A word from the editor

The book series “MARINE ECOLOGY – A Comprehensive Treatise on Life in Oceans and Coastal Waters” (organized and edited by Otto Kinne and contributed to by numerous outstanding experts over years) is now freely available with online Open Access.

Published in the years 1970 to 1984, the copyright for MARINE ECOLOGY was graciously transferred in 2008 by the original publisher, Wiley & Sons, to the editor.

The technical problems involved in the re-publication of the Treatise were mastered by Konstantin Kambach (Inter-Research). Unavoidably, the print quality of the final product is somewhat inferior to the original.

Otto Kinne

Oldendorf/Luhe
29.04.2008

MARINE ECOLOGY

A Comprehensive, Integrated Treatise on Life in Oceans and Coastal Waters

Volume I ENVIRONMENTAL FACTORS

Volume II PHYSIOLOGICAL MECHANISMS

Volume III CULTIVATION

Volume IV DYNAMICS

Volume V OCEAN MANAGEMENT

MARINE ECOLOGY

A Comprehensive, Integrated Treatise on Life in Oceans and Coastal Waters

Editor

OTTO KINNE

Biologische Anstalt Helgoland
Hamburg, West Germany

VOLUME I

Environmental Factors

Part 1

1970

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INTRODUCTION
to the
TREATISE

No words can introduce a Treatise on Marine Ecology more adequately than those by JOHANN WOLFGANG VON GOETHE[1] (1749–1832). I am quoting here the German text, as well as a favourite English translation by JOHN ANSTER:

'Alles ist aus dem Wasser entsprungen!!
Alles wird durch das Wasser erhalten!
Ozean, gönn uns dein ewiges Walten.
Wenn du nicht Wolken sendetest,
Nicht reiche Bäche spendetest,
Hin und her nicht Flüsse wendetest,
Die Ströme nicht vollendetest,
Was wären Gebirge, was Ebnen und Welt?
Du bist's, der das frischeste Leben erhält.'

'In Water all hath had its primal source;
And Water still keeps all things in their course.
Ocean, still round us let thy billows proud
Roll in their strength—still send up mist and cloud.
If the rich rivers thou didst cease to spread—
If floods no more were from thy bounty fed—
And the thin brooklet died in its dry bed—
Where then were mountains—valleys? Where would be
The world itself? Oh! thou dost still, great Sea,
Sustain alone the fresh life of all things.'

To modern science, the field of ecology comprises studies of organisms in relation to their environment, abiotic and biotic. Marine ecology is a branch of ecology dealing with the vast multiplicity of organisms living in oceans and coastal waters. The present treatise attempts to cover all major aspects of marine ecology. It consists of several volumes which, for convenience, in some cases have been subdivided into parts. At present 5 volumes are envisaged:

Volume I —Environmental Factors
Volume II —Physiological Mechanisms
Volume III—Cultivation
Volume IV—Dynamics
Volume V —Ocean Management

Environmental Factors is introduced on the following pages (Foreword). Volumes II to V are presently being organized and are scheduled to be published in the next few years.

Physiological Mechanisms will deal with support mechanisms, such as photosynthesis, respiration, reproduction; timing mechanisms, e.g. biological clocks, rhythms; orientation mechanisms; regulatory mechanisms, e.g. volume-, ion-, turgor-, osmo- and thermo-regulation; mechanisms of adaption; and communication mechanisms, such as sound production and perception, as well as visual and chemical communications.

Cultivation will be concerned with maintaining, raising, rearing and breeding marine and brackish-water organisms in laboratories, ponds, under-sea farms, restricted sea areas, etc., both for scientific and economic purposes; this volume will also include sections on technical aspects and diseases.

[1] Werke (Hamburger Ausg., 4th ed.) Vol. 3. Faust. Part 2, p. 255. Wegner, Hamburg, 1959.

Dynamics will focus on production, transformation and decomposition of organic matter in the marine environment; population dynamics; food-chain relations; nutritional requirements; as well as on flow and balance of energy and matter.

Ocean Management—a rather ambitious term for a young and virgin aspect of marine ecological research—will present a brief synopsis of important taxonomic groups, zonations, organismic assemblages; sea-water pollution (sources, biological consequences, avoidance, control, conventions); organic resources of the seas (distribution, use, control, conservation); and a general discussion concerning possible ways and means for management of important sea areas.

A comprehensive, integrated treatise on life in oceans and coastal waters cannot be written by a single author; it must draw from a multitude of talents and sources, and hence requires interdisciplinary and international co-operation. Neither a compendium nor an encyclopaedia, the treatise is intended to be an exhaustive systematic exposition summarizing and evaluating information obtained thus far on living systems in the seas and littoral areas. It has been conceived with the growing number of individuals in mind who are professionally concerned with life in the marine environment, especially investigators, engineers, teachers, students, administrators and businessmen. Although, for the benefit of the reader, integrated into a methodically arranged general concept, each contribution is intended to represent a detailed, authentic critical account in its own right; all contributors are free in choice of material and emphasis.

The first tentative outline of the treatise was circulated among several hundred marine ecologists in November, 1965. The warm response received from the international scientific community and the stimulating support from the publishers have encouraged me to proceed with my plans. Criticism, advice and assistance of numerous colleagues have greatly affected and improved the first proposal. I gratefully acknowledge all this support. It is not possible to list here the names of even the most active supporters; they will be mentioned in the forewords to the respective volumes.

A treatise such as this needs continued criticism and advice. Any comments—especially on outline, coverage and new points of view—will be most welcome.

July 21, 1969 O. KINNE

FOREWORD
to
VOLUME I: ENVIRONMENTAL FACTORS

'Environmental Factors' summarizes and evaluates all important information available to date on the responses of ocean and coastal-water living organisms to intensity variations of the major abiotic and biotic ecological factors. It is subdivided into 3 parts which contain the following chapters:

Part 1

Chapter 1 : Oceans and Coastal Waters as Life-supporting Environments
Chapter 2 : Light
Chapter 3 : Temperature

Part 2

Chapter 4 : Salinity
Chapter 5 : Water Movement
Chapter 6 : Turbidity

Part 3

Chapter 7 : Substratum
Chapter 8 : Pressure
Chapter 9 : Dissolved Gases
Chapter 10: Organic Substances
Chapter 11: Ionizing Radiation
Chapter 12: Factor Combinations

Chapter 1 considers oceans and coastal waters as life-supporting environments. It describes briefly the ocean basins, their principal water masses and circulation, the sea-land boundary, the properties of sea water and the chemical cycles in the seas.

Chapters 2 to 11 deal with responses to environmental factors. Of course, only factors about which enough information is available can be treated. Each chapter begins with a general introduction informing the reader about (1) general aspects of the environmental factor concerned, (2) methods of measuring its intensities, and (3) its intensity patterns in oceans and coastal waters. The chapter outline, suggested to all contributors, distinguishes between functional and structural responses. Functional responses are subdivided into tolerance, metabolism and activity, reproduction, and distribution; structural responses are dealt with under the subheadings size (body length, width, volume), external structures (shape, differentiation, etc. of external body parts) and internal

structures (organs, tissues, cells or parts thereof). The monofactorial approach used in Chapters 2 to 11 has been chosen because of the insufficient amount of information at hand on multifactorial relationships, and because organisms—whether bacteria, plants or animals—frequently exhibit comparable responses to intensity variations of environmental entities such as light, temperature or salinity. A monofactorial (univariable) design facilitates comparison, evaluation and generalization of reactions to a given environmental factor by members of different taxa. It is realized, of course, that in natural habitats organisms respond to their total environment rather than to single factors (selected by man for methodological, conceptual or historical reasons). Factor interactions, known or expected to be of special importance, are therefore referred to briefly in each chapter.

Chapter 12 presents a special, detailed account on organismic responses to factor combinations. There can be no doubt: investigation of responses to intensity variations of environmental factors acting in concert must be given priority if man wants to understand ecological dynamics and to achieve forecasting and controlling capacities in regard to life in the marine environment. There is great need for (i) conducting large-scale research projects based on multivariable designs and including all life-history stages of important food-web representatives, (ii) developing appropriate analyzing and evaluating techniques (computation, mathematical models and concepts of abstraction, formalization and generalization). Chapter 12 represents a pioneer effort to stimulate progress in this modern branch of ecological research.

Our intention to provide the reader with a well-organized source of information which enables him to find and compare facts and problems of interest to him quickly and easily created several difficulties. The first difficulty was to achieve general agreement in regard to gross taxonomic subdivisions. The subdivisions 'bacteria, fungi and blue-green algae', 'plants', and 'animals' have been adopted after long discussions; they are the result of a compromise between the need to keep the number of taxa as small as possible and to choose groups of organisms which can be conveniently treated by single authors; whenever necessary these groups are subdivided further, e.g. 'animals' into 'invertebrates' and 'fishes'. The second difficulty concerned the treatment of 'nutrition'. In bacteria, nutrients and substratum (Chapter 7) are hardly separable; in plants, nutrients overlap to a certain degree with salinity (Chapter 4), in animals with organic substances (Chapter 10). While some aspects of nutrition have been considered under various headings, nutritional aspects will be treated in detail in Volumes III and IV. The third difficulty was created by differences in thematic emphasis and in the usage of certain scientific terms in the fields of marine microbiology, botany or zoology. An example is the connotation of the term 'growth', which means increase in individual numbers in microbiology, but increase in organic matter of individuals in botany and zoology. Such terminological problems were solved by providing definitions or explanations.

The policy of placing the conceptual grid of the chapter outlines on the body of knowledge available and reviewing the material found near each 'point of intersection' (rather than following, as usual, the meandering path along which information happens to have accumulated) made us aware that many important areas of marine ecological research have hardly been touched upon, while others have

attracted unparalleled attention; such disproportions are reflected in the lengths of the respective contributions. The Chapter 'Water Movement: bacteria, fungi and blue-green algae' had to remain unwritten because of insufficient knowledge available.

Lack of information also created a serious gap in regard to biotic factors (e.g. behavioural and biochemical interactions between organisms of a given ecosystem) which may affect, or even govern, intra- and interspecific patterns of organismic co-existence. Little pertinent information is at hand on marine mammals and birds; their responses to environmental stress often depend on endogenous homeostatic mechanisms.

'Environmental Factors' concentrates on responses of intact organisms. However, if considered relevant, information obtained at the individual level is complemented by findings at the sub- or supra-individual levels. Functional and structural responses are primarily considered under the aspect of quantitative variability, i.e. in terms of changes in rates or intensities of performance. The physiological mechanisms involved will be dealt with in Volume II. General trends that have become apparent are documented by referring to one or a few well worked out examples rather than by presenting a long list of parallel findings. All literature cited appears in alphabetical order at the end of each chapter; it is hoped that such a procedure will help to strengthen interdisciplinary contacts between the fields of marine microbiology, botany and zoology and to facilitate a fast and convenient survey of important pertinent literature.

While an effort has been made to concentrate on marine and brackish-water organisms, in some instances information obtained on limnic forms has been included, especially in situations where knowledge on salt-water living organisms is scarce, or in which it appears safe to assume that both groups of aquatic organisms would exhibit comparable responses.

Much of our present knowledge on responses of marine and coastal-water living organisms to environmental stress has been obtained during casual observation or in insufficiently equipped and staffed laboratories. More complete studies require modern scientific dimensions: more space, better facilities and teams of scientists and technicians.

I am deeply indebted to all contributors for their patience, dedication and willingness to co-operate far beyond the usual demands; despite technical difficulties it was possible in most cases to adhere closely to the outlines proposed. The publishers have supported me wholeheartedly and considerably reduced the many problems by not imposing any space or time limits; I am grateful for this confidence and for excellent co-operation. It is a pleasure to acknowledge support, advice and criticism received by many colleagues, especially by D. F. Alderdice, J. R. Brett, A. W. Collier, M. Gillbricht, E. Hagmeier, M. Hoppenheit, H. W. Jannasch, R. I. Smith, R. W. Taylor and B. P. Ushakov. During the years of organizing and preparing Volume I, Mrs. J. M. Christian, Miss V. J. Clark and Miss F. C. Crouse have served as reliable and highly capable editorial secretaries and assistants. Mr. J. Marschall has given generously of his time and talent in altering or improving illustrations and Mr. W. Meiss was an indispensable and conscientious helper in all matters related to bibliographical problems. It is with a deep sense of gratitude that I acknowledge all this assistance.

July 21, 1969 O. Kinne

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CONTRIBUTORS
to
VOLUME I, PART 1

BLAXTER, J. H. S., *Marine Research Laboratory, P.O. Box 3; Oban, Argyll, Scotland.*

BRETT, J. R., *Fisheries Research Board of Canada, Biological Station; Nanaimo, British Columbia, Canada.*

COLLIER, A. W., *Department of Biological Science, The Florida State University; Tallahassee, Florida 32306, USA.*

GARSIDE, E. T., *Biological Department, Dalhousie University; Halifax, Nova Scotia, Canada.*

GESSNER, F., *Institut für Meereskunde an der Universität Kiel, Niemannsweg 11; 23 Kiel, West Germany.*

GUNKEL, W., *Biologische Anstalt Helgoland (Meeresstation); 2192 Helgoland, West Germany.*

HELLEBUST, J. A., *Department of Botany, University of Toronto; Toronto 5, Canada.*

JERLOV, N. G., *Institute of Physical Oceanography, University of Copenhagen, Sølvgade 83; Copenhagen K, Denmark.*

KINNE, O., *Biologische Anstalt Helgoland (Zentrale), Palmaille 9; 2000 Hamburg 50, West Germany.*

OPPENHEIMER, C. H., *The Florida State University; Tallahassee, Florida 32306, USA.*

SEGAL, E., *Department of Biology, San Fernando Valley State College, 18111 Nordhoff Street; Northridge, California 91324, USA.*

ENVIRONMENTAL FACTORS

1. OCEANS AND COASTAL WATERS AS LIFE-SUPPORTING ENVIRONMENTS

A. W. COLLIER

(1) Introduction

The marine ecologist strives for maximum comprehension of a biota which has been immersed in a saline medium since primeval times. The myriads of species composing the contemporary flora and fauna have been derived through the many failures and successes of opportunistic evolution (SIMPSON, 1949) from the biological primordium of ancient seas. The marine biota of today is the product of: (1) the tendency of living matter (and non-living matter) to assume every possible form compatible with the environment, (2) the capacity of living matter to utilize non-living and living matter as a source of energy and materials for survival and multiplication, and (3) nature's most abundant commodity: time.

The above paragraph offers a perspective which spans the appraisal of the oceans and their ancillary bodies as life-supporting environments. The purpose of this chapter is to describe briefly the oceans' basins and the pertinent attributes of the waters which they contain.

The attributes of sea water and the physical characteristics of the oceans have special meaning when they are viewed as parts of a system supporting an infinite variety of forms and functional specializations. The challenge of understanding an infinite variety of living organisms in a medium which has changed but little over many millions of years is one of the great fascinations of marine ecology.

(2) The Ocean Basins

The world ocean, as a responsive fluid, is subject to the remote but violent sun through the intermediary of the atmosphere; it is also a receptacle for organic and inorganic residues from a relatively small area of land which rises above it (slightly more than one quarter of Earth's total surface). The dissection of the hydrosphere by the land masses has been one of the important determinants in the development and distribution of both aquatic and terrestrial taxa. An examination of the general plan of articulation of the primary ocean basins and their ancillary bodies is fundamental to an evaluation of the marine environment.

In this section, I have chosen to organize the treatment of the basins to begin with the Arctic Ocean and to end with the Southern Ocean. Each major or primary ocean is presented with its adjoining secondary branches in geographical order.

The Arctic Ocean

The Arctic Ocean may be viewed as an inland sea with restricted communication with the world ocean. This ocean lies astride the North Pole as the continent of

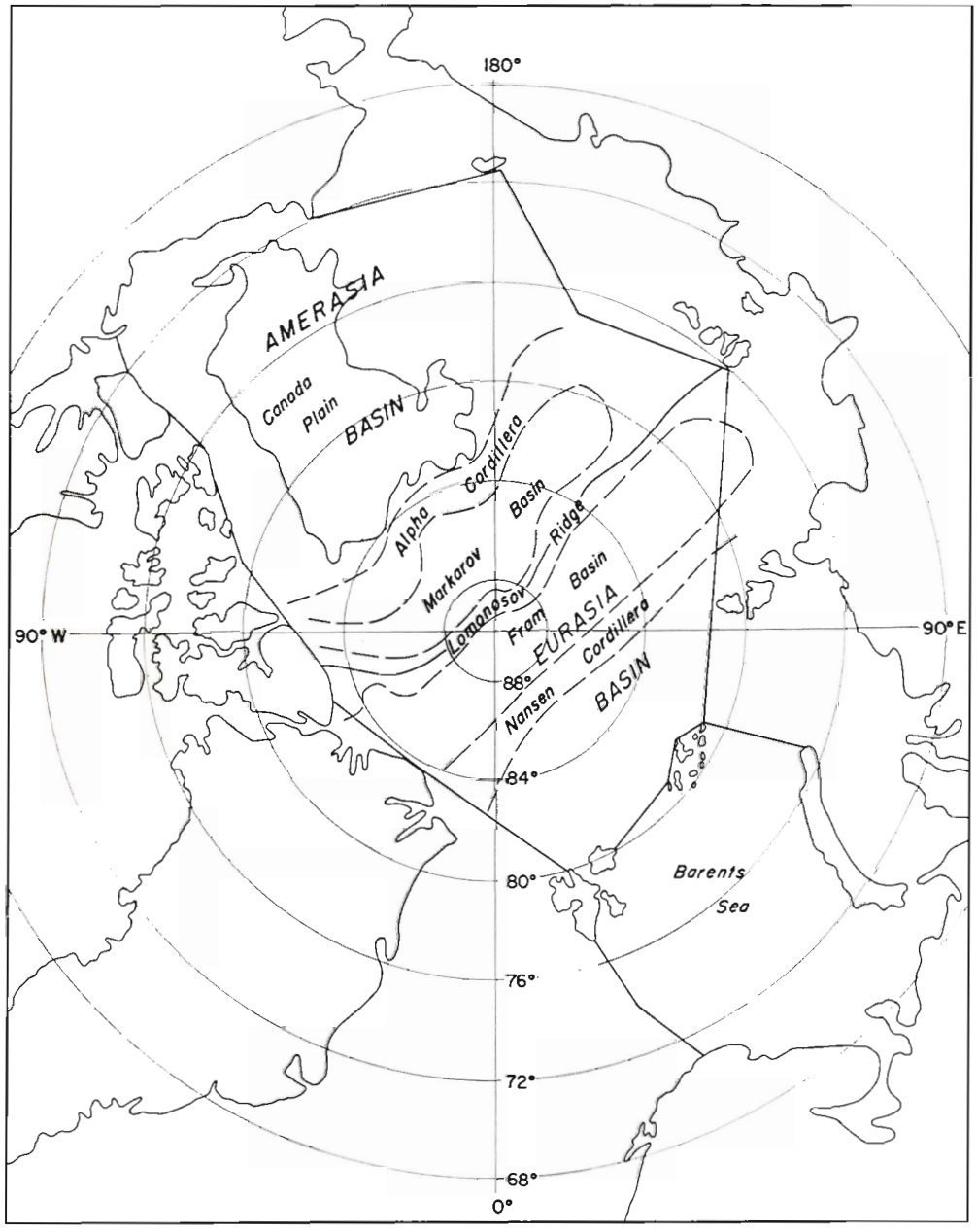


Fig. 1-1: The basins and the dominant bathymetric features of the Arctic Ocean. (After BEAL and co-authors 1966, and other sources.)

Antarctica embraces the South Pole. As an inland sea receiving continental drainage, Arctic waters are responsive to the balance of oceanic and terrestrial factors. By contrast, the Southern Ocean, peripheral to Antarctica, affects the character of a major part of the world ocean.

Arctic Basin

In this brief description of the Arctic Basin we shall follow the commentary on geographic names of the floor of the Arctic Ocean presented by BEAL and co-authors (1966). Beginning in the west, the Arctic Basin is divided into three easily identifiable segments: the Amerasia Basin, the Eurasia Basin, and Barents Sea (Fig. 1-1). Along the Eurasian continent there are the secondary seas, east to west: Chukchi Sea, East Siberian Sea, Laptev Sea, and Kara Sea. On the opposite side, from Greenland to Alaska, there are no secondary seas. 'Beaufort Sea' is given no hydrographic or geographic grounds for standing as a place name by BEAL and co-authors (1966).

The dividing line between the Amerasia Basin and the Eurasia Basin is the Lomonosov Ridge. It very nearly subtends the meridian 140° E to the North Pole; at a point just south of the pole, the ridge takes a turn to the west and parallels the meridian 85° W. Flanking the Lomonosov Ridge we find a series of parallel folds and correlated basins on either side. These features have been named, respectively, the Fram Basin and its dextrally-lying Nansen Cordillera in the Eurasia Basin, and the Markarov Basin with its sinistrally-lying Alpha Cordillera in the Amerasia Basin.

West of the Alpha Cordillera lies the Canada Plain bounded by a portion of the East Siberian Shelf, the Chukchi Shelf, and the Alaskan and Canadian coasts. The smaller details of the Arctic Basins are shown in Fig. 1-2.

Water Masses and Circulation of the Arctic Ocean

With respect to vertical distribution, three distinct water masses are recognized in the Arctic Ocean; they are related to the sources of water feeding into the ocean. The principal sources of water affecting the composition and differentiation of the masses are: Atlantic Ocean, Bering Sea, Norwegian coast and continental drainage from Asia. Horizontally, there is also differentiation. The vertically distributed masses are divided between the Amerasia and the Eurasia Basins.

COACHMAN and BARNES (1962) described the surface stratum, the Arctic Water Mass, as being composed of three layers: (1) from near the surface to 25 to 50 m, (2) from 25 to 50 m to 100 m, and (3) from 100 m to the Atlantic Water Mass, whose core lies at 250 to 300 m.

The deep Arctic is covered with an ice blanket which keeps the surface layer near the freezing point. An increase in density in the water just below prevents seasonal convection from being manifest to depths greater than 25 m, rarely to 50 m. This layer has a comparatively broad salinity range: 28 to 33·5 $^{0}/_{00}$.

The subsurface layer is characterized by a halocline reaching a maximum salinity of 34 $^{0}/_{00}$ at its lower limit of 100 m. The origin of this is postulated as arising from a mixture of Atlantic Water and continental drainage through an estuarine-like mechanism inherent in the canyon structures along the Eurasian continental slope (COACHMAN and BARNES, 1962).

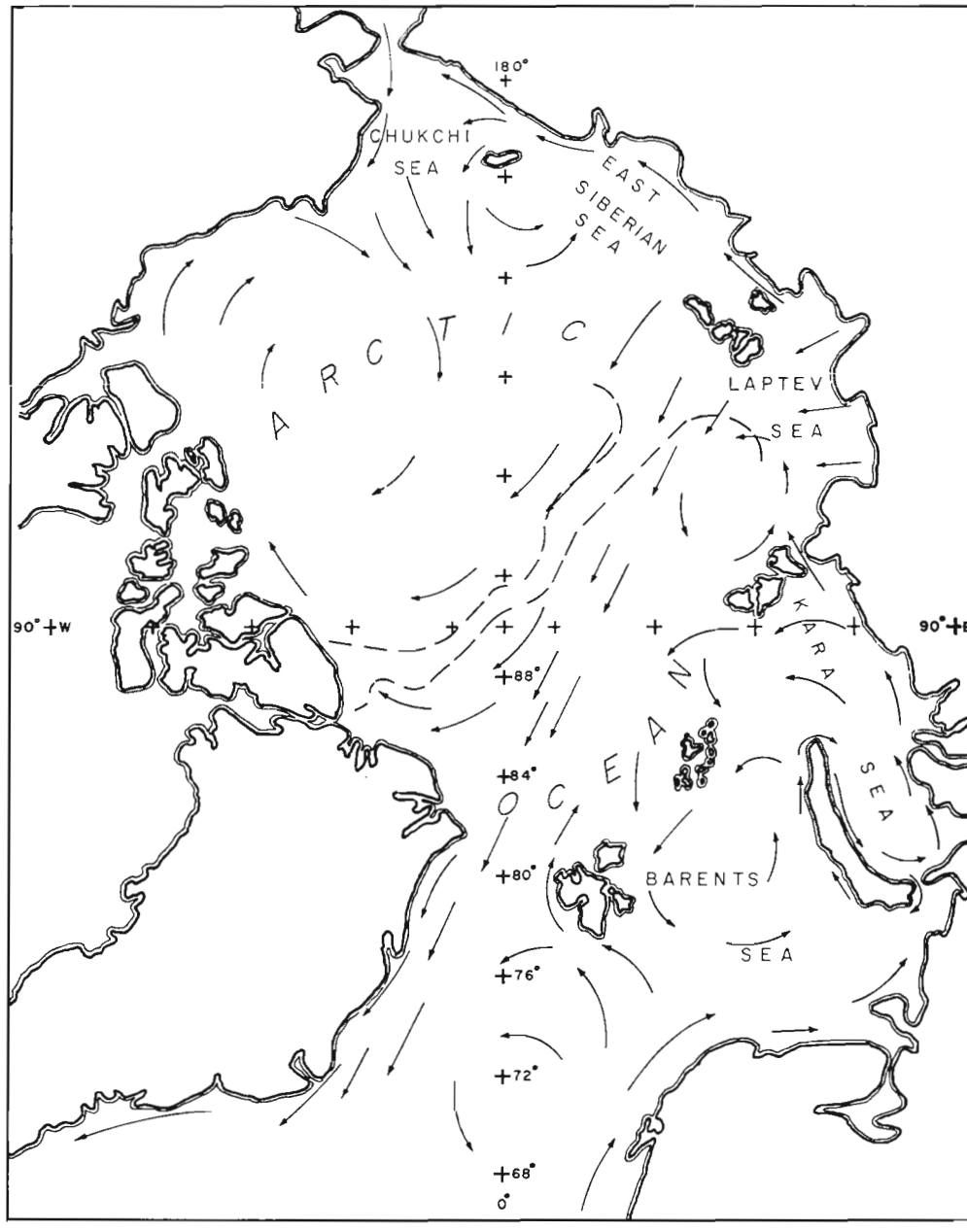


Fig. 1-2: The Arctic Ocean, its secondary seas and the principal routes of water circulation. (After various Sources.)

The third subdivision of the Arctic Water Mass extends from 100 m to the Atlantic Water Mass and is actually a mixture of the latter and the subsurface layer described above. Its properties are intermediate between the two.

It appears that Bering Sea water flows into the Amerasia Basin through Bering Strait and mixes with Siberian Shelf water after which it becomes a part of the Arctic circulation at a point northwest of Point Barrow (COACHMAN and BARNES, 1961). It is estimated that about 20% of this water comes from the Bering Sea. That water which passes through the Bering Strait in the summer causes a shallow temperature maximum and that which is brought in during the winter is believed to be associated with a deeper minimum temperature. It is these characteristics which differentiate the Amerasian Arctic Mass from the Eurasian Mass, the latter showing no shallow temperature maximum.

Using the core method of WÜST (1964), COACHMAN and BARNES (1963) made a study of the movement of the Atlantic Water in the Arctic Ocean. This water enters the Arctic near Spitsbergen and flows along the Eurasian continental slope to a point north of the Laptev Sea. Along this route segments of the mainstream curl off and flow back in a southwesterly direction towards the main exit of the Arctic—the current along East Greenland. This return movement aids in the rapid filling of the Eurasia Basin with the Atlantic water.

In a broad sweep from the slope of the Kara and Laptev Seas, the Atlantic water continues across the Lomonosov Ridge and moves parallel to the slopes of the East Siberian and Chukchi Seas. From there it proceeds across the southern aspect of the Amerasia Basin to recross the Lomonosov Ridge and exit through the East Greenland passage.

The Arctic Bottom Water seems to originate in the Norwegian Sea and reaches a temperature of $-0{\cdot}8°$ C in the Eurasia Basin at 2500 m, and $-0{\cdot}4°$ C in the Amerasia Basin at 2000 m. The reason for this differentiation is that the colder and deeper water does not flow over the Lomonosov Ridge. The relations between the various water masses and the general circulation are shown in Fig. 1-2.

The Atlantic Ocean

As a unit, the Atlantic Ocean is sigmoid in form and extends from the threshold of the Arctic to the open seas of the Southern Ocean. It is more or less closed on the north by the Greenland–Iceland, Faroe, British Isles complex. It may be further characterized by its two mediterranean seas, the European and the American. The Arctic Ocean is often considered as a secondary mediterranean sea of the Atlantic also.

North Atlantic Ocean

The least distance across the Atlantic Ocean lies near a line drawn on the mercator projection from Natal to the Arquipelago dos Bijagos (off Portuguese Guinea). This line provides a convenient boundary between the South and North Atlantic Oceans. It has some bathymetric validity because the Sierra Leone Ridge is roughly parallel to it, and extends from the African continent to the Mid-Atlantic Ridge. Between the latter and the South American bulge there is an unnamed plateau with limited relief which is flanked to the north and south by the Guiana and Brazil Basins, respectively.

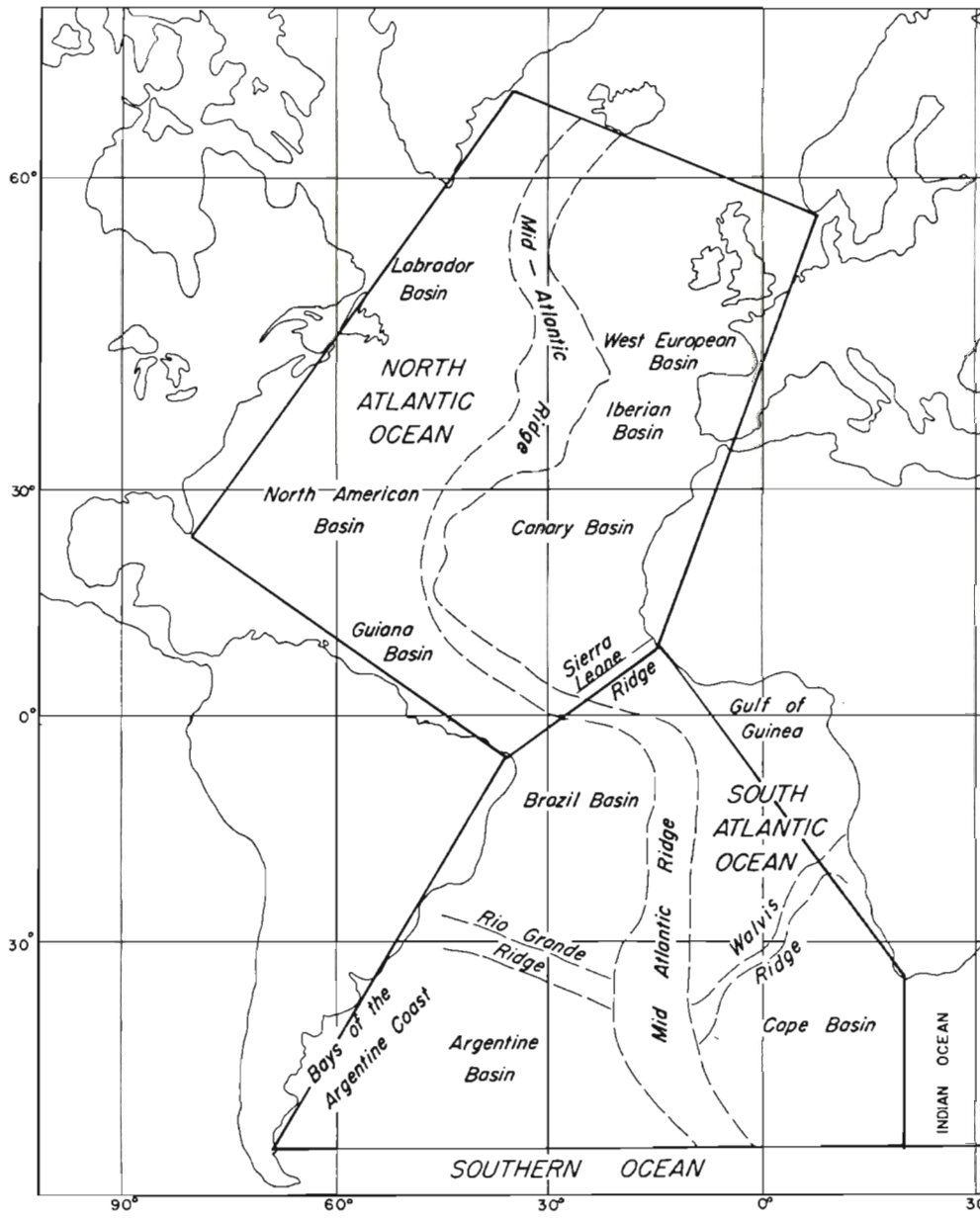


Fig. 1-3: A diagrammatic scheme to show the relations of the major basins and ridges of the North and South Atlantic. The boundary between the South Atlantic Ocean and the Southern Ocean is drawn at 52° S latitude. The South Atlantic Indian Ocean boundary is also by definition. (Adapted from US Naval Oceanographic Office Chart of the World No. H. O. 1262A, 10th Edition.)

A line drawn from the Arquipelago dos Bijagos to Kristiansand in Norway completes the east side of a rough rectangle which can be drawn to enclose the North Atlantic Ocean (Fig. 1-3). The principal bathymetric features of the North Atlantic can be most easily described by using the reference rectangle. It is seen that the Mid-Atlantic Ridge and associated structures divide the whole basin into almost symmetrical portions, each containing a series of basins. The east side of

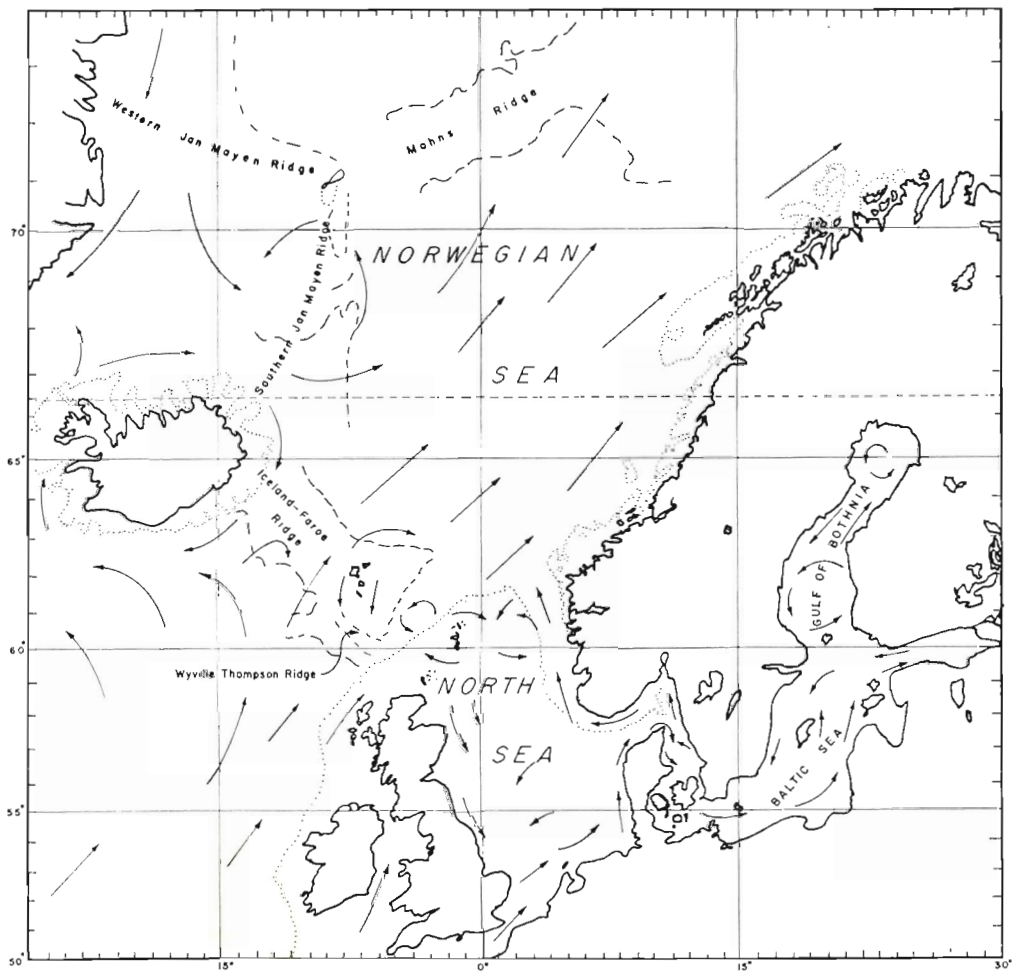


Fig. 1-4: The major geographic features in the region of the Norwegian Sea and the North Sea. The water circulation is shown. The dotted lines represent the 100 fathoms (183 m) contour. Ridges are indicated by dashes. (After various sources.)

the ridge is divided into the West European Basin, the Iberian Basin, the Canary Basin and the Cape Verde Basin. The region west of the Mid-Atlantic Ridge is divided into the Labrador Basin, the Newfoundland Basin, the very large North American Basin and the Guiana Basin.

The secondary seas of the North Atlantic are found on the periphery of the reference rectangle.

The Norwegian Sea and the Norwegian Basin lie in a semicircle formed around their southern perimeters by Norway, the British Isles, and Iceland. The Norwegian Basin is separated from its more northerly neighbour, the Greenland Basin, by Mohns Ridge (Fig. 1-4).

The North Sea is not a large geographic unit, but its location amidst one of the oldest population centres of the western world makes it one of the better known arms of the sea. The North Sea Basin is a segment of the Northwest European Shelf whose periphery extends from the coast of Norway to the coast of France in the Bay of Biscay (Figs. 1-4, 1-5).

The Celtic Sea (Fig. 1-5) is not a major arm of the sea and is not generally indicated on maps, but it is included here because of the frequent appearance of the name in oceanographic literature. COOPER and VAUX (1949) (see also COOPER, 1967) established the validity of the term and defined it as follows:

> '(1) On the east by the shortest line between the western point of the Island of Ushant (Ile d'Ouessant) and Lands End (Cornwall) and by the shortest line between Lands End and Ramsey Island, off St. David's Head, Pembrokeshire. (2) On the north by the shortest line from Ramsey Island to Carnsore Point, Co. Wexford, by the south coast of Ireland from Carnsore Point to Dursey Head, Co. Kerry, and by the shortest line from Dursey Head to the 200 m. (or alternatively the 100 fm.) contour. (3) On the west and southwest by the 200 m. (or 100 fm.) contour. (4) On the south by the shortest line from the western point of Ushant to the 200 m. (or 100 fm.) line.'

As the Celtic Sea stands on the northern flank of the English Channel, so stands the Bay of Biscay (Fig. 1-5) on the southern. The Cantabrian Mountains plunge through Asturias into the ocean to form the steep southern wall of the bay, and the northwest terminus of the Pyrenees marks the northward turn of the coast. At this point the continental shelf broadens and becomes confluent with that of the Celtic Sea.

The European Mediterranean is a double sea, all but isolated from the world ocean (Fig. 1-6). The western basin is characterized by deeper water than is found in the eastern basin (maximum depth of 4600 m), the comparatively restricted continental shelf, and limited communication with the Atlantic Ocean. The floor of the Western Mediterranean is characterized by the Balearic Abyssal Plain (HEEZEN and MENARD, 1963). The Tyrrhenian Sea, embraced by southern Italy, Sicily, Sardinia, and Corsica, is a separate basin within its own right with its deeper waters having limited access to the outside. The Western Mediterranean basin is separated from the eastern basin by the comparatively shallow and narrow passage between Sicily and Tunisia. The eastern basin is a common receiver for the waters of the Adriatic, the Aegean, and through the latter, the Black Sea. However small the total area, it contains the most extensive shelf area of the entire Mediterranean in three places: off Tunisia and Tripolitania, the inner two-thirds of the Adriatic and the Aegean. One would expect the Nile to have contributed more to the bottom relief of this basin but according to HEEZEN and MENARD (1963), tectonic activity in the area is too recent for the Nile sediments to register an effect.

The Labrador Sea is continuous with Baffin Bay to the north. The axis of the Labrador Basin is formed by an extension of the mid-ocean canyon originating in

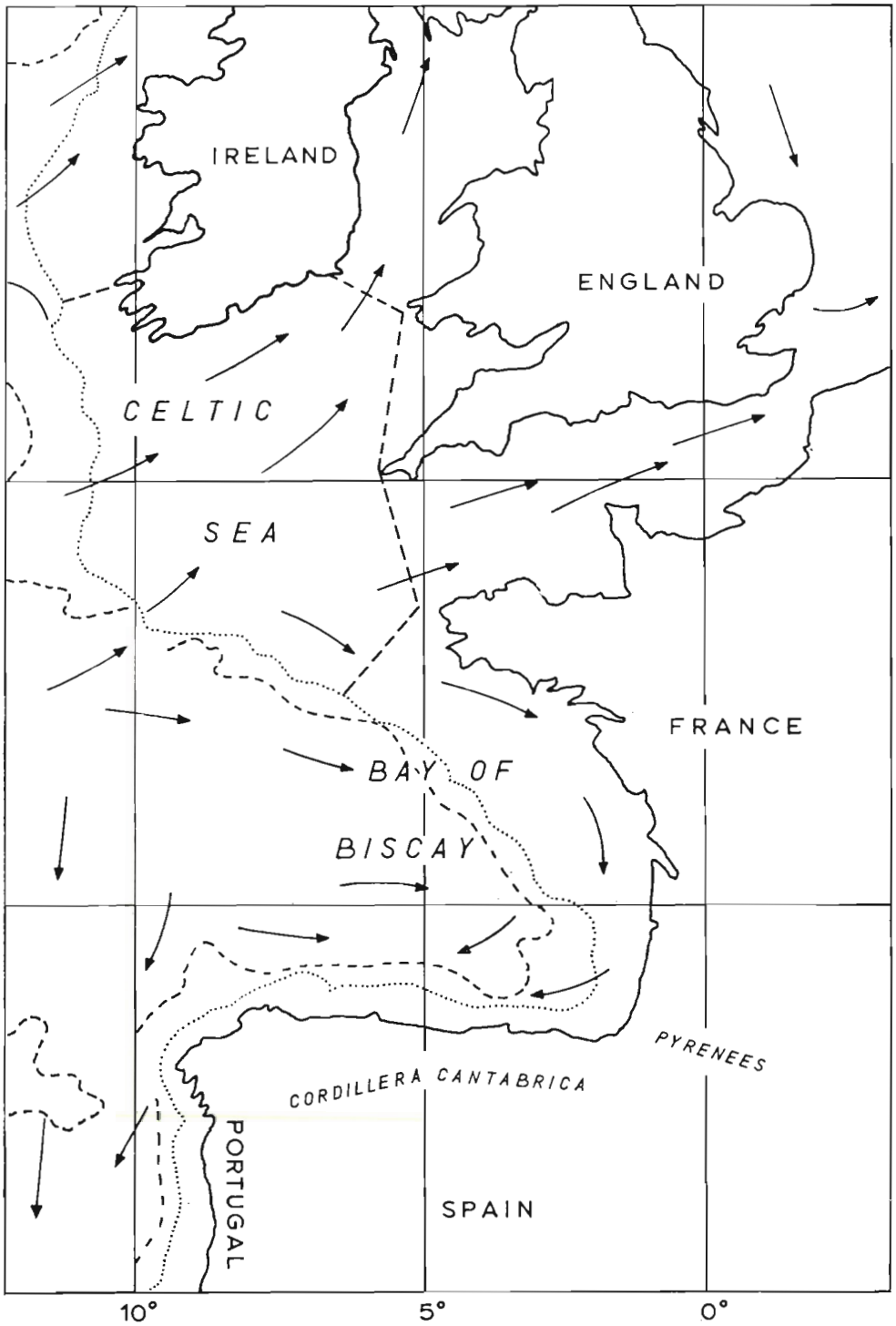


Fig. 1-5: The Celtic Sea and the Bay of Biscay. Dotted line: 100 fathom (183 m) contour. Arrows indicate surface currents. (From US Hydrographic Office Chart No. 5247, and GROSVENOR, 1963.)

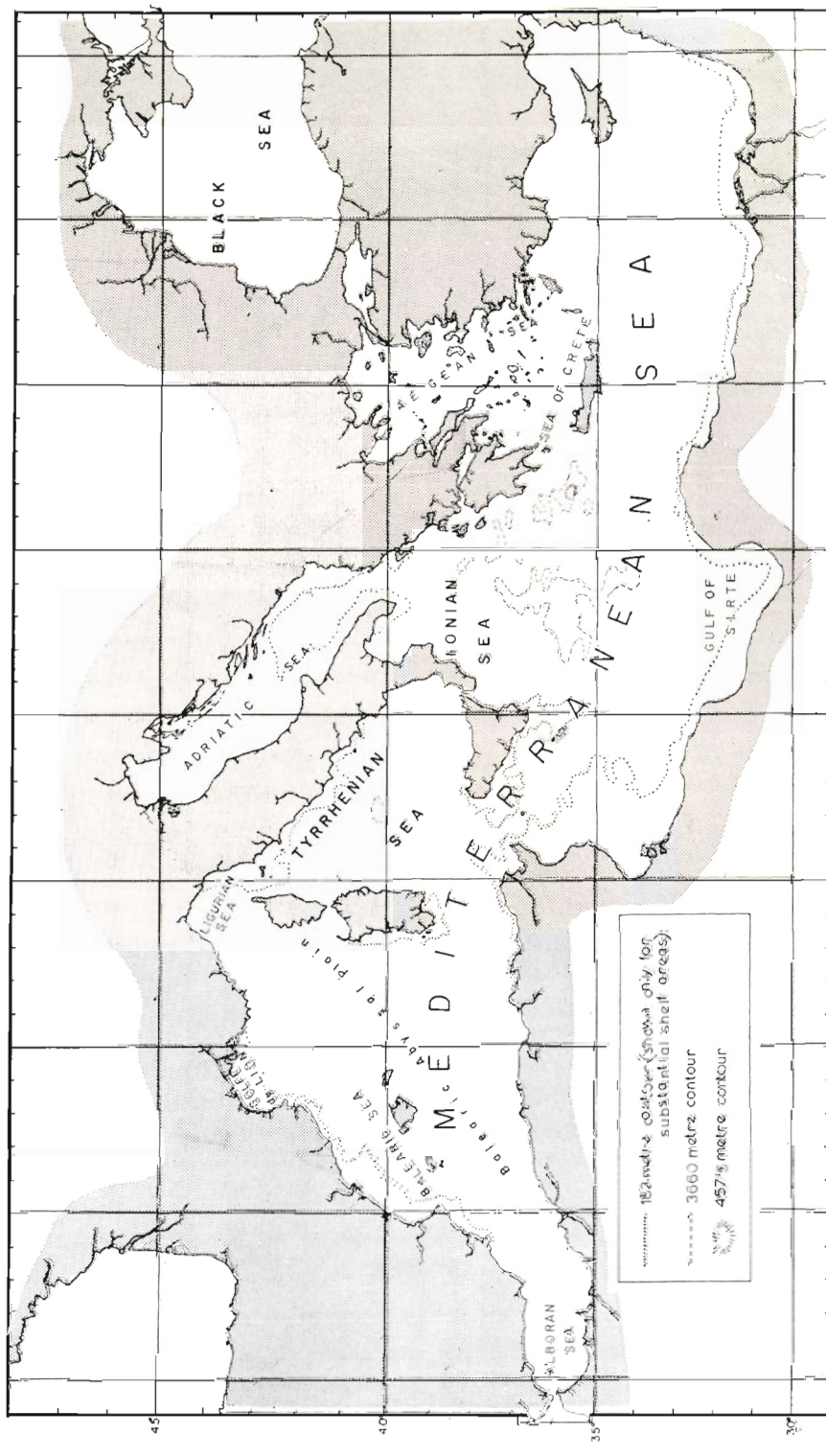


Fig. 1-6: Major geographic and bathymetric features of the European Mediterranean. (Adapted from US Navy Hydrographic Office Chart No. 4300, revised 5 June 1967.)

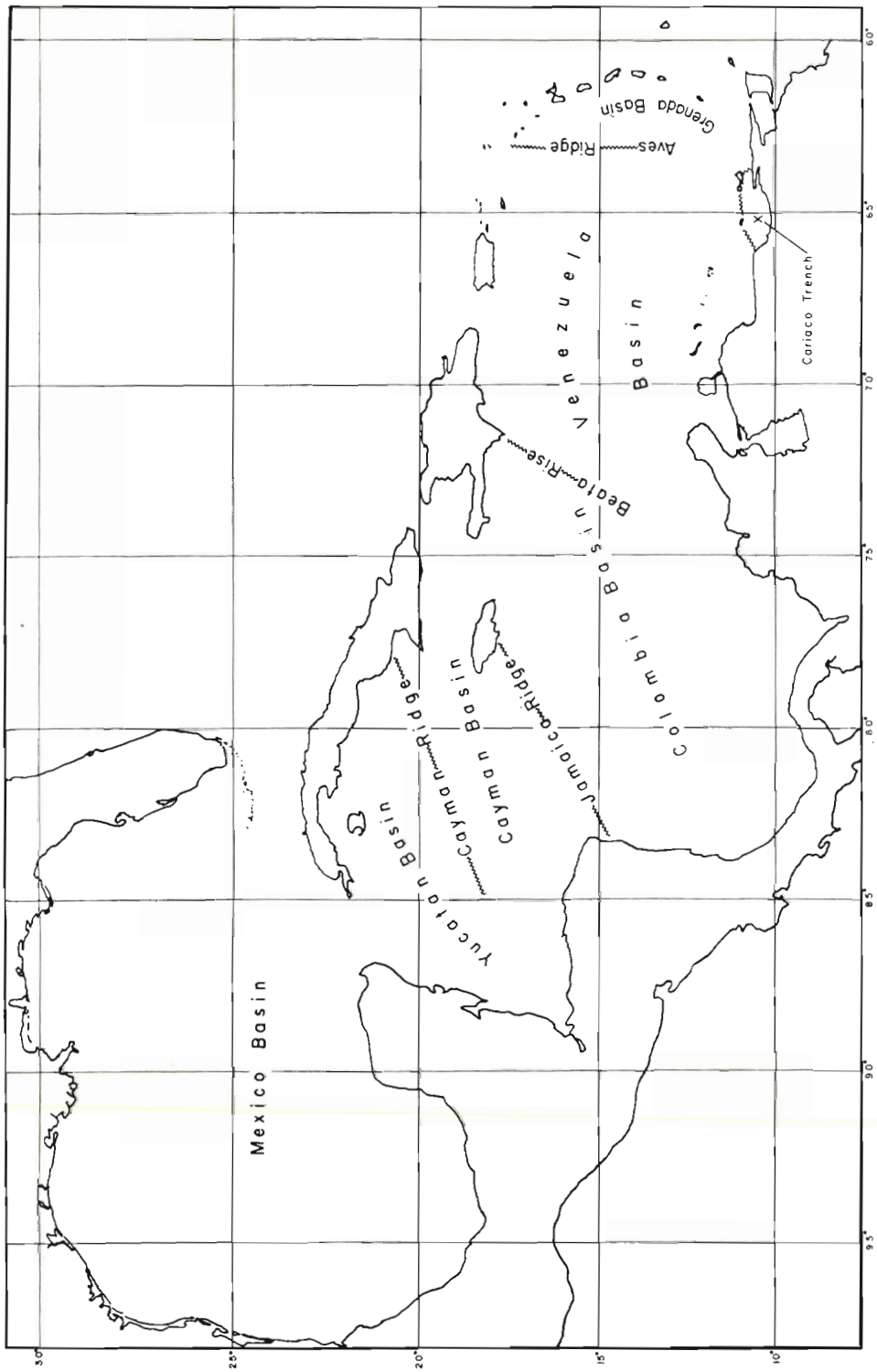


Fig. 1-7: Schema showing basins and ridges of the American Mediterrancan. (After various sources.)

the Newfoundland Basin to the northeast of the Azores. It is a northwestern arm of the Atlantic, which, but for the Ellesmere Island complex, would communicate directly with the Arctic Basin through Baffin Bay.

Although the Irminger Sea is referred to in the literature frequently, it does not appear on all maps. It is situated in the area between Iceland and Greenland occupied by the Irminger Current.

The Gulf of Mexico (Fig. 1-7) is unique among the mediterranean seas in that it receives terrestrial runoff directly from one of the world's larger rivers, the Mississippi. It is an enclosed sea whose circulation with the mother ocean is via the Caribbean and Yucatan Strait for ingress and Florida Strait for egress. It has a flat central basin of some 3600 m and is marked by steep escarpments along its eastern, south central and north central slopes (EWING and co-authors, 1958). The northwestern section of the island Cuba separates Yucatan and Florida Straits. The Florida Peninsula forms the eastern boundary. A southern extension embraced by the coast of Mexico forms the Golfo de Campeche and receives the waters of the Coatzacoalcos River, whose annual discharge is second only to the Mississippi among those rivers discharging into the Gulf of Mexico.

It is instructive to note certain analogies between the American Mediterranean and the European Mediterranean when the former is considered a unit composed of the Gulf of Mexico and the Caribbean Sea. On a relative scale the analogy is clear in these respects: there is first the generally smooth abyssal plain of the Gulf of Mexico and the similar condition for the floor of the western basin of the European Mediterranean; and, second, the parallel of the highly dissected floor of the eastern basin of the European Mediterranean with the same general conditions in the Caribbean. The Caribbean Sea may best be envisioned as two parts: (1) The southern portion consisting of a rectangle with its long axis running some 2400 km east and west. The north–south axis traverses approximately 900 km. The eastern boundary is formed by the islands of the Lesser Antilles, Guadelupe, Martinique and Barbados being some of the names of note. The western terminus is the coast of Honduras. Along the southern boundary lies Venezuela, Colombia, and Panama, while the northern traverse starts with Puerto Rico on the east and ends at the Caribbean coast of Guatemala. (2) The second segment of the Caribbean takes the form of a truncated trapezoid whose broad base rests on the north boundary of the above rectangle, covering one half the length plus an overhang formed by the north coast of Honduras. The truncated northern boundary of the trapezoid traverses Yucatan Strait.

The boundary common to these two geometric figures has a firm geographic basis because it lies on mated features of the Jamaica Rise and the Cayman Trough.

South Atlantic Ocean

It is not possible to resolve a natural boundary separating the South Atlantic Ocean from the North Atlantic Ocean. A purely geographic approach based on the equator is simple but not satisfactory from the environmental point of view; the use of ocean current regimes is not completely definitive (Fig. 1-8). Hence, a definition with more hydrographic and bathymetric application is given here.

The southwest–northeast side of the triangle described earlier roughly coincides

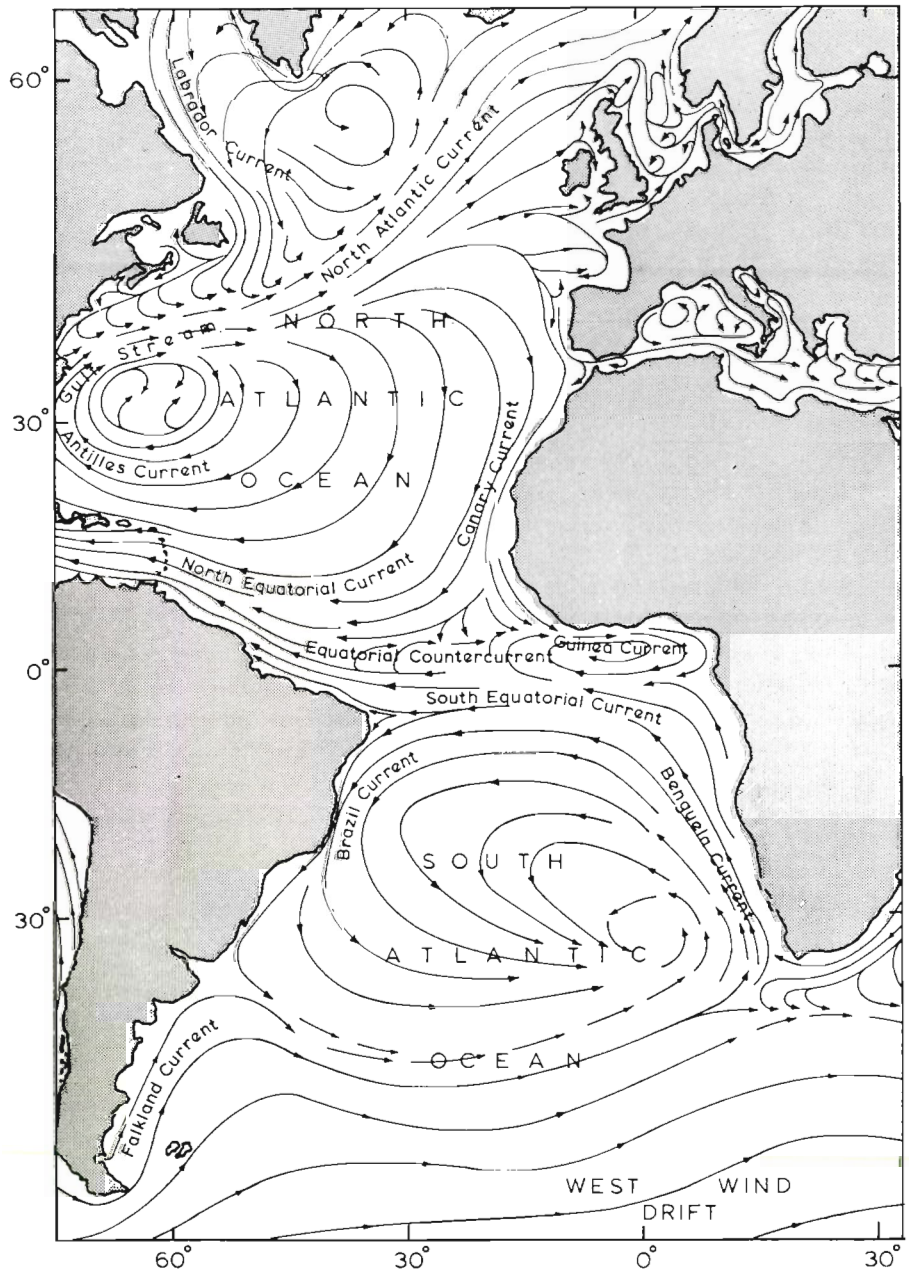


Fig. 1-8: Circulation of the North Atlantic Ocean and the South Atlantic Ocean for January. (Adapted from US Navy Hydrographic Office Pilot Chart No. H. O. 1400 N. A. January 1961.)

with the Sierra Leone Ridge as it proceeds toward Dakar from the Mid-Atlantic Ridge at a point near the intersection of the latter with the equator. The hydrographic implications of this definition will become clear later.

The southern boundary of the South Atlantic (and the other oceans) is fixed by convention (DIETRICH, 1963). Since it has been agreed that the polar oceans should not be separately defined and named and that the other oceans be demarcated in their southern extremities (see below), we can provide an imaginary boundary between the South Atlantic and the South Polar Sea.

BRODIE (1965) has set the northern boundary of the Southern Ocean as the parallel of 52° S. Since the Southern Ocean is discussed as a unit in this review, this line will also be regarded as an approximate southern limit of the Atlantic Ocean.

The eastern leg of the South Atlantic triangle (see above) bridges the easterly meander of the southwestern African coastline and so bounds roughly, in its more central aspect, the Gulf of Guinea. The gulf is not enclosed in any sense and lies as an extension of the Atlantic inward towards Nigeria. It is characterized by very little shelf area in its northern aspect, and off the coast of Ghana the bottom plunges to better than 4600 m within 100 km from the shore. (US Navy Hydrographic Office, Chart of the World, 1 : 12,233,000 at the equator, Mercator projection.) The related Guinea Basin is bounded by the Guinea Ridge on the south and opens into the Sierra Leone Basin to the northwest.

The coast of Argentina is crenulated with a series of embayments opening broadly upon the Atlantic Ocean, the bays of the Argentine coast. These cannot be properly considered as secondary seas, but they are sufficiently extensive and differentiated to be of possible distinctive importance insofar as biological environments are concerned. This point may be reinforced by the observation that this series of bays opens upon the most extensive continental shelf of the western hemisphere with the possible exception of the Northwest European shelves.

Principal water masses and circulation of the Atlantic Ocean

While continuing oceanographic research refines our knowledge of the details of the structure and circulation of the water masses in the Atlantic Ocean (MCLELLAN, 1965), the general features have been recognized for many years. A concise synopsis can most easily be given by following the approach of DIETRICH (1963).

With respect to the vertical distribution of temperature, the ocean profile shows a warm water shell lying over the cold water masses; the latter constitute by far the bulk of the ocean waters everywhere. The warm water shell averages about 500 m in thickness; steady influx of cold water from the polar regions into the deeper zones and the warmth of the upper level stabilizes the system and prevents mixing. Horizontally, the warm water shell extends from the parallel of 50° N to that of 45° S.

The ocean currents, as commonly thought of, are surface phenomena resulting from the contact of the sea surface with atmospheric circulation. In other words, they are largely wind generated. In Fig. 1-8 the large scale plan of the surface currents of the Atlantic Ocean is shown in the form of two large gyrals, one in the North Atlantic, the other in the South Atlantic.

The South Atlantic gyral is counter-clockwise and sends one branch northward as the Guiana Current, while another is turned southward by the South American continent as the Brazil Current. The water carried by the Guiana Current enters the Caribbean and further north joins the North Atlantic gyral. The principal flow of water into the southern gyral is from the circumpolar West Wind Drift via the Benguela Current. The northward flowing Falkland Current along the Argentine coast is derived from the West Wind Drift.

The gyral of the North Atlantic circulates in the clockwise direction. In its northern section it forms the North Atlantic Current which sends branches towards Iceland, the Norwegian Sea and the European coast. As it turns southward in the eastern Atlantic, it forms the Canary Current. The central part of the gyral is the area of the Sargasso Sea. The southern periphery of the gyral is the North Equatorial Current. WORTHINGTON (1962) has presented evidence for a two gyral system in the North Atlantic.

Between these two gyrals there is flow contrary to the North and South Equatorial Currents which is the Equatorial Countercurrent—a continuation of which forms the Guinea Current in the South Atlantic.

The cold water shell begins at the bottom of the warm water shell and extends to the bottom. It is composed of masses having distinct origins and characteristics. The movements of these masses are generated by archimedean forces more than by wind as is the case for the surface warm water shell. However, the temperature characteristics are ultimately generated by climatic conditions as we shall see.

The Weddell Sea of Antarctica produces a cold water which sinks and moves along the bottom of the oceans to form Antarctic Bottom Water, which as part of the Atlantic Cold Water Shell, extends as far north as 45° N. A second important stratum of the cold water shell originates in the Antarctic subpolar areas, between 45° and 55° S, and spreads northward as it sinks. It finds its level at about 900 m and here penetrates across the equator as far north as 25° N. This is the Antarctic Intermediate Water.

The north moving Bottom and Intermediate Waters seem to require a south moving compensation. This occurs in the form of the Deep Water, which is a mixture of Bottom and Intermediate Waters with the addition of water introduced from the North Atlantic in the vicinity of the Labrador and Irminger Seas. As the Deep Water approaches Antarctica, it ascends south of the 40th parallel.

Water masses and circulation of the Mediterranean Sea. The water masses of the Mediterranean fall into the following strata: Surface, Intermediate, Deep and Bottom. The Surface and Intermediate Waters seem to move together (OVCHINNIKOV, 1966) (Fig. 1-9). The Intermediate (or Levantine Intermediate Water) Water is characterized by high salinity resulting from the excess of evaporation over runoff. It is formed during the winter in the northern portion of the Levantine Basin, and flows between 200 and 600 m towards the Strait of Gibraltar where it enters the Atlantic Ocean with a salinity of 36·9 $^{0}/_{00}$ and a temperature of 15° C.

At the surface, excessive evaporation occurs in the winter months and the resulting high density water sinks and plunges through the Intermediate Water to become Deep Water. The areas in which this occurs are a subject of some

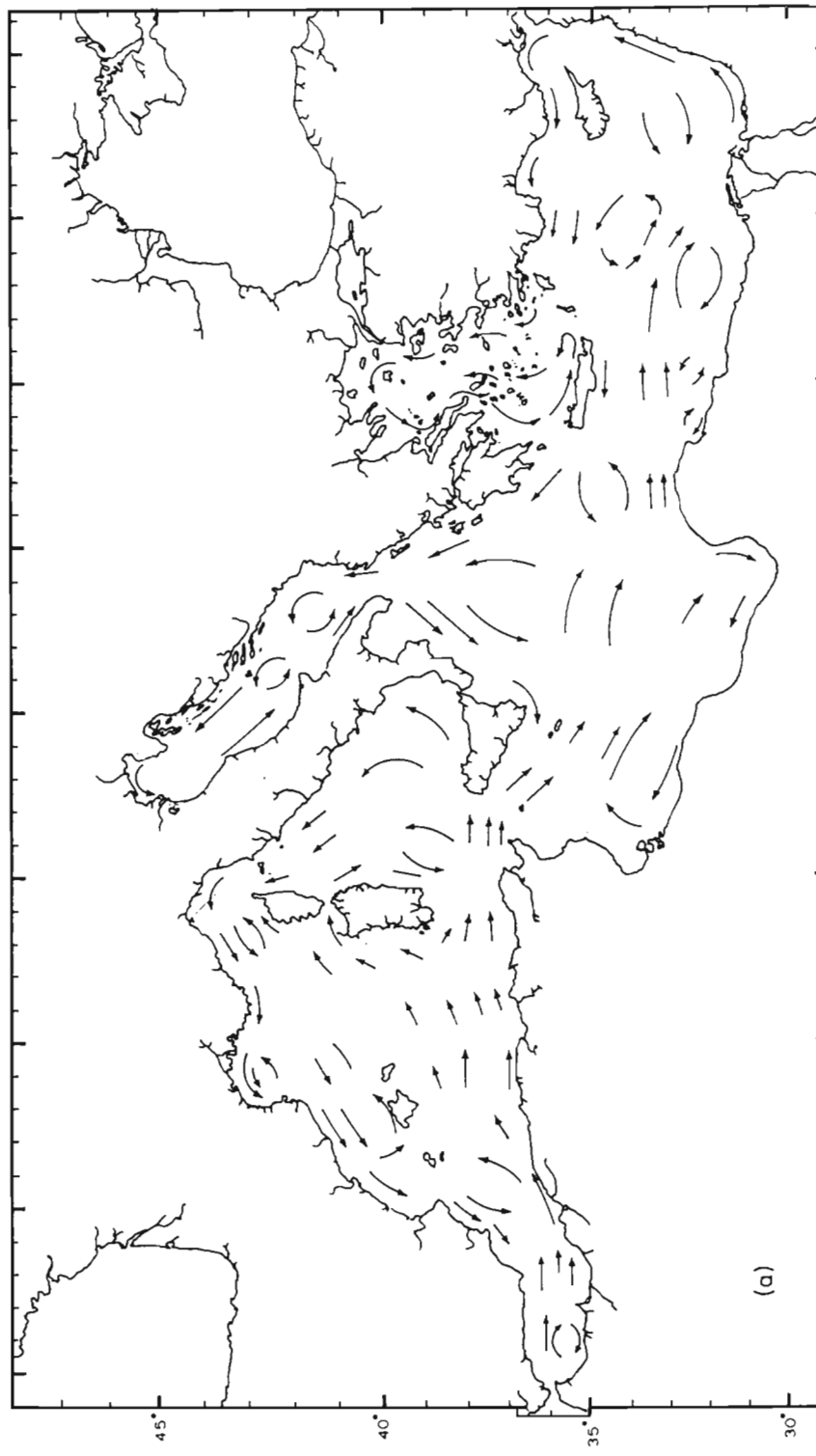


Fig. 1-9: The major basins and the large scale circulation pattern of the European Mediterranean. Surface circulation. (Adapted from Ovchinnikov, 1966.)

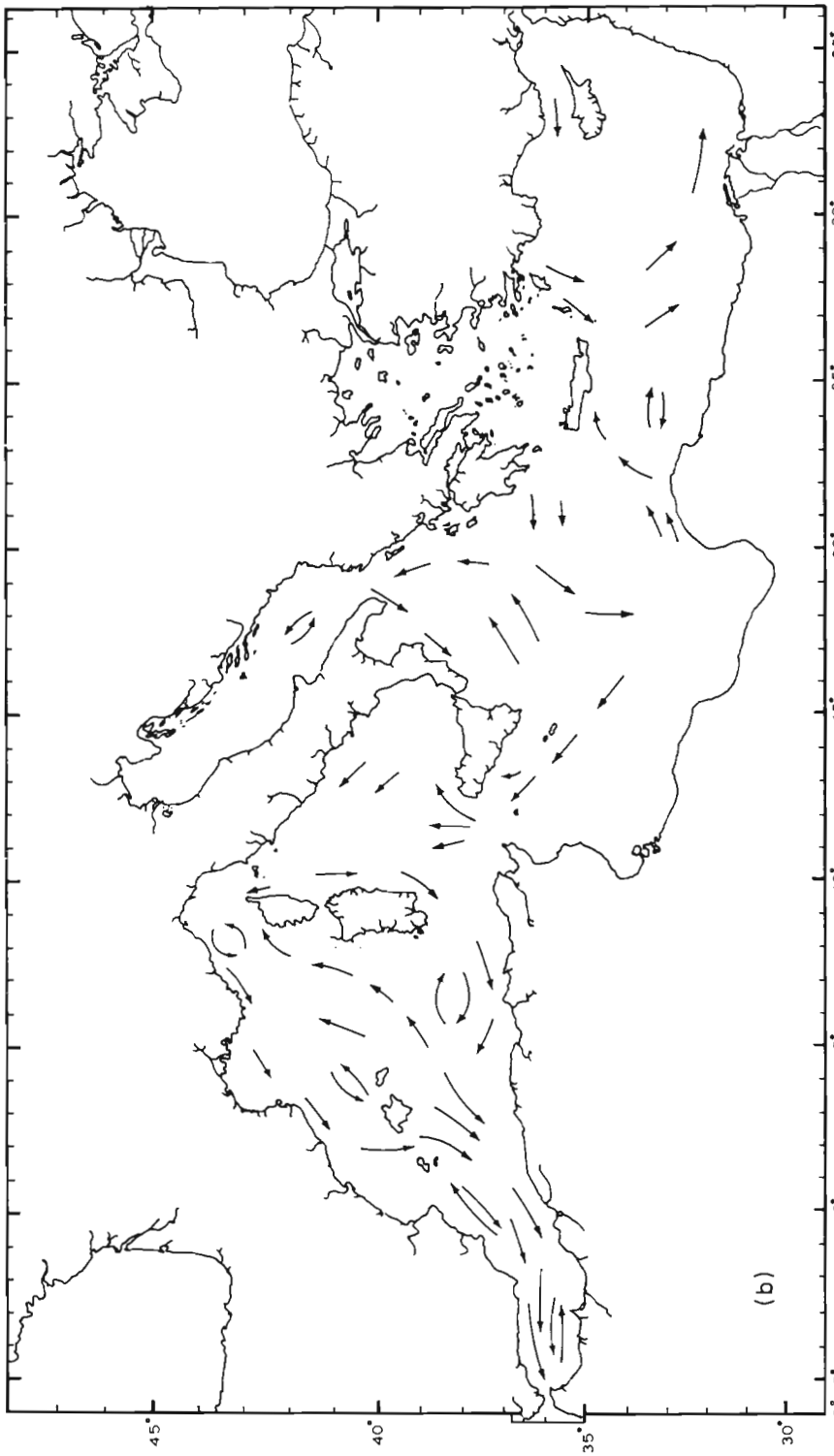


Fig. 1-9: The major basins and the large scale circulation pattern of the European Mediterranean. Circulation at 500 m. (Adapted from Ovchinnikov 1966.)

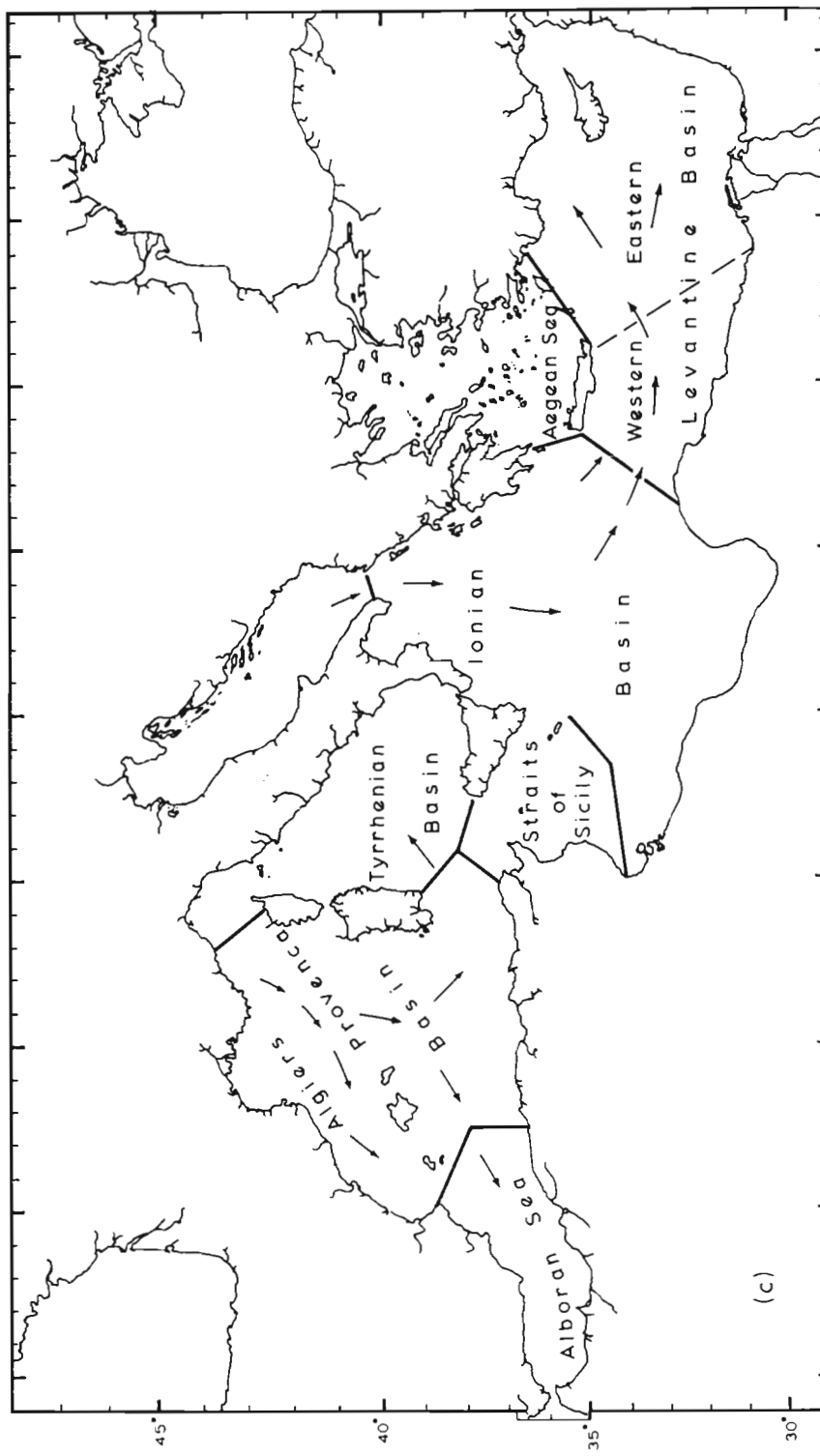


Fig. 1-9: The major basins and the large scale circulation pattern of the European Mediterranean. Movement of waters of bottom layer. (Circulation from OVCHINNIKOV and PLAKHIN, 1965; basin boundaries from MCGILL, 1961.)

disagreement. POLLAK (1951) assigns this role to the Adriatic Sea only for the eastern Mediterranean while OVCHINNIKOV and PLAKHIN (1965) present evidence that the Ionian Sea is also a site of Deep Water genesis. The latter authors also include the eastern areas of the Aegean Sea as well as the northeast of the Levantine Sea.

The circulation of the Mediterranean is greatly influenced by the irregular coastline and the intricate dissection of basins by islands and peninsulas. In general, the main surface current is the North African Current moving eastward from the Strait of Gibraltar. As implied by the name, it follows the African coast and can be traced to the Nile River. To the north there is a series of cyclonic and anticyclonic eddies. There are also some on the south in the region of the Libyan and Egyptian Seas. According to OVCHINNIKOV (1966), the circulation shows little seasonal fluctuation because of the dominant northwest winds.

Water masses and circulation of the Caribbean Sea and Gulf of Mexico (American Mediterranean). WÜST (1964, p. 29) objects to the use of the term 'American Mediterranean' for the Caribbean, although it has been used in the past as a collective term for the Gulf of Mexico and the Caribbean. The term was first used, according to WÜST, by KRÜMMEL in 1907. It alluded to similarities in geography such as the complex ridge and basin structure and the intercontinental situation. Hydrographically, as WÜST so clearly points out, the two are in completely different categories (Fig. 1-7).

The Caribbean is enclosed by an arc of islands born of diastrophic activities which are open to the north and east flowing main currents of the Atlantic Ocean. Hence, its principal water masses have their origins in the Subtropical Underwater and the Subantarctic Intermediate Water. The surface waters are derived from the Guinea Current.

Whereas the Bottom Water of the European Mediterranean originates in the Adriatic in the winter, the Aegean and in the northern regions of the western basin, in the American Mediterranean, the Bottom Water has its origin in the overflow of the Antarctic Bottom Current (WÜST, 1964) through the Virgin Islands Passage and Windward Passage. While the Caribbean Sea may not qualify as a mediterranean sea according to the criteria set up by WÜST, the Gulf of Mexico is itself a mediterranean sea by geographical criteria. It is not dissected by ridges and peninsulas but is an inland ocean with limited connections to the world ocean. It receives a direct flow from the Caribbean; the entrance of both Subtropical Underwater and the deeper water masses of the Atlantic certainly can be expected to be present if the work of WÜST can be extended to the Gulf of Mexico. The Mississippi River and many lesser ones contribute a large amount of land drainage to the Gulf. Its hydrography is further complicated by meteorological frontal activity. The surface circulation of the American Mediterranean is shown in Fig. 1-10.

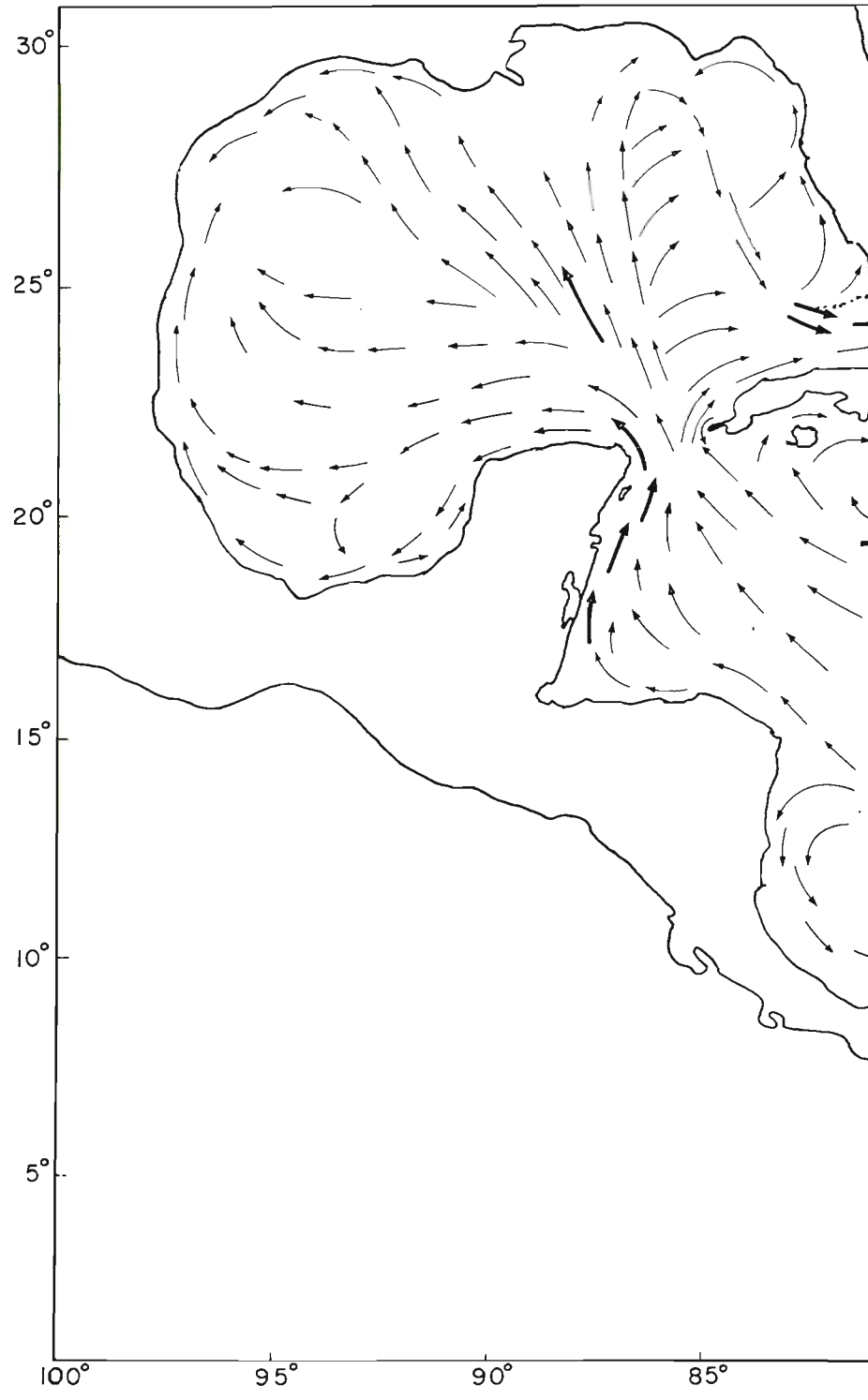
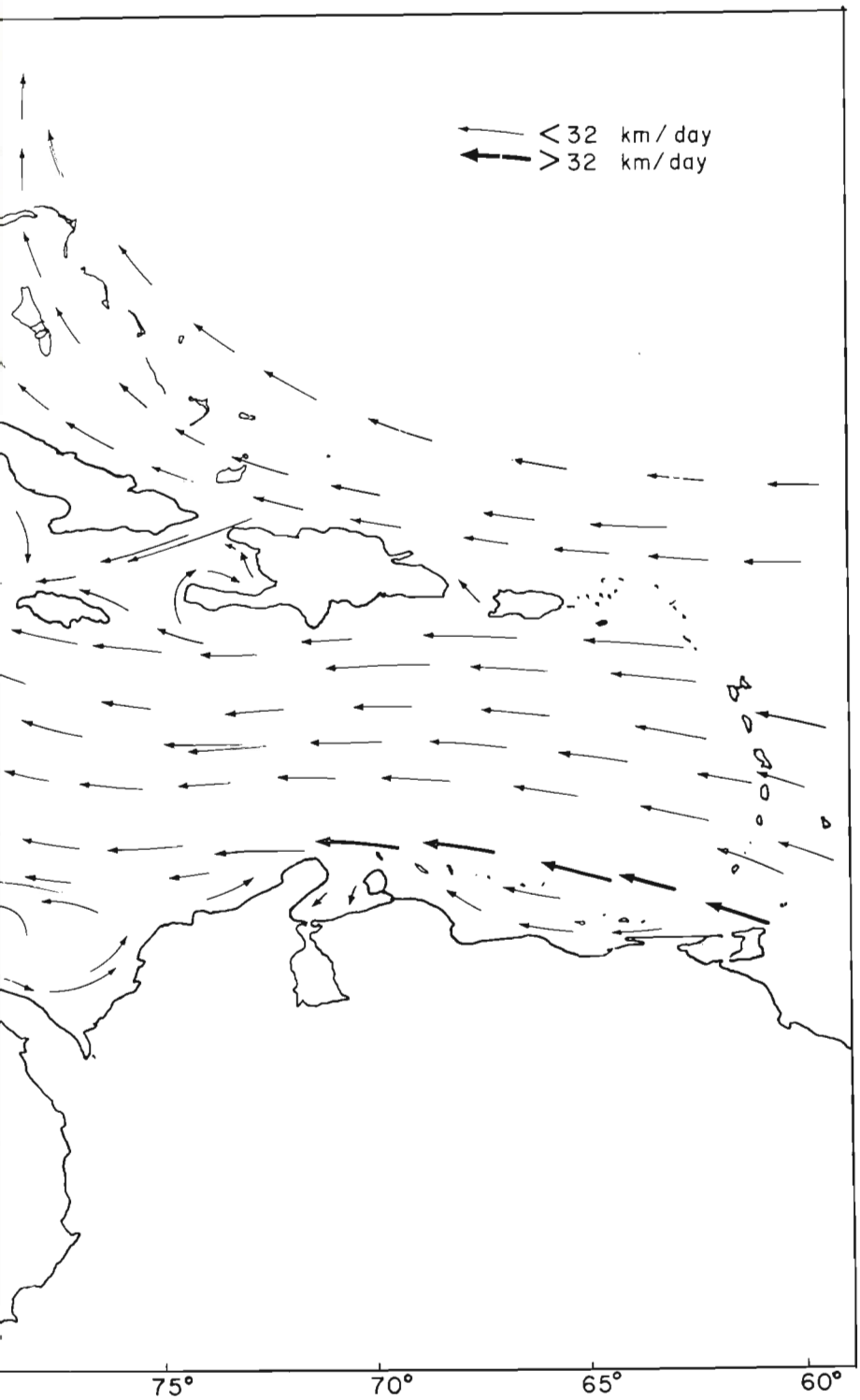


Fig. 1-10: Surface currents of the American Mediterranean. The figure is a generaliz
(After COLLIER, 1964.)



ata shown on US Hydrographic Office Pilot Charts for Central American waters.

The Pacific Ocean

One cannot truly comprehend the magnitude of the Pacific Ocean and its relation to the remainder of the oceans and the land masses without the aid of a globe. When viewed on a 45 cm globe at normal viewing distance with a line of sight normal to a tangent of the equator at 165° W, the east and west limits are beyond the globe's perimeter.

We shall organize the geography of this immense area in its most general terms before proceeding with a more detailed examination of the secondary seas.

The eastern boundary of the Pacific Ocean is much less dissected than the western boundary. It is noticeable that the American continents present themselves as an approximate southeast and northwest diagonal. This trend is also found in the island chains of the mid-ocean and southwestern areas. A parallel is also noticed beginning with New Zealand and proceeding toward the Indo-Chinese peninsula. In the latter case, it does not test the imagination to see that Antarctica continues this latter trend to the point of suggesting a continuation with the South American continent.

North Pacific Ocean

The North Pacific must be studied as a series of subunits rather than as a single basin (Fig. 1-11). The most pronounced subdivisions are the northeast and southwest sections. The northeast section is bound on the west and southwest by the Emperor Seamount Chain, the Hawaiian Islands and the Southwest Christmas Islands. Like the folds of a drape, the Aleutian Islands and the Aleutian Trench hang downward from the north. The comparatively smooth coastline (from distant perspective taken here) of North America forms the eastern limit.

This northeastern zone contains huge abyssal plains and fringing on the North American continent are a series of alternating seamount provinces and fracture zones. The series begins with the Gulf of Alaska Seamount Province on the north and terminates with the Clipperton fracture zone on the south.

Compared to the northeast section of the North Pacific Ocean, the northwestern section offers a great variety of topographic relief. It is rich in seamounts, island arcs and trenches, and has a comparatively restricted but well-defined Northwest Pacific Basin.

The Northwest Pacific Basin is bounded by the Marcus-Necker Seamount Ridge on the south, the Japan Trench, the Kuril-Kamchatka Trench on the west and the Emperor Seamount Chain on the east. South of the Marcus-Necker Seamount Ridge lies a large area of intermingled basins, ridges and island complexes.

The secondary seas of the North Pacific are described briefly in the following paragraphs.

The Bering Sea is the hydrographic mate of its northern counterpart, the Chukchi Sea. It has two obvious subdivisions: the extensive area within the 183 m contour which extends from Orimok Pass in the Aleutian Island Chain for slightly over 1800 km northwestward toward Mys Navarin off eastern Siberia, and the Aleutian Basin. The latter has the appearance of an extension of the Pacific which has been cut off by the Aleutian Island Chain.

The Sea of Okhotsk is a large marginal sea enclosed by the East Siberian

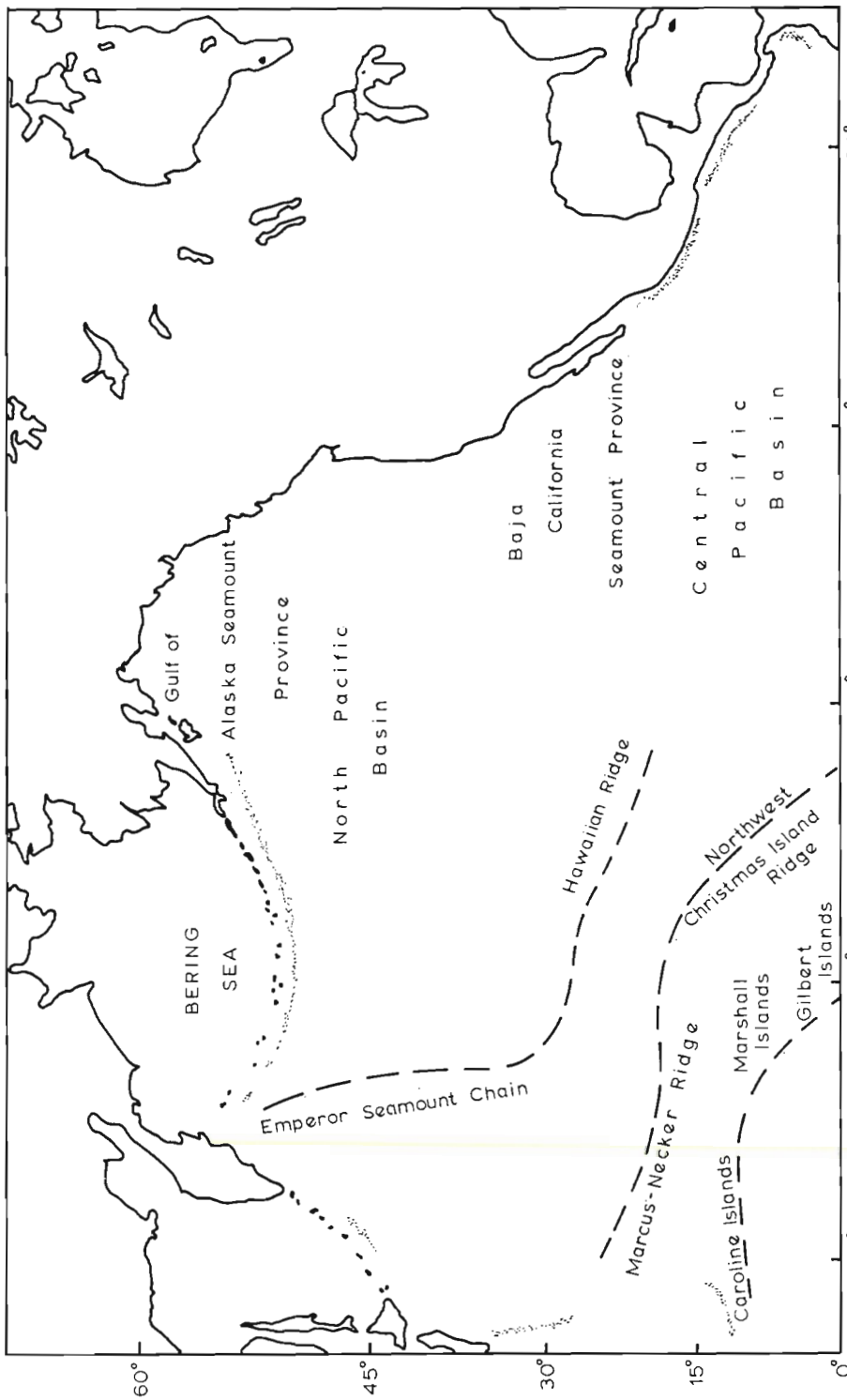
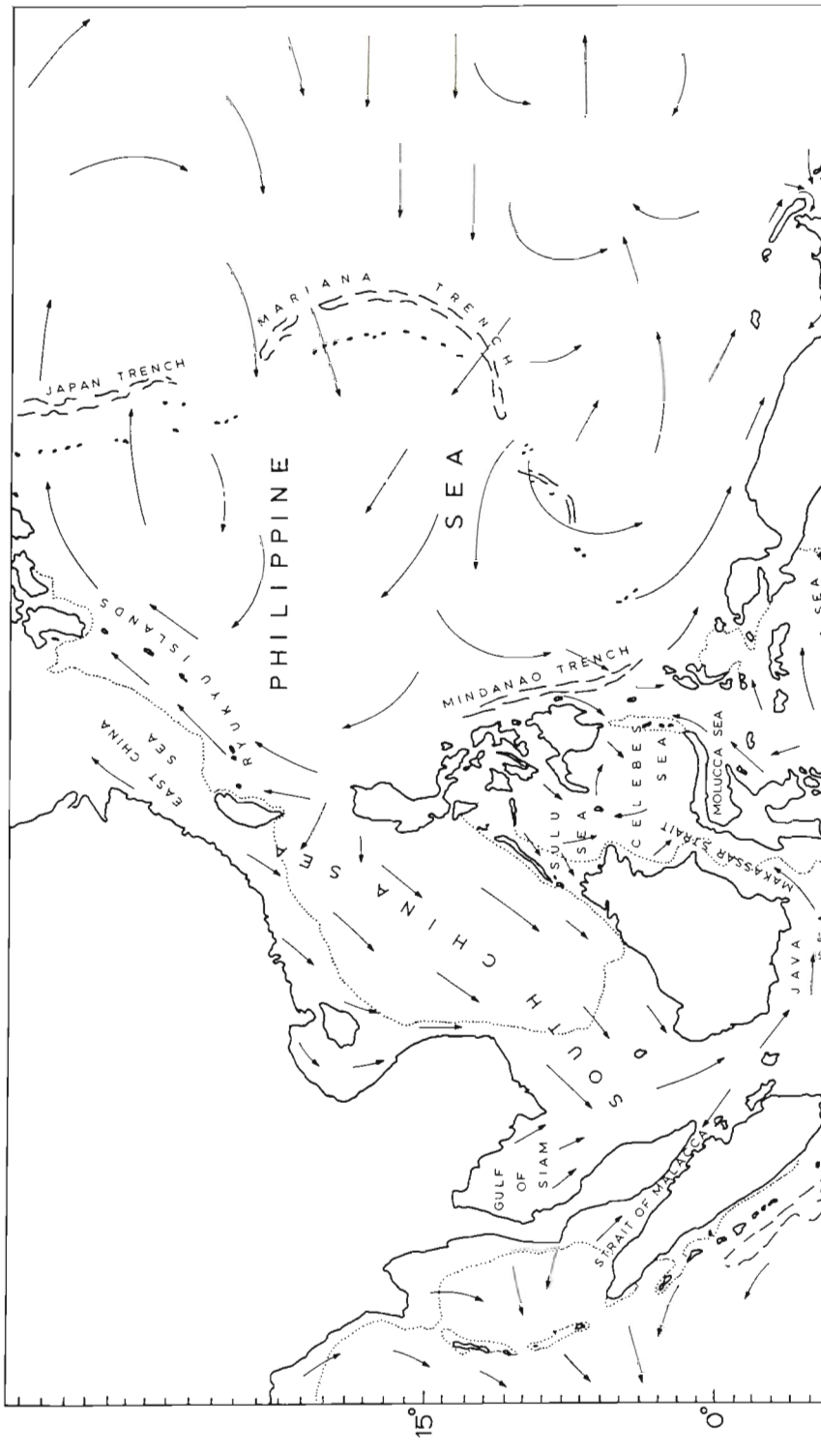


Fig. 1-11: Schematic representation of the major bathymetric features of the North Pacific. Stippled areas indicate location of trenches. (TROLL, 1966 consulted for nomenclature. Base map US Naval Oceanographic Office Chart of the World (1:39,000,000 at Equator) No. H. O. 1262A, revised 28 November 1966.)


JAPAN TRENCH
MARIANA TRENCH
PHILIPPINE SEA
RYUKYU ISLANDS
EAST CHINA SEA
MINDANAO TRENCH
SULU SEA
CELEBES SEA
MOLUCCA SEA
MAKASSAR STRAIT
SOUTH CHINA SEA
JAVA
GULF OF SIAM
STRAIT OF MALACCA
15°
0°

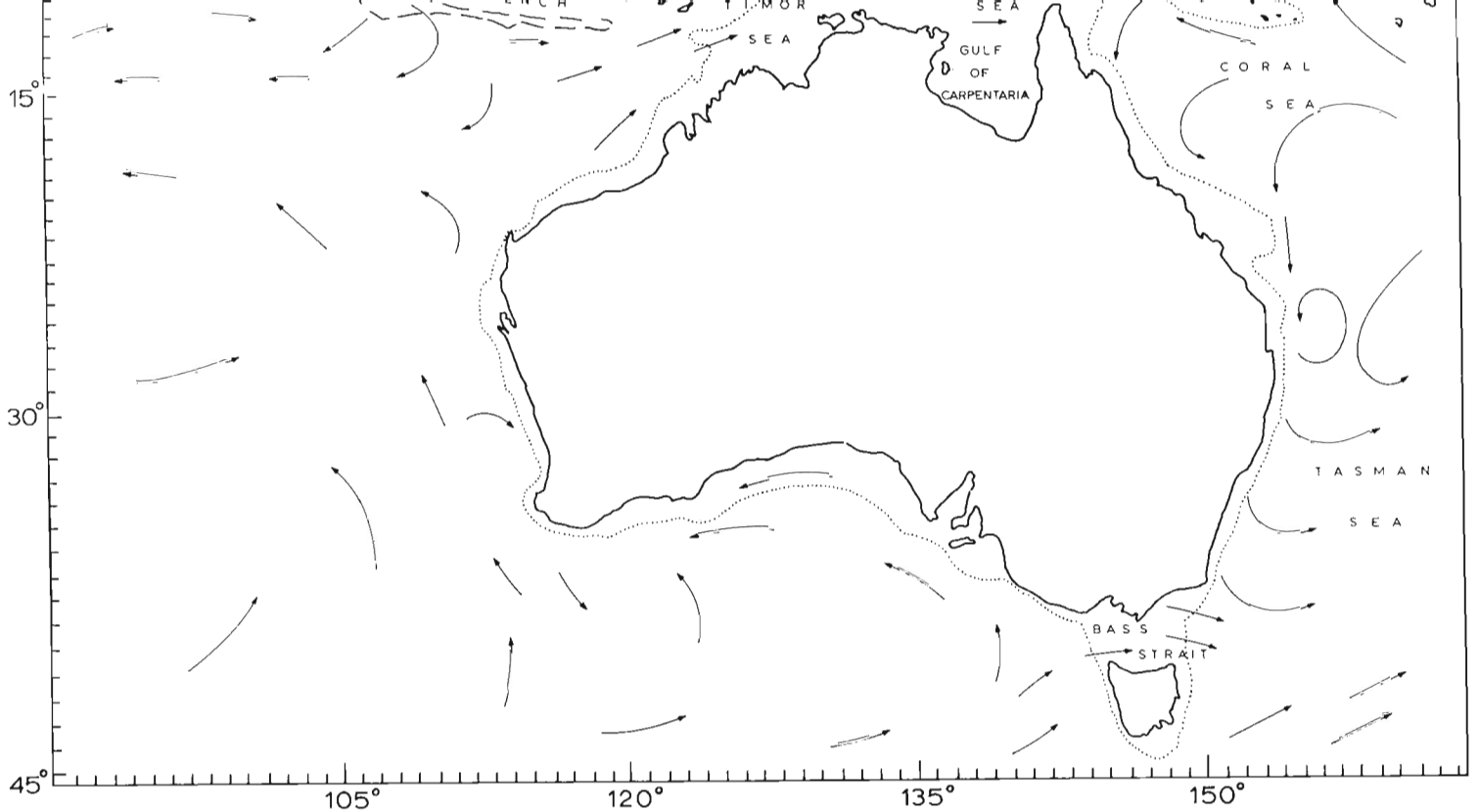


Fig. 1-12: The seas of Australasia showing a general plan of the currents. The currents vary in detail according to the season. (After various sources.)

mainland, and the Kuril Island group and Kamchatka. It is comparatively shallow with a basin of relatively small area reaching depths over 2700 m. The waters of the Zaliv Shelikhova form a northeastern extension of this sea between the mainland and Kamchatka.

The Sea of Japan represents a deep basin enclosed by the Asiatic mainland and the Japanese Islands. Its most notable characteristics are a lack of shelf waters and limited contact with the open sea.

The Yellow Sea is an inland body of water with all depths less than 183 m. It receives the Yellow River at its most inland aspect and opens seaward into the East China Sea.

The East China Sea may be regarded as a seaward extension of the Yellow Sea.

The Bering Sea, Sea of Okhotsk, Yellow Sea, and East China Sea all show signs of filling by erosional and volcanic products (HEEZEN and MENARD, 1963).

Consideration of the South China Sea brings us into the extreme southwest corner of the North Pacific and the vestibule of all Southeast Asia. It is a basin enclosed by the Philippines, Indo-China, the Malay Peninsula and Borneo. The most extensive sea entrances are by way of the passages between Taiwan and Luzon on the north and its southwest opening into the Java Sea. Its southwest sea floor provides the most extensive floor less than 183 m, while its northeast sector is occupied by the South China Basin. The South China Sea, together with the Philippine, Molluca and Banda Seas (see below) comprise a complex which may be considered as the seas of Australasia (Fig. 1-12).

In rough outline the Philippine Sea resembles a diamond with one of the acute angles resting on the equator. It is truly a vestibule which serves as a common entrance to the marginal seas of Southeast Asia. It is bounded on the east by the South Honshu Ridge and its flanking islands, and the complex of ridges and small islands (Nampo-Shoto) along the Japan Trench. The apex formed at the juncture of the Japan Trench and Honshu marks the northern limit of the Philippine Sea. At this point one may traverse the north and west boundaries by following the coast of Honshu, Shikoku and Kyushu islands, thence along the Ryukyu Chain to Taiwan. The southwest boundary of this sea is formed by the Philippine Islands. The long axis of the sea is marked by Palau-Kyushu Ridge. There is very little water in this sea with depths less than 183 m.

Around Borneo and with direct and indirect connections to the South China Sea there are a group of small seas which may be considered as satellite seas of the China Sea. The Gulf of Siam is an oceanic cul de sac terminating at Krung Thep (Bangkok) and dependent entirely upon the South China Sea for its circulation. To the south, between Java and Borneo, lies the Java Sea roughly symmetrical with the Gulf of Siam with respect to the long axis of the South China Sea. An important point here is that the Java Sea also connects with the Indian Ocean through the Straits of Malacca. North of Borneo lies the Sulu Sea as it connects with the South China Sea at both ends of Palawan. To the southeast the Sulu Sea is in communication with the Celebes Sea. This little sea serves as common vestibule for the Java Sea through Makassar Strait and the Philippine Sea via the unnamed opening between Mindanao and the extreme northerly tip of Celebes. At the periphery of this group of Indonesian seas lie the Molluca and the Banda Seas. These and some of the above are not actually in the North Pacific domain, but

there would be little point in separating their treatment. Water depths in all except the southwestern portion of the South China Sea, the Gulf of Siam and the Java Sea are much greater than 183 m. In those cases listed as exceptions we find considerable areas at depths ranging between 18 and 75 m.

The Gulf of Alaska is a segment of the Northeast Pacific Ocean demarcated by an approximately 90° turn from the northeast bearing of the coastline of Alaska to the southeast. It is penetrated along its northwest periphery by a projection of the Aleutian Trench. If one must delineate a seaward boundary, it might be arbitrarily considered as coincident with the outer limits of the Gulf of Alaska Seamount Province. This line may be described as a line extending northwest from Vancouver Island to coincide with the Alaska Peninsula, a distance of approximately 2300 km (1 nautical mile = 1·852 km). This more natural boundary is more extensive than one based on the political boundary of Alaska and Canada which coincides with Dixon Entrance.

The Golfo de California is a large canyon-like diverticulum of the Pacific Ocean which lies parallel to the west coast of Mexico. It is approximately 1100 km along its southwest to northwest axis and is separated from the Pacific by the peninsula of Baja California. The 2750 m contour penetrates the Golfo about 210 km above Cabo San Lucas and the 915 m contour is found about 660 km from the same reference point. The mouth of the Golfo de California, Cabo San Lucas to Cabo Corrientes is some 480 km in breadth.

The arc of the Isthmus of Panama and the Peninsula de Azuero embrace the Golfo de Panama. Its seaward boundary is marked by the 183 m contour. From the point of view of marine bathymetry, however, one might well consider the seaward extension to include the basin bounded by the coast of Colombia, Ecuador, the Carnegie Ridge, the Archipelago de Colon and the Cocos Ridge, all in clockwise sequence.

South Pacific Ocean

With the exceptions noted above in connection with the seas of Indonesia, which have already been discussed, this treatment includes all of the waters south of the equator (Fig. 1-13). The eastern and western boundaries of the South Pacific are established by convention. For the latter, the meridian of 147° E (near South East Cape, Tasmania) has been designated; for the former, the shortest line between the Cabo de Hornos, the South Shetland Islands, Deception Island and the Palmer Peninsula is the accepted boundary between the Pacific and Atlantic Oceans.

The southern boundary of the South Pacific (as with the Atlantic) is difficult to set. As before, we shall follow Brodie (1965) and consider 52° S as an arbitrary limit.

The South Pacific Ocean may be divided into eastern and western portions for descriptive purposes. The 125th meridian west marking the most eastern point of the Tuamotu Archipelago provides a convenient division. East of this, the Pacific has few islands, and to the west lies the well known complex of south sea islands. The southeast Pacific between the equator and 52° S and east of 125° has not been completely explored oceanographically. The most prominent bathymetric feature is the Easter Island Cordillera and its branches, the West Chile Rise and another

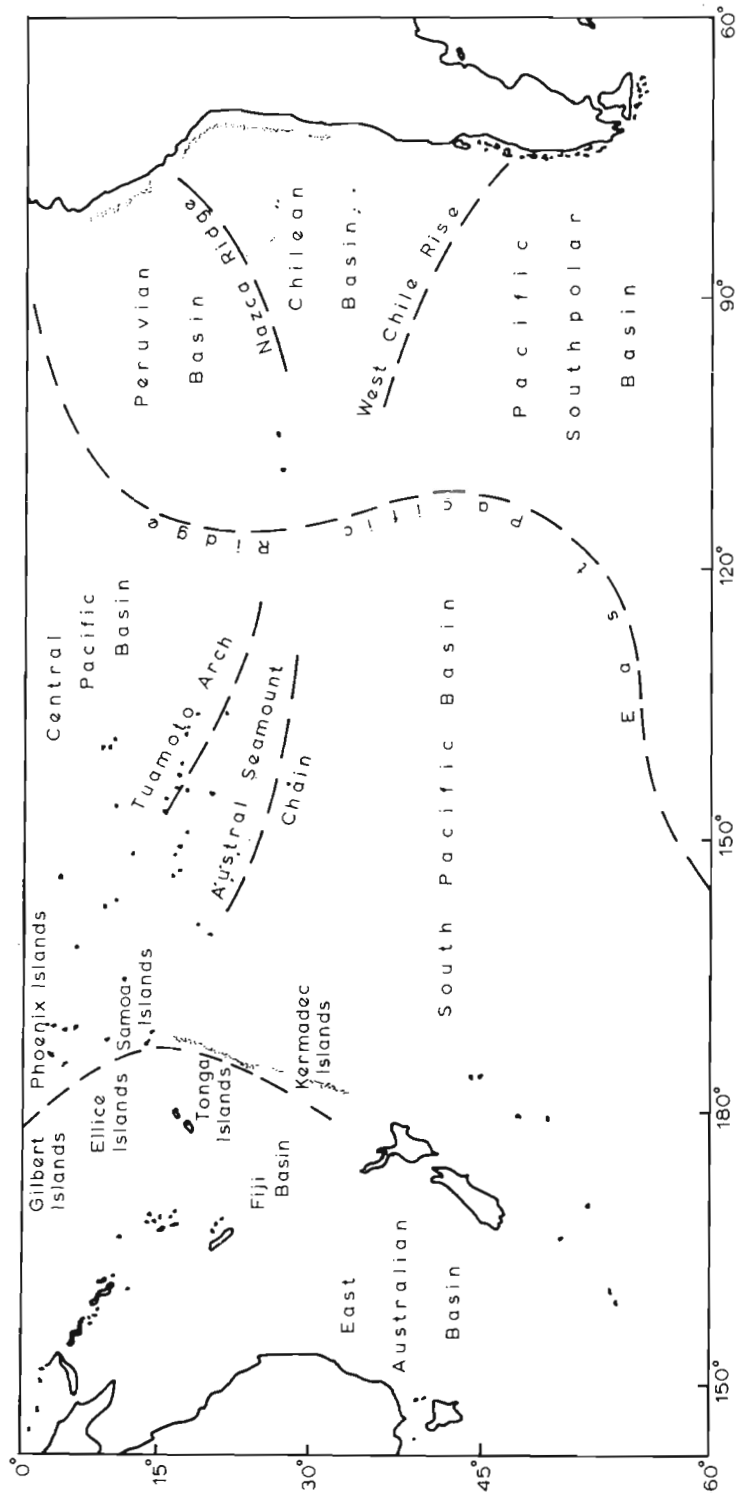


Fig. 1-13: Major bathymetric features of the South Pacific Ocean. Trenches indicated by stippled areas. (Authorities as in Fig. 1-11.)

almost continuous with the Nazca Ridge, subtending southwestward from the Peruvian coast.

To approach the western portion of the South Pacific we shall turn to those seas surrounding the Australian continent.

Between New Guinea and Australia we find the Arafura Sea as a rather spacious shelf area providing communication between the Indian Ocean and the Coral Sea by way of the small Timor Sea. The Gulf of Carpentaria hangs as an appendage from the northeastern quarter of the Arafura Sea.

The Coral Sea is continuous with the Tasman Sea on the south. Seaward, the former is roughly bounded by New Guinea, the Solomon Islands, and the New Hebrides.

Between New Zealand and the Samoan Islands there is a long and deep scar in the floor of the sea. This scar is the Kermadec-Tonga Trench. The 180th meridian passes midway between the southern tip of the trench and East Cape (North Island of New Zealand). The Kermadec-Tonga Trench marks the eastern extent of the South Fiji Basin; the North Fiji Basin lies between the Fiji and New Hebrides Islands. In the vicinity of the above islands we find the eastern termini of the two great island arcs, Melanesia and Micronesia. Towards the Society Islands further east we find the southern terminus of Polynesia.

Water masses and circulation of the Pacific Ocean

In turning from the Atlantic Ocean to the Pacific Ocean, the task increases in the same proportion as that of taking up a treatment of the Atlantic Ocean after dealing with the European Mediterranean. The immediate problem is one of reducing the tasks to manageable sections. DIETRICH (1963) presented a useful solution in his system of hydrographic regions of the world, and STEPANOV (1965) illustrated division of the oceans based on eight major water types. MUROMTSEV (1963) published a comprehensive treatment of the waters of the Pacific. The large elements of classification are probably correct, but no doubt there will be revisions as new data become available. Lack of data from the southeast Pacific is particularly noticeable. In STEPANOV's classifications we find some important characteristics in the Pacific as contrasted to the Atlantic (Fig. 1-14).

Beginning with the equatorial region, we note the expanded area of the equatorial structure. It is shown as extending completely across the Pacific, largely from the equator westward to a latitude of 15° N on the east and about 12° on the west. The Atlantic counterpart of this structure is shown as a relatively small triangle covering roughly the Guinea and Sierra Leone Basins on the southern aspect of the African bulge.

With respect to its tropical structure, the Pacific comes nearer to expectation than the Atlantic. There are two broad belts of tropical water on either side of the equatorial structure, with the exception that the north tropical mass is not shown as extending completely to the eastern boundary of the Pacific; its eastern boundary is marked by confluence of the equatorial and north temperate tropical structures.

Again the temperate–tropical mass of the Pacific occupies a narrower band of the earth's surface than does the analogous band in the Atlantic. In the latter case, there is no well-defined south tropical mass.

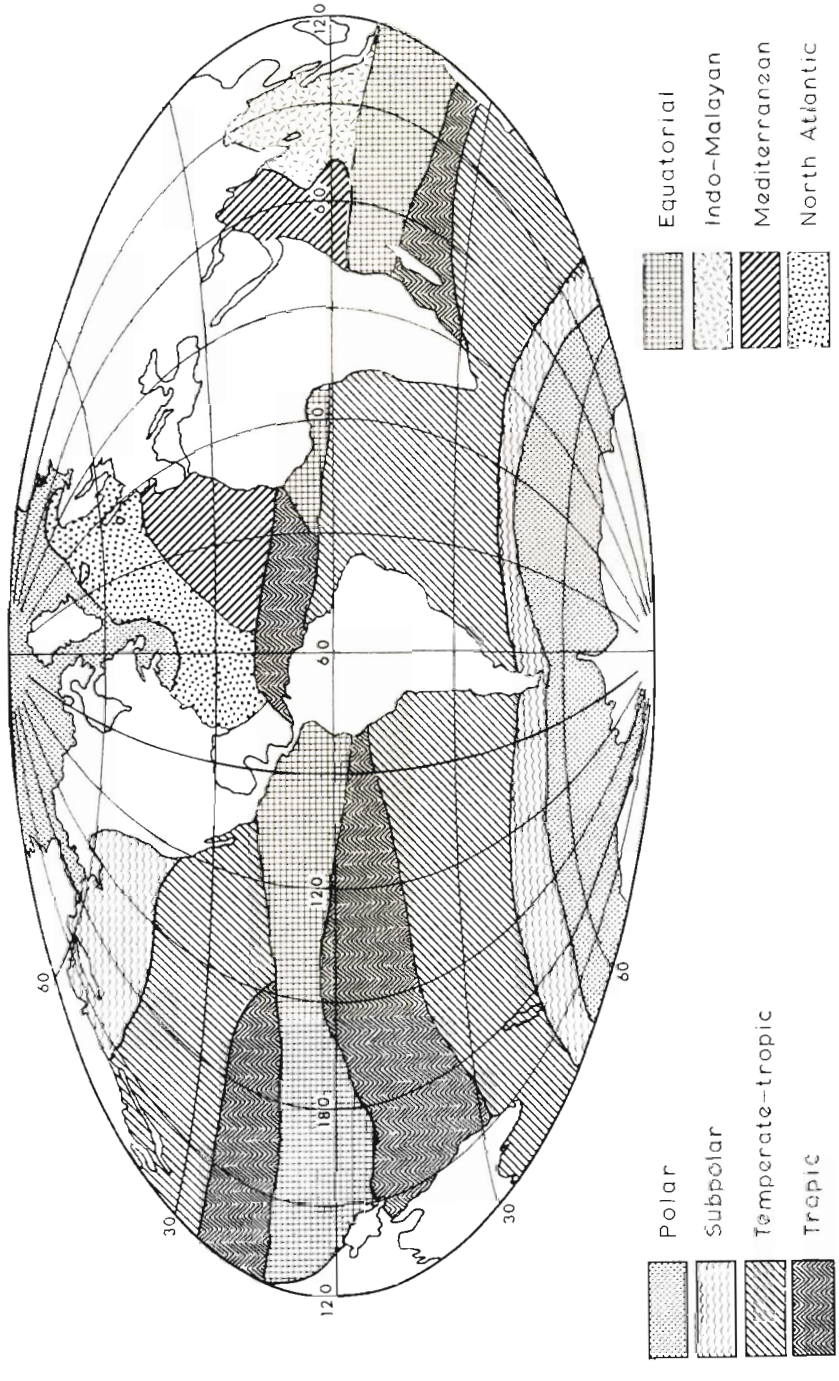


Fig. 1-14: Geographic limits of water masses as described by STEPANOV. (After STEPANOV, 1965; modified.)

Table 1-1

Characteristics of Pacific water masses
(After MUROMTSEV, 1963)

Water mass	°C	S ‰	O_2 ml/l
Surface Water			
Kurilo–Aleutian	4–9	33·0–33·6	6·0–7·0
Alaska Bay	4–12	32·2–32·9	4·5–6·0
California	9–20	33·5–34·5	4·5–5·8
North tropical	25–28	34·5–34·8	4·0–4·8
Kuroshio	10–26	34·2–34·8	4·5–5·5
North–temperate	10–20	34·0–34·5	4·8–5·6
North–central–subtropic	18–25	35·0	4·7–5·2
Equatorial	26–29	34·0–34·5	4·2–4·8
Southern–tropic	25–29	35·0–35·5	4·0–4·6
Peru	14–23	34·5–35·5	0·2–5·0
South–central–subtropic	20–25	35·5–36·45	4·0–5·2
South–temperate	5–15	34·0–34·5	5·8–6·8
Antarctic	− 1·85 + 2·00	33·5–34·0	6·4–8·2
Subsurface Water			
Kuril	1–2	33·3	6·8–7·2
North Pacific	3·5–3·8	33·65–33·95	1·8–4·3
Northern subtropic	15–20	34·7–35·33	4·5–4·8
Western–equatorial	20–25	34·8–34·9	2·0–3·5
Eastern–equatorial	12–15	34·7–34·9	0·0–1·9
South subtropic	10–20	34·8–36·3	0·4–4·5
Antarctic	− 0·45 − 1·87	34·0–34·6	6·2–7·6
Intermediate Water			
Kurilo–Aleutian	3·1–3·5	34·0–34·26	0·8–1·5
North Pacific	3–5	33·9–34·3	0·3–4·3
South Pacific	3–6	34·1–34·5	0·3–5·8
Equatorial	4·5–6·5	34·55–34·65	0·0–2·5
Deep Water			
South Pacific (upper)	2–2·5	34·61–34·66	2·81–3·84
North Pacific (upper)	2–2·5	34·61–34·66	1·6–2·6
Underlying	1·7–2·0	34·63–34·73	3·5–4·2
Bottom Water			
Antarctic	0·24–0·85	34·7–34·72	4·6–4·7
Pacific	1·0–1·6	34·64–34·71	3·7–4·5

The subpolar masses of the Pacific are more symmetrical structures than are found in the Atlantic; the latter being shown without a northern subpolar structure. The relations of the two oceans to the Arctic Basin and the size of the Pacific are in part responsible for these differences.

The more specific details of water mass distribution in the Pacific as given by MUROMTSEV (1963) will be briefly reviewed. The salinity and temperature characteristics are given in Table 1-1. Fig. 1-15 shows the boundaries of the regions. MUROMTSEV has given the most comprehensive treatment of the circulation of the

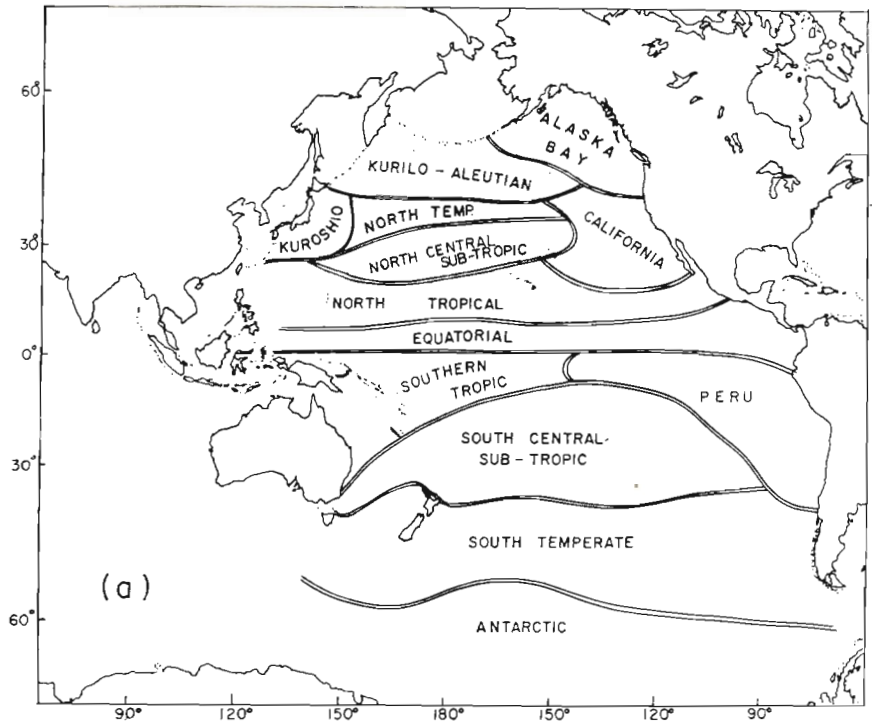


Fig. 1-15(a): Schematic representation of the water masses characterized in Table 1-1. Surface waters. (After MUROMTSEV, 1963; modified.)

Pacific Ocean which is available in recent literature. With respect to the large scale oceanography of the Pacific Ocean the treatment of the intermediate waters by REID (1965) should be mentioned. The description of the Equatorial Undercurrent by MONTGOMERY and STROUP (1962) is also of interest.

In its broadest terms, we may consider the circulation in terms of the surface layer, the intermediate layer, and the deep layer. The surface layer is responsive to the predominant atmospheric circulation and the result is the well-known system of gyrals (Fig. 1-16). Contrary to the case in the Atlantic Ocean, the South Equatorial Current does not send branches into the northern hemisphere. While a detailed description of the circulation as shown in Fig. 1-17 will not be given, a few remarks on the general circulation are in order. According to MUROMTSEV

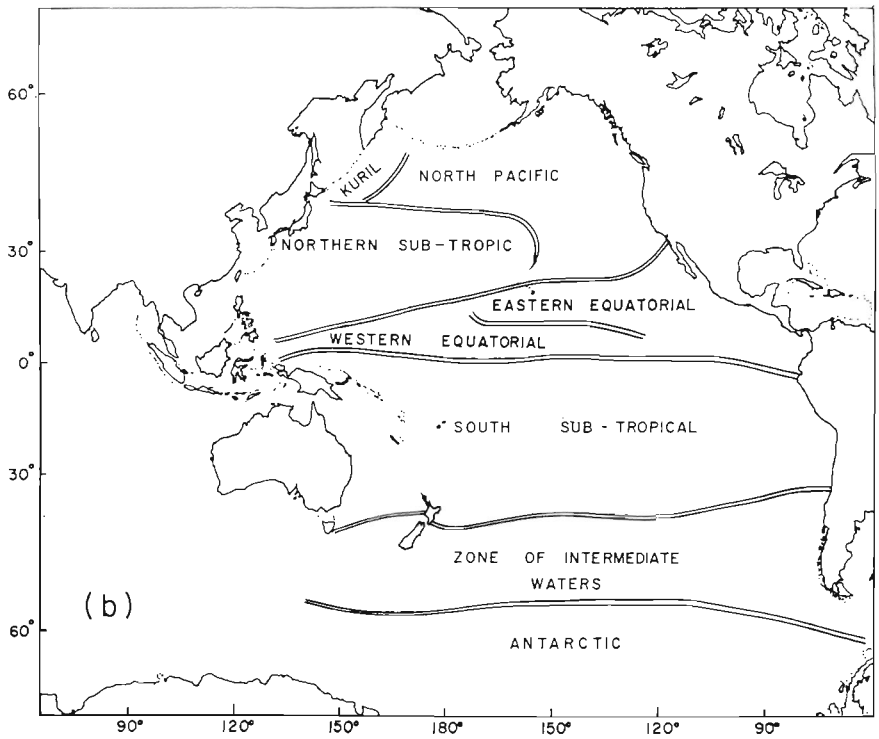


Fig. 1-15(b): Schematic representation of the water masses characterized in Table 1-1. Subsurface waters. (After MUROMTSEV, 1963; modified.)

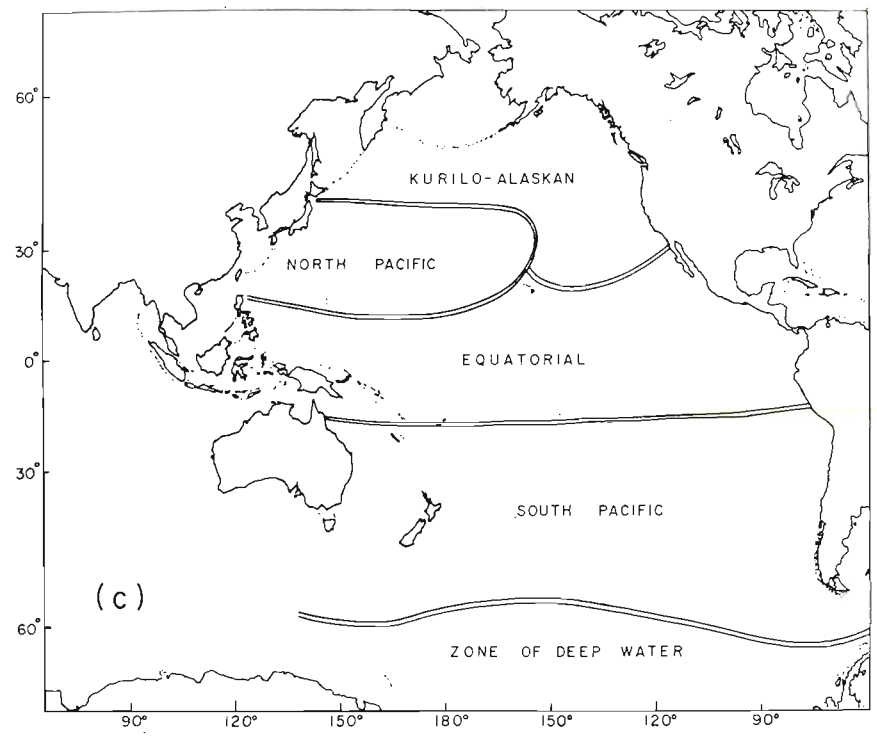


Fig. 1-15(c): Schematic representation of the water masses characterized in Table 1-1. Intermediate waters. (After MUROMTSEV, 1963; modified.)

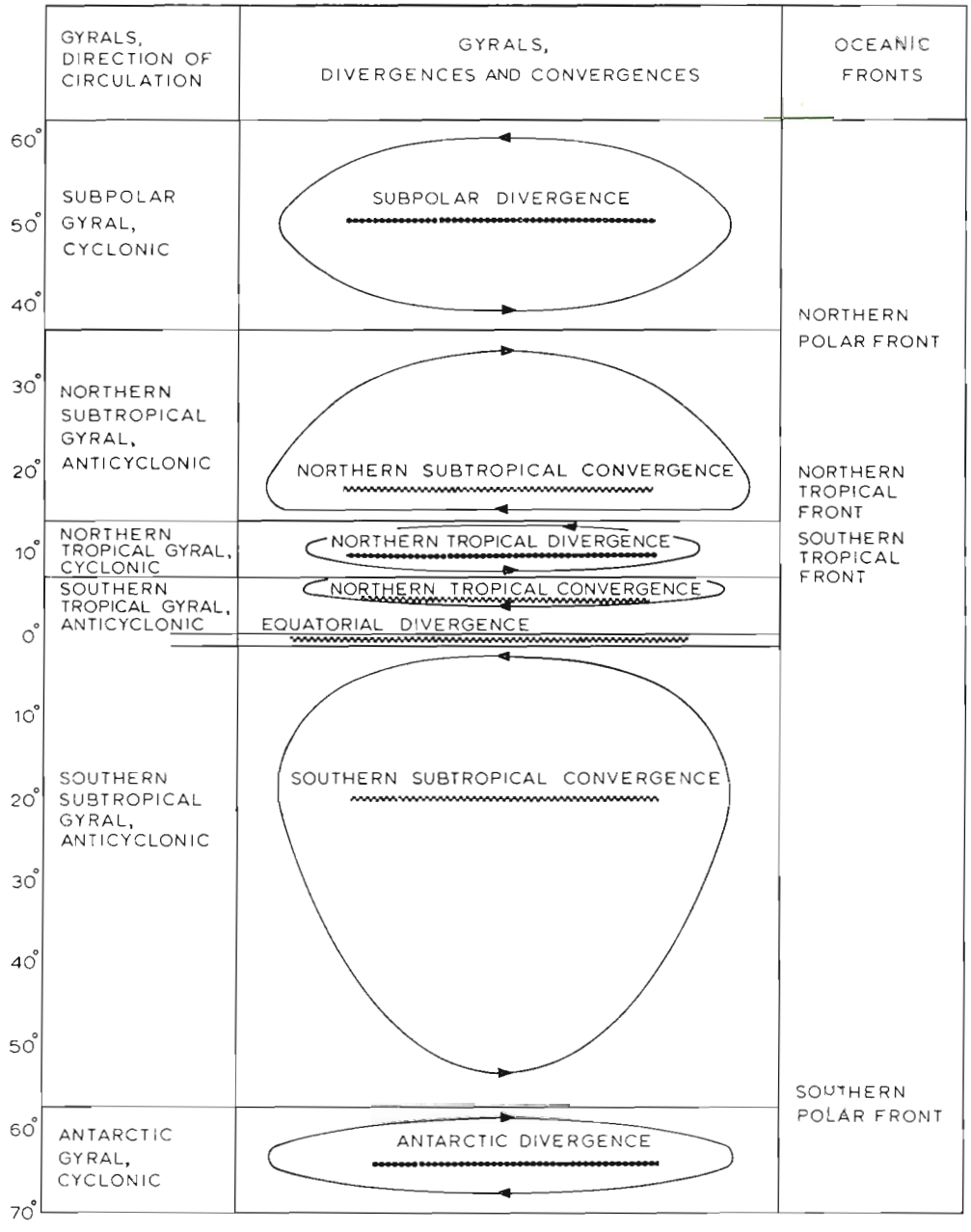


Fig. 1-16: Scheme of gyrals and related water mass structures of the Pacific Ocean. (After Burkov, 1966; modified.)

(1963) the longitudinal circulation begins with the sinking of water masses in the high latitudes of the southern regions. These move eventually into the Bering and the Okhotsk Seas where they are brought to the surface and enter the North Pacific areas. Here they sink again in the Arctic Convergence to be returned southward by the 'upper deep current'. They are then picked up in the West Wind Drift and carried into the Atlantic Ocean. In addition to that occurring in the Bering Sea and the Sea of Okhotsk, there is some upwelling from the depths in

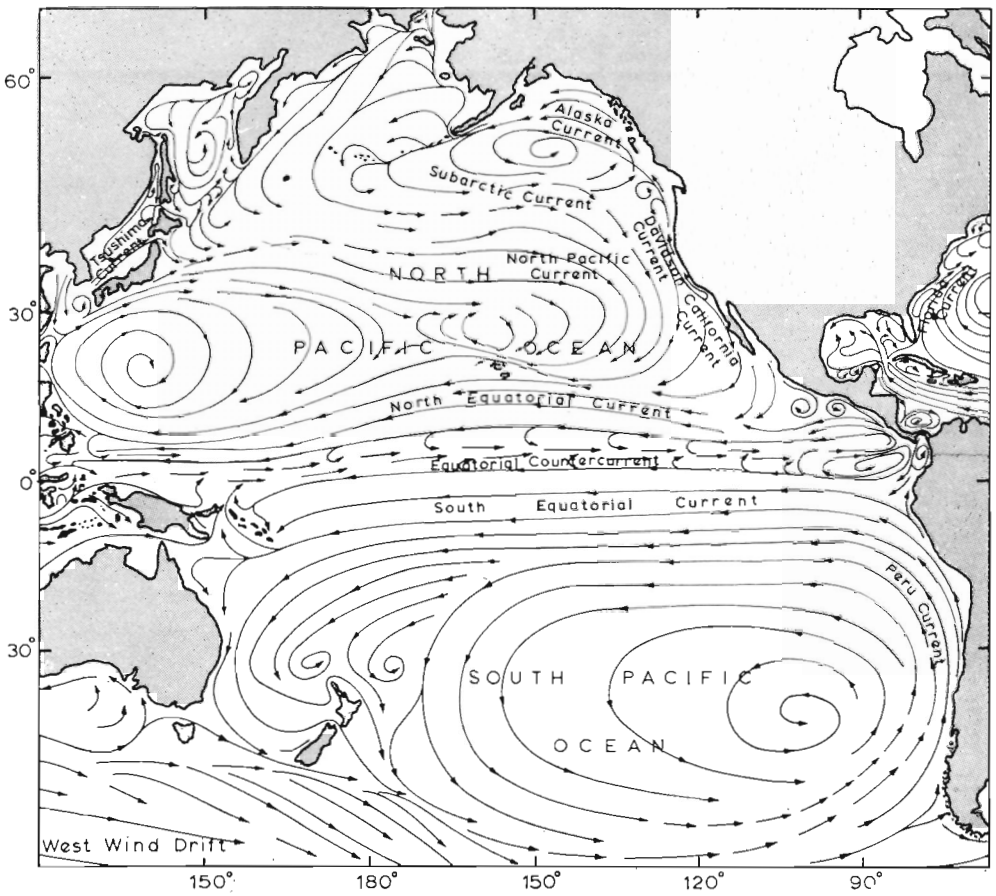


Fig. 1-17: Surface circulation of the Pacific Ocean. (Authority as in Fig. 1-8.)

the Banda Sea and the East and South China Seas, but the water does not reach the surface. It enters the circulation of the Intermediate Water.

The transfer from the Arctic Ocean through the Bering Strait and the Indian Ocean by way of Sunda Strait is small and of local significance.

The monsoons with their alternating maxima of precipitation and evaporation cause unusual variations in the surface salinities of the Bay of Bengal, the Andaman Sea and the South China Sea. The amplitude of the fluctuations may be as much as 3 $^{0}/_{00}$ S (DIETRICH, 1963).

The Indian Ocean

The eastern and western boundaries of the Indian Ocean are quasi-symmetrical about a line drawn from Cape Comorin, the southernmost point of India, to the Kerguelen Islands near the 50th parallel south. To the east and west of the Indian Peninsula lie the Bay of Bengal and the Arabian Sea, respectively. In the broad

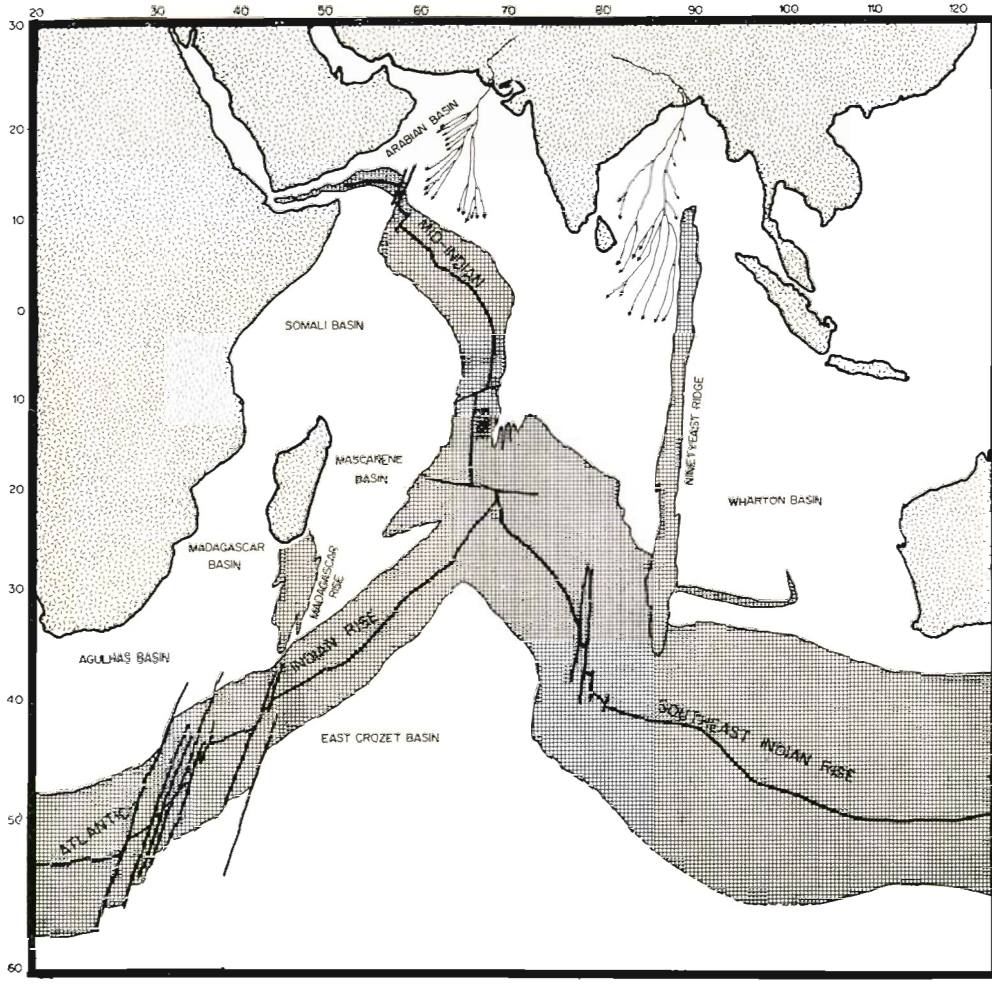


Fig. 1-18: Some of the major bathymetric features of the Indian Ocean. (After HEEZEN and THARP, 1965.)

sense the most characteristic feature of Indian Ocean bathymetry is its mesh work of ridges and basins. These have been most recently detailed by HEEZEN and THARP (1964–65). Some of the major features are shown in Fig. 1-18.

Tributary to the Arabian Sea, the Gulf of Aden serves as a vestibule to the Red Sea. The Gulf of Aden has very little water less than 183 m in depth, and contains

a basin of 2700 m in depth which is cut off from the Arabian Sea by a sill at some 1830 m.

The entrance to the shallow Persian Gulf from the Arabian Sea is through the Gulf of Oman and the Strait of Hormuz. The greatest depth shown for the Persian Gulf is approximately 75 m.

On the opposite side of the Indian Ocean we find the Andaman Sea isolated by a ridge which surfaces in the form of the Andaman and Nicobar Islands. It contains a deep basin (more than 2700 m) of limited area and a comparatively extensive shelf area. This sea communicates with the South China Sea through the Strait of Malacca.

Water masses and circulation of the Indian Ocean

The Indian Ocean may be hydrographically differentiated from the other oceans by these characteristics: (1) The major part of its area lies below the equator. (2) It is bounded on the north by a complex of irregular land masses. (3) The surface circulation is subject to alternating southwest and northeast monsoons. (4) The entire equatorial current system is located further south than those of the other oceans.

The surface water masses are marked by variable salinities in the northern region because of the variation in precipitation associated with the monsoons. There is a subtropical high in salinity (ca 36 $^{0}/_{00}$) west of Australia, and another high is found in the Arabian Sea (36·5 $^{0}/_{00}$). During the prevailing southwest monsoons, there is an area of upwelling along the coast of Arabia.

There are three principal subsurface water masses in the Indian Ocean. The Indian Ocean Central Water lies between 800 and 1000 m and the Indian Ocean Equatorial Water extends to 2000 m; below the latter is found the Deep Water with its characteristic temperature and salinity, 1° to 3° C and 34·6 to 34·8 $^{0}/_{00}$, respectively. At mid-depths, Antarctic Intermediate Water can be made out, and coming from the north, Red Sea Water can also be identified.

The mechanism of water exchange between the Red Sea and the Indian Ocean is analogous to that of the Mediterranean Sea and the Atlantic Ocean. The outflow over the 125 m sill is compensated by an inflow. Inside the sill the Red Sea Water has a temperature of 24° C and a salinity of 39·8 $^{0}/_{00}$. As the water discharges over the sill, it is mixed with the Indian Ocean water with resulting temperature and salinity of 15° C and 36 $^{0}/_{00}$ respectively (NEUMANN and MCGILL, 1962).

The southern limit of the Indian Ocean is considered to be in the region of the Subtropical Convergence which centres at 40° S. In this region, there is a dominant east flowing current generated by the westerlies. Off southwest Australia, the broad current splits with one branch turning north along the west coast of Australia (Fig. 1-19). In the vicinity of Northwest Cape, a second branching occurs with the westward moving component becoming part of the South Equatorial Current which lies between 8° S and 20° S. Along the way sections of the water in the current peel off into the southern gyral which is a permanent feature of the Indian Ocean surface circulation. The South Equatorial Current continues to impinge directly on the coast of the island of Madagascar. Here there is another division and in the season of the southwest monsoon (May to September), the northerly branch becomes the Southwest Monsoon Current. The southward moving branch completes the circuit of the southern gyral.

With the reversal of the winds in November, the Southwest Monsoon Current is replaced by an Equatorial Countercurrent moving eastward and a North Equatorial Current moving westward. During this season, then, we have a more typical picture of oceanic surface circulation. The relatively minor circulations of the Arabian Sea and the Bay of Bengal alternate in direction with the changing wind patterns.

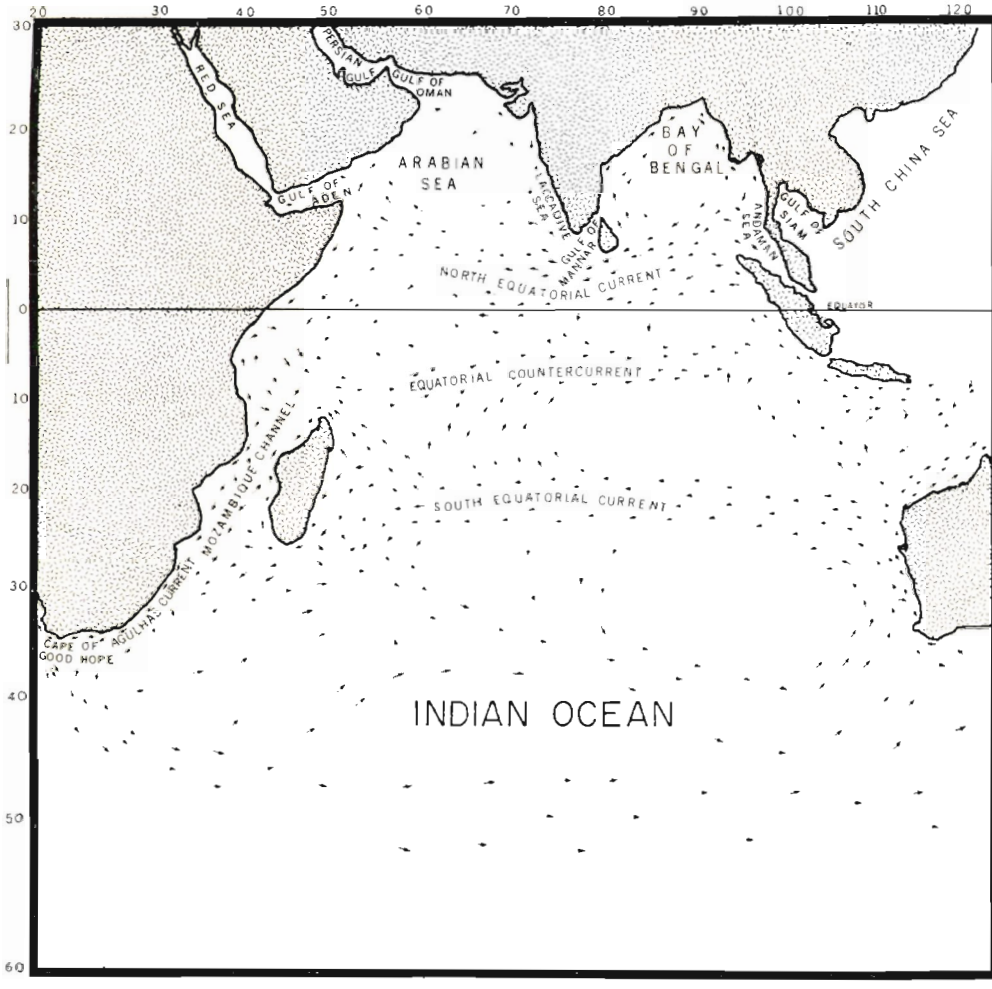


Fig. 1-19: The currents of the Indian Ocean following the reversal of the Southwest Monsoon in November. See Figure 1-20 for other details. (Base map after HEEZEN and THARP, 1965; currents from various sources.)

The currents along the east African coast during the southwest monsoon are notably swift (ANONYMOUS, 1930–31). By direct observation, the Agulhas Current shows a greatest mean drift of 50·3 miles per day in the two quarters of May to July and August to October, while the East African Coast Current has a value of 60 miles per day in the year quarter of May to July. One of the strongest currents in

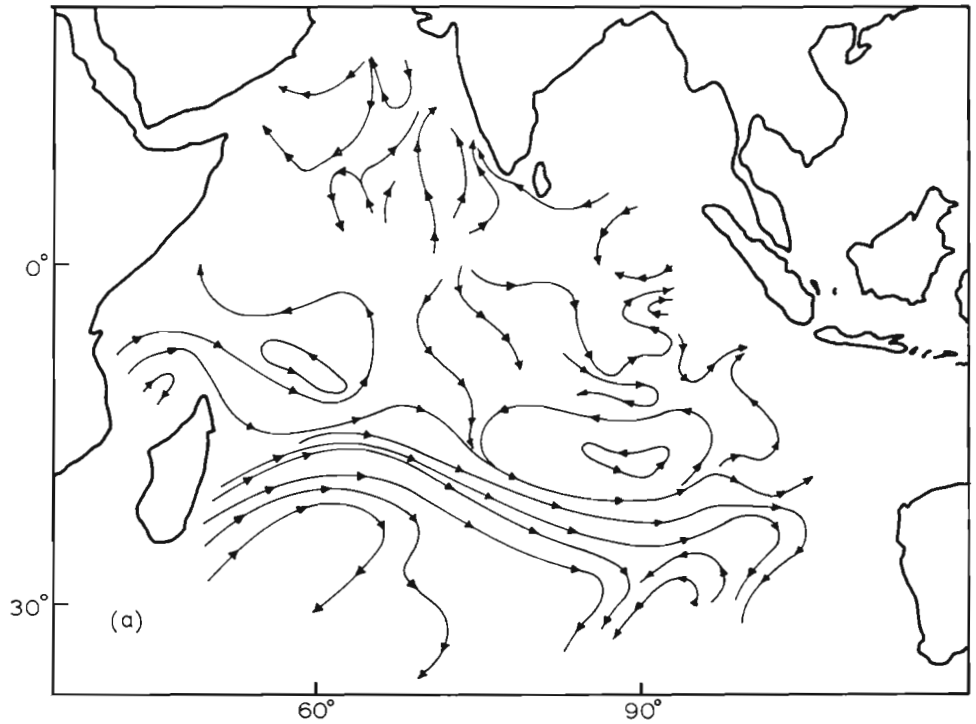


Fig. 1-20(a): Streamlines of currents at various levels in the Indian Ocean. 1500 m. (After diagram by ZALINSKII, 1964; modified.)

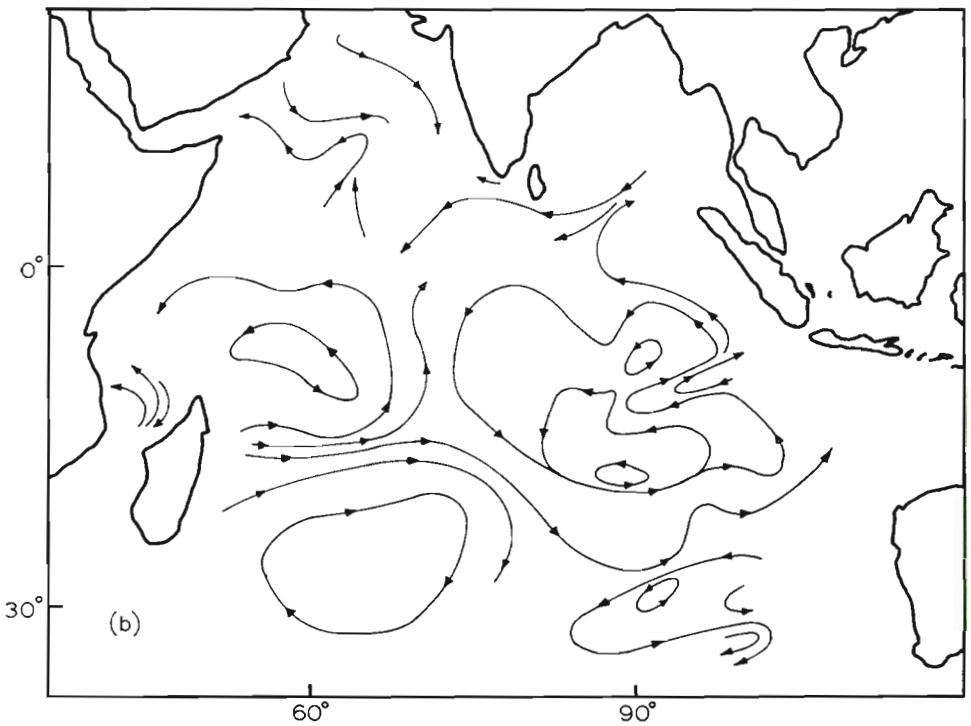


Fig. 1-20(b): Streamlines of currents at various levels in the Indian Ocean. 2000 m. (After diagram by ZALINSKII, 1964; modified.)

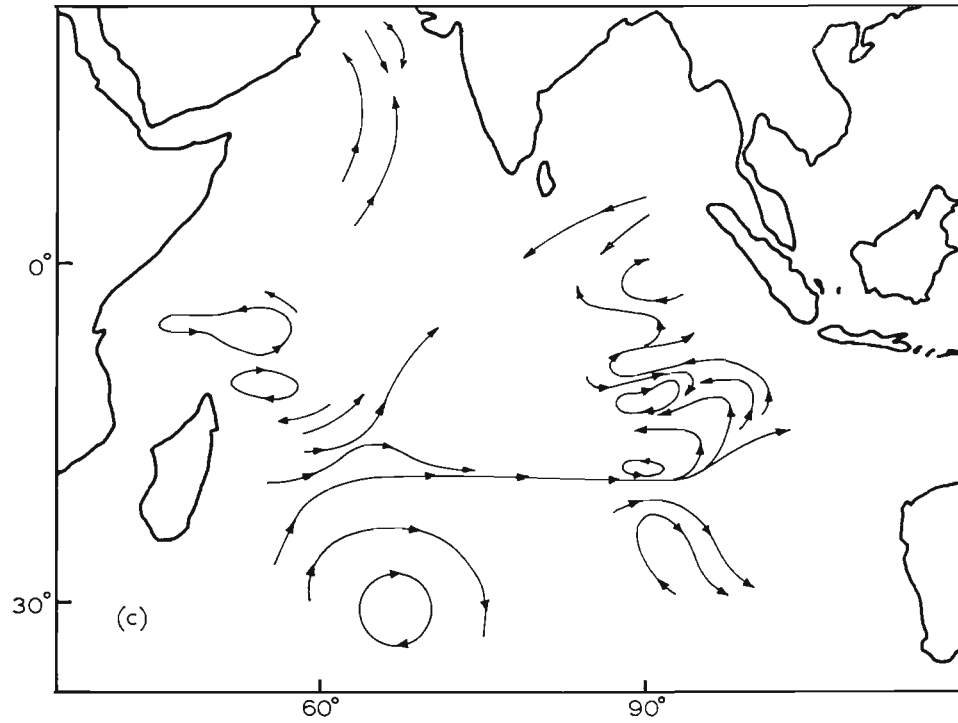


Fig. 1-20(c): Streamlines of currents at various levels in the Indian Ocean. 3000 m. (After diagram by ZALINSKII, 1964; modified.)

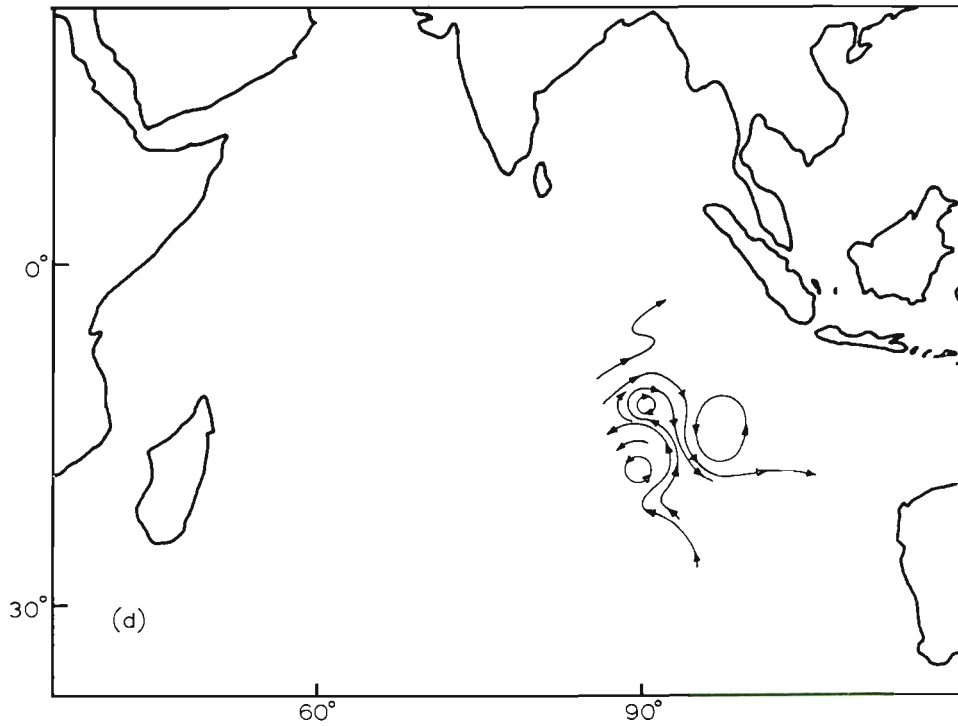


Fig. 1-20(d): Streamlines of currents at various levels in the Indian Ocean. 4000 m. (After diagram by ZALINSKII, 1964; modified.)

the world was reported in the region south of Socotra during the southwest monsoon. In an area within the bounds of 9° to 10° N and 54° to 55° E the mean drift exceeded 90 miles per day. However, it is considered that the East African Coast Current is the strongest extended current over a large area that has been so far reported (ANONYMOUS, 1930–31).

ZALINSKII (1964) has mapped the circulation of the Indian Ocean at the 1500, 2000, 3000, and 4000 m levels. His chart for the 1500 m level is reproduced in Fig. 1-20a. The circulation at the lower level roughly corresponds to that shown for 1500 m except that the large arc shown in the SE quadrant progressively intensifies as an eddy system with depth. Adjoining this flow and to the NE of Madagascar, a second and more complete eddy system is found. Lying just to the north of 20° S a third eddy system is shown. Common to all three of these is a broad current which sweeps nearly across the Indian Ocean along the south parallel of 20°. This structure, according to ZALINSKII, holds to the 3000 m level (Fig. 1-20c) beyond which it is broken up by the bottom topography.

It may be important to the biologist to note ZALINSKII's (1964) position that Atlantic Deep Water does not penetrate the Indian Ocean at depths beyond 3000 m because of bottom topography. It does enter through the Gulf of Mozambique to the south of Madagascar at 1500 to 2000 m. ZALINSKII also comments that the northward spread of Antarctic Bottom Water in the Indian Ocean has not been detected.

The Southern Ocean

The Southern Ocean is the ring sea of Antarctica (Fig. 1-21). As previously indicated, it is arbitrarily delineated northward by the 52nd parallel except for the Indian Ocean where the 40th parallel is considered the boundary. The Weddell Sea recurves to the west as it proceeds inland to a latitude of approximately 82° S. Central at 80° S and 50° W, Berkner Island marks the outer edge of Filchner Ice Shelf which fills the inner quarter of the area of the Weddell Sea.

A systematic discussion of the Southern Ocean may conveniently start at Graham Land (Palmer Peninsula or the Antarctic Peninsula according to the map consulted) and proceed eastward.

To the east of Graham Land we find the Weddell Sea which is the most pronounced indentation of the coast of Antarctica. Here we have one of the few exposures of a continental shelf in Antarctica. It extends tongue-like from beneath the ice and at its break (near the 1800 m contour) is at approximately 500 m. The abyssal plain of the Weddell Sea is probably one of the most extensive known (HEEZEN and LAUGHTON, 1963, p. 322). The Weddell Sea lies between 60° and 10° W.

Prydz Bay (70° to 80° E) represents a small embayment flanked by extensions of the continental shelf breaking at various depths. It is characterized by the Amery Ice Shelf.

The Ross Sea (170° E to 150° W) is not as wide at its mouth as the Weddell Sea but it penetrates the continent much farther; it reaches a little beyond the 85th parallel, almost to the South Pole itself. The inner half of its area is covered with the Ross Ice Shelf. As one approaches McMurdo Sound on the east side of the

Ross Sea, its left flank is guarded by the only active volcano in Antarctica—Mt. Erebus, 12,450 feet (4275 m) high. The continental shelf is extensive and breaks sharply at approximately 500 m.

The Amundsen Sea is a small sea midway along the coast between Ross Sea and Bellingshausen Sea. Captain Cook came within 200 km of land in the approach to

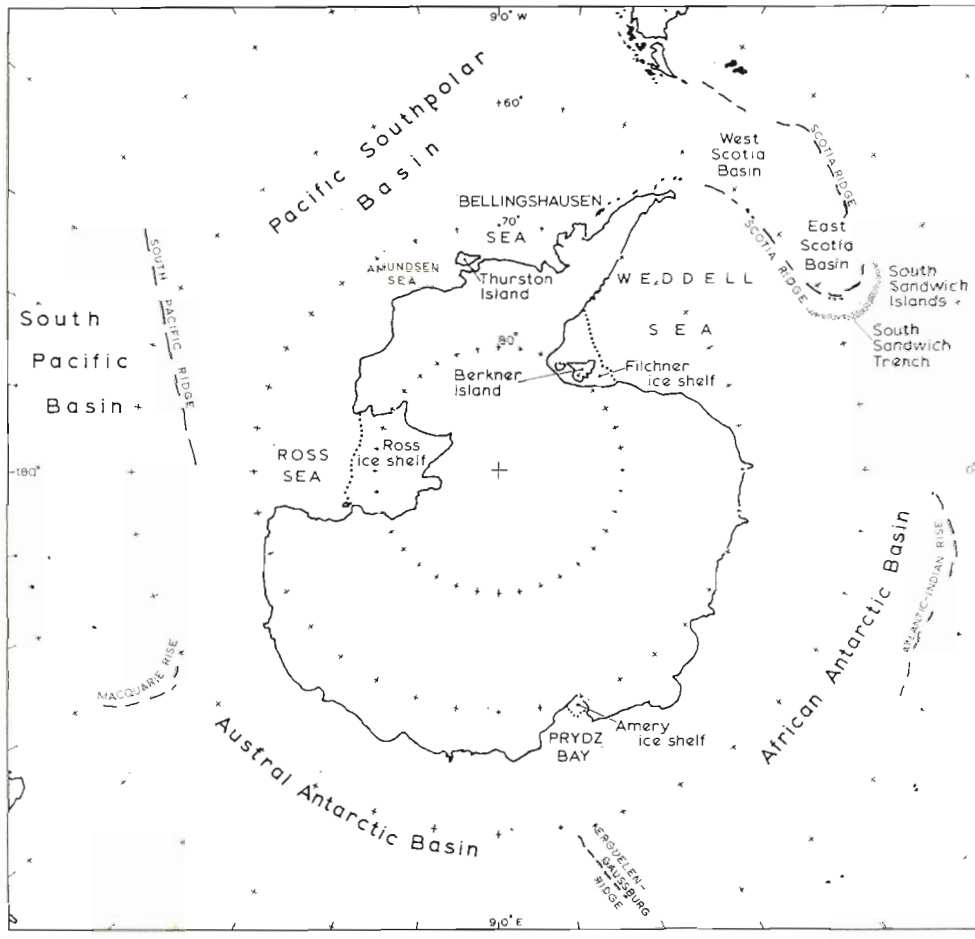


Fig. 1-21: Schematic representation of the major bathymetric features of the Southern Ocean. (Base map from US Navy Hydrographic Office 1957, publ. no. H. O. 705; some terminology after TROLL, 1966.)

this bay when he circumnavigated Antarctica in 1773 to 1775 (GROSVENOR, 1963, p. 150).

Separated from the Weddell Sea by Graham Land, the Bellingshausen Sea (70° to 100° W) stretches eastward to Thurston Island. It opens broadly to the Southern Ocean and Southeast Pacific, not possessing the well-defined geographic identity of Weddell and Ross Seas. Its continental shelf, breaking at some 550 m, is extensive.

If Antarctica and South America are imagined as joined between Graham Land and Cabo de Hornos, a giant pushing a finger through the continental masses might have left the bathymetric pattern we see on examination of this part of the Southern Ocean. The South Sandwich Islands and the mated South Trench appear to have been pushed eastward, leaving both limbs of the Scotia ridge and the eastward directed capes as stretch marks. The Scotia Sea and its east and west basins lie between the ridges and their associated islands.

Water masses and circulation of the Southern Ocean

Because they play such prominent roles in the deep circulation of the other oceans, the waters of the Southern Ocean have already been discussed to some

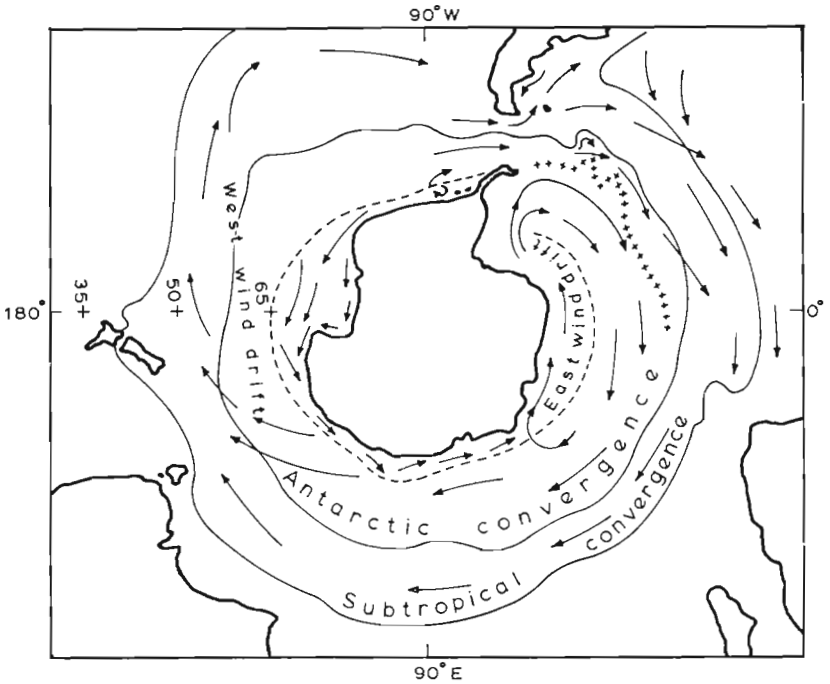


Fig. 1-22: Circulation of the Southern Ocean.

+ + + Northern boundary of Weddell Sea Current; – – – approximate boundary between East Wind Drift and West Wind Drift. (Adapted from DEACON, 1937 and US Navy Hydrographic Office 1957, publ. no. H. O. 705; modified.)

extent. However, this major component of the world ocean should be examined as a unit.

The southern boundary is the coast of Antarctica; the northern boundary must be defined in terms of water mass characteristics. It is characteristic that these waters are homogeneous in vertical profile and that the two counter-rotating annular currents extend to considerable depths (Fig. 1-22).

The innermost annulus, the East Wind Drift, flows in a counter-clockwise motion around Antarctica and only the Palmer Peninsula prevents the complete

cycle. The boundary between the East Wind Drift and the West Wind Drift constitutes the Antarctic Divergence, well known as a zone of very high biological production.

Outside of this divergence, the water flows in the opposite clockwise direction as the West Wind Drift. This is the slow and deep Circumpolar Current whose breadth extends to about 50° S in the Atlantic and Indian Oceans and 60° S in the Pacific Ocean.

(3) The sea-land boundary

Sea-land boundary denotes the interacting fringes of oceans and continents. Within this broad category, we treat estuaries, embayments, desert coasts, frozen fjords, jungle beaches and many of the more or less random configurations to be found. The element of randomness accounts for both the difficulty encountered in deriving a universally applicable classification scheme and the many schemes to be found.

But, there is good reason for classifying coasts: the process of classification necessitates analysis and organization. The marine ecologist thinks of coasts as habitats for living organisms; the geologist thinks of them as expressions of the physical forces operative in the geomorphological context. The classification schemes constructed by geologists are likely to be encumbered with more geological detail than is useful to the biologist. As shown so well by STEERS (1964), it is practically impossible to devise a scheme into which every segment of the sea–land boundary will find a place.

The sea–land boundary may be divided, for our purposes, into three broad categories: estuaries, embayments (non-estuarine), and ocean fronts. The term 'estuary' is used in the more restrictive sense of the geographer rather than with the more liberal interpretation of PRITCHARD (1967); specifically, it refers to the seaward terminus of a river. 'Embayments' include all other bodies separated from the open sea, for whatever reason. 'Ocean fronts' as sea–land contacts refer to beach lines, mountain cliffs and related areas exposed to unrestricted oceanic forces. Such subdivisions as the Gulf of Campeche, Gulf of Alaska, Bay of Biscay and the variously named indentations of the Argentine coast are regarded as cartographic conveniences.

Boundary morphology

Estuaries may be characterized as follows: (*a*) They receive the discharge of rivers and at the same time are exposed to the inflow of oceanic water. (*b*) Because of the admixture of saline and non-saline water, they contain a highly varied biota in relatively restricted areas. (*c*) Because of erosional processes in the river basins, the floor of a given estuary has a composition which reflects the composition and weathering of the continental masses drained by river systems. (*d*) As bottom texture responds to sedimentation phenomena, a varied benthic infauna is found. (*e*) Congruent with the erosional–depositional forces at work in estuaries is the process of nutrient enrichment extracted by runoff from continental top soils.

Most analytical studies of estuaries spring from interest in one or more of these characteristics.

The precise hydrography of a given estuary is determined by the dynamic balance between (*a*) types of solids carried by the river, (*b*) sediment load and its seasonal distribution, (*c*) tidal characteristics of the locale, (*d*) climatic regime prevailing and (*e*) structural geology underlying the locale.

There are few river–estuary systems that cannot be described with the aid of these criteria. The interested student will find well-selected illustrative material in papers by JENNINGS and BIRD (1967), MORGAN (1967), REDFIELD (1967), RUSSELL (1967), SCHOU (1967) and STEERS (1967).

As differentiated from estuaries, embayments receive land drainage either as local effluents (i.e. peripheral drainage channels and non-channelled direct drainage) or indirectly from neighbouring estuaries. Embayments may flank estuaries, and even owe their origin to the estuary, but still exist as geomorphologically independent units with distinct biological characteristics. Embayments include bays and lagoons which may be formed in the delta systems of the larger rivers.

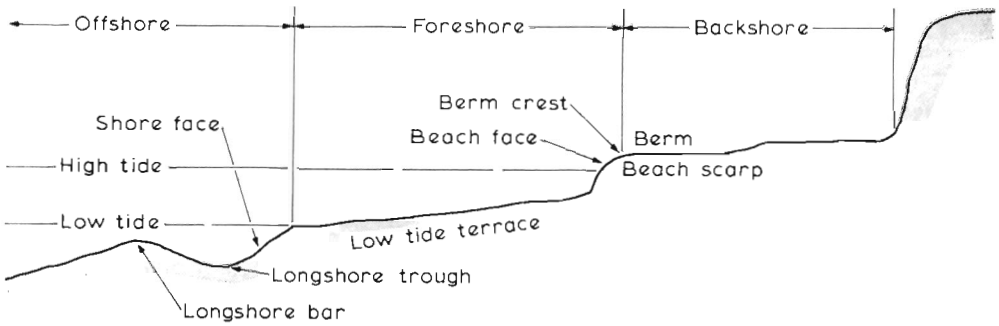


Fig. 1-23: Schematic diagram of sandy beach with principal terms used describing beach structure. (After SHEPARD, 1963; modified.)

There are pronounced embayments resulting from the construction of coastwise bars and islands by surf and wind. These coastal lagoons may have great length and narrow widths, receiving negligible quantities of land drainage. PRICE (1954) has given a detailed description of embayments and estuaries characteristic of coastal plains.

The following criteria may be useful in differentiating embayments: (*a*) Any axis of the embayment is independent of confluence with the axis of neighbouring estuaries. (*b*) It receives a limited local drainage only, with peripheral streams being dominantly tidal. (*c*) Hydrography and biota are dominated by oceanic regimes.

Ocean front refers to that part of the sea–land boundary zone which is exposed to the full force of the open sea. There are no protective bars, islands or peninsulas. Many schemes of classification can be outlined, but earlier remarks on the classification of coast lines apply here as well. We may, however, offer some general remarks on the oceanic beaches of two extreme types: sandy and rocky.

Sandy beaches have received a great deal of study because of their lack of stability where human habitation is concerned and because of their interest as a biological environment. Standard terminology for their description has been established. The most commonly used terms and their application are shown graphically in Fig. 1-23. Depending upon the physical nature of the beach material

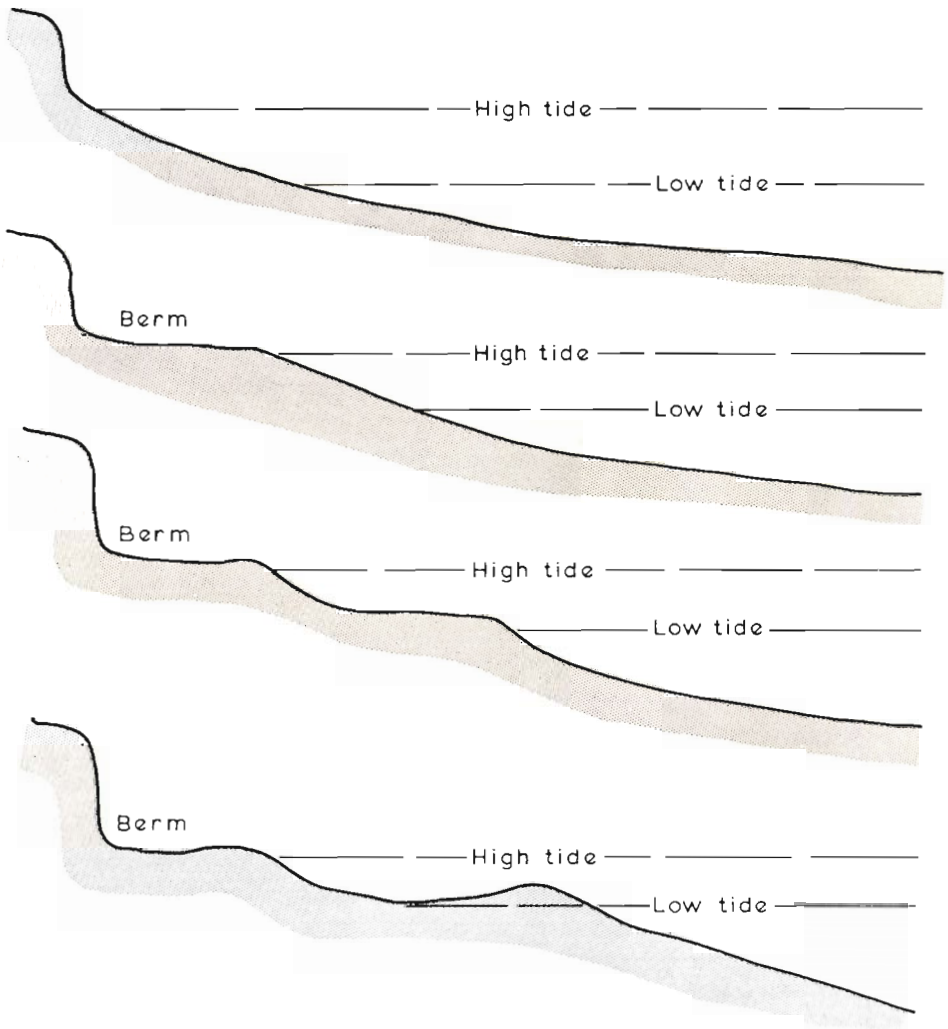


Fig. 1-24: Representative types of beach profiles in relation to tide levels. (After SHEPARD, 1963.)

and the sea conditions prevailing, we may find a variety of characteristic beach profiles. Some generalized types of these are shown in Fig. 1-24. The average slope of a beach can be associated with the particle size of the material. Beach slopes and associate particle sizes are given in Table 1-2.

Table 1-2

Average beach face slopes compared to sediment diameters
(After SHEPARD, 1963)

Type of beach sediment	Size (mm)	Average slope of beach face (°)
Very fine sand	1/16–1/8	1
Fine sand	1/8–1/4	3
Medium sand	1/4–1/2	5
Coarse sand	1/2–1	7
Very coarse sand	1–2	9
Granules	2–4	11
Pebbles	4–64	17
Cobbles	64–256	24

MEIGS (1966) has given an interesting treatment of coastal deserts which may be useful to the marine ecologist. The following outline is taken from his paper:

A Tropical deserts

1. Extreme (east coast type)—average temperature of warmest month above 86° F (30° C).
2. Modified (west coast type)—average temperature of warmest month below 86° F (30° C).

B Temperate deserts

1. Hot summer type—mean temperature of warmest month above 86° F (30° C). Persian Gulf, Arabian Sea, North Red Sea, Gulf of California.
2. Monsoon type—summer rain, spring temperature maximum.
3. Mediterranean type—warm sunny summers, mild winters. Desert shores of Mediterranean, western Sahara, western Australia.
4. Fog type—extreme west coast desert, no warm season, abundance of fog and low overcast. West coasts of South America, southwest Africa, Baja California.
5. Patagonian type—chilly winters, mild summers.

The rocky beach on the ocean front is the result of wave attack on exposed mountain structures. The process begins with the development of cliffs, proceeds with their subsequent undercutting and is completed with the degradation of the resulting boulder material. A comprehensive treatment of the marine erosion of rocky coastlines has been given by COTTON (1949). Fig. 1-25 represents a typical situation in which a sea cliff is under active erosion by the sea.

In his development of the ecology of rocky shores, LEWIS (1964) concludes that ecological characteristics (distribution, etc.) of organisms provide better criteria for the definition of environments than the dominant physical characteristics. In his discussion of zonation on rocky shores, he eliminates the designation of a 'supralittoral', the latter being a misconception based upon the supralittoral position of the *Littorina/Verrucaria* belt on exposed shores. LEWIS' arrangement of the zones is indicated in Fig. 1-26. The terminology for tidal ranges is shown in Fig. 1-27.

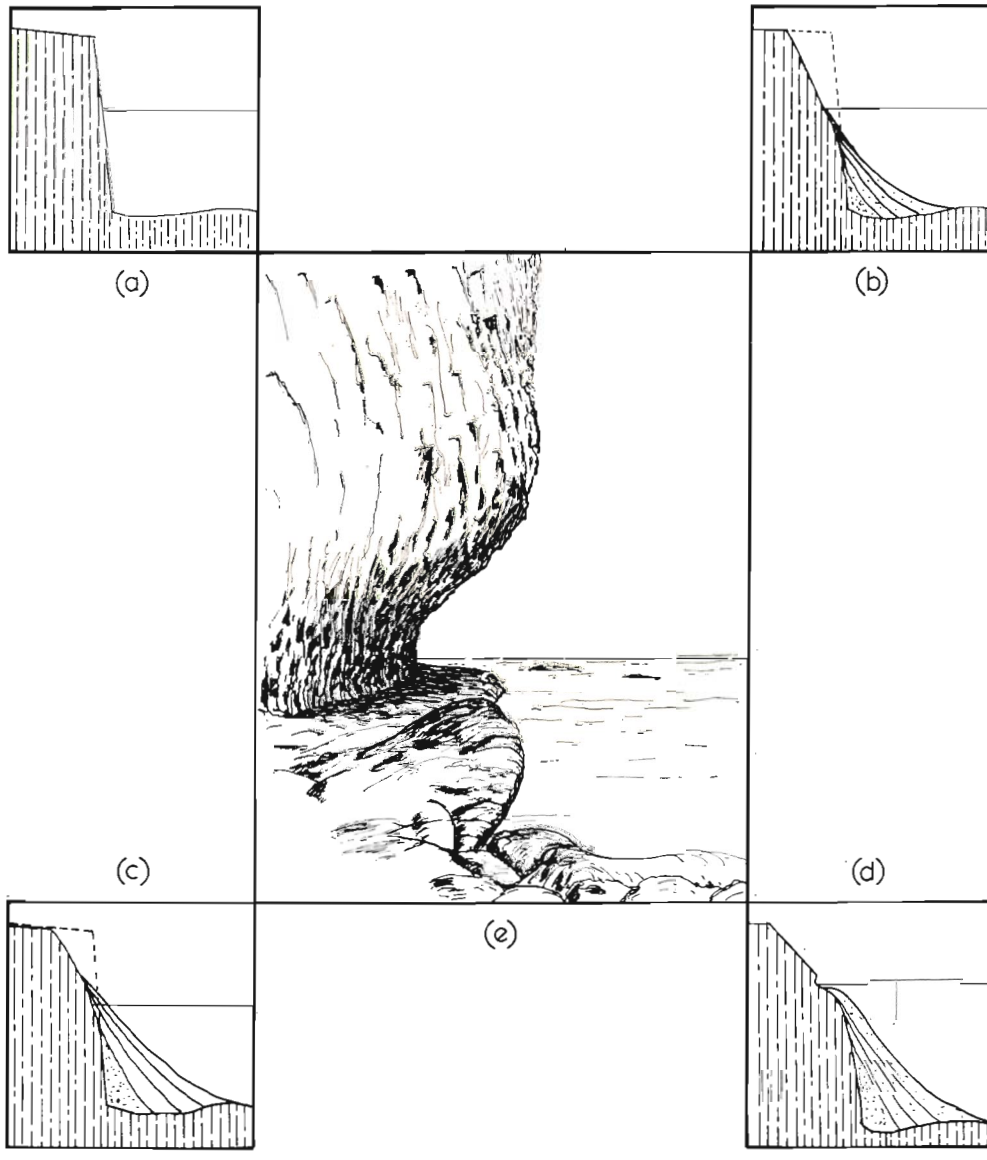


Fig. 1-25: Wave attack on steep coasts. (a) Initial profile; (b) and (c) change in slope resulting from accumulation of talus; (d) beginning of wave work; (e) nip at base of sea cliff under wave attack. (After COTTON, 1949; modified.)

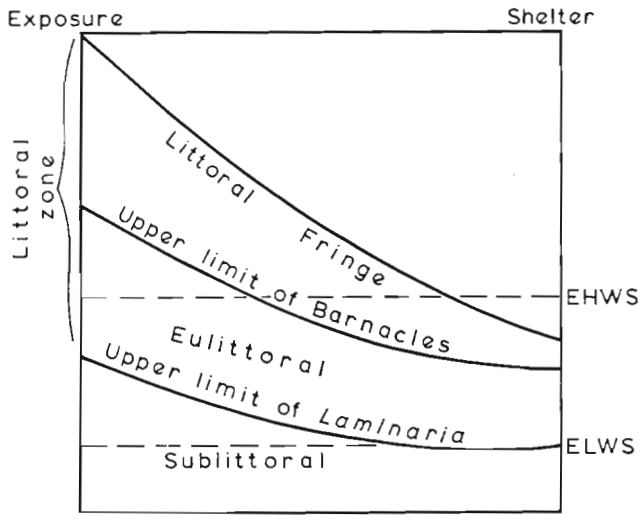


Fig. 1-26: Ecological zonation of rocky beaches. (After LEWIS, 1964.)

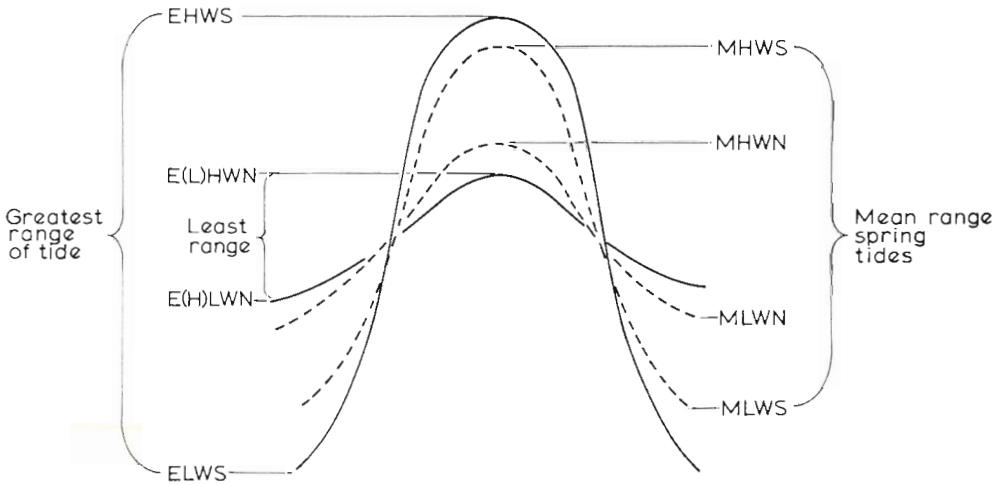


Fig. 1-27: Tidal regimes. MHWS: Mean high water—spring tides; MLWS: Mean low water—spring tides; EHWS: Extreme high water—spring tides; ELWS: Extreme low water—spring tides; MLWN: Mean low water—neap tides; MHWN: Mean high water—neap tides; E(L)HWN: Extreme lowest high water—neap tides; E(H)LWN: Extreme highest low water—neap tides. (After LEWIS, 1964.)

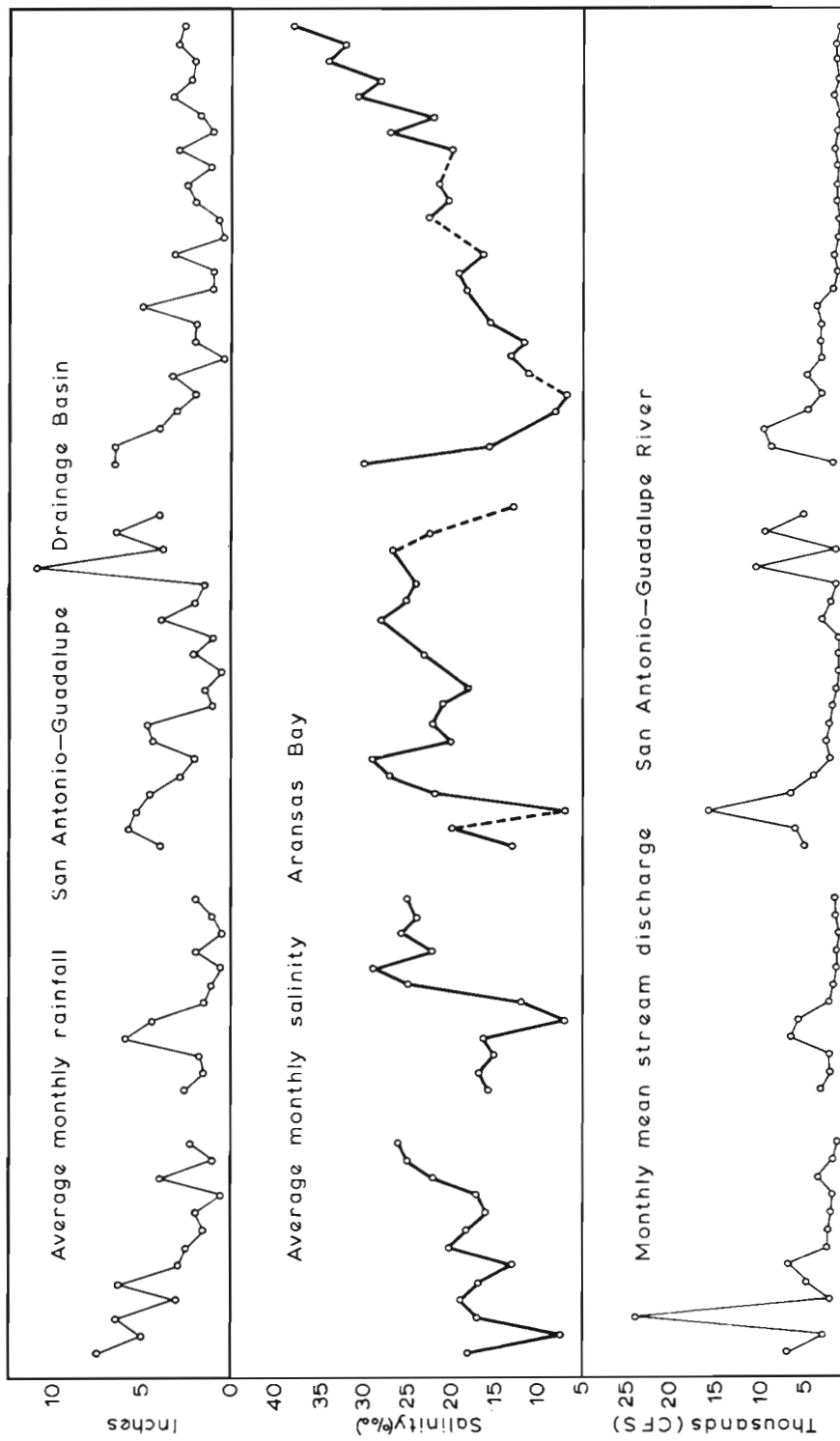


Fig. 1-28: Relationship between rainfall, salinity and stream discharge in a drainage basin-estuarial system in Texas (USA). Aransas Bay receives land drainage indirectly from the drainage basin through an estuary and a small intermediate bay. (After COLLIER and HEDGPETH, 1950.)

Hydrology of the sea–land boundary

The sea–land boundary generally, and its estuaries in particular, are subject to river discharge. The hydrologist uses the term 'runoff' to designate residual precipitation after transpiration, evaporation and seepage have claimed their fractions of the total precipitation. It is this residual which eventually reaches the ocean as a final act in the well-known hydrologic cycle. In the overall hydrologic picture it is said that transpiration and evaporation account for 15 to 25 inches (38 to 63 cm) of precipitation per year (MEYER, 1944).

COLLIER and HEDGPETH (1950) made a study of the relation between precipitation, runoff and salinity in a drainage basin–estuarial system in Texas, USA (Fig. 1-28). It is clear that these estuaries respond to climatic conditions in the drainage basin quite faithfully.

Circulation near the sea–land boundary

It is not in the province of an introductory statement to give a detailed exposition on circulation in estuaries and embayments. PRITCHARD (1967) gives an excellent summary for a generalized approach to this problem, and the interested reader is referred to that article. His 'estuary' covers both estuaries and embayments as I have defined them. The following groups set up by PRITCHARD refer to either of these: (*a*) The highly stratified estuary, (*b*) the moderately stratified estuary, (*c*) the vertically homogeneous estuary, (*d*) the laterally homogeneous estuary. PRITCHARD outlines the factors governing the position of a given estuary in this sequence as follows: volume and rate of freshwater inflow, tidal current velocities and the dimensions of the estuary.

Erosion at the sea–land boundary

Erosion is a continuing process at the sea–land boundary. In sandy areas the beach materials are picked up and moved from sector to sector, a process which has been much studied in recent years. JOHNSON and EAGLESON (1966) give an analysis of the forces at work in sediment transport (regarding sediment transport as an erosional process on sandy beaches). They consider the process as a duality of particle entrainment and particle transport. Entrainment requires that fluid velocities and accelerations in excess of some threshold value be present in the near bottom waters. Transportation requires that the orbit of the particle be open. Fig. 1-29 illustrates the beach zones as they are classified for the study of erosional processes by JOHNSON and EAGLESON.

Some biotic properties of the sea–land boundary

The environmental variability of the sea–land boundary challenges colonization with numerous obstacles, the greatest of which are probably the characteristically extreme salinity and temperature variations. KINNE (1967) analyzed the physiological responses to the stresses of this environment and found it helpful to group

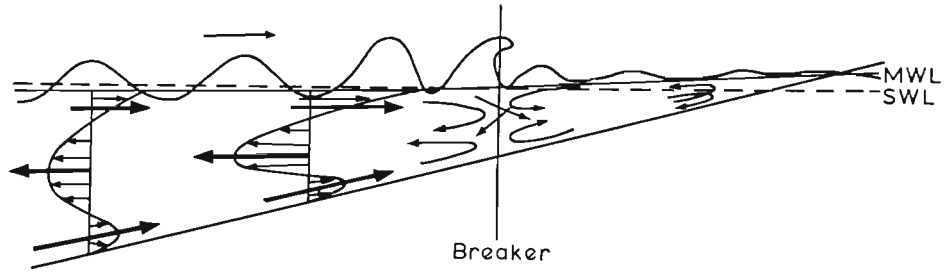


Fig. 1-29: Two-dimensional scheme of water circulation in which water depth decreases in direction of wave propagation. The relative mass transport velocity is indicated. Forward flow at the surface and near the bottom with a return in between is indicated. MWL—mean wave level; SWL—still water level. (After JOHNSON and EAGLESON, 1966.)

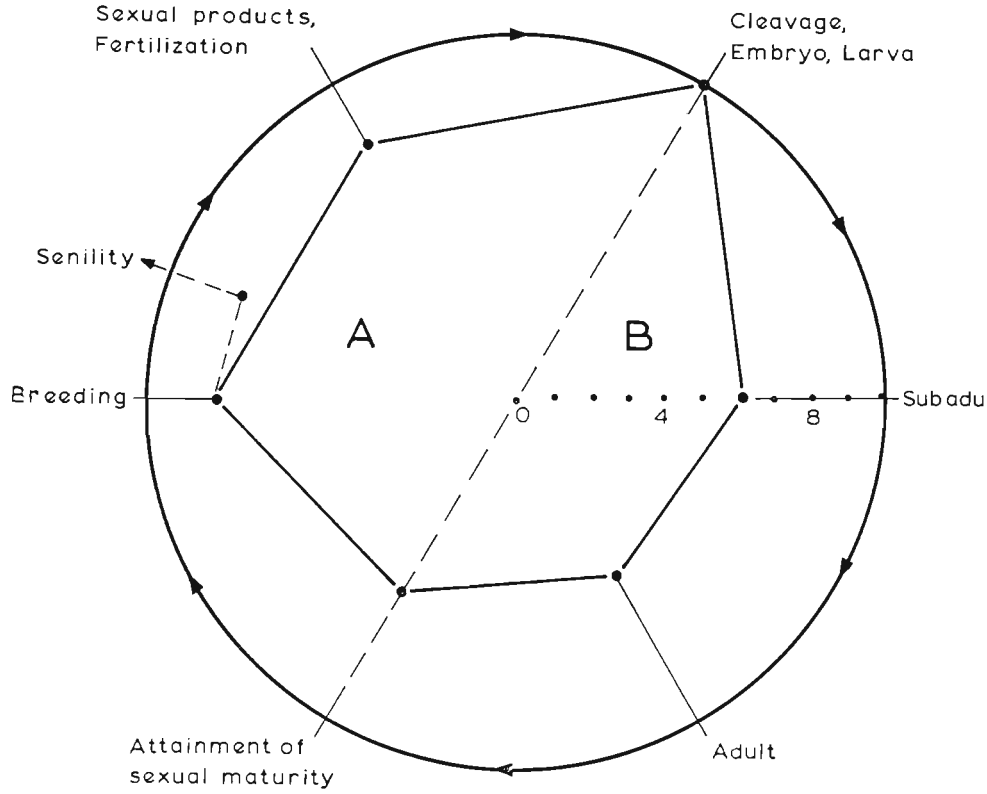


Fig. 1-30: Relative changes in sensitivity to salinity extremes during ontogenetic development of estuarine animals. Scale of intensities based on 10 for maximum sensitivity (embryo or larva). A: reproductive processes, B: growth from embryo or larva to adult. (After KINNE, 1966; modified.)

them under the following headings: escape, reduction of contact, regulation and acclimation.

Escape may be effected by vertical or horizontal migration into an area of more agreeable conditions. Vagile organisms may obviously move out of the area of stress, while others may simply burrow into the sediments where both the salinity and temperature are more equable. KINNE (1967) suggests an 'indirect escape' through the interaction of stress factors. The basis for this concept may be found in the work of COSTLOW and co-authors (1960) and KINNE (1964).

During a stressful change in the environment, *viz* freshwater inundation of an estuary due to floods, another class of response is possible: the reduction of contact with the offending factors. The responses in this case may be the secretion of a mucous coating or the closing of valves.

By far the most important class of response is that designated by KINNE (1967) as regulation. Regulation may be considered in three categories: ion regulation, volume regulation and osmoregulation. With respect to temperature, it should be pointed out that estuarine invertebrates and fishes lack the ability to regulate temperature; so, in general, escape is the only response available.

A total permanent adjustment of the life processes of an organism to varying stress patterns in the environment is considered by KINNE (1967) to be acclimation or non-genetic adaptation. This may be more important than escape, insofar as temperature is concerned, in many cases. KINNE (1966) considered estuaries as 'zones of reduced competition'. As such, the sea–land boundary zone in general may be characterized as a habitat in which the permanent residents are those with a genetically determined potential for resisting the stresses of intense variability in all stages of ontogenetic development (Fig. 1-30).

(4) Sea water

In the same sense that blood is a fluid whose function is to provide transport for nutrients, waste products, dissolved gases, metabolic regulators and heat, sea water may also be considered a biological fluid. It has been suggested (COLLIER, 1953) that the viewpoint of the physiologist in his study of blood as a body tissue might profitably be applied to sea-water studies. The coupling between organism and external medium is as intimate as that between cell and plasma. Only the scales of concentration differ.

Thermal properties of sea water

When two bodies are in thermal equilibrium, they are said to have the same temperature. Hence temperature is that property of a mass which indicates whether or not it is in thermal equilibrium with other masses (Chapter 3.0).

Specific heat refers to the heat capacity of a given mass and is dependent upon the physical and chemical characteristics of the material concerned, as well as the temperature at which the specification is made. For instance, the specific heat of sea water varies with salinity and temperature. The variation is shown graphically in Fig. 1-31 (see also Chapter 3.0, Fig. 3-1) (COX and SMITH, 1959).

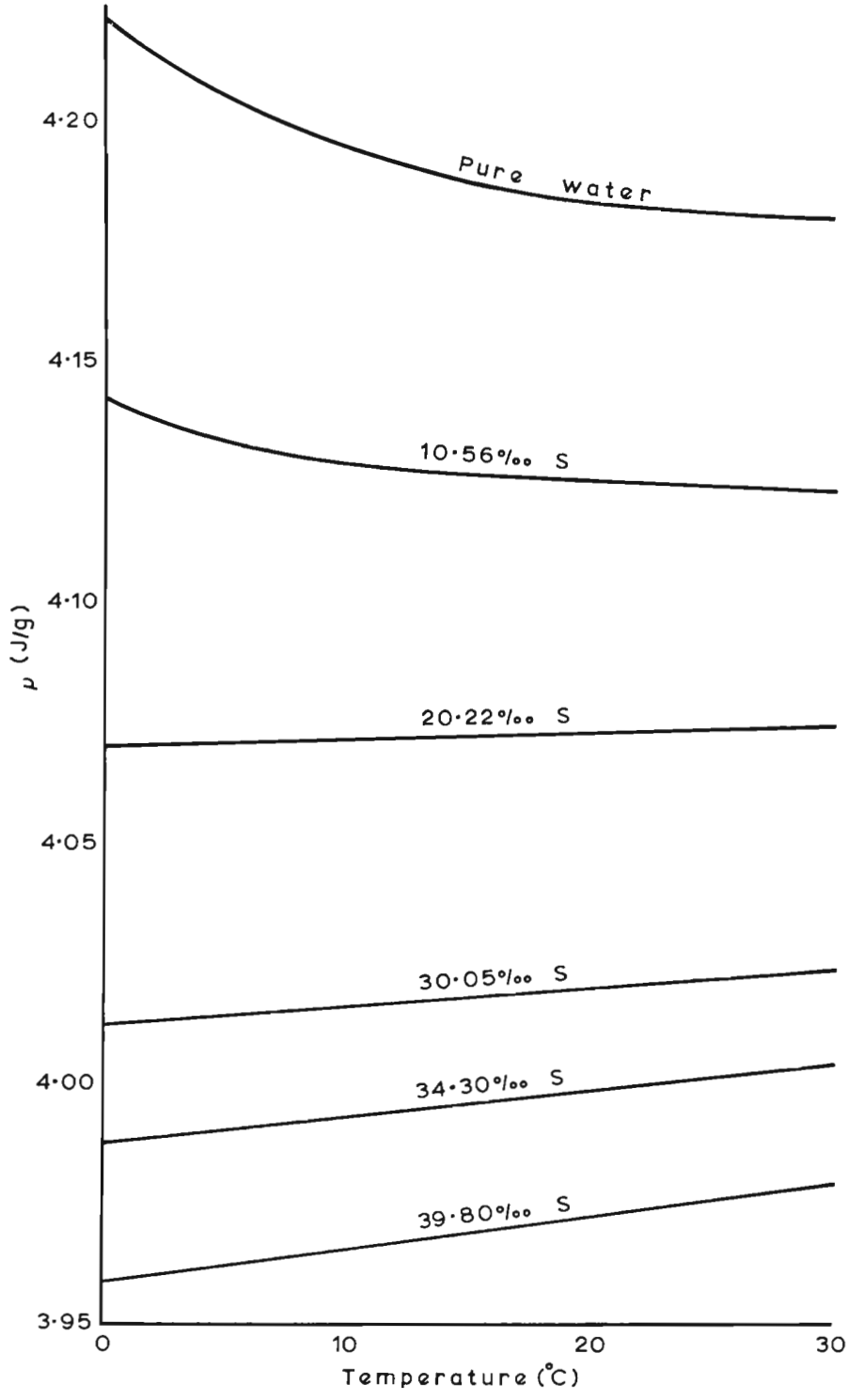


Fig. 1-31: Smoothed curves showing relation of specific heat of water to temperature and salinity. (After Cox and SMITH, 1959; modified.)

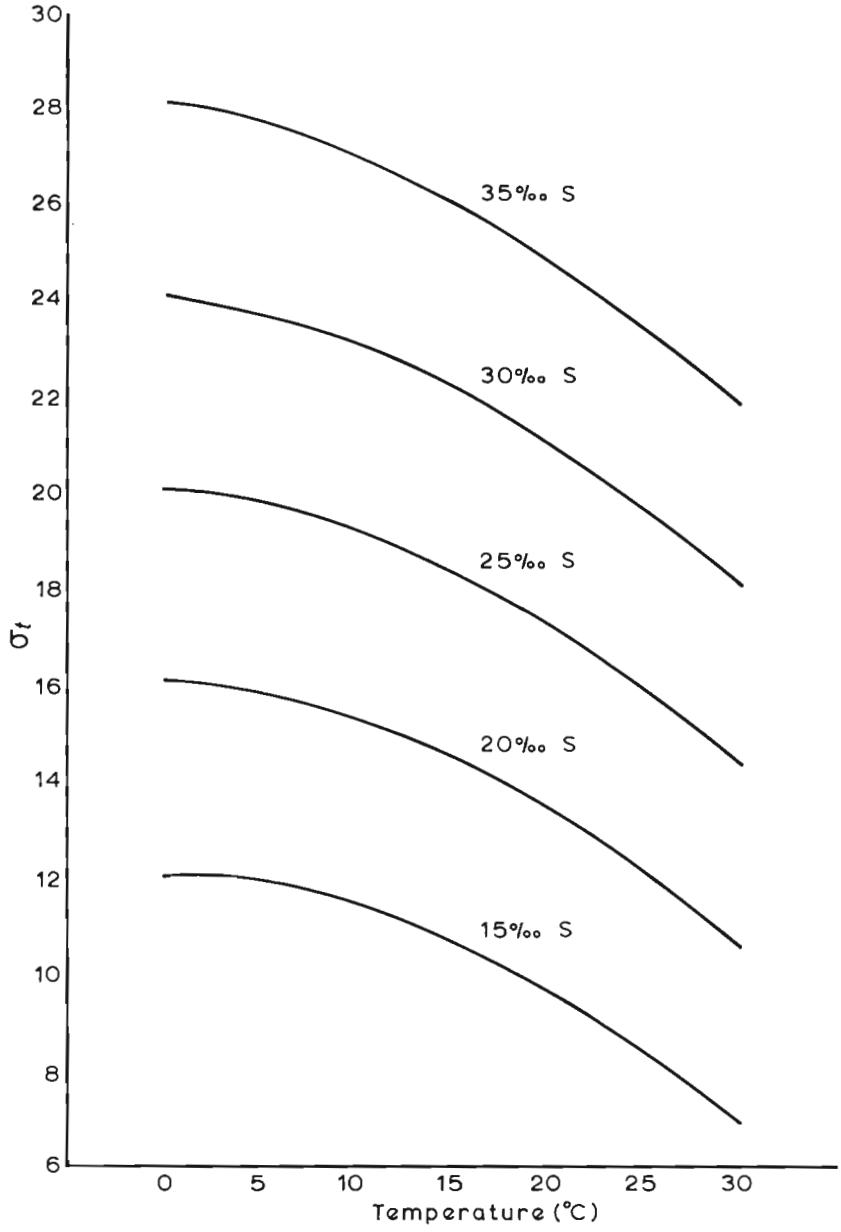


Fig. 1-32: Specific gravity of seawater as σ_t for certain salinities as a function of temperature. (Data from KNUDSON, 1901.)

The rate of heat conductance by water in the ocean is not of great significance to the oceanographer because the transfer of heat by mechanical mixing processes completely masks the purely conductive process. This is made clear by the computation showing that an ocean of 0° C with a surface maintained constantly at 30° C would show a temperature rise of 3 C° only after a passage of 1000 years if simple conductivity were the only method of transfer (DIETRICH, 1963). The classical equation for thermal conduction applies and the thermal conductivity coefficient (λ) is defined by the equation

$$Q = -\lambda(\delta v/\delta x)$$

where Q, in cal sec^{-1}, represents the heat passing through a 1 cm^2 plane normal to the direction of flow, $\delta v/\delta x$ is the temperature change (δv) in ° C along the distance (δx) in cm (DEFANT, 1961). According to DEFANT, the thermal conductivity of oceanic water (35 $^0/_{00}$ S) is about 42% less than that of pure water. At 17·5° C, DIETRICH gives thermal conductivity coefficients of $1{\cdot}40 \times 10^{-3}$ and $1{\cdot}34 \times 10^{-3}$ cal cm^{-1} $degree^{-1}$ sec^{-1} for salinities of 0 and 40 $^0/_{00}$ respectively.

The density of sea water is directly related to temperature and the coefficient of thermal expansion of sea water. It is further influenced by salinity. KNUDSEN's (1901) Tables give density values and their reciprocal, specific volume for normal ranges of temperatures and salinities found in the oceans. Fig. 1-32 compares the change of density with changing temperature for sea water at various salinities. Insofar as freezing point is concerned, the relation to osmotic pressure is of significance (Table 1-3).

Table 1-3

Freezing point and osmotic pressure of sea water at various salinities
(After DEFANT, 1961)

Salinity ($^0/_{00}$)	5	10	15	20	25	30	35	40
Freezing point (°C)	− 0·267	− 0·534	− 0·802	− 1·074	− 1·349	− 1·627	− 1·910	− 2·196
Osmotic pressure (atm)	3·23	6·44	9·69	12·98	16·32	19·67	23·12	26·59

Mechanical properties of sea water

Viscosity represents a mechanical interpretation of intermolecular forces of a fluid which cause resistance to the movement of a body moving through the fluid, or between a moving fluid and its container. It has biological significance with respect to the passive and active movements of plankton organisms, the velocities at which such organisms as fishes may swim and the work done by ciliary mechanisms (GRAY, 1928). Table 1-4 provides viscosity coefficients for a range of temperatures and salinities (MIYAKE and KOIZUMI, 1948).

In speaking of viscosity, the cohesive forces within a fluid mass were considered. The same cohesive forces operate to form a boundary between a liquid and a gas or between the interfaces of liquid–solid–gas. When the molecules of a liquid show

an attraction for the surfaces of other liquids and solids, the forces of adhesion are at work. Because the molecules in the surface of a liquid are unevenly held by the attraction of the cohering molecules beneath the surface, a surface tension develops. This tension can be measured in dyn/cm² and for pure water the values for various temperatures are given in Fig. 1-33 (see also Chapter 3.0, Fig. 3-2.) There is a slight correction for sea water and this has been expressed by FLEMING and REVELLE (1939) as follows:

$$\text{Surface tension (dyn/cm}^2) = 75{\cdot}64 - 0{\cdot}144t + 0{\cdot}0399\,\text{Cl}$$

The surface tension of natural waters, i.e. sea surface, may vary and at times is of interest to the biologist with respect to the formation of slicks, pollution studies and as indications of certain types of plankton populations. These phenomena,

Table 1-4

Viscosity coefficients of sea water in millipoise
(After MIYAKE and KOIZUMI, 1948)

	Cl ‰					
°C	0	4	8	12	16	20
0	17·94	18·11	18·29	18·45	18·62	18·90
2	16·76	16·92	17·10	17·29	17·46	17·74
4	15·71	15·85	16·03	16·23	16·41	16·68
6	14·75	14·89	15·07	15·28	15·46	15·71
8	13·81	14·03	14·20	14·41	14·59	14·83
10	13·10	13·24	13·41	13·62	13·80	14·03
12	12·39	12·52	12·69	12·89	13·07	13·29
14	11·73	11·87	12·04	12·23	12·40	12·60
16	11·13	11·27	11·43	11·61	11·79	11·97
18	10·58	10·72	10·88	11·05	11·21	11·39
20	10·07	10·21	10·36	10·52	10·68	10·85
22	9·60	9·74	9·89	10·03	10·19	10·35
24	9·16	9·30	9·45	9·58	9·73	9·88
26	8·75	8·90	9·04	9·16	9·31	9·44
28	8·37	8·52	8·65	8·77	8·91	9·04
30	8·02	8·17	8·30	8·40	8·54	8·66

often observable with the unaided eye, are the results of various impurities and contaminants of the water surface. The spreading of one liquid over another is determined by the balance between the cohesive and adhesive forces. GARRETT (1967) has given an account of a variety of organic materials present in the surface of natural waters and the nature of the surface-active compounds. He showed that a mixture of the more water-soluble and less water-soluble compounds exists in the natural state, and that the less soluble compounds tend to migrate to the surface and are more surface active. It is the latter that are responsible for slicks. The exact distribution varies locally according to meteorological and oceanographic conditions.

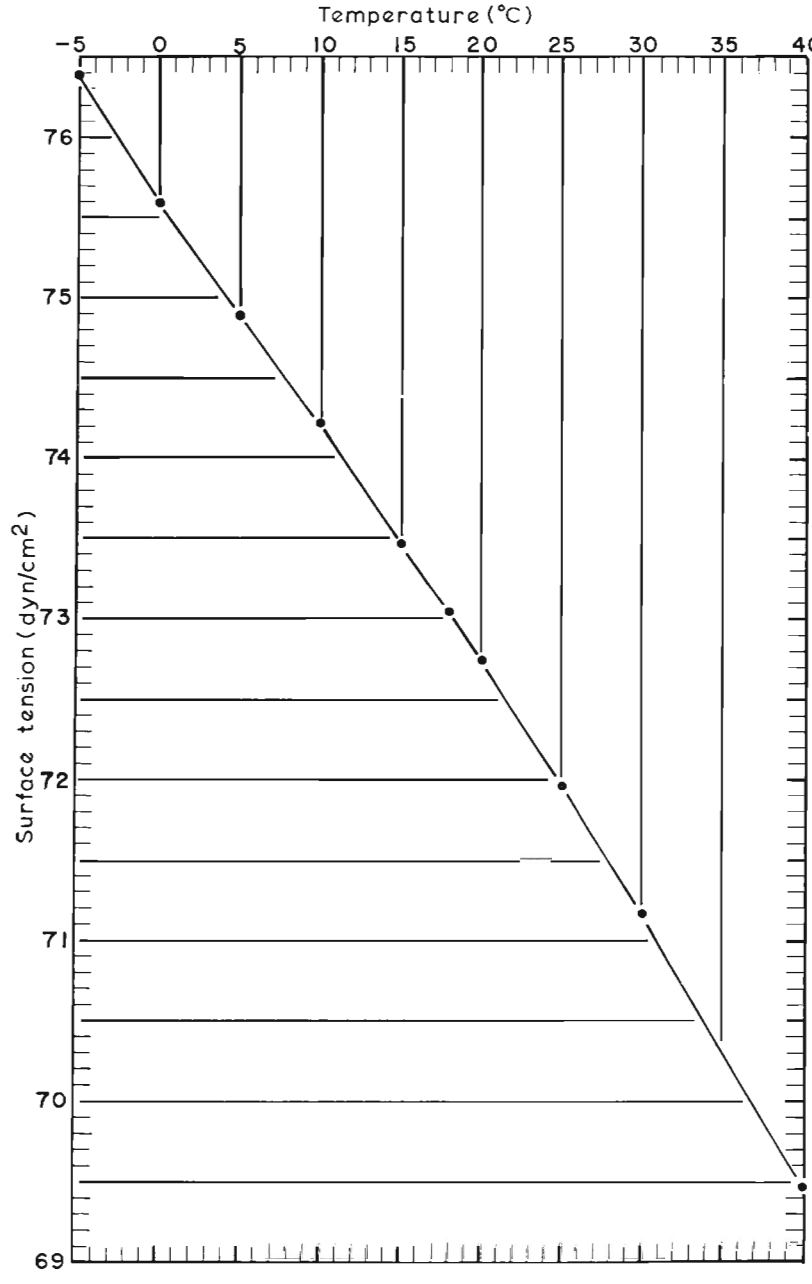


Fig. 1-33: Surface tension of pure water. (Data from WEAST, 1964.)

Photic properties of sea water

The solar radiation absorbed by the sea is an input of energy from the prime mover of the biosphere, the sun. As such, light is of profound interest to those who study the fundamental energy flow in the marine biosphere. Further, light *per se* as a by-product of chemical evolution in the form of bioluminescence (SELIGER and MCELROY, 1965), provides a challenge for the marine ethologist; as an illuminant for man submerged in lightless waters, a knowledge of aquatic optics becomes a practical need (Chapter 2.0).

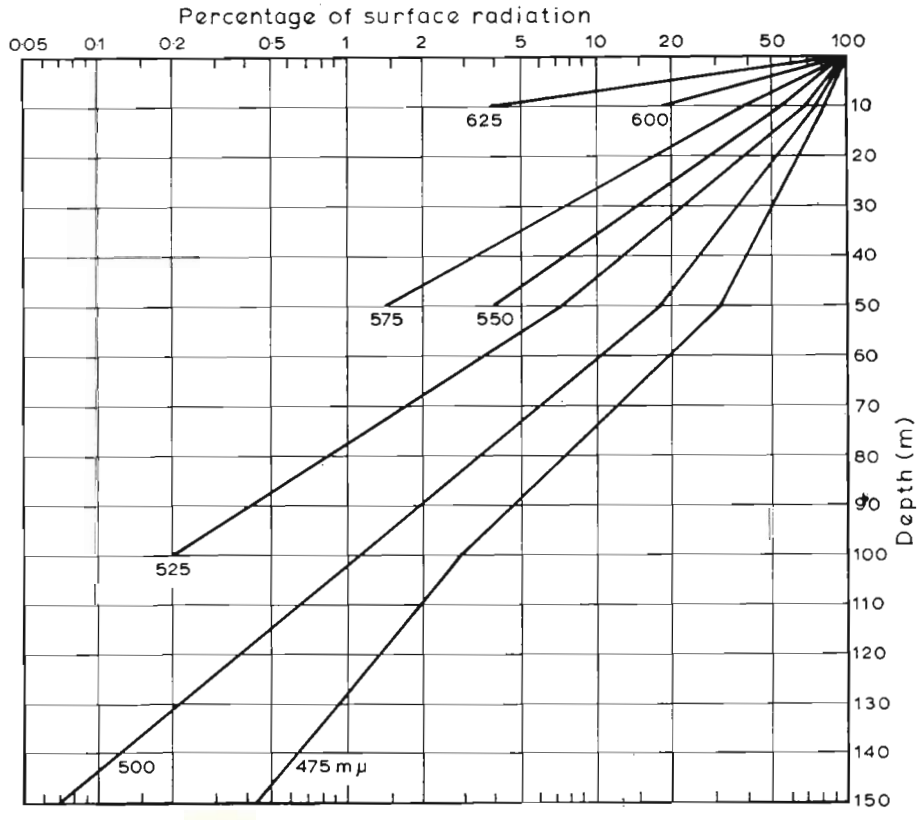


Fig. 1-34: Percentage surface radiation reaching different depths of the sea, and at 25 mμ intervals. Altitude of sun 65° to 90°. Sargasso Sea (Latitude 30° 38′ N, Longitude 56° 05′ W). (After JERLOV, 1951.)

Satisfaction of these divergent needs does not allow a simple treatment of the behaviour of light in the sea. To consider it as a biological energy source, we view it in terms of the quantum; as a product of bioluminescence, we look at it as the photogenic chemical process; as an illuminant for the activity of man, we consider it as emissions from a man-made source.

The attenuation of light by sea water is the result of two physical processes: absorption and scattering. In the first case, we are concerned with the individual

photons as they travel through the water and are modified irreversibly by thermodynamic processes; the energy input from the source which they represent may be converted to heat or chemical energy of one type or another. Scattering may be looked upon as a deflection in the direction of travel of photons with no changes of state. Absorption is responsive to wavelength, and scattering is not. If a represents absorption and s scattering, then

$$\text{attenuation} = a + s$$

DUNTLEY (1963) makes the point that no one index can specify the transparency of natural water satisfactorily because scattering and absorption are two entirely independent processes. The interested student will find a wealth of material based on modern physics in this work as well as in the papers of DUNTLEY (1962) and TYLER and PREISENDORFER (1962).

Many studies have been made on the spectral absorption of sea water, using artificial sources and daylight. Perhaps the most useful to the marine ecologist are those of JERLOV (1951). In Figs 1-34 and 2-6 the most pertinent of his findings have been summarized (see also Chapter 2.0). There are those who find reason to question the work in which filters have not been tested carefully for 'bandwidth error' or 'leakage'. The attenuation which is evident in these curves is primarily caused by absorption characteristics of different wavelengths. According to DUNTLEY (1963), the attenuation of 'clear blue ocean water' is about 40% due to absorption and about 60% due to scattering, this for a blue band of the spectrum centering on 480 millimicrons. For other spectral segments, absorption predominates over scattering (in water containing a minimum of particulate material).

Scattering is the alteration in the paths of photons without loss of energy brought about by water molecules themselves, fine clay particles, silts of various types, plankton organisms of all kinds and sizes and organic detrital particles of many types. It is obvious that the coefficient of scattering should vary considerably according to the kinds of plankton growth and the proximity to land drainage.

Acoustical properties of sea water

Sound is transmitted as a longitudinal pressure wave in an elastic medium. The propagation velocity of sound in sea water is equal to the square root of elasticity divided by the density. The following equation is used in place of this relation:

$$V = (\gamma/\rho K)^{1/2}$$

where V = velocity of propagation, γ = ratio of specific heats (specific heat at constant pressure/specific heat at constant volume), ρ = density, and K = adiabatic compressibility. The ratio enters because of the nature of sound as a compressional wave which causes the water to heat as it travels through (SVERDRUP and co-authors, 1942; DIETRICH, 1963). The values of γ, ρ, K are all dependent upon temperature, salinity and pressure, and to make the routine use of sound reflection methods possible, it has been necessary to compile special tables of corrections. This has been done for a large number of oceanic regions for layers at various depths (DIETRICH, 1963). Fig. 1-35 gives some of these data graphically.

The behaviour of sound in the ocean is subject to many vagaries, and these are derived from reflection, refraction, selective absorption, interference phenomena, etc. The propagation loss in terms of range (distance) varies with the frequency. This is illustrated in Fig. 1-36. In Fig. 1-37 we see an oscillograph recording of propagation from a source with constant output over a fixed range. The record clearly shows short time variations due to rapidly changing environmental conditions (HORTON, 1959).

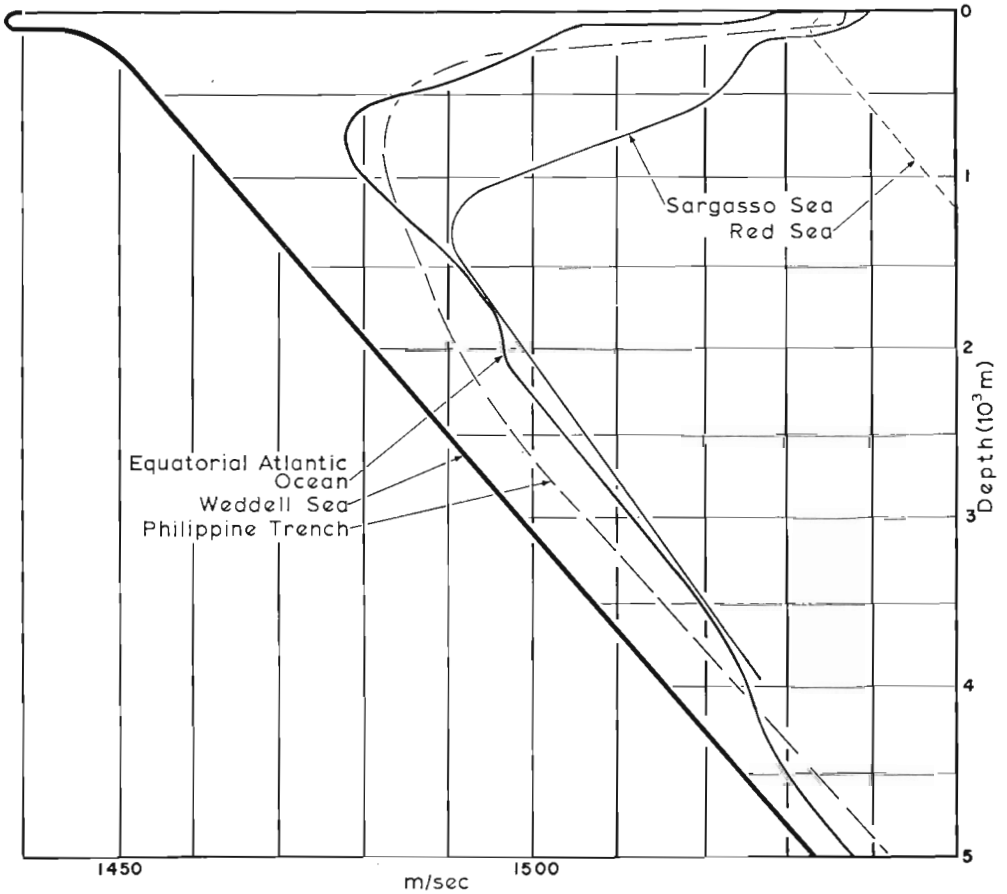


Fig. 1-35: Variation of sound velocity with depth in selected ocean waters. (After DIETRICH, 1963.)

There is an impressive array of ambient noises in the sea, and these have been divided into three principal classes (FURDUEV, 1964): (1) Ambient, from ocean waves, breakers, wind; (2) biological, from the fauna; (3) technical, from shipping and harbour facilities. Fig. 1-38 shows some of these. STEINBERG and co-authors (1962) studied faunal noises in the area of the Bahamas and listed 25 categories which fell into a variety of patterns. There were short bursts, daily patterns and seasonal patterns. They gave as tentative sources whales, porpoises, groupers, squirrel fish and grunts. The principal frequencies were mostly below 1000 cps.

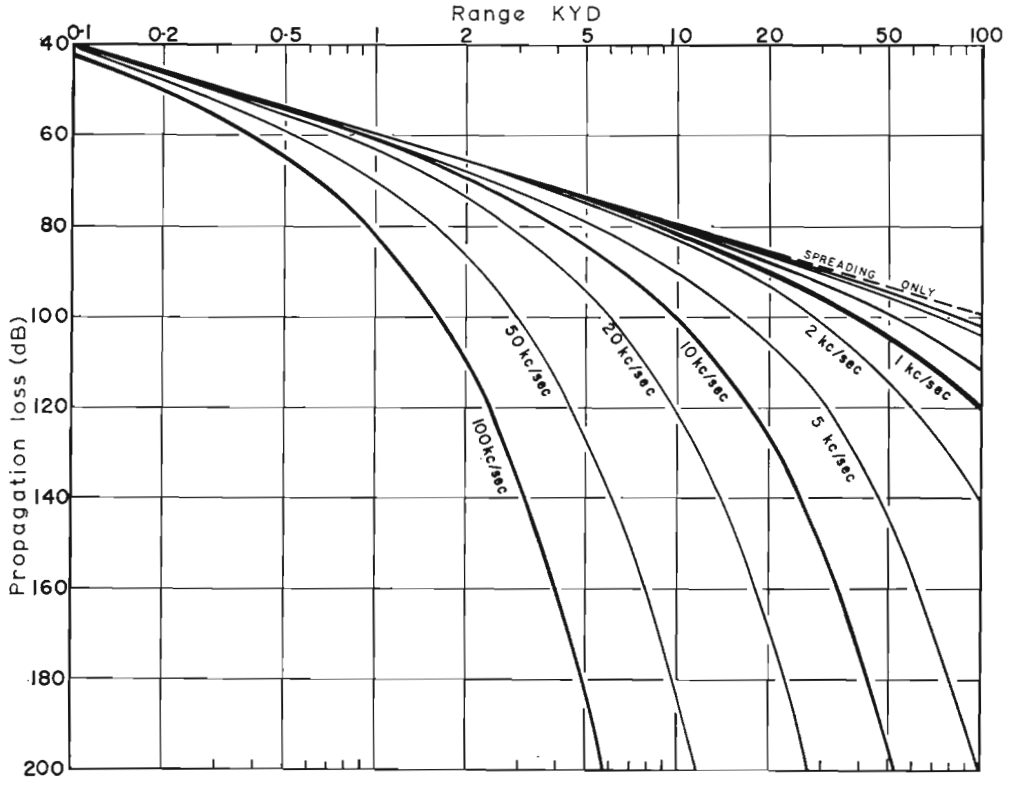


Fig. 1-36: Propagation loss of underwater sound relative to range (distance from effective centre of source) and frequency. (After HORTON, 1959.)

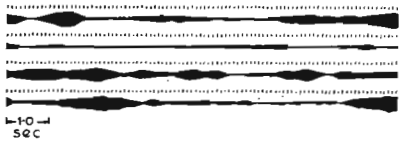


Fig. 1-37: An example of variation in sound propagation loss as recorded on oscillograms. These variations may be regarded as time and place deviations from the idealized curves of Fig. 1-36. They are believed to be due to short-term changes in sea conditions and interference effects. (After HORTON, 1959.)

The peak intensities were at times 20 dB above ambient. They found the peak sonic activity to be at sunset.

For the marine ecologist the most important phenomenon relative to the acoustical properties of sea water is the deep scattering layer, the well-known

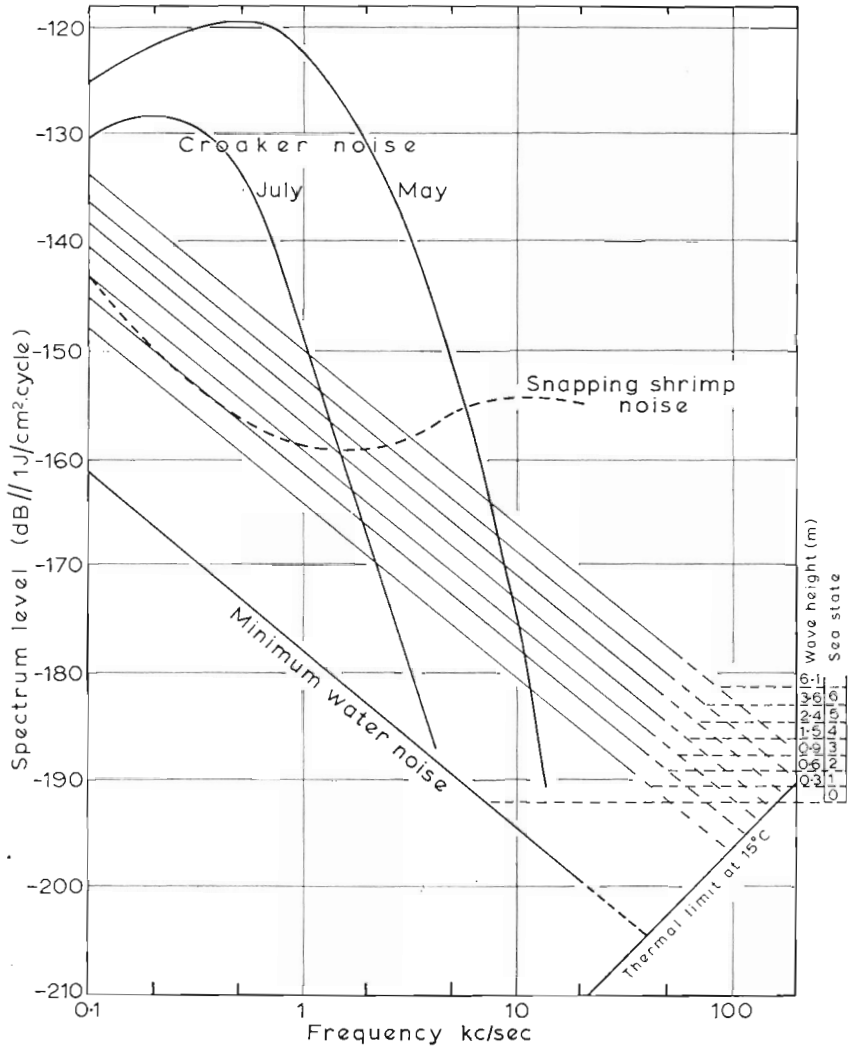


Fig. 1-38: Some contributors to ambient underwater sound (noise). Minimum water noise is that generated by impact of water on beaches, and other sources of water disturbance. The thermal limit is imposed by the instrumentation. Decibels relative to reference intensity per unit band (J_0=1 joule/cm². cycles). (After HORTON, 1959.)

DSL. This is a migratory stratum of sound scatterers found in most waters, with the exception of the Antarctic. Many attempts have been made to identify specific organisms with the deep scattering layer but there does not seem to be a simple answer. A variety of fishes and invertebrates have been designated as responsible. The DSL may be made up of a number of strata which migrate at different rates

and some not at all. CHAPMAN and MARSHALL (1966) made a study of the DSL in the western North Atlantic, making detailed observations at 37 points. During the day, scattering layers were found at depths of 300 to 900 m and persisted over distances of 700 km. Most of the low frequency reverberation came from the shallowest layer, which was the one that migrated towards the surface as sunset approached. They attributed the largest part of reverberation to the swimbladders of bathypelagic fish.

Electrical properties of sea water

Conductivity is the most important electrical property of sea water. It is due to the mobility of ions; hence, temperature, viscosity and pressure are factors which influence conductivity determinations. Fig. 1-39 illustrates the effects of

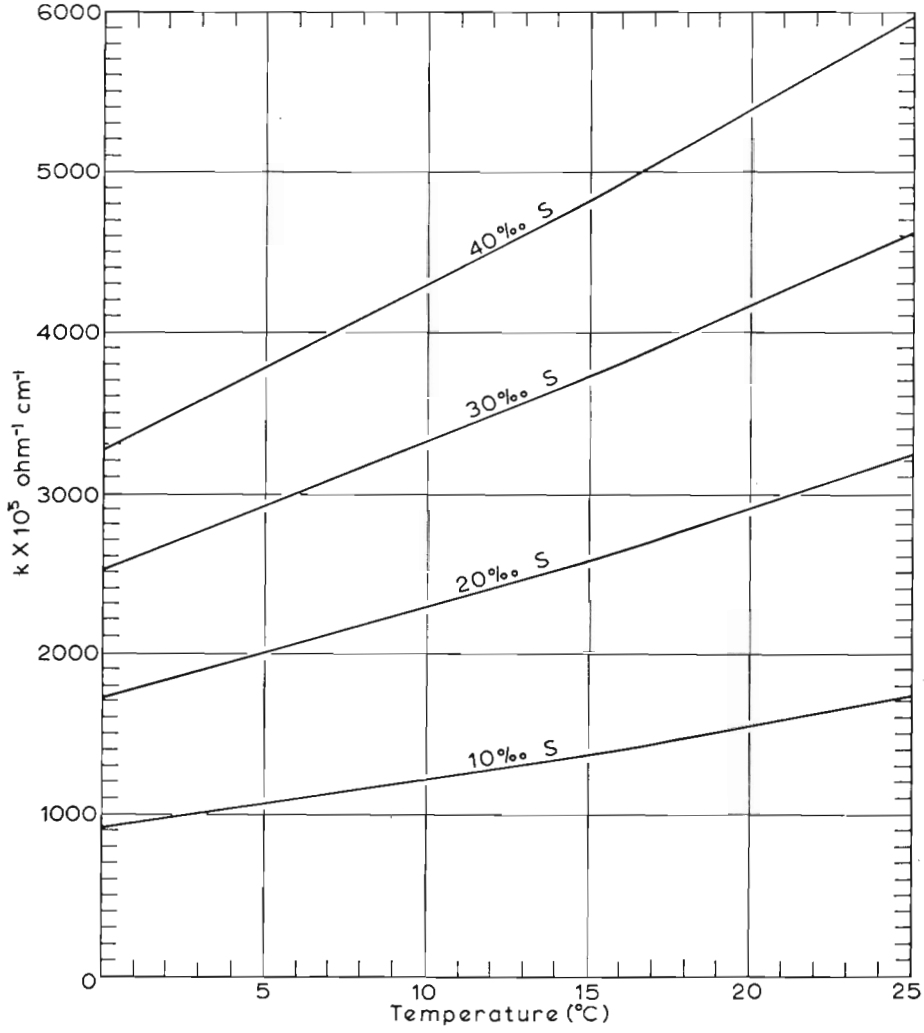


Fig. 1-39: Electrical conductivity of sea water for selected salinities as a function of temperature. (From data given by DIETRICH, 1963.)

salinity and temperature on conductivity. HAMON (1958) has shown that conductivity is suppressed with increasing pressure, with the greatest effects being at the lower temperatures.

Chemical properties of sea water

Water is a covalent polar molecule composed of two atoms of hydrogen and one atom of oxygen. The atoms are held together by shared electrons between the hydrogen and oxygen atoms in such a way that the angle between the radii

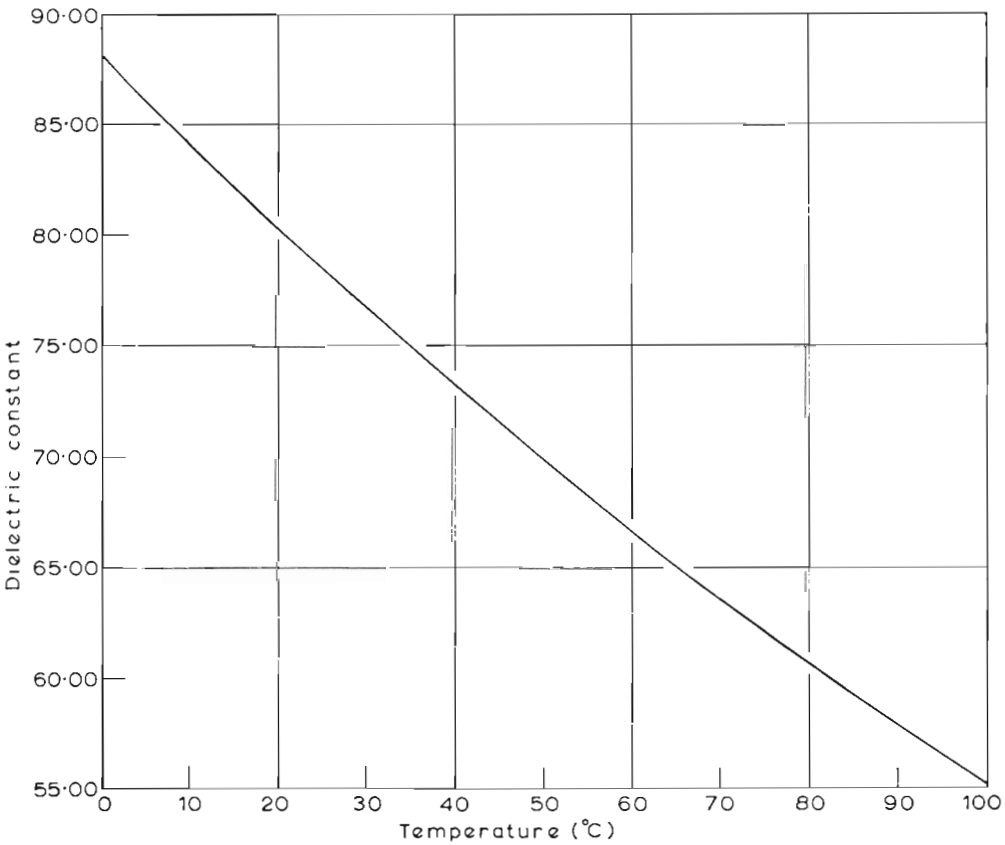


Fig. 1-40: The dielectric constant of water as a function of temperature. (Data from WEAST, 1964.)

occupied by the hydrogen atoms is 105°, a result of a sort of crowding by the two lone pairs of electrons on the oxygen atom. Inherent in this structure lies the capability of water molecules to form hydrogen bonds and polymers. A single water molecule is planar in configuration, but there is a temperature-dependent tendency to form two, four and eight molecule tetradic structures. The angular relation of the hydrogen atoms and the related densities of electron clouds causes a large dipole moment and dielectric constant. These properties, the hydrogen bonding and the degree of packing associated with polymer formation, are responsible for the solvation and hydration properties of water and its behavioural

states relative to temperature regimes. Fig. 1-40 gives the relation between the dielectric constant and temperature.

Water is the 'universal solvent' and the sea receives the dissolved residues resulting from the attack of the elements on every exposed geologic structure of the continents and those which are submerged in it. Hence, it is fair to say that it contains some portion of all known stable elements. For convenience, these are presented in a number of categories beginning with the major salts.

The major salts and their concentration in typical sea water are given in Table 1-5 (see also Chapter 4.0).

Table 1-5

Average composition of sea water of 19 $^{0}/_{00}$ chlorinity and 34·325 $^{0}/_{00}$ salinity (After NICOL, 1967)

Ion	Composition % of sea salt	Concentration g/kg of sea water	Concentration mM/kg	Concentration g/l at 20° C (Specific gravity 1·024)
Na^+	30·61	10·556	459·02	10·809
K^+	1·10	0·380	9·72	0·389
Mg^{2+}	3·69	1·272	52·30	1·303
Ca^{2+}	1·16	0·400	9·98	0·410
Sr^{2+}	0·04	0·0085	0·15	0·013
H_3BO_3	0·07	0·026	0·42	0·027
Cl^-	55·04	18·980	535·30	19·435
$SO_4^=$	7·68	2·649	27·57	2·713
HCO_3^- *	0·41	0·140	2·29	0·143
Br^-	0·19	0·065	0·81	0·067
F^-	0·004	0·001	0·05	0·001

* Bicarbonate and carbonate will vary according to the pH of the sea water

The universal dimension for indicating the total dissolved solids in sea water is salinity in parts per thousand (S $^{0}/_{00}$). This refers to the total weight in grams of solid matter dissolved in one kilogram of sea water. Salinity as thus defined is not determined directly as a routine method. It has been related to chlorinity, density and conductivity. The fundamental reference for all methods is chlorinity. Chlorinity is defined as the mass in grams of pure silver required to precipitate the halogens in 328·5233 g of sea water. The relation between chlorinity and salinity has been worked out as follows:

$$S\ ^{0}/_{00} = 1{\cdot}805\ Cl\ ^{0}/_{00} + 0{\cdot}030$$

This relation has been used almost universally for many years, but with the advancing technology and more demanding requirements of modern oceanography, some modifications have been adopted (JOHNSTON, 1964). The now famous old equation has been challenged and a Joint Panel (UNESCO, 1962) recommended that the equation for converting chlorinity to salinity be given the form

$$S = 1{\cdot}80655 \times \text{chlorinity}$$

The constant 0·030 in the old form was an allowance for the salinity of the diluting fresh water of the Baltic rivers. The elimination of this constant does not affect unduly the salinities ranging between 30 and 40 $^{0}/_{00}$. Below this range salinities are those of the sea–land boundary where the variability is great enough to minimize the error due to the elimination of the constant 0·030 (Chapter 4.0).

One should also bear in mind that the ion composition of sea–land boundary waters may vary significantly from those of pure oceanic sea water. Such waters generally have more carbonate and sulphate relative to chloride with an accompanying increase in ratio of calcium to sodium (KINNE, 1967).

While the major salts are largely responsible for the general solution properties of sea water, the inorganic trace elements are also significant from the biological point of view. These are shown according to magnitudes of concentration in Table 1-6.

Table 1-6

Partial list of inorganic trace elements in sea water of a chlorinity of 19 $^{0}/_{00}$ (After NICOL, 1967)

Element	mg/kg
Boron	5·0
Silicon	0·01–7·0
Nitrogen (as NH_4, NO_3, NO_2)	0·001–0·7
Phosphorus	0·001–0·17
Iron	0·001–0·29
Manganese	0·001–0·01
Copper	0·01–0·024
Zinc	0·005–0·014
Molybdenum	0·0003–0·016
Vanadium	0·0002–0·007
Chromium	0·001–0·003
Cobalt	0·0001–0·0005

Silicon is important biologically as a component of the frustules of diatoms, the spicules of some sponges and the hard parts of silicoflagellates and some radiolarians. Its greatest importance is with respect to the diatoms, and it is here that we are interested in its cyclical variations in concentration. It is found in both dissolved and particulate states in the abiotic form. Silica (SiO_2) is soluble in sea water to the extent of 100 to 140 mg/l; further, most of the dissolved silica in sea water is present as orthosilicic acid $Si(OH)_4$. It is also in the latter form that diatoms probably assimilate the material from the water (LEWIN, 1962).

In oceanic waters the distribution of silicate has a steep vertical gradient which is related to the photic zone. This is attributed to the growth, death and sinking of diatoms. It is well established that diatom blooms may exhaust the silicon content of these waters. It has been shown that following cell division new cell walls may be formed and silicified in 10 to 20 mins (REIMANN, 1960).

Table 1-7

Specific dissolved organic compounds identified in sea water (After DUURSMA, 1965)

Names of compounds and chemical formulae	Concentrations		Authors	Localities
I Carbohydrates				
Pentoses $C_5H_{10}O_5$	0–8	mg/l	COLLIER and co-authors (1950, 1953)	Gulf of Mexico
Pentoses $C_5H_{10}O_5$	0·5	µg/l	DEGENS and co-authors (1964)	Pacific off California
Hexoses	14–36	µg/l	DEGENS and co-authors (1964)	Pacific off California
Rhamnosides $C_6H_{12}O_5$	0·1–0·4	mg/l	LEWIS and RAKESTRAW (1955)	Pacific Ocean coast USA
Rhamnosides Dehydroascorbic acid $\ulcorner\!\!-\!\!O\!\!-\!\!\urcorner$ $COCOCOCHCH(OH)CH_2OH$	0·1	mg/l	WANGERSKY (1952)	Gulf of Mexico inshore water
II Proteins and their derivatives				
Peptides C:N ratio = 13·8:1			JEFFREY and HOOD (1958)	Gulf of Mexico
Polypeptides and polycondensates of:	(*a*) µg/l	(*b*) µg/l	(*c*) µg/l	(*d*) µg/l		
Glutamic acid $COOH(CH_2)_2CH(NH_2)COOH$		8–13	8–13	0·1–1·8	(*a*) PARK and co-authors (1962) (by ion-exchange)	Gulf of Mexico
Lysine $NH_2(CH_2)_4CH(NH_2)COOH$	< 1	?	trace–3	0·1–0·9	(*b*) TATSUMOTO and co-authors (1961) (by paper chromatography)	Gulf of Mexico
Glycine NH_2CH_2COOH		—	trace–3	1·2–3·7	(*c*) TATSUMOTO and co-authors (1961) (by ion-exchange)	Gulf of Mexico
Aspartic acid $COOHCH_2CH(NH_2)COOH$		3–8	trace–3	0·1–1·0	(*d*) DEGENS and co-authors (1964)	Pacific off California
Serine $CH_2OHCH(NH_2)COOH$		?	trace–3	1·8–5·6		
Alanine $CH_3CH(NH_2)COOH$		3–8	trace–3	0·7–3·1	(*a*) PARK and co-authors (1962) (by ion-exchange)	Gulf of Mexico
Leucine $(CH_3)_2CHCH_2CH(NH_2)COOH$	0·5–1	8–13	trace–3	0·9–3·8	(*b*) TATSUMOTO and co-authors (1961) (by paper chromatography)	Gulf of Mexico
Valine $(CH_3)_2CHCH(NH_2)COOH$		trace–3	trace–3	0·1–1·7	(*c*) TATSUMOTO and co-authors (1961) (by ion-exchange)	Gulf of Mexico
Cystine $[SCH_2CH(NH_2)COOH]_2$		trace–3	—	0·0–3·8	(*d*) DEGENS and co-authors (1964)	Pacific off California
Iso-leucine $CH_3CH_2CH(CH_3)CH(NH_2)COOH$		8–13	trace–3	—		
Leucine $CH_3CH_2CH_2CH_2CH(NH_2)COOH$		—	—	0·9–3·8		
Ornithine $NH_2(CH_2)_3CH(NH_2)COOH$		—	trace–3	0·2–2·4		
Methionine sulphoxide $CH_3S(:O)CH_2CH_2CH(NH_2)COOH$				—		

Phenylalanine $C_6H_5CH_2CH(NH_2)COOH$	—	—	0·1–0·3
Histidine $C_3H_3N_2CH_2CH(NH_2)COOH$	?	trace–3	trace–2·4
Arginine $NH_2C(:NH)NH(CH_2)_3CH(NH_2)COOH$	?	trace–3	0·1–0·6
Proline C_4H_8NCOOH	?	—	0·3–1·4
Methionine $CH_3SCH_2CH_2CH(NH_2)COOH$	—	trace–3	trace–0·4
Tryptophan $C_8H_6NCH_2CH(NH_2)COOH$	—	trace–3	—
Glucosamine $C_6H_{13}NO_5$	—	trace–3	—

Free amino acids	(*e*)	(*f*) µg/l
Cystine $[SCH_2CH(NH_2)COOH]_2$	det.	—
Lysine $NH_2(CH_2)_4CH(NH_2)COOH$	det.	0·2–3·1
Histidine $C_3H_3N_2CH_2CH(NH_2)COOH$	det.	0·5–1·7
Arginine $NH_2C(:NH)NH(CH_2)_3CH(NH_2)COOH$	det.	0·0
Serine $CH_2OHCH(NH_2)COOH$	det.	2·3–28·4
Aspartic acid $COOHCH_2CH(NH_2)COOH$	det.	trace–9·6
Glycine NH_2CH_2COOH	det.	trace–37·6
Hydroxyproline $C_4H_7N(OH)COOH$	det.	trace–2·8
Glutamic acid $COOH(CH_2)_2CH(NH_2)COOH$	det.	1·4–6·8
Threonine $CH_3CHOHCH(NH_2)COOH$	det.	2·8–11·8
α-Alanine $CH_3CH(NH_2)COOH$	det.	
Proline C_4H_8NCOOH	det.	0·0
Tyrosine $HOC_6H_4CH_2CH(NH_2)COOH$	det.	trace–5·0
Tryptophan $C_8H_6NCH_2CH(NH_2)COOH$	det.	—
Methionine $CH_3SCH_2CH_2CH(NH_2)COOH$	det.	—
Valine $(CH_3)_2CHCH(NH_2)COOH$	det.	0·3–2·7
Phenylalanine $C_6H_5CH_2CH(NH_2)COOH$	det.	trace–2·4
Iso-leucine $CH_3CH_2CH(CH_3)CH(NH_2)COOH$	det.	—
Leucine $(CH_3)_2CHCH_2CH(NH_2)COOH$	det.	0·5–5·5

(*e*) PALMORK (1963a, b) — Norwegian coastal water

(*f*) DEGENS and co-authors (1964) — Pacific off California

Table 1–7—*Continued*

Names of compounds and chemical formulae	Concentrations	Authors	Localities
Free compounds			
Uracil NHCONHCOCH:CH	det.	Belser (1959, 1963)	Pacific coast near La Jolla
Iso-leucine $CH_3CH_2CH(CH_3)CH(NH_2)COOH$	det.		
Methionine $CH_3SCH_2CH_2CH(NH_2)COOH$	det.		
Histidine $C_3H_3N_2CH_2CH(NH_2)COOH$	det.		
Adenine $C_5H_3N_4NH_2$	det.		
Peptone	det.		
Threonine $CH_3CHOHCH(NH_2)COOH$	det.		
Tryptophan $C_8H_6NCH_2CH(NH_2)COOH$	det.		
Glycine NH_2CH_2COOH	det.		
Purine $C_5H_4N_4$	det.		
Urea CH_4ON_2	det.	Degens and co-authors (1964)	Pacific off California
III Aliphatic Carboxylic and Hydroxycarboxylic acids			
	mg/l (0–200 m)	mg/l (200–600 m)	mg/l (>600 m)		
Lauric acid $CH_3(CH_2)_{10}COOH$	0·01–0·32	0·01–0·28	0–0·28	Slowey and co-authors (1962)	Coastal waters of Gulf of Mexico
Myristic acid $CH_3(CH_2)_{12}COOH$	0·01–0·10	0·01–0·05	0–0·07		
Myristoleic acid $CH_3(CH_2)_3CH:CH(CH_2)_7COOH$	trace–0·02	0·01–0·03	0–0·05		
Palmitic acid $CH_3(CH_2)_{14}COOH$	0·01–0·17	0·03–0·42	0–0·38		
Palmitoleic acid $CH_3(CH_2)_5CH:CH(CH_2)_7COOH$	0·02–0·16	0·02–0·16	0–0·21		
Stearic acid $CH_3(CH_2)_{16}COOH$	0·04–0·09	0·02–0·13	0–0·10		
Oleic acid $CH_3(CH_2)_7CH:CH(CH_2)_7COOH$	0·01	0·02	0		
Linoleic acid $CH_3(CH_2)_4CH:CHCH_2CH:CH(CH_2)_7COOH$	0·01	0·01	0		
		mg/l (1000—2500m)			
Fatty acids with: 12 C-atoms		0·0003–0·02		Williams (1961)	Pacific Ocean coastal

16 C ,, +1 double bond	0·0003–0·003		
18 C ,,	0·0037–0·0222		
18 C ,, +1 double bond	0·0083		
18 C ,, +2 double bonds	0·0000–0·0029		
20 C ,,	trace–0·0081		
22 C ,,	trace–0·0014		
	mg/l		
Acetic acid CH_3COOH	< 1·0	Koyama and Thompson (1959)	Pacific Ocean
Lactic acid $CH_3CH(OH)COOH$			
Glycollic acid $HOCH_2COOH$			
Malic acid $HOOCCH(OH)CH_2COOH$	0·28	Creac'h (1955)	Atlantic coastal water
Citric acid $HOOCCH_2C(OH)(COOH)CH_2COOH$	0·14		
Carotenoids and brownish waxy or fatty matter	2·5	Johnston (1955)	North Sea
		Wilson and Armstrong (1955)	English Channel
IV Biologically active compounds (see also Provasoli, 1963)			
Organic Fe compound(s)		Harvey (1925)	Deep sea water
Vitamin B_{12} (Cobalamine) $C_{63}H_{90}O_{14}N_{14}PCo$	3·4–1·6 mμg/l	Vishniac and Riley (1961)	Long Island Sound
Vitamin B_{12}	0·2 mμg/l (summer)	Cowey (1956)	Oceanic surface-water
	2·0 mμg/l (winter)		
Vitamin B_{12}	0·2–5·0 mμg/l	Daisley and Fisher (1958)	
Vitamin B_{12}	0–2·6 mμg/l	Kashiwada and co-authors (1957)	North Pacific Ocean
Vitamin B_{12}	0–0·03 mμg/l	Menzel and Spaeth (1962a)	Sargasso Sea 0–05 m
Thiamine (Vit. B_1) $C_{12}H_{18}ON_4SCl_2$	0–20 mμg/l	Cowey (1956)	Surface water, possibly from land drainage
Plant hormones (auxins)	3·41 mμg/l	Bentley (1960)	North Sea near Scotland
V Humic acids			
'Gelbstoffe' (Yellow substances) Melanoidin-like		Kalle (1949, 1962) Jerlov (1955) Armstrong and Boalch (1961a, b)	Coastal waters
VI Phenolic compounds			
p-Hydroxybenzoic acid HOC_6H_5COOH	1–3 μg/l	Degens and co-authors (1964)	Pacific off California
Vanillic acid $CH_3(HO)C_6H_3COOH$	1–3 μg/l		
Syringic acid $(CH_3O)_2(HO)C_6H_2COOH$	1–3 μg/l		
VII Hydrocarbons			
Pristane; (2, 6, 10, 14-tetramethylpentadecane)	trace	Blumer and co-authors (1963)	Cape Cod Bay

det. = detected — = not detected ? = possibly present

In offshore waters, the silicon supply must depend upon upwelling and resolution from dead diatoms. A living diatom possesses a means for protecting its silicious valves from dissolution; this process begins only after death (LEWIN, 1961). Thus, in oceanic waters, the silicon cycle is a simple one of uptake by and resolution from diatoms.

In the sea–land boundary zone there is evidently a supply of silica from various mineral silicates (kaolinite, monmorillinite, etc.) which produce silica on standing in sea water (MACKENZIE and GARRELS, 1965).

The presence of organic substances in sea water is due to either the decomposition of dead organisms or the escape of metabolites from living organisms. At some point in space and time there must be present in the sea a large variety of such compounds; in the richer waters of the temperate sea–land boundary they would be more in contrast to the more sterile oceanic waters of the tropics.

Some organic compounds are more stable than others and persist for long periods of time, even to the point of finding their way into the sediments. DUURSMA (1965) identified a great many of these compounds (Table 1-7).

Perhaps the greatest significance of these substances lies in their biological activity. This may fall into two roles: the activity of the substances as vitamins and auxin-type materials and their availability as energy sources.

PROVASOLI (1963) has reviewed this subject insofar as vitamin and auxin-like activity is concerned. The vitamin requirements of some algae are shown in Table 1-8.

It is well known that many marine organisms have well developed chemoreceptors and there is little doubt that these are aids in locating food. The salmon may sense differences in streams and thus locate natal areas to be used as spawning grounds. Sharks are heavily dependent upon olfaction for orientation in their pursuit of prey. Small fishes of the minnow family differentiate between related invertebrates and aquatic plants (WALKER and HASLER, 1949). These phenomena may be given as evidence that organic metabolites are present in the water in sufficient variety and quantities to serve as ecological communicators. This is of course the essence of the development of the idea of external metabolites as proposed by LUCAS (1961).

COLLIER and co-authors (1953) demonstrated the response of oysters to small amounts of material naturally present in sea water and responding to the N-ethylcarbazol test for reducing sugars. COLLIER (1959) further related the uptake of these substances to oxygen uptake, and proposed that they may be used as a source of energy for the cells of the ciliated epithelium of the gills. COLLIER (1963) has further shown that the N-ethylcarbazol materials exist in the sea in patterns of discontinuous distribution (Fig. 1-41).

The presence of oxygen in sea water is due to contact of the water with the atmosphere at the sea–air interface and to the metabolism of photosynthetic organisms. The oxygen concentration at any one moment at a given point is the resultant of a series of biological and physical factors. Once the mass of water has been in contact with the atmosphere and leaves the area of contact, it is subjected to the oxygen produced by photosynthetic processes, mixing with other masses of different oxygen concentration, and the uptake of oxygen during respiratory processes. The latter may include bacteria, plants or animals, or all three.

Diffusion of oxygen into the water from the atmosphere as a first step in ventilation is dependent upon the partial pressure of the gas in the atmosphere, the

Table 1-8

Vitamin requirements of marine algae (After PROVASOLI, 1963)

Species	B_{12}	Thiamine	Biotin
CHLOROPHYCEAE			
Dunaliella salina, *D. primolecta*, *D. euchlora*, *D. viridis*, *Nannochloris atomus*, *N. oculata*, *Pilinia* sp., *Platymonas* sp., *Prasiola stipitata*, *Stephanoptera gracilis*, *Stichococcus cylindricus*[b]	O	O	O
Stichococcus cylindricus[b], *Platymonas tetrathele*	R	O	O
Brachiomonas submarina, *Pyramimonas inconstans*	R	R	O
BACILLARIOPHYCEAE			
Amphora coffeaeformis[b], *Navicula* sp., *N. incerta*, *N. meniscus*, *Nitzschia putrida*, *N. angularis* var. *affinis*, *N. filiformis*, *N. frustulum*[b], *N. hybridaeformis*, *N. laevis*, *N. curvilineata*, *N. marginata*, *N. obtusa* var. *scalpelliformis*, *N.* aff. *ovalis*, *Phaeodactylum tricornutum*, *Stauroneis amphoroides*	O	O	O
Achnanthes brevipes, *Amphora perpusila* (*coffeaeformis*?), *A. coffeaeformis*[b], *A. lineolata*, *Cyclotella* sp., *Nitzshia frustulum*[b], *N. ovalis*, *N. punctata*, *Synedra affinis*, *Skeletonema costatum*, *Stephanopyxis turris*	R	O	O
Amphipleura rutilans, *Amphora coffeaeformis*[b], *Nitzshia closterium*[b]	R	R	O
Amphiprora paludosa, var. *duplex*, *Amphora coffeaeformis*[b], *Nitzschia closterium*[b]	O	R	O
CHRYSOPHYCEAE			
Stichochrysis immobilis	O	O	O
Hymenomonas carterae	R	O	O
Pleurochrysis scherffelii	O	R	O
Hymenomonas elongata, *Isochrysis galbana*, *Microglena arenicola*, *Monochrysis lutheri*, *Prymnesium parvum*	R	R	O
CRYPTOPHYCEAE			
Hemiselmis virescens, *Rhodomonas* sp. (10 strains)	R	R	O
Rhodomonas lens	S	R	O
DINOPHYCEAE			
Exuviaella cassubica, *Glenodinium foliaceum*, *Gonyaulax polyhedra*, *Gymnodinium splendens*, *Gyrodinium californicum*, *G. resplendens*, *G. uncatenum*, *Peridinium balticum*, *P. chattoni*, *P. trochoideum*	R	O	O
Amphidinium klebsii, *A. rhynchocephalum*, *Gynmodinium breve*, *Oxyrrhis marina*	R	R	R
Gyrodinium cohnii	O	S - R[c]	R
CYANOPHYCEAE			
Phormidium persicinum	R	O	O
RHODOPHYCEAE			
Goniotrichum elegans, *Bangia fuscopurpurea*	R	O	O

R = required; O = not required; [b]species represented by strains with different vitamin requirements; [c]slight but indefinite growth without thiamine; hundredfold increase (or more) when thiamine added

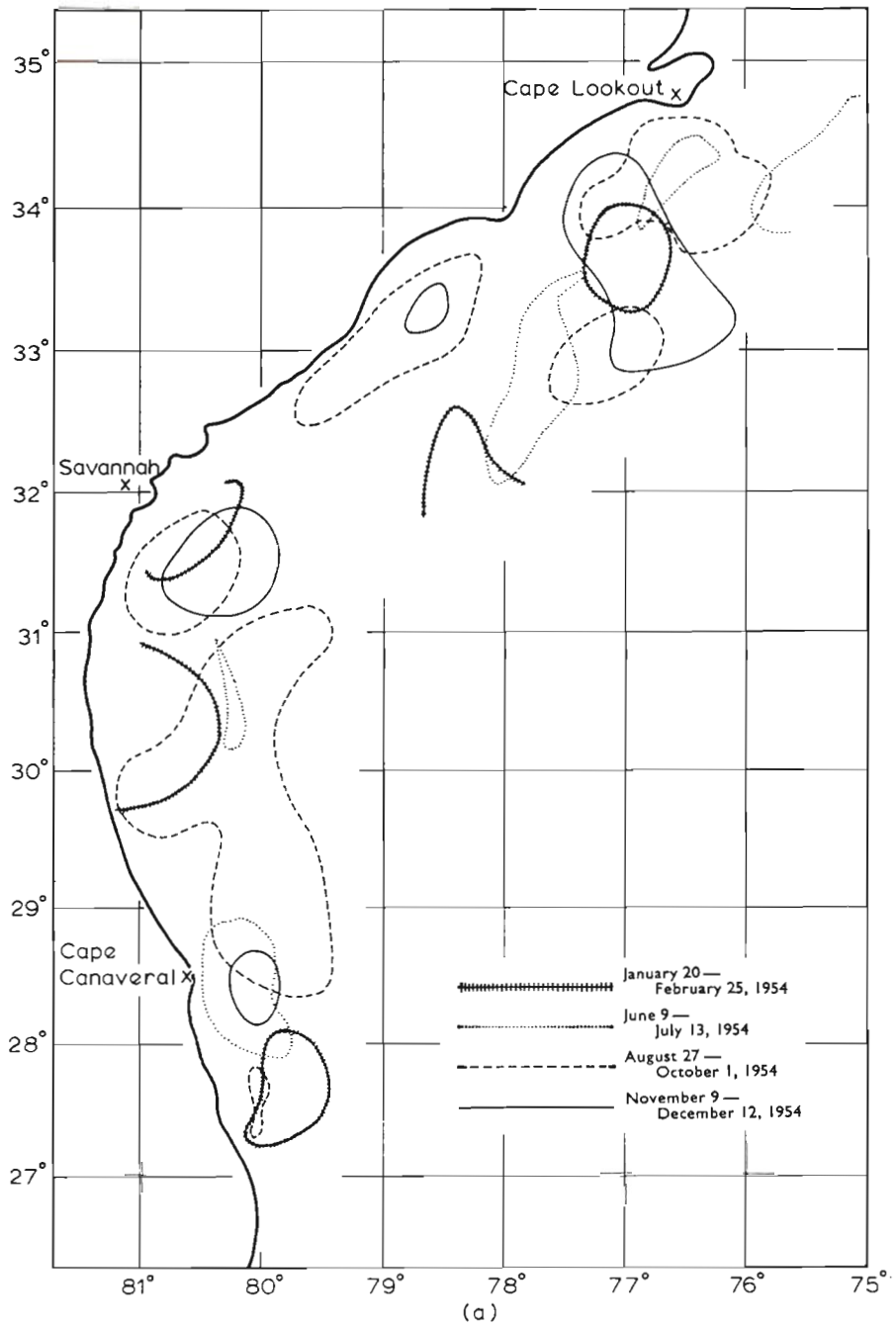


Fig. 1-41(a): Distribution patterns of carbohydrates in Atlantic waters off the south-east coast of the United States. Carbohydrates as measured by the N-ethylcarbazol reagent. Distribution of maximum values for the surface level. (Figure after COLLIER, 1963; data from ANDERSON and GEHRINGER, 1958a, b, and ANDERSON and GEHRINGER, 1959a, b, c.)

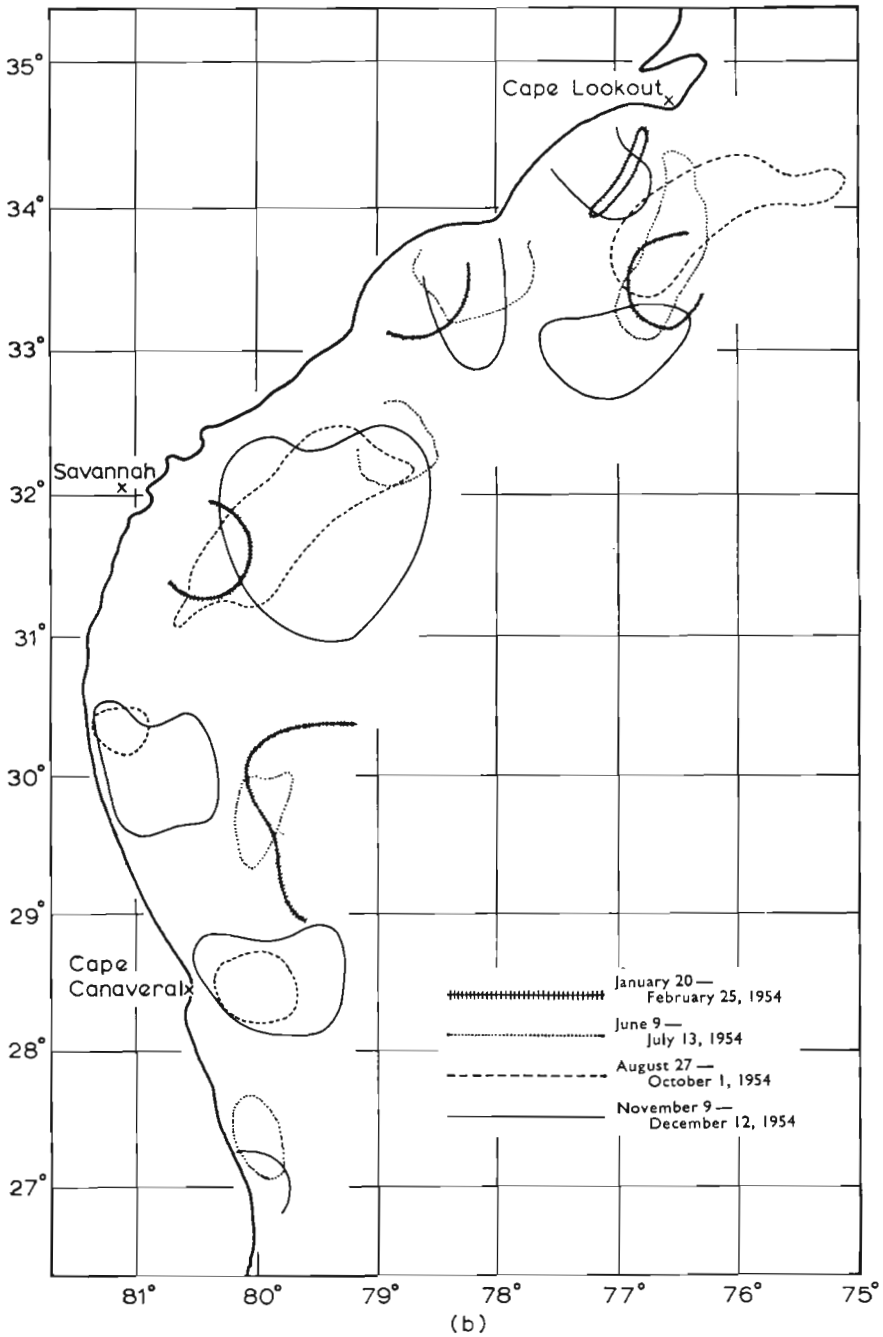


Fig. 1-41(b): Distribution patterns of carbohydrates in Atlantic waters off the south-east coast of the United States. Carbohydrates as measured by the N-ethylcarbazol reagent. Distribution of maximum values at the 10 m level. (Figure after COLLIER, 1963; data from ANDERSON and GEHRINGER 1958a, b, and ANDERSON and GEHRINGER, 1959a, b, c.)

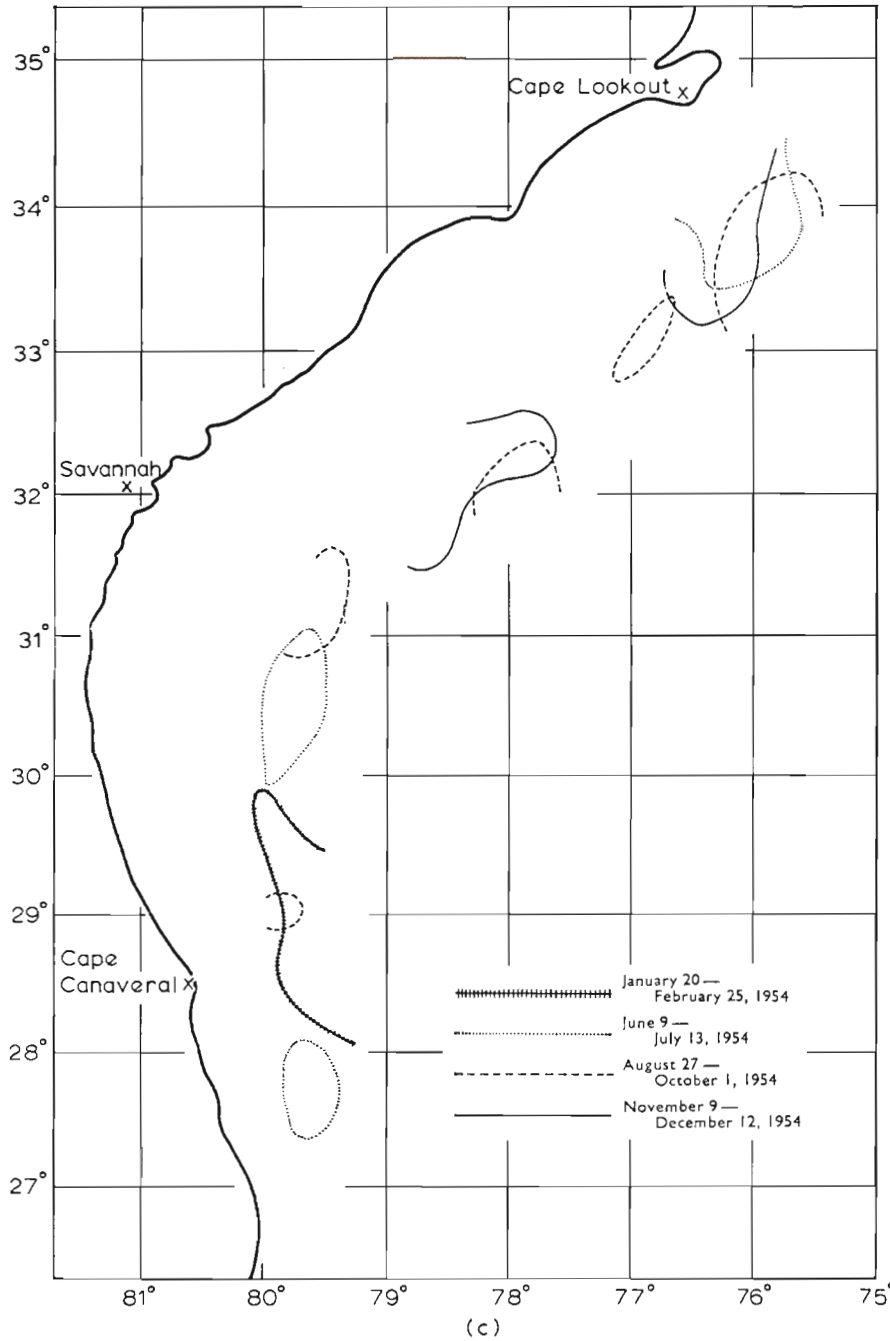
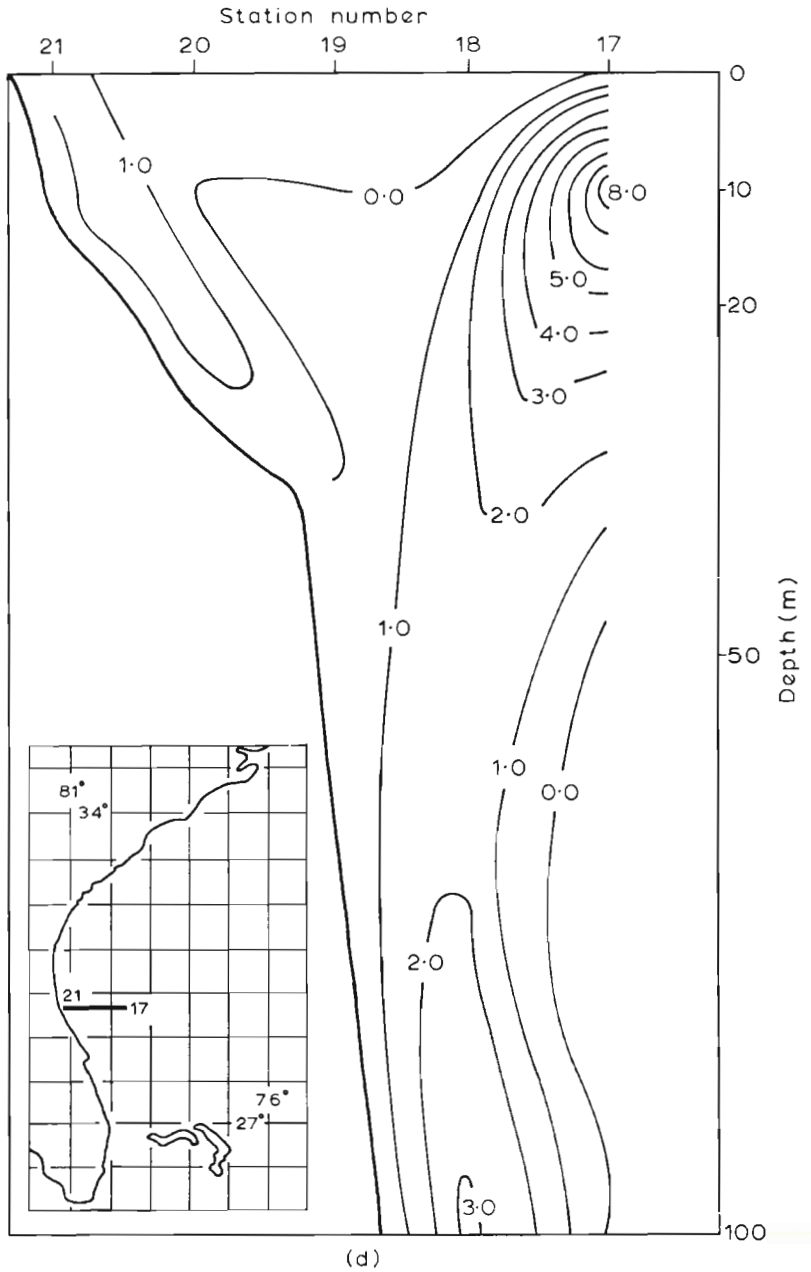


Fig. 1-41(c): Distribution patterns of carbohydrates in Atlantic waters off the south-east coast of the United States. Carbohydrates as measured by the N-ethylcarbazol reagent. Distribution of maximum values at the 100 m level. (Figure after COLLIER, 1963; data from ANDERSON and GEHRINGER, 1958a, b, and ANDERSON and GEHRINGER, 1959a, b, c.)



(d)

Fig. 1-41(d): Distribution patterns of carbohydrates in Atlantic waters off the southeast coast of the United States. Carbohydrates in mg/l as measured by the N-ethylcarbazol reagent. Vertical distribution between R/V *Gill* stations 17 and 21, cruise 5, January 20 to February 25, 1954. (Figure after COLLIER, 1963; data from ANDERSON and GEHRINGER, 1958a, b, and ANDERSON and GEHRINGER, 1959a, b, c.)

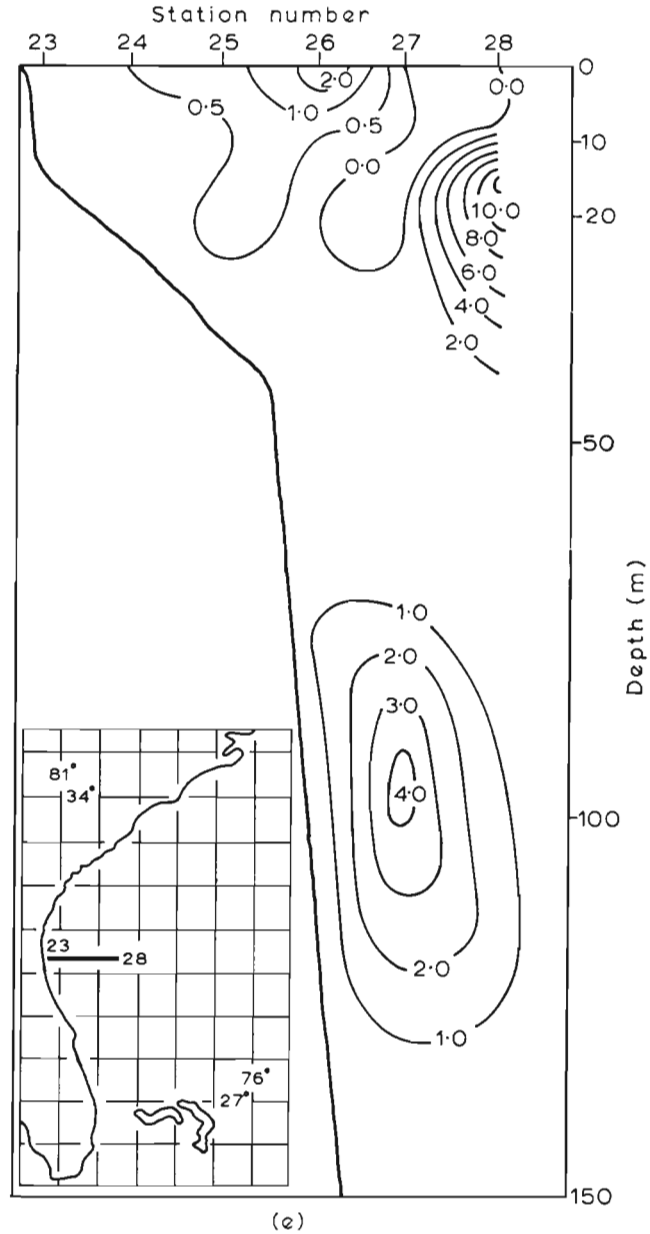


Fig. 1-41(e): Distribution patterns of carbohydrates in Atlantic waters off the southeast coast of the United States. Carbohydrates in mg/l as measured by the N-ethyl-carbazol reagent. Vertical distribution between stations 23 and 28, R/V *Gill* cruise 7, June 9 to 13, 1954. (Figure after COLLIER, 1963; data from ANDERSON and GEHRINGER, 1958a, b, and ANDERSON and GEHRINGER, 1959a, b, c.)

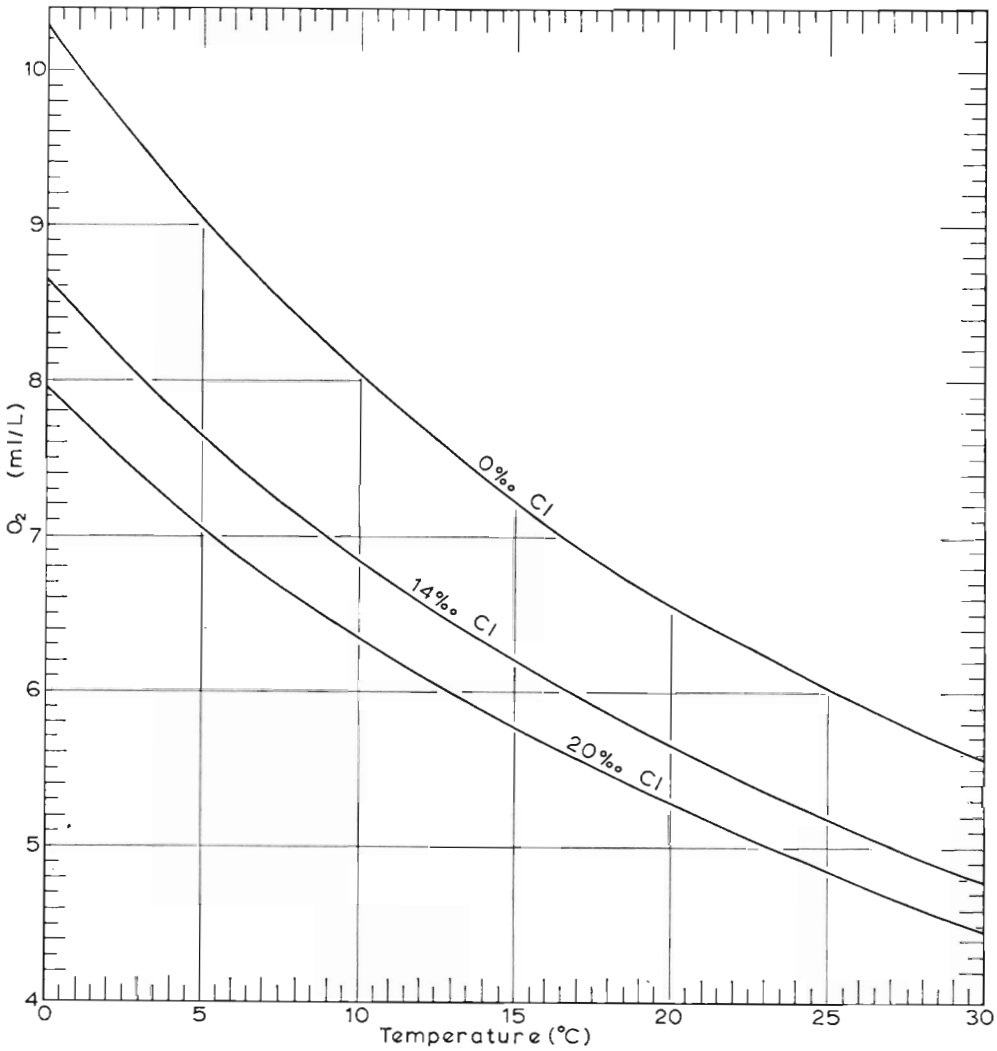


Fig. 1-42: Dissolved oxygen values at selected chlorinities as they vary with temperature. (Drawn from data of FOX as given by RICHARDS, 1965.)

concentration gradient in the surface layer, the atmospheric pressure, temperature and salinity. Several theoretical approaches to the problem of formulating the interrelations of these several factors have been offered (RICHARDS, 1965) but in most cases the empirically derived relations have been most practical. The comparison of the concentration of oxygen in water masses with saturation conditions at the surface serve most commonly for comparative studies. The percentage of saturation is usually given by

$$O_2\% = 100 \times O_2/O_2'$$

where O_2 is the observed value and O_2' is the saturated value. Oxygen saturation values for several intensities of temperature and chlorinity are given in Fig. 1-42.

As the surface water of oceanic regions sinks with its load of oxygen it may become supersaturated as a result of photosynthesis, but this is probably a transitory situation in most instances. However, an oxygen maximum is maintained in the photic zone, but below this there is a steady decline until an oxygen minimum is reached.

RICHARDS (1965) has summarized the vertical distribution of oxygen in the sea from which the following outline is taken: (1) A well-mixed layer in equilibrium with the atmosphere and a uniform oxygen content extends to the thermocline. (2) In stable water columns, such as those characteristic of the temperate regions in the spring, there is usually a subsurface maximum associated with photosynthetic maxima in the upper 50 m. (3) At depths below these, reaction with organic matter causes a variable decrease in oxygen with increasing depth. For example, in an eastern section of the North Pacific Ocean the decrease is from 5 ml to less than 0·1 ml/l in a change of depth of 100 m; in the Antarctic Convergence, a change in depth of 450 m produces a drop in oxygen concentration from 7·5 to 4·0 ml/l. (4) A minimum concentration is usually found at some depth between 700 and 1000 m, the exact level being more or less characteristic of the oceanic area being studied. (5) Because of the presence of water originating in the high latitudes, the oxygen concentration at depths below the oxygen minimum may increase slightly or remain constant as the depth increases.

It is important to emphasize the point that oxygen is removed from water in direct relation to the amount of organic residues being oxidized, and that as a consequence there is a thick layer of the tropical Pacific Ocean whose oxygen levels are much lower than the corresponding water masses of the Atlantic Ocean. The reason lies in the amount of organic matter being oxidized rather than the sluggishness of Pacific circulation. The greater amount of organic matter is due to the higher level of nutrients in the photic zone of the Pacific (RICHARDS, 1965).

(5) Chemical cycles in the seas

The carbon cycle

The fact that carbon can exist as a gaseous compound in the form of carbon dioxide and that plants have a mechanism for converting it to living tissue with the aid of sunlight are vital to the existence of all living things. Further, it is important that the well-buffered oceans can absorb excesses of the gas and maintain a certain equilibrium with the atmosphere. The latter relation is responsible for keeping the atmosphere clear of an accumulation of carbon dioxide resulting from the burning of fossil fuels. Since added carbon dioxide in the atmosphere would increase heat absorption by the atmosphere (the so-called 'greenhouse effect'), the entire world climate might be seriously altered. It has been estimated that between 1900 and 1935 the fractional volume of carbon dioxide in the atmosphere increased by approximately 9% (BATES, 1957). This was postulated to have come from the burning of fossil fuels, but it has also been suggested that the increase was due to the increase in ratio of cultivated land to forest land.

There is no difficulty in recognizing three carbon subcycles contributing to the

total flow. These are represented schematically in Fig. 1-43. The biologic cycle is essentially a closed circuit. The geologic cycle is made up of the various processes resulting in calcium carbonate deposition; some of these are no doubt physico-chemical and biological. These enter the lithosphere and from them carbon dioxide is released during metamorphosis and by slow dissolution of exposed rocks.

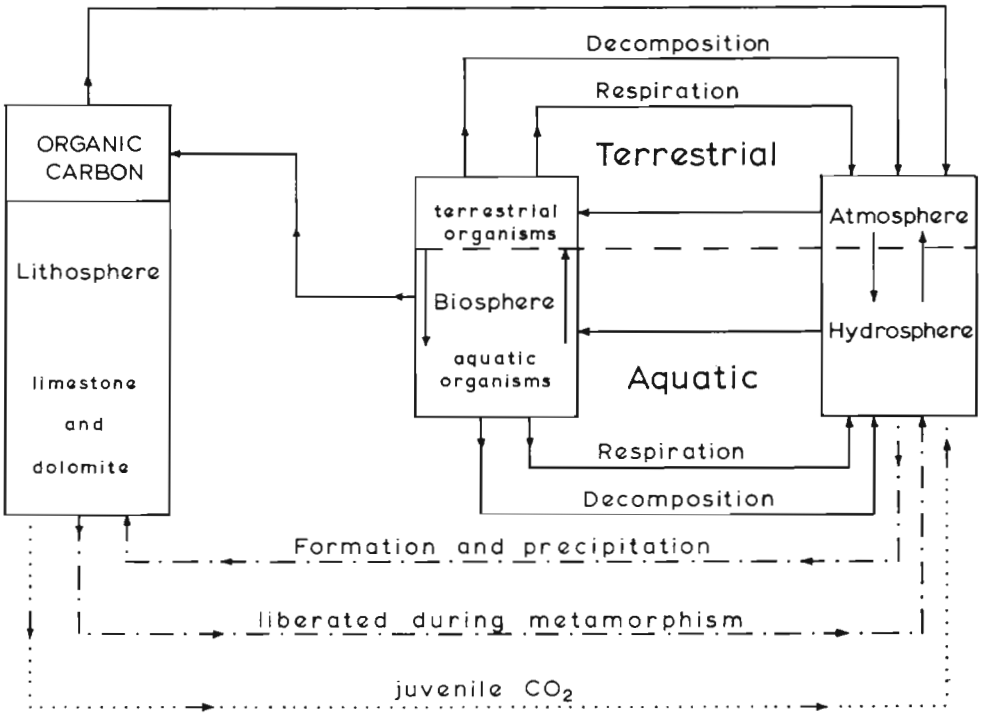


Fig. 1-43: General flow plan of carbon relating atmosphere, biosphere and the lithosphere with respect to aquatic and terrestrial organisms. (Original.)

The nitrogen cycle

The distribution of nitrogen in the seas has long been studied, and there is a great deal of literature on the subject (RAYMONT, 1963; VACARRO, 1965). In general, the concentrations are minimal in the surface waters and increase with increasing depth until the 700 to 1000 m level is reached. The major exception to this is in the Antarctic areas where the surfacing of the deeper strata brings nitrogen to the surface. This general pattern is illustrated in Fig. 1-44.

In this section, however, we are more concerned with the biological circulation of nitrogen, i.e. how it is transferred from one state to the next by the biological entities whose capability to carry on living processes is dependent upon it. The processes of nitrogen fixation, nitrification, denitrification and ammonification have been largely elucidated with respect to terrestrial regimes. For the marine environment, however, a great deal remains to be learned with respect to the specific organisms and their biochemistry. In the sea–land boundary, the situation

is confused because of the presence of many terrestrial forms. However, the best knowledge concerning the deep sea is gained largely by analogy with the boundary systems.

It is only within recent years that ammonia and molecular nitrogen have been found at least to supplement the nitrates as significant supplies for some phytoplankters. GOERING and co-authors (1966) have shown that in tropical waters

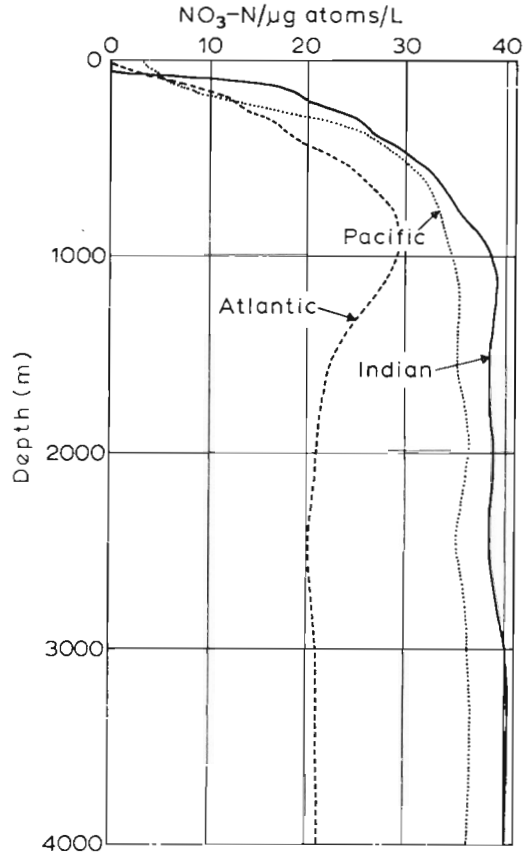


Fig. 1-44: Vertical distribution of NO_3–N in representative areas of the oceans. (After SVERDRUP and co-authors, 1942.)

Trichodesmium sp. is capable of fixing significant quantities of nitrogen. THOMAS (1966) studied the effects of certain nitrogenous materials in the growth of *Gymnodinium simplex*, *Chaetoceros gracilis* and *Nannochloris* sp. The results are summarized in Table 1-9 where it will be seen that ammonium ion is capable of supplying in a significant manner part of the nitrogen needs of these organisms. MENZEL and SPAETH (1962b) demonstrated that rain can contribute large quantities of ammonia to the surface waters of the seas in the vicinity of Bermuda. Fig. 1-45 shows the concentration of ammonium N as it varied with the five day

Table 1-9

Effects of various nitrogen sources on the growth of three phytoplankton cultures from the northeastern tropical Pacific Ocean. Cells of *Gymnodinium simplex* counted with Coulter electronic cell counter (incubation time: 9 days); cells of *Chaetoceros gracilis* and *Nannochloris* sp. counted with haemocytometer (incubation time: 8 days). Temperature 21° to 22° C, illumination 6,000 lux continuous, 40 W fluorescent lamps (After THOMAS, 1966)

Nitrogen source	*Gymnodinium simplex*	*Chaetoceros gracilis*	*Nannochloris* sp.
	Thousands of cells/ml		
NO_3^-	127·2	982·5	975·0
NO_2^-	32·7	60·5	1,041·5
NH_4^+	68·0	805·0	808·5
Glycine	26·8	379·0	2,210·0
Glutamic acid	3·6	78·5	165·3
Asparagine	4·4	121·5	174·4
Urea	42·0	695·0	111·6
Uric acid	60·8	133·3	1,975·0
None	0·4	50·0	9·0

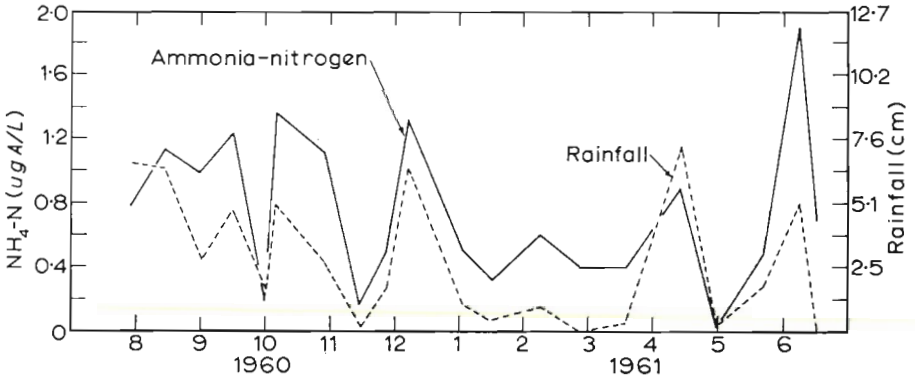


Fig. 1-45: Instantaneous values of ammonia-nitrogen (μg A/L) as related to accumulated rainfall of the preceding five days. Rainfall measured at Bermuda and ammonia-nitrogen in surface ocean water near Bermuda.(After MENZEL and SPAETH, 1962a.)

rainfall preceding each measurement. These findings have been incorporated in the diagram of the nitrogen cycle (Fig. 1-46).

The diagram illustrates the relation between the photic and aphotic zones. It is indicated that plants do not play a role in the aphotic zone; some of the more primitive algae may be of minor importance in these levels, but that remains to be

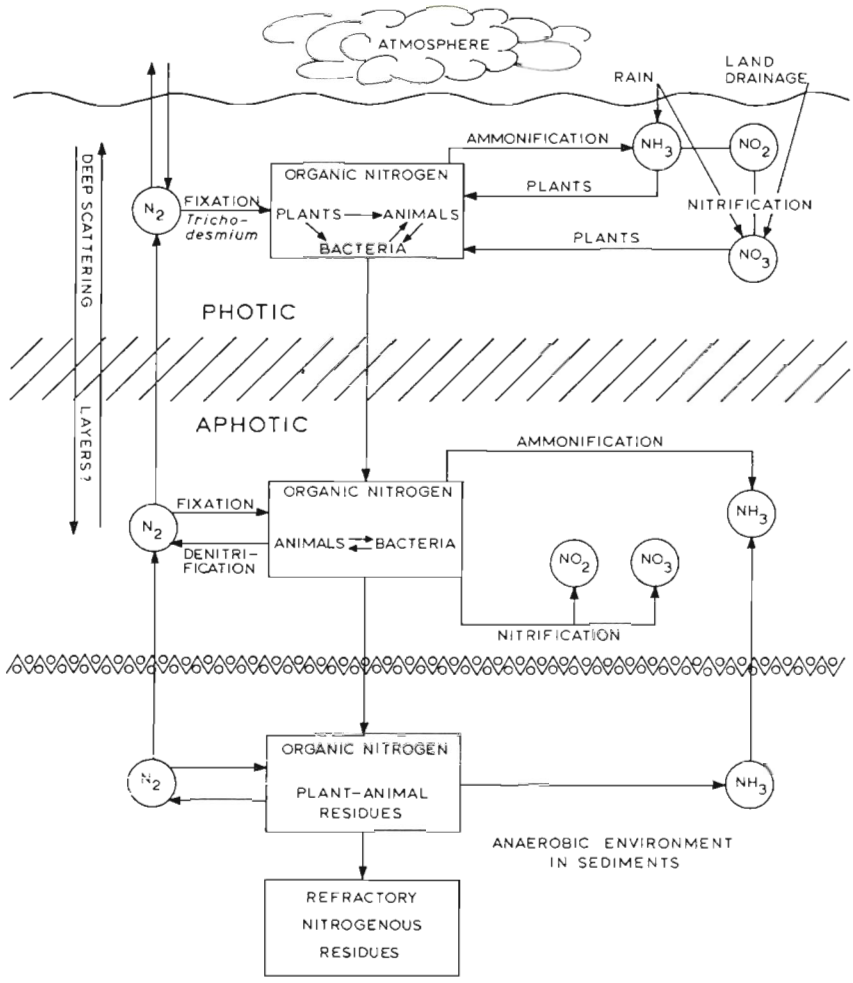


Fig. 1-46: A generalized scheme showing the sources of nitrogen and its organic circulation in the ocean. (Interpretation of data from various sources; see text.)

demonstrated. Another unknown but interesting portion of the nitrogen cycle is concerned with the magnitude of transport by those organisms migrating to the surface each night to return with their alimentary tracts filled with food organisms.

DUGDALE and GOERING (1967) completed a study on the uptake of nitrogen from various sources by using ^{15}N labelled compounds. Fig. 1-47 illustrates their concept of the circulation of nitrogen in the euphotic zone. They indicated the addition of small amounts of nitrate with precipitation as well as ammonia,

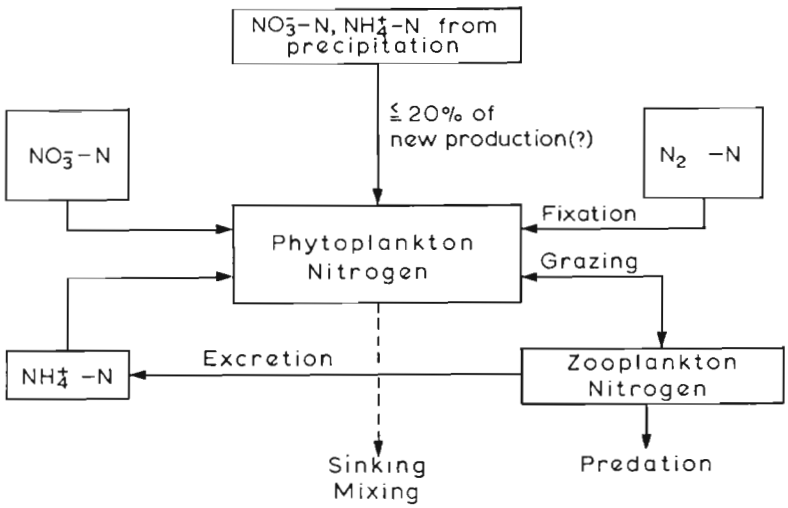


Fig. 1-47: Circulation of nitrogen in the euphotic zone. (After DUGDALE and GOERING, 1967; modified.)

although it was further indicated that this source of added nitrogen was not significant in the total picture of nitrogen utilization. The growth of *Trichodesmium* through its ability to fix nitrogen was found to be competitive with other elements of the phytoplankton using nitrate.

It appears that the study of primary production via the nitrogen route can add a new dimension to the knowledge gained from the approach of carbon fixation.

The phosphorus cycle

For 'average' sea water, the major nutrient elements occur in definite ratios, and the phytoplankton organisms utilize them in more or less definite proportions. REDFIELD and co-authors (1963) have given these figures in tabular form (Table 1-10).

Table 1-10

Availability of nutrient elements in 'average' sea water (2° C, 34·7 ‰ S) and the ratios of their availability and utilization by plankton (After REDFIELD and co-authors, 1963)

Nutrient elements and oxygen values	Availability in 'average' sea water mg atoms/m³	ratio	Utilization by plankton ratio	Ratio of availability to utilization
Phosphorus	2·3	1	1	1
Nitrogen	34·5	15	16	0·94
Carbon	2340	1017	106	9·6
Oxygen saturation values	735	320	276	1·16

It is not difficult to see why phosphorus can easily become the limiting factor and, following it, nitrogen. Unlike nitrogen, which is present in several inorganic forms as we have already seen, phosphorus occurs only as the phosphate. It is regenerated very rapidly. HAYES and PHILLIPS (1958) studied the regeneration of phosphates in a series of experiments utilizing P^{32}, mud and plants of various types and antibiotics. The materials came from freshwater lakes but the results are probably general enough to provide a basis for similar experiments with the marine biota.

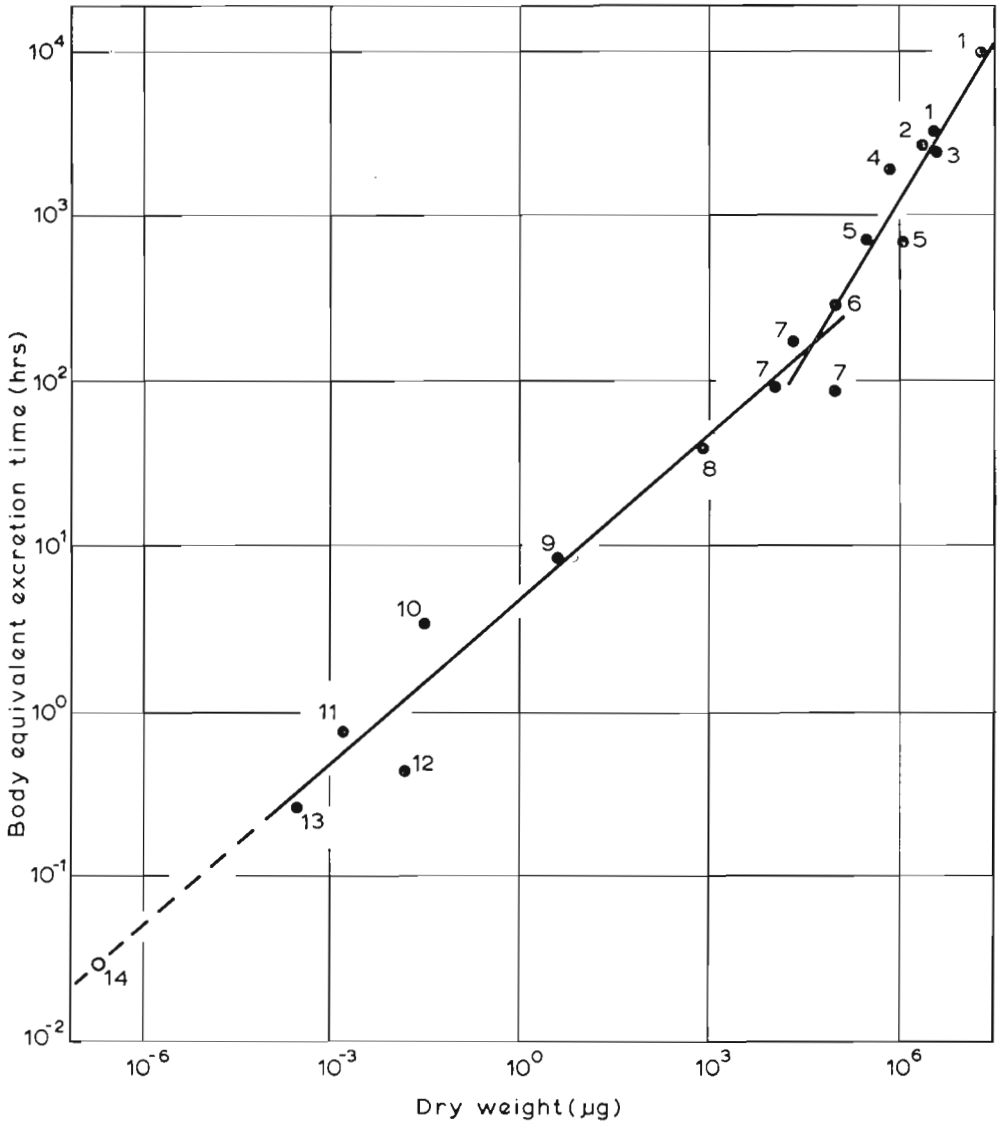


Fig. 1-48: Body equivalent excretion times (BEET) as related to dry weight of organism. BEET refers to the time required for an organism to excrete an amount of phosphorus equivalent to that contained in the body. (After JOHANNES, 1964; modified.)

The presence of antibiotics prevented the return of phosphorus to the aqueous medium even with the addition of dead plankton; in other words, autolysis alone cannot account for the return of phosphorus to the water.

JOHANNES (1964) reported on the excretion of phosphorus by a variety of organisms in terms of their body weight. He found that on the basis of body

Table 1-11

Algae in which polyphosphates have been demonstrated
(After KUHL, 1960)

CYANOPHYTA	*Spirogyra* sp.
Anabaena variabilis	*Ulothrix* sp.
Cylindrospermum licheniforme	*Zygnema* sp.
Gloeothece sp.	
Lyngbya aerugineo-coerulea	
L. amplivaginata	BACILLARIOPHYTA
Oscillatoria sp.	*Fragilaria* sp.
O. amoena	*Navicula* sp.
O. limosa	
Phormidium ambiguum	
P. frigidum	CRYPTOPHYTA
P. uncinatum	*Chilomonas* sp.
CHLOROPHYTA	RHODOPHYTA
Acetabularia mediterranea	*Ceramium* sp.
Chlorella sp.	
C. ellipsoidea	
C. pyrenoidosa	XANTHOPHYTA
C. vulgaris	*Vaucheria* sp.
Cladophora sp.	
Cosmarium sp.	
Enteromorpha sp.	EUGLENOPHYTA
Hydrodictyon reticulatum	*Euglena gracilis*
Mougeotia sp.	
Oedogonium sp.	
Rhopalocystis oleifera	CHAROPHYTA
Scenedesmus sp.	*Chara* sp.

equivalent excretion time the contribution of microzooplankton to the regeneration of phosphate may be much greater than would be indicated by the relative importance of their biomass. Fig. 1-48 shows the general relations discussed by JOHANNES.

There are indications that the response of phytoplankton organisms to phosphorus may be influenced by the ratio of magnesium to potassium (PROVASOLI and PINTNER, 1953).

Apparently, even less work has been published on specific bacteria active in the

regeneration of phosphate than is the case with the regeneration of nitrates. One would assume that there are many which will bring about the solubilization of organic phosphorus compounds in their attacks on tissue masses in general. We should look to those capable of bringing about the degradation of all of the phosphorus rich entities such as the nucleoproteins, phytins and lecithins. There must be some solubilization of the polyphosphates in the attached biota as well as the bacteria themselves as they are destroyed. The phosphates do seem to be stored in both algae and bacteria as polyphosphates (KUHL, 1960). Table 1-11 lists the algae in which polyphosphates have been demonstrated so far.

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2. LIGHT

2.0 GENERAL INTRODUCTION

N. G. JERLOV

(1) General Aspects of Underwater Daylight and Definitions of Fundamental Concepts

Radiant energy is carried by electromagnetic waves. A characteristic property of the energy is wavelength, generally given in nm (1 nm = 1 mμ = 10^{-9} m). Light is defined as the radiant energy, roughly covering the range 380 to 780 nm, which is capable of stimulating the human eye so as to produce the sensation of vision. The energy within specified wavelength intervals gives rise to typical colour sensations as illustrated in Table 2-1.

Table 2-1

Colour ranges in the light spectrum (Original)

Ultra-violet	Violet	Blue	Green	Yellow	Red	Infra-red
< 400 nm	400–420	420–480	500–560	580–600	620–780	>780

The propagation of radiant energy in a medium is always associated with attenuation due to two processes: absorption and scattering. The common definition of absorption is conversion of radiant energy into other forms of energy. Conversion takes place largely into sensible heat but also into photosynthetic energy, electronic energy leading to fluorescence, etc. Scattering, on the other hand, is an entirely different process produced by discrete particles. From a simple viewpoint it may be considered as deviation of the incident beam from rectilinear propagation. Thus the attenuation mechanism involves extinction of the radiant energy through absorption as well as change of its angular distribution through scattering.

Two fundamental quantities serve the purpose of exploring the underwater light field. The first is radiance which is defined as the energy per sec received by a surface from a certain direction. The second is irradiance which is the energy per sec falling on a surface from all directions. For routine research in the sea, measurements of the downward irradiance (the irradiance on a horizontal surface facing upwards) generally suffice to characterize the optical behaviour of the water mass.

By using physical (radiometric) concepts, the quantities of radiance and irradiance are expressed in units of watts (W) per m^2 and unit solid angle, and in watts per m^2 respectively. Both energy quantities are given per unit of wavelength or for a specified wavelength interval.

The photometric concepts, on the other hand, are psychophysical in nature. It

must be remembered that the definition of photometric quantities such as luminous intensity and illuminance is based on the spectral distribution of blackbody radiation multiplied with the photopic sensitivity of the human eye. For the marine environment there is no reason to involve the vision of man unless we deal with underwater visibility or colour of the sea. Furthermore, the underwater light from sun and sky is not blackbody radiation.

It follows that the relation between radiometric and photometric quantities is highly dependent on the spectral composition of the radiation. With zenith sun and clear sky the irradiance for the whole spectrum above the sea may be estimated at

$$100 \text{ g cal/cm}^2\text{/hr} = 1{\cdot}67 \text{ g cal/cm}^2\text{/min} = 1160 \text{ W/m}^2$$

which approximately corresponds to

$$10{,}000 \text{ foot-candles} = 107{,}600 \text{ lux}.$$

This relationship is drastically changed in the first metre of the sea where the total radiant energy from sun and sky loses half its value owing to the strong absorption of the infra-red (>780 nm). Most of the residual part is visible energy and may for the sake of simplicity be called underwater daylight.

For the photochemical processes, which are quantum phenomena, the proper characterization of light is in terms of quanta/sec/m^2/unit wavelength (λ). If the spectral distribution of underwater radiant energy is known, the corresponding quantum spectral distribution is obtained by the relation

$$1 \text{ quantum/sec} = \frac{1987}{\lambda \text{ (nm)}} \cdot 10^{-19} \text{ W}$$

However, complete spectral energy observations cannot be accomplished in routine work. For the study of photosynthesis Working Group 15 (*IAPSO, SCOR, UNESCO*) has suggested a direct measurement of the number of quanta/sec/m^2 within the range 350 to 700 nm.

(2) Measuring Light: Methods

Underwater light is conventionally measured by means of an irradiance meter provided with a selenium photovoltaic cell in a watertight enclosure. Light is collected from all directions preferably with the aid of an opal glass (collector). The simplicity of such measurements is somewhat illusory and several difficulties are involved which have not always been appreciated. In order to secure a linear relationship between light and photocurrent, the cell should be exposed to less than 1·5% of the brightest daylight, and the external load resistance should be low ($<50\Omega$) for the permissible upper light level. When the meter is lowered into the water its sensitivity is reduced by 15 to 30% due to reflection changes at the upper surface of the opal glass. Colour filters are placed between the opal glass and the cell. Attention must be paid to the bandwidth error which occurs with broad filters, and which is caused by a change in the width of the transmitted band and its position in the spectrum on account of the wavelength-selective absorption by

the water. In strong light, the narrow band interference filters can be used in combination with the photovoltaic cell.

A meter capable of recording number of quanta within the active range 350 to 700 nm has been devised at the Institute of Physical Oceanography, Copenhagen (Denmark).

(3) The Attenuation of Underwater Light

Sea water is an absorbing and scattering medium. When examining its optical properties, the action of different components will be dealt with in proper order. The water itself (without dissolved and suspended matter) exhibits a typical light-absorption effect which is little dependent on temperature. The attenuance values summarized in Table 2-2 demonstrate that pure water is most transparent to blue light (475 nm) whereas strong absorption takes place in red light; in fact water acts as a monochromator for blue light. The scattering by water, which is of molecular character, plays a relatively small part; it increases rapidly from long towards short wavelengths, being inversely proportional to the fourth power of the wavelength.

Table 2-2

Attenuance values for pure water (Original)

Wavelength (nm)	Attenuance (observed) (%/m)	Scatterance (theoretical) (%/m)
375	4·4	0·7
425	3·2	0·4
475	1·8	0·2
525	4·0	0·2
575	8·7	0·1
625	20·4	0·1
675	30·7	0·1
725	70·0	0
775	91·0	0

Among the dissolved substances, the sea salts exert only a weak influence on light, and their contribution may be ignored in the practical work. Certain dissolved decomposition products of organic matter, under the collective name of yellow substance, give rise to significant absorption which starts in the yellow and grows towards shorter wavelengths. Large quantities of yellow substance are brought to the sea by northern rivers but it is also formed in the sea, and, therefore, present in variable concentrations everywhere in the ocean.

Finally the particulate matter in the sea is responsible for absorption as well as scattering. The former process is on the average more marked for the shortwave than for the longwave end of the spectrum, whereas particle scattering is found to be virtually independent of wavelength. Important features in the scattering mechanism are that scattering is largely forward, i.e. in the direction of the

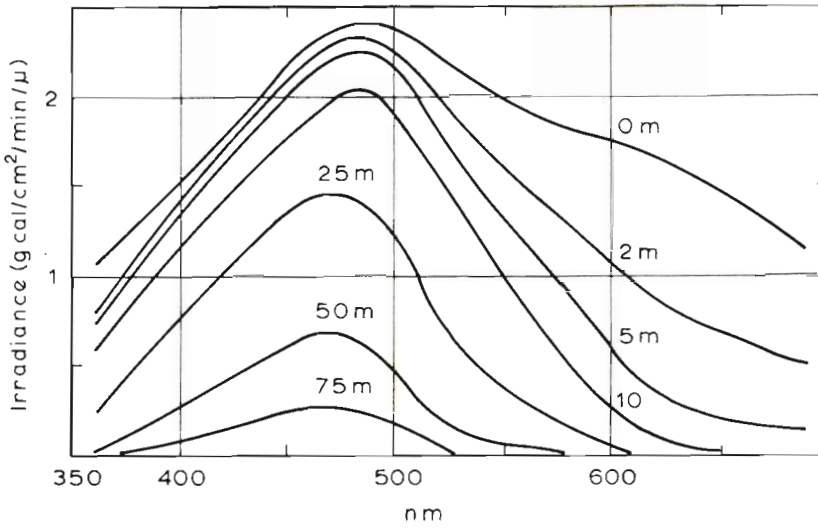

Fig. 2-1: Spectral energy distribution of downward irradiance at different depths in the east Mediterranean Sea. (Original.)

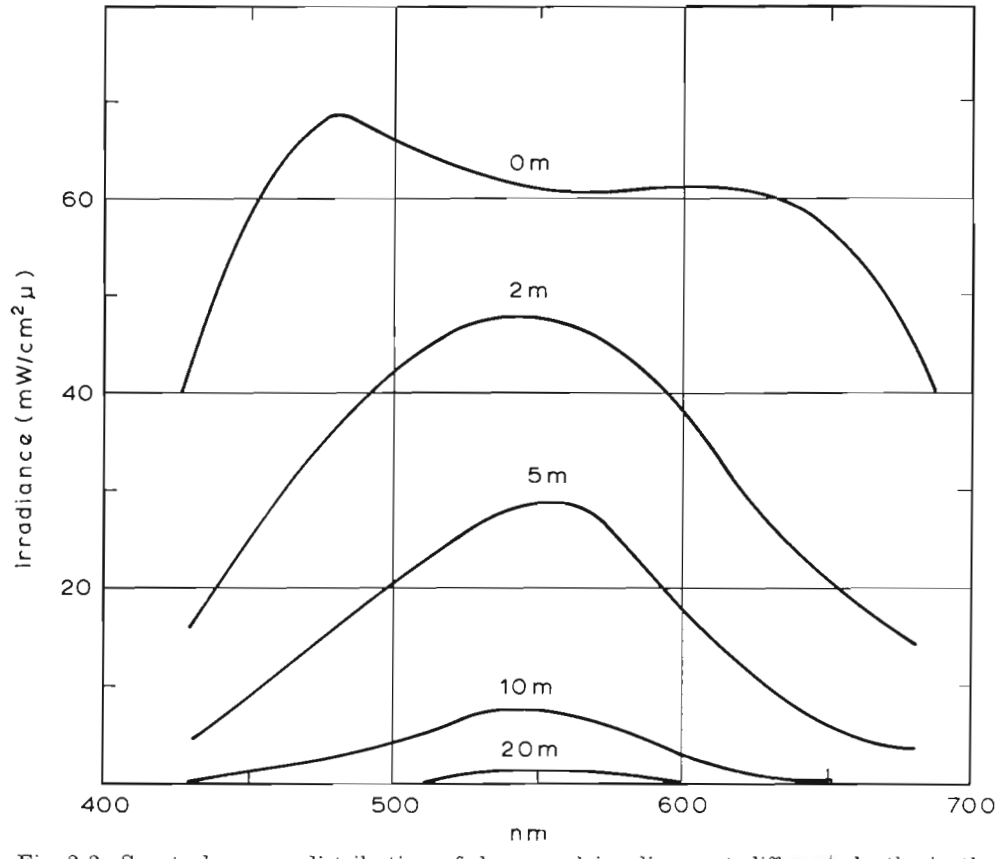

Fig. 2-2: Spectral energy distribution of downward irradiance at different depths in the northern Baltic Sea. (Original.)

propagating beam, and that the angular distribution of scattering shows relatively small variations from one oceanic area to another.

The attenuation of downward irradiance is determined by the behaviour of these different components. Spectral distribution curves for clear ocean water (Fig. 2-1) are peaked in blue light (470 nm) and the ultra-violet (u.v.) is fairly strong even at great depths. An entirely different picture is presented in Fig. 2-2 for the northern Baltic Sea. The wavelength-selective absorption by particulate matter and yellow substance, abundant in this water, leads to a shift of maximum transmittance towards 550 nm; the ultra-violet is rapidly extinguished in the surface stratum. These two extreme cases demonstrate the existence of a large span in optical properties of the sea.

(4) The Angular Distribution of Underwater Light

The reflection of sunlight from the sea surface is essentially a function of solar altitude. At high altitudes the reflectance of total light (sun + sky) from a horizontal sea surface is only about 3%; it becomes higher at low altitudes—for instance, theoretically 27% at 10° altitude—but this effect is strongly reduced due to wave action.

The refraction which takes place at the surface also modifies the distribution of the underwater light. For an angle of incidence of 90°, when the sun is at the horizon, the angle of refraction will be 48·6°. Therefore, the whole hemisphere of skylight is compressed in the water within a cone of apex angle $2 \times 48{\cdot}6°$. This is illustrated in Fig. 2-3 which also shows that underwater rays of obliquity $> 48{\cdot}6°$ are totally reflected at the underneath side of the sea surface. As a consequence, a considerable part of scattered light travelling upwards does not escape through the surface.

The light field in the sea is composed of direct sunlight, skylight, and light scattered chiefly from particles. On account of the reflection and refraction

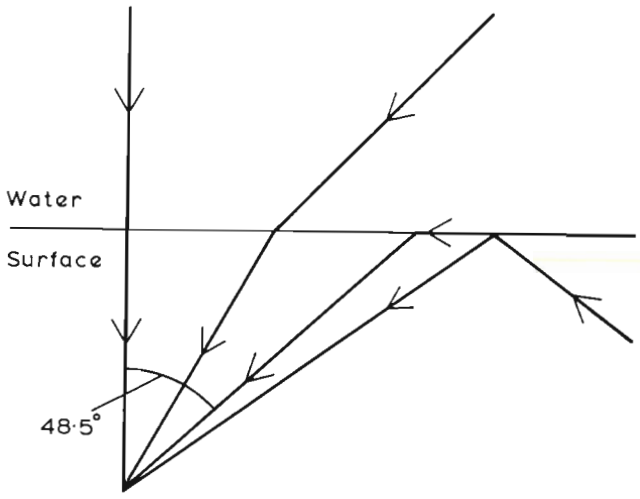

Fig. 2-3: Refraction at the sea surface. (Original.)

processes at the surface the radiance distribution has a rather complex structure in the uppermost layers. The most characteristic features are the strong dominance of radiance in the direction of refracted sun rays and the distinct reduction of radiance at the edge of the skylight cone (48·6°).

With increasing depth the light field alters its character into a less directed distribution and an approach of the direction of maximum radiance towards zenith gradually takes place. The final result of this transformation is an asymptotic radiance distribution which is symmetrical around the vertical (Fig. 2-4). This shape is independent of the surface lighting conditions and of the state of the sea surface; it depends only on the inherent optical properties of the water. Fig. 2-4 exhibits that near-asymptotic distributions are encountered at 400 m (blue light) in the Sargasso Sea and at 100 m (green light) in the Baltic Sea.

Another fundamental aspect of underwater light is its polarization. The pattern of polarization is dependent on the sun's position in the sky, as the degree of

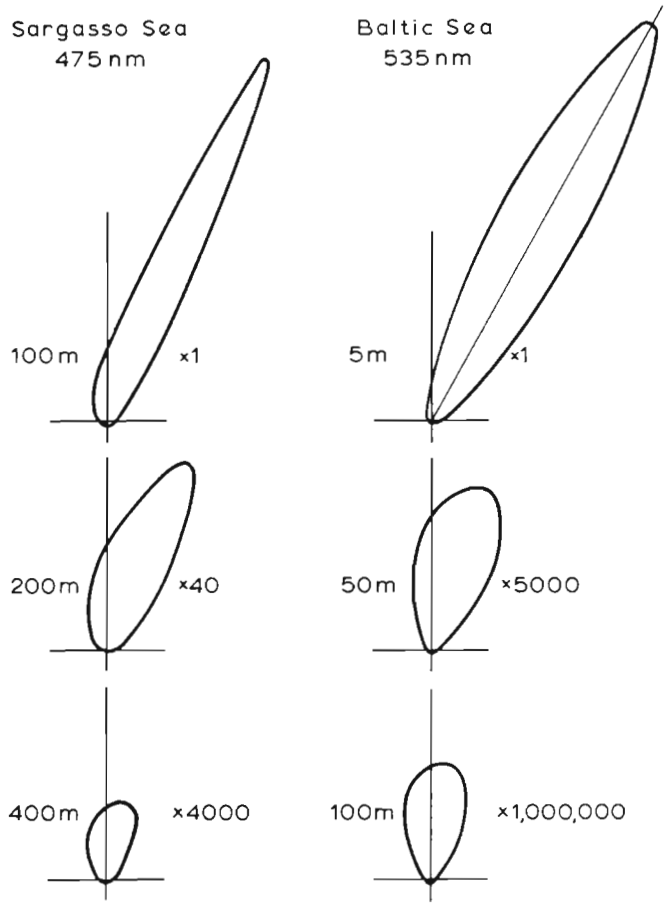

Fig. 2-4: Polar diagrams for Sargasso Sea and northern Baltic Sea showing the transformation of the radiance distribution with increase of depth to a final state which is symmetrical around the vertical. (Original.)

polarization is maximum in those lines of sight at about right angles to the direction of maximum radiance. Polarization is effected largely by particle scattering and by scattering of the water itself; in the upper layers linearly polarized skylight is also involved. The degree of polarization is most pronounced for light of high directionality, that is, for a clear blue sky, for shallow and clear water, and for the wavelength of least penetration. Since directionality of the light field persists down to infinite depths, polarization is a permanent property of underwater light.

(5) Regional Distribution of Optical Water Types

A systematic description of the penetration of light in different oceanic areas requires a classification in optical water types. Such a classification exists in terms of transmittance of downward irradiance in the upper layers and for high solar altitudes. Transmittance is here defined as the percentage left after the light has passed one metre. Fig. 2-5 presents three basic oceanic types, I, II, and III as well

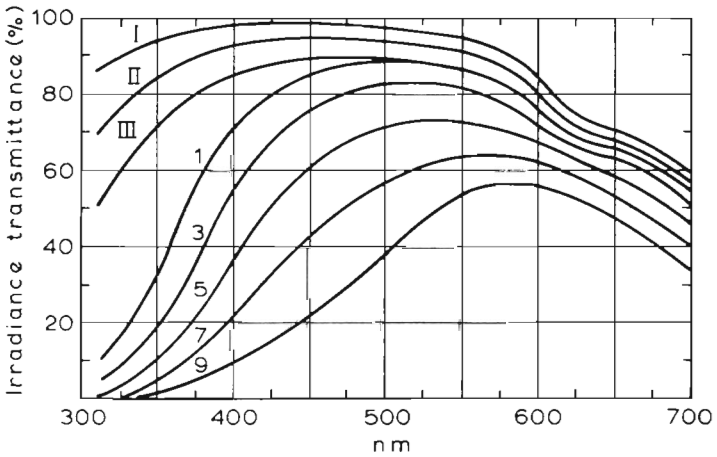

Fig. 2-5: Spectral transmittance (%/m) of downward irradiance for high solar altitudes in the upper layers of oceanic water types I, II, and III; and of coastal types 1, 3, 5, 7, and 9. (Original.)

as five coastal types 1, 3, 5, 7, and 9 representing areas off Scandinavia and northwestern USA. The trend of the two groups of curves indicates that decrease in transmittance from one type to the next is most marked for the shortwave light due to the wavelength-selective absorption by particles and yellow substance. In particular we notice the low transparency of coastal waters to the ultra-violet. It follows that reduction of transmittance is associated with a shift of maximum transmittance from blue, in the clearest waters, over green to brown in the most turbid waters. This is consistent with the behaviour of irradiance evidenced in Figs 2-1 and 2-2.

Another family of curves (Fig. 2-6) represents downward irradiance in the photosynthetic range 350 to 700 nm as a function of depth for the defined water types. Irradiance is here given in a logarithmic scale as percentage of the surface value.

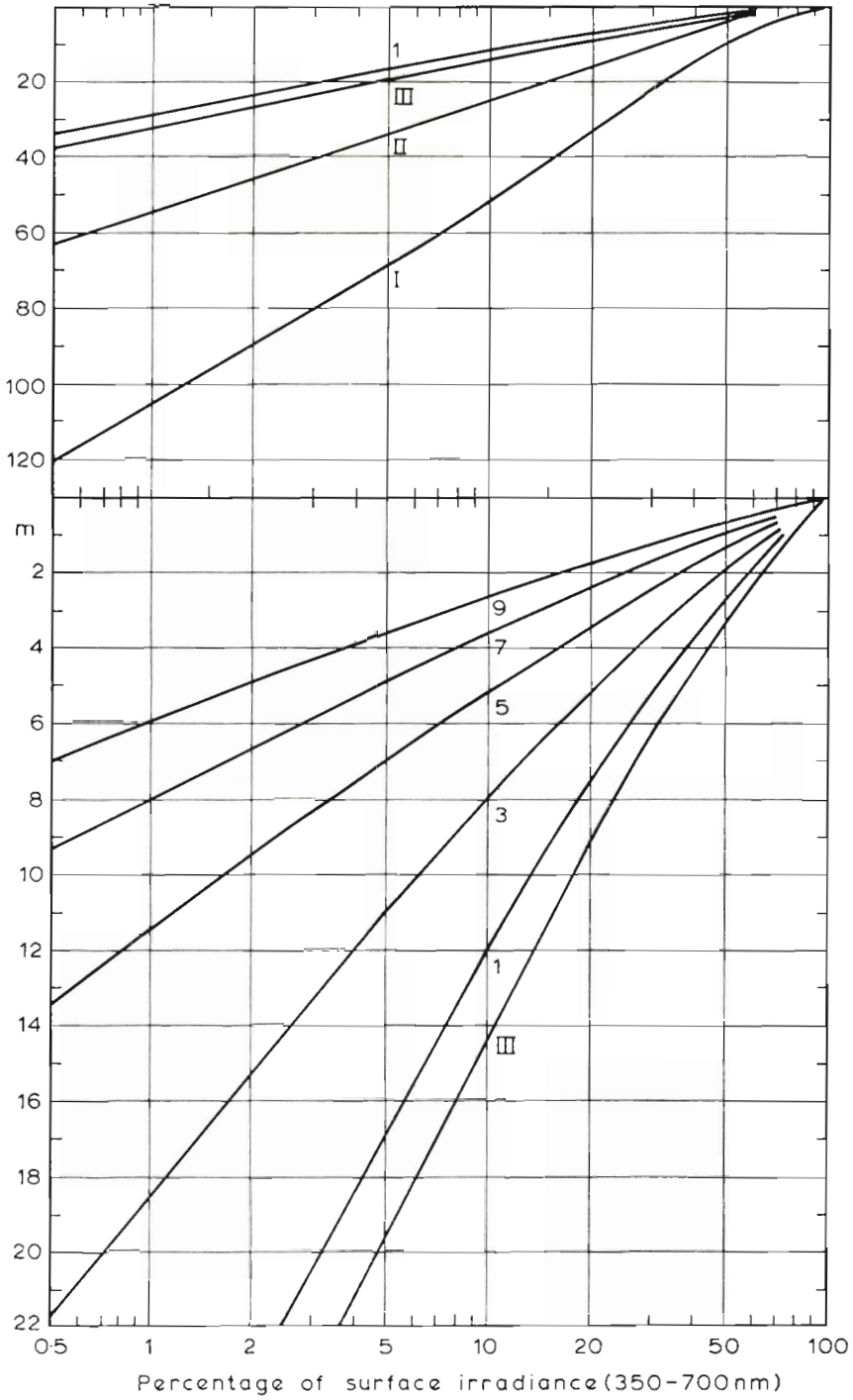

Fig. 2-6: Percentage of surface downward irradiance (350 to 700 nm) in a semi-logarithmic scale as a function of depth (m) in defined water types. (Original.)

2. LIGHT

2.1 BACTERIA, FUNGI AND BLUE-GREEN ALGAE

W. GUNKEL

(1) Introduction

Light is a basic prerequisite for life on earth. It furnishes the energy required for CO_2 fixation by plants and hence for synthesis of organic matter. The latter becomes available as a source of energy and carbon for bacteria and fungi either directly or after transformation by animals. Except for blue-green algae and some exceptionally specialized bacteria—such as purple bacteria and chemo-autotrophic forms—most micro-organisms are heterotrophic. The relation between micro-organisms and light is, therefore, to a large extent an indirect one.

Light is defined as that portion of the electromagnetic spectrum which is capable of stimulating the photoreceptors of the human eye (Chapter 2.0). The range thus delimited is conventionally considered to lie between 380 mμ and 780 mμ; however, this range is too narrow for the purposes of the marine ecologist concerned with micro-organisms, since portions of the solar spectrum interpreted as 'darkness' by the human eye may exert important photochemical effects on micro-organisms (STANIER and COHEN-BAZIRE, 1957). Furthermore, as GRIFFIN and co-authors (1947) discovered, the human eye can perceive light of wavelengths as long as 1150 mμ, provided that the stimulus is of sufficient intensity.

Wavelengths shorter than 270 mμ do not reach the earth's surface. However, these wavelengths are of considerable interest, since they comprise the absorption maximum of DNA, and hence are especially effective both as mutagenic and killing agents. We are better informed about the effects of these wavelengths on micro-organisms than about the effects of infra-red, visible light and ultra-violet (u.v.) of longer wavelengths. Also the so-called reactivation, the prevention of the manifestation of ultra-violet lesions by blue light, which is of considerable interest to the geneticist and molecular biologist, cannot be discussed here in detail. A comprehensive introduction to the importance of light in the natural environment, light absorption in different types of waters, distribution of radiation energy, as well as definitions and terms, has been published by STRICKLAND (1958).

Unfortunately, the units of light energy used by different authors are not consistent and the characterization of the light source employed is frequently insufficient. Doses are expressed in lux, calories, foot-candles, metre-candles, langleys, and often only in terms of radiation source distances. Different lamps with different spectra have been used even in parallel experimental series, and the doses expressed in lux. In experiments employing natural sunlight as an energy source, frequently only the time of exposure is given. There is great need for universal agreement on technical procedures and standardization of light units.

Considerable knowledge is available on the photobiology of micro-organisms. However, in spite of the many papers, reviews and books published, there is little

information which pertains directly to the topic of the present chapter. In order to present a sufficiently complete picture of the present status of our knowledge on the importance of light as an environmental factor in oceans and coastal waters, it proved necessary to include some investigations conducted in freshwater habitats and laboratory experiments on bacteria of neither marine nor limnic origin. In this chapter no attempt has been made to report extensively on the influence of visible light and ultra-violet light on the physiology and genetics of certain test strains of micro-organisms studied in laboratory experiments; readers interested in these problems are referred to SIMONIS (1956), RUHLAND (1961), SELIGER and MCELROY (1965), HARRISON (1967), and others.

High doses of light may damage or even kill micro-organisms. We are still far from understanding the effects of light as a killing agent for micro-organisms in the natural environment, in spite of the fact that numerous observations and experiments have been made to solve this problem. Due to the different methods employed, differing results have been obtained. A major problem presents the question as to what extent results obtained in laboratory experiments can be extended to interpret the situation in the sea.

In bacteria a special difficulty is caused by the fact that the capacity for multiplication, e.g. 'colony' formation, is used as a criterion of survival. Consequently, a bacterium which is fully alive but with critically reduced capacities for reproduction is considered dead. The bacteriologist has, so far, only worked with populations since it is not yet possible (or at least very difficult) to assess the responses of single individuals. Microbiological methods and techniques concentrate on the supra-individual (population) and sub individual (intracellular mechanisms of enzyme activities, protein syntheses, etc.) levels rather than on the individual level. Hence, reproduction in bacteria is considered as 'growth'.

Except for the paper by GOLDSTEIN (1963) there is hardly anything known about responses to light in marine fungi. The various physiological investigations concerned with responses to light in terrestial fungi, e.g. *Pilobolus kleinii* and *Phycomyces blakesleanus*, and the numerous investigations on phytopathogenic fungi, e.g. on light effects on the germination of fungal spores, are hardly pertinent to the concept of the present chapter. The influence of light upon the growth of fungal mycelia has been documented in many papers. However, the results obtained are not yet conclusive; there is considerable variation in the responses of different species, and even closely related species may react quite differently under identical culture conditions. The pertinent information has recently been discussed by MOHR (1961b); his review contains some 1000 references.

Sunlight. The light reaching the earth from the sun changes its composition and intensity as a function of season, daytime, latitude, cloudiness and altitude. In addition, the extent of sunlight absorption by the atmosphere changes. These changes are fundamental especially in regard to the ultra-violet portion of the sunlight which is biologically the most effective one.

Artificial light sources. Artificial light differs in its spectral composition from sunlight. Its spectral composition is mostly different in different light sources. Many artificial light sources do not have a continuous spectrum. Some authors have used combinations of different light sources; for this reason it is impossible to compare lux measurements of sunlight with lux measurements of artificial light.

(2) Functional Responses

(a) *Tolerance*

In order to assess tolerances of bacteria, fungi and blue-green algae to different light intensities a number of different approaches and techniques have been employed. It is necessary, therefore, to consider the results reported on the basis of the specific methodological procedure used.

Tolerances of micro-organisms to light have been tested in artificial liquid media, in samples of habitat water or in more or less solid media. The density of the cells during illumination was often different and so was the duration of light exposure. Some authors tested tolerances to light of populations contained in freshly sampled sea water, others of pure cultures, still others of cultures in media strongly enriched with various nutritives. In some cases the test populations were in the same growth phase, in others light tolerances have been determined in populations representing different growth phases. During long-term experiments lethal light effects can be masked by the multiplication of a few single resistant individuals which remain unharmed by light intensities not tolerated by the normal representatives of the test population. These few examples may suffice to illustrate the need for more consistent techniques in regard to the determination of micro-organismic tolerances to light.

Tolerance in the sea

Harmful effects of sunlight upon marine bacteria have been assumed to exist for a long time. This assumption was based on observations regarding the occurrence of bacteria in the sea. The older pertinent literature has been reviewed by ZOBELL (1946); FISCHER (1894) found more bacteria in the surface water of the North Atlantic at sunrise than in the afternoon. SCHMIDT-NIELSEN (1901) recorded 26 bacteria per ml near the sea surface and 420 per ml at a depth of 25 m. Both FISCHER and SCHMIDT-NIELSEN attributed these differences to the lethal effects of sunlight.

Several authors interpret the reciprocal quantitative relation between seasonal fluctuations in incident-light intensities and bacterial numbers in terms of the harmful effects of light. Thus GAARDER and SPÄRCK (1931) ascribed the paucity of bacteria in Norwegian oyster pools during summer to detrimental light effects. Similar interpretations have been put forward by MINDER (1920) and ZIH (1932) in regard to bacterial numbers obtained in lakes of Switzerland. ULKEN (1963) compared bacterial numbers found in the lower part of the river Elbe (Germany) to the incident light measured during two subsequent years and came to the conclusion that changes in both light intensity and spectral composition (higher percentage of ultra-violet light during summer) may contribute to fluctuations in bacterial numbers. On the other hand, KRISS (1961) determined the number of bacteria during noon and afternoon in the Black Sea, and found that at many stations the highest numbers were near the surface and gradually decreased with depth, indicating that light does not appreciably damage micro-organisms near the water surface.

It seems that the conclusion of ZOBELL (1946, p. 70) still stands:

'While it has been amply confirmed in nearly all parts of the world that there is often an apparent negative correlation between the abundance of bacteria in water and the intensity of light, there are no data which prove that the bactericidal action of sunlight is directly responsible for the diurnal, seasonal or vertical distribution of bacteria in either the ocean or large lakes.'

Practically nothing is known about light tolerances *in situ* in regard to marine fungi. Lethal light effects on blue-green algae have hardly been studied *in situ*. They are intimately related to the photophysiology of plants, and briefly touched upon in Chapter 2.2. Observations in the sea cannot provide conclusive data on the tolerances of bacteria, fungi and blue-green algae to light conditions. The degree of tolerance to specified qualities and quantities of light can be determined properly only in experiments under controlled environmental conditions, excluding interfering indirect effects of other concomitant environmental entities.

Tolerance experiments on natural populations

ZOBELL (1946) exposed bacteria present in freshly sampled sea water to direct midsummer sunlight at La Jolla, California, and kept aliquots in the dark. The temperature of the water was maintained at 25° to 26° C. After 2 hrs (11.00 am to 1.00 pm) samples were taken and the numbers of bacteria determined. The results demonstrate that sunlight does have a lethal effect on bacteria suspended in shallow layers of sea water (Table 2-3), but not in depths exceeding 20 cm. Even after light exposure lasting from sunrise to sunset, only a limited percentage of bacteria was killed (ZOBELL and MCEWEN, 1935).

Table 2-3

Average number of bacteria per ml of sea water (open battery jars) as a function of water depth and light intensity (After ZOBELL, 1946; modified)

Water depth (mm)	Number of bacteria per ml of sea water: at beginning of experiment	after 2 hrs in the dark	after 2 hrs of sunlight exposure	Percentage decrease attributable to the effect of sunlight
2	171	164	76	48·7
5	169	159	108	32·0
10	168	163	126	22·7
10	240	228	184	19·3
20	203	188	165	12·2
35	241	216	198	8·7

REYNOLDS (1965) introduced the intestinal bacterium *Escherichia coli* into concrete tanks containing more than 12 m³ of sea water by adding small amounts of sewage. Unfortunately, he did not determine the original bacterial population of the sea water used. In a series of consecutive samples he found that (i) the number of *E. coli* decreased, as would have been expected, with time, (ii) the rate of decrease was more pronounced during sun illumination than during the dark

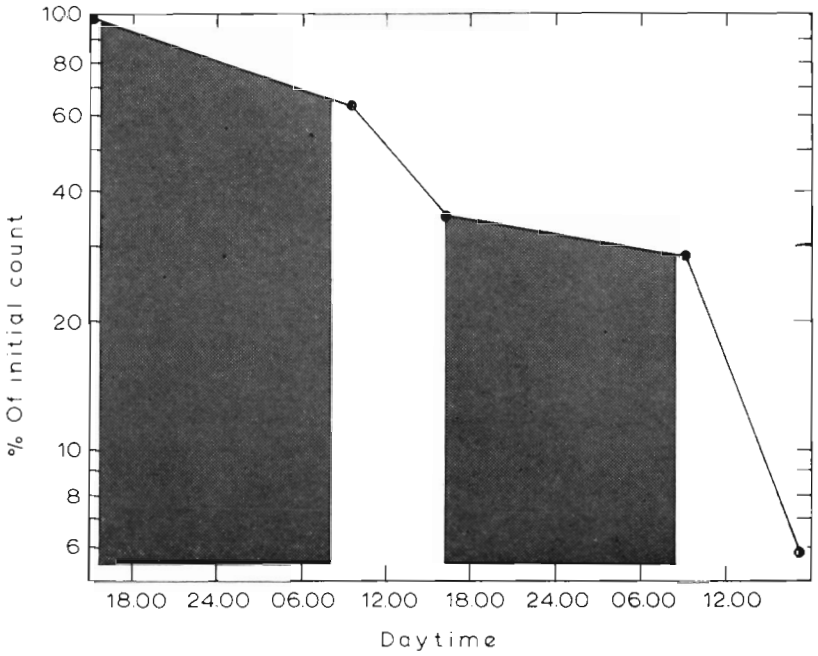

Fig. 2-7: Tolerance of intestinal bacteria *Escherichia coli* to changes in natural diurnal light intensity expressed as percentages of the initial count. Semilogarithmic scale. Dark areas represent periods without sunlight. The experiment was conducted in Conway, Caernarvonshire, Great Britain at a water temperature of 3° C. (After REYNOLDS, 1965; modified.)

periods. The results of a typical experiment are represented in Fig. 2-7. In a similar experiment, REYNOLDS recorded the decrease of *E. coli* numbers during a sunny afternoon for 5 hrs. He filled glass bottles with a mixture of sea water and sewage. Half of these bottles were painted black in order to prevent the sunlight from entering. All bottles were then submerged just below the water surface of the concrete tank. The subsequent decrease in *E. coli* numbers was smallest in the black bottles, larger in the tank water itself and largest in the transparent bottles. While these results reveal a pronounced reduction in bacterial numbers as a function of sunlight, the experimental conditions do not allow a more detailed analysis. Incident illumination was not measured and the population dynamics of the natural bacterial populations of the sea water used not considered. *E. coli* is a stranger in the marine environment. At least part of the decreases observed could have been caused by indirect effects, e.g. competition with endemic marine bacteria or algal excretes with photodynamic properties (SIEBURTH, 1965). Such possibilities were not excluded in REYNOLDS's experiments. No comparable experiments on fungi and blue-green algae have come to the reviewer's attention.

Tolerance experiments on pure cultures of bacteria

Quantitative aspects. Experimental results obtained with pure cultures of bacteria depend very much on the method used; it is necessary, therefore, to refer in all cases to methodological details.

SWART-FRÜCHTBAUER (1957) inoculated the surface of nutrient agar medium

with pure cultures of bacteria and determined the number of colonies which developed in illuminated and non-illuminated areas of the same petri dish. The criterion used to determine light tolerance was the capability of the tested cells to reproduce under the conditions offered. The experiments were conducted at noon in April in Göttingen (Germany) using the unfiltered light of the sun as illumination source. The results (percentage of survival) are presented in Tables 2-4 and 2-5. From the results presented it is obvious that light reduces the number of bacteria capable of forming a colony.

Table 2-4

Percentages of survival of two bacterial strains after different times of exposure to unfiltered sunlight (After SWART-FRÜCHTBAUER, 1957)

Exposure time (hrs)	*Serratia marcescens*	*Sarcina lutea*
1–1·5	56·7	67·2
2·5–4	40·9	33·2

Table 2-5

Percentages of survival of rods and cocci after different times of exposure to unfiltered sunlight (After SWART-FRÜCHTBAUER, 1957)

Exposure time (hrs)	Rods (average of 20 different strains)	Cocci (average of 17 different strains)
1	71·7	70·8
2	62·8	40·2
3	53·8	24·0

In spite of differences regarding method, tested bacteria species, latitude and time of the year, these values correspond well to the survival rates found by ZOBELL (1946); see also Table 2-3.

MÜLLER and SCHICHT (1965) conducted a number of experiments in regard to the photosensitivity of pure cultures of bacteria. As light source they mainly used a mercury pressure lamp HBO 500. The light intensity obtained with this lamp in their experimental design was $2{\cdot}8 \times 10^5$ erg/cm^2. The lamp emits a radiation from 280 to 900 mμ with a maximum at 400 to 500 mμ. MÜLLER and SCHICHT did not use quartz optic, therefore, only wavelengths greater than 300 mμ reached the bacteria. As 'critical doses' they selected the dose necessary to prevent all growth, i.e. multiplication at a densely inoculated agar surface. The tolerances of the individual strains tested differed considerably. Examples are presented in Table 2-6. The strains Hid. 38 and Hid. 5 were isolated from material obtained

Table 2-6

Illumination dose (mercury lamp) necessary to prevent growth of different pure cultures of bacteria (After MÜLLER and SCHICHT, 1965)

Bacterial species	Dose (W/cm²)
Serratia marcescens	85·9
Serratia marcescens (white mutant)	67·7
Bacillus mycoides	28·3
Pseudomonas aeruginosa	28·3
Sarcina urea	22·8
Pseudomonas sp. (strain Hid. 38)	21·2
Gram negative rod (strain Hid. 5)	16·0

at Hiddensee, Baltic Sea, at a local salinity of about 8 ‰. In interpreting the results one must keep in mind that the original number of cells inoculated influences the 'critical doses' in two ways: (i) If the original cell density is very high there is a 'covering effect'; the bacteria in the lower cell layers are somewhat protected against damaging effects of the light by the cells above them. (ii) Since the doses necessary to prevent growth (reproduction) were chosen as criterion to assess light damage, the results depend on the initial cell numbers.

Table 2-7

Degree of dilution of suspensions of the bacteria *Nitrobacter winogradskyi* and *Nitrosomonas europaea* at which they are still capable of exhibiting oxidizing properties (After BOCK, 1965)

Species	Suspensions kept in the dark	Illumination with light of 54,000 lux for 6 hrs	24 hrs
Nitrobacter winogradskyi	1:10,000,000	1:10,000	1:1
Nitrosomonas europaea	1:10,000,000	1:10,000,000	1:10

Some experiments on tolerances to light have been performed on the bacteria *Nitrosomonas europaea* and *Nitrobacter winogradskyi* by BOCK (1965). He tested the degree of dilution of untreated and illuminated suspensions—originally of the same cell density—still capable of conducting oxidations. According to Table 2-7, 6 hrs of illumination with 54,000 lux (light source: a combination of electric bulbs and one 1000 W mercury high pressure lamp) are tolerated by 10% of the *N. europaea* cells but by only 0·1% of the *N. winogradskyi* cells. The higher tolerance of *N. europaea* is consistent with the fact that a 5 hr exposure to 31,000 lux reduces the NH_4 oxidation of *N. europaea* by 10%, while the nitrite oxidation of *N. winogradskyi* is reduced by 43%.

Qualitative aspects. The effects of ultra-violet and visible light strikingly depend on wavelength. If light exposures required to produce the same result are compared for different wavelengths, the range around 265 mμ is found to be by far the most effective.

THIMANN (1955) has compiled the pertinent information published by various authors. He points out that the energy required to inactivate 90% of a bacterial population employing a wavelength of 254 mμ varies from 11,000 to 197,000 erg/cm² for different bacterial species (average: about 40,000 erg/cm²). A 30 W low-pressure mercury vapour lamp emits about 800 erg/cm²/sec measured at a distance of 1 m; since most of this energy has a wavelength of 254 mμ, an exposure of 1 or 2 mins should suffice to kill the vast majority of vegetative bacterial cells. At longer wavelengths of 350 to 450 mμ almost a million times as much energy is needed. The damaging effect of the light decreases further from 400 mμ (blue) to 700 mμ (red). The general tendency of decreasing light damage with increasing wavelength is exemplified in Fig. 2-8.

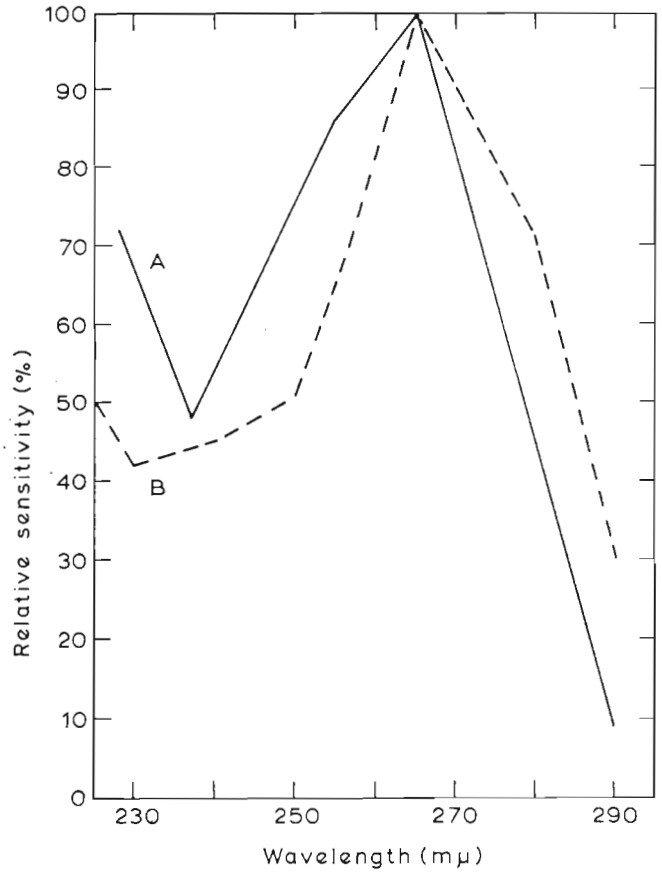

Fig. 2-8: Relative sensitivity of micro-organisms to ultra-violet light of different wavelengths. A: bacteria *Escherichia coli*; B: fungal spores. (After THIMANN, 1955; modified.)

The minimum tolerance occurs, according to Fig. 2-8, near 265 mμ. The pronounced damaging effects of this wavelength gain considerable scientific and practical importance in view of the fact that it coincides with the absorption peak of nucleic acids near 260 mμ. This wavelength is frequently used in science for inducing artificial mutations and, in practice, for sterilization (in hospital rooms and food and beverage packing rooms, for example).

Although bacteria exhibit a significantly higher tolerance to light of longer wavelengths, such light may still possess a definite killing potential. Since protein and DNA do not absorb visible light, other cell components must be damaged.

Reference to two experiments may suffice to exemplify the detrimental effects of longer wavelengths. In the first experiment, conducted by SWART-FRÜCHTBAUER and RIPPEL-BALDES (1951), natural sunlight was used as the illumination source

Table 2-8

Light tolerance of the bacterium *Serratia marcescens*
(After SWART-FRÜCHTBAUER and RIPPEL-BALDES, 1951)

Filters	Wavelength in mμ									Survivors
	281	302	313	334	366	405	436	480	509	(%)
WG 5	—	0·23	0·68	0·96	1·00	1·00	1·00	1·00	1·00	4
BG 12	—	—	0·02	0·39	0·75	0·86	0·85	0·48	0·12	42
UG 2	0·01	0·27	0·50	0·80	0·84	0·02	—	—	—	50
GG 13	—	—	—	—	0·20	0·92	0·98	0·99	0·99	66
BG 18	—	—	—	0·22	0·54	0·70	0·79	0·92	0·93	70
GG II	—	—	—	—	—	—	0·01	0·24	0·97	83
OG I	—	—	—	—	—	—	—	—	0·01	100

Of the sunlight used as light source, seven glass filters (left column) cut off different spectral portions. For each filter transmission values are presented for nine characteristic wavelengths; transmission values are expressed as percentages of incident light (= 1)

and a pure culture of the bacterium *Serratia marcescens* (syn.: *Bacterium prodigiosum*) as the test organism. Different wavelengths were filtered out by applying seven different glass filters (Schott & Genossen). The results are summarized in Table 2-8; they reveal that light tolerance (percentage of survivors) of *Serratia marcescens* increases with increasing wavelength. In the second experiment, performed by MÜLLER and SCHICHT (1965), the mercury high pressure lamp HBO 500 served as the light source, and seven pure cultures of different bacteria as the test organisms. Again, glass filters (Schott & Genossen) were used to filter out defined ranges of wavelengths. The filters BG12, UG5 and UG1 eliminate increasing portions of longwave sections of the total spectrum and lead to a reduction in light tolerance in all seven test organisms (Fig. 2-9) as shown by the decreasing total energy required to limit growth (reproduction). The sequence of the different strains is practically the same whether the total spectrum is used or different spectral portions are eliminated by glass filters. The transmission data of the filters are published, for example, in *Handbook of Chemistry and Physics* (see WEAST, 1966–1967.)

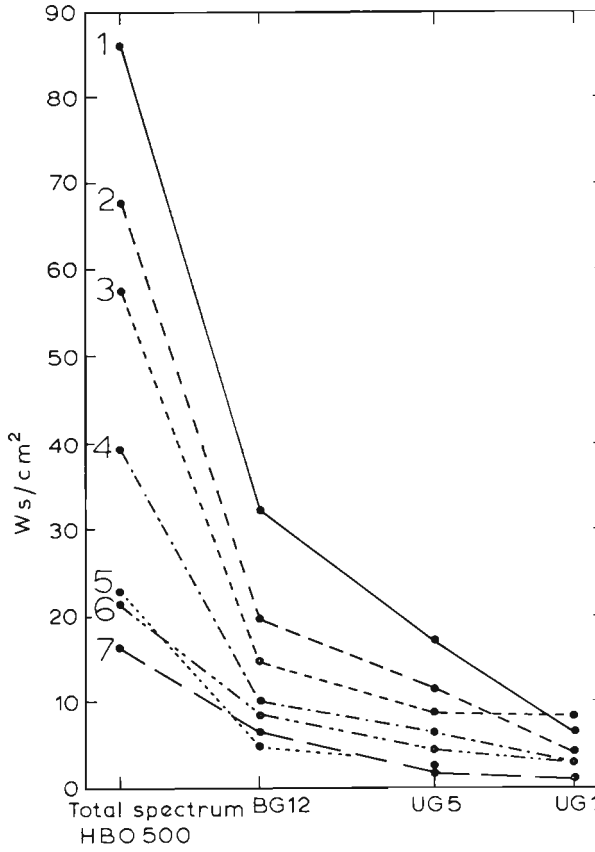

Fig. 2-9: Light tolerance of 7 pure cultures of different bacteria (1–7). Ordinate: Energy (Watt sec/cm²) necessary for total inhibition of population growth. Abscissa: Total spectrum of the mercury high pressure lamp HBO 500 and successive elimination of longwave fractions by Schott filters BG12, UG5, UG1. (After MÜLLER and SCHICHT, 1965; modified.)

Tolerance as a function of pigmentation, cell size and physiological condition

Several publications report that a considerable number of bacterial strains isolated from sea water contain pigments. For example, ZOBELL and FELTHAM (1934) found among several thousand colonies 69·4% with pigments. Of these, 31·3% contained a yellowish pigment, 15·2% an orange, 9·9% a brownish, 5·4% a red or pink, and 0·2% a green pigment; 7·4% possessed fluorescent colours. Occasionally, blue, black or silver shining colonies were found using special culture media. IMSENECKI (1946; *in*: SWART-FRÜCHTBAUER, 1957) reported faster killing of unpigmented bacteria sprayed into the air and radiated compared to pigmented ones. SWART-FRÜCHTBAUER (1951) gives examples for the occurrence of pigmented bacteria in different environments (Table 2-9) and expresses the opinion that under natural conditions there is a higher killing rate among unpigmented bacteria in the air (and consequently a percentage increase in the number of pigmented ones which may fall down into the oligotrophic lake). In

the eutrophic lake, on the other hand, there are such intensive microbial processes, together with a strong multiplication of autochtoneous bacteria, that those transported by the air into the lake do not play a significant role. The absolute numbers of bacteria are several orders of magnitude higher in the eutrophic lake than in the oligotrophic lake.

MÜLLER and SCHICHT (1965) found distinct differences in white and red strains of one bacterial species. Pigments absorb light within the visible portion of the spectrum and normally have absorption maxima in the shortwave range. According to SWART-FRÜCHTBAUER (1951), yellow-coloured bacteria, which absorb blue light and ultra-violet parts of the spectrum, exhibit a high light tolerance. The spectral portions absorbed by the yellow pigments can no longer damage vital structures and hence have a protective function. Bacteria with pink and orange pigments are less tolerant. The lowest tolerances are found among bacteria with greenish or no pigments.

The information presented above would seem to suggest relationships between

Table 2-9

Pigmented bacteria in different environments expressed as percentages of total numbers isolated (After SWART-FRÜCHTBAUER, 1951)

Environment	Pigmented bacteria (%)
Air	47
Oligotrophic fresh water	40
Eutrophic fresh water	12
Soil	16
Lake sediment	7

pigmentation and preferred depths of bacteria in the sea. However, such possible relationships have not yet been investigated.

According to SWART-FRÜCHTBAUER (1957) yeasts with identical pigmentation but different cell size can exhibit rather different light tolerances. Strains with larger cells are more resistant. The same relation between light tolerance and cell size was found in bacteria; in different species of the genus *Sarcina* for example, the biggest cells proved to be most light tolerant. Species of bacteria belonging to the family Micrococcaceae, especially of the genus *Micrococcus*, form cell aggregates which can be separated by employing ultrasonic techniques. Separated, individual cells are significantly less tolerant to light than undisturbed aggregates. Presumably, peripheral cells in the aggregation protect the more centrally located ones ('covering effect'). Analogue light-protecting effects may also play a role in regard to the increased light tolerance of larger single cells.

In general, tolerances of micro-organisms to environmental stress depend upon their physiological condition. There appears to be a reciprocal relation between the degree of physiological activity and tolerance. Thus, resting stages such as cysts and spores, as well as stationary phases, are considerably more resistant to environmental stress than physiologically more active phases (populations during logarithmic growth: cell division, reproduction).

Unfortunately, no detailed investigations have been undertaken so far to assess the specific responses to different light conditions in bacteria, fungi and blue-green algae as a function of their physiological condition.

(*b*) *Metabolism and Activity*

Our knowledge concerning light effects on metabolism and activity of bacteria, fungi and blue-green algae is very limited and largely restricted to the bacteria of the nitrogen cycle. VACCARO and RYTHER (1954) reported that sunlight has no significant effect on respiratory rates of marine bacteria suspended in 'light' and 'dark' bottles 25·4 cm below the sea surface.

In the following paragraphs I shall discuss the influence of light on metabolism and activity of nitrifying and denitrifying bacteria.

Nitrifying bacteria (pure cultures)

The comprehensive investigations of ENGEL and his associates have opened up first insights into the physiology of light effects on bacteria of the nitrogen cycle. The investigations by MÜLLER-NEUGLÜCK and ENGEL (1961), SCHÖN and ENGEL (1962), MÜTZE (1963), ULKEN (1963), BOCK (1965) and HARMS and ENGEL (1965) deal especially with bacterial species of the genera *Nitrobacter* and *Nitrosomonas*. *Nitrosomonas* oxidizes ammonia to nitrite; *Nitrobacter* oxidizes nitrite to nitrate.

MÜLLER-NEUGLÜCK and ENGEL (1961) showed that sunlight slows down the oxidative capacity of *Nitrosomonas europaea*. At higher light doses oxidation

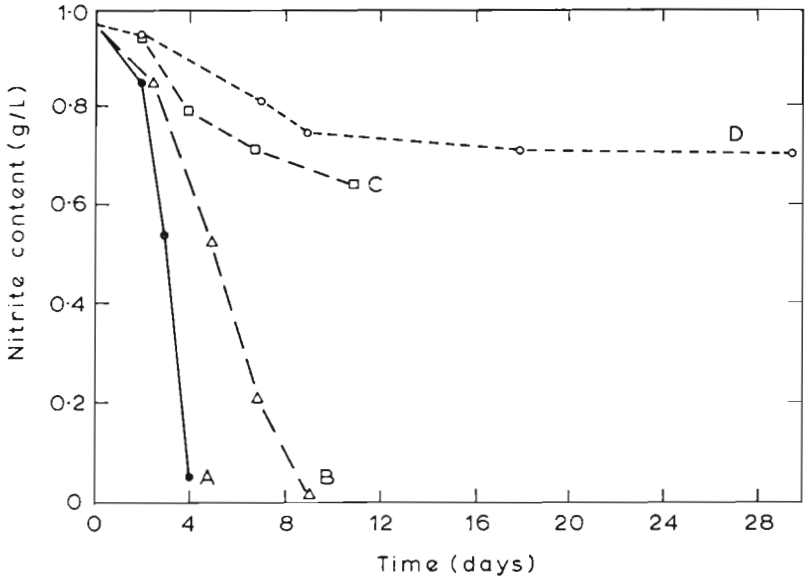

Fig. 2-10: Influence of natural sunlight on the rate of oxidation of nitrite to nitrate by a pure culture of bacteria *Nitrobacter winogradskyi*. A: complete darkness; B: dull weather (cloudy, misty); C: clear sky but in shadow; D: direct sunlight. Oxidation of nitrite (decrease in nitrite content) is fastest in complete darkness, slowest in direct sunlight. The experiments were conducted in Hamburg, North Germany, at 31° C. Information about the time of year is not available. (After MÜLLER-NEUGLÜCK and ENGEL, 1961; modified.)

ceases completely. Intensive sunlight can exert so strong an influence upon the cultures that they do not recover at night, but become more and more inactive from day to day. Fig. 2-10 illustrates the effects of different intensities of natural light on the intensity of oxidation of nitrite to nitrate by *Nitrobacter winogradskyi*. Rate of oxidation is fastest in complete darkness and decreases progressively under conditions of dull weather (cloudy, misty), clear sky in shadow, clear sky and direct sunlight. Direct sunlight significantly reduces the oxidative capacity and practically prevents all nitrite oxidation after 8 days. Experiments under conditions of artificial illumination reveal that the tolerance to light is rather small. An illumination of only 500 lux (fluorescent tubes 'Sylvania electric') clearly reduces the rate of nitrite oxidation as compared to the rate in complete darkness (Fig. 2-11).

Nitrosomonas europaea is more tolerant to light than *Nitrobacter winogradskyi* (SCHÖN and ENGEL, 1962). Fig. 2-12 illustrates the effect of artificial light on the

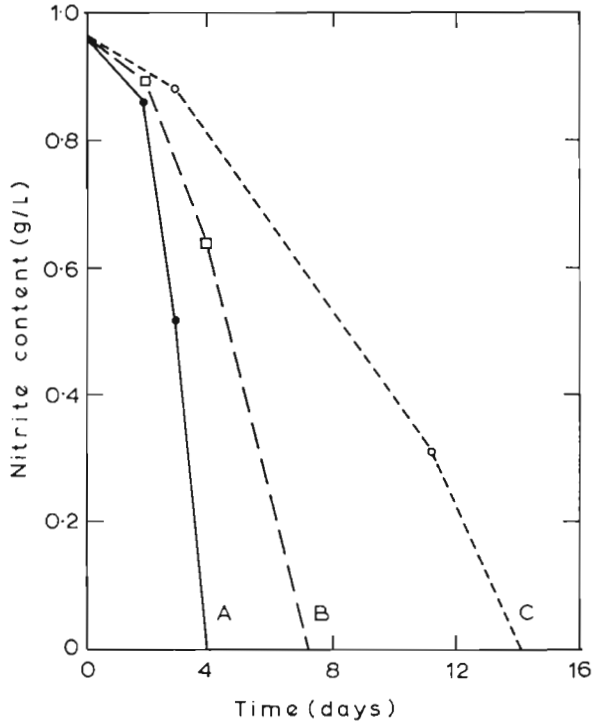

Fig. 2-11: Influence of artificial light on the rate of oxidation of nitrite by a pure culture of the bacteria *Nitrobacter winogradskyi*. A: complete darkness; B: 500 lux; C: 1000 lux. Light source: fluorescent lamps 'warm white deluxe' and 'soft white' of the Sylvania Electric Co. The lamps were arranged in alternating order. The first type emits light mainly in the region of 500 to 700 mμ, the second between 400 and 700 mμ. The maximum of both types is somewhat above 600 mμ. The experiments were conducted at 31° C. (After MÜLLER-NEUGLÜCK and ENGEL, 1961; modified.)

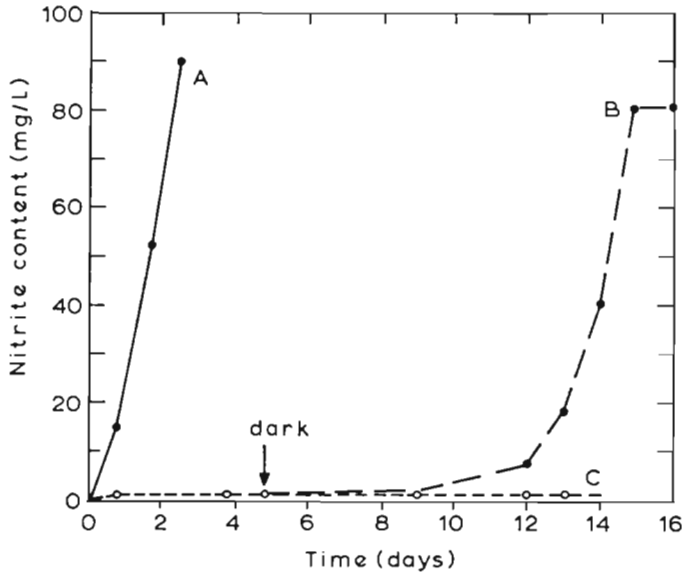

Fig. 2-12: Absorption spectra of resting, non-oxidizing cells of bacteria *Nitrosomonas europaea*. A: complete darkness; B: 10,000 lux illumination, the culture being transferred into the dark after 5 days; C: 10,000 lux illumination throughout the experiment. Light source: as in Fig. 2-11. Temperature: 30° C. (After SCHÖN and ENGEL, 1962; modified.)

intensity of oxidation of ammonia to nitrite. Exposure to a light intensity of 10,000 lux results in complete cessation of oxidation; however, if cultures exposed to 10,000 lux for 5 days are transferred to complete darkness they begin to recover within 7 days and regain normal oxidative intensities after about 9 days. This long delay in recovery suggests that major parts of the population were killed or critically incapacitated by the light and had to be replaced by reproduction.

Further experiments by SCHÖN and ENGEL (1962) with coloured glass filters (Schott & Genossen) showed that the blue portion of the light used was responsible for the decrease in oxidative capacity.

BOCK (1965) has demonstrated that the destruction of cytochromes by higher light intensities is the major cause for the decrease in oxidative performance of *Nitrobacter winogradskyi* and *Nitrosomonas europaea* and, at critical doses, leads to death. Fig. 2-13 illustrates absorption spectra of resting, non-oxidizing cells of *N. europaea* under different conditions of light. The absorption maximum at 422 mμ consists of the bands of cytochrome c and b and the β-band of cytochrome a. The peaks at 522, 551 and 600 mμ correspond to the β- and α-bands of a cytochrome of the c type and the α-band of cytochrome a. The illumination applied during the experiment causes a decrease of the extinction over the total spectral portion tested. After 8 hrs of exposure to 54,000 lux the positions of the various peaks are practically unchanged; however, their relative height (concentration) has decreased somewhat. After 24 hrs the cytochromes are destroyed; all typical bands have disappeared. This experiment reveals cytochromes as the vital light-sensitive cell components.

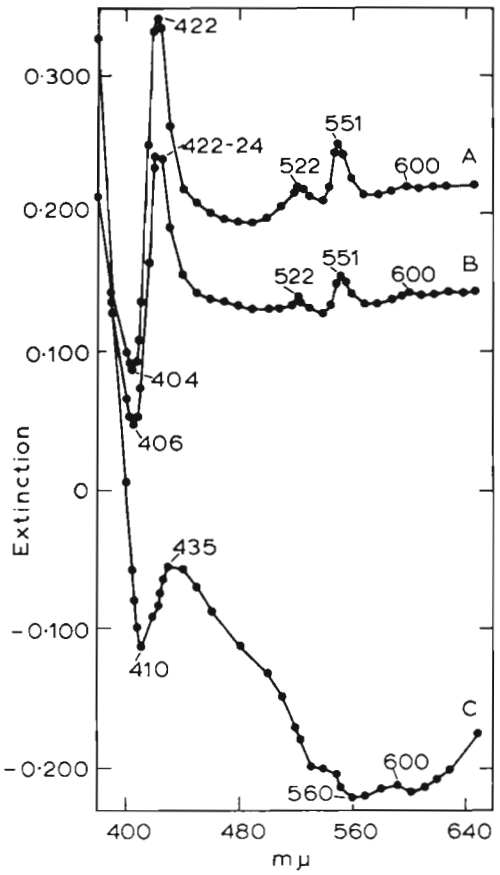

Fig. 2-13: Absorption spectra of resting, non-oxidizing cells of bacteria *Nitrosomonas europaea*. A: in complete darkness; B: after 8 hrs illumination (54,000 lux); C: after 24 hrs illumination (54,000 lux). Light source: combination of electric bulbs and 1000 W mercury high pressure lamp; temperature: 30° C. (After Bock, 1965; modified.)

Denitrifying bacteria (pure cultures)

Harms and Engel (1965) investigated the influence of visible light on the cytochrome system in resting cells of *Micrococcus denitrificans*. As in *N. europaea* high light intensities lead to destruction of cytochromes. The corresponding changes in the absorption maxima are also quite similar to those described for *N. europaea*. Destruction of cytochromes, diminution of the capacity for oxidation, and finally death of the bacteria are also, in this case, the subsequent steps of damage due to light. Harms and Engel used both natural sunlight and artificial light (250 W Phillips HPL lamp and 100 W Osram Krypton lamp).

Fig. 2-14 shows the influence of light on the nitrogen liberation by non-growing cultures of *Micrococcus denitrificans* in the dark and under artificial illumination (58,000 lux). Glycerin is oxidized by KNO_3. In the dark oxidation proceeds at a

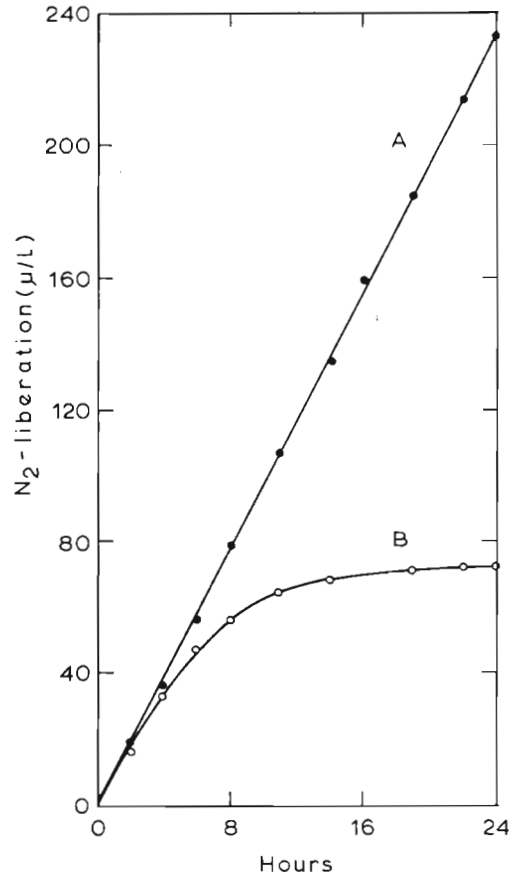

Fig. 2-14: Influence of light on the nitrogen liberation by a non-growing culture of bacteria *Micrococcus denitrificans*. A: complete darkness; B: 58,000 lux illumination. Light source: as in Fig. 2-13. (After HARMS and ENGEL, 1965; modified.)

constant rate but in the light N_2 liberation is strongly reduced. The diminution of a population of non-growing cells of *Micrococcus denitrificans* proceeds quite rapidly under the influence of light at 58,000 lux; in one experiment, after 16 hrs of light exposure, 99% of the bacteria were killed.

Nitrogen cycle in the aquatic environment

In the two preceding sections it became clear that light does affect metabolism and activity of pure bacteria cultures. It seems of importance to know whether similar responses can be demonstrated on natural, especially multispecies, populations.

ULKEN (1963) conducted experiments on multispecies bacterial populations from the river Elbe (Germany). She illuminated samples of river water with 4000 lux and obtained small but distinct differences between 'light' and 'dark' samples. As in pure cultures, the formation of nitrite from ammonia was somewhat slower

in the 'dark' samples. Pronounced differences were obtained at the second step of the oxidation process. The conversion of nitrite to nitrate was much faster in dark than in illuminated samples. In spite of convincing information concerning pure cultures and multispecies natural samples we are still not sure about the effect of light on the nitrogen cycle in the aquatic environment.

While it seems possible that light may affect the nitrogen cycle in clear water with high penetration values, in turbid waters—such as in the river Elbe—appreciable light effects can hardly be expected. According to RHEINHEIMER (1959), ULKEN (1963) and LUCHT (1964) the nitrite distribution in the Elbe does not show a significant relation to season—a fact which might be interpreted as an argument against ecologically significant light effects upon the nitrogen cycle in that river. One should also keep in mind that there is no constant light in nature and that both turbidity and mixing processes may considerably complicate the situation. Fig. 2-15 exemplifies the transparency of water from the river Elbe for different wavelengths and water depths.

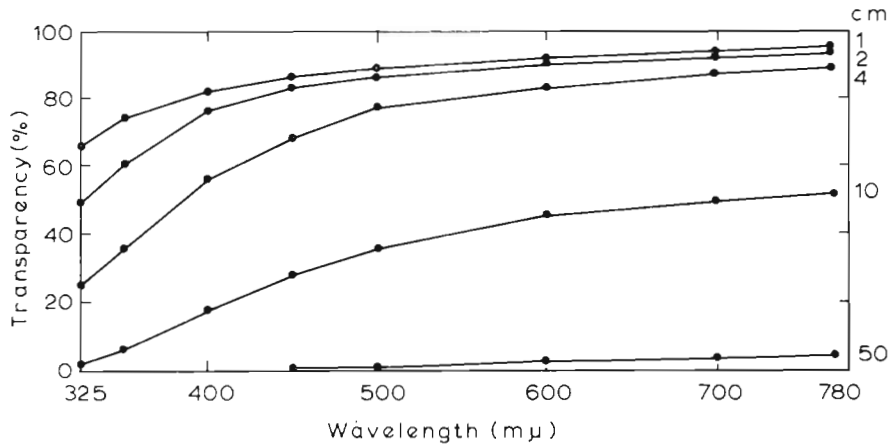

Fig. 2-15: Transparency of water from the river Elbe sampled at Hamburg (Germany) for light of different wavelengths as a function of water depth. The curves for water depths of 1, 2 and 4 cm (right scale) are drawn through individual values obtained by a photometer; the corresponding values at 10 and 50 cm are based on calculations. (After ULKEN, 1963; modified.)

(c) *Reproduction*

In bacteria, as well as in unicellular fungi and blue-green algae, it has, generally, not yet been possible to investigate responses of single individuals. The information available to date has been obtained at the supra-individual (population) level. Since 'population growth' is identical with the reproductive activities of the test population, most of the responses to light dealt with under 'tolerance' actually refer to rates of (largely asexual) reproduction.

In multicellular blue-green algae reproduction is closely related to rates of photosynthesis and growth dealt with in Chapter 2.2. Information concerning light effects on multicellular fungi is practically exclusively restricted to terrestrial and pathogenic forms. There is a great need for the investigation of the photobiology of marine fungi.

(*d*) *Distribution*

The distribution of bacteria, fungi and blue-green algae in oceans and coastal waters is significantly related to their nutritional physiology. While the distribution of photo-autotrophic micro-organisms tends to be directly affected by light, the relation between the light effects and distribution in heterotrophs is largely an indirect one. Heterotrophs require organic substances originally produced by the phytoplankton and gradually transferred through the food chain. Hence their horizontal and vertical distributions tend to be closely related to those of their respective food sources.

Among the photo-autotrophic micro-organisms are practically all blue-green algae, a few bacteria (purple and green) but no fungi. The purple and green bacteria live in anaerobic environments. Because most of them need hydrogen sulphide as well as light for photosynthesis their occurrence is restricted to very special habitats. They live mostly in shallow and muddy pools rich in organic materials. In some parts of wadden-seas (mud flats, tidal areas, marshes) they are more abundant. The heterotrophic micro-organisms are largely represented by fungi and many bacteria; few blue-green algae are facultative heterotrophic micro-organisms.

Direct light effects on microbial distributions

In regard to marine bacteria we may assume that direct light effects have a rather limited influence on their distribution. In several cases vertical distributions of bacteria appear to be related to light. However, a more detailed analysis reveals that such vertical gradients are primarily due to other factors such as phytoplankton distribution and hence only indirectly affected by the light regime.

The distribution of the photo-autotrophic blue-green algae is directly affected by light. This is especially true with respect to vertical distributions. However, substantial differences in average daily amounts of light received per unit water surface and in daylengths may be of considerable importance. The few detailed analyses available deal with different types of plants rather than with the distribution of cyanophyceans. The reader is, therefore, referred to Chapter 2.2 for further information.

Nothing is known about direct light effects on the distribution of marine fungi.

A special habitat, in which direct light effects on the distribution of micro-organisms have been studied, is the so-called 'Farbstreifensandwatt'. It comprises littoral sandy areas which contain vertical stratifications of different micro-organisms resulting in thin layers of different colours. The 'Farbstreifensandwatt' in the German Bight (southern North Sea) has been investigated by REMANE and SCHULZ (1934), SCHULZ (1937), SCHULZ and MEYER (1939), HOFFMANN (1942, 1949). It is composed of three thin layers (a few mm) and a thick layer (up to one or several m) of black muddy sand. The three thin layers consist of a surface layer composed of bleached rather white sand, a medium blue-green layer of cyanophyceans and a lower reddish layer of purple bacteria. The black colour at the thick bottom layer is caused by iron sulphides. The environmental factors primarily responsible for this vertical stratification are: light, redox potential, hydrogen donors, and pH.

Detailed lists of the micro-organisms in the blue-green and reddish layers are available. HOFFMANN (1942) found 29 species of blue-green algae in the 'Farbstreifensandwatt' of Kniepsand (Island of Amrum, southern North Sea); they belong to the following genera: *Microcystis*, *Gloecapsa*, *Chroococcus*, *Merismopedia*, *Calothrix*, *Hydrocoryne*, *Nodularia*, *Anabaena*, *Spirulina*, *Oscillatoria*, *Phormidium*, *Lyngbya*, *Microcoleus* and *Hydrocoleus*. The predominant purple bacteria responsible for the reddish colour of the next lower sand layer are: *Thiopedia rosea* and *Lamprocystis roseopersicina*. Less abundant are *Amoebobacter granula*, several species of *Chromatium* and *Thiospirillum rosenbergii*. In addition, the colourless *Beggiatoa alba* and *Achromatium oxaliferum* occur together with diatoms and colourless *Peridinium* species. Comparable lists of micro-organisms have been reported from similar habitats on the Danish coast by WARMING (1904, 1906; *in*: HOFFMAN, 1942).

There is some information available on light penetration through the uppermost white sand layer (HOFFMANN, 1949; see also TAYLOR and GEBELEIN, 1966). In wet sand light penetrates somewhat deeper than in dry sand; 37% of the incident sunlight is reflected by dry sand, but only 24% by wet sand. The transparency of wet sand (expressed as percentage of incident light) was, in a typical experiment, 52·2% at a sand thickness of 1 mm, 33·2% at 2 mm, 15·9% at 3 mm, 6·6% at 4 mm and 1·6% at 5 mm. In sand, red light (longer wavelengths) penetrates deeper than green or blue light (Fig. 2-16). The sand layer acts as a filter; beyond a certain thickness it permits only red light to penetrate. HOFFMANN (1949) did not present data on the penetration of infra-red light.

A compilation on typical absorption spectra of representatives of photo-auto-

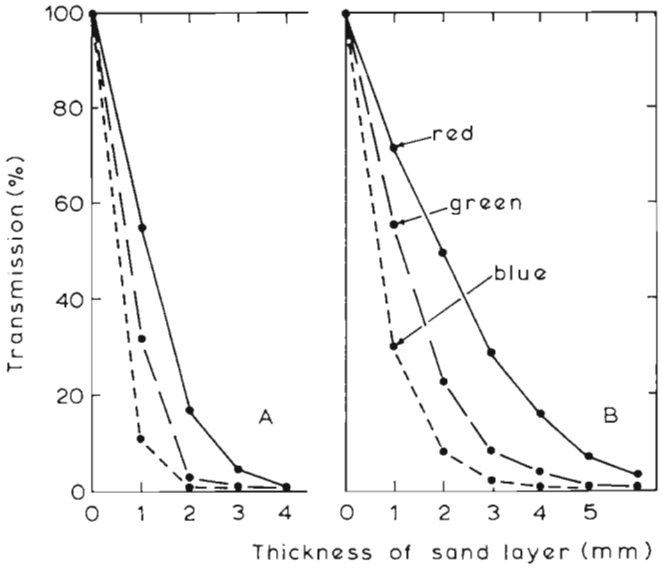

Fig. 2-16: Transmission of dry (A) and wet (B) sand (average grain size 0·2 mm) for red, green, and blue light. The transmission values are given in % of the incident light. Water content of the dry sand: 2·99%, of the wet sand: 17·55%. (After HOFFMANN, 1949; modified.)

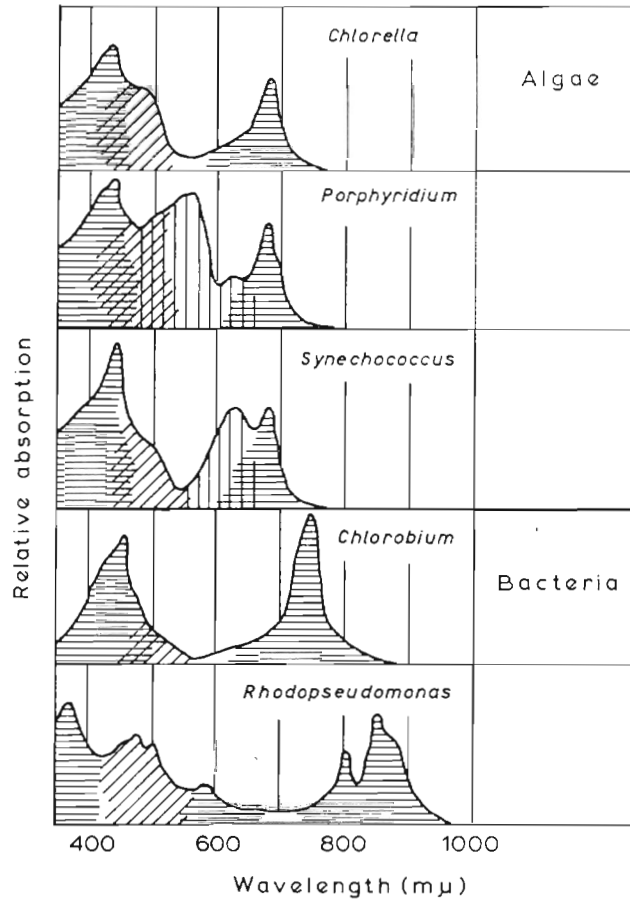

Fig. 2-17: Absorption spectra of some representatives of important taxonomic groups of phototrophic microorganisms: chlorophyte *Chlorella*, rhodophyte *Porphyridium*, cyanophyte *Synechococcus*, green bacterium *Chlorobium*, purple bacterium *Rhodopseudomonas*. The various classes of photosynthetic pigments are indicated as follows: chlorophylls by horizontal hatching, carotinoids by diagonal hatching and phycobilins by vertical hatching. (After STANIER and COHEN-BAZIRE, 1957; modified.)

trophic organisms has been given by STANIER and COHEN-BAZIRE (1957). Fig. 2-17 illustrates the absorption spectra of a chlorophyte (*Chlorella*), rhodophyte (*Porphyridium*), cyanophyte (*Synechococcus*), green bacterium (*Chlorobium*) and a purple bacterium (*Rhodopseudomonas*). Of these five groups cyanophytes and bacteria are represented by certain forms in the 'Farbstreifensandwatt'. The cyanophytes, occupying the blue-green layer, primarily absorb wavelengths between 600 and 700 mμ allowing light of higher wavelengths to penetrate. This infra-red portion of the light spectrum is used as an energy source by the purple bacteria which primarily absorb wavelengths between 800 and 900 mμ. Thus the purple bacteria of the 'Farbstreifensandwatt' occupy a rather special ecological

light niche. In addition to wavelengths, the vertical distribution of cyanophytes and bacteria are affected by the total light intensity, the redox potential, as well as by the presence of oxygen and hydrogen donors. Several factors appear to be responsible for the fact that cyanophytes are always found on top of the purple bacteria: total light intensity, wavelengths, oxygen (free oxygen is detrimental to purple bacteria) and hydrogen donors (required by purple bacteria for photosynthesis). Hydrogen sulphide, used by sulphur purple bacteria, is furnished either by proteolytic bacteria (degradation of organic sulphur-containing compounds) or by the activity of sulphate-reducing bacteria of the thick black bottom layer.

Indirect light effects on microbial distributions

Several cases of indirect light effects on the distributions of heterotrophic micro-organisms have come to the reviewer's attention. For example, ZoBELL (1946) has presented a general picture of vertical gradients in light intensity and temperature, as well as on the vertical distributions of phytoplankton and heterotrophic bacteria at a number of stations in the Pacific Ocean. He found the maximum numbers of bacteria at a water depth of about 50 m just below the greatest phytoplankton abundance (Fig. 2-18). One could interpret the bacterial

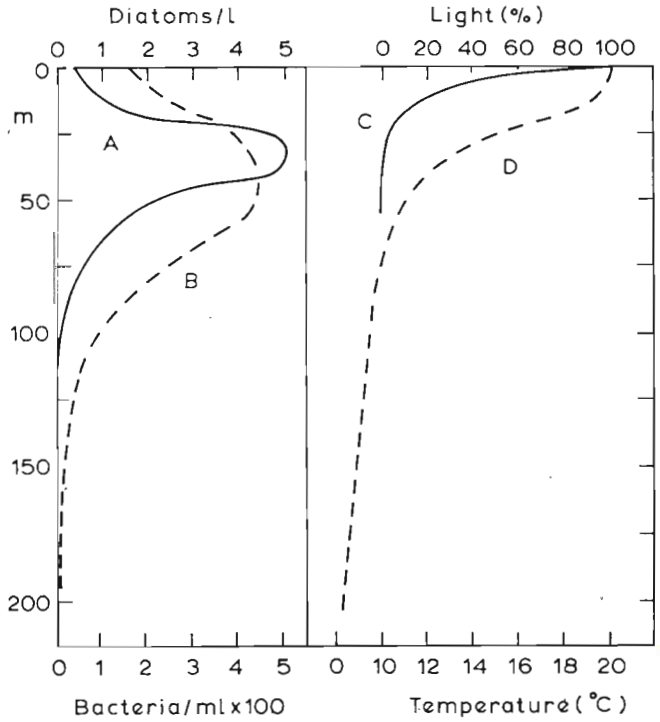

Fig. 2-18: Vertical distribution of phytoplankton diatoms (A) and bacteria (B), as well as vertical gradients of light (C) and temperature (D) in the Pacific Ocean, based upon averages obtained at several stations off the coast of southern California (USA). The abundance of bacteria is expressed as numbers per ml indicated by plate counts. (After ZoBELL, 1946; modified.)

maximum at about 50 m by assuming that light intensities and spectral compositions above and below that depth are less favourable. However, on the basis of existing knowledge it is most unlikely that lack of light acts as a direct inhibitor for heterotrophic micro-organisms. At the same time, harmful ultra-violet and blue-light wavelengths are practically completely absorbed in the uppermost metres of the water column.

ZoBell (1946) has, therefore, argued that the bacterial maximum in Fig. 2-18 depends largely upon phytoplankton distribution which, on the other hand, is affected primarily by light, temperature and availability of nutrients. Thus, as far as light is concerned, one could speak of an indirect light effect on bacteria via the phytoplankton.

Overbeck (1965, 1967) has suggested a close relationship between the vertical distributions of aerobic heterotrophic bacteria and the phytoplankton. Since photosynthesis provides the energetic basis for bacteria, a close spatial correlation between producers and decomposers would allow part of the remineralization process to take place in the immediate vicinity of the initial energy source.

Overbeck (1965, 1967) also reported a close correlation between the annual cycles of bacteria and phytoplankton. However, Gunkel (1968) found in water pools of the Düne (Helgoland, southern North Sea) that seasonal maxima of bacteria numbers can occur weeks after maximum phytoplankton abundance.

The phytoplankton not only serves as an energy source for bacteria; it may also produce antimicrobial substances and thus significantly suppress bacterial activities. Thus the cyanophycean *Phaeocystis pouchetii* produces acrylic acid which is highly toxic to bacteria (Sieburth, 1964, 1965).

(3) Structural Responses

No information is available on structural responses to light of marine micro-organisms. The reports concerning structural consequence of exposure to ultra-violet light of a wavelength of 254 mμ (changes in cell size, snake formation, etc.) are not pertinent to the concept of the present chapter.

2. LIGHT

2.2 PLANTS

J. A. HELLEBUST

(1) Introduction

Light serves as energy source for photosynthesis and hence plays a dominant role in all photosynthetic plants. Their functional and structural responses are largely affected by light intensity, quality and exposure patterns.

Basically, light may affect plants in three different ways (i) via photosynthesis, (ii) via processes only indirectly related to photosynthesis, (iii) via processes completely unrelated to photosynthesis.

It is the purpose of this chapter to consider the whole range of responses of marine plants to light. The physiological and biochemical mechanisms of photosynthesis will be referred to only as far as this seems necessary for the understanding of the responses considered; these mechanisms will be dealt with later in a separate volume of the present treatise.

(2) Functional Responses

(a) *Tolerance*

Upper tolerance limits to visible and ultra-violet radiation

Marine algae vary greatly in their resistance to high light intensities. Part of this variability is due to non-genetic adaptation to different levels of illumination, and part of it to genetic differences (see also Chapter 11.2).

It is well known that the rate of photosynthesis of marine phytoplankton is strongly depressed by exposure to direct sunlight for an extended period of time (RYTHER, 1956; STEEMANN NIELSEN and JENSEN, 1957). However, marine phytoplankton shows a remarkable ability to adapt to various light regimes; in general, plankton collected near the surface is more resistant to high light intensities than deep-water plankton (RYTHER and MENZEL, 1959; STEEMANN NIELSEN and HANSEN, 1959). Such differences in light adaptation of planktonic algae at different depths are, however, found only in water masses with vertically stabilized euphotic zones. In well-mixed euphotic zones, phytoplankton forms of intermediate light tolerances and photosynthetic characteristics are present.

Dunaliella tertiolecta, a marine green flagellate, exposed to direct sunlight of about 100 klux for as long as 9 hrs responded initially with a rapid, and then a more gradual decrease in photosynthetic capacity; only little bleaching of chlorophyll took place during the same period (HELLEBUST, unpublished a). Determination of the activities of two enzymes involved in photosynthetic dark reactions indicated that actually some net synthesis of these enzymes took place while the photosynthetic capacity was strongly inhibited. When the cultures were

placed in complete darkness following high light intensity exposure there was a rapid increase in photosynthetic light and dark reactions, as well as in chlorophyll and enzyme activities. These results indicate that no permanent damage was suffered by *D. tertiolecta* during the direct sunlight exposure. It is possible that many marine phytoplankton forms are equally resistant to direct sunlight, and respond only with a temporary decrease in photosynthetic rate; but this remains to be investigated. YENTSCH and RYTHER (1957) observed a decrease in chlorophyll content in marine surface phytoplankton during exposure to direct sunlight; this decrease may possibly have been due to pigment bleaching.

TAYLOR (1964) studied the effects of high light intensities on the intertidal benthic diatoms *Tropidoneis* sp. and *Hantzschia amphioxys* which appear on the substrate surface as golden-brown patches as the tide recedes. He found that a 1-hr exposure to full midday summer sunlight (74 gcal cm^{-2} or ca 110 klux) resulted only in a 10% inhibition of the photosynthetic capacity.

If *Chlorella pyrenoidosa* is exposed to intense light (SIRONVAL and KANDLER, 1958) it responds, during the initial induction phase, with a decrease in rate of photosynthesis, but not with pigment bleaching. The reduction of photosynthesis rate during this phase is reversible; normal photosynthetic capacity is gradually regained after exposure to low light conditions or complete darkness. Following the induction phase, bleaching of chlorophyll takes place (secondary effect) after the stabilizing chloroplast structure is partly destroyed due to light inhibition of metabolism.

Cultures of the green tropical alga *Acetabularia crenulata*, grown at very low light intensities and suddenly exposed to direct sunlight for 6 hrs, showed during the first 3 hrs only little pigment bleaching, and the activities of two enzymes involved in photo-assimilation of CO_2 (ribulose-1,5-diphosphate carboxylase and aldolase), too, changed very little (HELLEBUST, unpublished a). On the other hand, there was a 60% reduction in rates of light and dark reactions during the same time. After 6 hrs in direct sunlight about 70% of the chlorophyll had bleached and the photosynthetic capacity of the alga was almost completely lost; there was also a rapid loss of ribulose-1,5-diphosphate carboxylase during the last 3 hrs of exposure to sunlight. The specimens used in this experiment showed no evidence of calcification, and this may possibly be one reason for their high sensitivity to light.

The responses of marine phytoplankton to ultra-violet have received little attention. GESSNER and DIEHL (1951) exposed freshwater phytoplankton in flat glass vessels to direct sunlight and found that within one day $\frac{1}{2}$ to $\frac{3}{4}$ of the chlorophyll was destroyed. When the glass containers were covered with thick glass plates to exclude ultra-violet, no chlorophyll destruction took place in diatoms and dinoflagellates, and much less destruction in green flagellates. If marine surface plankton is kept in open glass bottles, full sunlight ultra-violet radiation affects the plankton algae in such a way that in subsequent experiments both rates of photochemical and dark reactions of photosynthesis are reduced (STEEMANN NIELSEN, 1964); full sunlight without ultra-violet has only slight effects.

MCLEOD and MCLACHLAN (1959) studied the comparative sensitivity of several marine and freshwater algae to ultra-violet radiation. The cells were irradiated using nearly monochromatic light of 254 nm at an intensity of 136 $\mu W\ cm^{-2}$ for 1 hr. Pigment concentrations and photosynthetic rates were determined after this

period. The algae exhibited widely different sensitivities to ultra-violet radiation. Diatoms, and the natural populations, which were predominantly diatoms, were the most sensitive forms. *Dunaliella tertiolecta* showed a relatively low sensitivity during the lag phase of growth, but a marked increase during the logarithmic phase.

DODGE (1965) investigated the effects of ultra-violet light on growth, nuclear structure and cell division of the dinoflagellate *Prorocentrum micans*. The cells were exposed to 70,000 μW cm^{-2} of radiation at 254 nm for varying periods of time. A 5-min exposure period scarcely affected cell growth; a 15-min exposure caused a delay in cell division; it took several days before cell division was resumed; a 30-min exposure resulted in a rapid decline in cell number; only 8% of the original population survived the treatment. Some chromosome breaks and exchanges giving rise to anaphase bridges were also observed. However, the percentage of cells showing chromosome aberrations was always very small and almost independent of dosage. Apparently, only cells in a particular phase of the mitotic cycle, presumably the stage of chromosome (or DNA) duplication, were susceptible to chromosome lesions by ultra-violet treatment.

That high light intensities may be damaging to attached marine algae has been known for a long time; a number of pertinent observations were made before the turn of the century by BERTHOLD (1882) and OLTMANNS (1892, 1905). They described the relative effects of intense light on seaweeds grown under shaded or exposed conditions and noted that the algae varied greatly in their tolerance to direct sunlight, and suggested that light tolerance plays an important role in the vertical distribution of seaweed species (see pp. 149–151).

MONTFORT (1933, 1953) studied the responses of attached marine algae, collected from intertidal and sublittoral regions, as well as from shaded cave environments, to high light intensities. He found that a deep-water *Laminaria* sp. and several red seaweeds from deep water as well as caves suffered pigment destruction and considerable depression of photosynthetic rates after short-term exposure to direct sunlight. Intertidal algae proved to be much more resistant. MONTFORT demonstrated that the longwave part of the visible spectrum contributes to pigment destruction, although the rate of destruction increases markedly after the addition of shortwave light.

Detailed quantitative studies on light tolerance of attached marine algae have been conducted by BIEBL (1952a, b, 1956, 1957). In 1952, BIEBL found that algae from tide pools and the intertidal zone which are normally exposed to high light intensities (*Porphyra laciniata*, *Cladophora utricularis*, *Plumaria elegans*, *Griffithsia flosculosa*, etc.) suffered no damage after 2 hrs of direct exposure to sunlight. *Ulva lobata*, *Cladophora trichotoma* and *Porphyra perforata*, collected in the upper intertidal region, were not damaged by direct exposure to sunlight (105 klux) for 5 hrs. Sublittoral algae (*Dictyota dichotoma*, *Neomonospora pedicellata*, *Polyneura hilliae*, *Antithamnion cruciatum*) accustomed to a low-light environment, however, were killed by a 2-hr exposure. In his second study BIEBL (1956) reported that certain sublittoral algae, *Pterochondria woodii*, *Microcladia californica*, and *Callophyllis marginifructa*, were partially or completely killed even after 1 hr of direct exposure to sunlight (97 klux). In almost all cases, the first visible responses to intense light were changes in shape and pigmentation of chromatophores. The

irregularly shaped chromatophores of the red seaweeds investigated became gradually more spherical and showed occasionally a large increase in volume. After an initial lag phase, a progressive destruction of pigments occurred, and, in most algae, cell death due to intense light expressed itself in the form of complete bleaching of chromatophores. However, not all light-killed cells were completely bleached. In *Griffithsia flosculosa*, the content of the cells remained red when the membranes had expanded enormously, and vital staining properties of the cytoplasm and the osmotic properties of the cells indicated that they were dead. In a few other cases (*Ceramium ciliatum*, *Acrosorium uncinatum*, *Polysiphonia furcellata*), a 4-day exposure to high light intensity caused an almost complete loss of photosynthetic pigments while osmotic and vital staining properties of the cells indicated that they were still alive. The upper and lower cell layers of the red seaweed *Callophyllis marginifructa* consist of photosynthetic cells containing numerous chromatophores separated by central layers of large cells poor in plastids. When BIEBL (1957) exposed one side of the thallus to direct sunlight for 60 mins, which is sufficient to kill the outer layer of photosynthetic cells, the lower cell layers suffered no essential damage.

Experiments with various ranges of filtered sunlight showed that the damaging light effects were primarily attributable to short wavelengths (BIEBL, 1956). However, wavelengths longer than 550 nm killed parts of the sublittoral algae *Pterochondria woodii* and *Callophyllis marginifructa* during a 5-hr exposure period, and produced inflation of the chromatophores and other morphological evidence of damage in *Botryoglossum farlowianum*.

The rate of photosynthesis of *Cladophora insignis* decreased about 40% during a 1-hr exposure to 100 klux when measured at this light intensity (STEEMANN NIELSEN, 1952). The rate of photosynthesis at 3 klux was less than the rate of respiration. This indicates a strong inhibition of both quantum yield and the rate of dark reactions. However, by keeping the alga in a window facing north for one day, following the high intensity light exposure, the rate of photosynthesis at 3 klux returned to normal.

Heavily calcified algae from locations exposed to high light intensities may show much less, or a complete lack of, calcification when grown in the shade; calcification may possibly protect the cells by reflecting part of the light (BERTHOLD, 1882). Uncalcified *Acetabularia* cells are very sensitive to direct sunlight, while older heavily calcified *Acetabularia* individuals, found in the upper intertidal region in the tropics and subtropics, are obviously much more tolerant to direct sunlight (DE BARY and STRASBURGER, 1877).

A difference in daylength tolerance has been observed for two species of *Ulva* from different latitudes (FÖYN, 1955). *Ulva lactuca* plants, collected on the coast of Norway or England, where they experience long days during summer, were able to tolerate continuous illumination, while more than 19 hrs of illumination per day resulted in injury for *Ulva thuretii* specimens collected from the Bay of Naples (Italy).

The degree of protoplasmic resistance to ultra-violet radiation (230 to 310 nm) of attached algae from different depths showed no correlation with the light conditions under which the algae grow (BIEBL, 1952b). This finding contrasts sharply with the very good correlation observed between resistance to visible light

and light exposure in attached algae (MONTFORT, 1933; BIEBL, 1956). BIEBL considers resistance against visible light 'ecological', resistance against ultra-violet light 'non-environmental–constitutional'. In the experiments referred to above (BIEBL, 1952a, b), the intensity of the ultra-violet radiation was much higher than the ultra-violet component of direct sunlight, and hence may be considered 'unecological'. Several studies have shown that shortwave components of sunlight are more effective in causing photodamage to algae than longwave portions. However, BIEBL (1957) exposed algae to an ultra-violet dose equivalent to that of unfiltered sunlight sufficient to kill the cells, and observed only little damage. This result indicates that ultra-violet radiation components of direct sunlight cause severe damage only if mixed with longer wave radiation (consult also Chapter 11.2).

From the information presented, it may be concluded that little is known about the effects of high light intensities on marine phytoplankton beyond the fact that surface algae suffer a strong, and presumably reversible, reduction in photosynthetic rate after prolonged exposure to sunlight. There is some indication of pigment bleaching in surface plankton under such conditions, but few studies have been performed with individual species to explore this problem. In general, planktonic algae seem very adaptable to varying light conditions; the effects of high light intensities on surface plankton appear to be mostly reversible.

We are quite well informed about the upper limits of light tolerance in many attached algae, and about damages to photosynthetic pigments, photosynthetic capacity and osmotic properties. Time–course studies on a few algal species indicate that initial effects are related to both light and dark reactions of photosynthesis, and that these effects are reversible during the induction phase. Continued exposure to intense light beyond the induction phase results in pigment bleaching and irreversible cell damage. Much remains to be learned about the biochemical nature of the damaging effects of intense light on cellular metabolism.

Prolonged exposure to ultra-violet light is lethal to most algae, but lethal doses vary with species and physiological condition. Ultra-violet irradiation appears to be particularly damaging in the presence of longer wavelength irradiation (radiation effects on marine plants are treated extensively in Chapter 11.2).

Lower tolerance limits to visible radiation

Since photosynthetic algae rely on light as energy source they will cease to grow and begin to degenerate beyond a certain lower tolerance limit. The exact determination of this limit is difficult. In response to environmental changes marine plants may gradually adapt to new conditions. It is necessary, therefore, to determine light compensations of algae under a large number of different factor intensities (e.g. temperature, light, nutrients), and after allowing a sufficient period of time to complete non-genetic adaptation at each condition, before one can reach meaningful conclusions regarding lower light tolerance limits. Temperature, in particular, is likely to affect significantly the lower tolerance limit; another important factor is heterotrophic utilization of dissolved organic substances (see Chapters 3, 10).

Living phytoplanktonic algae containing chlorophyll have been collected from water depths below 1000 m, where light could hardly play a significant role as

energy source (BERNARD, 1963; WOOD, 1963). It remains to be investigated as to whether heterotrophic utilization of organic substances contributes to survival and possible growth of algae found below the euphotic zone. MENZEL and RYTHER (1959) found no net photo-assimilation of CO_2 by chlorophyll-containing samples taken from below the euphotic zone (approximately 100 m) in the Sargasso Sea, indicating that the algae collected were photosynthetically inactive.

In survival, algae show great variations in tolerance to low light intensities or temporary complete darkness. YENTSCH and REICHERT (1963) placed the green flagellate *Dunaliella tertiolecta* in darkness at 20° C for 5 days, and recorded a complete loss of photosynthetic capacity and viability. HELLEBUST and TERBORGH (1967) exposed cells of the same alga to a light intensity considerably below its compensation point and found that its photosynthetic capacity was retained for a much longer period of time; furthermore, when *D. tertiolecta* was kept at 5° C, and exposed to continuous illumination of 20 μW cm^{-2} (approximately 50 lux) the cells remained photosynthetically active for 3 weeks without any increase in cell number. The kinetics of carbon loss from the cells in dim light indicated that the rate of respiration, and hence the compensation point, decreased appreciably with time.

In contrast to *D. tertiolecta*, young filaments of *Ectocarpus confervoides* were still viable after exposure to complete darkness at 15° C for 150 days (BOALCH, 1961). *E. confervoides* did not grow on several organic carbon sources in the dark; it, therefore, is probably an obligate photo-autotroph and must survive in the dark by an extreme reduction in metabolic activity. Recent collections of attached seaweeds from great depths in the Arctic (WILCE, 1964) and the Antarctic (ZANEVELD, 1966) indicate that these algae are able to tolerate conditions of extremely low light intensities for the greater part of the year. (For a more detailed account of compensation points and lower limits of light tolerance for individual algal species consult p. 145.)

In summary, the lower limits of light tolerance are rather poorly known for both unicellular planktonic and attached marine algae. The available data indicate a great deal of species variability, and also that individual algae may change their light requirements through physiological adaptation in response to varying environmental conditions.

(*b*) *Metabolism and Activity*

Pigment production and chromatic adaptation

In contrast to angiosperms which need light for converting protochlorophyll to chlorophyll, most of the algae examined so far do not require light for chlorophyll synthesis (BOARDMAN, 1966). However, some freshwater algae, particularly green flagellates, require light both for synthesis and maintenance of chlorophyll (PRINGSHEIM, 1954; NISHIMURA and HUZISIGE, 1959). Critical and comprehensive studies on light requirements for chlorophyll synthesis in marine algae are lacking; however, the marine flagellate *Dunaliella tertiolecta* rapidly increases its chlorophyll content upon transfer to complete darkness, similar to most freshwater algae examined (HELLEBUST and TERBORGH, 1967).

Although light generally stimulates the synthesis of carotenoids in plants, there

is apparently no absolute light requirement for their biosynthesis (GOODWIN, 1960). WOLKEN and MELLON (1956) demonstrated that the absence of light reduced the amount of carotenoids in *Euglena*, but did not entirely inhibit their production; carotenoid synthesis increases with increasing light intensity until it begins to drop again due to photodestruction of the pigments. In encysting *Haematococcus pluvialis*, found in tide pools, light is not essential for astaxanthin biosynthesis (DROOP, 1954). However, the presence of light considerably accelerates carotenoid synthesis in this alga (GOODWIN and JAMIKORN, 1954). A light quality effect on carotenoid synthesis has been observed in the marine diatom *Nitzschia closterium* (STRAIN and co-authors, 1944); cultures raised in white light produced more diadinoxanthin than when raised in red light.

Light intensity plays an important role in determining the chlorophyll content of algal cells. Unicellular algae grown under low light intensities ('shade cells') have much higher chlorophyll contents than cells grown under high intensities ('sun cells'). When cultures of *Skeletonema costatum*, *Dunaliella tertiolecta*, *Monochrysis lutheri* and *Amphidinium carteri* were transferred from low (0·02 ly/min) to high (0·35 ly/min) light intensity, the rate of chlorophyll a synthesis decreased relative to the rate of cell division (MCALLISTER and co-authors, 1964). Bleaching of chlorophyll did not appear to play a role during adaptation of 'shade' to 'sun' cells. When the cells were transferred from high to low light intensities the rate of chlorophyll synthesis increased relative to the cell division rate, resulting in cells with high chlorophyll contents.

Nitrogen deficiency increases the photolability of both chlorophyll and carotenoids of freshwater *Chlorella* (AACH, 1954). Nitrogen-deficient marine phytoplankters similarly become visibly chlorotic when exposed to even medium intense light (18 klux) for several days (YENTSCH and VACCARO, 1958).

Recent studies by YENTSCH (1965a, b) demonstrate conversion of chlorophyll a into phaeophytin when marine phytoplankton cultures are kept in complete darkness for several days. YENTSCH also showed that the ratio of phaeophytin to chlorophyll a increases with depth in the ocean, and is linked with a decreased capacity for photosynthesis. It appears that chlorophyll stability—both functional and chemical—in marine phytoplankton depends on the presence of light. A similar light-dependence for chlorophyll stability was reported earlier for *Euglena* (WOLKEN and co-authors, 1955).

The phenomenon of **complementary chromatic adaptation**—preferential synthesis of pigments with the highest absorption for incident wavelengths when an alga is exposed to light of a limited spectral region—was first discovered by ENGELMANN and GAIDUKOV (1902) in blue-green algae. Attempts to explain the different pigmentation of algae in view of the theory of complementary chromatic adaptation caused considerable controversy during many decades (RABINOWITCH, 1945). Complementary chromatic adaptation has been demonstrated clearly for the blue-green alga *Tolypothrix tenuis*, in which the relative amounts of phycocyanin and phycoerythrin are under intensity-independent chromatic control (HATTORI and FUJITA, 1959). It has also been reported for the red alga *Porphyridium cruentum* at low light intensities (BRODY and EMERSON, 1959); at higher light intensities **inverse chromatic control** of pigmentation was observed.

Little is known about the effects of light quality on pigment synthesis in marine

phytoplankton. *In situ* studies by YENTSCH and SCAGEL (1958) indicate differential effects of water depth, and, therefore, possibly of light quality, on the synthesis of chlorophyll a and carotenoid pigments. However, the pigment changes did not appear to follow a pattern indicative of complementary chromatic control. In a study on freshwater phytoplankton DUTTON and JUDAY (1944) found no evidence of chromatic adaptation with depth. A report on colour changes of cultures of a marine *Chaetoceros* species in response to changes in light quality indicates that the carotenoid/chlorophyll ratio in diatoms may be under chromatic control (MOTHES and SAGROMSKY, 1941); more thorough quantitative investigations on marine diatoms are desirable.

In a recent publication on light quality and intensity effects on the pigmentation of *Anacystis nidulans*, JONES and MYERS (1965) have attempted to resolve the argument concerning quality versus intensity as controlling variables. The light quality control of pigment production is viewed as a special case of intensity adaptation which has chromatic character by virtue of the presence of two different pigment systems linked to the two light reactions of photosynthesis. This hypothesis makes sense from a functional or teleological point of view, and is consistent with most of the available data. However, we still know next to nothing about the mechanisms of light quality or intensity control of pigment synthesis.

Pigments of *Chlorella* may be ranked in the following order of decreasing relative resistance to high light intensities: xanthophyll, chlorophyll a, chlorophyll b, and carotenes (SIRONVAL and KANDLER, 1958). No similar studies have been reported for marine algae, although qualitative observations indicate that the phycobilins in red seaweeds are more photolabile than chlorophyll a. Red seaweeds are frequently found to appear green or brownish-green in the upper part of their depth range (e.g. species of *Chondrus*, *Furcellaria*, *Laurencia*) presumably due to preferential photodestruction of the phycobilins (LEWIS, 1964). *Laurencia pinnatifida* in exposed localities becomes yellowish-green towards the end of the summer (REES, 1935); *Gigartina acicularis* loses its red colour and becomes yellowish-green in exposed parts of the intertidal region (SCHMIDT, 1929). In general, in red seaweeds the ratio (phycoerythrin/chlorophyll) tends to increase with increasing water depth (LUBIMENKO, 1925).

Few facts are available about light quality control of photosynthetic pigments in attached marine algae. YOCUM and BLINKS (1958) observed an inverse chromatic control of the pigments of two species of the red seaweed *Porphyra*.

Photosynthesis and respiration

Light supplies energy for the photosynthetic reactions; it also determines the long-term photosynthetic characteristics of plant cells (MYERS, 1946). Between light intensity and rate of photosynthesis exists a linear relation until light saturation is reached. Further increase of light intensity does not change the rate of photosynthesis until the rate begins finally to decrease at critical intensities which are determined genetically and phenotypically.

RYTHER (1956) obtained rate curves of photosynthesis for a variety of marine phytoplankton cultures exposed to different light intensities. He found that green algae, diatoms and dinoflagellates become both saturated and inhibited at progressively higher light intensities. In marine phytoplankton communities of

relatively stable euphotic zones, photosynthetic responses to light vary with habitat depths (RYTHER and MENZEL, 1959; STEEMANN NIELSEN and HANSEN, 1959; ICHIMURA and co-authors, 1962). Phytoplankton from near the surface becomes light saturated as well as photo-inhibited at higher intensities than that from greater depths. However, in the presence of intense water exchange there is not sufficient time for photosynthetic adjustments of phytoplankton to different water depths of the euphotic zone.

YENTSCH and LEE (1966) suggest that changes in environmental conditions, including light, mainly affect photosynthetic dark reactions. However, in view of the role which light intensity plays in regulating rates of pigment synthesis in marine phytoplankton (MCALLISTER and co-authors, 1964), the efficiency of absorption of incident light quanta must also be markedly affected through variations in concentrations of photosynthetic pigments of cells grown at different light intensity levels. When cultures of marine phytoplankton are kept in complete darkness there is a decrease in both photosynthetic light and dark reactions which eventually results in complete loss of photosynthetic ability after some days (YENTSCH and REICHERT, 1963; YENTSCH and LEE, 1966; HELLEBUST and TERBORGH, 1967).

Little is known about the effect of light on respiration in photosynthetic algae. The existence of metabolic intermediates common to both the reductive pentose phosphate cycle of photosynthesis and the oxidative pentose phosphate cycle of respiration suggest that a reciprocal influence is likely to occur. However, it has proved very difficult to demonstrate an immediate effect of visible light on plant respiration (ROSENSTOCK and RIED, 1960). Recent studies on higher plants indicate that photosynthetic cells have a respiration in the presence of light (photorespiration) which occurs by reactions different from those employed in the dark, in addition to normal dark respiration (FORRESTER and co-authors, 1966). No similar studies have been reported for marine algae. Low intensity red light was found to inhibit the rate of respiration in a psychrophilic marine diatom, while high intensity green and red light had the opposite effect (BUNT and co-authors, 1966).

Rapid oxygen utilization at high light intensities has been reported for *Chlorella* (MYERS and BURR, 1940; SIRONVAL and KANDLER, 1958), and for the coccolithophorid *Syracosphaera carterae* (MCALLISTER, 1961). However, excess consumption of O_2 under such conditions is probably due to photo-oxidation, a light-driven oxidation of cellular substrate accompanied by pigment bleaching, rather than an increased rate of respiration.

Chromatophore movement

Orientation movements of chromatophores of unicellular and multicellular marine algae in response to changes in light intensity were observed and described quite extensively by SENN (1908, 1917, 1919). SENN used an optical system which allowed him to expose either whole cells or portions of large diatoms, such as *Biddulphia pellucida* or *Striatella* spp., to intermediate or high intensity light. When the whole cell was exposed to direct sunlight, the chromatophores moved rapidly toward the centrally located nucleus (karyostrophy). If only a portion of the cell was exposed, all chromatophores moved towards the nucleus, but only

after prolonged light exposure. At intermediate light intensities the chromatophores were generally evenly distributed along the periphery of the cells (peristrophy). After long dark periods the chromatophores were found near the nucleus.

Orientation movements of chromatophores of red and brown seaweeds follow fairly similar patterns, although there are some variations depending on cell and thallus type (SENN, 1917, 1919). In general, when thalli of these algae are exposed to intermediate light intensities, most of the chromatophores are found along the outer walls (antistrophy). Under intense light, the chromatophores move and orient themselves along the side walls (apostrophy) where they receive a minimum amount of light due to mutual shading. A similar chromatophore distribution is often found after periods of darkness.

SWIFT and TAYLOR (1967) observed chromatophore movements in response to different light intensities and darkness in cysts of the dinoflagellate *Pyrocystis lunula*. In the dark, the cyst's four chromatophores contract distally. They spread out at intermediate light intensities and contract towards the centre of the cyst at high intensities. SWIFT and TAYLOR also found evidence for a 'biological clock' controlling a circadian rhythm of chromatophore movement from the distally contracted (dark) to the spread out (light) position. The marine pennate diatom *Surirella gemma* has only one large chromatophore; it expands in cultures exposed to intermediate light intensities of 500 to 1200 lux, but contracts in darkness and at light intensities over 2000 lux (HOPKINS, 1966a).

Virtually nothing is known about the mechanism of the chromatophore movements in algal cells. JAROSCH (1958) and KAMIYA (1959) have suggested that actomyosin-like contractile fibrils, located in the plasmagel at the gel–sol interfaces, may be involved. It is interesting to note that chromatophore distribution in the dark and in intense light is often similar; possibly, the strong inhibition of photosynthesis caused by both extremes produces similar cellular conditions, e.g. low ATP/ADP ratios.

Intermediary metabolism

One may expect light to exert strong influences on the relative rates of numerous metabolic reactions through its control of photosynthesis. However, few studies have been devoted to such indirect light effects on marine plants. In the freshwater alga *Chlorella pyrenoidosa* light plays an important role in the turnover of amino-acid pools and affects the relative rates of synthesis of cytoplastic and chloroplastic proteins (BASSHAM and co-authors, 1964). The same phenomena were observed in higher plants (HEBER, 1962; HELLEBUST and BIDWELL, 1963).

After allowing *Melosira nummuloides* and *Peridinium trochoideum* to take up ^{14}C-labelled alanine in the presence of light, isotopic carbon rapidly appears in glucose. However, in the absence of light, there is no transfer of isotopic carbon from alanine to glucose, indicating that the glycolytic pathway does not operate in reverse in the dark in these marine phytoplankters (HELLEBUST unpublished, a, 1968). In the diatom *M. nummuloides*, other reactions too are strongly influenced by light. Conversions of glutamic acid or arginine to proline, and of threonine to isoleucine, proceed very slowly in the dark, but are strongly enhanced by light.

In the marine facultative heterotroph *Cyclotella cryptica*, light prevents the induction of a glucose transport system (HELLEBUST unpublished, a, 1968). Cells

kept in the dark develop the ability to take up glucose. White light of only 4 klux prevents the induction. Assimilation of acetate by the green freshwater flagellate *Chlamydomonas mundana* is accelerated by light; probably via enhancement of biosynthetic pathways utilizing acetate (EPPLEY and co-authors, 1963).

Composition of plant cells

The composition of plant cells may be influenced by both light intensity and quality. Several workers have obtained evidence that the distribution of photo-assimilated carbon in early photosynthetic products is affected by light quality (KROTKOV, 1960). In *Chlorella vulgaris* blue light increases the proportion of photo-assimilated carbon entering the amino-acid and organic fraction as compared to the effects of red light (HAUSCHILD and co-authors, 1962, 1964). Synchronized cultures of *Chlorella vulgaris* grown in blue light produce a higher protein and a lower carbohydrate content than cultures grown in red light (KOWALLIK, 1962). Light-induced changes in the lipids of this alga have also been reported (NICHOLS, 1965).

The only clearly demonstrated light quality or intensity effects on the composition of marine algae concern photosynthetic pigments. Most of the studies on composition of marine algae are related to nutritional factors. There can be no doubt that light plays an important role in the striking seasonal changes which take place in the composition of seaweeds (BLACK, 1948; HAUG and JENSEN, 1954). However, because of the complexity of the ecological field situation (interactions of several important factors such as temperature, nutrient concentrations, etc.) it is not possible to deduce specific light effects from such studies. The more subtle effects of light quality and intensity on the formation of minor constituents such as morphogenetic substances will be discussed later (p. 155).

Ion uptake and ion regulation

There are two obvious ways in which light may influence ion uptake: (1) immediately via photosynthetic production of ATP, and possibly also electron transport, effecting ion uptake against concentration gradients; (2) on a long-term basis depending on photosynthetic assimilatory power, uptake of such ions as phosphate and sulphate through assimilation into organic compounds (in the case of phosphate also into polyphosphates).

The effects of light and darkness on the sodium and potassium content of the marine algae *Ulva lactuca* and *Valonia macrophysa* have been demonstrated very elegantly by SCOTT and HAYWARD (1955). When these algae are placed in darkness there is a gradual loss of potassium and a gain of sodium; illumination rapidly reverses these processes. Light stimulates the uptake of potassium by the red seaweed *Porphyra perforata* (EPPLEY, 1958). More recent work on the freshwater alga *Nitella translucens* demonstrates that the influx of potassium and chloride is light dependent. The active influx of chloride was 0·85 $\mu\mu$ moles cm^{-2} sec^{-1} in light, but only 0·052 $\mu\mu$ moles cm^{-2} sec^{-1} in the dark. Light affects both the influx and efflux of sodium in *Chara australis* (HOPE and WALKER, 1960). It appears that the energy for these transport processes is derived quite directly from light-dependent metabolism.

No information seems to be available about the effect of light on ion uptake and regulation in marine phytoplankton.

Permeability

Light may influence uptake or secretion of a substance either by causing a change in the permeability (diffusion coefficient) of the cell membrane, or by regulating the supply of energy-rich compounds, if an active transport system is involved.

Similar excretion rates were found in a large number of marine phytoplankters at 3 and 25 klux (HELLEBUST, 1965). However, when the algae were transferred to direct sunlight of about 110 klux, considerably higher rates of excretion of organic compounds resulted (Table 2-10). Increased excretion rates were also found in freshwater phytoplankton studied *in situ* at light intensities high enough to inhibit

Table 2-10

Excretion of photo-assimilated carbon by marine unicellular algae at different light intensities (After HELLEBUST, 1965)

Alga	Percentage of organic carbon excreted of total assimilated		
	3 klux	25 klux	120 klux
Exuviaella sp.	2·4	7·7	9
Skeletonema costatum	6·2	5·6	38
Thalassiosira fluviatilis	4·9	3·6	13
Phaeodactylum tricornutum	7·7	5·4	43
Pyramimonas sp.	5·0	7·8	20

photosynthesis (>50 klux) (FOGG and co-authors, 1965). It is possible that very high light intensities cause damage to the cell membranes and thus increase their permeability to organic substances.

Light influences ion fluxes through membranes of marine algae (MACROBBIE and DAINTY, 1958) probably mainly through active transport systems, although changes in permeability cannot be ruled out. Thus, in *Chara ceratophylla* illumination tends to increase permeability particularly to substances with low lipid solubility (JÄRVENKYLA, 1937); blue light is more effective than red.

The excretion of yellow substances by macerated thalli of the brown seaweed *Ascophyllum nodosum* was much higher in the light than in the dark (YENTSCH and REICHERT, 1962). However, this was possibly due to pH changes in the medium accompanying photosynthesis in the presence of light, since CRAIGIE and MCLACHLAN (1964) found essentially no difference between the amount of yellow substances excreted by *Fucus vesiculosus* in the presence or absence of light when the medium was buffered.

Bioluminescence

It is well known that bioluminescence in the surface layers of the ocean is mainly caused by dinoflagellates (KELLY and KATONA, 1966). Light exerts several

distinct effects on the intensity and circadian rhythm of bioluminescence both in cultured and natural populations of marine dinoflagellates. At light intensities below about 6 klux the endogenous rhythm of bioluminescence will persist in *Gonyaulax polyedra* even in continuous light (HASTINGS, 1964). At high light intensities rhythmicity disappears. Intermediate intensities of continuous illumination allow the endogenous rhythm of bioluminescence to continue, but affect the natural period of the rhythm; with increasing light intensities the period becomes shorter. Single light pulses may also change the phase of the rhythm. An increase of both duration and intensity of the light signal increases the amount of phase shift.

Under normal conditions of daily light intensity changes, luminescence attains its maximum during darkness, its minimum during daylight. Light inhibits luminescence at any time during the light–dark period. KELLY and KATONA (1966) demonstrated that the sensitivity of luminescent flashing of natural populations of dinoflagellates to light is controlled by an endogenous diurnal rhythm; it is greatest during midday when flashing is minimal. Bright light appears to inhibit luminescence via the mechanism controlling the cell's ability to trigger the reaction (HASTINGS and KEYNAN, 1965). Recent work by KELLY (1968) has shown that luminescence of non-photosynthetic dinoflagellates may also be inhibited by light.

Although the endogenous rhythm is not light dependent, the intensity of luminescence depends on the light intensity during pre-illumination (SWEENEY and co-authors, 1959). From the action spectrum of photo-enhancement of luminescence in *Gonyaulax polyedra* it appears that photo-enhancement is mediated through photosynthesis.

Bioluminescence in the euphotic zone of extensive areas of the North Atlantic Ocean is closely related to ambient light (YENTSCH and co-authors, 1964). It was concluded that the principal factors influencing the amount of dinoflagellate bioluminescence are photo-inhibition and photo-enhancement. However, studies by KELLY and KATONA (1966) on natural dinoflagellate populations indicate that this conclusion may be an oversimplification, and that an endogenous rhythm plays an important part in the observed changes in bioluminescence intensity on a 24-hr basis. Recently, YENTSCH and LAIRD (1968) found that natural populations of dinoflagellates exhibit an endogenous rhythm of bioluminescence only during summer. The endogenous rhythm disappears when water temperatures fall below approximately 12° C. The exogenous rhythm, in contrast, is a persistent feature of natural populations throughout the year. It appears, therefore, that, during the colder months of the year, the diurnal rhythm of bioluminescence is chiefly controlled through photo-enhancement and photo-inhibition effects of the existing light regime.

Phototactic movements and rhythmic migrations

Detailed studies of the phototactic movements of several marine dinoflagellates, *Ulva* gametes, *Platymonas subcordiformis* and *Dunaliella euchlora* have been reported by HALLDAL (1958). These algae show an active orientation of their locomotion relative to the direction of light by either swimming towards a light source (positive phototaxis) or away from it (negative phototaxis). It is now

possible to produce cultures of cells having either positive or negative phototaxis with a certain threshold value for the phototactic response. The balance of Ca, Mg, and K in the medium appears to play an important role in determining the phototactic response of algal cells (HALLDAL, 1959). Phototactic responses have been reported for zoospores and gametes of *Ectocarpus*, *Chorda* and *Fucus* (DAWSON, 1966), and for *Ulva*, *Cladophora* and *Bryopsis* (BLINKS, 1951; HAXO and CLENDENNING, 1953). Recent studies of phototactic movements of the marine dinoflagellate *Gyrodinium dorsum* have demonstrated short-term light regulation of a receptor mechanism involved in the phototactic light response (HAND and co-authors, 1967). Both blue- and red-absorbing pigments are involved in the receptor mechanism. There is a rapid loss of photoresponse sensitivity when the cells are placed in darkness. The photoresponse can be maintained or re-established by red light. Cells placed in blue light lose their sensitivity rapidly. However, if blue and red light are supplied simultaneously, the photoresponse is maintained at a high level.

Phototactic vertical migrations of dinoflagellates in respose to changing light intensities may be quite common in marine environments. *Ceratium furca*, *C. fusus*, *Peridinium triquetrum* and *Prorocentrum micans* were found to exhibit pronounced stratifications at different levels depending on light conditions (HASLE, 1950, 1954). In general, the cells migrated towards the surface during the day, and away from the surface at night. Evidence for a phototactic vertical migration of *Exuviaella baltica* in an estuary was reported by WHEELER (1964). Most of the population of this dinoflagellate was found near the surface in the morning; later in the day virtually all the cells had moved to deeper water, indicating a definite negative phototactic response. SOLI (1966) demonstrated a more complicated pattern of migration for *Pyrodinium bahamense* in which the dinoflagellate swam up and down twice in a 24-hr period. Further evidence for phototactic movement of dinoflagellates has been obtained by BACKUS and co-authors (1965) during a solar eclipse.

The vertical movement of several pennate diatoms through the sediments of intertidal mud and sandflats is influenced by changes in light conditions, although a diurnal, or tidal, rhythm of migration has been demonstrated to persist even under conditions of continuous illumination (PALMER and ROUND, 1967). Dinoflagellates, euglenoids and blue-green algae found in these sediments probably also undergo similar vertical-migration rhythms; however, detailed studies of light effects on the migration of these algae have not been reported. The diatoms are not found on the surface at night, and they can be kept from emerging on the surface during the day by artificially darkening the sediments. Apparently the events 'light off' and 'light on' act as signals for the phase relations of the migration rhythm. Diatoms already on the surface reburrow after artificial darkening. Light apparently has an attractive effect only during day, since the algae do not come to the surface during periods corresponding to the natural night phase. This observation indicates that the diatoms undergo rhythmic changes in their responses to light intensity. In accordance with this view, FAURÉ-FREMIET (1951) and PALMER (1960) found a reversal in the phototactic response of the diatom *Hantzschia virgata* (incorrectly named *H. amphioxys*: PALMER and ROUND, 1967) during the suprasurface phase of its rhythm. In another estuarine mudflat diatom

Surirella gemma, upward migration is inhibited by light, and there is a light requirement for the water induced motility of downward migration (HOPKINS, 1966b). Further studies are needed to interpret the different light effects on diatom migration reported by PALMER and ROUND, and by HOPKINS.

Growth

This section deals with general responses of cell division and growth of unicellular and multicellular marine plants to different light conditions. Other aspects of responses to light regarding growth, reproduction, and resulting shape and morphology are discussed on pp. 147–148 and 153–157.

Since photo-autotrophic plants depend on their photosynthetic capacity to supply the necessary organic substances and energy for growth, one might expect that growth and photosynthesis of a plant should show the same relation to light intensity and quality. If rates of photosynthesis and growth are measured at different light intensities over long periods of time, this is generally true. However, photosynthetic rates, which are generally measured over short time intervals, and growth rates, which are generally measured as increase in cell number or biomass over relatively long time intervals, are often light saturated at quite different levels of intensity (MYERS, 1946). Thus, *Chlorella*, cultured at relatively low light intensities, develops a much higher capacity for photosynthesis than it can actually utilize for growth at these intensities. Considerably higher light intensities are required for maximum photosynthetic rates than for maximum rates of growth. In contrast, in cells cultured at high light intensities, photosynthetic and growth capacities are more similar in magnitude and light intensity dependency.

A considerable discrepancy between light requirements for photosynthesis and growth of two marine coccolithophorids was demonstrated by JEFFREY and ALLEN (1964). The growth rate of *Hymenomonas* sp. was saturated at about 8000 lux, and that of *Coccolithus huxleyi* at about 2000 lux, while maximum photosynthetic rates for both algae were achieved at approximately 35,000 lux. The growth rate of *Acetabularia crenulata* under continuous light conditions is saturated at about 700 lux (TERBORGH and THIMANN, 1964), but its rate of photosynthesis at about 10,000 lux (HELLEBUST and co-authors, 1967). Extensive studies of cell division rates of marine phytoplankton as a function of light and temperature have been reported by JITTS and co-authors (1964). Light intensity requirements for maximum growth rates under optimal temperature conditions were found to be surprisingly high (0·02 to 0·15 ly/min, or 4000 to 30,000 lux), and are probably similar to those for maximum photosynthesis under the same conditions. THOMAS (1966) found much lower growth-saturating light intensities (6000 to 7500 lux) for a number of tropical oceanic phytoplankters; growth-compensating intensities ranged from 100 to 350 lux.

Under optimal temperature regimes growth rates of marine phytoplankton are not affected at intensities as high as 75 klux (0·4 ly/min) of light containing very little short wavelength radiation (JITTS and co-authors, 1964). However, at either high or low temperatures cell division rates are adversely affected by high light intensities. For instance, *Thalassiosira nordenskiöldii*, when kept below 8° C will only grow at light intensities below 20 klux. High light intensities (above 75 klux) are tolerated only within the comparatively narrow temperature range of 12° to

16° C. Nutrient conditions as well as temperature may influence the relation between light intensity and growth in marine algae (MADDUX and JONES, 1964). In general higher light intensities are required for maximal growth rates at optimal, than at less favourable, conditions of nutrition and temperature. It is possible that the extremely low light intensity requirement (about 800 lux) for maximum rates of cell division reported by SCHREIBER (1927) for the marine diatom *Biddulphia mobiliensis* was due to suboptimal growth conditions.

Most algae appear to grow perfectly well under continuous light, although some recent work indicates that, in particular, multicellular algae may behave quite differently when subjected to a variety of light–dark regimes (see p. 39). Studies on cultures of the dinoflagellates *Gonyaulax polyedra* (SWEENEY and HASTINGS, 1958), *Peridinium triquetrum* (BRAARUD and PAPPAS, 1951), the diatoms *Coscinodiscus granii* and *Biddulphia sinensis* (RIETH, 1939) and the green flagellate *Dunaliella tertiolecta* (EPPLEY and COATSWORTH, 1966) raised under alternating light–dark conditions revealed that cell division may be restricted to certain hours within a 24-hr light–dark cycle. In *G. polyedra*, kept under a 12-hr light–12-hr dark regime, maximum rate of cell division occurs at about the beginning of the light period (SWEENEY and HASTINGS, 1958) and *P. triquetrum* similarly divides most rapidly early in the morning (BRAARUD and PAPPAS, 1951). In contrast to this, members of the dinoflagellate genus *Ceratium* divide in their natural environment only at night (GOUGH, 1905; JÖRGENSEN, 1911; HASLE, 1954). Maximum division rates of the diatoms *Nitzschia palea*, *Biddulphia sinensis*, and *Coscinodiscus granii* occurred during the light period (RIETH, 1939; VON DENFFER, 1949). The effect of light in promoting or inhibiting the synthesis of 'cell division' factors is not well understood (PIRSON and LORENZEN, 1958; TAMIYA, 1966). EPEL and KRAUSS (1966) have demonstrated an inhibitory effect of light on the growth of the colourless alga *Prototheca zopfii* which appears to coincide with cell division. They suggest that this inhibition may be an important factor in the light–dark induced synchrony in algae.

A reduction of the lag phase occurs in the dinoflagellate *Prorocentrum micans* with increasing light intensity above saturation values for growth rate during exponential growth (KAIN and FOGG, 1960).

The effect of light offered in discrete photoperiods on the daily cell production of *Dunaliella tertiolecta* could be explained as a direct relation between cell production and the product of illumination intensity and length of photoperiod, at growth-limiting intensities (EPPLEY and COATSWORTH, 1966). Similarly, the unicellular red alga *Porphyridium cruentum* decreases its growth rate with decreasing daylength (JONES and co-authors, 1963). Growth of the marine diatom *Biddulphia sinensis*, however, is strongly inhibited when cultured under continuous light (RIETH, 1939). Continuous illumination is also less favourable for the growth of marine dinoflagellates than diurnal illumination (HASLE and NORDLI, 1951). The growth of the diatoms *Fragilaria striatula* and *Synedra tabulata* is 'daylength dependent' since cell division rates are significantly lower during short days than during long days, both above and below the saturating light intensity (CASTENHOLZ, 1964). Two other diatom species, *Melosira moniliformis* and *Biddulphia aurita* showed little or no dependence on daylength. In view of the varied responses of different plankton algae to light periodicity, further

work with more species is required for adequate evaluation of the importance of daylengths for phytoplankton growth under natural conditions.

Light quality affects photosynthesis (LEVRING, 1947); hence one may expect corresponding effects on growth. However, there appear to be more specific light quality effects on growth and cell division which cannot be explained simply by the wavelength dependency of photosynthesis. BAATZ (1941) reported considerable differences in cell division rates and morphology when marine diatoms were exposed to light of equal energy but different spectral composition (Fig. 2-19).

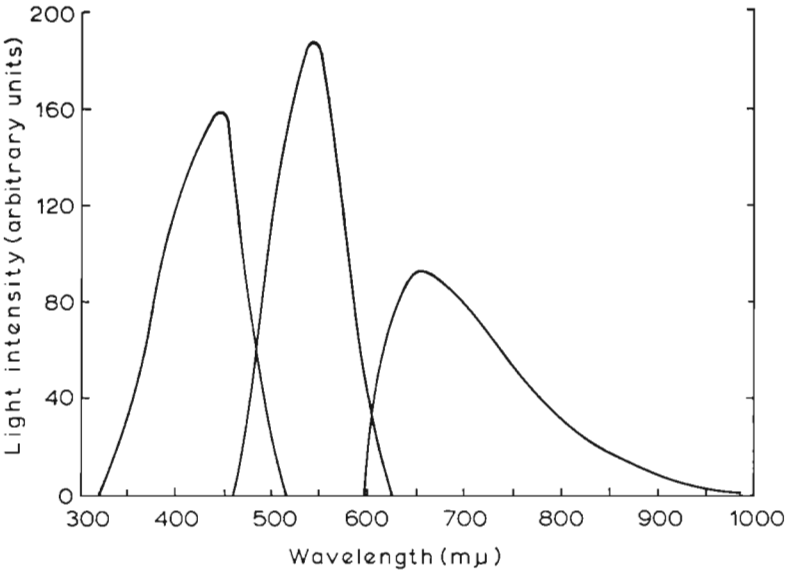

Fig. 2-19: Spectral distribution of light in 3 different culture chambers used for growth studies on marine diatoms. (After BAATZ, 1941.)

In general, the growth rate of diatoms exposed to green light was about 40% higher than in blue, and about 80% higher than in red light (Fig. 2-20). When *Biddulphia sinensis* was cultured in red light for longer than 8 to 10 days, visible distortions of cell shape, and further decreases in cell division rates resulted. BAATZ also observed some interesting transition effects. When cells previously raised under red light were transferred to blue light, a very high growth potential in blue light resulted. But when the cells were first grown in blue light and then transferred to red light, a growth depression resulted (Table 2-11). Both effects were only temporary and might have been partly due to chromatic effects on pigment composition. KAIN and FOGG (1958, 1960) found that incandescent and fluorescent lighting had very different effects on growth rates of the dinoflagellate *Prorocentrum micans*. Growth inhibition was observed at 3000 lux from 'white' fluorescent tubes, while 39,000 lux from tungsten lamps caused no growth inhibition. In view of the changes in spectral composition of light with depth in the ocean it is highly desirable to obtain more information about light quality effects on growth of planktonic algae.

The controversy between ENGELMANN (1883, 1884) and GAIDUKOV (1904), on

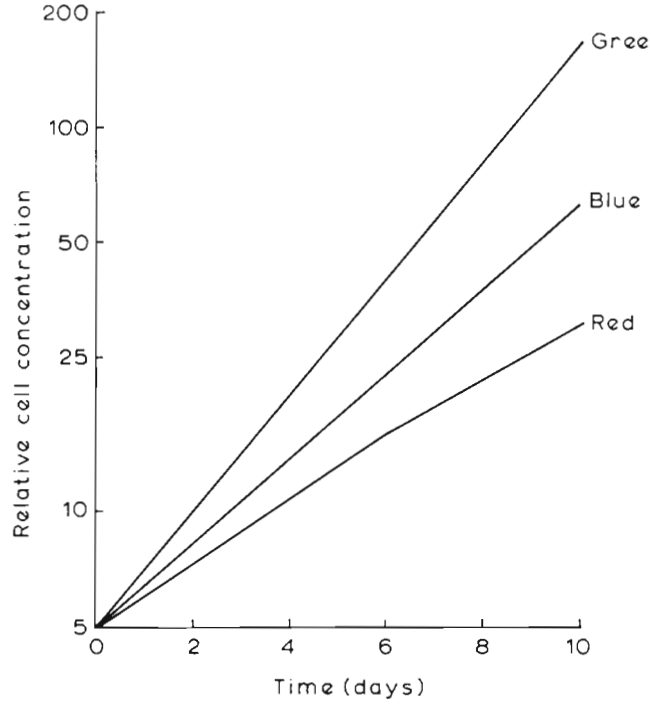

Fig. 2-20: Population growth of *Chaetoceros didymus* in green, blue and red light at 14° to 16° C. (After BAATZ, 1941.)

Table 2-11

Growth of *Biddulphia sinensis* during successive exposures to red and blue light of equal energies* (After BAATZ, 1941)

Experiment	Time (days)			
	0–2	2–4	4–6	6–8
	Light			
A	Red 0·34	Red 0·33	Blue 0·55	Red 0·25
B	Blue 0·41	Blue 0·50	Red 0·26	Blue 0·56

* The body of the table gives daily increment factors (averages).

the one hand, and BERTHOLD (1882) and OLTMANNS (1892), on the other, about the relative effects of light intensity and quality on growth and distribution of marine algae, stimulated a number of scientists during the first three decades of this century to investigate light quality effects on the photosynthesis of various green, brown and red seaweed species (LEVRING, 1947). However, little work was done to determine long-term effects of light of different spectral composition, but equal energy, on growth of macroscopic marine algae. The rather short periods (usually less than 24 hrs) used in measurements of photosynthesis do not allow plants sufficient time to become adapted to the experimental conditions, whereas growth experiments which usually last for several days or weeks will allow adaptation to take place. Thus, YOCUM (1951) found that *Porphyra perforata* grows initially much faster in green than in red light. However, after several days, the growth rate increases in red light, apparently due to chromatic adaptation.

Most of the recent work on light quality effects on seaweed growth has been done with young sporelings and gametophytes. Sporelings and gametophytes of several *Laminaria* spp. grow as well in blue light as in daylight, but red light inhibits both growth and reproductive development (HARRIES, 1932). Sporelings of the green seaweed *Monostroma* grow more rapidly in yellow, red or blue light than in brown or green light (ARASAKI, 1953). Since these experiments were not done with light of well-defined spectral composition and equal energy content, it is difficult to evaluate and compare the results. However, there can be no doubt that differences in spectral composition may cause important alterations in growth rates of at least some algae.

The growth of sporelings of the intertidal red algae *Plumaria elegans* and *Antithamnion plumula* is more than doubled by removing a few percent of the incident green light in the waveband 480 to 570 nm of either tungsten or fluorescent light sources (Table 2-12) (BONEY and CORNER, 1962, 1963). It appears that a critical balance of wavelengths in the incident light is necessary for optimal growth of these sporelings. The sporelings of the deep-water red alga *Brongniartella byssoides* respond differently to changes in the spectral composition of light; when about 4% of the green light is removed growth increases by about 20% over that of controls; when 42% of the green light is removed, growth is inhibited by over 40% (Table 2-12). BONEY and CORNER (1963) suggest that phycoerythrin serves

Table 2-12

Amounts of light transmitted by solutions of eosin yellow with corresponding effects on sporeling growth (After BONEY and CORNER, 1963)

Concentration of eosin yellow in screening solution (mg/l)	Percentage of total light energy transmitted (380–720 nm)	Percentage transmitted between wavelengths 380–480 (nm)	480–570 (nm)	570–720 (nm)	Percentage increase in cell production *Antithamnion plumula*	*Plumaria elegans*	*Brongniartella byssoides*
0	100	23·3	41·6	35·1	0	0	0
0·2	98·4	23·3	40·0	35·1	+150±5	+125±7	+19±2
2·0	92·7	23·1	34·5	35·1	+2±7	+5±2	−10±1
20·0	75·5	16·0	24·4	35·1	+1±5	+3±4	−41±6

different functions in red seaweeds depending on their vertical distribution: in intertidal algae, phycoerythrin may chiefly protect against damaging green light, while in deep-water species, the biliprotein may serve chiefly as an accessory pigment in photosynthesis.

Acetabularia crenulata grows more rapidly in blue than in white light of approximately the same intensity (Fig. 2-21) (TERBORGH, 1965). The test algae grew slowly in red light during the first few days of light exposure; thereafter growth ceased almost completely. However, if the cells grown in continuous red

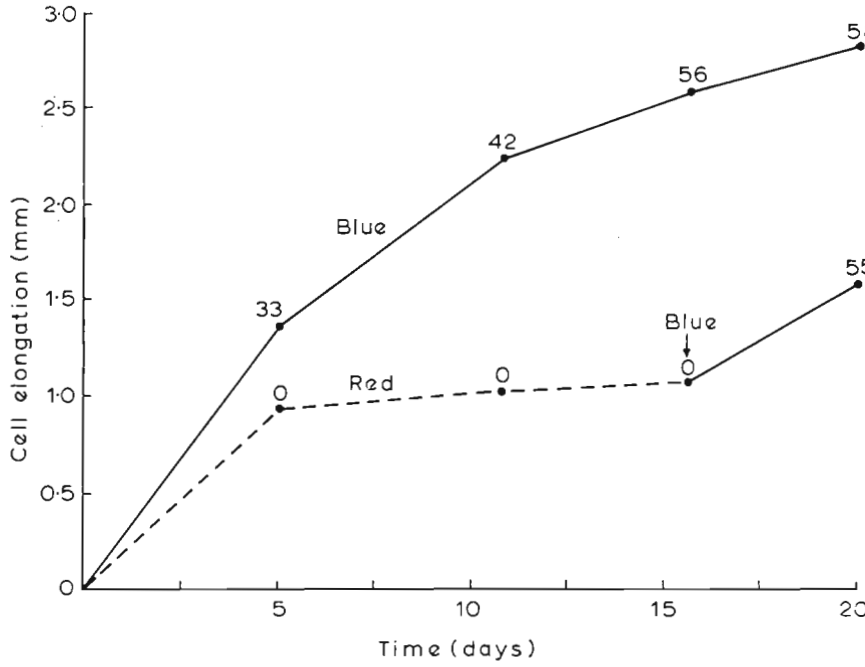

Fig. 2-21: Elongation of enucleate cells of *Acetabularia crenulata* in blue (1·5 mW cm^{-2}) and red (1·6 mW cm^{-2}) light. Cells given red light were transferred to blue light after 15 days. Numbers over points refer to the percentage of cap-bearing cells in sample.(After TERBORGH, 1965; modified.)

light were exposed for as little as 1 min to blue light of the same intensity (about 0·4 mW cm^{-2}), an appreciable (over 50% of that in continuous blue light) steady growth rate resulted (CLAUSS, 1963; TERBORGH, 1965). This blue-light effect probably acts via a special enhancement of photosynthesis, different from the classical Emerson enhancement effect of short wavelength light (TERBORGH, 1966).

As early as 1892, OLTMANNS reported his extensive investigations on light requirements for growth of marine macro-algae. Unfortunately, he did not provide quantitative data of light intensities, but he demonstrated clearly that seaweeds vary considerably in their light intensity–growth characteristics. He also observed that representatives of algal species living near the surface grew and matured considerably more rapidly than their counterparts at depths with lower light intensities. BERTHOLD (1882) made similar observations in the Gulf of Naples.

The light intensity regime of the environment is one of the most important

factors for establishment, growth, and successful development of algae *in situ*. Although seaweeds may show considerable phenotypic variability, the fact that certain species are confined to quite limited depth ranges indicates the presence of species-specific differences. Thus, the compensation point of the intertidal alga *Plumaria elegans* at 16° C is 50 lux (1·6 erg sec^{-1} mm^{-2}) and light saturation for growth is reached at 22,000 lux (75 erg sec^{-1} mm^{-2}) (Boney and Corner, 1962); in contrast, the shade-loving alga *Delesseria decipiens* has a light saturation of about 1200 lux (Haxo and Blinks, 1950). Sporelings of the red intertidal alga *Antithamnion plumula* reach maximum rate of cell division at about 500 lux (17 erg sec^{-1} mm^{-2}) of continuous illumination, while the corresponding value for the sublittoral alga *Brongniartella byssoides* amounts to only about 220 lux (7 erg sec^{-1} mm^{-2}).

Temperature may modify light requirements for growth. Thus, at 10° C growth of *Laminaria* sporelings is light saturated at about 350 lux (35 μgcal cm^{-2} sec^{-1}); at 17° C, however, saturation values lie between 1000 and 2000 lux (Kain, 1965). Minimum light intensity requirement for growth and development of gametophytes at 10° C is of the order of 20 lux (7 μW cm^{-2}) on a continuous illumination basis (Kain, 1964). The growth of young *Ectocarpus* sporelings is light saturated below 1350 lux (0·57 mW cm^{-2}) and light intensities as high as 16 klux (6·7 mW cm^{-2}) do not exert any inhibitory effect (Boalch, 1961). However, the lag phase is markedly affected by light intensity, and there is a marked optimum for a minimum lag phase at about 7000 lux (2·9 mW cm^{-2}).

Relatively little is known about light requirements for growth in older seaweeds *in situ* or under laboratory conditions. From the limited information available it appears that mature seaweeds may have higher light intensity requirements for growth than younger stages. This may of course be due partly to the larger bulk of the older algae causing mutual shading of cells in the thallus, and also mutual shading of branches of the larger algae. *In situ* studies indicate that the brown alga *Scytosiphon lomentarius* grows much better at a depth of 1 m than at the surface or at 2 m, which suggests that this alga requires a high light intensity for maximum growth (Klugh and Martin, 1927). The green seaweed *Enteromorpha linza* requires a lower light intensity: it grows best at a depth of about 2·5 m. The red alga *Gracilaria confervoides* has a high light intensity requirement for maximal growth rate and grows most rapidly when suspended just below the surface (Causey and co-authors, 1946).

Daylength may be an important factor for growth and development of marine macro-algae in nature, although the information available indicates that most macro-algae can be grown satisfactorily under continuous illumination. Beth (1955) measured growth rates of several species of *Acetabularia* in photoperiods ranging from 1 to 24 hrs per day. He found that the rate of stalk elongation strongly depends upon the duration of illumination up to light periods of 12 hrs per day. When *Acetabularia crenulata* is grown at low to moderate light intensities on a light–dark regime, growth can be accelerated either by lengthening the light period or by raising light intensity (Terborgh and Thimann, 1964). However, when relatively high intensities are used during 8-hr light periods, only the length of the light period is limiting, since the daily irradiance would be more than adequate to sustain a higher growth rate if given in longer photoperiods. Although the growth

rate of *A. crenulata* is sensitive to photoperiod, it does not appear to be subject to photoperiodic control in the same sense as applies to higher plants. However, recent studies on other marine algae indicate that true photoperiodic effects may regulate growth and development in at least some algae. IWASAKI (1961), and IWASAKI and MATSUDAIRA (1963) found that the life cycle of the red alga *Porphyra tenera* could be regulated by daylength. The life cycle of this alga includes two growth forms. The *Conchocelis* form is found only during long days (summer), and when cultured under long days it produces only *Conchocelis* colonies. The *Porphyra* form occurs during the short days of the winter and can be cultured only under short day conditions; if it is kept under long day conditions, the thallus disintegrates, releasing carpospores which will give rise to *Conchocelis* colonies.

Recent studies on growth and development of the perennial red seaweed *Constantinea subulifera* have revealed an interesting photoperiodic growth response (POWELL, 1964). Between 21 and 28 days of critical daylength of approximately 14 hrs is required for the initiation of a new blade. If the plant is returned to continuous light before the required number of critical days, the stipe tip rounds up and resumes apical growth. Length of the daily light period may also influence the growth of sporelings. Thus, *Enteromorpha* sporelings grow better under long-day conditions, whereas sporelings of *Monostroma* grow best initially under medium daylength, later under short-day conditions (ARASAKI, 1953).

(c) *Reproduction*

Few studies have been devoted to analyzing light effects on the reproduction of unicellular marine algae. BRUCKMAYER-BERKENBUSCH (1954) studied the auxospore formation in *Melosira nummuloides* under a variety of experimental conditions; reproduction is delayed by strong light and short or long photoperiods; it is enhanced by reduced light and intermediate photoperiods. *Lithodesmium undulatum* produces only oogonia under continuous light; low light intensity in a natural light–dark cycle causes only the formation of antheridia (VON STOSCH, 1954). In *Biddulphia sinensis* auxospore formation occurs much more frequently in blue than in red light (BAATZ, 1941).

Recent work indicates that both light intensity and daylength may be important for the reproduction of marine diatoms. When grown under 12-hr light–12-hr dark conditions *Stephanopyxis palmeriana* remains practically vegetative. Under short-day conditions asexual resting spores are formed, while sexual stages are induced under long-day conditions. Furthermore, when cells are grown under long days in fairly dim light (300 to 500 lux), only auxospore mother cells are produced, whereas at higher light intensities (2000 to 3000 lux) only male cells are formed (STEELE, 1965). The photoperiod also influences the range of other conditions under which the gametes develop and are released. In *Coscinodiscus concinnus*, under long days the range of conditions suitable for male gamete formation is considerably more restricted than in the case of short days. Auxospore formation is accelerated by short photoperiods (HOLMES, 1966).

Discharge of gametes and spores of attached marine algae may be affected by a variety of environmental conditions such as light intensity and regime, temperature, nutrient concentration and water movement. In many marine algae

endogenous, lunar or daily rhythms seem to be involved in triggering the discharge of reproductive cells (LANG, 1965); in general, the release of gametes or spores takes place around daybreak indicating the direct importance of dark–light transition. However, since endogenous rhythms are also often involved, it is necessary to ascertain whether one is dealing with direct, or indirect light effects. Furthermore, light probably also influences the formation of reproductive cells, but usually only its effect on their release has been studied.

A number of observations indicate that light intensity may be important for the reproduction of seaweeds. Relatively high intensities (6500 to 7500 lux) stimulate the production of plurilocular sporangia, and also the release and germination of the spores of *Ectocarpus confervoides* (BOALCH, 1961). The ratio of unilocular to plurilocular sporangia of *E. siliculosus* can be changed by varying light intensity as well as daylength (Table 2-13) (MÜLLER, 1962); the effect of daylength is not a

Table 2-13

Percentages of unilocular and plurilocular sporangia on *Ectocarpus siliculosus* grown at 16° C at various light intensities and daylengths (After MÜLLER, 1962)

Light intensity (lux)	3500	750	3500	3500
Daylength (hrs)	14	14	9	24
Percentage of unilocular sporangia	75	94	96	16
Percentage of plurilocular sporangia	25	6	4	84

photoperiodic phenomenon, but depends on the total light quantity. In *Vaucheria sessilis* high light intensities (above 3000 lux) inhibit zoospore formation, while low light (below 2500 lux) and darkness favour the formation of gametangia (HUSTEDE, 1957). Indoleacetic acid stimulates, and indolecarboxylic acid inhibits zoospore formation, indicating a possible relation between light effects and auxin metabolism in the reproduction of *Vaucheria sessilis*.

Light quality also appears to be important for the reproduction of attached algae. Thus, gametophytes of several species of *Laminaria* develop normally in blue light, while red light retards the formation of antheridia and inhibits strongly the formation of oogonia (HARRIES, 1932). In the red alga *Nitophyllum punctatum* blue light is more effective in enhancing tetraspore formation than green light, while red light is ineffective (SAGROMSKY, 1961). In *Monostroma nitidum* only light below 500 nm is effective in triggering gamete discharge (SHIHIRA, 1958).

Daylength and light periodicity greatly affect development and reproduction of marine macro-algae. In *Nitophyllum punctatum* tetraspore discharge occurs rhythmically under daily light–dark periodicity, with maxima following the onset of light: it is correlated with a daily periodicity of nuclear division. The discharge rhythm is apparently determined by periodic spore formation. Under continuous light or in continuous darkness, the discharge is aperiodic. In *Halicystis parvula* gamete formation takes longer under continuous light than under a light–dark

cycle. Plants kept under a light–dark cycle release their mature gametes immediately after dark-to-light transition. Gametes will also be released in the dark, but after a longer period of time. Gametangia formation is more synchronous under a light–dark cycle than in continuous light (ZIEGLER, 1966). In nature, gametes of *H. parvula* are released approximately biweekly, in relation to tides, with the appearance of light on the day of their maturation (HOLLENBERG, 1936).

The *Conchocelis* phase of *Porphyra tenera* forms monospores only under short-day conditions whereas the *Porphyra* phase produces carpospores only during long days (KUROGI, 1959; IWASAKI, 1961). The stimulation of spore formation in the *Conchocelis* phase by short-day conditions has recently been shown to be a genuine photoperiodic response mediated by phytochrome (DRING, 1967). The green alga *Monostroma* develops more rapidly under short-day conditions with a rich formation of spores (ARASAKI, 1953). HYGEN (1948) discovered interesting photoperiodic effects on the reproduction of the marine green alga *Ulothrix flacca*. Biciliate zoids, formed under different daylengths, are morphologically alike; however, spores produced under long-day conditions fuse in pairs and produce zygotes, while zoids formed under short-day conditions behave as asexual spores and develop directly into new filaments. Also, no germination of the zygotes formed under long-day conditions will take place unless the zygotes are transferred to short-day conditions. This daylength effect may be the key to the seasonal periodicity of appearance of *U. flacca* in northern waters.

Maturation of conceptacles and release of gametes in *Ascophyllum nodosum* on the Norwegian coast start at the beginning of June at latitude 58° N, but 40 to 50 days later at latitude 70° N (PRINTZ, 1959). It seems possible that this difference depends on the marked differences in relative daylengths at these two latitudes.

Gamete release in *Dictyota dichotoma* can be phased by light given during the dark period of a regular light–dark cycle (BÜNNING and MÜLLER, 1961; VIELHABEN, 1963). Light of only 0·3 lux (0·13 μW cm^{-2}) applied for 10 hrs during a normal dark period is sufficient to cause gametes to be released 10 days later, indicating that moonlight may be important as a phasing factor. A short dark period is necessary to stimulate discharge of gametangia from mature, fertile thallus sections of *Pelvetia fastigiata* (JAFFE, 1954); a 3-min period of darkness is sufficient to produce a substantial discharge. A similar requirement for darkness has been demonstrated for *Monostroma nitidum* (SHIHIRA, 1958). On the other hand, after a sufficient period of darkness, exposure to light appears to act as trigger for gamete release. The length of the required dark period is not additive since a short interruption by light will cancel the effect. After a sufficiently long dark period, liberation of gametes may be induced by a 1-sec light exposure of wavelengths shorter than 500 nm; light of longer wavelengths has the same effect as complete darkness. It appears that activation of gametes proceeds in two steps, one is inhibited, and the other triggered by blue light.

Summarizing the information presented above it may be said that light intensity, light quality, and photoperiod significantly affect the reproduction of unicellular as well as multicellular marine plants. We must know more about the mechanisms and the physiological and biochemical nature of the light effects reported. We also must find out just how important true photoperiodism is in regulating the reproductive capacity and the mode of reproduction of marine algae.

(*d*) *Distribution*

Planktonic algae are continually changing their vertical position in response to light conditions and as a result of water movement. The depth of the euphotic zone, in which the majority of the planktonic algae is found, depends primarily on the total amount of light received and the transparency of the water. In tropical regions with high average surface illumination throughout the year, the vertical distribution of photosynthetic algae often extends to depths of about 100 m. In higher latitudes and in more turbid coastal waters vertical distribution of phytoplankton is confined to a much more restricted vertical range. The low phytoplankton productivity of the North Atlantic during the dark winter period is due to the insufficient light received; the planktonic algae are transported by water mixing in layers considerably deeper than the depth at which photosynthesis equals respiration (SVERDRUP, 1953). Higher productivity is restricted to periods with increased light intensity (summers), and reduced vertical water exchange.

Distribution maxima of planktonic species with different light intensity requirements for growth are not often observed, due to vertical water exchange; even in quiet water vertical distributions may be modified by other factors, such as grazing and temperature. However, dinoflagellates may exhibit pronounced depth stratification as a function of light conditions (HASLE, 1950).

Light is probably the most important single factor determining the vertical distribution of marine attached plants. Since photo-autotrophic plants cannot exist for extended periods of time at light intensities too low to allow photosynthesis to equal respiratory losses of organic carbon, light intensity determines the lower limits of growth both in planktonic and attached benthic plants. However, there are other ecological factors, such as temperature, salinity, water movement, substratum and intertidal exposure which influence the distributional patterns of marine algae, particularly in the intertidal region. The interactions of all these factors make it difficult to assess specific light effects on field distributions, especially in near-shore habitats (see also Chapters 3, 4, 5, 7 and 12).

Both light intensity and quality change with water depth, and hence influence the vertical distribution of marine plants. Following the first, simple classification by ÖRSTED (1844) regarding the vertical distribution of attached marine algae into three zones (upper green, middle brown, lower red) ENGELMANN (1884) attempted to explain this vertical distribution of different coloured seaweeds on the basis of the changing light quality with depth. ENGELMANN (1884) and GAIDUKOV (1904) proposed the hypothesis of 'complementary chromatic adaptation', which maintains that efficient absorption of light requires pigments of complementary colour to that of the incident light. On the basis of this hypothesis red algae are found in the deepest plant zone where the incident light is mainly green, since they assimilate more efficiently than other algae in light of this composition; green algae, on the other hand, absorb and assimilate red light most efficiently, and hence occur near the surface, since red light attenuates quickly with depth; brown algae use red and blue light efficiently, but have a wider extension in the blue-green area of the spectrum, and consequently assume an intermediate position.

The view that light quality is the key factor determining the vertical distribution

of attached algae was strongly opposed by BERTHOLD (1882) and OLTMANNS (1892) who considered the vertical distribution to be chiefly determined by light intensity. Although one may superficially talk about a colour zonation of algae—green algae are abundant in the upper regions, red algae usually in deeper water—a strict zonation according to colour does not hold. Thus, OLTMANNS pointed to the frequent occurrence of red algae growing near the surface, often shaded by brown seaweeds, and BERTHOLD demonstrated the occurrence of green and brown seaweeds at considerable depths along with red algae. From observations in nature and culture experiments in the laboratory, BERTHOLD and OLTMANNS concluded that seaweeds have different, species-specific light intensity requirements for optimal growth, and that algae are distributed in nature chiefly according to their light intensity requirements. Algae with wide light intensity tolerances (euryphotic), such as *Gelidium crinale*, are found in the Bay of Naples near the surface in bright sunlight, at considerable depths, or in shadowed areas near the surface. Algae with high light intensity requirements and tolerance, such as *Fucus vesiculosus*, are found near the surface in exposed locations. Low light intensity-requiring species, such as *Callithamnion elegans*, are either found in deep water or in shaded locations near the surface.

Scientists have since tried to settle the controversy between ENGELMANN and GAIDUKOV on the one hand, and BERTHOLD and OLTMANNS on the other, regarding the relative importance of light quality and intensity as determining factors of the vertical distribution of marine algae (LEVRING, 1947). Most of them agree that both intensity *and* quality are important.

Red algae have an advantage over green algae at great water depths because of their efficient absorption of green light. However, a green alga with very high pigment content may still be able to absorb most of the incident green light, which can then be efficiently used for photosynthesis. If the green alga in question also has, at the same time, a low rate of respiration—and, therefore, a low compensation point—it may compete quite successfully with umbriophilic red algae in deep water. Although red algae are usually much more numerous than green or brown algae in the deeper plant zone, this is not always the case. At the Dry Tortugas, Florida, where the flora is typically tropical, TAYLOR (1928) found the following species composition at 19·5 m: 78% Chlorophyceae, 7% Phaeophyceae and 15% Rhodophyceae. Furthermore, the marine phanerogam *Halodule engelmanni* has a vertical distribution from 4·6 to 73·2 m below mean tide level, indicating that it must have a very wide tolerance to changes in both light intensity and quality. The more common marine phanerogam *Thalassia testudinum* requires relatively high light intensities and forms vast beds from near low tide level down to 11 m.

In general, marine plants penetrate to greater depths in the clear waters of the tropics than in the more turbid waters of temperate regions (see also Chapter 6.2). Along the North Sea coasts, attached algae are found down to a maximum depth of some 40 m, while on the Mediterranean coasts algae have been dredged from depths of almost 200 m (CHAPMAN, 1964). The high concentrations of dissolved yellow substances found in coastal waters of temperate regions may influence the vertical distribution of algae by reducing the transparency of the water. Maximum depth for seaweeds decreases from approximately 28 m at the mouth of the Trondheim Fjord to 10 m in the innermost part of the fjord. This difference has

been attributed to the high concentration of yellow substances supplied by rivers to the surface layers of the fjord (PRINTZ, 1926).

In contrast to the rather low maximum distributional depths of algae in temperate regions, e.g. only about 15 m on the Massachusetts coast (LAMB and ZIMMERMANN, 1964), seaweeds in Arctic and Antarctic environments may normally occur down to 40 m and even to depths exceeding 100 m (LUND, 1958; DELEPINE and co-authors, 1966; ZANEVELD, 1966; WILCE, 1967). In view of the very low light intensities penetrating to these depths during the greater part of the year, it is surprising that algae are able to grow at these great depths. The low water temperatures of polar waters probably permit them to reduce their respiratory losses so that the little light available may be used with great functional efficiency (EHRKE, 1931). KJELLMAN (1883) and WILCE (1967) have suggested that these algae may grow partly heterotrophically by taking up dissolved organic substances from the surrounding water.

Mutual shading may significantly modify development and growth, and thus the distribution, of many seaweeds, particularly in the intertidal region. Rapid changes in light intensity from full sunlight exposure to shaded conditions, appear to be tolerated by many algae which cannot withstand continued exposure to high light intensities. The movement of thalli of larger seaweeds, caused by wave action or currents, creates frequent changes in light intensities to which parts of these algae, epiphytes or algae growing under or between the larger seaweeds are subjected. Shade afforded by rocks, pilings, undercut platforms, caves or steep-sided cliffs is a key factor determining the distribution of marine plants (OLTMANNS, 1892; SCHMIDT, 1929; DELLOW and CASSIE, 1955; LEWIS, 1964). Light conditions caused by rocks, pilings, cliffs, caves, etc., and in micro-environments such as small cracks and crevices in solid substrata, as well as those created by other organisms, may affect germination and growth of plant propagules and thus their chances for successful settlement. In a small culture chamber with a continuous light gradient, ranging from complete darkness to full light exposure, swarmers of *Ectocarpus* and *Pylaiella*, contaminated by diatoms, developed into germlings occupying a well-defined band close to the darkest end of the chamber. Near the brightest side was a thick cover of diatoms, and at the darkest end no vegetation (OLTMANNS, 1892).

Little information is available about light effects on seasonal succession in marine phytoplanktonic species. Quite obvious is the important role of increasing light intensities for spring phytoplanktonic blooms in northern waters. Since light effects may be modified by temperature it is difficult to determine specific light effects from information obtained *in situ*. CONOVER (1956) explained the succession of *Thalassiosira nordenskiöldii* by *Skeletonema costatum* in Long Island Sound by the preference of the latter for higher light intensities and for temperatures exceeding 4° C. The recent observations by BRUCKMAYER-BERKENBUSCH (1954), STEELE (1965) and HOLMES (1966) that daylength affects growth and reproduction of marine diatoms (see p. 146) indicate that light periodicity may be an important factor in phytoplankton succession.

Changes in light intensity and periodicity throughout the year strongly influence seasonal succession of attached marine algae. Unfortunately, few studies have been published on such light effects. Many seaweeds occur only during

certain seasons. Seasonal changes in species composition are more pronounced in temperate regions, due to the extensive seasonal changes in temperature and light intensities, than in tropical areas with their much smaller changes in these physical parameters (FELDMANN, 1951, 1957).

Seasonal occurrence of *Ulothrix flacca* in the spring in northern waters is probably caused by changes in daylength and water temperature (HYGEN, 1948). While the formation of reproductive cells in the mature plant takes place only under long-day conditions, zygotes will germinate only when transferred to short-day conditions. Seasonal succession in life cycle phases has been observed in the red alga *Porphyra tenera* (IWASAKI, 1961); in nature, the filamentous *Conchocelis* phase grows only in the long-day season, the leafy *Porphyra* phase only in the short-day season. The transition between the two phases coincides practically with equinox.

Summarizing our present knowledge of light affecting distribution and seasonal succession (species composition) it may be concluded that there is much general information available from field studies; however, due to the complex interactions of physical, chemical and biotic factors, it is difficult to assign specific environmental effects to light from observations in nature. It is necessary, therefore, to develop satisfactory culture methods and to study light effects on distributional patterns and seasonal successions under controlled conditions in laboratories and in outdoor water bodies. We must improve our skills in growing complete life cycles of both attached and planktonic algae, so that we may learn more about the specific effects of light intensity and periodicity—and the role of interfering environmental factors—on distribution and succession of marine plants.

(3) Structural Responses

(*a*) *Size*

The relation between light conditions and final size of a plant has been analyzed only in a few studies. Under laboratory conditions, JITTS and co-authors (1964) observed an increase in size of *Skeletonema costatum* cells with increasing light intensity (0·005 to 0·4 ly min^{-1}) at low temperatures (8° to 12° C). They did not observe auxospore formation during their experiments, and it seems therefore likely that this light response took place during vegetative growth. BAATZ (1941) reported considerable differences in chain lengths of cells of *Biddulphia sinensis*, when exposed to lights of equal energy but different colour composition. In blue light 81% of the chains consisted of 4 or more individual cells; in red light only 10%. The average cell size of *Chaetoceros didymus* is larger in blue than in red light (BAATZ, 1941). In dinoflagellate populations, size variation appears to be a regular feature (BRAARUD, 1958), but no information is available on specific light effects on final cell size.

The fact that attached algae in the Arctic, which are exposed to very low light intensities throughout most of the year, are as a rule much smaller than representatives of the same species at lower latitudes where light is more abundant, indicates that light may affect the final size of the plants (WILCE, 1967). However, one cannot rule out simultaneous effects of temperature in arctic and boreal environments.

Mature thalli of the red algae *Grateloupia filicina* vary considerably in size and shape depending on their location. Where conditions are somewhat muddy the mature plants are small and virtually unbranched. This may be taken to indicate that *G. filicina* reaches a reduced final size at low light intensities, although responses to other factors such as high concentrations of organic substances, etc. may also be involved (DIXON, 1963). *Gelidium crinale* growing near the level of high water of neap tides has small erect fronds, usually less than 1 cm in height, while fronds at the level of low water of spring tides reach a maximum size of about 10 cm. This difference in final size results both from an increased growth rate, which is probably dependent on light conditions, and from a longer life span at the lower level (DIXON, 1963). Other seaweeds, such as *Chondrus crispus* and *Pterocladia capillacea* also exhibit considerable size variations depending on their location, and it seems likely that light conditions contribute to these variabilities.

(*b*) *External Structures*

It has been known for a long time that the morphological polarity of a germling may be determined by the direction of light during germination of spores of fertilized eggs. Photo-induction of polarity is the transformation of an apolar into a polar cell during early stages of development, resulting in an unequal division of the cell, or at least in an unequal distribution of cell contents. During germination of fertilized eggs of many Fucaceae unidirectional light generally causes the germling rhizoid cell to form on the side opposite to the light source (WHITAKER, 1940). The action spectrum for this effect shows that shortwave visible light is responsible (JAFFE, 1958). The decisive factor is not the direction of the light, but its intensity gradient (NIENBURG, 1922). During unilateral illumination the rear is less illuminated than the front because of strong attenuation of light inside the cell. If the direction of the light is reversed at hourly intervals, bipolar embryos can be obtained (CHILD, 1941). A minimum exposure to unilateral light of about 1 hr is necessary for the determination of a polarity gradient (HAUPT, 1958). This minimum exposure time cannot be reduced by an increase in light intensity.

If *Fucus* eggs are exposed to unilateral plane-polarized white light coming both from above and below, they tend to germinate horizontally in the plane of vibration, forming two rhizoids in opposite directions (JAFFE, 1956). A model illustrating the position of photoreceptor molecules in the *Fucus* egg has been proposed to explain polarity effects of light on germination (JAFFE, 1958).

Light has a polarity effect on a number of other brown algae. In germinating spores of species of *Cystoseira*, *Dictyopteris* and *Dictyota*, light direction determines the plane of the first division; the new walls are formed at right angles to the incident rays (WINKLER, 1900). Similarly, the rhizoids formed by germinating spores ordinarily grow away from the light, but in darkness they grow in all possible directions (PEIRCE and RANDOLPH, 1905). In general, rhizoids or holdfasts are negatively phototrophic, while the rest of the thallus is positively phototrophic.

Phototropism is orientation of growth in relation to light direction. Positive phototropic responses—growth of plants toward the light source—was reported by BERTHOLD as early as 1882 for a number of marine algae, including *Derbesia marina*, *Ectocarpus humilis* and *Antithamnion cruciatum*. Phototropic responses

have also been observed for the large multinucleate unicells of members of the Siphonales, *Caulerpa* and *Bryopsis* (NOLL, 1888; KLEMM, 1893). NASR (1939) demonstrated phototropism in *Acetabularia*. Little appears to be known about light effects on the polarity of germinating spores of red algae, or about phototropic effects on growth of red algae (BLOCH, 1943). BLINKS (1951) observed weak phototropism in *Cladophora* and *Griffithsia* and believes that this response may be fairly common in algae grown in quiet water.

An unusual phototropic response was reported by JONES (1959) for the red alga *Gracilaria verrucosa*; it shows a pronounced positive phototropism at high light intensities, but not in response to low or intermediate intensities. Since lower light intensities promote growth, JONES suggests that the response at high light intensities is not the result of auxin migration, which might be expected to occur under all intensities, but is due to growth inhibition of the thallus side facing light. The response was already observed after 3 hrs of intense illumination.

Phototropism of algae may change from a positive to a negative response with increasing light intensity above a certain threshold (BERTHOLD, 1882). Further studies of this interesting phenomenon are desirable. Much less is known about the mechanism of phototropic and polarity responses in algae than in higher plants. However, since a polar distribution of auxins has been demonstrated both in a brown alga *Fucus vesiculosus* (MOSS, 1966) and a green alga *Bryopsis* (JACOBS, 1951), it seems likely that light may affect the distribution of auxin. HAUPT (1965) recently discussed the nature of photoreceptors for polarity and phototropic responses in algae. On the basis of similarities of the available action spectra, he suggests that polarity induction in germ cells and phototropism in rhizoids have some fundamental processes in common.

Little is known about specific light effects on cell shape of unicellular algae. BAATZ (1941) found that red light causes distortion of the cell shape in the diatom *Biddulphia sinensis*, and also a shortening of the average chain length of cells.

BERTHOLD (1882) reported a number of interesting structural responses of attached seaweeds. When germlings of the green alga *Bryopsis* are kept in weak light, only prostrate filaments are formed. Relatively high light intensities are necessary for normal formation of the feather-like thallus of this alga. Even the mature thallus responds morphogenetically to different light intensities. BERTHOLD observed the formation of rhizoids from branches of the thallus when the plant was kept in very weak light. A number of other marine algae similarly produce rhizoids in response to reduced light intensity (OLTMANNS, 1905). When the brown seaweed *Sphacelaria fusca* is transferred from strong to weak light, shoot apices transform into rhizoids (ZIMMERMANN, 1923). Also the degree of thallus branching is light-intensity dependent in many algae. *Callithamnion corymbosum* becomes more heavily branched when kept at high light intensities than at low intensities; species of *Spermothamnion*, *Polysiphonia*, *Antithamnion* and of other genera respond similarly. With increasing light intensity axil cell length decreases, while branch cell length increases considerably. A differential growth rate response of axil and branch filaments to light intensity thus appears to be one of the key mechanisms by which light affects the external morphology of these plants (BERTHOLD, 1882).

The fronds of *Fucus vesiculosus* narrow in response to high light intensities both

in nature and in the laboratory (OLTMANNS, 1892). A number of red and brown seaweeds respond to high light intensities by forming additional hairs on their thallus surface (BERTHOLD, 1882; OLTMANNS, 1892). When the algae are grown at low intensities, these hairs are much less numerous, or completely absent.

Polysiphonia urceolata, distributed from mean low water spring tides to a depth of about 9 m below this level, exhibits morphological differences depending on its location (TAYLOR, 1966). Individuals growing in the upper levels are elongated with much branched filaments and without distinct main axes, and reach a length of 10 to 20 cm. Individuals at the lower levels have prostrate axes without branches and are smaller in size. Cultures of *P. urceolata* grown in the laboratory at very low light intensities over a period of many months respond by abnormal growth patterns; their thalli lack branches over long portions of their axes, while individuals grown at higher light intensities produce well branched thalli.

Structural responses to directional light have often been observed in marine macro-algae. When the red alga *Antithamnion cruciatum* is grown in diffuse light, it produces upright axes with opposite and alternating pairs of short branches (OLTMANNS, 1905). Directional light results in prostrate main axes with rhizoids on the lower side attached to the substratum. *Spermothamnion flabellatum*, *Callithamnion corymbosum* and *Halopteris filicina* exhibit similar although less complicated morphological responses to directional light (BERTHOLD, 1882). When *Caulerpa* is kept in a culture dish with one-sided illumination from a window, new proliferations form on the side of the thallus facing the window (KLEMM, 1893). Regeneration of *Caulerpa* occurs only on the illuminated side of its thallus, regardless of whether this is physically the upper or lower side (NOLL, 1888).

A large number of observations indicate that light gradients are important in establishing polarity in attached algae (BLOCH, 1965; HALBSGUTH, 1965; MÜLLER-STOLL, 1965; VON WETTSTEIN, 1965). *Cystoseira barbata* rhizoids or holdfasts form in the direction away from the light source, while in darkness the rhizoids arise in all possible directions from germinating spores (PEIRCE and RANDOLPH, 1905). The root pole of *Dasycladus clavaeformis* may become a shoot if exposed to stronger light intensity than the shoot pole (WULFF, 1910). In *Bryopsis* the morphological expression of polarity can be changed even in old plants (BERTHOLD, 1882); in weak light the apices of unicellular and multinucleate, pinnate, branched shoots develop rhizoids. Similarly, a complete reversal of rhizoid and leaf polarity of this alga occurs in response to a reversal of the light gradient (NOLL, 1888).

Recent studies have revealed a number of interesting morphogenetic responses to light in the green alga *Acetabularia crenulata*. When *A. crenulata* is grown at low light intensities (about 600 lux), no cap formation occurs (BETH, 1953); after transfer of such low-light grown, capless plants to high light-intensity conditions (5000 lux), caps are formed; it is sufficient to expose low-light grown plants for a short period of time, in order that cap formation may proceed upon return to low-light conditions. It appears that the conversion of precursors of morphogenetic substances to their active forms requires high light intensities. Strong light accelerates cap formation to such an extent that the plants may consist almost entirely of rhizoid and cap, the stalk being almost negligible in length (BETH, 1955).

Structural responses of external features to light quality have hardly been explored. They may be expected to yield rewarding insights into photoreceptor

mechanisms and morphogenetic co-ordination. Blue and violet light triggers the formation of leaf proliferation in *Caulerpa prolifera*, while red and yellow light are not effective (MICHEELS, 1911; DOSTAL, 1945). *Acetabularia crenulata* and *A. mediterranea* form caps in blue but not in red light. Only a very brief exposure (as little as 1 min) is necessary to allow red-light grown cells to increase their growth rate and form caps. Far-red light is ineffective in replacing blue light for this response (RICHTER, 1962; CLAUSS, 1963). In comparison to white light yielding the same growth rate, blue light causes both quantitative and qualitative morphogenetic effects in *A. crenulata* (TERBORGH, 1965): the time required for cap initiation is much longer, and the mean cell length reached is considerably greater in blue light. Cap morphology in blue light is similar to that of caps formed in nature, but differs considerably from caps formed in white fluorescent light.

External structural responses to varying daylengths have been examined only in a few cases. From the classical example of the effect of daylength on the life cycle of *Porphyra*, we know that a change in daylength may induce a different thallus form. For instance, when the leafy thallus, which thrives in short-day seasons, is exposed to long-day conditions, it becomes thick and degenerates, and scattered groups of large cells produce spores which germinate into filamentous thalli. It seems possible that light periodicity may similarly regulate the transition of one morphological form into another in the life cycles of other seaweeds.

(c) *Internal Structures*

Since marine plants respond to different light conditions by modifications in size and external structures, one would expect responses also on the cellular or subcellular levels. However, this again is an important aspect in the ecology and physiology of marine plants which has been badly neglected. Some careful observations were made by BIEBL (1956, 1957) on the appearance of cells of algal thalli which had been exposed to intense light for various periods of time. The cells responded by drastic changes in chromatophore shape, and inflation of cell membranes in tissues that were severely damaged, but not yet killed by the extremely intense light treatment. WILCE (unpublished a, b, c) investigated the morphology of a number of red and brown crustose algae collected at different depths throughout their range of vertical distribution. He found that these algae do not change their internal structure with depth, although the usual increase in photosynthetic pigment concentration with decreasing light intensity is evident.

The green siphonous alga *Tydemania expeditionis*, which grows abundantly at greater depths in the Eniwetok Atoll, differs from other members of the Codiaceae in having chloroplasts throughout its entire thallus instead of only in cells of the external layers. GILMARTIN (1966) suggests that low light intensity is the principal factor applying evolutionary pressure for the development of such a thallus which permits efficient utilization of low levels of light.

Light intensity may play an important role in the degree of calcification in calcareous algae. BERTHOLD (1882) observed that *Acetabularia* is heavily calcified in exposed conditions, but weakly calcified when grown under low light intensities.

Light quality may affect the cap morphology of *Acetabularia crenulata* (TERBORGH, 1965). Under white light of moderate intensity, caps are formed in

which the individual chambers are free and without particular orientation; caps formed in blue light were planar, each chamber laterally attached to the adjacent ones, and resembled caps formed under natural conditions.

No responses on the subcellular level have come to the reviewer's attention, although it may be assumed that the changes in pigment composition of marine algae grown under different light conditions can be accompanied by structural changes inside the chromatophores.

(4) Conclusions

Marine algae vary considerably in their tolerance to visible and ultra-violet light. This variability is due both to different abilities to adapt phenotypically to different levels of irradiation, and to genetic differences. In general, planktonic algae seem very adaptable to varying light conditions, and the effects of high light intensities on surface plankton appears to be mostly reversible. Prolonged exposure to ultra-violet light is lethal to most algae, but lethal doses vary with species and physiological conditions. The degree of protoplasmic resistance to ultra-violet radiation of attached algae from different depths shows no correlation with the light conditions. This contrasts sharply with the close correlation observed between tolerance to visible light and light exposure in attached algae. Lower limits of light tolerance are poorly known for marine plants. There appears to be a great deal of species variability, and individual algae change their light requirements through physiological adaptation in response to varying environmental conditions.

A large number of aspects of algal metabolism are strongly influenced by light conditions. The absolute and relative amounts of photosynthetic pigments depend on light intensity as well as quality. Light intensity and quality affect both the immediate rate of photosynthesis of plant cells as well as their photosynthetic characteristics through long-term adaptation. Since photosynthetic dark reactions and respiration have many intermediates in common, one may also expect light to influence respiration. However, little is known about such light effects as yet.

Chromatophore movement and orientation in both planktonic algae and macroalgae are light dependent. Such movements may serve either to protect the cell from light damage, or to allow maximum utilization of light for photosynthesis, depending on incident light intensity. The relative rates of many reactions in intermediary metabolism, as well as the composition of cells of marine plants, are probably strongly light-dependent. Furthermore, there is good evidence that the uptake and exchange of electrolytes, as well as the uptake and excretion of organic substances, are influenced by light. Other cellular activities, such as rhythmic migrations, bioluminescence and phototaxis respond to the light intensity and periodicity of the environment.

Marine algae vary considerably with respect to their light requirements for growth. Furthermore, nutrient conditions as well as temperature strongly influence the relation between light intensity and growth. Most algae appear to grow perfectly well under continuous light, although recent studies indicate that some algae—planktonic as well as multicellular forms—may grow and develop quite differently when subjected to different photoperiods. Seaweeds such as

Porphyra tenera and *Constantinea subulifera* exhibit very interesting photoperiodic growth responses, and at least in the case of *P. tenera* it appears that its photoperiodic response is mediated through phytochrome.

The reproduction of many multicellular and some unicellular marine plants shows a strong dependence on light intensity and quality as well as periodicity. Most of our information about light effects on reproduction of marine plants comes from work with attached algae where light is important both in the formation and discharge of reproductive cells. Light quality, in some cases, may affect the formation of male and female gametangia differently, and only relatively short-wavelength visible light is effective in triggering gamete discharge. It is particularly important to obtain more information about the physiological and biochemical nature of responses of marine plants to light intensity, quality and periodicity.

The distribution of algae, both horizontally and vertically, depends on various aspects of the light factor such as its intensity and quality, and daylength. The upper and lower tolerance limits of marine plants to light intensity play an important role in their vertical distribution according to local conditions of degree of light exposure. Seasonal occurrence of both unicellular and multicellular algae is probably light dependent, but only in a few cases do we have useful information about the nature of such relationships. Daylength is probably most important in determining the succession of species and life cycle forms of attached algae at higher latitudes.

The size and morphology of marine plants depend on light conditions of their environment, but very few detailed studies have been devoted to these important relationships. The photo-induction of morphological polarity in eggs and germlings of seaweeds is well known, and phototropic responses have also been described for a number of algae. The mechanisms of such responses in algae are, however, poorly understood. The external structures of marine plants respond to light intensity and quality as well as periodicity. Such responses—many of which were noted before the turn of the century—present many interesting problems that may be successfully attacked by modern techniques of physiology, biochemistry and structural analysis.

Many of the light-dependent functional and structural responses of marine plants are also to varying extents influenced by other factors such as temperature, salinity and nutrients. This chapter has, as far as possible, dealt with responses specifically due to light conditions of the environment.

2. LIGHT

2.3 ANIMALS

2.31 INVERTEBRATES

E. SEGAL

(1) Introduction

In this chapter an attempt is made to summarize our present knowledge of the effects of light on marine invertebrates. Throughout the euphotic and littoral regions of all oceans the various modalities of light (intensity, spectral composition, angular distribution, polarization and duration of light period or dark period) modified by the time of day and year, the latitude, the presence or absence of water and the depth and clarity of water, all exert effects upon functions and structures of marine invertebrates. Possibly no part of the sea is without light, for even in the depths of the ocean, below the level at which light from the surface may stimulate a photoreceptor, light is produced by luminescent organisms.

It is unfortunate that instrumentation and procedures for measuring light in the sea are not uniform (Chapter 2.0). Some workers measure underwater light in luminous watts/unit area squared. According to TYLER (personal communication) it is from this approach that all the 'mad units' are derived, e.g. foot candles and metre candles or lux. Other workers measure underwater light in radiant watts/unit area squared over either a unit solid angle (radiance, N) or from all directions (irradiance, H). The difficulty is that both groups of workers are not measuring the same thing, and attempts to convert from one set of measurements to the other is neither feasible nor sensible. Luminous watts are based upon the integration of the total energy flux and the spectral composition of the human eye over the range of visible wavelengths. In contrast, irradiance measurements are made over a narrow spectral band (near monochromatic light) with maximum intensities at specific wavelengths. Thus, the measured values can be selected to match or at least approximate the spectral sensitivity maximum of a migrating organism, if it is known, or of the water itself at specified depths where the organisms are found. It seems eminently more sensible to measure light in terms of the medium in which one is working and in terms of the sensitivity of the organisms in that medium. The use of foot candles and lux in underwater measurements should be avoided.

Of necessity, certain restrictions have been placed upon the contents of this chapter. While organismic responses to light will be covered, biochemical and physiological mechanisms underlying the responses will be treated only insofar as they lend clarity to an interpretation. The nature of the photoreceptors, visual acuity, spectral sensitivity, the neurophysiological correlates of the photoreceptor pathways and the special topic of bioluminescence will be the subjects of a

subsequent volume of this treatise and will, therefore, not be reviewed here. In all cases references will be provided in lieu of coverage.

(2) Functional Responses

(a) *Tolerance*

The statement that many marine invertebrates cannot tolerate strong light is not uncommon; however, direct evidence is scanty. An inference of lack of tolerance has usually been drawn from evidence such as the prevalence of diurnally migrating species, settlement of intertidal forms under shelter, nocturnal activity of benthic organisms, both sessile and motile, and withdrawal of tube dwelling or valve closure of shelled forms, when subjected to increased illumination. Many of the studies carried out on the tolerance of marine invertebrates to light are old and do not present reliable information on the subject.

Nauplii of the barnacle *Balanus perforatus* exposed to direct sunlight (no intensity given) died unless the ultra-violet component was filtered out (EWALD, 1912). Other studies showed that the polychaete *Myrianida pinnigera* died in light at a temperature much lower than could be tolerated in the dark (DEHORNE, 1918); the hydroid *Tubularia crocea* was killed in various intensities of ultra-violet (KLUGH, 1929); newly settled spat of the oyster *Ostrea commercialis* may be killed in direct sunlight (ROUGHLEY, 1933); polar bodies in the eggs of the polychaete *Nereis limbata* did not develop after exposure to ultra-violet light (JUST, 1933); larvae of the lobster *Homarus americanus* had a higher survival rate when reared in almost complete darkness than when reared in light (TEMPLEMAN, 1936); young stages of an unidentified ophiuroid (subsequently found to be *Ophiomyxa* sp.) were narcotized under strong light, all movement ceased and death followed protracted exposure (FELL, 1941); larvae of the oysters *Ostrea edulis* and *Crassostrea virginica* were damaged and, in some cases, killed by ultra-violet irradiation (ABOUL-ELA, 1958).

Harmful or inhibitory effects of light on metabolism or growth have been reported for the mysid *Mysis* (MERKER, 1926), the copepod *Calanus finmarchicus* (HARVEY, 1929; MARSHALL and co-authors, 1935), young colonies of the hydroids *Tubularia crocea* and *Pennaria tiarella*, the barnacle *Balanus eburneus* (MCDOUGALL, 1943), cypris larvae of *Balanus improvisus* and *B. amphitrite* (VISSCHER and LUCE, 1928) and growing *B. balanoides* (KLUGH and NEWCOMBE, 1935).

The lethal effect of ultra-violet radiation on cells and molecules is well documented (SELIGER and MCELROY, 1965); the action of visible light is an enigma. FRIEDRICH (1961) has put forth the suggestion that light damage to marine organisms is due to a photodynamic effect. Photodynamic action requires the presence of fluorescent materials which become photosensitized by light in the presence of oxygen. Can marine organisms be damaged when exposed to light in the presence of fluorescent substances? Yes, according to PEREIRA (1925) who showed that eggs, sperm and larvae of the sea-urchin *Arbacia* were not injured when exposed to light in pure sea water or with eosin in cultures in the dark but soon died when exposed to eosin in the light. TENNENT (1942) exposed eggs of the urchin *Lytechinus variegatus* to neutral red and a series of other dyes and found

that all the dyes were toxic to varying degrees depending upon the concentration of the dye and the intensity of light radiation; the damaging effect was primarily a surface phenomenon.

Significantly, *Lytechinus variegatus* can be photosensitized with injections of eosin Y, bengal rose and neutral red into the coelomic cavity so that they cover themselves (p. 185) in dim light (MILLOTT, 1956). OKAJIMA (1961) exposed the freshwater protozoan *Spirostomum* sp. to light in the presence of eosin and found an optimum concentration of dye (1×10^{-4} M eosin), at an unspecified intensity of illumination, which produced a maximum effect on contraction of the animal and reversal of ciliary beat. In a weak solution the action was on the surface; in a stronger solution the dye penetrated. In a different approach YANAGITA and KOUDA (1964) demonstrated a high sensitivity to photodynamic sensitization in the acontium of the anemone *Diadumene luciae*. Nematocysts, which normally do not respond to light, discharge stinging threads after photosensitization of the acontium. Exposure to illumination of 40 klux in 6×10^{-4} M eosin, or stronger, in sea water was sufficient to cause extrusion and explosion of the nematocysts. Concentrations of $1{\cdot}2 \times 10^{-4}$ M eosin or weaker caused capsule extrusion but no explosion. Nematocysts in isolation were found to be insusceptible to photodynamic activation. The time required for the dye to sensitize was very short, less than 1 min in $2{\cdot}4 \times 10^{-3}$ M eosin to 30 mins in 6×10^{-6} M eosin. This suggests that the photodynamic action is primarily on the cell surface, and YANAGITA and KOUDA (1964) postulate an action bringing about a loosening in the surface structure of the epithelial cells.

Visible light may also serve as a mutagenic agent in the absence of exogenous photosensitizers (LEFF and KRINSKY, 1967). Mutant cells lacking chlorophyll, chloroplasts and chloroplast DNA were produced by irradiating *Euglena gracilis* in aerobic conditions with visible or red light (greater than 610 mμ) of an intensity equivalent to that of direct sunlight. The photosensitizer is apparently the endogenous chlorophyll. Whether marine invertebrates possess endogenous photosensitizers that may serve as mutagenic agents is unknown.

Are there fluorescent substances in the ocean? Yes. Phycoerythrin and phycocyanin, algal pigments, are fluorescent and indications are that they may act as photosensitizers (MOORE, 1958). The sea itself contains a substance (yellow substance) which fluoresces in the blue region. KALLE (*in*: JERLOV, 1963) proposes that yellow substance or melanoidines originate from the breakdown of living material. DUURSMA (*in*: JERLOV, 1963) concurs and his findings, plus those of KOE and co-authors (1950), on fluorescent substances from the sea bottom, indicate the widespread occurrence of potential photosensitizing materials in the sea. Further, many tube-dwelling and burrowing annelids normally accumulate an excess of porphyrins in various tissues and blood (MANGUM and DALES, 1965). Human porphyriacs are afflicted with a pathologic excess of free porphyrins and porphyria is due to photodynamic sensitization. The worms, on the other hand, are infaunal animals which spend their lives in total or nearly total darkness. It is difficult to keep representatives of many annelid species in the laboratory when exposed to light; they die, just like human porphyriacs, with surface lesions all over the body (MANGUM, personal communication); porphyrin sensitization may explain this difficulty. It seems significant that the crowns of sabellids (*Myxicola infundibulum*,

Sabella penicillus and *Megalomma vesiculosum*), exposed to light when feeding during the daytime, contain no free porphyrin. Surprisingly, free chlorocruoroporphyrin has been demonstrated in the asteroids *Astropecten irregularis* and *Luidia ciliaris* (KENNEDY and VEVERS, 1954). Since porphyrins are known to render living tissues more sensitive to light, the free porphyrin may be involved in integumentary photoreception (VEVERS, 1966). The same suggestion was made by KENNEDY (1959) for the unscreened ventral surface of the porphyrin (uroporphyrin I)-bearing pulmonate slug *Arion ater*. For additional references on photodynamic effects in marine invertebrates and a discussion of the medical aspects of photodynamic sensitivity in man and animals consult BLUM (1964).

(*b*) *Metabolism and Activity*

Metabolism

Growth. Studies on the direct effect of light on growth in marine invertebrates are difficult to assess because of the variety of measures used as criteria for growth. Growth is not simply increase in linear dimension or mass but includes various tissue-forming and related activities that precede and follow the actual change in linear dimensions. Field studies on growth are difficult to interpret because of multiple factor interactions. For discussions of aspects of growth in decapod crustaceans, molluscs and echinoderms—the groups in which most of the studies have been conducted—consult PASSANO (1960), WILBUR and OWEN (1964), and SWAN (1966).

Light has long been recognized as a controlling environmental factor of primary importance in the growth of reef-building (hermatypic) corals. Reef corals always grow towards the light; they are rarely found in caves or other dark places. Further, reef-building corals, without exception, contain photosynthetic algal symbionts or Zooxanthellae (consult YONGE, 1963, for references and a discussion of the nature of Zooxanthellae) which are invariably confined within wandering or carrier cells in the endodermal tissues. Growth in corals is achieved by an increase in mass of the calcareous skeleton and a concomitant proliferation of the overlying tissues. Surprisingly, there is no constant relationship between these two kinds of growth. Attempts to measure growth rates of reef-building corals were, during the early years, confined to observations of coral colonies in their natural habitats (GOREAU, 1959). The approach to the problem was markedly changed by the introduction of a technique using radio-active calcium-45 as tracer to determine calcium deposition in the skeleton (GOREAU, 1959; GOREAU and GOREAU, 1959).

Under laboratory conditions (25·0° or 28·5° C, with continuous aeration), of seven species of coral, in which calcium deposition was measured both in the light (twin-bank of 20 W fluorescent tubes 30 cm above the experimental chambers; light intensity not stated) and in the dark, four species (*Porites divaricata*, *Acropora prolifera*, *Pocillopora damicornis* and *Oculina diffusa*) show significantly increased calcium incorporation (as μg Ca mg N/hr) in the light (Fig. 2-22). The other three species (*Porites compressa*, *Cladocora arbuscula* and *Montipora verrucosa*) showed increased calcium incorporation in the light but not significantly so (GOREAU, 1959). Under experimental field conditions (consult GOREAU and GOREAU, 1959,

for details), of 12 species in which calcium uptake was measured under sunny skies, overcast skies or at night (either all three or any two), all showed a marked increase with the increase in ambient light (underwater light intensities were not measured). In general, calcium uptake was fastest at noon on a sunny day, reduced by 50% on a cloudy day and reduced approximately by 90% at night.

The effect of the presence or absence of Zooxanthellae on calcification was determined in *Manicina areolata* and *Oculina diffusa* (GOREAU, 1959). During approximately 6 weeks in the dark, both species extruded their Zooxanthellae and,

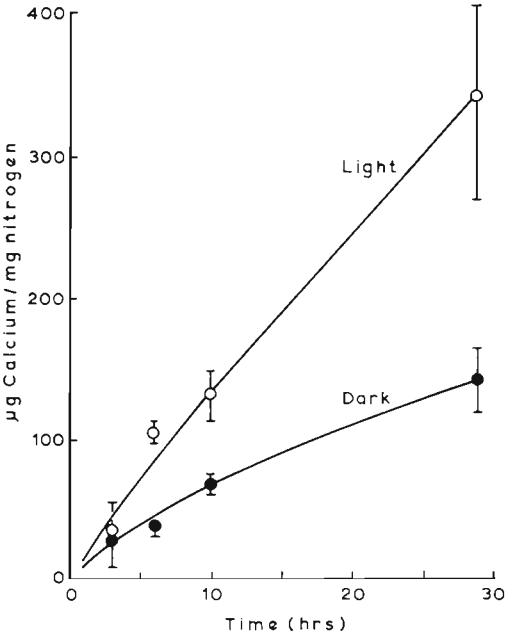

Fig. 2-22: Skeletal growth of *Acropora prolifera* as a function of calcium incorporation in the light and in the dark. Vertical lines through the points represent the standard deviation of the means. (After GOREAU, 1959.)

except for the absence of colour (the coenosarc was completely colourless and transparent), the polyps were fully expanded and appeared normal. In the light, calcium uptake in *O. diffusa*, with Zooxanthellae, was $1{\cdot}6 \pm 0{\cdot}38$ μg Ca/mg N/h while without Zooxanthellae it was $0{\cdot}37 \pm 0{\cdot}01$ μgCa/mg N/h. In the dark, with Zooxanthellae, the calcium uptake was $0{\cdot}81 \pm 0{\cdot}15$ μgCa/mg N/h while without Zooxanthellae it was $0{\cdot}26 \pm 0{\cdot}01$ μgCa/mg N/h. The data on *M. areolata* show the same relationship as in *O. diffusa*. It seems, then, that colonies with Zooxanthellae not only calcify faster in the light than in the dark, but faster in the dark when Zooxanthellae are present than in the light when they are not. Fortuitously, GOREAU and GOREAU (1959) were able to corroborate this finding with natural colonies of *M. areolata*, without Zooxanthellae, which were found alive and in good condition, growing unattached in semidarkness under a large hollow coral

head. The calcium uptake of the normal coral, with Zooxanthellae, was 13·4 ± 7·54 μgCa/mg N/h in sunshine and 1·8 ± 0·42 μgCa/mg N/h in darkness while the calcium uptake of the bleached colony (without Zooxanthellae) was 0·7 ± 0·31 μgCa/mg N/h in sunshine.

The role of Zooxanthellae in the growth process is not clear. While they seem to play an important role in determining calcification rates in reef-building corals, they do not appear to be directly linked with the calcification process since they are absent from deep-sea and cold-water corals (although ZAHL and MCLAUGHLIN, 1959, collected polyps, epizoic on a hexactinellid sponge, and a madreporarian coral from below 200 m off Key Largo, Florida, whose tissues bore dense concentrations of Zooxanthellae) and are present in many non-calcareous shallow-water cnidarians both in tropical waters (e.g. the actinarian *Condylactis* sp. and the scyphozoan *Cassiopeia* sp. from the Caribbean) and temperate waters (e.g. *Anthopleura elegantissima* and *A. xanthogrammica* from the southern California intertidal). Further, there seems to be no relationship between the process of calcification and the number of symbiont algae present in a given species or in different parts of the same species. According to GOREAU (1959), large apical polyps of some of the branching acroporid corals (*Montipora verrucosa, Porites compressa, Pocillopora damicornis* and *Acropora conferta*) contain few Zooxanthellae but calcify several times faster per unit of tissue nitrogen than the lateral polyps which are full of algae. In contrast, in the new buds of seriatopoid corals, Zooxanthellae aggregate at the site of the budding as though essential to the growth of new polyp tissue. In the dark, budding is inhibited (ATODA, 1951). GOREAU suggests that the presence of these algal symbionts, even when not photosynthesizing, may have a potentiating effect on the calcification rate of the coral host by exerting a stimulating effect on the host's metabolism. (Consult GOREAU, 1961, and YONGE, 1963, 1968, for discussions of possible calcium and carbonate pathways during calcification in reef-building corals and the possible role of Zooxanthellae in metabolic waste removal from the host.) Most significantly, Zooxanthellae isolated from the reef-coral *Pocillopora damicornis* and the reef-dwelling bivalve *Tridacna crocea* incorporate labelled CO_2 photosynthetically. In the presence of some component of host tissue up to 40% of the labelled algal photosynthate is liberated, primarily as glycerol (MUSCATINE, 1967). Preliminary experiments suggest that host tissue seems to stimulate photosynthesis, possibly indirectly through shading to yield more favourable light intensities incident on the algae, or directly by chemical catalysis.

There are a number of studies concerned with the role of light on the growth of freshwater crustaceans (PASSANO, 1960) but very few studies on light and growth of marine crustaceans. The one definitive study has been carried out by BLISS and BOYER (1964) on the decapod *Gecarcinus lateralis*. Growth in decapod crustaceans appears to be a discontinuous event. Increase in size occurs only when the animal sheds its shell (moults), and the shedding is the most conspicuous event associated with crustacean growth. CARLISLE and KNOWLES (1959) have proposed a terminology to describe the four principal stages of crustacean growth: 'proecdysis' which immediately precedes the shedding of the shell; 'ecdysis' which is the actual shedding of the shell; 'metecdysis' when the shell is hardening; 'diecdysis' which is a short period that occurs in continually moulting forms or

'anecdysis' which is a long period in seasonally moulting forms. The most significant event in each intermoult cycle is the beginning of proecdysis, a period of intensive growth. In *G. lateralis* and other decapods, a rapid, marked increase in size of a limb bud reflects rapid growth on the part of the entire animal.

In *G. lateralis*, darkness promotes growth. Under experimental conditions when crabs are exposed to constant darkness, at a favourable temperature (28° C), they enter the proecdysial stage and moult with minimum delay. When crabs are exposed to constant light, at the same temperature, they complete a preliminary growth phase then enter a long period of anecdysis before moulting (Fig. 2-23). Corroboration was obtained when crabs in constant light were moved into constant darkness and immediately initiated proecdysial growth and moulted. The converse was also true; proecdysial limb growth (in constant darkness) was stopped abruptly when crabs were exposed to constant light. Artificial eye covers clearly

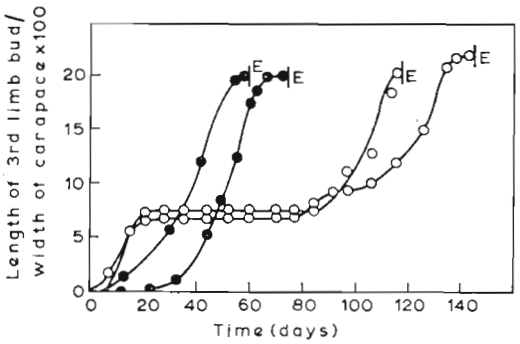

Fig. 2-23: Effects of constant darkness (●) and constant light (○) on limb regeneration in the decapod crab *Gecarcinus lateralis*. Each curve represents limb bud growth of 1 crab which typifies the responses of other individuals. E: ecdysis. (After Bliss and Boyer, 1964.)

showed that light acts via the compound eyes to inhibit growth. However, according to Bliss and Boyer (1964), constant darkness, while stimulating growth and moulting a first time, did not readily do so a second or third time. The crabs had to be exposed either to constant light or LD 12:12 for 24 hrs before being returned to constant darkness. Under these conditions, anecdysis following the first moult was shortened. Bliss and Boyer (1964) have also shown growth dependency upon temperature, size, presence or absence of moist sand and, most critically, seclusion. The duration of proecdysial growth may also be influenced by the background (Rao, 1966). On a white background *Ocypode macrocera* showed no difference in proecdysial growth in constant light or constant dark; on a dark background the proecdysial growth period was prolonged. All these environmental factors can act in combination with light modifying the resulting effects. Bliss and Boyer suggest that environmental factors, including light, operate through neuro-endocrine pathways to regulate growth in *G. lateralis* and possibly other decapod crustaceans.

Recent critical work on the freshwater crayfish *Orconectes virilis* has led AIKEN (1969) to propose that,

> 'Long days inhibit synthesis (by the X-organ) or release (by the sinus gland) of molt inhibiting hormone (MIH), and the inhibition is proportional to the day length (photophase). Maximum titer of MIH occurs in short days or constant darkness, but the X-organ sinus gland complex eventually becomes refractory and MIH titer decreases. MIH controls the molt cycle principally by preventing the tissues from reacting to MH (molt hormone), and proecdysis is induced when the endocrine balance shifts in favor of MH.'

Significantly, according to AIKEN, the moult cycle of the lobster *Homarus americanus* is not as sensitive to photoperiodic control as the moult cycle of *Orconectes virilis*. *H. americanus* is not a true seasonal breeder and may well represent the more primitive condition; MIH and photoperiodic influence may only be found in more specialized forms which have a need for a seasonal regulation of the moult cycle.

Studies on light effects on growth in *Balanus balanoides* and *B. crenatus* (BARNES, 1953), *B. balanoides* (KLUGH and NEWCOMBE, 1935; CRISP and PATEL, 1960), and the ectoproct *Bugula neritina* (MCDOUGALL, 1943) were poorly controlled and hence are not very revealing. It is clear that much remains to be done in this area of research.

O_2 *consumption and heart rate.* Light has been given little consideration with respect to its effects on metabolic rate functions of marine invertebrates. Earlier studies yielded conflicting results. In the planktonic copepod *Calanus finmarchicus*, exposure to light results in a steep decrease in heart rate (HARVEY, 1929) but a sharp increase in respiratory rate (MARSHALL and co-authors, 1935). Further, according to MARSHALL and ORR (1958), *C. finmarchicus* living at the same temperature in February and August has a higher O_2 consumption in August. Whether the difference in metabolic rate is a function of age as MARSHALL and ORR (1958) suggest, or is due to differences in light intensity, as FRIEDRICH (1961) suggests, is unresolvable. A study, such as that by GIMENO and co-authors (1967), in which visible light was shown to have a direct acceleratory effect upon the excised heart of the early chick embryo, has not yet been attempted with marine invertebrates.

More reliable and significant work is available on the effect of photoperiod on metabolic rate in marine invertebrates from a report by DEHNEL (1958). The decapod crustacean *Hemigrapsus oregonensis*—collected in the summer and maintained at 15° C, 35% sea water (approximate summer conditions) and LD 8:16—showed a higher O_2 consumption than crabs kept under the same temperature and salinity conditions with LD 16:8 or constant darkness (Fig. 2-24). Summer population individuals of the crab *H. nudus* exhibit the same increase in O_2 consumption as a result of maintenance under a short-day photoperiod (LD 8:16) as compared with a long-day photoperiod (LD 16:8) and constant darkness, but the differences are not as pronounced as in *H. oregonensis*. The response is evident in 1 week and persists for subsequent weeks. According to DEHNEL (1958), the increase in weight specific O_2 consumption in summer crabs exposed to short-day photoperiod may signify an adjustment of their metabolic rate to winter light conditions. If so, then the adaptive value of such a mechanism would be to prepare the animals to operate under low temperatures. A correlation between photoperiod and thermal resistance has been demonstrated in goldfish (HOAR,

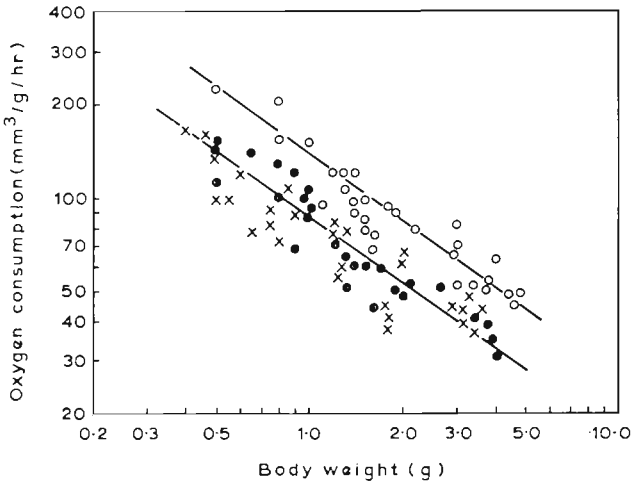

Fig. 2-24: Oxygen consumption in the decapod crab *Hemigrapsus oregonensis* after 2 weeks exposure to different photoperiods (○ LD 8:16; ● LD 16:8; X constant darkness) at 15° C and 35% sea water. Each point represents 1 individual. (After DEHNEL, 1958.)

1956b) and pulmonate slugs (SEGAL, 1963, and unpublished data). Clearly, the phenomenon requires further investigation in marine invertebrates.

Physiological colour change. Light has a profound effect upon the colour responses of large numbers of marine invertebrates. Slow colour transformation, due to the production or destruction of pigment, is known as morphological colour change and is covered under *Structural Responses* (p. 207). Rapid colour transformation, due to the degree of pigment dispersion within special pigment cells or chromatophores (Crustacea) or a change in the actual shape of a pigment organ (Cephalopoda) is known as physiological colour change. Extensive coverage of pigments, their chemistry, distribution and control may be found in PARKER (1948), KLEINHOLTZ (1961), NICOL (1964, 1967a), FINGERMAN (1965a, b, 1966), FOX (1966) and FOX and HOPKINS (1966). In general, pigments disperse with increasing and concentrate with decreasing light intensities.

Chromatophore responses may be brought about through a direct stimulatory action of light or through stimulation of ocular or extra-ocular receptors, and thus indirectly via humoral or nervous pathways to the chromatophores. However, classically, extra-ocular and direct responses have been referred to as 'secondary responses'. Since both extra-ocular and ocular responses may be mediated over comparable nervous or endocrine pathways, the distinction is artificial and confusing. For convenience I shall refer to the responses as direct or indirect.

A direct response of a chromatophore to light stimulus implies that the chromatophore is acting as an independent effector. However, although numerous workers have claimed the independent effector action of chromatophores in a variety of marine invertebrates, only in those in which isolated preparations were used can the demonstration be considered sufficiently rigorous. The echinoid *Diadema setosum* (YOSHIDA, 1956) and the decapod crustaceans *Leander serratus*

(KNOWLES, 1940) and *Macropipes vernalis* (BURGERS, 1959) appear to represent clear-cut cases of chromatophores responding as independent effectors to light stimulation. When a pigment-free area of a single branch of a chromatophore in *Diadema setosum* is illuminated with a light spot only 3 μ in diameter the cell disperses its pigment so as to cover the illuminated area (YOSHIDA, 1956). Further, the chromatophores are most sensitive to light of maximum wavelength at 470 mμ (YOSHIDA, 1957). Where the photosensitive pigments are located and how photic energy is transduced into pigment movement is entirely unknown (YOSHIDA, 1966). Experiments in which the test animals have been blinded or portions of them screened or illuminated (*Uca pugilator*, BROWN and co-authors, 1949; *Hippolyte varians*, KLEINHOLTZ and WELSH, 1937; *Leander adspersus*, KNOWLES, 1952; *Carcinus maenas*, POWELL, 1962; *Uca annulipes*, RAO, 1967; *Ligia oceanica*, SMITH, 1938) are more equivocal since it is possible that the changes observed were the result of mechanical, contact or local reflex action, and other possible receptors or coordinating mechanisms had not been eliminated. The presence of a persistent daily rhythm of colour change, manifested by dispersion of all chromatophoral pigments during the daytime and concentration at night (e.g. *Uca pugilator*, BROWN and SANDEEN, 1948; p. 174), combined with a response to total illumination which results in increased dispersion of both black and white pigments as the intensity of illumination increases (BROWN and HINES, 1952) and a red pigment that responds strongly to black and white backgrounds (BROWN, 1950), makes a proper analysis of independent effector activities indeed difficult. In fact, all of these responses may be observed in *Uca galapagensis herradurensis* in which black, white and red chromatophores respond to total illumination; all three pigments disperse with increasing light intensity of 5, 12, 32 and 120 foot candles. Further, black and red pigments concentrate on white background and disperse on black background; white pigments show the reverse response (BARNWELL, 1968b).

Indirect responses of chromatophores, whether ocular or extra-ocular both in marine invertebrates with and without formed eyes—are widespread (FINGERMAN, 1965a; NICOL, 1967a). Indirect responses may be caused by incident light or the state of background illumination. Some marine invertebrates can adapt to a variety of coloured backgrounds, e.g. cephalopods *Sepia officinalis* (HOLMES, 1940), *Stenoteuthis pteropus* (BOYCOTT, 1953), *Octopus vulgaris* (COWDRY, 1911), and decapod crustaceans *Palaemonetes vulgaris* (BROWN, 1935), *Hippolyte varians* (GAMBLE and KEEBLE, 1900), *Crangon vulgaris* (KOLLER, 1927). Others, with a more limited variety of chromatophore pigments, are restricted to blanching on light backgrounds and darkening on black backgrounds, e.g. the cephalopod *Loligo vulgaris* (BOYCOTT, 1953) and numerous isopods and brachyurans (KLEINHOLTZ, 1961; NICOL, 1967a).

Chromatophore responses to light, whether direct or indirect, have also been described for the siphonophore *Nanomia cara* (MACKIE, 1962), the echinoids *Centrostephanus longispinus* and *Arbacia lixula* (KLEINHOLTZ, 1938), and the polychaete *Platynereis dumerili* (PARKER, 1948). The regulatory control of indirect responses of crustacean chromatophores is firmly established as being solely hormonal while that of cephalopods is affected primarily through the nervous system with endocrines as a secondary slower mode of control (NICOL, 1964; FINGERMAN, 1965a).

Apparently, physiological chromatophore responses serve different functions in different marine invertebrates. The most widespread and obvious function is to adapt animals to their backgrounds (protective colouration); but thermoregulation, mating behaviour and protection from harmful effects of solar radiation (p. 160) have also been invoked. Our understanding of the functional significance of rapid chromatophore change in marine invertebrates awaits clarification.

In addition to chromatophores, which are responsive to light and serve to alter the colour or shade of an organism, higher Crustacea possess retinal pigment cells which also respond to light and serve to regulate the quantity of light impinging on the photoreceptive cells. Crustacea with compound eyes have three sets of retinal pigments commonly referred to as proximal, distal and reflecting. The photomechanical movements of the retinal pigments vary in different Crustacea, e.g. in *Palaemonetes* all three pigments move in response to light and dark while in *Homarus americanus* only the proximal retinal pigment moves (KLEINHOLTZ, 1961). Both distal and reflecting pigments appear to be under the control of light-adapting and dark-adapting endocrines, but the proximal pigments may well be independent effectors (DEBAISIEUX, 1944; KLEINHOLTZ, 1961; FINGERMAN, 1966). One or more retinal pigments of *Leander*, *Portunus*, *Pachygrapsus* and *Carcinus* have been shown to undergo rhythmic diurnal migrations synchronized with the normal day–night cycle. In constant dark, retinal pigment migration persists with reduced migration distances (HENKES, 1952; p. 174).

Cephalopods also possess pigment granules in the retinula and supporting cells of the retina. In *Octopus*, *Eledone*, *Sepia* and *Loligo*, illumination of the retina is followed by movement of the pigment towards the periphery; in the dark, pigment is rapidly withdrawn from the periphery. The same pigment movements occur in excised eyes (YOUNG, 1963), strongly suggesting a direct effect.

Activity

Responses of larvae. More than 80% of approximately 140,000 benthic marine bottom invertebrate species inhabit the photic zone of the sea, and about 80% of these possess a pelagic larval stage in which the young are free swimming in the water column (THORSON, 1950). Since the adults live in the realm of the photic zone, the larval stages, which are nearly all bound to relatively shallow waters, are exposed to regular periods of light and dark. Pelagic larvae, by the very nature of their mode of life, have problems of survival and maintenance which are quite different from those of the bottom-living adults. Pelagic larvae have developed responses which are adequate to cope with the environmental factors which challenge their survival while free swimming, and responses which would place them in ecologically acceptable situations for successful settlement and metamorphosis.

Much of the available information on the role of light in the life of pelagic larvae has been reviewed by THORSON (1964) in a most comprehensive manner covering photoresponses of early and late stage larvae, influence of light intensity, temperature and salinity on photoresponses, injurious effects of light and the role of substrate colour in larval settlement and metamorphosis. BANSE (1964) has reviewed the subject with particular emphasis on the role of light in vertical migration, diurnal activities, and settling and metamorphosis.

According to THORSON (1964), 116 out of 161 species of marine bottom invertebrates have larvae which are photopositive in their early pelagic phases. The phyla Cnidaria (Hydrozoa and Anthozoa), Ectoprocta, Annelida (Polychaeta), Echiuroidea, Rhynchocoela, Brachiopoda, Arthropoda (Cirripedia, Decapoda, Stomatopoda, Xiphosura), Mollusca (Prosobranchia, Opisthobranchia, Bivalvia, Cephalopoda), Echinodermata and Chordata (Tunicata) are represented in this category. The remainder of the larvae constitute 17 species in which the early stage larvae are indifferent to light, 8 species in which the early stage larvae appear to be photonegative and 20 species in which the early stage larvae rise to the surface immediately after hatching; whether this is due to photopositivity, geonegativity or a combination of the two is uncertain. However, there may be considerably more larvae in the last category than realized. Larvae of the nudibranch *Onchidoris fusca* exhibit a strong positive phototaxis while those of 10 other species swim upward during the first few days or even hours after hatching; but the response seems to be due to a strong negative geotaxis since it occurs both in the dark and in the light regardless of the direction of the light source (HADFIELD, 1963).

From both laboratory and field studies it is clear that by far the majority of pelagic larvae begin their larval life by swimming towards the light and thus the surface of the ocean. This is true for larvae of adults that inhabit both the tidal zones and deeper water. The initial photopositive response may be of extremely short duration, when the pelagic phase occupies but a few hours or days, or the response may last for a week or more when the pelagic phase is long (SCHELTEMA, 1968).

Some larvae remain photopositive to the moment when they stop swimming and begin to crawl. THORSON (1964) lists 15 species in this category; in all cases these are larvae of adults which live intertidally. In a few intertidal species, which seem to do equally well in direct sunlight or in shade, a percentage of the larvae remain photopositive until attachment while the remainder become photonegative before metamorphosis. Larvae of the remainder of the species studied become either photonegative (47) or indifferent to light (7) during the later developmental stages. Except for larvae which remain photopositive throughout their (larval) life and a few which change photoresponses at each larval stage (e.g. *Mytilus edulis*), the most common response—as THORSON phrases it 'The only reasonable response'—of larvae with a fairly long pelagic lifespan and adults living in somewhat deeper water, is to begin their life with photopositivity and, towards the end of their larval life, change to photonegativity.

In benthic marine invertebrates, the change-over from a positive to a negative photoresponse then seems to be a function of time i.e. of aging. This appears to be true also for larvae of pelagic adults undergoing diurnal vertical migrations (p. 194). Nauplius, metanauplius, and caliptopic stages of the euphausiids *Thysanoessa raschii* and *T. inermis* do not migrate vertically; they occupy the 0 to 15 m water layer day and night (LACROIX, 1961). The same is true for furcilia stages I to IV but older larvae begin to show the photic responses associated with extensive vertical migrations. Last stage furcilia and postlarvae are similar to adults.

The change in photic response depends on light intensity, temperature or salinity. A number of larvae (15 species according to THORSON, 1964), which are

normally photopositive, will become photonegative when exposed to bright light. But RYLAND (1960, 1962), who found that the change from photopositive to photonegative in a number of ectoproct larvae was independent of the intensity of illumination, is not convinced that the studies on light intensity were sufficiently conceived or controlled to permit reliable conclusions. On the contrary, in *Mytilus edulis* larvae, changes in intensity of directional illumination do affect the light response; most of the stages have an intensity threshold below which there is no response (BAYNE, 1964; see also below). Interestingly, stage II, III and IV Zoea of *Uca pugilator* demonstrate a positive phototaxis in light intensities between $3{\cdot}1 \times 10^{-3}$ to $1{\cdot}7 \times 10^{-5}$ μm/cm^2 but a negative phototaxis at intensities between $3{\cdot}1 \times 10^{-6}$ to $1{\cdot}7 \times 10^{-6}$ μm/cm^2 (HERRNKIND, 1968a).

Temperature, by virtue of its effect on metabolic systems, will influence the rate of change-over from photopositive to photonegative responses by speeding up development and shortening time to metamorphosis. THORSON (1964) lists at

Table 2-14

Percentages of larvae of the ectoproct *Cryptosula pallasiana* developing a photonegative response (After RYLAND, 1962)

Temperature (°C)	%	%
25·0	31·0 within 1 hr	70 within 2·5 hrs
20·0	21·5 within 1 hr	70 within 3·5 hrs
17·5	11·5 within 1 hr	70 within 7 hrs
15·0	6·0 within 1 hr	50 within 9 hrs
10·0	2·0 within 1 hr	50 within 12 hrs

least 12 species (Ectoprocta, Archiannelida, Polychaeta, Cirripedia, Decapoda, Stomatopoda) which turn from photopositive to photonegative at increased temperatures. The higher the temperature, within the physiological range of temperatures, the quicker and more decisive is the reversal of the response. The data for the ectoproct *Cryptosula pallasiana* are compiled in Table 2-14.

Reduced salinity also influences the photoresponse of marine larvae. THORSON (1964) lists 12 species (many are the same as those cited for the temperature response) whose larvae change from a photopositive to a photonegative response in reduced salinities. Introduction of the salinity factor opens up the complex problem of movement and distribution of planktonic larvae in estuaries. The subject cannot be covered in this chapter; the reader is referred to CARRIKER (1967) for a thorough discussion and an extensive list of references (see also Chapter 4).

BAYNE (1964), in a study which should serve as a model for future inquiries into the effect of light on marine invertebrate larvae, shows that when other environmental parameters (except the ever present gravitational effect) are not effective, the response to light depends upon stage of larval development and age. Although larvae of *Mytilus edulis*, with which BAYNE worked, are not

representative in their response to light, the effect of age is clearly evident (Table 2-15).

Temperature effects were significant and seem to have adaptive value. From 5° to 16° C the larvae showed light responses characteristic of the particular developmental stage. From 18° to 20° C no larval stages responded to directional light. Thus, higher temperatures tend to induce loss of positive phototactic responses and reversal of geotaxis. Loss of phototactic responses and reversal of geotaxis serve to keep planktonic stages clear of surface waters when these become overheated.

In *Mytilus edulis*, the key larval stage is the velichoncha which spends, at 15° C, 20 to 22 days in the plankton of the surface waters without a positive light response. What keeps these larvae in the surface waters? Velichoncha respond to a pressure increase of 0·54 atm above ambient hydrostatic pressure by increased rates of upward swimming (BAYNE, 1963; see also below). This response together with a strong negative geotaxis should keep the velichoncha near the surface.

Table 2-15

Responses to light in larvae of the lamellibranch *Mytilus edulis* as a function of age at 15° C (After BAYNE, 1964)

Larval stage	Age	Response
Trochophore	20–24 hrs	No significant response to light or gravity
Young veliger	16–18 hrs	Negative to light, no geotactic response
Straight hinged larvae	12–16 hrs	Positive phototaxis, no geotactic response
Velichoncha	20–22 days	No response to light, negative geotaxis
Eyed veliger	4–5 days	Positive phototaxis, negative geotaxis
Pediveliger (crawling–settling stage)	Older than 4–5 days	Negative phototaxis, positive geotaxis

If larvae are to be kept out of the water column for a period of time, then a negative phototaxis would be an appropriate response. This has been demonstrated in the propelagic stages (I, II, III) of the mantis shrimp *Gonodactylus bredini* (DINGLE, 1969). These stages (7–8 days) are spent in a chamber occupied and defended by the spawning female. The larvae show a strong thigmokinesis and negative phototaxis, with the first taking precedence over the second. Larvae cling to any suitable substrate and remain so even in the brightest light (to 145 foot candles). If the larvae are free swimming the photonegative response appears, thus keeping them within the chamber. During the moult to stage IV the thigmokinetic response disappears and photonegativity is replaced by photopositivity at all light intensities between 2·2 and 145 foot candles. Eye colour of larvae changes from black to green during the moult from stage III to stage IV. The change in photoresponse is adaptive and will get the larvae up into the plankton where they will disperse.

Pressure (Chapter 8), which seems to play a role incidental to light in the orientation responses of adult marine invertebrates (p. 195), may be of far greater significance in larval orientation responses. Larvae of numerous species of marine invertebrates respond to pressure changes, but the nature and direction of this

response and its relationship to light vary considerably in different species or in different stages of the same species. HARDY and BAINBRIDGE (1951) first demonstrated that decapod larvae are sensitive to small pressure changes, and RICE (1964) extended these observations to a wide variety of larvae. Ephyrae of *Aurelia aurita*, megalopae of *Carcinus maenas* and larvae of *Loligo forbesi* respond to rapid pressure changes (2 to 3 sec) of up to 1000 mbar by orienting entirely with respect to gravity. Increase in pressure produces upward movement, decrease downward movement, regardless of the direction of light, and in darkness. Stage I zoeae of 22 species of decapod crustaceans respond to pressure increase with an enhancement of their movements towards the light source, whether this involves upward, downward or horizontal swimming. Pressure decrease causes decreased swimming and consequent sinking with no active movements away from the light source. Nauplii of the barnacle *Balanus balanoides* and furcilia larvae of the euphausiid *Meganyctiphanes norvegica* respond to pressure increase as do the decapod larvae mentioned above. Pressure decrease, however, causes locomotion away from the light source.

Since so many larvae are photopositive during part or all of their life, their maintenance of position in the upper layers of the ocean during the hours of darkness is of vital significance. The effect of slow pressure changes brought about either by active swimming or passive sinking has not been investigated. But, if larvae respond to slow pressure changes as they do to rapid ones, it may well be that pressure effects are most significant in position keeping at night. Strong light is known to stimulate swimming activity in at least some larvae, for example, of oysters *Ostrea edulis* (COLE and KNIGHT-JONES, 1939), *Crassostrea virginica* (MEDCOF, 1955) and barnacles *Balanus* sp. (BOUSFIELD, 1955). According to HASKINS (1964), however, oyster larvae (assumed to be *Crassostrea virginica*) were most active in very dim natural light and completely inactive if exposed to daylight fluorescent lamps. In the absence of light most photopositive larvae sink or swim at minimal speeds. At night the tendency to swim upward at increased pressure would prevent the larvae from sinking too deep before dawn once more stimulates upward movement and hence attainment of normal day depth.

Although the majority of young larvae are photopositive they will rarely be found in the uppermost surface layers of the ocean. The change-over from photopositive to photonegative due to too strong light, increasing temperature and even reduced salinity—often found in the uppermost surface layers of coastal areas—may well account for proper vertical positioning. All these factors counteract the photopositive response tendency of the larvae and prevent them from occupying the uppermost surface layers. The resulting final vertical position of the larvae in the water masses may be considered a 'common denominator' for all environmental factors involved.

Settlement and metamorphosis are extremely critical events in the life cycles of marine invertebrates. Recent studies suggest that at least among many gregarious species of barnacles and oysters settlement and metamorphosis involve a recognition by the larvae of the insoluble protein layer of the shells (CRISP, 1965, 1967). Light seems not to be involved since settlement and metamorphosis take place both in light and dark. However, in the oyster *Ostrea edulis* light intensities of 1000 to 1250 lux are favourable for settlement; intensities of 0 to 250

lux are unfavourable. The light regime during a 24-hr period prior to settlement is important. While light during this period is favourable for settlement, it is inhibitory if it is of greater intensity than that during the period when the larvae are expected to settle. Although settling larvae are stimulated by light, their reactions to it appear to be negative (BAYNE, 1969).

Many larvae delay settlement so that they only settle in the presence of light when a choice between light and dark is available (THORSON, 1964). Since larvae of so many species become photonegative shortly before settlement they will tend to settle in dim or shaded places (DYBERN, 1963; CALLAME, 1965). Larvae which settle on a lighted surface may often crawl out of the light before final attachment. The complexity of the process has been well documented in *Mytilus edulis* (BAYNE, 1964). As described earlier in this chapter, *M. edulis* larvae are indifferent to light for most of their life. As eyespots develop, the larvae become photopositive again; when settlement is evident, they become photonegative. Prior to attachment, pediveligers avoid brightly lit surfaces; their geonegative behaviour on dimly lit surfaces results in their crawling away and thus in avoiding depressions in the substrate surface where silting-up is likely to occur. When crawling up a steep slope, illumination from above produces a loss of the negative geotactic response and the demonstration of a photonegative response. Final settlement (attachment of pediveligers by byssus threads) will occur more readily in dark than in light but not in dimly lit depressions (BAYNE, 1964).

Of course, if adults live in bright light their larvae will remain photopositive and settle in bright light. This has been well illustrated in the barnacles *Chthamalus stellatus*, from the upper intertidal, whose larvae settle most abundantly in direct sunlight; *Balanus amphitrite*, living lower in the intertidal, whose larvae settle most abundantly in daylight but not in direct sunlight; and *B. tintinnabulum*, living still lower in the intertidal, whose larvae settle abundantly during dusk and dawn rather than at noon (DANIEL, 1957).

Responses of adults. The activities of marine invertebrates, in their natural environment, fluctuate over a solar day cycle and, as has so often been observed, the fluctuations are not random but seem to be correlated with the rhythmic daily changes in intensity of illumination. One of the most dramatic cyclic activities is the diurnal vertical migration of many pelagic and benthic invertebrates (p. 194). But demersal (shallow water) and intertidal invertebrates similarly show diurnal changes in activity correlated with the natural periodicity of daylight to darkness over a 24-hr period. Diurnal rhythmic phenomena have been observed at many levels of biological organization from the cell to the whole animal. On the whole, animal diurnal cycles of activity are frequently complex and may be associated with feeding, courtship and reproduction, spawning, escape from predation and other as yet unidentifiable behaviour. Activity of an organism includes also its 'behaviour', and the reasons for a given activity may be as diverse as the number of organisms exhibiting it.

In addition to diurnal rhythms of activity marine invertebrates have also been shown to co-ordinate metabolism and behaviour in approximate synchronous phasing with tidal, semilunar, lunar and seasonal periodicities in their environment. Semilunar, lunar and seasonal periodicities, which are most significantly expressed

in reproductive events, are covered under *Reproduction*. Tidal rhythms, insofar as they may be superimposed upon diurnal rhythms or modified by light, are treated in this section.

The earlier literature has been well covered by CALHOUN (1944), KLEITMAN (1949), CLOUDSLEY-THOMPSON (1961), HARKER (1964) and REESE (1966, specifically echinoderms). As pointed out by WOODHEAD (1966) in regard to diurnal activities of fishes, few activity studies on marine invertebrates have been accompanied by light measurements (see also Chapter 2.32).

Diurnal activity patterns of marine invertebrates are diverse. Some species are active during the day and quiescent during the night. Others are active at night and quiescent during the day. Between these clear extremes range those forms that are active around dawn and dusk and inactive the rest of the time. Lastly, some species show no diurnal rhythmicity in their activities (YAMANOUCHI, 1956). Thus, *Carcinus maenas*, a decapod crustacean, raised in the laboratory under a 24-hr light/dark regime is active in the dark and inactive in the light with the rhythm continuing in constant dim light (WILLIAMS and NAYLOR, 1967). In nature the alcyonian *Cavernularia obesa* expands its club-shaped rachis above the sand at night and contracts beneath the sand in the daytime. Under conditions of constant darkness or constant light in the laboratory, the rhythmic activity persists with the original periodicity. When the light/dark cycle is reversed or altered, so that the light/dark periods are of different length, the rhythmic expansion and contraction of the colony synchronizes with the new cycles (MORI, 1960). The shrimp *Penaeus duorarum* shows a clear phase relationship in activity with artificial (13 lux incident on substrate; red light) and natural day–night cycles; at night the shrimps are active above the substrate, during the day they are inactive and buried (HUGHES, 1968). Emergence from the substrate is highly synchronized (20 to 30 mins) for the entire population. Under continuous dim light (3 days) a persistent cycle of activity is maintained, although there is a slowing of activity by the third day. According to HUGHES the rhythmic response of *P. duorarum* is keyed to the light–dark transition but it is modified by a 24-hr feeding rhythm since the animals will emerge from the substrate under high light intensity. Juvenile (less than 4 cm long) *P. duorarum* may be less dependent upon inherent rhythms and more receptive to external illumination.

The asteroid *Astropecten polyacanthus*, both in nature and in the laboratory, under simulated normal photoperiod, is active only at dawn and at dusk with the intensity of activity being stronger at dawn (MORI and MATUTANI, 1952). When the intensity of illumination exceeds 2000 lux the sea-stars do not move; when the intensity is below 100 lux they are most active although they rarely move at night. In continuous darkness the rhythmic activity persists for about 3 days. Interestingly, the responsiveness to light appears to have a rhythmic component since the 'sensibility' of the sea-star to sudden decrease of intensity during the daytime is highest at dawn, falls at midday then rises again toward dusk. PALMER (1964), using a choice chamber, demonstrated a diurnal light preference rhythm of activity in the decapod crustacean *Uca pugnax*; as the day progresses (*Uca* is a nocturnal crab), the attraction to light decreases. In contrast to *A. polyacanthus*, the asteroid *Luidia sarsi* is active and feeds at night and is quiescent during the day. In continuous darkness *L. sarsi* loses its activity rhythm at once (FENCHAL,

1965). *Opheodesoma spectabilis*, a giant (up to 2 m long when relaxed) non-burrowing endemic Hawaiian holothuroid, lives in aggregations in and on the beds of the alga *Sargassum*. Activity, as measured by the exposure of tentacle crowns, reaches a peak around sunset (95% crown exposure) and a low at noon (2 to 20% in direct sunlight, 50% when the sky is overcast). During the hours of peak activity the animals travel as much as 15 m over the *Sargassum*. After about 21·00 hrs travelling distances decrease to about 1 m and remain that way until dawn when the holothuroids re-enter the *Sargassum*. Under constant light in the laboratory (260 foot candles) the animals do not demonstrate an activity rhythm (BERRILL, 1966). The gastropods *Nassarius festivus* and *N. vibex* are active at night and inactive during the day both in nature and in the laboratory under simulated day–night conditions. OHBA (1954) was able to produce activity rhythms in *N. festivus* corresponding to a variety of LD periodicities (e.g. LD 15:3, 24:24). In constant light, the snails are essentially inactive. *Nassarius vibex* remains active with no evident rhythmic component throughout a 72-hr period in constant dark (HURST, 1965). Among barnacles, *Tetraclita squamosa* feeds at night and is quiescent during the day but only during normal strong wave action (MORI, 1958). However, SOUTHWARD and CRISP (1965) were unable to demonstrate diurnal feeding rhythms in eight species of barnacles.

EBLING and co-authors (1966), in a fascinating series of studies on ecological interrelations of important species of a marine invertebrate community, have shown rhythmic diurnal activity cycles of various members of the community which appear to be related to predation. The members of the dominant species in the community, the echinoid *Paracentrotus lividus*, are exposed and actively feeding during daylight hours, and largely hidden under boulders during the night. *Marthasterias glacialis*, a predatory asteroid, was only observed at night, primarily over a short period around midnight. The herbivorous gastropod *Gibbula cineraria* also exhibits a marked diurnal rhythm of activity, crawling up the boulders to feed at dawn and going down the boulders, out of sight, at sunset. *Carcinus maenas* and *Portunus puber*, predatory crabs, are both nocturnal foragers (MUNTZ and co-authors, 1965). Thus, the rhythmic activity movements of these community members (herbivores and omnivores by day, carnivores by night) limit extreme predation and, according to EBLING and co-authors (1966), maintain a measure of communal stability.

Swimming activities among marine invertebrates also depend upon diurnal changes in light intensity. The holothuroid *Labidoplax dubia* swims between early June and late July, but always in darkness. Swimming begins 1 hr after sunset and ends 1 hr before sunrise (HOSHIAI, 1963). The cephalopod mollusc *Sepia officinalis* swims during the night and is buried in gravel during the day. The buoyancy of *Sepia*, which permits this cephalopod to swim, depends upon its density which can be changed rapidly in bright light. If exposed to complete darkness for 1 to 2 days, *Sepia* becomes so buoyant that it is incapable of remaining at the bottom; it can stay at midwater only with difficulty (DENTON and GILPIN-BROWN, 1961). In and above *Fucus* beds in the Baltic Sea off Askö (Sweden) numerous marine invertebrates show a diurnal periodicity in swimming with the peak activity occurring between 21·00 and 03.00 hrs, with all species virtually absent from net catches at light intensities of approximately 4000 lux and higher.

In the laboratory, swimming activity of the amphipod *Gammarus oceanicus* increases significantly when the light intensity drops to a few lux, and decreases when the light intensity reaches 1000 lux and higher. The isopods *Idothea baltica* and *I. chelipes* show an abrupt increase in swimming activity at light intensities below 1 lux, and decrease in activity between 400 to 800 lux (JANSSON and KÄLLANDER, 1968).

Introduction of new techniques such as SCUBA and SUOC (static underwater observation chamber) which permit observation of marked and unrestrained marine organisms in their natural underwater habitat, although in its infancy, has opened up a new dimension in the study of the behaviour of marine invertebrates. SALSMAN and TALBERT (1965), using SCUBA and time-lapse photography at depths from 2 to 13 m, followed the activities of the echinoid *Mellita quinquiesperforata* off Panama City, Florida, USA. Activity in the community began during the early evening hours with emergence from the sand, and within 1 hr every member was actively moving with an average speed of approximately 1 cm/10 mins. At the approach of dawn, activity declined until by early morning the entire community was inactive and under the sand again. TSURNAMAL and MARDER (1966) observed the movements of marked individuals of the asteroid *Astroboa nuda* day and night on the coral reefs at Elat, Israel. During all seasons the animals fed actively at night and hid during the daylight hours in fixed shelters (usually cracks in the reef). The animals emerged from their hiding places 70 to 80 mins after sunset and began to move back to their shelters 45 to 60 mins before sunrise. FUSS and OGREN (1966) used a SUOC facility and a partially restraining *in situ* arrangement (1 m square bottomless metal frame cages covered with small mesh netting and attached to underwater viewing ports) to study the behaviour of the decapod crustacean *Penaeus duorarum* in the waters of St. Andrews Bay, Florida, USA. Both in the field and in aquaria in the laboratory, *P. duorarum* rhythmically burrows during the day and emerges from the sand around sunset reaching maximum activity approximately 1 hr after sunset. Although these workers took incident underwater light measurements, the restricted sensitivity of their instrument did not permit them to take readings below 0·01076 lumens/m^2 although maximum activity occurred below this level of illumination.

Numerous marine invertebrates demonstrate activity, O_2 consumption and chromatophore rhythms correlated with local tidal cycles (FINGERMAN, 1960; BARNWELL, 1968a). In many of these tidally synchronized invertebrates, laboratory analysis has shown that a tidal periodicity is often superimposed upon a diurnal periodicity. Activities, as measured by valve movement, in the bivalve *Venus mercenaria* (BENNETT, 1954); locomotion in various decapod species of *Uca* (WEBB and BROWN, 1965; BARNWELL, 1966), *Carcinus maenas* (NAYLOR, 1958; BLUME and co-authors, 1962) and *Emerita asiatica* (CHANDRASHEKAREN, 1965); O_2 consumption in the gastropods *Littorina littorea* and *Urosalpinx cinerea* (SANDEEN and co-authors, 1954), the decapods *Uca pugilator*, *Uca pugnax* (BROWN and co-authors, 1954) and *Carcinus maenas* (ARUDPRAGASAM and NAYLOR, 1964); and colour change in the crabs *Uca pugnax* (BROWN and co-authors, 1953) and *Callinectes sapidus* (FINGERMAN, 1955), ostensibly manifest both a diurnal and tidal periodicity (one of which may dominate the other or neither). A number of these workers have suggested that the periodic interaction of the diurnal and tidal cycles may account

for a semilunar (approximately 15 day) periodicity (but see p. 193). However, the intertidal amphipod *Synchelidium* sp. shows a strong conspicuous overt tidal rhythm without any evidence for a diurnal amplitude modification of the rhythm (ENRIGHT, 1963a). ENRIGHT (1963b, 1965) does not believe there is convincing evidence of any organism simultaneously possessing both endogenous (see below) diurnal and tidal rhythms.

It seems clear, from the studies cited, that the activities of numerous marine invertebrates are synchronized with the daily light–dark cycle in nature. However, in some of the studies, in which rhythmic activity persists under constant light or dark in the laboratory, there is obviously more to the manifest rhythms than simple synchronization. What these marine invertebrates are demonstrating is an endogenous (circadian) rhythm of activity which is synchronized or entrained by the daily changes in light. It is the generally accepted view (ASCHOFF, 1965; SOLLBERGER, 1965; BÜNNING, 1967; but see BROWN, 1965) that endogenous rhythms are brought about by innate oscillations in the animals' activity which become entrained by exogenous diurnal or tidal effects. According to PITTENDRIGH and MINIS (1964), virtually all organisms other than bacteria and blue-green algae manifest innate oscillations in their physiological functions.

Oscillations occur in time, and to measure time an organism needs a clock. The simplest clock is an interval timer (e.g. an hourglass) which only measures a preset duration (e.g. the time between dawn and sunset and sunset and dawn—the 24-hr day). If the interval timer has a scale, time may be measured continuously. If the interval timer rewinds automatically when ready to run down, we have a chronometer which is itself an oscillator and any oscillating system may be used as a true clock. Since living organisms can measure time intervals and orient in local or universal time, they must possess clocks of one kind or another. Biological clocks permit organisms to 'know' the time of day and year and thus permit them to anticipate environmental changes. The adaptive value of such a clock is evident. But, more than this, biological clocks may be used to measure the duration of a certain time stretch, regardless of the time of day. This aspect of the clock depends upon a 'recognition' of the annually changing day-length or night-length (the photoperiod). Longer term activities (semilunar, lunar and annual periods) may be timed in this way. Lastly, if a clock is consulted continuously it is a true chronometer and animals may use it for orientation (short distance movements; p. 184) by timing the movements of the sun (although which parameters of solar movement is not clear) and predicting its future path. Navigation (long distance movements) also requires the use of a continuously consulted clock plus a sextant. Whether marine invertebrates employ navigation or only orientation, using primarily the sun and possibly the moon as a reference point, has not been established.

The subject of endogenous rhythms and biological clocks is truly complex (ASCHOFF, 1965) and the literature is enormous (consult the COLD SPRING HARBOR SYMPOSIUM, 1960 and citations made above). Much of what we know about the subject comes from studies on plants, insects and vertebrates—to a considerably lesser degree from marine invertebrates. This situation may be changing. For example, for the first time the presence of an endogenous diurnal rhythm and even a semilunar rhythm in the spontaneous impulse rate of a neuron has been demon-

strated in the marine tectibranch gastropod *Aplysia californica* (STRUMWASSER, 1965). The rhythm becomes synchronized after application of a light–dark cycle (LD 12:12) to the whole organism for either 9 days or 3 days prior to isolation of the ganglion. Peak impulse rate was recorded, for at least 2 successive days, within approximately 1 hr of the time the lights would have gone on (simulated dawn). After 1 week in constant light, impulse rate still showed a diurnal rhythm but peak impulse rate was no longer synchronized with an environmental LD cycle. When *Aplysia* is maintained in constant darkness (5 days), prior to isolation of the ganglion, no rhythmic impulse rate was observed (LICKEY, 1967). Under LD 12:12, *Aplysia* is more active during the light period (2·6 m/min) than during the dark period (0·36 m/min) (KUPFERMANN, 1968). Mean activity, in the light, begins to decrease several hours before the dark period. In continuous darkness the gastropods maintain a higher activity (over 48 hrs) when the light would have been on (1·0 m/min vs 0·46 m/min). No attempt has been made to imply that the circadian rhythm of locomotion in the whole animal is dependent upon the circadian rhythm of the neuron (recall the differential response to constant dark) but synchronization of the rhythm in both depends upon the LD cycle and, at least in the neuron, some form of photic stimulation is necessary to maintain the circadian rhythm (LL experiments) or to trigger its expression.

Clearly, the ease of synchronization of biological rhythms is well known. How synchronization is attained is unknown. Many models have been proposed (PITTENDRIGH and MINIS, 1964) but the mechanism is still elusive.

Orientation. Light may act as an orientating stimulus for marine invertebrates by virtue of intensity gradients, directionality, wavelength or polarization. The responses of the animals may be very simple, consisting of random movements in which the speed of movement or the frequency of turning depends upon the light intensity (photokinesis), or directed movements in which the animal moves directly towards or directly away from the light source (phototaxis). More complex responses are seen when the light source (sun) is used as a reference point and the animal maintains some definite angle between the source and its direction of motion (light–compass reaction). If the sun is not visible, the polarization plane of the light will indicate its direction and may be used as an orientating stimulus. Other special responses to light stimuli are referred to as shadow reactions, dorsal-light reactions and covering reactions. Photo-orientation reactions are but one part of the complex mechanism involved in the behaviour of marine invertebrates. Since appropriate behaviour has survival value and light is one of the most important sensory guides to the ecological conditions in which marine invertebrates find themselves, the photoresponses of these animals are very important in maintaining them in optimum ecological conditions. However, according to WAINWRIGHT and DILLON (1969), orientation of sessile fan-shaped organisms, such as the sea-fan *Gorgonia*, is controlled by hydrodynamic forces.

If an animal is photoresponsive it must be photosensitive, and photosensitivity implies that photoreceptors (either formal or diffuse) are present. Marine invertebrates possess a wide variety of photoreceptive structures from the so-called 'dermal light sense' (STEVEN, 1963), pigment spots and cilia in Cnidaria (EAKIN and WESTFALL, 1962; YOSHIDA and OHTSUKI, 1966) and Ctenophora (HORRIDGE,

1964; see MOODY, 1964) to compound eyes in Crustacea (WATERMAN, 1961a) and lens focusing eyes in Cephalopoda (WELLS, 1966a). For details concerning the structure and physiology of photoreceptors of marine invertebrates and the underlying mechanisms of photoreception the reader is referred to BULLOCK and HORRIDGE (1965), CHARLES (1966), YOSHIDA (1966) and NICOL (1967a).

Many marine invertebrates will aggregate in the dark or in the light. Animals may aggregate (1) as a result of a change in the rate of forward movement due to a change in light intensity (speed up under unfavourable light conditions and slow down under favourable light conditions), or (2) as a result of increasing the rate of turning under favourable light conditions and decreasing the rate of turning under unfavourable light conditions (FRAENKEL and GUNN, 1961). Both of these responses may be in operation at the same time and reinforce each other. Unfortunately, it is difficult to find measurements of the effect of light intensity on the speed of locomotion or on the turning rate of marine animals; the classic kinetic studies have been carried out on terrestrial and freshwater invertebrates (CARTHY, 1958; FRAENKEL and GUNN, 1961). Analyses of photokinetic responses are complicated by the presence of phototactic responses in the same organism and its prior photic experience which may modify both kinds of responses.

Dark-adapted (6 hrs) gastropods *Littorina littorea*, at 19° C, crawl faster (approximately 25%) at high light intensities (3000 foot candles) than at low light intensities (10 foot candles) (NEWELL, 1958a). The gastropod *Peringia ulvae* burrows in darkness, and emerges and comes to the surface of the water (floating on a mucus raft) in full daylight. In the laboratory, a higher proportion of snails come to the surface and float in response to increased light intensities whether directed from above or below. The difference between the light intensity to which a snail is adapted, and the new intensity must be greater than 10 foot candles to cause 50% or more of the animals to float, and the greater the increase in illumination, the shorter is the time spent afloat. Dark-adapted individuals move faster than light-adapted ones in response to light, and the higher the intensity (600 vs 60 foot candles) the faster the rate of locomotion (NEWELL, 1962). The holothuroid *Opheodesoma spectabilis* moves more slowly under overcast skies as compared with sunlit skies and travels only short distances with a high rate of undirected turning. In field experiments, 30 out of 40 individuals remained within 2 m of the release point within 1 hr. In contrast, when released under direct sunlight 80 out of 100 individuals showed a strong negative phototaxis, moving directly away from the source of illumination following distinct paths at maximum rates of locomotion. The holothuroids slowed down and ceased movement when they encountered clumps of *Sargassum* where they remained aggregated throughout most of the daylight hours. In the laboratory, *O. spectabilis* gathered in shaded areas of the aquarium and avoided illuminated areas (BERRILL, 1966). According to BERRILL, the region of the tentacle crown of *O. spectabilis* is the primary light-sensitive area. The aggregating gastropod *Monodonta labio*, when dark adapted, responds to a rapid increase in intensity of illumination with marked locomotory activity. In the range of 5 to 2500 lux, locomotory activity is linearly correlated with the logarithm of the light intensity (OHBA, 1957). Light-adapted (200 lux, 30 mins or longer) starfish *Asterias amurensis* demonstrate a positive phototaxis at any time during a 24-hr period; dark-adapted starfish (4 hrs or longer) are photo-

negative (YOSHIDA and OHTSUKI, 1968). When one arm of light-adapted *A. amurensis* is illuminated, a high percentage of the animals move with the illuminated arm forward (80% of 100, with ocelli; 40% of 90, without ocelli). Dark-adapted animals move more or less randomly regardless of the presence or absence of ocelli. *A. amurensis* also shows a shadow response (p. 186), and YOSHIDA and OHTSUKI are of the opinion that light as well as shadow are perceived through ocelli, the animals moving towards the light and away from the shadow. They also suggest that an extra-ocellar diffuse photoreceptive system is present which, however, may play only a minor role.

Increased light intensity causes increase in swimming speed in the limnomedusan *Gonionemus murbachi* (YERKES, 1906), increase in rate of locomotion in the turbellarian *Plagiostomum* sp. (WELSH, 1933), reduction in rate of locomotion in *Uca pugnax* (HOLMES, 1908), acceleration of limb movements in the mysid *Hemimysis lamornae* (FRANZ, 1914), increase in the intensity of eye movements in response to a light source in the crab *Carcinus maenas* (HORRIDGE, 1966) and increase in the rate of expansion in the anthozoan coral *Oulastrea crispata* (KAWAGUTI, 1954). Related but probably more complex is the response of the interstitial archiannelid *Trilobodrilus heideri* which exhibits a patchy distribution in nature. In the laboratory, when given a choice between light and dark, the archiannelids gradually accumulate in shaded areas. When coming out of the dark, they rebound sharply at the light boundary (BOADEN, 1963). The response appears to be similar to that of the freshwater turbellarian *Dendrocoelum lacteum* on which the classic light–dark boundary studies have been carried out (ULLYOTT, 1936).

In a directional light field with an intensity gradient, most marine invertebrates will either move towards the light (photopositive) or away from it (photonegative). Diurnal vertical migration is a prime example of phototactic orientation to both direction and intensity of illumination (p. 194). Indifference to light is rare among marine invertebrates, and very possibly no marine invertebrate is indifferent during all of its life history. Phototactic responses may change with age (p. 169), nutritional state, reproductive condition, prior light history and other environmental factors. Lack of experimental standardization has produced considerable contradictory information (CARTHY, 1958; FRAENKEL and GUNN, 1961; PARDI and PAPI, 1961; YOSHIDA, 1966). Some reliable information has been obtained from studies in which two lights of equal or unequal intensity have been used and the animals dark or light adapted prior to experiments. PARDI and PAPI (1961) list four major response patterns of crustaceans in two light experiments. The test individuals orientate (i) between the lights, (ii) directly to one of the lights, (iii) either between or direct, and (iv) between, direct, or alternating from one light to the other. The response patterns appear to apply equally well to other marine invertebrates. For example, *Peringia ulvae*, when crawling on the substratum, orientates and moves directly to the brighter of two lights when these are switched on and off alternately (NEWELL, 1962). Some *Asterias rubens* and *Nassarius incrassata* may start by taking a path between two lights of equal intensity and then veering off to one or the other. Other animals may pass between the lights (VON BUDDENBROCK, 1952). Dark-adapted (4 days) *Littorina littorea* are positively phototactic, crawling directly towards a light source (250 foot candles); when a second light of equal intensity is turned on, at right angle to the first, the snails

usually ignore the second light and continue crawling towards the first (NEWELL, 1958b). Most of the more detailed studies have been carried out on insects and other non-marine invertebrates (CARTHY, 1958; FRAENKEL and GUNN, 1961).

Other experiments have demonstrated the importance of gravity and temperature on phototactic responses. The mobile, intertidal bivalve *Lasaea rubra* responds to directional light with negative phototaxis (MORTON, 1960). The higher the light intensity the more direct the path away from the light. However, negative geotaxis supersedes negative phototaxis when the stimuli work opposite each other. *Lasaea rubra* will climb against a light gradient if removed from a crevice. Lateral contact (crevice or depression) will normally supersede the usual responses to gravity and light. There is, therefore, a hierarchy of responses contributing to an increasing precision in securing shelter and maintaining position on the shore. Many of the relevant studies have been carried out on the ubiquitous littorinid gastropods. The results have been, in some significant respects, remarkably contradictory.

In the littoral gastropod *Littorina obtusata*, the sign of phototaxis changes with temperature (JANSSEN, 1960). From about 3° C and higher the animals are positively phototactic. But, the light response is much weaker than the gravity response which shows a sharp reversal from negative to positive at 2° C and below. Thus, when *L. obtusata* is negatively geotactic it is also positively phototactic; when it is positively geotactic (at 2° C and below) it is either weakly influenced by light or negatively phototactic. Gravity and immersion in water influences the phototactic response in the high intertidal *Littorina neritoides* (FRAENKEL, 1927a). Out of water *L. neritoides* is photonegative. Under water it is also photonegative and geonegative except when it is upside down and then it is photopositive. According to FRAENKEL, these tactic responses would take the animals out of water under favourable light conditions and prevent them from becoming trapped in crevices under water. In an experimental tidal tank, *L. neritoides*, *L. saxatilis* and *L. littorea* establish a zonation similar to that in nature. According to EVANS (1965), *L. neritoides* and *L. saxatilis* occupy the upper zones; they are positively phototactic in the horizontal plane but indifferent to light in the vertical plane (light from above or below). *L. littorea* shows a moderate positive phototaxis to light from below. Both *L. neritoides* and *L. saxatilis* reverse direction at a barrier (water barrier over a half-tide rock) and rezone on the vertical walls without a barrier. In the dark, zonation is broken suggesting that the snails lose their geonegativity. EVANS proposes that light is necessary not as an orientating stimulus but for the snails to see the surface of the water. The structure of the littorinid eye (*L. littorea*) may permit image formation in air (NEWELL, 1965) but probably not in water (CHARLES, 1966).

On the west coast of North America, *L. planaxis* and *L. scutulata* are the representative littorinids. Both species demonstrate a strong negative geotaxis sufficient to carry them out of the water in aquaria, and *L. planaxis* to the highest level on the shore in nature (above mean higher high tide). High temperature and desiccation will reverse the negative geotaxis in both species and, additionally, the algae *Pelvetiopsis* will affect the response to light in *L. scutulata*. *Littorina planaxis* is strongly photonegative (from 400 to 15,000 foot candles) while *L. scutulata* is much less so. Negative geotaxis supersedes negative phototaxis until

the snails reach physiologically suitable heights above water when the negative phototaxis dominates and drives them into cracks and crevices, their natural habitats (BOCK and JOHNSON, 1967). NEWELL (1958a, b; consult for earlier references) carried out his studies prior to JANSSEN, EVANS, and BOCK and JOHNSON but none of the later authors paid particular heed to his warnings. NEWELL compared the light and gravity responses of *Littorina littorea* to horizontal and vertical surfaces. *L. littorea* living on horizontal surfaces orientate solely by reactions to the direction of light while those from vertical surfaces orientate to the direction of light and to gravity. The differences are phenotypic since horizontal dwelling snails will, after a period of time, orientate to gravity when given the opportunity to do so. What NEWELL clearly demonstrated others have ignored: the immediate history of the animals (whether living on horizontal or vertical surfaces, the degree of dark or light adaptation, the nutritional state, the time of year) is of utmost importance in analyzing their phototactic and geotactic responses. Further, NEWELL followed individual animals and discovered recurring reversals of the sign of both phototactic and geotactic responses even under non-tidal laboratory conditions. The behaviour of these animals, in their feeding excursions and in their maintenance of position on the shore, appears to be far less 'stereotyped' than the data would lead us to believe.

An orientation in which an animal does not go towards or away from the light (taxis), but uses the light as a fixed point and maintains a particular angle between the light and the long axis of its body is called a light–compass reaction. The phenomenon was first recognized by SANTSCHI (1911) for the movements of ants to and from their nest and is best known in terrestrial arthropods. Among marine invertebrates it has been demonstrated in prosobranchs, opisthobranchs and crustaceans with formed eyes, and in a bivalve without any well-established receptors.

The most detailed study has been carried out with the opisthobranch *Elysia viridis* (FRAENKEL, 1927b). *Elysia* maintains a constant orientation angle to a horizontal beam of parallel light rays and alters its course to maintain this angle when the beam is moved through 90°. All the angles observed lay between 45° and 135°, if crawling directly towards the light is considered as an orientation angle of 0°. The limits on the orientation angles are due to the eyes which, because of their structure, only permit light received approximately within the angle 35° to 130° to reach the retina. *Elysia* cannot see directly ahead (0°) or directly behind (180°). Change in direction is usually accomplished by a smooth curve and a new orientation is reached with as little turning as possible. When crawling along a track orientated to a light, switching on a second light, even if brighter, usually fails to disturb *Elysia* provided the original light is left on. If the first light is turned off, the animal will re-orientate to the second light with the same angle of orientation.

Littorina littoralis demonstrates a strong light–compass orientation in the laboratory (BURDON-JONES and CHARLES, 1958) and in the field *L. littorea* will do the same (NEWELL, 1958b). On flat featureless sand, *L. littorea* will change direction and crawl parallel to its original course when the sun is blocked on one side and a mirror-reflected image of the sun is shone on the other side of the snail. Regardless of the direction of the original path, north to south or east to west,

the direction of crawling was reversed when the apparent direction of the sun was altered. However, *L. littorea* periodically reverses its course and its orientation to the sun (by changing the sign of its response to light) and traces a roughly U-shaped path leading it back to its starting point (NEWELL, 1958b). The bivalve *Macoma baltica* undertakes similar U-shaped feeding movements over sand flats (BRAFIELD and NEWELL, 1961). Under heavy cloud cover the orientations are random. CHARLES (1966) suggests that U-shaped compass orientations may be of widespread occurrence in certain littoral species, conferring the advantage of bringing the mollusc into contact with surrounding areas while still maintaining its station on the shore. This proposal needs to be checked.

Among crustaceans a light-compass reaction has been demonstrated in *Carcinus maenas* (WOLTER, 1936). However, in *Carcinus* the mobility of its eyestalks permits the animal to maintain a given body orientation when the light is displaced. If light is displaced less than 20°, the change is compensated for solely by ocular movements without change in the animal's course. If the eyes are immobilized and the light displaced, the whole crab re-orientates.

Something quite different, at least as it has been analyzed, is the light-compass orientation of *Talitrus saltator* and other beach amphipods. Actually it is believed that animals are using the horizontal projection of the sun's direction, its azimuth, in their compass orientation (BÜNNING, 1967). According to PARDI and PAPI (1961), *Talitrus* can return directly to the wet beach zone it normally occupies after displacement to dry sand or to water. The direction of its return is approximately at right angles to the shore. As long as they can see the sun or, if they are shaded from the sun, the polarized light from an area of blue sky (see below), they will return, though not very accurately, in the correct compass direction at all hours of the day. *Talitrus* living on differently orientated shores have different directions of such flight movements. The direction taken is independent of the nearness of the sea or the land and is entirely dependent upon the sight of the sun and sky. Since the direction of these escape movements remains constant during the course of a day, the angle of orientation to the sun must change continuously and in a regular manner. These animals must have a time sense, an endogenous physiological clock (p. 178). The daily periods of light and dark set the clock. Artificially shifting the phase of the day–night cycle 6 hrs from the normal day, results in the animals assuming flight angles at noon that they would normally have at 6 a.m. When *Talitrus* was taken from Italy to Argentina, their escape direction on the beach was orientated to the sun in Italy, where the clock had been set. A similar time-compensated light-compass orientation has been demonstrated in *Uca pugilator* (HERRNKIND, 1968b).

There is evidence (PAPI, 1960; PAPI and PARDI, 1963) that *Talitrus* can also use the moon in a light-compass orientation; it implies that *Talitrus* not only possesses an endogenous diurnal rhythm corresponding to the movement of the sun but also an endogenous lunar rhythm corresponding to the movement of the moon. However, the isopod *Tylos punctatus* on Baja California, Mexico shores does not demonstrate time-compensated orientation to either the sun or moon; it does orient to slopes, as small as 1°, moving uphill when the substrate is wet, downhill when it is dry. *Tylos punctatus* orients successfully on the beach by day or night (HAMNER and co-authors, 1968).

A number of marine gastropods (*Littorina*, *Nassarius*), cephalopods (*Octopus*) and crustaceans (*Carcinus*, *Goniopsis*, *Ocypode*, *Talitrus*, *Tylos*, *Uca*) have been shown to detect and possibly orientate to the plane of polarized light (polarotaxis, as suggested by WATERMAN, 1966) in the field and in the laboratory (CARTHY, 1958; PARDI and PAPI, 1961; WATERMAN, 1961a; DAUMER and co-authors, 1963; JANDER and co-authors, 1963; SCHÖNE, 1963; CHARLES, 1966; WELLS, 1966b; HERRNKIND, 1968b). There are two opposing views as to the nature of the discrimination process: (1) extra-ocular analysis dependent upon differential intensities in the pattern of light reflected by the environment or substratum and (2) intra-ocular analysis dependent upon the arrangement and analyzing faculty of the retinal cells capable of directly discriminating the plane of polarization. Recent studies (SHAW, 1966; HORRIDGE, 1967) on *Carcinus maenas* and earlier work (ROWELL and WELLS, 1961; MOODY, 1962) on *Octopus vulgaris* lend credence to the latter view.

A special response to light, demonstrated by a few marine invertebrates, is the dorsal light reaction. In this response the animals maintain themselves with their dorsal surfaces towards the light source. CARTHY (1958) and FRAENKEL and GUNN (1961) discuss the phenomenon at length. Cnidarian medusae, pelagic polychaetes, asteroids (DIEBSCHLAG, 1938) and a variety of malacostracan crustaceans show a dorsal light reaction. For example, the shrimp *Palaemon xiphias* possesses statocysts and stalked eyes; it uses its statocysts to maintain the normal position with the dorsal side up whatever the direction of the light. When the shrimp is suspended freely and held obliquely the legs on the lower side make pushing movements returning it to the normal position if it were free to move. Illumination from the side does not interfere with this static reaction. However, in lateral light, after removal of statocysts, the shrimp makes pushing movements with its legs on the side farthest from the light; when turned over on the side with its back to the light, it makes no pushing movements. Another crustacean, *Processa canaliculata*, which has no statocysts shows essentially the same light reaction as a *Palaemon xiphias* without statocysts. In marine invertebrates with statocysts and dorsal light reaction, the static reaction and the photic reaction reinforce each other but the static reaction takes precedence.

Echinoids display unique covering responses (NICHOLS, 1964). A large number of littoral sea-urchins cover themselves with opaque objects such as pieces of shell, gravel or algae. YOSHIDA (1966) lists a variety of urchins that exhibit covering responses and the author of this chapter has observed the reaction in *Strongylocentrotus purpuratus* and *S. franciscanus* in bright light when covering materials are available. The response is particularly striking in a number of tropical sea-urchin species. *Lytechinus variegatus* drops its cover at night and picks it up again in the light; if only part of the urchin is illuminated the cover is held over the lighted area. The amount of covering material picked up is greater in strong light, and pale individuals pick up faster than dark ones. Individuals injected with photosynthesizing dyes (eosin Y, bengal rose, bengal red) cover in dim light; normal individuals cover more readily after a period in the dark and lose the response when uncovered in strong light for a long period (MILLOTT, 1956; MOORE and co-authors, 1963a). If *L. variegatus* is illuminated on the wall of an aquarium it descends to the bottom and picks up covering materials. The response to ultra-violet is faster than to white light with the ultra-violet filtered out (SHARP

and GRAY, 1962). *Tripneustes esculentus*, in nature, begins to cover in the spring as the light becomes stronger and tends to seek shelter during bright summer days; in the laboratory it covers only in sunlight (LEWIS, 1958; MOORE and co-authors, 1963b).

MILLOTT (1956) has shown that covering is an elaborate and well-defined response involving the coordinated use of spines and podia to pick up objects (even other urchins) and carry them over the illuminated portion of their test. Since both continuous strong light and intensity changes are effective stimuli, there is no doubt that the response subserves a light protective mechanism and may well permit inadequately pigmented urchins (p. 207) to feed during daylight hours in sunlit shallow waters.

Shadow responses, including reactions to both increase ('on') and decrease ('off') in light intensity, are widespread among bottom-dwelling marine invertebrates (see MILLOTT, 1957, and particularly STEVEN, 1963, for thorough discussions and comprehensive lists of references). Marine invertebrates respond to both increase and decrease in light intensity, e.g. the echinoids *Diadema antillarum* (MILLOTT, 1954) and *D. setosum* (YOSHIDA, 1962) and the gastropod *Serpulorbis squamigerus* (KOOPOWITZ, personal communication); rarely to increase alone, e.g. the bivalve *Pinna nobilis* (BRAUN, 1954); and, most commonly, to decrease alone, e.g. the polychaete *Branchiomma vesiculosum* (NICOL, 1950). Shadow responses, mediated through the diffuse photoreceptive surface of marine invertebrates, may entail (i) rapid withdrawal of an exposed part such as siphons in tunicates; siphons, mantle edges and possibly closure of valves in bivalves; tentacle crowns in serpulid and sabellid polychaetes; limbs in cirripedia, (ii) movement of spines, podia and pedicellaria in echinoids, (iii) cessation of movement and pressing the girdle to the substratum, e.g. in chitons (AREY and CROZIER, 1919). Physiological analyses of shadow responses (consult HECHT, 1934 for a summary of the classic work on the bivalves *Mya arenaria*, *Pholas dactylus* and the tunicate *Ciona intestinalis* which laid the foundation for the photochemical theory of vision) have shown that the speed, duration and intensity of the light stimulus and previous illumination determines the reaction time and duration of the response. The response adapts to repeated or prolonged stimulation.

Shadow responses are normally executed in the absence of anything that can be called 'eyes' (but see below); many marine invertebrates are indeed photosensitive over their entire body surface. Attempts to define the photochemical systems (pigments and spectral sensitivity) subserving non-optic light responses have been very unrewarding. But, in an entirely different approach MILLOTT (1966) and YOSHIDA (1966) have shown that photosensitivity is co-extensive with the superficial nervous system (at least in the echinoid *Diadema*) and that dermal photoreceptors are nerve elements devoid of obvious structural differentiation at the microscopic level. In a series of elegant experiments on *Diadema* an explanation for the shadow response appears to have been worked out. The shadow response, which results in directed movements of the sea-urchins' spines, is brought about through neuronal adaptation and inhibition. Spontaneous spine movements are inhibited by light to a degree proportional to its intensity and duration. Shading initiates a reaction (directed spine movements) whose strength and duration are proportional to the preceding illumination. The sensitivity of the response

increases in darkness and declines in light even in body areas screened from the adapting light. All of this is integrated through an organization in the superficial nervous system and radial nerve which appears to show a complexity and sophistication one usually attributes to elaborate photoreceptors.

Physiologically the tube-dwelling gastropod *Serpulorbis squamigerus* has also been shown to possess 'on' and 'off' receptors but, in contrast to the echinoid *Diadema antillarum*, the eyes may play a role in shadow reactions. Individuals with eyes have shorter 'off' and 'on' response latency periods (550 to 400 msecs off; 1500 to 950 msecs on) than those with eyes removed (800 to 550 msecs off; 3000 to 1500 msecs on). In normal *Serpulorbis* 'off' response latencies are always shorter (50 to 70 msecs) than 'on' response latencies at all intensities between 3×10^{15} to 3×10^{13} photons/cm^2. The higher the intensities of both 'on' and 'off' responses the shorter are their latencies (KOOPOWITZ, personal communication). If eyes play a role in shadow responses, BARTH'S (1964) intracellular recordings from retinal neurons of the nudibranch *Hermissenda crassicornis* are relevant. *Hermissenda* retinal neurons show both excitation ('on') and inhibition ('off') impulse discharge with appropriate photic stimulation.

There is considerable similarity in withdrawal responses of *Serpulorbis squamigerus* and spine responses of *Diadema antillarum*. At 510 mμ, the larger the change in intensity of illumination (decrease), the greater the amplitude of withdrawal contraction; the more rapid the illumination change the more rapid the withdrawal contraction. Light can inhibit 'off' responses if the shadow period is brief. If the shadow period is not brief, light has no effect. When subjected to pulsing light (1·5 to 2/sec) *Serpulorbis* contracts ('on' response), then begins to recover and returns to baseline. If the flicker is stopped, the test individual contracts again ('off' response). As MILLOTT (1966) and YOSHIDA (1966) have proposed for *Diadema* and KOOPOWITZ (personal communication) for *Serpulorbis*, the 'off' response does not represent a specific 'off' receptor but an inhibitory rebound response.

Approaching enemies probably cast shadows, and shadow responses are assumed to be protective (VON BUDDENBROCK, 1952). The spines of *Diadema antillarum* are poisonous and constitute a formidable armament directed towards the shading object. The gastropod *Cassis tuberosa*, the predator of *Diadema*, secretes a saliva containing an active neurotoxin which blocks spine convergence on a shaded area, inhibits spine movement under steady illumination and increased movement under increased light (CORNMAN, 1963). As MILLOTT (1966) points out, although divining 'purpose' or 'usefulness' is sometimes considered a misguided pursuit, the elaborate means employed by *Cassis*, in order to inhibit spine reactions of *Diadema*, must surely have their ecological implications.

Behaviour. Ample portions of this chapter have dealt with descriptions and interpretations of the effect of light on the behaviour of marine invertebrates. What has not been covered are aspects of behaviour modified by, and thus dependent upon, the immediate experience of the individual. According to THORPE (1963), we may justifiably call such behaviour 'learning'. A simplistic definition as THORPE's, includes within a single category an enormous range and complexity of behaviour influenced by individual experience. But, as pointed out by PANTIN (1965):

'Thorpe's definition is excellent because it gives the minimum qualities needed for a phenomenon to be classed as an example of learning, and it does not fall into the common error of entangling a definition with contemporary hypotheses of how the phenomenon is brought about.'

Three recent reviews (THORPE and DAVENPORT, 1965; WELLS, 1965; MCCONNELL, 1966) summarize most of what is known about learning in invertebrates, including marine ones.

Habituation is the simplest light-related learning process in marine invertebrates. In habituation the organisms stop responding to repeated light stimuli ('on' or 'off') that initially caused a response. There is considerable individual variation in habituation responses to light and a variety of other external stimuli; many of the older studies did not take adequate account of this. Reliable data on habituation to light has come primarily from studies on polychaetes and more recently a gastropod (NICOL, 1950; CLARK, 1960a, b and KOOPOWITZ, personal communication).

The sabellid polychaete *Branchiomma vesiculosum* (NICOL, 1950; consult for earlier references) shows the characteristic shadow response to a decrease in light intensity or to passing shadows and habituates rapidly. Habituation to a decrease in light intensity is more rapid than to a passing shadow. The errant polychaete *Nereis pelagica*, kept in glass tubes in the laboratory, responds to decrease and increase in light intensity and to moving shadows with a sudden contraction of the longitudinal muscles of its body wall. Light-adapted worms (1 hr) subjected to a sudden decrease in light intensity (33·9 to 0·08 foot candles applied at 1-min intervals with light off for 9 sec) habituate in the first 15 trials. The response to a moving shadow (same intensity change but over a 0·5 sec interval) revealed a fast contraction, which habituates in about 4 trials, and a slow contraction which habituates by the 16th trial. When the shadow is moved slowly across the worms (2 to 3 secs) they do not respond. Dark-adapted individuals (2 hrs) exposed to a sudden increase in light intensity (0·08 to 33·9 foot candles applied at 1-min intervals with light on for 9 secs) usually respond with a complicated series of fast and delayed slow contractions with the fast contraction habituating in 50 to 60 trials. Habituation is, therefore, faster to decrease than to increase in light intensity (CLARK, 1960a). *N. pelagica* also habituates to other stimuli (e.g. mechanical shock) and the slowest habituation takes place with a sudden decrease in light intensity combined with a mechanical shock. Habituation to one of these stimuli lengthens habituation to the other. *Nereis diversicolor* has a similar rate of habituation to both a sudden decrease in light intensity and moving shadows, but habituation to one factor does not appear to influence habituation to the other (CLARK, 1960b).

Recovery from habituation is a slow process and depends on the number and frequency of stimuli to which the animal has habituated. Thus, recovery from habituation to sudden decrease in light intensity took 5·5 hrs when the interval between trials was 30 secs, and 17 hrs when the interval was 3 mins (CLARK, 1960b).

Habituation to light stimuli has also been demonstrated for the first time in a gastropod (KOOPOWITZ, personal communication). The tube-dwelling gastropod *Serpulorbis squamigerus* responds to both decrease and increase in light intensity above 1×10^{14} photons/cm^2 with a fast contraction followed by a slow contraction of the body wall. With repeated stimuli at the same intensity the fast contraction

drops out first. If the intensity of stimulation is increased the fast contraction takes longer to drop out, which means habituation to low intensity stimulation is faster. For example, at an intensity of $1{\cdot}2 \times 10^{15}$ photons/cm^2 sec, the fast contraction drops out after 13 contractions, at $3{\cdot}9 \times 10^{14}$ after 6 contractions, and at $2{\cdot}2 \times 10^{14}$ after 1 contraction. Similar responses were obtained with a decrease in light intensity.

Recovery from habituation in *Serpulorbis* is a slow process but not to the extent shown in *Nereis*. No matter what the level of stimulation, *Serpulorbis* will not respond in less than 10 secs. By about 15 secs 30 to 40% of the original response is obtained; by about 1 min up to 70% of the original response is obtained. After habituation to either increase or decrease in light intensity it takes at least 20 mins to return to the normal response level.

Recent neurophysiological studies on giant cells of the abdominal and pleural ganglia of the sea-hare *Aplysia* provide information on one possible aspect of a cellular response which may underlie the mechanism of habituation (TAUC, 1966).

A shadow response—usually manifest by withdrawal into a tube, or pulling back of all or part of the body, in non-tube-dwelling marine invertebrates—is assumed to be a defence mechanism against predators. Rapid habituation would leave the organisms vulnerable to attack unless recognition of the approach of a predator is not by any single stimulus but by a complex of stimuli. Contraction every time a small change in light intensity occurs would hardly be of adaptive value to the animal involved. Withdrawal, particularly of tube-dwelling invertebrates, interrupts numerous maintenance activities including tube building, feeding and possibly respiration. Large changes, single, multiple or cumulative, would be biologically important; small changes would not.

Only a scatter of more complex light-connected learning has been demonstrated among marine invertebrates. When fed under red light for some time the decapod crustaceans *Dardanus* and *Palaemonetes* took food only when offered under red light (MIKHAILOFF, *in*: SCHÖNE, 1965). The polyclad turbellarian *Leptoplana*, normally photonegative, was trained to remain in the light by contact punishment (HOVEY, 1929). SCHÖNE (1961) trained the decapod crustacean *Panulirus argus* to make a brightness choice, although learning was faster when the animals were required to make a left–right choice. According to LANDENBERGER (1966), the asteroid *Pisaster giganteus* was able to associate light and food and descend to a feeding area of an aquarium when the light was turned on even though food was no longer presented. *Limulus polyphemus* was conditioned to move its tail in response to light stimulation in place of electrical stimulation, the adequate stimulus (SMITH and BAKER, 1960). However, associative learning in polychaetes, originally proposed by COPELAND (1930), has been challenged by EVANS (1966). EVANS (1966), in controlled experiments, has shown that food sensitizes *Nereis diversicolor* to light so that they become more responsive to sudden increases in illumination; the behavioural modification is therefore non-associative. Appropriate sun compass orientation, either directly or from the plane of polarization appears to involve a learning component in *Talitrus* and other beach amphipods (PARDI, 1960) and in the crabs *Ocypode* (DAUMER and co-authors, 1963) and *Goniopsis* (SCHÖNE, 1965). Some of the most impressive learning responses among marine invertebrates have been demonstrated in cephalopod molluscs, particularly *Octopus vulgaris*.

Octopus can make a wide variety of visual discriminations including discrimination of the plane of polarization of the light source (consult WELLS, 1965, 1966b for a thorough review on learning in cephalopods).

(c) *Reproduction*

Few detailed investigations have been made on environmental stimuli which trigger the various aspects of reproductive processes in marine invertebrates, so that there are serious gaps in our knowledge of their breeding biology. In many marine invertebrates, reproduction encompasses the greater part of their lives. Factors that may initiate spawning, and integrate the more immediate aspects of reproductive behaviour in a population, are more readily amenable to investigation and understanding than factors that synchronize a population, and are instrumental in bringing them to the point where spawning and possibly the coordinated release of gametes may occur.

Photic stimulations represent important extrinsic factors controlling aspects of reproduction in many marine invertebrates. The manner in which control takes place ranges from the direct effects of illumination on tissues, to the psychological impact of specific visual impressions. Further, changes in relative lengths of diurnal light and dark periods, the so-called photoperiod, is an essential component of the seasonal calendar by which many marine organisms seem to regulate their reproductive activities.

In its simplest manifestation, light, passing through the integument of transparent or translucent organisms, appears to act directly on germ cells. Alternating periods of light and dark, in varying sequences, may initiate spawning in the hydroids *Hydractinia*, *Pennaria* (BAKER, 1936; BALLARD, 1942) and the limnomedusan *Gonionemus* (RUGH, 1929); the ectoprocts *Bugula* (LYNCH, 1960) and *Cryptosula* (RYLAND, 1962); and the ascidians *Ciona* and *Molgula* (LAMBERT and BRANDT, 1967; WHITTINGHAM, 1967). Under constant light or dark these invertebrates do not spawn.

SCHARRER and SCHARRER (1963) assume that there are substances in the germ cells which are sensitive to light or its absence, whose reaction to illumination change initiates sexual maturation and spawning. Rarely stated is the point that organisms which spawn in response to illumination changes are mature individuals ready to spawn; non-gravid individuals cannot, of course, spawn, regardless of the light regime. LAMBERT and BRANDT (1967) found that the oviduct of the tunicate *Ciona intestinalis* was packed with ova prior to spawning. Maturation of gametes and release of mature gametes are separate processes both in regard to time and function (see below).

Photo-induced spawning responses have received some attention. Both male and female colonies of the sea-pen *Cavernularia obesa* normally release gametes 2 to 2·5 hrs after sunrise during October even when reared in separate vessels. If the light–dark cycle is reversed, within 2 to 7 days gamete release will take place 2 to 2·5 hrs after the onset of the light phase. The intensity of illumination determines the time course for the change-over to the new cycle of gamete release; between 1230 lux and 7 lux change-over takes 2 or 3 days, at 1·2 lux 6 days and at 0·3 lux 7 days for about 50% of the colonies tested (MORI, 1960). The ascidian *Corella*

parallelogramma, which normally spawns during the early morning hours, can be induced to spawn after exposure to light for 2 mins following a period of dark adaptation (HUUS, 1939). The time between illumination and spawning ('dormant' period) is temperature dependent and ranges from 11 mins at 24° C to 17 mins at 10·5° C. HUUS (1941) proposed that light causes spawning by eliciting the production of a hormone, and that the dormant period is due to the delay in hormone action. WHITTINGHAM (1967) stimulated the tunicate *Ciona intestinalis* to begin releasing gametes 4 mins after light exposure but gave no indication of the temperature. He did find an intensity threshold since in both species there was a marked reduction in release of gametes between 0·67 foot candles and 0·40 foot candles with a complete inhibition in *Ciona* and a 25% reduction in *Molgula* at 0·21 foot candles. Spawning occurred in the anthomedusan *Polyorchis kerafutoensis* following 1 to $1\frac{1}{2}$ hrs of light (no intensity given) preceded by 2 to 3 hrs of dark; when animals were kept in continuous light or dark, spawning did not occur (ZEN, 1963).

Further work by LAMBERT and BRANDT (1967) on *Ciona intestinalis* was directed at establishing the minimum reliable dark-adaptation time and the time required for spawning after illumination. More significantly, these workers obtained an action spectrum for spawning. *Ciona* requires 1 hr of dark adaptation followed by illumination which may be as short as 1 min for 78% of the population to spawn. At 15° to 16° C, an average of 27 mins elapsed between the end of the dark-adaptation period and the initiation of spawning. The action spectrum obtained by LAMBERT and BRANDT is most interesting. There are three peaks of maximum effectiveness for the induction of spawning. The most effective peak is at 415 mμ which requires a dose of light about one-third that of the next most effective wavelength, 550 mμ; the third peak at 520 mμ is about as effective as 550 mμ. LAMBERT and BRANDT suggest that a haemoprotein, possibly reduced cytochrome c, may be the chromophore (Fig. 2-25). If so, it is apparently the first demonstration of a haemoprotein involvement in a photo-induced reproductive response of an animal.

ARVANITAKI and CHALAZONITIS (1961), studying the effect of light on the visceral ganglion of the sea-hare *Aplysia*, demonstrated the involvement of two chromophores, a haemoprotein at maximum absorption of 579 mμ and a carotene–protein at maximum absorption of 490 mμ. The haemoprotein is involved in an 'on' response, the carotene–protein in an 'off' response. Both pigments are contained within the neurons of the ganglion. Photosensitive neurons have been described (KENNEDY, 1960; TAKAHASHI, 1964), but the question arises whether all neurons or only specialized ones are endowed with the capacity of recording photic stimuli (consult STEVEN, 1963 for a discussion of the 'dermal light sense'). CHALAZONITIS (1964) has proposed a scheme for the conversion of light energy into electrical energy in neuronal membranes, but the path to an organismic response, in this case spawning in *Ciona*, is not known. We also do not know whether light is acting directly on the gametes, reproductive structures, neurons serving the oviduct musculature or an integrative centre removed from the reproductive elements. In transparent forms, such as *Ciona*, light impinges on a variety of pigmented and non-pigmented structures to varying degrees. In *Ciona* (and other ascidians) the close approximation of the neuronal ganglion–neuronal gland

complex to the oviducts and siphons, the determination of neurosecretory cells in the neural ganglia of a number of species of tunicates (DAWSON and HISAW, 1964), and the latent period between illumination and spawning which suggest hormonal action, point to the need for investigation of a photoneuro-endocrine pathway subserving photo-induction of spawning if not numerous other aspects of the reproductive process. Significant, too, is the fact that as gametes and reproductive organs become shielded from light, in the majority of marine invertebrates that are not translucent, the effect of light and darkness becomes, of necessity, an indirect one. A discussion of the neurosecretory neurone in neuro-endocrine regulatory mechanisms and photoneuro-endocrine systems is beyond the scope of this chapter. The reader is referred to E. SCHARRER (1964), B. SCHARRER (1967), and the symposium *Neurosecretion of invertebrates other than insects* (1966).

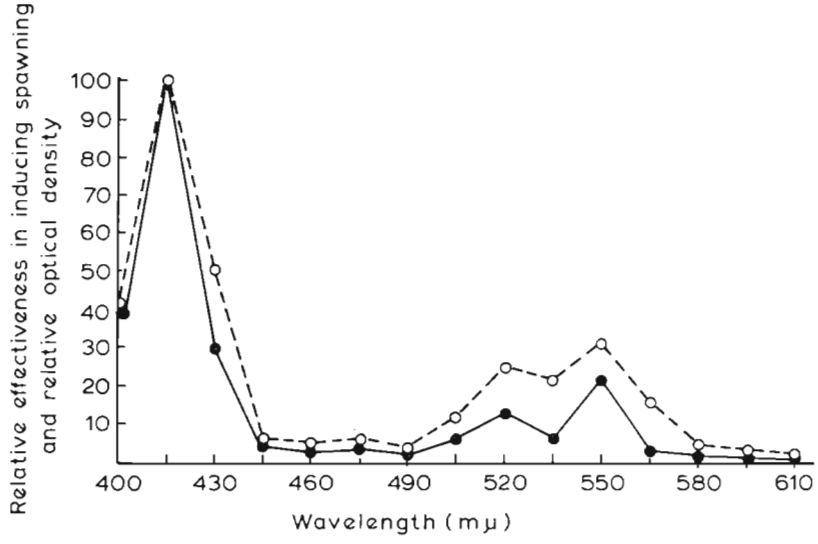

Fig. 2-25: Comparison of the action spectrum for spawning of the tunicate *Ciona intestinalis* (○) with the absorption spectrum of reduced horse heart cytochrome c (●). (After LAMBERT and BRANDT, 1967.)

Studies on long term photoperiodic effects on reproductive processes—effects that are instrumental in preparing individual organisms and possibly synchronizing entire populations for the culminating activity, spawning—are not numerous and certainly not very revealing at this time. Spawning time in three Hawaiian species of *Littorina* was altered by imposing a series of LD cycles on the females (STRUHSAKER, 1966); normally, *Littorina* spawns throughout the year in tropical regions. The crabs *Hemigrapsus nudus* and *Lophophanopeus bellus* begin to copulate during and after the shortest day of the year and progress steadily as photoperiod lengthens (KNUDSEN, 1964). According to BARNES (1963), the barnacle *Balanus balanoides* requires a period of 4 to 6 weeks at less than 12 hrs of light per day below a specified critical temperature for gamete maturation. Constant illumination inhibits breeding by interfering, in some way, with the later stages of development. Geographically separated populations of the urchin

Strongylocentrotus purpuratus show identical peaks of spawning; minimal day lengths may be responsible for this synchrony (BOOLOOTIAN and GIESE, 1959). Subsequently, BOOLOOTIAN (1963) demonstrated that long day photoperiod (LD 14:10) primarily stimulates the production of eggs while short day photoperiod (LD 6:18) primarily stimulates the production of spermatozoa in *S. purpuratus*. A population of the sea-urchin *Stylocidaris affinis*, at 70 m depth near the Isle of Capri, undergoes an annual gametogenic reproductive cycle in both males and females (HOLLAND, 1967). Since temperature (13·7° to 14·8° C), O_2 concentration (7·4 to 8·4 mg/l) and salinity (37·58 to 38·06 $^0/_{00}$) show a marked lack of annual variation at this depth, the author invokes the annual change in photoperiod as a possible reference point to synchronize the rhythm. The shrimp *Palaemonetes pugio* may be induced to spawn in winter by slowly raising the temperature and increasing the photoperiod. Winter animals at 10° C and LD 10·5:13·5 spawned when subjected to a gradual temperature increase to 25° C and photoperiod increase to LD 14·5:9·5 over a period of 32 days (LITTLE, 1968).

Most of the species referred to are relatively heavily and uniformly pigmented forms. According to MILLOTT (1966), who has worked extensively with the urchin *Diadema setosum*, the white aboral areas overlying the gonads of certain urchins may be the windows through which light exerts an effect on the reproductive activities of these animals. Further, since it is well known that spawning in a few urchins can stimulate other members of the population to follow suit, those with windows (white areas) may be light-triggered reproductive 'pacemakers' in echinoid populations.

Sex determination in the amphipod *Gammarus duebeni* has also been demonstrated to be under the influence of the photoperiod (BULNHEIM, 1967). In rearing experiments, short-day photoperiod (LD 8:16) resulted in an increase in the number of females, while long-day photoperiod (LD 16:8) resulted in an increase in the number of males. The photosensitive period is more or less restricted to the interval between the second and fourth moult. BULNHEIM offers an interpretation of a photoperiodic influence on sex realization in terms of a photoneuro-endocrine pathway. In cephalopods, sexual maturity may be light dependent (WELLS and WELLS, 1959). Indirect evidence suggests that, among cephalopods such as *Octopus*, nervous inhibition of the optic gland is conditioned by photic stimuli. Maturation of the gonads is determined by secretion from the optic gland which is normally held in check by an inhibitory nerve supply from the basal lobe area of the brain. The action of this region of the brain is, in turn, dependent upon the integrity of the optic nerves and thus presumably upon light. ALAIN (1967), using the change in colouration of the nidamentary gland as an index of sexual development in the squid *Sepia*, has demonstrated that the development of the gonad and associated structures is dependent upon at least 12 hrs of darkness out of 24 hrs; less than this inhibits maturation of the gonad. Temperature (Chapter 3.3) also influences the growth of the gonad but the minimal dark period is necessary for complete development.

Both semilunar (15 day) and lunar (30 day) reproductive activities also appear to depend upon the influence of light. In the field, a semilunar and diurnal periodicity of hatching and emergence in the intertidal chironomid *Clunio marinus* is synchronized with tidal conditions which parallel certain times in the semilunar

(15 day) cycle of spring and neap tides (NEUMANN, 1966). The restriction of hatching to particular days of the month was achieved in the laboratory by subjecting individuals to a regime of periodic night-time illumination with artificial moonlight (4 'nights' with 0·4 lux every 30 days). The restriction of emergence to particular times of the day was achieved by altering the phasing of the diurnal light–dark cycle. According to NEUMANN, both the semilunar and diurnal periodicities are endogenous rhythms (p. 178) and differ in different populations depending upon local tide conditions.

The entire question of lunar swarming periodicity (KORRINGA, 1947, 1957) also seems to rest upon the influence of light other than the moon itself, which may act as a trigger or synchronizer. CLARK (1965) presented a summary for the role of light, endocrines and swarming periodicity in annelids. HAUENSCHILD (1960, 1966) has experimentally supported the view that lunar swarming periodicity, at least in *Platynereis*, observed under natural conditions, is due to photoperiodic suppression of cerebral endocrine activity. Graded ultra-violet irradiation of the brain of intact animals with germ cells results in precocious maturation. The average time span between irradiation and maturation equals that between decrease of photoperiod and maturation.

(*d*) *Distribution*

Vertical distribution

Diurnal vertical migration is one of the most conspicuous phenomena observable in oceans and coastal waters. It occurs in both shallow and deep water and, although most of the observations and experiments have been carried out with crustaceans (Copepoda and Cladocera, also Decapoda, Isopoda, Amphipoda, Euphausiacea and Mysidacea), vertical migrations seem to take place in all groups with planktonic representatives. The attention devoted to the diurnal vertical migration of marine forms, other than fish, has been considerable; numerous reviews are available, e.g. CUSHING (1951), BAYLOR and SMITH (1957), BAINBRIDGE (1961), BANSE (1964), RINGELBERG (1964); for earlier literature consult RUSSELL (1927). WOODHEAD (1966) covers the literature dealing with diurnal vertical migrations in fishes (see also Chapter 2.32).

A general picture of diurnal vertical migration has been proposed by CUSHING (1951). In his opinion the execution of the basic plan depends upon the penetration of light and the aggregation of animals in an optimum band of light intensity. As postulated, the phases of the migration are (i) an evening ascent towards the surface from day depth, (ii) a departure from the surface at or before midnight, (iii) a return to the surface shortly before dawn, (iv) a sharp descent to day depth when the sunlight begins to penetrate the water and (v) maintenance of a variable day depth. BAINBRIDGE (1961) lists the widespread field observations of diurnal vertical migration among crustaceans and maintains that CUSHING's cyclic schema is an idealization and is, in fact, revealed only upon the rarest of occasions. The natural order of things is variability of performance whether due to the physical parameters of the environment or to the inherent variability of organismic response demonstrated at different times, different places and by different age and/or size groups (p. 169). BANSE (1964) has summarized the significant literature on night/day ratios of plankton volumes and concludes that, in the upper layers of

the open ocean, usually less than half of the plankton retained by nets with mesh aperture of about 0·3 mm does not migrate so that a large part of the grazers are always present in the photic zone. In the upper layers of the shelf, he maintains, even fewer species migrate. Earlier, BOGOROV (1958) had implied that the small, non-migrating species usually contribute little to the biomass of the net plankton, and that possibly three-quarters of the zooplankton mass migrate diurnally.

Criticism has been levelled at studies based solely upon net plankton tows (BARY and co-authors, 1958; HANSEN and ANDERSON, 1962; CASSIE, 1963). Numerous species of euphausiids avoid nets (BRINTON, 1967), and the escape capabilities of zooplankton must be overcome to be able to obtain a representative cross section of a zooplankton community or to make accurate estimates of the population structure of any given species (FLEMINGER and CLUTTER, 1965). The latter study was conducted on captive populations of zooplankton (six species of copepods and one mysid shrimp) where light conditions, time of sampling and path of sampling could be precisely repeated. The results clearly demonstrate that zooplankton can avoid capture and that accuracy in sampling can be affected significantly by the behaviour of the animals. Net size, interaction between net size and population size, light intensity (particularly with the mysids) and an apparent avoidance difference between species, even within the same genus, all contribute to a diminution of whatever accuracy may be claimed for net sampling techniques. As CASSIE (1963) has stated:

> 'An important consequence of vertical migration is that no two samples, unless they represent the entire water column, can be strictly comparable unless they are taken at the same time of day and under the same lighting conditions.'

All in all—notwithstanding organismic variability, physical parameters and pelagic species not vertically migrating or reversely migrating (BAINBRIDGE, 1961; ROEHR and MOORE, 1965; consult BANSE, 1964 for an extensive list of references and a discussion of both pelagic and shallow-water non-migrating species)—it remains clear that diurnal vertical migration of marine populations is a widespread and significant phenomenon. The search for initiating or controlling factors in vertical migration really amounts to a search for the factors which permit marine forms to gauge depth (Chapter 8). Vertical migration, whether the excursions are short or extensive, would be impossible if a depth-gauging mechanism were not present. Both light and pressure may act as adequate stimuli, but the overwhelming evidence has led most research workers to conclude that light plays the major role in initiating and controlling vertical migrations of marine invertebrates (RUSSELL, 1927; CLARKE, 1933; SPOONER, 1933; CUSHING, 1951; HARDY and BAINBRIDGE, 1954; KAMPA and BODEN, 1954; CLARKE and BACKUS, 1956; MOORE, 1958; HERMAN, 1963; BARY, 1967; BODEN and KAMPA, 1967 and others).

This is not to say that pressure is without effect either alone or in conjunction with light (BAINBRIDGE, 1961; Chapter 12). According to KNIGHT-JONES and MORGAN (1966) many planktonic animals tend to regulate their depth through pressure responses. However, the nature of the response, its direction and relation to light, varies considerably in different species or different developmental stages of the same species (p. 172). Animals may respond to pressure by orientating to light or gravity or both. For contributions to the role of gravity as an orientating

factor in vertical migration see SIEBECK (1960), BAINBRIDGE (1961), RINGELBERG (1964), and MOORE and ROEHR (1966). It is interesting to note that the mechanism of pressure sensitivity is still obscure. DIGBY (1967), in an extension of a proposal raised earlier (DIGBY, 1961), discusses the possibility that pressure sensitivity is due to an electrode effect arising from the compression of hydrogen produced electrolytically on the outer surface of organisms; however, ENRIGHT's (1963c) work on the amphipod *Synchelidium* sp. showed that if such a gas film is present it would apparently undergo thickness changes of less than 2 Å during pressure changes perceptible to the animal, hence, the sensory amplification system would have to be remarkably refined. KNIGHT-JONES and MORGAN (1966) discuss the possible mechanisms of barosensitivity in their comprehensive review (for further details consult Chapter 8).

Migration of deep-water invertebrates from below approximately 1000 m, usually assumed to be the lower level of surface light penetration measurable in the sea (CLARKE and DENTON, 1962), suggests that these organisms are initiating their upward migration without light cues from the surface. However, even man has visibility at approximately 700 m (BUSBY, 1967), and the full transmissibility of ambient light in the open ocean still remains to be demonstrated. According to VINOGRADOV (1959; consult also ZENKEVITCH, 1963), who has summarized data on the migration of deep-sea zooplankton, invertebrates such as Mysidea live at about 4000 m and may feed at the surface. Numerous marine invertebrates have been reported to show a 'dawn rise' during the night hours before any surface illumination cues could be present, or at least cues that the human observer could detect. KAMPA (personal communication) is of the opinion that the 'dawn rise' is associated with light decrease brought about by increased cloud cover.

If the migration of deep-water invertebrates without obvious light cues and the 'dawn rise' phenomenon are real, the approximate regularity of activities of many migrating forms in the temporary absence of normal environmental stimuli remains to be explained. Work on the marine copepod *Calanus finmarchicus* and the freshwater cladoceran *Daphnia magna* has led HARRIS (1963) to propose the operation of an endogenous diurnal rhythm of activity in vertical migration. At times of peak illumination, the depth maintained is assumed to be governed by phototactic responses and to be determined entirely by light intensity. Whatever their distribution in the vertical column, the organisms move towards the surface as the illumination diminishes. They maintain themselves in or near the surface layers until the light fails and then they begin to sink (midnight sinking). It is during the hours of darkness, HARRIS proposes, that the intrinsic rhythm of activity is able to become manifest. If the phasing of this rhythm is appropriate, a rise towards the surface could occur at any time well before true dawn. When surface illumination increases at dawn it would reinforce and finally predominate over the intrinsic rhythm, and the population would follow its optimum intensity by actively maintaining itself near the surface or actively moving downward as the intensity of illumination increases with time. If such a rhythm is in operation it would prevent migrating invertebrates from sinking beyond the level in the water column where the normal stimulus, light, would have its effect. HERMAN (1962) was unable to demonstrate an endogenous rhythm in the vertical migration of the mysid *Neomysis americana*. In total darkness, in the laboratory, *Neomysis*

revealed no significant movements towards the surface at the time of day when the animals in nature were ascending. RICE (1964) and KNIGHT-JONES and MORGAN (1966) suggest, although without experimental evidence, that pressure (Chapter 8) may set bounds to the vertical migration of planktonic animals and may also affect the precise timing of endogenous cyclic rhythms of activity.

ENRIGHT and HAMNER (1967) attempted to reassess the possible contribution of internal rhythmicity to the vertical migration of a variety of nearshore zooplankton held in a 2·5 m deep concrete tank. Light–dark cycles of about 100 lux maximum at the surface during the light phase and 0·02 lux minimum during the dark phase were imposed on the animals. The transition period at artificial twilight took 30 mins. Net sampling techniques provided information only on the changes in abundance of the various species in the upper 30 cm of the water column. During the first experiment, simulated daylight was imposed from noon to midnight for 3 days; in the second experiment the light period ran from midnight to noon for 6 days. In both experiments, the majority of the species demonstrated vertical migratory behaviour (9 out of 13 species, with 7 of the 9 at the surface during the dark phase and 2 during the light phase in the first experiment; 11 out of 16 species, with 9 of these at the surface during the dark phase and 2 during the light phase in the second experiment). According to ENRIGHT and HAMNER, the amphipod *Nototropis* sp. and possibly two peltidiad copepod species (not further identified) demonstrated a persistent endogenous rhythm synchronized by the environmental light cycles; two copepod species (a lacophontid, not further identified, and *Euterpina* sp.) revealed an inverse vertical migratory pattern which did not persist in constant dim light; the amphipod *Tiron* sp. showed a non-rhythmic migratory pattern; and the remainder of the species tested exhibited migratory patterns directly responsive, in varying degrees, to the prevailing experimental light regime. These results raise numerous questions and possibly indicate, as the authors suggest, that the physiological mechanisms underlying vertical migration in nature are '. . . by no means uniform.' However, the procedures and the very nature of the experimental conditions do not allay concern about the physiological state of the organisms and the normality of their behaviour.

Other environmental factors, such as temperature (Chapter 3), salinity (Chapter 4), and oxygen (Chapter 9), have, at one time or another, been implicated as initiating or controlling vertical migration. Both BAINBRIDGE (1961) and BANSE (1964) discuss the respective possibilities. There is no good evidence that any one of these factors, or any other factor, is directly involved in diurnal vertical migration but sharp thermal, saline or oxygen gradients, acting as physical barriers or modifying behaviour stimuli, may restrict the extent, upward or downward, or modify the patterns of vertical migrations (CLARKE, 1933; HANSEN, 1951; BODEN and KAMPA, 1958; BANSE, 1959; LACROIX, 1961; HERLINVEAUX, 1962; LANCE, 1962; BRUSCA, 1967). Also, there may be a mechanical interaction of diurnally migrating zooplankton with the ocean floor, as on a seamount, resulting in less extensive migrations (ISAACS and SCHWARTZLOSE, 1965). Age (BOYD, 1967), maturation and reproductive needs (KOMAKI, 1967) may modify (daytime swarming) or terminate the migration pattern.

Although most of the evidence leads to the conclusion that light is the primary initiating and controlling factor in vertical migrations, that evidence is, for the

most part, indirect and circumstantial. Recent studies have begun to dispel any lingering doubts on the role of light and attempts have been made to understand how the organisms interpret light stimuli, i.e. the physiological bases for vertical migration. Two theories are currently vying for attention: (i) migrating organisms are responding to the rate and duration of the relative change in light intensity (with the implication that they can adapt to a wide range of light intensities), and (ii) migrating organisms are following an optimal light intensity, usually referred to as an isolume, attempting to remain within a comfortable and/or useful photo-environment. Evidence for each theory rests upon an entirely different approach to the problem.

RINGELBERG (1964) is the prime mover for the notion that migrating organisms can adapt to a wide range of light intensities, and that the rate of the relative change from each adapted intensity represents the adequate stimulus for the migratory response. His postulations result from a series of elaborate experiments on the freshwater cladoceran *Daphnia magna*, some corroborative observations of *Daphnia* migrations in nature and certain assumptions and recalculations of sonic-scattering layer data from the work of KAMPA and BODEN (1954), and CLARKE and BACKUS (1956). RINGELBERG's experiments were limited to decreases in light intensity and, therefore, concerned with upward movements in the afternoon when the light intensity is decreasing. He concludes:

> 'Relative decreases in light intensity of sufficient rapidity and of sufficient duration evoke an upward swimming during a certain short time. As long as the light intensity is decreasing at a sufficient rate new stimuli are furnished over and over again, which cause renewed reactions. When the decrease in light intensity is slow in the afternoon the upward swimming is interrupted by periods of no swimming. These periods become shorter and shorter with increasing change in illumination when time progresses.'

RINGELBERG's daphnids maintained constant swimming speed during the period of upward movement but at specified stimulus levels the swimming speed increased. In a later paper (RINGELBERG and co-authors, 1967) the intensity range within which the phototactic reaction of *Daphnia magna* will adapt was established at $3{\cdot}4 \times 10^{1}$ to $3{\cdot}4 \times 10^{4}$ erg cm^{-2} sec^{-1}. At lower intensities the threshold value changes rapidly with absolute intensity.

There are studies on vertically migrating sonic-scattering layers in the ocean which, as pointed out by BARY (1967), tend to support RINGELBERG's contention. If, during the ascent towards the surface, the sonic-scattering organisms are migrating at different lower light intensities than during the descent (indicating a differential adaptation to the different light conditions prior to ascent and descent), or if the organisms pass isolumes by swimming at a speed differing from that of a descending or ascending isolume, they are not following an isolume but must be swimming in response to the relative rate of intensity change, such that at each new response threshold swimming movements would change. BARY refers to the sonic-scattering studies of CLARKE and BACKUS (1956, 1964), BODEN and KAMPA (1965) and to his own work (BARY, 1967) in support of this theory.

The theory, as proposed, has a number of drawbacks which must be accounted for before widespread acceptance will be forthcoming.

Extrapolations from experimental laboratory results on a small freshwater

crustacean such as *Daphnia*, to larger marine forms making up the bulk of the migrating organisms is, at best, a precarious endeavour. While *Daphnia* can easily be maintained in the laboratory and behaves in a 'sensible' manner to experimental procedures, extensive migrators, such as the euphausiids *Euphausia pacifica* and *Thysanoessa raschii*, certainly do not. BODEN and KAMPA (personal communication) kept *E. pacifica* in captivity for one month and could no longer pick up action potentials from the eyes after the first week; in essence, the animals were blind.

Extrapolations from either field or laboratory studies on the smaller marine forms living in the surface waters, e.g. copepods, cladocerans and a wide variety of larval forms, are similarly precarious. These invertebrates may not migrate or, if they do, are relatively shallow migrators. Further, they may show considerable modification in migratory patterns due to a variety of environmental conditions and physiological states (BJÖRNBERG and WILBUR, 1968). *Calanus finmarchicus*, which has been intensively studied, seems not to migrate during the winter in temperate seas (MARSHALL and ORR, 1955); it migrates during spring and autumn but not during the continuous darkness of winter and not at all, or to a limited extent, during the continuous light of polar summers (BOGOROV, 1946). MARSHALL and ORR (1960) found considerable differences in diurnal vertical migration of *Calanus finmarchicus* from one year to another, and further discovered that ripe females migrate more and remain higher in the water than males or immature females. A similar situation has been reported for the sergestid decapod *Lucifer faxoni* (WOODMANSEE, 1966a). Also, a relation between body-fat content and intensity of vertical migration has been noticed in *Calanus* by SUSHKINA (*in*: BANSE, 1964). In contrast, the euphausiid *Thysanoessa raschii* performs regular diurnal vertical migrations in winter and summer (15 hrs of darkness as opposed to 6 hrs of darkness), showing no difference between males and females and no vertical layering of size classes (MAUCHLINE, 1966).

It is now obvious that we cannot place much reliability on human estimates of underwater light conditions (p. 202) and exact measurements of the relative changes in underwater light intensity have not yet been made. BARY (1967) conducted no surface or underwater light measurements at all: 'Light measurements would have been desirable with all records, but were not taken.' Instead, the events BARY recorded were referred to the times of dawn and sunrise, dusk and sunset, '. . . the dominant natural phenomena in the daily fluctuations of light in the sea.' An evaluation of the relative light-intensity change theory cannot be made until adequate underwater light measurements have been made.

The optimum intensity theory—the theory that migrating zooplanktonic forms are attempting to follow an optimum light intensity—was first put forward by RUSSELL (1927). It has since gained wide acceptance, but the evidence upon which the acceptance was based has been, for the most part, circumstantial. With the development of sophisticated sonar equipment operating at various frequencies and capable of detecting scattering layers of obvious biological origin (LENZ, 1965, carrying out sonic soundings in the western Baltic Sea believes he detected two different kinds of scattering layers one of biological origin, and the 'real' scattering layer due to a thermocline and, therefore, of physical origin), precision underwater light meters that can measure the intensity of light at a specific wavelength

(BODEN and co-authors, 1960; BODEN and KAMPA, 1967; TYLER and SMITH, 1967), the advent of submersible vehicles (BARHAM, 1966; BUSBY, 1967), design of improved underwater collecting gear (FOXTON, 1963) and the neurophysiological and biochemical techniques (BULLOCK and HORRIDGE, 1965) available for some time, we are now at the point where we can work on the physiology of migrating organisms where they live—in the sea—in conjunction with complementary physiological and biochemical studies in the laboratory.

Polar studies on sonic-scattering layers corroborate the net haul studies of BOGOROV (1946) that diurnal migration does not take place under conditions of permanent or almost permanent daylight (DIETZ, 1948; from analysis of fathograms taken on board the USS *Henderson* during the US Navy Antarctic Development Project, 1947). Towards the end of January and the return of a day–night cycle, there was a redevelopment of a sonic-scattering layer and the diurnal migration of the scatterers. HUNKINS (1965) found Arctic Ocean scattering layers to occur at relatively shallow depths (50 to 200 m during the day as compared to 200 to 600 m in non-polar seas). The Arctic scattering layers have a pronounced annual rather than diurnal cycle related to the polar light conditions. Beneath the permanent ice cover the light is relatively weak, the 'day' becomes effectively one year long at these high latitudes so that scattering layers are present at moderate depths during the summer light period and then disappear during the winter dark period.

In temperate waters (200 miles south of Woods Hole, Massachusetts, USA), BACKUS and co-authors (1965) obtained records of the upward movement of sonic-scattering layers during daytime as illumination was reduced during the solar eclipse of July, 1963. On the day of the eclipse a greater than normal rate of ascent of three scattering layers was observed about 20 mins after the eclipse began, and continued for about 5 mins after mid-eclipse. With the uncovering of the sun and increasing light the layers descended.

SUZUKI (1963a, b) measured submarine illumination off Hokkaido (Japan) in conjunction with the movements of a sonic-scattering layer. Net collections, at prescribed intervals and depths, suggested that the most obvious scatterer was *Euphausia pacifica* which migrated vertically following a 0·2 to 0·8 lux isolume. The sonic-scattering layer stayed at the depth of this range of light intensities on the way up and on the way down. No temperature correlation was obtainable during the series of measurements. HERMAN (1963), working with the mysid *Neomysis americana* in Narrangansett Bay, Rhode Island (USA), took surface light readings and calculated underwater light intensities at depth from extinction coefficients. *N. americana*, a relatively shallow bottom-dwelling mysid, undergoes a regular diurnal vertical migration which often includes midnight sinking and dawn rise. HERMAN calculated that the animals were congregating at a level where light intensity varied from 5×10^{-1} to 1×10^{-3} foot candles. A number of physical and biological factors influenced the diurnal pattern (thermoclines during July and August, flood and ebb tide, strong tidal currents, and predation by the shrimp *Crangon septemspinosa* during certain times of the year) but did not obscure the basic pattern.

In 1962, HERMAN showed that *N. americana* requires at least 12 hrs in continuous darkness to become photonegative (in contrast to RINGELBERG's hypothesis)

and, if kept in weak light for any period of time, becomes photopositive or, if the light source is substantially increased, photonegative. Therefore, whether or not *N. americana* undergoes a dawn rise depends upon the length of time spent in the dark during the night. From March through August this mysid shows a dawn rise because it had been in the dark less than 12 hrs and is still photopositive, so that at first light it moves towards the surface. However, from October through February the mysids encounter dark periods exceeding 12 hrs, and hence become dark adapted. Consequently, as the first light appears they are photonegative and, in nature, the increase in light is sufficient to keep them photonegative; they move towards the bottom. Under experimental conditions in the laboratory, continued exposure to light intensities approximating dawn light brings about a reversal from photonegative to photopositive within 3 to 5 mins. *Neomysis americana* is highly sensitive to light having a wavelength of about 515 mμ and will actively seek this in preference to light of other wavelengths; some individuals may be attempting to follow both an optimum light intensity and an optimum wavelength (HERMAN, 1962).

The proposition that organisms respond to wavelengths of light with specific behaviour characteristics is not new. BAYLOR and SMITH (1957) have described colour dances in *Daphnia*, three marine copepods and the larvae of the stomatopod *Squilla*. DINGLE (1962) has observed colour dances in the copepods *Temora* and *Labidocera*, stomatopod larvae and anomuran zoeas, but not in *Acartia*, *Centropages* or a number of species of *Calanus*. Basically, the colour dances lead to a concentration in red light and a spreading in blue light. None of the authors believes that colour dances among marine forms make a contribution to vertical migration of planktonic Crustacea. Instead, they assume that colour dances, where demonstrated, may function as a behavioural pattern leading to food. In herbivores and omnivores, red dancing tends to congregate the organisms in areas of abundant algae or diatoms (plants filter out blue light and leave red light). Blue dancing increases the probability of encountering such phytoplankton should it be scarce. HERMAN's (1962) suggestion that migrators like *N. americana* may be following a specific wavelength in diurnal vertical migration, opens up an entire new area of inquiry.

CLARKE (1966) put into operation a system composed of two nets (a 2 m Isaac Kidd mid-water trawl and a cod-end sampler), sensors for light, temperature, depth, water flow in a unit mount combined with shipboard readout equipment and a fathometer. In this way, measurements of environmental parameters and collections of biological samples could be taken simultaneously with both the sampling depth and the rate and method of sampling controlled. While the objections to net sampling, raised earlier, still apply and the collections in the nets may not be true representatives of all organisms that make up the sonic-scattering layer(s), the entire system is a considerable improvement on equipment used in earlier studies. Sampling was conducted by following one or two constant light levels (isolumes) in conjunction with oblique tows, which were made to obtain samples from different strata of water between the maximum sampling depths and the surface both while light conditions were changing and when light conditions were stable.

Two principal groups of migrating invertebrate organisms—euphausiid shrimps,

and sergestid shrimps (not further identified but probably *Euphausia pacifica* and *Sergestes similis*)—and a lantern fish showed a definite peak in concentration at a particular light level. The euphausiids were most abundant in the 1×10^{-3} to 1×10^{-4} μW/cm^2 light range, and the sergestids in the 1×10^{-5} to 1×10^{-6} μW/cm^2 light range. Two types of siphonophores and one ctenophore also showed major concentrations at particular light levels; a prayid siphonophore within 1×10^{-2} to 1×10^{-3} μW/cm^2, a diphyid siphonophore no higher than the 1×10^{-6} μW/cm^2 level

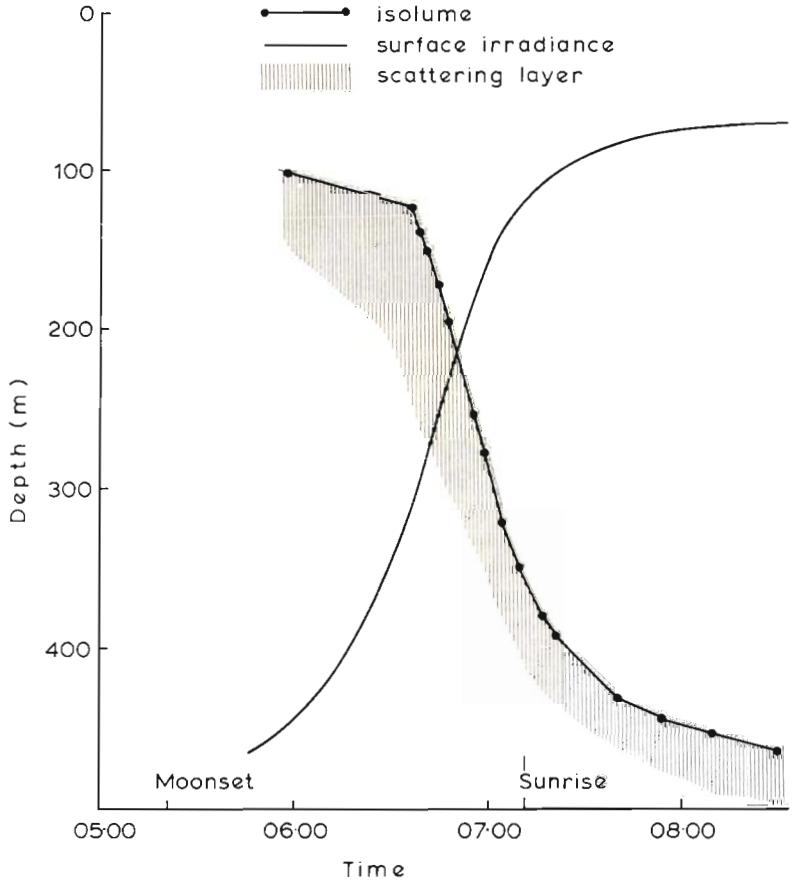

Fig. 2-26: Downward migration of the sonic-scattering layer, depth of the 5×10^{-4} μW/cm^2, 474 mμ isolume, and surface light intensity during one dawn. (After Boden and Kampa, 1967.)

(very close to the sensitivity limit of the photometer) and the ctenophore at 1×10^{-3} to 1×10^{-4} μW/cm^2. Two other species of deep-water shrimps, which are non-luminous in contrast to the other forms collected, showed no correlation with specific light levels within the light measuring range of the photometer employed.

Some of the most exciting and precise work on the role of light in vertical migration has been published by Kampa and Boden (1954) and Boden and Kampa (1958 to 1967). Off the Canary Islands, these workers used a narrow band irradiance meter (depth and temperature were also recorded), with maximum

transmission at 474 mμ, lowered to the depth of a migratory sonic-scattering layer. An initially measured intensity of irradiance was followed up and down (at dusk and dawn) with the time to reach each depth recorded in measured steps. The selected level of irradiance followed was the 5×10^{-4} μW/cm^2 isolume. The precision echo sounder operating at 10 kc/s actually detected the trace of the irradiance meter and of the scattering layer which it was monitoring simultaneously. BODEN and KAMPA (1967) then introduced a new element not present in previous studies,

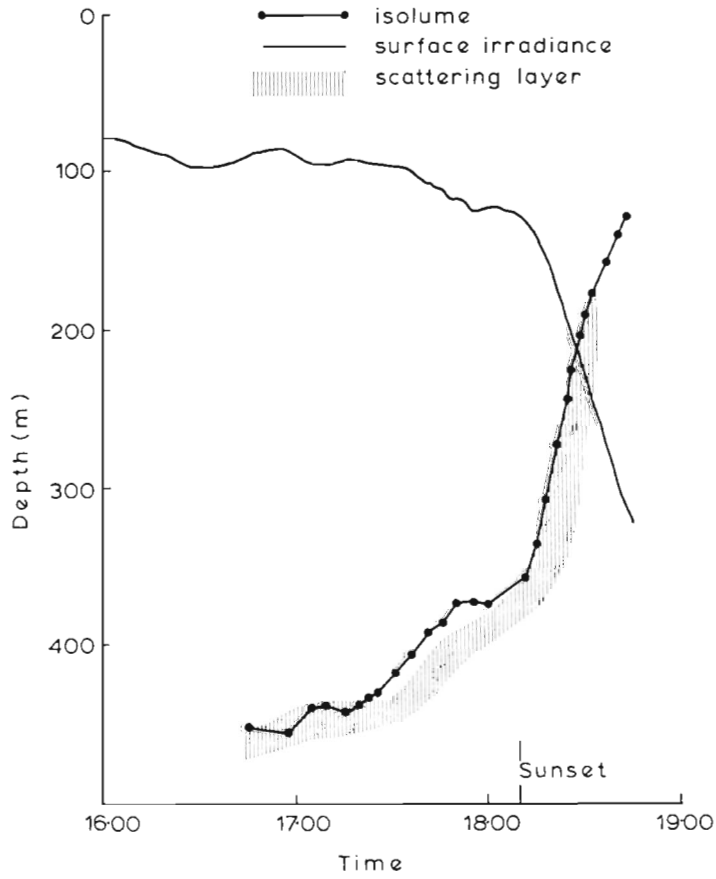

Fig. 2-27: Upward migration of the sonic-scattering layer, depth of the 5×10^{-4} μW/cm^2, 474 mμ isolume, and surface light intensity during one dusk. (After BODEN and KAMPA, 1967.)

a surface irradiance meter, to monitor changing conditions of sun and sky and provide a check on the performance of the light meter at depth.

Downward and upward migrations of the organisms in the sonic-scattering layer coincided closely with the isolume (Figs 2-26 and 2-27). In all measurements, during two dawns and two dusks, the depth of the migratory layer was never more than 12 m above or below the depth of the level of the intensity of irradiance at 474 mμ with which the layer was associated at the beginning of migration. The surface irradiance meter detected differences in irradiance on two successive

evenings and accounted for the fact that the scattering layer was 85 m closer to the surface on the second day, 20 mins after sunset, as compared with the scattering layer on the first day at the same time (Fig. 2-28). As BODEN and KAMPA (1967) state:

'If an investigator, interested in the vertical movements of animals in the sea and equipped solely with an echo sounder and visual observations of sun and sky, had attempted to calculate the depths of a constant value of light on these two successive evenings from the information in nautical almanacs, tables of variation of light with season and latitude and published data on the transparency of various types of ocean waters, he would probably have been wrong on one or the other, if not on both evenings.'

Thus, the organisms in this individual sonic-scattering layer seek to live within

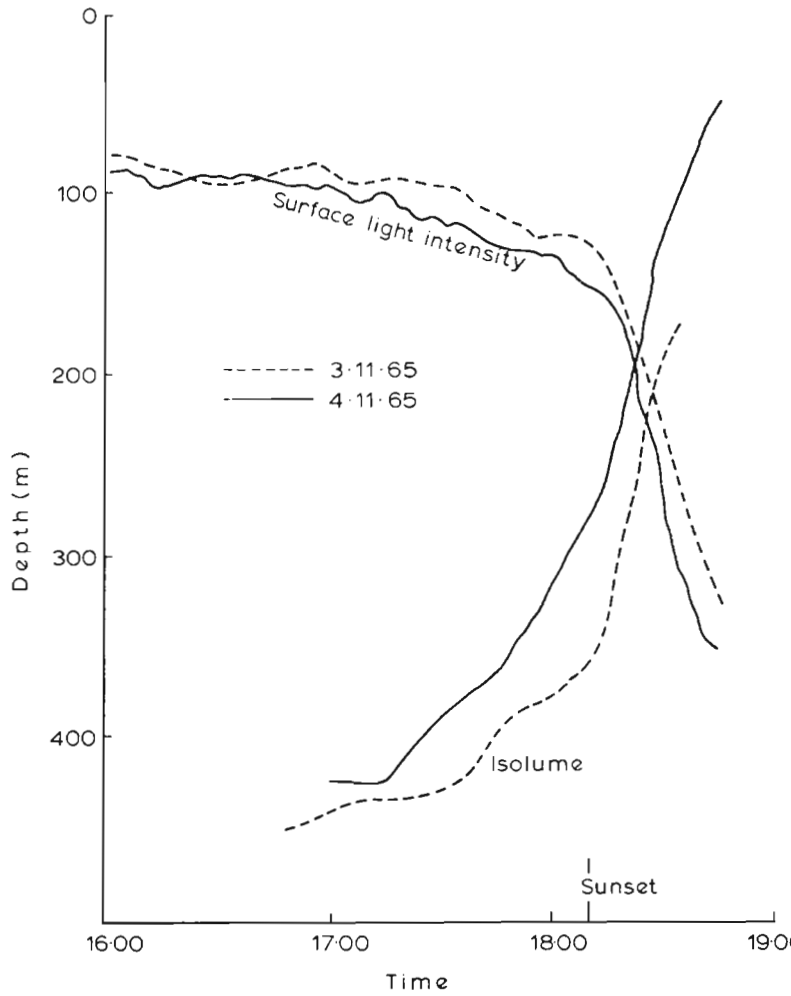

Fig. 2-28: Decrease in light intensity at the surface and the corresponding rise of the 5×10^{-4} $\mu W/cm^2$, 474 mμ isolume in the water column during 2 successive dusks on November 3 and 4, 1965. (After BODEN and KAMPA, 1967.)

the narrow limits of 0·00035 and 0·00075 $\mu W/cm^2$ (calculated for 12 m above or below the depth of the measured isolume through which the migratory layer could range) when, at least at midday, they could range upwards to more than 10,000 $\mu W/cm^2$. BODEN and KAMPA (1967) did not detect any dark adaptation of the animals in the scattering layer during the night. This finding is in contrast to their early work (KAMPA and BODEN, 1954) with a scattering layer off San Diego, California. Marked improvement in the underwater light meter and the use of a surface light meter suggest to the authors (personal communication) that the earlier dark adaptation was spurious.

Finally, BLAXTER and CURRIE (1967) were able to influence the movements of a sonic-scattering layer at dusk and during the night. At night, downward movements of 20 m or more were recorded as responses to artificial lights of 1000 to 1500 W. Lower intensity sources produced smaller movements. On one occasion, gradual progressive lowering of the source forced down a layer from 60 to 300 m. At dusk, it was possible to delay the upward migration of both deep layers (350 m) and shallow ones (100 m) by at least 15 mins. Daytime results were inconclusive because of technical problems.

Since no biological samples were taken by BLAXTER and CURRIE (1967) or BODEN and KAMPA (1967), the makeup of the scattering layers is uncertain. However, this is not of particular importance here since the biological nature of the scattering layers can no longer be questioned. There can be very little doubt that diurnal vertical migrations of organisms living at depth in the sea where light is appreciable are directly controlled by light and represent efforts, as BODEN and KAMPA have put it, '. . . to remain within a comfortable and/or useful photoenvironment.'

Horizontal distribution

While the role of light in vertical distribution and migration is unequivocal, its role in horizontal distribution and migration remains to be demonstrated. Horizontal migration may be subdivided into short-term diurnal and tidal migrations, and long-term annual migrations (consult BAINBRIDGE, 1961 and ALLEN, 1966 for a thorough coverage of migratory patterns of crustaceans, particularly decapods). It is only in the short-term diurnal migrations, whether by swimming, crawling or walking on the bottom, that light may play a direct role (ELMHIRST, 1931, 1932). However, many marine forms are nocturnal foragers who may exhibit both vertical and horizontal components in their nocturnal wanderings before returning to their daytime abode. Whether these diurnal movements should be considered 'migrations', i.e. directional mass movements, is a moot point. Such movements are considered on p. 174.

Movements—inshore and offshore, landward and seaward, alongshore and long-range benthic and oceanic—seem to be initiated by the physiological state of the organisms relative to the drives for feeding, moulting, mating, breeding and recolonization. O'DONOGHUE (1924), however, notes migrations of entire populations of sea stars *Pisaster ochraceus* and *Evasterias troschelii* exposed to direct sunlight in summer in British Columbia, Canada.

The state of the organisms may—in addition to light—be modified by various environmental factors such as temperature (Chapter 3), salinity (Chapter 4), and water movement (Chapter 5), but there are few data concerning the factors which

actually govern horizontal migrations. Of course, migration implies orientation, unless transport is passively carried out in water layers or tidal currents (HARDY, 1956; ALLEN, 1966; WOODMANSEE, 1966b; CARRIKER, 1967). Orientation may be accomplished directly by use of the sun or by the polarized light components of the sun (p. 179).

(3) Structural Responses

(*a*) *Size*

In colonial marine invertebrates, particularly corals, it is difficult to differentiate final body size from body form, both of which are growth functions (p. 161). The question is essentially semantic in an inverebrate in which size and number of asexual individuals determines the form of the colony. For simplicity's sake both categories will be grouped together.

Final body size and form among sessile marine invertebrates forming large colonies, e.g. reef-building corals, are highly variable and depend primarily upon water movement and conditions of illumination. ABEL (1959) has shown a change of shape and height in the madreporarian *Cladocora cespitosa* and the gorgonian *Eunicella verrucosa* as a function of the intensity of illumination and agitation of the water. In calm water, the higher the intensity of illumination, the more branched are the colonies; in agitated water, colonies are more prostrate but the branching and intensity relationship still holds. The hydrozoan coral *Millepora* has a diversity of growth forms. YONGE (1963) suggests that BOSCHMA's (*in*: YONGE, 1963) explanation may well serve for many other genera of madreporarian corals. According to BOSCHMA, there are numerous species of *Millepora* whose variability is such that under the influence of external conditions, primarily water movement and illumination, each species may assume a form which is more or less typical for another species. If a *Millepora* larva settles where the conditions are ideal for the species, it grows out to a colony of the typical form. If a larva settles where the conditions for existence are unfavourable, it may grow out to a colony with a growth form quite different from that of the typical form. *Echinopora lamellosa* normally forms flat horizontal plates with polyps restricted to the upper illuminated surface (BOSCHMA and VERWEY, 1930). When plates grow vertically the polyps appear on both surfaces altering the shape of the colony. When light impinges upon the underside of horizontal plates polyps appear whose numbers are apparently in direct relation to the intensity of illumination. Moreover, size and form of individual polyps are modified since they elongate on stalks towards the source of illumination.

There are very limited observations on the effect of light on final body size or form of non-colonial marine invertebrates. According to DYBERN (1963), *Ciona intestinalis* living under a *Zostera* (eel-grass) bed in very shallow water (0 to 3 m) are smaller in size at maturity than *C. intestinalis* living in deeper water (10 to 15 m) or in protected shallow-water habitats. On the other hand, *Balanus balanoides* on pilings in the sun do not grow as large as *B. balanoides* on the same pilings in the shade (KLUGH and NEWCOMBE, 1935). Coral skeleton formation occurs only in the light and the condition of the skeleton depends upon the state of expansion or contraction of the organisms' tentacles. Thus, solitary corals which expand

their tentacles during daytime (*Fungia actiniformis*) lay down the skeleton in the expanded state and produce a soft, enlarged skeleton while corals that expand their tentacles at night (*Fungia echinata*) lay down the skeleton in the contracted state and produce a hard, dense, reduced skeleton. Corals that are partial day expanders (*Fungia repunda*) produce a skeleton between the extremes (KAWAGUTI, 1954; see also ATODA, 1953 for a discussion of this point in reef-building corals). Attempts to determine the effect of light on body size and form in bivalve molluscs gave conflicting and unreliable results (MEDCOF and KERSWILL, 1965).

Clearly, the entire question of the effect of light on size and body form of marine invertebrates needs extended investigation both in the field and in the laboratory. As YONGE (1958) points out, more critical observations can be carried out *in situ* by the use of SCUBA. Light intensity could be determined and coral colonies marked and measured. The ratio of growth (body size and form) of similar colonies living under different light intensities could then be determined.

(*b*) *External Structures*

Slow transformations in body pigments (morphological colour change) are brought about either by pigment deposition (an increase in the number of chromatophores or an increase in the amount of pigment) or pigment destruction. Where environmental factors are influential in colour variation, light plays a prominent role. According to NICOL (1967a), morphological colour change has adaptive value in bringing about closer resemblance to the animals' habitual environment, or protection from the harmful rays of the sun (p. 160).

The isopod *Idothea montereyensis* occurs in red, green, and brown colour varieties which usually match the colour of the plant on which this isopod is found (LEE, 1966). When transferred from plants of one colour to plants of another, the isopods are capable of changing to the colour of the new background. Once the substrate has been changed, the isopod first responds by slowly reversing the existing state of contraction or expansion of its chromatophores (physiological colour change). Then new pigment is produced and is either placed in the old cuticle or in a new one underneath the old. Complete colour change may take from 2 to 4 weeks and this colour change only takes place in the presence of light (LEE, 1965). The nature of the food is not involved. On the open coast of California (USA) the holothuroid *Cucumaria curata* is darkly pigmented while specimens from *Mytilus* beds have very little body wall pigment (SMITH, 1962). Interestingly, darkly pigmented individuals do not contract when a strong light is directed on their body; pale individuals are very sensitive to strong light and move rapidly away. Populations of the brachyuran crab *Ocypode ceretophthalma* may be found on the white sand beaches of Oahu Island and on the black sand beaches of Hawaii (GREEN, 1964). Hawaiian beach crabs possess approximately twelve times as many black chromatophores as Oahuan beach crabs. In the laboratory when white sand crabs are kept on a black background there is an increase in black chromatophores (chromatophore index + 0.3 black chromatophores/mm^2/day). When black sand animals are maintained on a white background there is a decrease in black chromatophores (− 0·76 black chromatophores/mm^2/day).

Direct effects of light on pigment deposition or destruction have been described

in echinoids. When the echinoderms *Diadema antillarum* (JACOBSON and MILLOTT, 1953) and *Arbacia punctulata* (HARVEY, 1956) are subjected to ultra-violet radiation there is a marked increase in melanin formation. *D. antillarum* raised in normal light deposits more pigment in the spines than when it is raised in dim light (KRISTENSEN, 1964), and lightly pigmented individuals of *A. lixula* slowly darken (1 month) in the light while darker individuals slowly pale in the dark (HARVEY, 1956).

Pigment variation correlated with distributional depth are common. The sea-urchin *Lytechinus variegatus* in deeper water, off the North Carolina coast (USA), are white but in shallow water, on the Florida Gulf coast, they are reddish brown or reddish purple (FOX and HOPKINS, 1966). Intertidal populations of *Arbacia punctulata*, at Beaufort, North Carolina, have a higher percentage of individuals with complete spine pigmentation as compared with subtidal populations living in approximately 7 m of water (HOPKINS, *in*: FOX and HOPKINS, 1966). Shallow-water (0 to 3 m) tunicates *Ciona intestinalis*, on the Swedish west coast, subject to direct illumination, number 1 to a few per m^2 and are heavily pigmented red. Deeper-water (10 to 15 m) *Ciona*, which may also number only a few per m^2, and shallow-water (1 to 10 m) protected *Ciona* (under overhangs, in caves, on steeply sloping walls) may number up to several thousand per m^2 and are not pigmented (DYBERN, 1963). FONTAINE (1962) collected the ophiuroid *Ophiocomina nigra* at depths from 10 to 45 m and found an increasing frequency of light-coloured individuals with depth. In the laboratory, *O. nigra* tended to die rather quickly in bright light but the lighter-coloured individuals died more quickly than the darker ones. Individuals in aquaria shielded from direct light lived much longer and could tolerate warmer water. The dark pigment is a melanin.

The echinoids *Dendraster excentricus* and *D. laevis* from shallow (1 m) water (see GOODWIN and FOX, 1955 for the original observations on their pigments) are more darkly pigmented than individuals from deeper (12 m) water (MERRILL and PORTER, personal communication). In shallow-water *D. excentricus*, the buried end is lighter coloured than the exposed end; the author of this chapter could confirm this by field observations. When comparing the species, the darkest *D. laevis* (shallow) are lighter than the lightest *D. excentricus* (deep) but less light is transmitted through the test of the shallow *D. laevis*. Since shallow *D. laevis* are exposed to more light than deep *D. excentricus* either the former can tolerate more light than the latter or there is a further compensation for the greater illumination penetrating through the test. Also, since shallow *D. laevis* and shallow *D. excentricus* are sympatric and the same intensity of illumination impinges upon them, MERRILL and PORTER (personal communication) reasoned that a compensation for the low order of epidermal pigmentation must exist. They scraped the epidermis off the tests of both species, left the internal organs intact and discovered that less light still passed through *D. laevis* than through *D. excentricus*. The authors conclude that there is a qualitative and/or quantitative difference, probably in internal pigments, between the two species.

If pigment deposition is a protective device against the harmful effects of light (p. 160), then we should expect that marine organisms living permanently in the surface waters of tropical and subtropical seas would be particularly well protected against the high intensity illumination found there; indeed, many of the neustonic

animals are strikingly pigmented with an intense blue colour (DAVID, 1965). It is not at all clear, though, what the predominance of blue means in animals of the sea surface. FOX and HAXO (1959) suggested that blue colouring in the siphonophore *Vellela lata* might be a protection, not for the animal itself but for the symbiotic algal cells within its tissues. However many blue neustonic forms do not possess algal commensals, as CHEESMAN and co-authors (1967) point out, and experimental proof remains to be provided. According to HEINRICH (1960) and HERRING (1965), the blue and purple pigments of tropical and subtropical pelagic invertebrates act as a protective screen against strong solar radiation, and DAVID (1967) proposes that the widespread occurrence of blue in many diverse groups of marine animals indicates some selective advantage to an animal which is so coloured; however, there is no experimental evidence to substantiate this suggestion.

The blue pigment is a combination of a carotenoid (astaxanthin) with protein. According to HERRING (1967), the absorption spectrum of blue carotenoids gives no indication of any obvious function as a protection against ultra-violet or near ultra-violet, which are generally considered to be biologically most harmful. Whether blue pigments strongly absorb in these regions is not known. Light, of the wavelength of the pigment's peak absorption (625 to 650 mμ), is not generally considered to be particularly harmful, though it is in the proportion of the red and infra-red wavelengths that the light composition in the upper few cm of the water column will differ most from that in slightly deeper water. The distribution of the pigment is variable from species to species and in some its presence over the gut and muscles and its absence over such potentially vulnerable organs as the brain and nervous system, makes such a protective function unlikely. Further, carotenoproteins in the stalk fluid of the barnacle *Pollicipes polymerus* could not possibly provide protection against solar radiation since the fluid is completely bounded by a thick, black epidermis (HOLTER, 1969).

It is well known that carotenoids and proteins are capable of mutually stabilizing each other. Carotenoids, in simple solution, are rapidly bleached in high light intensities while carotenoid–protein complexes are much less susceptible to photo-oxidation. HERRING (1967) suggests that if an animal requires astaxanthin for any purpose, it could well be stored in the more stable complex. According to HERRING, this seems quite feasible for animals subsequently developing chromatophores, the astaxanthin being transferred from the blue complex to the chromatophores during development. Another possibility is that one of the roles of carotenoid in nature is to stabilize the polypeptide configuration of the protein (CHEESMAN, 1958; CHEESMAN and co-authors, 1967). In this case the resulting blue colour would be accidental because astaxanthin is the stabilizing carotenoid. Other than the possibility that the blue carotenoproteins are used in cryptic colouration, i.e. as a method of concealment or as warning colouration (HERRING, 1965), it is clear that the question of the role of these pigments remains unanswered.

(*c*) *Internal Structures*

Other than the extrusion of algal symbionts, Zooxanthellae, in the dark (YONGE, 1931; ATODA, 1951; GOREAU, 1959; GOREAU and GOREAU, 1959; ZAHL and

McLaughlin, 1959) in numerous marine invertebrates (Yonge, 1944), there is no information on the effect of light on internal structures in these organisms. Studies on the effect of light and light deprivation on the ultrastructure of cells of non-marine invertebrates are being carried out (White and Sundeen, 1967), and it is assumed that marine invertebrates will eventually be utilized as experimental animals.

(4) Conclusions

There are few aspects in the ecology of marine invertebrates that are uninfluenced by light in one or more of its modalities. Responses to light are inevitably complex; unfortunately, the interests of ecologists, physiologists, and ethologists have not necessarily assisted in unravelling the complex. Some areas of the subject are embarrassingly rich in information while others are lacking.

Thus, our knowledge of tolerance levels to light is completely insufficient because of the scarcity of reliable quantitative data. It is merely a truism to say that marine invertebrates are differently adapted to light and thus tolerate it to a greater or lesser degree. The lethal effects of ultra-violet are well documented but the lethal effects of visible light are an enigma. Current theory suggests a photodynamic sensitization involving fluorescing compounds in the sea or free porphyrins in the organisms.

Metabolic processes, including growth, rate functions and physiological colour change are all influenced by light. Light promotes growth in reef-building corals while darkness promotes growth in a crustacean. Short-day photoperiod stimulates, and long-day photoperiod depresses O_2 consumption in a crustacean. The latter response appears to be an acclimation, a phenomenon which has not yet received critical attention in relation to light. In contrast, chromatophore responses (rapid colour change) and retinal pigment movements have been studied in many cases, particularly in crustaceans and cephalopods. Chromatophores may be stimulated directly by light (independent effectors) or through stimulation of ocular or extra-ocular pathways. Background adaptation appears to be the most obvious function of physiological colour change although protection from the harmful effects of solar radiation should not be dismissed.

Pelagic larvae of marine invertebrates, bound to relatively shallow waters, are strongly influenced by light. The majority of larval species are photopositive in their early phases and a majority of these, unless the adults live in direct sunlight, become photonegative before settlement. Light intensity, temperature (Chapter 3) and salinity (Chapter 4) all markedly affect the photic responses of larvae.

Adult marine invertebrates show a wide variety of light-connected activities. Many show diurnal cycles of activity (locomotion, feeding, swimming, spawning and other more complex behaviour) coordinated with the cycle of day and night. Some of these rhythms persist under constant light or dark in the laboratory suggesting the presence of an endogenous (circadian) rhythm synchronized or entrained by the daily changes in light and dark (photoperiod). It is well established that many marine invertebrates possess physiological clocks permitting them to 'know' the time of day and year and to anticipate environmental changes. Such clocks are used to maintain a fixed 'escape' route regardless of the time of day. The clock also permits recognition of the annually changing photoperiod by

measuring the duration of a certain time stretch, also regardless of the time of day. Semilunar, lunar and annual periods may be timed in this way, particularly reproductive activities.

Light, by virtue of its intensity gradients, directionality, wavelength, or polarization may act as an orientating stimulus. Responses may be relatively simple (photokinetic and phototactic movements) or complex (light-compass reactions). Other special responses are shadow reactions, dorsal light reactions and covering reactions. Indifference to light is rare among marine invertebrates. Since appropriate activity has survival value and light is one of the most important guides to ecological conditions, the photoresponses of marine invertebrates are very important in maintaining them in optimum ecological conditions.

Aspects of behaviour which are modified by and thus dependent upon the immediate experience of the individual (learning) may be light related. Habituation of the shadow response has been demonstrated in polychaetes and a gastropod. Generally, marine invertebrates habituate rapidly to small light changes and slowly to large changes, which, we must assume, are biologically more important. More complex light-connected learning (associative) has been proposed but—except for cephalopod molluscs which show the most impressive learning and certain decapod crustaceans which may include a learning component in their sun-compass orientation—the arguments are not very compelling.

Light is most significant in reproductive activities of marine invertebrates. Both short-term (initiation of spawning) and long-term (maturation of gonads and gametes, sex determination, and synchronization of spawning) reproductive activities are light dependent and appear to be mediated over photoneuroendocrine pathways.

Diurnal vertical migration of planktonic and benthic marine invertebrates represents one of the most widespread and conspicuous phenomena in oceans and coastal waters. Current theory, on good experimental grounds, is that light is the initiating and controlling factor. Whether endogenous rhythms contribute to the phenomenon is not clear. New techniques and instrumentation now permit precise measurements of migration movements of the animals in the sea. Most migrators appear to follow intensity isolumes. There is little information on the role of light in vertical distribution of non-migrating marine invertebrates. There are few data concerning the role of light in horizontal distribution and migration.

Structural changes in size and form have been demonstrated to be light connected but the observations are limited and, in general, poorly controlled. Slow colour transformations (morphological colour change), in which pigment is either deposited or destroyed, are light dependent for many marine invertebrates and adaptively bring about closer resemblance to the animals' habitual environment or possibly contribute to protection from the harmful rays of the sun.

Other than the extrusion of Zooxanthellae in the dark from the cells of animals harbouring them in the light (reef-building corals), there is no information on the effect of light on internal structures of marine invertebrates.

2. LIGHT

2.3 ANIMALS

2.32 FISHES

J. H. S. Blaxter

(1) Introduction

(a) General Aspects

The selective absorption and scattering of light results in greater variability of light conditions in water than on land. Aquatic animals thus have greater potential variations with which to contend; at the same time many of them have a much greater ability to move in both horizontal and vertical directions. Light has the advantage of only limited diffraction and is thus a good directional stimulus; variations in intensity, wavelength and duration provide information concerning the environment, daily and seasonal changes being of particular significance. From the aspect of signalling between animals it is less satisfactory than sound because of rather rapid attenuation and because less information can be encoded in a light source than in sound stimuli. On the other hand, orientation by sound stimuli is considerably more difficult.

The various ways in which light may affect fish is shown in Fig. 2-29. This figure is, to a great extent, a simplified version of the complexity which will emerge from the following pages.

Light effects on fish have been considered recently by a number of authors, for example, Nicol (1963), more from a physiological angle, and Woodhead (1966) with more emphasis on ecological aspects. The latter author treats the subject comprehensively though not in great detail.

The units of light intensity used by different authors are diverse. Most commonly, experimentalists have used foot candles (ft.c) or metre candles (mc) also called lux, and occasionally millilamberts (mL), which is a measurement of brightness, or quanta. Oceanographers have tended to use $\mu W/cm^2/sec$. Where possible, measurements quoted here have been standardized in metre candles as follows: 1 mc = 0·1 ft.c = 0·1 mL. Comparisons between units of illumination or brightness and units of energy vary depending on the spectral response of the measuring instruments. It appears that 1 mc is equivalent to about 0·4 $\mu W/cm^2/sec$ (4 erg/cm^2/sec) at the surface (e.g. Westlake, 1965); Clarke and Wertheim (1956) consider the visible energy of the summer sun to be about 53,000 $\mu W/cm^2/sec$ or 11,000 ft.c. Jerlov (p. 96) estimates the irradiance for the whole spectrum above the sea surface with clear sky and zenith sun at 116,000 $\mu W/cm^2$. About half this is infra-red light which is absorbed in the first metre or so. Wavelength in this chapter is expressed as nm (1 nm = 1 mμ = 10°A).

Such comparisons of intensity may be justified because logarithmic changes of

light have to be considered in the study of light reactions of fish and hence small discrepancies in the above standardization can be ignored. A number of authors (e.g. CRAIG, 1964; WESTLAKE, 1965) have been aware of the need for more general adoption of a particular unit, but so far this has not been achieved. All units employed tend to have shortcomings in that the photometer used in an investigation may have a spectral response different from the eye of the experimental

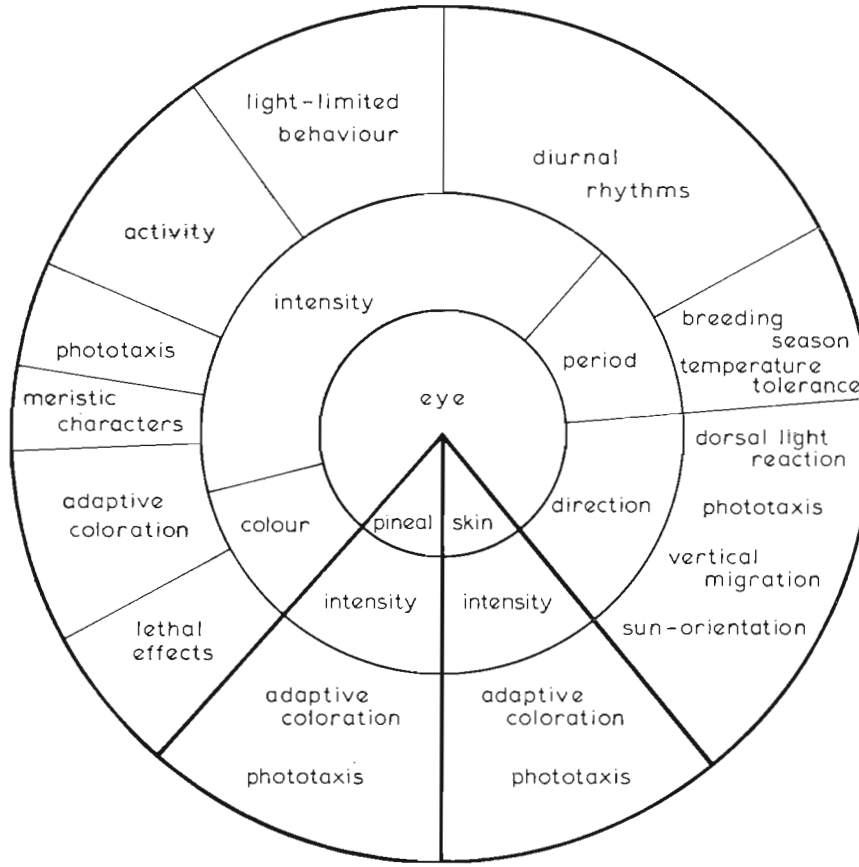

Fig. 2-29: Diagram to show how various characteristics of light stimuli may affect the sense organs and so induce changes in the physiology and behaviour of fishes. (Original.)

organism and light may thus be measured which is not of functional significance. BLAXTER and PARRISH (1965) avoided this problem by adjusting the response of their photometer to that of the eye of the herring which they were studying. Another problem which should be mentioned is the reflection of light from the surfaces of experimental tanks. HUNTER (1968) rightly points out that these reflections may be as important as the downwelling light in determining the state of adaptation of the eye.

Comparisons between measurements in metre candles and day–night conditions are given in Fig. 2-30.

(*b*) *Light Perception*

The eye

Abundant data are available in publications such as those of BRETT (1957), ROCHON-DUVIGNEAUD (1958) and WALLS (1963); however, only certain aspects will be selected which seem of especial interest to the theme of the chapter.

Originally, the presence of an adipose eyelid was thought to be a streamlining device. In clupeoids, mugilids, carangids and scombrids, anterior and posterior halves are separated by an elliptical opening over the pupil; in elopids, engraulids, stromateids and polynemids there is no aperture, while in salmonids only a small posterior part of the eyelid covers the eye. These eyelids are now known to be birefringent (STEWART, 1962). Their potential role for orientation to polarized light or for cohesion in schooling is mentioned on pp. 231–232 to which may be added a possible role in improving the range of vision, see p. 272.

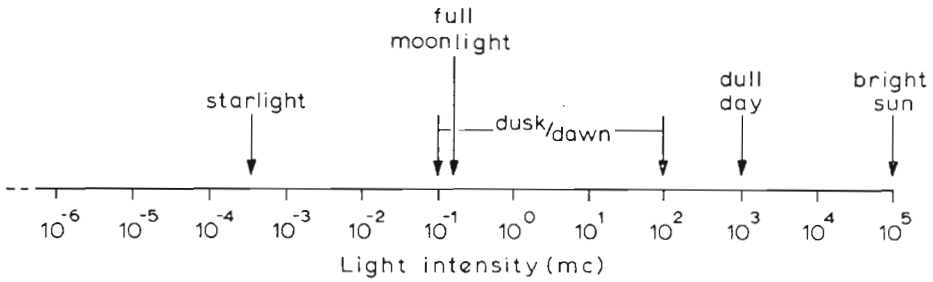

Fig. 2-30: Light intensities in metre candles (mc) associated with different types of natural light. (Original.)

The retina of fish is enormously variable in the size, number, density, distribution and type of the visual cells. WUNDER (*in*: HERTER, 1953) attempted to associate the density of rod and cones with the habits of the fish. The extensive studies of BARON and VERRIER (1951), TAMURA (1957a), ENGSTRÖM (1963), O'CONNELL (1963), TAMURA and WISBY (1963) and ANCTIL (1969) show, in fact, how difficult such correlations are. Certain features emerge, however, of which many apply to other vertebrates. The rods are responsible for scotopic vision at low light intensities, the cones for photopic vision at intensities above the rod threshold (p. 272). The summating effect of a number of rods connected to one intermediate or bipolar neuron means that their several responses may reinforce each other to fire the bipolar, thus giving high sensitivity. With cones, the degree of summation is very much less, resulting in lower sensitivity. On the other hand, the reduction in cross connections between the cones leads to much greater acuity (p. 222). While many species have a duplex retina with both rods and cones, some elasmobranchs and deep-sea fish have a retina consisting purely of rods. A pure-cone retina seems to be typical of the larval stages of fish, for example, in Pacific salmon *Oncorhynchus* spp. (ALI, 1959), in herring *Clupea harengus* (BLAXTER and JONES, 1967), in plaice *Pleuronectes platessa* (BLAXTER, 1968b) and in other species (BLAXTER and STAINES, 1970).

The retina may be specialized into a true foveal region (KAHMANN, 1936; BARON

and VERRIER, 1951) in the blenny *Blennius* and some serranids; here small cones are highly concentrated, giving good acuity and visual capability along a particular visual axis. More commonly an area temporalis is found where a large patch of the retina contains cones of smaller size and higher density. TAMURA (1957a) and TAMURA and WISBY (1963) related the position of this area to the visual axis of the eye and the habits of fish, describing 3 groups: (i) Axis in anterior–downward ('lower-fore') direction as in bottom feeders, for example, sea bream *Sparus*; (ii) axis in anterior–horizontal ('fore') direction as in fish taking food immediately in front of them, for example, sail fish *Istiophorus*; (iii) axis in anterior–upward ('upper-fore') direction as in pelagic feeders such as horse mackerel *Trachurus* which take food slightly from below.

Many fish have a wide field of view, amounting to 300° or more, where the eyes are laterally placed and the lenses protruding from the side of the head. Binocular vision is also common; TANSLEY (1950) quotes values of 20 to 40° for the average degree of overlap. In many cases binocular vision is enhanced by sighting grooves along the surface of the head. TAMURA (1957a) used an ophthalmoscope to measure the degree of binocularity by reflections of light from the eye both in the horizontal and vertical plane. The maximum degree of binocularity lay between an angle of 30° above the horizontal to 20° below, depending on the direction of the visual axis and position of the area temporalis in the retina. Binocular vision would seem well fitted for the appreciation of distance, by permitting simultaneous comparisons to be made of an object and by convergence of the visual axes; it would also enable a better appreciation of the object by stereoscopy. TANSLEY (1950) has questioned the need for partial decussation of the optic nerve, as found in mammals, to obtain stereoscopy. Complete decussation, which is a feature of lower vertebrates, is so often present in animals with overlapping visual fields, that it may be assumed it provides for stereoscopic vision.

Vision is thus enhanced by specialization in the retina and by coordination between the eyes. Colour vision (p. 221) and increased sensitivity are also of common occurrence. Sensitivity is improved by raising the number of rods present; in some species of elasmobranchs and in many deep-sea fish the retina may be composed entirely of rods. A tapetum is found in many elasmobranchs; this is a reflecting layer of guanine crystals in the choroid behind the retina. The crystals are orientated (DENTON and NICOL, 1964) to reflect light along the incident path whatever their position in the eye, thus doubly stimulating the visual cells nearby. The orientation also prevents stray reflection of light which could cause reduction in acuity. The advantages of this reflector over other devices, such as longer outer segments or higher densities of visual pigment in the rods, may be that dark adaptation (pp. 272–275) is accelerated if the visual pigments can be kept at a fairly low density. Similarly the signal: noise ratio at low light levels may also be more favourable. A reflecting layer within the retina is found in engraulids (O'CONNELL, 1963).

The rather unusual tubular form of the eyes of deep-sea fish has been described by MUNK (1966). These eyes are often directed dorsally, presumably to make use of downwelling light at low intensities. The tubular eyes often have considerable binocularity and their shape is considered as an adaptation to increase the size of the pupil, lens and eye (thus leading to improved light-collecting ability and a

larger, though not brighter, image on the retina, which would improve acuity) without taking up undue space in the head. Only the axially-placed main retina will perceive focussed images in the binocular field. As well as improving judgement of distance, binocularity may also increase sensitivity. The lateral accessory retina, around the sides of the tube, probably responds mainly to movement; it is unlikely that the lens can accommodate adequately to focus images in these lateral positions. Other deep-sea adaptations are found in the aphakik apertures around the lens where light can reach the retina without interposition of the refracting media, thus increasing sensitivity and the field of view.

The pineal

This organ, associated with the diencephalon, has a function in some light responses (Breder and Rasquin, 1950; Steven, 1963). The blind characin *Anoptichthys* tends to swim into dim light when the pineal is screened by pigment. When this pigment is removed, the fish tends to aggregate in brighter conditions. The closely-related species *Astyanax* seems unaffected by stimulation of the pineal. The pineal or associated areas of the diencephalon may affect colour change in the ammocoete of *Lampetra*; the melanophore pigment disperses, causing darkening, and diurnal changes disappear with removal of the pineal and its associated region. When the pineal area is illuminated in artificially-blinded minnows there is a similar darkening, and a paling when it is shaded. Colour change in tuna *Thunnus*, juvenile salmonids and other teleosts is almost certainly under some pineal influence (Healey, 1957). In most instances, the relative importance of the pineal itself or the associated part of the brain has not been determined.

Breder and Rasquin (1950) divided fish, by experiments, into 3 groups: (i) Light positive fish in which the tissue over pineal transmits light (examples: *Sardinella maxophthalmus*, *Jenkinsia lamprotaenia*, *Leptocephalus* larvae); (ii) light negative fish in which the tissue over pineal is opaque (examples: *Astyanax mexicanus*, *Ameiurus nebulosus*); (iii) fish exhibiting variable responses in which the tissue over pineal varies in transmission by chromatophore change (examples: *Sphyraena*, *Strongylura*).

The dermal light sense

Sensitivity to light of parts of fishes other than the eye or pineal organ seems to be common in cyclostomes but limited in teleosts and elasmobranchs (Steven, 1963). Few authors have, however, conclusively eliminated the pineal as a receptor. The eyeless ammocoete larva of the lamprey *Lampetra* exhibits changes in the speed or incidence of movement (an 'orthokinesis') depending on the intensity of light. High activity in bright light (from 5·5 to 54 mc) tends to cause aggregation in dimmer areas. Below this range of intensity, changes in the rate of turning ('klinokinesis') bring about a similar result. Kineses also occur in teleosts such as the minnow *Phoxinus*, the catfish *Ameiurus* and the grouper *Epinephelus* which have been blinded experimentally. A particular study has been made of cave characinids such as *Anoptichthys*; different forms vary in the degree of degeneration of the eye and some seem to have a photonegative behaviour, although the eye must be non-functional.

Response to dermal light stimulation is usually slow. The reaction time is

inversely related to the intensity of stimulation and its duration, for example in the hagfish *Myxine* and in the ammocoete of *Lampetra*, while the threshold for response may decrease during dark-adaptation. The response has an action spectrum similar to a spectral sensitivity curve (Table 2-16). The light-sensory cells

Table 2-16

Characteristics of light reactions mediated by the dermal sense*
(After STEVEN, 1963)

Species	Threshold light intensity for response (mc)	λ maximum of action spectrum (nm)	Author
Lampetra planeri (ammocoete)	2·7–10·7	530	STEVEN (1950)
Lampetra planeri (ammocoete)	5·4	—	JONES (1955)
Anoptichthys jordani (characin)	0·12	490	THINES and KÄHLING (1957)
Phoxinus laevis (minnow) blinded	< 0·017	—	SCHARRER (1928)
Phoxinus laevis (minnow) blinded	0·0034–0·024	—	JONES, F. R. H. (1956)
Myxine glutinosa (hagfish)	—	500–520	STEVEN (1955)

* The pineal was not necessarily eliminated as the light receptor.

have rarely been located, though in cyclostomes cells in the head and tail region have been provisionally identified. Other cells such as chromatophores (p. 270) are known to respond directly to light. The iris (of the eel *Anguilla*) and pigment cells in the retina and tapetum seem to be almost entirely independent of both the nervous and endocrine systems. In *Lampetra* larvae, the spinal cord can be directly stimulated by light. One wonders how such transparent forms as fish larvae prevent over-stimulation of their unscreened nervous systems.

(c) *Visual Abilities*

Brief mention must be made of the ability of fish to perceive various characteristics of visual stimulation. Much of the earlier work was done by the German school of visual physiologists (e.g. HERTER, 1953). After a gap of 20 to 25 years there has been a resurgence in the study of the sensory physiology of fish using training experiments and new physiological techniques.

Thresholds for vision

The range of light intensity over which light- and dark-adaptation take place is dealt with on pp. 273–275. Absolute thresholds of the rods depend to a great extent

on the technique used. KOBAYASHI (1962) measured the intensity of white light of 10 millisecs duration required to produce an ERG response in the retinae of a number of species. His results range from 100 to 0·05 mc, being lower in those species normally inhabiting greater depths. They seem very high compared with the rod threshold for sunfish *Lepomis*, estimated by GRUNDFEST (1932a) to be 10^{-6} mL (about 10^{-5} mc) or with thresholds of 10^{-5} to 10^{-6} mc using a phototaxis technique in fish larvae (BLAXTER, 1968a, 1969). CLARKE (1936), DENTON and WARREN (1957) and CLARKE and DENTON (1962) used GRUNDFEST's and other human eye values in their assessments of the visual abilities of deep-sea fish. Basing their arguments on the greater pupil size, higher pigment density and other attributes of the eyes of deep-sea fish, they concluded that such fish might just appreciate intensities 10 to 100 times less than the human threshold (given as about 10^{-8} μW/cm^2). Assuming a threshold of 10^{-10} μW/cm^2 and an extinction coefficient of 0·04 in clear oceanic water, light would just be visible at about 900 m on a bright day. In fact, bioluminescence (pp. 224–226) is of such general occurrence that the ambient light at great oceanic depths more often depends on it than on downwelling natural light.

Brightness discrimination

Brightness discrimination may be important in the regulation of vertical migration and in sun orientation (pp. 260, 262). The increment of intensity just distinguishable (ΔI) as a fraction of the ambient intensity (I), that is ΔI I or Weber's fraction, is usually expressed as a percentage. It was originally thought to be constant over all values of I, but the work of HECHT (1937) and others has shown that where it may sometimes remain constant over a restricted range of I, ΔI/I usually falls as I increases; thus small percentage changes in brightness are more easily discriminated at high light intensities. HECHT found values of ΔI/I from 200% to 2% varying with species (not fish) and intensity. In fish, Weber's fraction has been estimated in a few instances. SGONINA (1933) trained the minnow *Phoxinus laevis* to distinguish different shades of grey. The ratio ΔI/I was only constant over the range of greys used (from black to white) when the greys being compared were rather dark, containing less than 25% white. The best performance was a discrimination of greys different by about 2% in content of white. In this instance Weber's fraction varied from 50 to 100%. PERKINS and WHEELER (1931) trained goldfish *Carassius auratus* to distinguish between feeding compartments lit by different intensities of light. Absolute, but not percentage, increases in brightness were more difficult to distinguish at high intensities, which is to be expected if Weber's Law is valid. Differences of 33% in brightness were discriminated (i.e. the difference between a compartment lit with an intensity of 45 units compared with one lit by 60 units). LOUKASHKIN and GRANT (1965) tested the preference of the anchovy *Engraulis mordax* for different intensities without training. Their results show a discrimination between intensities differing by 100%. Better data are available from the results of KOBAYASHI (1962) who measured brightness discrimination by the electroretinogram (ERG). The minimum values found for ΔI/I are given in Table 2-17, together with the intensity of adaptation, and further results in Table 2-18 and Fig. 2-31. Some species are very insensitive, for instance

Table 2-17

The adaptation level at which the % increment of light intensity $\Delta I/I$ (Weber's fraction) discriminated is minimal, as shown by ERG
(After KOBAYASHI, 1962)

Species	Adaptation intensity (I) (mc)	Increment discriminated $\Delta I/I$ as a percentage
ELASMOBRANCHS		
Mustelus manazo (dogfish)	0·2	1400
Narke japonica (electric ray)	0·2–10	60
Urolophus fuscus	0·1–1·2	7
Dasyatis akajei (sting ray)	4	5
Holorhinus tobijei	1–12	0·6
TELEOSTS		
Anguilla japonica (eel)	0·2–15	540
Trachurus japonicus (horse mackerel)	10	320
Chelidonichthys kumu	3	180
Stephanolepis cirrhifer	15	90
Misgurnus anguillicaudatus	3	40
Chrysophrys major	3–15	36
Kareius bicoloratus	3	2

Table 2-18

Increment of light intensity discriminated as percentage of the intensity of adaptation for various species as shown by ERG
(After PROTASOV, 1964)

Species	Increment discriminated $\Delta I/I$ as a percentage
Gadus morhua (cod)	1
Pollachius virens (coalfish)	1
Mallotus villosus (capelin)	< 0·01
Pleuronectes platessa (plaice)	7–10
Hippoglossoides platessoides (long rough dab)	7–10
Anarhichas lupus (catfish)	10–12
Myoxocephalus quadricornis (sculpin)	3
Raja radiata (ray)	7–10

dogfish *Mustelus* and *Anguilla*. In others a response is found to an intensity increment of only 0·6 to 2% above the level of adaptation. It should be stressed that these are increments determined physiologically; only training experiments would show whether they were perceived 'subjectively' by the fish. Recently

HESTER (1968) has described some elegant experiments on brightness discrimination in goldfish using a conditioned cardiac-response technique. In particular he showed that brightness discrimination improved with size (increase of lens diameter). It also varied with temperature, being best at 20° C, and with the position of the target on the retina, the size of the target and the level of light adaptation.

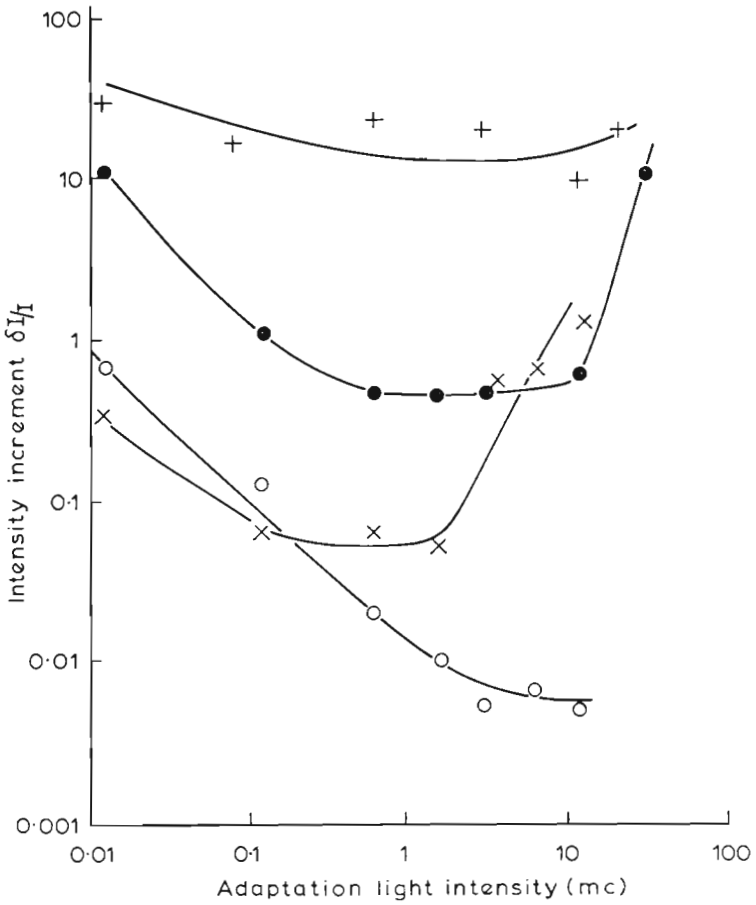

Fig. 2-31: Brightness discrimination, absolute increase of light intensity required to give an ERG response at different levels of light adaptation. ● electric ray *Narke japonica*; ○ eagle ray *Holorhinus tobijei*; × ray *Urolophus fuscus*; + eel *Anguilla japonica*. (After KOBAYASHI, 1962; redrawn.)

Colour vision

Whether colour vision exists in fish was at one time the centre of considerable controversy (HERTER, 1953; WALLS, 1963). The physiological or anatomical requirements for colour vision are the presence of cones reacting to 3 primary colours, different combinations of which will give any colour in the visible range. Evidence of various sorts has been used to determine whether fish have colour vision. TAMURA and NIWA (1967) studied the S potential (an electrophysiological

response to light) in isolated retinae of fish and concluded that 7 out of the 10 species used probably had colour vision, including one elasmobranch, the sting ray *Dasyatis akajei*. In the mullet *Mugil cephalus*, carp *Cyprinus carpio* and goldfish *Carassius auratus* it was especially well developed. This response of the eye to coloured light is not conclusive evidence that the fish see colour, which must be at least partly a feature of the central nervous system. Circumstantial evidence may be obtained from observing the precise adjustment of some species of fish, for example *Phoxinus*, pleuronectids and labrids, to coloured backgrounds. Experiments where fish are offered, and make, a choice between coloured lights (LOUKASHKIN and GRANT, 1965) are not valid as proof of colour vision unless they are designed to remove the possibility of choice by a brightness difference. It is not sufficient to adjust the brightness of 2 coloured lights photometrically; they must be adjusted 'subjectively' according to the spectral sensitivity of the light-adapted fish. Alternatively, a correct choice must be made between one colour against a wide range of intensities of another colour. Where either of these criteria has been satisfied, and a successful choice of colour made, a colour sense would appear to exist. Choice experiments of this sort have shown that many species of fish prefer the blue or blue-green.

Some of the best colour vision experiments were done by VON FRISCH and co-authors (*in*: HERTER, 1953). A number of species such as the minnow *Phoxinus laevis*, the ide *Idus*, the bitterling *Rhodeus* and tench *Tinca* were trained to take food from a coloured container placed amongst a large number of other containers of different shades of grey. Without colour vision one or more of the grey containers would have been confused with the coloured one in terms of brightness. These experiments give good proof of colour vision in these species, and showed, in the minnow, an ability to discriminate between 20 different colours within the visible spectrum. Colour vision is lost when the intensity of adaptation drops below 0·25 to 0·01 mc. Other workers, for example, MUNTZ and CRONLY-DILLON (1966), have recently taken up training techniques to test the ability to see colour. According to WALLS (1963), no teleost has ever been shown not to have colour vision, and this statement still represents current thinking.

Acuity

Acuity or resolving power is the power to discriminate detail. It is measured as the ability to distinguish 2 parallel lines closely adjacent to each other. To avoid the problem of distance from the eye, acuity may be given as the minimum separable angle in minutes subtended at the eye. Thus a small angle indicates high acuity. Presumably image lines are only resolved if they are separated by one unstimulated visual cell; extensive summation will reduce acuity. Acuity is also dependent on the focal length of the lens. TAMURA and WISBY (1963) give the formula:

$$\text{Sin } \alpha = \frac{1}{F}\left[\frac{0{\cdot}1(1 + 0{\cdot}25)}{\sqrt{n}} \times 2\right]$$

where α is the minimum separable angle, F is the focal length of the lens, 0·25 is the degree of shrinkage and n is the number of cones in 0·01 mm^2. These authors and TAMURA (1957a) calculated the acuity of over 30 species from fresh water and

the sea, finding particularly low values, of 2–4′, for some pelagic fish, and a higher range, of about 6–9′, in other species. The values vary greatly depending on the part of the retina from which the value n is taken. TAMURA concluded that the resolving power of the lens is much better than that of the retina and hence acuity is mainly dependent on the density of cones.

Acuity can also be measured by behaviour responses. GRUNDFEST (1932a, b) used wide stripes for optomotor experiments in dark-adapted *Lepomis* and narrow stripes for the experiments on light-adapted fish. BRUNNER (1934) working on *Phoxinus*, and BAERENDS and co-authors (1960) on *Aequidens*, trained their fish to distinguish a striped background from a grey one when selecting a feeding location; where the stripes could not be resolved training was unsuccessful, thus giving a measure of acuity. BRUNNER found in *Phoxinus* that the width of stripes which could be resolved became smaller (from 3·0 to 0·25 mm) as the light was increased from 10^{-3} to 10^{3} mc, with a particularly rapid change at the dark-light adaptation range (Table 2-27). In *Aequidens* the light was kept constant, but better resolution was found in larger fish, the width resolved varying from 1·5 to 0·3 mm at body lengths from 3 to 11 cm. NAKAMURA (1968) trained skipjack tuna *Katsuwonus pelamis* and little tunny *Euthynnus affinis* to distinguish between horizontal and vertical stripes. The fish varied in length from 36 to 47 cm. Acuity was better at high light intensities, the lowest separable angle measured being 5·6′ in skipjack and 7·4′ in little tunny. Similarly YAMANOUCHI (*in*: NAKAMURA, 1968) obtained a value of 5·0′ for coral fish *Microcanthus strigatus* 9 to 11 cm long. Considering fish generally, the density of cones (n) decreases with age but the focal length (F) increases; although these compensate each other to some extent, the focal length dominates the relationship, so that older fish have a higher acuity. This was calculated for the herring by BLAXTER and JONES (1967) who found that acuity in the peripheral retina improved from 200′ to 25′ in fish from 1 cm to 30 cm in length and from 50′ to 7′ in the pure-cone area temporalis.

Directional perception

Directional perception is important for both primary orientation, that is in the control of posture, and in secondary orientation, the control of movement. VON HOLST's (1935) classical work on *Crenilabrus rostratus* shows the importance of the dorsal light reaction in maintaining posture. There is an interplay between the labyrinth and dorsal light stimulation as can be shown by changing the direction of light and by unilateral or bilateral labyrinthectomy. In aquatic organisms of similar specific gravity to water an additional means of maintaining posture other than by gravity is obviously of value.

Directional perception for secondary orientation is presumably used in the various types of vertical and horizontal movement to be discussed. The ability is improved by the development of binocular vision, foveae or areae or any adaptation which localizes stimulation of the retina or improves acuity.

Shape discrimination

HERTER (1953) summarized the immense amount of work done by German physiologists on shape discrimination by fish. Suffice it to say that some of the

more common freshwater laboratory species can discriminate squares, rectangles, rhombuses, circles, ellipses, stars, crosses, stripes, lines, points, pyramids, cubes and letters. They are also deceived by the optical illusions which affect the human eye. True stereoscopic vision has also been demonstrated. More recent work by SUTHERLAND (1963) and MATTHEWS (1964) on *Carassius auratus*, and the tropical *Tilapia* and *Aequidens*, has tested the nature of discrimination and shown that the complete shape is probably of more importance than any limited characteristics.

Movement discrimination

Again this is an ability closely related to acuity and has been tested by optomotor responses, or by the electroretinogram. Two ingenious earlier experiments have been described by HERTER (1953). In the first, Siamese fighting fish *Betta splendens* were trained to distinguish a grey disc from a rotating disc composed of black and white sectors. Where there was complete flicker–fusion, the disc divided in sectors appeared grey and could not be discriminated. In the same species, which attacks its own image in a mirror, a rotating sector was interposed, and the frequency of rotation measured at the point when the image became clear and the fish started its attacks. The highest flicker–fusion rate varied from 30 to 55/sec in these 2 experiments. KOBAYASHI (1962) used the ERG technique and found the maximum flicker–fusion frequencies varied from 32/sec in *Trachurus trachurus* to 15/sec in *Gymnothorax reticulatus*. In elasmobranchs the maximum values ranged from 10 + to 4·4/sec. PROTASOV (1964) reported frequencies varying from 14/sec in *Carassius auratus* to 67/sec in smelt *Atherina*, again using the electroretinogram. HANYU and ALI (1964) using an ERG on the Atlantic salmon *Salmo salar* found an effect both of light intensity and temperature, flicker–fusion frequencies increasing from 10 to 100/sec with temperature between 5° and 25° C, and with light between 10 and 5000 mc. ALI and KOBAYASHI (1967) made further studies on *Lepomis gibbosus*. In this species, flicker–fusion frequencies increased with both temperature and light intensity, from 10 to 90/sec between light intensities of 40 to 7000 mc and temperatures of 10° to 20° C.

The fall of flicker–fusion frequency with light intensity is reported by all authors who studied light effects. The fall-off is not linear; the relationship between light and flicker–fusion changes with intensity, especially at the transition from cone to rod vision (Fig. 2-32). This may be used for assessment of dark- or light-adaptation (Table 2-27) (WOLF and ZERRAHN-WOLF, 1935–1936; CROZIER and WOLF, 1940).

(*d*) *Bioluminescence*

Photophores are confined to marine fish, usually oceanic in distribution. The occurrence and physiology of these organs has been reviewed by MARSHALL (1954), HARVEY (1957) and especially by NICOL (1962, 1967b). The light may be produced continuously by symbiotic bacteria, for example in the macrourid *Malacocephalus*, the anomalopids *Anomalops* and *Photoblepharon*, and in the leiognathids. In the stomiatoids and myctophids light is produced by photocytes and here it tends to be more intermittent. These organs may be simple, with or without a pigment layer, and are often superficial and widely distributed over the body; for example,

several thousand are found in *Chauliodus*. The light organs on the illicium of deep-sea ceratioids are also simple in structure. Amongst the more complex organs are 3 groups: (i) Accumulations of photocytes on the integument associated with a reflecting and pigment layer and often with a lens and filter to concentrate and colour the light emitted. The skin usually has a 'window' where it overlies the organ. Such organs are found in *Cyclothone*, myctophids and in the batrachoidid *Porichthys*. (ii) Alveolar organs or sacs in the body wall, as in *Photoblepharon*, usually consisting of a mass of secretory tubules parts of which are surrounded by a reflecting layer and masking pigment; they contain symbiotic bacteria and have a

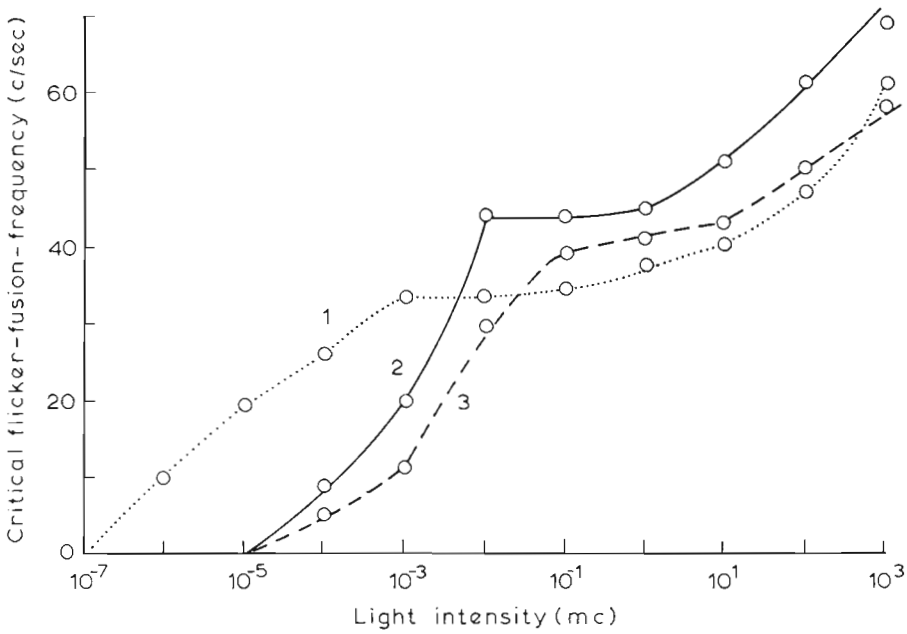

Fig. 2-32: Critical flicker-fusion-frequency as a function of light intensity. 1: Sea bream *Sargus annularis*; 2: anchovy *Engraulis mordax*; 3: young smelt *Atherina mochon pontica*. (After PROTASOV and co-authors, 1960; redrawn.)

'window' overlying them and often a pore to the exterior. (iii) Visceral light organs, glandular structures sometimes containing symbiotic bacteria; they are associated with the oesophagus in leiognathids or with parts of the intestine, as in the serranid *Apogon*. The argentinoid *Opisthoproctus* has a rectal organ of some complexity and light escapes from within the body over a wide ventral area or 'sole'.

The light emitted by the photophores has a λ_{max} of 460 to 470 nm in *Myctophum* and *Apogon ellioti*; if this is a general characteristic it would mean that the light emitted is similar in spectral composition to the light best transmitted by oceanic sea water. Records of bioluminescence measured by an underwater photometer also showed that the intensity is greatest around 470 nm (CLARKE, 1961).

NICOL (1967b) classified the possible function of the photophores as follows: (i) Attraction. The tentacular or illicial organs of ceratioid angler fish, and other organs found within the oral cavity, as in *Chauliodus*, are almost certainly acting as lures

to attract prey. Light attraction is involved in the courtship of *Porichthys*, and the specific or sexual pattern of the photophores in some myctophids suggests a species or sexual recognition. Unfortunately, schooling or territorial habits of deep-sea fish are unknown. (ii) Repulsion. *Porichthys* is apparently avoided by predators whenever it flashes, suggesting a warning device. Sudden flashing or the discharge of a luminous secretion, as in *Searsia*, may also distract predators. (iii) Illumination. MARSHALL (1954) advocated this role for those photophores giving out a beam of light. The general illumination produced by cheek organs or lateral photophores could enhance feeding. He also suggests that the orbital light organs found in *Cyclothone*, *Argyropelecus* and *Chauliodus* might pre-adapt the eye to light before flashing starts. (iv) Obliterating. CLARKE (1963) suggested this originally and the idea has been elaborated by NICOL (1967b). If deep-sea fish could match the downwelling light by ventrally-directed photophores the silhouette effect would be reduced or lost. It is well known that photophores are directed in this way and that the eyes of deep-sea fish often point dorsally. *Opisthoproctus* with its illuminated sole would seem particularly well-adapted to this, as would fish like *Chauliodus* and *Porichthys* which emit a continuous glow. CLARKE (1961) and CLARKE and BACKUS (1964) measured flashes of bioluminescence ranging from 10^{-2} to 10^{-7} $\mu W/cm^2$ or even less, which overlap the range of downwelling light. High intensity flashes were found just below the depth at which the same intensity of ambient light occurred. Assuming an absolute threshold for deep-sea fish of 10^{-10} $\mu W/cm^2$ (p. 219) there is abundant flexibility in the photophores for matching downwelling light in terms of intensity and colour. Because the deep-sea fish with a pure-rod eye must have relatively poor acuity, and is probably myopic, the photophores of other fish may well appear as a dim glow rather than as a point source; this may help to reduce silhouette effects. However, the problems to the fish of matching the intensity of the light organs to diurnal changes of ambient light or during vertical migration could be considerable.

(2) Functional Responses

(a) *Tolerance*

Light as a harmful factor

An abundance of experimental work has been conducted on the effects of X-rays, ultra-violet, infra-red and visible light on the early stages of fish (EISLER, 1961). X-rays will not be considered further here. The action of ultra-violet light has been studied principally in freshwater fish; in the killifish *Fundulus*, for example, it causes abnormalities of the skeleton, particularly in the tail, cyclopia and twinning. A general increase in mortality may occur in fish such as the rainbow trout *Salmo irideus* and the pike *Esox lucius*. In the eggs and alevins of sockeye salmon *Oncorhynchus nerka*, BELL and HOAR (1950) found that irradiation with light from 280 to 310 nm led to premature hatching, abnormalities of the vertebral column, high mortality and, surprisingly, delayed pigmentation. MARINARO and BERNARD (1966) exposed the eggs of pelagic marine fish to sunlight, with and without the ultra-violet component filtered out, finding a lower hatching rate in the pilchard *Sardina pilchardus*, mullet *Mullus*, *Trachurus* and *Diplodus annularis* where the ultra-violet light was not removed.

Various salmonid species—e.g. *Salmo irideus*, *Oncorhynchus kisutch* and *O. tshawytscha*—have been subjected to visible light in the early stages of development, up to complete yolk resorption (HAMDORF, 1960; EISLER, 1961) causing early hatching, mortality, poor growth and darker pigmentation. In *S. irideus* an intensity of about 1600 mc for 72 hrs causes a high mortality. Exposures of 168 hrs at a similar intensity during different stages of the development of *O. tshawytscha* cause abnormalities and increased mortality; both decrease when the exposure is made later in development, becoming particularly reduced after the onset of pigmentation, and, in the case of *S. irideus*, after the heart starts to beat. Susceptibility to light is reduced at lower intensities of exposure. In *O. tshawytscha* deleterious effects decreased in experiments where the intensity was lower (intensities used were 1500, 900, 370 and 0·2 mc). While with ultra-violet light harm can clearly be caused at wavelengths which coincide with maximum absorption of the nucleic acids, with visible light it is thought that there is significant destruction of lactoflavine.

A low percentage hatch in salmonid eggs on exposure to light is not unexpected since they normally develop in the semi-darkness of the spawning redd. Similarly other species with eggs developing in sand, for example, the grunion *Leuresthes tenuis* (MCHUGH, 1954), or on the sea bed, as in the herring *Clupea harengus* (BLAXTER, 1956), may show a poorer hatching in lighted conditions. Where the eggs are pelagic it might be expected that there would be a fairly high resistance though DANNEVIG and HANSEN (1952) found a higher hatch of plaice *Pleuronectes platessa* in the dark, and of cod *Gadus morhua* in light. Careful controls are required in experiments of this sort to avoid other, indirect effects of light such as warming and phytoplankton growth.

Mortality in the sea due to light, especially ultra-violet, has been mentioned earlier. Other less precise ecological investigations indicate the possible effects of light on mortality of young fish which may be due either to light or changes of surface temperature. LJUBICKAJA (1957) found a higher proportion of dead eggs and larvae of *Sardinella* in the Sea of Azov near the surface than near the bottom. DEMENTEVA (1958) reported that engraulid eggs die at temperatures above 26° C thus emphasizing that temperature change may sometimes be the dominant effect.

The transparency of pelagic eggs and larvae may be an adaptation to reduce absorption of light in the tissues as well as an anti-predation device. The possibility of direct light effects on the nervous system and spinal cord cannot be ruled out and this is certainly found in the ammocoete larvae of the lamprey. Fish with transparent young stages have an unguarded pineal, while those with opaque or pigmented eggs have one protected by pigment, which suggests that adults with transparent larvae have a pineal organ which is inactive (BREDER, 1962).

Darkness as a harmful factor

The freshwater *Astyanax mexicanus* can live for long periods in complete darkness, but there is a progressive development of thyroid hyperplasia, malfunction of the adrenal and pituitary, and distortion of the vertebral column (RASQUIN and ROSENBLOOM, 1954). This species represents a rather special category since its close derivative *Anoptichthys* lives in the darkness of limestone caves. ONEFF (*in*: PFLUGFELDER, 1952) found retinal degeneration in *Carassius auratus* kept in

darkness for 3 years, while PFLUGFELDER himself claimed a reduction in size of the optic tectum in the guppy *Lebistes* and of the pseudobranch in *Lebistes* and *Hyphessobrycon* after unilateral and bilateral blinding or in darkness. The question of the effect of sensory deprivation of all kinds both in the development of the sense organs and in the normal life of fish requires further study. In the same way that locomotor activity plays a role in the development of muscles, sensory input may well be required for proper development and continuous functioning of the sense organs.

Temperature tolerance and photoperiod

In *Carassius auratus* resistance to cold is greater in winter, and resistance to heat greater in summer. This rather unspectacular finding is due to an interesting photoperiodic effect (HOAR and ROBERTSON, 1959) probably mediated via the pituitary. Experiments altering the photoperiod out-of-season change temperature tolerance independently of ambient temperature variations. It would be valuable to extend such experiments to other species. The freshwater *Lepomis gibbosus* (ROBERTS, 1964) shows a significant difference in respiratory rate, but not opercular frequency, when subjected to a 9-hr and 15-hr day. This only occurs in autumn and winter fish above 10° C and may be linked with a conditioning for reproduction. Spring and summer fish at lower temperatures do not exhibit this response.

Limiting effects of light

In many species of fish, sometimes called 'optic' or 'visual' species, light plays the dominant role in perception. Its importance in the clupeoids for schooling, feeding, spawning and avoidance of fishing gear has been stressed by BLAXTER and HOLLIDAY (1963). Light above a certain threshold is essential for certain patterns of behaviour; around this threshold there is a gradual reduction in behavioural performance and usually a general reduction in activity as well. While in some groups other senses may dominate, in the 'visual' species these other senses may only assume some importance below the light threshold.

Limiting light effects on schooling. Social groupings of fish have been discussed at some length by BREDER (1959). They vary from the tightly-packed 'pod', through the polarized 'school', to the looser, unpolarized 'aggregation'. The term school will be used here to characterize a group of fish polarized or orientated to one another, usually with members evenly spaced and swimming at similar speeds. Where possible this definition should include the requirement that the fish are responding to each other rather than to a common external stimulus whether this be light, tide, current, predator or fishing gear.

Schooling is found in widely-separated groups of fish, being especially prevalent in the planktonophage, pelagic species such as engraulids and clupeids. SHAW (1962) estimated about 2000 or more marine schooling species including the above and such families as the mugilids, scombrids and trachurids, and a further 2000 freshwater species principally amongst the cypriniforms.

The importance of vision in the maintenance of schools has been reviewed by a number of scientists (for example, MORROW, 1948; BREDER, 1959; LOUKASHKIN and GRANT, 1959; SHAW, 1961, 1967, 1969). SHAW and TUCKER (1965) suggested

that schooling may be due to an optomotor response (p. 262) between the members. Perhaps the best evidence for visual contact comes from observations where the reduction of schooling has been related to light intensity. An instance of such work is given in Fig. 2-33 and a summary of other results in Fig. 2-34, from which it can be seen that the most general reduction takes place between 10 and 10^{-2} mc. Other techniques which have been used involve blinding or straight-

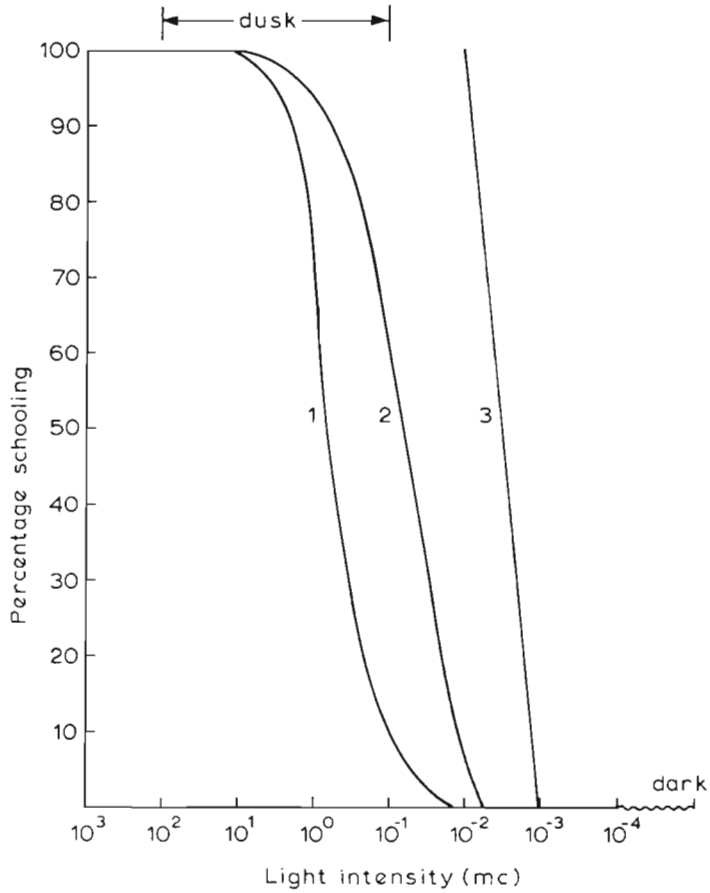

Fig. 2-33: Schooling of herring *Clupea harengus* at different light intensities. 1, 2: large tanks (different experiments); 3: small tank. (After BLAXTER and PARRISH, 1965; redrawn.)

forward observations of fish kept in the dark. Lists of species which disperse in the dark (MORROW, 1948) include many gadoids such as cod *Gadus morhua*, coalfish *Pollachius virens*, whiting *Merlangius merlangus*, hake *Merluccius*, red fish *Sebastes* (WOODHEAD, 1966), reef fishes of the Clupeidae, Lutjanidae and Pomadasyidae (HOBSON, 1965) and clupeids such as *Clupea harengus*, sprat *Sprattus* and sardine *Sardina melanosticta* (BLAXTER and HOLLIDAY, 1963). The work of KEENLEYSIDE (1955) on the freshwater rudd *Scardinius erythrophthalmus* showed that schooling does not occur in blinded specimens, though odour has some aggregating influence.

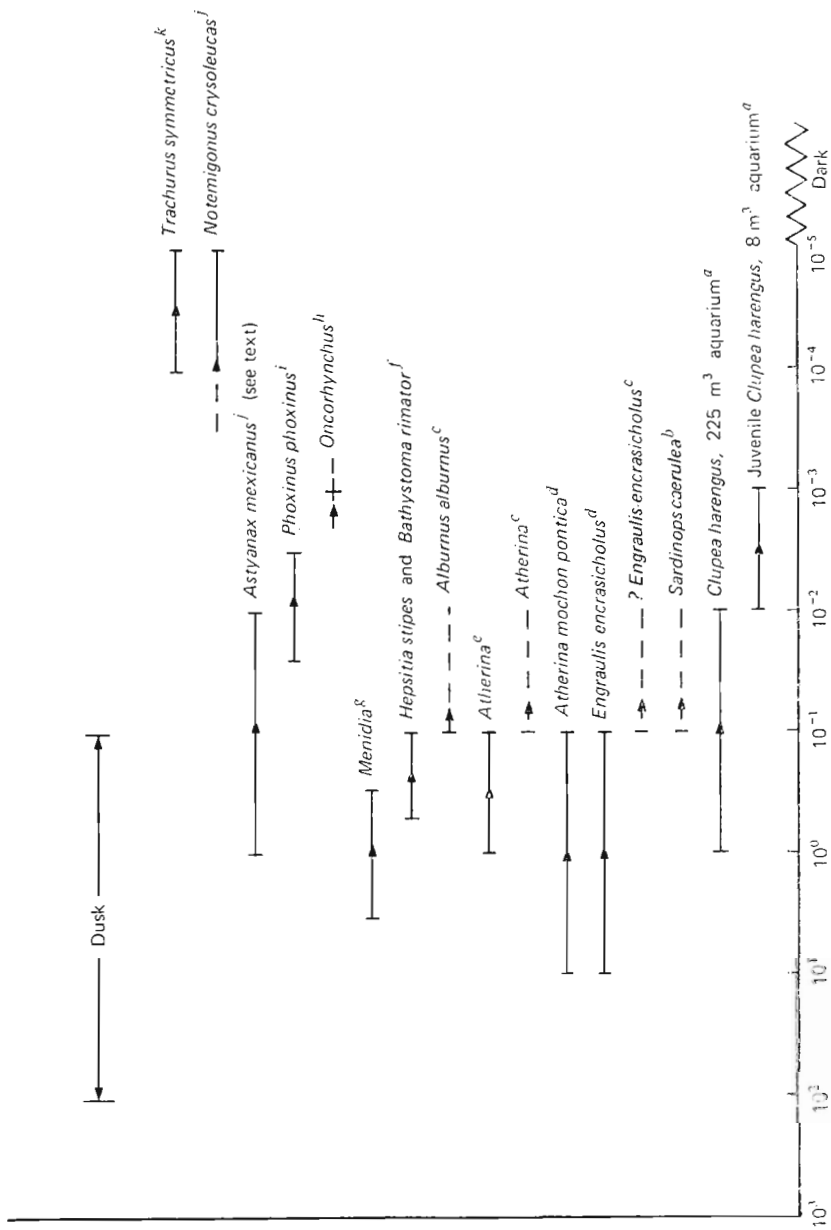

Fig. 2-34: Range of light intensities over which schooling drops. – – – complete range not determined; arrows indicate direction of decrease. (After (*a*) BLAXTER and PARRISH, 1965; (*b*) LOUKASHKIN and GRANT, 1959; (*c*) GIBSA, 1961; (*d*) PROTASOV and co-authors, 1960; (*e*) PAVLOV, 1962; (*f*) STEVEN, 1959; (*g*) SHAW, 1961; (*h*) ALI, 1959; (*i*) JONES, F. R. H., 1956; (*j*) JOHN, 1964; (*k*) HUNTER, 1968.)

It is thus possible that schools may be kept together to some extent by olfaction.

The best observations available on schooling changes by night and day in the natural habitat are contradictory. CRAIG and PRIESTLEY (1960) used electronic flash to photograph *Clupea harengus* on a spawning ground in the Clyde estuary, finding close schooling during the night when the ambient light must have been well below threshold. WELSBY and co-authors (1964) used a high resolution sector-scanning sonar, adequate to show young clupeids as individuals, in the turbid water of the Forth river, finding a dispersal at night in sub-threshold light conditions.

A more complicated relationship between light and schooling may well exist in some species. This was brought out in the work of JOHN (1964) on *Astyanax mexicanus*. Observations at different light intensities using an infra-red image convertor showed that the intensity of schooling alters with light reduction depending on the state of dark- or light-adaptation of the eye (Fig. 2-35). Using

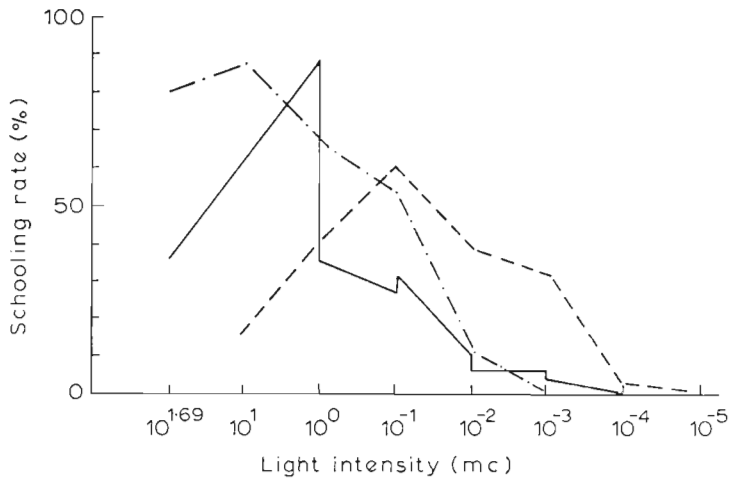

Fig. 2-35: Schooling of *Astyanax mexicanus* at different light intensities using different procedures. Fish maintained in artificial light. —— sudden progressive reductions of illumination at 'dusk'; — · — · — sudden reduction of illumination for light-adapted fish by 'day'; – – – sudden increase of illumination for dark-adapted fish at 'night'. (After JOHN, 1964; redrawn.)

entirely artificial lighting, he found that in sudden reductions of illumination by 'day', schooling dropped to zero between 10^{-2} and 10^{-3} mc, while sudden increases of illumination by 'night' permitted schooling down to 10^{-4} to 10^{-5} mc. At an artificial 'dusk' schooling dropped most rapidly between 10^{0} and 10^{-2} mc. While these experiments were not performed in natural light, and only small groups were used, they indicate the need for careful standardization of technique and suggest that the best defining of thresholds might be at natural dusk or dawn.

Before dealing with criticisms of the light-schooling relationship, a paradox which has recently been developed should be mentioned. It arises from the work of DENTON and NICOL (1965a, b, 1966) on the silvery-sided horse mackerel *Trachurus trachurus*, herring *Clupea harengus* and bleak *Alburnus alburnus* which

showed that adaptation to background by means of a mirror-like reflecting layer was so good that the resulting invisibility might well make visual schooling exceedingly difficult. It should be mentioned that this camouflage effect depends on a homogeneous distribution of light from all azimuths. This will be least true at dusk and dawn, the times which are most critical for maintenance of the school from the light-intensity aspect.

The instances when schools were found in the dark are either infrequent or, in many cases, open to criticism. MOULTON (1960) found tight schools of *Anchoviella choerostoma* and *Caranx latus* in the dark. This, and his finding that blinded *Anchoviella* would school with intact fish as long as movement was sufficiently rapid, constitute some of the best evidence available. Echo-sounding records of 'schools' at night, for example in herring *Clupea harengus* (JONES, 1962), or records from results of fishing, for example, in the chub mackerel *Pneumatophorus grex* (SETTE, 1950) do not provide proof of polarization, though they are evidence of aggregation. Observations from submarines of schools of *Clupea harengus*

Table 2-19

Degree of adhesion (low values are equivalent to close schooling) in *Rasbora heteromorpha* under different light conditions (After THINES and VANDENBUSSCHE, 1966)

Experimental condition	Alarm substance present		Alarm substance absent	
	Day	Night	Day	Night
Tanks lighted	3·64	19·70	14·00	24·18
Tanks in darkness	14·50	22·20	20·43	21·27

(RADAKOV, 1960) and others by eye, for instance by ZUSSER (1958) of *Anchoviella* and *Sprattus* in the Sea of Azov, and by DEELDER (1958) of *Anguilla* elvers remaining together at night, are not accompanied either by a definition of schooling or by values of ambient light at the time. Indeed, how were the observations made without providing artificial lights to see the fish? Similar criticism may be applied to the work of HATANAKA and co-authors (1957) who photographed young mackerel *Pneumatophorus japonicus* by flash, but made no measurements of ambient light. For similar reasons records need to be kept of the possible effects of bioluminescence.

Evidence of 'visual' schooling from aquarium work was criticized by JONES (1962) on the grounds that possible olfactory cues which could operate in the natural environment at night would pervade the whole restricted volume of a tank. It is more likely that such olfactory stimuli could only help to keep a group of fish aggregated, as found in *Scardinius*; they could not provide a means for polarization. THINES and VANDENBUSSCHE (1966) found that the 'alarm substance' ('Schreckstoff') produced by *Rasbora heteromorpha* was of assistance in bringing the fish together by day but not by night; it also helped when the light intensity was reduced during the day (Table 2-19). They suggested that olfactory cues can be of assistance in this species for aggregation purposes, but activity patterns,

which are high by day and low by night, are overriding. In cases where polarization becomes reduced but not lost in the dark, for example, in *Pneumatophorus grex* (SHLAIFER, 1942), non-visual reinforcing stimuli must be looked for. Apart from olfaction the schooling drive may vary with the degree of satiation; for instance ZADULSKAIA and SMIRNOV (1939) reported that hungry fish tend to concentrate more than satiated ones, while HUNTER (1965) found the reverse in *Trachurus trachurus*; when deprived of food the interval between fish increased. Many species break school to feed (e.g. *Clupea harengus*, BLAXTER and HOLLIDAY, 1958) and this can have a profound influence on school maintenance at dusk when feeding may be at a peak. For further information concerning the role of schooling consult SHAW (1967, 1969) and HOBSON (1968).

Limiting light effects on feeding. DE GROOT (1969) studied feeding in some species of flatfish using food models with and without olfactory stimulation. Taking the sole *Solea solea*, plaice *Pleuronectes platessa*, flounder *Platichthys flesus*, turbot *Psetta maxima* and brill *Scophthalmus rhombus* his results were at first surprising. *Solea solea*, which is a night feeder, displayed many more positive responses to models of food without olfactory cues than did *Pleuronectes platessa* and *Platichthys flesus*, which required additional olfactory stimulation. These 2 species and *Psetta* and *Scophthalmus*, which did not react to models of food at all, were considered as day-feeders and their lack of response was probably due to a more exacting and specific type of choice in visual conditons.

The minimum light intensity for initial detection of food and visual recognition and selection are of great importance in many species. An analysis of stomach contents over a 24-hr period is one method for determining the influence of light. The difficulties lie in assessing rates of digestion, the possibility of regurgitation and the effects of fixation where the fish are preserved. The work of ZADULSKAIA and SMIRNOV (1939) is one example of extensive use of this technique. They found that feeding in *Gadus morhua* of the Barents Sea depends on tide, time of day, illumination and season. The stomachs were fullest at the following times: winter 16 to 20 hrs; spring 12 to 16 hrs; summer 8 to 12 hrs; autumn 8 to 12 hrs. Digestion may take 5 to 6 days, hence precision in deducing peaks for feeding is difficult to attain.

Based on similar analyses, diurnal feeding rhythms have been reported, for instance in adult *Clupea harengus* (MUŽINIĆ, 1931), *Pleuronectes platessa* (DAWES, 1930; JONES, 1952; HEMPEL, 1956) and *Thunnus alalunga* (IVERSEN, 1962). With a more rapid turnover in the gut it was easier for these workers to assess when peaks occurred, the most usual finding being a peak at dusk and dawn with no feeding at night. Comparable rhythms have been found for the larvae of marine fish belonging to widely divergent groups; for example, larvae of *Clupea harengus* (HENTSCHEL, 1950; BHATTACHARYYA, 1957), *Engraulis encrasicholus* (DEMENTEVA, 1958), *Pleuronectes platessa* (SHELBOURNE, 1953; RYLAND, 1964), *Ammodytes lanceolatus* (RYLAND, 1964) and *Seriola* sp. (ANRAKU and AZETA, 1966) feed by day, either continuously, or with certain peak periods, and cease to feed after dark. An example of the results obtained is shown in Fig. 2-36.

Other species are known to feed at night. The sand eel *Ammodytes personatus* (SENTA, 1965) and some species of reef predators such as *Gymnothorax* (BARDACH

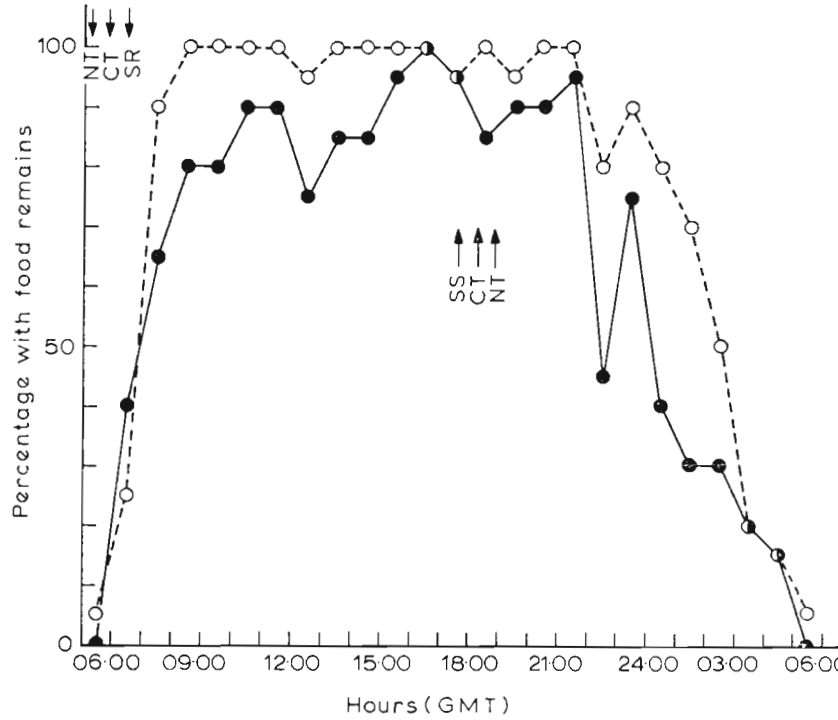

Fig. 2-36: Feeding periodicity of plaice *Pleuronectes platessa* ○ - - - ○ and sand eel *Ammodytes marinus* ● —— ●. NT: nautical twilight; CT: civil twilight; SR: sunrise; SS: sunset. (After RYLAND, 1964; redrawn.)

and co-authors, 1959) feed nocturnally, with olfaction presumably being an important sensory factor. Judging by comparisons between the ratio of food in the first to the second part of the gut, *Solea solea* feeds during the night (KRUUK, 1963; Fig. 2-37).

Straightforward observations that larvae of Georges Bank haddock *Melanogrammus aeglefinus* stalk their prey visually (MARAK, 1960), or that *Clupea harengus* can take food in bright moonlight—estimated to be 0·25 mc—(BATTLE and co-authors, 1936), provide information that light is required for feeding. More exact information is obtained by feeding experiments conducted over a range of light intensities. Examples are given in Fig. 2-38 which has been compiled from the results of several authors. The figure reveals different effects of illumination depending on species and food supply. A more comprehensive survey of the range of light intensity over which feeding activity becomes reduced is presented in Fig. 2-39. While some species show feeding into darkness the main fall-off for 'visual' feeders is between 10^{0} and 10^{-2} mc.

The relationship between predator and prey can depend on illumination. GIRSA (1961) showed how the predators *Molva molva*, *Silurus glanis* and *Corvina* are most active by night, feeding on 'visual' planktonophage species such as anchovy *Engraulis* and smelt *Atherina* which have broken up from their daylight schooling formation (Fig. 2-40). By day the predators are either inactive or the food is not so vulnerable to attack. This is shown in more detail in Fig. 2-41 for young

Atherina being preyed on by smarids (PAVLOV, 1962). At high light intensities schooling acts as a protection: low light levels are insufficient for smarids to take their prey: it is only at intermediate light intensities, as the schools break, that *Atherina* becomes vulnerable. HOBSON (1968) considers in some detail the predatory behaviour of Californian shore fishes, showing that nocturnally active species are usually predators.

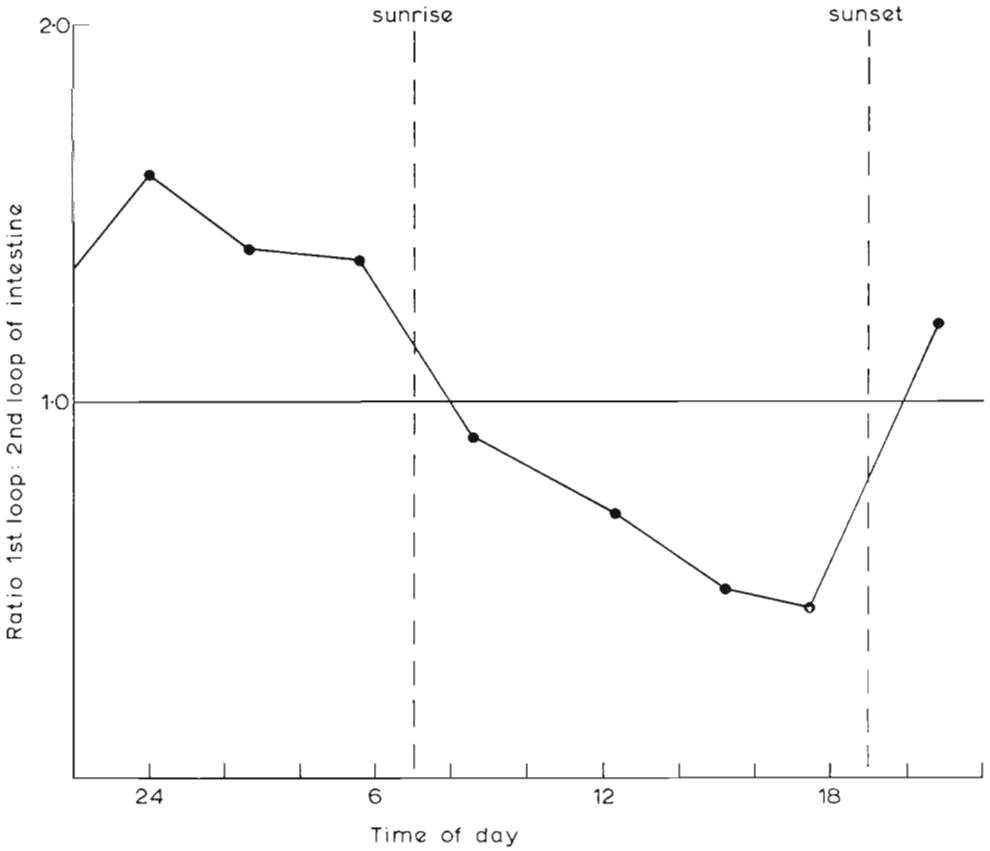

Fig. 2-37: Feeding periodicity of the sole *Solea solea*. The movement of food through the gut is indicated on the ordinate by the ratio of the number of guts with the first loop filled to the number with the second filled. (After KRUUK, 1963; redrawn.)

Feeding by night under tank conditions is not necessarily evidence of nocturnal feeding behaviour in the natural environment. For instance, in a confined space a learning factor may be involved, as found by HOAR (1942). Young *Salmo salar* which fed on chopped earthworm in the dark (compare with BRETT and GROOT, 1963 in Fig. 2-38) were being presented with inanimate food in a particular position in a tank where learning could operate. ALI (1964b) reported a similar result with yearlings of *S. salar*, while JONES, F. R. H. (1956) using the freshwater *Phoxinus phoxinus* and BLAXTER (1968b) using metamorphosing larvae of *Pleuronectes platessa* found residual feeding in the dark. There can be no doubt that

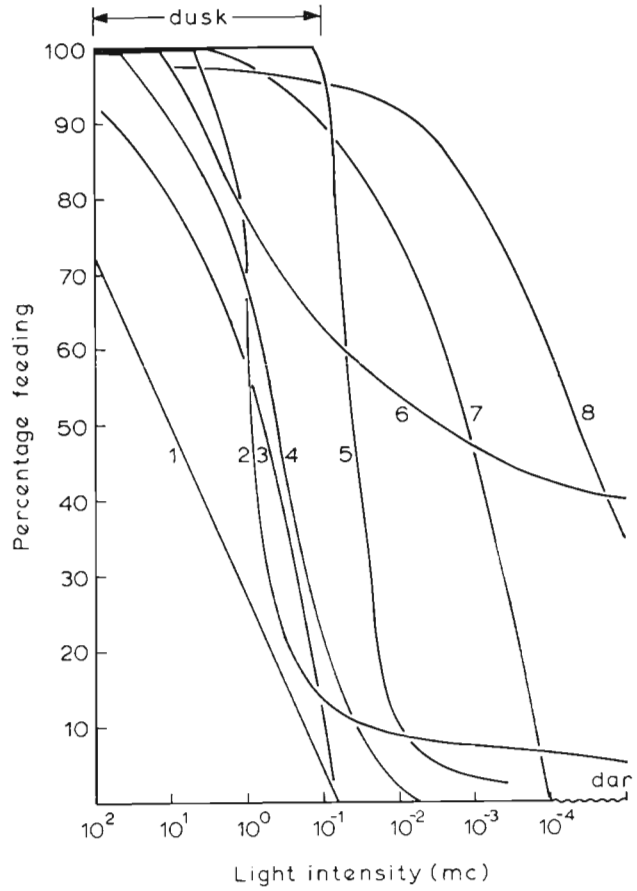

Fig. 2-38: Percentage feeding of fish at different light intensities. 1: Larvae of the herring *Clupea harengus* feeding on *Balanus* nauplii (after BLAXTER, 1966); 2: bleak *Alburnus alburnus* feeding on plankton (after GIRSA, 1961); 3: larvae of *Clupea harengus* feeding on *Artemia* nauplii (after BLAXTER, 1966); 4: cod *Boreogadus saida* feeding on plankton (after GIRSA, 1961); 5: young pike *Esox lucius* feeding on plankton (after GIRSA, 1961); 6: crucian carp *Carassius carassius* feeding on plankton (after GIRSA, 1961); 7: young coho salmon *Oncorhynchus kisutch* feeding on *Daphnia* (after BRETT and GROOT, 1963); 8: minnow *Phoxinus phoxinus* feeding on *Daphnia* (after JONES, F. R. H., 1956).

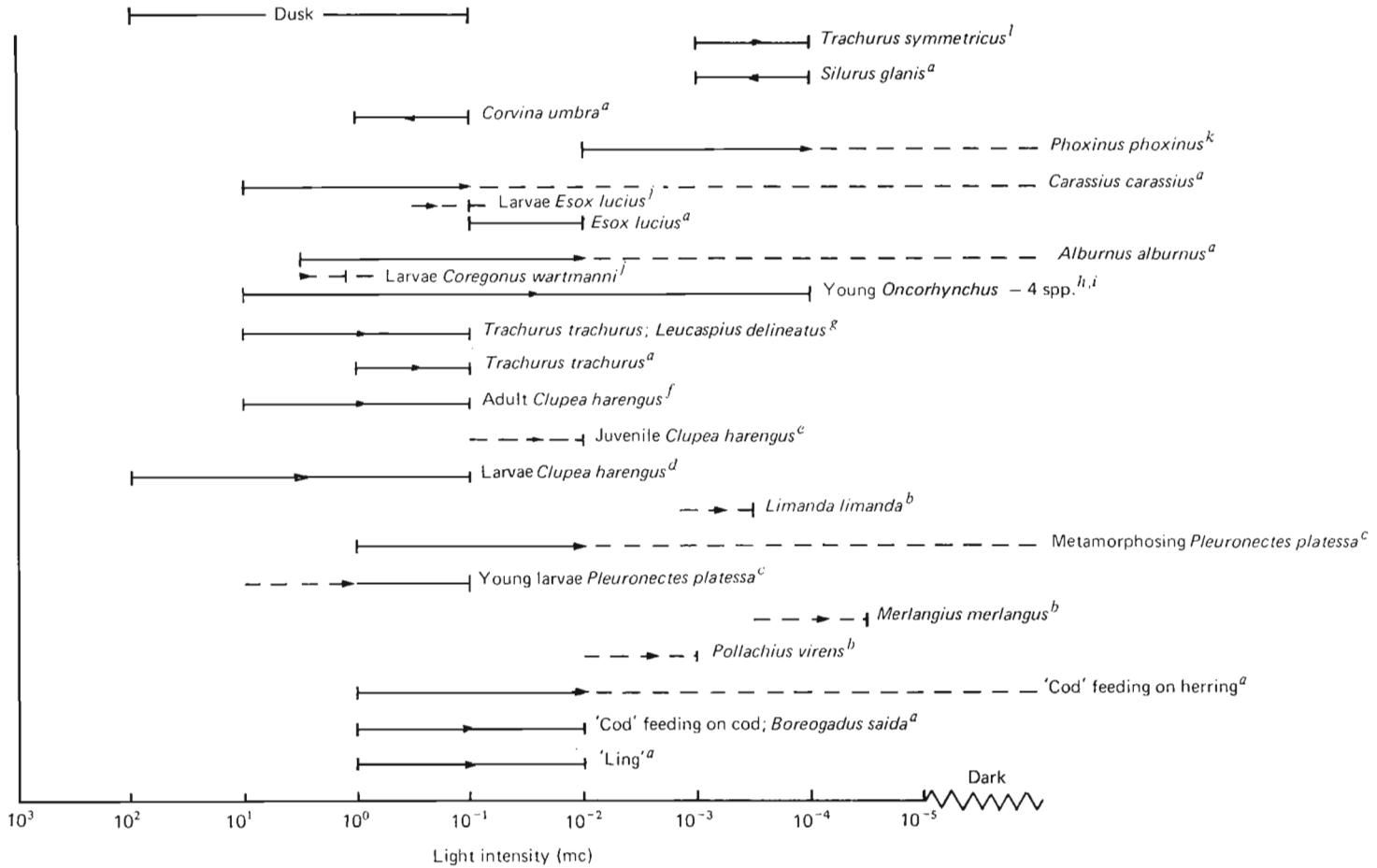

Fig. 2-39: Range of light intensities over which feeding activity declines. – – –: complete range not determined or feeding continues into the dark; arrows indicate direction of decrease in feeding intensity. (After (*a*) GIRSA, 1961; (*b*) BLAXTER and LITTLE, unpublished; (*c*) BLAXTER, 1968b; (*d*) BLAXTER, 1966; (*e*) BLAXTER, 1964; (*f*) BLAXTER and HOLLIDAY, 1958; (*g*) PROTASOV and co-authors, 1960; (*h*) BRETT and GROOT, 1963; (*i*) ALI, 1959; (*j*) BRAUM, 1964; (*k*) JONES, F. R. H., 1956; (*l*) HUNTER, 1968.)

learning and the type of food (including its mobility) play an important part in the outcome of this type of experiment.

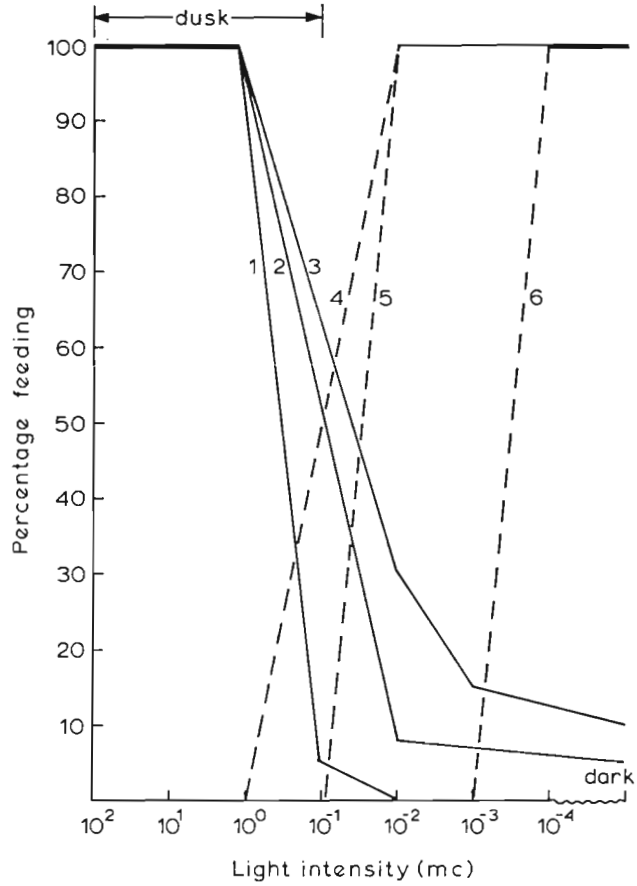

Fig. 2-40: Feeding of fish at different light intensities; predatory fish feeding on planktonophage fish. 1: Horse mackerel *Trachurus trachurus*; 2: 'cod' feeding on cod; 3: 'cod' feeding on herring; 4: 'ling'; 5: corb *Corvina umbra*; 6: *Silurus glanis*. (After GIRSA, 1961; redrawn.)

Limiting light effects on spawning. Spawning is rarely observed either at sea or under aquarium conditions. Many marine fish species have a rather insignificant sexual dimorphism and for this reason courtship and mating may be a less involved procedure than in some freshwater or tropical fish. Where elaborate displays occur, as for instance in marine pomacentrids (REESE, 1964), vision must be important.

In tanks light was shown to be necessary for the spawning act of *Clupea harengus* (HOLLIDAY, 1960) both in the interaction between male and female and in the choice of substrate for depositing the demersal eggs. BRAWN (1961) found that *Gadus morhua* spawned in very dim light in aquaria, but she did not observe

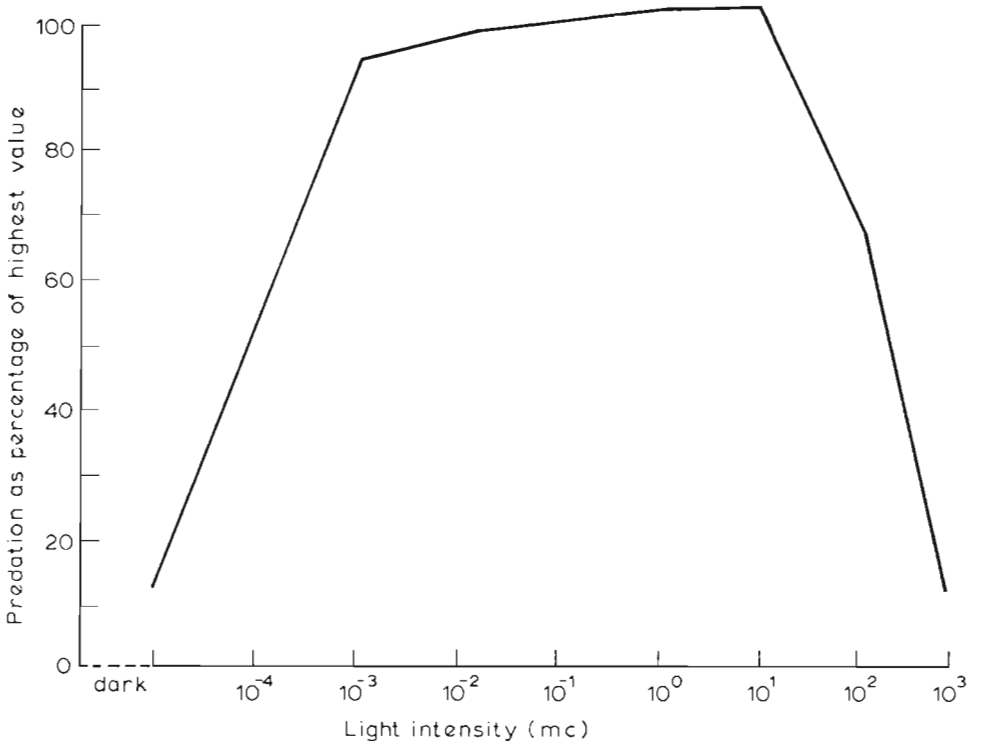

Fig. 2-41: Feeding of smarid fish on young smelt *Atherina* at different light intensities (After PAVLOV, 1962; redrawn.)

whether this continued in darkness. In the sea, results of surveys for eggs show that spawning seems to occur in the late evening or around dusk in many clupeoids; in *Pleuronectes platessa* kept for hatching purposes eggs are rarely released by day; see also WOODHEAD (1966).

Limiting light effects in gear avoidance. The possible role of light in determining the capture success of fishing gear may be deduced in a number of ways: (i) By comparisons of day and night catches in the sea (p. 262); (ii) by use of nets of different visibility in the sea; (iii) by experimental studies in tanks with model gear; (iv) by experimental studies under 'field' conditions.

The use of nets of different visibility has been developed by a number of countries, especially Britain, Germany and Japan. A summary of some of the findings is given in Table 2-20; many of them point to the great advantages of using transparent synthetic fibres, especially for passive capture by gill nets. These materials may even permit daytime fishing which has hitherto been uneconomic. In other instances fishing in turbid water may improve the catch by day. The reverse effect is desired where netting is required to herd fish; it should then be as visible as possible. This applies with encircling nets or with the peripheral parts of trawls or seines. The visibility of netting in different sea areas has recently been studied by HEMMINGS (1966) with tests of sighting distances by a group of divers. He concluded that brightness rather than colour was the more significant factor. As

Table 2-20

Visibility effects in fish capture (Original)

Species	Result	Author
Clupea harengus (herring)	Taken by day with monofilament nylon nets.	VON BRANDT (1954)
Clupea harengus	Ability to avoid nets in tanks is least when nets are of low visibility or twine is very thin; threshold twine diameter 0·2 mm.	MOHR (1961a)
Clupea harengus	Monofilament nylon nets very effective in catching fish in tanks. Cannot avoid nets with opaque plastic over eyes (see also Table 2-21).	BLAXTER and PARRISH (1965)
Anchovy	Gill nets less effective in clear water.	ASLANOVA (1958)
Gadus morhua (cod)	Avoid gill nets by day.	SUNDNES (1964)
Gadus morhua	Greater catches by perlon nets.	SCHWARZ (1959)
Thunnus alalunga (albacore)	Gill nets seem more effective in turbid water, visual lures (trolling) better in clear water (see also Fig. 2-42).	MURPHY (1959)
Lateolabrax japonicus (sea bass) *Konosirus punctatus* (gizzard shad)	Better fishing when illumination poor, nets dull in colour, water turbid.	NOMURA (1959)
Coregonids (white fish)	Monofilament nylon nets take seven times, and multifilament nylon four times, the catch with cotton nets.	MOLIN (1959)
Oncorhynchus spp. (Pacific salmon)	Monofilament nets outfish multifilament by at least 2:1.	LARKINS (1963–1964)
Perca fluviatilis (perch) *Rutilus rutilus* (roach)	Better catches with inconspicuous nets (also tested by optomotor response to netting).	STEINBERG (1961)
Salmon	Entangling properties best in the order grey = blue-green > brown.	KOIKE (1958)
Trachurus trachurus (horse mackerel) *Atherina elymus* (sand smelt) *Cyprinus carpio* (carp)	Experimental observation that *barrier* effect is best in the order red > yellow > green.	KANDA and co-authors (1958)

an example of the relative importance of vision for different types of fishing gear the results of MURPHY (1959) for albacore tuna *Thunnus alalunga* are given in Fig. 2-42. They suggest that high transparency of the water is advantageous for trolling but not for gill nets.

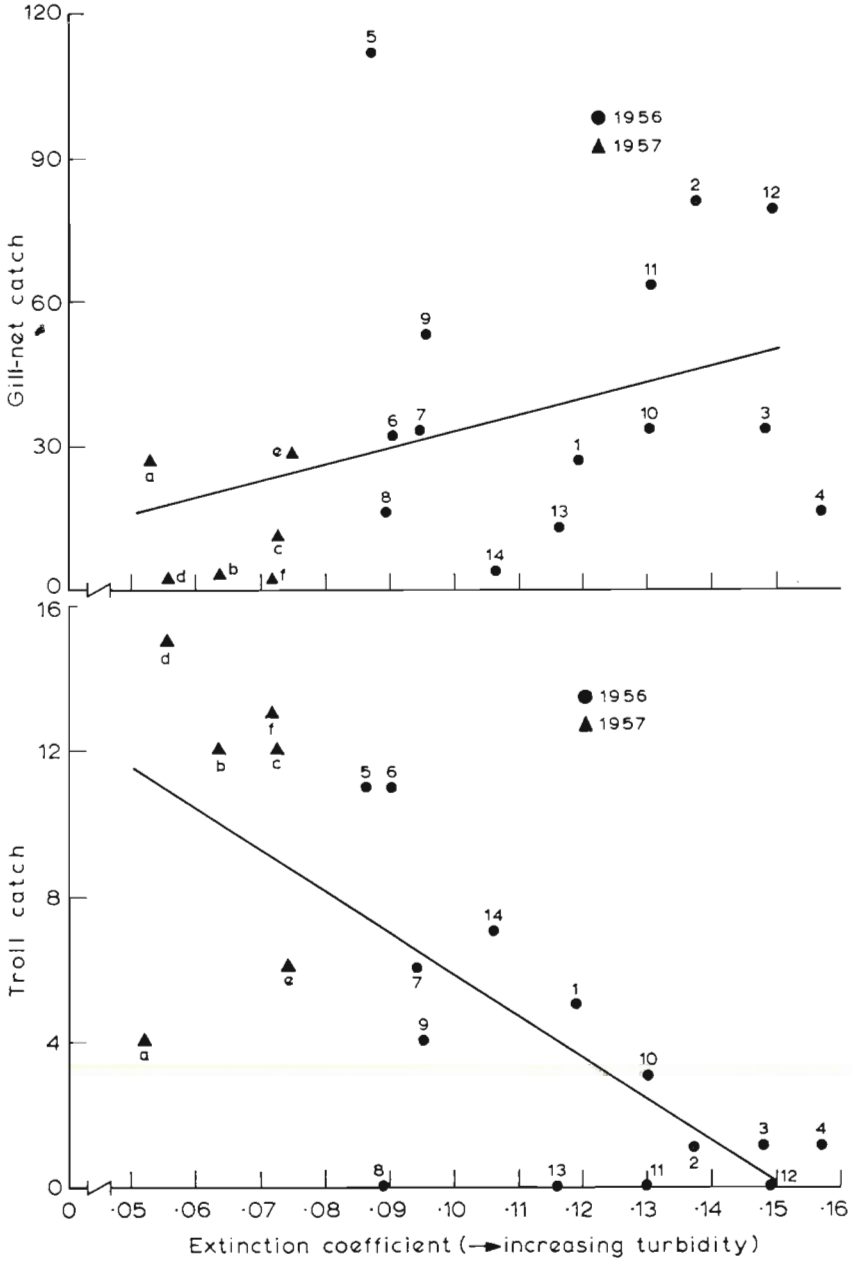

Fig. 2-42: Catch of albacore *Thunnus alalunga* by gill net and troll in water of different turbidity, showing a tendency for gill net catches to improve and troll catches to worsen in more turbid water. Letters and numbers refer to station positions. (After MURPHY, 1959; redrawn.)

Some of the more experimental studies, particularly on the driving effects of nets should be mentioned. Thresholds of light intensity at which *Clupea harengus* swam into gill nets under different conditions are presented in Table 2-21. Aquarium studies on the effects of models of moving nets on *Clupea harengus*, *Melanogrammus aeglefinus* and *Gadus morhua* showed that herding ability varied with the conspicuousness of the models. In all cases there was a great reduction in herding as the illumination dropped at dusk, the thresholds being given in Table 2-22; while there is much variability the most general reduction seemed to be occurring at about 0·1 mc.

Table 2-21

Light intensities (mc) at which herring start to swim into netting which they avoid in daylight (After BLAXTER and PARRISH, 1965)

Experimental condition	Colour of twine	Background Grey	White	Black
Small tank	Black	1×10^{-3}	—	—
	White	$< 10^{-3}$	—	—
Large tank	Black	—	8×10^{-3}	3×10^{-2}
	White	—	3×10^{-3}	2×10^{-3}

Table 2-22

Light intensities (mc) at which the herding of fish drops to 50% of the daylight value (After BLAXTER and PARRISH, 1966)

Model	*Clupea harengus*	*Gadus morhua*	*Melanogrammus aeglefinus*
Ground rope and attachments	0·1–0·55	0·07–0·6	0·01–0·5
Panels of netting	0·08	?0·3–0·5	0·3
Underwater lights	0·005–0·66	0·005–0·7?	0·7
Air bubble screen	0·09–0·25	—	0·45

Limiting light effects in fish-guiding experiments. Slow-moving curtains of air bubbles have been tested recently, both at sea and experimentally, as a means of guiding fish into pound nets or for other herding purposes. For instance SMITH (1964) tested such a device on *Clupea harengus* and *Brevoortia tyrannus*, concluding that it was more effective in clear water. When used and found to be effective through the dusk period and even in darkness, it was observed that the bubbles could still be seen by the human eye, perhaps partly due to bioluminescence. Aquarium experiments on *Oryzias latipes*, *Carassius auratus*, *Salmo trutta*, *Anguilla anguilla*, *Clupea harengus* and *Melanogrammus aeglefinus* (KOBAYASHI and co-authors, 1959; MOHR, 1960; BLAXTER and PARRISH, 1966) evaluated the herding properties of these air-bubble curtains and found them to be mainly effective when moving slowly and under good conditions of illumination.

A different type of guiding may be seen in the extensive work aimed at deflecting Pacific salmonids from the spillways or intakes of power stations. Chiefly performed by Americans and Canadians, it has been reviewed by FIELDS (1957) and BRETT and ALDERDICE (1958). With certain exceptions there is an up- and downstream migration by night; in attempts to control or deflect this migration various devices were used such as barriers of air bubbles, stationary and moving curtains of vertically hanging chains, batteries of lights usually above the surface (of various intensities and colours) and bright or illuminated plates on the bottom; in some cases these were combined with sound or electrical stimuli. With the variety of species and ages used and the differences in conditions of water velocity, turbidity, bottom topography, time of day and season, it is hardly surprising that there is some inconsistency in the results. They indicate, however, a general antipathy for visual stimuli amongst nearly all the species, which may vary with the degree of dark-adaptation. Bubble barriers were never very effective unless illuminated; considering the aeration found in rivers this is not surprising. Chain or cable barriers were also not particularly effective but became more so if vibrated, moved or illuminated. There were also critical distances between the components. While flashing light barriers above the surface led to conflicting results, steady lights were sometimes effective depending more on their intensity than colour. Of great significance for deflection is the angle of the barrier in relation to the flow of water; the nearer the barrier was in line with the current the more effective it became. Where the velocity of the current was high, guiding was more difficult. Multiple barriers increased the percentage of fish guided. Of the various types of barriers studied, those above the surface have the advantage of not being clogged by debris in the river or stream.

(*b*) *Metabolism and Activity*

The limitation of behaviour by light is not always a straightforward relationship; often metabolism and activity become reduced in the dark, due to some endocrinal or nervous factor, and cannot immediately be restored by providing artificial light during a period of darkness. Many diurnal activities may be due to an endogenous rhythm continuing in constant light or dark which is only modulated by a change in light conditions. The term 'diurnal' rhythm is now in such wide use for denoting patterns of behaviour which cycle approximately once every 24 hrs that the etymologically more correct expressions 'diel' or 'circadian' will not be used; the 3 expressions may be considered as synonymous. Since in many instances no attempt has been made to test whether diurnal rhythms, for example of feeding, are brought about by inability to feed, or by a drop in activity due to reduced light, much of the work which might have been described in this section has been dealt with under tolerance. In many cases light is really limiting; there is loss of visual perception which reduces the sensory information reaching the brain to a level which is inadequate to control behaviour. This section, however, deals with changes in metabolism and activity which are not necessarily light-limited, although in some instances they bear a close relationship to behaviour described in the previous section.

Metabolism

WINBERG (1960) reviewed the literature on diurnal variations in oxygen consumption with some scepticism, pointing to inadequate experimental technique or analysis of data in the results of a number of authors. In the largemouth bass *Hucho salmoides* maximum values were found in the morning and evening which were twice the minimum. The work of OLIFAN (*in*: WINBERG, 1960), showing fluctuations in O_2 uptake with peaks especially at dusk and dawn and low levels by day and night, is open to criticism, especially since these variations have not been correlated with activity levels. In carp *Cyprinus carpio*, studied more critically, diurnal variations in O_2 uptake were not significant, being of the order of 15% or less.

More recent experiments have not shown a particularly impressive rhythm either. ALI (1964a) certainly found a tendency for O_2 consumption to be higher by day, with an afternoon peak around 14·00 hrs, in yearling *Salmo salar*, but an imposed light regime of alternate dark and light lasting either 6 or 12 hrs produced inconsistent results with little relationship in the earlier stages of the experiments. At later stages O_2 consumption fell off in each dark period. In continuous dark, but not continuous light, there was some evidence for an endogenous rhythm, but the experiments lasted only 4 days. Similarly, the respiratory rates obtained by HOLLIDAY and co-authors (1964) on larvae of *Clupea harengus*, although showing a tendency for a reduction by night, were inconsistent from one replicate to another. HEMPEL (1964), recording a greater activity of *Pleuronectes platessa* at night, correlated this with a greater O_2 consumption at that time, by 14, 25 and 40% in 3 experiments. DAVIES (1966) used a calorimetric technique to measure output of heat by *Carassius auratus* and found a depression in heat production during darkness.

It is to be expected that a decrease in respiratory rate should follow a reduction in activity by night, but whether a drop in respiration by some physiological means could impose a decrease in activity seems uncertain. HOLLIDAY (personal communication) has recently developed a hypothesis that the pseudobranch–chorioid gland complex plays a part in activity. These 2 organs are always found linked together in fish and it seems possible that the pseudobranch controls the oxygen dissociation curve of the blood, in fact imposing a Bohr shift. The chorioid gland, which is situated behind the retina, may provide some sort of visual control of this pseudobranch effect.

Seasonal variations in metabolism may also occur. WELLS (1935) found that the killifish *Fundulus parvipennis* had a high rate of metabolism from February to March and a low rate from July to August, both at seasonal temperatures and when held at a constant high or low temperature. BEAMISH (1964) reported a reverse effect in brook trout *Salvelinus fontinalis*. Individuals held at 10° C in natural daylight exhibited a low rate of standard metabolism from March to April, about half the rate found in late autumn. In brown trout *Salmo trutta* the autumn rate of standard metabolism was about 50% higher than that in winter or spring. These responses are probably related to changes in photoperiod and to maturation.

Activity

Cycles of locomotor and feeding activity. A number of devices have been used

both to measure and record activity of fish by day and night, especially some type of vane or barrier agitated by fish moving in a tank. Thus SPOOR (1946) built an aluminium paddle wheel and JONES, F.R.H. (1956) a celluloid vane causing a make-and-break circuit to record on a kymograph drum. HARDER and HEMPEL (1954) devised a false bottom in an aquarium for the study of activity in flatfish, movements being recorded in a similar way on a kymograph drum. KRUUK (1963) suspended lead balls in the water, the suspension wire, acting as one contact, running in a concentric ring acting as the other. A relay system again permitted recording on a kymograph. DAVIS (1964) used the same suspension technique for a framework of aluminium supporting a mesh of rubber bands. DE GROOT and SCHUYF (1967) and LILLELUND (1967) independently developed a magnetic tag, for flatfish and carp respectively, which distorted a magnetic field set up in the tank.

Other techniques involve measurement of respiration rate, but the limitations of this lie in the accumulation of an oxygen debt and in the chance of respiration changes which are not paralleled by changes in activity. BEAMISH and MOOKHERJII (1964) designed an ingenious warm-bulb activity recorder: activity causes heat loss from a small heater unit and the current input required to make good this loss is recorded. HEUSNER and ENRIGHT (1966) used a rather similar principle, measuring the change in heat conductance of water due to activity of animals by means of a thermistor. Other authors, for example, KOBAYASHI and co-authors (1956), measured feeding activity by recording the agitation of a food container. Three elegant developments have recently enabled observations of activity to be made in poor illumination. The use of infra-red light, to which fish are insensitive, with an infra-red image convertor (e.g. DUNCAN, 1956; JOHN, 1964) allows fish to be watched, provided that the depth of water is not too great. SWIFT (1964) assessed cycles of activity as fish disturbed electric fields set up in underwater cages. The recent developments in high resolution sector-scanning sonar, which can show fish as individuals on a P.P.I. display (cathode ray tube), as reported by WELSBY and co-authors (1964) and JONES (1969), give a means of observation in the dark and in turbid water at any depth.

Many of the aquarium experiments just described show a tendency for activity to drop by night or in the dark. Field studies such as those described by HOAR (1956a) and ALI (1959) on different stages and species of the Pacific salmon, chum *Oncorhynchus keta*, pink *O. gorbuscha* and sockeye *O. nerka* clearly show how much more involved behaviour may be than would appear in the artificial environment of the aquarium tank. Much migration takes place at night. Fry and smolts of these species rise to the surface from the stream bed at dusk and are either passively displaced or swim downstream, cover often being sought again at dawn. It seems likely that active swimming is more prevalent than was originally thought. As will be described later, BRETT and GROOT (1963) found that young *O. nerka*, after one year or more in a lake, will make a mass exodus in a diurnally-pulsed migration, especially at dusk, but also at dawn. The migrations of the elvers of *Anguilla vulgaris* provide an interesting parallel. Here the vertical movements are closely related to the tidal cycle in estuaries; they use the flood tide to make a 'landfall' by migrating vertically to the surface on the flood tide, and keeping to the bottom on the ebb, as long as they are physiologically in condition to with-

stand the salinity drop (CREUTZBERG, 1961). During early stages near the freshwater boundary the elvers are highly photonegative, becoming less disturbed by light later on (DEELDER, 1958).

Flatfish have been a frequent subject of activity studies. HARDER and HEMPEL (1954), DE GROOT (1964) and VERHEIJEN and DE GROOT (1967), for example, showed high activity in *Pleuronectes platessa* by night; this result does not fit very well with observations on stomach contents from fish caught at sea, which indicate feeding by day. In addition, daytime catches also tend to be higher, except perhaps in the spawning season. DE GROOT was able to explain this discrepancy when he

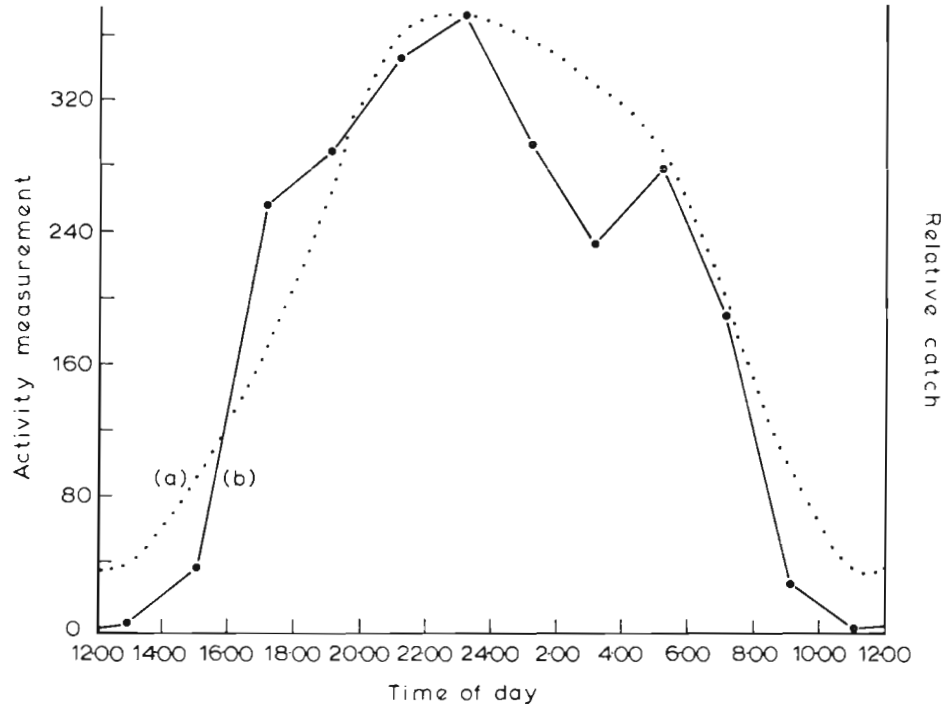

Fig. 2-43: Line (a) shows relative catch of sole *Solea solea* for January and February at different times of day, and (b) activity measurements on similar fish in aquaria. (After KRUUK, 1963; redrawn.)

kept his fish at much lower light intensities in the daytime, similar to those found on the sea bed; this led to some increase in day activity. VERHEIJEN and DE GROOT also found some feeding activity in tanks by day when a more sensitive recording techique was used. *Solea solea*, however, shows a nocturnal activity rhythm which correlates well with night feeding as deduced from stomach analyses (Fig. 2-37) and indeed with higher catches at night (Fig. 2-43). This activity starts when the light falls to 0·008 mc and 'digging-in', a behaviour characteristic of lighted conditions, starts at 0·035 mc during a gradual increase in light intensity (KRUUK, 1963).

Observational data such as those of II and co-authors (1953) on about 20 species show that fish may be classified into groups which are either active by night, by day, or by night and day. Coastal fish especially tend to be nocturnal. HOBSON (1965, 1968)

studied a number of inshore species in the Gulf of California. The herbivores and omnivores showed a tendency to feed by day (for example, pomacentrids, labrids and scarids). The nocturnal species, such as holocentrids and pomadasyids, were usually predators sheltering by day and feeding by night. Some clupeid and carangid species were in rather inactive schools by day, dispersing offshore at night to feed. This type of casual observation, while giving information on the habits of fish, does not help in deciding whether the behaviour is light-limited or whether visual cues are involved in feeding.

Research into habits based on hourly changes in stomach contents is extensive and has been reviewed by WOODHEAD (1966). It is also relevant in the study of vertical movements and diurnal changes in catches (pp. 262–264), both of which may involve behaviour limited by light and diurnal activity rhythms.

A problem of special concern is the extent to which locomotor and feeding rhythms may be endogenous. This has been discussed in general by CLOUDESLEY-THOMPSON (1961) and HARKER (1964). Endogenous rhythms certainly do seem to occur in fish. In *Pleuronectes platessa* and *Solea solea* kept in constant light or dark a locomotor rhythm persists at least for some days (DE GROOT, 1964; KRUUK, 1963). Often a continuous light regime or artificial photoperiods may reduce, but not suppress, such rhythms. They are manifested also in what are called 'pre-feeding' rhythms of activity as those described by DAVIS (1964) for the bluegill *Lepomis m. macrochirus* and the largemouth bass *Micropterus salmoides*. These species show a peak of activity before dawn, which is a learned response and which can be changed by altering the photoperiod. DAVIS and BARDACH (1965) using the tomcod *Microgadus tomcod*, scup *Stenotomus versicolor* and killifish *Fundulus heteroclitus* concluded that these species related the act of feeding to an endogenous activity rhythm which was itself being timed by feeding or daily changes in light.

Some findings have shown how aquarium observations on activity can lead to spurious conclusions. Apart from light itself being critical, with often a change in activity level at a certain threshold, for example, at about 0·2 mc in *Phoxinus phoxinus* (WOODHEAD, 1956), a reverse pattern may be observed if some species are given shelter during periods when they are normally active. This occurs in *Phoxinus phoxinus* (JONES, F.R.H., 1956) while BREGNBALLE (1961) found that *Platichthys flesus* swam actively until sand was put in the aquarium.

The control mechanism of endogenous rhythms has been considered by BÜNNING (1964). In many instances they eventually do die out but may persist for weeks. The persistent rhythms, which are not necessarily of exactly 24 hrs, are modulated by an external stimulus or 'Zeitgeber' which is usually light. Changing the phase by the use of artificial photoperiods often allows the rhythm to be gradually retimed (hence the advantage of it not being exactly 24 hrs in length). This, of course, happens as the seasons progress anyhow. While the times for maximum light change, such as dusk and dawn, are of great importance, intensity alone or the relative periods of light and dark may have an influence. In fish, and in other animals, there are practically no data available on the action spectra or thresholds for photoperiodic stimulation of this sort.

A significant factor in endogenous rhythms is the almost complete independence of temperature; where Q_{10}'s have been measured they are usually 1·0 to 1·1. This

raises interesting problems of the localization of the 'clock' and if chemical reactions are involved how temperature is compensated for.

The value of an endogenous rhythm has been discussed by ASCHOFF (1964). The advantage of being pre-adapted to a change in the environment is obvious, so long as it does not make the organism temporarily less viable under the existing environmental conditions. Such rhythms also provide a double safety mechanism preventing an animal sleeping through the dawn period. A mechanism is also provided, though this is less likely in fish, so that an endogenous rhythm which has adaptive value in relation to a particular stimulus may be timed by quite a different one. For instance, endogenous rhythms which adapt the animal to day and night humidity changes may be timed by light rather than humidity, light providing a more regular and easily perceived cue. On the species level endogenous rhythms may provide a means by which different stages in the life history may be accommodated in one environment without competition, if their rhythms are out of phase (p. 260); similarly competition between species could be reduced. As ASCHOFF puts it—this is sympatry in space but allopatry in time.

Sleep. The suggestion that fish sleep is open to criticism. Whether highly inactive fish are sleeping, as recorded in the literature, in the sense that higher vertebrates do, requires a far stricter analysis than has been used by the investigators concerned. The criteria of brain rhythms, reaction times and waking need to be critically applied. That activity, however, drops in some species by night is irrefutable. Observation from the Russian submarine *Severyanka* (RADAKOV and SOLOVYEV, 1959; ZAITSEV and RADAKOV, 1960) of *Clupea harengus* resting in the water by night at various angles to the horizontal, or those of ZUSSER (1958) of clupeids in the Caspian in motionless 'schools', and the aquarium observations on *C. harengus* (BLAXTER and PARRISH, 1966), the Californian sardine *Sardinops caerulea* (LOUKASHKIN and GRANT, 1959) and mackerel *Scomber* (II and co-authors, 1953) show how inactivity becomes almost total in the dark, the fish often losing all horizontal orientation. Examples especially of clupeids are quoted by WOODHEAD (1966) as evidence of a contrary effect, while other species such as *Euthynnus affinis* continue to swim actively at night.

Instances of fish 'falling asleep' are given by KAWAMOTO and KONISHI (1955) who quote the case of *Rudarius ercodes* and by UCHIHASHI and co-authors (1962) who made an experimental study of sleep in the *Carassius auratus*, purporting to show sleep by a reduction in learned (conditioned) responses.

'Sleep' as a survival factor in rearing fish larvae is mentioned by QASIM (1959). He showed a higher survival in the larvae of the shore species *Blennius pholis* and *Pholis gunnellus* under a day–night regime than in continuous light. This work is of such interest in fish farming that it should be repeated on other species, but a great many replicate experiments are required to obviate the unknown factors which may so easily affect the viability of fish larvae.

The deleterious effects of continuous dark have already been dealt with. What must be considered is the condition of life in more extreme latitudes where both continuous light or dark can prevail naturally. The effect of this on the marine fauna is almost unknown. BLAXTER (1966) showed how the time available for feeding and the volume of water searched by *Clupea harengus* larvae and adults

could vary by a factor of 2 to 3, depending on the season, in more northerly races. Vertical migrations disappear in the polar night or day (ZUSSER, 1958). Polar animals may well require rather special mechanisms to overcome the seasonal extremes of day and night.

Lunar rhythms. Moonlight at its maximum has an intensity of only about 10^{-6} of full sunlight. Nevertheless, it represents the order of intensity when the eye changes from the light- to the dark-adapted state (p. 274) and when many of the light-limiting types of behaviour only begin to phase out. It is thus sufficient for many types of activity to continue. As the lunar cycle has a considerable effect on the tides it is often very difficult to decide how much of a lunar cycle is due to tidal height or current velocity, and how much to light. KORRINGA (1957) reviewed lunar rhythms but his examples were taken mainly from invertebrates. However, the grunion *Leuresthes tenuis*, an atherinid of southern California, spawns on the beaches through spring and summer only on the 3 or 4 nights following each full or new moon and then only 1 to 3 hrs after high water. The eggs are deposited in the sand and hatch about 15 days later when the spring tides recur. The extent to which this is due to tide or light is uncertain. Presumably there is a rhythmical maturation of the gonads which might be controlled overall by seasonal photoperiod, with a more precise modulator due to lunar light or tide. If the former is of importance the question arises of thresholds of light for such effects and the problem of light reduction by cloud cover or other factors which might disturb the cycle.

Another well-known instance of a lunar cycle is found in the pre-war catches of *Clupea harengus* in the southern North Sea (SAVAGE and HODGSON, 1934). Around the full moon the catch sometimes doubled, but the date of full moon was also important. If it was in the second week of October there was often good fishing for 5 weeks with a second peak after a month. If full moon was towards the end of October there was only one peak of good catches. Since the war the declining fishery and spells of bad weather at certain stages of the lunar cycle have reduced its significance. How it operates is uncertain. It is in part due to an increase in the activity level of the fish (the 'swim'), but how much this is caused by bright moonlight or high-tidal velocities and whether these affect vertical migration, crowding, predators or ability to see the nets is uncertain.

BOËTIUS (1967) found that the escapes of experimental eels were much higher in the third quarter of the moon. The stimulus concerned seemed not to be light as the eels were kept in constant darkness.

Effect of artificial lights. Attraction to, or repulsion from, artificial lights is used as a fishing practice and much experimental work has been done on it in recent years (BLAXTER and PARRISH, 1958; LOUKASHKIN and GRANT, 1965; WOODHEAD, 1966). SCHÄRFE (1953) has reviewed fishing methods employed in both primitive and more sophisticated fisheries of the sea and fresh water. Apart from simple torches, fire 'baskets' and petroleum, acetylene and electric lamps, mostly used above the surface to attract fish to where they can be reached by spears, harpoons, hooks, explosives or electrical fishing apparatus, banks of lights above or below the surface are now in use, which may be controlled from ship or shore. Various

types of nets, such as purse seines or pull nets, may be used to encircle the fish, or they may be lured into set nets. Lights are used in all parts of the world and perhaps the clupeoids and scombroids are most predominant in the catch. Amongst the most intriguing of these luring devices are the light organs of *Sepia*, fish and glow worms which may be used as bait.

Of the more elaborate apparatus the Japanese stick-held dip net fishing gear is illustrated in Fig. 2-44(a). The fish, often scombroids or trachurids, are attracted

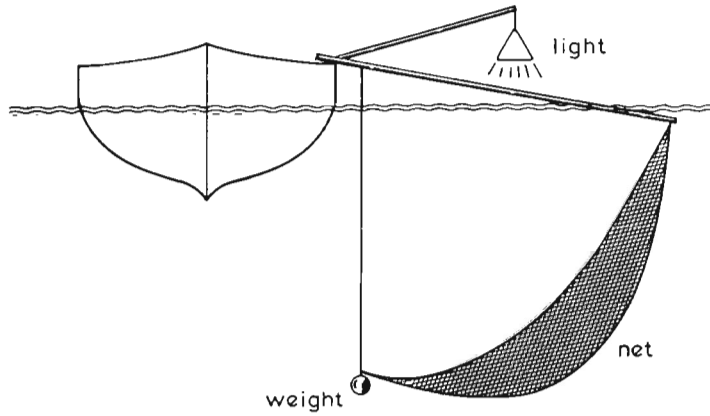

Fig. 2-44(a): Light fishing gear. Stick-held dip net; fish are attracted by the light above the surface and the net is then closed. (Original.)

to the surface by light; the dip net is then hauled up by means of 2 booms to trap them. The Americans (RADOVICH and GIBBS, 1954) have used a similar technique experimentally as a sampling device. The Japanese (SASAKI, 1959) have also developed a set net with a train of lights which are successively switched on and off to lead fish towards the shore (Fig. 2-44(b)). Both Americans and Russians (SMITH, 1955; DETHLOFF, 1964; NIKONOROV, 1964) have used lights with an electrical fishing and pumping apparatus (Fig. 2-44(c)). The fish, usually small clupeoids, are attracted into the electric field by a light of 1000 W or more. Here they are either further attracted or else narcotized by the electrical field and drawn into the pump intake associated with the anode. The fish are then pumped on deck. A fishery for kilka *Clupeonella* sp. in the Caspian Sea and for saury *Cololobis saira* in the Sea of Okhotsk depends on this technique.

Experimental studies on fish attraction have been reviewed by VERHEIJEN (1958) and LOUKASHKIN and GRANT (1965) and much of the British, Dutch, German, Norwegian and Russian work on clupeoids in North Sea, N.E. Atlantic, Caspian Sea and Pacific has been summarized by BORISOV (1955) and BLAXTER and HOLLIDAY (1963). In the case of clupeoids there is, in general, an attraction of younger stages and repulsion of older ones with lights ranging from 5 to 1500 W. There are also sex differences in the reaction to lights, for example, in *Clupeonella* sp. High intensities usually result in a quicker and greater attraction. BORISOV (1955) divided the fish studied by Russian workers into 3 groups: the first avoided light (*Anguilla* and *Lampetra*), the second were attracted in the absence of food

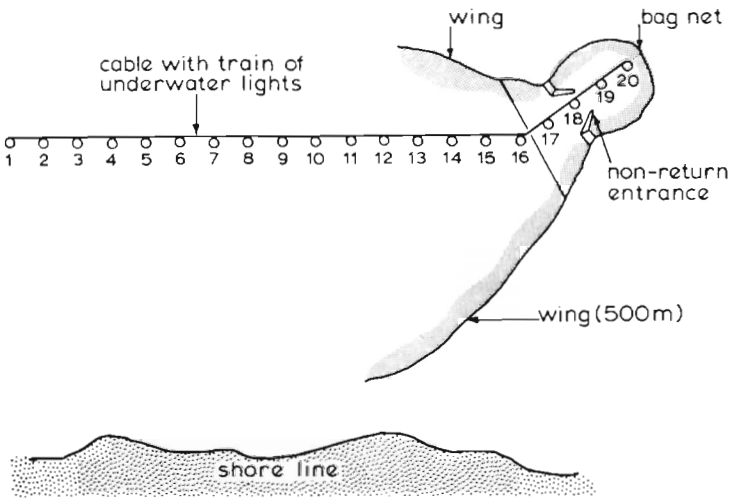

Fig. 2-44(b): Light fishing gear. Bag net with train of underwater lights; the lights are successively switched on and off, attracting the fish progressively towards the net. (After SASAKI, 1959; redrawn.)

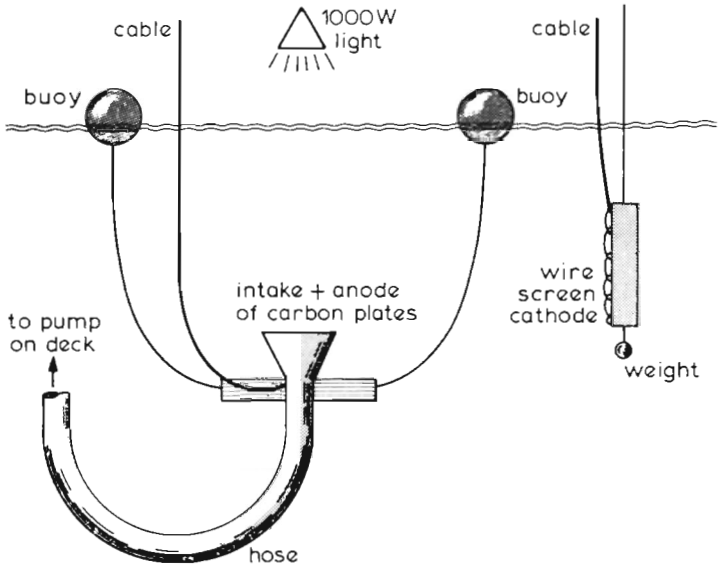

Fig. 2-44(c): Light fishing gear. Electric fishing with lights; fish are first attracted by the light into the electric field, eventually being sucked into the hose intake and pumped on deck. (Original.)

(kilka *Clupeonella*, smelt *Osmerus*), while the third group were attracted only when food was present (*Clupea harengus*, *Belone belone*, *Scomber scombrus*). The Japanese have investigated the influence of different intensity and colour of light on a large number of species by day and night both in turbid and clear water and at different seasons. Two papers are of particular interest. KAWAMOTO and KONISHI (1955) found a diurnal rhythm of phototaxis, for example in *Girella punctata*, where a stronger tendency to phototaxis was observed by day than by night. MAEDA (1951) introduced the concept of the 'lamp community' and showed how organisms arrived at a lamp in a regular order, the first being some of the smaller organisms, many of which were showing phototactic behaviour, these being later followed by the predator species. Such artificial feeding communities varied with light intensity and colour, season, currents, etc.

Repulsion by lights is used as a fishery practice to frighten fish away from shelter or from the mouth of an encircling net. Experimentally it has been used in a study of the light factors involved in vertical migration. BLAXTER and CURRIE (1967) used underwater sources of light on acoustic scattering layers in the Atlantic and found it possible, progressively, to force down a surface layer at night from about 60 m to 300 m. The dusk ascent to the surface could be delayed by lights for at least 15 mins.

The explanation for light attraction has been speculated on by many authors. BELYAEVA and NIKONOROV (1960) attributed it to a number of possible factors such as curiosity, feeding plus a positive phototaxis, hypnosis, following of optimum light conditions, disorientation or conditioned responses. Russian thinking has tended to favour the idea of conditioning, light becoming associated with feeding under normal conditions. The idea of a light optimum is supported by the work of BLAXTER and PARRISH (1958) on *Merlangius merlangus*. This species remained at varying distances from lamps of different wattage, aggregating where the ambient intensity was about 0·1 mc, equivalent to the light intensity at which they were normally found by day. Optima are also mentioned by BORISOV (1955) for *Engraulis encrasicholus*, *Gadus morhua* and *Ammodytes*. VERHEIJEN (1958), in particular, advocated the idea of 'mass disorientation' of fish near a lamp, likening it to the effect of lighthouses or lights on insects and migrating birds. Certainly a lamp is an unusual stimulus with a rather rapid attenuation of intensity around it and giving a different spectrum than daylight. Whether it could often be acting as a point source, only stimulating one eye and causing the 'circus' movements suggested by VERJEIJEN, is questionable. Firstly, circus movements are unusual in fish, though found in invertebrates; secondly, a light is unlikely to act as a point source except in the clearest of water. The explanation may apply in a few instances where fish swim very close to a lamp, e.g. in *Clupeonella* sp., *Cololobis saira* and *Belone belone* (BORISOV, 1955; VERHEIJEN, 1958), but in the case of marine lamp communities or fish remaining at a distance from lamps this explanation cannot hold.

The requirements for light attraction as a fishing method depend on the ability to accumulate fish. Thus acclimation is undesirable. Perhaps it is particularly successful in schooling species which may 'lock on' to each other near a light, the intensity being above the schooling threshold. However, an explanation for attraction, in view of its universal occurrence, is unlikely to be found in any single theory.

An interesting recent development concerns the attraction of fish to floating objects. HUNTER and MITCHELL (1968) used a variety of plastic sheets in different orientations, finding that most fish were attracted to a plastic sheet bent at 60° in its midline and resembling a small tent. While devices of this type are already used in local fisheries, they clearly have potential value on a larger scale.

(c) *Reproduction*

The need for light to enable courtship and mating has already been considered as a limiting factor in nature. Photoperiodism as a timing device for maturation is well known in birds and mammals and also in freshwater fish (PICKFORD and ATZ, 1957; PINHORN and ANDREWS, 1963). While the spring increase in daylength is important for some species, as can be shown experimentally, autumn decrease may operate in fish such as salmonids which spawn later in the year.

A summary of the results of experiments on photoperiodic effects on the reproduction of marine, estuarine or anadramous fish is given in Table 2-23. There is an unfortunate lack of work on marine species, and an undesirable inconsistency in the light conditions, such as intensity and wavelength, used in many experiments (some experiments on purely freshwater species are not included in the table). Undoubtedly several species are refractory to photoperiodic effects at certain times of year, for example, the cyprinid *Notropis bifrenatus* (HARRINGTON *in*

Table 2-23

Photoperiodic effects on some fish species (where no date is given, the reference may be found in PICKFORD and ATZ, 1957) (Original)

Species	Photoperiodic or other light effect	Author
Ameiurus nebulosus (catfish)	Increasing DL[a] causes enlargement of gonads.	BUSER and BLANC
Gobius cobitis (goby)	Increasing DL causes enlargement of gonads.	BUSER-LAHAYE
Ameiurus nebulosus (catfish)	Increasing DL causes enlargement of gonads.	
Mugil ramada (mullet)	Increasing DL causes enlargement of gonads.	
Julis (Coris) vulgaris (wrasse)	Increasing DL causes enlargement of gonads.	
Gasterosteus aculeatus (stickleback)	Some light required for maturation.	KAZANSKII
Gasterosteus aculeatus	Increasing DL accelerates maturation and reproductive behaviour.	VANDEN EECKHOUDT
Gasterosteus aculeatus	Increasing DL accelerates maturation (threshold perhaps 150–300 mc).	BAGGERMANN (1957)
Oncorhynchus nerka (blue back or sockeye salmon)	Increasing DL delays spawning, decreasing DL accelerates it.	COMBS and co-authors (1959)

[a] Day length

PINHORN and ANDREWS, 1963), which is only responsive to increasing daylength from mid-November to mid-July. The effects of photoperiodism on maturation in high latitudes compared with the tropics would be of great interest, as would experiments on maturation in deep-sea fish, were it possible to establish them in tanks. BOËTIUS and BOËTIUS (1967) were unable to find any influence of light on the maturation of the male eel *Anguilla anguilla*.

(*d*) *Distribution*

Vertical distribution

Vertical distribution and migration are not light-limited, though, as will be shown, migration seems often to be controlled by changes of light intensity. Vertical distribution may be affected by a diurnal migration resulting in daily changes in preferred depth, or it may result in a particular depth distribution in a species or in an age-group of a species.

Pelagic fish. The vertical movements of the herring *Clupea harengus* are now well known (BLAXTER and HOLLIDAY, 1963; WOODHEAD, 1966). As with demersal and deepsea species it is only since the invention of the echo-sounder in the last 30 years that the extent of vertical migration has been appreciated. Up to the present, movements of schools or aggregations have been recorded; only with larger fish can individuals be detected. The perfection of equipment with higher resolution (WELSBY and co-authors, 1964; JONES, 1969) will make individual movements of smaller fish also visible. Most commonly, schools are found towards the bottom by day; they move to the surface at dusk and break up at night to form a scattering layer. This process is probably accelerated by feeding. At dawn the schools reform and move downwards again. The amplitude of the vertical movement may vary with age and with the depth of water and similarly the day and night depths maintained may vary enormously. In immature herring of the east coast of Canada and the USA no correlation between the mean depth by day and daytime solar radiation was found. From May to December the day depth was 9 to 13 m, and in January to April 25 to 38 m. At all seasons there was a movement to the surface at night (BRAWN, 1960). In mature oceanic herring the depth may vary from 200 to 400 m by day and from 40 to 80 m by night (RYZHENKO, 1961). The light intensity at the depth of schools was measured by BLAXTER and PARRISH (1965) in the North Sea. These intensities varied greatly by day, from 10^3 to 10^0 mc, with little apparent effect of cloud cover. Other workers had more success in finding the factors controlling depth by day or by night. CHESTNOY (1961) claimed that the depth of the schools could be correlated with isolux lines and the appropriate depth for shooting nets could be predicted from this. Herring were observed by echo-sounder to leave the bottom earlier on overcast evenings (BALLS, 1951) and were found near the surface in foggy or overcast weather by JOHNSON (1939).

The upward and downward migrations are more clearly related to rapid changes of light. They do not occur in Polar conditions of continuous day or night according to ZUSSER (1958). SCHÜLER (*in*: WOODHEAD, 1966) observed an upward movement of 10 to 20 m of herring schools near the Faroe Islands during an eclipse; a subsequent, though somewhat smaller, downward movement was recorded later. At

dusk and dawn, herring of the North Sea are either found to follow isolux lines (Richardson, 1952; Postuma, 1957) or to move when the rapid fall or rise of light intensity reaches certain values (Blaxter and Parrish, 1965). Postuma found that the herring were following a preferendum of about 1 mc, and Blaxter and Parrish that light intensities varied from 10 to 0·1 mc (Fig. 2-45) when the movement began; they also showed that the schools broke up at sea at about the same light threshold as that measured experimentally in tanks (0·1 mc). In the Pacific herring *Clupea pallasii*, *Sprattus sprattus*, *Clupeonella* sp., *Sardina pilchardus*, *Sardinella aurita* and *Sardinops caerulea* vertical migration has been observed, and in some cases similar data on light are available. *Sardinops melanosticta* remains by day in a wide variety of light conditions, ranging from 10 to 1000 mc (Nomura, 1958), moving upwards when the light intensity drops to values between 0·1 and

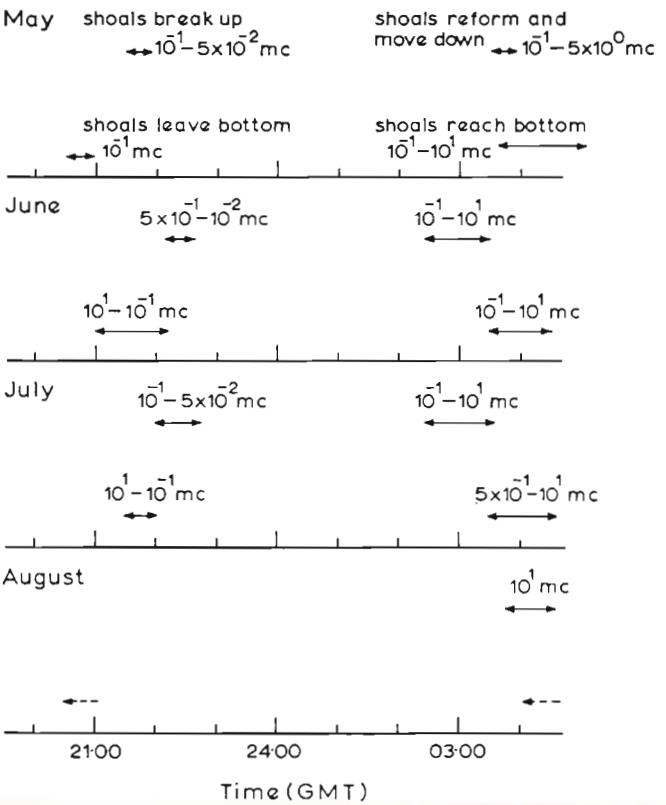

Fig. 2-45: Light intensities for vertical migration and school formation in herring *Clupea harengus* of the northern North Sea. (After Blaxter and Parrish, 1965; redrawn.)

0·01 mc. While the general evidence is rather conflicting about the role of light in maintaining particularly a daytime depth, the larger scale vertical movements at dusk and dawn seem to be caused either by following a preferendum or are at least triggered off by sudden changes in light intensity.

Demersal fish. Vertical movements of so-called demersal fish have been most adequately dealt with by WOODHEAD (1965, 1966) and BEAMISH (1966); the following account is condensed from their reviews. Vertical movements have been assessed by observations at the water surface, echo-sounding, catch data from midwater trawls, lines and drift nets, or from diurnal changes in catches by bottom trawl. Information on the latter will be found on p. 262. There is extreme variability in the findings due to seasonal, age and depth differences, but the general tendency is found, as in pelagic species, for an upward movement by night. *Solea solea* have been seen swimming at the water surface, especially around spawning time, while other flatfish species such as *Limanda limanda* and *Platichthys flesus* have been caught at night by midwater trawls or surface drift nets. Amongst the gadoids, *Gadus morhua* off Greenland are caught by pelagic longlines. Echo-sounders show quite frequently that cod are found in compact groups by day and move to the surface at dusk and disperse; coalfish *Pollachius virens* may make similar vertical migrations of 100 m or more. Young coalfish have been taken near the surface by purse seines off the Icelandic and Norwegian fjords and *Merlangius merlangus* by drift nets and midwater trawls in the North Sea. Some examples of changes in vertical distribution as plotted from echo-sounder records are shown in Fig. 2-46. It can be seen that even *Melanogrammus aeglefinus* will sometimes make vertical excursions. Amongst other species *Sebastes* is known to make large scale vertical movements, as much as 300 m in amplitude.

Fish larvae. Many of the findings of the earlier plankton surveys by day and night, for example those of RUSSELL, are reviewed by WOODHEAD (1966). The central problem of these surveys has always been the question of whether absence of larvae in the catch is due to real distributional differences or differential avoidance by day and night. High speed samplers—such as Gulf III, Miller net, plankton recorder and indicator—have given a less equivocal picture. The work on clupeoid larvae was summarized by BLAXTER and HOLLIDAY (1963). It showed that with the slow nets used for clupeoid larvae, night catches of medium-sized larvae were 4 to 30 times greater than those by day. Frequently larger larvae over 15 to 20 mm in length were never taken by day. When workers such as BRIDGER (1958) used high speed nets many of these differences disappeared. This, and later work on other species, pointed to a residual effect due to vertical movement. Thus RYLAND (1964) made a careful study of *Pleuronectes platessa* and *Ammodytes marinus* larvae in the North Sea using a high speed net and flow meter. By day both species were at depths from 4 to 11 m (light intensity 100 to 5000 mc) and at night the distribution ranged from 1 to 36 m, the average light intensity being very much lower. COLTON (1965) used the continuous plankton recorder to sample larvae of *Melanogrammus aeglefinus* in the Georges Bank–Gulf of Maine area, finding no diurnal differences in size, where hitherto there had been a bias in favour of larger larvae in the night catches.

Deep-sea fish. It is only in the last 10 to 20 years that it has been appreciated how widely distributed are vertically-moving scattering layers over deep water. These are caused, amongst other organisms, by the mesopelagic fish species found by day from about 200 to 1000 m, the upper ones moving from 200 to 500 m towards or to the surface at night (HERSEY and BACKUS, 1962; WOODHEAD, 1965; CLARKE,

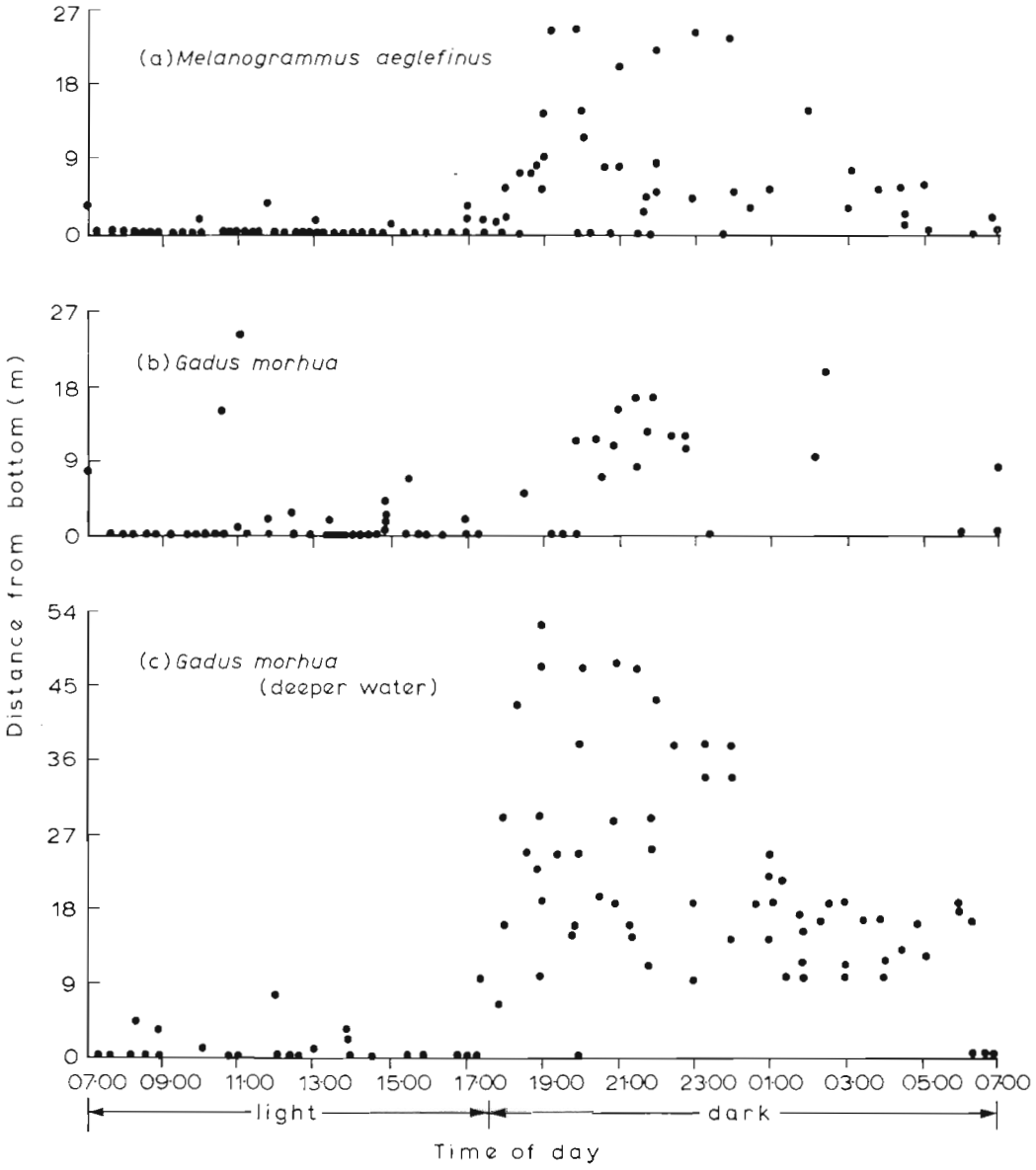

Fig. 2-46: Vertical movements of haddock *Melanogrammus aeglefinus* and cod *Gadus morhua* in the N.W. Atlantic Ocean related to time of day. (After BEAMISH, 1966; redrawn.)

1966; PEARCY and LAURS, 1966). They are present at lower densities than the organisms described in the earlier sections, ranging perhaps from 1 per 20 m^3 (BLAXTER and CURRIE, 1967) to 1 per 650 m^3 or even less (HERSEY and BACKUS, 1962; PEARCY and LAURS, 1966). The most common species are myctophids, for example of the genera *Diaphus*, *Lampanyctus* or *Tarletonbeania*, or melanostomatids such as *Tactostoma* (PEARCY, 1964).

Light intensity as a controlling factor has already been mentioned in the work of BLAXTER and CURRIE (1967) who were able to modify or initiate vertical movements by the use of artificial lights off the Canary Islands. CLARKE and BACKUS (1964) measured the light at different levels during dusk and dawn and found a fairly close correspondence between isolux lines (isolumes) of 10^{-1} to 10^{-5} μW/cm^2 and movements of various layers between 50 and 450 m (Fig. 2-47). There was a

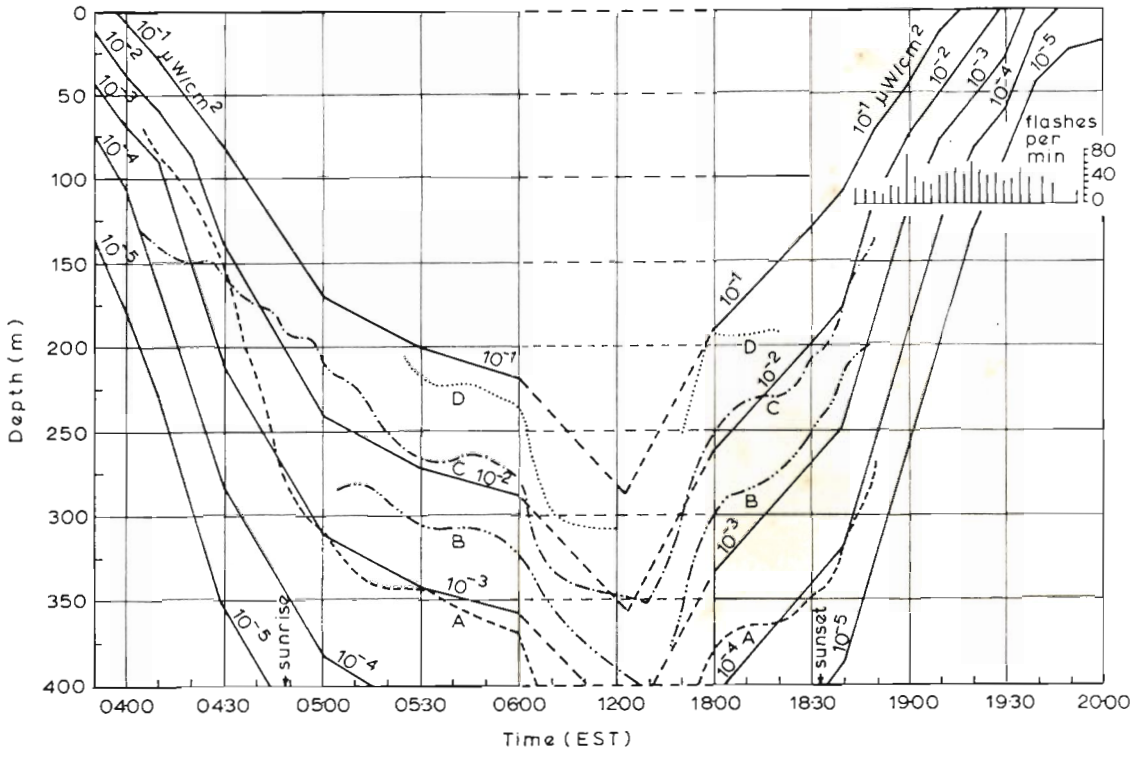

Fig. 2-47: Movements of acoustic scattering layers (A to D) at dawn and dusk, related to isolumes of downwelling natural light. From 18·45 to 19·55 the frequency of flashes of bioluminescence is given at 115 m. (After CLARKE and BACKUS, 1964.)

tendency to 'hunt', in that the layers seemed alternately to over- and under-compensate for the changes of light as they moved vertically. These authors used a photometer with a wide spectral response from 320 nm to 650 nm with a peak at 480 nm. CLARKE (1966) found that lantern fish concentrated at a level of less than 10^{-6} μW/cm^2. BODEN and KAMPA (1967), using a photometer equipped with remotely-controlled interference filters, found a rather precise following of an isolume when light of a particular wavelength (474 nm) was measured. Other evidence for a light effect has been reported by DIETZ (1962) who found that the moon had a modifying influence on the depth of a scattering layer in the eastern Pacific.

Theories of function and mechanism of vertical migration. In view of its diversity, to attempt a single explanation for vertical migration is difficult. The range of

movement varies from a few metres in some flatfish to perhaps 400 m in mesopelagic species. Light, temperature, age and season, as well as depth, have modifying influences of various sorts. Without doubt the exploitation of more than one environment within each day has potential adaptive value. It may provide more variety in food supply, or the differences in the velocity and direction of the current may play a part in horizontal distribution. JONES (1965) has advanced the thesis that apparently orientated horizontal migrations could be explained by passive drift and selective vertical migration in relation to tidal and other currents, as has already been mentioned for elvers of *Anguilla anguilla*. Passive drift by herring in tidal currents has been observed, and it is now generally accepted that fish cannot orientate to a current out-of-sight of some fixed reference point or out-of-contact with the sea bed.

Vertical migration has often been considered as a regular movement to the surface in order to feed and especially as the following of prey species upwards to the surface layers at dusk. The credibility of hypotheses relating vertical migration to feeding rests on a consideration of the relative vulnerability at the surface and the depths by night and day. It may be assumed that the night is the safest time for filter-feeding herbivorous prey species and also that their food is only available near the surface. Possibly a downward movement by day permits them to reduce their density, and therefore vulnerability, because they can take up a greater range of vertical distribution. Predatory fish (or zooplankton) will then find their food supply at its highest concentration by night at the surface. As many of these species are 'visual' feeders they will have a limited period at dusk and dawn during which they can feed.

Why do the predators not continue to feed in the depths by day? While it is certainly true that peaks of feeding occur at dusk and dawn, some feeding also continues by day, presumably at depth. This lower level of feeding may be partly due to the reduced density of the prey and, in the case of predators which are themselves prey species, e.g. herring, due to the need to retain school formation as a safety measure. What is quite clear is that light is adequate for visual feeding during the day down to substantial depths, for example over most of the North Sea (BLAXTER and PARRISH, 1965); it is sufficient for herring to feed and to be fed on. Why do not many of the prey species stay in the region of the surface by day instead of making vertical downward movements, wasteful in a metabolic sense, in order to feed at a low level on poor densities of food? Is the surface more vulnerable by day than the depths? As already stated, in terms of light intensity there is adequate light in the North Sea for predation at any depth during the day. A few metres below the surface larger prey species, such as clupeoids, are secure from diving sea birds. If they were to make no vertical migration at dawn such prey species would be in a concentrated stratum near the sea–air interface and therefore vulnerable to searching predators. In practice, however, they often move down and form vulnerable concentrations at the sea–sea bed interface. It may be that silvery-sided fish, at any rate, are safer at depth because there the light is more homogenous in its distribution and the requirements for maximum camouflage are met (p. 271). The critical dusk and dawn periods, when feeding is at a maximum, are only safe, or relatively safer, if the planktonophage fish can continue to feed after, or start to feed before, their own predators. In fact, the relative

visual powers of predator and prey are vital for survival at all levels of the food chain.

Other somewhat isolated explanations for vertical migration have been given which cannot be generally applicable. Often the bottom water is cooler and metabolic demands might be reduced there during an inactive, daytime phase. Nevertheless, the energy expended in vertical movement at dusk might well cancel out this credit balance. KALLE (1965) speculated on the possibilities of the oxygen level becoming limiting in a school, causing an explosive vertical movement when the % saturation level became too low. However, rapid horizontal movements would be equally effective. As an explanation for regular movements it seems hardly applicable.

Vertical stratification of fish might be a means of reducing both intra- and inter-specific competition. There is some evidence (p. 262) that different size-groups of a species may vary in their distribution, preventing both competition for food and even cannibalism. In this context the possible role of vertical migration as an epideictic device (WYNNE-EDWARDS, 1962) is relevant. The concentration of a species into a thin surface stratum at dusk could provide a means of 'testing' population density and lead to compensating reactions to maintain an optimum density, and would be especially valuable in zooplankton or fish species where the daytime depths showed a very wide stratification.

Accepting, from the earlier evidence, the role of light in controlling migration, it is possible to speculate on another potential advantage of vertical movements at dusk. If any weight can be attached to ALI's (1959) suggestion that fish may undergo a period of night blindness, because light falls more rapidly at dusk than the eye can compensate for, a vertically upward movement would prolong the dusk period (and a downward movement at dawn, the dawn period), perhaps preventing this temporary loss of visual ability.

While the evidence conflicts about the closeness with which fish can follow a particular light intensity to the surface, in some cases it seems to be very precise. It is of interest to speculate (BLAXTER, 1968c) how good the brightness discrimination of fish must be to appreciate, as they move vertically and dusk falls, whether it is getting brighter or less bright as they reach different levels. Unfortunately brightness discrimination in fish (p. 219) has been rather inadequately studied for the scope of this discussion. Such evidence as exists suggests that the increment of brightness (ΔI), which can just be discriminated from the ambient level (I) on simultaneous presentation, is related to I as a constant fraction ($\Delta I/I$ or Weber's fraction—usually given as a percentage) only over a very limited range of brightness. Values for Weber's fraction in fish vary from 0·06% to 100% or more depending on the species and level of ambient brightness (Table 2-17). Values from 5% to 30% are common. What values of $\Delta I/I$ must obtain for the appreciation of vertical test migrations of different amplitude? The results of calculations for different turbidities (Chapter 6) are given in Fig. 2-48. The increase in brightness for quite small movements of 1 m or 5 m is considerable even in clear oceanic water. Assuming a Weber's fraction of around 10%, that is an ability to perceive an increase in brightness of 10% from the ambient level, a fish would need to move less than 1 m in coastal conditions and only 2 to 3 m in the ocean. Should discrimination only be possible with a change of 100%, that is a doubling of the initial brightness,

a coastal fish would have to move 5 m or less and an oceanic fish 10 to 15 m in order to perceive this. Appreciation of brightness in these circumstances is from consecutive stimulation, hence these calculations are entirely speculative. It can be seen how the logarithmic attenuation of light with depth assists brightness discrimination by giving rather large changes over short distances; this should reduce any 'hunting' (over-compensation) during ascent and descent at dusk and dawn.

The powerful potentialities of appreciating changes in pressure (Chapter 8) may

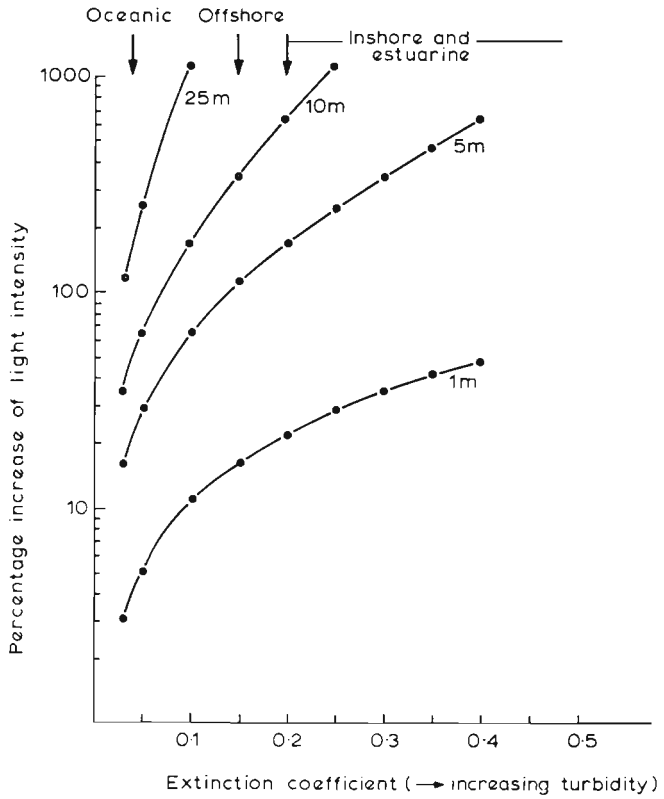

Fig. 2-48: Percentage increase of light intensity for a 1 m, 5m, 10m or 25m 'test' migration, related to the turbidity of the water. (Original.)

also have a modulating effect on any form of vertical movement. Apart from the gross limitations set by expansion of the swim bladder, recent experiments (McCUTCHEON, 1966) have shown how extraordinarily responsive some teleosts are to very small pressure changes. In 12 species of teleosts, responses (subjectively assessed by 'yawning' and erection of the dorsal fin) were made to changes of about 2·0 cm of water. In the pinfish *Lagodon rhomboides* and Black Sea bass *Centropristes striatus*, there seemed to be a sensitivity to less than 0·5 cm of water with a reaction time of about 0·1 sec. A subsequent latency probably prevents reaction to short-term changes of pressure as would be caused by waves.

Diurnal variations in catches by trawl. These are of great importance both in the economics of fishing and in the attempt to assess abundance of stock. The subject has been reviewed by PARRISH and co-authors (1964) and WOODHEAD (1966); much of it is summarized in Table 2-24. A general tendency is seen for catches of various gadoids, *Clupea harengus* and *Sebastes marinus* to fall at night, except in the clear water of the Faroe Islands. In general, flatfish—with the exception of *Pleuronectes platessa*—are caught in greater numbers by night. The differences in catch may be due to: (i) Changes in activity associated with burying behaviour (flatfish), feeding (*Pleuronectes platessa*), spawning (*Gadus morhua*, *Clupea harengus*) or vertical migration (many species); (ii) diurnal changes in ability to avoid the trawl; (iii) diurnal changes in the herding ability of parts of the trawls. Almost certainly the main reductions by night are due to fish leaving the sea bed. In the case of flatfish such as *Solea solea*, and sometimes in *Pleuronectes platessa*, movement may be only just off the bottom from a daytime position buried in the sand, leading to higher catches by ground trawl. The greater ability of some species to avoid nets by day may be compensated for, in terms of catch, by the greater herding ability of the warps and peripheral parts of the net. At night less efficient avoidance, but poorer herding, may to some extent cancel each other out. The poor day catches in the clear waters of the Faroes in the absence of a marked diurnal vertical movement may be due to avoidance of the net by day.

Day/night differentials are often greater in young fish. This seems true of some flatfish, and for *Gadus morhua*, *Melanogrammus aeglefinus*, *Pollachius virens*, *Merluccius merluccius* and *Clupea harengus* (PARRISH and co-authors, 1964; WOODHEAD, 1964) and suggests that varying ranges of distribution for different age groups of a species help to reduce competition. The extent to which this is an artificial factor brought about by sampling methods, for instance different mesh selection factors or escape through other parts of the net by day and night, is not certain.

Horizontal distribution

Rheotropism. The ability to maintain position in a current or to swim against it, rheotropism, is due to either visual or tactile stimulation and does not occur out-of-sight of stationary reference points or out-of-contact with the bottom. The action of a current can be simulated by moving a background of stripes past a fish in static water, the optomotor or pseudorheotropic response. This response has been used to measure swimming abilities. JONES (1963) worked on a number of marine species including *Clupea harengus*, *Gadus morhua*, whiting-pout *Gadus luscus*, weaver *Trachinus vipera* and some flatfish, finding that the first 4 mentioned and also *Osmerus eperlanus* responded to background movements equivalent to water velocities of 1 to 2 cm/sec. The response has also been used to study the visual abilities of fish (p. 274). For instance GRÜNDFEST (1932a, b) measured spectral sensitivity in *Lepomis* and WOLF and ZERRAHN-WOLF (1935–36) and CROZIER and WOLF (1940) flicker–fusion frequency in *Lepomis* and *Fundulus*, while STEINBERG (1961) assessed the visibility of model nets by their optomotor effect.

Navigation. Some species of fish have the ability to maintain a compass direction using the sun as a reference point. This demands a time as well as a directional

Table 2-24

Diurnal variations in catch by bottom trawl (Original)

Species	Area	Season	Catch higher Day	Catch higher Night	Ratio	Author
Gadus morhua (cod)	N. Norwegian coast	January–March	√		av. 2:1	WOODHEAD (1964)
	Faroe Islands	April		√	4–5:1	JONES, R. (1956)
	E. Scottish coast	November, January	√		2–3:1	PARRISH and co-authors (1964)
	W. Scottish coast	April–October	√		2–3:1	BAGENAL (1958)
	St. Lawrence, Cape Breton	All year	√		av. 1·9:1	BEAMISH (1966)
Melanogrammus aeglefinus (haddock)	Barents Sea (Skolpen Bank)	November	√		av. 4:1	WOODHEAD (1964)
	Barents Sea (N. Deeps)	November		√	av. 2:1	WOODHEAD (1964)
	N. Norwegian coast	January–March	√		av. 2·8:1	WOODHEAD (1964)
	Faroe Islands	April		√	4–5:1	JONES, R. (1956)
	W. Scottish coast	April–October	√		5–33:1	BAGENAL (1958)
	E. Scottish coast	All year		√	1–10:1	PARRISH and co-authors (1964)
	North Sea area	December–February	√		2–5:1	PARRISH and co-authors (1964)
	Sable–Emerald Banks	All year	√		av. 1·2:1	BEAMISH (1966)
	Cape Breton	All year	√		av. 1·5:1	BEAMISH (1966)
Merlangius merlangus (whiting)	W. Scottish coast	April–October	√		2–17:1	BAGENAL (1958)
	North Sea area	All year		√	1–3:1	PARRISH and co-authors (1964)
Pollachius virens (coalfish saithe)	Iceland and Norway	November–March	√	√	depending on age	SCHMIDT (1955)
	N. Norwegian coast	January–March	√		av. 2:1	WOODHEAD (1964)
Merluccius merluccius (hake)	Irish Sea	June–December	√		2–6:1	HICKLING (1933)
Sebastes marinus (redfish)	Sable Island Bank Gulf of St. Lawrence	?	√		2·8:1	BEAMISH (1966)
Clupea harengus (herring)	North Sea	September–October	√		av. 7:1	LUCAS (1936)

Table 2-24—*Continued*

Species	Area	Season	Catch higher Day	Catch higher Night	Ratio	Author
Pleuronectes platessa (plaice)	W. Scottish coast	April–October	√		2–4:1 in 4 out of 5 expts.	BAGENAL (1958)
	E. Scottish coast	All year		√	av. 2:1	PARRISH and co-authors (1964)
	North Sea (Haddock Bank)	April–May	√		av. 1·4:1	WOODHEAD (1964)
	North Sea	All year except January, February	√		1·2–1·3:1	DE GROOT (1964)
	North Sea	All year		√	av. 1·3:1	BOEREMA (1964)
	North Sea (off Sylt)	All year	√		av. 1·4:1	HEMPEL (1964)
Hippoglossoides platessoides (American 'plaice')	Cape Breton and Sable Island	?	√		av. 1·8:1	BEAMISH (1966)
Hippoglossoides platessoides (long rough dab)	W. Scottish coast	April–October	√		2–5:1	BAGENAL (1958)
Hippoglossoides platessoides and *Limanda limanda* (common dab)	E. Scottish coast	All year		√	av. 4:1	PARRISH and co-authors (1964)
Limanda ferruginea (yellowtail)	Sable Island and Emerald Bank	?		√	av. 2·5:1	BEAMISH (1966)
Glyptocephalus cynoglossus (witch)	W. Scottish coast	April–October	√		up to 3:1 in 4 out of 5 expts	BAGENAL (1958)
Glyptocephalus cynoglossus (American grey sole)	Scatari Bank	February		√	av. 2·6:1	BEAMISH (1966)
Solea solea (sole)	North Sea	?		√	av. 2·6:1	WOODHEAD (1964)
	North Sea	All year		√	about 10:1	BOEREMA (1964)
Microstomus kitt (lemon sole)	E. Scottish coast	All year		√	av. 3:1	PARRISH and co-authors (1964)
	Faroe Islands	April		√	20:1	JONES, R. (1956)
Pseudopleuronectes americanus (winter flounder)	Bay of Fundy	November		√	av. 1·4:1	BEAMISH (1966)

sense, for these compass directions can be maintained regardless of time of day.

The training experiments pioneered by HASLER and his associates (HASLER and co-authors, 1958; BRAEMER, 1960; HASLER and SCHWASSMANN, 1960; BRAEMER and SCHWASSMANN, 1963; HASLER, 1966) on the centrarchid *Lepomis gibbosus* and *L. macrochirus* and cichlids such as *Aequidens* yielded the following results: (i) The

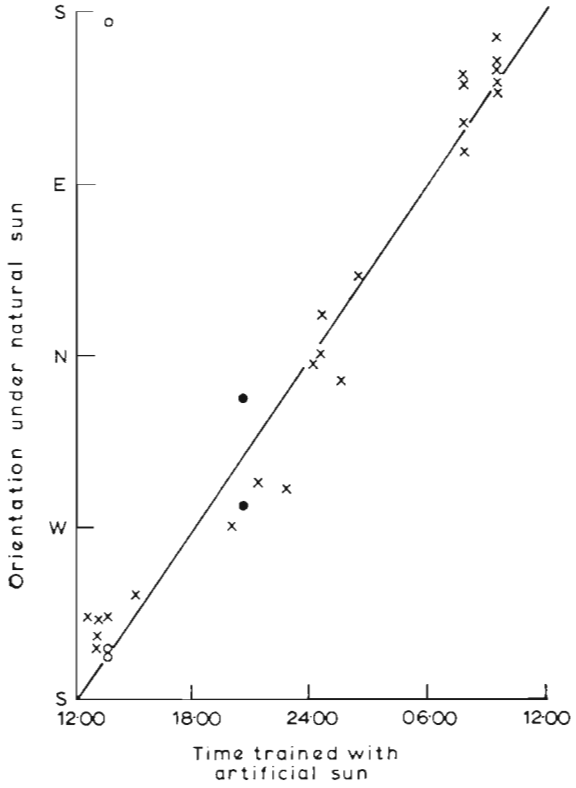

Fig. 2-49: Fish trained to swim towards an artificial sun at the times shown on the abscissa, swam in the direction indicated on the ordinate when subjected to natural sunlight not at the training time. × sunfish *Lepomis gibbosus*; ○ cichlid *Aequidens portalegrensis*; ● salmon *Oncorhynchus kisutch*. Note how a compass direction can be maintained at night. The diagonal represents an azimuth change of 15°/hr. (After BRAEMER, 1960; redrawn.)

ability is lost in overcast conditions. (ii) Artificial lights can be used instead of the sun. (iii) Gradual changes in photoperiod (time of 'dusk' and 'dawn' under artificial light conditions) are compensated for by the fish so that the compass direction is modified appropriately on subjection to the natural sun again. (iv) After considerable changes in photoperiod, followed by exposure to the natural sun during the 'night', fish (in the Northern Hemisphere) orientate as if the sun continued to move clockwise during the night (Fig. 2-49). (v) Experiments at the

equator show that fish can be trained there despite the differences in the movements of the sun which change twice per year from a clockwise to anti-clockwise direction. Compensation for this may require a few weeks. The changes in the azimuth of the sun (its compass bearing) may also be very small, though altitude (sextant angle) varies greatly. Altitude may be used by fish at the equator as well as azimuth and here compass bearings can be maintained until the sun is within about 5° of its zenith position. Of fish trained away from the equator and then transported there, *Lepomis* could maintain the appropriate compass direction in the forenoon but not in the afternoon. Cichlids tended to move in compass directions at equal angles on either side of the sun. It seems that transported fish will tolerate the 'wrong altitude' at least to some extent. (vi) In the Southern Hemisphere fish can be trained to allow for the sun moving anti-clockwise, though *Lepomis* transported there after training in the Northern Hemisphere behaved as if the sun were moving clockwise. (vii) Rearing in artificial light followed by training suggests that *Lepomis*, which is indigenous in high latitudes of the Northern Hemisphere, has an innate compensation for clockwise movement of the sun, while the equatorial cichlids have to learn either a clockwise or anti-clockwise movement. This seems a logical adaptation to the characteristics of the sun's movement at the different latitudes.

Sun–compass orientation requires remarkable perception if it is to be exact. For instance, the rate of change of azimuth of the sun is not constant at 15°/hr (Fig. 2-50). When using this ability over a long period, or over long distances, a fish might have to contend with changing daylength, changing altitude (with change of latitude) and even a change from clockwise to anti-clockwise movement of the sun between the Tropics.

Three facts must be emphasized. In the first place, with the exception of BRAEMER's (1960) work on *Oncorhynchus kisutch*, these training experiments have been done on non-migratory species. Secondly, all they have done is to show that an ability to orientate exists, but not that it is used. Thirdly, they point to an ability to maintain a compass course using the sun, but not to navigate. That is, there is no suggestion that fish could locate their position on the earth's surface by a true coordinate type of navigation.

Some evidence is now accumulating of the possibility of sun-orientation in the 'field'. HASLER and co-authors (1958) found that tagged white bass *Roccus chrysops* in Lake Mendota could return to their spawning sites if displaced. Fish released with floats attached moved generally northwards on clear days, but at random on overcast days or if their eyes were covered with caps. WINN and co-authors (1964) studied the diurnal movements of Bermudan parrot fish *Scarus*. Adult fish released with floats and tracked were mainly found to swim in a southeast direction. Comparisons were made of orientation on overcast days and at night, and also using fish with opaque eyeshields or subjected to a delayed photoperiod. The results supported the hypothesis that the sun was being used as a reference point. DE VEEN (1967) collated information on the direction of swimming of soles *Solea solea* at night in the southern North Sea and found they were only at the surface when the tidal streams were heading between northeast and south. The preference for easterly tidal currents seemed to be related to the lack of cloud cover, suggesting celestial cues might be operating. BRETT and GROOT (1963) and GROOT (1965)

described observations on young *O. nerka*, which migrate from lakes in early spring, in diurnal pulses at dusk and dawn. Using traps, sonar and observation by eye from high ground, it was noted that the fish seem to maintain a compass course down the lake well clear of the shore line and apparently not related to any hydrographical

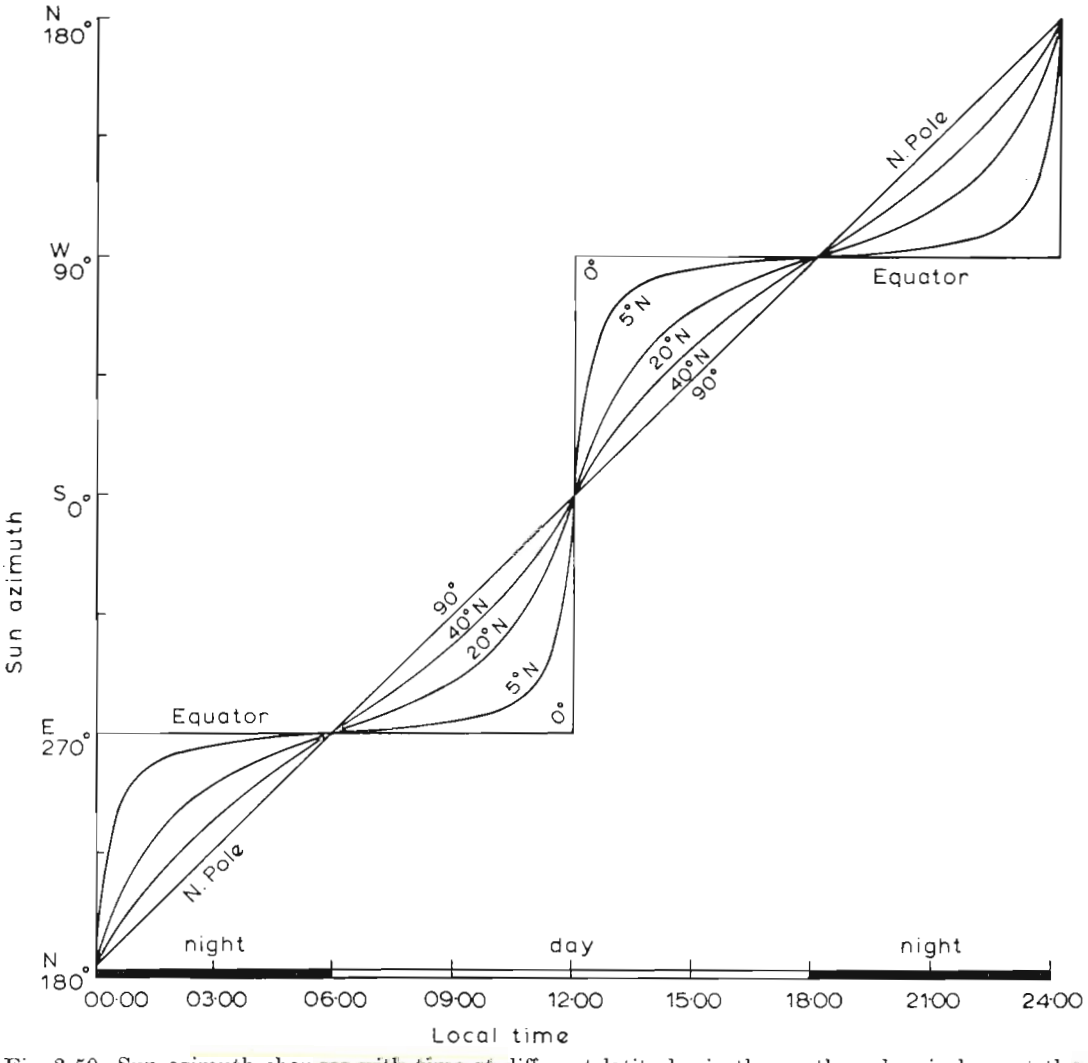

Fig. 2-50: Sun azimuth changes with time at different latitudes in the northern hemisphere at the equinox. (After BRAEMER, 1960; redrawn.)

features. The rates of movement, 4 to 5 miles per day, are small, yet there is here an indication of a sun-orientation mechanism. More direct evidence is to be found in experimental octagonal or circular tanks where this species exhibited a 'migration restlessness' similar to that of migratory birds. Using techniques developed on birds, such as altering the position of the sun with mirrors and making comparisons between overcast and sunny days (but not using training) the conclusion was reached that the sun was acting as a reference point and, with a

time sense, a compass direction was maintained in tanks which was related to the normal direction of migration. This direction could be maintained to some extent with up to 70% cloud cover, a subsequent increase in ability with greater cloud cover indicating another unknown mechanism coming into play. Use of polaroid filters and observation on orientation under blue sky out of sight of the sun suggested that polarized light as a factor could not be ruled out.

Whether salmon in the open sea might use such a mechanism was questioned by SAILA and SHAPPY (1963) who developed a 'numerical probability' model to explain the return of salmon to the west coast of America from their feeding grounds in the Pacific. Allowing a return distance of 1000 miles, a maximum time limit of 175 days and a cruising speed of 2·5 mph in the ocean and 1·25 mph along the coast, they concluded that about 37% of fish could return to their home river by means of random movement with only a small element of orientation. This value is considerably higher than the 10 to 20% return of tagged fish, though, of course, such fish are subject to predation and tag shedding. These authors pointed out that too good an orientation or compass course would lead to deflection by ocean currents. PATTEN (1964) criticized this model on the basis of the severity of some of the constraints and the lack of its relation to salmon biology. Nevertheless, developing a different model of search behaviour, he came to a similar conclusion! JONES (1965) is another author who has suggested that migration may be less strictly orientated than had earlier been supposed. The value of selective vertical migration and the utilization of currents and tides has been discussed earlier (p. 259). Sun-orientation at sea seems feasible because light can retain a directional component underwater despite the effects of refraction and turbidity which tend to reduce this. JONES (1968) has recently discussed the problems of sun orientation from the point of view of the underwater light environment. Both refraction at the surface and scattering make it more difficult to appreciate altitude and azimuth of the sun. The ability of a fish to discriminate differences in brightness in different directions is of major importance for sun orientation. Assuming that fish have an ability to discriminate brightness similar to that of man and that the azimuth must be correct to $\pm 20°$, JONES calculated that fish could appreciate azimuth to a depth of 54 m in a lake in the Columbia River and to depths of 129 to 172 m in the Sargasso Sea, 23 to 30 m off Woods Hole, 33 to 44 m in Crystal Lake, Wisconsin, 2 to 12 m in Lake Mendota (USA) and 10 to 13 m in Lake Windermere (UK). Generally speaking, in clear water with a smooth surface, fish should be able to detect both azimuth and apparent altitude of the sun to 6° at depths of 5 to 10 m. The sun is unlikely to be usable as a reference point at depths where the light has fallen to 0·1 to 0·01% of the subsurface value. HENDERSON (1963) analyzed the patterns of glitter and twinkling underwater, both theoretically and from diving and surface observations, and concluded that while fish might lose some precision in determining the position of the sun compared with terrestrial animals, other cues were available underwater which might be of use in sun orientation. WATERMAN (1961b) showed there was considerable polarization of light transmitted across the sea surface and in view of GROOT's (1965) report of polarization affecting orientation in 'migration restlessness' and the presence of a birefringent adipose eyelid in some species (STEWART, 1962) this cannot be ruled out as another factor.

(3) Structural Responses

(*a*) *Size*

No data have come to the reviewer's attention which would indicate direct effects of light on body size.

(*b*) *External Structures*

There is no information available concerning direct light effects on external structures such as shape of fins, dermal differentiations, etc. Adaptive colouration is dealt with under '*Internal Structures*'.

(*c*) *Internal Structures*

Vertebrae and fin rays

Light, at least experimentally, affects counts of vertebrae and fin rays, perhaps by altering the relative speed of growth and differentiation. Some results are given in Table 2-25.

Table 2-25

Effect of light on meristic characters (Original)

Species	Stage treated	Meristic character	Effect of light	Author
Gadus morhua (cod)	?	Vertebrae	? Bright light reduces average	Dannevig (1932)
Leuresthes tenuis (grunion)	1st month	Vertebrae	Bright light reduces average	McHugh (1954)
Oncorhynchus nerka (sockeye salmon)	Embryo	Vertebrae; anal fin rays	Longer duration of light per day decreases average	Lindsey (1958)
Oncorhynchus nerka	Embryo	Scales; fin rays	Brighter light or longer duration decreases average	Canagaratnam (*in*: Eisler, 1961)
Oncorhynchus tshawytscha (chinook salmon)	Embryo 8–13 days old	Vertebrae; dorsal fin rays	Lower average at 370 mc than at 0·2 mc or 1500 mc	Eisler (1961)
Salmo salar (Atlantic salmon)	Embryo	Vertebrae	Lower count in total dark or full light than in partial dark	Vibert (1954)

Adaptive colouration

Lack of colouration in most fish larvae and in some of the polar 'ice fish' (Chaenichthyids) may well be an adaptation for camouflage. More often adults are adapted by other devices, either to the background of the bottom or the water itself.

Chromatophores. Apart from simple countershading as found in some elasmobranchs, fish may adapt themselves closely to the background or substrate. This is especially true of flatfish. The processes of colour change have been reviewed by PARKER (1948) and ODIORNE (1957) and it is not intended to do more here than summarize the results and describe the more recent developments.

The numbers of chromatophores may change with long-term alterations in light. On the other hand short-term changes, which last from a few seconds to a matter of minutes, are brought about by pigment dispersion giving a darkening effect, or aggregation causing a lightening of the body. The effect of various experimental treatments on teleosts may be summarized as follows: (i) Removal of the pituitary generally causes pallor, which is thought to be due to absence of intermedin, a hormone causing dispersion of the pigment in the chromatophores. (ii) Injection of adrenalin gives pallor. (iii) Removal of the eyes causes darkening. (iv) Interruption of the nervous supply often causes a local darkening followed later by paling. (v) Stimulation of the nervous system gives pallor. In general a nervous mechanism might be expected to give a fast result, an endocrine mechanism a slower one.

The role of the eye in colour change is of great importance, especially in such exact adaptations as take place, for instance, in the summer flounder *Paralichthys dentatus*. Evidence from the use of eye shields in different positions over the pupil, and of rotation experiments of the eye, show that the balance between stimulation of the dorsal and ventral retina by light is the main factor for general control of colour, but presumably the pattern of stimulation on the dorsal retina must give the more detailed adaptations.

Long-term changes in colour are found in animals which show sexual dimorphism of colour or other visual features in the breeding season. Melanophores will even develop on the white ventral surface of flatfish or in pale regions of *Ameiurus melas* when light is shone from below for a considerable period. Colour abnormalities may appear in times of stress as SHELBOURNE (1963) found in rearing experiments on *Pleuronectes platessa*. A high proportion of albino or semi-albino fish occurred in crowded tank conditions, especially amongst the smaller specimens.

In cyclostomes the pineal or the associated areas of the diencephalon are responsible for diurnal changes of colour, that is paling by night and darkening by day. In elasmobranchs the changes of colour are slow and under hormonal control; they are similar to those of teleosts in that hypophysectomy causes pallor, and blinding leads to a darkening of the body.

Reflecting layers. The recent reports of DENTON and NICOL (1965a, b) on the silvery sides of *Alburnus alburnus*, *Trachurus trachurus* and *Clupea harengus*, and later DENTON and NICOL (1966) on some other species, describe 2 kinds of reflecting layers, an argenteum containing long, thin guanine crystals whose reflecting surfaces are parallel to that of the adjacent body surface, and a layer of crystals on the inner surface of the scales, or in the subdermis, where the orientation of the crystals varies. The reflecting surfaces of these crystals vary with the position of the scale on the flank, so that they tend to lie always vertical. This gives a mirror effect to the side of the body, an effect which is not disturbed by the lateral curvature. So long as the light from the surface is homogeneously distributed from all points of the compass, a mirror hanging vertically will provide the best

camouflage against the background from whatever angle it is viewed (Fig. 2-51) because the light reflected is seen against similar light coming from the background. The fish have, so-to-speak, inserted small vertical mirrors at all points in their flanks to give the reflexion effect. This describes the phenomena only in very simple terms; the argenteum layer, for instance, seems to play a part in increasing reflectivity at near-normal angles of incidence, while the reflecting layers in the scales may be effective only when there is a considerable overlap and a precise spacing of the crystals, because interference phenomena are involved. The back of the fish is usually black to prevent reflexion of downwelling light while the ventral

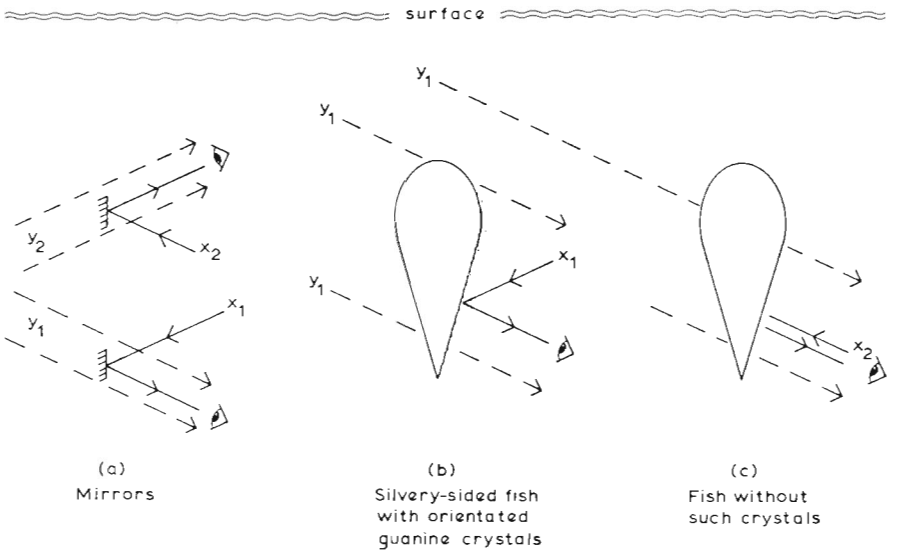

Fig. 2-51: Comparisons between reflected and background light: (a) for mirrors; (b) for a silvery-sided fish with orientated guanine crystals; (c) for a fish without such crystals. On the assumption that the distribution of light intensity is symmetrical with regard to azimuth, reflected (x_1, x_2) and background (y_1, y_2) light will be similar where a vertical reflecting surface is available. In (c) where this is not so, the flank of the fish will appear darker compared with brighter background light (y_1). (After DENTON and NICOL, 1965a; modified.)

surface is keel-like, presumably as an adaptation to reduce a silhouette effect. The downwardly-directed photophores of some deep-sea fish might also be an adaptation to reduce silhouetting if the light from the photophores matches the ambient light.

It should be stressed that this adaptation to the background will be somewhat less effective when the light impinging on the fish is not homogenous in its distribution. Refraction and scattering reduce the directional effects of the sun; presumably, however, the light will be least directional near the surface at dusk or dawn with clear skies and clear water. Vertically migrating fish often arrive at the surface after sunset and leave before sunrise and could be considered as avoiding places where they might be more conspicuous than usual. The seeming paradox between this high degree of inconspicuousness and the need for visual contact in schooling has already been discussed (p. 231). It might be mentioned again, however, that because light will be less homogeneously distributed at dawn the

reforming of schools may be aided by the somewhat poorer camouflage effect at that time. The bottom may be safer by day because homogeneity of light distribution increases with depth.

Exceptions or unexpected phenomena are common in biological observation. HOBSON (1963), for instance, reported that in mixed schools of flat iron herring *Harengula thrissina* and anchovetas *Cetengraulis mysticetus*, the latter were much more conspicuous by reason of their distended opercula. The stomach contents of predators apparently confirmed a selective predation on the anchoveta.

DENTON and NICOL (1965c) also measured the amount of polarized light reflected from *Alburnus alburnus*, finding it rather small. Whether the birefringent adipose eyelid could be acting as an analyzer for detecting polarized light coming from other members of the school must remain an open question until other species have been examined. The birefringent eyelid may have another function, at least in those species where it filters light entering the eye (LYTHGOE and HEMMINGS, 1967). Recent underwater observations using polaroid filters over the human eye have shown that the resultant reduction of the polarized component of scattered light increases the range of vision and enhances the contrast between an object and its background.

Dark–light visual adaptation

Light may affect various internal structures such as the pupil, retinal masking pigment and pigment in the tapetum. The changes in these, together with the presence of visual cells of various sensitivities, endow the eye with great flexibility and it can appreciate light varying in intensity over 10^{12} units. The main change-over is during the process of dark- and light-adaptation when the visual process is transferred between the cones and rods of the duplex retina. The characteristics of this change are shown schematically in Table 2-26.

Table 2-26
Dark–light visual adaptation (Original)

Dark-adapted	⟷	Light-adapted
Low intensity scotopic vision by rods High sensitivity More sensitive in the blue (though not seen as a colour)	⟵ Purkinje Shift ⟶	High intensity photopic vision by cones Low sensitivity More sensitive in green-yellow
No colour vision Low acuity (much summation) Low frequency for flicker-fusion		Colour vision High acuity (less summation) High frequency for flicker-fusion
	⟵ Change in many behaviour patterns (see earlier) ⟶	

Pupillary movement. This occurs (NICOL, 1963) in many elasmobranchs and in a few teleosts such as *Anguilla*, *Lophius* and *Uranoscopus*. Contraction seems to be the direct effect of light in *Anguilla* and some selachians. In the other teleosts mentioned contraction seems to be controlled by the sympathetic, and dilation by the parasympathetic nervous system. The action spectrum for contraction in *Anguilla* has a peak at 500 nm, similar to the absorption maximum for the visual pigment rhodopsin.

Retinal pigment movement. In species with a duplex retina there is a pigment migration within the outer sensory layer. In the dark-adapted state the pigment is aggregated peripherally, the rod myoids are contracted to bring the outer segments clear of the pigment, and the cone myoids are extended, taking the large cones out of the light path to the rods. In light-adaptation the pigment disperses inwards towards the lens, covering the rods which extend into it. The cone myoids contract and bring their outer segments out of the extending pigment layer (Fig. 2-52).

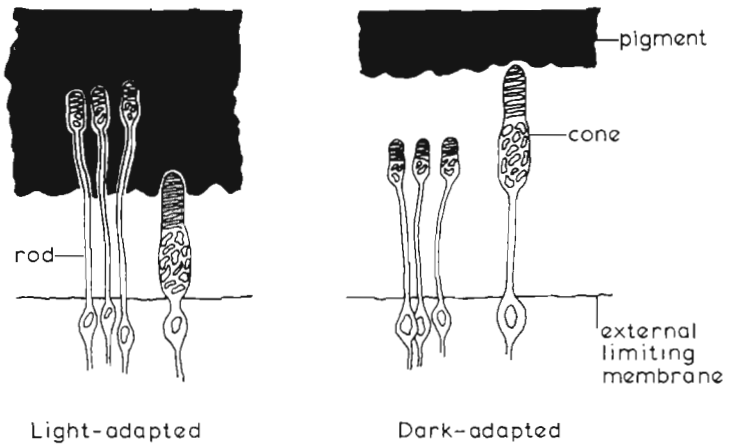

Fig. 2-52: Changes in the retinal pigment, rods and cones in the light-adapted and dark-adapted state. (Original.)

These retino-motor responses have been reviewed by NICOL (1963) and have been worked on of late by ALI (1959, 1961) in salmonids, NICOL (1965a) in flatfish and BLAXTER and JONES (1967) and BLAXTER (1968b) in *Clupea harengus* and *Pleuronectes platessa*. The responses do not occur in some larval stages, which are often without rods in the retina (ALI, 1959; BLAXTER and JONES, 1967; BLAXTER and STAINES, 1970) nor do they occur in pure-rod eyes such as those of elasmobranchs and deep-sea fish. They are also absent in the species of Dipnoi and Brachiopterygii studied (PFEIFFER, 1968). Of particular interest is the range of light intensity over which the response takes place, since this gives a measure of the light conditions when fish become dark-adapted. The results of experiments of various kinds are given in Table 2–27. The most general range of values, 10^{1} to 10^{-3} mc, may be correlated with the thresholds for many types of behaviour which have been shown to be light-limiting; it is equivalent to the change of light found at dusk or dawn.

Table 2-27

Range of intensity over which visual adaptation takes place (Original)

Species	Light intensity for dark⇌light adaptation from histology of retina	from flicker-fusion frequency	from behaviour	Author (remarks)
Engraulis encrasicholus (anchovy)	10^{0}–10^{-1}	10^{-2}	—	PROTASOV and co-authors (1960)
Clupea harengus (herring)	10^{1}–10^{-1}	—	—	BLAXTER and JONES (1967)
Trachurus trachurus (silver mackerel)	10^{0}–10^{-2}	—	—	KOBAYASHI (1957)
Sargus annularis (sea bream)	10^{-1}–10^{-2}	10^{-3}	—	PROTASOV and co-authors (1960)
Gadus morhua (cod)	10^{-2}–10^{-3}	—	—	PROTASOV (1964)
Pollachius virens (coalfish)	10^{-2}–10^{-3}	—	—	PROTASOV (1964)
Mallotus villosus (capelin)	10^{-2}–10^{-3}	—	—	PROTASOV (1964)
Hippoglossoides platessoides (long rough dab)	10^{-2}–10^{-3}	—	—	PROTASOV (1964)
Pleuronectes platessa (plaice)	10^{1}–10^{-2}	—	—	BLAXTER (1968b)
Pleuronectes platessa	10^{-2}	—	—	PROTASOV (1964)
Lateolabrax japonicus (sea bass)	c. 10^{-2}	—	—	TAMURA (1957b)
Anarhichas lupus (catfish)	10^{-2}–10^{-3}	—	—	PROTASOV (1964)
Salmo salar (Atlantic salmon)	10^{-1}–10^{-3}	—	—	ALI (1961)
Oncorhynchus spp. (Pacific salmon)	10^{1}–10^{-3}	—	—	ALI (1959)
Atherina mochon pontica (smelt)	10^{1}–10^{0}	10^{-1}	—	PROTASOV and co-authors (1960)
Leuciscus rutilus (roach)	10^{-3}–10^{-4}	—	—	ENGSTRÖM and ROSSTORP (1963)
Cyprinus sp. (carp)	c. 10^{-4}	—	—	TAMURA (1957b)
Carassius auratus (goldfish)	$>10^{0}$–10^{-2}	—	—	KOBAYASHI (1957)
Phoxinus laevis (minnow)	—	—	10^{-2}–10^{-3}	BRUNNER (1934) (from acuity change)
Phoxinus laevis	—	—	10^{-1}–10^{-2}	VON FRISCH (*in*: HERTER, 1953; loss of colour vision)
Misgurnus anguillicaudatus (loach)	10^{-1}–10^{-2}	—	—	KOBAYASHI (1957)
Fundulus heteroclitus (killifish)	—	c. 10^{1}	—	CROZIER and WOLF (1940) (using optomotor response)
Astyanax mexicanus (black-banded tetra)	—	—	10^{-1}–10^{-2}	JOHN (1964) (change in schooling)
Lepomis sp. (sunfish)	—	c. 10^{-1}	—	WOLF and ZERRAHN-WOLF (1935–1936) (using optomotor response)
Enneacanthus sp. (sunfish)	—	10^{0}	—	CROZIER and WOLF (1940) (using optomotor response)
Platypoecilus sp.	—	10^{1}	—	CROZIER and WOLF (1940)
Xiphophorus sp.	—	10^{0}	—	CROZIER and WOLF (1940)
Hybrid of the above two species	—	10^{1}–?	—	CROZIER and WOLF (1940)

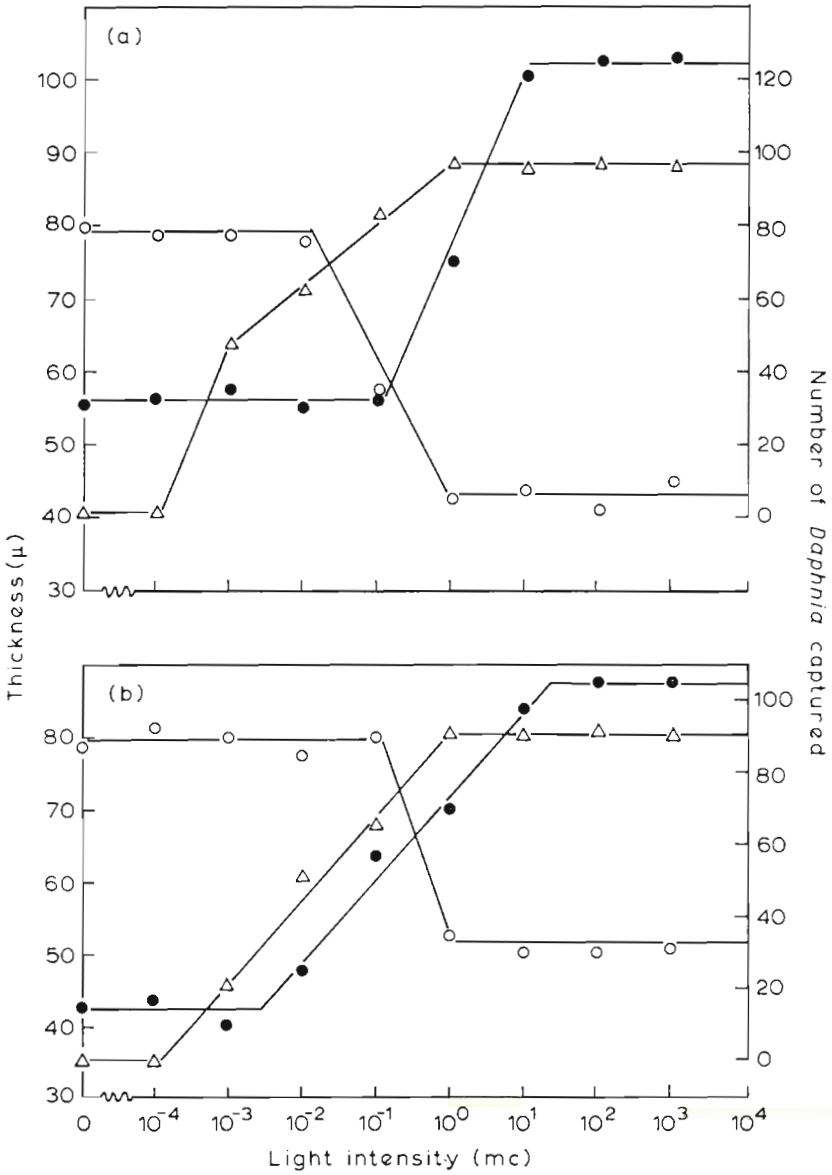

Fig. 2-53: Effect of light intensity on pigment (●), cones (○) and rate of feeding (Δ). (a) Coho smolts *Oncorhynchus kisutch*; (b) sockeye smolts *O. nerka*. (After ALI, 1959; redrawn.)

Dark-adaptation, as judged histologically, has been related by ALI (1959) to changes in behaviour such as feeding in young salmonids (Fig. 2-53). In *Clupea harengus* BLAXTER and JONES (1967) found a similar close correlation between feeding and retino-motor phenomena. The time taken for the latter to occur has been reviewed by NICOL (1963) based mainly on ALI's work. Dark-adaptation, as judged by histological measurements, takes 30 to 45 mins (range 20 to 70 mins) in salmonids. This length of time led ALI (1959) to speculate that retino-motor changes might lag behind the fall of light at dusk, leading to short periods of night-blindness. This could be of great ecological importance and requires careful study, although it seems from an adaptive standpoint to be a rather unlikely occurrence. Certainly vertical migration upwards at dusk and downwards at dawn would prolong the dusk and dawn periods and might obviate such an effect, should it occur. However, dusk and dawn periods vary greatly in length depending on season in higher latitudes and this must be taken into account when making comparisons.

The evidence for endogenous rhythms in retino-motor changes is rather equivocal. WELSH and OSBORN (1937) found no signs of such rhythms in rods and cones of *Ameiurus nebulosus* exposed to constant light; in constant dark there was a persistence for at least 2 days, but the movements were reduced in amplitude. AREY and MUNDT (1941), repeating some of this work, found a greater elongation of cones at midnight than at noon when the fish were kept in constant darkness; this effect persisted for 4 days. The pigment and rods showed less marked changes and the effect of continuous light seemed unimportant. WIGGER (1941) reported that dark-adapting *Carassius auratus* by day lead to a less marked retino-motor response than dark-adaptation by night, suggesting the modifying effect of a rhythm and pointing to the dangers of assessing retino-motor changes at times other than when natural changes of light are occurring. JOHN and co-authors (1967) later showed that the cones of goldfish exhibit a diurnal rhythm for at least 3 days in constant darkness, the amplitude of the shift decreasing after the first night. Similar results with *Lepomis macrochirus* kept in constant darkness for up to 42 hrs were reported by JOHN and GRING (1968). ALI (1961) measured pigment movements in young *Salmo salar*, finding a diurnal rhythm in constant darkness only. JOHN and HAUT (1964) observed similar changes during behaviour studies on *Astyanax mexicanus*. When dark-adapted artificially by day they schooled in 15 secs after being subjected to an intensity of 50 mc; when dark-adapted at night they required 6 mins to school when similarly illuminated, again suggesting that dark-adaptation by day is a less extreme process. It thus seems that an endogenous rhythm underlies at least some retino-motor changes, being more prevalent in continuous darkness. However, in continuous light it can be important enough to prevent complete light-adaptation at certain times. It would not seem, from the experimental evidence available, that fish are likely to be preadapted to dusk though they should be partially pre-adapted to dawn.

The control of the retino-motor changes was reviewed by ALI (1964b) who found that enucleated eyes of goldfish *Carassius auratus* and bullhead *Ictalurus nebulosus* do not show a typical response when transferred from light to dark conditions. Other authors, using similar techniques on other species, found either no response or an incomplete one. The technique itself is suspect because of the problems of

keeping the eye alive and the answer to this question of control remains open. Recently ALI and CROUZY (1968) measured the action spectrum for retinal pigment migration in *Salvelinus fontinalis*, finding maximum sensitivity at 520 nm. They related this to the breakdown of rod pigment. This gives a clue to the interrelationships within the retina.

Tapetal pigment movement. Tapetal pigment in elasmobranchs such as *Squalus* and *Mustelus* migrates in an analogous way to the retinal pigment of teleosts, with an inward dispersion of pigment over the reflecting layers following transfer to light, and an outward withdrawal and aggregation of pigment peripherally on transfer to darkness (DENTON and NICOL, 1964; NICOL, 1965b). In more benthic elasmobranchs such as *Scyliorhinus* a tapetum is present except in the ventral part of the eye and pigment migration may be slight or non-existent. Pigment migration or 'occlusion' requires about 2 hrs but there appear to be no data on the threshold range of light intensity over which it occurs. NICOL (1965b), in a comprehensive series of experiments, showed that the pigment must be an independent effector system, sensitive to light, at least in *Squalus*. No response was found following nerve section, hormone injection or extirpation of the pituitary and pineal.

The function of occlusion is presumably to protect the rods from over-stimulation due to reflection by day, and probably to reduce 'eyeshine'. Thus, the non-occlusible tapetum of *Scyliorhinus* does not extend to the ventral part of the eye where the greatest eyeshine would occur from downwelling light near the sea bed. In *Squalus* the occlusion is not complete by day; perhaps this is an adaptation to prevent the eye appearing too black and, therefore, contrasting with the grey of the surface of the head.

Visual pigments and spectral sensitivity

Rod pigments. Extraction and photochemical studies of rod pigments (visual purple or rhodopsin) have allowed speculation on the adaptive value of possessing pigments with certain spectral characteristics. Pigments are usually referred to by the wavelength where they maximally absorb light (λ_{max}) and it is assumed that this is the wavelength at which the pigment is most sensitive to light. Originally, WALD (1946, 1960) distinguished 2 main groups of pigment in the rods: (i) The rhodopsins with a λ_{max} around 500 nm, related to vitamin A_1 and found in elasmobranchs, and in many marine species such as swordfish, sea bass, sand flounder, herring, haddock and whiting; (ii) the porphyropsins with a λ_{max} around 522 nm, related to vitamin A_2 and found in freshwater species such as catfish, perch, carp, goldfish and bluegill. Later work (DARTNALL and LYTHGOE, 1965; SCHWANZARA, 1967) has shown that the original concept was too simple. For example, in 55 species of freshwater tropical fish 7 had rhodopsin based on vitamin A_2, 19 on vitamin A_1 and the remaining 29 had a mixture. There are also mixtures or changes of visual pigment in fish inhabiting fresh water and the sea at different times of their life history. In *Lampetra* there is a mixture of the 2 pigments, with porphyropsin predominating. MUNZ and BEATTY (1965) and BEATTY (1966) measured the proportions of rhodopsin (λ_{max} 503 $\pm$1 nm) and porphyropsin (λ_{max} 527 $\pm$1 nm) in 5 species of *Oncorhynchus* and 4 species of

Salmo. The proportions varied; in particular there was an increase of porphyropsin in the adults of *Oncorhynchus* during the spawning migration with a rise in vitamin A_2 in the liver. In the anadromous perch *Morone americana* the pigment is pure porphyropsin. In the catadromous eel *Anguilla anguilla* rhodopsin predominates in the freshwater phase but on migration to the sea for spawning the pigment changes to one with a λ_{max} transposed 33 nm towards the blue end of the spectrum (CARLISLE and DENTON, 1959). In fact the adult eel has pigment with a λ_{max} similar to that of the deep-sea fish studied by DENTON and WARREN (1957). Their pigments, visual golds, or chrysopsins have maximum absorption at about 485 nm.

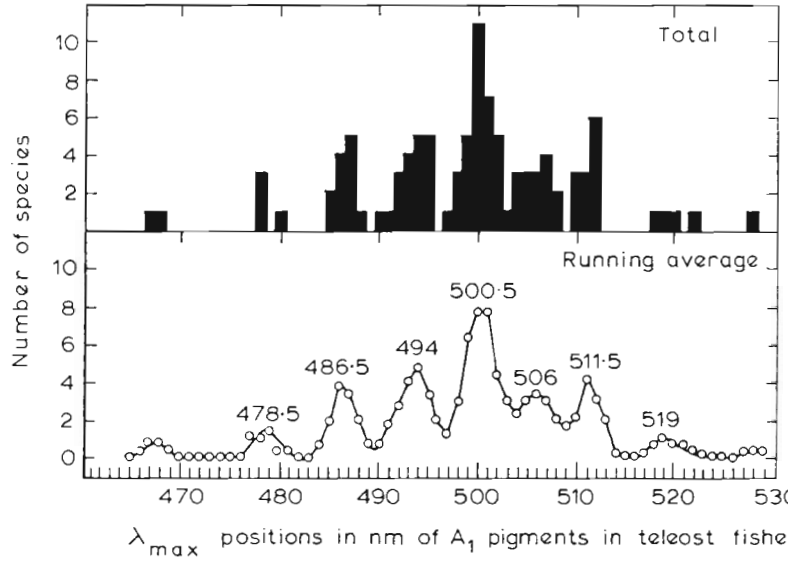

Fig. 2-54: Distribution of rhodopsins in teleosts; above as a histogram, below as a running average (obtained from the histogram by averaging the frequencies over 3 consecutive wavelengths). (After DARTNALL and LYTHGOE, 1965; redrawn.)

The idea that the λ_{max} of the visual pigment coincides with the wavelength where the water transmits light best (sometimes called λ_{min}) has to some extent stood the test of time. Thus blue oceanic water has a λ_{min} of from 470 to 490 nm, offshore shallower water transmits best around 500 nm, while further inshore or in fresh water there is a progressive increase of yellowish humic acids which act as a blue filter and shift the λ_{min} into the green or yellow. SCHWANZARA (1967) suggests that the differences in rhodopsins of freshwater fish may be explained on the basis of their distribution in terms of latitude. The spectral quality of sunlight penetrating the water will vary with latitude, the red component being reduced in the tropics; thus rhodopsins which are more blue-sensitive predominate there. That this is an oversimplified explanation appears from the work of BRIDGES (1965), DARTNALL and LYTHGOE (1965) and LYTHGOE (1966). Plots of reliable data for the rhodopsin system (Fig. 2-54) show a clustering effect with 5 or 6 main peaks.

LYTHGOE (1966) questioned more closely a simple correlation between λ_{max} of

the rhodopsin system and the λ_{min} of the environment, initially finding exceptions in the Mediterranean where the pigments cluster at 500 nm but the λ_{min} of the water is around 465 nm. The relationship he found between these characteristics is listed for different environments in Table 2-28. He showed firstly that fish would need different visual pigments near the surface compared with depth if the pigments

Table 2-28

Characteristics of visual pigments in different environments (After LYTHGOE, 1966)

Area	λ_{max} pigments (nm)	λ_{min} water (nm)
Mediterranean	493–506	465
Deep sea	478–490	485
Coastal	494–501	530
Estuarine	504–512	590

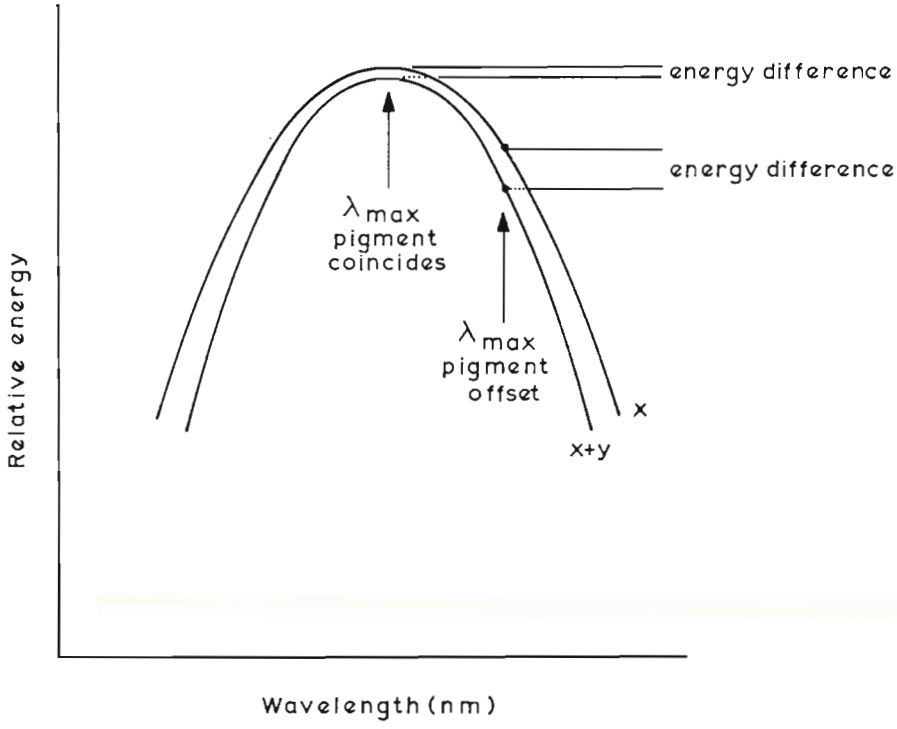

Fig. 2-55: Relative energy of different wavelengths at depth x and depth $x+y$. Energy differences between light reflected from the background (path length from surface $x+y$) and from a nearby object (path length x) are shown where maximum sensitivity (λ_{max}) coincides with the λ_{min} of the water and where it is offset. Note the contrast between background and object will be greater where the pigment is offset. (Original.)

were to be closely related to brightest wavelengths. Secondly he suggested the interesting idea that the offsetting of the λ_{max} of pigments from the λ_{min} of the sea water, although decreasing sensitivity, has the effect of enhancing contrast between objects and the background. This is explained by the difference in path length for surface light reflected by the background and by an object nearer the eye. The intensity difference, and therefore the contrast, between object and background is greater when the pigment is offset than where its λ_{max} coincides with the λ_{min} of the water. This is shown schematically in Fig. 2-55. Later experimental work in the Mediterranean (LYTHGOE, 1968) confirmed that offset pigments were more suitable for detecting small grey objects in shallow water.

Cone pigments. The density of the cone pigments is low and extraction and measurement in vitro is difficult. Most theories of colour vision require 3 types of cone with a pigment absorbing in the blue or violet, green and red. Superseded for some time by more involved explanations, the Young–Helmholtz theory has of late gained new respectability by the findings of MARKS (1965). Using an elegant microspectrophotometer technique he succeeded in measuring the absorption characteristics of the pigment in individual outer segments of the cones in the excised retina of *Carassius auratus*. He found 3 groups with maxima of pigment absorption at 455, 530 and 625 nm. TOMITA and co-authors (1967), recording from single cones in carp, found maxima at 462, 529 and 611 nm.

Spectral sensitivity. The sensitivity of the eye to different wavelengths or action spectra can often be fairly closely related to the absorption of the visual pigment. This was shown in *Lepomis* sp. by the pioneer work of GRUNDFEST (1932a, b). Using the optomotor response he measured for various wavelengths the threshold at which the response disappeared. The action spectrum had a λ_{max} at 540 nm in dark-adapted fish with a Purkinje shift in light-adapted specimens to a λ_{max} of 570 to 600 nm. Spectral sensitivity measurements using a number of behaviour criteria such as feeding, phototaxis and avoidance of a net were related to the absorption characteristics of the visual pigment in *Clupea harengus* by BLAXTER (1964).

Information on spectral sensitivity has been supplemented by electrophysiological studies of Japanese, Russian and British scientists. The results of KOBAYASHI (1962) are given in Table 2-29 and of PROTASOV (1964) in Fig. 2-56. Subsequent work has shown that the photopic curve of the goldfish is not very satisfactorily derived from a simple additive model of a trimodal cone system and that more complex interactions may be involved (BURKHARDT, 1966). HAMMOND (1968), using the plaice, found responses, using suprathreshold stimuli for cones, which had 4 components with spectral peaks at 440 to 460 nm, 470 to 490 nm, 510 to 540 nm and 560 to 590 nm. At low intensities there was a single peak at 510 to 530 nm. Electroretinograms show the Purkinje shift (except where a pure-rod retina exists, as in some elasmobranchs) and sometimes a variability of the maxima of sensitivity which can be related to the maximum transmission characteristics of the habitat. The Purkinje shift presents something of an anomaly. The photopic curve applies by day when the ambient light is extremely blue with a colour temperature of 7500° K. At dusk as the shift occurs to give maximum sensitivity of the eye more in the blue, the colour of the ambient light, now about

4800° K, changes in such a way as to give more energy in the red (colour values taken from LYTHGOE, 1966).

Table 2-29

Maxima of spectral sensitivity curves of various species determined by ERG (After KOBAYASHI, 1962)

Species	λ max Dark-adapted (nm)	λ max Light-adapted (nm)	Remarks
Elasmobranchs			
Dasyatis akajei (sting ray)	525	575	
Holorhinus tobijei (eagle ray)	525	575	
Narke japonica (electric ray)	500	500	Benthic
Raja porosa (skate)	500	?500	Deep water
Urolophus fuscus (ray)	500	525	Deep water
Mustelus manazo (dogfish)	500	?	Benthic
Teleosts			
Acanthogobius flavimanus (goby)	575	?	Littoral
Anguilla japonica (eel)	500	?	Fresh water
Argyrosomus argentatus (croaker)	500	?	Inshore benthic
Carassius auratus (goldfish)	525		Fresh water
Chelidonichthys kumu (sea robin)	500	575	Benthic
Chrysophrys major (scup)	470	525	Coastal
Cyprinus carpio (carp)	550	600	Fresh water
Dictyosoma burgeri (blenny)	600	?	Littoral
Gymnothorax reticularis (moray)	500	530	Littoral
Halichoeres poecilopterus (wrasse)	—	600	Pure cone retina; littoral
Hoplognathus fasciata	500 -600	?	Littoral
Inegocia crocodila (flat-head)	550	550	Inshore benthic
Lagocephalus lunaris (puffer)	525	?	Coastal
Misgurnus anguillicaudatus (loach)	550	?	Fresh water; hides in mud
Pseudorhombus cinnamoneus (lefteye flounder)	500	?	Inshore benthic
Scorpaenodes guamensis (rock-fish)	525	575	Benthic
Stephanolepis cirrhifer (file-fish)	—	550	Littoral; pure cone
Trachurus japonicus (mackerel)	500	?	Coastal

(4) Conclusions

An attempt has been made to relate the change in behaviour of fish to the physiology of the eye, especially to the process of dark-adaptation. A light intensity of about 10^{-1} mc, corresponding to late dusk, may be quoted as a general threshold. The importance of such a threshold in relation to season and latitude has only rarely been emphasized for fish (BLAXTER, 1966). At certain seasons in high

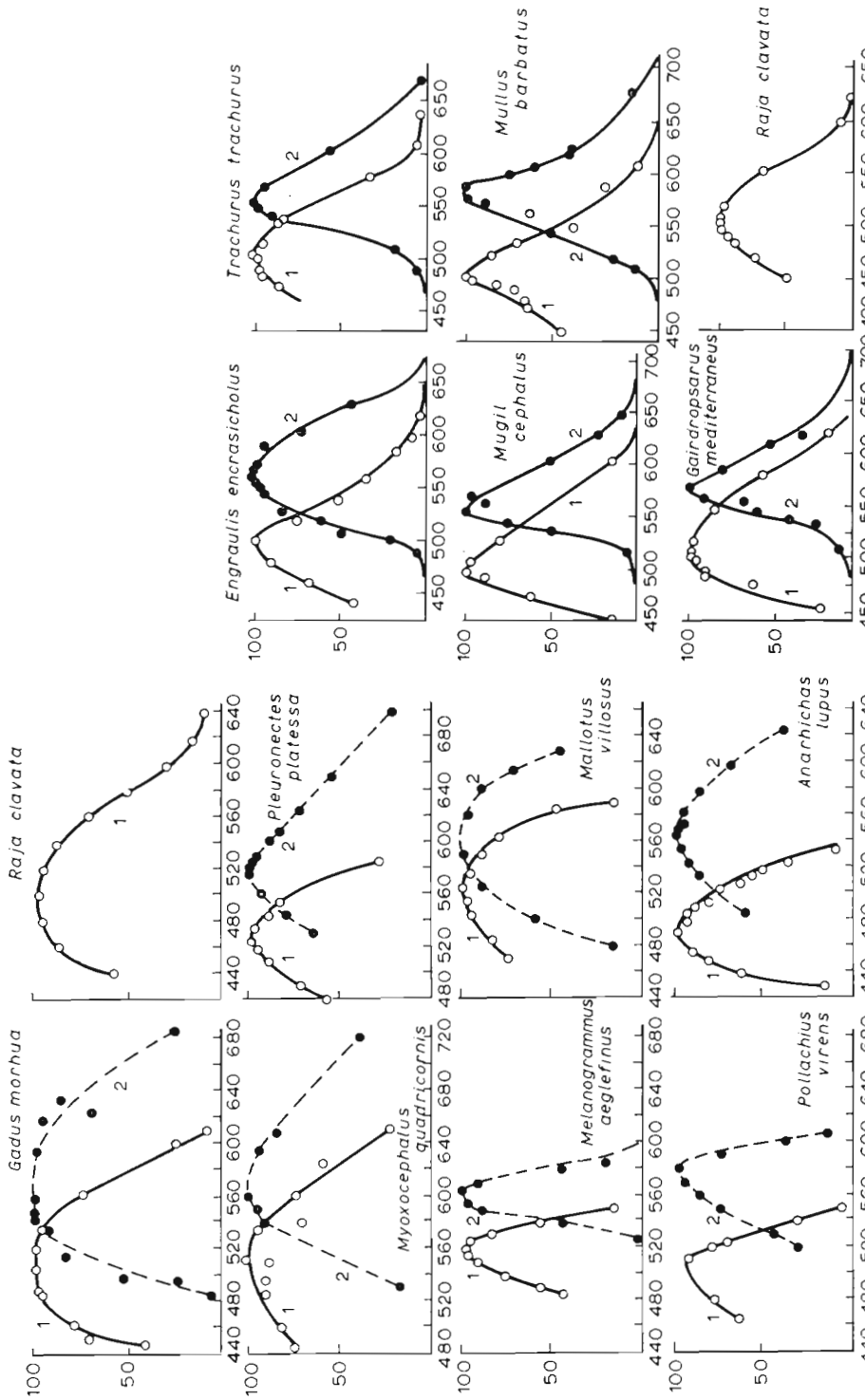

Fig. 2-56: Spectral sensitivity of various species obtained by ERG. (After Protasov, 1964; redrawn.)

latitudes some types of behaviour may not occur at all. At some times the ability to feed (and grow) may be hampered by short length of day, while at others light-limited behaviour can continue 24 hrs in each day. The hours per day during which the light intensity at the surface is above 0·1 mc are given for different

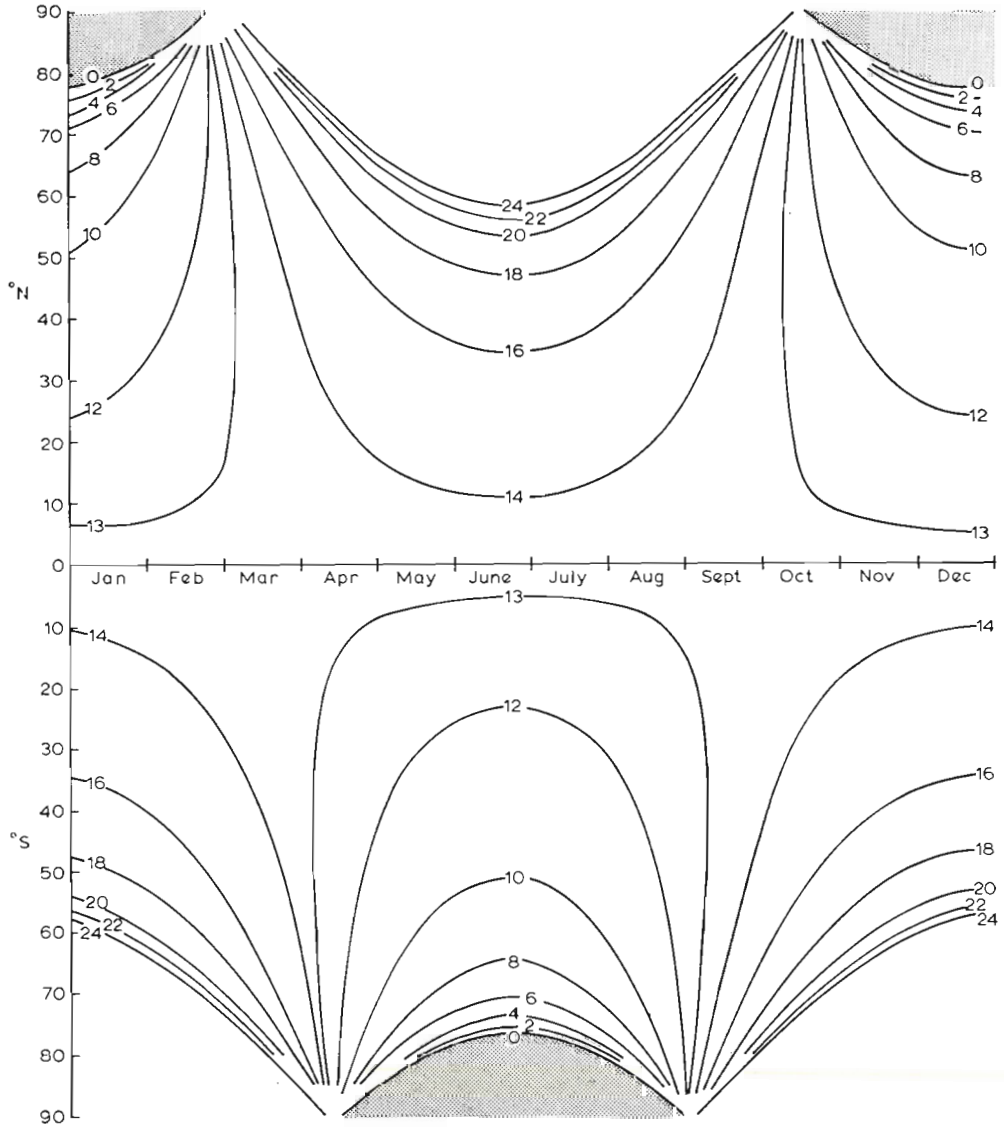

Fig. 2-57: Hours per day at which the surface light intensity is above 0·1 mc, related to season and latitude. (Original.)

latitudes and seasons in Fig. 2-57 using data from illumination charts (BROWN, 1952). The figure demonstrates the great seasonal variability of surface light conditions at high latitudes compared with the rather insignificant changes near the equator.

The importance of attenuation in varying the light still further, depending on

depth and area, is shown in Fig. 2-58. Here attenuation in different types of water is shown related to depth and to the thresholds of various kinds discussed in this chapter. As a further exercise in predicting the light environment for fish, Fig. 2-59 illustrates the areas of the N.W. Atlantic in which light on the sea bed may vary enough diurnally to cause changes in the light- and dark-adaptation of fish, and a further, deeper area still, where light is at least just above the absolute threshold on the sea bed for a time each day. This figure shows the vast areas of the ocean bed where light never penetrates from the surface, and emphasizes once again the great range of light conditions available to fish in the aquatic environment.

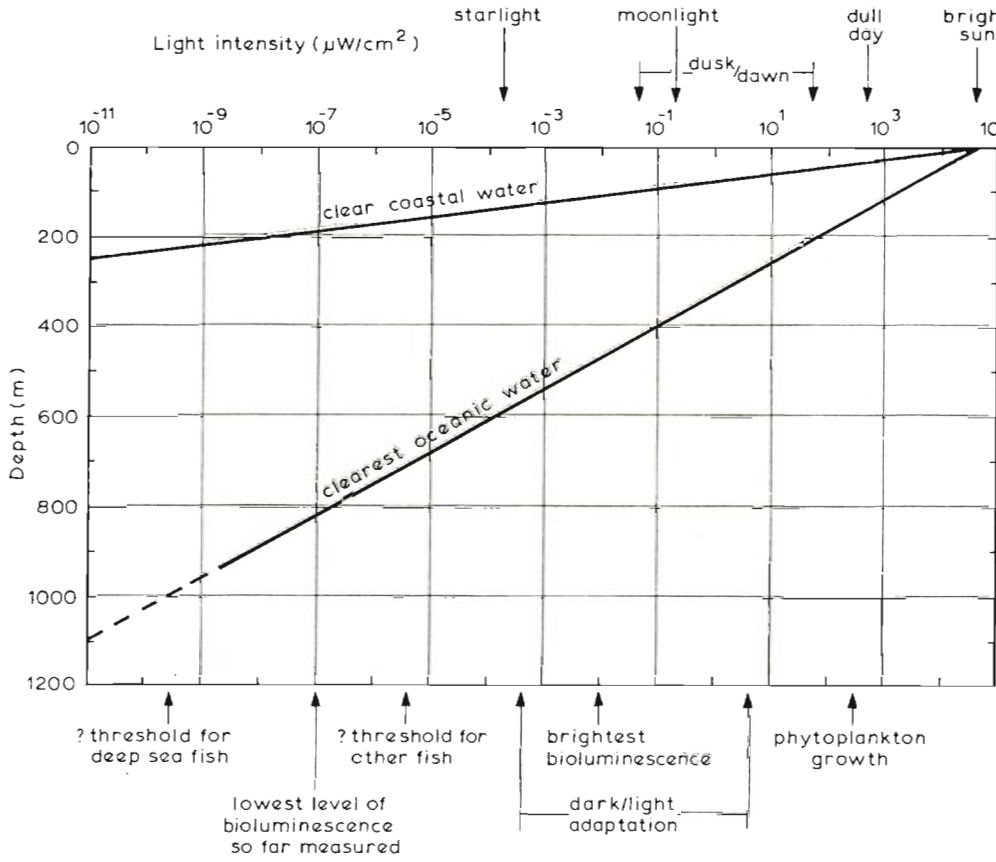

Fig. 2-58: Penetration of bright sunlight into clear coastal and clearest oceanic water (heavy lines). Also shown are intensity values for other conditions of natural light and thresholds for various biological processes; 1 $\mu W/cm^2$ is approximately equivalent to 2 metre-candles at the surface. (After CLARKE and DENTON, 1962; modified.)

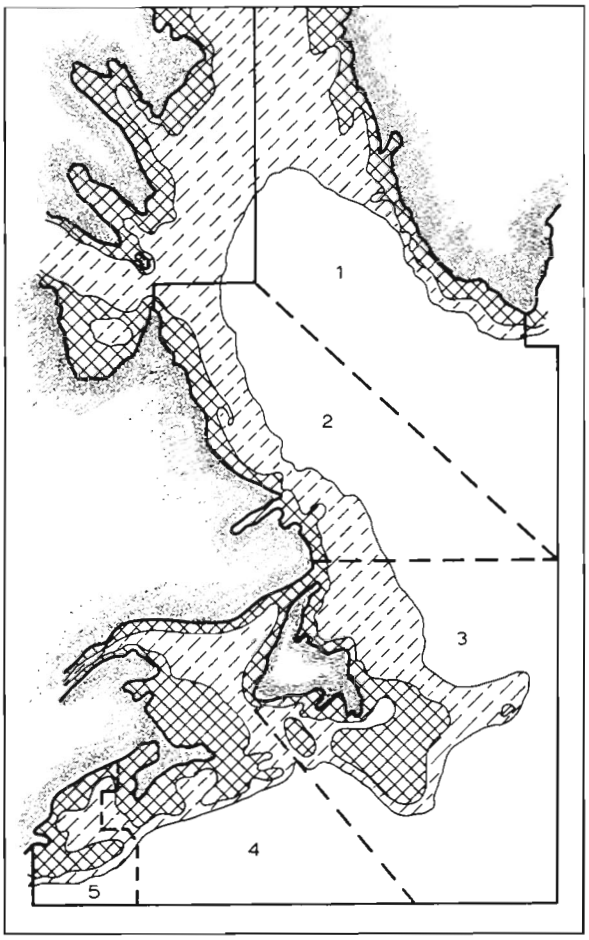

Fig. 2-59: The N.W. Atlantic Ocean area showing in cross hatching, the area of the sea bed where light should penetrate well enough to cause changes in light- and dark-adaptation of fish (assuming the threshold is 10^{-1} mc and extinction coefficient 0·13). The area in broken hatching shows the additional area of the sea bed where light should reach the absolute threshold at noon (based on an absolute threshold of 10^{-10} mc and an extinction coefficient of 0·045). Numbers represent areas for fisheries regulation. (After BLAXTER, 1965; redrawn.)

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3. TEMPERATURE

3.0 GENERAL INTRODUCTION

O. KINNE

(1) General Aspects of Temperature

(*a*) *Physical Aspects*

Heat is energy of molecular motion. It can be transformed into other forms of energy (mechanical, chemical, electrical, radiant, etc.) and obtained by transformation from these other forms. Heat alters the state of a given material and is capable of passing from warm to cold materials until equable diffusion is attained. It is measured in calories and can be transferred from one place to another by radiation, convection or conduction.

Temperature is a measure of the condition caused by heat; it expresses the intensity of warmth and is measured in degrees. While the quantity of heat contained in a given material is a function of its mass (at the same degree of warmth, 2 kg of water contain more heat than 1 kg), temperature is mass-independent. Living organisms cannot sense the quantity of heat but differences in heat intensity, i.e. in temperature. Temperature may be defined as measure of the thermal state of a given material (relative to its capacity to communicate heat to other materials).

The dimension of temperature is not related to the basic dimensions mass, length, time (g, cm, sec); it is expressed in a basic unit of its own right: degrees centigrade (° C)[1], or more generally, t. The absolute lowest temperature (cessation of molecular motion) has been determined to be −273·15° C, a condition which is, in practice, not attainable. This is the zero point of the 'absolute temperature scale', designed as T_0. For many scientific purposes the absolute temperature scale is the most convenient one. It is basically identical with the thermodynamic temperature scale proposed by the English physicist LORD KELVIN and expressed as ° K (degrees Kelvin); hence the absolute zero point of temperature is $T_0 = 0°$ K.

The primary source of heat on earth is the sun. Solar radiation is converted into heat when the rays strike absorbing substances. In oceans and coastal waters, solar radiation is absorbed and converted into heat primarily at the water surface. It is transferred by convection (water movement) or conduction (contact and passing on from one contiguous particle of matter to the next). In most cases, radiation, convection and conduction are operative simultaneously and the resulting combined effect is of considerable complexity.

(*b*) *Biological Aspects*

All biological processes require some degree of heat. They are restricted to specific lower and upper temperature limits and, within the ranges of tolerance, greatly

[1] Temperature intervals are expressed as centigrade degrees (C°), e.g. the temperature interval between 10° and 20° C is 10 C°.

affected by temperature both quantitatively and qualitatively. With regard to life on earth, temperature is—next to light—the most potent environmental component.

Temperature affects living systems in 3 principal ways: (i) it determines the rate and mode of chemical reactions and hence of biological processes; (ii) it affects the state of water, the basic life-supporting medium; (iii) it modifies basic properties of living matter. In the following paragraphs we shall briefly consider these 3 principle aspects.

Originally, many biologists assumed that temperature would affect rates of biological processes to the same degree as it determines the rate and mode of chemical reactions outside living organisms. It was soon found, however, that even the 'thermal conformers' (p. 329) exhibit some capacity of regulation, counteraction or adjustment to detrimental temperatures within their species specific thermal limits, and hence are not 'ein Spielball der Umwelt'. Responses of living organisms to temperature have been expressed quantitatively in terms of the temperature coefficient Q_{10}, which denotes the ratio of the rate of a metabolic process (e.g. growth) at one temperature to the rate at a 10° C lower temperature, i.e.

$$Q_{10} = \frac{K_{t+10}}{K_t}$$

where K = velocity constant and t = temperature. Q_{10} varies over the temperature range of a given organism; hence the absolute value of Kt must be stated. A more appropriate way of expressing temperature effects on organisms is the **Arrhenius equation,** which—like the Q_{10} concept—had originally been employed to describe temperature effects on rates of chemical reactions. Some biological temperature functions are linear, most are logarithmic. For further details regarding Q_{10}, Arrhenius equation and related matters consult BĚLEHRÁDEK (1935), JOHNSON and co-authors (1954), PRECHT and co-authors (1955), JOHNSON (1957), PROSSER and BROWN (1961), QUANTITATIVE BIOLOGY OF METABOLISM (1964, 1966, 1968) and ROSE (1967).

The effects of temperature on the state of both the external water and the water in the living cells have been subject to a multitude of studies. The effect of temperature on the specific heat (number of calories required to increase the temperature of 1 g of a substance 1 centigrade degree) of sea water has been illustrated in Fig. 1-31. The specific heat of pure water, 1·00 cal g^{-1} $C^{\circ -1}$ at 18° C, reveals a minimum near 35° C (Fig. 3-1; see also Chapter 1, Fig. 1-31). Animal tissues, except compact bone, require 0·7 to 0·9 cal to raise the temperature of 1 g of tissue 1 centigrade degree. A plot of the surface tension of pure water as a function of temperature is shown in Fig. 3-2; it demonstrates that surface tension decreases with increasing temperature (see also Chapter 1, Fig. 1-33). There is evidence that the degree of organization of water also decreases with increasing temperature (e.g. KLOTZ, 1965). However, the degree of organization of water molecules around weakly hydrated ions seems to increase with increasing temperature (NÉMETHY and SCHERAGA, 1962). In liquid water the molecular structure may change (kink theory); DROST-HANSEN (1967) has interpreted such temperature-dependent structural changes of water as a discrete change in molecular aggregation. The heat conductivity of water is 0·0014 cal cm^{-1} sec^{-1} $C^{\circ -1}$ and hence higher than that of most other liquids.

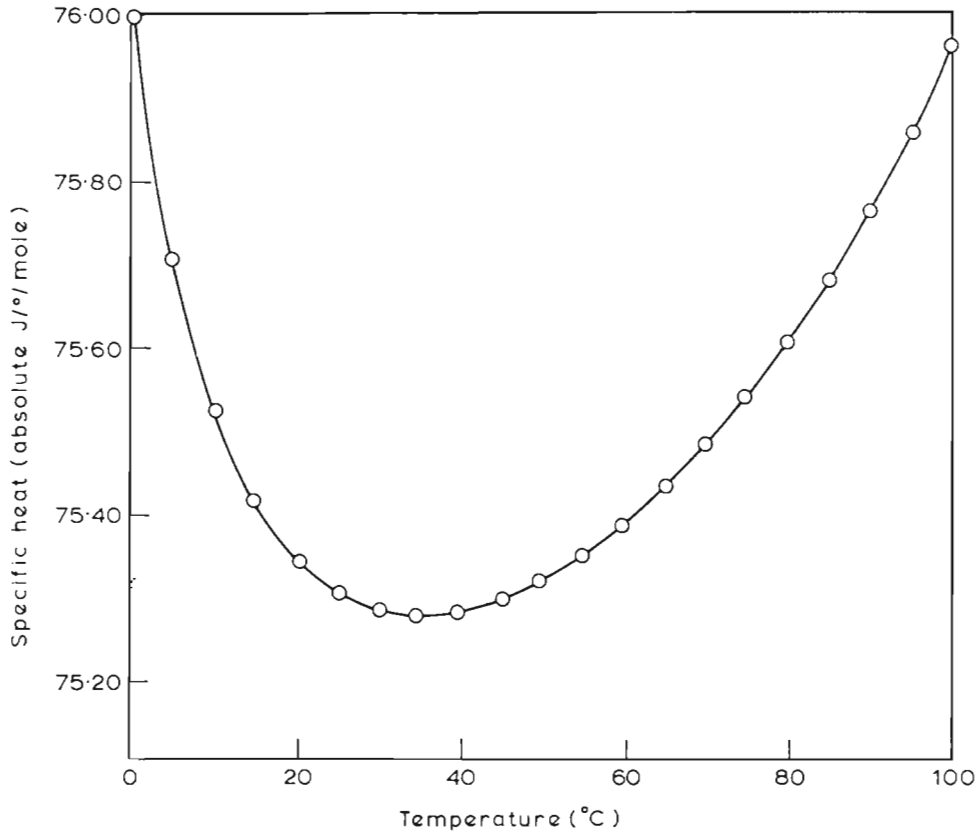


Fig. 3-1: Specific heat of pure water as a function of temperature at a constant pressure of 1 atm. The specific heat minimum occurs at about 35° C. (After GINNINGS and FURUKAWA, 1953.)

The effect of temperature on the state of water within the living cells has recently been reviewed by LING (1967). This subject poses a difficult problem since there is still no agreement on the structure of pure water itself (FRANK, 1965); 'as regards the state of water in living cells, the situation is even more obscure' (LING, 1967, p. 5). Recent studies imply that cell water possesses a much higher degree of organization than pure liquid water. In the past phase of cell physiology, cell properties have been interpreted in terms of membrane permeability and metabolic pumps; LING attempts to interpret these aspects in terms of fundamental parameters of modern physics.

Studies concerned with responses to temperature of living organisms originally centred almost exclusively on the intact individual. Hence, at the individual level, there exists today an extensive literature on temperature responses of a large variety of marine and brackish-water living organisms, both in the sea and under laboratory conditions. While such research is of great importance, studies at the subindividual and at the supra-individual levels have opened up new avenues for a more complete understanding of temperature effects on living systems. Unfortunately, there still exists but little information on responses to temperature at the supra-individual level (populations, ecosystems) except in microbiological studies

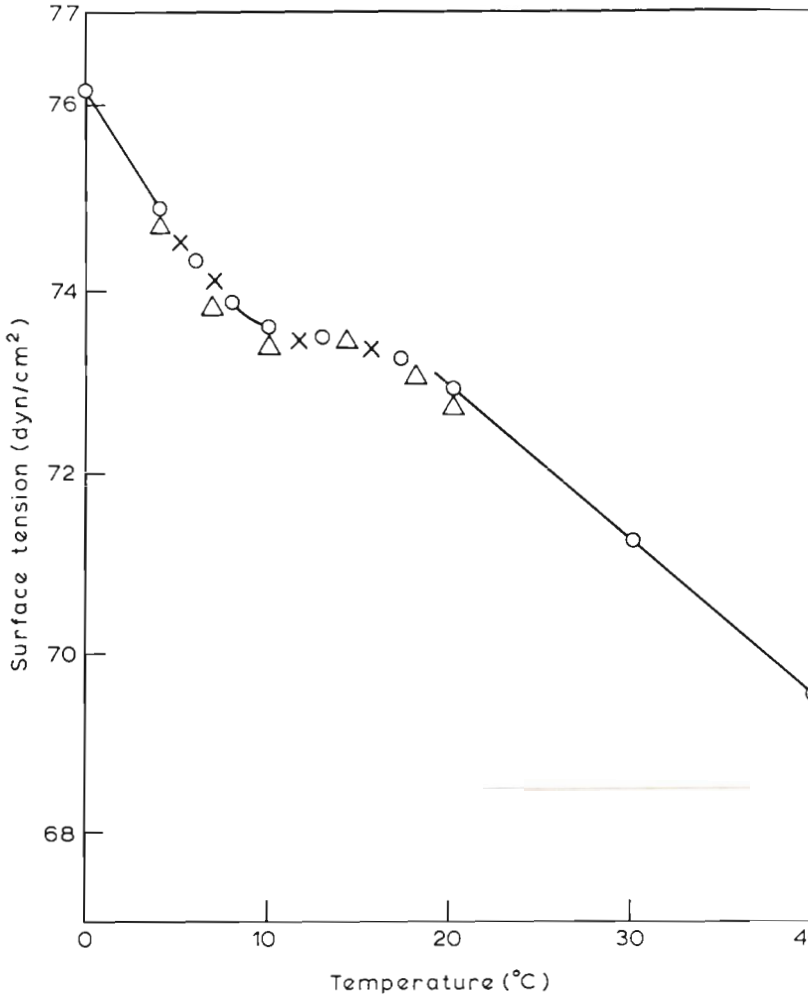


Fig. 3-2: Surface tension of pure water as a function of temperature. Data obtained by the capillary rise method (o), the drop weight method (△) or by bubble pressure (x). (From data of TIMMERMANS and BODSON, 1937; after LING, 1967.)

where, on the other hand, hardly anything is known about temperature responses of individuals, since population responses serve as criteria. Inadequate knowledge of ecological principles, lack of agreement as to how to assess temperature responses of multispecies systems and an insufficient capacity to breed important representatives of the marine food chain has largely impeded progress of research at the supra-individual level. No doubt, such research is of utmost importance if man is to achieve forecasting, controlling and managing capacities in regard to life processes in the sea.

Studies at the subindividual level have provided new insights into the cellular and molecular bases of temperature responses of such fundamental processes as thermal injury, photosynthesis, metabolism, adaptation and reproduction (PROSSER, 1967; ROSE, 1967; TROSHIN, 1967). In the following paragraphs we shall briefly

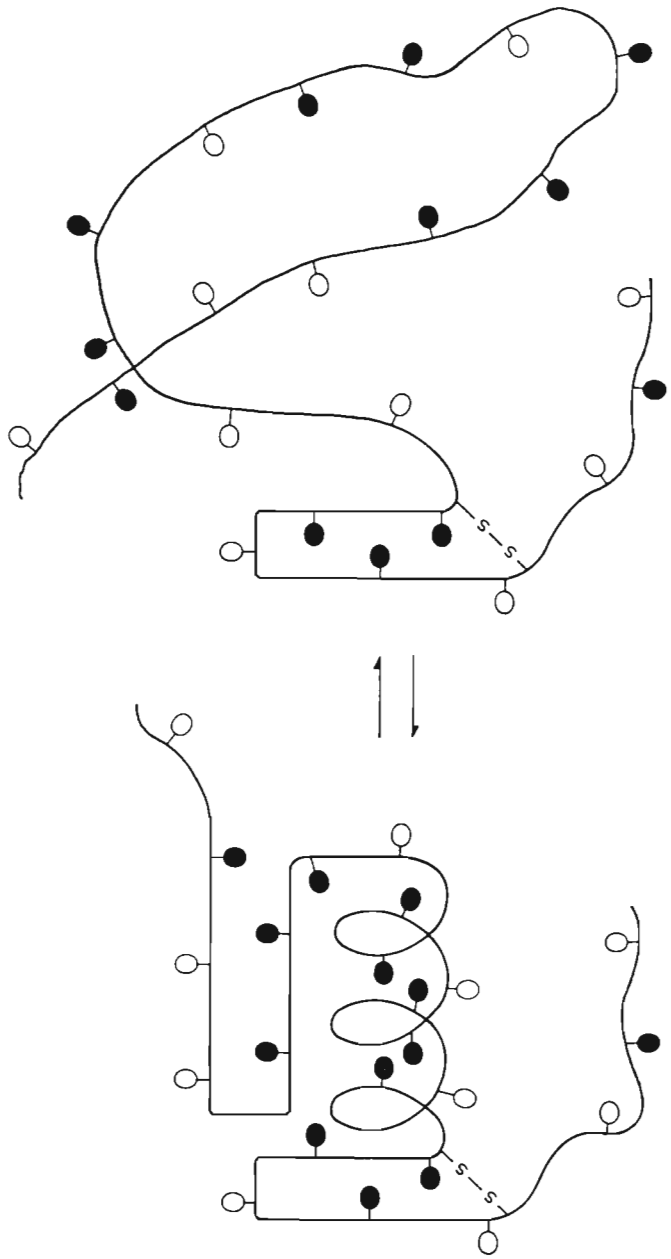


Fig. 3-3: Denaturation of a protein molecule; diagrammatic representation of average conformational states. In the native state, hydrophobic side chains (filled circles) are mostly buried in the molecule; in the denatured state they are exposed to the solvent; polar and ionic side chains (open circles) are largely solvated in both the native and denatured states. (After BRANDTS, 1967.)

consider some temperature effects on proteins, enzymes, nucleic acids and cell membranes.

The pertinent literature on temperature effects on proteins and enzymes has recently been reviewed by BRANDTS (1967). The native conformation of globular proteins, governed by the amino-acid sequence and the immediate solution conditions, is thermodynamically controlled. In view of the intimate relation between enzyme conformation and physiological response, an 'understanding of protein denaturation is the necessary first step toward the interpretation of biological activity, and the way in which this depends upon temperature, pressure and local solvent conditions' (BRANDTS, 1967, p. 27). The denaturation process is illustrated schematically in Fig. 3-3, showing average conformational states. The accommodation of hydrophobic side chains of proteins in the denatured state must be viewed with respect to a solvent order–disorder transition (Fig. 3-4) which may

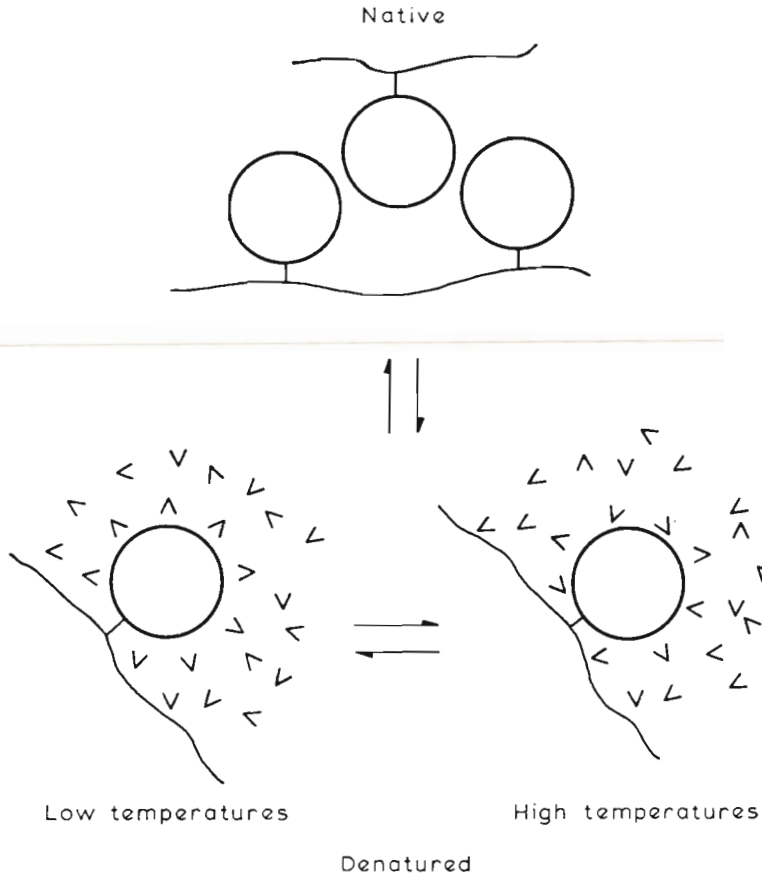


Fig. 3-4: Hypothetical temperature effects on the hydrophobic bonding reaction and the clathrate melting transition in proteins. In the native state, non-polar side-chains are surrounded locally by other non-polar groups. In the denatured state, the exposed, non-polar groups will be accommodated by an ordered solvation shell of water molecules (v) at low temperatures but by a disordered solvation shell at high temperatures. (After BRANDTS, 1967.)

be referred to as 'clathrate melting'. In the native state, the solvent assumes no importance since the local environment of the non-polar side chain consists of other protein groups. However, in the denatured state, the solvent assumes the dominant role, particularly in view of the clathrate melting transition which can be expected to impart unusual aspects to the thermal stability of proteins.

The basic effect of elevated temperature is to supply enough kinetic energy to disrupt the bonds between atoms and molecules. In regard to basic biological structures such as proteins, enzymes and nucleic acids, it is, therefore, necessary to know which of the bonds are most susceptible to the effects of temperature under given solvent conditions (Fig. 3-5). Elevated temperatures have 2 principal effects on nucleic acids: (i) Disruption of the secondary structure held together by non-covalent bonds, including hydrogen bonds, and a variety of stacking forces; (ii) cleavage of the N-glycosidic and of phosphate ester bonds (SZYBALSKI, 1967). Effect (i) leads to a very abrupt change in the conformation of double-stranded native DNA with a disruption of the double helix and a dissociation of the complementary strands. Following small temperature changes, this reaction is rapidly reversible, but it becomes irreversible upon rapid temperature decrease, as soon as all hydrogen bonds are broken and the strands fully separated. Such completely denatured DNA does not regain the helical double-stranded configuration. Thus, heat denaturation of helical DNA followed by chilling is an all-or-nothing phenomenon: the DNA either regains its native configuration or collapses into the denatured form, a rather random coil structure. Cleavage of N-glycosidic bonds and of phosphate ester bonds is the chief reason for the loss of biological activity by nuclease-free DNA at temperatures below heat denaturation. Heat inactivation of nuclease-free RNA is caused by the cleavage of the phosphate ester bonds. Although single-stranded RNA is resistant to depurination, its biological activity is 30 times more sensitive to thermal inactivation than that of single-stranded DNA.

Cell membranes and their constituents are, at present, receiving considerable attention. However, there is still lack of definite information, and a number of different physiological definitions of a cell membrane have been put forward. According to CHAPMAN (1967), the cell membrane is a dynamic system with a turnover in fatty acid and phospholipid composition in which phase transitions from lamellar to some other phase (spherical, micellar or hexagonal) may occur. The cell membrane is also associated with a variety of important exchange phenomena involving ion and molecule transport as well as probably providing a quasi-catalytic surface for the activation of chemical or enzymic reactions. Freezing may cause changes in the immediate environment of the cell membrane which are sufficient to denaturate its lipoprotein. Although the crushing effect of growing ice crystals has been considered to be a major cause for cold damage (p. 442), secondary changes in osmoconcentration and pH may play an important part (e.g. LOVELOCK, 1957; PROSSER and BROWN, 1961; JANKOWSKY and co-authors, 1969). Temperature variations may also affect the rate of proton interchange along membrane interfaces.

The effects of ambient temperatures on marine and brackish-water living organisms can be complicated by the fact that the temperature of the responding individual or its parts may not be identical with that of the surrounding water.

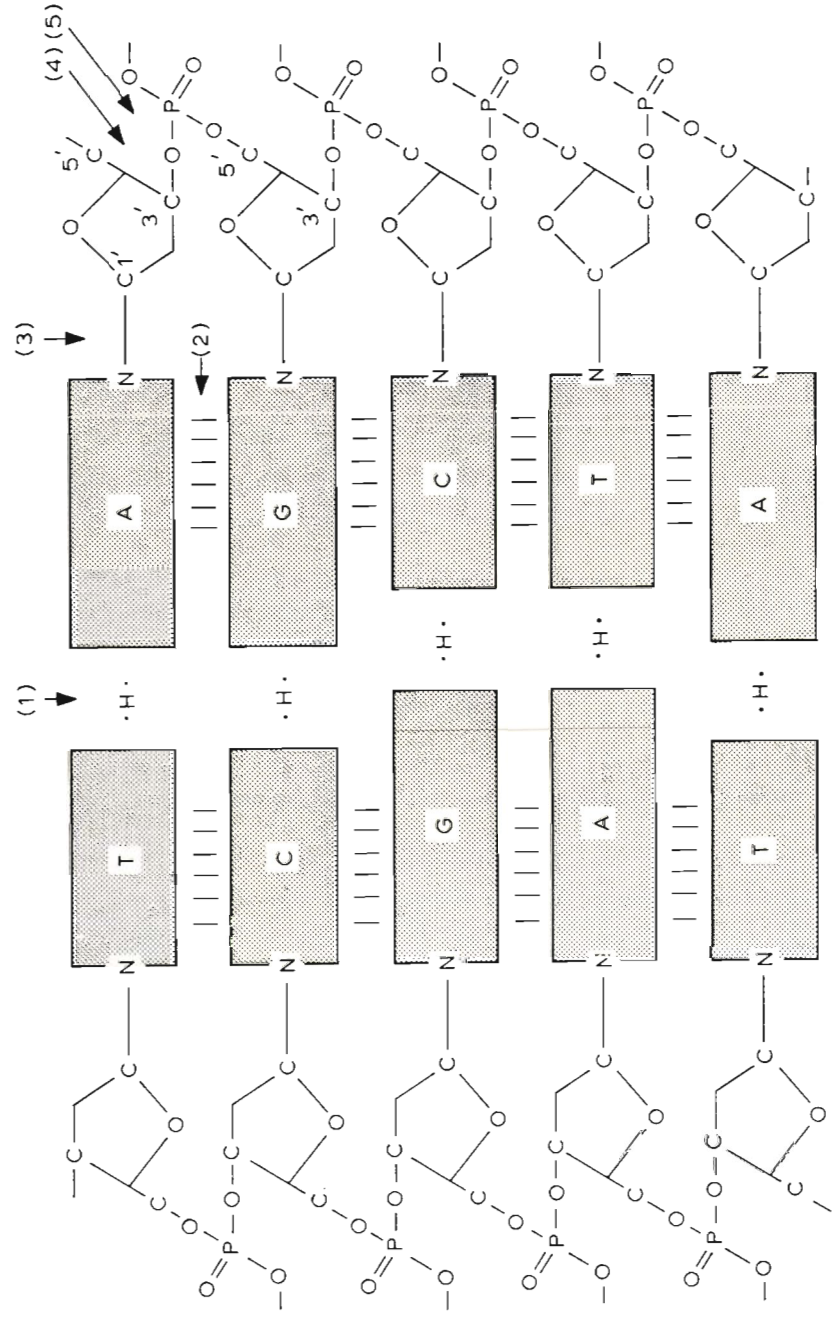


Fig. 3-5: Diagrammatic representation of a fragment of a double-stranded (native) DNA molecule. The bonds which are most sensitive to elevated temperatures include (1) hydrogen bonds between the complementary bases thymine (T) and adenine (A), or cytosine (C) and guanine (G); (2) stacking interactions between the bases, moderated by the supporting water envelope; (3) N-glycosidic bonds; (4) C(3′)—O and C(5′)—O bonds; (5) O—(3′)P and O—(5′)P phosphate ester bonds. (After SZYBALSKI, 1967.)

Marine birds and mammals maintain a rather constant temperature in their central body parts, which is species specific and may range from some 36° to 38° C in mammals and some 40° to 43° C (extremes: 38° to 44° C) in birds. These animal groups, the **thermal regulators** or **homeotherms**, are able to maintain—under extreme conditions of ambient temperatures gradients between internal and external temperatures of some 50 to more than 100 centigrade degrees. Such impressive regulatory capacities are attained by variations in metabolic heat production, adjustments in insulation (tissue fat, feathers, hair), heat transfer via circulating body fluids, as well as by behavioural regulations. For further information on body temperatures of marine birds and mammals consult DAWSON and SCHMIDT-NIELSEN (1964), IRVING (1964), KING and FARNER (1964) and SCHOLANDER (1964).

The body temperature of the vast majority of organisms living in oceans and coastal waters follows—due to rather low metabolic heat production and intensive heat exchange (respiration, body fluid circulation) between the organism and its external medium—more or less closely the temperature of the surrounding water. These organisms are referred to as **thermal conformers** or **poikilotherms**. However, heat gain through metabolic activity and absorption of radiant energy may, at least temporarily or locally, be higher than heat loss through conduction, convection, or radiation, and result in appreciable temperature differences and gradients between ambient and body temperatures, especially in large and rather active aquatic poikilotherms. HALSBAND (1953) measured body (intestine) temperatures of the trout *Salmo gairdnerii* which is confined to a rather restricted temperature range and of the chub *Leuciscus cephalus* which is able to exist under relatively wide ranges of temperature. Thermo-electric measurements at 5°, 10° and 15° C revealed that the body temperature of *S. gairdnerii* was on an average 0·012° C, that of *L. cephalus* 0·024 to 0·066° C higher than the respective environmental temperature. MORROW and MAURO (1950) recorded up to 6 centigrade degrees higher body temperatures (dorsal muscle mass; thermocouple harpoon) in striped marlin *Makaira mitsukurii* under conditions of violent activity. They suggest, however, that under normal activity conditions body temperature of *M. mitsukurii* does not differ greatly from that of the ambient water. BARRETT and HESTER (1964) measured deep-muscle temperatures of 62 live yellowfin tunas (*Thunnus albacores*) and 31 live skipjack tunas (*Katsuwonus pelamis*) shortly after they had been captured at sea temperatures ranging between 19·4° and 30·6° C. At an ambient temperature of 20° C, *T. albacores* had on an average a temperature of about 23·5° C, *K. pelamis* 28° C; at an ambient temperature of 30° C, the respective values were about 31·7° and 33·8° C. For further information concerning body temperatures of poikilotherms consult Chapter 3.3, GUNN (1942), BRATTSTRÖM (1963), SCHMIDT-NIELSEN and DAWSON (1964) and FRY (1967). The small body mass of micro-organisms responds quickly to temperature changes and may be affected by minute changes in the thermal microdistribution or the direct capture of radiant energy (Chapter 3·1). In spite of such largely temporary differences between ambient and body temperatures, aquatic micro-organisms, plants, and poikilothermic animals are decisively affected by the temperature of the surrounding water.

Aqueous solutions may supercool by several centigrade degrees, especially in

capillary spaces, and bound water is resistant to freezing. Hence some organisms supercool, and partially dehydrated organisms, or those with some extracellular water replaced by organic solvents ('antifreeze substances'), often can withstand temperatures far below 0° C without their tissues becoming frozen (KANWISHER, 1957; PROSSER and BROWN, 1961).

Effects of ambient temperatures on aquatic organisms may be modified by selection (genetic adaptation), non-genetic adaptation (functional and structural acclimations at the individual level), behavioural and metabolic regulations, and other simultaneously effective environmental factors. Considering the effects of temperature as an ecological factor, attention has to be paid not only to the acute temperature intensity but also to its past and present pattern of variation. A distinction must be made between constant and fluctuating temperatures, between temperature gradients, ranges, averages, frequency and intensity of changes, duration of a given pattern, and the total summation per period of time. Within the same species the biological effects of a given temperature pattern may be different (i) at different intensities of other environmental factors such as light, salinity, pressure, dissolved gases, or quantity and quality of the food available; (ii) in genetically different populations; (iii) at different levels of non-genetic adaptation; (iv) at different physiological states of the tested individual (age, life history stage, sex, environmental history). Up to this date most of the laboratory work on biological temperature effects has been performed under conditions of constant temperature. There is urgent need for experiments conducted under fluctuating temperature patterns. Many aquatic organisms encounter, in their natural habitat, daily or seasonal temperature variations, and these may, in some cases, represent an important prerequisite for their well being and the normal completion of their life cycle (KINNE, 1963a).

According to current knowledge, life on earth began in an aqueous environment similar to sea water as we know it today. All present forms of life still require liquid water. In the state of latent life, organisms (especially cysts of micro-organisms such as bacteria and protozoans) may survive very low temperatures; some forms tolerate the lowest temperatures recorded on earth, i.e. − 88·3° C (new record low temperature established at the Soviet Antarctic Station 'Vostock' on August 24, 1960; *Soviet News*, August 26, 1960; see NEW RECORD low temperature in Antarctica, 1961). The red alga *Porphyra yezoensis* survived a 24-hr exposure to − 196° C (TERUMOTO, 1965b). According to ALLEE and co-authors (1949), protoplasm in the state of latent life has survived temperatures as low as about − 270° C and as high as 150° C. Continued active aquatic life exists only within a rather limited temperature range, some − 10° to 70° C in micro-organisms and some − 2° to 40° C in marine plants and animals (many polar forms, including fishes, are active between − 2° to 0° C). However, the vast majority of marine and brackish-water organisms live within much narrower temperature ranges (Chapters 3.1, 3.2, 3.3).

Extreme low or high temperatures may disable an individual critically without the ambient temperature *per se* being lethal within the period of exposure. Such incapacitation (thermal shock) often follows abrupt temperature change; it may, however, also result from prolonged exposure to sub- or supranormal temperatures. It is characterized by severe distortions of metabolic or activity patterns.

The concept of the critical thermal maximum (c.t.m.) has originally been elaborated particularly on reptiles and amphibians (LOWE and VANCE, 1955; HUTCHINSON, 1961); however it is, in essence, also applicable to other organisms. Initially, the c.t.m. may cause occasional failures in orientation and other directed activities and, at a later stage, complete disorientation and cessation of directed activities. Thus, locomotory activity may become incapacitated to an extent where the individual involved loses its ability to escape from conditions that will soon cause its death. Even if temperature itself is not lethal, a c.t.m. condition may lead to death from predation by a more temperature-tolerant predator, or by failure to perform life-preserving activities such as respiratory movements (e.g. decapod crustaceans), ciliary cleaning activities (e.g. substrate-living suspension feeders), or hold on to solid substrates (e.g. rock-living gastropods).

In general, the total range of temperature tolerated in the state of active life is smallest in marine forms, larger in brackish and freshwater forms and largest in terrestrial species. Organisms that can tolerate wide ranges of temperature are called **eurytherm**; those restricted to narrow ranges are called **stenotherm**. The latter may be either oligotherm (cold stenotherm) or polytherm (warm stenotherm). Such terms are useful to characterize large groups of organisms, even though they are relative in connotation. Eurytherm species appear to be less in number than stenotherm ones. Among marine and brackish-water invertebrates and fishes the majority of the eurytherm species live near the coast, especially in littoral areas. Of these, sessile or hemisessile forms tend to be more eurytherm than vagile ones, and those with a cosmopolitan distribution are usually more eurytherm than stenotopic species. The majority of the stenotherm marine species live in the open oceans. In both eurytherm and stenotherm organisms, the temperature range tolerated is often more restricted during the sexual phase than during the asexual phase; in many species it is narrow during very early ontogenetic development, then increases somewhat and finally decreases again in the senile adult (KINNE, 1963a).

(2) Measuring Temperature: Methods

Even though temperature is considered one of the easiest measurable environmental components, none of our present measuring methods is entirely satisfactory. Physically, the units of temperature, and hence all temperature measurements, are still provisional arrangements which must later be amended (BERGMANN and SCHAEFER, 1965, p. 453). The measurement of temperature (thermometry) is based on the assumption of an exact relation between the degree of warmth of a given material and its properties such as volume, electrical conductivity, elasticity (deformation) and colour. The volume of most materials increases with increasing heat; under constant pressure, this increase is largest in gases, less in fluids and least in solids. Theoretically, it would be most convenient to use gases for measuring temperature; however, the volume of gases is not only a function of temperature but—in contrast to that of fluids and solids—depends also to a large extent on pressure. Insufficient knowledge on the behaviour of gases forces us to use volume changes in fluids as a basic method in thermometry.

The most frequently used fluid in thermometry is mercury. In order to determine

the lower fixed point, the mercury thermometer is submersed in a bath of melting ice (air-saturated water) until heat equilibrium is established and the mercury column has stopped moving; the position of the column top (at 760 mm barometric pressure) is the lower fixed point. The upper fixed point is similarly determined in the steam of boiling water, and the position of the top of the mercury column carefully marked. Between both fixed points, the interval has been divided into 80 degrees (parts of equal volume) by Réamur (° R), 100 degrees by Celsius (° C) and 180 degrees by Fahrenheit (° F). These scales have been extended below and above the fixed points accordingly. The subdivision of the Fahrenheit scale into smaller fractions offers certain advantages and is said to be the main reason for retaining it in several English-speaking countries. However, the centigrade scale, proposed by Anders Celsius (Swedish astronomer at Uppsala, 1701 to 1744), due to its simpler arithmetical concept, is now employed in most scientific studies. A conversion table for Celsius versus Fahrenheit degrees is presented in Table 3-1.

Table 3-1

Conversion table for Celsius (° C) and Fahrenheit (° F) scales. For conversion of ° C into ° F first multiply by $\frac{9}{5}$, then add 32. For conversion of ° F into ° C first subtract 32, then take $\frac{5}{9}$ the remainder

° C	° F	° C	° F	° C	° F	° C	° F
−50	−58·0	8	46·4	21	69·8	34	93·2
−40	−40·0	9	48·2	22	71·6	35	95·0
−30	−22·0	10	50·0	23	73·4	36	96·8
−20	−4·0	11	51·8	24	75·2	37	98·6
−10	14·0	12	53·6	25	77·0	38	100·4
0	32·0	13	55·4	26	78·8	39	102·2
1	33·8	14	57·2	27	80·6	40	104·0
2	35·6	15	59·0	28	82·4	50	122·0
3	37·4	16	60·8	29	84·2	60	140·0
4	39·2	17	62·6	30	86·0	70	158·0
5	41·0	18	64·4	31	87·8	80	176·0
6	42·8	19	66·2	32	89·6	90	194·0
7	44·6	20	68·0	33	91·4	100	212·0

Mercury becomes solid at about −39° C and gaseous at about 356·7° C, hence one has to use different thermometer fluids for different ranges of temperature (e.g. alcohol, toluol). The need to employ different thermometer fluids introduces uncertainties since, for example, mercury and alcohol thermometers show exactly equal values only at the lower and upper fixed points, not on the scale between these.

Our knowledge of functional and structural responses of marine and brackish-water living organisms is essentially based on temperature measurements conducted with the mercury thermometer.

Within the ranges of temperature tolerated by organisms in the state of active

life, mercury thermometry with narrow capillaries may be accurate to $\frac{1}{100}$° C. Such sensitive thermometers, however, are available only for narrow temperature ranges. The **Beckmann thermometer** indicates temperature differences as small as $\frac{1}{1000}$° C. Maximum temperature differences during a given period of time can be measured by using a **maximum–minimum thermometer.**

The basic thermometric tools of the marine ecologist working at sea have been the Nansen bottle and the reversing mercury thermometer. In recent years, new devices for recording water temperatures have become available and greatly advanced our knowledge of macro- and microthermal dynamics, e.g. **bathythermograph, electrical resistance thermometer, thermistor,** and **infra-red thermometer.** The bathythermograph consists of a stylus which rests against a small smoked glass slide and is moved horizontally by a long tube filled with a fluid which expands with increasing temperature; the slide, in turn, is affected by a pressure element causing it to move up or down with changing hydrostatic pressure; as the bathythermograph is lowered into the sea, the stylus moves down with increasing pressure while its horizontal position is simultaneously determined by the water temperature. An example of the resulting depth versus temperature plot is shown in Fig. 3-6. The electrical resistance thermometer is composed of materials which increase their electrical resistance with increasing temperature.

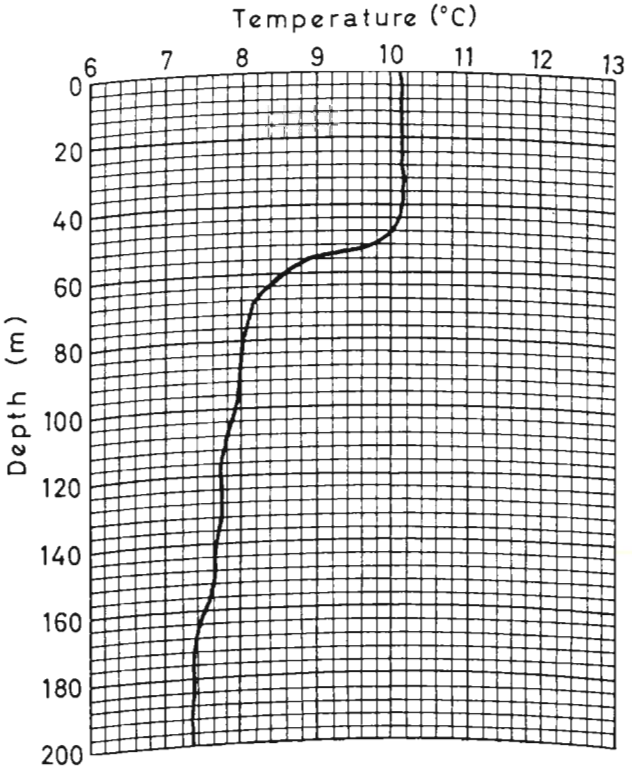


Fig. 3-6: Example of a typical vertical temperature recording as obtained with a bathythermograph. (Original.)

The thermistor consists of semiconducting materials which decrease their resistance as temperature increases; it is more sensitive than the resistance thermometer. Fast temperature changes in the sea have been successfully measured with the thermo-electrical 'Schlierenmesser' first described by KALLE in 1942 and since then continually improved (e.g. DIETRICH and KALLE, 1965). A new device, operating on a principle new to temperature measurement, is the quartz thermometer which contains 2 quartz crystal resonators, with companion electronic circuitry generating an audio frequency that varies linearly with changes in temperature through the range $-2°$ to $40°$ C. The frequency is transmitted by cable to the recording device. Since digital techniques are employed, multiple sensor probes can be scanned sequentially with the display read out on a single measuring device. It is claimed that the new '2832A Temperature Sensor Assembly' (Hewlett-Packard, Palo Alto, California, USA) measures ocean temperatures even in great depths with resolution to $0{\cdot}0001°$ C. While all these devices measure temperature by being in direct contact with the surrounding water, the infra-red thermometer is used from low-flying airplanes and provides a convenient picture of the surface temperature distribution.

The principles and methods of gas thermometry, mercury-in-glass thermometry and electrical thermometry have been discussed by FAIRCHILD (1958) and BERGMANN and SCHAEFER (1965). Thermometric methods used in biological, chemical and physical oceanography have been described by VINE (1952), HERDMAN (1958, 1963), DEFANT (1961), BRUNS (1962), WILLIAMS (1962), SVERDRUP and co-authors (1963), DIETRICH and KALLE (1965), GROEN (1967), SIEDLER (1968) and others.

(3) Temperature in Oceans and Coastal Waters

The total heat budget of the earth has undergone considerable changes throughout its history. However, since man began to record the temperature of land masses and oceans, the total heat budget has not changed significantly, even though we have become aware in recent decades of slight local temperature increases and their biogeographical consequences. Hence, during past centuries, the total amount

Table 3-2

Heat budget of the oceans (After SVERDRUP and co-authors, 1963)

Processes heating the ocean water	Processes cooling the ocean water
(1) Absorption of radiation from sun and sky	(1) Back radiation from the sea surface
(2) Conduction of heat through the ocean bottom from the earth interior	(2) Convection of sensible heat to the atmosphere
(3) Transformation of kinetic energy into heat	(3) Evaporation
(4) Heating due to chemical processes	
(5) Convection of sensible heat from the atmosphere	
(6) Condensation of water vapour	

Table 3-3

Average amounts of radiation from sun and sky, expressed in g cal/cm²/min, which reach the sea surface every month in the stated localities (Computed from KIMBALL, 1928, after SVERDRUP and co-authors, 1963)

Latitude	Longitude	January	February	March	April	May	June	July	August	September	October	November	December
60°N	7°E–56°W	0·002	0·053	0·125	0·207	0·272	0·292	0·267	0·212	0·147	0·074	0·006	0
60 N	135–170 W	0·005	0·078	0·155	0·208	0·269	0·260	0·242	0·185	0·127	0·077	0·015	0
52 N	10 W	0·048	0·089	0·148	0·219	0·258	0·267	0·251	0·211	0·160	0·104	0·062	0·041
52 N	129 W	0·053	0·091	0·135	0·185	0·246	0·250	0·230	0·214	0·158	0·097	0·058	0·039
42 N	66–70 W	0·094	0·138	0·212	0·272	0·306	0·329	0·302	0·267	0·230	0·174	0·115	0·086
42 N	124 W	0·100	0·151	0·210	0·286	0·331	0·360	0·320	0·274	0·231	0·174	0·113	0·092
30 N	65–77 W	0·146	0·165	0·238	0·285	0·317	0·310	0·301	0·282	0·239	0·188	0·169	0·142
30 N	128–130 E	0·141	0·153	0·199	0·241	0·258	0·238	0·256	0·260	0·219	0·178	0·153	0·135
10 N	61–69 W	0·254	0·276	0·299	0·305	0·272	0·276	0·285	0·292	0·287	0·269	0·248	0·239
10 N	116 E–80 W	0·226	0·257	0·292	0·278	0·255	0·239	0·240	0·242	0·247	0·237	0·224	0·219
0	7–12 E	0·239	0·248	0·244	0·230	0·210	0·196	0·188	0·194	0·220	0·240	0·239	0·235
0	48 W and 170 E	0·261	0·265	0·282	0·297	0·309	0·300	0·300	0·340	0·366	0·362	0·339	0·278
10 S	14 E; 36–38 W	0·329	0·328	0·301	0·254	0·219	0·206	0·232	0·278	0·312	0·324	0·317	0·320
10 S	72–171 E	0·290	0·308	0·315	0·289	0·266	0·253	0·269	0·306	0·332	0·313	0·301	0·303
30 S	17 and 116 E	0·452	0·406	0·340	0·254	0·186	0·148	0·166	0·214	0·274	0·362	0·401	0·430
30 S	110 W	0·380	0·330	0·260	0·209	0·162	0·130	0·145	0·176	0·237	0·321	0·340	0·390
42 S	73 W; 147 E	0·343	0·297	0·223	0·154	0·104	0·085	0·092	0·135	0·187	0·264	0·310	0·348
52 S	58 W	0·289	0·237	0·167	0·112	0·062	0·039	0·049	0·097	0·150	0·222	0·273	0·302
60 S	45 W	0·213	0·171	0·105	0·056	0·011	0	·003	0·054	0·111	0·156	0·204	0·221

of heat received per year from the sun must have been balanced rather accurately by heat loss via reflection and radiation into outer space. As is well known, lower latitudes receive more heat by radiation than they lose by reflection and back radiation, while in higher latitudes the gain is less than the loss. This difference is compensated for by heat transport from lower to higher latitudes via the atmosphere (winds) and, to a lesser degree, via the hydrosphere (currents).

The processes determining the heat budget of the oceans are listed in Table 3-2. Of these processes, absorption of radiation from sun and sky, back radiation from the sea surface and evaporation are the most important. Heat conduction through the ocean bottom could conceivably play a part in determining temperature distributions only in basins with quasi-stagnant, heavily stratified, deep water; no such case has yet become known with certainty (heating of bottom water via deep thermal springs appears to be restricted to a few rather special situations, e.g. p. 340). Transformation of kinetic energy into heat is of no significance to the general heat budget of the oceans. Heating due to chemical processes can be disregarded; convection of sensible heat is of much less importance than evaporation and so is condensation of water vapour (SVERDRUP and co-authors, 1963).

The shortwave radiation which reaches the sea surface comes partly direct from the sun and partly from the sky as reflected or scattered radiation. The amount of incoming radiation depends mainly upon sun altitude, atmospheric absorption and

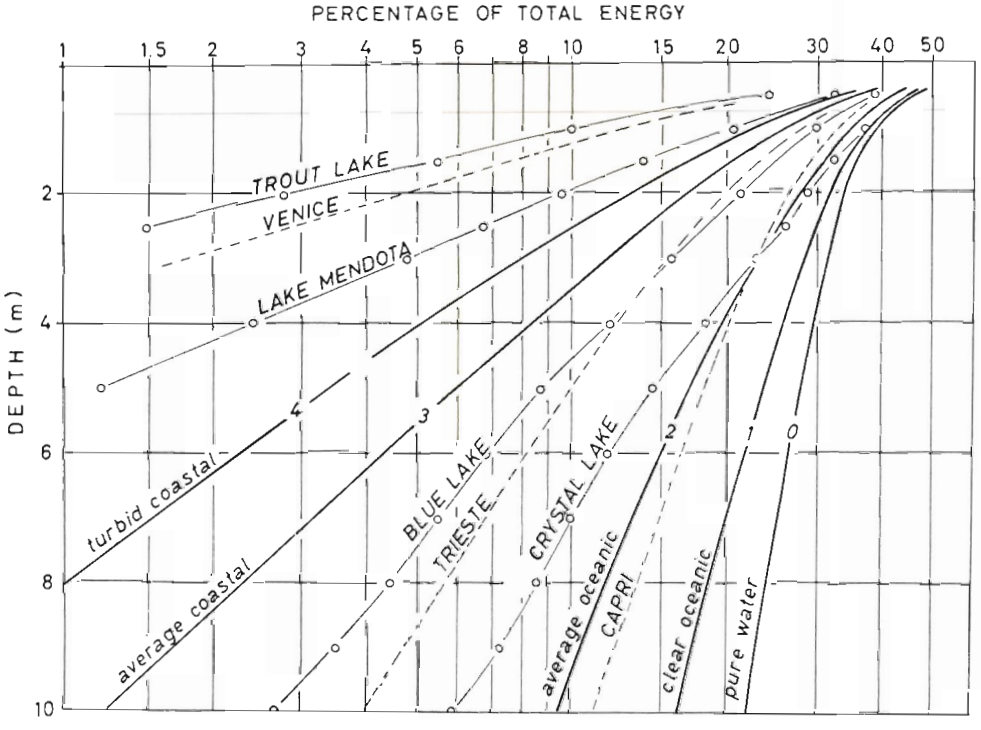


Fig. 3-7: Percentages of total energy reaching different depths in turbid coastal sea water, average coastal, average oceanic, clear oceanic and pure water computed from extinction coefficients and corresponding to observed values in 4 lakes, and at 3 localities in the Mediterranean Sea. (After SVERDRUP and co-authors, 1963; modified.)

the presence or absence of clouds. With a clear sky and a high sun, about 85% of the radiation comes directly from the sun and about 15% from the sky, but with a low sun, the proportion of sky radiation increases up to about 40% of the total with the sun 10° above the horizon. The amount of radiation energy absorbed per unit sea volume depends upon the amount of energy reaching the sea surface, the degree of reflection, and the absorption coefficients for total energy (SVERDRUP and co-authors, 1963).

The average monthly amounts of incoming radiation which reach a horizontal ocean surface are presented in Table 3-3. The differences between the parts of the oceans in the same latitudes are mainly due to differences in cloudiness. The penetration depths of energy (percentage amounts of the total energy) between surface and 10 m vary considerably in different waters (Fig. 3-7; see also Chapter 1, Fig. 1-34). An estimate of the degree of heating due to absorption of radiation can be obtained by computing the increase of temperature at different depths resulting from a penetration of 1000 g cal/cm² through the sea surface. The results (Table 3-4) indicate that the greater part of the energy is absorbed near the surface,

Table 3-4

Computed temperature increase (in ° C) at different depth intervals and in different types of water, corresponding to an absorption of 1000 g cal/cm² (After SVERDRUP and co-authors, 1963)

Interval of depth (m)	Oceanic water		Coastal water	
	Clearest	Average	Average	Turbid
0–1	6·24	6·48	7·32	7·72
1–2	0·610	0·720	0·970	0·960
5–6	0·236	0·282	0·164	0·120
10–11	0·104	0·096	0·030	0·0140
20–21	0·040	0·030	0·0016	0·0003
50–51	0·0096	0·0024	$0{\cdot}0_5 34$	$0{\cdot}0_7 15$
100–101	0·0016	$0{\cdot}0_4 11$		

particularly in turbid water. These values show no similarity to temperature changes occurring in open oceans, because here mixing processes mask the direct effect of absorption. However, in small, landlocked water bodies temperature distributions near the surface may be governed primarily by absorption of short-wave radiation (SVERDRUP and co-authors, 1963). The spectrum of the sunlight changes considerably on passing through the water and its intensity decreases fast with increasing depth. Thus, in 1 cm water depth, wavelengths $>1{\cdot}5\ \mu$ are completely eliminated and the spectrum extends only to $0{\cdot}9\ \mu$; for water layers 100 m thick the remaining energy has fallen to less than 1·5% (DEFANT, 1961).

The average temperature of all water masses of all oceans is only about 3·8° C. Even at the equator, the average temperature of the whole water column amounts only to about 4·9° C. Oceanic warm-water habitats are restricted to the surface

layers at the lower and middle latitudes; these serve as heat reservoirs which—due to the high specific heat of water—are capable of storing gigantic amounts of thermal energy. Part of the heat stored is transported to higher latitudes by ocean currents and, following heat transfer into the atmosphere, by winds. The surface layers of the oceans thus serve as important regulators and stabilizers in the heat budget of the earth (DIETRICH and KALLE, 1965).

The temperature of the open oceans ranges from about $-2°$ to $30°$ C and that of sea- and brackish-water areas closer to the continents from about $-2°$ to $43°$ C (KINNE, 1963a). These ranges are small in comparison to the temperature extremes observed on the continents, which may be as low as $-88{\cdot}3°$ C (p. 330) and as high as $70°$ to $85°$ C in hot springs containing living blue-green algae.

The average surface temperatures of the oceans and their average annual ranges are shown in Table 3-5 and Fig. 3-8 respectively. The annual variations in

Table 3-5

Average surface temperatures (° C) of Atlantic, Indian and Pacific Oceans between parallels of latitude (After SVERDRUP and co-authors, 1963)

North latitude (°)	Atlantic Ocean	Indian Ocean	Pacific Ocean	South latitude (°)	Atlantic Ocean	Indian Ocean	Pacific Ocean
70–60	5·60			70–60	−1·30	−1·50	−1·30
60–50	8·66		5·74	60–50	1·76	1·63	5·00
50–40	13·16		9·99	50–40	8·68	8·67	11·16
40–30	20·40		18·62	40–30	16·90	17·00	16·98
30–20	24·16	26·14	23·38	30–20	21·20	22·53	21·53
20–10	25·81	27·23	26·42	20–10	23·16	25·85	25·11
10–0	26·66	27·88	27·20	10–0	25·18	27·41	26·01

temperature are almost negligible in the tropics and in the highest latitudes; they reach a maximum in the middle latitudes. In general, annual temperature ranges decrease with increasing water depth.

The average daily surface temperature range of the oceans is about $0{\cdot}2°$ to $0{\cdot}3°$ C (SVERDRUP and co-authors, 1963). It is quite similar in secondary seas; only in shallow areas with appreciably restricted vertical exchange are the daily temperature fluctuations more pronounced. Thus, in June, the maximum daily temperature fluctuation in the southern North Sea (about 50 m) is $0{\cdot}24°$ C, while it is $1{\cdot}90°$ C in the shallow (6 m) Finnish rocky littoral in the Gulf of Bothnia of the Baltic Sea (DIETRICH, 1953). Under extreme conditions, diurnal temperature variations in the upper water layer may reach $3°$ C (WILLIAMS, 1962). It is difficult to determine the depth to which daily temperature fluctuations penetrate into the water layers of the seas because of hydrographic interferences, especially by internal waves, which mask small diurnal variations. Daily temperature fluctuations may be important in regard to biological activities; they represent the fastest rhythm of heat transfer in oceans and coastal waters.

The vertical temperature distribution in the upper layers of the sea often reveals an isothermal surface layer (identical temperatures at different depths), a

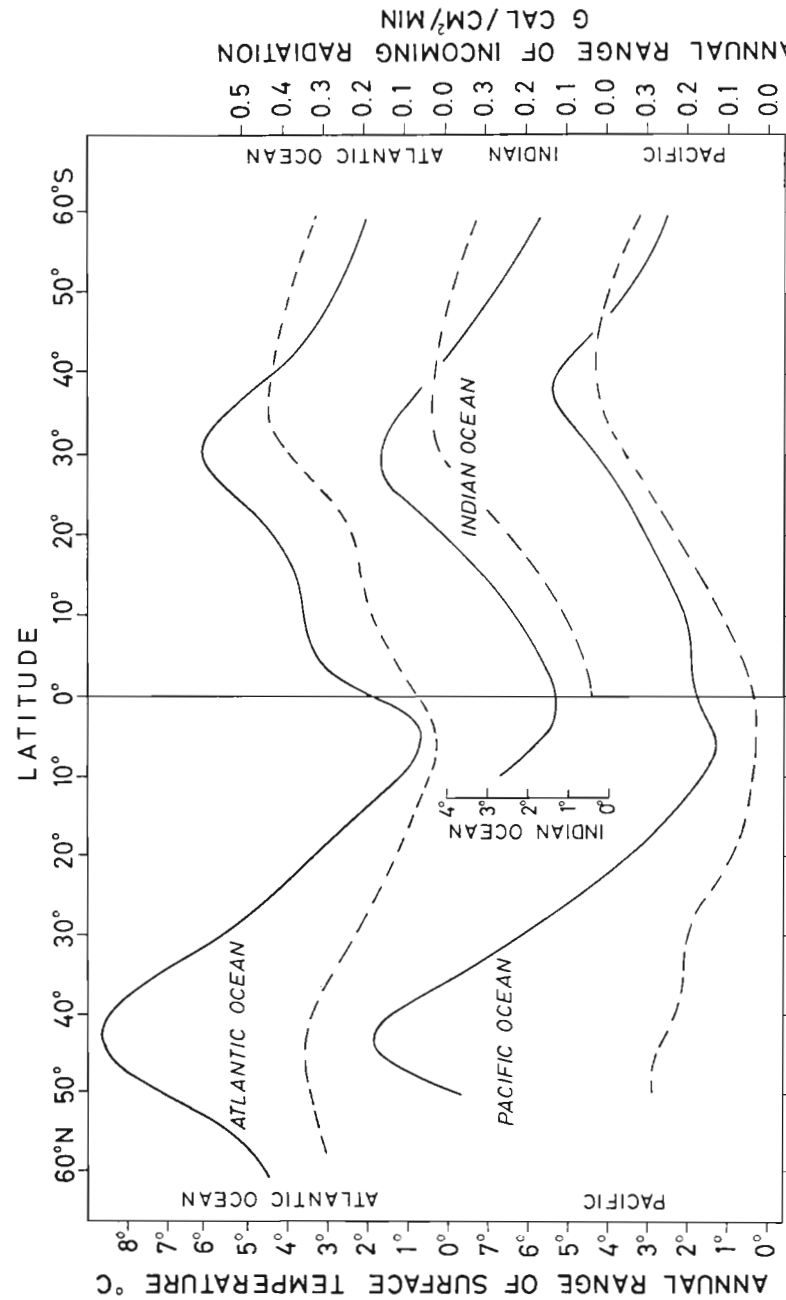


Fig. 3-8: Average annual ranges of surface temperature in Atlantic, Pacific and Indian Oceans plotted against latitude, and corresponding ranges in the radiation income (broken lines). Temperature ranges represent the differences between average temperatures in February and August. (After SVERDRUP and co-authors, 1963; modified.)

layer with maximum temperature decrease per unit depth (the thermocline) and a thick lower layer with slowly decreasing temperatures (Fig. 3-6). The thermocline is, in general, the result of temporary increased radiation from sun and sky. In the northern hemisphere, for example, the increasing amounts of thermal energy received during spring by the surface layer decrease its density and thus produce a vertical stratification of progressively increasing stability. The resulting thermocline begins to restrict the vertical heat and water exchange, entertained largely by turbulence as well as by wind-produced waves and currents. Further addition

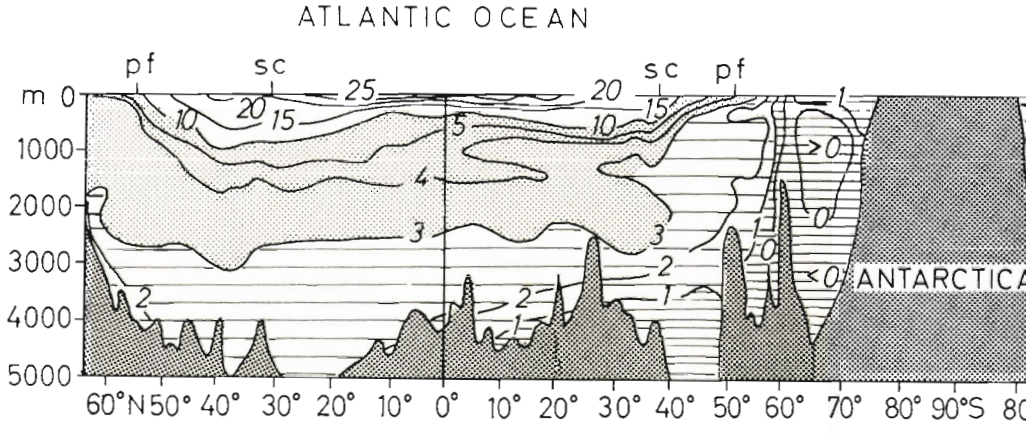


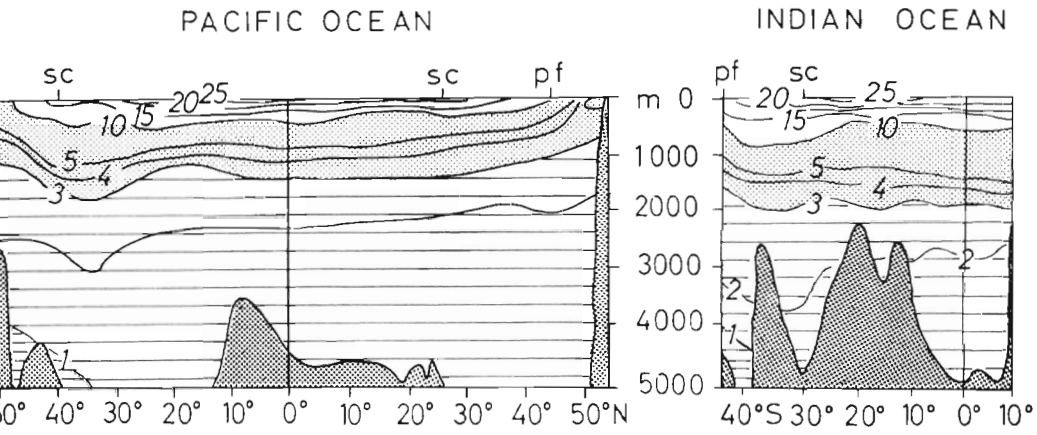
Fig. 3-9: Vertical temperature distribution in Atlantic Ocean (longitudinal section on its western side) gence; depth exaggerated 1000 times. (Compiled after various authors by DIETRICH and KALLE, 1965; m

of heat leads to heat storage in the surface layer, increased temperature gradients and a lowering of the thermocline to somewhat greater depths. A strong thermocline can largely inhibit physicochemical and biological vertical exchanges and thus greatly affect both the hydrographical and ecological dynamics within the sea area concerned. The thermocline breaks down when heat loss critically increases the density of the surface water (e.g. in autumn) resulting in full vertical convection which, in turn, facilitates the distribution of biologically important nutrients and gases. The steep vertical temperature gradient in the tropics has considerable consequences both in regard to vertical exchanges and animal distributions. On the equator, water temperature is approximately 26° C at the surface, 13° C at 200 m, 7·5° C at 400 m, 4·5° C at 1000 m, and 3·3° C at 2000 m (EKMAN, 1953; see also FLEMING, 1957 and SVERDRUP and co-authors, 1963).

In exceptional cases, the vertical temperature gradient may be inverse. Thus, hot water occurs in several deep holes of the Red Sea. On her recent cruise to the Indian Ocean, the German R.V. *Meteor* recorded deep hot water of a high salt content in the 'Discovery Deep' and in the area of the 'Atlantis Deep'. In the Discovery Deep, for example, the temperature increased within a thermocline of 45 m thickness from 21·6° to 44·8° C (KRAUSE and ZIEGENBEIN, 1966). The causes for the presence of this deep hot water have been discussed by BREWER and co-authors (1965). It is assumed that the deep hot water has escaped from briny thermal springs below the sea bottom.

The general vertical distribution of temperature in the Atlantic, Pacific and Indian Oceans is illustrated in Fig. 3-9. Longitudinal sections reveal a thin, warm, surface layer (25° to 10° C) and a mighty, several 1000 m thick, cold water layer which extends poleward of 40° latitude all the way up to the surface. The greatest depths of the oceans are characterized by almost constant, very low temperatures.

The average annual fluctuations of the surface temperature of the oceans are presented in Fig. 3-10. The surface temperature in February is shown in Fig. 3-11, that in August in Fig. 3-12.



(at about 170° W) and Indian Ocean (on its western side). pf: polar front; sc: subtropical surface conver-

In his recent review, BUNT (1967) presents details on the temperature regimes in arctic and antarctic regions and their effects on polar life. In contrast to air temperatures, polar water temperatures are very stable. In the bottom waters of McMurdo Sound, for example, water temperatures deviate only about 0·1° C from the annual mean. BUNT also stresses the biological importance of sea ice. The polar ice layer, commonly 1 to 3 m thick, minimizes heat and gas exchange between hydrosphere and atmosphere, and modifies intensity as well as spectral quality of submarine light. The abrasive action of sea ice renders effective colonization of the polar intertidal zones impossible. Annual freezing and thawing of ice modifies salinities and hence may cause physiological stress situations. Sea ice further affects migratory activities as well as predator–prey relations of marine mammals and birds, and provides a substrate for various organisms, especially unicellular plants and micro-organisms (Chapter 7).

A rather new aspect is the change of temperature regimes in aquatic habitats due to man's activities. Of growing concern is the 'thermal loading' or 'thermal pollution' of ecosystems by electric power plants. The nuclear plants will produce greater amounts of waste heat per kilowatt of electricity than conventional power installations, since they are less efficient. Although there are other causes of changing temperature regimes (dams, irrigation, industrial waste heat), the steam electric station (S.E.S.) industry represents the major factor. In the USA, power requirements in 1980 will use $\frac{1}{5}$ to $\frac{1}{6}$ of the total freshwater runoff for cooling water;

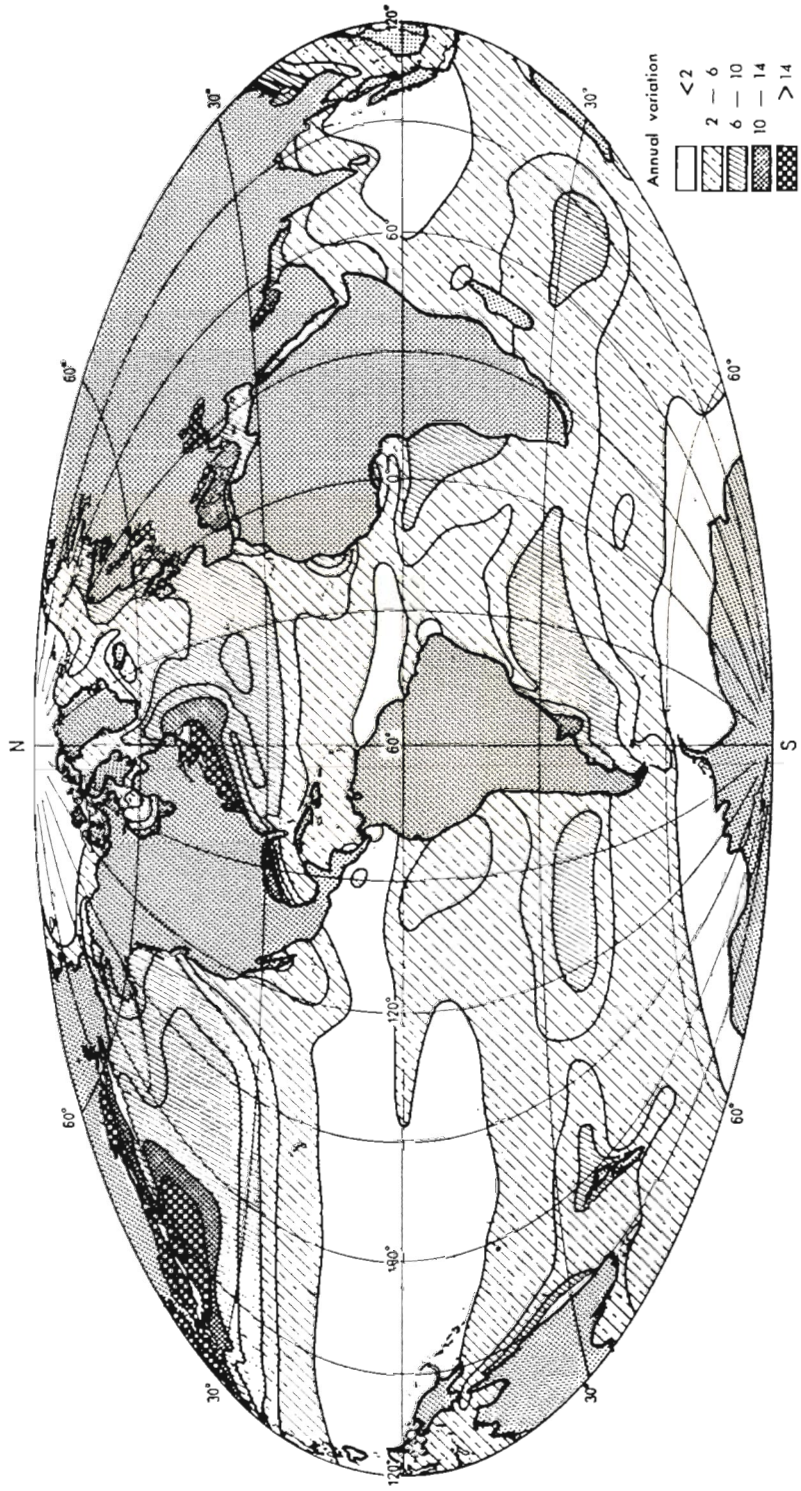


Fig.3-10: Average annual fluctuations of the oceanic surface temperatures. (After SCHOTT, 1942.)

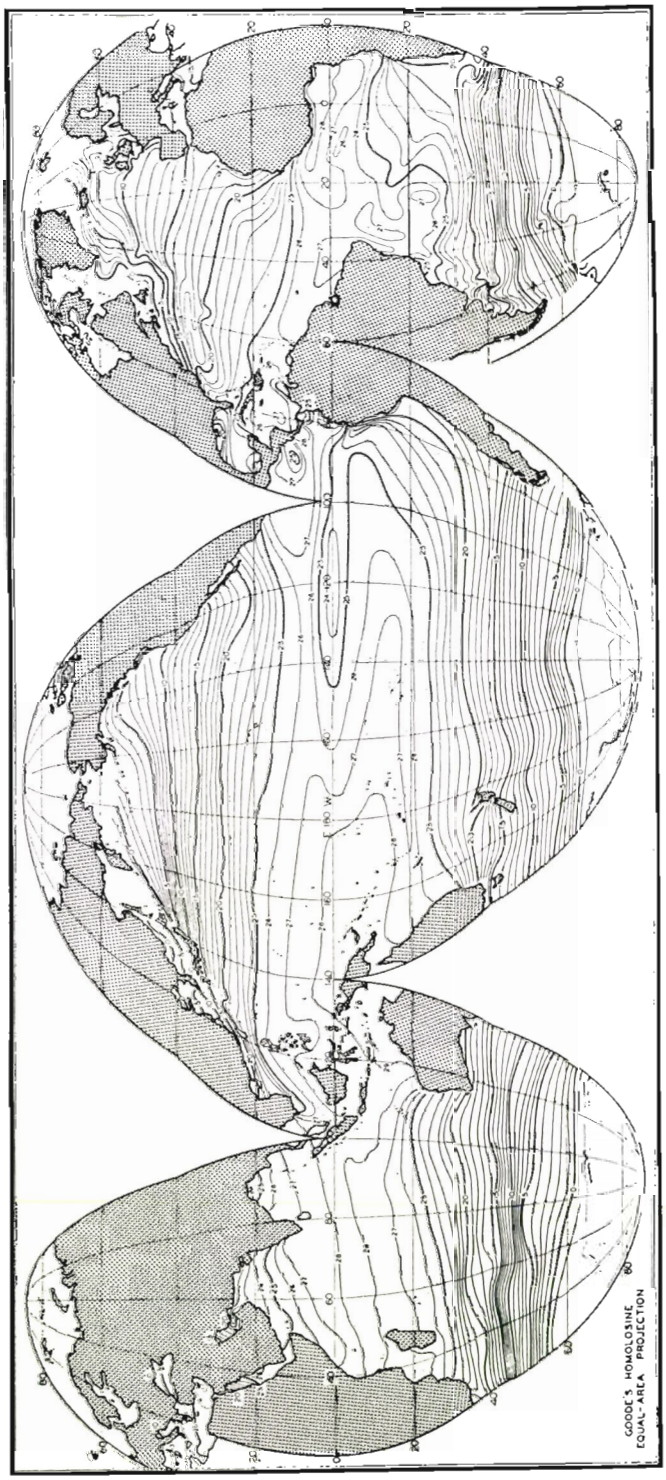


Fig. 3-11: Surface temperatures of the oceans in February. (After SVERDRUP and co-authors, 1963.)

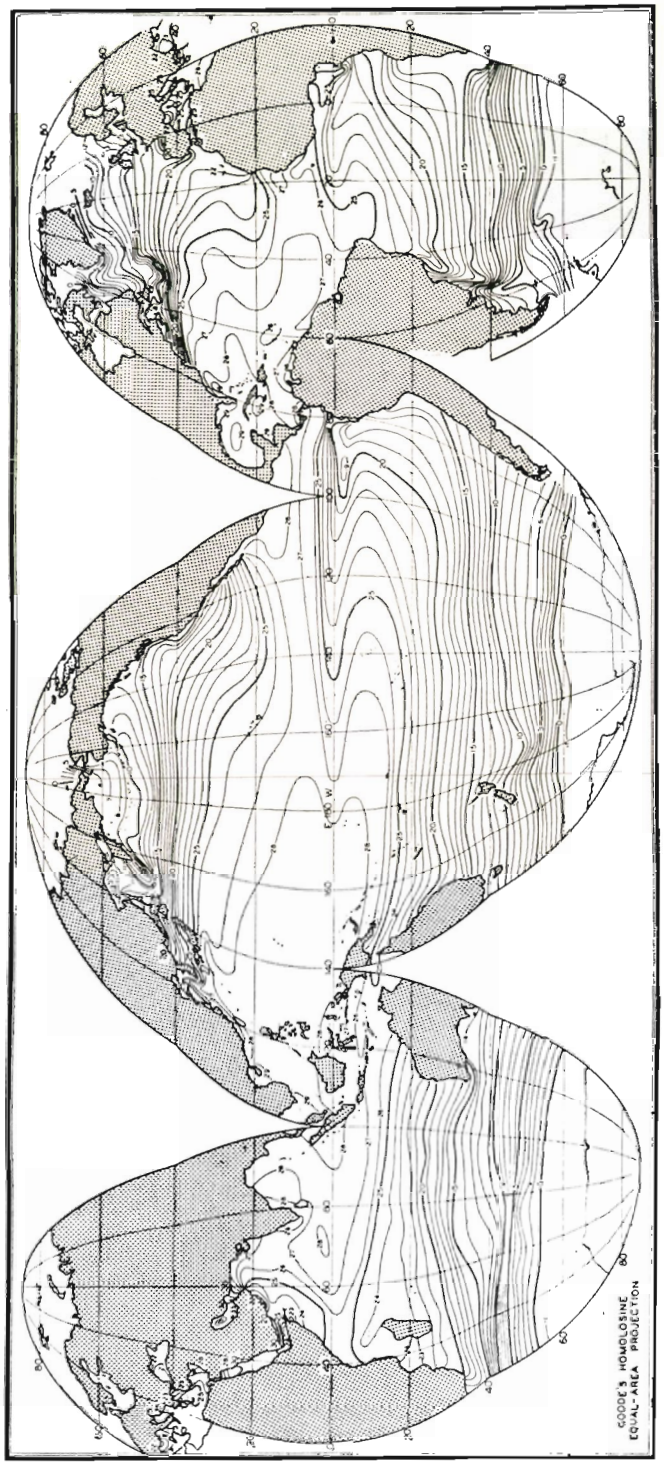


Fig. 3-12: Surface temperatures of the oceans in August. (After SVERDRUP and co-authors, 1963.)

discounting flood flows, which occur about 4 months of the year, the S.E.S. industry will require about one half of the total runoff for the remaining 8 months (MIHURSKY and KENNEDY, 1967). The S.E.S. discharge temperatures may range between 37·7° C and 46·1° C, and up to 35° C almost 8 km downstream from an S.E.S. No engineering designs appear to be envisioned which could appreciably reduce waste heat release into streams during this century. In Pennsylvania (USA) tremendous quantities of water are withdrawn from streams and lakes for industrial use. Approximately 80% of all water withdrawn by industry is used for cooling. The resulting thermal pollution of lakes, rivers and coastal waters has led to the adoption of regulations against critical temperature increase due to human activities (ARNOLD, 1962). The rapidly increasing industrial potential of modern mankind and the projected installation of larger power plants along the length of major rivers are bound to cause significant temperature elevations in certain coastal and marine waters within the next few decades.

In this general introduction it is not possible to mention all important contributions to temperature distributions in oceans and coastal waters. In addition to the accounts already referred to, the reader will find extensive information in BÖHNECKE (1936), WÜST and DEFANT (1936), WORLD ATLAS OF THE SEA SURFACE TEMPERATURE (1948), and ACADEMY OF SCIENCES OF THE U.S.S.R. (1958). The worldwide increase in oceanographic and marine biological activities has, in the last few years, considerably augmented our information on temperature distributions in oceans and coastal waters, and progressive use of automatic registration as well as of computers has multiplied our measuring and recording capacities. The reader is referred to the following recent publications:

DHI (1960)
DIETRICH (1960, 1965)
FUGLISTER (1960)
NORPAC COMMITTEE (1960)
IGY WORLD DATA CENTER (1961)
HILL (1962)
ICES (1962)
COACHMANN (1963)
MUROMTSEV (1963)
SAINT-GUILY (1963)
SCRIPPS INSTITUTION (1963)
TULLY and GIOVANDO (1963)
BOCHKOV (1964)
GOEDECKE (1964, 1968)
LAFOND (1964)
PANFILOVA (1964)
SCHEMAINDA and co-authors (1964)
WÜST and ARNOLD (1964)
WYRTKI (1964, 1965)
BABENKOV (1965)
BERRIT (1965)
BRUCE and CHARNOCK (1965)
CARSOLA and co-authors (1965)
CURRIE (1965)
MERTSALOVA (1965)
NEUMANN (1965)
NEUMANN and WILLIAMS (1965)
REID (1965)
STOMMEL (1965)
WOLFF and co-authors (1965)
BAKAEV (1966)
BARANOV and SHMATKO (1966)
BOGUSLAVSKIJ (1966)
KOSAREV (1966)
KRILOV (1966)
LEE and COX (1966)
MANN and co-authors (1966)
ORREN (1966)
ROBBLES (1966)
SHANNON (1966)
VOORHIS and PERKINS (1966)
WORTHINGTON (1966)
DARBYSHIRE (1967)
DÜING and KOSKE (1967)

DÜING and co-authors (1967)
GARNER (1967)
KUSUNOKI and co-authors (1967)
MANN (1967)
MCFADDEN (1967)
PUGH (1967)
SQUIRE (1967)
TAIT and co-authors (1967)
BANSE (1968)

3. TEMPERATURE

3.1 BACTERIA, FUNGI AND BLUE-GREEN ALGAE

C. H. Oppenheimer

(1) Introduction

Discussion of the effect of temperature on the more general aspects of marine micro-organisms, other than environmental description, is not abundant. However, temperature, as defined in Chapter 3.0 (*Physical Aspects*), is an influential physical property that directly affects most biological activities. Microbial responses to changes in temperature in water are due to effects of solubility of molecules, viscosity, density, conductivity, hydrogen bonding, osmotic effects of membranes, ion transport and diffusion, dipole moment, surface tension and many colloidal properties of matter in water systems. A large variety of temperature information has been summarized by Precht and co-authors (1955) and Rose (1967).

Heat in the marine environment may have its origin from sunlight either by direct absorption or sky irradiation (calculated at 0·21 g cal/cm²/min), from the earth's centre through the sediments (at $6{\cdot}2 \times 10^{-5}$ g cal/cm²/min), from metabolic oxidation of organic or inorganic materials, from kinetic energy (water movement through tides or currents), or from radio-active disintegration of natural radio-nuclides (Hill, 1963; see also Chapter 3.0). Whereas most of the sources of heat other than the sun are considered negligible in relation to the gross heat budgets of the earth, such sources are of the utmost importance to micro-organisms within the size range of 0·5 to 50 microns. The small mass of the micro-organisms will respond quickly to heat change and because of their small heat capacity may be affected by the minute changes within a thermocline, the air–water interface, the sediment–water interface, the direct capture of quanta of energy from the infra-red or visible spectra in the euphotic zones of the ocean, or the proximity of a natural radio-nuclide.

One must consider the rather unusual properties of water in order to explain the significance of heat to the activities of micro-organisms. Although water is made up of simple H_2O molecules, the various anomalies of ice, steam, maximum density, etc., suggest macromolecular associations. Considerable discussion has arisen to describe the molecular structure of water. According to Pauling (1957), Drost-Hansen (1967), and others, water may consist of various molecular aggregations, from ice which is a tetrahedral structure, to water which is a dodecahedron, to steam in which the molecules behave somewhat like a true gas. Within the liquid state the molecular structure may change, as suggested by the kink theory of Drost-Hansen (1967). Hydrogen bonding plays a very important role. As water changes from ice to a liquid it goes through a state of maximum density at 4° C which, according to Pauling (1957), is due to the disruption of a tetrahedral orientation and subsequent packing of the water molecules. As the temperature increases beyond 4° C the water undergoes an organized pattern of complexing in

which the individual molecules are held together by hydrogen bonding and molecular aggregation changes occur through changes in bonding forces. DROST-HANSEN (1967), has explained this as a discrete change in the molecular aggregation with anomalies evident at organized temperature increments of 15°, 30°, 45°, and 60° C (see also PRECHT and co-authors, 1955). OPPENHEIMER and DROST-HANSEN (1960) have suggested that these anomalous kinks in the structure of water are responsible for affects which account for the general separation of the psychrophile, mesophile, thermophile classification of micro-organisms.

Because of its heat capacity, water provides a relatively stable temperature environment except in areas where large temperature differences exist between water, sediment or air. Thus, micro-organisms at the sea surface may be exposed to daily or seasonal temperature changes as compared to organisms having negligible temperature variation in the more stable regions of the sea. In addition to temperature changes caused by the absorption of energy by the water, micro-organisms within the photic zone may selectively absorb various wavelengths of light thus directly capturing energy that is converted to heat or body substances. Such phenomena may be of direct importance to the activities of micro-organisms in arctic waters or on ice where water temperature may never reach 5° C and yet large masses of organisms grow during spring.

Thus, microbial activity in oceans and coastal waters may be directly related to temperature through the control of ion or food transport across cell membranes, solubility of gases, through changes in viscosity affecting surface phenomena or movement, by density changes within the organism or water which may affect buoyancy, by regulating metabolism, by controlling reproduction or growth rates, by altering diffusion rates by which food may be brought to cell surfaces or removed especially within sedimentary environment or within large detrital particles, and through the direct capture of light which may result in a heat change or specific reactions such as photosynthesis.

Indirect effects may be related to the thermal movement of water masses during large-scale currents, thus bringing the micro-organisms into a more or less favourable environment, the creation of temperature gradients which may attract higher organisms, or particulate material as food sources or solid surfaces, through upwelling and mixing processes, and, of course, by the various wind effects that may produce waves, slicks, aerosols containing micro-organisms, evaporation–cooling, etc.

(2) Functional Responses

(*a*) *Tolerance*

The marine environment may be considered to consist of an area from the shoreline to the depths of the sea, with a wide variety of conditions from the tropics to the polar regions. In general, the shoreline will have the same temperature relation as we normally consider in terrestrial weather boundaries. In the water, however, because of the high heat capacity, temperature variations will differ within a wide variety of environmental conditions.

In general, the temperature range for growth and reproduction of micro-organisms ranges from about – 17° to 70° C. Many micro-organisms will tolerate tempera-

ture extremes to well below freezing and above boiling. Thus, the marine habitat which offers a range of temperatures from approximately 0° to 40° C is well within the normal range of most micro-organisms. Although 90% of the marine environment is perpetually lower than 5° C the majority of the microbial biomass and activities are found at the surface layers or near shore where water temperatures are higher. The lack of large amounts of organic material in the depths of the sea is an indication that the micro-organisms are active, although their rates of activity may be rather slow due to low rates of material fallout from the overlying warmer waters. There is continued evidence that most mineralization takes place within the upper layers of the oceans.

Marine micro-organisms respond to temperature change with the typical growth–temperature curve as shown in general microbiology text books (THIMANN, 1963) with the usual Q_{10} response (ROSE, 1967). Increase in pressures up to 1000 atm, appears to increase the upper thermal tolerance of bacteria (ZOBELL, 1958) but it is doubtful whether this is significant in the depths of the sea where low temperatures predominate.

Very little information is available on the physiological causes of cold and heat death of marine micro-organisms living within the marine environment and all reports related to such phenomenon follow the general effects of temperature as summarized by PRECHT and co-authors (1955) and ROSE (1967). No information is available to the author's knowledge on specific physiological effects of extreme temperature varying between the bacteria, fungi and blue-green algae.

At the sea surface, where many micro-organisms may concentrate in surface films, slicks or on floating materials, temperature will fluctuate widely with atmospheric conditions, surface mixing and depth. Theoretically the surface may be defined as the area of water bounded by air with no depth relation. However, for practical purposes we must define the surface with respect to 'Lebensraum' and thus give it depth. Micro-organisms may, therefore, orientate themselves in layers only a few microns thick depending on surface mixing and the type of organism, or they could be orientated in a gradient to a depth of 1 to 5 cm and still be considered surface organisms by some investigators. Of course, those organisms below the immediate surface should be considered within the water when one attempts to determine temperature relations.

Micro-organisms in the surface layer 1 to 10 microns thick may be exposed to heat from direct absorption or from the water, and hence to rapidly fluctuating temperatures; cloud cover, light reflection from waves, etc., may result in an immediate temperature change of several degrees within the top few microns. Because of the direct absorption of infra-red by micro-organisms, additional temperature response can be expected during sun variations other than water absorption. GATES (1962) illustrates the energy of sunlight absorbed by *Ficus* leaves where the surface temperature in direct sunlight was 49° C in still air of 28° C and when a cloud passed over the leaf, the temperature dropped to 30° C in 30 secs (Fig. 3-13). No comparable information has been found in the marine biological literature but the above example can be extrapolated to the sea surface.

Surface-film micro-organisms, therefore, may be exposed to widely fluctuating temperatures usually not considered in the laboratory.

Along the edges of continental or island shelves the water-temperature profile will

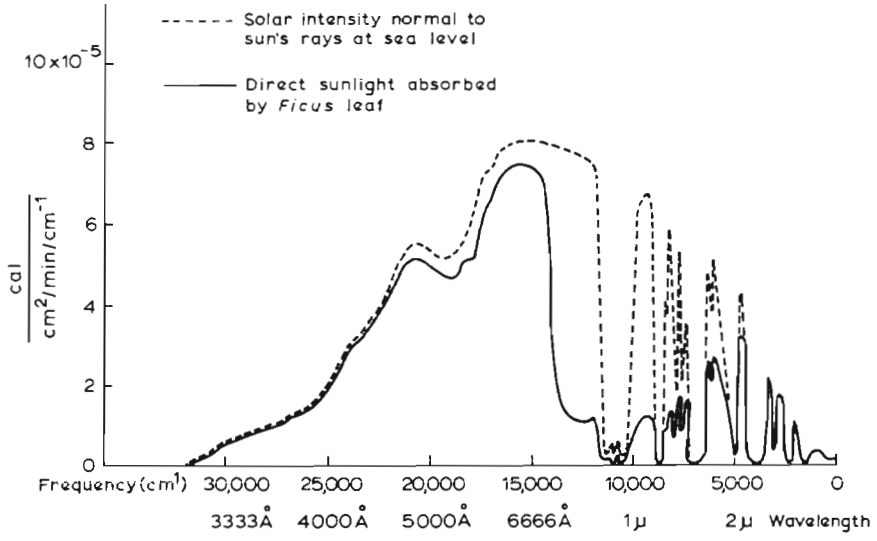


Fig. 3-13: Solar intensity at the earth's surface at sea level normal to the sun's rays for the sun in the zenith. The atmosphere is hazy and very moist (25 mm of precipitable water vapour). The total energy under this curve is 1·03 cal/cm²/min. The solar energy absorbed by a *Ficus* leaf normal to the direct rays from the sun is shown in the lower curve. The average absorptivity to the solar energy is 71·2%. (After GATES, 1962.)

vary according to locality. In shallow bays, lagoons, etc., the water temperature rapidly follows changes in air temperature usually due to mixing processes (LAUFF, 1967). The amount of lag between air and water temperature will be a function of mixing, temperature variation, latitude and time of year. In the tropics, shallow-water temperatures during the day may exceed air temperature. This may also be true for tidal pools along rocky coasts in northern latitudes where reflection of radiant energy from the rock will cause considerable warming. It is not unusual to find 30° C pool temperatures along the coast of California during sunny summer days. In contrast some Texas hypersaline bays may have localized water temperatures up to 50° C and the author has measured temperatures in water at Searles Salt Lake in California which was 60° C. Again these high temperatures are due to back radiation from the bottom, sides and particulate matter.

Sand and mud flats will also have large temperature fluctuations at the surface due to radiant energy. Exposed beach sands may often be quite warm as evidenced by walking barefoot on the beach in summer. Temperatures as high as 60° C have been measured by the author in sands of the Texas coast. Such temperatures will be a function of the back irradiation and absorption characteristics of the sediment surface. For example, in exposed sunlight in Texas a blue-green algal mat on the sand surface will have a temperature of 30° C, adjacent quartz sand will show 45° C and mud may be only 35° C.

(*b*) *Metabolism, Activity, and Distribution*

The activities and distributions of bacteria, fungi and blue-green algae in nature are quite complicated and, therefore, will be discussed in terms of temperature and

environment. Since metabolism, activity and distribution of these organisms are intimately correlated, they are discussed under a common heading in this chapter.

The bacteria, comprising both heterotrophic and autotrophic types, are ubiquitous in oceans and coastal waters. The heterotrophic forms are found everywhere in the marine environment although the specific species may vary from place to place. Autotrophic bacteria of the photosynthetic groups are found usually in environments having the presence of reduced sulphur and are commonly found on the surface of reducing sediments exposed to sunlight. Some photosynthetic bacteria are heterotrophic in the absence of sunlight. Chemosynthetic bacteria are only found in relation with reduced ions or molecules that are available for oxidative energy metabolism. These organisms may be associated with reduced decaying particulate material or within anaerobic sediments where oxygen is available at the interface.

Fungi are also widespread in the marine environment. JOHNSON and SPARROW (1961) have summarized information on the distribution of marine fungi up to 1960. Normally, fungi are found near shores associated with terrestrial materials and living organisms although their resistant spores may be widely distributed throughout the oceans.

The blue-green algae (DAWSON, 1966) are normally associated with algal mats along the coasts although there are planktonic forms such as *Trichodesmium* (WOOD, 1965) that may produce non-toxic red tides over wide areas of the tropical sea surface. They also occur in anaerobic sediments and are quite resistant to both high temperatures and desiccation. Some blue-green algae are able to live heterotrophically (FOGG, 1965) and most are able to fix nitrogen.

The effects of temperature on general physiology, metabolism, and growth characteristics for micro-organisms have been detailed in various books on general microbiology. As these subjects are readily available the present account will concentrate only on specialized aspects related to environmental temperature. Of course it is always difficult to relate idealized laboratory experiments to environmental conditions and laboratory temperature responses are generally more restrictive than evidenced by the same organism in the natural environment. Perhaps this is related to the fact that temperature response may be related to food type and availability, which is difficult to replicate in the laboratory.

Although most of the marine environment is at less than 5° C, the dynamic areas with respect to microbial activity are at sea surface within the photic zone and along the edges of land masses or in shallow seas. Such microbial activities are clearly a function of the availability of nutrients or sunlight. As ZOBELL (1946) has shown, the lower limits of nutrient concentration for heterotrophs are within the values of dissolved organic matter (DUURSMA, 1960). Therefore microbial activity will be related primarily to particulate matter either in the form of the remains, or whole bodies of organisms, or absorbed organic materials on solid surfaces such as clays or other inorganic particulate material in sea water. Because the metabolic rates are a function of the availability of food, the temperature and other ecological parameters, all must be considered when attempts are made to evaluate microbial activities in marine environments.

During diagenesis or mineralization of organic matter, micro-organisms develop in a sequential pattern depending on the specific enzymatic function of the bacteria

and the type of materials present from immediately prior microbial or biological activity. Each process may be temperature dependent.

Micro-organisms may be classified according to their temperature optimum as psychrophiles (MORITA, 1966) having optima below 20° C, mesophiles having optima between 20° and 45° C and thermophiles having optima above 45° C (THIMANN, 1963; OPPENHEIMER, 1968). Bacteria have been known to metabolize from −11° to 70° C although growth at the extremes is quite low.

Although many micro-organisms have been classified as to their optimum- and total-temperature response (BREED and co-authors, 1948), few investigators have compared optima with organisms that are found in a wide range of *in situ* temperatures such as in the oceans. SIEBURTH (1964) has shown that a marine *Arthrobacter* sp. has multiple-temperature optima that are influenced by nutrient content of media (Fig. 3-14), Multiple-temperature optima have been shown also for terrestrial

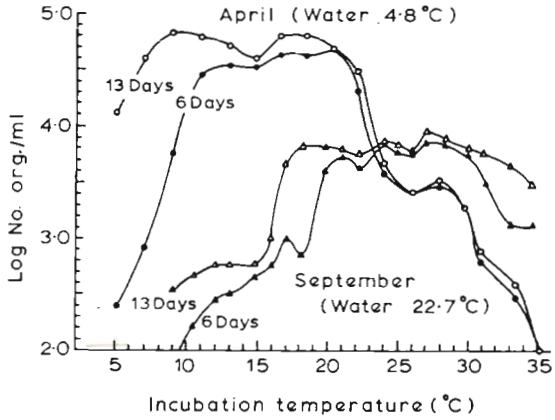


Fig. 3-14: Extremes in seasonal variation of the growth-temperature spectra of the gross bacterial flora from Narragansett Bay, Rhode Island, USA. (After SIEBURTH, 1964.)

organisms (OPPENHEIMER and DROST-HANSEN, 1960) and they seem a logical explanation for optimal activities of single strains of micro-organisms distributed between tropic and polar regions. In membrane-potential studies of the green algae *Valonia*, DROST-HANSEN and THORHAUG (1967) showed that the potential was constant between 15° and 30° C whereas below and above those temperatures the potential demonstrated rapid increase. If membrane potential is significant to uptake, then one could assume that at different temperatures different nutrients may be required. SIEBURTH (1968) studied the seasonal distribution of bacteria which grew at 18° C as a function of water temperature (Fig. 3-15). Isolates from 18° C counts were then separately determined for optimal temperature. The summer months showed a preponderance of higher optima cells with lower optima cells predominant in the winter.

Because of the limitation of shipboard space and equipment most bacterial cultures are incubated at one or two temperatures, usually at 20° to 23° C. However, with the modified polythermostat (OPPENHEIMER and DROST-HANSEN, 1960)

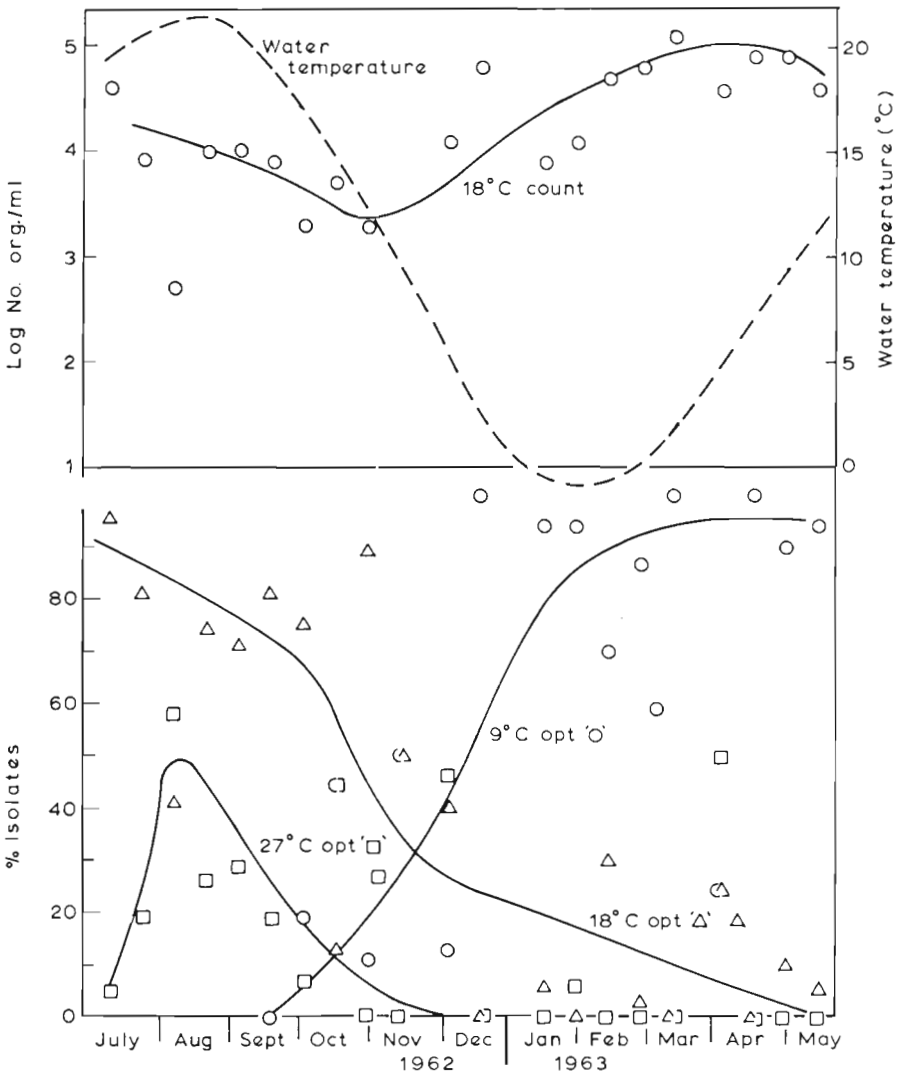


Fig. 3-15: Top: Comparison of the 18° C count with water temperature for 1962–1963 in Narragansett Bay, Rhode Island, USA. Bottom: Seasonal variation in the optimum temperature of representative isolates from the 18° C counts. Note the decrease in the 27° and 18° C optimum isolates and the increase in isolates with a 9° C optimum during the cold-water period. (After SIEBURTH, 1968.)

it is possible within equipment limits to determine the number of bacteria during surveys at *in situ* temperatures as shown by SIEBURTH (1968) (Fig. 3-14).

BEDFORD (1933), ZOBELL (1946) and others have shown that most marine bacteria grow at 0° C, have an optimum of 18° to 25° C, and rarely grow above 30° C. Bacteria of the more temperate or tropical zones, however, do not fall into this category (OPPENHEIMER, personal observations; SIEBURTH, 1968; Fig. 3-16). MORITA and associates have published a series of papers on the metabolism and temperature effects of psychrophilic marine bacteria (MORITA, 1966). ZOBELL

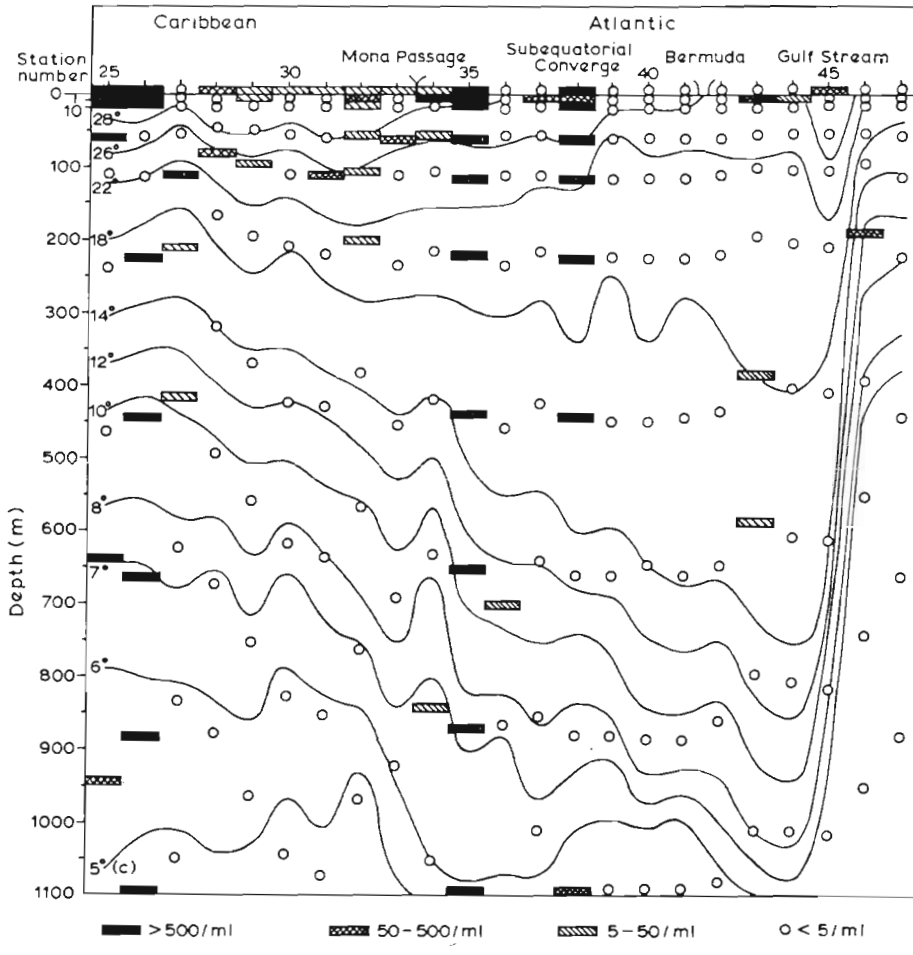


Fig. 3-16: Comparison of the distribution of bacteria (grown at *in situ* water temperatures) with the isotherms, geographical and hydrological features for R/V *Trident* Cruise 1; stations 25 through 47 in the Caribbean Sea and Atlantic Ocean. 5 different groups of bacterial abundance (number of bacteria per ml are indicated at the bottom of the figure). (After SIEBURTH, 1968.)

(1946) demonstrated that marine bacteria collected off the California coast (USA) had a temperature preference of 18° C and were later adapted to higher temperatures. MORITA and HAIGHT (1964) showed that *Vibrio marinus* MP-1 had an optimum temperature of 18° C and was killed above 20° C. According to LANGRIDGE and MORITA (1966), the enzyme malic dehydrogenase from MP-1 was stable between 0° and 20° C and was inactivated above 20° C. HAIGHT and MORITA (1966a, b) found that MP-1 held above 20° C leaked protein and electron micrographs of the organism showed that the cell envelope was damaged by the heat (COLWELL, 1968). According to UPADHYAY and STOKES (1963), enzyme systems in some psychrophilic organisms are sensitive to heat.

Although there are not much data concerning the mechanism of heat sensitivity for marine micro-organisms, it is obvious from the above reports that bacteria from

the depths of the sea are sensitive to surface temperatures. For example, during a 24-hr sampling period SIEBURTH (1968) showed that morning samples contained a majority of psychrophilic bacteria and evening samples from the same area had a majority of bacteria that grew optimally above 20° C. SIEBURTH explained this as due to bacteria brought up from colder regions during the night attached to plankton forms as these migrated upward by diurnal movement (DIETZ, 1962).

The so-called 'psychrophiles' found in the colder parts of the sea may have rapid growth at sea-floor temperatures as shown by MORITA and ALBRIGHT (1965) who reported cell counts up to 1000/ml (Fig. 3-17). LISTON (1968) indicated that the

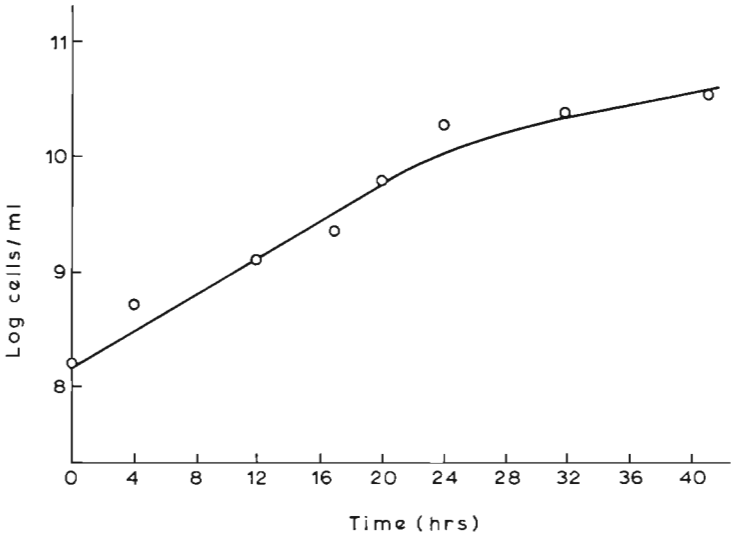


Fig. 3-17: Population growth of *Vibrio marinus* MP 1 at 3° C as estimated by MPN in PYM medium. All values are the average of duplicate assays. (After MORITA and ALBRIGHT, 1965.)

percentage of psychrotrophic bacteria varied through a profile from the Columbia River (Oregon, USA) to off the shelf. The majority of the organisms had a wide range of temperature tolerance (Table 3-6). MCDONALD and co-authors (1963) found proteolytic activity of bacteria in arctic sediments to be quite high at 0° C.

Whereas bacteria from the colder regions of the ocean may have low optimal temperatures, bacteria found in tropic or warm seas have much higher temperature ranges as shown in Fig. 3-16 (SIEBURTH, 1968). OPPENHEIMER and VOLKMANN (1962) found a seasonal increase of bacteria in sediment between 15° C in winter and 25° C in summer.

In the classical discussion of temperature and biological activity, typical growth responses follow the pattern shown by MORITA and BURTON (1963) where the maximum is close to the thermal death point (Fig. 3-18). However, if organisms show multiple temperature optima as previously described, then the Vant Hoff Q_{10} rule will not hold and each environmental niche may create its own optima. If one assumes that the major function of the micro-organisms is the regeneration of minerals from protoplasm, the micro-organisms should be ubiquitous with a

Table 3-6

Characteristics of bacteria from sediments off the Washington/Oregon Coast, USA. Samples were taken in the region of the Columbia River from upriver to various depths off the coast from the river mouth (After LISTON, 1968)

Stations	Characteristics of bacteria				
	Obligate sea water	Euryhaline	Psychrotrophic	Eurytherm	Stenotherm
Upriver	55[a]	45	55	41	4
River mouth	25	75	75	18	7
54 m depth	23	77	66	32	2
90 m	11	89	26	67	7
135 m	6	94	23	68	9
180 m	4	96	58	23	19
270 m	15	85	31	62	7
360 m	12	88	75	25	0
450 m	7	93	25	52	23
540 m	22[b]	78	67	33	0
620 m	3	97	34	60	6
810 m	1	99	22	56	22
1250 m	0	100	10	47	43
1620 m	13	87	52	26	22
Total %	14·0	86·0	39·5	50·0	10·5
Total No.	64	388	177	226	49

[a] Percent of total isolates
[b] Small sample

metabolic capability for the wide range of temperatures in the sea and during the continual movement of water from one environment to another. Because of the heat capacity of water, micro-organisms are usually not subject to rapid temperature changes except in surface waters or beaches and, therefore, may be able to adjust to different optima as ZOBELL (1946) has indicated. However, the case may be—there is no evidence, except for petroliferous material accumulations—that organic matter is preserved in the marine environment. Even the most resistant organic molecules are ultimately broken down, although the time factor may not be significant for materials deposited in the deeper parts of the sea where sediment deposition is measured in cm per thousands of years.

Very little work has been done on the temperature response of fungi and blue-green algae. These organisms are active throughout the marine environment. The fungi produce resistant spores that will carry them through the most severe ecological conditions and the blue-greens appear to have a resistance to high temperature and desiccation. Most marine fungal studies have been made *in situ* on wood panels (MEYERS and REYNOLDS, 1958). Such studies show that the wood is quickly infested with mycelia in a wide variety of marine locations in the world. Sporulation does not occur easily *in situ* but can be shown after incubation of the exposed panels in the laboratory.

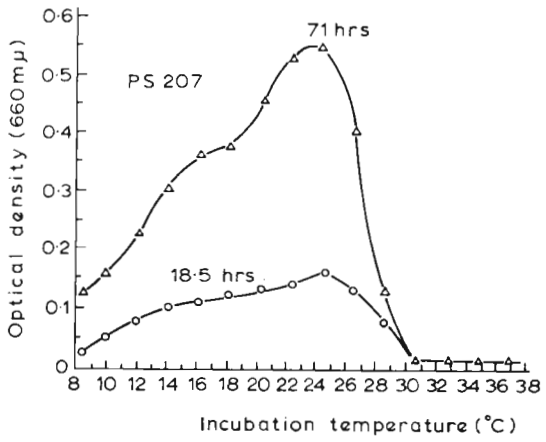


Fig. 3-18: Influence of temperature on population growth of marine psychrophile PS 207. Average values of quadruplicate readings. (After MORITA and BURTON, 1963.)

Yeasts were reported in the Indian Ocean by FELL (1967) who found them more numerous in the Somali Current and Antarctic intermediate water whereas fungi were related to waters with terrestrial materials. The marine yeast *Candida parapsilosis* was only found in warm surface waters above 16° C whereas *Rhodotorula rubra* was present in all positive samples. MEYERS (1966) found that *Lulworthia* species from Biscayne Bay (Florida, USA) environments grew faster at 30° C than at 25° C indicating that the organisms had adapted to the warm semi-tropical environment. A salinity–temperature relation in a northern estuary was noted by GOLD (1958): *Ceriosporopsis halima* developed on wood in salinities of 35 to 37‰ at 25° to 29° C, whereas when the temperature was 7° C the organism would not grow above 15‰ S. *Lulworthia floridana* was found to grow in high salinities within a wide temperature range. HUGHES (1960) reported the same situation for various fungi indicating a wide variation of temperature–salinity response for some fungal activities in an estuary.

Fungi have been reported present in deep-sea cores by various workers (SPARROW, 1937; MORITA and ZOBELL, 1955; HÖHNK, 1959; and others). It is apparent then that these organisms can survive the cold temperatures of the depths although their activity is relatively little known to this date.

There is a considerable amount of literature on the blue-green algae (DESIKACHARY, 1959) but most of it is related to terrestrial forms or general marine taxonomy. Certain interest in nitrogen fixation has created literature on metabolism, but few data are concerned with responses to temperature variation. In general, the marine blue-greens are most predominant in the temperate or tropical environments. WOOD (1965) reports widespread bloom and incidence of *Trichodesmium* and *Nostoc* in warm waters. Other forms are able to grow and be active in arctic regions as reported by TAYLOR (1954) for *Gloecapsa* and *Nostoc* species.

The blue-green algae are noted for their growth in hot waters. COPELAND (1936) gives a good review of algae from hot springs and their temperature tolerance.

Although some warm-spring forms such as *Westiellopsis prolifica* in pure culture had optimum growth at 40° C, the specific nitrogen-fixing system in the organism had an optimum between 30° and 35° C; much of the nitrogen was released as organic material into the environment.

There is a large amount of information on the responses to temperature related to the microbiology of fish processing which is not included in this paper as the material is mostly related to non-environmental conditions.

(c) *Reproduction*

Reproduction rates of the marine bacteria in natural environments have been under continued question because of the lack of experimental procedure for *in situ* experimentation. Most of the laboratory techniques involve large amounts of nutrients with optimal temperatures, and as a result micro-organisms have a high growth rate. Thus, it is quite impossible to extrapolate from laboratory experiments, actual growth rates in the marine environment. Since enumeration techniques for marine micro-organisms sample only a small percentage of the population, it is also quite difficult to determine standing crops (ZoBell, 1946).

Table 3-7

Average ratio of daily production of bacteria to their biomass (P/B) at various depths in the seas; exposure of slides for 24 hrs (After Kriss, 1963)

Depth (m)	Black Sea			Caspian Sea	Pacific Ocean	
	0·7 miles May 1953	11 miles May 1953	50 miles December 1952	Station 1 August 1953	Station 3 July 1951	Station 4 July 1951
0	0·1	0·2	0·2			
10	0·1	0·01	0·2			
15	0·07	0·2	0·3			
25	0·1	0·2	0·3	0·5		
50	0·1	0·2	0·2			0·7
75			0·2			0·2
100	0·05	0·1	0·02	0·3		1·0
150	0·1	0·1	0·1	0·3		
200	0·01	0·03				0·2
250		0·1	0·1		1·0	
300						1·2
350			0·03			
475						0·5
500				0·5	2·0	
550			0·05			
600				0·2		
700				0·3		
750			0·09		0·2	
950			0·08			
1250			0·05			
1450			0·1			

Bacteria are adventitious and their populations and activities must be a reflection of the total abundance of available food and 'Lebensraum'. As the soluble food is quite dilute, usually less than 2 ppm, the bacteria will usually have the most rapid growth rate at the surface of particulate material. It is this growth characteristic that complicates enumeration procedures (JANNASCH and JONES, 1959).

KRISS (1963), however, believes that bacteria in the open sea are individual and not in clumps. Thus, they may be studied for growth and reproduction through glass-slide techniques using regular time intervals. Tables 3-7 and 3-8 show the

Table 3-8

Daily increase of biomass of micro-organisms at various depths in the ocean in the region of the North Pole (After KRISS, 1963)

Depth (m)	Biomass of micro-organisms (mg/m³)	Average daily coefficient P/B	Daily increase in microbial biomass (mg/m³)	Relationship of daily production of micro-organisms to their biomass (%)
0	7·8	0·576	4·5	58
10	1·5	0·456	0·69	46
25		0·552		55
50	0·5	0·312	0·15	31
75	0·5	0·576	0·29	58
100	1·2	0·720	0·86	72
150	0·8	0·504	0·40	50
200	0·3	0·384	0·11	38
250	0·3	0·144	0·04	14
300	0·1	0·480	0·04	48
400	0·11	0·600	0·06	60
500	0·15	0·288	0·04	29
600	0·02			
750	0·05			
1000	0·17	0·240	0·04	24
1500	0·05	0·288	0·014	29
2000	0·05			
2500	0·02			
3000	0·01	0·456	0·004	46
3400	0·007	0·120	0·0008	12

daily production of bacteria for various water masses. It is significant to note that the Polar water has the same reproduction rates as the more temperate areas. However, there is some question as to the validity of the glass-slide technique because of the possibility that the bacteria can be washed off or have different rates of attachment even when separated by small distances between slides.

Under optimum conditions bacteria will reproduce in 20 mins whereas under natural oceanic conditions it has been assumed that the growth rates are much smaller. ZHUKOVA (1963) found that in the Sea of Azov, micro-organisms were able to increase 1 to 6 times their mass in 24 hrs whereas in the Caspian Sea the rate was 5 to 6 times their weight in 24 hrs. ZHUKOVA credits the relatively low total

numbers of bacteria in the sea as evidence of active grazing by large organisms. WOOD and CORCORAN (1966) found that the net generation time of phytoplankton in the Tongue of the Ocean (Bahamas) and the West Coast of Africa were 8 and 4 hrs respectively. They also showed that diurnal migration accounted for an appreciable grazing effect on the phytoplankton at the surface.

Recent experiments using the biostat or chemostat (VACCARO and JANNASCH, 1966; JANNASCH, 1967) may provide more information on the activities *in situ* in the oceans. Although VACCARO and JANNASCH state that the marine micro-organism *Achromobacter aquamarinus* can detect glucose at concentrations as low as 4×10^{-8} M this is a reflection of 10^5 or more cells which means that an individual cell can detect 10^{-13} M concentrations assuming that the energy and carbon can be used.

The presence of marine bacteria within the entire ocean system provides the mechanism for the ultimate mineralization of the complexity of organic matter produced by living organisms. If the small number of bacteria of 1 to 10 per ml in the open sea as shown by ZOBELL (1946) and KRISS (1963) is true, then their ability to produce mineralization is a rather fascinating process involving either the auto-infection of the water by a more diverse population or the syninfection of the water mass through the process of carrying the micro-organisms as part of the particulate organic material that is to be mineralized. Of course one could visualize a situation whereby a dead organism as it falls through the water column will pick up the necessary organisms to ensure its complete mineralization at any level.

The data at hand indicate that we are still not assured of a complete explanation of the reproduction rates of micro-organisms within the seas. This includes most micro-organisms. A point of note is the fairly common occurrence of *Trichodesmium* blooms that occur at the obvious deficiencies of phosphate ions. The author has watched a one-square-metre bloom of *Trichodesmium* off the Texas Coast growing into several acres within 24 hrs in a water mass where phosphate and nitrate are obviously lacking. It is rather interesting to speculate as to where the essential minerals originate. There are some who suggest that phosphate sharing could account for the large growth phenomenon. WOOD (1965) has mentioned blue-green blooms that extend to 2500 square miles (6475 km^2). Of course these blooms are only within the top 5 m of water and some might explain that the phosphate or nitrogen originates from the underlying water. However, there is really no physical or chemical effect that explains either mixing or diffusion of the essential nutrients within the ecological situation.

No data are available related to temperature effects on sexual reproduction of marine micro-organisms.

(*d*) *Experimental Aspects*

The experimental procedures for the enumeration of marine micro-organisms have suffered from the classical medical implication for the cultivation of micro-organisms. One of the first serious scientists to study marine micro-organisms was FISCHER who was the medical doctor on the Humboldt Expedition of 1889 where he described various microbes during his spare time.

Since FISCHER'S time the marine micro-ecologist has persistently followed the

doctrine of the medical bacteriologist that a little nutrient could only be bettered by more nutrient. Thus, most of the media for the enumeration of marine micro-organisms provide for an excess of various nutrients some or none of which may be found within the marine environment.

Incubation temperatures have followed either medical 37° C thermostats or room temperature, whatever that may be. The classical thermostat was so involved that only a few boxes were found in each laboratory. Most of the information has been obtained at temperatures of 10-degree intervals; 10 except for 37·5° C. The description of the polythermostat of OPPENHEIMER and DROST-HANSEN (1960) allowed the evolution away from the 10 C° interval. It is suspected that many temperature-dependent phenomena will be revealed in the future due to the simple control of multiple temperatures in the laboratory.

Storage of samples of bacteria from the sea have provided multiple problems. ZOBELL (1946) elucidated the complexity of the problem when he demonstrated that storage time and temperature were critical to the accurate evaluation of sea water or sediment samples. During storage the number of bacteria increases while the number of species decreases. The change in temperature between collecting and bringing in a sample from the depth to the surface was 2° to 20° C. The average time to retrieve a hydrographic sample from a depth of 11,000 m is 6 hrs. During this transport through the water column any sample changes. Thus a water sample containing bacteria that had existed under static conditions for several thousands of years could be subject to a temperature transition from 2° to 20° C in 6 hrs. It is well known that micro-organisms can withstand a slow temperature transition much better than a rapid transition. The transport of a sample through the water column could impose quite abnormal situations which are reflective of the experimental accounts of marine bacteria. Even greater effects could be expected if the samples were stored at room temperature during the usual manipulations necessary for experimental procedures.

(3) Structural Responses

It is generally recognized (SVERDRUP and co-authors, 1963) that organisms in northern latitudes tend to be larger than the more tropical forms. This is apparently not true for micro-organisms. There are no reports known to the author that describe the morphological relationship of micro-organisms to latitude or temperature.

External and internal structures in micro-organisms are unknown to change because of temperature. Very little experimental evidence can be found in the literature to substantiate morphological internal or external changes of micro-organisms due to temperature with the exception of the work of SIEBURTH (1964).

3. TEMPERATURE

3.2 PLANTS

F. GESSNER

(1) Introduction

Temperature influences all life processes, particularly those involving chemical transactions; it is necessary, therefore, to be selective in evaluating the influence of temperature on marine plants. In this chapter, only those temperature effects will be considered which are largely responsible for the reactions we observe in individual marine plants or associations. We shall discuss responses which are primarily caused by temperature. Secondary temperature effects act through temperature-induced changes in other environmental factors, which then, in turn, influence the living system. As these secondary effects can cause still further effects (tertiary, etc.), and as primary, secondary and tertiary effects can also simultaneously influence various life processes, we are dealing with a complicated system of effects which is often difficult to analyze. A rise in the temperature of sea water may, for example, at first directly influence the response of a given marine plant. Immediately following the rise in temperature, however, the amount of dissolved oxygen decreases causing secondary modifications in the respiratory rate. Changes in temperature can further lead to alterations in the dissociation ratio of carbonic acid, which can subsequently affect photosynthesis.

It would be wrong to focus our attention only on temperature changes occurring *in situ*, i.e. in oceans and coastal waters. We can gain ample information on temperature effects on life processes in artificial environments offered in the laboratory; the responses of the test organisms obtained under such conditions may 'answer questions' for which they are 'not prepared'.

(2) Functional Responses

(*a*) *Tolerance*

Terrestrial plants can exist within a temperature range of about 100 centigrade degrees. The capacity to tolerate such extremes is related to a series of specific adaptations; these have been dealt with by MERYMAN (1966) and ROSE (1967).

In contrast, marine plants are restricted to a much narrower temperature range. This is due to the fact that the freezing point of sea water is $-1{\cdot}9°$ C, and to the high specific heat of water which reduces the temperature extremes encountered in oceans and coastal waters. Only in small bodies of water, like shallow rockpools and lagoon rims of coral reefs, can temperatures of up to 43° C be attained. Thus, the range between minimum and maximum temperatures within which marine plants must survive or exist amounts to only approximately 30 C°, which represents one-third of the temperature range of terrestrial plants. Littoral marine plants, however, are exposed to quite different conditions. Due to air exposure and drying,

which may last several hours during low tides, they are temporarily subjected to the rough thermal climate of terrestrial plants and must be able to tolerate very high and very low temperatures. While terrestrial plants can tolerate extreme temperatures for several weeks or months, littoral plants have to endure extreme temperatures only during a few hours. Exceptions are arctic and antarctic areas where algae can be covered with ice for up to 5 months. Littoral plants seem to have developed adaptations for enduring extreme temperatures to a lesser degree than most typical terrestrial plants and to exhibit no major seasonal differences regarding their ability of adaptation.

The degree of temperature tolerance of algae depends on (i) the absolute intensity of the temperature extreme, (ii) the duration of exposure to the extreme temperature, (iii) the speed of temperature change, both in regard to extreme values attained and re-establishment of normal temperatures, (iv) the plant material tested (organ, state of development, geographic origin), (v) the physico-chemical conditions during, before, and after exposure to extreme temperatures, (vi) the criterion used as tolerance indicator.

Point (i) is self-explanatory; it should not be expected, however, that the degree of damage increases linearly with the extremeness of the temperature. An exponential relationship is more likely because increasing temperatures will progressively damage more and more vital cellular processes. Points (ii) and (iii) are related to the well-known fact that the time factor is immanent in every process; however, in one case time is measured in minutes or hours, in the other in days or weeks. Certain influences manifest themselves only at a later time after return to normal temperature conditions, as has been shown by SCHRAMM (1968) regarding the consequences of drying in the brown alga *Fucus vesiculosus*. Examples illustrating point (iv) will be presented later on. Points (v) and (vi) refer to the fact that extreme temperatures produce manifold direct and indirect effects which, in turn, depend upon the physico-chemical environment (pressure, pH, O_2, salinity, etc.), and on the criterion employed (changing of cell colour, plasmolysis, vital staining, protoplasmic streaming, rate of metabolism, etc.) (ALEXANDROV, 1964; ASAHINA, 1967).

Tolerance to low temperatures

Cold hardiness. The term 'winter hardiness' embraces all properties of the plant that permit it to survive the severities of winter. The multiplicity of such characteristics is indicated in Table 3-9. In some climates, it has been suspected that survival may depend upon the plant's ability to prevent or tolerate excessive water loss from leaves at a time when the transport of water to them is impossible due to freezing of other plant parts.

The first investigations into cold resistance of marine algae were published by KYLIN in 1917. He exposed algae from the Swedish west coast to temperatures of $-2{\cdot}9^{\circ}$ C down to -20° C for 3, 6 and 10 hrs respectively and ascertained the occurrence of death by observing the cells after staining, as well as by absence of plasmolysis. The northern origin of the algae examined (Sweden) accounts for the fact that only temperatures below 0° C could not be tolerated (Table 3-10). KYLIN's experiments revealed that algae from deeper waters are more susceptible to cold (Table 3-10, left column) than littoral algae which may occasionally

Table 3-9

The components of winter hardiness. The 2 main components are indicated by italics (After LEVITT, 1966)

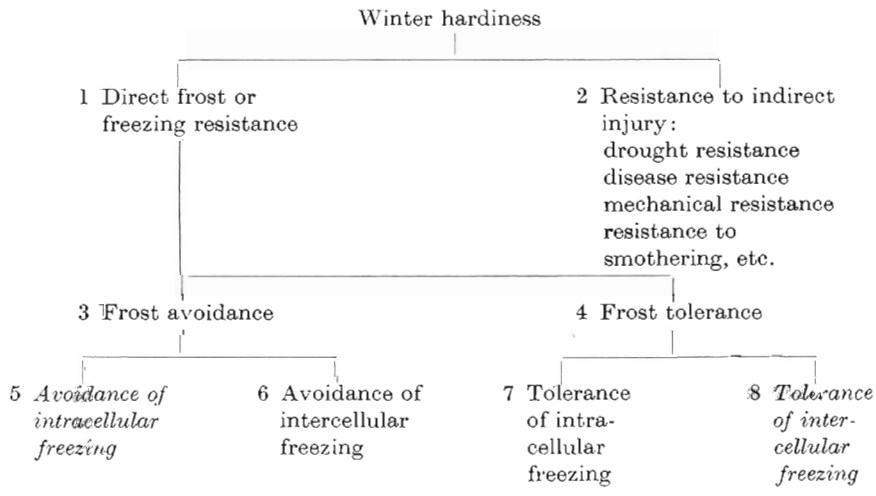


Table 3-10

Tolerance to low temperatures in marine algae from Swedish waters (After KYLIN, 1917)

Cold-sensitive species Death temperature −3° to −5° C	Cold-resistant species Death temperature −10° to −20° C
Trailiella intricata	*Chondrus crispus*
Delesseria sanguinea	*Nemalion crispus*
Delesseria sinuosa	*Porphyra hiemalis*
Laurencia pinnatifida	*Bangia fuscopurpurea*
Laminaria saccharina	*Fucus vesiculosus*
Laminaria digitata	*Fucus serratus*
	Ascophyllum nodosum

encounter very low temperatures in their natural habitats. Moreover, young thallus parts proved to be more sensitive than older ones, e.g. in *Laminaria saccharina*.

KYLIN (1917) assumed that ice formation is essential for death by freezing. The thalli of Fucales do not die, however, even if surrounded by an ice-coating. After removal of the ice-coating, the thallus still proves soft and flexible and hence unfrozen. Recent investigations have shown that death due to freezing occurs only at still lower temperatures. Since during ice formation 80 cal are released for 1 g of water, the quantity of ice formed can be determined calorimetrically and related

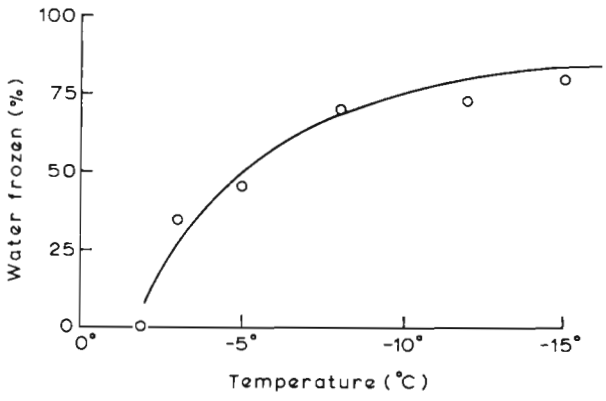


Fig. 3-19: Relation between ambient temperature and the percentage amount of water frozen in the brown alga *Fucus vesiculosus*. (After KANWISHER, 1957; redrawn.)

to the temperature. At $-15°$ C, approximately 80% of the water is frozen in the thallus of *Fucus vesiculosus* without causing death (Fig. 3-19); in fact, this brown alga may be frozen in the Arctic region for months at a temperature of $-40°$ C. According to KANWISHER (1957), the percentage of frozen water of the total water amount at $-15°$ C is 76% in *Ascophyllum nodosum*, 74% in *Chondrus crispus* and 69% in *Ulva lactuca*. The freezing of a portion of the cell water causes an enormous

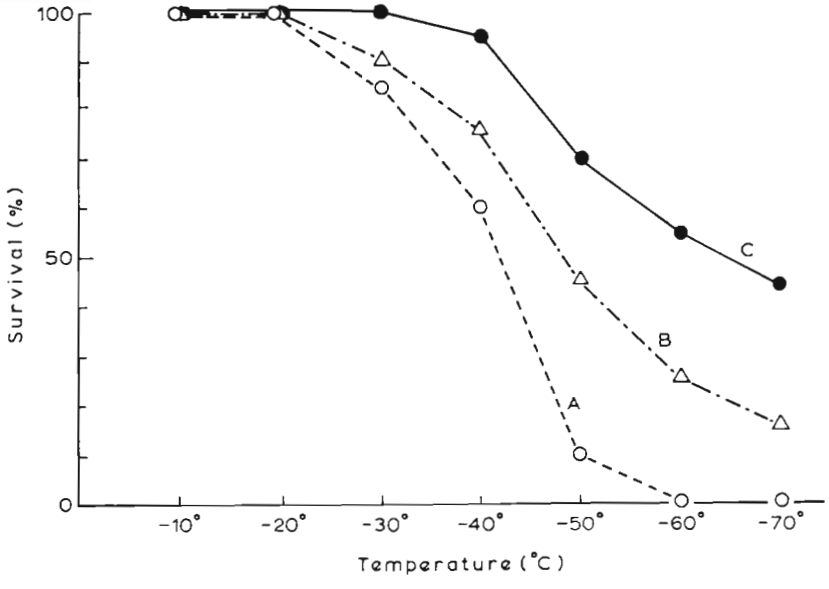


Fig. 3-20: Cell survival (%) of thalli of the red alga *Porphyra tenera* frozen at different temperatures. A: Freezing in sea water after cooling at a rate of about 50 C°/min; B: freezing in sea water after cooling at about 10 C°/min; C: freezing of half-dried thalli (30% water content) after cooling at about 10 C°/min. (After MIGATA, 1966; modified.)

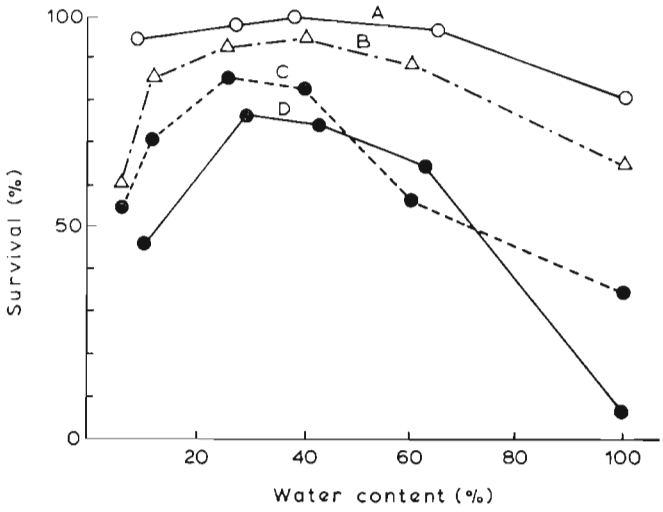


Fig. 3-21: Relation between cell survival (%) and water content (%) of *Porphyra* thalli which had been 'freeze-preserved' for 2 months at about −20° C. A: *Porphyra suborbiculata*, vegetative cell; B: *P. yezoensis*, vegetative cell in adult thalli; C: *P. tenera*, vegetative cell in adult thalli; D: *P. tenera*, vegetative cell in young thalli of about 1 cm length. (After MIGATA, 1966; modified.)

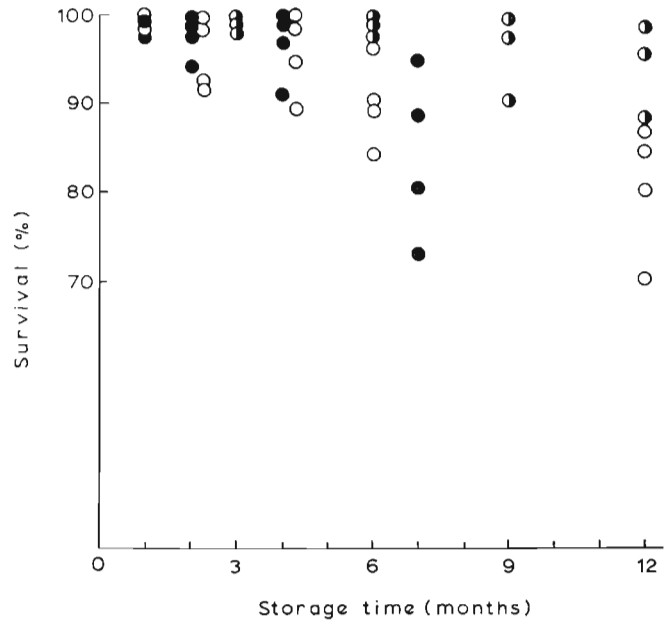


Fig. 3-22: Changes with time in cell survival (%) of *Porphyra* thalli during 'freeze-preservation' at about −20° C in a half-dried state. ○: *P. tenera*, ●: *P. yezoensis*, ◑: *P. suborbiculata*. (After MIGATA, 1966; redrawn.)

loss of free water which—together with the resulting increase in salt concentration—may be the real cause of cold death. Loss of free cell water frequently leads to frostplasmolysis; this was observed, for example, in *Ulva pertusa* and *Enteromorpha intestinalis* by TERUMOTO (1960a, 1961). *U. pertusa* can tolerate $-10°$ C for a period of approximately 24 hrs, *E. intestinalis* $-20°$ C for about 3 days.

Species of the genus *Porphyra* exhibit the highest amount of freezing resistance, a fact which gained great practical importance in Japanese *Porphyra* cultures during the last few years (KURAKAKE and HORI, 1966; MIGATA, 1966, 1967). If the thalli of this red alga have a water content of 20%, they can be held at $-20°$ C up to one year. An important factor is the speed of temperature change. If cooling takes place at a rate of 0·5 C°/min down to $-20°$ C (prefreezing), 55% of the cells survive at $-75°$ C, while less than 5% survive without prefreezing (Fig. 3-20). In culture practice, the nets with the thallus remainders are dried in the open air until the water content is 20%. This lowering of the water content is important because very low temperatures can only be tolerated in such a dried state (Fig. 3-21). Fig. 3-22 indicates changes in cell survival of half-dried thalli of 3 *Porphyra* species during 'freeze preservation' at about $-20°$ C.

TERUMOTO (1964) found the following critical temperatures (50% survival in 24 hrs) in Japanese littoral algae exposed to low temperatures:

Alga	°C
Enteromorpha linza	−20
Monostroma angicava	−20
Bangia fuscopurpurea	−20
Porphyra onoi	−10
Porphyra pseudolinearis (♀♀)	−55
Porphyra pseudolinearis (♂♂)	−70

In 1965 TERUMOTO reported that *Porphyra yezoensis* survived exposure to $-196°$ C for 24 hrs. It is noteworthy that—probably due to lower tissue-water content—Japanese algae are more frost tolerant than Swedish ones, that in *Porphyra pseudolinearis* the male thallus is more resistant than that of the female, and that *P. yezoensis* exhibits the greatest known frost tolerance of all multicellular plants.

If minimum winter temperatures determine the degree of cold hardiness, relations between geographical distribution and winter hardiness are to be expected. BIEBL (1962a, b, c) compared the cold tolerance of some species occurring in Roscoff (France) and at tropical latitudes in Mayaguez (Puerto Rico) and indeed found a greater cold tolerance in the individuals obtained in Roscoff (Table 3-11). On the other hand, certain species are found in the tropics (*Ulva fasciata, Enteromorpha flexuosa*) which tolerate temperatures of $-10°$ C.

In 1958, BIEBL found that many marine algae from Roscoff (France) die at a temperature of $+5°$ C during a 12-hr exposure, e.g. *Sphondylothamnium multifidum* var. *piliferum, Drachiella spectabilis, Rhodophyllis divaricata* and *Cryptopleura ramosa*. Similar results have been obtained on algae from the coast of Venezuela (BIEBL, 1962c; Table 3-12).

In spite of the occurrence of some species in Puerto Rico which can tolerate temperatures down to $-2°$ C in temperate seas, not a single deep-water alga was

Table 3-11

Intraspecific differences in cold tolerance of algae from Roscoff (France) and Mayaguez (Puerto Rico). Listed are the lower limiting temperatures tolerated by 50% of the algae for 12 hrs (After BIEBL, 1962c)

Species	Roscoff (° C)	Mayaguez (° C)
Ulva lactuca	−8	−2
Dictyota dichotoma	+3	+5
Falkenbergia rufolanosa	+3	+14
Laurencia obtusa	+3	+14

Table 3-12

Cold tolerance of marine algae at the coasts and islands of Cumana, Venezuela (After BIEBL, 1962c)

Algae	Cold-resistance				Control
	ice (−10° C)	+3° C	+7° C	+11° C	+27° C
Bostrychia tenella	+	1	1	1	1
Struvea anastomosans	+	1	1	1	1
Centroceras clavulatum	+	+	1	1	1
Hypnea musciformis	+	+	1	1	1
Heterosiphonia gibbesii	+	+	1	1	1
Chaetomorpha crassa	+	+	+	1	1
Spyridia filamentosa	+	+	+	1	1
Halymenia floresia	+	+	+	1	1
Acanthophora spicifera	+	+	+	+	1

1: Alive
+: Dead

found which could tolerate a temperature below +5° C. This fact suggests that the extent of cold sensibility of deep-water algae from warm seas has a stronger genetic basis than the cold tolerance of the local algal populations found in temperate seas. Thus, it seems that algae penetrating into warmer seas tend to lose their capacity for cold tolerance more quickly than species moving from warm to cold seas are able to acquire cold tolerance.

It is not easy to explain the damaging effects of chilling temperatures above zero. In terrestrial plants death can be caused by thermally induced reduction of

water permeability of the protoplasm. In marine algae, damages to vital metabolic processes may be assumed to be primarily responsible for cold death above zero (see also Chapter 3.3).

Seasonal changes in cold hardiness. It has been known for more than 30 years that leaves from terrestrial plants, especially those from alpine environments, show seasonal changes in frost tolerance within a range of more than 30 C°. PARKER (1960) published a study on seasonal changes in cold hardiness of the brown alga *Fucus vesiculosus*. Summer plants can withstand about − 30° C (lowest temperature at which 50% of the frond is still alive after a 3-hr treatment). The viability was tested by the use of 2,3,5-triphenyl tetrazolium chloride which is reduced by the dehydrogenase activity to its red formazan derivative, produced only in living cells. In February and March *F. vesiculosus* plants withstand − 45° C to nearly − 60° C. The growing tips are the hardiest parts of the plant in winter and early spring, but the least hardy in the late summer.

FELDMAN and LUTOVA (1963) investigated seasonal changes in cold hardiness in some brown algae of the Arctic littoral. The time to withstand extreme low temperatures was measured in minutes. In February, *Fucus vesiculosus* was killed at − 28° C after 268 mins, in August after 184 mins. *Ascophyllum nodosum* tolerated − 30° C in February for 293 mins, in August for 79 mins. In contrast, *Fucus serratus* of the lowest littoral showed no appreciable changes in February and August (in February death occurred after 36 mins, in August after 32 mins).

It may be assumed that sublittoral algae show only small seasonal changes in cold hardiness or none at all. Resistance adaptation to new temperature regimes is probably a rather rapid process. FELDMAN and LUTOVA (1963) exposed *Ascophyllum nodosum* to temperatures of 16° and 20° C for 24 hrs in February. This was already sufficient to reduce the survival time at − 30° C from 375 to 154 mins.

The causes of seasonal changes in cold hardiness have been investigated in numerous studies devoted to terrestrial plants; however, no pertinent studies have been conducted on marine plants.

Tolerance to high temperatures

Heat hardiness. Knowledge of the degree of tolerance to high temperatures is of considerable ecological importance. In general, permanently submerged marine plants are less tolerant to high temperatures than shallow-water forms temporarily exposed to air during low tides. While submerged algae are usually not confronted with very high temperatures in their natural habitat, littoral algae may have to withstand considerable heating due to sun radiation, especially during low tide. Thus, investigations carried out by SCHÖLM (1966) on the coast of California (USA) show that algae from deeper waters (12 to 15 m) are less heat hardy than algae growing at water depths between 2 and 5 m. The difference in lethal temperatures (after 30-min exposures) is about 3 to 4 C° (see also SCHÖLM, 1968). In the intertidal brown alga *Fucus vesiculosus* of northern European waters SCHRAMM (1968) recorded, during air exposure, a maximum tissue temperature of 54° C.

AYRES (1916) exposed the red alga *Ceramium tenuissimum* to different levels of high temperature and determined their survival periods. His main results are presented in Table 3-13.

Table 3-13

Tolerance of the red alga *Ceramium tenuissimum* to high ambient temperatures expressed in terms of the length of survival periods at different test temperature levels (After AYRES, 1916; modified)

Length of survival periods (min)	Test temperature (° C)	Medium temperature coefficient Q_1	Q_{10}
7–10	38	1·64	8·5
12–16	37	2·14	14
25–35	36	1·58	30
40–55	35	1·42	47·5
60–75	34	1·18	67·5
75–85	33	2·12	80
160–185	32	1·15	172·5
185–215	31	1·16	200
210–255	30	1·12	232·5
240–285	29	1·21	265·5
300–400	28		320

Table 3-14

Maximum temperatures tolerated during 90 to 120 mins (After VILHELM, 1927)

Algae	Highest temperature tolerated after gradual warm-up (° C)
Green algae:	
Ulva lactuca var. *rigida*	45
Cladophora prolifera	46
Bryopsis disticha	45
Caulerpa prolifera	43
Codium tomentosum	39
Udotea desfontainii	45
Brown algae:	
Dictyota dichotoma	39
Stypocaulon scoparium	45
Red algae:	
Bornetia secundiflora	43
Gymnogongrus griffithsiae	45
Phyllophora rubens var. *nervosa*	44
Nitophyllum punctatum	40
Griffithsia phyllamphora	42
Ceramium rubrum	46
Ceramium lomation	47
Lithothamnium crassum	46
Peyssonnelia squamaria	46

VILHELM (1927) investigated the maximum temperatures which were tolerated during a period of 90 to 120 mins by a number of green, brown and red algal species (Table 3-14). These upper temperature limits are very distinct and occur rather suddenly in most cases; many algae withstand temperatures of only 1 C° below the maximum temperature without harm, provided they are subsequently retransferred into normal temperatures. The tolerated maximum temperatures vary in different species; this applies especially to algae which withstand drying without being damaged. Thus SCHRAMM (1968) found that high-temperature tolerance in *Fucus vesiculosus* increases with decreasing tissue water content (Fig. 3-23).

Bangia fuscopurpurea which normally dies in sea water at 35° C within 12 hrs, survives, air-dry, a temperature of 42° C during an equal period (BIEBL, 1939).

Another factor which may influence the heat tolerance of marine plants is respiration (oxygen supply). As a rule, respiration is impaired at high temperatures

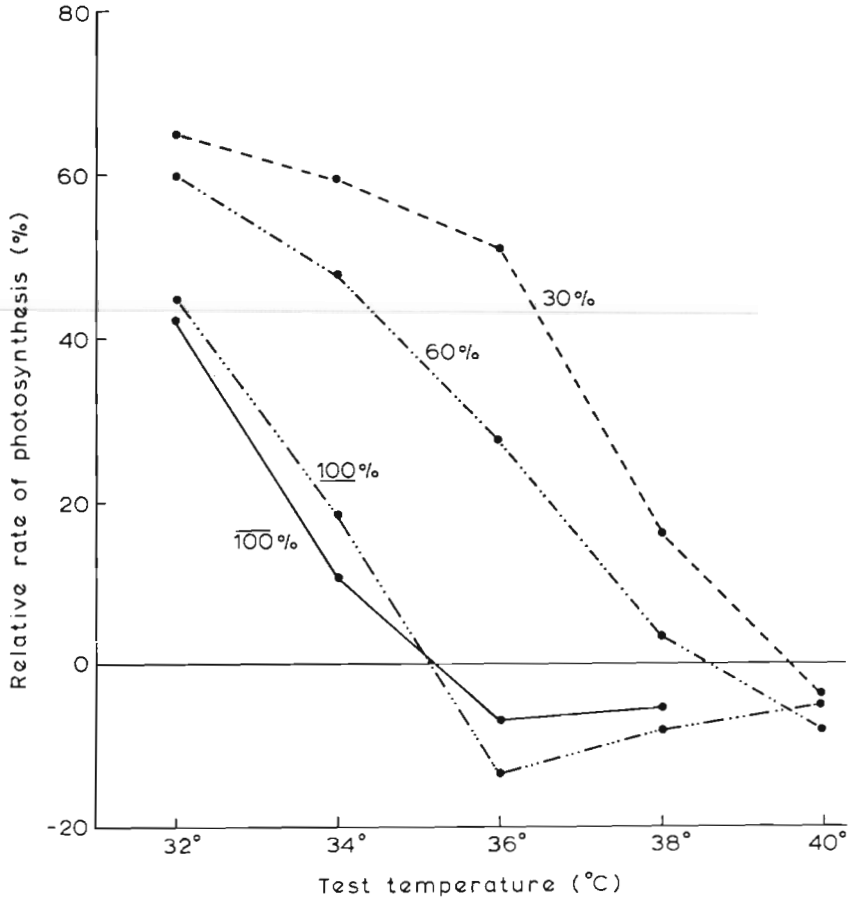


Fig. 3-23: Tolerance to high temperature (expressed in terms of percentage relative rate of photosynthesis) in *Fucus vesiculosus* as a function of tissue water content and temperature. The algae were air-exposed to the test temperatures for 2 hrs at 100% humidity (100%) or exposed sea water ($\overline{100}$%), and subsequently dried to 60 or 30% of their saturation weight. (After SCHRAMM, 1968; modified.)

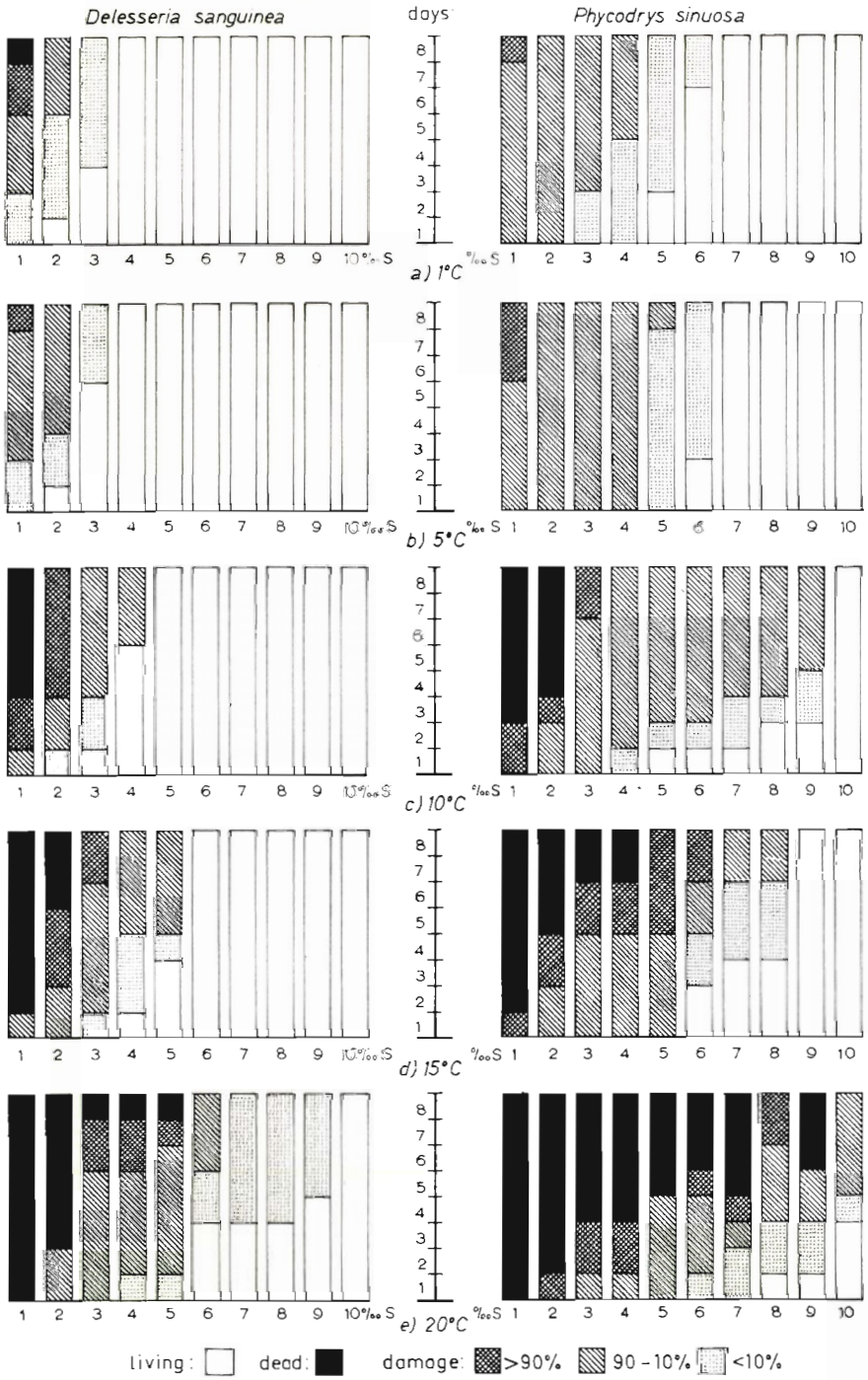


Fig. 3-24: Relations between temperature, salinity and time of exposure in 2 red algae of the western Baltic Sea. (After SCHWENKE, 1959; modified.)

and, unless the available oxygen supply is sufficient, reduction of respiratory rate is the immediate cause of high-temperature damage. SCHRAMM (personal communication) demonstrated this by exposing *Fucus vesiculosus* to 30° C in air and sea water for 14 hrs. Thalli suspended in air were only slightly damaged (extent of damage measured as rate of photosynthesis), while those submersed in sea water did not recover afterwards. Following equal periods of exposure 28° C caused slight damage both in air and sea water, while 31·5° C led to considerable damage under both conditions.

SCHWENKE (1959) made experiments on 2 red algae (*Delesseria sanguinea* and *Phycodrys sinuosa*) from deeper waters of the Baltic Sea, varying temperature, salinity and duration of exposure. He found, at 20° C, an increasing degree of damage with decreasing salinity and increasing time of exposure (1 to 8 days) (Fig. 3-24). At 35° C, damage already became apparent after 40 to 90 mins; following retransfer into normal temperatures it manifested itself in many cases 3 days later as an after-effect.

Tropical algae are not very heat resistant. According to BIEBL (1962c), most of them are killed at temperatures between 32° and 35° C (exposure time 12 hrs), and only a few littoral species survive 40° C.

Seasonal changes in heat tolerance. FELDMAN and LUTOVA (1963) determined the upper thermal limits which kill littoral brown algae at different times of the year. Their main results are summarized in Table 3-15. Due to the short exposure time of 5 mins the lethal temperatures are very high, and the seasonal differences small. Peculiarly, heat tolerance of all species tested tends to be lower in May than in February; it is highest in August in all cases.

Table 3-15

Upper lethal temperatures (mean values in ° C and standard deviations) of littoral brown algae as a function of season (After FELDMAN and LUTOVA, 1963)

Species	February	May	August
Fucus vesiculosus	41·6±0·1	41·4±0·1	42·5±0·1
Fucus distichus	41·0±0·2	40·3±0·1	42·3±0·1
Fucus serratus	39·1±0·1	38·9±0·1	40·7±0·1
Ascophyllum nodosum	39·3±0·1	38·8±0·2	41·5±0·1

MONTFORT and co-authors (1957) investigated the heat tolerance of marine surface and deep-water algae. Representatives of 21 common species were exposed for 3 hrs to temperatures of 22°, 27°, 32° and 37° C, respectively, and after-effects in rates of photosynthesis and respiration recorded for a period of 12 days. It was found that the individual species exhibit considerable gradual differences in heat tolerance over a temperature range of approximately 13 centigrade degrees; after a

3-hr exposure, the most susceptible species reveal the first irreversible damages at 25° C, the most resistant ones at 38·5° C.

These experiments clearly demonstrate the extensive genetic fixation of the degree of heat tolerance. A significant modifying influence of environmental conditions was found only in a few species; but, even in these, the differences in heat tolerance attributable to the modifying influences of ambient climatic conditions are much smaller than those between different species of the same general habitat.

(*b*) *Metabolism and Activity*

Photosynthesis and respiration

KNIEP (1914) was the first author who investigated the effects of temperature on rates of photosynthesis and respiration of marine plants. He found that respiratory rate of *Fucus serratus* drops more rapidly with decreasing temperature than the intensity of its photosynthesis, so that at low temperatures a greater surplus remains for synthesis of organic substance than at high temperatures.

These findings initiated similar experiments by HARDER (1915) who confirmed KNIEP's results in various species of marine and freshwater algae. HARDER determined, for instance, in freshwater *Cladophora* a photosynthesis/respiration quotient (Q) of 0·428 for the temperature range 20° to 22° C, and a Q of 1·608 at

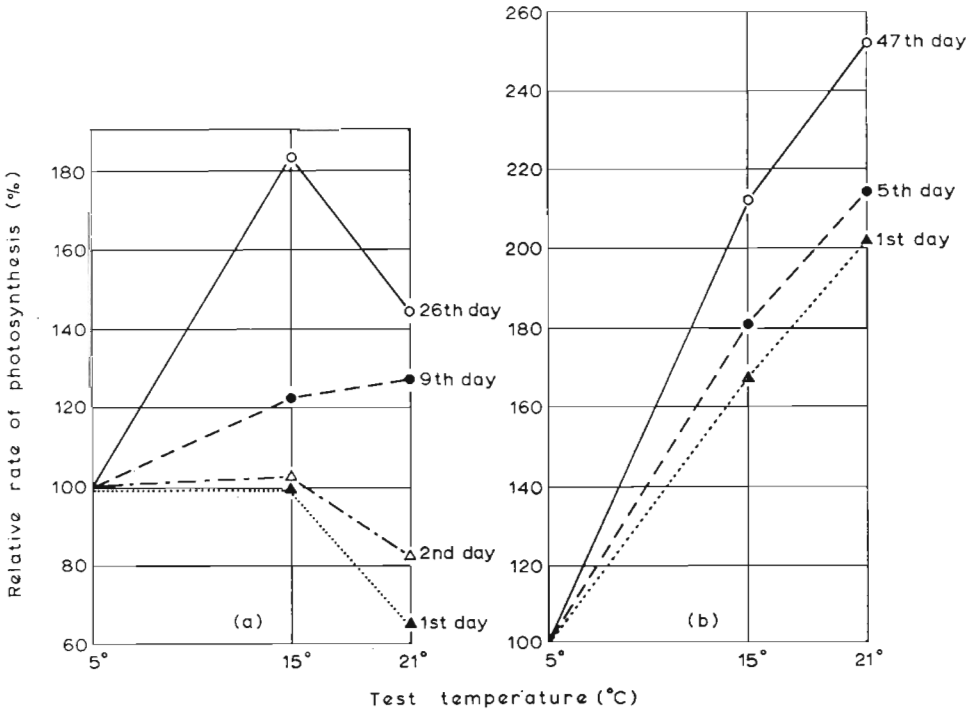


Fig. 3-25: Winter individuals of *Fucus serratus* exposed to different test temperature levels at low (*a*) and high (*b*) light intensities. Adjustment of rate of photosynthesis. (After LAMPE, 1935; modified.)

temperatures between 2° and 3·5° C. Both KNIEP and HARDER have suggested that decreasing Q values at reduced temperatures are responsible for the fact that cold seas harbour rich floras and large seaweed; even arctic seas have a richer flora than is characteristic of terrestrial polar areas. However, in more recent studies it has become obvious that the situation is not quite as simple as originally suggested.

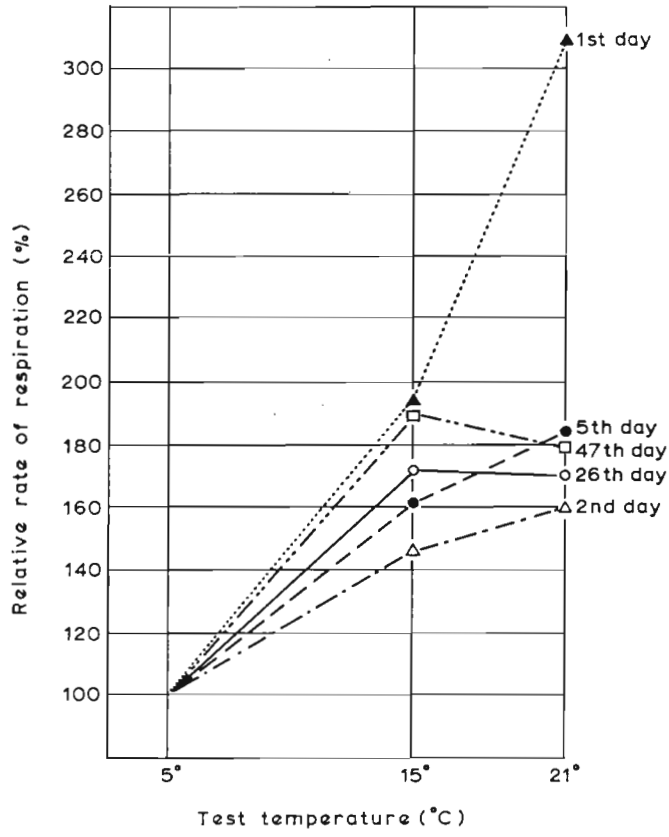


Fig. 3-26: Winter individuals of *Fucus serratus* exposed to different test temperatures at low light intensities. Adjustment of rate of respiration. Substantial non-genetic adaptation is already acquired on the 2nd day of exposure to 21° C. (After LAMPE, 1935; modified.)

Firstly, the statements made by KNIEP (1914) and HARDER (1915) apply only to conditions of faint light under which there is actually little photosynthetic activity. Secondly, it was recognized only later that most plants are capable of plasmatic adaptation to temperature.

Marine plants adjust rather rapidly to different light regimes (Chapter 2.2), and thus can take optimum advantage either of faint light ('shadow plant') or of strong light ('solar plant'). As shown by LAMPE (1935) the same applies to the temperature. When establishing, in summer and winter, temperature curves for respiration and photosynthesis of the same algal individual, entirely different

slopes will result. If, for instance, a winter plant of *Fucus serratus* (initial temperature 5° C) is transferred to summer temperatures of 15° or 21° C the values for low and high light intensities shown in Fig. 3-25 will result. At low light intensities (Fig. 3-25a) the gain in photosynthesis at 15° C increases substantially with time (gain in non-genetic thermal adaptation); after 26 days maximum rate of photosynthesis is achieved at 15° C. In contrast, at high light intensities (Fig. 3-25b) maximum rate of photosynthesis is achieved—irrespective of acclimation time—at 21° C. The respective time course of non-genetic adaptation of the respiratory

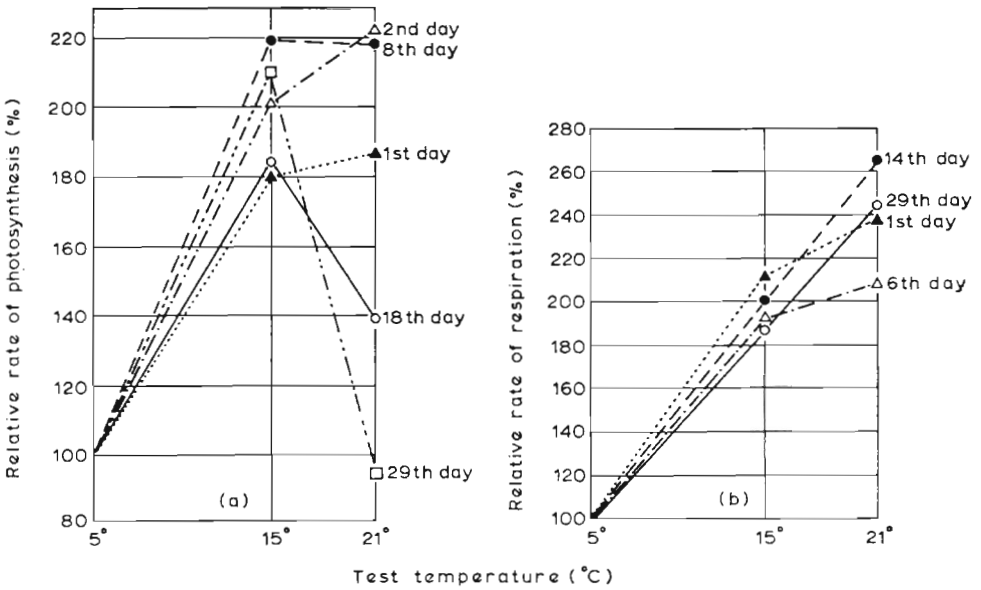


Fig. 3-27: Winter individuals of the cold-stenotherm red alga *Porphyra hiemalis* exposed to different test temperatures. (*a*) Relative rates of photosynthesis; (*b*) relative rates of respiration. (After LAMPE, 1935; modified.)

rate is illustrated in Fig. 3-26. If we compare Figs 3-25 and 3-26 it becomes apparent that the low photosynthetic value determined at 21° C on the first day after transfer from 15° C is due to the initially very high respiratory rate at that temperature. Already on the second day at 21° C, however, the winter plant has adjusted its respiration which subsequently remains almost constant (Fig. 3-26). It should be pointed out that these conditions apply only to eurythermal plants which, like *Fucus serratus*, occur all year round. The cold-stenothermal alga *Porphyra hiemalis*, which develops mainly in winter, cannot adapt its respiratory rate when transferred to high temperature and consequently exhibits a decreasing rate of photosynthesis with time at 21° C (Fig. 3-27).

Accordingly, the hypothesis advanced by KNIEP (1914) and HARDER (1915) maintaining that periods of minimum temperature are most advantageous for photosynthesis, does not appear to be quite correct. Ecologically, it is as important to know the season when a given alga reaches its highest efficiency of producing additional organic matter as it is to recognize the temperature at which the alga

can resist most successfully unfavourable light conditions. In the upper littoral, high light-intensity plants undoubtedly dominate among the brown algae; their optimum productivity is attained at summer temperatures. Just as polar *Fucus* species may be considered 'cold plants', *Fucus serratus* of the North and the Baltic Seas may be called a 'warm plant'. In general, shallow-water perennial algae of North Sea, Baltic Sea and Norwegian west coast are capable of adapting physiologically to local seasonal conditions in such a way that they act as 'cold plants' during winter and as 'warm plants' during summer (LAMPE, 1935).

Recent investigations by KANWISHER (1966) reveal that the concept of LAMPE (1935) requires qualification. KANWISHER studied respiratory rates of some algae in summer and winter (Fig. 3-28). In *Ascophyllum nodosum*, respiratory rates of

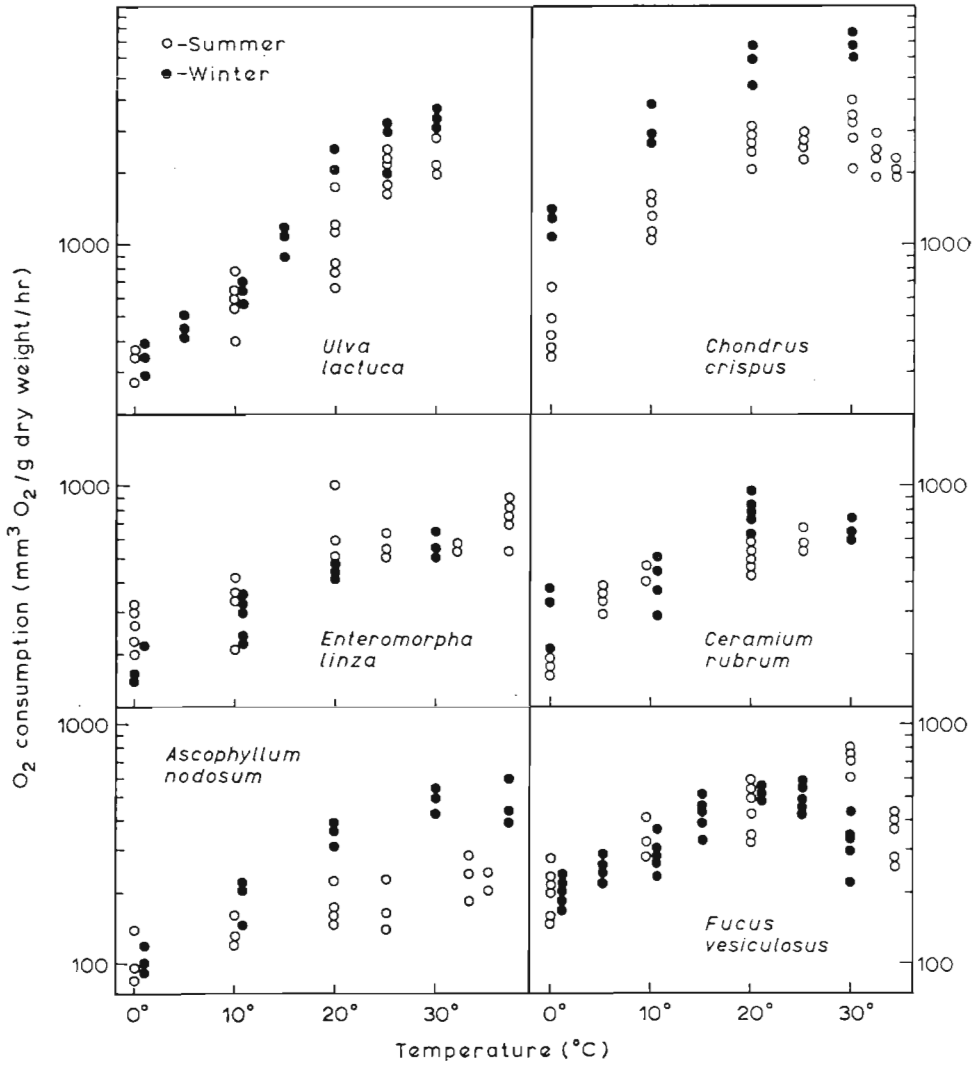


Fig. 3-28: Respiratory rates of seaweed in summer and winter. Semilogarithmic co-ordinates. (After KANWISHER, 1957; modified.)

winter and summer plants are equal at low temperatures, but with rising temperature increase more significantly in winter individuals. *Fucus vesiculosus* does not show such differences. In *Chondrus crispus* respiration of winter forms is, as expected, higher at high temperatures; though it is surprising that respiration values at 0° C are also higher in winter plants. *Fucus vesiculosus* respired down to – 15° C at a rate equivalent to 1% of the 15° C value (Fig. 3-29). A comparison of brown algae from Woods Hole (USA) with those of Labrador (Canada) did not produce enough data to decide whether northern algae have higher metabolic rates at the same temperature than those from warmer climates.

In 1930, EHRKE studied the relations between temperature and photosynthetic rate and respiration. The curves obtained for *Fucus serratus*, *Plocamium coccineum* and *Enteromorpha compressa* are illustrated in Fig. 3-30. It would be an illusion, however, to assume that for a given algal species one standard curve could express the relation between temperature, photosynthesis and respiration. Since temperature effects depend on the length of exposure time, a multitude of curves can be obtained for a single alga. Fig. 3-31 demonstrates the rapid decrease of photosynthesis at 30° C in the green alga *Bryopsis plumosa*. At 30° C, the protoplasm

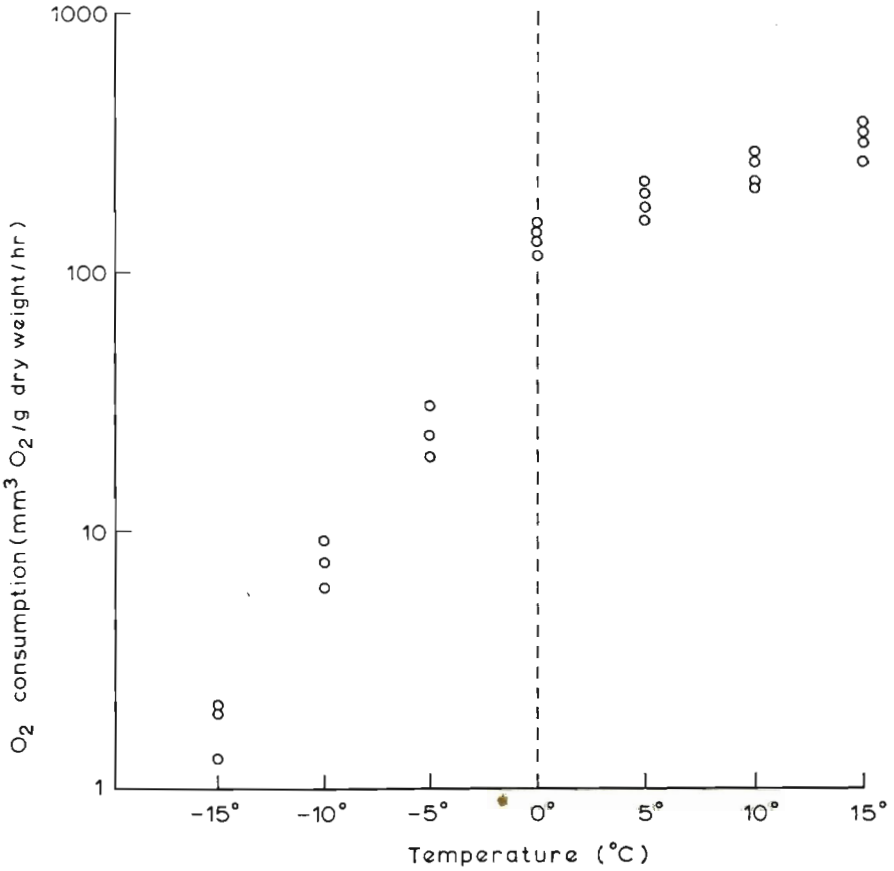


Fig. 3-29: Respiratory rate of *Fucus vesiculosus* over a wide temperature range. Semi-logarithmic co-ordinates; see also Figure 3-28. (After KANWISHER, 1957; modified.)

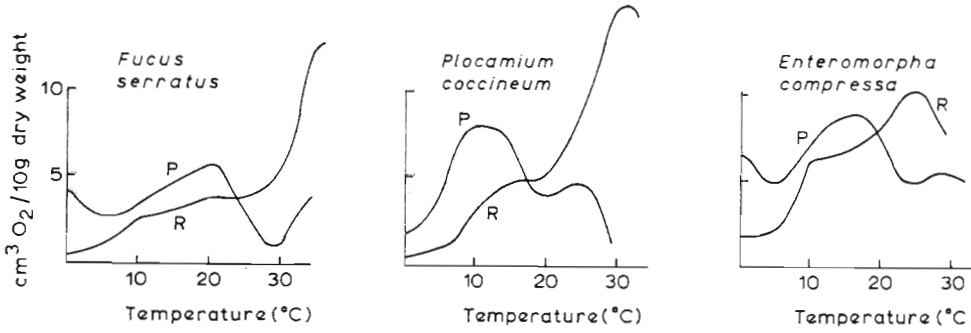


Fig. 3-30: Temperature effects on rates of photosynthesis (P) and respiration (R) in the brown alga *Fucus serratus*, the red alga *Plocamium coccineum* and the green alga *Enteromorpha compressa*. Exposure time to the respective test temperatures was 3 hrs. (After EHRKE, 1930; modified.)

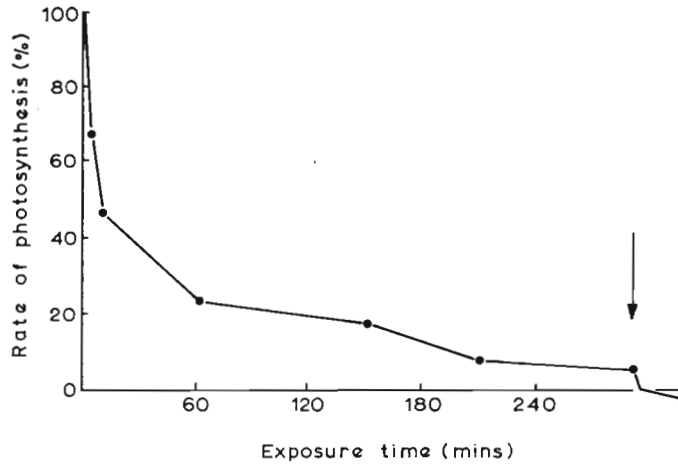


Fig. 3-31: Rate of photosynthesis of the green alga *Bryopsis plumosa* at 30° C as a function of exposure time. Arrow: destruction of protoplasmic structures caused by shaking the thallus. (Original.)

quickly loses its stability and shaking of the thallus is followed by a sudden breakdown of the photosynthetic system (GESSNER, unpublished).

Since EHRKE published his paper, the complicated interrelated effects of temperature and light on photosynthesis have also been discussed. In this chapter, devoted to temperature effects, it may suffice to note that planktonic and benthonic algae with high light maxima for photosynthesis can make the best use of high light intensities at high temperatures (STEEMANN NIELSEN and HANSEN, 1959).

Growth

Since temperature influences all metabolic processes it also affects the growth of algae. FRIES (1966) published a short note on temperature-growth relations in 3 red algae: *Goniotrichum elegans*, *Nemalion multifidum* and *Polysiphonia urceolata* in axenic cultures. *N. multifidum* shows optimal growth at 20° C, while the other

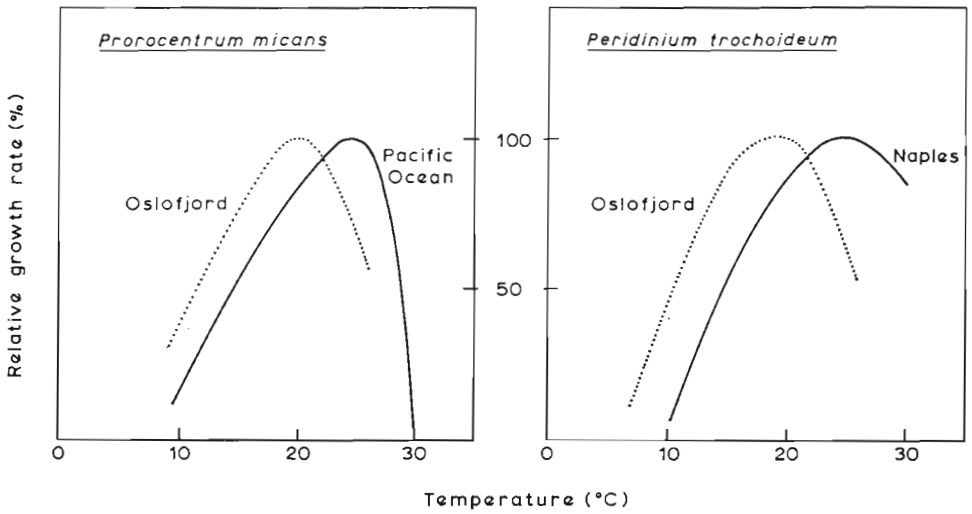


Fig. 3-32: Relative growth rates (rates of population growth) as a function of temperature in unicellular planktonic algal strains from different geographic regions. (After BRAARUD, 1961; modified.)

2 species prefer 22·5° to 27·5° C. 30° C is lethal to *G. elegans* and *N. multifidum*; *P. urceolata* survives at that temperature but does not grow. The optimal temperatures are well above the average temperatures for the warmest month occurring in the natural habitat. It can be presumed that a physiological temperature optimum exists for algae kept under axenic conditions, and an ecological optimum for algae living in non-axenic cultures, i.e. together with bacteria. Unfortunately, FRIES did not compare temperature-growth curves from algae in axenic and non-axenic cultures. BRAARUD (1961) studied the rate of cell division (population growth) of unicellular phytoplanktonic algae and found different rates in strains from different geographic regions at identical test temperatures (Fig. 3-32). These

Table 3-16

Temperature–growth relationships in marine planktonic diatoms; based on data by OSTENFELD (1913), SCHREIBER (1927), GRAN and BRAARUD (1935), BRAARUD (1937) and GRØNTVED (1949) (After BRAARUD, 1961)

Species	Temperature during maximum abundance *in situ* (° C)	Optimum temperature for growth in culture (° C)
Biddulphia aurita	1	(5)
Biddulphia sinensis	13	(16)
Asterionella japonica	8 (GRAN) >20 (Danish waters)	20 to 25
Thalassiosira nordenskiöldi	2 to 3	Excellent growth at 10 to 11

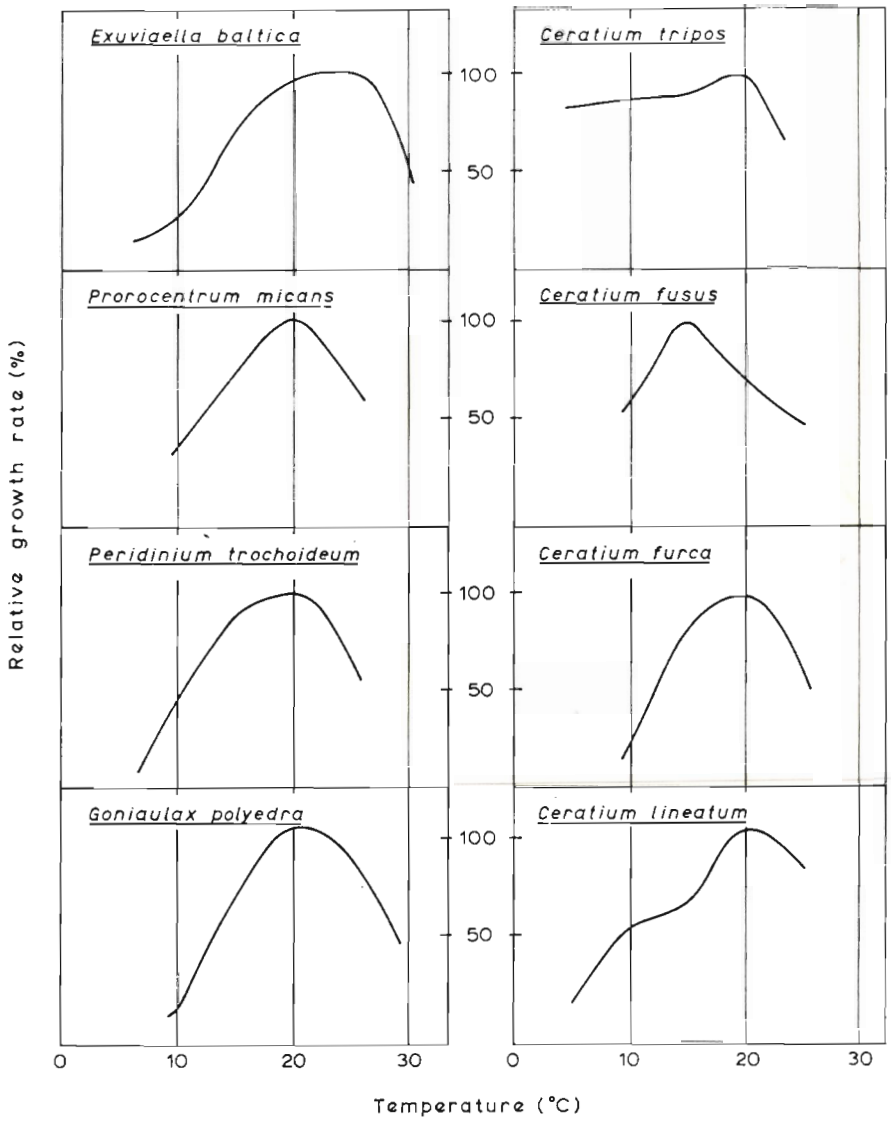


Fig. 3-33: Growth (as percentage of maximum growth rate) of dinoflagellates of the same geographic area at different temperatures. (After BRAARUD, 1961; modified.)

differences indicate climatic adaptations. In many cases, species-specific temperature optima coincide with thermal conditions prevailing during maximum abundance in the sea. However, there may also be considerable differences (Table 3-16).

There exist numerous examples proving general agreement between field data and experimental results, e.g. in dinoflagellates of the Oslofjord (Norway), and there are many cases of pronounced disagreement, e.g. in *Asterionella japonica* and *Thalassiosira nordenskiöldi*. Two explanations may be suggested to explain these discrepancies and both may be involved simultaneously: (i) the experimental

technique has been unsatisfactory and produced false results; (ii) the deductions from biogeographical data were erroneous, as in the case of *Thalassiosira nordenskiöldi*.

A major objection to the culture techniques used is that most cultures are not bacteria free. Hence, 2 effects may be responsible for different growth rates of a culture at different temperatures: (i) the response of the alga and (ii) the response the algal population.

> 'As long as we have no parallel temperature experiments with and without bacteria as associates, we are unable to judge how important the latter effect may be, but the recent discovery of the vitamin requirements of the planktonic algae lends some support to such a view. It would not seem unreasonable to suggest that the difference between the temperature optima observed in the experiments with strains of *Peridinium trochoideum* and *Prorocentrum micans* from widely separated localities might be due to the difference in the bacterial populations of the 2 cultures, since that latter may, presumably, provide vitamins necessary for growth. The other alternative, that temperature is not a decisive environmental factor for the abundance of a species such as *Thalassiosira nordenskiöldi* at low temperature and its absence at higher temperature, as indicated by the experiments, finds some support in the fact that the rise in temperature in spring in northern Atlantic waters coincides with a decline in the supply of inorganic nutrients. Species demanding fairly high concentration of nutrients, therefore, might show a similar seasonal occurrence as a cold-water species. Only new experiments with bacteria-free cultures can give us a clearer picture of the actual temperature effect upon growth' (BRAARUD, 1961).

Nevertheless, it may be pointed out that phytoplanktonic species of the same geographic area show very similar temperature-growth curves (Fig. 3-33).

Numerous experiments have also been made to ascertain temperature effects on growth rates of multicellular algae. KUROGI and co-authors (1962), for example, studied the growth of the *Conchocelis* phase in various *Porphyra* species (Fig. 3-34). Their experiments illustrate how different species of one and the same genus can respond to given temperatures.

In situ observations are usually not suitable for the assessment of direct correlations between growth and temperature. In his paper on *Laminaria digitata*, SUNDENE (1964) made the following pertinent remarks:

> 'In southern Norway growth was most rapid from February to April and slowest in late summer when the temperature was highest. Growth became slower as the temperature increased up to 18° C. At higher temperatures no growth was observed. Temperatures above 20° C were very unfavourable. When the temperature decreased in early autumn, new growth started again becoming more rapid in late autumn and winter according to the fall in temperature.'

Since, together with temperature, light intensity and daylength also vary *in situ*, it is not possible without experimental studies to assess the direct role of temperature.

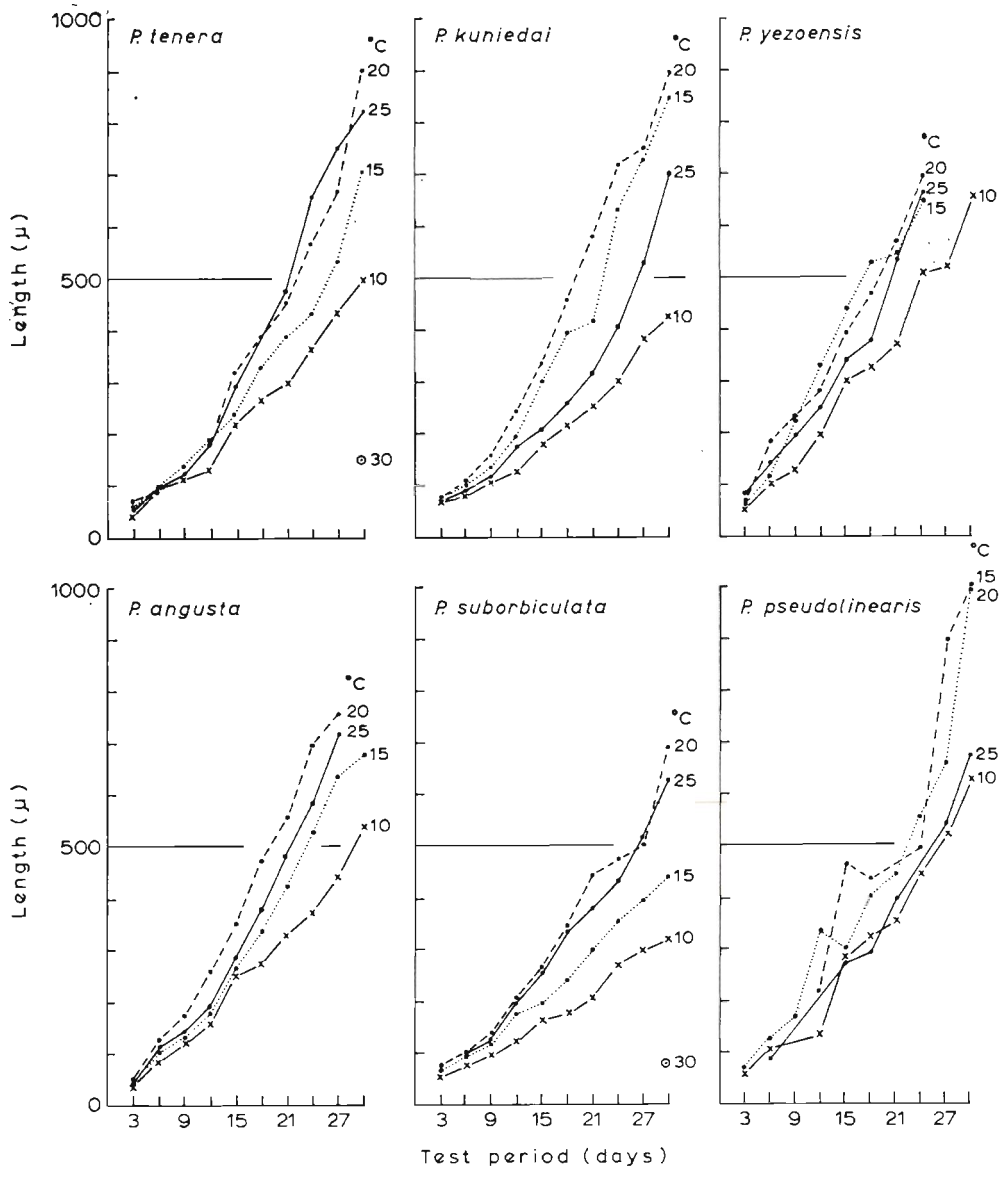


Fig. 3-34: Growth at different temperatures in 6 species of the red alga genus *Porphyra* (*Conchocelis* phase). (After KURUGI and co-authors, 1962; modified.)

The responses to temperature may change with age and development of algae. LI and LI (1966) showed that in young plants of *Undaria pinnatifida* temperatures between 5° and 15° C cause maximum growth; however, if thallus length exceeds 60 cm, rapid growth also occurs at lower temperatures.

Information on temperature effects on the internal metabolism of marine plants is very limited and often hidden in special papers. Therefore, an example concerning a unicellular freshwater alga must suffice. COOK (1966) investigated 2 strains of *Euglena gracilis* and found maximum growth at 29° C. Lower tempera-

tures resulted in increased levels of protein and RNA; both protein and RNA were found to be exponential functions of cell-growth rates, and the rate of protein synthesis was a linear function of the rate of RNA synthesis in both strains tested.

(c) *Reproduction*

KUROGI and HIRANO (1956) and KUROGI and co-authors (1967) conducted detailed investigations into the effect of temperature on monospore formation in the *Conchocelis* phase of the red alga *Porphyra*. Rate of monospore formation is very high at 10° C and very low at 20° C, irrespective of daylength. This applies only to the month of May, since water temperature in August has not the same importance for formation of spores (KUROGI and co-authors, 1967). Consequently, seasonal differences also seem to exist in regard to the temperature influence related to the stage of propagation. LI and LI (1966) found good sporangia development in *Undaria pinnatifida* between 10° and 20° C, but poor sporangia formation below 10° C and above 20° C.

According to AKIYAMA (1965), gametophytes of *Undaria pinnatifida* can survive within a temperature range of − 1° to 27·5° C. At 30° C, they die within 2 to 3 days. The most suitable temperatures for growth and maturation of the gametophytes, and for the formation and growth of the sporophyte, lie between 10° and 20° C (especially between 15° and 20° C). At 5° and 27·5° C gametophyte growth is slower and sporophytes decrease in number.

In many cases, marine plants inhabiting littoral areas fructify during winter, those of the sublittoral in summer (PIGNATTI, 1962).

ZIEGLER-PAGE and KINGSBURY (1968) studied, in culture experiments, the formation of gametangia in the green alga *Halicystis parvula* (*Derbesia tenuissima*) at different temperatures. Their results are shown in Table 3-17.

Table 3-17

Relation between culture temperature and number of gametangia in *Halicystis parvula* (After ZIEGLER-PAGE and KINGSBURY, 1968)

Culture temperature (° C)	Average number of gametangia per plant
16·1	0·8
16·6	0·7
21·7	2·7
23·0	2·0
25·2	1·7

A critical assessment of all available data on temperature effects on reproduction in marine plants does not yet reveal any general trends or rules.

(*d*) *Distribution*

Benthonic algae

The large scale horizontal distribution of marine benthonic algae depends largely upon temperature, while the distributional patterns of terrestrial plants are also influenced by the extent of precipitation and the chemical properties of the substrate. Since the chemical milieu of marine algae is very uniform, except for brackish-water areas, temperature effects may be particularly pronounced. The average annual surface temperatures range from 0·2° C in Spitsbergen over 6·3° (Tromsö), 9·9° (Helgoland), 12·7° (Brest), 15·7° (Banyuls sur Mer), 18·8° (Naples), 22·8° (Alexandria) and 26·8° (Aden) to 27·0° C in Puerto Rico. Such gradients are bound to affect algal distributions.

In the European-Atlantic area, NIENBURG (1930) studied the horizontal distributions of benthonic algae. He compared the distributional areas of various species to different isotherms. In this way it became evident that the 10° C annual surface isotherm determines the northern border of the meridional flora. Except for the cosmopolitan species *Ulva lactuca*, *Enteromorpha compressa*, *Ceramium rubrum* and *Phyllitis fascia*, most algae reveal restricted distributions which are clearly related to temperature. Thus NIENBURG was able to distinguish northern European, Arctic, Arctic–French, meridional, west European–Baltic and meridional–Norwegian species. The last-named group contains species (e.g. *Bryopsis plumosa*) which occur from the southern Mediterranean to northern Norway and hence appear to be temperature independent in regard to their distribution within wide ranges. However, in reality, these species prefer medium-temperature intensities and are distributed so far to the north only because the Gulf Stream transports warm-water masses northwards along the Norwegian coast.

Thus, oceanic currents are especially suitable for proving the importance of temperature for the geographical distribution of algae. The south coasts of Africa, for example, provide an outstanding opportunity for such studies. Since on the west side the cold Benguela Current runs northwards, while on the east side the Agulhäs Current transports warm water from the equator to the south, the temperatures on the west coast are much lower than those on the east coast. Hence in the Lüderitz Bight of the west coast, the annual mean of the surface water temperatures is 13·1° C, while in Durban, on the east coast, it is 21·8° C. These temperature differences result in significant differences in the species composition of littoral algae. Tropical genera such as *Turbinaria*, *Caulerpa*, *Chamaedoris* and others are restricted to the east coast, while the west coast often harbours world-wide distributed genera (ISAAK, 1954).

If, on the other hand, oceanic currents flow along the coast and maintain a rather constant temperature, the marine vegetation may remain largely unchanged over many latitudinal degrees; this has been demonstrated, for example, by SCAGEL (1963) along the coast of British Columbia. He could show that the more resistant species occupying the littoral have a wider distribution than the inhabitants of the sublittoral.

The attempt to use certain species of the marine vegetation as temperature indicators encounters difficulties which SCAGEL (1963) characterizes as follows:

'But just as the thermometer is an essential tool of the physical oceanographer, taxonomy is the tool of the biological oceanographer. In both fields, the degree of reliability of the data obtained is a function of the accuracy of the tool. Unfortunately, the analogy breaks down at this point because of the different nature of the units used. The physicist's units of temperature (degrees) are static; the temperature may change, but the units do not. The ecologist's units are species; as the environment changes, so does the species composition of an area, in direct relation to the environmental changes. But at the same time there may be more subtle but fundamental changes in the units themselves as a result of their genetic flexibility. Species of sexually reproducing organisms merge and diverge because of this potential genetic flexibility. If this were not so, the problem would be much simpler; the biologist's units would be static and lend themselves to the precision and prediction usually possible in the physical sciences.'

Numerous species of benthonic algae have a tropical distribution and do not, or only in exceptional cases, cross the tropical boundaries. Examples are the following species:

Chlorophycea	Rhodophycea
Anadyomene wrightii	*Lithophyllum okamurai*
Anadyomene brownii	*Lithophyllum acrocamptum*
Anadyomene plicata	*Rhodomela crassicaulis*
Struvea anastomosans	*Champia ceylanica*
Struvea tenuissima	*Laurencia ceylanica*
Valonia forbesii	*Corallopsis opuntia*
Valonia fastigiata	*Claudea multifida*
Dictyosphaeria versluysii	*Claudea elegans*
Dictyosphaeria intermedia	*Porphyra suborbiculata*
Neomeris dumetosa	*Dermonema fasciculatum*
Neomeris van bosseae	

On the other hand, there are genera—especially among the brown algae—which prefer cold or at least temperate waters. Thus, *Fucus*, for example, occurs on all coasts of the North Atlantic Ocean but reaches its southern border at the coast of Morocco. The only *Fucus* species of the Mediterranean is *Fucus virsoides*; it is restricted to the northern Adriatic. The genus *Laminaria* is not quite as strictly limited to the northern hemisphere. Even though it attains maximum numbers of species and individuals in median latitudes, it still penetrates far into the Arctic; however, 1 species occurs also in the South Atlantic, and recently 2 *Laminaria* species (*L. abyssalis* and *L. brasiensis*) have been found off the Brazilian coast in tropical latitudes (22 to 23° S) (JOLY and DE OLIVEIRA FILHO, 1967). Like *Fucus* and *Laminaria*, *Macrocystis pyrifera* also prefers colder water, even though it can live at quite different temperatures: in South Georgia between 0° and 5° C, at the Kerguelen between 5° and 10° C, in South Chile between 10° and 15° C, in South Africa and off the North African west coast between 15° and 20° C. The southern border of *Macrocystis* in North America is located near the middle of the

California peninsula; however, it fluctuates to the north or south as a function of seasonal temperatures. The far penetration of *Macrocystis* towards the south is due to the upwelling of cold water along the Californian coast. The kelp is absent in the inner parts of the Bay of California where upwelling does not occur.

The species' composition of the marine benthonic vegetation is clearly related to temperature in coastal areas, extending over several degrees of latitude or exposed to oceanic currents of different origin. KANG (1966) divides the Korean coast into 5 sections: (1) northeastern, (2) southeastern, (3) southern and (4) western section; section (5) is related to the volcanic Cheju Island which is located south of Korea. Table 3-18 shows the percentages of the marine vegetation components of different origin found in each of the 5 sections mentioned.

Table 3-18

Horizontal distribution of benthonic marine algae along the coasts of Korea. The figures represent percentages of the total number of species of different biogeographic origin present in 5 coastal sections (After KANG, 1966)

Biogeographical origin	Coastal sections 1 North-eastern	2 South-eastern	3 Southern	4 Western	5 Cheju Island
Boreal	29	10	6	6	2
Temperate	52	70	76	71	74
Subtropical	2	4	5	4	10
Cosmopolitan	18	16	13	20	15

Toward the coldest ocean areas, Arctic and Antarctic, the decreasing water temperature progressively exerts a negative effect. This fact is illustrated, according to SVENDSEN (1959), by a comparison between the number of species found in Finnmark and in Spitsbergen (Table 3-19).

Table 3-19

Comparison of the number of algal species found at 2 localities in the northern parts of Norway (After SVENDSEN, 1959)

Localities	Brown algae	Red algae
Finnmark	60	65
Spitsbergen	30	37

Spitsbergen offers these marine algae the northernmost habitats. Their temperatures are, due to the Gulf Stream, higher than can be accounted for on the basis of

the geographic latitude. The vegetation is characterized by the examples listed in Table 3-20.

Table 3-20

Examples of marine algal species found near Spitsbergen (After SVENDSEN, 1959)

Species	Supralittoral	Littoral	Sublittoral
Rhizoclonium riparium	+		
Ulothrix pseudoflacca	+	+	
Urospora penicilliformis	+	+	
Fucus distichus	+	+	
Pylaiella littoralis	+		
Chordaria flagelliformis		+	+
Ralfsia sp.		+	
Alaria grandifolia			+
Laminaria digitata			+
Laminaria solidungula			+
Phyllaria dematodea		+	+
Desmarestia aculeata			+
Desmarestia viridis			+
Hildenbrandia prototypus	+		
Rhodymenia palmata			+
Polysiphonia arctica			+
Ptilota pectinata			
Phycodrys rubens			+
Antithamnion boreale			+

+ Species present

Ten of the algal species found near Spitsbergen were arctic, 38 sub-arctic and 10 boreal forms.

Compared to the older papers by KJELLMANN (1875, 1877), SVENDSEN (1959) reports 10 additional species. Since these 10 species are, in general, rather common, it seems improbable that they had been overlooked by KJELLMANN. The more likely conclusion is that they represent new immigrants from the south which could expand their distributional area because of the universal temperature increase during the 20th century. This temperature increase may be documented on the basis of multi-annual means measured in the North Sea; the mean annual surface temperature at the lightship *Weser* has increased during the 20th century 0·31° C, at *Elbe I* 0·60° C and at *Elbe IV* 1·3° C (GOEDECKE, 1954).

Of course these are rather small temperature changes; but many marine algae respond to such shiftings very sensitively and significantly alter their distributional areas. Thus, the red alga *Dasya pedicellata* may be visualized as a recent immigrant from the south into the Swedish Gullmarfjord. The species composition of littoral algal communities is not constant but underlies modifications related to long-term climatic changes. Alterations in species composition and geographic distribution can be clearly established only if the species-specific areas of distribution are exactly known.

The most pronounced temperature differences, both in regard to space and seasonal gradients, are found along the coasts of Japan for which some 1000 algal species have been recorded. Due to the influence of currents of different origin at least 3 areas can be distinguished in which the composition of the marine vegetation is extremely different (ARASAKI, 1966). If one compares well-studied coastal areas of different latitudes, one usually finds a gradient of decrease in species number from south to north. This gradient is not only due to temperature, but also to light (arctic night). An example of a south–north gradient of species numbers is presented in Table 3-21.

Table 3-21

Example of decreasing numbers of algal species from southern to northern latitudes (Original)

Locality	Number of species found
Naples	383
West Norway	220
North Norway	125
Southwest Iceland	129
Northeast Iceland	100
Spitsbergen	67
White Sea	134
Siberian Sea	55

The temperature regimes in arctic and antarctic areas are basically different and hence one may expect significant differences in the distribution of marine benthonic algae. Near the North Pole, a large ice cap exists but no mainland. The high-arctic seas are, therefore, accessible to oceanic currents which transport heat from low latitudes. In exchange, cold arctic waters flow southwards along the sea bottom. Consequently, we find in the Arctic at identical latitudes rather different water temperatures and hence differences in the species' composition of the marine vegetation.

This situation is quite different in the Antarctic. Here exists a large continent which is surrounded by a westwardly directed circulating current. This circular oceanic current system largely prohibits north–south water exchange. Consequently, water temperatures at respective latitudes are quite similar and so is the marine vegetation. The algae, which are in the northermost areas still represented by genera and species from the Arctic, are, therefore, usually distributed in areas which parallel the latitudinal degrees (DELEPINE, 1966).

In general, the map of FRITSCH (1952) demonstrates convincingly the close relation between the horizontal distribution of marine plants and water temperature (Fig. 3-35).

Temperature effects on the composition of the marine vegetation may be exemplified by results obtained in 1938 by FELDMANN who pointed out that the ratio number of red algal species to number of brown algal species increases with

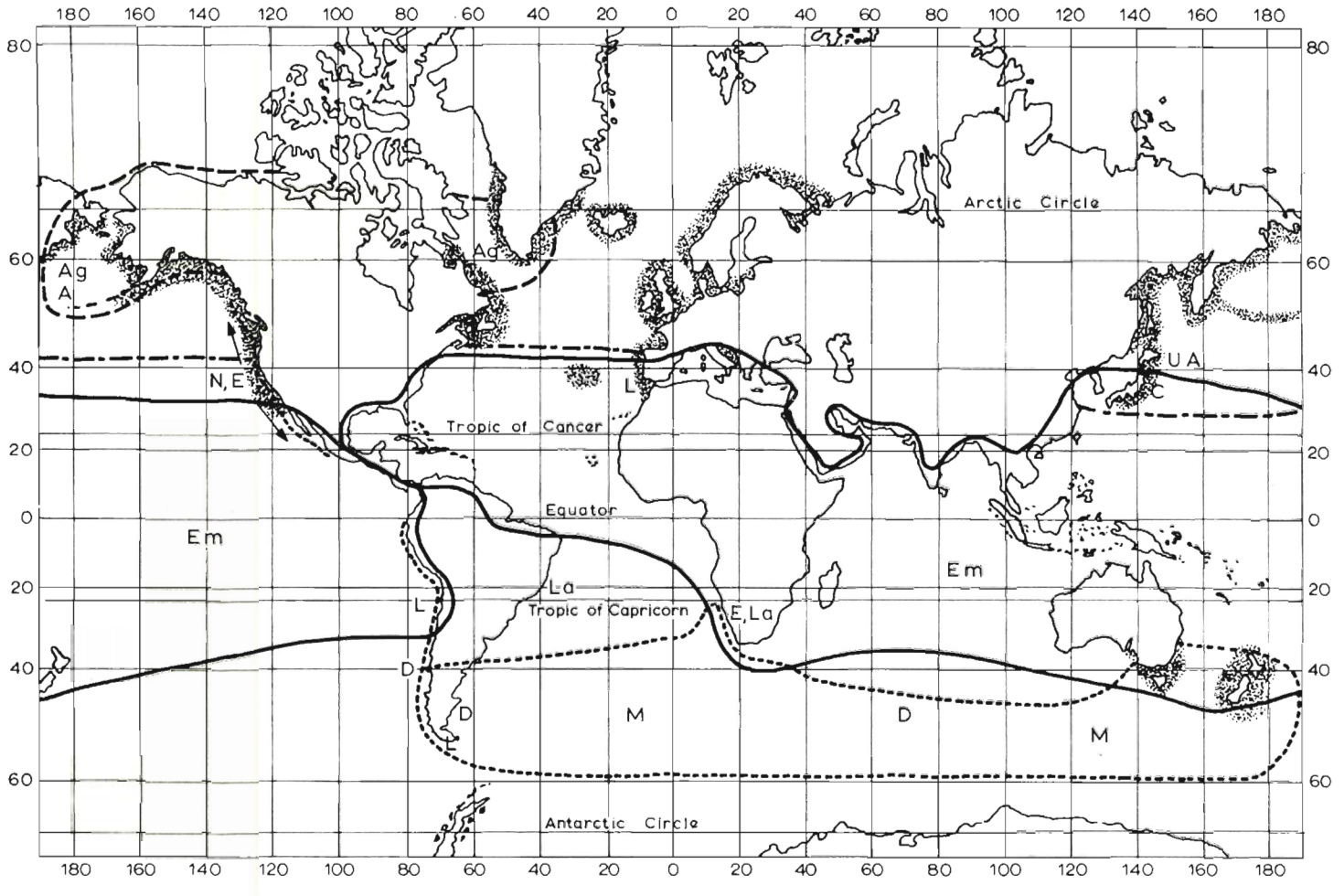


Fig. 3-35: Distribution of Laminariales and Fucales. The dots in the Northern Hemisphere show the area occupied by the genus *Fucus*, in the Southern Hemisphere that occupied by the Australasian Fucales. The continuous line encloses the area occupied by the species of *Eusargassum* (Em), the dotted line that occupied by *Macrocystis* (M), the broken line the area occupied by the Agareae (Ag); the line composed of dots and dashes shows the southern limit of Laminariales in the Northern Hemisphere. The distribution of the following is shown by letters: A: *Arthrothamnus*, C: *Coccophora*, D: *Durvillea*, E: *Ecklonia*, L: *Lessonia*, La: *Laminaria* (outside the northern zone), N: *Nereocystis*, U: *Undaria*. (After FRITSCH, 1952; modified.)

increasing temperature. Based on this relation, FELDMANN introduced the R/P quotient (species number of Rhodophyceae divided by species number of Phaeophyceae) as indicator of the temperature regime. This quotient amounts to values between 1 and 1·5 in the Arctic, 2 in the English Channel, 2 to 3 in the Mediterranean and 4 to 5 in tropical seas. The R/P quotient does not seem to be valid in the Antarctic where a value of 3 was calculated in 550 antarctic and subantarctic species (PAPENFUSS, 1964). But, in marine-plant geography, arctic and antarctic regions cannot be directly compared. The arctic area 'is more arctic than the antarctic is antarctic'. The R/P value of 3 is the result of the overlapping of subantarctic and subtropical areas.

Not only algal distributions show close relations to temperature conditions in the sea. Among the 47 real marine-phanerogam species it is possible to distinguish between cold-water genera (*Zostera*, *Phyllospadix*), genera which prefer the temperate conditions of the Mediterranean (*Posidonia*, *Cymodocea*), and tropical genera (*Halophila*, *Thalassia*, *Syringodium*); *Ruppia maritima* shows a cosmopolitan distribution independent of temperature within a wide range.

Distributional overlapping of the genera mentioned above seems to mask phytogeographic temperature relations. Thus, in the Mediterranean, both *Zostera* and *Posidonia* occur but *Zostera* dominates in the northern part, *Posidonia* in the southern part. During the last few years, *Halophila stipulacea* was also often observed in the southeastern part of the Mediterranean. Since the main distributional areas of this plant are the Indian Ocean and the Red Sea, it may be assumed that it immigrated via the Suez Canal.

The composition of the marine vegetation reflects not only mean annual temperatures, but also seasonal temperature fluctuations. The differences between highest and lowest local-water temperatures are usually greatest in the middle geographic latitudes (see also Chapter 3·0). This is evident already over relatively small latitudinal distances. At Banyuls sur Mer (France) the annual mean of the surface temperature is 15·7° C and the annual temperature amplitude 12·0 C°; in Alexandria (Egypt) the respective values are 22·8° C and 8·0 C°. In purely tropical seas, e.g. in the Caribbean Sea, the annual amplitude is usually less than 3 C°. However, it may come to pronounced seasonal temperature fluctuations of 10 C° and more, also in the tropics, if upwelling brings cold deep water to the surface under appropriate wind conditions. Short-term decreases in surface temperatures may thus exert considerable selective pressures and explain why most tropical algae are capable of surviving exposure to temperatures far below their normal ecological temperature range (BIEBL, 1962c). Such examples make it also clear that not monthly or annual temperature means but short-term extremes are the important circumstances which decisively control algal distributions; this fact has long been known in terrestrial plant ecology.

We have seen that mean annual temperatures of the surface water, which differ some 10 or 20 C°, may cause a completely different species' composition. In view of the fast growth of many marine algae, seasonal temperature fluctuations may also be expected to affect the marine vegetation in various ways. Of course, one must not forget that the temperature fluctuations are largely an expression of the differences in intensity of sun radiation, and hence intimately related to fluctuations in light conditions. In most cases it will prove difficult to distinguish

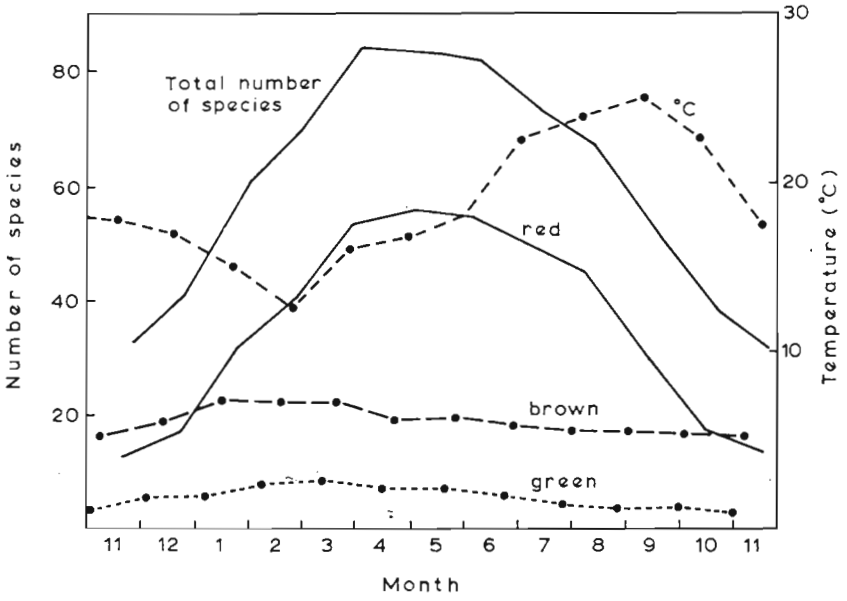


Fig. 3-36: Seasonal variations in the number of red, brown and green littoral algae species present at the Manadzuru Reef, Pacific coast of Japan. (After MATSUURA, 1958; modified.)

between ecological effects of temperature proper and effects of sun radiation. Annual changes in the marine vegetation are usually a consequence of a temperature–light interaction which can be analyzed in detail only in laboratory experiments conducted under a variety of controlled temperature and light conditions. Furthermore, in certain cases, one cannot exclude an endogenous annual rhythm. Thus, in the rocky sublittoral of the North Sea island Helgoland, *Laminaria hyperborea* begins to grow in December and stops growing in June at near maximum light intensities. The growth stop in June is due to an accumulation of photosynthetic products in the plant's tissues (LÜNING, 1968).

Seasonal differences in a given marine vegetation may exist in regard to (i) species number, (ii) number of representatives from certain taxonomic groups, (iii) biomass, (iv) development of reproductive organs, (v) structural aspects of the algal habitus. Of course, such differences usually occur in certain combinations whereby the extent of the effectiveness of the temperature may be quite different. Direct temperature effects as a consequence of seasonal changes may be expected especially in the middle latitudes (approximately 35 to 55° South or North). MATSUURA (1958) investigated the seasonal abundance changes in a number of species and reproductive stages in the Manadzuru Reef on the Pacific coast of Japan. He found pronounced variations in the numbers of red, green and brown algal species present (Fig. 3-36). Among the red algal species, there was a definite seasonal relationship in regard to species with tetraspores, cystocarps and those exhibiting maximum growth (Fig. 3-37).

RAUNKIAER (1934) distinguished between 5 types of adjustment to life under low-temperature conditions. His system was expanded in 1937 by FELDMANN to also

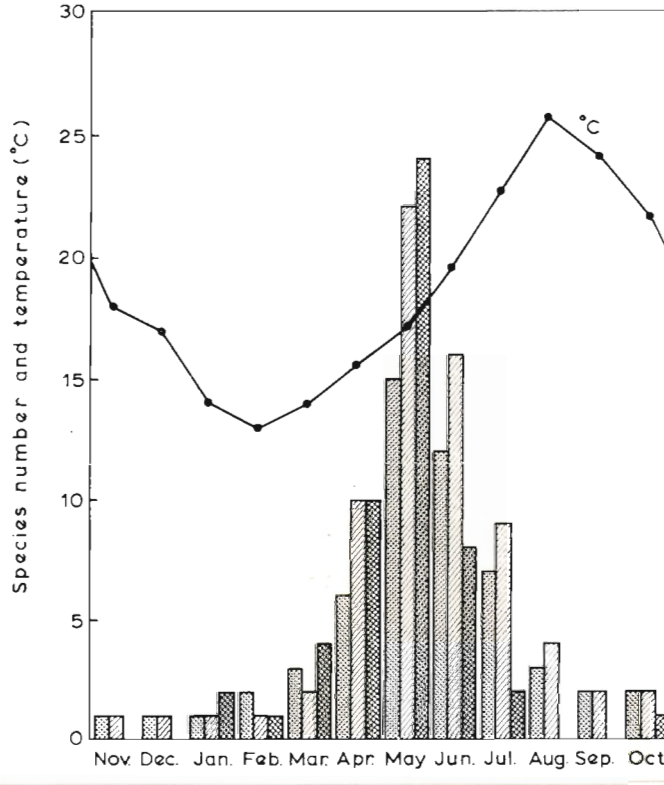


Fig. 3-37: Seasonal variations in the number of red algae present at the Manadzuru Reef, Japan, with tetraspores (dotted), cystocarps (hatched) and species exhibiting maximum growth (cross-hatched). (After MATSUURA, 1958; modified.)

include marine algae. In middle latitudes, these too must be adjusted to tolerate low temperatures during winter, even if not to the same extent as terrestrial plants. FELDMANN modernized his system in 1966 (Table 3-22).

The vertical distribution of benthonic algae depends more on light conditions (Chapter 2.2) than on temperature. Possible temperature effects are likely to be masked or dominated by vertical light-regime changes which have been shown in numerous papers to largely determine vertical-distribution patterns of macroscopic attached marine plants.

The vertical distribution of marine vascular plants with intracellular spaces depends, apart from light, also on the hydrostatic pressure (Chapter 8.2) (GESSNER, 1961).

Planktonic algae

The planktonic algae (phytoplankton) are subject to considerable displacement by oceanic currents; hence their distribution is much more difficult to analyze than that of benthonic algae. However, some benthonic plants may also be subject to current drifting, especially representatives of the genus *Sargassum* which in East Asia even serve as current indicators (YOSHIDA, 1963b); also the turtle grass

Table 3-22

Biological types of marine algae (After FELDMANN, 1966; modified)

I *Annual algae* Present all year round, mostly in several sequential generations			Ephemerophyceae	
Present only during a certain period of the year		occur during the rest of the year in a microscopic but vegetatively active form	Eclipsiophyceae	(1) with small or microscopic gametophytes (2) with microscopic sporophytes (3) in form of microscopic filaments
		occur during the rest of the year in resting stages	Hypnophyceae	(1) with oospores (2) with hormogonia (3) with akinetes (4) with resting spores
II *Perennial algae*				
Perennial part represented by	whole thallus	Thallus erect	Phanerophyceae	
		Thallus in form of a crust on the substrate	Chamaephyceae	
	part of the thallus	part of the erect thallus persists	Hemiphanerophyceae	
		only the basal part persists (all erect thallus parts disappear)	Hemicryptophyceae	a basic attachment disc persists attachment claw persists

Thalassia testudinum has sometimes been found drifting at the ocean surface 1000 km north of its tropical distribution area in the Caribbean Sea; there are many other examples (MENZIES and co-authors, 1967). Numerous phytoplanktonic species, if not the majority of that group, have a world-wide distribution.

Let us first consider the dinoflagellates; *Dinophysis caudata* occurs frequently in tropical and subtropical waters but is not abundant in cold waters. Such wide distributions are typical for the majority of the species of this flagellate group. Cold-water species are, for example, *Dinophysis arctica* and *Ceratium arcticum*. The greatest variety of dinoflagellates is doubtlessly attained in warm waters, especially in tropical seas. Several tropical species are listed in Table 3-23. Definite

Table 3-23

Tropical dinoflagellates (After ABÉ, 1967)

Ornithocercus splendidus	*Ornithocercus thurnii*
Ornithocercus heteroporus	*Ornithocercus steini*
Ornithocercus magnificus	*Ornithocercus francescae*
Ornithocercus quadratus	*Histoneis pietschmani, Amphisolenia thrinax*

relations between temperature and distribution of dinoflagellates have been established by KÄSLER (1938) who studied the Dinophysiales which were collected during the German South Atlantic *Meteor* Expedition (1925 to 1927). It could be shown that in the South Atlantic the 16° C isotherm acted as a distributional border line, especially for the genera *Ornithocercus* and *Amphisolenia*. Of 90 species, 68 were restricted to the area north of that isotherm, 17 occurred only south of it and 5 were found in both areas. In 1967 HALIM investigated samples from the southeast Carribean; among 116 species and varieties he found 16 strictly tropical representatives (*Ceratium humile*, *C. incisum*, *C. lunula*, *Peridinium grande*, *P. quinquecorn*, *Pyrodinium bahamense* and others). The establishment of relations between dinoflagellate distributions and temperature is simplified by the fact that their exoskeleton is soon destroyed after their death, and thus does not persist as long as in diatoms.

Clear relations to temperature have also been found in regard to the distribution of the 'red tides', a mass accumulation of various dinoflagellates near the sea surface, which give the water a red colour. According to RYTHER (1955), the following authors found 'red tides' only at higher water temperatures:

	°C
BARKER (1935)	18–25
BRAARUD and PAPPAS (1951)	18
NÖRDLI (1953)	15–20
PROVASOLI (unpublished)	20–25

Compared to purely tropical seas, temperatures between 15° and 18° C may, of course, already be considered to be low, and thus it seems understandable that

there are statements in literature according to which 'red tides' coincide with decreasing temperatures (HAMMER, 1965).

SMAYDA (1958) devoted an extensive paper to the relation between temperature and phytoplankton distribution and postulated a number of species to be arctic or antarctic, respectively (Table 3-24).

Table 3-24

Separation of phytoplanktonic forms into arctic and antarctic species (After SMAYDA, 1958)

Antarctic species	Arctic species
Chaetoceros criophilus	*Achnanthes taeniata*
Chaetoceros neglectus	*Bacteriosira fragilis*
Eucampia balaustium	*Ceratium arcticum*
Fragilaria curta	*Chaetoceros furcellatus*
Peridinium applanatum	*Fragilaria oceanica*
Synedra reinboldii	*Navicula vanhöffenii*

Since diatoms, characteristic of high latitudes, often occur near melting-ice masses, it seems understandable that they can tolerate not only low temperatures but also salinities below $35^0/_{00}$ (Figs 3-38 and 3-39). In contrast to the numerous cold-stenothermal species among the diatoms the number of true tropical species is rather small. Tropical diatoms include the species *Chaetoceros laevis*, *Gossleriella tropica*, *Hemiaulus membranaceus* and *Rhizosolenia robusta*.

On the other hand, there exists a large number of diatom species which occur between widely different temperature areas and thrive in warm-temperate or even in colder seas; examples are *Planktoniella sol* and *Thalassionema nitzschioides* (Figs 3-40 and 3-41).

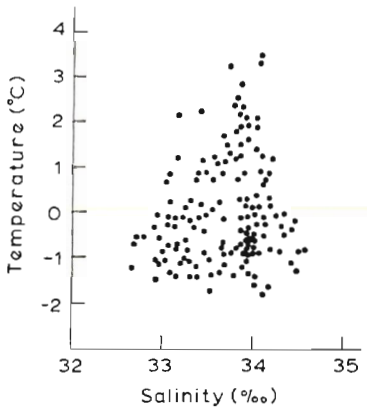


Fig. 3-38: Distributional temperature-salinity relationships in the planktonic diatom *Thalassiosira antarctica*. (After SMAYDA, 1958.)

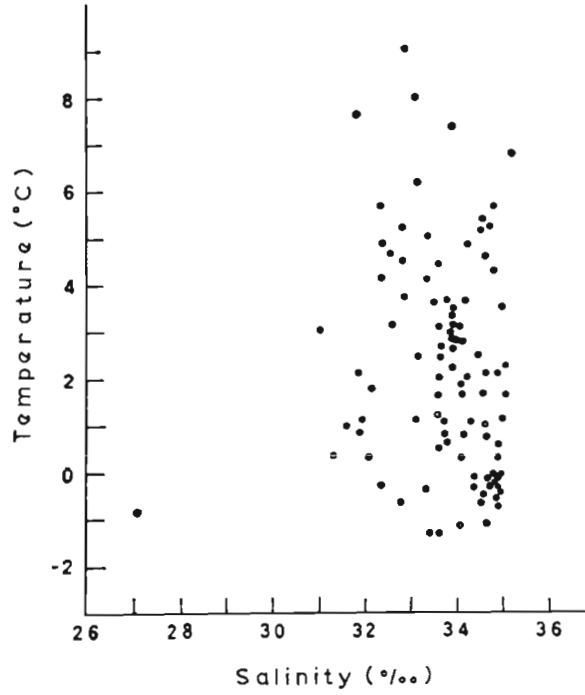


Fig. 3-39: Distributional temperature-salinity relationships in the planktonic diatom *Thalassiosira hyalina*. (After SMAYDA, 1958.)

A special phenomenon in connection with temperature distributions is the phenomenon of bipolarity. A bipolar distribution has been ascribed to a number of phytoplanktonic species. *Thalassiothrix longissima* and *Rhizosolenia hebetata* f. *semispina* are the classical examples given in literature. The concept of bipolarity, in its strictest sense, refers to the occurrence of an organism in both polar regions and its absence in tropical regions; it stresses a discontinuous distribution no matter whether the organism in question is polar or subpolar.

KARSTEN (1905) listed 31 marine phytoplanktonic species as being bipolar; however, all of these are now known to live in the tropics as well. Indeed, true bipolarity at the species level probably does not exist among marine phytoplanktonic forms. The greatest obstacle appears to be the problem of transtropical migration. Passing from one pole to the other necessitates transport through the tropics. A stenothermal cold-water form like *Thalassiosira antarctica* or *T. hyalina* must, therefore, be able to withstand tropical temperatures if it is to reach the opposite pole in a viable state. Unlike zooplankton, phytoplankton cannot take advantage of the more suitable thermal conditions in the colder depths as these invariably lie underneath the euphotic zone. In order to traverse the tremendous distances, active cell division must continue and for this light is a prerequisite. It would seem that neritic species are well equipped to become bipolar, since many produce resting spores, supposedly capable of withstanding extreme environmental conditions. Following their formation, resting spores may be carried to suitable

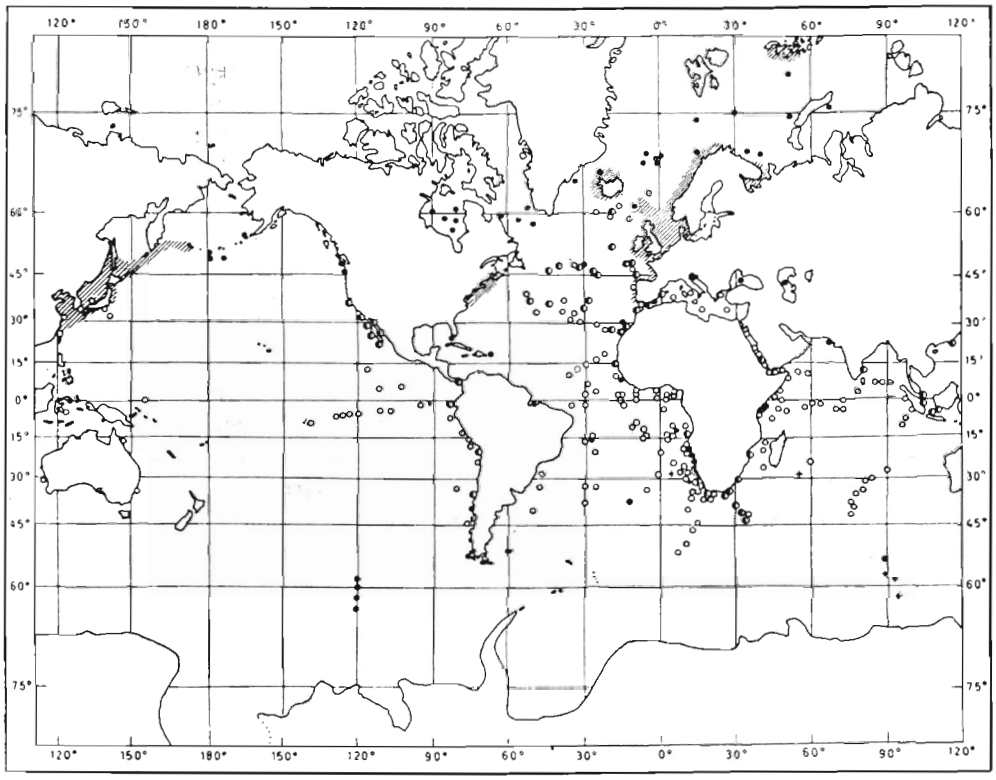


Fig. 3-40: Geographic distribution of the planktonic diatoms *Planktoniella sol* (open circles) and *Thalassionema nitzschioides* (hatched areas, closed circles). Half-filled circles represent occurrences of both species; plus marks indicate findings recorded as varieties of *T. nitzschioides*. (After SMAYDA, 1958.)

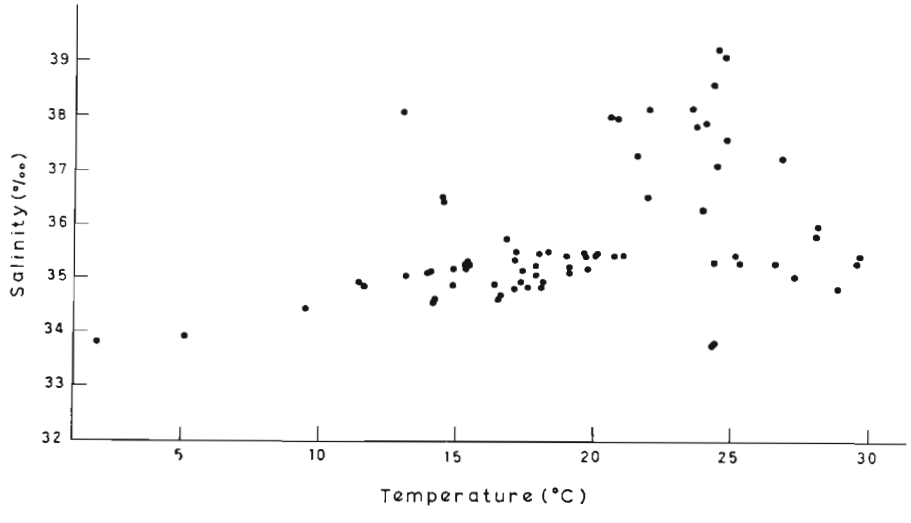


Fig. 3-41: Distributional temperature-salinity relationships in the planktonic diatom *Planktoniella sol*. (After SMAYDA, 1958; modified.)

habitats and germinate; newly formed resting spores may then repeat the cycle. Thus, the species could stepwise extend its distributional range toward the opposite pole. However, as a general rule, only a few of the vegetative cells of a given species capable of producing resting spores do so, and of these only a limited number, if any, are likely to gain access to transport via the proper current system. In addition, dispersal during transport and loss, due to sinking and grazing, continues to decimate the initial number. Even if a species succeeds in this way to establish itself in a new area, it will eventually be confronted with the problem of maintaining populations in a tropical environment as well. If it fails to do so, it must have its resting spores transported from the marginal areas of its distributional range over considerable distances to the opposite polar region. Should these resting spores reach the opposite pole, permanent bipolarity is only assured if a sufficient population density enables the species to withstand the dangers of extinction due to grazing and if resting spores can be produced. It is maintained that the attainment of a bipolar distribution through the mechanism of resting spores is ineffective for marine phytoplankton. This is borne out by the absence of a single known bipolar neritic species (SMAYDA, 1958, p. 172). According to present knowledge, bipolarity does not occur in benthonic algae. Many cosmopolitan species can be found in the check lists of arctic and antarctic areas but not a single species with a real bipolar distribution.

In the North Pacific Ocean, MARUMO (1967) found a close relationship between water temperatures, currents and phytoplankton distributions. The distributional patterns of the diatom communities correspond well to those of the currents (Fig. 3-42). A subarctic cold-water community appears in a cold-current system extending from the Oyashio and the Aleutian Currents to the Alaskan Current. *Rhizosolenia* and *Hemiaulus* communities occur in a warm-water current system

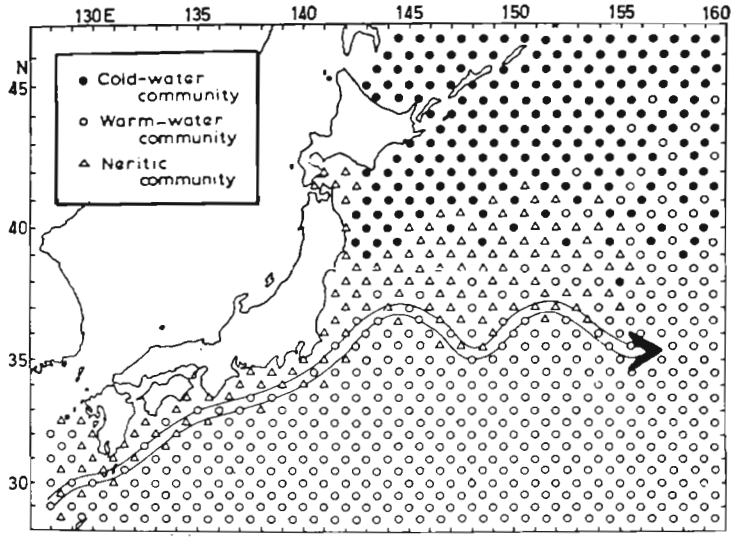


Fig. 3-42: Diatom communities near Japan in summer. The long, wavy arrow indicates the direction of the Kuroshio Current. (After MARUMO, 1967.)

(Kuroshio Current, Kuroshio Extension, North Pacific Current, part of the California Current, North Equatorial Current). Between these 2 current systems a *Nitzschia* community is found. There is no doubt that pelagic diatoms can be widely distributed in subarctic or tropical waters by such circular current systems. In fact, MARUMO found almost identical communities in eastern and western parts of the same latitude, except for endemic coastal species.

The Kuroshio Current and its Extension play an important role in limiting distributions of surface-plankton communities; they represent a barrier for the mixing of biologically different water masses. For example, *Eucampia zoodiacus*, a neritic diatom from the coastal waters of northern Japan, was found only north of the Kuroshio Current and its Extension.

GEMEINHARDT (1934) published an impressive figure on the silicoflagellate distribution on the basis of plankton samples obtained during the German South Atlantic *Meteor* Expedition. From this figure, the distributions of the 2 major genera have been compiled in Table 3-25.

Table 3-25

Number of stations at which species of the silicoflagellate genera *Dictyocha* and *Distephanus* have been found in the Atlantic Ocean and the water temperatures recorded during the South Atlantic *Meteor* Expedition (After GEMEINHARDT, 1934)

Water temperature (° C)	*Dictyocha* species	*Distephanus* species
below 0	1	4
0 to 5	7	41
5 to 10	6	16
10 to 15	—	3
15 to 20	47	4
20 to 25	23	3
above 25	12	—

Dictyocha fibula with its subspecies was found especially at temperatures above 15° C, while *Distephanus speculus* with its subspecies was caught most frequently between 0° and 5° C.

Of course, the large-scale seasonal temperature changes in the middle latitudes affect the distribution of the phytoplankton considerably. In the free oceanic water, seasonal temperature fluctuations are, however, intimately correlated to fluctuations in incoming radiation and nutrient concentrations. Proper analysis of direct temperature effects is, therefore, only possible in experiments conducted under controlled environmental conditions.

The planktonic blue-green alga *Trichodesmium*, occurring in all tropical oceans, is a good indicator for high water temperatures between 27° and 30° C (SOURNÍA, 1968). Among all groups of phytoplankton the coccolithophorids represent the best indicators for water temperature. MCINTYRE and BÉ, (1967) found that definite biogeographic species boundaries can be equated with specific surface water isotherms. They distinguish 5 groups of species (Table 3-26). These groups

Table 3-26

Species of the Atlantic coccolithophorid floral assemblages arranged in descending order of importance within each group (After McINTYRE and BÉ, 1967)

I Tropical	II Subtropical
Umbellosphaera irregularis	*Umbellosphaera tenuis*
Cyclolithella annulus	*Rhabdosphaera stylifera*
Cyclococcolithus fragilis	*Discosphaera tubifera*
Umbellosphaera tenuis	*Cyclolithella annulus*
Discosphaera tubifera	*Gephyrocapsa oceanica*
Rhabdosphaera stylifera	*Umbilicosphaera mirabilis*
Helicosphaera carteri	*Helicosphaera carteri*
Gephyrocapsa oceanica	*Cyclococcolithus leptoporus*
Coccolithus huxleyi	*Cyclococcolithus fragilis*
Cyclococcolithus leptoporus	*Coccolithus huxleyi*
III Transitional	IV Subarctic
Coccolithus huxleyi	*Coccolithus pelagicus*
Cyclococcolithus leptoporus	*Coccolithus huxleyi*
Gephyrocapsa ericsoni	*Cyclococcolithus leptoporus*
Rhabdosphaera stylifera	
Gephyrocapsa oceanica	V Subantarctic
Umbellosphaera tenuis	*Coccolithus huxleyi*
Coccolithus pelagicus	*Cyclococcolithus leptoporus*

occupy 4 floral zones in the Atlantic Ocean (Fig. 3-43). *Coccolithus huxleyi* and *Cyclococcolithus leptoporus* occur in the subarctic and subantarctic; they are eurytherm rather than bipolar forms (Fig. 3-44). Moreover, it is uncertain whether all *Coccolithus huxleyi* found really belong to one and the same species. Electron microphotographs show remarkable differences between specimens from cold and warm waters (Fig. 3-45).

Comparisons of coccolith distributions in the plankton and the sediment reveal discrepancies indicative of recent species' migrations due to the post-glacial warming of the Atlantic. In the sediment of the northern hemisphere post-glacial coccoliths of warm-water species are located 15° (latitude) farther to the south than today (McINTYRE and BÉ, 1967).

(3) Structural Responses

The information available on temperature effects on size and external and internal structures of marine plants is very limited and rather vague. General trends or rules have not yet become apparent aside from the fact that many algae tend to attain a larger final size in the colder parts of their species-specific distributional areas, and may show pronounced seasonal changes in their habitus (Fig. 3-46). Temperature effects on coccosphere structures of *Coccolithus huxleyi* are illustrated in Fig. 3-45.

At the cellular level interesting correlations between functional and structural

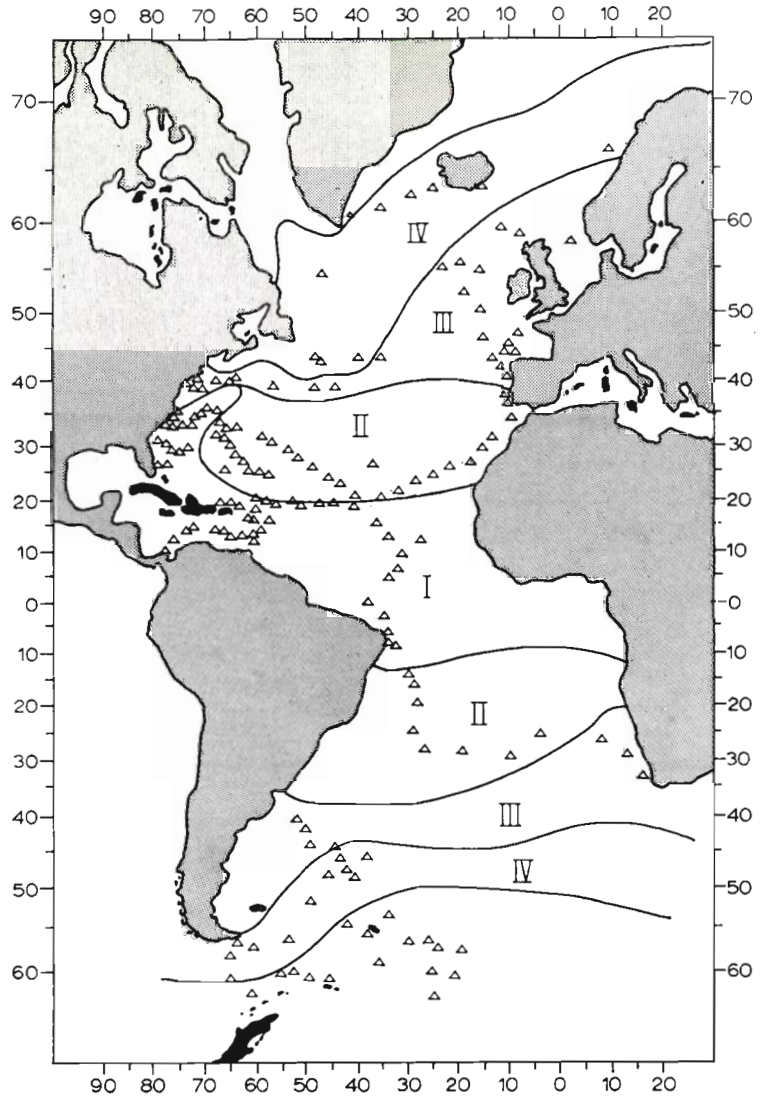


Fig. 3-43: The coccolithophorid floral zones of the Atlantic Ocean. I tropical, II subtropical, III transitional and IV subarctic-subantarctic zone. (After McIntyre and Bé, 1967.)

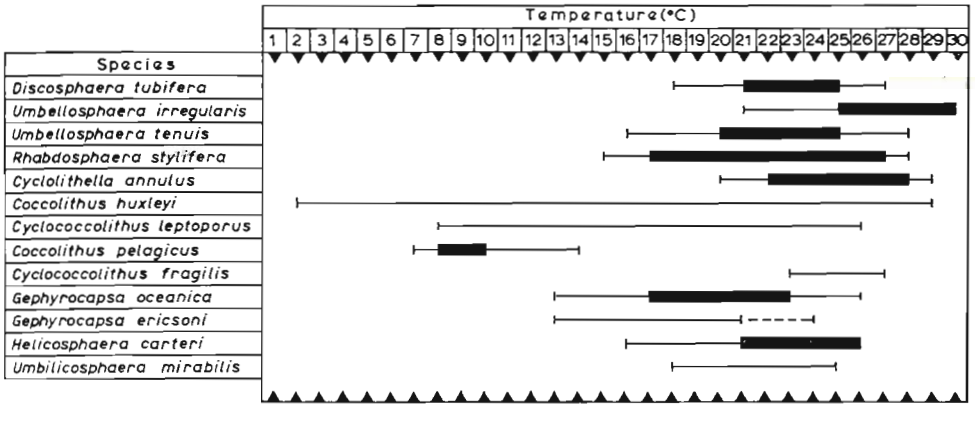


Fig. 3-44: Maximum (lines) and, where ascertained, optimum (black columns) temperature ranges of 13 dominant placolith and cyrtolith species in the Atlantic Ocean. (After McIntyre and Bé, 1967.)

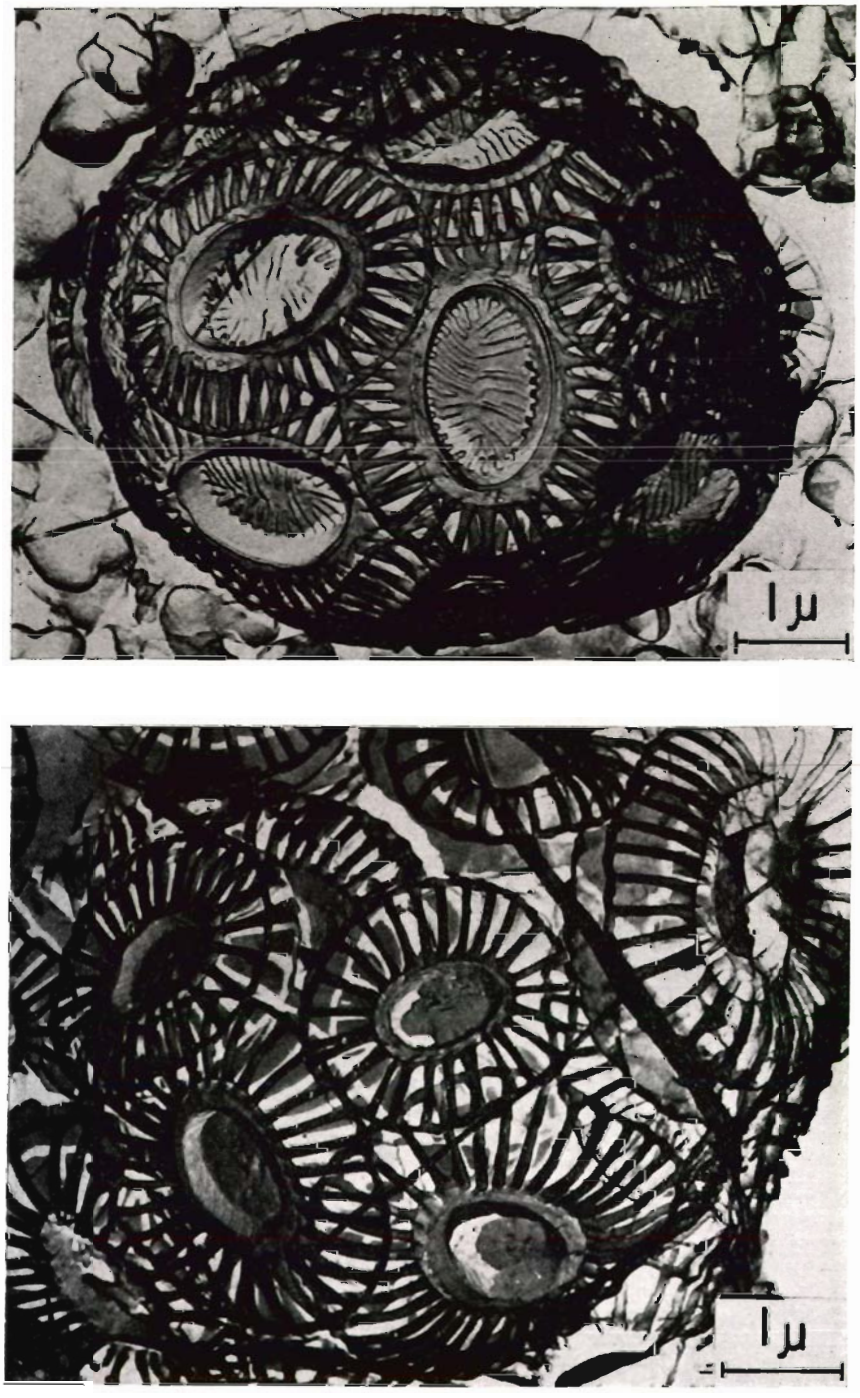


Fig. 3-45: Effects of water temperature on coccosphere structures in the coccolithophorid phytoplankton species *Coccolithus huxleyi*. (*a*) Warm-water type with openwork grill covering the central pore and T-shaped structures in both shields. An organic membrane covers, and partially obscures, these features (Vidal 10). (*b*) Cold-water type (portion of coccosphere) revealing the solid proximal shield and the pore covering (Eltanin 9-13). (After McIntyre and Bé, 1967.)

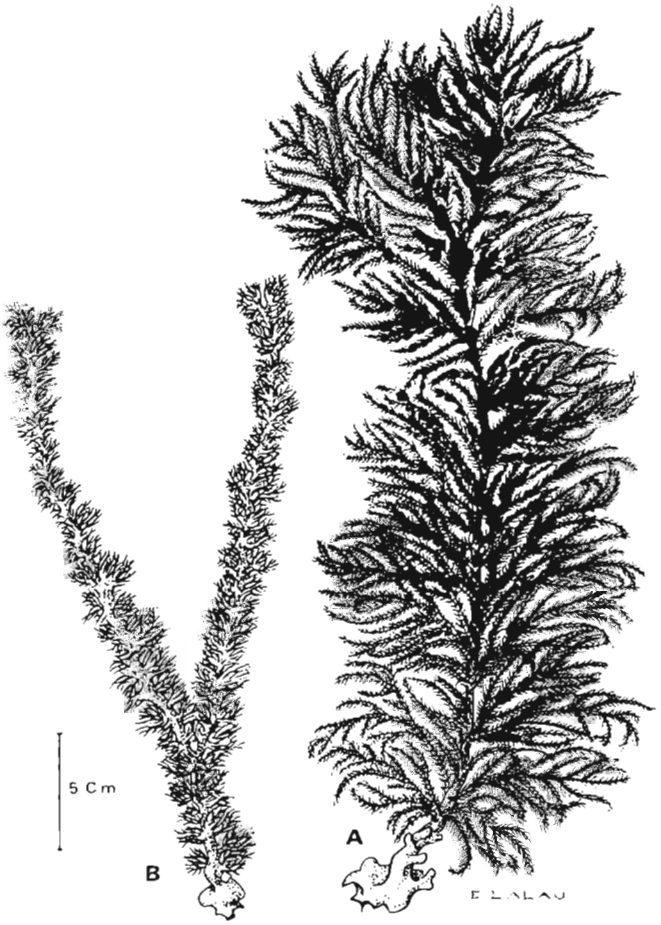


Fig. 3-46: Example of seasonal modifications in size and shape: Hemiphanerophycea *Cystoseira sedoides*; A: collected in July; B: collected in January. Collection area: Coast of Alger. (After FELDMANN, 1966.)

responses to temperature have been reported by STEEMANN NIELSEN and JÖRGENSEN (1968). In *Skeletonema costatum* the rate of light-saturated photosynthesis decreases with decreasing temperature. Cells adapted to 20°, 14° and 8° C show identical light-intensity photosynthetic curves, also for light-saturated rates of photosynthesis. The adaptation to the different temperatures is paralleled by increasing concentrations of enzymes at low temperatures (Table 3-27). The amount of organic matter (μg C) assimilated by one cell generation increases with decreasing temperature. The same is true for proteins. In two series of experiments JÖRGENSEN (1968) demonstrated that the protein concentration is twice as high in cells adapted to 7° C than in cells adapted to 20° C. These differences also influence the cell volume, being 218 μ^3 at 7° C and 127 μ^3 at 20° C. The average height of the cells at 7° C is 7·7 μ, at 15° C 6·1 μ and at 20° C 4·5 μ. Thus

there exists a close relationship between temperature, metabolism, cell size and cell structure.

Investigations into temperature effects on structural aspects can be expected to reveal important new insights both at the individual and subindividual levels.

Table 3-27

Number of cell divisions during the exponential growth phase of *Skeletonema costatum* and the amount of carbon assimilated during one cell generation The tested cells were acclimated to the different temperatures (After JÖRGENSEN, 1968)

Temperature (° C)	Cell divisions (per 24 hrs)	Amount of carbon (C) assimilated in one cell generation (10^{-6} µg)
20	2·3	10·2
15	1·9	12·7
10	1·6	16·5
7	1·0	19·5

3. TEMPERATURE

3.3 ANIMALS

3.31 INVERTEBRATES

O. KINNE

(1) Introduction

Temperature affects both a multitude of environmental properties and of biological processes. Functional and structural responses of organisms to temperature should, therefore, be evaluated in context with other environmental factors and the past and present physiological and morphological states of the living system under consideration (see also Chapters 3.0, 3.1 and 3.2).

In nature, aquatic invertebrates are subjected to a variety of environmental changes; they respond to the total resulting stimulus or stress rather than to single environmental entities. Organismic response patterns to the complex natural environments are multidimensional. However, due to the difficulties of simulating nature in the laboratory, of designing meaningful multivariable experimental conditions, and of critically evaluating the results obtained in terms of cause and effect, most experimental studies devoted to the analysis of temperature effects have been conducted under considerably simplified laboratory conditions. In fact, our present knowledge on temperature responses of marine and brackish-water invertebrates is largely based on univariable designs in which the experimenters tried to keep all factors, except temperature, as constant as possible. While such unifactorial approaches are useful in focussing attention on a given environmental aspect, there is great need for the study of responses to multivariable factor intensity patterns (Chapter 12).

Many aquatic invertebrates encounter, in their natural habitat, specific daily or annual temperature variations—sometimes correlated to concomitant variations in other factors such as light and food—and these may, in some cases, represent an important prerequisite for their well-being and the normal completion of their life cycle (KINNE, 1963a).

Responses of marine invertebrates to temperature may be modified by variations in intensity of other simultaneously effective environmental factors, especially light (Chapter 2), salinity (Chapter 4), pressure (Chapter 8) and dissolved gases (Chapter 9). Different individuals may show remarkable variations in their thermal responses, even in cases of identical biological and environmental backgrounds. While cases of such individual variation are usually exceptions in the sense of experimental statistics, they may be of ecological significance, especially in populations under increased environmental stress, since they provide a basis for selection and population survival.

On the whole, responses to temperature are similar in marine and freshwater invertebrates. In some cases reference will, therefore, also be made to freshwater forms.

Innumerable papers have been published concerning the effects of temperature on marine and brackish invertebrates. Reviews on or including this subject have been written by BULLOCK (1955), PRECHT and co-authors (1955), PROSSER (1955), GUNTER (1957), MOORE (1958), REMANE and SCHLIEPER (1958), BRETT (1960), PROSSER and BROWN (1961), KINNE (1963a, b, 1964a, 1967), MIHURSKY and KENNEDY (1967). For basic considerations concerning temperature relations of organisms, temperature-rate functions, their mathematical formulation, and the so-called temperature rules consult BĚLEHRÁDEK (1935), ALLEE and co-authors (1949), HEILBRUNN (1952), ANDREWARTHA and BIRCH (1954), PRECHT and co-authors (1955), HEDGPETH (1957), JOHNSON (1957), PROSSER and BROWN (1961), QUANTITATIVE BIOLOGY OF METABOLISM (1964, 1966, 1968).

(2) Functional Responses

Body temperature. There may be temporary differences between the environmental temperature and the body temperature of poikilotherms resulting in measurable temperature gradients. Such gradients can modify the response pattern of internal body parts. Temperature gradients between ambient and body temperature may be caused by internal heat production through metabolic processes (especially muscular activities), absorption of radiant energy, and insufficient time for attainment of isothermy after a fast change in environmental temperature. Absorption of radiant energy and heat exchange with the environment may be modified by changes in body shape and colour (see also Chapter 3.0). Hardly any

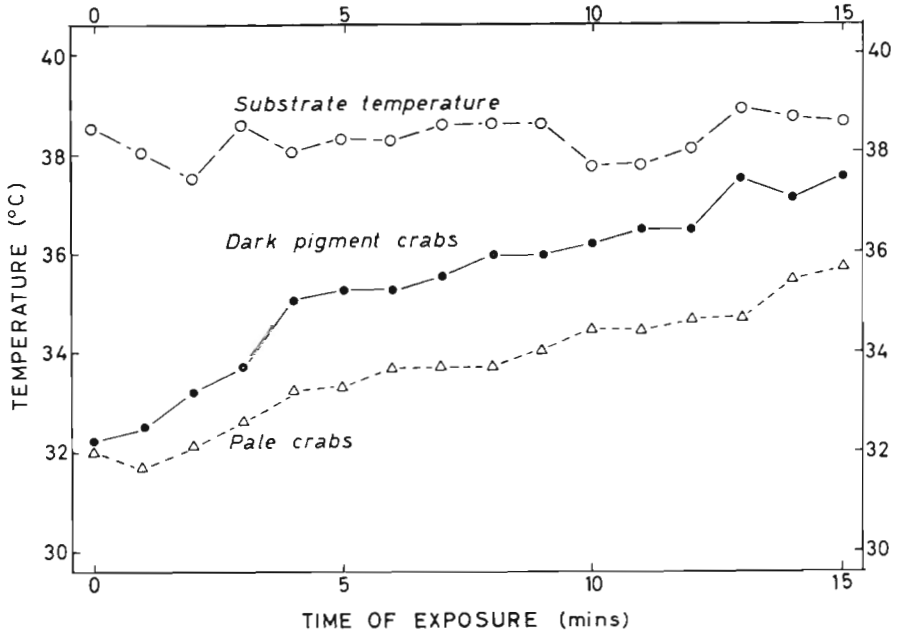


Fig. 3-47: Body temperature (thermocouples; near midgut) of semiterrestrial crabs *Uca pugilator* as a function of body pigmentation and time of exposure to sunlight. (After WILKENS and FINGERMAN, 1965; modified.)

critical analyses regarding the time course, and extent of temperature gradients between body parts of marine invertebrates and the surrounding water, are available.

WILKENS and FINGERMAN (1965) have studied body versus ambient temperatures in the semiterrestrial decapod *Uca pugilator*. On hot days, the crabs return to their dark, moist burrows in 18 to 24-min cycles. This behaviour is likely to result in replenishment of water lost through evaporation and in a periodic lowering of the body temperature. Evaporation rate increases as water saturation of the air decreases. In saturated air, *U. pugilator* can temporarily survive at 40·7° C, in dry air at 45·1° to 47° C. In bright sunshine, dark-pigmented crabs had body temperatures about 2 C° higher than pale ones (Fig. 3-47).

LEWIS (1963) measured body temperatures of 3 tropical intertidal invertebrates, the barnacle *Tetraclita squamosa*, the limpet *Fissurella barbadensis*, and the gastropod *Nerita tesselata*. Measurements were conducted by thrusting the thermocouple (fine wire, copper-constantan, insulated with lacquer) tip under the operculum of *Nerita*, through the apical hole of *Fissurella*, and between the plates of the carapace of *Tetraclita*. The 3 intertidal invertebrates do not absorb radiation as do inanimate bodies or black bodies. Thus, on a sunny day, the tissue temperatures of *Tetraclita squamosa* were below black body temperatures by about 12·9 C°, *Nerita tesselata* by 10 C°, and *Fissurella barbadensis* by 12·2 C°; similarly, body temperatures were all below the temperature of an inanimate body. The most obvious reduction of the heating effect of the sun is attained by evaporation. On the whole, body temperatures of the 3 tropical invertebrates were considerably above ambient air temperatures on a hot sunny day; these gradients were less marked on a cloudy day.

SOUTHWARD (1958) conducted field measurements of the body temperature of intertidal barnacles and limpets while exposed to air (near Plymouth, England; with thermocouples). Under many weather conditions, the body temperatures were higher than would be expected from local meteorological values of air temperature. These differences are interpreted as being due to retention of sea temperature by invertebrates and rocks and to the heating effects of sunlight. Similar studies have been conducted by EDNEY (1951) on body temperatures of woodlice.

In future experiments, more attention should be paid to possible gradients between internal and external temperatures. Regarding our present knowledge, it appears that differences between ambient and body temperatures do not significantly affect the thermal responses of marine invertebrates.

Supercooling. Some organisms can tolerate body temperatures considerably below 0° C without ice formation. Freezing-point determinations performed on marine invertebrates have shown that the freezing point of body fluids is similar to, or lower than, that of the external medium. Exceptions are estuarine and brine shrimps and semiterrestrial crabs; in salinities close to or above that of sea water, these forms maintain hypo-osmotic body fluids, which would be expected to freeze at higher temperatures than sea water (KINNE, 1963a). Various circumstances, however, may suppress or delay freezing: (i) as is well known, aqueous solutions can supercool by several degrees, particularly if contained in capillary

spaces; (ii) exposure to decreasing temperature leads first to extracellular freezing, dehydration, and gelation, resulting in an increase in osmoconcentration of cell fluids, and thus delaying freezing and augmenting cold resistance of cells; (iii) bound water is more resistant to freezing than free water; (iv) organic solvents with anti-freeze effect may be added to body fluids. Hence certain marine animals can withstand supercooling well below the freezing point of sea water without internal ice formation.

An increase in blood osmoconcentration at low temperatures (winter) has been shown for several crustaceans, especially in salinities significantly below that of sea water, for example, in various aquatic and semiterrestrial species (WIDMANN, 1935), *Rhithropanopeus harrisii* (OTTO, 1934; KINNE and ROTTHAUWE, 1952), *Eriocheir sinensis* (OTTO, 1937), *Palaemonetes varians*, *Leander serratus* (PANIKKAR, 1940b), *Gammarus duebeni* (KINNE, 1952) and *Crangon crangon* (BROEKEMA, 1941; FLÜGEL, 1959, 1966). In supranormal salinities, however, blood osmoconcentration may be lower at low temperatures than at high temperatures, for example, in *Gammarus duebeni* and *Rhithropanopeus harrisii*. In *Nereis diversicolor* no effect of temperature on blood osmoconcentration could be demonstrated (BEADLE, 1943). The phenomenon of supercooling is not confined to aquatic organisms; certain insects may be supercooled to as low as $-40°$ to $-50°$ C (SALT and MAIL, 1943). Some frost-hardy insects use glycerol in high concentrations as antifreeze and supercooling facilitator (SALT, 1958). SALT (1961) considers $-30°$ C to be a practical limit for supercooling.

(*a*) *Tolerance*

The species-specific degree of temperature tolerance of marine invertebrates may change during ontogeny. It is often smaller in gametes and developmental stages than in the adult. Hence, for ecological considerations knowledge of temperature conditions which limit the reproductive activities or the viability of gametes, fertilized eggs, embryos or post-embryonic stages, are of particular importance. The degree of temperature tolerance at these critical life-cycle stages is largely species specific since no or only small adjustment capacities are available during early ontogeny. Thermal tolerance may also be a function of sex, age, physiological or nutritive condition, environmental history, and season.

Thermal death in the sea

Death from low sea temperatures is as universal in marine and brackish-water invertebrates as death from extreme high temperatures. Both are particularly prevalent in habitats which are subjected irregularly to thermal stress (e.g. BRONGERSMA-SANDERS, 1957).

Cold death in the sea has been reported from Florida by BANGS (1895), FINCH (1917), STOREY and GUDGER (1936) and MILLER (1940); from Danish waters by BLEGVAD (1929), JOHANSEN (1929) and SMIDT (1944); from the Bermuda Islands by VERRILL (1901); from the coast of Texas by GUNTER and HILDEBRAND (1951) (in Bermuda and Texas, temperatures did not fall below 7° and 4° C respectively); from the North Sea by COURTNEY and WEBB (1964), CRISP (1964a, b), ZIEGELMEIER (1964); from the vicinity of Seto (Japan) by TOKIOKA (1963). STOREY (1937)

and GUNTER (1957) claim that, in Florida and Texas, death during cold spells occurs at intervals of about 10 years.

The lower temperature limit is generally higher in warm-water species than in cold-water forms. Particularly in marine invertebrates with lower temperature limits above 0° C, a sudden fall in temperature may be more detrimental than low temperatures. Gradual, slow temperature decrease is tolerated much better than abrupt change; some species tolerate gradual slow changes of up to 30 or 35 centigrade degrees.

A number of marine and brackish-water invertebrates cannot withstand freezing. In the Arctic, for example, populations of intertidal forms, such as the gastropod *Littorina littorea*, suffer high mortality rates unless they avoid freezing by moving down below the low-water mark when winter approaches. Other temperate invertebrates undertake annual migrations in order to avoid critically low water temperatures. On a sandy beach in Denmark, 2 months of unusually severe freezing killed the total populations of the polychaete *Scoloplos armiger* and the molluscs *Mytilus edulis*, *Scrobicularia plana* and *Littorina littorea*; *Arenicola marina* suffered 95% mortality, *Cardium edule* and *Mya arenaria* 80%, *Nereis diversicolor* 70% and *Macoma baltica* 33% (BLEGVAD, 1929). In Danish offshore waters, high mortality of shallow-water species during 'severe ice winters' seems to be responsible for the fluctuations in abundance from year to year of invertebrate larvae (THORSON, 1946b, p. 473). Similar reports have been published by DELPHY (1917), CAULLERY (1929), JOHANSEN (1929), ORTON and LEWIS (1931) and SMIDT (1944).

During the extreme cold winter of 1962/1963, sea-water temperatures near Helgoland (North Sea) fell to an abnormal low of $-1{\cdot}5°$ C. At least 50% of the *Branchiostoma lanceolatum* population died, and none of the autumn settlement of newly metamorphosed individuals survived; death rate was as high as 90% among the largest *B. lanceolatum*. It was suggested that activity (muscular movement, swimming, burrowing, functioning of pharyngeal mechanism) was greatly reduced below 3° C and that the depth to which lancelets of different sizes burrow into the sandy substrate could account for differential mortality through cold (COURTNEY and WEBB, 1964). During the same cold winter, the southeast coasts of Great Britain suffered extreme low temperatures; northern forms were not seriously affected, but some celtic and southern forms suffered very high mortalities in the intertidal zone, particularly in embayed areas. Death resulted not only from direct tissue damage, but also from lowering of activity (failure to remove silt by ciliary action, to cling to the rock surface and to burrow). Even where high mortalities occurred, a few, perhaps more resistant, individuals survived in favourable habitats, so that, in general, distribution limits were little affected (CRISP, 1964a). Near Helgoland, most benthic invertebrates suffered tremendous losses. Death rates were highest among the Lamellibranchia; thus the *Angulus fabula* population was almost completely killed, and most *A. tenuis* died; only 2 lamellibranch species suffered relatively few mortalities: *Macoma baltica* and *Nucula nitida*. Among the other marine invertebrates the highest mortalities were observed in the gastropod *Lunatia nitida* and the echinoderms *Amphiura filiformis*, *Echinocardium cordatum* and *Astropecten irregularis*. Death rates were lower in the crustaceans and lowest in the polychaetes. In general, juvenile benthic

invertebrates were more tolerant than mature and older individuals. The degree of cold damage was modified by water depth, type of substrate, zoogeographical affiliation, body size and, presumably, motility (ZIEGELMEIER, 1964).

CRISP (1964b) edited a special series of papers concerned with the effects of the severe winter 1962/1963 on marine life along the British coasts. The general conclusions drawn (CRISP and co-authors, 1964) reveal that the largest number of cases of severe mortality was found among the southern or lusitanian elements of the British fauna, whose distribution is confined to the south and west (Table 3-28).

Table 3-28

Tolerance to severe cold in the sea (British coasts) of 3 different faunistic elements (selection of species for which the evidence of cold damage was clear). Severe mortality: at least 50% losses in the coldest areas of the west and south, or values approaching 100% in the southeast. Less severe mortality: some definite mortality. Unaffected mortality: normal rates of survival (After CRISP and co-authors, 1964; modified)

Faunistic elements	Severe mortality number of species (%)	Less severe mortality number of species (%)	Unaffected mortality number of species (%)	Total number of species
Southern	57	24	19	21
Celtic	39	47	14	36
Arctic	0	15	85	26

The celtic elements, which occur all round the coasts of Britain and extend to southern Scandinavia, were not as seriously reduced in numbers, although in the southeast some of these hardier species suffered quite heavily, indicating that in cold winters they may be living near their endurance limits. The boreal–arctic elements, with a few exceptions, revealed no unusual mortality; their range of distribution extends into the Arctic Circle and to the south of the British Isles.

CRISP and co-authors (1964) considered also the losses of the few introduced forms. *Elminius modestus* showed high survival under all but the most extreme conditions; it turned out to be hardier than would have been expected for a temperate–subtropical Australasian species. But the cold tolerance exhibited by *Venus mercenaria*, *Urosalpinx cinerea*, and to a lesser extent by *Crepidula fornicata* was not unexpected in view of the climatic extremes of their 'home' areas at the east coast of North America.

Several southern invertebrates tolerated the extreme cold winter of 1962/1963 over much or all of their distributional range, e.g. *Chthamalus stellatus*, *Clibanarius misanthropus*, *Xantho incisus*, *Paracentrotus lividus* and, to a lesser degree, *Patella intermedia*. CRISP and co-authors (1964) stress that caution is required in the interpretation of the complete survival of the more extreme lusitanian species such as *Paracentrotus lividus*, because, even at the northern limits of their range, it was less cold than elsewhere to the southeast. These species may well be more

susceptible to cold than the celtic elements which showed high mortalities in the southeast. Had the pattern of temperature anomaly been different, these lusitanian forms might not have survived as successfully. It seems likely that their northern and eastern distribution limits are not primarily controlled by minimum winter temperatures (MOORE and KITCHING, 1939; CRISP and SOUTHWARD, 1958), and that the upper temperature level during the breeding season is of importance via its influence on fecundity and reproductive rates (CRISP and co-authors, 1964)—a limitation which might act quite independently of tolerance to cold in winter (HUTCHINS, 1947; SOUTHWARD and CRISP, 1956).

The immediate circumstances leading to cold death in the sea are complex. Direct lethal damage of body structures seems largely to be restricted to cases involving ice formation. More important seem critical reductions in life-supporting functions such as motility, respiratory movements, muscular strength, as well as in coordination and integration of body functions and critical decrease in resistance to parasitic and microbial infections. This view is supported by the fact that many organisms did not die during exposure to minimum temperatures but days, weeks or even months later. According to CRISP and co-authors (1964), barnacles, limpets and topshells began to show mortalities at the beginning of the cold period; however, *Elminius modestus* were only enfeebled and lived many weeks before eventually succumbing; such delayed death was also observed in *Chthamalus stellatus* (heaviest mortalities occurred a month or more after coldest weather), *Actinia equina*, razor shells and other bivalves, and, possibly, in *Corystes cassivelaunus*. In several species it was noted that young adults were less subject to torpor and mortality than older (larger) ones. Mass mortalities of scallops *Placopecten magellanicus* have been reported from the southwestern Gulf of St. Lawrence (Canada); extreme temperatures, fast changes in habitat temperature and temperature gradients (thermocline) rate among the most likely causes next to disease and predators (DICKIE and MEDCOF, 1963).

In most temperate marine invertebrates, tolerance to cold is more pronounced in winter than in summer. In addition to conditioning by the thermal history, such annual variations in thermal resistance may be related to the photoperiod (long days frequently tend to increase activity and to lower thermal resistance) and to the quality and quantity of food (glycogen, fatty acids and lipid contents in the food, and its total amount, may affect cold hardiness; however, conclusive data are still lacking). A number of aquatic invertebrates die at water temperatures well above 0° C; some tropical forms may suffer severe cold damage at temperatures as high as 20° C. A malacostracan from warm brackish waters of 37° to 47° C is reported to have a lower lethal temperature as high as 30° C (BARNES, 1959).

In regard to death from high sea temperatures, many invertebrates are killed by thermal conditions not far above those to which they are accustomed (SEMPER, 1881; MAYER, 1914, 1918; SHELFORD, 1916; GOWANLOCH and HAYES, 1927; HENDERSON, 1929; NEWCOMBE and co-authors, 1936; BROEKHUYSEN, 1940; KINNE, 1954a, 1963a). The upper critical temperature may be different in different areas of a species' distributional area. Thus *Limulus* from Massachusetts (USA) died at 41° C, but specimens from Florida died at 46·3° C; *Aurelia* from Halifax (Canada) died at 26·8° to 28° C, from Florida at 40° C (MAYER, 1914). Among intertidal animals from different parts of the world, heat tolerance tends to increase

as a function of habitat–height above low-water level. In South Africa, marine gastropods occupying the upper intertidal (longest exposure to high temperatures) had an average lethal temperature of 43·0° C; the respective values in the lower tidal levels were: 41·7° C in the midtidal, 39·5° C in the lower intertidal and 34·1° C in the sublittoral (BROEKHUYSEN, 1940). Echinoids, notably *Lytechinus variegatus* and *Tripneustes ventricosus*, and other reef flat invertebrates (crabs, chitons and ophiurids) suffer heavy mortalities in Puerto Rico during sudden extreme midday low waters in spring and summer; death often results from prolonged exposure to temperatures up to 40° C (GLYNN, 1968). Other incidents of extensive mortalities due to extreme high temperatures in the sea have been reported by VAUGHAN (1918), HODGKIN (1959) and TOKIOKA (1966).

Only under extreme climatic conditions may thermal death in the sea be attributed to temperature alone with some degree of certainty. Other factors may interfere and make a detailed analysis of cause and effect difficult.

Thermal death in the laboratory.

Prior to determining thermal responses under laboratory conditions, it is customary to stabilize the test individuals for some days or weeks by keeping them under defined environmental and nutritive conditions. The lower and upper lethal temperatures are then determined either by a slow decline or raise of water temperature from non-lethal intensities, or by abrupt exposure to critically low or high constant temperatures. In both cases the time to death of given percentages of the test population is recorded (for further details consult CRISP and RITZ, 1967 and FRY, 1967).

The latter approach is based on the classic pharmacological assay method. Lower and upper lethal limits are expressed in terms of the lethal dose to kill 50% of the test population within a given period of time, frequently 24 hrs (LD_{50}–24 hrs). For a more complete analysis it is necessary to determine also LD_{10}, LD_{20}, LD_{30}, etc. to LD_{100}, within different periods of time. It is further desirable to determine the lethal limits of all life-history stages (acclimated to different temperature conditions) and to test the modifying influences of other simultaneously effective environmental factors such as light (Chapter 2), salinity (Chapter 4), pressure (Chapter 8), dissolved gases (Chapter 9), etc. Such comprehensive studies require modern scientific dimensions: considerable laboratory facilities and a team of scientists and technicians; they have not yet been conducted.

Most of our present knowledge on thermal death of marine invertebrates in the laboratory has been obtained from adults or subadults. For ecological considerations it is important to know the thermal tolerances of the most sensitive life-cycle stages (adults during breeding season, gametes, fertilized eggs, developing earliest ontogenetic stages) and the most resistant (non-reproducing adults, dormant stages, cysts, etc.).

Plotted assay data typically reveal sigmoid patterns. Fig. 3-48 shows heat–death curves for adults of 7 estuarine invertebrates (MIHURSKY and KENNEDY, 1967). The least heat-tolerant species shown is the mysid crustacean *Neomysis americana*; collected from the Patuxent estuary in Maryland, this mysid is near its southern limit of distribution in the USA (TATTERSALL, 1951). The most heat-tolerant species is the polyp stage of the scyphozoan coelenterate *Chrysaora quinquecirrha*;

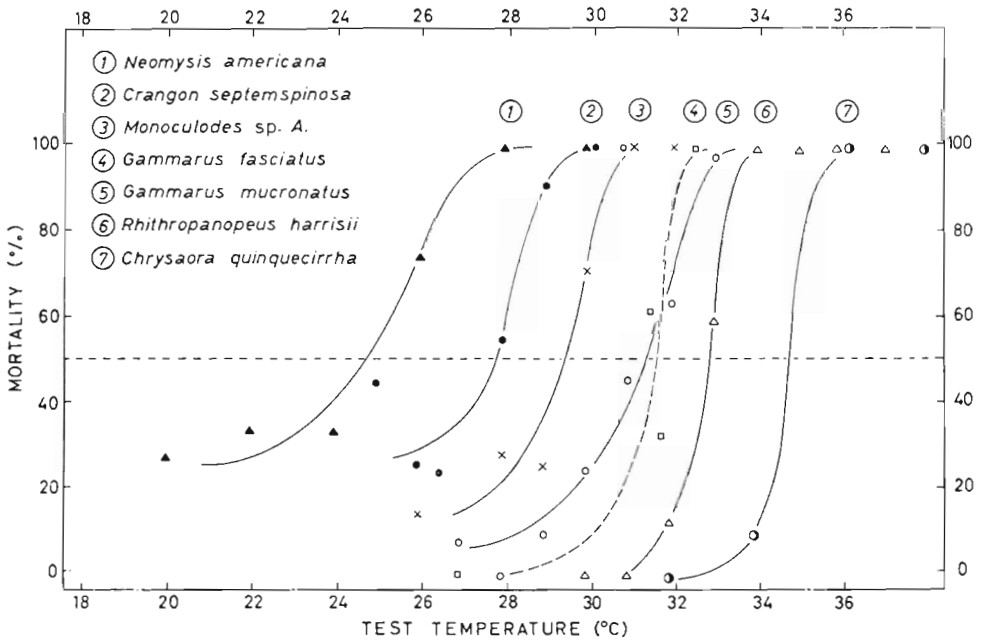


Fig. 3-48: Comparative heat death curves for adults of 7 estuarine invertebrates. (Acclimation temperature: 15° to 16° C; time of exposure to test temperatures: 24 hrs; N = 2707). LD_{50} – 24 hrs is indicated by the horizontal broken line. (After MIHURSKY and KENNEDY, 1967; modified.)

its LD_{50}–24 hrs level lies some 10 centigrade degrees above that of *N. americana* even though both forms had been acclimated at identical temperatures. The decapod crustacean *Crangon septemspinosa* is comparable to *N. americana* in regard to its zoogeography, and is also rather heat sensitive. The curves of 3 species of amphipod crustaceans (*Monoculodes* sp. A, *Gammarus fasciatus* and *Gammarus mucronatus*) are grouped in the centre of the graph; the deep-water living *Monoculodes* shows less thermal tolerance than either of the 2 shallow-water shelf species which inhabit areas with higher temperatures. The decapod crab *Rhithropanopeus harrisii* is a temperate–tropical form (e.g. KINNE and ROTTHAUWE, 1952); it exhibits a rather high heat tolerance. Interestingly, its abundance has been reported to increase in estuarine areas below steam electric stations which caused ambient-temperature increases due to the release of large amounts of heated effluents (NAYLOR, 1965).

Limulus polyphemus has been reported to tolerate 44° C for 1 hr (exposure to constant critically high temperatures, LD_{50}); *Littorina littorea*, 40° to 41° C; and *Pagurus longicarpus*, 36° C (FRAENKEL, 1960). The intertidal Mediterranean gastropod *Littorina neritoides*, which spends most of its adult life on rocks out of the water, exhibits an unusually high degree of short-term heat tolerance. It is able to resist 46° to 47° C for 1 to 2 hrs when submerged, and about 48° to 49° C when in air (FRAENKEL, 1961). In 1966, FRAENKEL studied the heat tolerance of adults of 12 species of intertidal gastropods from the surroundings of Shirahama (Japan). He submitted the snails to constant critically high temperatures while they were submerged in sea water, for 1 and 2 hrs, and then determined the highest temperature from which they were able to recover, i.e. to resume normal loco-

motion. The degree of heat tolerance was found to be closely correlated to the position of the gastropods in the intertidal zone. The highest tolerance, 47° to 48·5° C (1-hr exposure), is exhibited by *Nodilittorina pyramidalis*, *N. granularis*, *Planaxis sulcatus* and *Littorina brevicula* which inhabit the highest littoral zone; a similar degree of resistance to heat is found in *Peasiella roepstorffiana* which lives in shallow tide pools. *Heminerita japonica* and *Theliostyla albicilla*, inhabitants of the midtidal zone, tolerate 46° and 44° C, respectively. Gastropods from a still lower region, *Lunella coronata*, *Morulina granulata*, *Thais clavigera* and *Monodonta labio*, withstand 42° to 43° C, and the topshell *Chlorostoma argyrostoma lischkei*, which inhabits the water's edge, 39° C.

FARMANFARMAIAN and GIESE (1963) analyzed the thermal tolerance of well-fed adult purple sea-urchins *Strongylocentrotus purpuratus* of 3 to 5 cm test diameter (200 to 250 g wet weight). Specimens transferred into sea water of 25° ± 0·5° C become limp within 4 hrs and invariably die within 24 hrs. Individuals first acclimated for 10 days at 20° C similarly lose activity within 4 hrs; they die after about 3 days. It is, therefore, remarkable that specimens kept at 23·5° C remain normal, climb up the container and feed essentially like controls. Obviously, there exists a sharp upper thermal-tolerance limit between 23·5° and 25° C. Low-temperature experiments indicate that *S. purpuratus* endures 8° C without harm; some individuals survive 1·9° C, depending on successful acclimation to cold (no evidence of resistance adaptation to heat was obtained).

Tolerance to cold is much more variable and more difficult to measure than tolerance to heat. Certain invertebrates such as rotifers, nematodes and tardigrades can, in a desiccated condition, survive several hours of exposure to temperatures as low as − 272° C if cooled and warmed quickly to prevent internal ice formation (LUYET and GEHENIO, 1940; GUNTER, 1957). The ability of *Littorina rudis*, *L. littorea* and *Balanus balanoides* from the inner Oslofjord (Norway) to tolerate freezing conditions was greatest during the middle of the winter; at this time adult representatives of all 3 species survived for several days at − 10° C; at − 20° C all specimens were killed after brief exposures (SÖMME, 1966).

CRISP and RITZ (1967) studied changes in temperature tolerance of the cirripede crustacean *Balanus balanoides* during its life cycle. They employed the method of gradually raising the ambient temperature and withdrawing samples at intervals to estimate survival rates (see also SOUTHWARD, 1958). The lower lethal temperatures were measured by placing the barnacles dry, or the larvae in sea water, in a series of low-temperature jackets held constant to ± 0·2 degrees. *B. balanoides* exhibits little seasonal variation in upper lethal temperatures (North Wales, UK), but there are marked seasonal changes in tolerance to subzero temperatures, the lower lethal varying from − 6·0° C in June to − 17·6° C in January (Fig. 3-49). Exceptional tolerance to cold is acquired between December and January and is lost between February and April. Although these dates coincide with oviposition and naupliar liberation respectively, cold tolerance does not necessarily depend upon, or accompany, the breeding cycle. Cold tolerance is not acquired by individuals kept cold in the laboratory during winter, nor is it lost in specimens kept in the laboratory during spring; there is no evidence that changes in nutrition or in light regime lead to cold-tolerance loss. Cyprids are considerably less tolerant to both low and high temperatures than overwintering adults and late-stage embryos

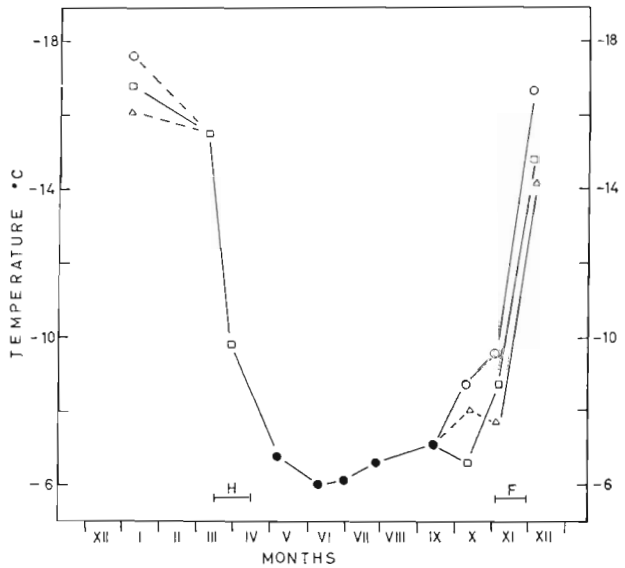


Fig. 3-49: Seasonal variations in cold tolerance of adult barnacles *Balanus balanoides* from Menai Bridge (UK). Median lethal temperatures of specimens from high water (open circles), mean tide level (squares), low water (triangles), and from high water and mean tide level combined (black circles). H: Hatching period; F: fertilization period. (After CRISP and RITZ, 1967.)

but tolerance increases markedly at metamorphosis. The appearance of cold tolerance in adults coincides with 'physiological hibernation', involving loss of certain tissues and reduction of feeding activity, respiration and biosynthesis.

FOSTER (1969) determined the upper thermal limits tolerated by some cirripedes of the British coasts in two ways: (i) He measured 'upper lethal temperatures' by raising the test temperature at a constant rate of 0·2 C°/min; (ii) he established 'time-temperature-survival' curves by increasing the temperature at a rate of 0·2 C°/min to the required level, and then maintaining the test temperature constant. In *Elminius modestus* and *Balanus crenatus* thermal tolerances are the same in summer and winter. In *Balanus balanoides*—although the upper lethal temperature does not vary seasonally—adults are more susceptible in winter than in summer to prolonged exposure to temperatures a little below the upper lethal limit. In general, upper lethal temperatures of British barnacles turned out to correspond to the geographical and intertidal distributions of the species concerned. Consideration of 'time-temperature-survival' curves indicates that intertidal barnacles are living closer to lethal habitat temperatures than would be expected on the basis of 'upper lethal temperature' measurements alone. In *Balanus balanoides* there is a 3 C° increase in upper thermal tolerance from the free-swimming cyprid stage to the recently metamorphosed barnacle stage. Apparently, settling stages must quickly assume the wider tolerance range required to meet the extended variations of environmental factors encountered in the intertidal region.

However, FOSTER warns that increased thermal tolerance during metamorphosis is paralleled by synchronous changes in the adults; hence more work is required to decide whether the changes reported are linked with developmental processes or induced by the environment.

The only study concerned with thermal death in the laboratory under conditions

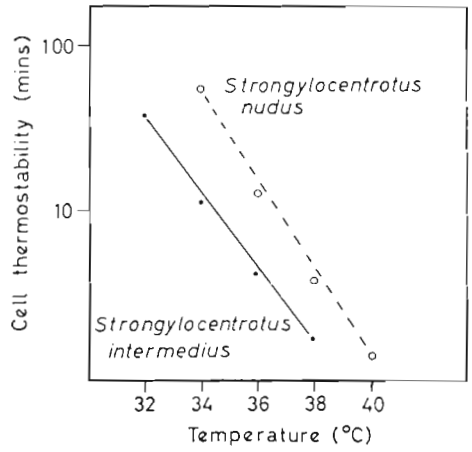


Fig. 3-50: Heat tolerances of spermatozoa of the sea-urchins *Strongylocentrotus intermedius* and *S. nudus*. Ordinate: period of heat exposure in mins (logarithmic scale) causing loss of motility in 100% of the spermatozoa tested. (After ANDRONIKOV, 1965, 1967; modified.)

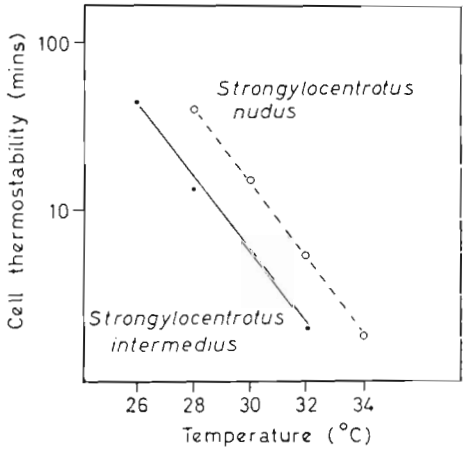


Fig. 3-51: Heat tolerances of unfertilized ova of the sea-urchins *Strongylocentrotus intermedius* and *S. nudus*. Ordinate: period of heat exposure in mins (logarithmic scale) causing loss of cleavage capacity in the ova tested. (After ANDRONIKOV, 1965, 1967; modified.)

of cyclic temperature changes that has come to the reviewer's attention has been conducted by COSTLOW and BOOKHOUT (1970) on larvae of the mud-crab *Rhithropanopeus harrisii*. The larvae were kept from hatching to the first crab stage in a constant salinity of 25‰ combined with eight 24-hr cycles of temperature. The 5° temperature cycles were 15° to 20° C, 20° to 25° C, 25° to 30° C, 30° to 35° C and 35° to 40° C; the 10°-cycles, 15° to 25° C, 20° to 30° C and 25° to 35° C. Each day the larvae were fed recently hatched nauplii of *Artemia salina*, transferred into freshly filtered sea water of the same salinity and temperature, and survival rates recorded. Comparable data were obtained for larvae kept in the same salinity but at constant temperatures of 15°, 20°, 25°, 30° and 35° C respectively. Survival rates to the crab stage were slightly lower in the 10°-cycles 15° to 25° C and 20° to 30° C than at the constant levels 15°, 20°, 25° and 30° C, and considerably lower in the 25° to 35° C cycle. In the 5°-cycles survival was lower at 20° to 25° C than either at constant 20° or 25° C. In the cycle 25° to 30° C survival was lower than at 25° C but considerably higher than at constant 30° C. The highest percentage survival was observed in a cycle of 30° to 35° C.

Of special importance for marine ecological considerations is the knowledge of the thermal tolerances of gametes. Investigations carried out on spermatozoa and ova of taxonomically closely related species of molluscs and echinoderms reveal species-specific differences in gamete heat tolerances (SVINKIN, 1961; ANDRONIKOV, 1963, 1965, 1967). Figs 3-50 and 3-51 illustrate heat tolerances of spermatozoa and ova of different sea-urchin species. On the basis of the criteria used (loss of motility in spermatozoa, loss of cleavage capacity in ova), spermatozoa of a given species are more heat tolerant than unfertilized eggs. Heat tolerance of spermatozoa is independent of thermal acclimation or habitat temperature of the donating male of the species under consideration. Fertilized eggs exhibit the same degree of heat resistance as unfertilized ones. The zygote obtained by fertilization of *Strongylocentrotus nudus* ova via *S. intermedius* spermatozoa shows the same level of heat tolerance as does a normal *S. nudus* zygote (ANDRONIKOV, 1967), indicating the dominating influence of the egg's thermal characteristics.

Other papers dealing with thermal death of marine and brackish-water invertebrates under controlled laboratory conditions have been published on the scallop *Placopecten magellanicus* by DICKIE (1958), semiterrestrial fiddler crabs of the genus *Uca* by VERNBERG and TASHIAN (1959), EDNEY (1961), WILKENS and FINGERMAN (1965), on postlarval stages of the brown shrimp *Penaeus aztecus* by ZEIN-ELDIN and ALDRICH (1965), on the European oyster *Ostrea edulis* by DAVIS and CALABRESE (1969), on the ctenophore *Pleurobrachia pileus* by GREVE (1969), and on the polychaetes *Diopatra cuprea* and *Clymenella torquata* by KENNY (1969).

The determination of lethal temperatures provides a useful tool for assessing (i) inter- and intraspecific differences in temperature tolerance, (ii) the physiological condition, (iii) the status of acclimation to a given temperature (HATHAWAY, 1927; FRY and co-authors, 1942; FRY and co-authors, 1946; FRY, 1947, 1957a, b; BRETT, 1956; MCLEESE, 1956; SOUTHWARD, 1958). A list of upper lethal temperatures for various marine molluscs has been compiled from data by BROEKHUYSEN (1940) and EVANS (1948), and published by GUNTER (1957). A certain amount of dehydration and gelation tends to increase resistance to both heat and cold (HEILBRUNN, 1952; CHRISTOPHERSEN and PRECHT, 1953; KINNE, 1953a, 1956a;

PRECHT and co-authors, 1955; REMANE and SCHLIEPER, 1958; JANKOWSKY and co-authors, 1969).

Thermal tolerance at the subindividual level

It is the objective of the ecologist to study integrated responses of living systems to environmental variations. Hence, his attention is focussed on the individual and supra-individual levels. However, research at the subindividual level has opened up new insights into the mechanisms of thermal tolerance which are also of importance for ecological considerations. While the study of thermal tolerance at the individual level has revealed a remarkable diversity, the multitude of specific functional and structural responses tends to decrease as the experimenter moves down to organs, tissues, cells or cellular components, and basic universal generalities become apparent (Chapter 3.0).

Thermal tolerance at the subindividual level has recently been reviewed and discussed by DILL and co-authors (1964), PROSSER (1967) and ROSE (1967). The following paragraphs are largely devoted to information which has not been presented in these 3 important reviews.

THEEDE (1965) investigated the cellular freezing tolerance of lamellibranchs from the North Sea. He froze small isolated gill areas (about 4 to 8 mm²) of littoral and sublittoral species for different periods of time (a few mins to 6 hrs, depending on the species-specific degree of freezing resistance) at $-10°$ C and studied the activity of the gill cilia after subsequent thawing at room temperature of about

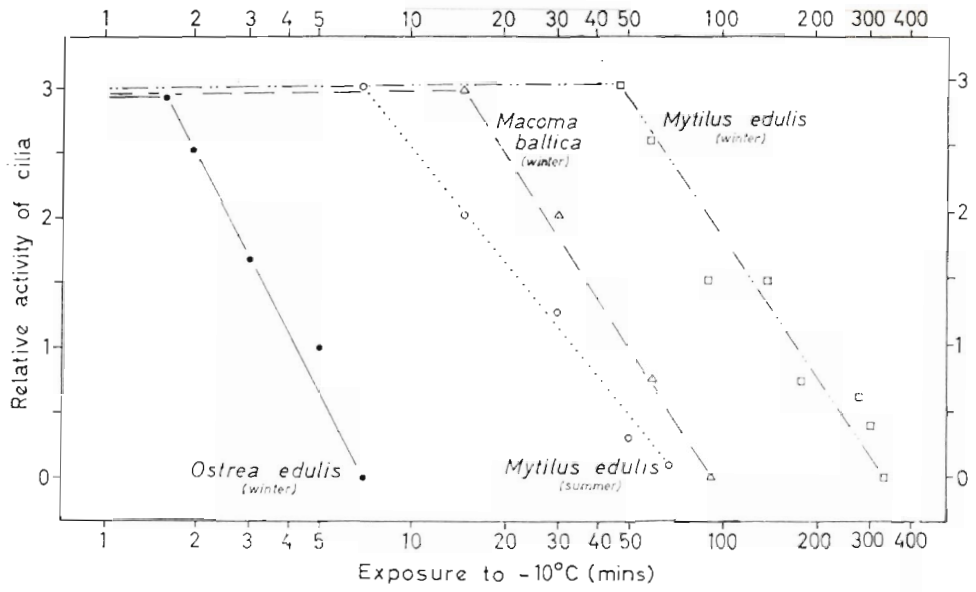


Fig. 3-52: Cellular tolerances of excised surviving gill pieces of North Sea bivalves to freezing during winter. Gill pieces of *Mytilus edulis* tested during summer (dotted line) are considerably less cold resistant than in winter (extreme right). Ordinate: relative activity (beating) of gill cilia; 3: normal activity, 2: slightly reduced activity, 1: strongly reduced activity, 0: complete cessation of beating in all cilia. Semi-logarithmic plot. (After THEEDE, 1965; modified.)

20° C. Thawing was completed after 15 to 20 secs. Controls (excised gill pieces of respective sizes exposed to normal environmental conditions, i.e. 10° and 20° C, $30^0/_{00}$ S) survived at least for 3 days while exhibiting normal ciliary activity in all species tested. An example of THEEDE's results is illustrated in Fig. 3-52. The cellular freezing resistance decreases in the order: *Mytilus edulis*, *Cardium edule*, *Macoma baltica*, *Modiolus modiolus*, *Spisula solida*; *Ostrea edulis* exhibits the same degree of resistance as *Modiolus modiolus*. Isolated gill pieces of the intertidal *Mytilus edulis* survive 5 hrs freezing at – 10° C and subsequent thawing at 20° C,

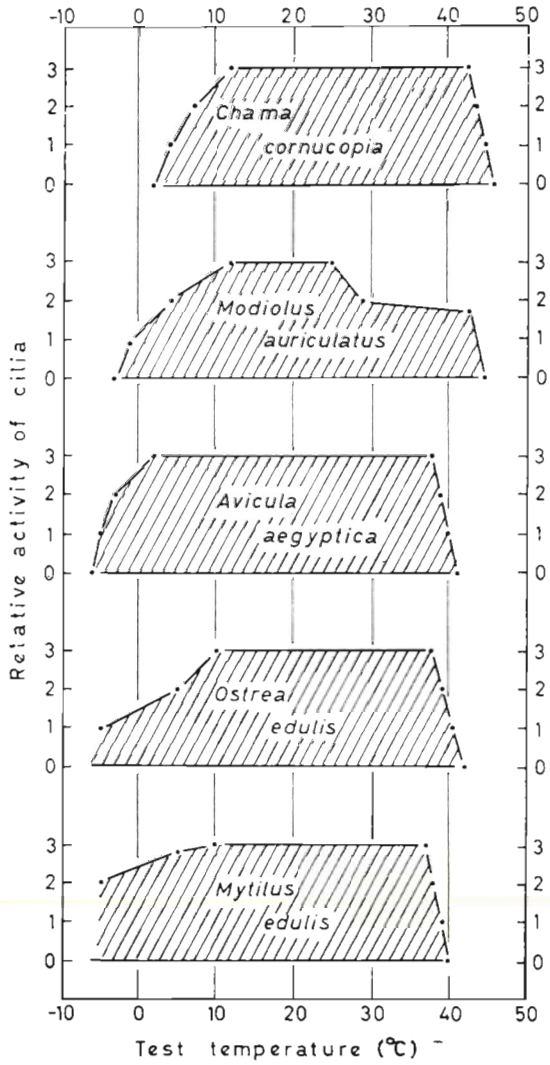


Fig. 3-53: Cellular tolerances of excised surviving gill pieces of various bivalves exposed to slowly increasing or decreasing temperatures. Relative activity of gill cilia as in legend to Figure 3-52. (After SCHLIEPER and co-authors, 1967; modified.)

whereas gill pieces of the sublittoral *Spisula solida* reveal irreversible cell damages after an exposure to $-10°$ C of only 4 mins.

SCHLIEPER (1966) and SCHLIEPER and co-authors (1967) exposed excised gill pieces of marine molluscs to slowly decreasing or slowly increasing temperatures. The rate of temperature change ranged from 1 C° per 5 mins in experiments with increasing temperatures to 1 C° per 1 min in those with decreasing temperatures. Fig. 3-53 summarizes the results obtained. Gill tissue of the tropical *Chama cornucopia* shows the greatest tolerance to high test temperatures but the smallest tolerance range. Tolerances to cold and tolerance ranges increase in the sequence *Modiolus auriculatus, Avicula aegyptica, Ostrea edulis, Mytilus edulis.*

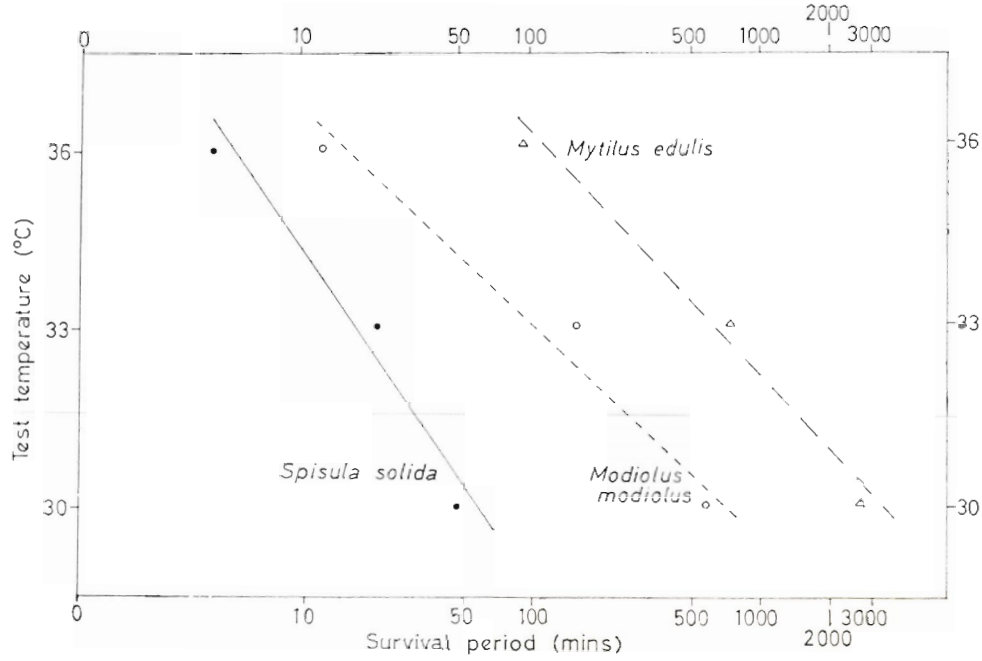


Fig. 3-54: Cellular tolerances to heat in 3 bivalve species from the North Sea, acclimated for at least 3 days at 10° C and abruptly transferred into critically high test temperatures. 30‰ salinity. Semilogarithmic plot. (After RESHÖFT, 1961; modified.)

The degree of cellular thermal tolerances of molluscs reflects the relative species-specific differences observed at the individual level; it may change due to differences in environmental histories of the test individuals. Fig. 3-54 exemplifies species-specific differences in cellular tolerance of 3 lamellibranch species, which occur at different depths in the North Sea, after sudden transfer into critically high constant test temperatures. In tropical and temperate zones, genetic cellular heat tolerances tend to decrease with increasing habitat depth.

The degree of cellular freezing tolerance may be a function of salinity (*Mytilus edulis* from brackish waters of about 15‰ S have a lower tolerance than those from North Sea waters of about 32‰ S) and season (cold tolerance is usually

higher in winter than in summer; see also Fig. 3-52); it increases if organic substances such as sucrose, glucose and glycerol are added to the ambient water (THEEDE, 1965).

Cellular resistance to heat tends to increase with the Ca content of the external medium (SCHLIEPER, 1966). Cilia of isolated gill pieces of the sublittoral mollusc *Aequipecten irradians* ceased beating when exposed to 37° C for about 100 mins, while those of intertidal molluscs *Modiolus demissus* and *Crassostrea virginica* survived, during the same period of time, a temperature of 44° C (VERNBERG and co-authors, 1963).

Euryoecous species with large distribution areas show a wider range of cellular thermal resistance than stenoecous species distributionally restricted to narrow temperature ranges. The species-specific differences in cellular thermal resistances represent, according to RESHÖFT (1961), to a large extent true cell-physiological species characteristics. Hence, carefully conducted analyses of cellular tolerances to cold and heat may provide useful criteria for the assessment of the ecological thermopotential of a given population, both in regard to its basic genetic capacity and its potential for non-genetic (individual) adjustments.

According to USHAKOV (1968), evidence concerning heat tolerance of cells and proteins indicates that, at early stages of embryogenesis of multicellular animals, the cellular level of organization becomes 'naked'; the cells become exposed to the direct influence of natural selection. The result is a species-specific level of cell thermostability. This level is related to the temperature at which the species in question reproduces. Upon further ontogenetic development, heat tolerance of the majority of somatic cells of the individual increases and, hence, variations in their thermostabilities can no longer limit the degree of resistance of the whole intact individual. Non-genetic resistance adaptation to temperature involves the same pattern of stability changes in protozoans and in somatic cells of multicellular invertebrates.

USHAKOV (1968) distinguishes between obligatory and situational changes in heat tolerance of cells and proteins. Obligatory changes are caused by factors endogenous to the individual but not, as a rule, to its cells (e.g. growth, cell differentiation, metamorphosis). They are repeated conservatively in subsequent generations. Obligatory changes are, to a considerable extent, independent of alterations in the surrounding media and, usually, are not connected with changes in environmental temperatures. Examples have been presented by KUSAKINA (1963a). Situational changes in cell thermostability are induced by exogenous factors and represent the response of an individual to alterations in its environment. An increase in salinity, for example, tends to result in an increase of cellular heat resistance in poikilosmotic animals (e.g. KINNE 1954a; SCHLIEPER and KOWALSKY, 1956; DREGOLSKAYA, 1961; IVLEVA, 1967).

Seasonal changes in cell thermostability are repeated from year to year and from generation to generation (DREGOLSKAYA, 1962, 1963; IVLEVA, 1967). These changes occur in different tissues of the individual in a similar way (PASHKOVA, 1967). In higher animals, seasonal changes in cell thermostability are caused by functional changes of endocrine glands; the most pronounced changes in heat tolerance of cells and tissues are observed during reproduction. In some species, seasonal changes are correlated to alterations in the environmental temperature. In the

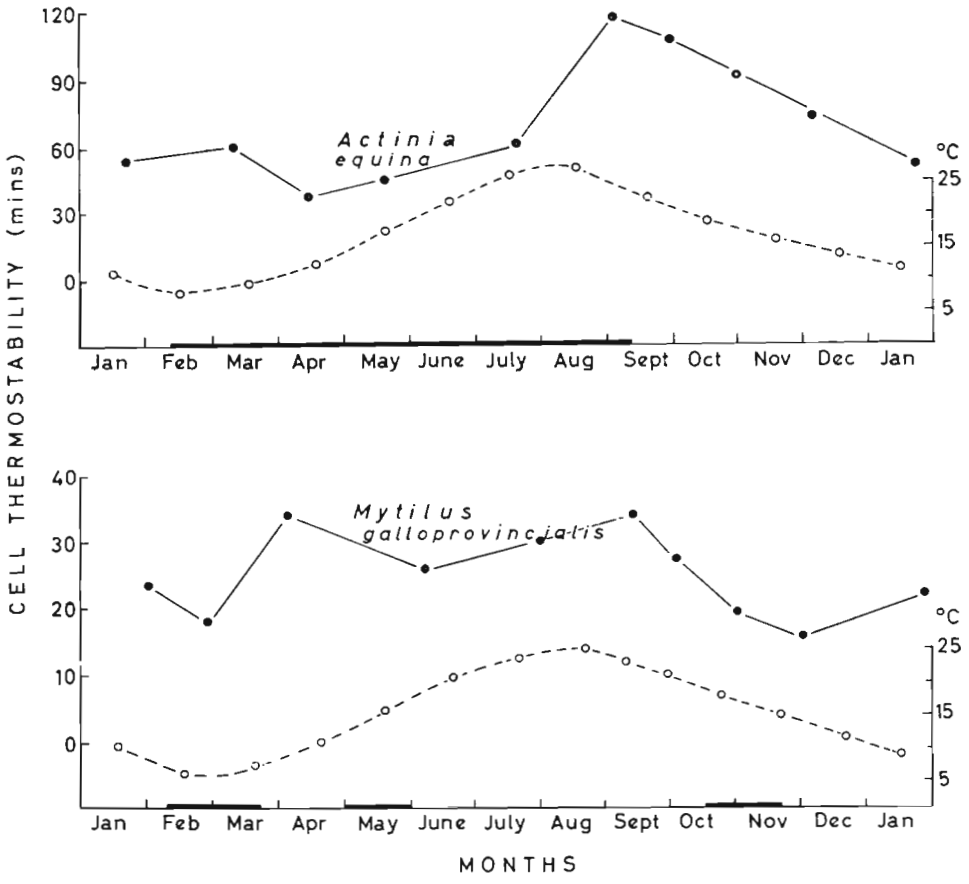


Fig. 3-55: Seasonal changes in thermostability of cells (ciliated epithelium) of the anthozoan *Actinia equina* (from DREGOLSKAYA, 1962) and the lamellibranch *Mytilus galloprovincialis* (from DREGOLSKAYA, 1963). Ordinate: cell thermostability, expressed as survival times of cells at 39° C in mins; broken lines: sea-water temperatures (right scale). (After USHAKOV, 1968; modified.)

anthozoan *Actinia equina*, such correlation is a result of a temporary coincidence of obligatory changes in cell thermostability with monthly changes in sea-water temperature (Fig. 3-55); in summer, changes in water temperature do not affect the variations in its cell thermostability (ZHIRMUNSKY, 1959; DREGOLSKAYA, 1967). In contrast, in the polychaete *Nereis diversicolor* seasonal changes in cell thermostability are mainly determined by situational responses to fluctuations in ambient water temperature (IVLEVA, 1967). The results obtained by USHAKOV and his associates indicate that in different species seasonal changes in cell thermostability may be controlled by different mechanisms (obligatory, situational, mixed). Ambient temperatures may alter the rate of obligatory changes and/or induce specific situational changes in cell thermostability. Hence, experimental analyses must differentiate between these 2 temperature effects. Several experimenters have neglected to record obligatory changes; consequently, a cell-physiological interpretation of their results is difficult or impossible.

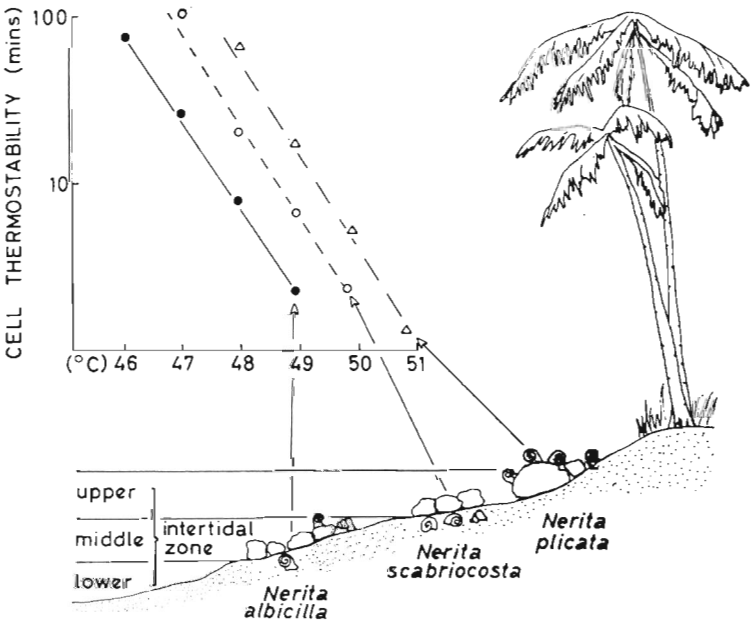


Fig. 3-56: Thermostability of cells (ciliated epithelium) of 3 species of the gastropod genus *Nerita*, and their respective distributional areas in the upper, middle and lower intertidal zone. Ordinate: cell thermostability, expressed as survival time of cells in mins (logarithmic scale); abscissa: test temperatures (°C). (From ZHIRMUNSKY and CHU LI-CHUN, 1960; after USHAKOV, 1968; modified.)

Situational variations in cell thermostability correlated to fluctuations in ambient temperature are usually observed only during summer (PASHKOVA, 1963, 1965). Among marine invertebrates such responses seem to be normal in eurytherm littoral species; they have not been found in stenotherm sublittoral invertebrates (VERNBERG and co-authors, 1963; SCHLIEPER, 1966, 1967).

Most poikilotherm invertebrates exhibit no intraspecific, but significant interspecific, differences in the thermostability of homologous cells and proteins (USHAKOV, 1968). The interspecific differences are not determined by the taxonomic category of the species but by their present and past environmental temperature conditions (USHAKOV, 1964; ZHIRMUNSKY, 1966; DZHAMUSOVA, 1967). The level of cellular thermostability is assumed to reflect both contemporary species-specific thermal requirements and thermal conditions during the species' evolution. The higher the contemporary ambient temperatures required during reproduction and during the non-reproductive (vegetative) period of a species, the higher is the heat resistance of cells and proteins. For example, cells and proteins of littoral species exhibit higher thermostabilities than those of sublittoral species (DZHAMUSOVA, 1960, 1967; ZHIRMUNSKY, 1960, 1967; READ, 1963, 1964), and thermal tolerance of cells in littoral forms increases with increasing habitat height relative to the mean water level (Fig. 3-56). Interspecific differences in protein thermostability were discovered even in closely related species; this evidence

led USHAKOV (1966) to conclude that associated changes in protein thermostability occur during speciation. Studies on intraspecific groups, performed on several animal species, suggest that these changes are accomplished by natural selection in a certain succession finally involving the major portion of the individuals' proteins. As a result, species evolve which differ progressively in their protein thermostability with increasing differences in ambient temperatures during the individuals' reproductive and non-reproductive periods.

Heat tolerance of individual cells of poikilotherm invertebrates is a phylogenetically conservative species-specific property (USHAKOV, 1959, 1964, 1967a, b; RESHÖFT, 1961; DREGOLSKAYA, 1967; DZHAMUSOVA, 1967; ZHIRMUNSKY, 1967). Studies on protein thermostability lead to the same conclusion (KUSAKINA, 1963b, 1967; USHAKOV, 1966; BROWN and co-authors, 1967; GLUSHANKOVA, 1967; KUSAKINA and VINOGRADOVA, 1967). ALEXANDROV (1967) suggested that interspecific differences in protein thermostability result from differences in the flexibility of protein molecules. Most of the somatic cells studied can tolerate temperatures many centigrade degrees higher than the intact whole individual (USHAKOV, 1968).

USHAKOV (1966) and USHAKOV and co-authors (1966) report coupling between thermostabilities of different proteins of individuals belonging to the same species; they consider this coupling to be of great biological importance, and have described the relation between the thermostability levels of proteins differing in their function by a system of linear equations:

$$T_0 = A_1T_1 + B_1 = A_2T_2 + B_2 = A_3T_3 + B_3 = \ldots = A_nT_n + B_n,$$

where T_0, T_1, $T_3 \ldots T_n$ are the denaturational temperatures of different proteins, while A and B are constant values. This equation holds for all poikilotherm animals studied.

Other pertinent reviews, including the problem of thermal death at the subindividual level, have been published by PRECHT and co-authors (1955), MEWS (1957), PROSSER (1958, 1967), PROSSER and BROWN (1961), HANNON and VIERECK (1962) and PRECHT (1964).

Thermal tolerance at the supra-individual level

Thermal death at the population level may be brought about by the immediate killing of all individuals composing the population in question or by suppressing their reproductive activities. The effects on individuals have been dealt with above; the effects on reproduction will be discussed on p. 486.

Thermal death at the ecosystem level has hardly been studied. It is probably rare and likely to occur only over geological periods of time as a consequence of pronounced general temperature changes (e.g. glacial and interglacial periods). However, increasing temperatures have led to noticeable changes in species' composition of ecosystems and in species' distributions during the last few decades, for example, in arctic and subarctic seas and in the North Sea.

Man-made heat, such as the gigantic amounts of waste heat disposed of by industrial plants—especially by steam electric stations (Chapter 3.0)—may be expected to cause 'thermal death' of present estuarine ecosystems (e.g. MIHURSKY and KENNEDY, 1967).

Thermal tolerance under multivariable conditions

Thermal responses may be modified by other concomitantly effective environmental variables such as light (Chapter 2), salinity (Chapter 4), etc. Responses to such factor combinations will be dealt with in detail in Chapter 12; however, influences on thermal tolerances of marine invertebrates via other environmental factors require brief treatment in the present context.

Of the various environmental factors which are known to modify thermal tolerances, salinity has received the greatest attention. Among the first authors to study temperature–salinity relations were PANIKKAR (1940a, b, 1941a, b), BROEKEMA (1941), KINNE (1952, 1953a, 1954a), KINNE and ROTTHAUWE (1952), MCLEESE (1956) and SCHLIEPER and co-authors (1960). Several aquatic invertebrates which live in habitats with greatly fluctuating temperature and salinity conditions can tolerate subnormal temperatures better at the lower end of their salinity range, and supranormal temperatures better at the upper end of their salinity range. Beneficial effects of such low/low and high/high combinations have been found in regard to survival and performance in *Gammarus duebeni* (KINNE, 1952, 1953a), the decapod crab *Rhithropanopeus harrisii* (KINNE and ROTTHAUWE, 1952), and the colonial hydroid *Cordylophora caspia* (KINNE, 1956b, 1958). In the amphipod *Gammarus duebeni*, temperature and salinity tolerances are reciprocally related in that the range of temperatures tolerated tends to be widest in optimal salinities, and the range of salinities tolerated tends to be widest at optimal temperatures (KINNE, 1953a).

A lowering of the upper lethal temperature due to a decrease in the normal habitat salinity has been reported for the polychaete *Nereis* (*Neanthes*) *diversicolor*, the amphipod *Gammarus duebeni* and the isopod *Sphaeroma hookeri* (KINNE, 1954a). While in these forms an increase in salinity beyond normal habitat conditions tends to increase heat resistance, very high salinities may become a severe stress *per se* and thus ultimately reduce the overall vitality including resistance to cold and heat (KINNE, 1964a). Some papers which report reduced thermostability in supranormal salinities may possibly be interpreted on this basis; others indicate a different response pattern and require special interpretations. Better survival in low salinities at high temperatures, or in high salinities at low temperatures, has been reported in shrimps: *Palaemonetes varians*, *Leander serratus* (PANIKKAR, 1940b), *Penaeus duorarum*, *P. aztecus* (WILLIAMS, 1960), and claimed for *Crangon crangon* (BROEKEMA, 1941). *Crangon crangon* has, however, been shown to belong to the first described response type with better survival in low salinities at low temperatures (FLÜGEL, 1959, 1966). In a 10-day experiment, adult *Crangon crangon* survived at 5° C in salinities ranging from 1 to 50‰, at 15° C from 4 to 50‰, and at 20° C from 4 to 35‰ (FLÜGEL, 1966). Various authors have suggested that increased thermal stability in supranormal salinities might be due to a reduction in the amount of free cellular water or changes in the distributional pattern of such water (e.g. HEILBRUNN, 1952; KINNE, 1954a, 1956a; PRECHT and co-authors, 1955). Increased thermostability is often paralleled by a decrease in metabolic rate and vice versa.

Some physiological and physical aspects of temperature–salinity relations have been discussed by KINNE (1956a), VERWEY (1957) and ROSE (1967). VERWEY'S

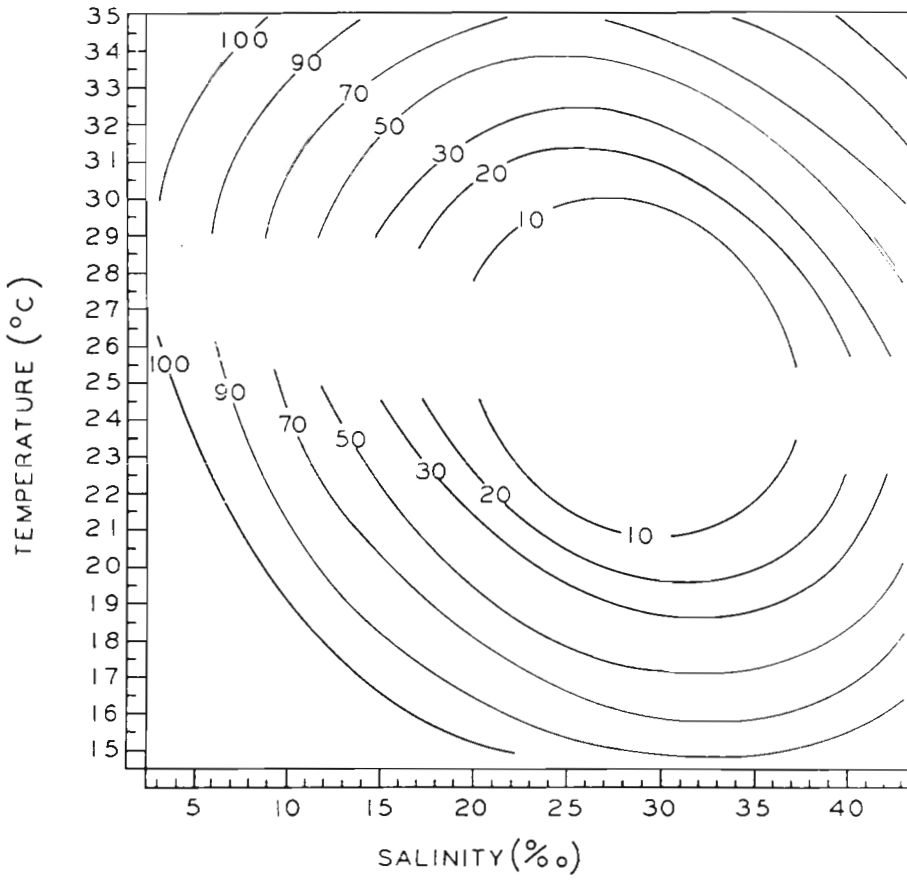


Fig. 3-57: Estimation of per cent mortality of zoea stage I of the decapod crab *Sesarma cinereum* based on the fitted response surface to observed mortality under 12 combinations of temperature and salinity. (After COSTLOW and co-authors, 1960.)

concept (relative constancy of osmotic pressure under changed temperature conditions) has been criticized by FLÜGEL (1966) who points out that VERWEY's calculations are based only on the electrolyte content of the blood of *Crangon crangon*, neglecting possible quantitative changes in dissolved organic blood components which would affect the resulting total osmotic pressure.

In experiments with the decapod crabs *Hemigrapsus nudus* and *H. oregonensis*, maintenance at the combination 20° C/75‰ sea water led to the highest tolerance to supranormal test temperatures, while maintenance at the combination 5° C/35‰ sea water produced the lowest tolerance (TODD and DEHNEL, 1960). Thermal tolerance of the ciliate protozoan *Zoothamnium hiketes*, which lives epizoic on brackish-water gammarids, has been shown (VOGEL, 1966) to depend upon acclimation temperature (high acclimation temperatures augment heat tolerance and decrease cold tolerance; low temperatures have opposite effects), salinity (increase in habitat salinities up to 20‰ augment, lower or higher salinities decrease heat resistance), and daylength (long-day conditions increase, short days decrease heat

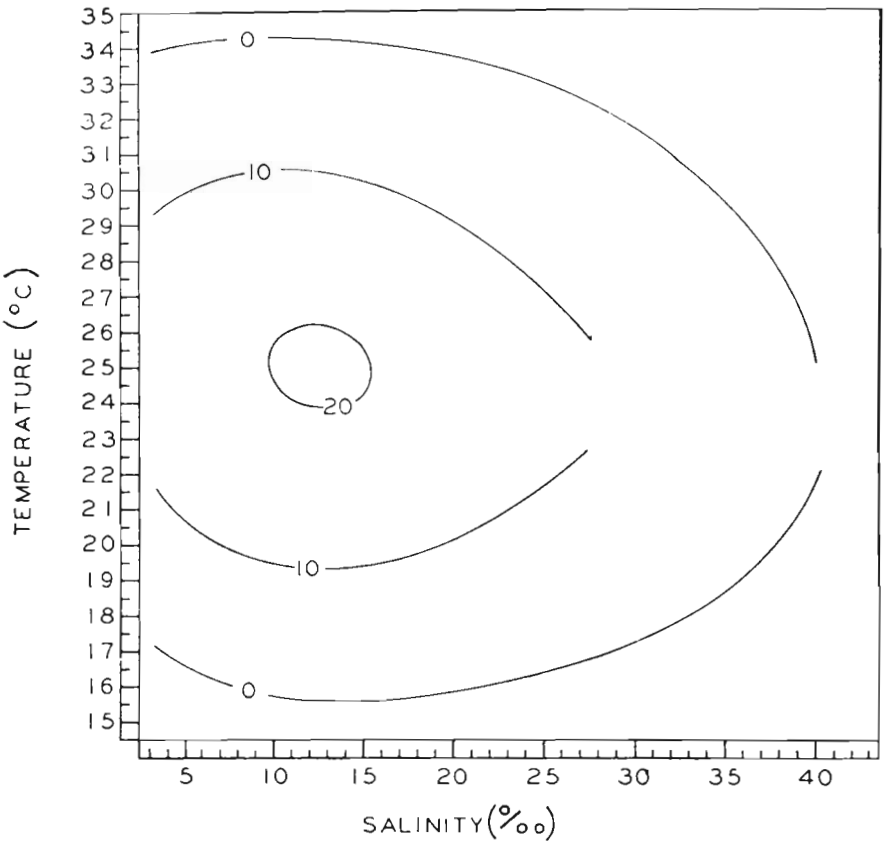


Fig. 3-58: Estimation of per cent mortality of zoea stage II of the decapod crab *Sesarma cinereum* based on the fitted response surface to observed mortality under 12 combinations of temperature and salinity. (After COSTLOW and co-authors, 1960.)

tolerance). An increase in ambient Mg content tends to increase heat tolerance but does not affect cold resistance; this, and related findings, support POLJANSKY's (1957, 1959) hypothesis that heat and cold resistances are governed by different physiological mechanisms.

Detailed analyses of the combined effects of temperature and salinity on the thermal resistance of marine invertebrates require a large number of factor combinations and fully acclimated test individuals. COSTLOW and co-authors (1960) have employed 12 different temperature–salinity combinations and estimated the responses of different life-cycle stages of the decapod crab *Sesarma cinereum* on the basis of response surfaces (Chapter 12). The authors postulated the existence of a continuous response (% mortality) as a function of temperature and salinity, and either unique optimum combinations of the 2 factors or several combinations of temperature and salinity producing the same response. They calculated the contours of the surfaces for several selected mortality percentages (10, 20, 30, etc.) and plotted them for the different larval stages tested (Figs 3-57, 3-58, 3-59, 3-60, 3-61). These plots represent the predicted values of temperature and salinity which would produce the mortality indicated by the contour lines. COSTLOW and

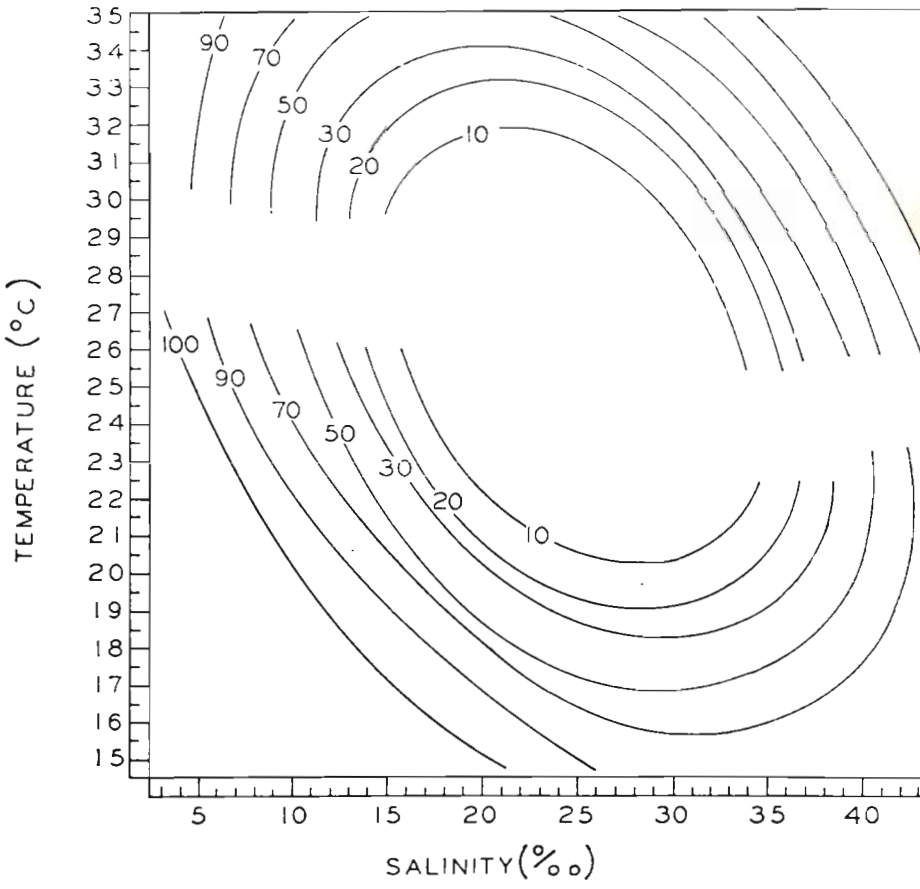


Fig. 3-59: Estimation of per cent mortality of zoea stage III of the decapod crab *Sesarma cinereum* based on the fitted response surface to observed mortality under 12 combinations of temperature and salinity. (After COSTLOW and co-authors, 1960.)

co-authors stress the point that the usual dangers of extrapolation beyond the ranges of observed data are as inherent in this method of prediction as in any other. The larval stages I (Fig. 3-57) and II (Fig. 3-58) are characterized by approximately concentric contour circles indicating no factor interactions. Stage III (Fig. 3-59) shows a distortion of contours into pronounced ellipses. Stages IV and V (Figs 3-60, 3-61) reveal a 'ridge' pattern manifesting the interaction and the lack of a unique maximum or minimum. The basic equations may be simplified by eliminating those factors which showed no effect and refitting the simpler model to the observed data. In some cases this may be desirable or even the objective of the study. COSTLOW and co-authors, however, attempted to describe the totality of the response surface and to infer from the changing patterns with each zoea stage a possible explanation of the mortality associated with each moult.

> 'We have, therefore, a sort of predicted mortality pattern as a function of temperature and salinity from which to postulate about the basic mechanisms involved in the system' (COSTLOW and co-authors, 1960, p. 200).

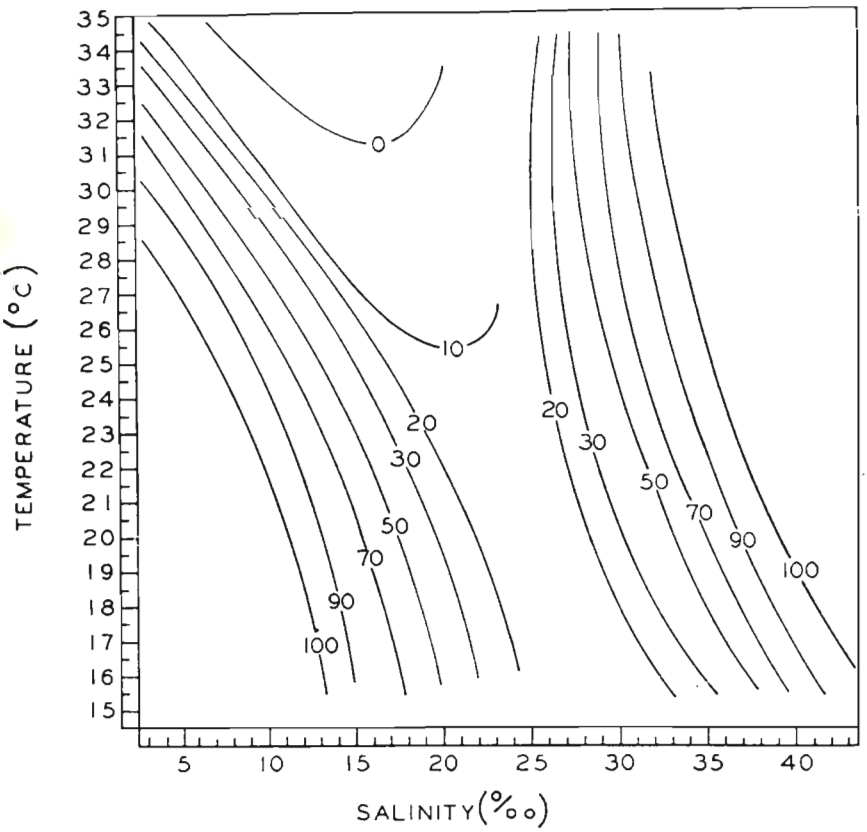


Fig. 3-60: Estimation of per cent mortality of zoea stage IV of the decapod crab *Sesarma cinereum* based on the fitted response surface to observed mortality under 12 combinations of temperature and salinity. (After COSTLOW and co-authors, 1960.)

In zoea stage I (Fig. 3-57) mortality of 20% or less may be expected in the rectangular area bordered by 21° to 31° C and 23 to 32‰ S. In zoea stage II (Fig. 3-58) less than 20% mortality can be expected in all temperature–salinity combinations other than 24° to 26° C and 10 to 15‰ S. Thus it appears that the second larval stage is tolerant to almost any temperature–salinity condition which might exist in an estuary. The tolerances of stage III (Fig. 3-59) are somewhat similar to those of stage I. The pattern of tolerance of stage IV (Fig. 3-60) does not correspond to that of any other larval stage; as temperatures increase up to 35° C, stage IV can withstand reductions in salinity to as low as 3‰. Stage V, the megalops (Fig. 3-61), is tolerant to a wide range of temperatures at high salinities (30 to 40‰) and, at high temperatures, it can withstand low salinities. As the temperature decreases, however, tolerance to low salinity is more restricted.

A similar study has been devoted to larval stages of the crab *Panopeus herbstii* (COSTLOW and co-authors, 1962). The differences in tolerance of the various larval stages of *P. herbstii* are less pronounced than in *Sesarma cinereum*, and succeeding stages show minimum mortality under different factor combinations.

ZEIN-ELDIN and ALDRICH (1965) studied the effects of temperature and salinity

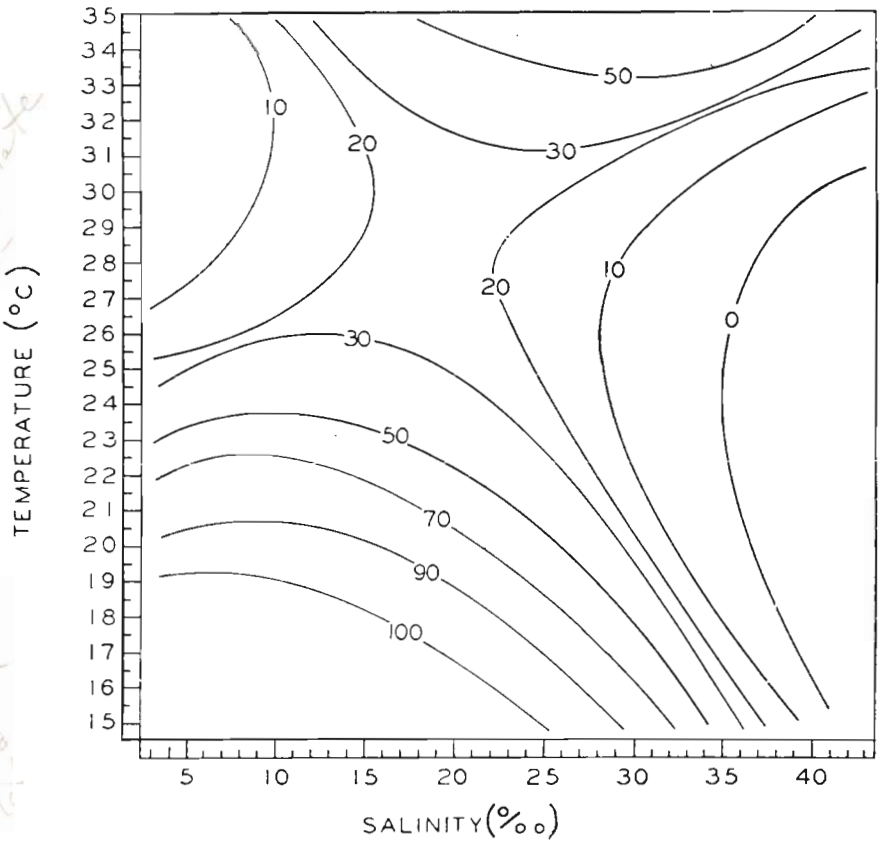


Fig. 3-61: Estimation of per cent mortality of larval stage V (megalops) of *Sesarma cinereum* based on the fitted response surface to observed mortality under 12 combinations of temperature and salinity. (After COSTLOW and co-authors, 1960.)

on postlarval stages of the brown shrimp *Penaeus aztecus*. The general design of their experiments was comparable to that of COSTLOW and co-authors (1960, 1962). However, they did not use the fitted response surface method—originally described by BOX and YOULE (1955)—because they felt that the complex nature of biological responses to temperature and salinity renders extrapolation too speculative. Tolerances of postlarval *Penaeus aztecus*, observed in 24-hr and 28-day experiments, to different temperature–salinity combinations are illustrated in Fig. 3–62. With relatively short periods of acclimation, postlarval brown shrimp tolerated wide ranges of both temperature and salinity for 24 hrs; the degree of tolerance was only slightly less over periods of 28 days. The postlarvae survived temperatures as low as 11° C with almost no growth for 1 month in salinities of $15^0/_{00}$ or more.

Further studies on the combined effects of temperature and salinity on the survival capacity of marine invertebrates have been conducted by SCHMITT (1955) in turbellarians, RANADE (1957) in the copepod *Tigriopus fulvus*, COSTLOW and BOOKHOUT (1959) in larvae of the blue crab *Callinectes sapidus*, COSTLOW and

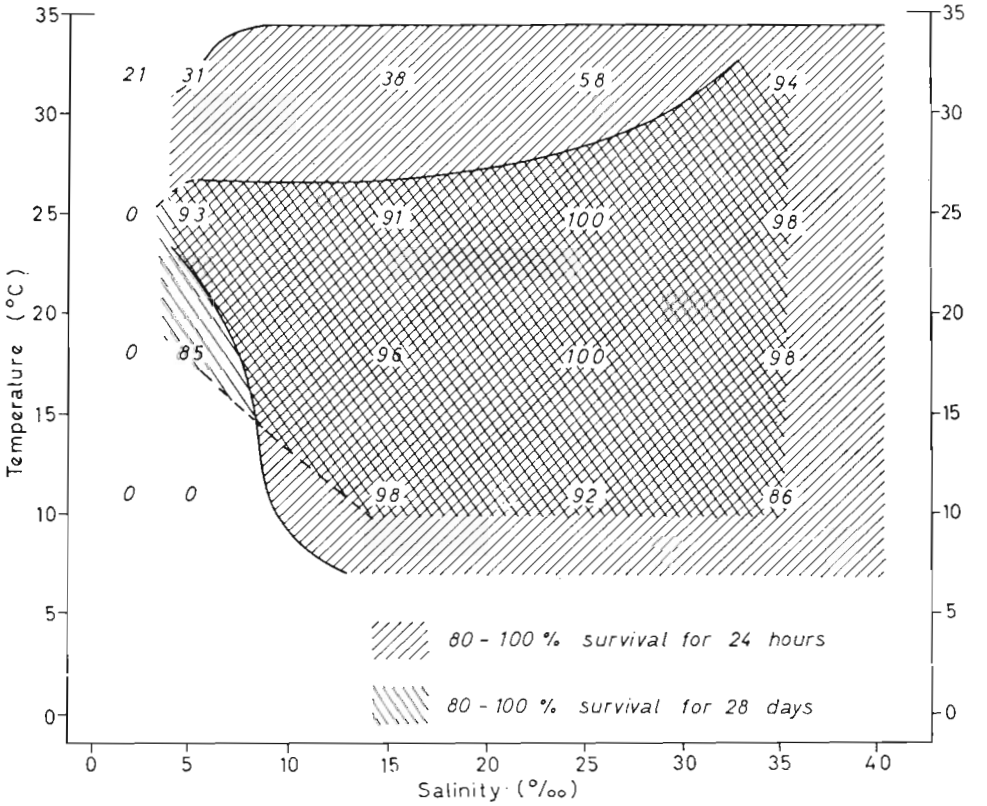


Fig. 3-62: Survival of postlarval *Penaeus aztecus* as a function of temperature and salinity. The graph presents results obtained both in 24-hr and 28-day experiments. Numbers indicate 28-day survival in per cent. The postlarvae tolerate wide ranges of temperature and salinity. The tolerated temperature range narrows as salinities decrease below 15‰ and, particularly, below 8‰ S. (After ZEIN-ELDIN and ALDRICH, 1965.)

BOOKHOUT (1962a) in larvae of the crab *Hepatus epheliticus*, COSTLOW and BOOKHOUT (1962b) in larvae of the crab *Sesarma reticulatum*, COSTLOW and co-authors (1966) in larvae of the crab *Rhithropanopeus harrisii*, COSTLOW (1967) on megalops of the blue crab *Callinectes sapidus*, and others.

For general considerations of physiological and ecological aspects of temperature-salinity relations consult HARTMANN (1918), STEINER (1935), HEILBRUNN (1952), PRECHT and co-authors (1955), KINNE (1956a), GUNTER (1957), REMANE and SCHLIEPER (1958), PROSSER and BROWN (1961), DILL and co-authors (1964) and ROSE (1967).

Other factors which have been reported to modify temperature tolerances are oxygen availability, pressure, light and food (at elevated temperatures inadequate food quality or insufficient quantity may cause death at non-lethal temperature intensities). While insufficient information on marine invertebrates is available with regard to light and food, we shall briefly illustrate concomitant oxygen and pressure effects.

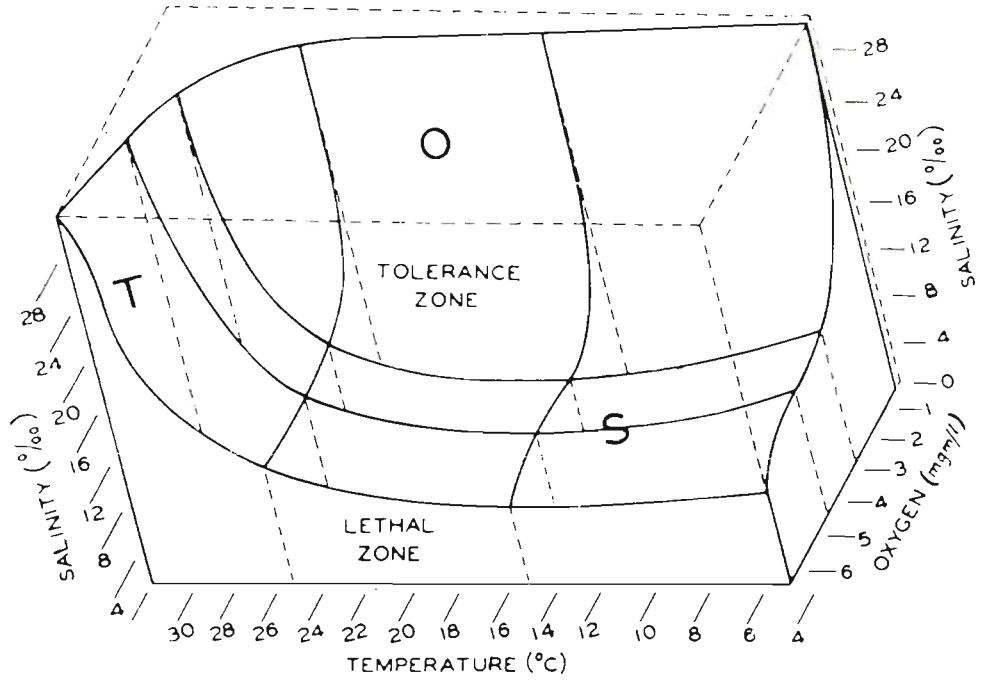


Fig. 3-63: Diagram of the boundaries of lethal conditions for American lobsters *Homarus americanus* in various combinations of temperature, salinity and oxygen. T, S, O: regions in which temperature, salinity or oxygen alone act as a lethal factor. (After McLEESE, 1956.)

McLEESE (1956) studied the responses of the American lobster *Homarus americanus* to different constant levels of temperature, salinity and dissolved oxygen. His results are discussed in more detail in Chapter 12. Fig. 3-63 shows the boundary lines of lethal conditions for these 3 environmental factors. It also indicates the regions in which the factors are effective independently and in combination. The upper lethal temperature is lowered by a decrease in salinity, and the lower lethal salinity raised by an increase in the level of thermal acclimation. These relations are, in addition, a function of the oxygen content of the water (Table 3-29).

SCHLIEPER and his associates studied various aspects of the relation between thermal tolerance and hydrostatic pressure. In his recent review SCHLIEPER (1968) reports that non-genetic adaptation of euryoecous marine invertebrates to supranormal temperatures—as well as to supranormal ambient osmotic concentrations and high Ca contents of tissues—results in increased pressure resistance both of excised tissues and intact whole individuals. In the eurythermal lamellibranch *Mytilus edulis* cellular pressure tolerance is higher at 20° C than at 10° C (Fig. 3-64); however, the pressure resistance increases during adaptation to cold.

> 'We can only expect that a eurythermal species is more pressure resistant in the warmth, if we compare its individual pressure resistance at two temperatures within the range of the genetically determined thermal resistance or if the higher test temperature lies near the thermal optimum of the species' (SCHLIEPER, 1968, p. 9).

Table 3-29

Levels of upper lethal temperature and lower lethal salinity and oxygen for lobsters *Homarus americanus* kept at 27 different combinations of temperature, salinity and oxygen (After McLeese, 1956)

Acclimation conditions			Upper lethal temperature	Lower lethal salinity	Lower lethal oxygen
Temperature (° C)	Salinity (‰)	Oxygen (mg/l)	(° C)	(‰)	(mg/l)
		2·9	20·6	11·0	0·72
5	20	4·3	22·0	9·0	0·77
		6·4	23·7	9·0	0·72
		2·9	22·4	12·0	0·57
5	25	4·3	22·1	12·4	0·51
		6·4	24·6	9·2	0·24
		2·9	24·0	10·8	0·29
5	30	4·3	25·2	11·5	0·33
		6·4	25·7	6·0	0·20
		2·9	27·3	9·0	0·86
15	20	4·3	27·7	9·0	0·79
		6·4	27·8	8·2	1·20
		2·9	27·5	10·7	0·80
15	25	4·3	28·2	10·7	0·90
		6·4	28·0	9·5	1·00
		2·9	27·8	10·6	0·66
15	30	4·3	28·2	11·0	0·83
		6·4	28·4	11·2	0·83
		2·9	28·5	11·5	1·72
25	20	4·3	29·0	11·5	1·58
		6·4	29·3	11·1	1·26
		2·9	29·0	14·3	1·17
25	25	4·3	29·5	14·8	1·20
		6·4	29·6	14·0	1·60
		2·9	28·7	15·4	1·30
25	30	4·3	29·5	16·0	1·25
		6·4	30·5	16·4	1·17

According to Naroska (1968), the decapod crustacean *Crangon crangon* is more tolerant to high pressures in the cold (Fig. 3-65).

Non-genetic resistance adaptation

The term 'adaptation' is used in different ways and hence requires qualification. Adaptation is visualized here as an ecological phenomenon comprising adjustments of organisms to alterations in the intensity pattern of variables in their environment, which ultimately result in a relative increase in their capacity to survive, reproduce or compete under the new conditions (Kinne, 1964b, c). Such adjustments can be assessed quantitatively by measuring differences in tolerance or per-

formance of individuals with different environmental histories. The definition presented separates adaptation from the more general term 'response' which refers to any reaction to an environmental stimulus whether it be adaptive or not; another difference between adaptation and response is that the former requires more time to develop and involves changes in the adapted organism which persist beyond the environmental circumstance which induced it. Adaptation involves practically all levels of organismic organization.

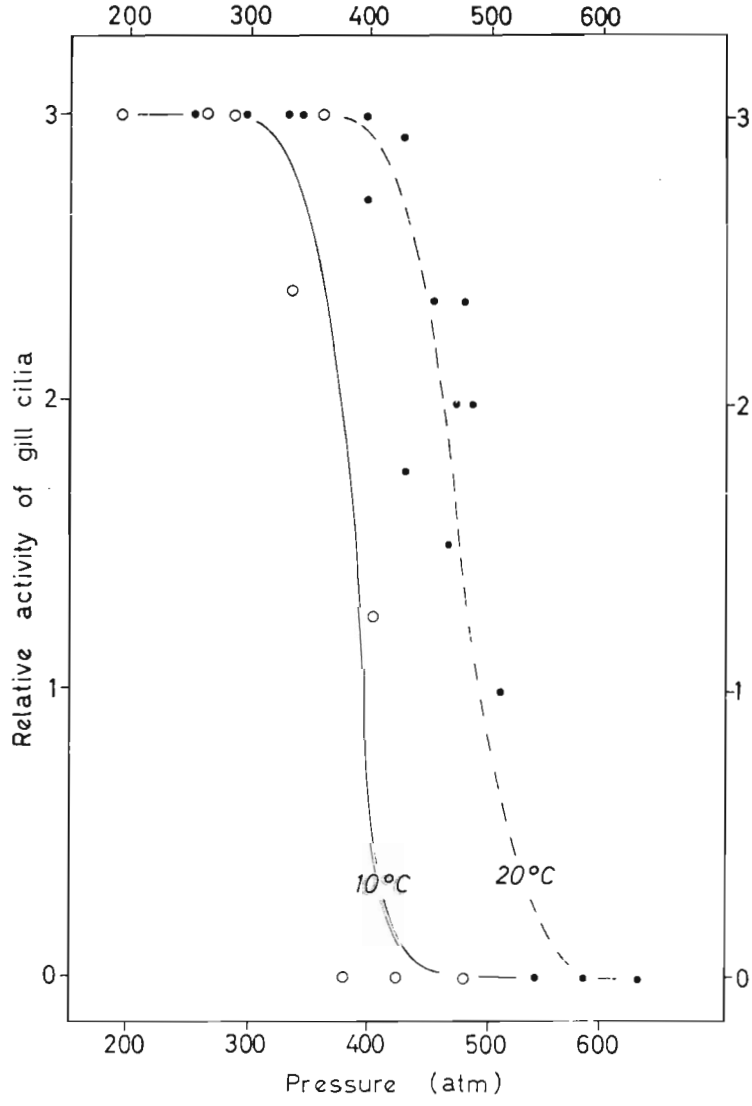


Fig. 3-64: Influence of temperature on resistance to high water pressures in excised surviving gill pieces of the lamellibranch *Mytilus edulis*. Vertical: relative activity of terminal cilia; 3: normal activity, 2: slightly reduced activity, 1: strongly reduced activity (50 to 90% of the cilia have ceased to beat). 0: complete cessation of activity. Horizontal: test pressures. (After SCHLIEPER, 1963; modified.)

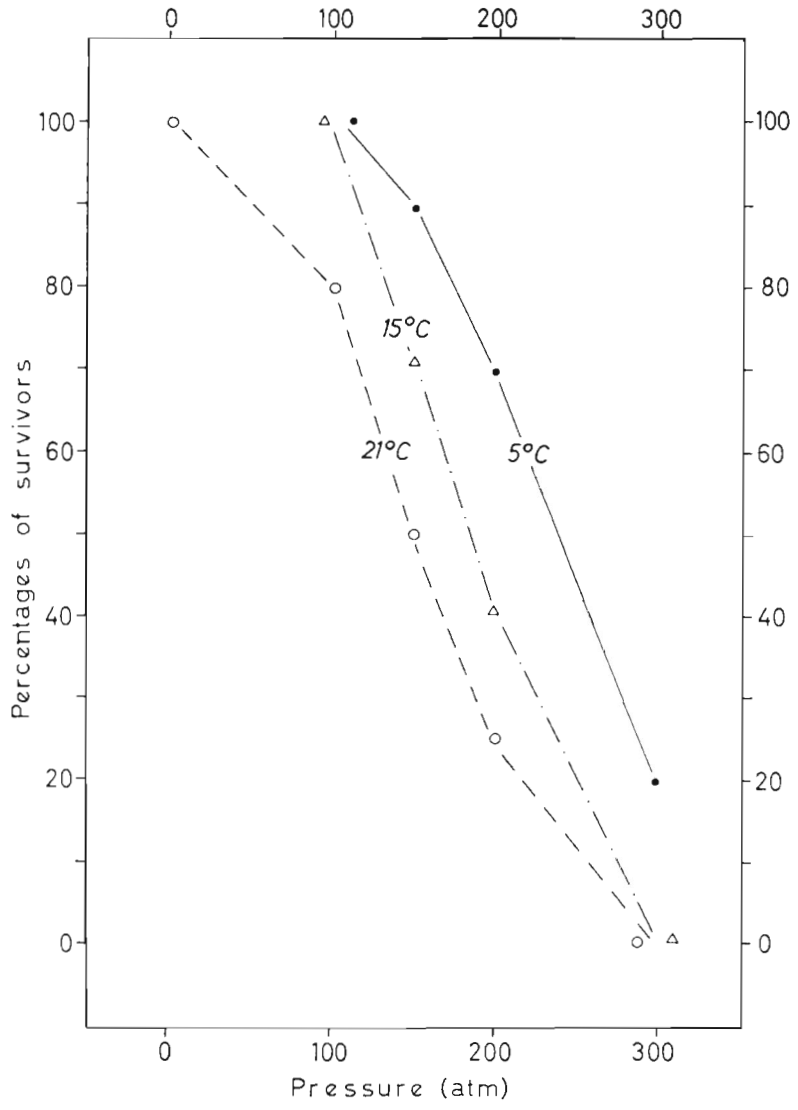


Fig. 3-65: Influence of temperature on resistance to high water pressures in the decapod crustacean *Crangon crangon*. (After NAROSKA, 1968.)

Adaptations to temperature often consist of a variety of adjustments, of both functions and structures. They may be genetically determined (genetic adaptation) or environmentally induced (non-genetic adaptation). Genetic adaptations involve changes in the genotype and are the result of speciation and evolution. Non-genetic adaptations (acclimations, acclimatizations) involve gradual adjustments of individuals within their genetic limits which are directly induced by the environment and not passed on as such to the next generation. Adaptations to given temperature conditions often consist of a genetic plus a non-genetic component. These are distinguishable by cross-acclimation experiments.

With respect to both genetic and non-genetic adaptations to temperature, one may (with CHRISTOPHERSEN and PRECHT, 1953; PRECHT and co-authors 1955; PRECHT, 1964, 1967) differentiate between resistance adaptations (variations in tolerance to extreme temperatures) and capacity adaptations (variations in performance within the tolerated temperature range). These 2 types of adaptation are closely related and may occur simultaneously in one and the same individual; they are useful analytical concepts rather than basically different biological phenomena.

Thermal resistance adaptations of marine invertebrates have been studied at the individual and subindividual (tissues, cells, cell components) levels (e.g. TODD and DEHNEL, 1960; KINNE, 1963a, b, 1964b, c; USHAKOV, 1963a, b, 1965, 1966, 1968; PRECHT, 1964; SCHLIEPER, 1966). Non-genetic resistance adaptation may significantly affect the degree of tolerance to cold and heat. In most cases reported, non-genetic adaptation to subnormal temperatures tends to shift the lower lethal limit downward, and acclimation to supranormal temperatures tends to shift the upper lethal limit upward. According to PRECHT (1958), the resulting adjustments may be meaningful (complete, partial or overcompensation) or paradoxical (reverse compensation). The paradoxical acclimations reported thus far need critical attention and ought to be repeated under adequate ecological conditions.

Meaningful non-genetic resistance adaptations have been found, for example, in the amphipod *Gammarus duebeni* (KINNE, 1953a), the fairy shrimp *Strepto-*

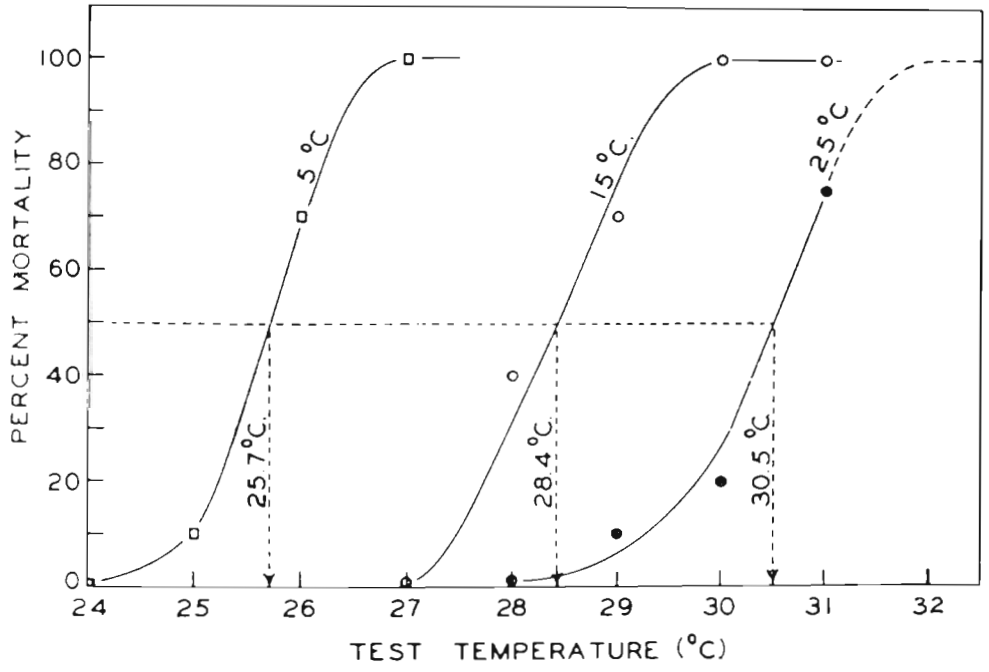


Fig. 3-66: The effect of non-genetic temperature adaptation on the upper lethal temperatures in the American lobster *Homarus americanus*. Acclimation temperatures: 5°, 15°, and 25° C, respectively; test temperatures are indicated on the horizontal axis. The sigmoid curves are drawn through points representing per cent mortalities at the respective test temperatures after 48 hrs; the temperature that would cause 50% mortality (LD_{50} – 48 hrs) is indicated by dotted lines and arrows. 30‰ salinity; 6·4 mg O /l. (After MCLEESE 1956.)

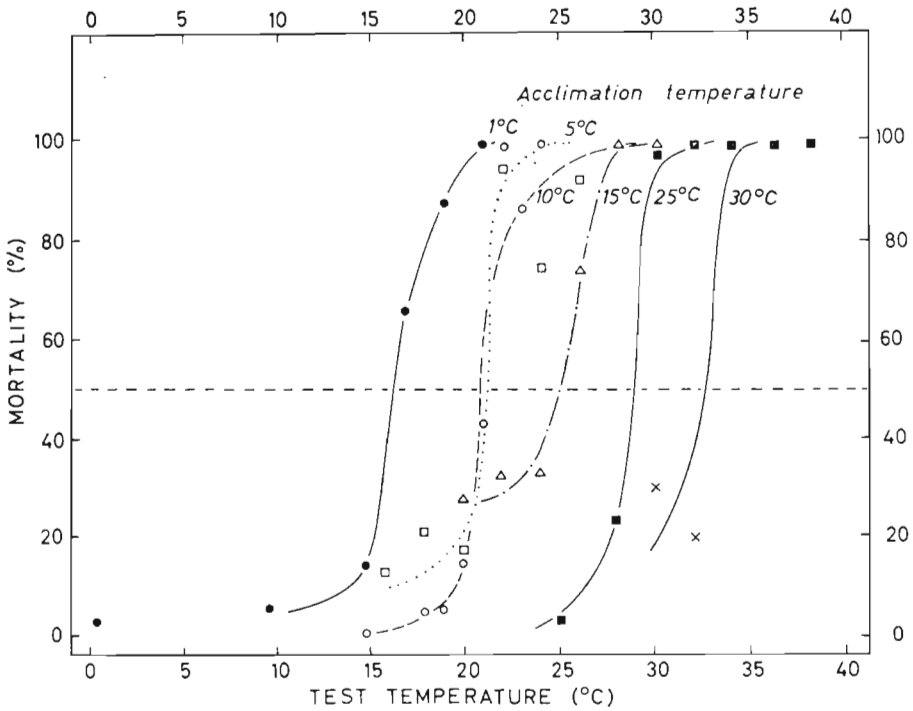


Fig. 3-67: Heat death curves of the mysid *Neomysis americana* acclimated to 6 different temperatures prior to heat-tolerance determination. LD_{50} – 24 hrs levels increase with increasing acclimation temperature. N = 1800. (GIBSON, unpublished; after MIHURSKY and KENNEDY, 1967; modified.)

cephalus seali (MOORE, 1955), the American lobster *Homarus americanus* (MCLEESE, 1956), the brine shrimp *Artemia salina* (GRAINGER, 1958), the decapod crabs *Hemigrapsus nudus* and *Hemigrapsus oregonensis* (TODD and DEHNEL, 1960), the isopod *Ligia oceanica* (EDNEY, 1960), and the mysid *Neomysis americana* (MIHURSKY and KENNEDY, 1967). MATUTANI (1960) reported a case of reverse resistance adaptation for the marine copepod *Tigriopus japonicus*: while 30° C-acclimated *Tigriopus* exhibit a higher heat tolerance than 20° C-acclimated ones, acclimation temperatures below 20° C (10° C; 5° C) cause a progressively increasing tolerance to heat. According to PRECHT (1964), non-genetic resistance adaptation of intact vertebrates seems always to be meaningful, whereas invertebrates often adapt to one temperature extreme only, and cellular resistances may show reverse adaptations.

Fig. 3-66 illustrates the effect of non-genetic temperature adaptation on the upper lethal limits in the lobster *Homarus americanus*. The lobsters were exposed to various test temperatures following acclimation to 5°, 15° or 25° C. Average LD_{50}–48 hrs values vary from 25·7° over 28·4° to 30·5° C. Thus the mean heat tolerance increased almost 5 centigrade degrees. Fig. 3-67 exemplifies the effect of different acclimation temperatures on the heat tolerance of the mysid *Neomysis americana* (compare with Fig. 3-48). The LD_{50}–24 hrs levels are raised with increasing acclimation temperature until maximum acclimation is attained. The highest

incipient lethal temperature that can be achieved by acclimation is the ultimate upper incipient lethal temperature (FRY and co-authors, 1946; FRY, 1947). Since rate of acclimation is temperature dependent, most invertebrates acclimate faster to temperatures near the upper end of their species-specific range than to those near the lower end. DICKIE (1958) demonstrated that heat tolerance in the mollusc *Placopecten magellanicus* acclimates rapidly (1·7 C°/day) at high temperatures, but that it may take up to 3 months to lose this heat resistance again (see also KINNE, 1964b).

As pointed out by USHAKOV (1968), non-genetic resistance adaptation has been studied in many protozoans (e.g. POLJANSKY, 1957, 1959; PROPPER, 1965; POLJANSKY and SUKHANOVA, 1967). In the marine protozoans *Zoothamnium hiketes* and *Anoplophrya filum*, adaptive changes in heat resistance were accomplished within 24 hrs, and to cold, within several days (POLJANSKY, 1957, 1959; VOGEL, 1966). In *Paramecium caudatum*, heat hardening begins several seconds after initiation of heat stress (POLJANSKY and IRLINA, 1967). Non-genetic resistance adaptations of protozoans are a function of salinity and light (LOSINA-LOSINSKY, 1948; VOGEL, 1966). Prolonged heat treatment (28° to 30° C) induces a long-lasting increase in heat resistance of infusoria (POLJANSKY and ORLOVA, 1948); different infusoria clones may exhibit different, genetically fixed, degrees of thermostability.

According to USHAKOV (1968), early (oligocellular) stages of ontogenesis of multicellular marine invertebrates (gametes, zygotes, developing eggs) have the smallest capacity for non-genetic resistance adaptation within the individual's life span. Supracellular mechanisms of homeostasis, and adjustments in the degree of resistance are still lacking and adaptation of the developing young individual is provided only at the cellular level. Mature spermatozoa usually exhibit a higher degree of thermostability than mature ova (Figs 3-50, 3-51). The heat tolerance of gametes and cleaving eggs is a rather stable species-specific characteristic (MOORE, 1939; ANDRONIKOV, 1967), closely related to the temperatures of reproduction of the tested invertebrates. Intraspecific differences in thermostability of gametes and eggs at early stages of development have been observed only in a few species.

With regard to the mechanisms of adaptation in unicellular organisms, recent results indicate that adaptive changes in cold resistance depend on an increased capacity of the cells to withstand supercooling and, in case of ice formation, on an increase in resistance to dehydration (MAZUR, 1966; MERYMAN, 1966; USHAKOV, 1968). Both non-genetic cold and heat adaptation are associated with an increase of antidenaturants in the cell (SALT, 1958; HEBER and SANTARIUS, 1967). The mechanisms of cellular resistance adaptations are not yet sufficiently understood; there is a great need to expand our knowledge

> 'since there is every reason to believe that stenothermy of animals during their period of reproduction is determined by the fact that, at this moment, animals possess the smallest adaptive abilities' . . . 'In other words, stenothermy of marine animals during the reproductive period is a stabilizing adaptation which serves normal oligocellular stages of ontogenesis when the adaptive capacities of the organism are minimal' (USHAKOV, 1968, p. 155).

Ontogenetic temperature conditions may affect the iodine numbers of lipids which are related to the number of double bonds in the molecule. Poikilotherms grown at subnormal temperatures tend to contain increased proportions of unsaturated fatty acids. Insects which are fed diets containing unsaturated fatty acids exhibit lower tolerances to extreme high temperatures than their counterparts which consume higher saturated fatty acids. Terrestrial homeotherms exposed to low environmental temperatures contain larger proportions of unsaturated fatty acids in their surface lipids than under normal temperature conditions (CHAPMAN, 1967). Comparable situations may exist in marine invertebrates and could conceivably affect their capacity for non-genetic resistance adaptation.

Non-genetic adaptation of marine invertebrates to temperature at the subindividual (cellular) level has been studied by several authors. It may suffice here to refer to the recent reviews by SCHLIEPER (1966) and USHAKOV (1968).

SCHLIEPER (1966) distinguishes between 'specific' and 'non-specific' cellular non-genetic resistance adaptations. In specific adaptations the lower and upper thermal limits shift in the same direction (adaptation to heat results in increased heat resistance and decreased cold resistance of excised tissues). In non-specific resistance adaptations, 'the total cellular resistance extent (against heat, cold, frost, pressure, etc.) may be enlarged or diminished in several directions' (SCHLIEPER, 1966, p. 498).

USHAKOV (1968) considers the role of cells and proteins in the process of adaptation, and comes to the conclusion that all adaptations are ultimately a result of natural selection. Since the primary object of natural selection appears to be the intact whole organism, adaptations are accomplished at the individual or supra-individual levels of organization. According to this consideration, the term 'cellular adaptation' may be applied only to unicellular forms and to multicellular organisms at early (mono- or oligocellular) stages of ontogenesis. The analysis of the role of cells and proteins in the process of adaptation of multicellular organisms reveals not cellular or molecular adaptations, but cellular and molecular mechanisms of adaptation which serve higher, supra-individual levels of organization (population, ecosystem).

Genetic resistance adaptation

All living organisms are somehow genetically adapted to their ecological niche. Their mere presence is proof of such a statement. Strictly conservative systems cannot exist indefinitely in a changing environment, and there is no environmental aspect—abiotic or biotic—which does not change over long periods of time (KINNE, 1963a, b).

Evidence for genetic resistance adaptation comes from comparisons of thermal tolerances in species from different latitudes, different water depths or different climatic zones and hence is discussed in this chapter under various headings.

Causes of cold and heat death

The causes of cold and heat death have been considered in a number of reviews (e.g. BĚLEHRÁDEK, 1935, 1957; HEILBRUNN, 1952; PRECHT and co-authors, 1955; GUNTER, 1957; PROSSER and BROWN, 1961; KINNE, 1963a; DILL and co-authors 1964; PROSSER, 1967; ROSE, 1967; TROSHIN, 1967; see also Chapter 3.0). They

are complex and may manifest themselves at different levels of organization.

Evidence from field observations suggests that the primary causes of cold or heat death in the sea are related to the breakdown in physiological integration rather than to direct cell damages. Heat or chill coma suffered near the critical temperature maximum, c.t.m. (Chapter 3.0) usually precedes actual cell damage and critically incapacitates the individual concerned.

Extreme low temperatures cause insufficient integration of nervous and metabolic processes, insufficient rates of energy liberation, changes in water and mineral balance and in the colloidal relations with water, such as formation of ice crystals (disrupture of intracellular organization), increase in osmoconcentration resulting from extracellular freezing and followed by dehydration of cells, as well as liquefaction of cortical protoplasm and gelation of the interior. Fatal effects of disrupture of protoplasmic organization by ice crystals have been reported for amoebae (CHAMBERS and HALE, 1932) and plants (LEVITT, 1958).

In intertidal invertebrates, especially molluscs, frozen at $-15°$ C, only 55 to 65% of the body water was actually frozen. Such freezing was accompanied by a rapid decline in oxygen consumption, which may have been the result of increased intercellular osmoconcentration rather than of the low temperature *per se* (KANWISHER, 1955, 1957, 1959). Freezing modifies the pattern of water and salt distribution in the living organism. In a slowly freezing salt solution, water crystallizes and salt is concentrated and trapped in interstices of the crystals. Osmoconcentration of the yet unfrozen fraction of the solution rises and, since initial freezing is usually extracellular, water is drawn out of the cells (MERYMAN, 1956). As freezing continues, the water balance becomes seriously disturbed.

While a sudden drop of temperature to 0° C may have harmful effects on a variety of cells, gradual cooling to 0° C or even below often causes non-critical and usually reversible changes as long as no freezing occurs. Temperatures below the freezing point of sea water (ca $-1{\cdot}9°$ C) cause rapidly spreading ice formation in extracellular fluids which initially does not extend into cells (except dead or injured ones) since the cell membrane acts as a barrier. Intracellular freezing occurs only upon further cooling or seeding (introduction of small ice crystals into the cell). The water–protein system of the myofilaments cannot be frozen into ice since the water molecules in this system are so strongly oriented that it would be energetically very unfavourable for them to turn around and to re-organize into the tridymite structure of ice (LING, 1967).

Extreme high temperatures tend to cause an insufficient supply of oxygen, failures in process integration and water loss by evaporation (desiccation); enzymes pass the phase where inactivation exceeds activation and synthesis, lipids change in state, protoplasmic viscosity increases, and cell membranes become increasingly permeable; at still higher temperatures protein denaturation occurs and toxic substances may be released from damaged cells (e.g. KINNE, 1963a).

Heat denaturation of proteins is a co-operative phenomenon (e.g. SCHELLMANN, 1955; LING, 1962, 1964). As in other co-operative phenomena, there is a sharp transition temperature corresponding to the lambda point. In native ribonuclease, for example, large sections of the molecule exist in an α-helical form. Heating in a near-neutral solution causes the α-helical structure to disappear suddenly between

60° and 70° C, and the denaturated protein molecules assume a form often referred to as a random coil. If the pH value of the solution decreases below the pK value of the β- and γ-carboxyl groups (4·6 to 4·7), the lambda point drops to a much lower temperature, indicating, in a general way, that salt linkages, formed by the carboxyl groups with fixed cationic groups, stabilize the α-helical structure. Each native protein possesses a specific complex water structure surrounding it. Once the protein is denatured, one may anticipate that the hydrophobic groups tend to aggregate to form a core from which the hydrophilic groups are directed outwards. Thus, heat denaturation involves not only the protein but the entire protein–water system; without water, protein cannot undergo denaturation (Ling, 1967). Most marine invertebrates die at temperatures between 25° and 30° C; only a few tropical forms tolerate significantly higher temperatures. Heat denaturation of proteins is a function of primary structures and hence depends strongly upon genetic characteristics.

(*b*) *Metabolism and Activity*

Within the range of temperature conditions tolerated, the functions of an organism may be considered under 2 aspects: metabolism and activity. Metabolism comprises the total of all processes which use and convert material and energy for maintenance, repair, growth and reproduction of the living system under consideration. Activity represents, in a sense, the result of the integrated, co-ordinated metabolism; it comprises such processes as locomotion, feeding, fighting, and courting.

The literature available on the effects of temperature on metabolism and activity of marine invertebrates easily fills several volumes. This section is, therefore, largely restricted to quantitative aspects of performance, i.e. rates of metabolism and activity. The general trends that have become apparent will be elucidated on the basis of a few examples; details of the intermediary metabolism and mechanisms of muscular activity will not be treated.

In general, rates of metabolism and activity increase with increasing temperature over most of the species-specific temperature range tolerated and decrease suddenly near the upper lethal limit (critical temperature maximum; Chapter 3.0). The rates of increase are usually different for different species (populations), and frequently also for different biological processes. They depend on the absolute temperature intensity employed, the speed of temperature change, the previous environmental history (season), the physiological state of the tested individual and on other simultaneously effective environmental factors. The use of the temperature coefficient Q_{10}, the Arrhenius equation and other quantitative expressions of biological temperature functions must, therefore, be considered in the light of the specific experimental circumstances. Especially the use of Q_{10} values as tools in ecology should be considered critically (e.g. Kinne, 1963a). Numerous attempts to formulate the relation between temperature and the velocity of physiological and ecological processes mathematically have been presented (e.g. Quantitative Biology of Metabolism, 1964, 1966, 1968), and in several cases led to promising new concepts.

Metabolism and activity are interrelated. Variations in metabolic rate modify

the scope for activity, and the degree of activity affects the metabolic rate. However, rates of metabolism and activity may not necessarily attain comparable intensities synchronously. For example, after a sudden burst of activity, metabolic debt is often only slowly repaid, and a temporary decline in activity may not be accompanied by a comparable decline in metabolic rate but a level higher than can be accounted for by the present rate of activity. Three quantitative aspects of metabolism have been recognized (see also Chapter 3.32, p. 538): (i) **standard metabolic rate**, referring to minimum energy requirements for maintenance of all vital functions; (ii) **routine metabolic rate**, energy demands for spontaneous normal activity; (iii) **active metabolic rate**, energy requirements during sustained forced activity.

Unfortunately, many reports dealing with temperature effects on rates of metabolism and activity of marine invertebrates have not taken these considerations into account, nor have they allowed for the modifying effects of other simultaneously effective environmental factors or the physiological state of the tested individuals. The study of temperature effects on rates of metabolism and activity is indeed more complex than originally expected; it requires the development of new techniques which allow a better differentiation between the 3 quantitative aspects mentioned, and the assessment of functional performances under adequate environmental circumstances.

Most of our knowledge on temperature effects on metabolic rates in marine invertebrates has been obtained by determining respiratory intensities per unit body mass during short-term experiments employing small respiratory chambers. Such procedure may, especially in 'higher' forms such as molluscs and crustaceans, lead to abnormal responses. It seems that long-term assessments of energy budgets under experimental conditions which allow normal growth rates or even normal reproductive activities are to be preferred in ecological studies. Such studies attempt to record intake, transformation and output of energy at different levels of temperature and activity over weeks, months or even years, and hence may be expected to yield important ecological information.

Metabolism

The effects of ambient temperature conditions on metabolic rates of marine invertebrates have been discussed in a large number of papers. In most of the experiments conducted, the criterion employed was the rate of oxygen consumption.

Rate of oxygen consumption. Since temperature affects rate of O_2 consumption via the speed of biochemical reactions, many authors have expressed temperature/O_2 consumption relations in terms of Q_{10} values. For several crustaceans such Q_{10} values have been reported to range between 2·0 and 3·0. In the same individual, Q_{10} values usually increase with decreasing temperature. Crustaceans of different body sizes exhibit either a weight-dependent or a weight-independent Q_{10} (WOLVEKAMP and WATERMAN, 1960).

The O_2 consumption of many aquatic invertebrates tends to decrease in the presence of high CO_2 concentrations. Under conditions of gradually diminishing ambient O_2 concentrations a number of species maintain or slowly reduce the rate

of their O_2 consumption down to a critical pressure (*Pc*) below which their O_2 consumption declines rapidly; such 'metabolic regulators' are characterized by a wide range of oxygen independence. This response pattern is exemplified in Figs 3-68, 3-69, which illustrate metabolic rates of 2 barnacle species at 25·0° ± 0·5° C after abrupt transfer into various constant levels of ambient O_2 concentrations. In *Balanus amphitrite amphitrite* O_2 consumption remains largely constant over a considerable range (4·0 to 2·5 ml O_2/l); however, below 2·5 ml O_2/l it decreases rapidly (Fig. 3-68). In *Balanus tintinnabulum tintinnabulum*, the critical point below which metabolic rate begins to decrease lies near 3.5 ml O_2/l (Fig. 3-69). In both species no gaseous exchange was observed at 0·5 ml O_2/l. It seems possible that at, or below, this level these barnacle species change to anaerobic metabolism which would allow them to tolerate periods of extreme low oxygen availability (Prasada Rao and Ganapati, 1968). The mud-shrimp *Callianassa californiensis* shows oxygen-independent respiration above 10 to 20 mm Hg (6–12·5% air saturation), the mud-shrimp *Upogebia pugettensis* above 45 to 50 mm Hg (28–31% air saturation). Within the independent range, *C. californiensis* has a mean metabolic rate of 0·029 ml $O_2 \times$ g wet weight$^{-1} \times$ hr^{-1}, which is significantly lower than that of *U. pugettensis* (0·059 ml $O_2 \times$ g wet weight$^{-1} \times$ hr^{-1}). Preliminary data suggest that postmoult *U. pugettensis* do not regulate and therefore are oxygen dependent throughout the range of ambient O_2 concentrations tested (Thompson and Pritchard, 1969). The spiny lobster *Panulirus interruptus* regulates between 25 and 45% air saturation (Winget, 1969).

In other invertebrates—the 'metabolic conformers'—O_2 consumption is more or less directly proportional to variations in ambient O_2 concentration. Regulators and conformers are not always clearly distinguishable.

Examples of metabolic regulators are (unless indicated otherwise, critical pressures are given as partial pressures of O_2 in mm Hg): most protozoans, larvae of some polychaetes (*Pc* = 40 to 50); *Arbacia* eggs unfertilized (*Pc* = 40), fertilized (*Pc* = 50); *Mya* (*Pc* = 40 to 50); *Ostrea* (*Pc* = 100); *Ancylus* (*Pc* = 80); *Mytilus* (*Pc* = 50% air saturation); *Calanus* (*Pc* = 204 ml O_2/l); *Pugettia* (*Pc* = 70); *Uca pugilator* and *Uca pugnax* (*Pc* = 4). Examples of metabolic conformers are numerous actinias, nematodes, *Sipunculus*, *Urechis*, *Nereis*, *Limulus*, sea-stars and sea-urchins (Zeuthen, 1955; Prosser and Brown, 1961). Relative independence of variations in oxygen supply may be related to body size. In large animals without special respiratory organs or circulation, long diffusion distances may result in O_2 dependence (actinias, *Sipunculus*, nematodes). When the actinia *Metridium* was cut into pieces, these were less O_2 dependent than the intact individual (Henze, 1910). In protozoans where the diffusion path is short, the critical O_2 pressure is extremely low (2·5 mm Hg in *Tetrahymena*).

The critical pressure values presented above must be viewed with reserve unless additional data on temperature regime, amount of space available, degree of locomotory activity, etc., are provided. McLeese (1964), using prestabilized adult *Homarus americanus* tested at temperatures to which they had been acclimated for 3 or more weeks, found that at a test temperature of 10° C 2 individuals increased their routine rate of O_2 consumption over the range of ambient O_2 concentrations from 2·3 to 9·0 mg O_2/l, while a group of 25 individuals consumed O_2 at a practically constant rate of about 28·3 mg O_2/kg/hr at concentrations of 1·0

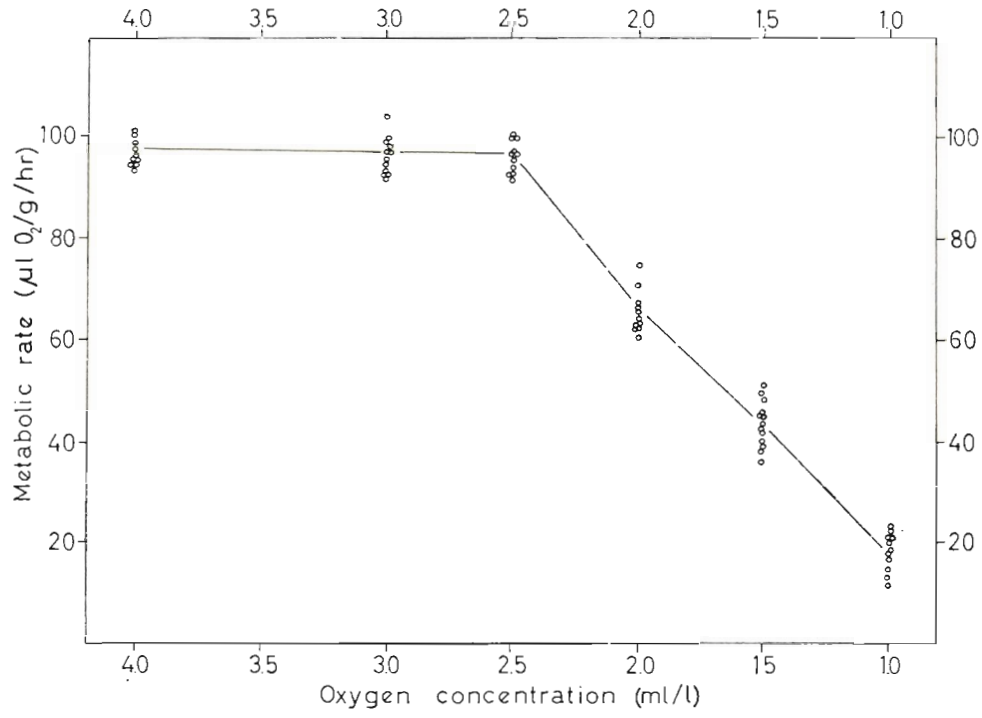


Fig. 3-68: Metabolic rate (0_2 consumption at 25° C) as a function of ambient oxygen concentration in *Balanus amphitrite amphitrite*. Individual measurements. (After PRASADA RAO and GANAPATI, 1968.)

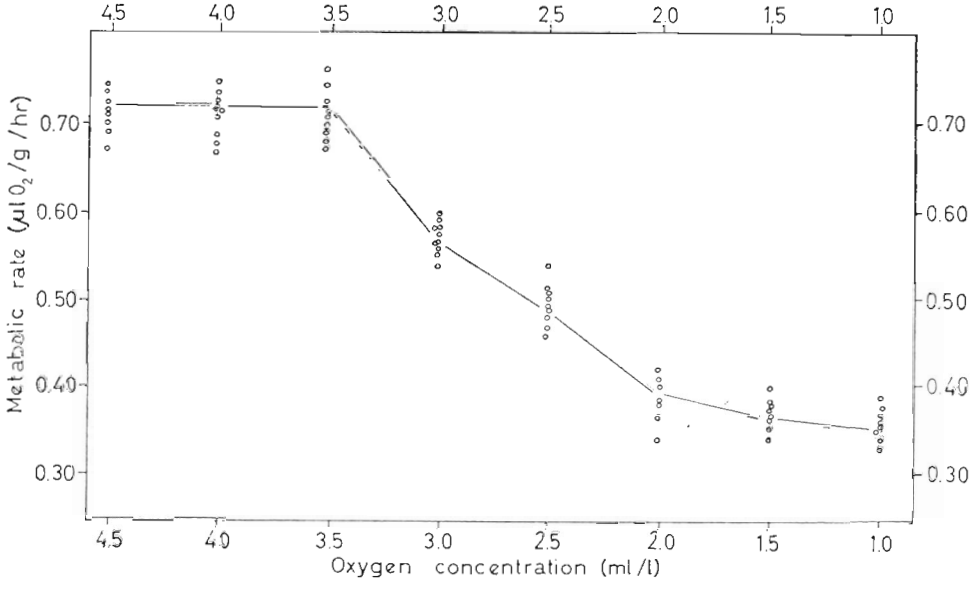


Fig. 3-69: Metabolic rate (0_2 consumption at 25° C) as a function of ambient oxygen concentration in *Balanus tintinnabulum tintinnabulum*. Individual measurements. (After PRASADA RAO and GANAPATI, 1968.)

to 8·6 mg/O_2/l. At 15° C, however, 4 individuals and groups of 35 to 50 lobsters both showed comparable increases in routine O_2 consumption with increasing ambient O_2 concentration. The rates of routine O_2 consumption at 15° C and 5 mg O_2/l for the 4 individuals and the groups of 35 and 50 lobsters were 29, 38, and 55 mg O_2/kg/hr, respectively. When the activity of the lobsters was increased by crowding, the general rate of O_2 consumption was higher. Active O_2 consumption is considerably higher (at 15° C and 5 mg O_2/l, 60 to 70 mg O_2/kg/hr) and related to higher critical O_2 pressures.

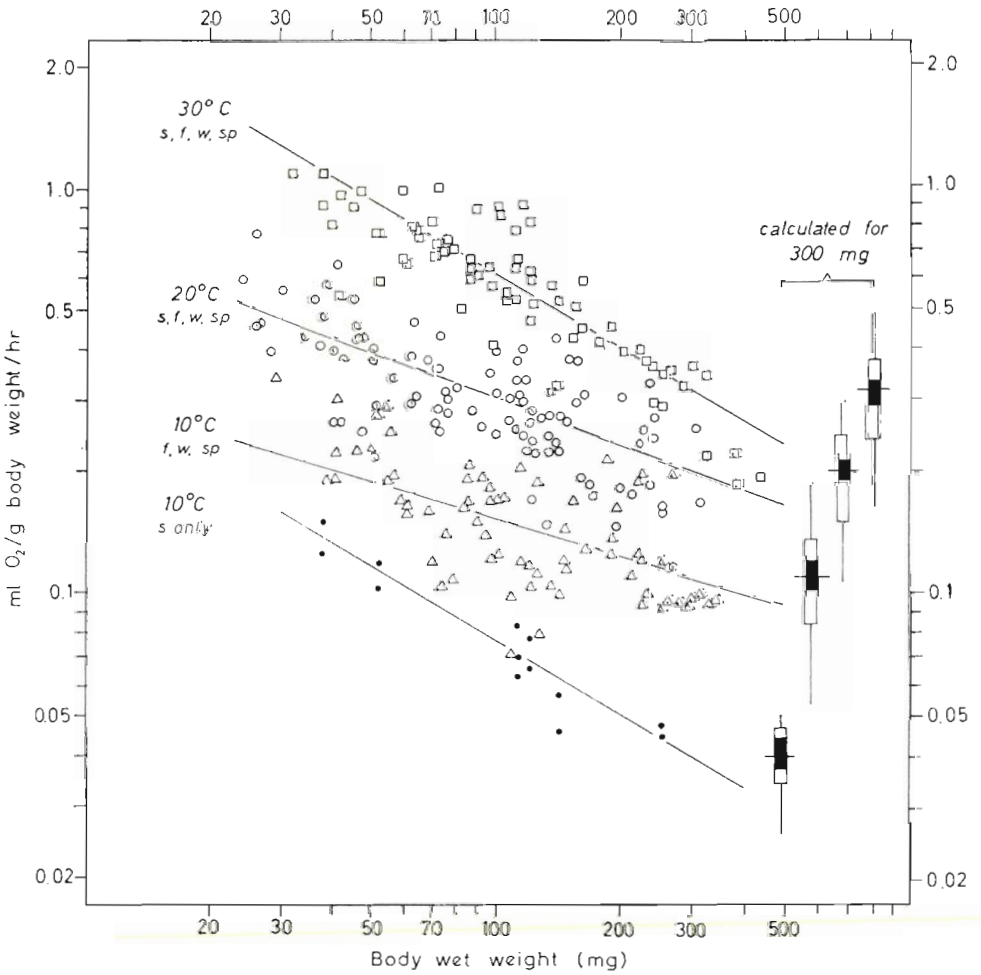


Fig. 3-70: Standard metabolism (0_2 consumption) after acute exposure to 10°, 20°, and 30° C in *Palaemonetes vulgaris* collected during summer (s), fall (f), winter (w), and spring (sp). The symbols on the right express oxygen consumption rates of the 4 shrimp groups, calculated for 300-mg body weight; horizontal line: mean; vertical black bar: ± 2 standard error of the mean; vertical open-face bar ±: 1 standard deviation; vertical line: range of values. Shrimps obtained at all seasons have been grouped at each test temperature, except for summer shrimps tested at 10° C; with that exception, which is associated with loss of equilibrium, season has no significant effect on standard metabolic rates. (After McFarland and Pickens, 1965; modified.)

These data, and similar results by other authors, reveal that experiments concerning metabolic responses of marine invertebrates to temperature must take into account ambient O_2 and CO_2 concentrations. Since both are a function of temperature and salinity, respiratory research on marine and brackish-water invertebrates is indeed a domain which requires most critical attention. For further details regarding the effects of dissolved gases on functions and structures of marine organisms consult Chapter 9.

McFARLAND and PICKENS (1965) studied adult grass shrimp *Palaemonetes vulgaris* from Nueces County, Texas, USA. The standard metabolic rate was determined in the dark (Warburg respirometer). *P. vulgaris* collected during the 4 seasons of the year and exposed to 3 different constant temperatures reveal increasing rates of O_2 consumption with increasing test temperature, but no significant seasonal effects on standard O_2-consumption rates (Fig. 3-70). With the overhead lights on, O_2 consumption was 20 to 25% higher. This shrimp is eurytherm and exhibits a high degree of independence of individual thermal history, except at extreme temperatures. Its standard O_2-consumption rate is, therefore, a predictable function of the test temperature over a wide range of thermal conditions. Active metabolic rate was determined by making the shrimp swim against a water current (sustained work); it is significantly higher, and independent of thermal history only during acute exposure to temperatures between 15° and 30° C; active rates at lower or higher test temperatures are affected by the previous temperature regime. Warm-acclimated *P. vulgaris* swim faster per unit O_2 consumption than do intermediate- or cold-acclimated ones.

McLEESE (1964) determined O_2 consumption of individual adult lobsters *Homarus americanus* at high ambient O_2 concentrations and constant temperatures of 12°, 15°, 20° and 25° C using a manometric respirometer (Table 3-30). Average O_2 consumption increases with temperature at a constant rate between 12° and 25° C.

THOMAS (1954) found a similar relation between routine rate of O_2 consumption and temperature for the European lobster *Homarus gammarus*. However, at com-

Table 3-30

Average routine O_2 consumption of the decapod crustacean *Homarus americanus* at high ambient O_2 concentrations as a function of temperature. All test individuals (380 to 520 g wet weight) had been kept at temperatures identical to the later test temperatures for 3 or more weeks prior to the experiment (After McLEESE, 1964)

Temperature (° C)	Average O_2 consumption ($mgO_2/kg/hr$)	Standard deviation	Number of individuals tested
12	30·6	9·8	14
15	39·5	11·3	26
20	56·0	19·1	21
25	61·7	25·0	21

parable test temperatures his values, which range from about 35 to 110 mg O_2/kg/hr at 6° to 18° C, are approximately twice as high as those for *Homarus americanus*. According to McLeese (1964), it is likely that these differences are due to differences in activity. Krüger (1964b) investigated the effects of temperature and body size on the O_2 consumption in the polychaete *Arenicola marina*. Examples of his measurements are presented in Table 3-31.

Table 3-31

Routine O_2 consumption of the polychaete *Arenicola marina* as a function of temperature and body size. The measurements were made in September and October 1961 on Helgoland (North Sea). The body of the table contains average amounts of O_2 consumption of individuals, expressed as cm^3O_2/hr (After Krüger, 1964b)

Body wet weight (g)	Test temperatures (° C)							
	2	3	5	10	15	20	25	30
0·38	10·60	12·35	13·50	21·25	26·00	35·00	18·10	72·75
0·48	—	—	10·75	—	37·25	31·50	—	—
0·69	—	—	15·68	41·50	57·43	54·00	—	90·75
0·86	—	—	—	—	69·50	87·75	—	—
0·87	—	13·50	—	35·25	40·50	50·00	62·50	100·75
1·03	21·25	18·25	36·25	35·75	46·00	62·33	61·25	89·75
1·32	18·50	21·00	31·25	35·75	52·75	74·67	86·75	127·25
1·53	17·25	21·00	31·75	83·75	77·80	91·00	110·25	132·75
1·75	9·50	60·00	34·75	98·33	108·00	116·50	130·25	—
1·82	—	45·75	—	—	—	—	—	169·67
2·24	—	—	—	—	106·60	—	—	—
2·54	32·00	—	56·67	139·33	134·33	141·00	242·00	—
2·89	24·25	30·00	35·75	41·17	99·00	131·50	170·25	277·00
3·29	—	—	88·25	153·75	166·20	232·25	224·75	311·00
3·37	—	—	70·50	137·25	198·83	216·33	—	317·75
3·39	—	—	83·75	—	198·75	251·33	—	367·25
4·23	31·00	48·00	63·00	119·50	190·50	144·75	189·50	260·25
4·95	56·00	60·50	145·50	128·50	236·50	247·50	379·25	565·25
5·00	—	—	—	87·00	121·33	—	—	—
5·97	48·00	44·00	76·00	115·83	210·75	222·50	334·50	503·75
6·37	—	—	80·75	173·00	290·57	304·67	—	530·75
6·70	43·00	83·75	89·25	179·00	192·60	174·00	275·75	381·25
8·09	—	—	—	—	—	437·25	520·50	—
8·19	—	—	—	—	—	—	—	542·80
9·08	—	—	174·25	335·50	398·14	394·00	—	567·50
10·31	126·60	156·75	182·75	282·00	351·60	384·50	517·75	—
10·68	140·00	149·75	248·50	397·00	437·43	585·75	633·25	914·50
11·30	140·40	164·25	163·75	292·00	394·40	386·25	512·75	—
11·96	161·00	164·67	225·25	323·75	341·50	565·00	618·00	689·00
12·64	—	—	—	—	—	—	—	838·60
12·71	145·25	171·25	151·50	350·75	329·40	—	—	—
13·16	164·75	128·75	167·25	322·00	306·00	204·00	633·75	—
13·29	203·00	215·50	235·00	483·00	448·57	274·50	327·00	—

KRÜGER expressed the modifying effects of body size by the allometric formula: $y = b \cdot w^{\alpha}$, where b represents the rate of O_2 consumption of an individual of a given weight, and α the decrease of metabolic rate during growth (increasing body weight). The exponent turned out to be not the same at all test temperatures; in most cases it lies between 0·7 and 0·8, i.e. between a weight-proportional and a surface-proportional respiratory rate. Minimum values for a were found during summer at 20° C, and spring at 15° C. According to KRÜGER, these minimum values are indicative of an optimum efficiency of the metabolism at these temperatures. Determinations of b demonstrated that metabolic rates of *A. marina* are significantly less affected by temperature in spring (10° to 20° C) and autumn (10° to 25° C) than would have been expected on the basis of the normal temperature dependence of biological processes.

Standard O_2 consumption of adult sea-urchins *Strongylocentrotus purpuratus* collected near Yankee Point, California, USA, was determined by FARMANFARMAIAN and GIESE (1963). One group of urchins was acclimated for 50 days at 5° C and the other kept at 14° to 19° C (controls). Both groups were tested at 5°, 10°, 15°, and 20° C respectively (Fig. 3-71). For each 5 C°-interval Q_{10} values

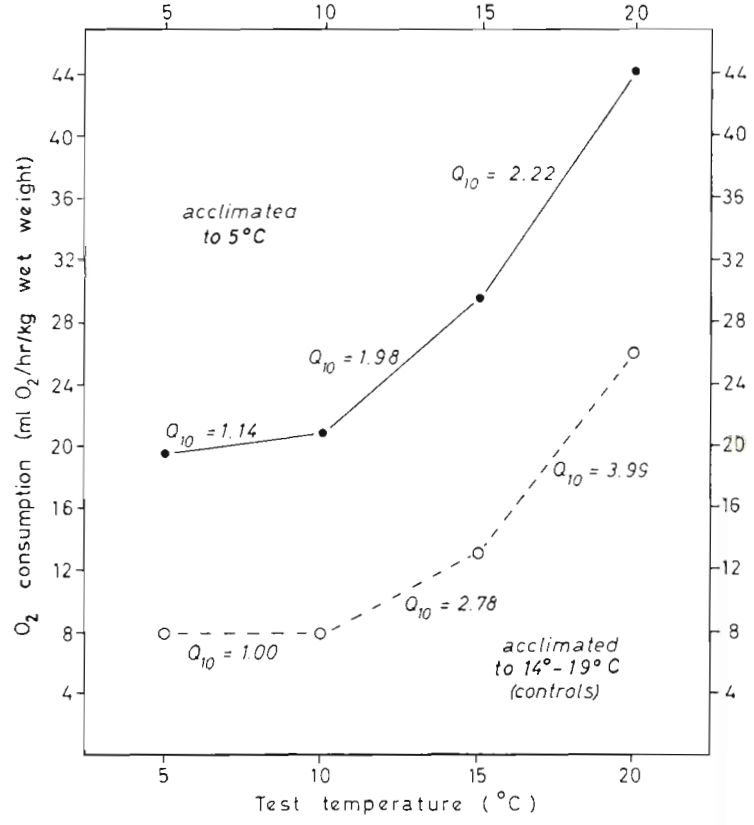


Fig. 3-71: Rates of 0_2 consumption of adult sea-urchin *Strongylocentrotus purpuratus* acclimated to 5° and 14° to 19° C, respectively, and tested at the constant temperatures indicated. Q_{10} values are given for the 5 C°-intervals. (After FARMANFARMAIAN and GIESE, 1963; modified.)

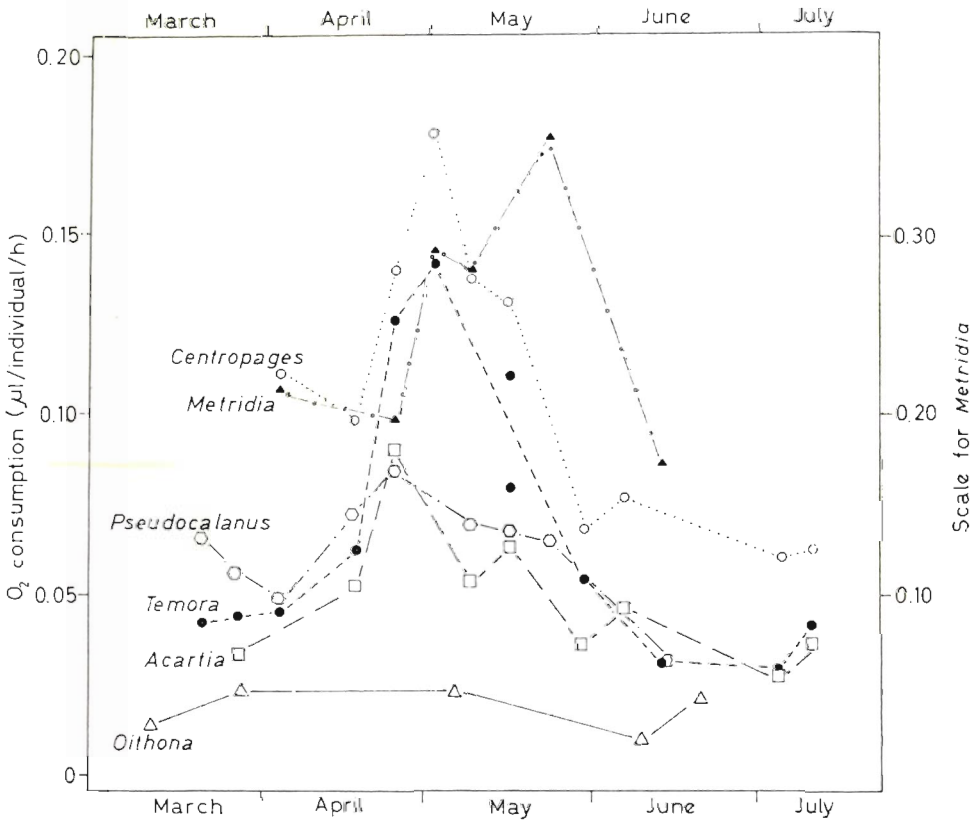


Fig. 3-72: O_2 consumption in a number of common marine copepods in relation to season. Note that the scale for *Metridia* is half that of the rest. (After MARSHALL and ORR, 1966; modified.)

are presented. O_2 consumption increases with temperature at all test temperatures; it is significantly higher in specimens stabilized at 5° C, than at 14° to 19° C. For further examples of temperature effects on respiratory rates in echinoderms consult FARMANFARMAIAN (1966).

Respiratory rates of marine copepods have been reported by RAYMONT and GAULD (1951), GAULD and RAYMONT (1953), CONOVER (1956, 1959, 1960, 1962), RAYMONT (1959), BERNER (1962), and MARSHALL and ORR (1966). The latter 2 authors made observations on rates of feeding and respiration in the following common small copepods of the Clyde sea area: *Pseudocalanus elongatus*, *Centropages hamatus*, *Temora longicornis*, *Acartia clausi* and *Oithona similis*, with occasional observations on *Paracalanus parvus*, *Metridia lucens* and *Diaixis hibernica*. They used cultures labelled with ^{32}P for feeding experiments and the Winkler method for respiratory measurements. In all species, except possibly in *Oithona similis*, there is a rise in O_2 consumption following the spring diatom increase. This rise is linked with the increased size of the copepods at that time. The respiratory values compare fairly well with those of other authors (Fig. 3-72). Most respiratory measurements were done on females but males of *Centropages*, *Temora*, *Acartia* and *Metridia* were also used; their O_2 consumption was always

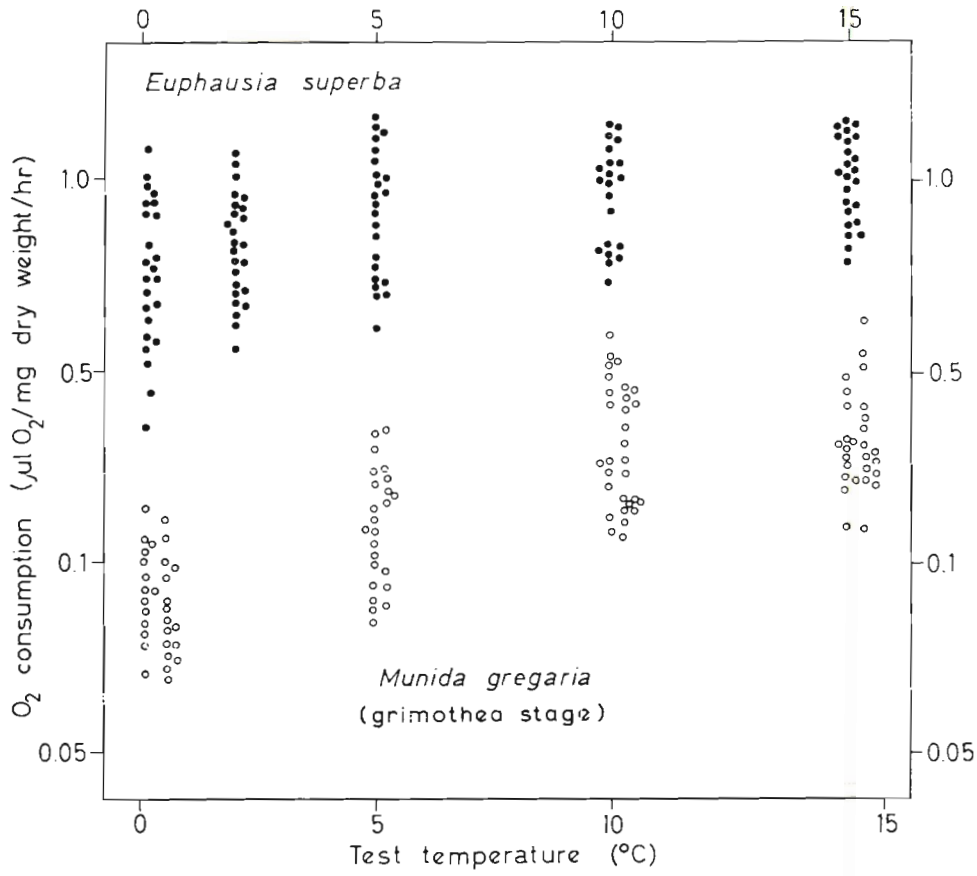


Fig. 3-73: O_2 consumption of antarctic crustaceans at different test temperatures. The krill *Euphausia superba* was tested immediately after collection from surface waters of −0·9° and −1·27° C. The grimothea stage of the anomuran decapod *Munida gregaria* was tested after a 4-day stabilization period at 2° and 13° C respectively. (After McWHINNIE, 1964; modified.)

lower than that of the females. In *Calanus hyperboreus* from the Gulf of Maine (USA) or nearby slope waters, availability of food is the most important environmental factor influencing the rate of respiration. In the sea, highest respiratory rates correspond with the spring diatom bloom. Fed individuals of *C. hyperboreus* have higher rates of O_2 consumption than starved ones; gravid females exhibit higher rates than unripe ones, regardless of their nutritional history (CONOVER, 1962).

Little information is available on O_2 consumption of oceanic invertebrates. McWHINNIE (1964) measured acute respirometric responses of the antarctic planktonic crustacean *Euphausia superba*, collected at −1·27° to 2° C from surface waters in the Bransfield Strait and Weddell Sea, and *Munida gregaria* (grimothea stage), collected at 8·8° C from subantarctic waters in the Straits of Magellan. Mortality was rather high; euphausiids of the North Atlantic Ocean are said to be most difficult to maintain in the laboratory, 17 days being the maximum survival period (CONOVER, 1960). O_2 consumption of *E. superba* (4 to 6 cm long; 30 to

60 mg dry weight) at temperatures between 0° and 15° C was measured within 30 mins of collection. The data were obtained from 2 groups collected at 62° S, 57° W and 62° S, 63° W with water surface temperatures of −0·9° and −1·27° C, respectively. There was no significant difference between the 2 groups (Fig. 3-73); the general response to increasing temperature was a slight increase in O_2 consumption between 0° and 5° C with no further increase above the 5° C level. The normal temperature range of *E. superba* at the sea surface seems to be 0° to 2° C; the responses illustrated indicate that they exhibit a considerable degree of metabolic independence within this range. Grimothea stages of the anomuran decapod *Munida gregaria* were collected by surface netting at 54° S, 68° W and transferred to 2° and 13° C. O_2 consumption was measured 4 days after introduction to the test temperatures (Fig. 3-73). The differences in O_2 consumption between the 2° C individuals (left group at each test temperature) and the 13° C individuals (right group) were not significant and indicated no marked increase in O_2 uptake by specimens held at 2° C relative to those kept at 13° C. However, extension of the stabilization period resulted in metabolic acclimation.

Further studies on O_2 consumption as a function of ambient temperature in marine invertebrates have been presented by MARSHALL and co-authors (1935), CLARKE and BONNET (1939), and MARSHALL and ORR (1958, 1966) in various planktonic copepods, especially *Calanus finmarchicus*, and by BARNES and co-authors (1963) in *Balanus balanoides* and *B. balanus*. Respiratory systems of aquatic invertebrates have been discussed by DITTMER and GREBE (1958), KROGH (1959), WATERMAN (1960), PROSSER and BROWN (1961), MCCUTCHEON (1964) and others.

Rate of growth. The temperature range allowing growth is usually narrower than that for metabolic regulation or activity; it is often smaller for gametes, developing embryos and hatching stages than for subadults or adults. The first statement may be exemplified by the well-known fact that moulting, and hence growth, in several crustaceans is blocked by low temperatures which still allow metabolic regulation and locomotory activity; the second, by the narrower temperature ranges for growth of gametes, embryos and larvae of many planktonic or meroplanktonic invertebrates such as molluscs and crustaceans (developing eggs and larvae of the European lobster *Homarus gammarus* require temperatures above 15° C for growth while adults keep on growing in colder water).

In the majority of marine invertebrates, growth appears to continue under suitable environmental conditions throughout most of their life. In temperate forms there is usually a marked retardation or complete cessation of growth during the colder season; frequently also at, or after, attainment of maturity and during the breeding season. In the latter cases, body growth often alternates with gonad growth (MOORE, 1935, 1937). Some corals grow at normal rates only at temperatures near 21° C (e.g. HUTCHINS and SCHARFF, 1947; HESSE and co-authors, 1951). Also some polar invertebrate species are said to require very definite and narrow thermal ranges for growth. Much of the information available on temperature effects on growth rates of marine invertebrates is based on casual observations. We shall concentrate here on a few examples based on laboratory experiments. For general aspects of temperature effects on growth consult BRODY (1945), VON

BERTALANFFY (1951, 1960, 1964), PRECHT and co-authors (1955), WATERMAN (1960), KRÜGER (1962, 1963, 1964a, 1966) and ROSE (1967). Since growth is associated with body size and shape, further reference to growth will be made in the section on *Structural Responses* (p. 511).

Fig. 3-74 illustrates growth curves of males of the euryplastic amphipod *Gammarus duebeni*, obtained under different experimental conditions. Growth rates are expressed as increase in body length (distance between base of first antenna and base of telson with the body straightened out). Curve (a) represents a typical growth curve obtained under the given food and space conditions at 19° to 20° C in $10‰$ S, a near optimum salinity. Curve (b) gives the growth in a much less favourable salinity ($37‰$) under conditions of gradually increasing temperatures (simulating nature; averaged for 50-day intervals); after 98 days,

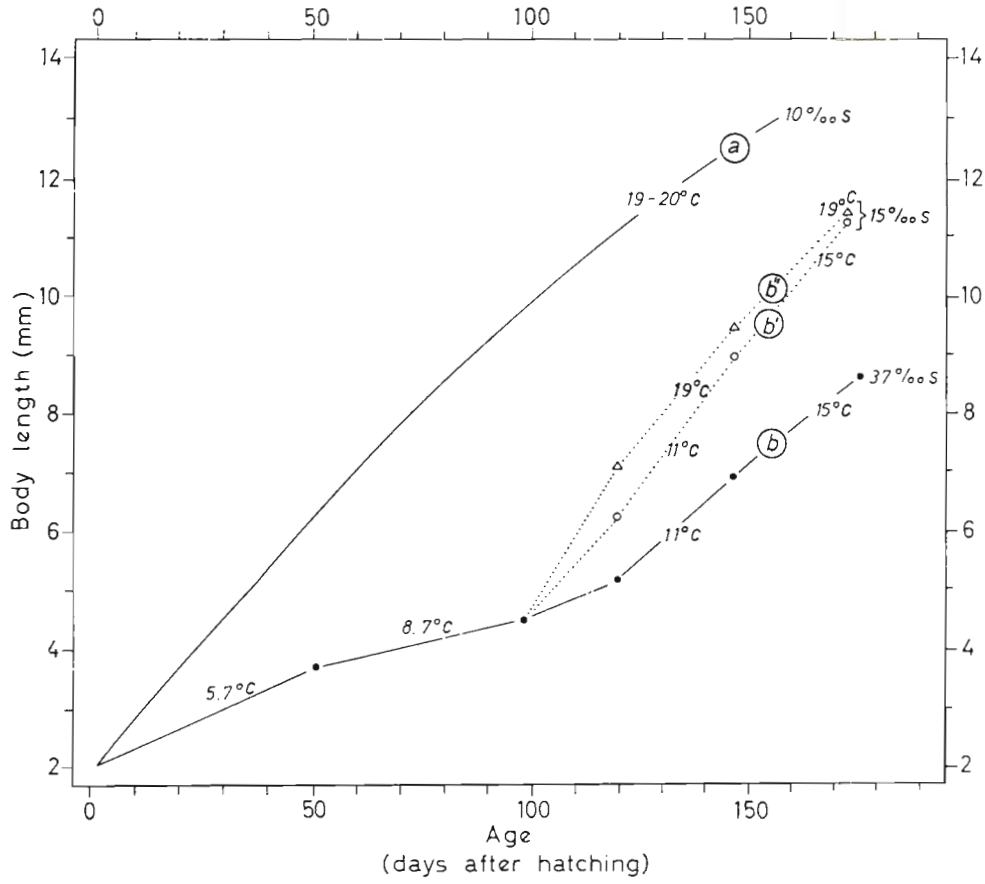


Fig. 3-74: Growth rates of males of the brackish-water amphipod *Gammarus duebeni*, based on average values of increase in body length, under varying conditions of temperature and salinity. (*a*): Growth rates of 17 males at 19° to 20° C and $10‰$ S. (*b*): Growth rates of 38 males kept for the first 98 days after hatching in $37‰$ S under conditions of slowly increasing temperatures; 20 of them were then transferred into $15‰$ S (dotted curves); of these 10 grew under identical temperature conditions as those in $37‰$ S (b'), and 10 at a constant temperature of 19° C (b''). (After KINNE 1953a; modified.)

part of the males were transferred into 15‰ S (dotted lines); of these, one half remained under temperatures identical to those in 37‰ S (curve b'); the other half was exposed to a constant temperature of 19° C (curve b"). After initial exposure to adverse conditions, growth rates increase beyond the intensity achieved in curve (a) even though the environmental conditions are similar and certainly not more favourable (KINNE, 1953a). Such compensations for a 'bad start' are also known from other organisms.

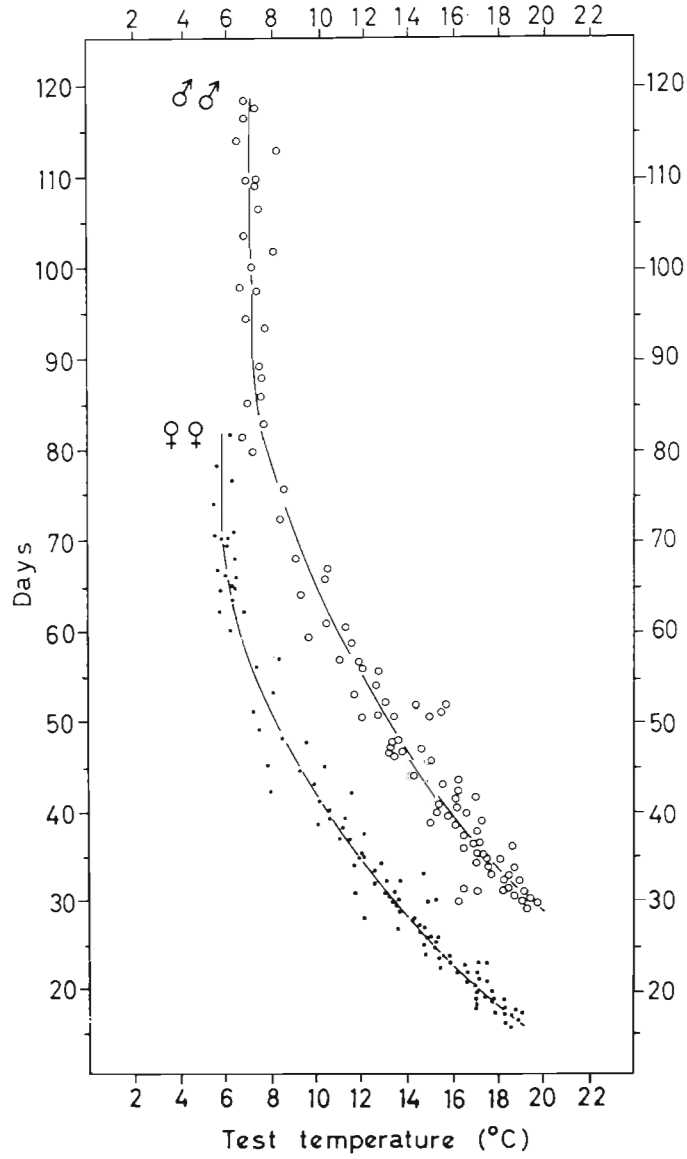


Fig. 3-75: Intervals between successive moultings (in days) as function of temperature in adult females and males of the amphipod *Gammarus duebeni*. Salinity: 10‰. Individual data. (After KINNE, 1953b; modified.)

In crustaceans, growth is closely correlated to moulting. Hence, temperature effects on moulting frequency are of importance for assessing growth intensities. In freshly hatched *Gammarus duebeni*, moulting frequency is thermally rather independent within normal ranges of temperature. However, moulting frequencies of adults depend closely on variations in ambient temperature (Fig. 3-75). At identical temperatures, intervals between successive moults are significantly longer in males than in females. The data plotted in Fig. 3-75 were obtained from specimens kept in pairs under temperature and light conditions simulating natural seasonal variations (habitat regime). Water temperatures in the culture vessels

Table 3-32

Moulting frequency of adult amphipods *Gammarus duebeni* kept in pairs throughout the year at 2 different temperature regimes. Habitat regime: temperature conditions simulating seasonal habitat variations ranging from ca 2° C in winter to 20° C in summer; warm regime: ranging from 16° to 25° C. In both cases the accompanying light regime was seasonally synchronous (daylight through windows). Table body: average intervals between successive moults in days (After KINNE, 1953b; modified)

	Mean temperature between successive moultings (° C)	Habitat regime (days)	Warm regime (days)	Difference (days)
Females	17	21	30	9
	18	18	24	6
	19	16	20	4
Males	17	37	66	29
	18	34	56	22
	19	31	50	19

(absolute midday temperatures and the small diurnal fluctuations) were determined daily; from these measurements mean values per moulting interval were calculated. Specimens kept in pairs at higher temperatures (warm regime; minimum 16° C, maximum 25° C, average 19° to 20° C) revealed quite different thermal relations (Table 3-32). At identical average moulting interval temperatures their moulting frequency was considerably slower, and a 1 centigrade degree change resulted in more pronounced responses than in the specimens kept under close-to-natural habitat temperatures which ranged throughout the year from about 2° to 20° C. Irrespective of temperature conditions, females kept without males tend to prolong their moulting intervals; in contrast, isolated males maintain

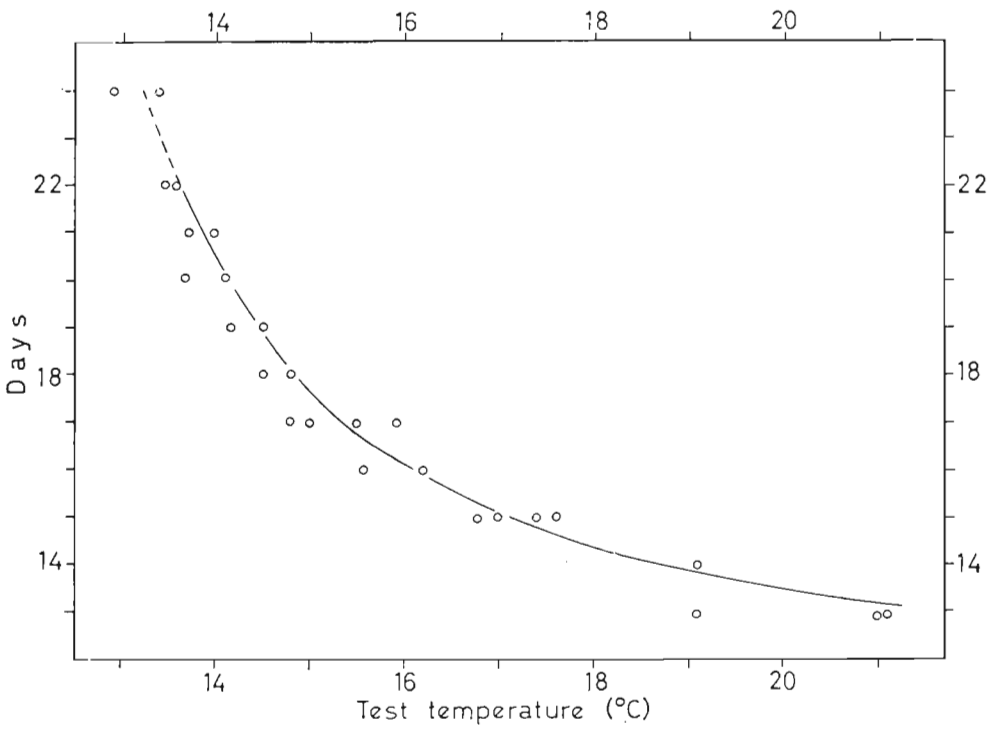


Fig. 3-76: Intervals between successive moultings (in days) as function of temperature in adult females of the amphipod *Gammarus zaddachi*. Salinity: 10‰. Individual data. (After KINNE, 1961; modified.)

normal temperature relations. The 2 sexes also respond differently to loss of appendages (amputation of legs): amputated males significantly shorten their moulting intervals, rather independently of the thermal regime, while females do not appreciably alter their moulting frequency (KINNE, 1953b).

Under conditions strictly parallel to those described above for the *Gammarus duebeni* population kept under thermal and light regimes simulating nature, moulting frequency of adult *Gammarus zaddachi* females revealed the thermal relations illustrated in Fig. 3-76 (KINNE, 1961). This curve is similar to the one established under comparable conditions for *Gammarus salinus* (KINNE, 1960b). Both *Gammarus zaddachi* and *G. salinus* exhibit shorter moulting intervals and faster growth at given temperatures than does *G. duebeni*.

Growth and moulting frequency in the shore crab *Carcinus maenas* increase with increasing test temperatures (BÜCKMANN and ADELUNG, 1964). Body volume doubles at each moult. Intermoult periods increase with increasing body size; they also depend on nutrition (starvation lengthens the intervals), presence of a larger specimen (lengthens intervals) and loss of appendages (tends to shorten intervals). The combined effects of temperature and body size are illustrated in Fig. 3-77.

PASSANO (1960) studied the effect of 10 temperatures on proecdysis resulting from eye-stalk removal in a uniform male population of the crab *Uca pugnax*. Proecdysis duration is shortest at 29° to 32° C; it lengthens significantly at lower temperatures. The initiation of proecdysis is markedly temperature sensitive and

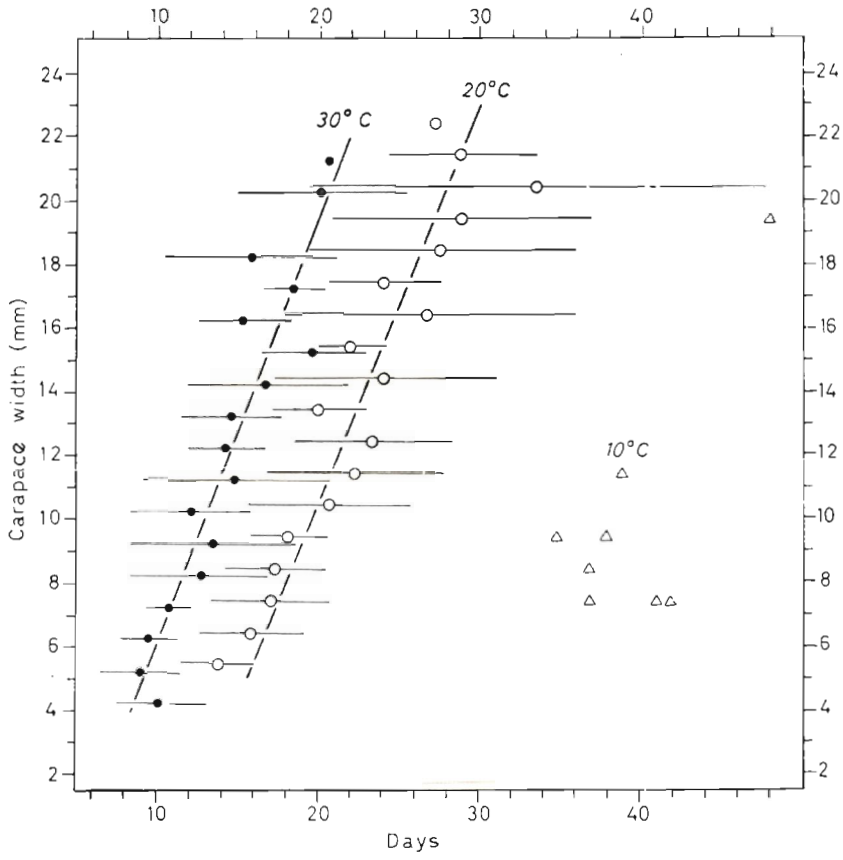


Fig. 3-77: Intervals between successive moultings (in days) as function of temperature and body size in subadult crustacean decapods *Carcinus maenas*. Circles: mean values of 10 to 25 individuals; horizontal lines through circles: standard deviations. Triangles: individual data. (After BÜCKMANN and ADELUNG, 1964; modified.)

becomes completely blocked at 15° C or below; between 15° and 20° C a substantial proportion of the crabs fail to begin proecdysis. It seems unusual that a temperature of 15° C or even higher can block completely a crab's moulting, and hence growth, even though it experiences lower ambient temperatures through much of its life cycle. PASSANO further reports that temperatures which block proecdysis initiation also inhibit basal limb bud regeneration (a moult-independent growth process) and hypothesizes that a metabolic event common to both processes becomes thermally blocked.

Until recently, virtually nothing was known about moulting frequency in deep-sea crustaceans. LASKER (1964) succeeded in keeping *Euphausia pacifica* in the laboratory for more than 7 weeks on a diet of flagellates (*Dunaliella primolecta* and/or *Platymonas subcordiformis*). Within the range of the experimental temperatures (9° to 14° C), moulting frequency was 5 days with a standard deviation of 1 day (range: 4 to 7 days). *E. pacifica* is an ecologically important and abundant component of the deep-sea plankton with a wide distributional range (north of Japan across the Bering Sea to Baja California, Mexico). If it moults every 5 days

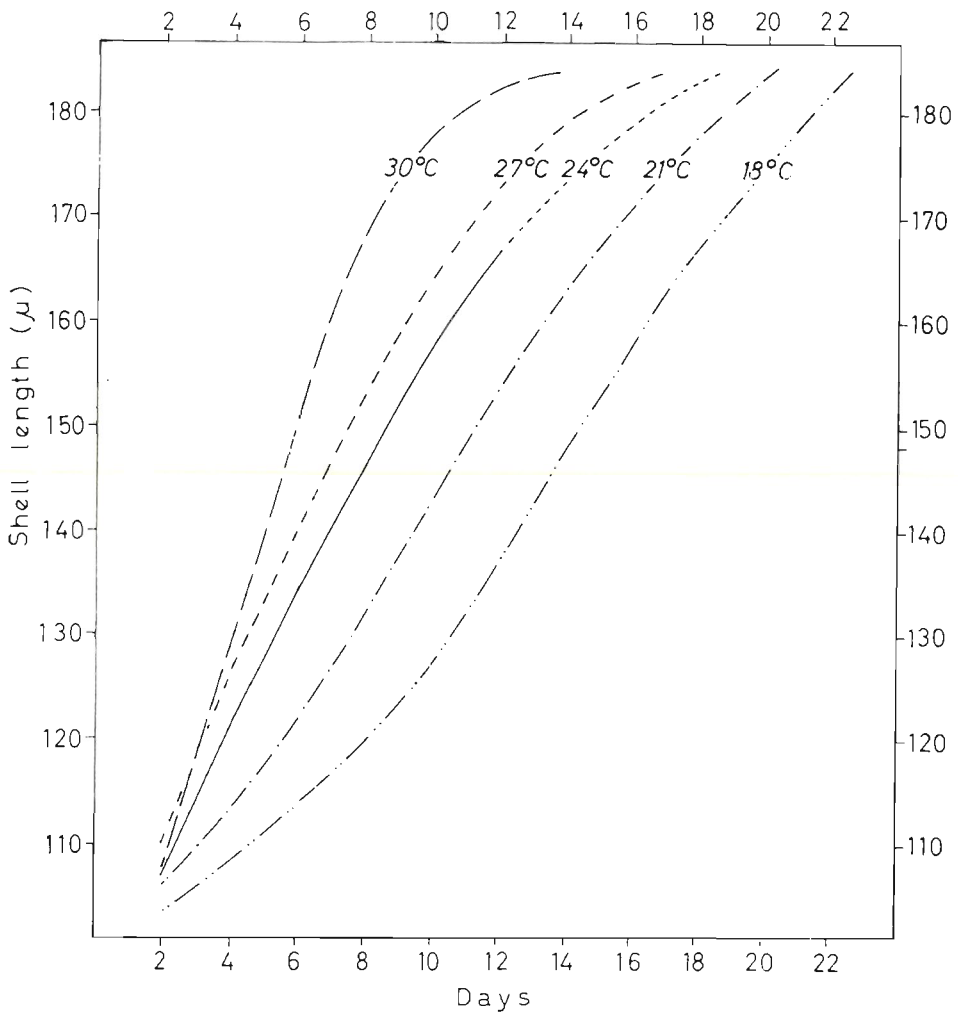


Fig. 3-78: Growth rates of larvae of the lamellibranch *Mercenaria mercenaria* at different constant temperatures. General trends based on 4 experiments. Food: mixture of *Chlorella* sp. (ca 300,000 cells per cm³ of water) and sulphur bacterium *Chromatium perty* (400,000 cells per cm³). (After Loosanoff and co-authors, 1951; modified.)

also *in situ* the resulting 'rain' of organic material could add considerably to the detritus in the sea (see also Lasker, 1966).

Loosanoff and co-authors (1951) grew larvae of the hard-shell clam *Mercenaria mercenaria* to metamorphosis at 5 different constant temperatures and obtained the general trend of increase in length illustrated in Fig. 3-78. The rate of growth of the larvae is usually, but not always, more rapid at high than at low temperatures. Larvae from the same sources and grown under identical conditions often show considerable individual variations in growth rate and time required to reach metamorphosis. At 30° C, setting of larvae begins as early as the 7th day after fertilization; setting of the entire test population was accomplished within 5 to 7 days. At 18·0° C, larvae setting begins 16 days and ends 24 days after fertilization. The mean setting dates for larvae grown at 30·0°, 27·0°, 24·0°, 21·0° and

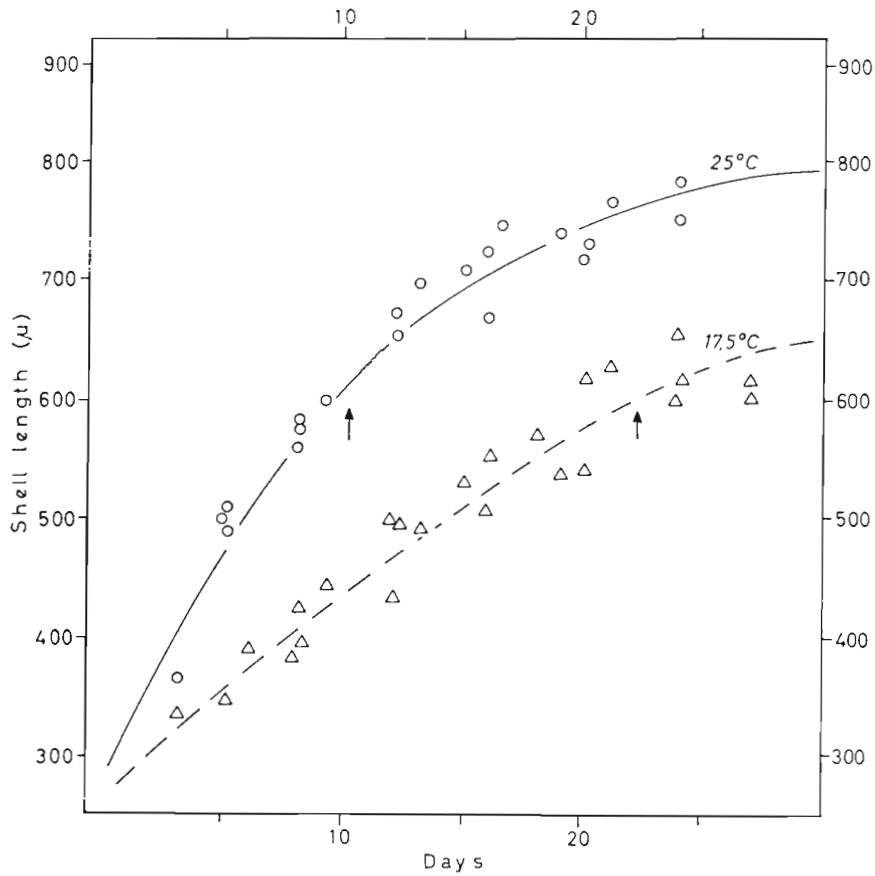


Fig. 3-79: Growth rates of larvae of the gastropod *Nassarius obsoletus* at different temperatures. Attainment of 'creeping-swimming stage' is indicated on each curve by an arrow. Food: alga *Phaeodactylum tricornutum* (ca 200,000 cells per ml of water). (After SCHELTEMA, 1967; modified.)

18·0° C lie on a straight line according to the equation $y' = -1{\cdot}00x + 37{\cdot}91$, where y' = predicted setting date, and x = temperature (LOOSANOFF, 1959). Under the same laboratory conditions, growth rates of the larvae of *Mercenaria campechiensis* and *M. mercenaria* are identical, and larvae setting begins at the same time.

These pioneering experiments on temperature responses of pelagic mollusc larvae were followed by a series of similar studies by WALNE (1958) on *Ostrea edulis*, DAVIS and CALABRESE (1964) on *Mercenaria mercenaria* and *Crassostrea virginica*, STICKNEY (1964) on *Mya arenaria*, BAYNE (1965) on *Mytilus edulis* and SCHELTEMA (1962a, b, 1964, 1967) on *Nassarius obsoletus*. SCHELTEMA's study on the common marine intertidal prosobranch gastropod *N. obsoletus* yielded the cumulative growth curves of its planktonic veliger larvae illustrated in Fig. 3-79. A temperature of about 25° C causes maximum growth rates, while 17·5° C is close to the lowest temperature at which larval development to settlement is completed. SCHELTEMA is not sure whether the growth maximum at 25° C is an intrinsic characteristic of the veligers or whether growth may have been, to some extent,

influenced via the alga *Phaeodactylum tricornutum* used as food source. DAVIS (1963) and DAVIS and CALABRESE (1964) have shown that growth rates of larvae of *Mercenaria mercenaria* and *Crassostrea virginica* at different temperatures are critically affected by the type of food organism available. The larvae can utilize naked chrysophytes—such as *Monochrysis lutheri*, *Isochrysis galbana* and *Dicrateria* sp.—at lower temperatures than chlorophytes - such as *Chlorella* sp.—which have thicker cell walls. This implies that the enzymes required by the mollusc larvae for digesting naked flagellates are active at lower temperatures than are the enzymes necessary to digest forms with more resistant cell walls, or that digestion proceeds more intensively at the higher temperatures.

The temperature allowing maximum growth in larvae of the oyster *Crassostrea virginica* lies between 30·0° and 32·5° C at salinities ranging between 10·0 and 27·5‰; at 7·5‰ S maximum growth occurs at 27·5° C. The time required for the larvae to reach the setting stage ranges, under laboratory conditions, from 10 to 12 days at 30° to 32·5° C, to 36 to 40 days at 20·0° C. Larvae reared to setting size at about 27·0° C and transferred to lower temperatures can set at temperatures as low as 12·5° C, but the percentage of cases of successfully completed metamorphosis decreases progressively with decreasing test temperature (DAVIS and CALABRESE, 1964).

In larvae of the European oyster *Ostrea edulis*, the temperature range for satisfactory growth (70% or more of optimum rates) ranges, at 27‰ S, from 17·5° to

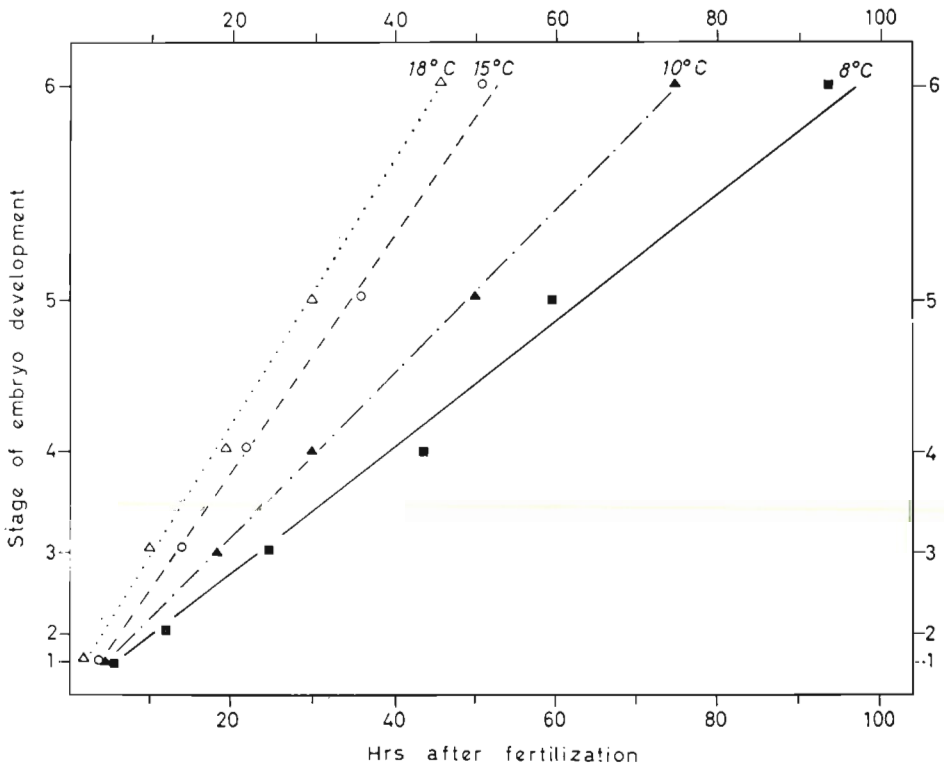


Fig. 3-80: The effect of temperature on cleavage and embryonic development of *Mytilus edulis* from Talyfoel (Anglesey, North Wales). (After BAYNE, 1965; modified.)

30° C (DAVIS and CALABRESE, 1969). Approximate setting times are: 26 days at 17·5° C, 14 days at 20° C, and from 8 to 12 days at 25°, 27·5° and 30° C. It is suggested that the larvae be reared to setting size at temperatures between 25° and 27·5° C and then kept at 20° to 22.5° C during setting to obtain fastest growth of larvae and highest setting percentage. Spat kept at 10° C shows virtually no growth. Between temperatures from 12·5° to 27·5° C growth rates of spat increase with the progressively higher temperature levels employed.

Since few dinoflagellates or diatoms can grow equally well over wide temperature ranges, both their numbers and food values may differ as a function of temperature. It is necessary, therefore, when relating laboratory experiments to situations in the sea, to take into account possible temperature effects on the food organisms offered to the tested invertebrates (SCHELTEMA, 1967).

BAYNE (1965) investigated the effect of temperature on growth rates of larvae of the lamellibranch *Mytilus edulis* fed on *Isochrysis galbana* and *Monochrysis lutheri*. Growth rate increases with increased cell concentration to 100 cells of *I. galbana*/μl, and 2·0μl packed cell volume of *M. lutheri*/l. A mixture of these 2 species supports more rapid larval growth than either species individually. Growth rates of *Mytilus edulis* larvae increase with temperature from 10° to 21° C

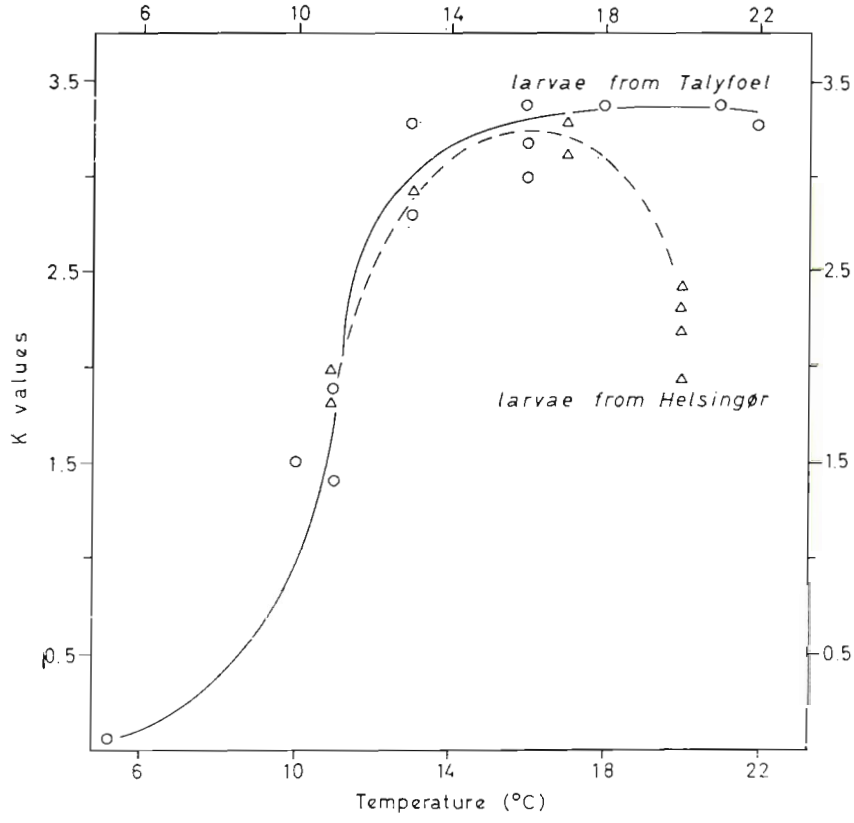


Fig. 3-81: The effect of temperature on growth rates of *Mytilus edulis* larvae from Talyfoel (Anglesey, North Wales) and Helsingør (Denmark). Each value of K calculated for L_1 = 130-140 μ and t = 20 days. (After BAYNE, 1965; modified.)

(Fig. 3-80) but above 13° C growth is relatively temperature-independent; at 5° C, the larvae remain swimming for more than 30 days but do not feed (after the first 3 days there was no additional growth). With increasing shell length all larvae reduce their growth rates irrespective of the ambient temperature.

DEHNEL (1955) and WALNE (1963) have used the instantaneous relative growth rate, K, to compare rates of growth in larvae under different conditions:

$$k = \frac{\log_e L_2 - \log_e L_1}{t},$$

where L_1 = initial mean length, and L_2 = mean length at time t. This equation has also been used by BAYNE (1965) for larvae of *Mytilus edulis* ($K = 100\ k$); the values of K for 20 cultures, all of which were reared on a diet of 20 to 25 cells of *Isochrysis galbana*/μl, have been plotted against temperature in Fig. 3-81. The resulting curves are similar for the larvae from Talyfoel (N. Wales) and Helsingør (Denmark) between 11° and 17° C; at higher temperatures growth rates of Talyfoel larvae remain constant while those of Helsingør larvae decline. These differences show a relationship to ambient temperature regimes at the respective 'home' habitats. At 11° C, the pediveliger stage is reached on an average after 34 to 38 days, at 16° C after 16 to 20 days. The developmental rate of *M. mercenaria* larvae is most rapid at 30·0° C and 27·0‰ salinity (Table 3-33). The temperature range for satisfactory

Table 3-33

Percentage increase in mean length of larvae of the clam *Mercenaria mercenaria* kept at different combinations of temperature and salinity for 10 days. Percentages given in the body of the table are means of duplicate cultures; the mean length increase of the most rapidly growing set was considered 100% in each case. The most satisfactory development occurs in the combinations indicated by italics

(After DAVIS and CALABRESE, 1964; modified)

Salinity (‰)	Temperature (° C)								
	12·5	15·0	17·5	20·0	22·5	25·0	27·5	30·0	32·5
12·5	0	0	0	0	0	2	0	0	0
15·0	0	<1	3	9	20	31	17	12	0
17·5	<1	5	21	36	59	66	68	63	15
20·0	5	17	39	60	*80*	*82*	*87*	*85*	54
22·5	12	25	48	68	*83*	*88*	*85*	*91*	61
27·0	16	30	53	*71*	*83*	*93*	*83*	*98*	65

growth of clam larvae narrows as the salinity decreases. At 27·0‰ S at least some larvae approach setting size by the 12th day at temperatures from 15·0° to 32·5° C; at 17·5‰ S satisfactory development is limited to the range from 20·0° to 30·0° C; at 15‰ S there is no significant growth except at 25·0 C (DAVIS and CALABRESE, 1964).

Mytilus planulatus and *M. edulis*, common lamellibranchs of Australian and northern seas respectively, show almost identical temperature ranges for successful larval settlement (12·5° to about 19° C with insignificant settlement above 22° C);

also other thermal responses appear to be quite similar in these southern and northern hemisphere representatives (ALLEN, 1955). In regard to temperature effects on the duration and delay of metamorphosis in *M. edulis* consult BAYNE (1965).

Growth rates of pelagic stages of meroplanktonic invertebrates may significantly affect the length of their pelagic period and hence their chances of dislocation (currents) and survival (predators). However, length of pelagic life may also depend on other factors such as food and the availability of an adequate substrate for settlement. According to KORRINGA (1941), larvae of the Dutch oyster *Ostrea edulis* have a pelagic life of 6 days at 22° to 23° C, 9 to 10 days at 18° to 21° C and 13 to 14 days at 16° to 17° C. In American oysters *Ostrea virginica*, the free-swimming period is 7 days at 24° to 27° C, 13 days at 23° C and 17 days at 20° C (NELSON, 1908). Growth parameters of the Pacific cockle *Cardium corbis* are correlated to mean air temperatures in North American localities (TAYLOR, 1960). For further information concerning thermal responses of lamellibranch larvae consult MEDCOF (1939) and the reviews by THORSON (1946), BAUGHMAN (1947), KORRINGA (1952) and CARRIKER (1961).

The colonial hydroids *Cordylophora caspia* (*C. lacustris*) and *Clava multicornis* show exponential growth rates (KINNE, 1956b, 1958; FULTON, 1962, 1963; KINNE and PAFFENHÖFER, 1966; PAFFENHÖFER, 1968). Temperature effects may be exemplified on the basis of experiments conducted on *Clava multicornis* by PAFFENHÖFER (Table 3-34). Growth rates accelerate with increases in temperature and daily food rations. At 6° C and minimum daily food ration, organic dry substance doubles in 76·6 days, at 16° C and maximum daily food ration, in 11·6 days. Organic dry substance per colony increases at 6° C and minimum ration at a rate of 1·3% per day, at 16° C and maximum ration at 8·6% per day.

Metabolic regulation. Rate and capacity of metabolic regulations of marine invertebrates are affected by temperature. This may be illustrated by reference to osmoregulation in marine and brackish forms. Rate and capacity of osmoregulation in hypo- or hyperosmotic salinities may increase or decrease as a function of temperature (e.g. KINNE, 1963a). A number of euryhaline crustaceans maintain their internal osmoconcentration more successfully near the lower end of their temperature range, when under hypo- or hyperosmotic stress. Examples are the decapod crabs *Rhithropanopeus harrisii* (OTTO, 1934; KINNE and ROTTHAUWE, 1952), and *Eriocheir sinensis* (OTTO, 1937), the amphipod *Gammarus duebeni* (KINNE, 1952), and the shrimp *Crangon crangon* (FLÜGEL, 1959, 1966). In *Crangon crangon* BROEKEMA (1941) originally reported that the osmoregulative capacity was greater at high temperature (21° C) than at low temperature (4° C). Her results were obtained by measuring the electrical conductivity of the blood. They have been superseded by recent investigations (FLÜGEL, 1966), conducted at 5°, 10°, and 15° C respectively, and employing the freezing-point technique. In general, the osmoregulative capacity of a given species appears to be greatest at near-optimum temperatures or somewhat below (KINNE, 1952, 1953a), and to decrease at supranormal temperatures. Close to the lower or upper limits of the tolerated temperature range, osmoregulation breaks down completely (see also Chapter 4).

Growth of the colonial hydroid *Clava multicornis* at different temperatures and daily food rations in sea water of 32‰ S. Food: larvae of *Artemia salina*. Daily food rations: minimum = smallest amount of food which allows existence without premature reduction of the hydranths, maximum = greatest amount of food not yet causing detrimental effects due to overfeeding, medium = intermediate amounts between minimum and maximum rations. *a*: regressions, *b*: doubling times (number of days within which colonial weight doubled), *c*: daily growth rates (increase in mg organic dry substance per day divided by colony dry weight). *d*: average deviation from mean; *v*: variability; in parentheses: number of data (After PAFFENHÖFER, 1968)

Temperature (° C)	Daily ration		Organic dry substance	*d*	*v* (%)	Total lenght of Polyps	*d*	*v* (%)	Polyp number	*d*	*v* (%)
6	minimum	*a*	0·00456	±0·000513	11·2	0·00457	±0·000543	11·9	0·00331	±0·000844	25·5
		b	76·6 (12)			76·6			112·8		
		c	1·3%			1·3%			0·9%		
6	maximum	*a*	0·00593	±0·000570	9·6	0·00602	±0·000828	13·8	0·00349	±0·000654	18·7
		b	61·0 (10)			58·8			104·5		
		c	1·6%			1·7%			1·0%		
11	minimum	*a*	0·00625	±0·000743	11·9	0·00619	±0·000851	13·7	0·00668	±0·001084	16·2
		b	54·2 (10)			56·0			45·2		
		c	1·8%			1·8%			2·2%		
11	medium	*a*	0·00931	±0·000817	8·8	0·00953	±0·000557	5·8	0·01001	±0·001162	11·6
		b	32·3 (8)			31·8			30·2		
		c	3·1%			3·1%			3·3%		
11	maximum	*a*	0·01212	±0·00131	10·8	0·01174	±0·00131	11·2	0·01161	±0·00101	8·7
		b	25·0 (8)			25·3			25·4		
		c	4·0%			3·9%			3·9%		
16	minimum	*a*	0·2105	±0·00176	8·4	0·02025	±0·00166	8·2	0·01808	±0·00182	10·1
		b	14·3 (11)			14·9			16·6		
		c	7·0%			6·7%			6·0%		
16	medium	*a*	0·02664	±0·00208	7·8	0·02509	±0·00175	7·0	0·02191	±0·00174	8·0
		b	11·4 (8)			12·0			13·8		
		c	8·8%			8·3%			7·2%		
16	maximum	*a*	0·02612	±0·00138	5·3	0·02730	±0·00186	6·8	0·02429	±0·00317	13·1
		b	11·6 (8)			11·1			12·3		
		c	8·6%			9·0%			8·1%		

Metabolic efficiency. The efficiency with which an organism functions under a given thermal regime appears to be a more suitable criterion for ecological assessments than the rate of performance. Even though nature does not always seem to select for functional economy, it is a basic ecological fact that within a given habitat a number of different forms of life compete for the resources of food available. Hence, an organism which can obtain and use these resources most efficiently, under the climatic conditions given, is in a more favourable situation than another competing one, which functions less efficiently in terms of its energy budget for internal and external work, maintenance, repair, growth and reproduction.

A complete energy budget of an organism requires measurements of intake, transformation and output of energy and matter:

INTAKE	=	TRANSFORMATION	+	OUTPUT
Energy and matter obtained		into Body functions and structures		Energy and matter non-utilized

The transformation of energy and matter obtained in form of food consists of the sequential steps digestion, absorption and conversion (assimilation). Part of the food taken in is digested and part of the digested food subsequently absorbed; the rest is removed in form of faeces. The absorbed food—minus urine excretions—is converted into body functions (internal and external work) and body structures (body growth and reproductive material). Of the energy absorbed, the portion transformed into body functions is ultimately lost as heat (it is measured in terms of respiration or heat loss), the portion transformed into growth and reproductive material is temporarily stored. The reproductive material (gametes, spores, buds, etc.) is released when the transforming individual reproduces. A point neglected in pertinent studies but deserving attention is the possibility that energy budgets of individuals may be measurably affected by gain or loss of (dissolved) matter via non-intestinal and non-renal routes; organisms may, furthermore, gain energy via radiation.

The efficiency with which the intake is transformed into energy available for biological functions and body structures is expressed as percentage intake transformed, whereby gross efficiency refers to the total intake, and net efficiency to the intake fraction actually assimilated. The efficiency of transformation depends on the ambient temperature regime, and presumably also on other environmental factors such as light (Chapter 2), salinity (Chapter 4), and dissolved gases (Chapter 9), as well as on the quality and quantity of food consumed per unit time. Temperature may exert differential effects on food intake, digestion, absorption and assimilation (enzymes), and modify the proportional utilization of the protein, fat and carbohydrate components contained in the food consumed.

Complete energy budgets of marine invertebrates kept at different defined ambient temperature conditions are lacking. A few investigators have attempted to assess energy budgets at different seasons, or at one temperature, or have studied partial aspects of such budgets at different temperatures.

The most complete study conducted throughout a year (seasonal, but not closer defined temperature conditions) has been conducted by FUJI (1967), who

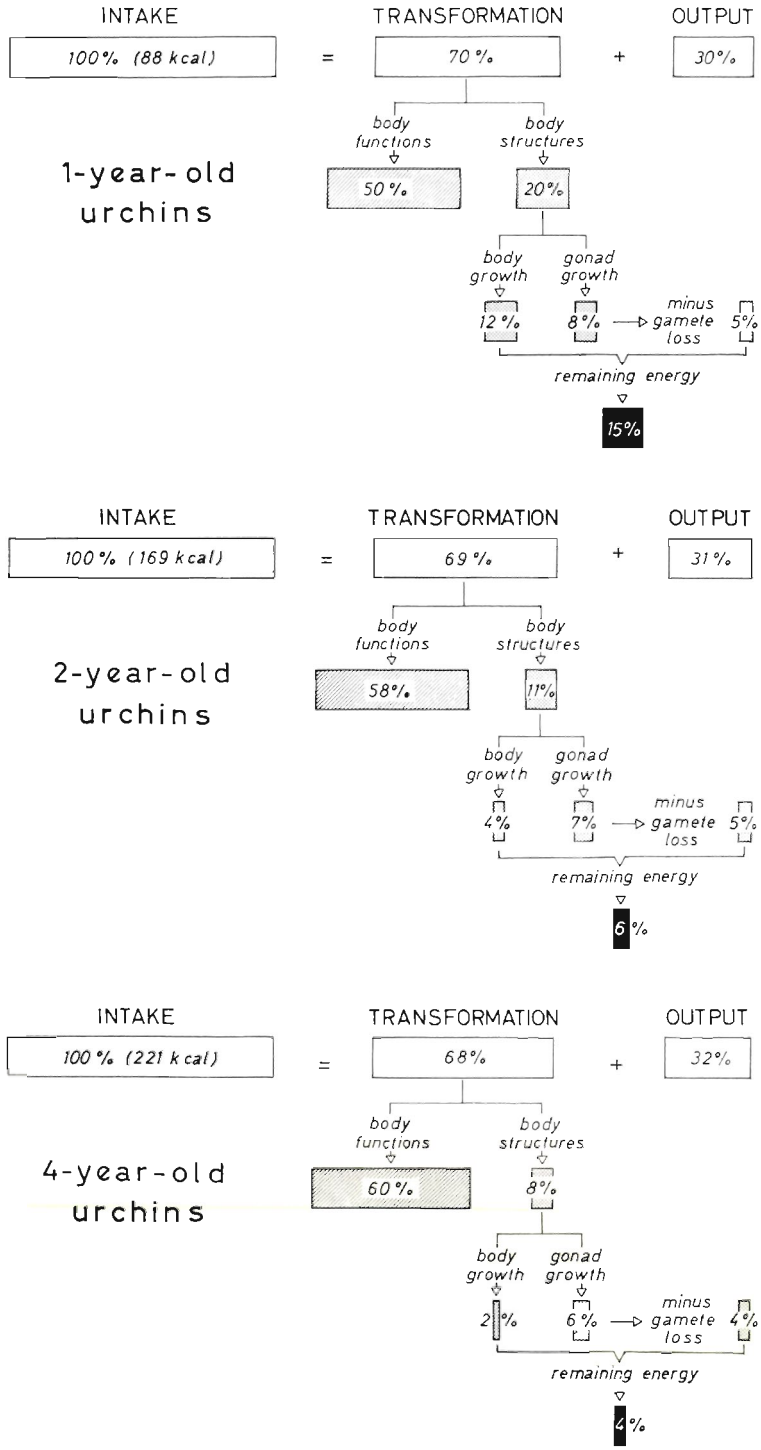


Fig. 3-82: Assessment of energy budgets in 1-, 2- and 4-year-old sea-urchins *Strongylocentrotus intermedius*. Approximate, rounded-off figures based on data by FUJI (1967).

examined important links in the energy budget of the sea-urchin *Strongylocentrotus intermedius* from Japanese waters near Hokkaido. FUJI comes to the conclusion that the rate of flow of energy through the sea-urchin body differs markedly at different seasons and different stages of development. The percentage energy required for growth (body structures) decreases with age, while that necessary for maintenance (body functions) increases (Fig. 3-82). The total remaining amount of energy decreases from about 15% of the total intake in 1-year-old urchins to 5% in 2-year-old, and to 4% in 4-year-old ones.

Food intake has been investigated by PAINE (1965) in the opisthobranch *Navanax inermis* at 17° C (average habitat temperature of the Pacific Ocean near San Diego, USA). *N. inermis* was fed other opisthobranchs of the order Bullacea. Small individuals consumed daily 9·5% of their own dry weight (11·5% in terms of calorie contents of prey and predator). ANRAKU and OMORI (1963) examined feeding rates of 6 copepods (*Calanus finmarchicus*, *Acartia tonsa*, *Centropages hamatus*, *C. typicus*, *Labidocera aestiva* and *Tortanus discaudatus*), offered 3 different foods (diatom *Thalassiosira fluviatilis*, diatoms plus nauplii of *Artemia salina*, *Artemia salina* alone) at different temperatures, and related the resulting responses to morphological features of the copepods' mouthparts. CONOVER (1964) assembled data on the efficiencies of assimilation, gross growth and net growth for stages IV and V of the copepod *Calanus hyperboreus* (Table 3-35). Data on carbon assimilation in the crustacean *Euphausia pacifica* have been published by LASKER (1966).

PAFFENHÖFER (1968) studied colonial hydroids *Clava multicornis*, obtained from the North Sea near Helgoland. He fed his colonies with larvae of *Artemia salina* and kept them at 3 different constant temperatures while offering 3 different daily food rations: minimum ration (empirically determined amount of food which allows the test colonies to exist without premature reduction of their hydranths), maximum ration (highest amount of food not yet causing detrimental effects due to overfeeding) and medium ration (intermediate between minimum and maximum rations). The results of his food intake experiments are presented in Table 3-36. At all 3 feeding schedules, the amount of food consumed increases with increasing temperature. According to STEPHENS and SCHINSKE (1961), hydroid polyps (*Tubularia crocea* and *Schizotricha tenella*) are able to absorb dissolved organic matter (amino acid glycin) at an initial concentration of 150 mg per 1000 ml sea water, which is about 5 times higher than the maximum values recorded at sea. However, in PAFFENHÖFER's *Clava* cultures, the sea water contained only between 0·7 and 1·2 mg dissolved organic matter per litre, a quantity which can hardly be expected to significantly affect his results.

The time elapsing between food intake and defaecation may also provide a simple but useful tool for assessing temperature effects on processes of food transformation. KINNE and PAFFENHÖFER (1965) determined the effects of different temperature–salinity combinations on the time span between swallowing and defaecating of *Artemia salina* larvae by *Clava multicornis* (beginning: closure of mouth rim of the fed hydranth over the swallowed prey; ending: completed defaecation). Fully grown hydranths, raised at test temperatures and starved 24 hrs previous to experiments, were hand fed *Artemia* larvae of about 1·40 mm length; completed food intake was determined to the nearest 5 mins, defaecation

Table 3-35

Assimilation efficiency, gross growth efficiency, and net growth efficiency of copepodid stages IV and V of the marine copepod *Calanus hyperboreus* (After CONOVER, 1964)

Copepodid stage	° C	Food organism	Food concentration (mg ash free dry wt/l)	Assimilation efficiency	Gross growth efficiency (based on weight)	Net growth efficiency (based on weight)	Gross growth efficiency (based on calories)	Net growth efficiency (based on calories)
IV	2	*Thalassiosira fluviatilis*	6·4	44·0	3·7	8·5	5	12
V*	2	,,	6·4	47·6	17·3	36·4	24	50
IV*	5	,,	6·7	52·7	13·0	24·7	18	34
V*	5	,,	6·7	50·9	14·6	28·6	20	40
V*	5	*Thalassiosira nordenskiöldii*	2·6	39·6	13·9	32·4	—	—
V	2	*Thalassiosira fluviatilis*	1·7	71·1	28·4	39·4	39	55
V	5	,,	1·7	64·1	18·6	27·6	26	38
V*	2	*Ditylum brightwellii*	0·6	53·0	32·3	60·6	46	86
V	2	*Rhizosolenia setigera*	1·7	65·4	29·0	44·2	41	62
V*	5	,,	1·4	63·1	30·4	48·4	43	68
V	4	*Thalassiosira fluviatilis*	0·3	57·2	13·3	23·3	18	32
V*	4	,,	1·8	56·6	36·4	64·3	50	89

* Statistically significant growth

Table 3-36

Food intake in the colonial hydroid *Clava multicornis* offered minimum, medium and maximum daily food rations and kept at 3 different constant temperatures in a salinity of $32^0/_{00}$ (After PAFFENHÖFER, 1968; modified)

Food intake (%)	6° C		11° C			16° C		
	minimum	maximum	minimum	medium	maximum	minimum	medium	maximum
of colony dry weight (mg)	2·3	3·2	4·0	5·7	7·1	13·4	17·2	19·0
of colony calorie content (cal)	2·4	3·1	4·4	5·9	7·0	14·1	17·2	18·5

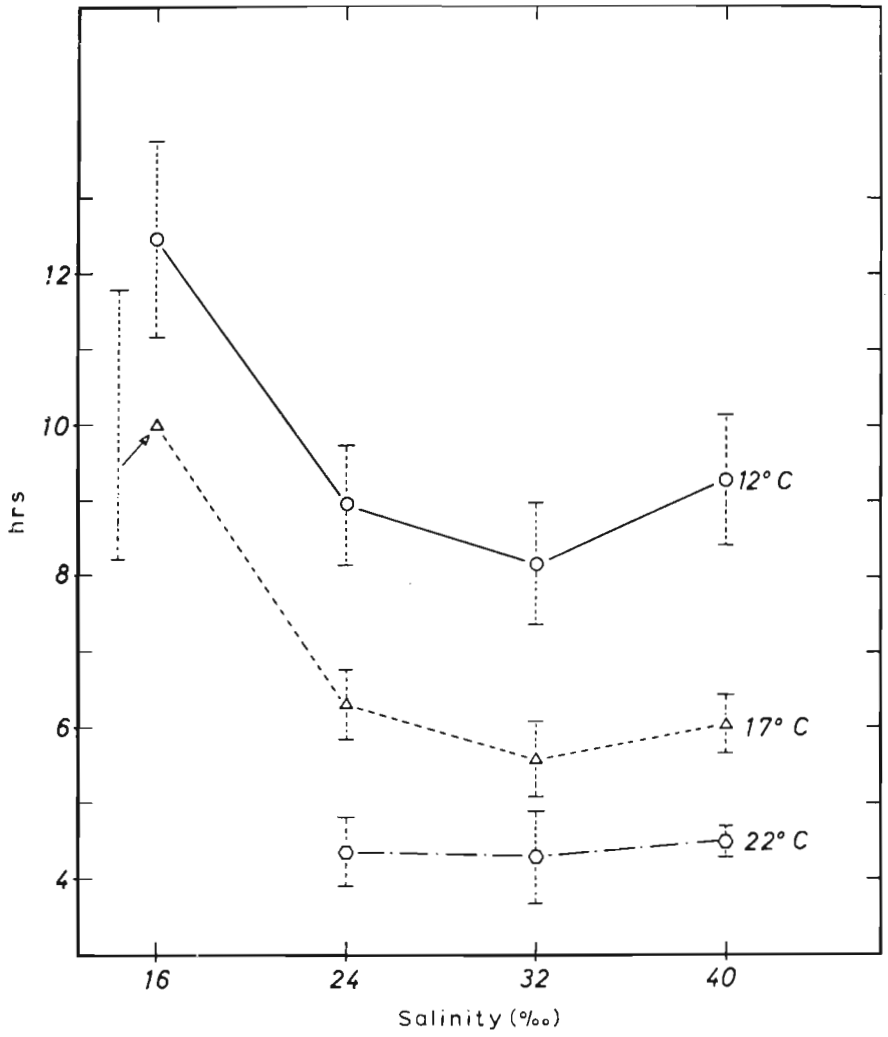


Fig. 3-83: Time required for intestinal food (1·40 mm long *Artemia salina* larvae) passage as a function of temperature and salinity in the colonial hydroid *Clava multicornis*. Each value represents the average of 25 measurements. Vertical broken lines indicate standard deviation. (After KINNE and PAFFENHÖFER, 1965.)

to the nearest 10 mins. The periods of food passage are graphically plotted in Fig. 3-83. They decrease with increasing temperature. The time required at 22° C is approximately half that at 12° C. Irrespective of temperature or hydranth size, the periods are shortest in $32^0/_{00}$, the normal habitat salinity of the *Clava* population near Helgoland. At both 12° and 17° C the periods are longest in the lowest salinity employed ($16^0/_{00}$).

The efficiency of food transformation into body substance of *Clava multicornis* is a function of both temperature and daily food rations (Table 3-37). It decreases with increasing temperature in all 3 feeding schedules; low temperatures allow a more efficient use of the food consumed. In contrast, the rate of food transfor-

Table 3-37

Efficiency (in italics) of food transformation into body substance in the colonial hydroid *Clava multicornis* as a function of temperature and daily food ration (minimum, medium, maximum rations: see text). The per cent values following the + signs at 11° and 16° C represent compensations for gonophore loss. S: standard deviation of mean (After PAFFENHÖFER, 1968; modified)

Temperature (° C)	Minimum (%)	S	Medium (%)	S	Maximum (%)	S
6	*44·6*	±5·70	—		*49·3*	±4·24
11	37·1	±4·65	40·1	±4·06	43·6	±3·83
	+2·6		+2·5		+2·0	
	39·7		*42·6*		*45·6*	
16	37·9	±2·56	39·3	±2·14	38·0	±3·09
	+0·6		+1·0		+1·3	
	38·5		*40·3*		*39·3*	

Table 3-38

Rate of food transformation per 24 hrs in *Clava multicornis* colonies as a function of temperature and daily food ration (minimum, medium, maximum; see text) (After PAFFENHÖFER, 1968)

Temperature (° C)	Minimum (%)	Medium (%)	Maximum (%)
6	1·09	—	1·56
11	1·73	2·53	3·18
16	5·44	6·94	7·28

Table 3-39

Energy budget of the colonial hydroid *Clava multicornis* at 16° C and 3 daily food rations (minimum, medium, maximum: see text) (After PAFFENHÖFER, 1968; modified)

Intake		Transformation				Output	Daily food ration
Energy (food) obtained (cal)		Energy transformed into body functions (cal)		body structures (cal)		Non-utilized matter (faeces) (mg dry weight)	
103·7%	=	39·2%	+	38·5%	+	26·0%	minimum
106·6%	=	31·7%	+	40·3%	+	34·6%	medium
106·3%	=	27·7%	+	39·3%	+	39·3%	maximum

mation (per cent intake converted into body substance per unit time) increases with temperature (Table 3-38).

The energy budget for *Clava multicornis* has been worked out thus far only for a constant temperature of 16° C (Table 3-39). PAFFENHÖFER points out that it was not possible for technical reasons to express the output in calories; he presented the values in mg dry weight instead, which resulted in percentages of the initial intake exceeding 100 by up to 6·6%. The percentage utilization of the intake at 16° C for body functions (metabolic rate; O_2 consumption), body structures (growth rate) and output (amount of faeces) reveals the following situation: the percentage of energy transformed into functions decreases with increasing daily food ration, while the percentage of faecal discharge changes in the opposite direction, indicating maximum food utilization at a minimum daily food ration; the percentage energy transformed into body structures remains rather unaffected by the different feeding schedules offered. PAINE (1965), during his studies on the opisthobranch *Navanax inermis*, was able to determine also the calorific contents of faeces and sexual products (eggs). The energy budget of *N. inermis* at 17° C is presented in Table 3-40.

Table 3-40

Energy budget of the opisthobranch *Navanax inermis* at 17° C (After PAINE, 1965; modified)

Intake		Transformation				Output
Energy (food) obtained (cal)		Energy transformed into body functions (cal)		body structures (cal)		Non-utilized energy (faeces) (cal)
98·9%	=	31·0%	+	30·1%	+	37·8%

According to MARSHALL and ORR (1958), a ripe female of the copepod *Calanus finmarchicus* requires daily, at 10° C, from 3·9 to 7·2% of its body weight (dry matter) in summer, and from 2·8 to 6·7% in winter; stage V requires 2·3 to 3·1% in summer, and 1·4 to 3·3% in winter; the higher values are for carbohydrate, the lower for fat. In winter, *C. finmarchicus* will hardly be able to find enough food by filtration alone but depends more on predation.

Seasonal variations in respiration and feeding of the common small copepods of the Clyde sea area (near Millport, Scotland) have been investigated by MARSHALL and ORR (1966), using the Winkler method for respiration measurements and cultures labelled with ^{32}P for feeding experiments. With the possible exception of *Oithona similis*, all species examined revealed an increase in O_2 consumption following the spring diatom bloom. This rise is interpreted as linked with the body size increase of the copepods rather than with water temperature.

In temperate seas most invertebrates exhibit significantly reduced food requirements during the cold months. In the Danish *Macoma baltica* community no predation and no growth seem to occur from late November to late April (THORSON, 1958). Winter starvation has been reported also for the gastropods *Ocinebra*

erinacea (ORTON, 1929), *Urosalpinx cinerea* (FEDERIGHI, 1931; GALTSOFF and co-authors, 1937; HANCOCK, 1954), *Busycon carica* and *B. canaliculatum* (MAGELHAES, 1948), *Polinices heros* and *P. duplicata* (SAWYER, 1950; TURNER, 1950). In spring and early summer, food requirements and growth rates increase rapidly. In the amphipod *Gammarus duebeni*, the isopod *Sphaeroma hookeri* and the mysid *Neomysis integer*, for example, food intake and growth cease practically at temperatures below 2° C; both increase drastically during spring when water temperatures rise (KINNE, 1963a).

Metabolic efficiency may be influenced by temperature via the thermal characteristics of digestive enzymes. There is some evidence that enzymes required by mollusc larvae for digestion of naked planktonic flagellates are active at lower temperatures than those involved in the digestion of certain other food organisms with thicker cell walls (DAVIS and CALABRESE, 1964).

Non-genetic capacity adaptation. According to the definitions given on p. 435ff, non-genetic capacity adaptations (acclimations, acclimatizations) refer to variations in performance of individuals within the tolerated temperature range. Practically all information available on non-genetic capacity adaptation to temperature in marine invertebrates has been obtained under conditions of constant temperature. Future studies should put more emphasis on fluctuating temperature conditions and multivariable designs. Our knowledge of non-genetic capacity adaptation in marine invertebrates has been reviewed by KINNE (1963a, b, 1964b, c), BULLARD (1964) and MCWHINNIE (1967).

In the time course of non-genetic adaptation, 3 phases may be distinguished (KINNE, 1964c): (i) Immediate response; it begins seconds or minutes after a change in ambient temperature and is characterized by increased variation of performance (shock reactions; over- or undershoots of metabolic rates). The immediate response does not seem to be an integrant part of the subsequent acclimation process in all cases. (ii) Stabilization; it begins minutes or hours after the temperature change and leads to a progressive constancy of performance, thereby gradually approaching a new steady level. (iii) New steady state; it begins hours, or weeks after the change, i.e. after attainment of near maximum adjustment. Several examples of immediate responses have been presented by KINNE (1964b, c).

The duration of the phase of stabilization may be different depending on the species tested and the life process measured. In representatives of a given species it depends upon age (it tends to increase with age), metabolic rate (it tends to decrease with increasing metabolic rate), life-cycle stage, the degree and pattern of the temperature change and other environmental variables. In American lobsters *Homarus americanus* kept at 14·5° C and transferred into 23·0° C for periods ranging from 1 to 31 days, thermal acclimation was practically complete after 22 days (MCLEESE, 1956). In the intertidal mollusc *Acmaea limatula*, low-tide level individuals transplanted to high-level localities exhibit a subsequent decrease in heart pumping rate; within 29 days heart rate becomes equal to that of high-level individuals when measured at a given temperature; half-acclimation time is about 6 days (SEGAL, 1956). A similar situation exists in *Mytilus californianus* (RAO, 1953). In the shore crab *Pachygrapsus crassipes*, respiratory acclimation to a change

in environmental temperature of 7·5 centigrade degrees requires a half-time of about 6 days (ROBERTS, 1957). Decapod crabs *Uca pugnax* kept at 22° to 27° C need about 14 days for complete acclimation to 15° C (VERNBERG, 1959). In most marine invertebrates examined thus far, 50% or more of the total resulting amount of metabolic acclimation seems to have been achieved within the first quarter or one-third of the stabilization period or even before that; later, the amount of non-genetic adaptation acquired per unit time decreases progressively. The giant scallop *Placopecten magellanicus* acclimates rapidly to increasing ambient temperatures (1·7 centigrade degrees per day), but may take up to 3 months to lose this acclimation when exposed to lowered temperatures (DICKIE, 1958).

All possible quantitative differences between the original level of performance and the new steady state following a change in temperature have been considered and classified by PRECHT (1949a, b, 1958; see also PRECHT and co-authors, 1955) and later, in a modified version, by PROSSER (1958); they are dealt with in detail in Chapter 12. Capacity acclimation to temperature involves not only variations in metabolic rate but also changes in temperature preferenda, orientation, migration and in other behavioural aspects such as territorialism and schooling, as well as in biological rhythms.

CONOVER (1962) reports that the O_2 uptake of the planktonic copepod *Calanus hyperboreus* acclimates almost perfectly over a range of experimental temperatures commensurate with habitat temperatures, which may vary between 0° and 10° C. Looking for a comparable copepod, but with a wider habitat temperature range, HALCROW (1963) selected *Calanus finmarchicus* which occurs at sea temperatures between − 2° and 22° C. He constructed graphs of acclimated O_2-uptake curves and superimposed acutely determined curves for *C. finmarchicus* collected in spring and in summer. From these curves it appears that the copepods do not acclimate to temperatures outside their seasonal thermal range but are able to compensate for temperature changes in the vicinity of the temperature of the water from which they are collected.

On the other hand, the potential for non-genetic capacity adaptation may exceed the immediate demands by seasonal habitat variations. An example is the presumably antarctic circumpolar amphipod *Orchomonella chilensis* which, in its habitat, lives at rather constant temperatures. ARMITAGE (1962) measured the O_2 consumption of adult *O. chilensis* at 8 different temperatures between − 1·8° and 12° C and found metabolic compensation between − 1·8° and 6° (8°) C indicated by a vertical downward displacement of the R-T (rate of O_2 consumption versus test temperature) curve. Such differences between the potential for acclimation and environmental demands may be indicative of the species' capacities for extending its distributional range beyond the present temperature regime and/or of its phylogenetic temperature history.

According to VERNBERG (1959), the temperate-zone decapod crab *Uca pugnax*, collected on the coast of North Carolina, USA, shows higher metabolic rates after acclimation to 15° C than individuals kept at 22° to 27° C when O_2 consumption is measured at 7°, 17° and 27° C; however, at test temperatures 33° and 39° C, metabolic rate is lower or about the same in both cold- and warm-acclimated crabs (Fig. 3-84). When the crabs are starved during the period of acclimation, they only begin to show acclimation, but after 6 to 8 days lose their potential for non-genetic

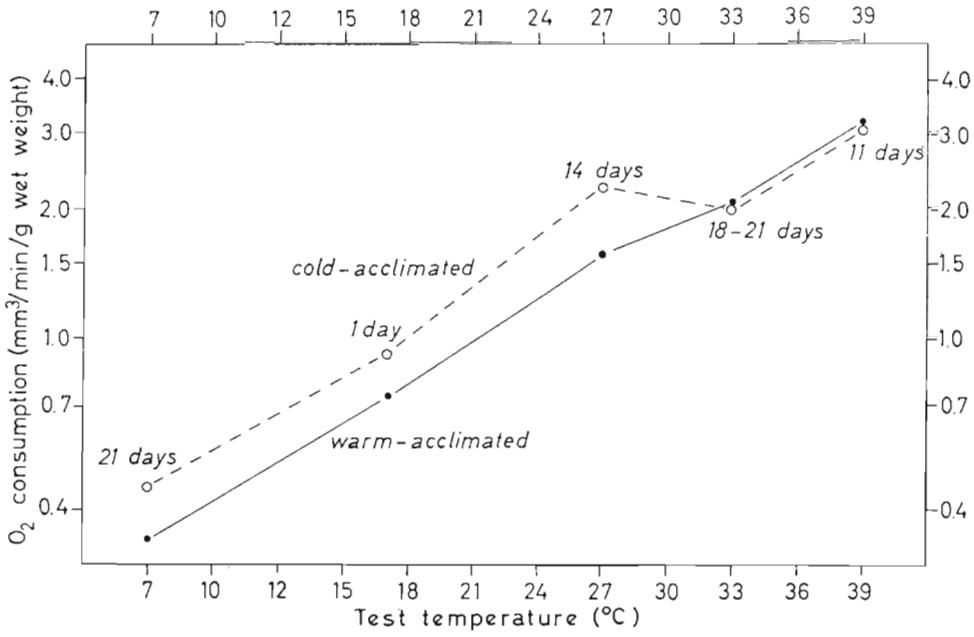


Fig. 3-84: Rate of 0_2 consumption of warm- (22° to 27° C) and cold- (15° C) acclimated decapod crabs *Uca pugnax* from Beaufort, North Carolina, USA. 0_2 consumption of 21 warm-acclimated crabs was determined at 27° C; then these crabs were transferred into 15° C and their 0_2 consumption re-determined after the number of days indicated at 27° C. (After VERNBERG, 1959; modified.)

capacity adaptation; feeding restores this potential. *Uca rapax* from Jamaica, West Indies, does not show any shift in metabolic rate during acclimation to 15° C, except when tested at 36° C, where cold-acclimated individuals exhibit higher rates than warm-acclimated ones. In the antarctic crustacean *Euphausia superba*, thermal acclimation follows the pattern of rotation (Chapter 12; type 3 of PRECHT, 1958) providing metabolic independence within a narrow environmental temperature range with no capacity adaptation at higher temperatures (MCWHINNIE, 1964).

MOREIRA and VERNBERG (1968) determined the non-genetic capacity adaptation of dimorphic males of the world-wide distributed planktonic copepod *Euterpina acutifrons*. In this species one group of males is distinctly smaller than the other and shows also morphological differences in antennules, antennae and second leg pairs. Both groups were fed daily on fresh cultures of the algae *Phaeodactylum tricornutum* and cold- (15° C) or warm- (25° C) acclimated. Warm- and cold-acclimated small and large males were then tested at both 15° and 25° C. At 15° C, the cold-acclimated small males show a lower metabolic rate than the large ones; at 25° C, the warm-acclimated large males have a lower metabolic rate than the small ones. Cold- and warm-acclimated small males consume O_2 at a similar rate at 25° C, but the cold acclimated ones have a lower rate at 15° C; coldacclimated large males consume O_2 at a similar rate at 15° C, but the cold-acclimated ones exhibit a higher rate at 25° C (Fig. 3-85). The presence of 2 forms of males or females in

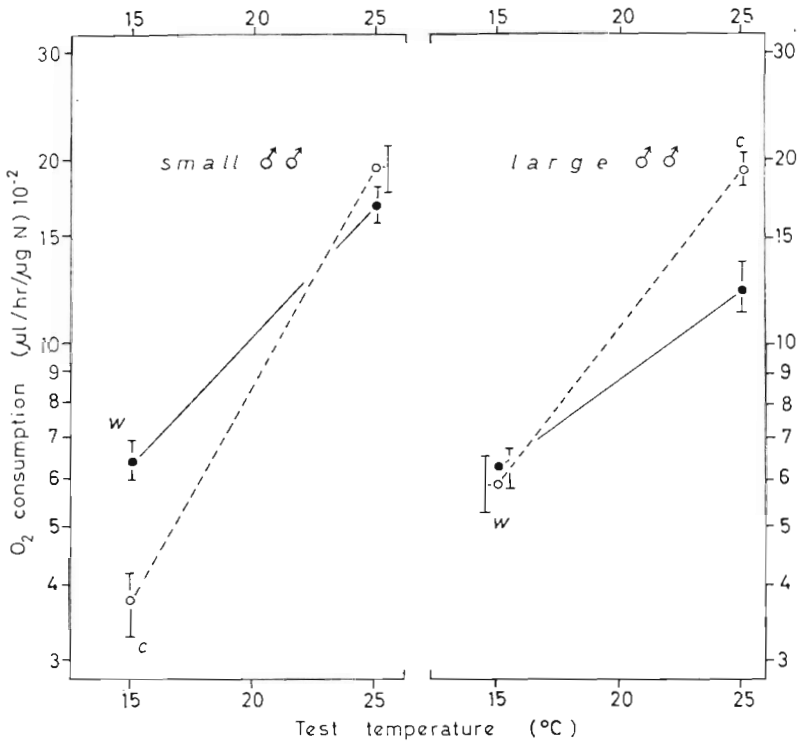


Fig. 3-85: Non-genetic capacity adaptation in dimorphic males of the copepod *Euterpina acutifrons*. w: warm-acclimated at 25° C; c: cold-acclimated at 15° C. (After MOREIRA and VERNBERG, 1968; modified.)

marine copepods is known from several species. Such dimorphism has been related to different environmental histories, seasonal effects or genetic factors. The small males of *Euterpina acutifrons* acclimate at low but not at high temperatures, while the large males adapt at high but not at low temperatures. Such differences in thermal responses may affect survival chances and metabolic performance of the respective groups and hence their distributional patterns in water bodies of different thermal (hydrographic) conditions.

Seasonal capacity acclimation has been demonstrated in the decapod crab *Emerita talpoida* by EDWARDS and IRVING (1943); at all test temperatures below 20° C, O_2 consumption is lower in summer than in winter crabs. Further examples may be found in TODD and DEHNEL (1960). For additional information on non-genetic capacity adaptation to temperature consult BULLOCK, 1955; PROSSER, 1958; KINNE, 1963a, 1964b; DILL and co-authors, 1964; MCWHINNIE, 1967 and Chapter 12.

The potential for non-genetic capacity adaptation depends primarily on the genetic background. However, it may also vary with physiological condition, life-cycle stage, age and sex of the individual involved; in most cases it seems to reach maximum values during early subadult and adult life and minimum values in gametes, embryos, dormant stages and senile adults. The total cumulative amount achievable throughout an individual's life appears to increase with the length of

time during which a given thermal regime was effective; it may reach maximum values only if the individual was subjected to this regime throughout its life (including fertilization and embryonic development). The rate of acclimation tends to increase with increasing rate of metabolism. The intensity of acclimation—expressed as persistence of a given non-genetic adaptation beyond the environmental situation which caused it or as the amount of reinforcement required to maintain it—tends to decrease with increasing age; it depends on the degree of thermal stress involved.

Genetic capacity adaptation. Some examples of genetic capacity adaptation to temperature are based on comparisons between closely related communities, genera or species in arctic and tropical waters. The most fundamental difference between arctic and tropical seas is the temperature (THORSON, 1958). In spite of the great differences in temperature, however, an arctic community displays rates of metabolism and activity at 0° C which are similar or not very different to its boreal counterpart at 8° C, its Mediterranean counterpart at about 12° C, and its tropical counterpart at still higher temperatures. Such relative independency of metabolic performance was first suggested by ORTON (1923), SPÄRCK (1936), and THORSON (1936) and later confirmed by THORSON (1952), BERG (1953), SCHOLANDER and co-authors (1953b), and DEHNEL (1955); see also the reviews by RAO and BULLOCK (1954), BULLOCK (1955), PRECHT (1955, 1958), PROSSER (1955), KINNE (1963a, b). SCHOLANDER and co-authors (1953b) showed that the metabolic rate (oxygen consumption) of a number of arctic poikilotherms is much higher at a given intermediate temperature than that of their tropical counterparts; they write (p. 90):

> 'The arctic curves are displaced toward cold, and the arctic forms at the normal temperature of their habitat, 0° C, have a three to ten times lower metabolic rate than have the tropical forms at a habitat temperature of 30° C. If the tropical curves are extrapolated to 0° C, they would be lowered by thirty to forty times, and hence there is a very considerable, although not complete, metabolic adaptation in the arctic forms relative to the tropical forms'.

These adjustments may be considered genetic adaptations of basal metabolic rates to life at low temperatures, since locomotory activity appears to be similar in both groups and metabolism in isolated tissues shows parallel adjustments. Such adaptations can result in considerable differences in lower and upper limiting temperatures (KROG, 1954; TAKEDA, 1954; SPOOR, 1955; SOUTHWARD, 1958) and in temperature optima (WINGFIELD, 1939). They may consist of a genetic as well as a non-genetic component. Reviewing the pertinent literature, GUNTER (1957) comes to the conclusion that the commonly held idea about life proceeding at a faster pace in the tropics than in the arctic appears to be correct, but that the difference is probably not so great as is usually supposed.

Results obtained on antarctic crustaceans are not in complete agreement with those reported by SCHOLANDER and co-authors (1953b) for arctic ones. According to MCWHINNIE (1967) cold-water forms show little metabolic adaptation when

compared with tropical species; however, R–T curves are displaced farther to the left than those of animals from tropical environments.

> 'From this, one can infer adaptation only by increased rates of reactions. It was interpreted that species in regions of low temperature variation, such as polar forms, do not require as broad a competence for physiological adaptation as do those from more widely varying temperature environments' (McWHINNIE, 1967; p. 358).

More information on the responses of polar versus tropical invertebrates is needed before we possess a satisfactory picture of the degree of their genetic capacity adaptation to the different thermal regimes encountered.

A closely related problem concerns genetic adjustments of metabolic rate in invertebrates from tropical and temperate zones. Comparisons between the O_2 consumption of tropical versus temperate-zone fiddler crabs of the genus *Uca* (VERNBERG, 1959) have confirmed that temperate species show higher rates of O_2 consumption at elevated temperatures than do tropical species when both have been acclimated at 15° C (see also VERNBERG and TASHIAN, 1959; VERNBERG, 1962; VERNBERG and VERNBERG, 1964, 1966; McWHINNIE, 1967).

While the examples quoted above refer largely to interspecific differences in genetic capacity adaptation, there is also evidence for intraspecific differences. Thus, thermal responses of the amphipod *Gammarus duebeni* are apparently quite different in populations from North Germany and warm-water habitats (warm springs) in Ireland, suggesting the existence of genetically different populations with significantly different thermal response patterns.

Activity

The relation between temperature and cirral activity of cirripede species from Europe and America has been discussed in detail by SOUTHWARD (1964). Cirral activity has been observed with the tested barnacles subjected to a flow of water, gentle for some species, strong for others; such water flow minimizes responses to other stimuli (light, mechanical shock) which might otherwise interfere with the regular beating activity of the barnacles' appendages. Some typical results are illustrated in Fig. 3-86 for the 2 common European barnacles *Balanus balanoides* and *Chthamalus stellatus*. In addition to a difference in rates of activity, there is a shift in position of the curves, indicating adaptation to low ambient temperature in the northern species (*B. balanoides*) and adaptation to higher temperatures in the southern species. This shift is such that the northern species ceases cirral beating completely at a temperature at which the warm-water *C. stellatus* exhibits maximum activity. In the limited areas of Britain, France and N.W. Spain, where these 2 species occur together, the local temperature regime must—as pointed out by SOUTHWARD—be a most important factor determining their relative ecological success.

Comparable differences, though smaller than in some other invertebrate groups, exist in arctic barnacles versus tropical ones. SOUTHWARD (1964) compared 2 pairs of species of about the same body size but not the same ecological niche: (i) *Balanus crenatus* from Point Barrow (Alaska) and *B. amphitrite* from Miami (Florida); (ii) *Balanus balanus* from Point Barrow and *Tetraclita squamosa* from

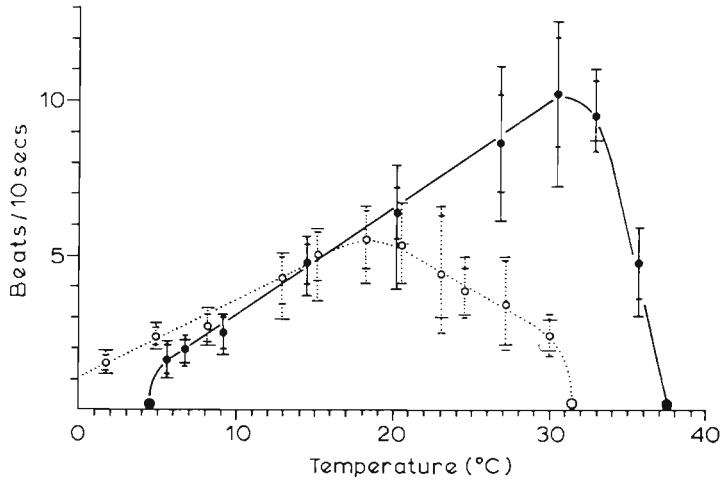


Fig. 3-86: Cirral activity as a function of temperature in the cirripedes *Balanus balanoides* (dotted line) and *Chthamalus stellatus* (solid line). Small circles indicate mean rate at each temperature, large cross lines the range of observations and the small cross lines the standard deviation on each side of the mean. The large circles indicate absence of cirral beating. (After SOUTHWARD, 1964.)

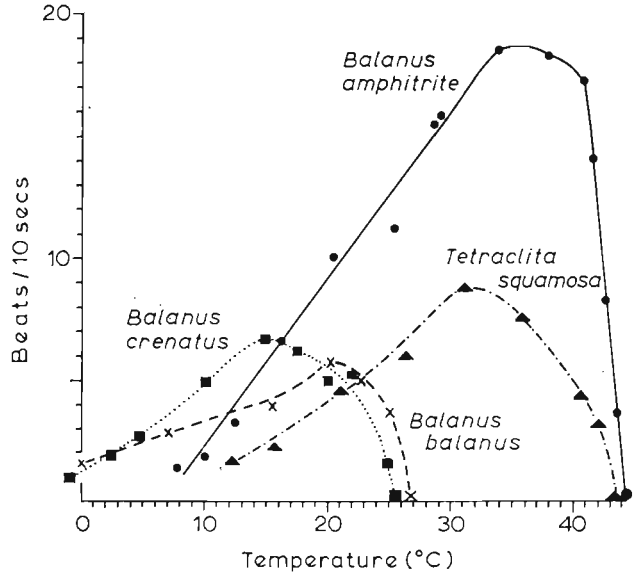


Fig. 3-87: Cirral activity as a function of temperature in pairs of arctic (*Balanus crenatus*, small, sublittoral; *B. balanus*, large, sublittoral) and tropical (*Balanus amphitrite*, small, sublittoral; *Tetraclita squamosa*, large, midtide) Cirripedia. (After SOUTHWARD, 1964; modified.)

Miami (Fig. 3-87). He considers these cases classical examples of activity adaptations to the particular thermal environments, ranging from below – 1° C to about 6° C for the arctic specimens, and from 22° C to over 30° C for the tropical ones. SOUTHWARD also studied activity–temperature curves for barnacles from the Atlantic coast of the USA in which the differences in activity rates are not always quite as pronounced, and draws attention to the interesting distributional problems encountered on the Pacific coast of North America where the cool temperate region is expanded at the expense of the warm temperate and arctic regions. On this coast, *Balanus balanoides* appears to be restricted to the coldest parts of the temperate zone (southeastern Alaska), and near its southern limit it is abundant only in the presumably cooler inlets. The temperature–activity curve is, however, very similar to that of European specimens, displaying an insignificant amount of low temperature shift. In the Pacific, *B. balanoides* is in competition with the more widely distributed *B. glandula* which occurs from Mexico to the Aleutians. *B. glandula* is obviously better equipped for life in this area since, at low temperatures, its activity rate is comparable with that of *B. balanoides*; yet it is able to continue its activity at temperatures some 10 centigrade degrees higher before showing signs of disturbance. Thus, comparative studies on animal activity rates may produce important clues as to the ecological potential of the species concerned relative to the local temperature regime.

Another example of temperature effects on rates of activity, presented by SOUTHWARD (1964), concerns the warm-temperate cirripede *Chthamalus fissus* which occurs from north Mexico to Monterey (USA). It shows only slight adjustments to high temperature compared with the more widely (south California to arctic regions in the Chukchi Sea) distributed *Chthamalus dalli*. Within this wide area of distribution *C. dalli* exhibits almost identical temperature–activity curves. Specimens from Cape Thompson in the Chukchi Sea survive 6 months frozen in the ice foot, and begin breeding at 5° C, yet display in their rate curves only the slightest low temperature adjustment, statistically insignificant, compared with specimens from the warm temperate region where the water temperature never falls below 15° C. However, *C. dalli* does show some differences in activity rates of specimens from different tidal levels and habitats. High-water specimens have a depressed rate of cirral beating compared with low-water specimens.

> 'In the absence of significant adaptation with latitude, it can hardly be maintained that these differences are a matter of adaptation to temperature, as suggested for other groups of intertidal animals (e.g. SEGAL and co-authors, 1953; DEHNEL, 1956; SEGAL, 1956; see also SEGAL, 1961), and an alternative theory of correlation with relative rates of growth—usually maximal at low water and minimal in high water wave-beaten places—would seem to be confirmed' (SOUTHWARD, 1964, p. 401).

RÜPPELL (1967) recorded the daily locomotory activity of the semiterrestrial marine amphipod *Orchestia platensis* in the field and in the laboratory. Below 5° C, rate of activity becomes closely dependent on temperature; at higher temperatures it depends primarily on light and humidity (floods). Endogenous patterns of activity become apparent under constant environmental conditions in the laboratory but are overruled by climatic fluctuations under field conditions.

McWHINNIE (1964) maintained the antarctic planktonic crustacean *Euphausia superba* (collected at −1·27° to 2° C; 60 to 62° S between 49 and 63° W) and *Munida gregaria* (grimothea stage; collected at 8·8° C; 54° S in the Strait of Magellan) immediately after collection at different temperatures. *E. superba* showed greatest locomotory activity at −1·5° C, which was greatly reduced or absent at 4° C; *M. gregaria* was most active at 8° to 10° C and did not survive rapid transfer into 0° C (see also MARR, 1962).

The relations between locomotory activity (walking rate), acclimation temperature and thermal tolerance in the American lobster *Homarus americanus* have been studied by McLEESE and WILDER (1958). Their results are discussed and illustrated in Chapter 12 which is devoted to organismic responses to factor combinations.

SCHWAB (1967) studied the locomotory activity of the turbellarian *Polychoerus carmelensis* collected from tide pools and the midtide horizon at Point Pinos, California, USA. After dark-conditioning for at least 24 hrs at 13° to 14° C, individual flatworms were placed on a horizontal plastic grid and quickly submerged to a depth of 1 cm into sea water of different temperatures. Illumination during experiments (fluorescent room lights) was 60 foot candles at water level—sufficient to induce photokinetic responses in dark-conditioned specimens. Locomotory responses across the grid were recorded and rate of locomotion computed in mm/min. Transfer into a temperature of 3° C led immediately to contraction resulting in a U-shaped posture; after several minutes disintegration of epidermal cells commenced and shortly thereafter gentle water movements resulted in body-tissue disintegration. Exposure to 5° C led also to U-shaped body contraction and cessation of locomotory activity for several minutes; subsequently, most test individuals were capable of locomotion at rates ranging from 5·0 to 32·5 mm/min. Changes in ambient temperature clearly affected locomotion rates. However, the manner of locomotion differed. Several of 20 individuals exposed to 8° C began to move while still in a U-shaped posture by action of their dorsal cilia (the only body portion in contact with the grid). These individuals soon re-orientated to the typical flatworm posture and thereafter travelled—as did the other specimens tested—at an average rate of 44·9 mm/min. At higher temperatures, rate of locomotion increased to averages of 64·8 mm/min at 11° C, 83·0 at 14° C and 90·4 at 17° C respectively (Table 3-41). In response to a 12-degree centigrade rise (5° to 17 C°) rate of locomotion increased—at a nearly uniform rate of 6·1 mm/min/C°—from 17·4 to 90·4 mm/min. Temperatures higher than 17° C led to decreased locomotory activity, resulting in a steady decrease of about 4·4 mm/min/C° at temperatures between 17° and 33° C. At 29° C, *P. carmelensis* usually contracted into a curled posture with the posterior body portion drawn up under the more anterior one. Locomotion in this position was primarily accomplished by the anterior body in contact with the grid. At 33° C, most specimens curled up and were capable of locomotion for only 1 to 3 mins; thereafter tissue disintegration took place. At 35° C, tissue disintegration occurred within 60 secs, and at 38° C death resulted immediately.

SCHWAB (1967) points to the fact that the highest rate of locomotion of *Polychoerus carmelensis* occurred at a temperature (17° C) comparable to that measured at the respective time of the year in the natural habitat. This suggests that the

maximum scope for activity may be associated with seasonal climatic habitat conditions. Comparable rates of locomotion had earlier been obtained by ARMITAGE (1961) whose observations indicate that activity in *P. carmelensis* is affected not only by temperature but also by light intensity and water movement.

ANDERSON and REISH (1967) subjected 3 species of the wood-boring isopod genus *Limnoria* to different temperatures and O_2 concentrations and found that burrowing activity, as measured by egestion rate of faecal pellets, depends on O_2 and ambient temperature.

In the polychaete *Nereis* (*Neanthes*) *succinea* the nightly swimming activity associated with spawning is related to variations in surface water temperatures.

Table 3-41

Locomotory activity as a function of ambient water temperatures in the acoelous turbellarian *Polychoerus carmelensis*. A total of 20 individuals was tested at each of the temperature levels (After SCHWAB, 1967; modified)

Test temperature (° C)	Rate of locomotion (mm/min)			
	Range	Average	Standard deviation	Standard error of mean
5	5·0–32·5	17	6·8	1·5
8	25·0–62·5	45	9·8	2·2
11	40·0–90·0	65	14·2	3·2
14	62·5–115·0	83	14·7	3·3
17	57·5–122·5	90	17·1	3·8
21	45·0–95·0	79	13·9	3·1
25	45·0–87·5	66	11·4	2·5
29	35·0–62·5	50	7·4	1·7
33	17·5–65·0	33	11·5	2·6

In the harbour of Kiel (Germany) spawning activities extended in the summer of 1953 through June, July and August. During these months intensive swimming activity occurred at temperatures above 16° to 17° C with a maximum at 21° to 22° C (the highest local sea temperatures recorded); below 16° C only a few specimens were observed, below 13° C none (KINNE, 1954b).

Temperature variations can modify the locomotory activity pattern of planktonic organisms. The technical difficulties in recording activities of small or even unicellular planktonic organisms have been largely overcome by new technical developments. DAVENPORT and co-authors (1962) described an electronic tracking device which makes it possible to obtain, with great accuracy and rapidity, activity data on linear velocity and rate of change in direction. Results obtained on dinoflagellate protozoans indicate thermal independence of activity rates over appreciable temperature ranges. Thus *Gonyaulax polyedra* (the causative agent of 'red tides') and an unidentified *Gyrodinium* species maintained their locomotory

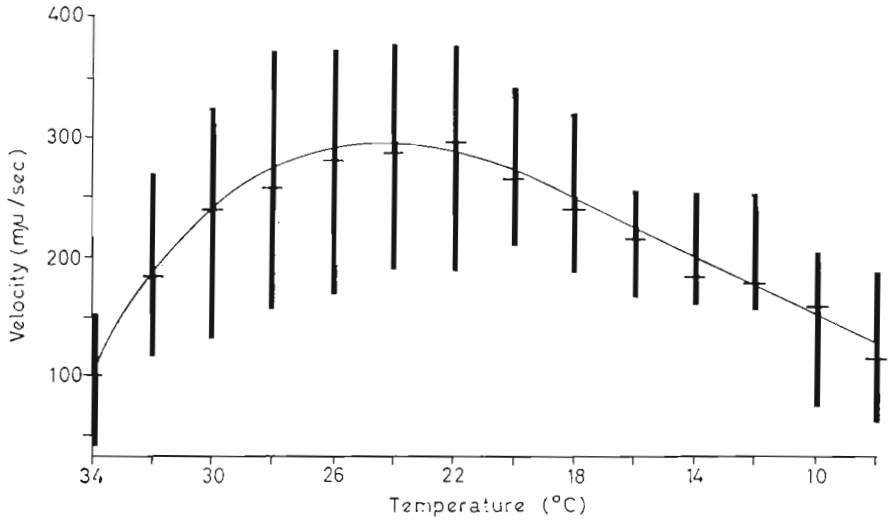


Fig. 3-88: Linear velocity (motility) as a function of temperature in the dinoflagellate *Gonyaulax polyedra*. (After HAND and co-authors, 1965.)

velocity through a rather wide variety of temperature conditions (HAND and co-authors, 1965). *G. polyedra* was exposed to a rapid temperature decline from 20° to 8° C within 10 mins. The cells maintained their motility down to 16° C (which took 6 mins), whereupon they began to cease their locomotory activity and to settle to the bottom of the culture flask. All cells lost motility at 12° C; cells kept at 8° C for 12 hrs did not recover motility; those returned to 20° C immediately after the initial decline to 8° C recovered activity within 12 hrs. Rapid temperature increase from 20° to 34° C within about 20 mins resulted in motility loss at 28° C; cells maintained at this temperature recovered motility in about 1 hr. If *G. polyedra* was exposed to slower temperature increase (approximately 2 C°/30 mins) locomotory activity ceased only at 34° C. Cells maintained at 34° C for 12 hrs never recovered activity; those returned to 20° C immediately after a temperature rise to 34° C likewise never recovered. In another experiment, *G. polyedra* was exposed to a temperature decrease in 2 C° decrements from 20° C to a temperature where motility disappeared. The temperature decline between subsequent 2-degree levels was achieved over a 30-min period (the shortest interval possible which would not cause a 'subjectively observable' number of cells to lose motility). At each temperature interval a sample was taken from the culture and subjected to microscopic examination. The relationship of linear velocity to temperature in *G. polyedra* is illustrated in Fig. 3-88. Strictly parallel experiments with *Gyrodinium* sp. provided the data shown in Fig. 3-89. The littoral *G. polyedra* and the lagoon-inhabiting *Gyrodinium* sp. maintain similar locomotory velocities through a wide temperature range; however, the former exhibits a more pronounced temperature independence as one might expect in view of the thermal characteristics of its habitat.

Rates of locomotory activity which are, within a certain range, independent of ambient temperature variations may be of value to dinoflagellate populations com-

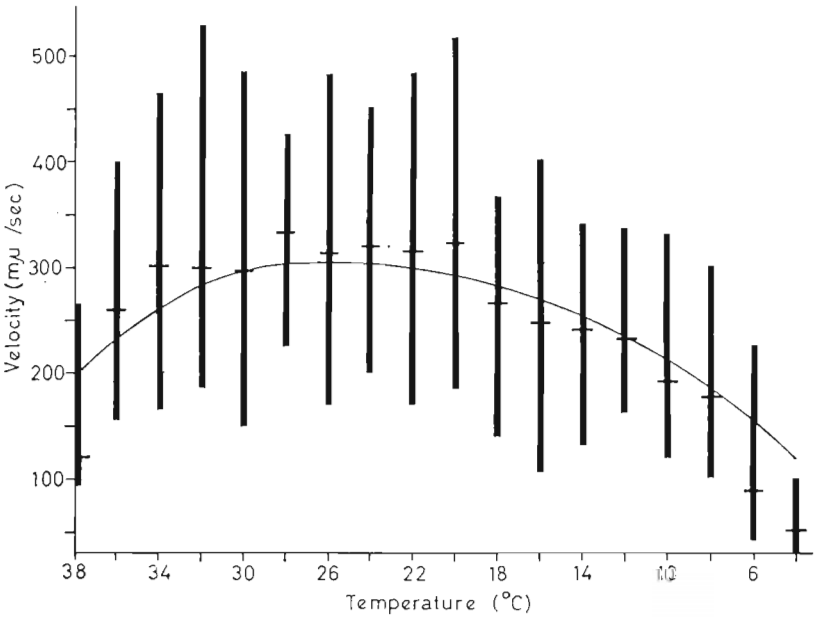


Fig. 3-89: Linear velocity (motility) as a function of temperature in *Gyrodinium* sp. (After HAND and co-authors, 1965.)

peting with each other under varying hydrographical conditions (temperature, salinity, light, nutrients), particularly in forms with phototactically controlled diurnal migrations such as *Gonyaulax polyedra* (RYTHER, 1955; HAND and co-authors, 1965). Locomotory rates of *G. polyedra* are, with approximately 250 μ/sec, well within the order of magnitude necessary to accomplish the amount of diurnal migration established by HASLE (1950, 1954) for this species in a Norwegian fjord (HAND and co-authors, 1965). Nothing is known about the locomotory behaviour of unicellular planktonic organisms in the presence of steep temperature and salinity gradients in the sea such as occur in thermoclines.

> 'We do not even know whether as a discrete and independently motile unit such a cell ever crosses an interface under natural conditions. We have not as yet directed our attention to the technical problem of "facing" the single cell with such a condition. We believe that when we have done this and investigated the correlation of such behavior with responses effected by changes in light intensity and wave length, we may be better able to understand the so-frequently reported "spotty" distribution of these phytoplankters' (HAND and co-authors, 1965, p. 100–101).

CROZIER (1916) investigated the rate of cloacal pulsations in the echinoderm holothuroid *Stichopus moebii*. Pulsation activity reaches a maximum near 26° C and decreases both at lower and higher temperatures. According to his graph, time for 10 pulsations is about 220 secs at 12·5° C, 185 at 16° C, 144 at 20° C, 90 at 26° C, and 135 at 30° C; below 12·5° and above 32·0° C pulsations cease. Similarly cloacal pulsations per min vary in *Paracaudina chilensis* from 3 to 6 between 8° to 28° C,

9 to 10 at about 30° C and less than 1 at 32° C (TAO, 1930). In *Stichopus japonicus* time for a 'single breath' decreases with increasing temperature between 12° C and 18° C while at higher temperatures a rather steady rate of about 1 pulsation per min is maintained up to about 28° C while the holothurian reduces other activities (CHOE, 1962).

Temperature may, finally, control to a large extent the alternation of active and dormant life-cycle stages. This may be exemplified on the basis of field and laboratory studies of the colonial hydroids *Laomedea loveni*, *Cordylophora caspia* and *Perigonimus megas*. All 3 species tend to 'reduce' their hydranths below certain critical temperatures 'waiting' in the non-active, dormant or menont stage for suitable temperature conditions to return and then, after rebuilding their hydranths, begin to feed and grow again. In the Kiel Canal (north Germany) *Laomedea loveni* shows only partial hydranth reduction in mid-winter and mid-summer, suggesting that water temperatures below 2° to 3° C and above 19° to 20° C tend to cause hydranth dormancy; in *Cordylophora caspia* complete hydranth reductions occur during the coldest winter months at temperatures below 2° to 4° C, and reactivation in spring at temperatures above 6° C; in *Perigonimus megas* dormancy begins in October at temperatures below 9° to 12° C and ends in May at temperatures above 9° to 12° C. Such differences in the relative lengths of active and non-active periods may significantly affect the ecological potential of the species in a given habitat and modify aspects of population dynamics and competition as a function of season (KINNE, 1956b, c).

(c) *Reproduction*

Reproduction always involves growth; both processes make heavy demands on the energy resources of the organism, and hence body growth and gonad growth tend to be incompatible with each other. Usually, reproduction begins only after body growth has declined markedly; in many species body growth alternates with gonad growth or reproductive activities. Physiologically, the relation between growth and reproduction is governed by cytochemical and hormonal mechanisms which, in turn, are influenced by environmental factors, especially temperature, light and nutrition.

Few marine invertebrates can as yet be bred under controlled laboratory conditions from egg to egg. Hence much information concerning temperature effects on reproduction is based on occasional observations both in the sea and in the laboratory. Reviews dealing with, or including problems of, temperature effects on reproduction in marine invertebrates have been written by GUNTER (1957), GIESE (1959), KINNE (1963a) and BOOLOOTIAN (1966b).

In most marine invertebrates reproduction tends to be confined to narrower thermal ranges than the majority of other life processes. The gastropod *Urosalpinx cinerea* requires higher temperatures for oviposition (15° to 20° C) than for drilling (10° to 15° C) or locomotion (5° to 10° C) (STAUBER, 1950); the American oyster *Crassostrea virginica* can feed and grow at much lower and higher temperatures than are required for spawning (GUNTER, 1957); according to rough approximations, the amphipod *Gammarus duebeni* (north Germany; 10‰ S) can move about and feed at temperatures between −1° and 26° C while reproduction is possible only

between about 3° and 22° C (KINNE, 1953a). The temperature ranges for existence and reproduction in 3 colonial hydroids are 2° to 20° C versus 7° to 19° C in *Laomedea loveni*, 2° to 24° C versus 12° to 19° C in *Cordylophora caspia* and 9° to more than 25° C versus 14° to 23° C in *Perigonimus megas* (KINNE, 1956b, c).

It is necessary, therefore, to distinguish between the vegetative temperature range and the reproductive temperature range of an organism. In habitats with considerable annual temperature variations, an organism with vegetative eurythermy and reproductive polystenothermy can make use of its eurytherm capacities only if seasonal temperature variations provide high enough temperatures for a sufficiently long period, or if it undertakes periodical reproductive migrations into areas with suitable thermal conditions. Conversely, a vegetatively eurytherm organism with reproductive oligostenothermy can exist in temperate seas only if sufficiently long periods with low temperatures occur during the coldest season or if it migrates into colder areas for reproduction.

While the initiation of reproduction depends on several environmental factors in most marine invertebrates, it seems justified to generalize that—once certain prerequisites such as appropriate physiological condition and nutritional demands are satisfied—the time of reproduction (breeding season) is often decisively affected by temperature. A few species seem to breed all year round; however, most marine invertebrates begin to reproduce when a certain temperature level is reached after a period of either increasing or decreasing temperature, or in response to sudden temperature changes.

The idea introduced by SEMPER (1881) that tropical organisms have continuous breeding seasons requires qualification (GUNTER, 1957). YONGE (1930) has shown that at the Great Barrier Reef many organisms have definite breeding rhythms; it seems that the majority of tropical species spawn either exclusively or most intensively during the warmer months (STEPHENSON, 1934). On the whole, the breeding seasons of tropical marine animals of a given community appear to be arranged so as to make the best use of time, space and food available with the result that planktonic larvae are present all year round (THORSON, 1946). In many temperate marine invertebrates the duration of the breeding season tends to increase with decreasing latitude. Literature information on breeding seasons (periods during which fertilizable gametes are present) has been summarized for many species of crinoids, holothuroids, asteroids, echinoids and ophiuroids by BOOLOOTIAN (1966b). While the reproductive processes of echinoderms show clear relations to season, the role of temperature *per se* still remains to be ascertained. In 2 separate populations of the echinoderm *Strongylocentrotus purpuratus*, which inhabit side by side water masses with different temperature regimes in California (USA), reproductive cycles are strikingly similar, except for an extended duration and lower amplitude of gonadal activity in the warm-water population near Tres Hermanas compared to the cold-water one near Papalote Bay (BOOLOOTIAN, 1966b).

In many cases seasonal variations of temperature appear to act in concert with those of light and nutrition as well as with endogenous factors. No detailed analyses are available. LITTLE (1968) succeeded in inducing winter breeding in the shrimp *Palaemonetes pugio* both by increasing the temperature and by employing a combination of increasing temperature and photoperiod. His results indicate

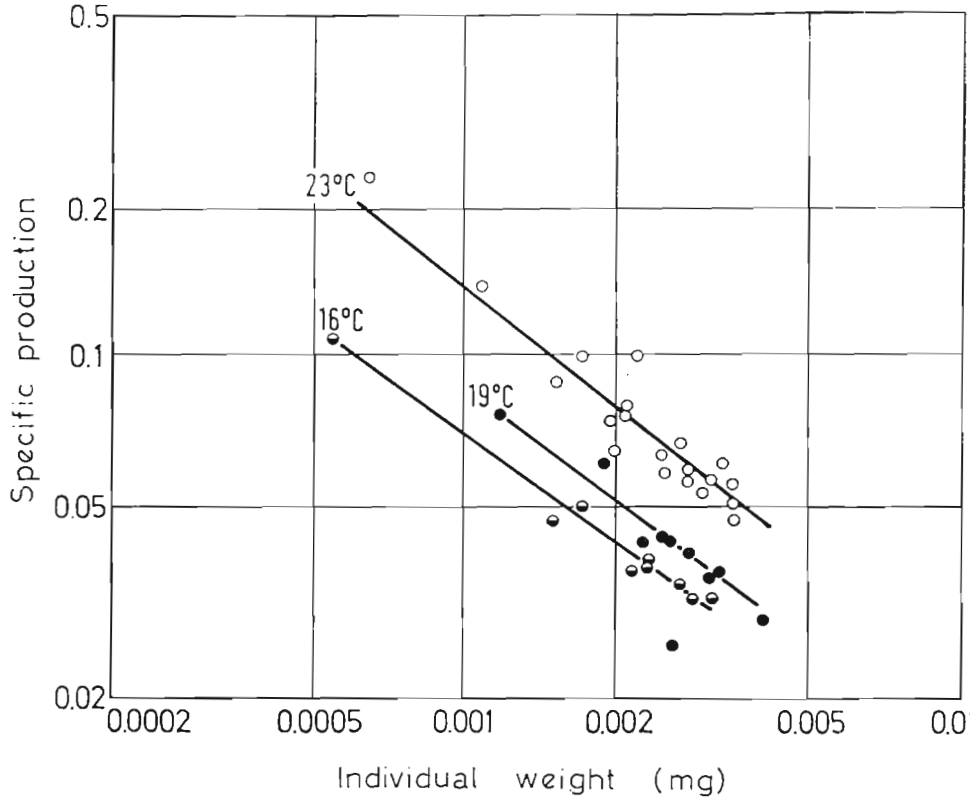


Fig. 3-90: Relation at different temperatures between 'specific production' and average individual weight in the copepod *Acartia clausi* from the Azov Sea. (After ZAIKA and MALOWITZKAJA, 1967; modified.)

that a combination of temperature and light may be more effective than temperature alone. Several other cases—each one hardly conclusive in itself—suggest that seasonal changes in temperature plus light, as well as parallel changes in food quality and quantity, may be required for maximum responses in regard to inducing reproduction; for a number of species such a combination may be obligatory.

When comparing the reproductive rates of different populations, the concept of 'specific production' (the production rate per unit biomass) can be of use. ZAIKA (1968) demonstrated for 3 calanid species from the Azov Sea, that the ratio annual production/average annual biomass is relatively stable and the relation between specific production and average individual weight is close to a straight line in a log/log graph; it depends upon temperature (Fig. 3-90), increasing from 16° over 19° to 23° C as does growth rate.

Sexual reproduction

Sexual reproduction of marine invertebrates comprises several processes following the vegetative phase: gonad growth, gamete maturation, gamete release (spawning, mating, copulation, etc.) and embryonic development. Since these sequential steps may be affected differently by temperature, a detailed analysis

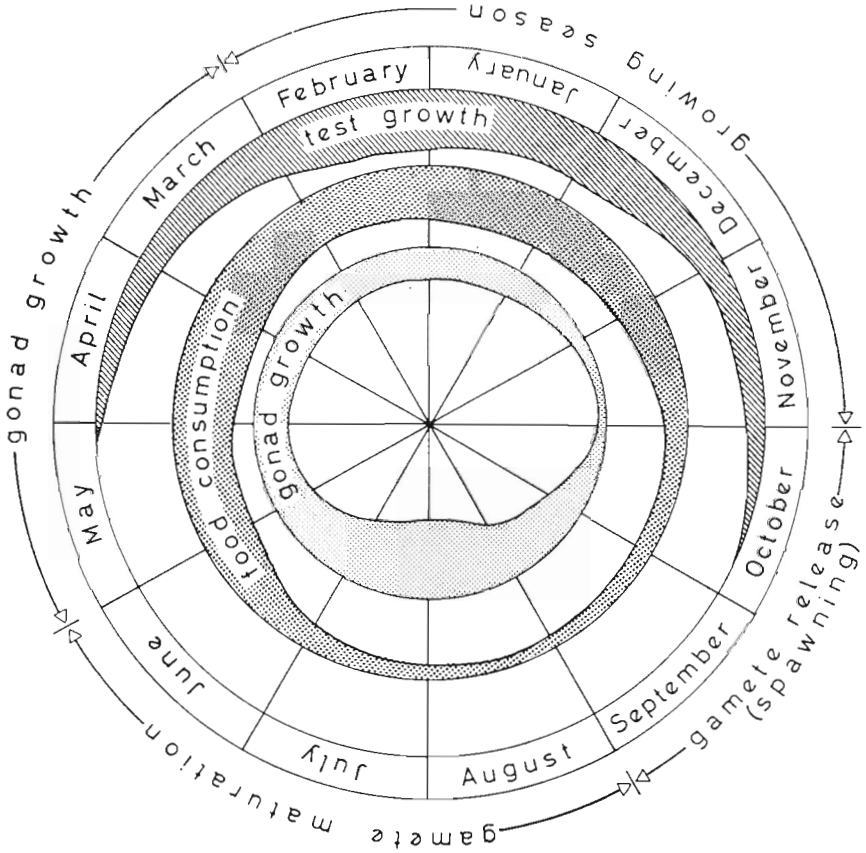


Fig. 3-91: Gonad growth, test growth and food consumption in the sea-urchin *Strongylocentrotus intermedius* throughout the season. (After FUJI, 1967; modified.)

requires a separate assessment of the thermal effects on each process. Only few such studies have been conducted. For echinoderms, pertinent methods and discussions have been presented by GIESE (1959), BOOLOOTIAN (1966b) and FUJI (1967; see Fig. 3-91), for the scallop *Aequipecten irradians* by SASTRY (1961, 1966). Gonad growth and gamete maturation frequently occur simultaneously and may be different aspects of one and the same general phenomenon. However, in practice, gonad growth is usually determined on a weight or volume basis whereas gamete maturation is assessed histologically in terms of gametogenesis stages or gamete diameter. Pertinent papers reflect these methodological differences; hence both aspects will be treated separately.

Gonad growth. Assessments of gonad growth have been made by determining the gonad volume or weight divided by body volume or weight times 100 ('gonad index', e.g. GIESE, 1959). In bay scallops *Aequipecten irradians*, gonad growth and body growth take place simultaneously during the beginning of their first reproductive period (SASTRY, 1966). Gonad growth is possible only in the presence of food. Scallops exposed to various ambient temperatures during the period of gonad

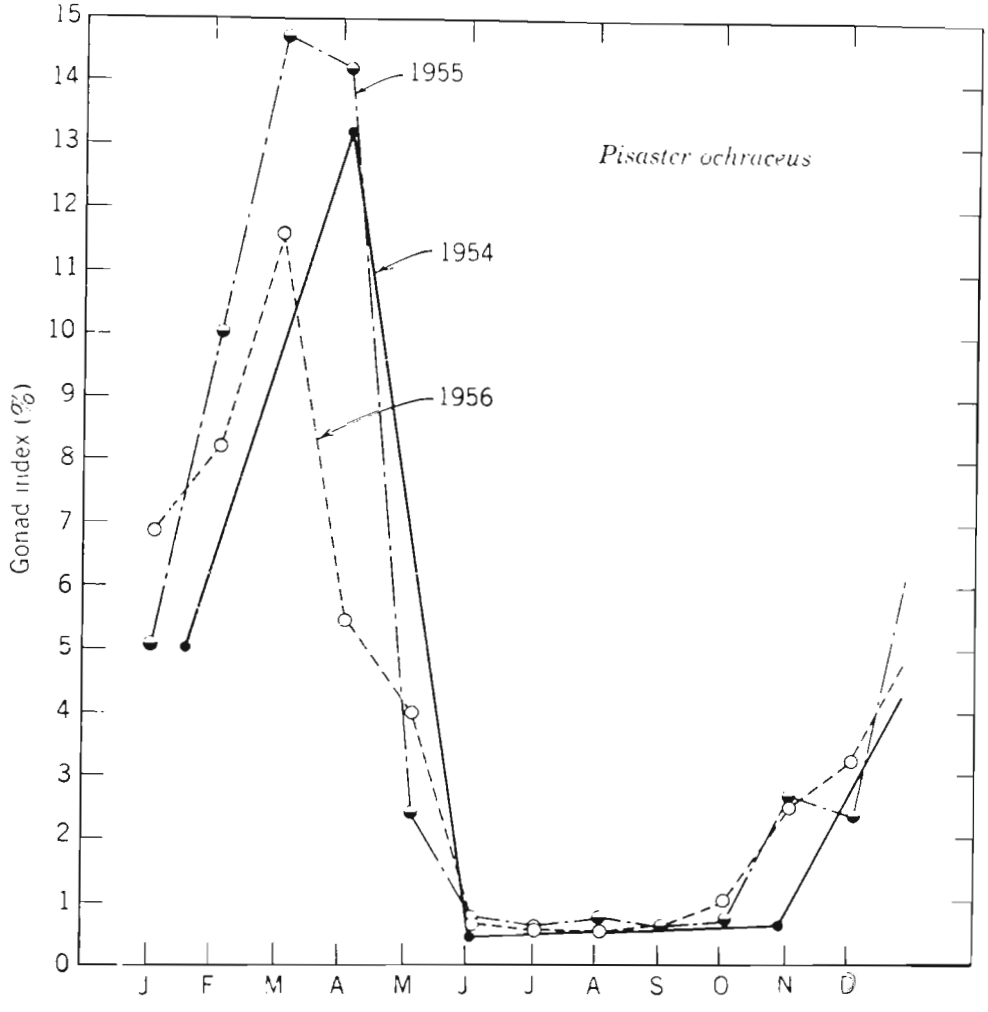


Fig. 3-92: Seasonal changes in gonad index of the sea-star *Pisaster ochraceus* (coast of north California, USA) during 1954 (according to FEDER, 1956), 1955 and 1956 (according to FARMANFARMAIAN and co-authors 1958). The points represent averages for 10 individuals. (After BOOLOOTIAN, 1966a.)

growth, without food supply, show a decrease of the gonad index. SASTRY suggests that gonad growth in *A. irradians* might normally take place in the presence of abundant food and under temperature conditions at which nutrient mobilization to gonads is permitted after the basic metabolic needs of the scallop have been met.

An example of gonad-index changes as a function of season is presented in Fig. 3-92 for the echinoderm asteroid *Pisaster ochraceus* from the coast of northern California (USA). The curves obtained during 3 years show the same general pattern of increase and decrease of gonad size throughout the year. Quite similar values have been obtained for the years 1957 and 1958 by GREENFIELD (1959).

Gonad growth of most hitherto examined marine invertebrates appears to depend primarily on nutrient supply, temperature and photoperiod.

Gamete maturation. Near Beaufort, North Carolina (USA), gametogenesis of bay scallop *Aequipecten irradians* begins when the gonads have a minimum amount of reserve material at temperatures slowly increasing above 20° C (May, June; Fig. 3-93). Continued nutrient transfer to gonads appears to be necessary for further gamete maturation. In the laboratory, starvation during gonad growth results in the absorption of oogonia and oocytes at all test temperatures. The time–temperature relation for spawning of *A. irradians* from different collections indicates that the development of oocytes to maturity might be a function of ambient temperature within the species-specific range, if the gonads have already accumulated sufficient reserve materials to support gamete maturation (SASTRY, 1966).

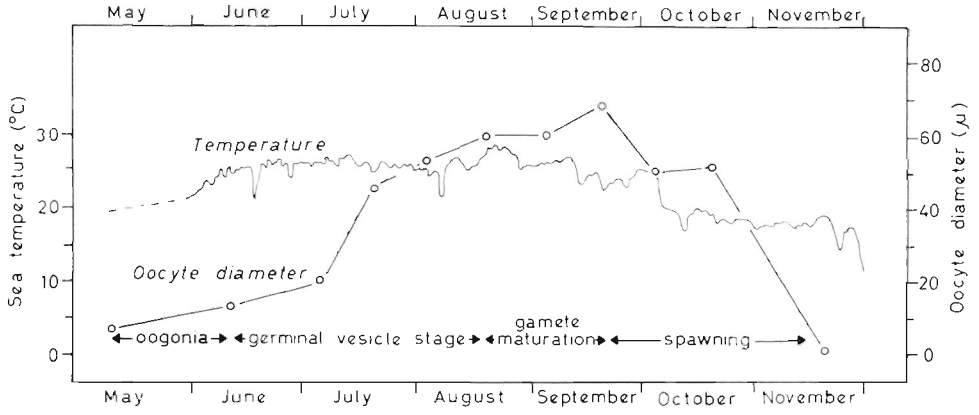


Fig. 3-93: Sea temperature (daily noon-time measurements) and reproductive cycle of the scallop *Aequipecten irradians* near Beaufort, North Carolina, USA. Scallops were collected at intervals and their average oocyte diameters (main curve) and reproductive condition (bottom) determined. (After SASTRY, 1966; modified.)

Oocytes of the scallop *Pecten yessoensis* were accelerated to maturity *in vitro* by exposure to high temperatures; they reached maturity long before the oocytes of the natural population (YAMAMOTO, 1951a). In the oyster *Crassostrea virginica*, the time required for gamete maturation depends on the maintenance temperature; individuals with poor glycogen reserves fail to reach sexual maturity (LOOSANOFF and DAVIS, 1952). In cirripedes, starvation may accelerate gamete maturation (CRISP, 1957). Interactions of temperature and light in regard to gamete growth and maturation have been demonstrated in the barnacle *Balanus balanoides* (BARNES, 1963) and the sea-urchin *Strongylocentrotus purpuratus* (BOOLOOTIAN, 1963).

HOLLAND (1967) studied gametogenesis during the annual reproductive cycle of the sea-urchin *Stylocidaris affinis*. In view of the observed lack of seasonal fluctuations in temperature, oxygen concentration and salinity, he concludes that these environmental factors do not control or synchronize gametogenesis and spawning of *S. affinis*. The long periods of oocyte growth and spermatocyte accumulation also show no close relation to the photoperiod, nor do the short periods of initiation of oocyte growth and initiation of spermatocyte accumulation.

However, HOLLAND feels it may be possible that, even if light does not have a direct influence on reproduction in *S. affinis*, photoperiod might possibly be used as periodic reference point. For details on light effects on marine invertebrates consult Chapter 2.31.

CHIA (1964) followed the annual reproductive cycle of the sea-star *Leptasterias hexactis* for 4 successive years and measured in monthly intervals the diameters of maturing oocytes both in fresh and fixed specimens. Maturation of an oocyte takes almost 2 years; yet sexually mature *L. hexactis* spawn annually. During the first few months of the year an increasing separation of oogonia into 2 size groups can be observed; one group attains maturity between July and August and is, thereafter, ready for spawning; the other group consists of smaller cells which reach a diameter of only about 100 μ by the end of the first year and attain spawning size during the following midsummer (Fig. 3-94). Detailed accounts on seasonal effects on gametogenesis both in females and males of the sea-urchins *Strongylocentrotus nudus* and *S. intermedius*, have been presented by FUJI (1960a, b, c). For additional

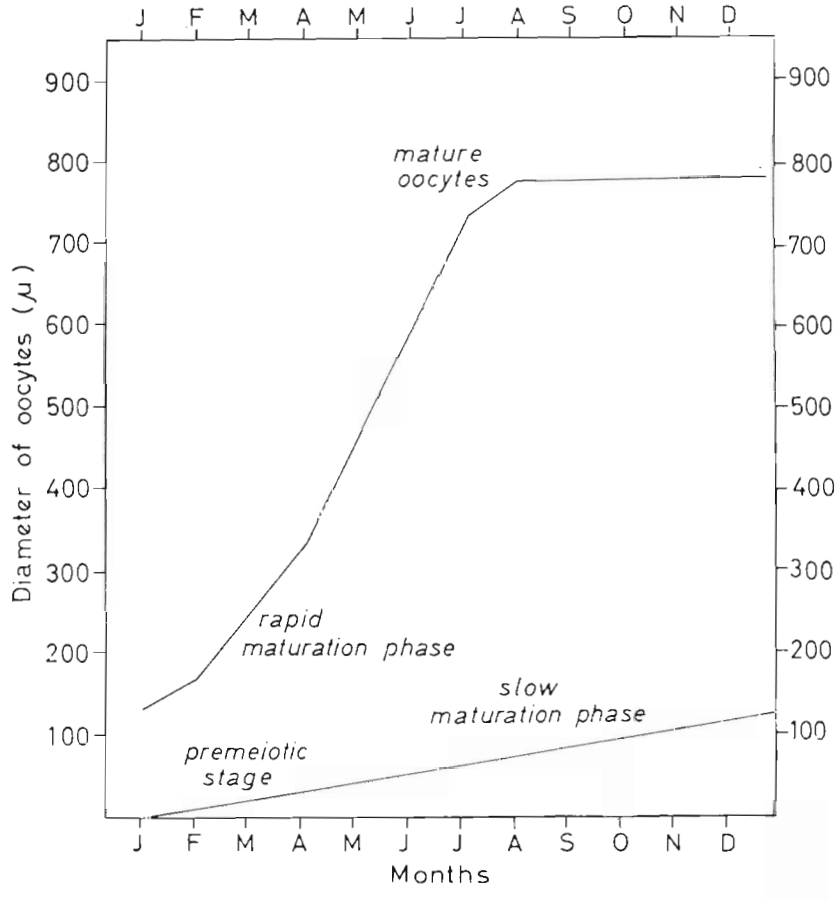


Fig. 3-94: Gamete maturation in the echinoderm asteroid *Leptasterias hexactis*. Diagrammatic extrapolation of seasonal changes in oogonium or oocyte diameter reveals a phase of slow growth during the first year and a phase of rapid growth during the next. (From CHIA, 1964; after BOOLOOTIAN, 1966a; modified.)

information on gamete maturation in echinoderms consult GIESE (1959) and BOOLOOTIAN (1966a, b).

Gamete release. Marine invertebrates release their gametes (i) by (synchronous) shedding of ova and spermatozoa into the surrounding water, i.e. spawning; (ii) by mating without copulation or by pseudo-copulation; (iii) by various modes of copulation. The majority of accounts reporting temperature effects on gamete release are concerned with spawning. While gamete release may occur repeatedly within one year at certain intervals or over longer periods of time, it is, in most marine invertebrates, restricted to shorter periods than the preceding preparatory phases of gonad growth and gamete maturation and, in individuals with mature gametes, may be induced rapidly by a variety of stimuli. For further details consult GIESE (1959) and BOOLOOTIAN (1966a, b).

APELT (1969) maintained laboratory populations of the euryoecous acoelous turbellarian *Archaphanostoma agile* at different constant temperatures in North Sea water of about $32‰$ S. Egg masses were released between about 3° and 22° C. The number of eggs released per individual within 50 days amounts to 17 at 3° to 4° C, 62 at 5° to 6° C, 100 at 8° to 9° C, 75 at 14° to 15° C, 81 at 16° to 18° C and 26 at 22° C. Average numbers of eggs per egg mass is 3·5 (1–10) at 3° to 4° C, 4·0 (1–13) at 5° to 6° C, 3·9 (1–17) at 8° to 9° C and 1·8 (1–7) at 16° to 18° C. The number of eggs per individual reaches comparable high values in the range between 5° and 18° C, while the average egg number per egg mass drops from about 4 at 5° to 9° C to 1·8 at 16° to 18° C. Adult individuals kept at 5° to 9° C are larger (1,350 μm long, 315 μm wide) than those maintained at 16° to 18° C (1,100 μm long, 260 μm wide). The fewer number of eggs per egg mass laid by the smaller individuals is compensated for by a shortening of egg-laying intervals, resulting in the practically equal egg production per individual per unit of time. An important prerequisite for normal gamete release performance is continuous optimal nutrition (food: diatoms of the genus *Nitzschia*).

When kept at 20° C or above, *Aequipecten irradians* with accumulated gonad reserves release their mature gametes even when starved. This observation demonstrates that once a certain amount of reserves is present in the gonads and the ambient temperature conditions are suitable for gamete maturation, gamete release (spawning) proceeds irrespective of food supply. *A. irradians* seems to require temperatures slightly above 20° C for maturation of oocytes to the stage prior to release. However, minimum temperature requirements for spawning decrease with increasing maturity of the oocytes; at early stages of gametogenesis (oocytes at the beginning of growth phase) individuals maintained at 20° C and below fail to spawn; at later stages of gametogenesis (oocytes at end of growth phase), they do spawn. Only individuals exposed to 15° and 10° C never release gametes (SASTRY, 1966).

In the gastropod *Nassarius obsoletus*, gametogenesis is always completed several months before spawning; hence a short period of warming can easily initiate gamete release. Such a condition occurs when the low tide falls near noon on clear sunny days during early spring (SCHELTEMA, 1967).

According to CHIPPERFIELD (1953), the lamellibranch *Mytilus edulis* spawns off the coasts of Great Britain from the end of April to the end of May when water

temperatures approach 11° to 13° C (at Portree, Scotland, the temperature was as low as 10° to 10·5° C). In the coastal waters of Scotland the gonads of *M. edulis* attain maturity in March or April (WILLIAMSON, 1907). In the Limfjord (Denmark) spawning has been observed in May and June (SPÄRCK, 1920); along the Atlantic coast of North America primarily in April, but continuing as long as September (FIELD, 1922). In the southwestern archipelago of Finland, spawning began somewhat below 12° C, attained maximum intensity slightly above 12° C (May, June) and ceased at 15·5° to 16° C (HEINONEN, 1961).

Spawning of oysters *Crassostrea virginica* and clams *Mercenaria mercenaria* can be delayed by transferring ripe or nearly ripe individuals into subnormal temperatures. This was demonstrated by LOOSANOFF and DAVIS (1951) who transplanted Long Island Sound individuals to Boothbay Harbour, Maine (USA) where the temperature—although high enough to permit gamete maturation—was too low to induce spawning. In *C. virginica* spawning could be postponed until 6 or 8 weeks after the Long Island Sound population was completely spent; *M. mercenaria* held over healthy summer spawn throughout autumn and winter into the following spring and may be induced to spawn at this time, releasing viable gametes which develop into normal larvae. *C. virginica* kept at subspawning temperatures resorb unspawned gonads in late autumn. Exposure to supranormal temperatures advances maturation and spawning in *Aequipecten irradians* (SASTRY, 1963).

Under normal conditions many invertebrates spawn either at a definite temperature or at a definite temperature change (ORTON, 1920; THORSON, 1946). According to ORTON, marine animals can be divided into those that spawn at rising or maximum temperatures and those that spawn at falling or minimum temperatures. Slowly rising or falling temperatures often lead to maturation of sexual products; spawning or copulation may then be induced by more extensive or more sudden temperature change in the same direction (YAMAMOTO, 1951a, b), specific substances released by either or both sexes or by other organisms (LUCAS, 1947, 1961; MARSHALL and ORR, 1952), light (KINNE, 1954b; HAUENSCHILD, 1960), tides and moon (FRIEDLÄNDER, 1898; KRÄMER, 1899; CASPERS, 1951; KORRINGA, 1957a; NEUMANN, 1967; HAUENSCHILD and co-authors, 1968).

In arctic and antarctic polar species, spawning usually occurs for limited periods during spring and summer plankton blooms when conditions are more favourable for development and settling of larvae or young. Light often seems to play a more important role than temperature. While most polar forms appear to have only one annual spawning season, some pelagic species among the ctenophores, chaetognaths and cnidarians have probably several broods per year (THORSON, 1936; GIESE, 1959).

In temperate and higher latitudes, gamete release is usually closely associated with the warmer seasons of the year. In spring, rising temperatures induce maturation of gametes, and spawning takes place when a specific temperature level is reached (GUNTER, 1957; GIESE, 1959). In Dutch waters the oyster *Ostrea edulis* breeds at temperatures above 15° to 16° C (but only if exposed to these temperatures for several weeks), and stops breeding long before sea temperatures have fallen below 15° C. A detailed investigation revealed, however, that the correlation between breeding and water temperatures cannot be a very close one (KORRINGA, 1957b).

Induction of gamete release by low temperatures has been reported in several cases and may be exemplified by referring to results obtained on the cold-water barnacles *Balanus balanoides* and *B. balanus* (CRISP, 1957). 'Vegetative' individuals kept in the laboratory between 15° and 18°C do not copulate; however, when kept between 3° and 10° C for several months they begin to copulate. If maintained at 15° to 18° C after the fertilized eggs have developed, normal copulation, fertilization and embryonic development occurs, indicating that such high temperatures do not inhibit these processes but that a period of low temperatures is required to induce breeding (see also PATEL and CRISP, 1960). In their recent paper, CRISP and PATEL (1969) point out that *Balanus balanoides*, *B. balanus* and *B. crenatus* require conditioning for several weeks below a critical temperature to reach the breeding condition. For *Balanus balanoides* the critical temperature lies between 10° and 12° C, for *B. balanus* between 10° and 14° C, and for *B. crenatus* at about 17° C. In *B. balanoides* high light intensities exert an inhibitory influence delaying the onset of breeding; but if the temperature is low, breeding will eventually take place. It is suggested that also other factors, not yet known, have an important influence on breeding in these barnacle species. Under laboratory conditions, feeding delays gamete release, though only to a slight degree. Whereas *B. crenatus*, and perhaps *B. balanus*, can be induced to breed prematurely by lowering the temperature, gamete release in *B. balanoides* can be advanced very little before its normal breeding season. *B. balanoides*, can, however, be made to breed by the experimenter, also out of season, when keeping it at supracritical temperatures (to delay breeding), and then providing a subsequent conditioning period at subcritical temperatures to induce gamete maturation. The fact that the breeding season of *B. balanoides* cannot be significantly influenced by abnormal conditions of temperature and light between March and September suggests that the earliest time for the onset of breeding is determined endogenously. There is some evidence of a

Table 3-42

Spawning in arctic–boreal, boreal and Mediterranean–boreal invertebrates near Bergen, Norway (After RUNNSTRÖM, 1927; modified)

Fauna group	Invertebrate species	January	February	March	April	May	June	July	August	September	October	November	December
Arctic–boreal	*Strongylocentrotus drobachiensis*	x	x	x									
	Cucumaria frondosa		x	x	x								
	Dendronotus frondosus	x	x										
Boreal	*Mytilus edulis*			x	x	x	x						
	Echinus esculentus			x	x	x	x	x					
	Asterias rubens			x	x	x	x						
Mediterranean–boreal	*Psammechinus miliaris*					x	x	x	x	x			
	Echinocyamus pusillus					x	x	x	x				
	Echinocardium flavescens					x	x	x	x	x			
	Echinocardium cordatum						x	x	x	x			
	Ciona intestinalis					x	x	x	x	x	x		

critical period in late summer, when processes leading to gamete release in autumn are initiated. Breeding then proceeds normally, if the temperature and illumination are not excessive. CRISP and PATEL (1969) assume that a similar endogenous cycle may exist in *B. balanus*, but probably not in *B. crenatus*.

Along the Norwegian coast, arctic, boreal and Mediterranean invertebrate species live side by side but spawn at different times of the year. Near Bergen, arctic–boreal, boreal and Mediterranean–boreal species spawn in winter, spring and summer respectively (Table 3-42). In some oysters there may be 2 spawning peaks during one year if the warm season is long enough (HOPKINS, 1931). Of 157 benthic marine species in the Adriatic, 64 breed in spring, 49 in summer, 26 in autumn and only 18 in winter (VATOVA, 1949).

Cosmopolitan species and species occuring over 2 or several climatic zones usually exhibit non-genetic or genetic adaptations to local temperature conditions, or both. Thus in Delaware Bay, Biddeford River, and Long Island Sound (USA), spawning of oysters begins at about the same time of year although the corresponding temperatures are respectively 25°, 20° and 16·4° C (STAUBER, 1950). Oysters, *Crassostrea virginica*, in Long Island Sound may spawn at temperatures as low as 16° C while southern oysters require 20° C (LOOSANOFF and NOMEJKO, 1951; see also KORRINGA, 1957b). *Gammarus duebeni* cannot reproduce at temperatures above approximately 22° C near Kiel, Germany, but establishes populations in warm springs of Ireland at 25° C (SCHWABE, 1936; KINNE, 1953a, 1963a).

Little is known about gamete release in deep-sea invertebrates. The echinoderm *Allocentrotus fragilis* which lives at 90 to 840 m depth has a distinct breeding cycle; its gonads increase in size until about September or October, and spawning takes place between January and April although ambient temperatures vary only 2° C (GIESE, 1959).

Once marine invertebrates have reached the prespawning condition, the stimulus required for initiating gamete release tends to decrease with time both in regard to intensity and specificity. At later stages a variety of environmental stimuli may induce spawning, including changes in temperature, light, salinity, dissolved gases, water movement and pressure, as well as vibrations, handling, electrical shock and various chemicals. In some sea-stars spawning could be induced by radial nerve extracts (NOUMURA and KANATANI, 1962). In species with a complex reproductive behaviour, gamete release is usually more stimulus specific.

Embryonic development. In the acoelous turbellarian *Archaphanostoma agile* the duration of embryonic development was studied as a function of temperature by APELT (1969). In North Sea water of about 32‰ S embryonic development is completed in 15 (12–26) days at 3° to 4° C, in 8 (7–13) days at 5° to 6° C, in 5·5 (4–8) days at 8° to 9° C and in 3 days (2–4) days at 16° to 18° C. While percentages of successful hatchings amount to 91% or more at temperatures above 5° C, they drop to 80% at 3° to 4° C.

In the scallop *Aequipecten irradians* the lowest temperatures for early cleavages of fertilized eggs lie between 15° and 20° C (SASTRY, 1966). In a number of marine invertebrates, RUNNSTRÖM (1936) determined the critical temperatures for egg development. An example for temperatures and salinities limiting marsupial

egg development in the euryplastic amphipod *Gammarus duebeni* is presented in Table 3-43. A parallel example refers to the embryonic development of the clam *Mercenaria mercenaria* (Table 3-44). In general, thermal conditions during the breeding period tend to lie within the limits for egg development and larva growth (THORSON, 1950).

After completion of their embryonic development, the larvae of the common intertidal gastropod *Nassarius obsoletus* emerge through an opening at the free

Table 3-43

Limiting conditions of temperature and salinity for complete embryonic development (fertilization of eggs to hatching of marsupium young) in the amphipod *Gammarus duebeni*. The table gives approximate average percentages of successfully completed egg developments; the estimated average egg number initially deposited into the marsupium was considered 100% in each case (Data from KINNE, 1953a)

Salinity (‰)	Temperature (° C) 8	16	20
2	87	60	0
10	90	90	65
30	85	55	0

Table 3-44

Limiting conditions of temperature and salinity for eggs of the clam *Mercenaria mercenaria* developing to the straight-hinge stage. The table gives percentages (means of duplicate cultures); the highest number of eggs developing at any combination of temperature and salinity was considered 100% in each case. Only at temperature–salinity combinations given in italics is embryonic development comparatively normal. (After DAVIS and CALABRESE, 1964; modified)

Salinity (‰)	Temperature (° C) 12·5	15·0	17·5	20·0	22·5	25·0	27·5	30·0	32·5
12·5	0	0	0	0	0	0	0	0	0
15·0	0	0	0	0	0	0	0	0	0
17·5	0	0	0	0	0	0	0	0	0
20·0	0	0	0	<1	0	5	0	0	0
22·5	<1	1	52	56	*73*	*79*	65	36	<1
27·0	0	24	*94*	*95*	*92*	*95*	*93*	*81*	39

end of the egg capsule into the sea. The relation of temperature to the time required between spawning and emergence of the veliger larvae from egg capsules has been studied by SCHELTEMA (1967) at different thermal levels (11·5°, 16·5°, 19.5°, 28° C). No larvae emerge from the capsules held at 11·5° C. Between 11° and 13° C embryos do not complete their development but a large portion remains viable for a period of up to at least 9 weeks; when returned to warmer water such embryos develop normally (SCHELTEMA, 1962a). Fig. 3-95 gives the number of

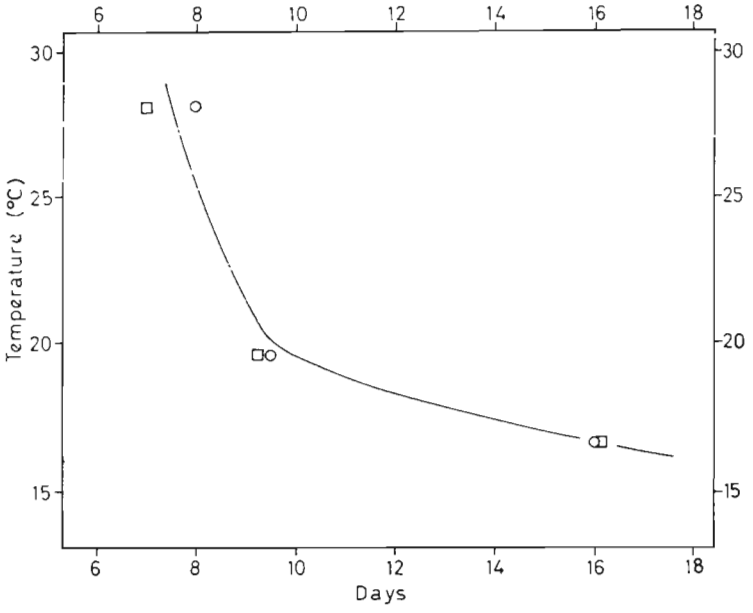


Fig. 3-95: Temperature effects on the time required between spawning and emergence of the larvae of the intertidal marine gastropod *Nassarius obsoletus* from egg capsules. 250 to 300 egg capsules were tested at each temperature in experiments with material from Cape Cod (Massachusetts, USA) (□), and about 100 in experiments with material from Beaufort (North Carolina, USA) (○). No significant differences are discernible between temperature requirements of egg capsules from the 2 geographically isolated regions. (After SCHELTEMA, 1967; modified.)

days required for the liberation of the first 50% of the larvae. The time required for emergence increases slightly between 28° and 20° C (about 0·25 day/C°), more rapidly below 20° C (2 days/C° between 20° and 16·5° C). There are no significant differences in populations from Beaufort, North Carolina, and Cape Cod, Massachusetts (USA). In sea-urchin eggs, rates of development increase 2·5 times for every 10-degree increment in temperatures between 2·5° and 25° C (PETER, 1906).

DEHNEL (1955) reports differences in developmental rate in embryos of several intertidal gastropod species collected at different geographic regions along the west coast of North America and exposed to identical temperatures. A typical example of the rate of embryonic development at different temperatures is illustrated in Fig. 3-96 which presents the duration of embryonic development in the amphipod

Gammarus duebeni kept under slowly changing temperature and light conditions simulating diurnal and annual habitat fluctuations.

In spite of the considerable ecological importance of euphausiids, very little is known about the rates of their early development. During cruises of RV *Vityaz* (USSR) in the western part of the Indian Ocean, PONOMAREVA (1969) was able to

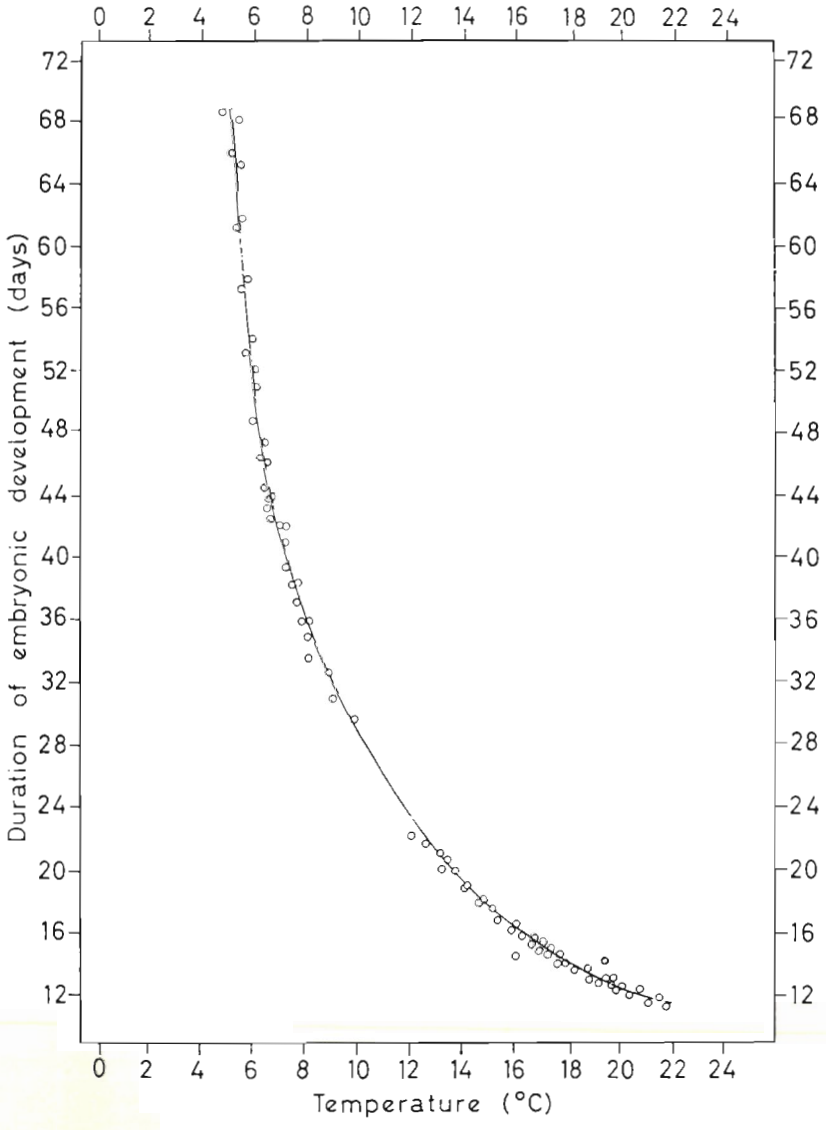


Fig. 3-96: Rate of embryonic development in the amphipod *Gammarus duebeni* as a function of ambient temperature, expressed as the number of days elapsing between oviposition (release of eggs into marsupium) and hatching (emergence of young from egg capsules into marsupium). 10‰ S. Thermal and light conditions simulated diurnal and annual temperature variations, recorded in the habitat, in smoothed patterns. Average temperatures per developmental period were calculated on the basis of diurnal fluctuations (0·5–1·0 C°) around daily 'mean' temperatures. Individual data. (After KINNE, 1953a; modified.)

establish that at water temperatures between 22° and 26° C the time between fertilization and hatching of the nauplius amounts to about 16 hrs; the metamorphosis stage lasts 2 days, the calyptopsis stage I also 2 days, and the calyptopis stage III up to 4 days.

CORKETT (1970) has adapted BĚLEHRÁDEK's equation to relate development time with temperature and thus succeeded in describing and predicting the rates of development of the planktonic copepod *Pseudocalanus minutus* from egg to adult female.

In order to ascertain the temperature effect on cleavage stages, several *Mytilus edulis* were induced to spawn at 17° to 18° C, and eggs and sperm pipetted directly from spawning trays into small dishes containing sea water of temperatures ranging between 5° and 22° C. Fertilization occurred at all temperatures; however, normal cleavage took place only between 8° and 18° C; at 5° C no cleavage occurred, and at 20° to 22° C cleavage was abnormal. The rate of cleavage was assessed by selecting 6 stages of development from fertilization to the appearance of the pro-

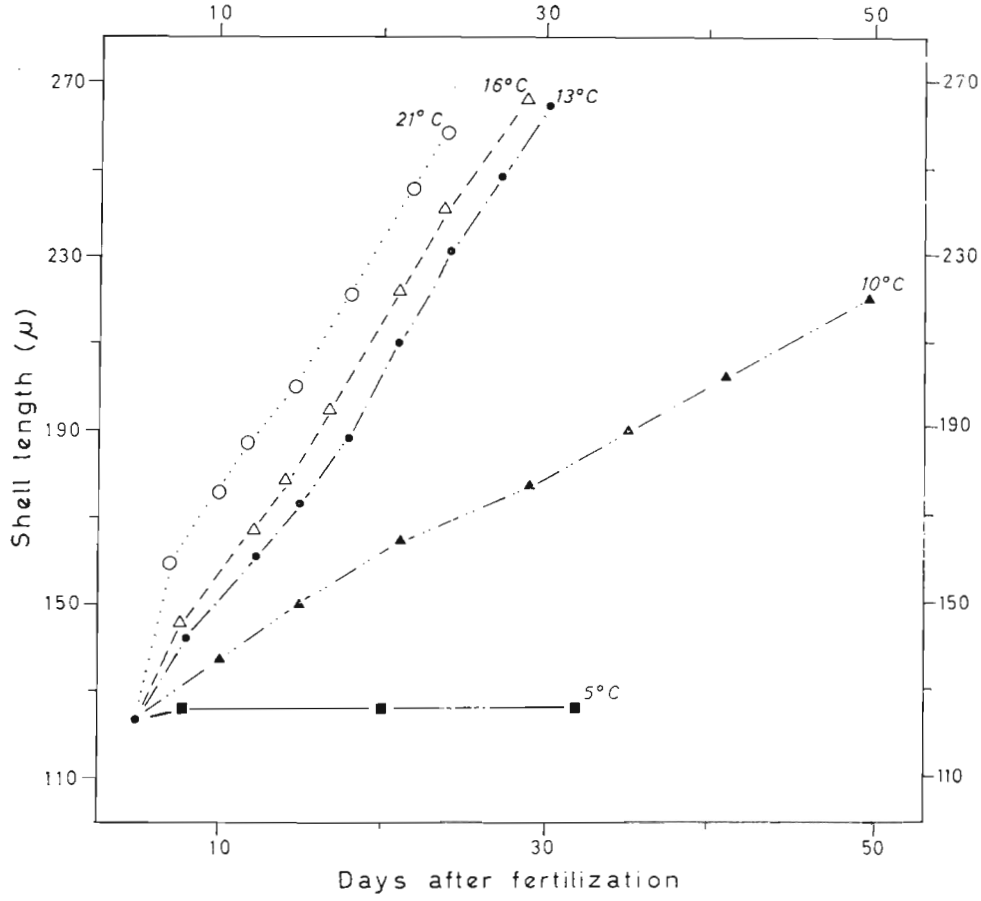


Fig. 3-97: Growth rates of larvae of the lamellibranch *Mytilus edulis* from Anglesey (North Wales) fed on 25 cells of *Isochrysis galbana*/μl, at different constant temperatures; 31‰ to 33‰ S. (After BAYNE, 1965; modified.)

dissoconch I shell and by recording the times at which 50% of the embryos reached each stage. Stages were chosen for ease of recognition rather than embryological significance. They were as follows: stage 1: appearance of first polar lobe; stage 2: macromeres surrounded by micromeres, first appearance of cilia, embryo begins to rotate slowly; stage 3: young trocophore; stage 4: young veliger; stage 5: first appearance of shell; stage 6: straight-hinge larva with the prodissoconch I shell fully developed but the prodissoconch II shell not yet secreted. Results are plotted in Fig. 3-97. The scale of the ordinate was determined by the length of time required to reach each stage at 10° C, expressed as the percentage of the total time. There is an increase in the rate of cleavage and embryo development with increased temperature; the effect of temperature increase is greatest at the lower temperature levels. The straight-line relationship at each temperature suggests that a constant proportion of the total time is spent at each stage; the same finding has been reported by WALNE (1965) in the oyster *Ostrea edulis*. On the whole, the cleavage stages of *Mytilus edulis* require a slightly narrower temperature range than the shelled larvae (BAYNE, 1965).

Modus of sexual reproduction. Temperature may also modify the modus of reproduction. Of the various examples available only one will be quoted here. The anthomedusa *Margelopsis haeckeli* produces 2 kinds of eggs: 'subitan' eggs which develop directly into polyps, and larger 'resting' eggs in which development becomes arrested about 48 hrs after the egg has been released from the gonad ('sterroblastula'). The sterroblastula separates from the manubrium of the medusa, sinks to the sea bottom, attaches itself to a solid substrate and overwinters; in the following spring, it gives rise to a small polyp. The production of subitan eggs depends on temperature, nutrition and possibly population density. At 7° to 15° C the medusae first produce numerous subitan eggs, and later resting eggs. At 15° to 20° C (especially at 17° to 20° C) subitan egg formation becomes entirely or largely suppressed (WERNER, 1955).

Asexual reproduction

Asexual reproduction (uniparental fission, budding, etc., with the result that a part of the parental body develops into a separate individual) and sexual reproduction (fusion of nuclei from different gametes into one zygote nucleus) often alternate in one and the same organism. This alternation may be affected or even controlled by temperature.

The anthomedusa *Rathkea octopunctata* reproduces asexually by forming buds on its manubrium, sexually via gametes. WERNER (1956b, 1958, 1963) was able to demonstrate that in female medusa asexual or sexual reproduction can be induced by appropriate changes in ambient temperature: below 6° to 7° C, the medusa buds asexually new medusae on its manubrium; above 6° to 7° C, it produces gametes (Fig. 3-98). Similarly, the hydrozoan polyp *Coryne tubulosa* reproduces asexually by forming new hydranths and stolons at 14° C; transfer into lower temperatures of about 2° C causes the polyps, after a latent period of 2 to 3 weeks, to produce medusae (the sexually reproducing life-cycle stage); this shifting from producing hydranths to producing medusae is entirely reversible and strictly controlled by the ambient temperature regime. Corresponding temperature effects have been

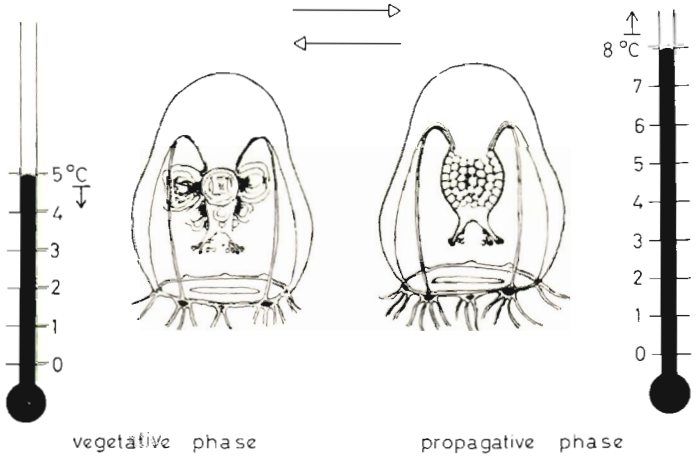


Fig. 3-98: Reversible temperature effects on the mode of reproduction in the medusa of *Rathkea octopunctata*. Below 6° to 7° C the medusa produces asexually new medusae, above 6° to 7° C gametes. (After WERNER, 1963; modified.)

observed *in situ* (southern North Sea). Further experiments revealed that the critical temperature lies near 6° to 8° C (WERNER, 1963). In additional experiments, WERNER transferred *C. tubulosa* cultures from 2° C to a higher temperature level of 6° to 8° C and observed the fate of medusa buds present at the moment of transfer; the buds exhibit 3 types of response: (i) far-developed buds continue their development at an increased rate due to the elevation in temperature: (ii) younger buds exhibit signs of growth inhibition and reduction of certain body parts (especially the umbrella); (iii) the youngest buds develop into more or less typical polyps (hydranths).

(*d*) *Distribution*

Distributions of invertebrates in the sea are the result of a multitude of environmental and organismic properties, interrelated in various ways and all subject to changes in time. Consequently, attempts to explain distributions must consider a variety of historical as well as present-day aspects. Even if such considerations are restricted to the present situation, the causes underlying distributions in the sea are presumably so complex that temperature can be expected to represent the primary controlling factor only if (i) habitats are compared with widely different thermal regimes, (ii) attention is focussed on areas with extreme or significantly changing temperatures, or (iii) organisms are considered which have rather specific temperature requirements.

The principal methods applied to investigate the effects of environmental factors on distributions of marine animals are based on the collection of sufficient data on (i) organismic abundance and hydrographic conditions relative to space and time and (ii) organismic requirements for survival, growth, metabolism, activity and reproduction. Even a geographically perfect match of organismic abundance and temperature conditions can only provide circumstantial evidence for a causal relation between distribution and temperature — evidence which can further be

strengthened by congruent organismic requirements as revealed by long-term culture experiments. Definite proof necessitates experiments *in situ*, i.e. defined changes in the usual thermal patterns with the rest of the environment remaining essentially unaltered. Such changes may occur occasionally in the sea (extreme cold or warm seasons, long-range climatic changes, change in direction of warm or cold oceanic currents, etc.); they may be simulated by transplanting parts of a given population into comparable areas with different thermal regimes, or they may be artificially created in restricted areas, small bays etc., and in the laboratory in artificial ecosystems or multispecies cultures.

The vast majority of reports claiming temperature effects on distribution of marine invertebrates is based on circumstantial evidence referring to more or less parallel patterns in organismic abundances and thermal regimes. The pertinent literature has recently been reviewed by DUNBAR (1963), KINNE (1963a) and BUNT (1967).

The importance of temperature for animal distributions was first stressed by APPELLÖF (1912) and later emphasized by ORTON (1920). Distributional patterns primarily controlled by temperature are found particularly among stenotherm forms such as polystenotherm corals and oligostenotherm polar forms. Some reef-building corals are confined to temperatures above 18° to 19° C, and reef formation takes place between the surface minimal isotherm lines (isocrymes) of 20° C (GUNTER, 1957; WELLS, 1957). The polar lamellibranch *Portlandia* (*Yoldia*) *arctica* usually lives in water below 4° C and *Pecten groenlandicus* has never been found in water above 0° C (JENSEN, 1942).

In temperate seas, distributional limits may often be determined by occasional temperature extremes occurring at intervals of several years rather than by intermediate 'normal' thermal patterns.

The most obvious effect of temperature on invertebrate distributions is exclusion of certain species from areas with unsuitable thermal regimes. However, temperature can affect distribution also by modifying rates and efficiencies of performance and hence the dynamics of interspecific coexistence. There can be hardly any doubt that temperature effects on rates and efficiencies of organismic functions may shift differentially the ecological potentials of coexisting populations and thus modify their relative distributional limits. Of special importance appear to be temperature-induced changes in functional efficiency, time to maturity, and reproduction (length of breeding period, number, survival and development of offspring).

Horizontal distributions

In regard to horizontal distributions, north–south distributions are of particular importance and often appear to be largely controlled by temperature; they are not only affected by the overall geographic temperature gradient but also by winter or summer seasonal conditions (see KINNE, 1963a for references).

An example of a temperature-dependent horizontal distribution has been provided by WERNER (1962) who examined the 2 closely related metagenic cnidarians *Rathkea octopunctata* and *Bougainvillia superciliaris*. Both species are circumpolar and widely distributed in the northern hemisphere. WERNER based his distributional study on numerous recordings on the abundance of these 2 species in the sea, hydrographic data from the areas inhabited and results of rearing

experiments conducted under a variety of controlled temperature conditions in the laboratory. In both species, the polyp is eurytherm during its vegetative phase, but stenotherm during asexual reproduction. The medusa—the sexually reproducing life-cycle stage (which, however, in the case of *Rathkea octopunctata*, is also capable of asexually budding secondary medusae)—is stenotherm in both species. The distributional areas and the seasonal appearances of polyps and medusae of *R. octopunctata* and *B. superciliaris* in the sea can be explained exclusively on the basis of local temperature conditions and the temperature requirements revealed in laboratory studies.

Another, comparable, example has been reported by BECKMAN and MENZIES (1960) who studied the thermal requirements for vital life processes in the wood-destroying isopod *Limnoria tripunctata* and found that these agree well with the known geographic range of this species. The euryplastic *L. tripunctata* feeds at temperatures ranging from approximately 10° to 30° C and reproduces between 15° and 30° C; under test conditions its greatest population increase occurs in the neighbourhood of 25° C; excessive mortality results at 30° C. Gravidity and number of young depend upon the season and do not appear to be immediately modified by favourable reproductive temperatures.

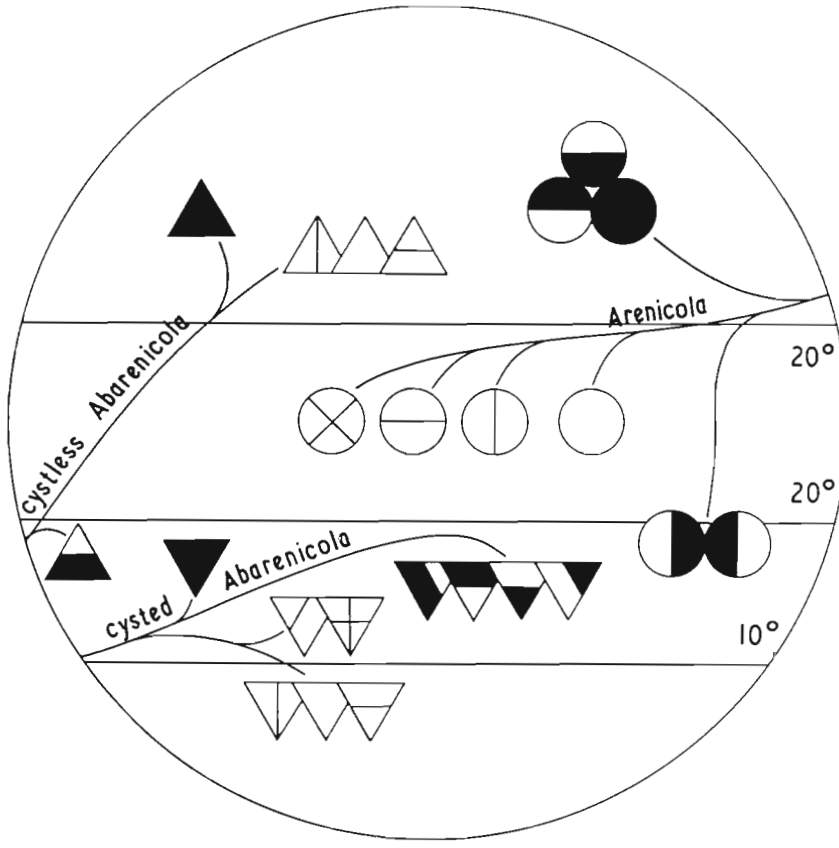


Fig. 3-99: The horizontal distribution of the polychaete family Arenicolidae. (After WELLS, 1964.)

The horizontal distribution of the 24 caudate species of the polychaete family Arenicolidae has been studied by WELLS (1964). In regard to the distribution of these species, of which *Arenicola marina* is a well-known example, the surface of the earth may be divided into 3 great zones, each with a distinct *Arenicola* fauna on its shores. The boundaries correspond roughly with the summer surface-water isotherms at 20° C, and they separate a northern cool-water, an intermediate warm-water, and a southern cool-water zone (Fig. 3-99), the latter showing a subdivision of minor importance along the 10° C isotherm. The main zones are characterized by endemic forms which seem to have evolved and differentiated within the zones. The temperature barriers must have persisted for long enough to allow a considerable degree of intrazonal evolutionary differentiation to take place. The genus *Arenicola* is represented in Fig. 3-99 as radiating from an ancestral stock in the northern cool-water zone, because *Arenicola marina*, a northern species, exhibits several characteristics that are probably primitive. The genus *Arenicola* consists of (a) *Arenicola marina* with 3 subspecies, all in the north (black or horizontal half-black circles), (b) a group of closely interrelated species, the '*cristata* group', occurring in warm water right around the earth (white circles), and (c) *Arenicola loveni* with 2 geographically separated subspecies, both found near the southern 20° C boundary line (vertical half-black circles). The cysted *Abarenicola* species are presumably more primitive than the cystless ones, and it seems likely that the genus radiated out from ancestral forms in southern cold water. The cysted forms include 3 species, with 1, 4, and 5 subspecies respectively—all restricted to southern cool water; most of them live north of the 10° C boundary line, but 3 subspecies of *Abarenicola assimilis* occur only below it. WELLS supposes that the cystless *Abarenicola* species evolved from cysted forms, probably somewhere in the south; the southern hemisphere still harbours the curious *Abarenicola pusilla*, but most of the cystless *Abarenicola* forms live in northern cold water, where 2 species are found, 1 with 3 subspecies. A more detailed map of the distributions of the various species and subspecies has been published by WELLS in 1963.

AURICH (1967) studied the horizontal distribution of the copepod *Calanus finmarchicus* in the Irminger Sea. He found *C. finmarchicus helgolandicus* restricted to northeast Atlantic waters, and *C. finmarchicus glacialis* to east Greenland waters, whereas *C. finmarchicus sensu stricto* occurred throughout the whole area in several populations differing from each other in medium body size. These differences in body size are negatively related to local water temperatures.

Since temperature affects the length of the planktonic phase—the oyster *Ostrea edulis* has, according to THORSON (1946), a planktonic larval phase of 7 days at 24° to 27° C, 13 days at 23° to 24° C, 17 days at 20° C and of at least 21 days at still lower temperatures—it may influence the distance over which the larvae are transported by oceanic currents. Species restricted to a certain geographic area by reproductive stenothermy may occupy additional space by establishing a sterile zone of distribution which is maintained by a continuous flow of individuals from the reproductive distributional centres. This has been demonstrated, for example, in the medusa *Aglantha*, the amphipod *Parathemisto* and the chaetognath *Sagitta elegans* (e.g. KINNE, 1963a).

In the Norwegian and Barents Seas, MILEIKOVSKY (1965, 1966, 1968) has studied the large-scale patterns of distribution of pelagic larvae of 16 different

taxonomic groups of bottom invertebrates. The distributions of the planktonic larvae are primarily determined by the distributional patterns of their benthic parents. Dispersion via oceanic currents modifies larval distribution only in a small proportion of the total larval population without significantly affecting the general pattern. On the basis of his data and those obtained in other seas, MILEIKOVSKY comes to the conclusion that such dependence of the distribution of pelagic larvae of shallow shelf bottom invertebrates on the distribution of their parents is typical for the world oceans.

There is a remarkable resemblance between species and genera occurring near the North and South Poles—'a bipolarity of analogous phenomena' (EKMAN, 1953, p. 251); animals of higher latitudes are more closely related taxonomically to each other than to those of lower latitudes. Examples of bipolarity are the gephyrean *Priapulus caudatus* of the northern hemisphere which is represented in the southern hemisphere by a subspecies, and the pteropods *Limacina helicina* and *Clione limacina* of the north which have related forms in the south. Bipolarity is not confined to species. The counterparts may be genera or families; higher taxonomic categories imply that the bipolarity is of an older standing. Bipolarity is presumably related to the similar temperature conditions near the poles (WIMPENNY, 1941; HESSE and co-authors, 1951; GUNTER, 1957). Associated with the phenomenon of bipolarity is the tropical submergence of cold-stenothermal invertebrates. Provided they are sufficiently eurybath, northern littoral or epipelagic forms may have a continuous distribution from high northern to high southern latitudes by living closer to the colder ocean floor in equatorial regions.

According to GUNTER (1957), it is generally accepted that oceanic life is most abundant in the colder parts of the world. Polar and temperate seas appear to have a more abundant fauna at any given time than tropical ones. However, turnover of energy and matter, and the amount of living material produced per year appears to be greater in the tropics. In tropical waters the number of species and of different organizational types is larger, but the number of individuals per species smaller than in colder waters. HESSE and co-authors (1951), for example, report 635 ascidian species from tropical waters but only 145 species from both poles; CLEVE (1900) found 34 copepod species in the Atlantic at temperatures between 20·3° and 27·5° C, 19 species between 11·4° and 19·6° C, and only 8 between 0° and 11·1° C; WIMPENNY (1941) accumulated similar information from various sources for sponges, tunicates and crustaceans; and FILATOVA (1957) showed that the bivalve-molluscan fauna of the northern seas of the USSR and the adjacent parts of the Arctic Ocean is poorer than the corresponding faunas of the North Atlantic and of the North Pacific Ocean, respectively, the ratios of the number of species being approximately 1:3:4 (a total of 119 species and 45 subspecies of bivalve molluscs are presently known in the northern seas of the USSR). According to FILATOVA, one of the characteristic features of the bivalve fauna of the northern seas is the impoverishment of systematic categories; several families are represented by one genus or species only. Apparently, numerous stenobiontic and conservative species of boreal origin cannot live under arctic sea conditions. Many invertebrate genera and families are found only in the tropics; few have no tropical representatives, and most families have the majority of their species in tropical seas (GUNTER, 1957). In East Greenland waters, phytoplankton pro-

duction lasts only a few weeks per year; very few planktotrophic larvae can complete their development in such a short period of time. Thus there are no prosobranchs in the high arctic and antarctic seas, but towards the tropics the number of prosobranch species increases considerably (THORSON, 1950).

In the open oceans, temperature gradients are less pronounced than in coastal areas. 'Nevertheless, the cold or warm currents in certain places constitute barriers as effective as if they were solid walls' (GUNTER, 1957, p. 173). Thus the Gulf Stream divides the craspedote medusae into 2 groups (STEUER, 1910), and a sudden change in its flow may amount to a catastrophe. In benthic animals, an example of the effectiveness of temperature gradients as a barrier to distribution in the open ocean has been provided by MURRAY and HJORT (1912), who studied the fauna on both sides of the Wyville Thomson Ridge. Over this 500 m deep ridge which connects the Shetland and Faroe Islands, the Gulf Stream flows into the cold Norwegian Sea. South of the ridge, bottom temperatures are higher (4° C) than north of it (−0·41° C), while above it, temperatures on both sides are quite similar. An analysis of the faunas on each side showed that only about 11% of a total of 433 species and varieties are common on both sides. In the northeast Atlantic and the northeast Pacific, temperature gradients are smaller and so are the differences in species' composition of the respective faunas.

Horizontal migrations into warmer water in winter have been reported for many invertebrate species. Pertinent cases in the Arctic have been documented by BLEGVAD (1929). Examples in the temperate regions are: the polychaete *Arenicola marina* (WERNER, 1956b), the crustaceans *Crangon crangon* (HAVINGA, 1930; BROEKEMA, 1941; TIEWS, 1954); *Neomysis integer*, *Mesopodopsis slabberi*, *Praunus flexuosus*, *Rhithropanopeus harrisii* ssp. *tridentatus*, to a lesser degree *Gammarus oceanicus*, *G. salinus*, *G. zaddachi*, *G. duebeni*, *Jaera albifrons*, *Sphaeroma hookeri* (KINNE, 1955); and various invertebrates at the northern Gulf Coast, USA (GUNTER, 1938, 1945, 1950). Distribution and relative abundance of the squid *Loligo pealei*, reported from otter trawl samplings in the mid-Atlantic Bight during late winter, suggest that this common inhabitant of the Atlantic Ocean migrates up to 200 km to come inshore during spring. Since *L. pealei* populations were found restricted to water temperatures of 8° C or higher, seasonal migrations appear to be related to temperature (SUMMERS, 1969). On the intertidal beaches of the North Sea island Sylt (Germany) numerous species of Gastrotricha (mostly of the order Macrodasyoidea) tend to occupy somewhat deeper sand layers in winter than in summer (SCHMIDT and TEUCHERT, 1969). In temperate regions, winter migrations into warmer water have often a horizontal as well as a vertical component since shallow coastal waters are more subject to critically reduced temperatures than deeper offshore areas. Cases of the opposite type of seasonal migration, that is into colder water in summer, are known from some glacial relicts in extra-arctic areas; examples are *Pontoporeia affinis* and *Mysis oculata* mod. *relicta* (SAMTER and WELTNER, 1904; THIENEMANN, 1925; SEGERSTRÅLE, 1937).

Vertical distributions

Vertical distributions of marine invertebrates may be affected by temperature in 3 ways (KINNE, 1963a): (i) by exclusion from water depths with unsuitable temperatures, (ii) by migrations to suitable thermal levels within the vertical

gradient, (iii) by passive transport, accumulation or dissipation due to hydrographical conditions (density and viscosity of the water, thermocline, water movement). Hydrographical conditions are of vital importance for the vertical distribution of passively floating planktonic forms. Although many planktonic organisms possess a remarkable capacity for keeping afloat, their suspensory structures often cannot completely compensate for the constant pull of gravity; they can retard sinking but cannot prevent it. Consequently, many individuals tend to sink gradually below the euphotic zone and may be considered lost from the reproducing population, unless before death they are returned to the lighted water by ascending water movements (SVERDRUP and co-authors, 1963). At a thermocline the rate of sinking may be sufficiently retarded to allow accumulation of planktonic organisms that would have otherwise been lost to deeper waters. A thermocline may also restrict the upward migrations of deeper forms and modify the dynamics of exchange of energy and matter between waters above and below.

Vertical temperature gradients are more pronounced in low latitudes than in higher ones, and consequently vertical distributions tend to be influenced more by the thermal regime in tropical and temperate regions than in polar waters. On the continental shelf near Cape Cod, Massachusetts (USA), vertical temperature gradients determine increasingly the distribution of boreal plankton when summer surface temperatures rise above 14° C (BIGELOW and SEARS, 1939).

There is little information available which pertains directly to temperature effects on vertical distributions of individual invertebrate organisms. On the basis of unpublished data by W. B. CLARKE and his associates, LASKER (1966) has calculated the average preference temperature for a population of *Euphausia pacifica* (off San Diego, California, USA). During daylight hours, regardless of the month, *E. pacifica* resides in 8° to 10° C water and rises rapidly into surface waters at dusk. The overall average temperature at which the bulk of the population was found during 1965 was 11·05° C.

In the deepest parts of the oceans, temperature is very low and almost constant (Chapters 1 and 3.0). Some old as well as new evidence supports the view that truly abyssal species are cosmopolitans. Comparisons between continental shelf areas, medium water depths and the greatest oceanic depths reveal a tendency of the number of species to decrease in the deep sea. Thus colder waters in general—polar regions as well as great oceanic depths—appear to be less favourable for variation and speciation (KINNE, 1963a).

The *Vitiaz* Expedition (USSR) and the *Galathea* Expedition (Denmark) found no Turbellaria, Solenogastres, Decapoda, Bryozoa or Brachiopoda at depths greater than 6000 m. Of 125 identified species 77 did not occur at depths less than 6000 m. The plankton below 6000 m contained only Calanoida, Gammaridea, Ostracoda and possibly Radiolaria (BIRSHSTEIN, 1959). The bottom fauna below 6000 m exhibits peculiarities which distinguish it as a special 'ultra-abyssal fauna' (ZENKEVITCH, 1954; ZENKEVITCH and BELIAEV, 1954) or 'hadal fauna' (BRUUN, 1956, 1957) from the abyssal fauna. A major peculiarity of the ultra-abyssal fauna is its highly individual character in each trench. Every one of 9 ultra-abyssal species of isopods, 6 species of actinians, as well as 4 out of 5 species of holothurians and 2 out of 3 species of polychaetes collected by the *Galathea* were recorded from one trench only and the oldest trenches harboured the most

highly differentiated endemic ultra-abyssal fauna (BIRSHSTEIN, 1959). The biomass of plankton in 6000 to 9000 m is 0·48 mg per 1 m^3 in the Kurile-Kamchatka trench, 0·085 mg per 1 m^3 in the Kermadec trench and about 0·01 mg per 1 m^3 in the Bougainville trench. The biomass of the benthos in depths of 9000 to 10,000 m varies from 260 to 930 mg per 1 m^2 in the Kermadec trench to 1 mg per 1 m^2 at a depth of 10,500 m in the Tonga trench, and 7 mg per 1 m^2 at about 9000 m in the Bougainville trench (see also BELIAEV, 1959; FILATOVA, 1959; MENZIES and IMBRIE, 1959; RASS, 1959; USHAKOV, 1959; VINOGRADOV, 1959; VINOGRADOVA, 1959a, b).

Distribution and composition of ecosystems

Temperature effects on distribution and composition of ecosystems have been reported by GOLIKOV and SCARLATO (1967). The bottom ecosystems (biocoenoses) in the Possjet Bay (Sea of Japan) reveal modifications in their distribution, species' composition, relative degree of complexity and stability which can be, in part, attributed to temperature. The quality and quantity of bottom organisms in the Possjet Bay depend on temperature, other environmental factors – especially the nature of the substratum—as well as on the quantity of food available, but also on the 'biocoenotic background' (conditions created by aggregations of representatives of certain species whose presence modifies the general ecological condition and creates additional niches). Average temperature intensities and temperature fluctuations are, according to GOLIKOV and SCARLATO, the most effective force in determining the dynamics of such systems. Thus biocoenoses of shallow waters and half-closed coastal areas are less resistant (degree of resistance or stability of biocoenoses: length of time of their being in a state close to climax or of their existing in an invariable state) than those in deeper, open waters, presumably because of the more pronounced climatic changes in the near shore habitats mentioned.

Widely scattered information on marine and brackish-water ecosystems seems to support this view. It appears that climatic conditions, suitable for many forms of life and rather uniform over long periods of time, are favourable for the formation of ecosystems composed of many diverse species characterized by complex nets of interrelations and high degrees of integration and stability. Conversely, areas with extreme or intensively fluctuating climatic conditions tend to contain ecosystems composed of few species, tolerant to the adverse environment and characterized by simple immediate and not well buffered interrelationships; such ecosystems often reveal pronounced short-term changes in intra- as well as interspecific population dynamics and tend toward instability. While members of 'stable' systems seem to be governed in regard to their coexistence largely by biotic factors (competition, behaviour, predator–prey and food-chain relations), the members of 'unstable' systems tend to be governed primarily by abiotic factor intensities. The first group may be considered bio-euryplastic and abiostenoplastic, the second biostenoplastic and abio-euryplastic.

Temperature-dependent chronological co-ordination and integration of life cycles of species within an ecosystem are of particular importance in species which compete for food or space or show predator–prey relations. This statement may be exemplified on the basis of results by THORSON (1946, 1950, 1955, 1958) in Danish

waters. Brittle stars of the genus *Amphiura*, for example, go annually through a period of about 2 months during which they breed and feed little or not at all; during this non-feeding period many larvae of meroplanktonic species (especially molluscs) sink down from the waters above and can settle without being eaten by the brittle stars. An additional period elapses before the larvae hatched from the predator's eggs settle on the bottom; thus larvae of prey species settling when the predator begins its non-feeding period have not only a time span without predation from the adult predator, but also a period of appeasement before the voracious newly-hatched predators settle and begin to feed. In view of the great population density of *Amphiura* at the bottom of the Danish waters studied, settling meroplanktonic prey larvae would hardly stand a chance of escaping predation outside of the non-feeding and appeasement periods. Only proper chronological co-ordination of the prey larvae's settling and the predator's breeding activities allow the prey species to replenish their stocks and many of their offspring to reach a sufficient body size fast enough that they can no longer be eaten when the predator has completed its breeding activities and begins to feed again. Similar cases of chronologically co-ordinated and integrated life cycles of marine invertebrate prey and predator species have been reported by other authors (see KINNE, 1963a) and seem to be a common feature on the sea bottom.

In view of the known effects of temperature on gamete maturation, spawning, embryonic development, length of planktonic phase and larval settling, one must expect considerable disturbances of such delicate interrelations between species of an ecosystem in case of abnormal or changing temperature conditions, since most species tested thus far reveal differences in their respective thermal responses. The scallop *Placopecten magellanicus* cannot compensate for the temperature extremes encountered in the Gulf of St. Lawrence as well as the sea-star *Asterias vulgaris*. Consequently, during periods of extreme temperatures, the scallop can no longer successfully escape by swimming away and heavy predation is, apparently, the result (DICKIE and MEDCOF, 1963).

Seasonal temperature changes may affect the species' composition of an ecosystem by causing migration (periodic appearance and disappearance of species) or formation of resting stages, such as cysts, menonts, etc. (temporary disappearance of active life-cycle stages), and temperature changes amounting to catastrophes can lead to temporary or permanent elimination of species in the area concerned.

Historical aspects

While we have restricted our brief assessment of temperature effects on invertebrate distributions largely to the present day situation, it may be in order to recall that overall decreases or increases of temperature over centuries have—according to paleozoological findings—repeatedly changed faunistic borders in vast areas of the earth, for example, during glacial and interglacial periods. The 'glacial relicts' among our recent marine invertebrate species are living proofs of such a statement.

Moreover, the well-known fact that whole faunas may differ in their horizontal distribution (warm-water fauna of the shelf, Mediterranean–Atlantic fauna, boreal fauna of the north Atlantic, temperate fauna of the north Pacific, arctic fauna) and in their vertical distribution (arctic–benthal fauna, abyssal fauna, epipelagic

fauna, bathypelagic fauna) is probably related to present as well as to historical temperature conditions (EKMAN, 1935, 1953; SVERDRUP and co-authors, 1963).

(3) Structural Responses

The differentiation between functional and structural responses of organisms is a methodical convenience rather than a division into basically different biological aspects. Functions and structures of an organism are intimately interrelated and, if moving down from the individual to the subindividual level, or if applying time-lapse techniques, proper distinction becomes increasingly difficult. It is hardly surprising therefore, that functional responses to temperature are often paralleled by structural ones.

Ever since ecologists and physiologists began to investigate organismic responses to temperature they have focussed their main attention on functional aspects, considering structural aspects to belong to the domain of morphologists. This attitude is only now beginning to change, not least because of important new information produced at the cellular and subcellular level by biochemists and molecular biologists (Chapter 3.0).

(*a*) *Size*

Many marine invertebrates attain a larger final body size in the colder parts of their distributional area than in parts with normal or supranormal temperatures. Increase in size with increasing latitude has been reported in individuals of the same species, representatives of a given genus, or higher taxonomic groups (RHUMBLER, 1911–13, MURRAY and HJORT, 1912; WIMPENNY, 1941; SVERDRUP and co-authors, 1963). Larger final sizes in colder parts of the distributional area have been reported for various taxonomic groups, for example, for protozoans (KOFOID, 1930), copepods (SVERDRUP and co-authors, 1963), amphipods (STEPHENSEN, 1929, 1940; SEGERSTRÅLE, 1950), molluscs (WEYMOUTH and THOMPSON, 1931; WEYMOUTH and co-authors, 1931; BUTLER, 1953), and fishes (Chapter 3.32). Some radiolarians exhibit increasing final sizes with water depth, a phenomenon which is presumably related to the concomitant lowering of temperature (POPOFSKY, 1908). MANN (1948) claims that giant size of invertebrates is a characteristic of antarctic seas and that a combination of large size and small body surface area is advantageous for life in cold areas. Detailed pertinent information has been published on the molluscs *Cardium corbis* and *Siliqua patula* by WEYMOUTH and his associates in 1931. However, there exists also a number of exceptions to the rule that larger final size is attained in colder parts of the distributional area: the sea-urchin *Echinus esculentus* reaches its largest size in warmer water (MOORE, 1937) and so does the gastropod *Urosalpinx cinerea* (FRASER, 1931); further examples have been presented by ODHNER (1915) and MOORE (1958).

Large final body size is indicative of slow, long-continued growth rather than of rapid growth. Most invertebrates grow more slowly if exposed to subnormal temperatures and need a longer time to reach sexual maturity than at normal or supranormal temperatures; at the same time they extend their growth phase,

prolong their life span and attain a larger final size. This is true, for example, of the chaetognath *Sagitta elegans* (RUSSELL, 1932), various amphipods (KINNE, 1953a; HYNES, 1955), the isopod *Sphaeroma hookeri* (KINNE, 1954c) and the mysid *Neomysis integer* (KINNE, 1955).

Relationships between growth, maturation, length of life and maximum size have also been demonstrated under controlled conditions in the laboratory, for example, in the amphipod *Gammarus duebeni* (KINNE, 1953a) and the hydroid *Cordylophora caspia* (KINNE, 1956b, 1958). Males of the brackish-water *Gammarus duebeni* reared in $10^0/_{00}$ salinity have an average life span of 480 days at temperatures between 18° and 20° C, of 700 days at simulated annual habitat temperature changes (from 0° C in winter to 23° C in summer), and of about 1000 days if the simulated summer habitat temperatures do not exceed 16° C; the respective average final body lengths (distance base of first antenna to base of telson with the body straightened out) are 20·8, 22·3, and 24·5 mm. In *G. duebeni*, postponement of sexual maturity is, however, not the only prerequisite for prolongation of life and attainment of a larger final size. Females born and raised in $10^0/_{00}$ S at 19° to 20° C were, immediately after attaining sexual maturity, paired with males of identical environmental history; 200 pairs were subsequently exposed to simulated annual habitat temperatures, while the rest (120 pairs) remained at higher temperatures between 19° and 20° C. In the first group, the females reached an average age of 450 days and a final body length of 15·2 mm; in the second group, the corresponding values were 275 days, and 14·7 mm (KINNE, 1953a, 1959).

Biogeographic 'size-rules' are discussed critically in Chapter 3.32.

(*b*) *External Structures*

Temperature-induced differential growth of body parts may lead to modifications in body shape and in externally visible morphological characteristics such as appendages or dermal differentiations. Although many of such characteristics have been considered to be of taxonomic importance, little has been done to assess the degree of their dependence upon environmental temperature.

Seasonal changes in body shape are documented by the phenomenon of cyclomorphosis in Cladocera (WESENBERG-LUND, 1900; OSTWALD, 1904; WOLTERECK, 1913; BROOKS, 1946, 1947, 1957; LIEDER, 1951) and Copepoda (MARGALEF, 1955). The best analyzed cases have been reported in freshwater living species of the genus *Daphnia*. In high-temperature latitudes, *Daphnia cucullata* and *D. retrocurva* exhibit remarkable structural variations of helmet, head, crest and spines, particularly if the parthogenetic young developed at high temperatures of at least 18° to 20° C. Such changes in external structures seem to represent incidental expressions of functional adjustments to seasonal changes, especially to high temperature and increased turbulence. Temperature and water movement affect relative growth presumably through an increase in metabolic rate (BROOKS, 1957; HRBÁČEK, 1959).

In several species of planktonic marine copepods differences in external structures (and body size) have been reported both in males and females. The structural alterations have been related to different environmental histories in *Calanus finmarchicus* (RUSSELL, 1928), seasonal effects in *Calanus finmarchicus* (MARSHALL,

1933), or genetic factors in *Euterpia acutifrons* (HAQ, 1965) and *Pseudocalanus minutus* (MCLAREN and co-authors, 1966).

Increase in number and size of dermal differentiations, cilia, spines, etc., as a consequence of exposure to high temperatures is known for a number of protozoans and invertebrate metazoans. It can be demonstrated by intra- as well as interspecific comparisons. In temperate seas, autumn and winter generations often have shorter spines than summer generations, and specimens from cold waters have shorter spines than individuals from warm waters. The same situation is found in fresh water, where winter forms of protozoans, rotifers and entomostracans have been shown to be less spinose than the respective summer forms (WESENBERG-LUND, 1910). It has been claimed in various papers that such structural changes in planktonic forms are related to their floating capacity compensating for the decrease in water viscosity caused by increasing temperatures.

In the Kiel Canal, north Germany, the colonial hydroids *Laomedea loveni*, *Cordylophora caspia* and *Perigonimus megas* exhibit structural modifications in colony growth, hydranth shape and tentacle number, which appear to be related to habitat temperature (KINNE, 1956c). Comparable modifications in shape of colonies and hydranths, as well as in tentacle number per hydranth and tentacle length, could be induced under laboratory conditions and clearly attributed to the thermal conditions offered in the brackish-water living *Cordylophora caspia* by

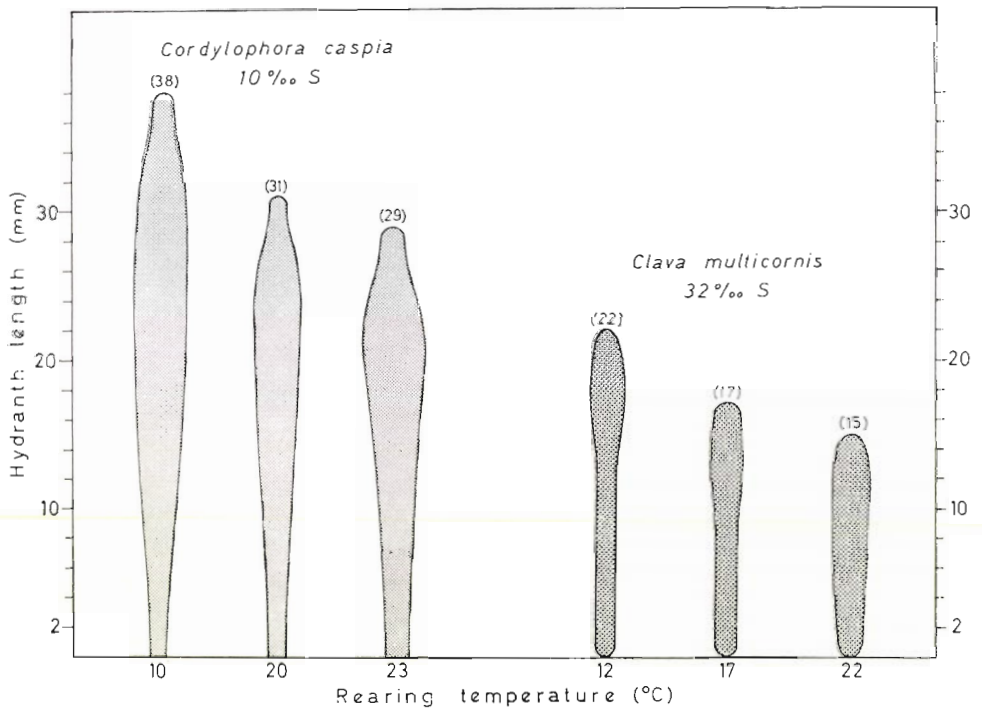


Fig. 3-100: Shapes of hydranth bodies of *Cordylophora caspia* and *Clava multicornis* (constructed on the basis of average length and width values) reared at 3 different temperature levels in each case. The average number of tentacles per hydranth is given in brackets. (Based on data by KINNE, 1957 and KINNE and PAFFENHÖFER, 1965.)

KINNE (1956b, 1957) and the marine colonial hydroid *Clava multicornis* by KINNE and PAFFENHÖFER (1965). In both species the temperature experiments have been conducted on genetically identical material: hydranths were cut off from an individual 'primary colony' and subsequently gave rise to new 'secondary colonies'. *C. caspia* was fed oligochaetes *Enchytraeus albidus*; *C. multicornis* received 4-day old larvae of the brine shrimp *Artemia salina*. Both species respond to increasingly higher temperature levels by progressively reducing their hydranth length; the corresponding changes in maximum hydranth width are less pronounced but width also tends to decrease with temperature (Fig. 3-100). Tentacle number per hydranth decreases in both species with increasing temperature. The average length of the fully extended tentacles is difficult to determine; however, it, too, appears to be influenced by thermal conditions. The described changes in body shape bring about significant alterations in the ratio of surface area to volume of the individual hydranths. Since the hydranths are the major sites of metabolic exchange between colony and environment, such alterations may conceivably affect rate and efficiency of metabolism and hence present means of compensation for thermal stress. External structures of colonies, hydranths and tentacles are also influenced significantly by salinity (Chapter 4.31).

(c) *Internal Structures*

Hardly anything is known about temperature effects on size and shape of organs, tissues, or cells in marine invertebrates. In genetically identical hydranths of the colonial hydroid *Cordylophora caspia* cell dimensions change in different combinations of temperature and salinity (Chapter 4.31), and the nuclei of hydranth cells have a larger diameter at 10° C than at 20° C in all salinities tested; the same applies to the length and width of nematocysts (KINNE, 1958). In regard to temperature effects on subcellular structures consult Chapter 3.0.

3. TEMPERATURE

3.3 ANIMALS

3.32 FISHES

J. R. Brett

(1) Introduction

Among the vertebrates, fish are the only members which can be termed obligate poikilotherms throughout their life span, although there seems to be reason to doubt this in a few specialized forms and possibly in some of the aerial excursions of lungfishes (Dipnoi). Essentially they are thermal conformers, expending no energy nor exerting any significant influence on maintaining body temperature by specialized metabolic or behavioural means. This circumstance derives from the fact of breathing in a medium with particularly high specific heat. On the basis of equal volumes, water requires over 300 times the amount of energy to raise its temperature by 1 C° than is necessary for air. The need for effective exchange of gases has resulted in an efficient heat exchanger between the blood and external environment across the respiratory surfaces.

This does not mean that no adaptive or compensative mechanisms have evolved to meet the vicissitudes of wide variations in temperature which may occur geographically, seasonally or daily. It does mean, however, that every response and every process proceeds within a thermal range dictated by the immediate environment. Hence, the rates of all reactions within the organism are environmentally dependent. This is the physical–chemical fact of life. But temperature has a far more diverse meaning when examined by way of the organism's responses. At one and the same temperature, according to the state of adaptation, a fish may survive or die, be hyperactive or benumbed into inactivity, be stimulated to migrate or be passively related, be sexually mature or remain immature. Its responses are multiple because temperature is itself a complex factor in life. It cannot be considered as a single entity despite our conditioning in thinking derived mainly from physics and chemistry, and promoted by the simplicity of measurement. To the organism temperature has a quality which, like light, is significantly different from its quantity. Recognition and elucidation of this property for fishes was provided by Fry (1947) in an examination of environmental entities in relation to how they act rather than what they are. Thus, temperature may act as a lethal agent destroying the organism, as a controlling factor setting the pace of metabolism and development, as a limiting factor restricting activity and distribution, as a masking factor interacting with other environmental entities by blocking or altering their potential expression, and finally by providing a directing agent as a gradient stimulating sensory perception and oriented response.

From a functional point of view the first consideration is a critical examination

of the evidence bearing on the possible capacity of fish to maintain an internal temperature distinct from that of the external environment. The second issue concerns the ability of the organism at all stages of development to tolerate extremes of temperature together with any mechanisms which have evolved to extend this capacity. Within the limits of tolerance a series of functional relations must next be examined which relate to (i) all metabolic demands including those of maintenance and activity, (ii) the capacity of the organism to take on adequate energy including nitrogenous compounds, and (iii) the elaboration of gonads which will suffice in the production of sufficient gametes to offset the heavy mortalities which may characterize early stages of life.

The inherent complexity of response to temperature alone and in relation to most other environmental factors, not excluding the dimension of time, accounts for much of the diversity in the literature as well as the difficulty of piecing the evidence together in revealing principles. Although this chapter attempts to provide some insight into the relation exhibited among marine and estuarine fishes, it is necessary to draw on the greater experimental evidence which has been derived in many instances for freshwater fishes. With the exception of stages in early development when ultimate control of electrolyte balance has not been achieved by the organism, and some cases of supercooling, this extension does not appear subject to serious objection in principle. Physiological aspects will be considered with a particular view to their ecological significance. Temperature is an environmental factor which, if not considered, would render a good many ecological studies devoid of meaning. Not only must it be assessed in its absolute value but also in a relative sense (degree of excitation within and between species), as well as a dynamic factor which fluctuates providing variation in range and rate of change. Among the abiotic entities of a fish's environment there is no greater contender for the position of ecological master factor than temperature.

It should be appreciated that the assessment of the state of knowledge in any one field necessitates taking inventory of the existing literature. A full inventory is virtually impossible. The basis of generalization is, therefore, drawn from a sample; the hope is that the sample is adequate and representative. Since this compilation was completed, FRY (1967) has published a review on 'Responses of vertebrate poikilotherms to temperature' which the reader should consult for additional relevant information on fish.

(2) Functional Responses

Maintenance of body temperature in homeotherms has been shown to derive mainly from metabolic heat in the muscles and liver (SMITH, 1958). In consequence it might be expected that during periods of muscular exertion, particularly in large fish which may have as much as 70% of their body weight attributed to muscle (MARSHALL, 1965), internal heating might exceed the rate of loss through respiratory and peripheral circulation (DAVIS, 1955). This possibility was the subject of early investigation by SIMPSON (1908). GUNN (1942) reviewed body temperatures in poikilothermic animals providing evidence for close conformity among fishes. This has been confirmed by HALSBAND (1953) for trout, by HIRANO and MATSUI (1955) for carp, and by SMITH and DAVIS (personal communication)

for free-swimming Pacific salmon when performing in a respirometer at the upper limits of active metabolic rate. Deep muscle temperatures did not become elevated by more than 0·02 C°; rapid equilibration (8 to 10 mins) occurred when environmental temperatures were altered by 5 C°. Exceptions to this have been recorded, notably in the case of the striped marlin *Makaira mitsukurii*, where a 6·2 C° differential was obtained when a thermo-electric tip was plunged into the deep musculature, and also for the large ocean sunfish *Mola mola* which had a temperature of 2 to 4 C° lower than the sea-surface temperature (Morrow and Mauro, 1950). These authors discuss the problem of interpretation where large fish weighing over 90 kg are brought aboard dead or nearly dead after 10 to 30 mins of struggling on a hook, or have come from cooler, subsurface water. They suggest that under normal conditions the body temperature of striped marlin does not differ greatly from that of the environment.

The methodological limitations were largely overcome by Barrett and Hester (1964) who examined muscle temperatures of 62 live yellowfin tunas *Thunnus albacores* and 31 skipjacks *Katsuwonus pelamis* within 1 min of capture or when swimming in the sea while hooked. Convincing evidence is provided for body temperatures of the 2 species respectively averaging 3·5 and 8·0 C° higher than a sea-surface temperature of 20° C, and 1·7 and 3·8 C° higher at 30° C (see Zharov, 1965). If such elevated temperatures are possible, remarkably enough placing some members of the fishes in the category of heterotherms, what mechanism could account for the maintenance of elevated body temperatures? If considerable oxygen debt can be tolerated by the muscles during high activity, thermal difference could result from the lag in adequate circulation producing a temporary gradient. However, the fact that a greater differential exists for both species at lower environmental temperatures suggests the possibility of an actual controlling mechanism. The only way to retain heat prior to rapid loss at the gill or epidermal surfaces would be by a closely associated countercurrent arrangement of arterial and venous vessels before entering the cardinal vein prior to the gills. A suggestion of this possibility is present in the anatomical studies of scombroid fish by Kishinouye (1923). Still further indication of possible control was provided by the work of Walters (1961, 1962) who reported on the presence of specialized cutaneous vascularization in tunas and skipjacks in the posterior body surface. This author hypothesized that either or both thermal control and reduced surface viscosity have resulted in the evolution of a cutaneous heat exchanger. Final confirmation for the existence of heterothermy in 2 species of tuna has come from observations by Carey and Teal (1966) who recorded elevated temperatures of 10 to 12 C° in the deep lateral muscles behind the pectoral fin, diminishing externally and posteriorly. A thermal barrier is produced by a highly developed countercurrent vascular system in the muscle, trapping metabolic heat. Carey and Teal (1969a, b) have further confirmed the presence of circulatory heat traps in the body musculature of other adult tunas, as well as in mako and porbeagle sharks. No evidence for heterothermy in other areas of the body has been obtained. The age and size at which elevated temperatures can be maintained has yet to be determined.

Despite this fascinating development, which may be found to occur in yet other large fast-swimming fishes, it can only be treated as a significant exception. The

consideration of temperature relations in fishes can proceed on the basis that external and internal temperatures are approximately identical.

(*a*) *Tolerance*

Natural occurrence of death. Mass mortalities of fish in the sea are not infrequently observed but the causal relations may be obscure. BRONGERSMA-SANDERS (1957) has reviewed many such cases citing instances of death from volcanic eruptions (poisonous gases, ash), seaquakes (shock, H_2S), waterbloom (oxygen lack, toxic release), severe storms (damage, stranding) and sudden changes in salinity and temperature. The consequences of drift, flotation, decomposition and secondary infection can often erase any possibility of diagnosis. Also the opportunity of obtaining such records is handicapped by the sinking of dead fish. SCHWARTZ (1964) observed the lethal effect of severe winter conditions in Maryland (USA) on 15 species of captive marine fish. Although some surfaced during the final phases of death, almost all sank to the bottom. Nevertheless, death from extreme temperature has been well documented, particularly from sudden cold spells in subtropical areas or prolonged periods of abnormally low temperatures in more temperate zones (STOREY, 1937; GUNTER, 1947; GUNTER and HILDEBRAND, 1951; WELLS and co-authors, 1961). An instance of massive cold death is that recorded by GALLOWAY (1941) when no less than 55 species were identified blown on shore in the cold winter of 1939–1940 along the southern tip of Florida, USA. The universality of these cases may be judged by the detailed records cited by BRONGERSMA-SANDERS (1957) which include the Baltic Sea, North Sea, the Black Sea, the Sea of Azov, Bellingshausen Sea (Antarctic), and coastal areas of the Atlantic including the southern tip of Africa as well as around the Bermuda Islands. In addition to this extensive documentation, the subject has been considered in reviews by GUNTER (1957), KINNE (1963a), and specifically by TEMPLEMAN (1965) for the Newfoundland area (N.E. Atlantic).

An interesting case was that predicted in the North Sea during the severe winter of 1962–1963 based on previous observations during comparable winters of 1929 and 1947 (WOODHEAD, 1964). A prolonged cold spell brought surface temperatures down to 0·6° C, with a peak mortality in mid-March. On this occasion 16 species were involved, many brought up in trawl nets including sole *Solea solea*, dab *Limanda limanda*, plaice *Pleuronectes platessa*, and whiting *Gadus merlangus*. To these may be added the mass deaths among redfish *Sebastes marinus* and cod *Gadus morhua* when temperatures of $-1°$ C were recorded to depths of 100 m in fjords of West Greenland (HORSTED and SMIDT, 1965).

Fewer cases have been reported for death from high temperatures, which appear to occur more frequently among freshwater fish than marine species (for instance, HUNTSMAN, 1946; BAILEY, 1955; GRAHAM, 1956), although this may relate to greater ease of observation. In unusual years the Pacific equatorial countercurrent sweeps far south along the coast of Peru. Wholesale destruction of organisms from plankton to fish occurs; this mortality is, however, involved with the appearance of noxious 'red water' (BRONGERSMA-SANDERS, 1957).

Two cases of mass death from warming have been reported during the larval stage. That for frigate mackerel *Auxis* sp., in the Hawaiian Islands, appears to

have occurred when the larvae were carried by currents through an area of marked thermal discontinuity, with surface temperatures ranging from 25·8° to 26·7° C (STRASBURG, 1959). Dead larvae of yellowtail flounder *Limanda ferruginea* and whiting *Merluccius bilinearis* were obtained by COLTON (1959) when sampling in the area of Georges Bank off the east American coast where an intrusion of Gulf Stream water had elevated surface temperatures from 8° to 20° C. Only boreal forms had succumbed whereas subtropical and tropical species had not. The extreme fluctuations in year–class strength of such fish as haddock, cod and hake are considered by COLTON (1959) to arise in some instances from an overly rapid temperature change. Unfortunately the chances of documenting natural mortalities during early stages of development are indeed slim. LASKER (1965) has commented that temperature may at times be one of the most decisive factors which govern year–class strength but the biological phenomena which affect the survival of larval fish are most complex, as studies on the biology at this stage in the life history reveal.

Historical development. Relatively critical studies of temperature tolerance in fishes date back to the last century (DAVENPORT and CASTLE, 1895; MAUREL and LAGRIFFE, 1899). However, the early method of determining the lethal end-point by slow heating or cooling (HUNTSMAN and SPARKS, 1924) was supplanted by the more precise method of immediate transfer to a series of preset temperatures from which the percentage mortality and rates of dying could be obtained (LOEB and WASTENEYS, 1912; HATHAWAY, 1927; SUMNER and DOUDOROFF, 1938). These experiments demonstrated the significant effect of the past history of the fish, in particular the acclimation temperature[1] (FRY and co-authors, 1942), or the influence of variation in environmental temperature (seasonal acclimatization) determined from field collections (BRETT, 1944; KEIZ, 1953; MIZUOKA, 1962; HEATH, 1967). Appreciation of this phenomenon resulted in efforts to explore systematically the relation between acclimation temperature, upper and lower lethal temperature, and exposure time (FRY and co-authors, 1946; BRETT, 1952; HART, 1952). The results led FRY (1947, 1964) to define a zone of thermal tolerance bounded by upper and lower lethal temperatures within which fish could be expected to survive the primary effects of extreme temperatures (biokinetic range). Outside this zone death was inevitable, being a function of temperature × time (thermal resistance). Thus, temperature tolerance was progressively extended in concept from a single end-point to a linear sequence of responses, and thence to an area of tolerance. Although referable to subsequent sections throughout much of the text, it should be recognized here that extensive research on a variety of animals including fish had led PRECHT and associates (PRECHT and co-authors, 1955; PRECHT, 1964, 1967) to investigate capacity adaptation (within the normal temperature range) and resistance adaptation (extremes of temperature) in regard to the types of response and homeostatic mechanisms involved. These works provide a broad perspective to the phenomena of organismic, systemic, and cellular response.

The frequent involvement of temperature response with other environmental

[1] Applied to temperatures imposed in the laboratory, usually at fixed levels; a relatively rapid, non-genetic, reversible response considered as 'resistance adaptation' by PRECHT (1958).

factors, particularly natural variations in salinity and oxygen concentration, has led to exploring the response surfaces of tri-axial configurations, and can be extended mathematically to greater multidimensional series (ALDERDICE, 1963). Increasing complexity has proceeded in an ever-expanding array from the original simple approach. Tabulation of multiple responses resulting from multifactorial experiments on fish characterizes some of the recent literature, particularly for developmental stages, which includes defining isopleths with temperature tolerance as one variable (FORRESTER and ALDERDICE, 1966). The need for such involved systems of research is predicated on the justifiable premise that normal environments are both complex and dynamic. The approach also permits an evaluation of interaction effects (Chapter 12).

While response systems may be accurately defined with appropriate statistical limits the problem of interpretation can only proceed in the light of a clear understanding of the contributing elements. Just as the organism must be dissected and studied in all its parts or 'elements', so the immediate problem posed by temperature change alone must remain a central theme of inquiry in its unique but multiple role.

Modifying factors. Temperature tolerance is genetically controlled. Systematic differences between species of known history have demonstrated that the lethal temperature may be used as a taxonomic tool (FRY, 1957b). At any one state of acclimation phenotypic expression is subject to modification (frequently reversible) by a number of variables which include salinity, photoperiod, endocrine activity, season, diet and size. Studies on some of these factors have been prompted from speculation as to the cause of death (BĚLEHRÁDEK, 1935, 1957; HEILBRUNN, 1952). Various types of adaptive responses are recognized but difficulty in clarifying the underlying mechanisms remains (PRECHT, 1958).

Salinity. For larval and postlarval stages of some fish a fairly wide range of salinities may have little effect on temperature tolerance. BLAXTER (1960) has shown that herring larvae in sea water could withstand temperatures ranging from $-1{\cdot}8°$ to 24° C. Although this range tended to be narrowed by unfavourable salinities these lay beyond a tolerable range of 5 to $36^0/_{00}$ (BLAXTER and HOLLIDAY, 1963). Experiments by BRAWN (1960) also indicated that adverse effects of temperature on Atlantic herring would be minimal at levels above $5^0/_{00}$ S. Larval Atlantic menhaden *Brevoortia tyrannus* could not tolerate fresh water but showed high survival at a temperature of 4 C° and above when exposed to salinities from 5 to $30^0/_{00}$ (LEWIS, 1966). SCHLIEPER and co-authors (1952) have demonstrated a significant effect of certain cations (Mg^{2+}, Ca^{2+}) on temperature tolerance in freshwater fishes. However, for the freshwater cyprinodont *Lebistes reticulatus*, ARAI and co-authors (1963) found only a 0.2 C° difference in upper temperature tolerance for an exposure time of 72 hrs when tested in fresh water and 25% sea water; somewhat greater differences were obtained when exposed to rapidly lethal temperatures of 36° to 38° C. Adaptation of fingerling sockeye salmon *Oncorhynchus nerka* to salt water reduces their heat tolerance by 1 C° (BRETT, unpublished). Salinities of 21 to $37^0/_{00}$ had no measurable influence on the lethal temperature of 3 species of cottids studied by MORRIS (1960). Above this range some reduction

occurred except in the case of *Leptocottus armatus* which remained unaffected as high as 60‰ S. The temperature resistance times of plaice *Pleuronectes platessa* and flounder *P. flesus* were determined by WAEDE (1954) at salinities of 30, 15, and 7·5‰. No significant change occurred in the response of the flounder; a reduction of approximately 0·5 C° was manifested by the plaice. Tolerance to salinity change is considered by GORDON (1964) to be greater at low than high temperatures, although the interaction is such that an optimum range for each species could be expected. The estuarine striped bass *Roccus saxatilis* can stand abrupt transfer from salt water to fresh water over a range of 7° to 27° C as an adult but is more restricted in the juvenile stage (TAGATZ, 1961; TALBOT, 1966). An optimum resistance to high temperature (3-hr exposure) occurred at 12 to 14‰ S among 10 species of salt- and freshwater-marsh fishes studied by STRAWN and DUNN (1967). Except in one case extreme differences in tolerance did not exceed 1 C°.

This relative stability is not displayed in the embryonic stage. Mortalities, abnormalities and unsuccessful hatch may be induced at otherwise tolerable temperatures when salinity is altered from an optimum range, usually in the region of 28 to 36‰ (SENO and co-authors, 1926; FORRESTER and ALDERDICE, 1966).

Endocrine influence. The relation of thyroid activity to temperature tolerance in teleosts is stated by CHEVERIE and LYNN (1963) to be variable and confused, with both increased and decreased tolerance of 1 to 2 C° reported. DODD and DENT (1963) repeated the work of FORTUNE (1958) and could not confirm the large increase of 10 C° supposedly induced by hypofunction. HOAR (1965) has reviewed research on the effect of photoperiod, season, thyroid hormone and gonadectomy in goldfish *Carassius auratus* with significant effects reported for all but gonadectomy although male fish were more resistant to cold than female fish. A winter reduction in tolerance of from 2 to 4 C°, depending on acclimation test temperature, was reported by TYLER (1966) for red bellied dace *Chrosomus eos*. Seasonal changes in association with corresponding photoperiod change appear to be adaptive in their relation to sharp temperature changes in spring and autumn. PRECHT (1958) reports that hormones can influence heat resistance and heat adaptation (see THIEDE, 1965).

Although such circumstances have unquestionable biological significance it would appear that none of these factors matches the extensive effect of acclimation temperature on resistance; they may indeed be looked upon as changes which promote the seasonal response to temperature by facilitating acclimatization.

Size. Lack of any influence of size has been reported in the majority of experimental studies particularly where upper lethal temperatures have been determined (TSUKADA, 1960b; TIMET, 1963; LEWIS, 1965). However, BRAWN (1960) noted larger herring dying more quickly than smaller ones and SPAAS (1960) obtained a significant increase in the upper lethal temperatures of 3 species of Salmonidae. BRETT (1952) reported a greater susceptibility to extremes of low temperature among the smaller members of juvenile Pacific salmon (*Oncorhynchus*), but not for high temperature tolerance.

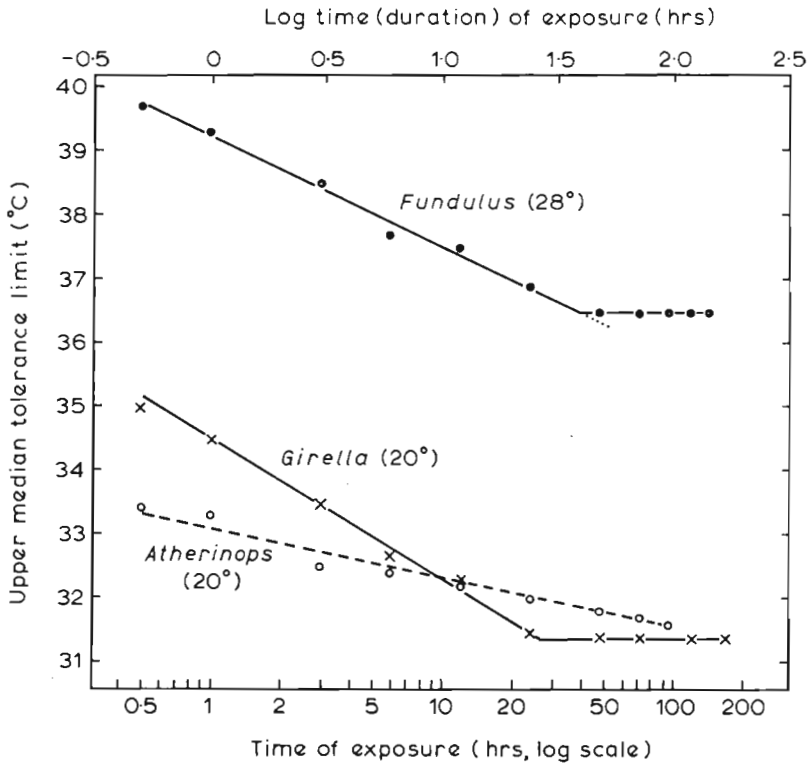


Fig. 3-101: Time-temperature curves for heat resistance of 3 species of marine fish acclimated to temperatures of 20° and 28° C as indicated. (After DOUDOROFF, 1945.)

Time. The duration of exposure to any potentially lethal temperature (Fig. 3-101) has been shown to be highly significant in all cases studied (DOUDOROFF, 1942, 1945; FRY, 1947; HART, 1952; ORR, 1955). An example may be cited from FRY and co-authors (1946) for the speckled trout *Salvelinus fontinalis*. When acclimated to 3° C a test time of 12 hrs was sufficient to establish the upper lethal temperature where continued exposure produced no significant change in response. At an acclimation temperature of 24° C the necessary exposure time was extended to nearly 100 hrs. These responses apply to death from temperature as a primary cause. Prolonged stress from high temperature accompanied by adverse growth relations can result in death from secondary causes (COCKING, 1959).

The major known factors modifying temperature tolerance have been treated briefly. Somewhat greater consideration has been given to salinity effect because of its biologically complex interrelation with temperature and the large variation in this factor, from estuary to offshore concentrations. The necessity for documenting these pertinent aspects when conducting temperature-tolerance experiments or recording natural occurrences of mortality is abundantly clear.

Lethal limits. Many records on the upper and lower lethal temperatures of fish have been reported. ALTMAN and DITTMER (1966) include 434 cases in their compila-

tion for *Biological Handbooks*, derived from 47 references. With improved understanding of the modifying factors, and the established need for a critical approach, minimum standards for acceptable values have been set. Although not exhaustive, the survey of records on 46 marine and estuarine fishes (Table 3-46) serves to illustrate the limits of tolerance in relation to acclimation or field temperature, geographical location and habitat. Only results for direct exposure to fixed temperatures are included. Those cases involving slow heating or cooling have been omitted (for example, 20 tropical reef fishes tested by TAMURA, 1944). The case for using this latter method has been made by TSUKUDA and OHSAWA (1958) and TSUKUDA (1960a). When detailed studies are conducted on the rate of temperature change in relation to the level causing distress a variety of physiological responses can be investigated with profit. However, this approach does not permit comparison with much of the existing literature. As an example GIBSON (1954), working with *Lebistes reticulatus*, obtained a median lethal level 7 to 8 C° lower than that for heat coma as recorded for the same species by TSUKUDA (1960b). Similar differences occurred between the 'critical thermal maximum' (heating at 0.5 C°/min) and the lethal temperatures for 3 species of shallow-water marine fish (HEATH, 1967).

These latter records were not available at the time of compiling Table 3-46. They lend supporting evidence for the upper lethals plotted in Fig. 3-103, and should be consulted for their ecological significance in demonstrating genetic adaptation to living in the extremely high temperatures of subtropical inshore waters where diurnal fluctuations in temperature may exceed the lethal level. In addition the study on temperature resistance of marsh fishes at various salinities (STRAWN and DUNN, 1967) is a contribution of significance which was not included.

Because of the significance of exposure time in determining the lethal level, a correction (Table 3-45) has been applied to all cases involving a test time of less than 72 hrs, since temperatures which permit continued survival have most ecological significance. The correction is at best a limited one. It was derived from the resistance times recorded for 11 species of fish at various levels of acclimation by DOUDOROFF (1945), BRETT (1952), BRETT and ALDERDICE (1958), and HOFF

Table 3-45

Values for adjusting lethal temperatures to a 72-hr exposure time. See text for basis of compilation (Original)

Test time used (hrs)	Adjustment	
	Upper lethal (° C)	Lower lethal (° C)
3	−1·3	+1·0
6	−0·9	+0·8
12	−0·74	+0·6
24	−0·41	+0·25
48	−0·15	+0·08

A. Upper and lower lethal temperatures of post-embryonic stages of marine and est
adjusted to a minimum exposure time of 72 hrs according to Table 3-45. Notati
remarks'). Salinities have been bracketed whenever not specified; frequently re
B. Tolerance limits for embryos arranged as in (A) with similar notation, Columns or
hatch at the upper and lower limits. (Original)

A. (post-embryonic).

Species	Family	Habitat (Place collected)	Latitude collected (Normal range)	Size range	Age or stage	S
				(cm/gm)	(years)	
Tilapia mossambica	Cichlidae	FW* to estuarine (India)	13° N (0–35°)	7·5–10·5 cm	—	
Cyprinodon dearboni	Cyprinodontidae	Littoral (Caribbean Islands)	18° N	1·0–5·0 cm	0–2	
Poecilia sphenops	Poeciliidae	,, ,,	18° N	1·0–10·0 cm	0–2	
Rivulus marmoratus	Cyprinodontidae	,, ,,	18° N (13–30°)	1·0–7·0 cm	0–2	
Kuhlia sandricensis	Kuhliidae	Tidepools (Hawaii)	20° N	3·0–7·0 cm	0–2	
Tilapia mossambica	Cichlidae	FW to estuarine (Transvaal, Africa)	25° S (0–35°)	8·0–12·0 cm 10·0–17·0 gm	0·3–0·5	
Atherinops affinis	Atherinidae	Littoral–open coast (California, USA)	33° N (32–42°)	6·0–6·2 cm	—	
Fundulus parvipinnis	Cyprinodontidae	Littoral and estuarine (California, USA)	33° N (32–36°)	6–7 cm	Adult	
Gillichthys mirabilis	Gobiidae	Littoral (California, USA)	33° N (30–46°)	10·0–11·0 cm	—	
Girella nigricans	Kyphosidae	Littoral (California, USA)	32° N (28–37°)	7·1–8·0 cm	Immat.	
Brevoortia tyrannus	Clupeidae	Estuarine and pelagic (N. Carolina, USA)	36° N (28–47°)	1·7–3·4 cm	Larva	
Engraulis japonicus	Engraulidae	Pelagic (Japan)	37° N (30–46°)	6–14 cm	—	
Sardinops melanosticta	Clupeidae	Pelagic (Japan)	37° N (31–46°)	12–15 cm	—	
Menidia menidia	Atherinidae	Benthic (New Jersey, USA)	40° N	4·3–5·2 gm	—	
Pseudopleuronectes americanus	Pleuronectidae	Benthic (New Jersey, USA)	40° N (25–55°)	10·3–14·9 gm 6·0–7·1 gm†	—	
Spheroides maculatus	Tetraodontidae	Benthic (New Jersey, USA)	40° N (25–45°)	—	—	
Apeltes quadracus	Gasterosteidae	Estuarine (Maryland, USA)	42° N (36–45°)	2·1–2·9 cm 2·1–4·7 cm	— —	
Gobiesox strumosus	Gobiesocidae	,,	42° N	2·9–5·3 cm	—	
Lucania parva	Cyprinodontidae	,,	42° N	1·6–3·2 cm	—	
Tautogolabrus adspersus	Labridae	Littoral (Massachusetts, USA)	42° N (41–60°)	25–70 gm 25–70 gm	— —	
Clinocottus globiceps	Cottidae	Littoral (Oregon, USA)	43° N (37–60°)	2·0–3·5 cm	—	2
Oligocottus maculosus	Cottidae	Littoral (Oregon, USA)	43° N (37–60°)	2·0–3·5 cm	—	2
Leptocottus armatus	Cottidae	Littoral (Oregon, USA)	43° N (30–60°)	2·0–3·5 cm	—	2

arranged in order of approximate latitude where collected. The lethal levels have been sterisk or other symbol refers to the last column for each species ('References and 'salt water'. Unpublished records kindly supplied by authors indicated.
re not applicable. 'Test time' represents the incubation period for 50% of optimum

imation Time	Field temp.	Test time	Upper lethal	Adjusted	Lower lethal	Adjusted	Tolerance range	References and remarks
(days)	(° C)	(hrs.)	(° C)	(° C)	(° C)	(° C)	(C°)	
30	—	33	—	—	16·0	16·2	—	KUTTY (unpublished) *fresh water. Euryhaline
—	25–40	2–3	37·0	35·7	14·0	15·0	20·7	KRISTENSEN (unpublished) *fish found in salinities ranging from 5 to 47‰
—	25–33	2–3	37·0	35·7	15·0	16·0	19·7	
—	25–35	2–3	37·0	35·7	14·0	15·0	20·7	
—	20–30	24	34·4	34·0	13·8	14·1	19·9	TESTER and TAKATA (1953)
4	23–26	83	36·9	36·9	—	—	—	ALLANSON and NOBLE (1964) *occurs in estuaries: tested in fresh water †Maximum acclimation temperature
4	23–26	83	37·9	37·9	—	—	—	
4	23–26	83	38·2	38·2	—	—	—	
60	—	24	—	—	13·5	13·8	—	DOUDOROFF (1945) maximum environmental temperature = 25° C. *24-hr lower lethal = 9·7° C. †Maximum temperatures of 30° C.
28	19–20	72*	31·7	31·7	10·4*	10·4	21·3	
21	16	24	30·5	30·1	8·8	9·1	21·0	
60	—	24	—	—	7·6	7·8	—	
60	19–21†	72	36·5	36·5	—	—	—	
30–50	19–21†	72	35·1	35·1	3·6	3·6	31·5	
60–70	19–21†	72	32·3	32·3	1·2	1·2	31·1	
30	—	72	39·3	39·3	—	—	—	SUMNER and DOUDOROFF (1938)
20–60	19–20	24	37·7	37·3	—	—	—	
7	—	24	36·5	36·1	—	—	—	
—	—*	72	31·4	31·4	13·0	13·0	18·4	DOUDOROFF (1942) *weekly average extremes of environmental temperature = 12°–25° C
—	—*	72	31·4	31·4	8·0	8·0	23·4	
—	—*	72	28·7	28·7	4·6	4·6	24·1	
0·5 +	4–8	72	—	—	3·4*	3·4	—	LEWIS (1965) *determined by graphical interpolation from published data
0·5 +	4–8	72	—	—	4·1*	4·1	—	
0·5 +	4–8	72	—	—	4·4*	4·4	—	
30·0	4–8	72	—	—	5·2*	5·2	—	
—	22	3	31·0	29·7	11·0	12·0	17·7	SUEHIRO (1951)
—	22	3	29·0	27·7	7·0	8·0	19·7	
2–5	17·5–18·5*	72	32·5	32·5	8·7	8·7	23·8	HOFF and WESTMAN (1966) *held in lab for 2–30 days †weights for lower lethal ††longer acclimation considered likely to lower the lower lethal
1	,, ,,	72	30·4	30·4	4·3	4·3	26·1	
1	,, ,,	72	25·0	25·0	2·0	2·0	23·0	
2–5	,, ,,	72	22·0	22·0	1·5	1·5	20·5	
2–5	17·5–18·5*	72	29·1	29·1	6·0	6·0	23·1	
1	,, ,,	72	27·0	27·0	1·4	1·4	25·6	
1	,, ,,	72	23·7	23·7	< 1·0	1·0	22·7	
2–5	,, ,,	72	22·0	22·0	< 1·0	1·0	21·0	
2–5	,, ,,	72	32·5	32·5	13·0	13·0	19·5	
1	,, ,,	72	31·2	31·2	10·7	10·7	20·5	
1	,, ,,	72	30·2	30·2	8·8	8·8	21·4	
2–5††	,, ,,	48	27·5	27·4	7·5††	7·6	19·8	
6–8	26–28	24	32·5†	32·1	—	—	—	KENNEDY and MIHURSKY (unpublished) *Est. = estuary †lethals given within ±0·5° C
16–18	12	24	30·5	30·1	—	—	—	
16	7	24	31·5	31·1	—	—	—	
6–7	26–30	24	37·5	37·1	—	—	—	
—	18–22	(48)*	29–30	30·0	5·0	5·0	25·0	HAUGAARD and IRVING (1943) *likely 48 hrs or more
—	1–3	—	25–26	26·0	< 0·6	0·6	25·4	
0·5–11	12–16*	14	26·0	25·3	—	—	—	MORRIS (1960) *maximum temperature = 17–18° C
0·5–11	12–16*	14	26·5	25·8	—	—	—	
0·5–11	12–16*	14	29·5	28·8	—	—	—	

Table 3-46 (*continued*)

Species	Family	Habitat (Place collected)	Latitude collected (Normal range)	Size range	Age or stage	S
				(cm/gm)	(years)	
Box salpa	Sparidae	Littoral (Rovinj, Yugoslavia)	45° N (37–45°)	—	—	
Crenilabrus ocellatus	Labridae	,,	45° N (37–45°)	—	—	
Gobius paganellus	Gobiidae	,,	45° N (37–45°)	—	—	
Mullus barbatus	Mullidae	,,	45° N (30–45°)	—	—	
Mullus surmuletus	Mullidae	,,	45° N (30–45°)	—	—	
Sargus vulgaris	Sparidae	,,	45° N (37–45°)	—	—	
Scorpaena porcus	Scorpaenidae	,,	45° N (37–45°)	—	—	
Clupea harengus	Clupeidae	Pelagic (New Brunswick, Canada)	47° N (33–60°)	10–18 cm 9–12 cm 17–30 cm	— — —	
Oncorhynchus keta	Salmonidae	Littoral–Pelagic (British Columbia, Canada)	52° N (38–66°)	3·4 cm; 0·5 gm 3·1 cm; 0·3 gm 13·9 cm; 23·5 gm	0·3 0·3 1	
Oncorhynchus nerka	Salmonidae	,, ,,	52° N (42–66°)	10·5 cm; 12·4 gm 10·7 cm; 12·9 gm	1·2 1·2	
Pleuronectes flesus	Pleuronectidae	Benthic, brackish (Kiel, Germany	55° N (30–73°)	5·0–10·0 cm	—	(
Pleuronectes platessa	Pleuronectidae	Benthic (Kiel, Germany)	55° N (35–73°)	5·0–10·0 cm	—	(
Clupea harengus	Clupeidae	Pelagic (Aberdeen, Scotland)	57° N (33–78°)	0·6–0·8 cm 0·6–0·8 cm 0·6–0·8 cm	larva* larva* larva*	
Clupea harengus	Clupeidae	,, ,,	57° N (33–78°)	0·6–0·8 cm	larva†	
Trematomus bernacchii	Nototheniidae	Benthic (McMurdo Sound, Antarctic)	78° S (60–78°)	34–177 gm	—	
Trematomus borchgrevinki	Nototheniidae	,, ,,	78° S (60–78°)	34–177 gm	—	
Trematomus hansoni	Nototheniidae	,, ,,	78° S (60–78°)	34–177 gm	—	

B. (embryonic)

Species	Family	Habitat (Place collected)	Latitude collected (Normal range)	Sali
				(‰
Atherinops affinis	Atherinidae	Littoral and estuarine (California, USA)	33° N (32–46°)	(3
Fundulus parvipinnis	Cyprinodontidae	,, ,,	33° N (32–35°)	(34
Hypsoblennius sp.	Blenniidae	Littoral (California, USA)	33° N (30–36°)	(3
Leuresthes tenuis	Atherinidae	Littoral and pelagic (California, USA)	33° N (32–38°)	(3
Cyprinodon macularius	Cyprinodontidae	Littoral, estuarine (California, USA)	33° N (30–36°)	3
Sardinops caerulea	Clupeidae	Pelagic (California, USA)	33° N (30–45°)	(3
Calotomus japonicus	Scaridae	Coastal (Japan)	37° N (27–37°)	(34
Scomber scombrus	Scombridae	Pelagic (Massachusetts, USA)	42° N (35–57°)	(3
Parophrys vetulus	Pleuronectidae	Benthic (pelagic egg) (British Columbia, Canada)	50° N (32–58°)	25
Gadus macrocephalus	Gadidae	Benthic (British Columbia, Canada)	52° N (32–66°)	26
Gadus callarias (morhua)	Gadidae	Benthic (Denmark)	56° N (55–66°)	23
Pleuronectes platessa	Pleuronectidae	,,	56° N (35–73°)	23 23
Clupea harengus	Clupeidae	Pelagic (Scotland)	57° N (50–75°)	3

nation Time	Field temp.	Test time	Upper lethal	Adjusted	Lower lethal	Adjusted	Tolerance range	References and remarks
(days)	(° C)	(hrs)	(° C)	(° C)	(° C)	(° C)	(°C)	
3–4	22–25	3	32·5*	31·2	—	—	—	TIMET (1963) *determined graphically from original data
3–4	22–25	3	32·8*	31·5	—	—	—	
3–4	22–25	3	31·8*	30·5	—	—	—	
3–4	22–25	3	32·4*	31·1	—	—	—	
3–4	22–25	3	30·7*	29·4	—	—	—	
3–4	22–25	3	32·8*	31·5	—	—	—	
3–4	22–25	3	32·5*	31·2	—	—	—	
8	—	48	19·6	19·5	—	—	—	BRAWN (1960)—June tests *October tests, fish seen swimming at − 0·3° C †Tank observations
—	9·6	48	21·2	21·1	< − 0·3*	− 0·2	21·3	
—	9·6	48	19·5	19·4	< − 1·1†	− 1·0	20·4	
21	7–9	24	—	—	− 0·4	− 0·1	—	BRETT and ALDERDICE (1958) *adjusted for salinity effect from unpublished experiments
21	7–9	24	—	—	− 0·4	− 0·1	—	
49	7–9	24	21·5*	21·1	− 0·7	− 0·5	22·0	
30	8–9	24	23·2*	22·8	—	—	—	
28	7–9	24	22·0*	21·6	− 0·7	− 0·5	22·5	
28	7–9	24	—	—	− 0·6	− 0·4	—	
(20–40)	—	48	29·0	28·9	—	—	—	WAEDE (1954) *determined graphically from original data
(20–40)	—	48	26·5*	26·4	—	—	—	
7–15	—	24	22·3	21·9	− 1·8	− 1·5	23·4	BLANTER (1960) *Spring spawned †autumn spawned
7–15	—	24	22·7	22·3	− 1·5	− 1·2	23·5	
7–15	—	24	23·5	23·1	− 0·7	− 0·4	23·5	
7–15	—	24	22·0	21·6	− 1·0	− 0·7	22·3	
7–15	—	24	22·8	22·4	− 0·5	− 0·2	22·6	
7	− 1·9 ± 0·2	70 to 170	6·0	6·0	− 2·5	− 2·5	8·5	SOMERO and DE VRIES (1967) Fish occur under ice and in ice tunnels
7	− 1·9 ± 0·2	70 to 170	6·0	6·0	< − 2·5	− 2·5	8·5	
7	− 1·9 ± 0·2	70 to 170	6·0	6·0	< − 2·5	− 2·5	8·5	

rtion ature	Field temperature	Test time	Upper lethal	Lower lethal	Tolerance range	References and remarks
)	(° C)	(hrs)	(° C)	(° C)	(C°)	
7	—	480–1200	26·8	< 12·8	14·0	HUBBS (1965) *development apparently similar in fresh water, although larvae died quicker
7	—	480–1200	28·5	16·6	11·9	
7	—	480–1200	26·8	< 12·0	14·8	
7	—	480–1200	26·8	14·8	12·0	
8	—	94–800	34	15	19·0	KINNE and KINNE (1962)
	13–22	—	21*	14*	7·0	LASKER (1964) *24 to 13° C—see AHLSTROM (1943, 1954)
	24	12–58	28·6	20·5	8·1	SENO and co-authors (1926) *abnormal hatch below 32‰
	12–18	49–207	21·0	11·0	10·0	WORLEY (1933) Optimum = 15 – 16° C
	5–7	84–288	12·5	4·5	8·0	ALDERDICE and FORRESTER (1968) *optimum salinity
	—	167–479	8·0	2·0	6·0	FORRESTER (1964a)
·7*	—	—	11–12	—	—	JOHANSEN and KROGH (1914) *fertilization temperature
4*	—	—	—	− 1 to 0	—	
	—	to (1250)	14	—	—	
	—	(1250)	—	0	—	
	—	180–960	16	2	1·40	BLAXTER (1956)

and WESTMAN (1966). In the case of larval menhaden LEWIS (1965) obtained somewhat greater differences than those applied in Table 3-45.

Maximum heat-tolerance ranges from an upper lethal temperature of 6° C for 3 species of antarctic fish (SOMERO and DE VRIES, 1967) to 39° C for the littoral goby *Gillichthys mirabilis*. Limits of cold-tolerance may occur as high as 16° C for a number of species, ranging down to – 2·5° C among the cold-hardy polar species.

These extremes of temperature tolerance are illustrated in the two provisional zones of tolerance plotted in Fig. 3-102. That for *Menidia menidia* demonstrates

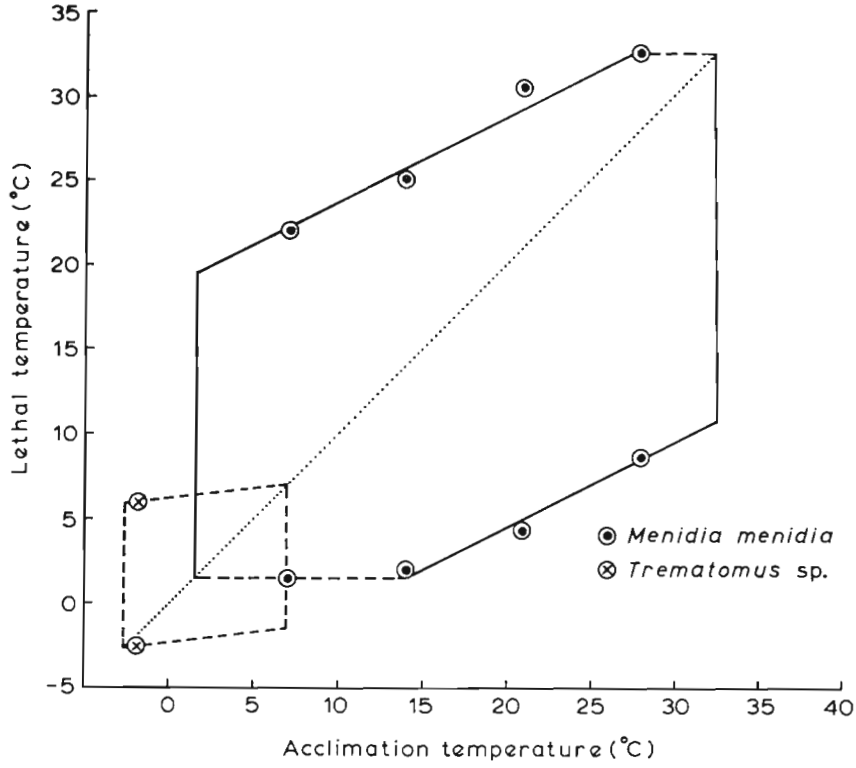


Fig. 3-102: Provisional zones of temperature tolerance illustrating extreme difference between a temperate species *Menidia menidia* from the Atlantic coast and a polar species *Trematomus* sp. from the Antarctic. Broken lines represent likely relation; dotted construction line is where lethal temperature equals acclimation temperature. (Data from HOFF and WESTMAN, 1966; and SOMERO and DEVRIES, 1967.)

the tremendous effect of acclimation temperature, already noted for some freshwater species, resulting in a maximum recorded upper lethal temperature of 32·5° C with an extrapolated possible limit of 37° C, although this latter is often not achieved due to a restricting plateau (indicated by broken heavy lines in Fig. 3-102). There is also some question regarding the lower lethal plateau which may not be accurately defined in this case because of the short acclimation times involved. However, the data represent some of the best documentations for marine species. The lethal effect of temperatures well above 0° C, for acclimation tem-

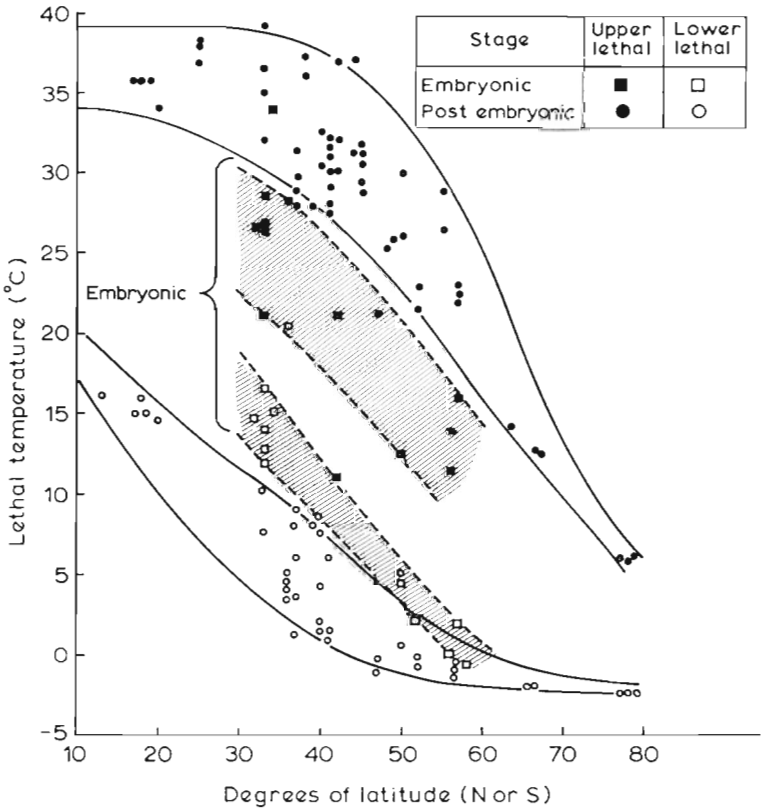


Fig. 3-103: General distribution of upper and lower lethal temperatures for embryonic and post-embryonic stages in relation to latitude. Data are included only for acclimatization temperatures within the normal range of the species tested. (From Table 3-46A and B with some records for arctic fish from SCHOLANDER and co-authors, 1953a; original.)

peratures of 15° C and above, is a phenomenon which has repeatedly attracted attention (DOUDOROFF, 1942, 1945; FRY and co-authors, 1942).

The process of acclimation, permitting increased tolerance to high temperature, is accompanied by a decreased resistance to low temperature. The upward shift frequently results in a reduction in tolerance range leaving the organism temporarily more vulnerable to cold. The calculated area for the zone of tolerance of this species is 715° C squared with an average of 675° C squared for the 3 species tested by HOFF and WESTMAN (1966). Although these represent some of the more tolerant marine species (eurythermal) nevertheless they have a tolerance rating which is less than 75% of the 23 cases cited for freshwater fish by BRETT (1956). The very confined zone of tolerance of *Trematomus* amounting to less than 100° C squared is derived from the data of SOMERO and DE VRIES (1967) and the limited acclimation which WOHLSCHLAG (1960) has found in the metabolic response of antarctic species. Although provisional, the narrow temperature tolerance (stenothermal) which characterizes species subject to very little variation in

environmental temperature is clearly demonstrated. It is highly likely that this would apply to most bathypelagic fishes.

These observations are more broadly represented in Fig. 3-103, relating upper and lower lethal temperatures to geographic distribution. Tolerance limits can only be plotted against latitude without regard for the obvious lack of close correspondence which ocean currents and seasonal changes impose on the relation between temperature and latitude. For instance HUBBS (1965) has observed that, in southern California, fish breeding in the summer tend to have more warm-tolerant eggs than the winter-spawning species. Also experiments on embryonic tolerance are frequently handicapped by mortalities under most conditions of incubation. This has led some investigators to use 50% of the optimum hatch as a survival criterion. Factors of this sort contribute a measure of uncontrolled variability. Nevertheless, the plotted data demonstrate that for the larval stage and older the range of tolerance varies from about 20° C in the tropical latitudes to 27° C in the temperate areas, narrowing to 8° C when nearest the poles. There is limited evidence that larval stages may be more sensitive than juveniles (LEWIS, 1965). The exceptionally small tolerance range of 3 to 4 C° reported by KUTHALINGHAM (1959) for 10 marine species appears to be questionable in its lower lethal limits (27° to 29° C).

Although similar information on embryonic stages is restricted to temperate and subarctic regions, they exhibit a significantly reduced tolerance span with an average ranging from 11° down to 8° C. This is corroborated by the research of PERTSEVA-OSTROUMOVA (1961) on the temperature conditions under which eggs of a variety of species of flounder (Pleuronectidae and Bothidae) survive experimentally and in nature. Off the coast of Kamchatka (USSR) the most northerly distributed species tolerated temperatures from – 2° to 6° C (for instance, *Liopsetta pinnifasciata*). In the sea of Japan such species as *Cleisthenes herzensteini* and *Limanda aspera* were killed by temperatures below 11° and above 20° C. Vulnerability during early development is consequently much greater than at later stages.

The observations on marine fish confirm the general relation established for freshwater species. Temperature tolerances of juvenile and older fish may correlate with but rarely define the limits of distribution, particularly for upper lethal temperatures which may occur 4° to 7° C above the ambient levels. The stenothermal embryonic stage, coupled with greater salinity sensitivity, undoubtedly defines distributional limits for some species and imposes demands on reproductive behaviour of the adult to release eggs in suitable thermal environments.

Acclimation relations. Acclimation temperature has been studied in regard to the magnitude of influence on heat and cold tolerance, the rate of change of thermal tolerance in nature and under imposed laboratory conditions, and the underlying mechanisms responsible for the adaptation response (FISHER, 1958). Among the first to examine the phenomenon critically in marine fishes were LOEB and WASTENEYS (1912), SUMNER and DOUDOROFF (1938) and DOUDOROFF (1942, 1945). Acclimation temperatures ranging from 12° to 28° C were shown to alter the heat and cold tolerance of the opaleye *Girella nigricans* by 4 and 9 C° respectively. No greater limits of tolerance have been obtained than those for the goldfish *Carassius auratus* (FRY and co-authors, 1942) which responds to extremes of

Table 3-47

Rates of acclimation to sudden changes in temperature measured in terms of (A) heat tolerance and (B) cold tolerance. Estimates of 90% response time have been derived from graphs or tables in references cited (Original)

Species	Temperature increased		Temperature decreased		Reference
	Temperature change (° C)	90% response (days)	Temperature change (° C)	90% response (days)	
(A) Heat tolerance					
Gillichthys mirabilis	20 to 30	1	30 to 20	> 23	Sumner and Doudoroff (1938)
Girella nigricans	14 to 26	1	26 to 14	> 25	Doudoroff (1942)
Ictalarus punctulosus	20 to 28	1	—	—	Brett (1944)
Pimephales promelas	—	—	24 to 16	14	Brett (1944)
Carassius auratus	4 to 12	16	—	—	Brett (1946)
Carassius auratus	20 to 28	3	—	—	Brett (1946)
Pleuronectes platessa	7 to 24	1	—	—	Waede (1954)
Lebistes reticulatus	18 to 23	10	23 to 18	20	Tsukuda (1960a)[a]
Lebistes reticulatus	23 to 28	20	28 to 23	13	Tsukuda (1960a)[a]
Rhinogobius similis	8 to 17	7	—	—	Mizuoka (1962)
Rhinogobius similis	17 to 24	3	—	—	Mizuoka (1962)
Tilapia mossambica	25 to 30	1	25 to 15	> 20	Allanson and Noble (1964)
(B) Cold tolerance					
Girella nigricans	14 to 26	15	26 to 14	25	Doudoroff (1942)
Rhinogobius similis	8 to 17	7	—	—	Mizuoka (1962)
Rhinogobius similis	17 to 24	3 to 7	—	—	Mizuoka (1962)

[a] Reversible heat-coma used

acclimation (1° to 38° C) by altering its upper lethal temperature by 14 C° (27° to 41° C) and lower lethal temperature by 17 C° (0° to 17° C). Observations of seasonal changes in temperature tolerance in relation to environmental temperature have been shown to amount to 7 C° for both the catfish *Ictalurus nebulosus* (BRETT, 1944) and the gobioid fish *Rhinogobius similis* (MIZUOKA, 1962).

Studies on the rate of acclimation have not received as much attention, particularly in regard to cold tolerance. Nevertheless, as the limited compilation in Table 3-47 reveals, pertinent information is available. Four responses may be followed, namely, rates of change of either heat or cold tolerance with increased temperature, and similar rates of change with decreased temperature. Ecologically the rate of acclimation of heat tolerance prior to summer heatwaves and of cold tolerance in preparation for winter chill are of greatest importance.

Before considering the significance of the results the methods of assessing the rate of change in tolerance must be examined. Three techniques have been employed: (i) the change in median temperature tolerance by applying a series of appropriately selected extreme temperatures (DOUDOROFF, 1942), (ii) the change in tolerance to a single extreme temperature which causes rapid death in unacclimated fish but little or none when fully acclimated (WAEDE, 1954; ALLANSON and NOBLE, 1964), and (iii) the change in coma produced by a steady increase or decrease in temperature (TSUKUDA, 1960a). The first method is in keeping with that most commonly used for establishing the lethal temperature; it shows almost immediate improved survival. The second indicates an initial latent period (BRETT, 1944) before a favourable response occurs; this apparent delay is probably an artifact inherent in the experimental method. The third involves two rate relations resulting in responses which are more complex than in the other two cases.

It is apparent (Table 3-47) that the rate of acclimation to increased temperature, in terms of heat tolerance, is a rapid one mostly occurring within one day except where the temperatures are low, and except in the case of the guppy *Lebistes reticulatus* (TSUKUDA, 1960a). Almost all other cases whether involving heat or cold tolerance take much longer to approach completion, amounting to 2 to 4 weeks. The general pace of the response is apparently set by the level of the new temperature and is exponentially related to time, being most rapid at the start (Fig. 3-104). This relation, however, is subject to some modification by the magnitude of the change imposed which has led TSUKUDA (1960a) to postulate an optimum acclimation rate.

The ecological significance of these rates of change in temperature tolerance is apparent in the rapidity with which fish keep pace with increasing temperatures in nature, and the lag that follows temperature depressions (BRETT, 1944, 1946). This provides for summation in heat tolerance conferring on the organism an enhanced ability to cope with rapid temperature elevations which lie within the ultimate lethal level. The likelihood of mass mortalities from this cause is correspondingly reduced. Alternatively death from sudden cold spells can occur as a direct result of inherently slow acclimation rates.

Just as the basis for death from extremes of temperature has been sought by studies on the limiting physiological systems which centre around neural, neurohormonal, electrolyte, and bound-water relations (CHRISTOPHERSEN and PRECHT, 1952; BĚLEHRÁDEK, 1957; USHAKOV, 1964; HEINICKE and HOUSTON, 1965), so

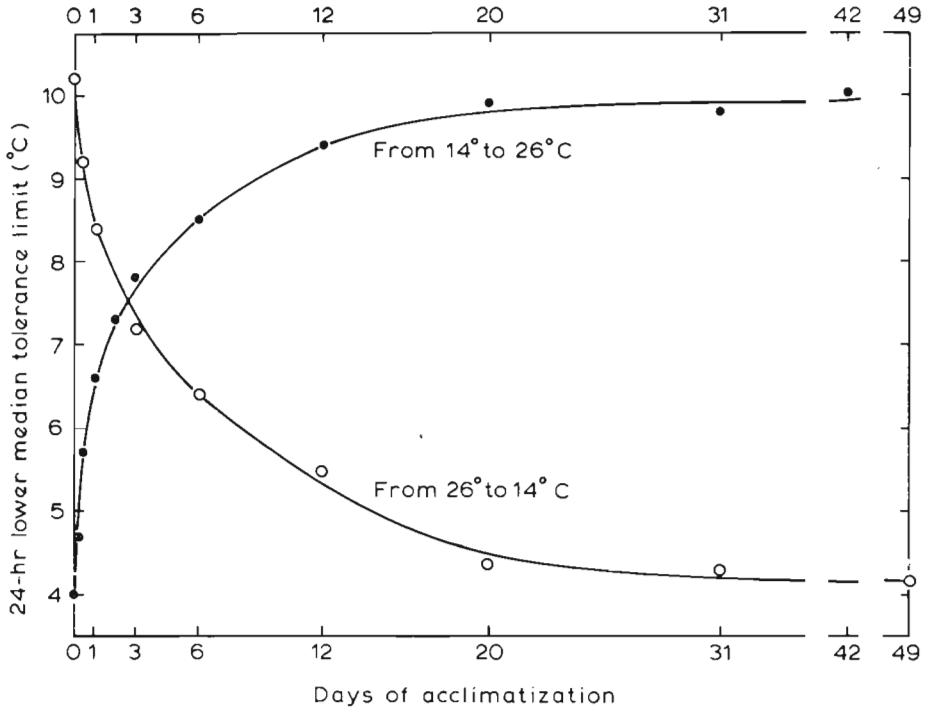


Fig. 3-104: Rate of change of cold tolerance for *Girella nigricans* when acclimated at one temperature and transferred to a higher or to a lower temperature. (After DOUDOROFF, 1942.)

the underlying mechanism for acclimation has received attention along similar lines (TSUKUDA, 1961; ROOTS and PROSSER, 1962; BASLOW and NIGRELLI, 1964; HICKMAN and co-authors, 1964; KONISHI and HICKMAN, 1964; THIEDE, 1965). The two phenomena appear to be closely related and may prove to have a common basis (BASLOW, 1967).

Acclimation rates have been considered here only in relation to induced changes in thermal tolerance. A variety of other physiological responses have been studied. For a recent account of changes in the frequency of opercular movements the experiments of PRECHT and co-authors (1966) are of particular interest.

Supercooling. Evidence concerning the ability of fish to withstand temperatures below the normal freezing point of their body fluids varies according to the species, the season, the state of acclimation, and the conditions of the experiment. The blood of most teleosts has a freezing point depression (ΔF) of $-0{\cdot}5°$ to $-0{\cdot}8°$ C, yet a variety of cold-tolerant species are known to live naturally at temperatures of $-1{\cdot}75°$ C, approximately the ΔF of sea water. This phenomenon has been investigated by SCHOLANDER and co-authors (1957), LEIVESTAD (1965), and WOODHEAD and WOODHEAD (1965). SMITH (1958, 1961) has reviewed the problem generally.

Ability to cope with such low temperatures occurs as a result of either an increased osmolarity or a capacity to live in a supercooled state. The former is

characteristic of some littoral arctic and subarctic species (for example, *Gadus ogac*, *Myoxocephalus scorpius*) which undergo a shift in plasma freezing point from $-0{\cdot}8°$ C in summer to a range of $-1{\cdot}4°$ to $-1{\cdot}6°$ C in winter (SCHOLANDER and co-authors, 1957). Protection appears to be afforded in part by a non-salt fraction involving small organic molecules of non-protein nitrogen (not urea or glycerol) in the blood of the fjord cod *Gadus ogac* acting as a biological antifreeze (GORDON and co-authors, 1962). Experiments performed by UMMINGER (1967) on *Fundulus heteroclitus* acclimated to temperatures ranging from 20° to $-1°$ C demonstrated significant increases in some serum electrolytes at low temperatures, with a dramatic increase in glucose at $-1°$ C. Deep-water species like *Boreogadus saida*, *Liparis koefoedi* and *Gymnacanthus tricuspis* manage to live in a supercooled state by almost 1 C° in the absence of any seeding agent. LEIVESTAD (1965) was able to acclimate *Cottus scorpius* to $-1{\cdot}5°$ C in the laboratory. Seeding by contact with ice caused immediate death from rapid formation of cellular crystals. The low lethal temperatures of $-2{\cdot}5°$ C for some antarctic species (Table 3-46) which inhabit ice tunnels indicate that they must be endowed with particularly high osmotic or antifreeze properties. DE VRIES and WOHLSCHLAG (1969) have discovered that glycoproteins account for a considerable proportion of the ΔF.

The ability to withstand temperatures 1 to 2 C° below zero is particularly distinctive of marine species inhabiting circumpolar regions and areas where cold arctic water like the Labrador Current flows southward into the Atlantic. It is not only a phenomenon of physiological and ecological interest but also one of commercial importance affecting the distribution and survival of such valuable species as cod *Gadus morhua* and haddock *Melanogrammus aeglefinus* (WOODHEAD and WOODHEAD, 1965). On occasion, mass mortalities of these species have been noted apparently involved with intolerance as in the case of Greenland halibut *Reinhardtius hippolossoides* or ice-seeding of supercooled fish like the pelagic capelin *Mallotus villosus* caught in the presence of surface ice crystals.

(*b*) *Metabolism and Activity*

Within the framework which defines the zone of temperature tolerance for any species, among the most important features contributing to survival and success in nature are the energetics of living, which relate to metabolism and activity, and the capacity of the organism to develop (differentiate cells) and grow (multiply cells and store reserves). The revealing observation of FRY (1947) that temperature, like a good many other environmental factors, acts through metabolism on activity directed attention to the need for a precise description of metabolic relations before any clear understanding of what governs the energetics of activity could be achieved. This was undoubtedly appreciated by WINBERG (1956) in his extensive analysis of metabolism, food requirements and growth of fishes. Metabolic relations are treated first and occupy more than two-thirds of the review.

Metabolism

Metabolism represents the sum total of energy expended by the organism for the ingestion and transformation of food, growth, maintenance of vital processes, activity, and excretion. These processes which are basically chemical in nature, but

influenced by such physical properties as viscosity and diffusion rate, are temperature dependent. Among the most significant of vital chemical reactions are the enzymatic processes which relate to oxidative metabolism. Most enzymes show an optimum temperature at which they reach maximum catalytic activity. Hence it is not uncommon to find temperature optima among the various metabolic processes. These may differ in their peaks according to the functions involved, for example, digestion, development, growth and locomotion. It appears to be a feature of the genetic complex that enzymes related to similar functions are subject to selection such that optima may shift according to the thermal habitat of the species (BULLOCK, 1955). There is also a marked diversity between species within the same general habitat. It is well known that thermal optima may occur as a result of interaction with such other environmental factors as salinity, oxygen and pH. The physiological importance of optimum temperatures for some teleosts has been discussed by SCHMEING-ENGBERDING (1953).

Basically there are four ways of measuring the metabolism of animals: (i) the heat produced (direct calorimetry), (ii) the oxygen consumed (indirect calorimetry), (iii) the utilization of body constituents, and (iv) the food consumed less the amount directed into growth, biochemical transformations and excretion. Fortuitously the oxygen requirements for obtaining equal amounts of energy from one or other of the basic fuels (fat, protein or carbohydrate) only differ by $\pm 3\%$ from their mean oxycalorific value of 4·75 calories per litre of O_2 consumed (BRODY, 1945; WINBERG, 1956). Hence the rate of utilization of body constituents may be converted directly into the equivalent rate of oxygen consumption with negligible error. This is of particular importance in studies of starving animals or where food supply is known, as in egg development.

The rate of energy expenditure in fishes has most often been measured by examining respiratory metabolism or rate of oxygen consumption which provides an instantaneous measure, as long as no oxygen debt is being accumulated. Reviews of the techniques employed and results obtained may be found in FRY (1947, 1957a, 1964) and WINBERG (1956). Certain modifications and extensions in technique for studies on juvenile or older fish have been described in the experiments of BLAZKA (1960), BEAMISH (1964a), BRETT (1964) and MUIR and co-authors (1965). Although these serve to elaborate on the diversity of metabolic rates and extend the known limits between minimum and maximum levels, the basic concepts set forth by FRY (1947, 1957a) can be usefully employed at this point.

Before proceeding, two aspects deserve comment. As was stated in the introduction, the majority of studies on temperature relations relate to freshwater fish, among which members of the Salmonidae have received a great deal of attention. Although the influence of salinity on metabolic rate has been examined in a number of cases (POTTS and PARRY, 1964; Chapter 4.32) there is still too little evidence to arrive at a set of principles which could be considered adequate to generalize on what appears to be a fairly involved temperature–salinity–metabolism phenomenon. Undoubtedly there is a complex interaction between water balance, ionic retention, tissue tolerance, irritability, osmotic work and active transport which deserves a great deal of attention at all stages of development as well as during periods of salinity change. Without better evidence and more extensive knowledge on marine fishes, which is sorely lacking, it will be assumed that the reduction in

osmotic work (and probably in active transport) which sea water provides tends to reduce the energy demand on the maintenance metabolism of marine species (WIKGREN, 1953). Fish have a blood concentration of about 9 to 12‰ which would lead one to suspect that osmotic work would be minimal in environments of comparable salinity. Recent work in our laboratory has shown that fingerling sockeye salmon at the migrating stage (smolts) show a 20 to 30% reduction in metabolic rate when passing from fresh to salt water (28‰ S). GORDON (1964) has elaborated on the 'perennial and still unresolved question of the metabolic requirements of fishes in relation to salinity.' He states that 'in the majority of cases it does appear that metabolic rate is more or less inversely related to salinity.' In the survey by WINBERG (1956) approximately 100 species are considered, only a small fraction of which are marine or estuarine. Again there is conflicting evidence as to the influence of salinity on metabolic rate; however, it would appear that the metabolic requirements of active transport tend to be reduced in the marine environment. RAO (1968) has recently reported that a 20% reduction occurs in total metabolism of rainbow trout *Salmo gairdneri* at an isosmotic salinity of 7·5‰. The cost of osmoregulation was somewhat higher at 5° C than at 15° C. (For further information concerning responses to salinity, consult Chapter 4.)

This intrusion into the realm of salinity as an environmental factor has been necessary in order to provide perspective on the relation of temperature to metabolism and activity. The discussion of the effect of temperature on metabolism of fishes must be conducted therefore without the benefit of distinguishing between marine and freshwater species. It will also be limited in most instances to a number of fishes best known to the author in an attempt to demonstrate the principles without getting involved in a great deal of literature citation. A synopsis of this sort may be found in the review of WINBERG (1956) which could be profitably updated.

The second aspect deserving comment concerns the significant but relatively limited research on metabolic rate which has been performed on the egg, embryo and larval stages of fish. LASKER (1964) obtained a linear relation between yolk absorption and temperature for the Pacific sardine *Sardinops caerulea* with a relatively high Q_{10} of 4·0 (Fig. 3-105). Further, LASKER and THEILACKER (1962) have commented that oxygen-consumption measurements of planktonic fish eggs or larvae have been confined to very few species. Records on temperature effects appear to have dealt mainly with rates of development. The microtechniques of ZEUTHEN (1943, 1950) and SCHOLANDER and co-authors (1952) using a Cartesian diver have provided delicate means of determining the respiration rate of single cells (GLICK, 1961). This technique was employed effectively by NAKANO (1953) during maturation and fertilization of the eggs of *Oryzias latipes*. Oxygen uptake of developing salmon eggs (*Salmo salar*) has been studied by HAYES and associates (HAYES and PELLUET, 1945; HAYES, 1949; HAYES and co-authors, 1953) in relation to development, growth and activity including a consideration of temperature effects. Oxygen consumption per gram of embryo was unaltered during normal development and best described in relation to temperature by the same equation for embryonic growth, namely, Temperature × Time = Constant, within viable limits.

It is important to note that activity of the salmon embryo could elevate the

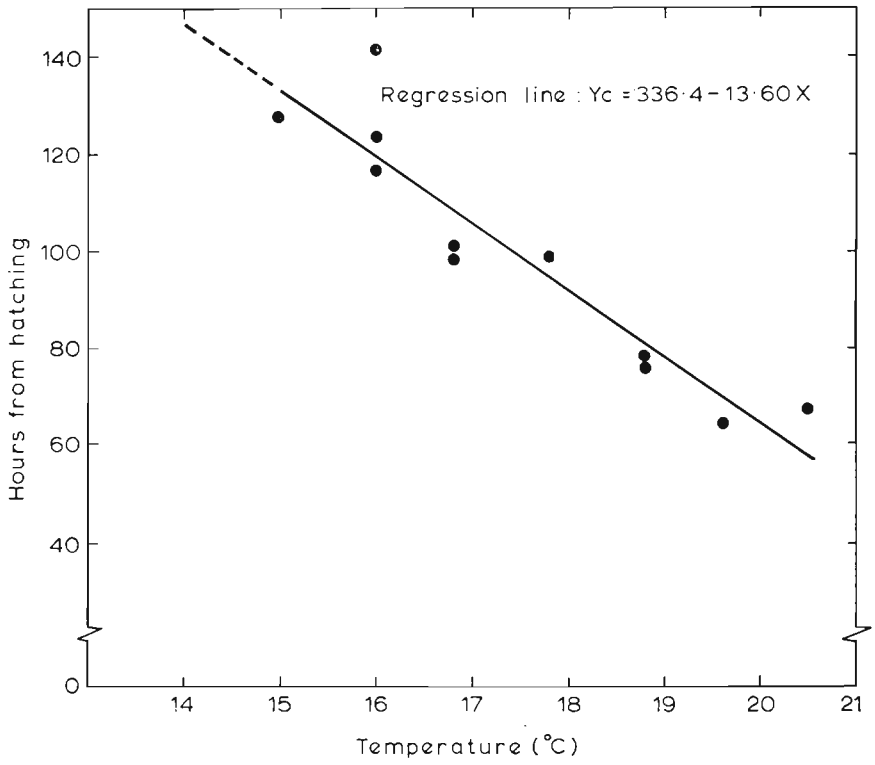


Fig. 3-105: The effect of temperature on yolk absorption of *Sardinops caerulea*. Q_{10} of yolk absorption is 4·0 for the temperature interval from 15° to 21°C (After LASKER, 1965.)

metabolic rate by a factor of three times. A doubling of the rate was recorded by HOLLIDAY and co-authors (1964) for activity of herring embryos at 8° C; in addition the metabolic rate increased as a result of elevating the temperature from 8° to 12° C providing a Q_{10} of 3·5. Different levels of spontaneous activity may be associated with various levels of temperature, consequently the need for activity meters may be extended to even this early stage. LASKER and THEILACKER (1962) observed a significant increase in metabolism of Pacific sardine eggs and larvae from various forms of activity, sufficient to mask the demands for osmoregulation, the object of their studies. Indeed these authors concluded that the energy requirement for osmoregulation was insignificant when compared to the total metabolic requirement of the larva—a relatively temperature-dependent phenomenon.

The parallel relation between metabolic rate measured by heat production (SMITH, 1957) and specific growth rate of the embryo of *Salmo irideus* adds convincing evidence that the effect of temperature on metabolic rate is quite similar to that for development except for some divergence in the late stages. SMITH (1957) has analyzed the possible mechanisms of temperature effect on the efficiency of embryonic development in relation to the distinct processes of maintenance and growth.

BLAXTER and HOLLIDAY (1963) compiled a table on the oxygen-consumption rates of clupeid larvae with associated temperatures; LINDROTH (1942) records that the metabolic rates of *Salmo salar* eggs just prior to hatching were 23 mg O_2/kg/hr at 5° C and 41 mg O_2/kg/hr at 17° C. Beyond these relatively few records there appears little to add to temperature relations and metabolism in the early stages of development. With this brief account it is possible to turn to the more extensive studies on juvenile and adult stages.

Metabolic rate. Three levels of metabolic rate have been commonly recognized for fish: (i) **standard metabolism**, representing that fraction which is necessary to maintain all vital functions, (ii) **routine metabolism** which includes the energy demands of spontaneous activity, and (iii) **active metabolism** which pertains to the maximum level at which oxygen can be consumed. The amount of energy available for external work has been termed **metabolic scope**, representing the difference between active and standard metabolism. Each of these is related to temperature in a different way, and, in turn, subject to modification by such factors as size, age, maturity, season, aggregation and starvation (ZEUTHEN, 1953; WOHLSCHLAG and JULIANO, 1959; EVANS and co-authors, 1962; SAUNDERS, 1963; BEAMISH, 1964a, b).

Standard metabolism. Because of the extremely responsive nature of metabolism to most forms of activity any measures of standard metabolic rate which do not take this into account are subject to considerable variability and uncertainty. The inclusion of activity meters or the imposing of fixed velocities in tunnel or annular respirometers has permitted better assessment of both standard and active metabolism (BEAMISH and DICKIE, 1967). As a result, a great many records of standard rates are now considered to be on the high side, bordering on routine rates. Since temperature can excite activity it was not until the careful work of BEAMISH (1964b) that seasonal influence could be separated from the confounding element of temperature-induced excitement. Nevertheless, by critically examining all the evidence on temperature effects, and aware that the metabolic levels might border on routine rates for other than sluggish fish, WINBERG (1956) concluded that KROGH'S (1916) 'normal curve' for temperature still provided the best descriptive relation. Since the generalized form of this curve had yet to be transformed into any simple mathematical expression WINBERG set up a table of multipliers based on the Q_{10} values:

Temperature interval (° C)	0–5	5–10	10–15	15–20	20–25	25–30
Q_{10}	10·9	3·5	2·9	2·5	2·3	2·2

Although metabolic rate continues to increase throughout the full range, the rate of increase diminishes. When plotted as the logarithm of standard metabolism against temperature KROGH'S curve follows a convex shape (Fig. 3-108). BARLOW (1961) obtained close correspondence to KROGH'S curve for *Gillichthys mirabilis* over the range 10° to 30° C. However, a number of exceptions occur (BRETT, 1964; WOHLSCHLAG, 1964) which points to the inescapable need to establish the species-specific response although the generalization may be accepted.

PROSSER and BROWN (1961) have considered the quantitative laws governing

the acceleration of vital processes. They also point out that the most widely used is still the Q_{10} (BĚLEHRÁDEK, 1957), but the temperature range and size must be included. Q_{10} often increases with body size. It has been convenient in reviewing temperature effects to use this simple index and the exponential presentation of Fig. 3-108. However, the critiques of MCLAREN (1963, 1964) and the mathematical analyses of KRÜGER (1961, 1964a) provide transformations which satisfy many of the temperature relations and should be consulted.

WOHLSCHLAG (1957, 1960) and WOHLSCHLAG and JULIANO (1959) using a circular, rotating respirometer chamber have performed field studies on marine and freshwater fish, widely distributed geographically. To account for the major factors, multivariable analysis was applied using the equation,

$$Y = a + b_1X_1 + b_2X_2 + b_3X_3,$$

where Y is log oxygen-consumption rate, X_1 is log weight, X_2 is velocity, X_3 is temperature, and b_1, b_2, b_3 are the partial regression coefficients. This assumes an exponential relation of metabolic rate to temperature. Lack of conformity to this relation may account for some of the variability reported by WOHLSCHLAG. A seasonal shift in Q_{10} was obtained for the bluegill *Lepomis macrochirus* whereas temperature effect on the antarctic fish *Trematomus bernacchii* under the limited conditions of its normal environment ($-2°$ to $+2°$ C) showed a slightly increasing trend up to 0° C. It is of interest to note that with respect to temperature a minimum maintenance metabolism of about 50 ± 10 mg O_2/kg/hr (weight 15 to 300 g) was obtained for this antarctic species, a rate which is in the same range for 2 species of Salmonidae estimated by BEAMISH (1964a) and BRETT (1964) for a temperature of 0° C.

WOHLSCHLAG (1964) has used multiple regression analysis extensively both for determining weight and temperature coefficients. The range of values for the weight coefficient falls within the expected range of 0·75 and 0·85 in many cases. However, the temperature coefficients show such a variety of values usually ranging from 0·02 to 0·06, but not infrequently with greater extremes, that it would appear to allow little of the generality of application which the weight coefficient has provided. MORRIS (1965) has reported temperature coefficients of 0·05 to 0·07 for *Ictalurus natalis* depending on temperature acclimation, and considered that a re-examination of KROGH's curve was desirable.

Beyond the generalization of increased molecular agitation resulting from increased temperature no one has yet been able to define just what the controlling mechanism governing the standard metabolic rate is, and hence what temperature is primarily affecting. Opinion has at times favoured certain enzymes, for example, tryptophan peroxidase-oxidase (KNOX and co-authors, 1956), cytochrome c (DRABKIN, 1950), cytochrome oxidase, succinodehydrase, or malicodehydrase (VON BERTALANFFY, 1957, 1964; SCHULTZE, 1965), and catalase (MINAMORI, 1964). For a recent discussion of the temperature relation of enzymes affecting acclimation and metabolic rates the review by HOCHACHKA and SOMERO (1969) should be consulted. It is of interest to note that thermal optima for rate reactions are affected by substrate saturation concentrations, which are seldom if ever found *in vivo*. In principle, thermal shunts may therefore occur in much the same way as is represented for growth rates in Fig. 3-109. Seasonal shifts suggest neurohormonal

involvement, with adaptive changes occurring in the central nervous system (JANKOWSKY, 1966). CHRISTOPHERSEN and PRECHT (see critique in FRY, 1958) have hypothesized that viscosity of protoplasm involving the extent of bound water is intimately related to the mobilization rate of metabolites. For the whole organism ZEUTHEN (1953) reviewed the evidence for relating rates to total nitrogen (reflecting protein content); no advantage over dry or wet weight relations was demonstrated. Similar results were obtained for sockeye salmon (BRETT, 1964). The problem remains one of great interest and importance to environmental ecologists.

Active metabolism. The maximum levels of metabolic rate have not received as much attention as the minimum levels. Since standard metabolism relates to the maintenance costs of a non-feeding, non-digesting, non-growing, non-active fish, there is reason for WINBERG's (1956) appeal for increased studies on active metabolism. When swimming, a major increase in demand for oxygen arises from the

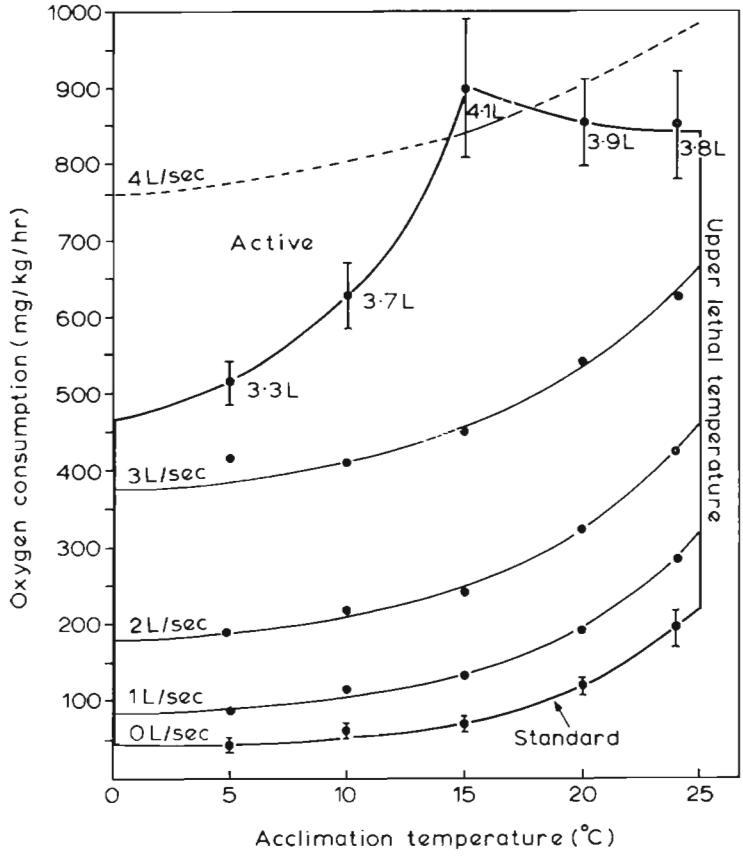


Fig. 3-106: Relation between rate of oxygen consumption and acclimation temperature at various swimming speeds (L/sec = total length per second) for *Oncorhynchus nerka*. The broken line for 4 L/sec is drawn in an area where rapid fatigue would occur since the speed at these temperatures demands a metabolic rate in excess of the active rate. (After BRETT, 1964.)

contractions of the large lateral muscles and is consequently not so likely to be influenced by salinity relations as might be expected in the resting state.

The effect of acclimation temperature on active metabolism has been considered by FRY and associates (FRY, 1957a). A different set of temperature relations than those for the standard rate apply. There may be either an optimum followed by a decrease (for example, *Salvelinus namaycush*), or an intermediate upper limit which levels off (*Oncorhynchus nerka*), or a continuous increase up to the lethal limit (*Ameiurus nebulosus*). No mathematical expressions have been attempted, nor does there appear to be a likely basis since the physiological phenomena are so involved. As Fig. 3-106 shows, for sockeye salmon the metabolic rates accompanying intermediate levels of swimming speed follow an approximate exponential series; but this does not apply to the active rate. A maximum for this species occurs at 15° C (900 mg O_2/kg/hr) which may be compared with the rate at 5° C (510 mg O_2/kg/hr) providing a Q_{10} of 1·8. The lack of any increase above 15° C appears to be the result of atmospheric oxygen acting as a limiting factor.

Metabolic scope. Since this derivative of metabolism represents the difference between two other rates (active minus standard) it may be expected in most cases to be strongly dome-shaped in relation to temperature. A singular exception is that for *Ameiurus nebulosus* which is characterized by an increasing scope permitting a high level of activity in the vicinity of the lethal limit (FRY, 1957a).

Scope may be considered as the metabolic requirement for locomotion, and studied in its relation to temperature at swimming speeds including those less than the maximum sustained rates. In the case of sockeye salmon fingerlings a progressive decrease in thermal dependence occurred with increasing speed (BRETT, 1964). It was predicted that burst speeds would be independent of temperature, a phenomenon which has subsequently been supported (p. 549).

Oxygen debt. Any sudden activity or excessive effort involves a large anaerobic fraction in the metabolic process. It is known that fish can accumulate considerable oxygen debt following strenuous exercise, which may take 8 to 12 hrs to repay (BLACK and co-authors, 1962). The effect of temperature on the total debt tolerated by young sockeye was found to be doubled by an increase from 5° to 15° C; higher temperatures were accompanied by a reduction in the tolerable debt (BRETT, 1964). Post-fatigue death occurred above 15° C rising to 40% at 24° C. This aspect of temperature relations in fish appears to be a field of inquiry which has received comparatively little attention to date.

Acclimation rate. Sudden or progressive environmental-temperature changes undoubtedly elevate or depress metabolic rate as a result of diurnal fluctuations, vertical or horizontal migrations, and seasonal changes. An interaction with photoperiod is reported by ROBERTS (1964). From experimental studies the rate of metabolic acclimation to temperature change, unlike temperature-tolerance acclimation, is less dependent on the direction of change (Fig. 3-107). An initial, rapid response over the first 3 to 7 hrs occurs, usually accompanied by some overshoot, followed by a slower response of small magnitude which may extend from 3 to 9 days and in some cases appears to require up to 3 weeks (AUERBACH, 1957). WELLS (1935)

observed a rapid response in *Gillichthys mirabilis* but did not consider acclimation to be complete within 50 hrs. A comparison of 3 stenothermal species (all Salmonidae) and 4 eurythermal species led FLÖRKE and co-authors (1954) to conclude that the former were the most responsive whereas the latter showed slower initial responses (24 to 48 hrs). They reported a seasonal difference in standard metabolism of *Trutta iridea*, the winter rate exhibiting a compensatory shift to twice the summer rate when compared at 10° C. A similar sort of seasonal response was reported for the bluegill *Lepomis macrochirus* (WOHLSCHLAG and JULIANO, 1959) but not for the cunner *Tautogolabrus adspersus* (HAUGAARD and IRVING, 1943).

KLICKA (1965) has conducted one of the most thorough studies attempting to determine possible hormonal involvement in metabolic acclimation of goldfish *Carassius auratus*. No evidence of relationship with adrenal activity was obtained. KLICKA did conclude, however, that acclimation was completed sooner at low than

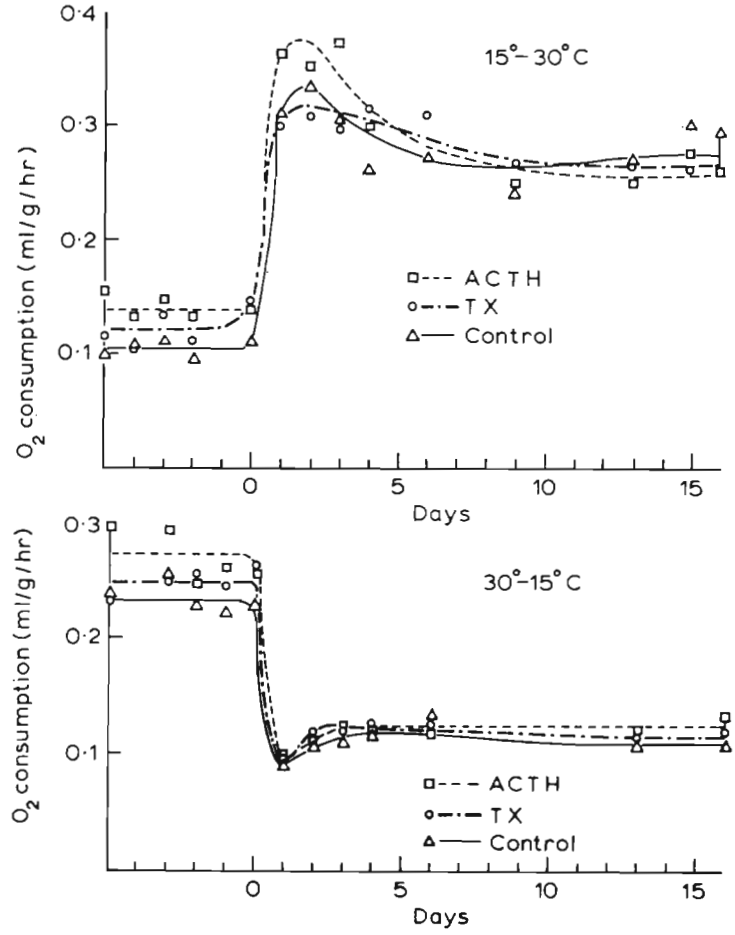


Fig. 3-107: Metabolic acclimation patterns of *Carassius auratus* following transfer on day zero from initial to new acclimation temperatures. (Two examples from KLICKA, 1965; different symbols represent hormonal treatments which were not considered to produce any significant difference.)

at high temperatures, suggesting that cold acclimation may involve a partial shifting from aerobic to anaerobic metabolism for this species. A case for two types of response is made by MORRIS (1965) for the yellow bullhead *Ictalurus natalis*.

It is important to recognize the complexity of this phenomenon when different rates and levels of temperature are involved, coupled with seasonal, size, age and species differences. Measures of activity have yet to accompany the experimental procedures, so that a clear distinction between standard and routine metabolic rates has not necessarily been made, both within and between species.

Compensation. Unlike metabolic acclimation which is a non-genetic reversible response of the organism to environmental change, temperature compensation is an evolved adaptation permitting higher (or lower) metabolic rates at extremes of polar (or tropical) environments which could not be predicted from studies conducted in one or other of the normal habitats (BULLOCK, 1955; FRY, 1958; ROBERTS, 1966, 1967). SCHOLANDER and co-authors (1953a) were among the first to recognize this phenomenon in fish by comparing the standard metabolic rates of tropical and polar species. The expected rates of arctic species were 20 to 30 times higher than would be predicted by applying KROGH's curve. It was observed that the polar species were not only shunted to the left and elevated in their standard rates (Fig. 3-108) but because of the constricting influence of low tempera-

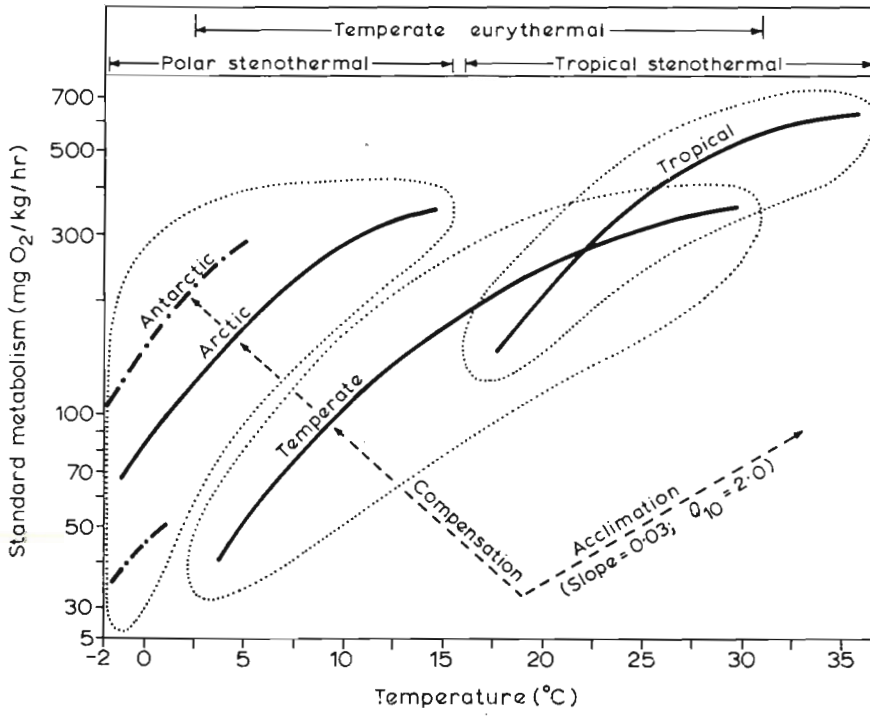


Fig. 3-108: Schematic representation of relation between temperature and standard metabolic rates of marine fish from different climatic zones. Dotted lines indicate range of variability within each zone. The direction of metabolic compensation between species and metabolic acclimation within species is represented by construction lines. (Drawn from compilation of WOHLSCHLAG, 1964.)

ture they tended to live nearer their upper metabolic limit when active. The comparison could of course be reversed if the polar species were taken as the reference point. As a basis for comparison the phenomenon should be considered from the environmental circumstance surrounding the likely origin of teleosts. It will, therefore, be treated from the standpoint of adaptive radiation from temperate seas. MORRIS (1961) adopted such an approach in the study of 6 species of Pacific cottids distributed from Alaska to southern California, conducting inter- and intraspecific comparisons of metabolic rate in relation to temperature. Both nongenetic (seasonal acclimation) and genetic (temperature compensation) adaptations were demonstrated in the invasion of new habitats and an extension of geographic range.

The work of WOHLSCHLAG (1960, 1964) on antarctic fishes and his compilation of pertinent data for tropical, temperate and polar species has done much to elucidate the phenomenon. The tropical fish appear to have undergone less compensatory shift in their temperature–metabolism relations except at the limits of their tolerance range. An average change of about 50% increase over that for temperate species occurs at 30° C. Their response has been to live at a higher pace in accordance with an extension of metabolic rate corresponding to a Q_{10} of approximately 2·5. Accompanying this has been an upward shift in temperature tolerance to become warm stenothermal. In addition they have become somewhat more depressed in their metabolic rate at the lower limit of temperature tolerance than their temperate counterpart. To extrapolate this metabolic relation for the tropical fish to the extreme cold-lethal temperatures naturally tolerated by the polar stenothermal species is to apply a 'correction' beyond reasonable physiological comparison. The compensatory shift which can justly be compared is that with the temperate species, within mutually tolerable temperatures (Fig. 3-108). On this basis the arctic species show an upward displacement in standard metabolic rate of about 3 times. The antarctic species are split into 2 groups. One group which characterizes all but a single species among the 8 studied by WOHLSCHLAG (1964) exhibited an adaptive upward shift of about 5 times that for the temperate fish and appears to be even more compensated than those studied in the arctic. The single species, a zoarcid *Rhigophilia dearboni*, showed less than twice the expected rate as derived from the relation for temperate species. The widespread distribution of members of this family, including representatives in temperate regions, led WOHLSCHLAG to speculate that this antarctic species was not well adapted to cold in its southern limits and only secondarily a deep-water form.

A point of interest arising from studies on antarctic fishes was the excessive metabolic variability (increased rates) which occurred at the lowest temperatures. In WOHLSCHLAG's opinion this is a natural phenomenon gone unrecognized previously although it also appears to be present in some of the arctic species reported earlier. It could be a metabolic response to produce just enough internal heat to resist freezing.

A deviation from the general pattern of metabolic response to temperature has recently been reported by ROBERTS (1967) who obtained no significant change in the standard metabolism of sunfish *Lepomis gibbosus* between 10° and 17·5° C under controlled photoperiod. A form of metabolic homeostasis occurs in this particular temperature range, apparently subject to seasonal modification. The

response was thought to be systemic, rather than cellular, involving neural and endocrine functions.

Growth and food conversion. Few other aspects in the study of fishes have received more attention than growth rate, one of the essential parameters in the assessment of populations and productivity. By the very nature of rings on scales, bones and otoliths, marked changes in rate are imprinted. In the absence of limiting factors growth is a multiplicative process which under ideal conditions, as in the early stages of life, follows an exponential curve. However, development is the product of many interacting processes woven in a web of metabolic relations subject to both hormonal stimulation and a counteracting inhibition with age. Its overall configuration tends to follow the sigmoid shape of a logistic curve, but no universal pattern prevails. The quantitative laws including many of the factors governing growth have been treated generally by such authors as CLARK and MEDAWAR (1945), VON BERTALANFFY (1957) and NEEDHAM (1964) with more specific consideration of the process in fish provided by BROWN (1957), BEVERTON and HOLT (1959), TAYLOR (1962) and PALOHEIMO and DICKIE (1965).

Among the most important environmental factors influencing growth, aside from salinity, are temperature and photoperiod. In nature these are usually correlated with each other and with seasonal abundance of food as well as growth hormone (SWIFT, 1955, 1960), so that the unravelling of how temperature affects growth has been sought by experimentation. As any investigator will attest, such an approach is not without obstacles. Biotic problems of crowding, hierarchy, activity, diet and excretory products must be considered. Among the relatively few revealing studies of this sort are the experiments of DAWES (1930a, b) on plaice *Pleuronectes platessa*, PENTELOW (1939) and BROWN (1957) on trout *Salmo trutta* and KINNE (1960a) on the desert pupfish *Cyprinodon macularius*. These works and others have been the subject of further analysis by URSIN (1963), and PALOHEIMO and DICKIE (1966a, b).

With the exception of cases where food rations have not been provided above the maintenance level, increasing temperature enhances growth up to an optimum beyond which moderate or rapid diminution occurs. Examples of such optima variously recorded for different species are presented in Table 3-48. KINNE (1960a) has shown how different levels of salinity can alter the thermal response of a cyprinodont, not only by shifting the optimum to a lower temperature at lower salinities, but also by altering the range for good growth. In experiments on brown trout an interacting effect of increased spontaneous activity at intermediate temperatures resulted in a bimodal growth response (BROWN, 1957) which would appear to be an experimental anomaly judging from the more general cases and results obtained on another species of salmonid. In the latter case BRETT and co-authors (1969) demonstrated a continuous shift and reduction in the optimum for young sockeye salmon when fed a series of reduced rations while induced to swim at a fairly uniform speed (Fig. 3-109). Experiments conducted on young mackerel *Pneumatophorus japonicus* by HATANAKA and co-authors (1957) when fed anchovy showed a continuous decrease in growth rate as temperature was reduced from 18·4° to 14·7° C over a 30-day period. Optimum conversion efficiency occurred at an intermediate temperature of 16·4° C (TAKAHASHI and HATANAKA, 1960).

Table 3-48

Examples of temperatures for optimum growth derived (i) experimentally, (ii) observed in nature, and (iii) computed from published data. Arranged in order of increasing temperature optima (Original)

Species	Optimum (° C)	Salinity (‰)	Size (cm, g)	Comment	Reference
Salmo trutta	8	Fresh water	50 g	lower optimum	BROWN (1957)
Oncorhynchus nerka	10	Fresh water	8 g	3·0% ration[a]	BRETT and co-authors (1969)
Pleuronectes platessa	12	Sea water	4·6 mm[b]	computed	URSIN (1963)
Pleuronectes platessa	12	Sea water	2·0 cm	observed	JANSEN (1938)
Gadus morhua	13	Sea water	Large	computed	URSIN (1963)
Pleuronectes platessa	15	Sea water	1·7 cm	observed	JANSEN (1938)
Oncorhynchus nerka	15	Fresh water	25 g	6·0% ration[a]	BRETT and co-authors (1969)
Salmo trutta	17	Fresh water	50 g	higher optimum	BROWN (1957)
Pseudopleuronectes americanus	18	Sea water	10 g	computed	URSIN (1963)
Cyprinodon macularius	28	15‰	20–30 cm	experimental	KINNE (1960a)
Cyprinodon macularius	30	35‰	20–30 cm	experimental	KINNE (1960a)

[a] Food ration as percentage of dry body weight

[b] Larval stage

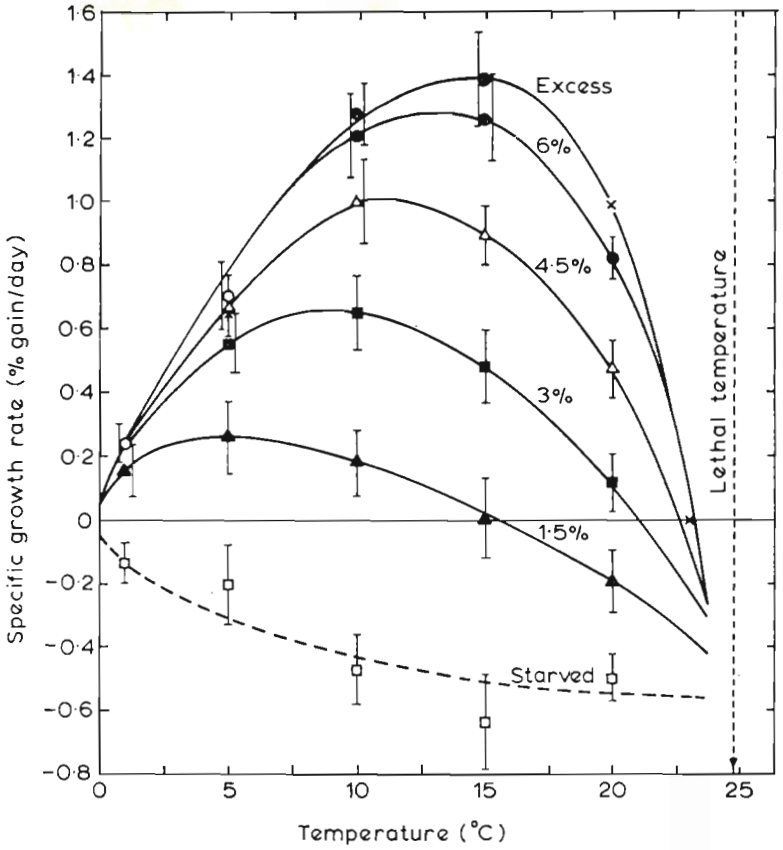


Fig. 3-109: Relation between temperature and specific growth rate (±2 S.E.) of young *Oncorhynchus nerka* when fed various rations as percentage of body dry weight. Points marked (X) and (O) are from separate experiments using excess ration. (After BRETT and co-authors, 1969.)

The presence of growth optima has led WARREN and DAVIS (1967) to propose a 'scope for growth' which, in the manner of metabolic scope, could be considered as the interaction between growth-promoting and growth-restricting processes differentially affected by temperature. These authors reported for *Cichlasoma bimaculatum* that within the range of 20° to 36° C, food consumption, scope for growth, and assimilation efficiency were greatest at 28° C. Faecal losses amounted to 30% of the calorific intake at 36° C. Some of the reduction in growth above the optimum temperature appeared to result from an increase in the energy requirements for food conversion. This is supported by the tripling in maintenance requirements for *Salmo trutta* which BROWN (1946) discovered when temperature was increased from 5° to 20° C. Above 23° C young sockeye showed no ability to grow despite the presence of abundant food (DONALDSON and FOSTER, 1940; see also Fig. 3-109).

Although low temperature usually retards and may even inhibit growth completely this obviously does not apply to fish which frequent areas where either depth, cold currents or polar distribution impose such a potential restriction.

Growth compensation with its complement of metabolic compensation has evolved, accompanied by a slower growth rate, longer life and later maturation so that the ultimate size is not necessarily reduced (TAYLOR, 1958; LIU and WALFORD, 1966). The common antarctic fish *Trematomus bernacchii* which lives under ice cover at $-1{\cdot}9°$ C may reach a weight of 350 g in about 10 years (WOHLSCHLAG, 1961).

In general the efficiency of food conversion decreases with age so that for mature fish which have minimum growth the energy demand is essentially for metabolic rate and gonad production. The highest gross efficiency is that during embryonic growth which frequently exceeds 60%. A reduction from this level to 42% occurred at 5° C in *Salmo salar* (HAYES and PELLUET, 1945). MARR (1966) re-examined the case for salmonid embryos presenting evidence for an optimum approaching 70% at 10° C falling to 64% at 7·6° C and at 14·3° C. In the post-embryonic stage, the analysis of data for the desert pupfish (PALOHEIMO and DICKIE, 1966b) indicated that despite some exceptions efficiency of conversion was independent of temperature but negatively correlated with ration and weight. These authors concluded that temperature changes affected the rate of turnover of energy rather than the distribution within the fish.

The rate of food conversion and the primary process of digestion are highly temperature dependent, increasing by a factor of 2 to 3 times for a 10 C° change (KINNE, 1960a; NIKOLSKY, 1963). Increased proteolytic activity of digestive enzymes has been reported by MEWS (1957) for the goldfish at high acclimation temperatures. In the larval stage of some clupeids BLAXTER (1965) records that the digestion time decreased from 8 hrs at 7° C to 4 hrs at 15° C ($Q_{10}=2{\cdot}4$). By means of X-ray and force-feeding MOLNAR and TOLG (1962) followed the gastric digestion rate in the largemouth bass *Micropterus salmoides* during seasonal temperature change. The rate of emptying the stomach was 5 to 6 times faster in summer (25° C) than in winter (5° C). In view of the relation of growth rate to temperature it is interesting to find that an optimum in gastric secretion has been recorded by SMIT (1967) for the brown bullhead *Ictalurus nebulosus* at 25° C when acclimated over a range of 10° to 30° C.

It can be seen that since growth and food conversion are intimately bound to metabolic rate, both through energy demand and by accumulation of energy stores, the response to temperature and food supply for different developmental stages and sizes of fish is complex and may be confounded by interaction. Thus, the long-term effect of temperature on metabolic rate appeared to follow KROGH's curve when food was abundant but was significantly lower when only a maintenance diet was presented (PALOHEIMO and DICKIE, 1966a, b). It is apparent that adaptive responses in the metabolic pathways and activity patterns of fish exist which act in a homeostatic manner governing growth. Hence in the long term no simple relation to temperature can be expected either in nature or in the laboratory, despite being able to illustrate certain temperature-dependent responses experimentally. These, however, reveal an essential aspect of the fabric of growth.

Activity

Swimming speed. The metabolic capacity to convert chemical energy into mechanical thrust governs locomotory performance and is, therefore, dependent on the aerobic

and anaerobic processes involved. A variety of levels of performance are recognized according to the time they can be maintained. For vertebrates the maximum sustained speed, like the marathon, depends on the continuous supply of oxygen and metabolites to maintain performance. This level is governed by the metabolic scope and accordingly subject to temperature effects. In most instances there is an optimum temperature corresponding to that for maximum metabolic scope such that excessively high or low temperatures reduce the level of sustained performance. Both FISHER (1958) and FRY (1964) have reviewed the subject.

Short-term burst speeds have very little aerobic fraction. Oxygen debt is accumulated rapidly limiting the time of the burst though not necessarily the magnitude. In the final analysis the upper limit would be expected to be a product of the contractile capacity of muscle fibres and the immediate source of energy, derived from available ATP. BAINBRIDGE (1960, 1962) studied the duration of burst speeds concluding that approximately 20 secs characterized the limit for the species tested.

An analysis of the fatigue curve (BRETT, 1964, 1967a) has provided evidence for an intermediate level of performance, distinguished by steady swimming with periodic vigorous efforts, which may last from a few mins to a maximum of 2 to 3 hrs, terminating in fatigue. This has been termed 'prolonged performance' as a distinction between sustained and burst speeds. It would appear to depend not only on a combination of aerobic and anaerobic functions but on the rate of mobilizing metabolites from carbohydrate and lipid sources.

Since these levels of performance differ in their physiological basis it is not surprising that they should differ in relation to temperature. On the basis of studies on metabolic rate in relation to performance of young sockeye salmon it was hypothesized that burst speeds would be independent of temperature (BRETT, 1964). This conjecture has recently been supported by experiments of GROVES (personal communication) who discovered that although the maximum burst speed achieved was not affected by temperature the duration was.

Prolonged performance has not been examined sufficiently to allow any statement on temperature relations other than supposing that it would occupy an intermediate position, displaying some temperature dependence. There is evidence for a seasonal reduction for sockeye salmon in winter although acclimated to summer temperatures (BRETT, 1967b).

Although performance studies on marine species have received attention (HELA and LAEVASTU, 1962) these have almost invariably been concerned with the speed attained at any one temperature, not with a systematic examination of the factorial relation. The observations of SCHOLANDER and co-authors (1953a) on the relatively high level of performance among arctic fishes in relation to their maximum ability has been noted. Among the species of *Trematomus* studied by WOHLSCHLAG (1962) in the Antarctic only the pelagic species *T. borchgrevinki* could be induced to swim steadily in a rotating chamber at $-1{\cdot}8^{\circ}$ C, the normal temperature of its habitat. At higher temperatures swimming became inconsistent and ceased at $+2^{\circ}$ C. BLAXTER and HOLLIDAY (1963) have summarized records on swimming speeds of herring and other clupeids, including environmental temperatures. An account of the interrelations remains to be elaborated.

In the interaction between predator and prey, and the demands on endurance

which competition imposes, temperature–performance relations must play a prominent role. By inference the distribution and habits of 2 species of Pacific salmon provide evidence of this nature. Although possessing almost identical upper lethal temperatures, young coho salmon defend territory along lake shores and in streams during the warmth of summer whereas sockeye remain in the limnetic zone frequenting cooler, deeper water. The temperature permitting optimum sustained swimming speed occurs at 20° C for coho, some 5 C° higher than that for sockeye (BRETT and co-authors, 1958). Among two other species of salmonids, where they occur in the same area, the brown trout is found in greater abundance further downstream than the speckled trout. This corresponds with a higher optimum in the temperature–activity relations of the brown trout (KING, 1943; HOLTON, 1953). The ecological relation, however, is far from simple. MCCAULEY (1958) in a study of two subspecies of *Salvelinus alpinus* found a significant difference in lethal temperatures but not in the activity–temperature curves.

Spontaneous activity. KERKUT and TAYLOR (1958) note that poikilotherms normally become less active at low temperatures but that anomalous temperature responses are not unknown. These latter are attributed to transient increases in the discharge from sensory perceptors, below an optimum temperature, whereas spontaneous discharges from the central nervous system increase above the optimum.

The frequency of spontaneous movements in the speckled trout showed two maxima, one in the region of the preferred temperature at 10° C ± 2 C° and the other at 24° C ± 1 C°, close to the upper lethal temperature; destruction of the dorsal part of the cerebellum eliminated the intermediate response (FISHER and SULLIVAN, 1958). As noted previously (p. 545) spontaneous activity of *Salmo trutta*, although complicated by appetitive behaviour, resulted in two growth optima (BROWN, 1957). No such optima were observed for shoals of young mackerel *Pneumatophorus japonicus* swimming freely in aquaria. Influenced by both size and temperature the mean speed increased from 38 cm/sec at 15°C ± 2 C° to 57 cm/sec at 22° C ± 2 C° for fish 18 cm in length (HATANAKA and co-authors, 1957).

These few examples which may be supplemented by records on diurnal changes (ALABASTER and ROBERTSON, 1961) and routine metabolism (FRY, 1957a) serve to illustrate the diversity in response. Cycles of activity have been studied more in relation to photoperiod, feeding behaviour, and daily or seasonal patterns of movement (SWIFT, 1962). The influence of temperature on spontaneous activity has not received as much attention. Evidence for temperature *per se* resulting in rhythms of activity is not presented in the review of HARKER (1958). Indeed, appropriate compensation for temperature fluctuations is a requisite for the timing mechanism of biological clocks. Nevertheless HEATH (1963) using acclimation thermoperiods of one-quarter to twice the 24-hr cycle has shown that optimum temperature tolerance in cutthroat trout *Salmo clarkii* was induced by 24-hr periods, indicating a naturally timed, physiological adaptation of thermal acclimation.

The ecological significance of temperature-induced spontaneous activity has been variously attributed to (i) inducing aggregation under favourable thermal conditions for greatest scope for activity, (ii) as a response to extremes of temperature presumably contributing to escape from unfavourable stress and (iii) for the

production of a life-saving small increment of heat at subzero temperatures.

Gradient responses. Numerous observations on the concentration of fish within a limited range of both horizontal and vertical temperature gradients have provided ample demonstration of preferred or selected temperatures. DOUDOROFF (1938) documented the selective response and effect of acclimation temperature among young opaleye *Girella nigricans* and Pacific killifish *Fundulus parvipinnis*. The response of the latter was not as pronounced as the former. Extensive difference between species occurs. FRY (1964) has reviewed much of the evidence, quoting the work on freshwater species of FERGUSON (1958) who concluded that there was a good correspondence between laboratory and field observations with the provision that experimental records tended to be on the high side, a difference which could be attributed to use of young fish for laboratory work. The reaction of young rainbow trout *Salmo irideus* and Baltic salmon *Salmo salar* was reported by MANTELMAN (1958) to be more rapid than in older fish, with a particularly sensitive stage when 2 to 4 weeks old. The fact that preferred ranges could be related to temperatures providing maximum scope for activity (and coincided with optimum spontaneous activity in some species) led FRY and associates to postulate that this provided an adaptive mechanism of survival value (BRETT, 1956).

In nature there seems no reason not to support this general view based on physiological grounds, particularly where open waters permit free movement. However, seasonal influences (SULLIVAN and FISHER, 1953; MANTELMAN, 1958) and special behaviour patterns involving temperature-oriented migrations may become overriding features. In the case of *Girella nigricans*, NORRIS (1963) conducted extensive field and laboratory studies clearly demonstrating that at one stage of life this eurythermal species showed a remarkably precise selection centred around 26° C, independent of thermal history and geographic range (Fig. 3-110). This was associated with a period when prejuveniles migrated inshore to intertidal waters prior to adult transformation; maximum feeding rates were also shown to correlate with the selected temperature. Prolonged acclimation in the laboratory tended to produce increased excitability resulting in a masking of the specific reaction.

A delicate sense for temperature discrimination is displayed by *Jenkinsia lamprotaenia* (BREDER, 1951). Schools of this species were observed to avoid a temperature of 30° C, although moving freely in a temperature of 29·0° to 29·5° C and capable of withstanding 35° C. A minimum difference of 0·5 C° was required to produce an unconditioned orientation response in 2 species of *Pomolobus*, the alewife and the glut herring (COLLINS, 1952). Such observations of natural responses which depend on an innate, specific drive or reactive state do not indicate the limits of sensitivity. MURRAY (1962) has reviewed the results obtained from conditioning experiments and electro-physiological recording. Drawing on the work of BULL (1936) who examined 19 marine species, and supported by the tests of BARDACH and BJORKLUND (1957) on 5 freshwater species from diverse habitats, there is evidence among teleosts of a threshold of ± 0·05 C°. Free nerve endings over most of the body surface appear to be the effective reception.

Among the few elasmobranchs studied the threshold is much higher, being about 0·8°C. Although the ampullae of Lorenzini, with extensive distribution of jelly-

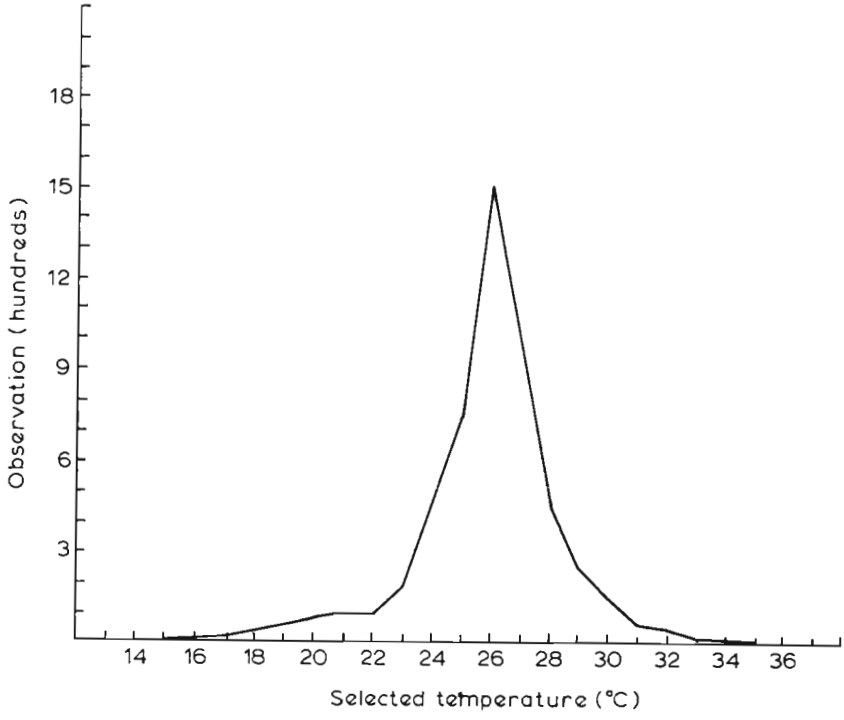


Fig. 3-110: Selected temperatures of unacclimated, prejuvenile *Girella nigricans*, approximately 3 to 6 cm standard length. (After NORRIS, 1963.)

filled tubes connected to cutaneous pores, are more responsive to temperature change than any other sense organ, nevertheless their function does not appear to be in this category.

A distinction between temperature responses which confer such physiological attributes as optimum activity and metabolic scope, and behavioural responses in which temperature acts as a directive cue must be considered in the deciphering of temperature-related phenomena. NORRIS (1963) concluded that temperature selection and orientation are undoubtedly

> 'widespread phenomena among both freshwater and saltwater fishes serving a variety of uses such as assuring optimum food supplies for growth, escape from predators, timing of migrations and reproduction'.

Temperature discrimination constitutes one of the mechanisms for habitat selection, but the multitude of biotic and abiotic factors which attend life can override the adaptive expression. An example may be cited for the cod and haddock which on occasion are killed by freezing temperatures, apparently in pursuit of capelin (ICNAF, 1965).

(c) *Reproduction and Development*

The sequence of events relating to maturation, spawning migration, release of gametes, and subsequent development of the egg and embryo represents one of the most complex phenomena in nature. Physiological, environmental (factorial),

ecological and applied (fishing and fish-cultural) studies have each contributed a share in elaborating various aspects (ARONSON, 1957, 1965; HOAR, 1957; HOLLIDAY, 1965). By far the majority of investigations have been conducted on freshwater fish, although an increased effort to describe the distribution, spawning relations and survival of the young of marine species is apparent (PERTSEVA OSTROUMOVA, 1961; LASKER, 1965; LUCAS, 1965).

Sensory receptors are known to stimulate the pituitary gland, resulting in a chain of interacting responses within and between the organism and its environment culminating in reproduction (PICKFORD and ATZ, 1957). In some cases the events may be remarkably precise. Reproduction occurs only within a limited geographic range and under relatively specific conditions apparently dictated by the particular environmental requirements of the egg and embryo (USHAKOV, 1964). The reproductive timing of the grunion *Leuresthes tenuis* which spawns only on beaches along the California coast can be annually predicted usually within a fraction of an hour (CLARK, 1938).

Among the environmental factors involved are light (photoperiod), temperature, salinity, water currents, tides and food abundance which are all seasonally related one way or another. Experimental evidence has been sought in an effort to define the respective roles but not without difficulty and apparent contradiction. HENDERSON (1963) has pointed out that diversity of experimental conditions, variation in species response, lack of adequate controls in some instances and insufficient duration to allow proper assessment (ATZ, 1957) have made interpretation difficult. It is perhaps unreasonable to expect any ready clarification where such a complex interplay between environment and organism has evolved. On the whole there appears to be a more pronounced relation to light, particularly where precision of timing (internal clock?) and migration (celestial orientation?) are involved. However, one of the reasons for this precision may be the need imposed by a restricted temperature range for early development. In general, temperature may affect the rate of maturation; it is known to act as a timing and/or releasing factor; it undoubtedly imposes a marked confining effect on reproductive limits. Some examples of these respective roles may be considered.

Reproduction

BAGGERMAN (1957), working with the three-spined stickleback *Gasterosteus aculeatus*, has conducted one of the most thorough studies on breeding relations. Gonadal development was found to increase with temperature when on a 16 hr daylength at any time between December and May; on an 8 hr day the response was quite limited. Other cases are cited, for example, *Phoxinus laevis* shows no response to temperature change whereas males of *Rhodeus amarus* can be induced to mature in midwinter by high temperatures; the females only respond if on a long daylength. Rate of maturation in *Salvelinus fontinalis* was not altered at temperatures of 16° and 8·5° C when on normal daylength but significant differences were noted under long or short photoperiods (HENDERSON, 1963). Maturation of males of *Cyprinodon macularius* did not occur in a 12 month period at 20° C or below, but averaged only 99 days at 30° C (KINNE, 1960a). Detailed studies on the reproductive physiology of the viviparous sea-perch *Cymatogaster aggregata* (WIEBE, 1968) revealed that spermatogenesis would occur at cold temperatures

(10° C) provided the daylength was long enough; the process was hastened by warm temperature (20° C). High temperature and short photoperiod inhibited maturation. Oocyte formation was influenced more by temperature than photoperiod. The relation of environmental factors (temperature, light and season) to the various stages of reproductive development and behaviour in this species is shown to be highly complex.

Reproductive cycles have been recorded for many marine species, with an advance or retardation of reproduction closely related to the temperature of the months preceding spawning, as in the cod *Gadus morhua* (HELA and LAEVASTU, 1962). In a survey of 115 marine or estuarine species off the coast of Texas (USA), GUNTER (1945) observed that over 85% of the fishes spawned in the spring and summer. This does not define the temperature influence, a fact which BLAXTER and HOLLIDAY (1963) and HOLLIDAY (1965) well recognize in their discussion of the maturation of clupeids. Different races of herring may mature at different times of year despite occupying the same environment.

The difference in the effect of temperature governing a rate phenomenon and temperature acting as a timing or releasing factor is clearly revealed in those cases where falling temperature induces spawning. This has been noted for the char *Salvelinus alpinus*, the Caspian sturgeon *Acipenser güldenstädti* (BAGGERMAN, 1957), the whitefish *Coregonus* sp. (in conjunction with a particular character of bottom layer; FABRICIUS, 1950), the lake trout *Salvelinus namaycush* (ROYCE, 1951), and many species of characins and cyprinids (ARONSON, 1957). An experimental case is recorded for herring *Clupea harengus* which responded after an imposed delay of 3 months to a rise in temperature; however, as BLAXTER and HOLLIDAY (1963) note, other environmental changes have resulted in similar responses. The general pattern of the spawning bed may be most important for this species.

Temperature appears to confine spawning to a narrower range than the majority of other functions (KINNE, 1963a). This is apparent for marine fish from the ranges and optima recorded in Table 3-49. The average range for spawning is of the order of one-quarter to one-third that for the lethal range. When the optima are compared with the temperature limits for embryonic survival (Fig. 3-103) they fall in an intermediate position supporting the view of USHAKOV (1964) that the extent of thermal independence which poikilotherms have achieved is the product of cellular organization and adaptability of the adult which, when it approaches the stage of liberating single reproductive cells, must seek the appropriate stenothermal (and stenohaline) conditions for embryogenesis. The existence of anadromous and catadromous species constitute striking examples of this relation.

It can be concluded that although temperature may set narrow limits for spawning it is not alone in this environmental relation. Nor can it be considered other than in a complex of interaction in which temperature and light may reinforce each other. Species response is highly variable and may even differ between races and sexes of one species.

Development

While in most instances temperature is probably subordinate to light in its relation to spawning, once the reproductive cell is released its fate is very dependent

Table 3-49

Spawning temperatures (° C) of some marine fishes, showing range and optimum. Lethal temperatures of the adults are presented for comparison from Table 3-45. (Additional references listed in footnotes) (Original)

Species	Locality	Spawning temperature		Lethal		Reference
		Range	Optimum	Lower	Upper	
Liopsetta pinnifasciata	Kamchatka Coast	−2 to 4	−1 to 2	—	—	Pertseva-Ostroumova (1961)
Platessa quadrituberculata	Kamchatka Coast	−1 to 6	1·5 to 4	—	—	Pertseva-Ostroumova (1961)
Gadus callarius (*morhua*)	Barents Sea to Atlantic	0·4 to 7	1·5 to 4	−2	22 ± 2[a]	Hela and Laevastu (1962)
Clupea harengus (spring)	Barents Sea to Atlantic	0 to 12	4 to 9	−1·8	23	Hela and Laevastu (1962)
Pleuronectes platessa	North Sea	4 to 7	6 to 7[b]	—	26	Hela and Laevastu (1962)
Clupea pallasii	Hokkaido West Coast	4 to 8	5 to 6	—	—	Tamura (personal communication)
Clupea harengus (autumn)	North Sea to Atlantic	6 to 15	9 to 13	−1·8	23	Hela and Laevastu (1962)
Sardinia pilchardus	English Channel	9 to 16·5	—	—	—	Hela and Laevastu (1962)
Scomber scombrus	North Atlantic	10 to 15	—	—	—	Hela and Laevastu (1962)
Girella nigricans	California Coast	12 to 19	—	4·6	31	Norris (1963)
Sardinops melanosticta	Sea of Japan	13 to 17	14 to 15·5	8	28	Hela and Laevastu (1962)
Sardinops caerulea	California Coast	13 to 22[c]	15 to 16	—	—	Hela and Laevastu (1962)
Plecoglossus altivelis	Sea of Japan	14 to 19	—	(10)	24	Tamura (personal communication)
Sardina ocellata	Southwest Africa Coast	15 to 19·6	—	—	—	Hela and Laevastu (1962)
Cyprinodon macularius	Salton Sea (California)	20 to 30 ± 2	—	<9	>40	Kinne (1960a)

[a] Altman and Dittmer (1966)
[b] Shelbourne (1964)
[c] Ahlstrom (1954); Lasker (1964)

on temperature within the natural limits of salinity. An inevitable but temporary return to the minimum level of organization for the species has occurred. Development involves both growth and differentiation, which, in turn, relate to metabolic rate, biochemical transformation and the complex organization of embryonic tissue. Limits of successful development have already been considered under *Tolerance* (p. 530), where it was noted that the capacity to survive temperature extremes was significantly restricted during early life; for instance HEUTS (1956) found that the eggs of *Gasterosteus aculeatus* were differentially adapted to narrow temperature–salinity niches. The cause of mortality at this stage may be attributed to cessation or derangement of differentiation blocking successful hatching, as well as to tissue intolerance.

In the section on *Metabolism* (p. 536) it was further seen that yolk transformation was not only dependent on temperature as a rate function, but also the efficiency of conversion was influenced by temperature. LASKER (1965) has studied the incorporation efficiency of yolk during development of Pacific sardine which ranged from 90% to 45% at 14° C, with 78% conversion for the entire period.

Differentiation means that the growing organism is in a constant state of organizational change, unlike any other stage except for those species which metamorphose. Temperature-sensitive stages in development have been noted, coupled with shifts in tolerance limits (PERTSEVA-OSTROUMOVA, 1961). SMITH (1957) has reported on early development of 2 species of *Salmo* in which the periods of cleavage, gastrulation and gastrular overgrowth showed marked differences in thermal response. This author comments further that cod eggs are much more resistant once the blastopore has closed. Both Atlantic and Pacific cod have a period of high susceptibility to mortality just prior to hatching (FORRESTER, 1964a). Improvement in the artificial propagation of plaice *Pleuronectes platessa* was obtained by incubating at 6° to 7° C and subsequently raising the temperature by stages to reach 10° to 12° C at metamorphosis (SHELBOURNE, 1964).

The presence of sensitive stages, differential growth patterns and periods of velocity change during development can make the quantitative expression between incubation time and temperature a difficult one. Probably because of the major control imposed by metabolic rate, and the high conversion efficiency, sufficient consistency of response is exhibited to permit a number of mathematical transformations, within the range of good viability. Rate of development (hyperbolic function) approximates a linear relation to temperature for *Gadus macrocephalus*, *Gadus morhua*, *Parophrys vetulus*, *Pleuronectes platessa*, *Pleuronectes flesus*, *Lepidopsetta bilineata* and *Clupea harengus* (JOHANSEN and KROGH, 1914; BLAXTER, 1956; FORRESTER, 1964a, b; ALDERDICE and FORRESTER, 1968). Semi-log (exponential function) and double-log transformations have been applied to *Sardinops melanosticta*, *Sardinops caerulea*, *Clupea harengus* and *Osmerus eperlanus* (LILLELUND, 1961; HELA and LAEVASTU, 1962; LASKER, 1964), whereas the logistic equation was used effectively for chinook salmon *Oncorhynchus tshawytscha* by SEYMOUR (1956) and is more generally suitable for growth (see also HAYES, 1949).

Detailed studies on the rate of embryonic development of *Cyprinodon macularius* (KINNE and KINNE, 1962) were presented in relation to temperature at one salinity, using a variety of transformations (Fig. 3-111). This eurythermal species

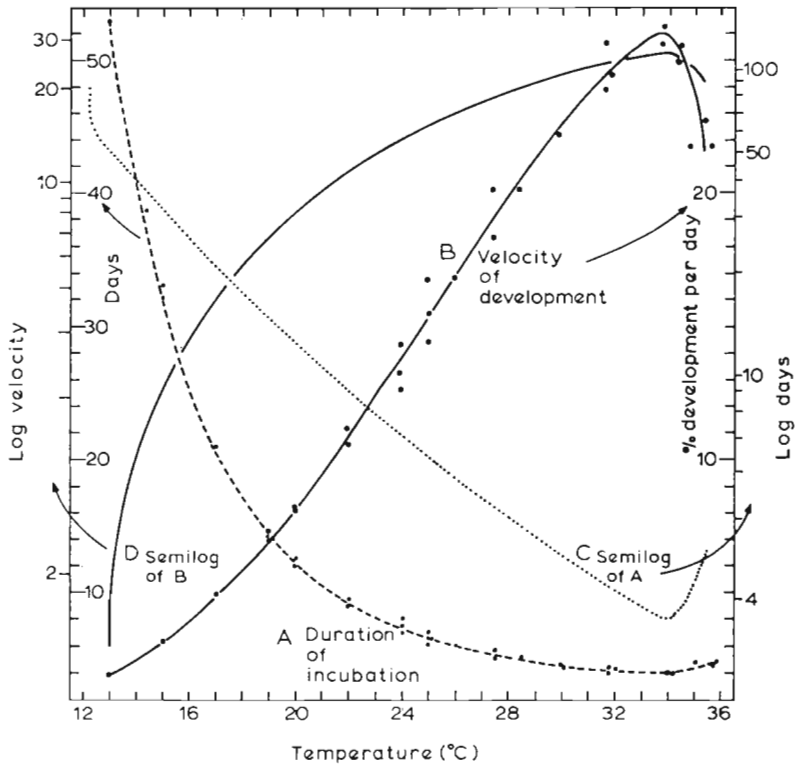


Fig. 3-111: Time-temperature relation in *Cyprinodon macularius* eggs, developing in 100% air-saturated sea water of 35‰ salinity, at different constant temperatures. A: incubation periods in days; B: reciprocals of A multiplied by 100 showing velocity of development expressed as average percentage development per day; C: semilogarithmic plot of incubation periods; D: semilogarithmic plot of developmental velocity. (After KINNE and KINNE, 1962.)

exhibits a close conformity to either hyperbolic or exponential functions between temperatures of about 16° to 32° C. Deviations occur beyond these extremes with a sharp inflection at 34° C, the 50% tolerance limit. Such analyses facilitate comparisons among species which may exhibit marked differences in slopes, intercepts and thresholds. Temperature exerts an exceptionally high controlling influence on developmental rate which is frequently characterized by a Q_{10} in excess of 4, particularly for temperature elevations at the low end of the tolerance range. Fig. 3-111 illustrates a case where the maximum rate, requiring only 4 days at 34° C to hatching, may be compared with a time of 33 days at 15° C and 90 days at 13° C (where only 10% hatch). Two other examples may be cited. The small planktonic eggs released by *Sardinops caerulea* have an incubation time of only 1 day at 21° C increasing to 3 days at 14° C (LASKER, 1964), whereas the littoral, adhesive eggs of *Clupea harengus* require from 9 days at 15° C to 40 days at 3° C (BLAXTER, 1956). These members of the Clupeidae amply demonstrate the genetic diversity between species and the thermal effect on development within species.

Besides determining the limits and rates of development there are two important

features for survival which bear close scrutiny, namely, the optimum temperature for growth and the optimum time for hatching. The former relates to the highest conversion efficiency with lowest metabolic demand, but does not necessarily provide the best timing for the start of feeding or the most propitious period of drift in ocean currents to suitable niches. Beyond the complexity of physiological response lies the important sequence of ecological events which govern survival at this critical stage.

(*d*) *Distribution*

It has been stated that temperature largely determines the distribution of marine organisms (GUNTER, 1957). Much has been written on the significance of temperature, one of the easiest measured and most recorded environmental variables (ANDREWARTHA and BIRCH, 1954; VERNBERG, 1962; KINNE, 1963a; MACAN, 1963; NIKOLSKY, 1963). In view of the evidence presented on restricted spawning requirements, sensitive embryonic stages, optimum growth and activity relations, and sharply defined tolerance limits, it could hardly be denied that temperature must play one of the most important roles in governing the distribution of fishes, both in time and space. Yet the evolution and consequent adaptive relation of species to their environment is the product of an unfathomable interaction of abiotic and biotic factors occurring during geological periods, for which remarkable but nevertheless limited evidence of the environmental conditions may be deduced. As a result the case for temperature-dependent distribution is not so readily made. In an extensive symposium dealing with the effects of environmental factors on the distribution of fishes in the Northwest Atlantic, temperature relations featured in the majority of cases concerning the physical environment (ICNAF, 1965). Despite the many associations few conclusions could be drawn where temperature was indisputedly the governing factor. LUCAS (1965) emphasized the inherent complexity of ecological systems, warning against the elementary assumptions that follow from good correlations leading to causal interpretations. Temperature structure is related to such oceanic features as upwelling, circulation, oxygenation, nutrient concentration, depth contours and plankton abundance such that the circumstances inducing the aggregation of fish may be only remotely involved with temperature. This does not refute the usefulness of temperature as an indicator for locating concentrations of fish but it requires a far more detailed examination to draw any direct conclusions.

In the realm of physiological ecology, particularly the studies on metabolic compensation and homeostatic mechanisms which permit fish to live successfully anywhere from tropical reefs to ice tunnels, it has been noted that a relative freedom from the restrictions of temperature has evolved. This inference may be contrasted with the view of some zoogeographers (HUBBS, 1948) who consider the fish fauna to reflect the past and present temperature regime so that the presence of fish classed as tropical, subtropical, boreal, etc., can be considered as indicator species. ROSENBLATT (1967) has reviewed the zoogeographic relationships of 479 genera of fishes distributed along the Atlantic and Pacific coasts of tropical America. A profound physical and biological difference exists between the two environments influenced by oceanic currents and topographical dissimilarities.

The tropical fish fauna of the Atlantic coast extends some 30° of latitude beyond the relatively restricted boundaries of the Pacific coast. Despite the difference, an essential correspondence between the separate fish fauna occurs for more than half the genera. However, a number of families and 38 genera considered to be of Indo-Pacific origin are found in the Atlantic but are absent in the Pacific. ROSENBLATT comments that

> 'it has been hypothesized that late Pleistocene cooling may have extirpated much of the eastern Pacific fauna (HUBBS, 1960). This would account nicely for what is missing, but how are we to explain the 344 genera still there?'

Despite the apparent conundrum from these various sources of information they all have relevance to the problem of distribution in which phenotypic and genotypic relations must be distinguished. As stated in the introduction, temperature is not a simple factor so that the variety of direct and indirect effects requires careful sifting of evidence before causal relations can be established (NORRIS, 1963). In addition, although physiology has provided insight regarding the sorts of temperature responses which fish exhibit, the distribution problem for even such a well-known species as the Atlantic herring *Clupea harengus* has yet to receive sufficient attention to resolve the controlling influences (PARRISH and SAVILLE, 1965). BARTHOLOMEW (1958) has expressed the view regarding the role of physiology in the distribution of terrestrial vertebrates as having either no direct implication or offering a contribution so broad that little assistance in the analysis of any specific instance is afforded. While this author is of the opinion that such a statement might not apply to fish, particularly in open waters, it would be hard to refute except in a few well-documented cases. Such an attempt has been made by BLACKBURN (1965) in a review of oceanographic conditions and the ecology of tunas (Scombridae). Members of this family are widespread, mostly in tropical and temperate waters; one species (*Thunnus thynnus*) does occur as far as 70° N in the eastern Atlantic. The distribution and movements of the various species have been documented from detailed catch records, exploratory fishing and systematic oceanographic surveys. Some adult fish occur to depths of 150 m but information on vertical distribution is considered quite incomplete. Larvae have not been found as extensively distributed in colder waters as the adults. By comparing changes in isotherms with changes in tuna abundance and examining many of the accompanying oceanic properties (salinity, oxygen, transparency, phosphate, primary production) and dynamic features (surface currents, water masses, fronts, upwelling, thermocline structure), BLACKBURN systematically eliminates evidence which would not support the hypothesis that limits of distribution correspond closely with particular isotherms. Thus, albacore *Thunnus alalunga* occur from 23° to 14° C and are sufficiently abundant between 21° and 15° C to support commercial fishing. These temperatures define the boundaries of distribution. What governs the movements and relative abundance within the limiting isotherms remains to be determined.

It is of interest that further north in the Pacific the highly mobile scombrids appear to be replaced in their general ecological relations by salmon (*Oncorhynchus*). Members of this genus occur from 15° to 1° C with an optimum abundance in the region of 9° to 3° C (NEAVE and HANAVAN, 1960; MANZER and co-authors,

1965), yet the adults are able to tolerate temperatures up to 23° C (Table 3-46). Very different temperature-dependent metabolic and activity relations may account for the geographic separation eliminating competition between these two groups of highly successful predators.

In the various papers dealing with the distribution of cod *Gadus morhua* (ICNAF, 1965) which occur in waters from −1° to 17° C there is ample evidence that this species frequently aggregates in the vicinity of cold fronts from 0° to 2° C. Seasonal migrations onshore and offshore show a marked tendency to avoid passing through colder water masses. However, as noted, mass mortality may occur when caught by particularly low temperatures.

One final example may be cited from the combined works of KETCHEN (1956) and ALDERDICE and FORRESTER (1968) on the lemon sole *Parophrys vetulus*. This species of flatfish occurs from Baja California (29° N) to western Alaska (55° N), releasing pelagic eggs in midwinter. A close correspondence exists between the mean sea-surface temperatures at the limits of the geographic range at that time of year and temperatures causing 50% hatching mortality (above 12° and below 4° C). Furthermore an inverse correlation was found to occur between year–class strength and water temperatures during the period of pelagic life. The possibility of such a relation was attributed to the interaction of drift currents, prevailing temperatures and rates of development affecting the success of reaching suitable rearing grounds at the time of metamorphosis. This interesting hypothesis serves to illustrate the complexity of factors which may govern abundance and distribution, both directly and indirectly influenced by temperature.

Consideration of the possible relation of temperature to distribution has served to review many of the ways in which this all-pervading environmental factor may influence the lives of fishes. There can be no doubt about the exclusion of species from areas of unsuitable temperature conditions despite being within tolerance limits. Breeding and early stages of development are mostly stenothermal but it does not follow that embryogenesis is necessarily the time of greatest mortality in nature. Adequate physiological description of fishes, particularly marine species at all stages of development, is singularly lacking. Various intriguing phenomena such as acclimation, compensation, and supercooling have attracted particular attention. However, the catalogue of well-documented information on any one aspect cannot be considered extensive. The basic relations of temperature and metabolic rate, of paramount importance in the field of bio-energetics, have yet to be evaluated with any measure of thoroughness for marine species. It is no wonder that reviews on temperature relations, touching as they do on the varied manifestations of response, leave little of the mark of certainty regarding the precise role of temperature in distribution. The complexity cannot be escaped. There remains an immense but rewarding task to match morphological and taxonomic understanding with comparable physiological insight.

(3) Structural Responses

E. T. GARSIDE

The processes which determine structural responses are differentiation and growth. Temperature, operative on fishes as a controlling factor (FRY, 1947), affects these processes in the same direction but at differing rates so that interaction varies with temperature. In this subchapter I have assembled evidence to support the proposition that, in fishes and perhaps other groups of animals, many conditions of structure including several drastic malformations are induced by such plastic interaction of these processes and that, to a considerable degree, they are governed by environmental temperature. Obviously temperature is but one of several prime controlling factors of the marine environment which act simultaneously on early developmental stages and the situation becomes even more complex when the effects of limiting factors are integrated. As nearly as possible I have chosen examples in which control of most environmental variables allows reasonable assurance that temperature is the basic causative variable.

It has not been possible to use examples of marine species for all general trends presented. Thus, some of this review has been based on experiments conducted on freshwater or anadromous fishes.

(*a*) *Size*

Analyses of growth in fishes and the consequent states of size and form in relation to environmental temperature have been studied imperfectly; there is great need for extensive, controlled experimentation. General reviews of growth have been presented by ROUNSEFELL and EVERHART (1953), and BROWN (1957), the latter containing numerous considerations of the role of environmental factors including that of temperature.

In the great majority of fishes growth is more or less continuous throughout life, but it is characterized by a progressive diminution of the specific growth rate following inflection of the growth curve which occurs coincidently with sexual maturity. Since final size (final length) is not attained in most cases growth is 'indeterminate'. 'Determinate growth' is known to occur commonly in the families Poeciliidae and Cyprinodontidae. This condition is characterized by the attainment of a final size relatively early in the life-span, approximately coinciding with the onset of reproductive competence.

Recognition of the role of growth rate and the attainment of specific body sizes in fishes was stated by HUBBS (1926). He observed that those individuals of a species which grow more slowly, as a result of retarding environmental conditions such as lower temperatures, attain greater final sizes than those of the same species which exist in more accelerating conditions. The extent of applicability of this hypothesis, ontogenetically, is not known but there is some substantiation from laboratory studies.

Embryos of clupeid and salmonid fishes are frequent subjects for developmental studies because of their large size which facilitates mensuration and their slow pace of development. GRAY (1928), WOOD (1932) and MERRIMAN (1935) have

demonstrated that trout *Salmo trutta* incubated at higher temperature weighed less at hatching or at the completion of absorption of yolk than those which had developed more slowly at lower temperatures. Similarly, BLAXTER (1956) has shown that alevins of herring *Clupea harengus* tend to weigh less and be shorter through an increasing series of incubation temperatures. HALL (1925) and PRICE (1940) reported pronounced reduction in length of alevins of lake whitefish *Coregonus clupeaformis* with high incubation temperatures. Since these species have indeterminate growth, consideration of this early phase of growth, prior to active feeding, may not be a valid demonstration of HUBBS' statement. Fish culturists know well that, other conditions being similar, yearling salmonids which are incubated and reared at higher temperatures are considerably larger than those maintained in lower temperatures. Verification for such species would require many years to complete since most are capable of continuous growth to considerable ages.

Species of fish with determinate growth, however, can exhibit the phenomenon described by HUBBS. Studies on two cyprinodonts, the guppy *Lebistes reticulatus* by GIBSON and HIRST (1955) and the euryhaline desert pupfish *Cyprinodon macularius* by KINNE (1960a) and by SWEET and KINNE (1964), indicate that individuals incubated and reared at higher temperatures, although growing more rapidly through the earlier phase of independent life, eventually undergo such declines in specific growth rates that those growing at somewhat lower temperatures surpass the former groups and attain greater final sizes.

The observation frequently reported for aquatic poikilotherms (GUNTER, 1957), that individuals of species and species of genera which in either case are represented through considerable latitudinal ranges, tend to attain larger sizes in poleward or cooler latitudes, is apparently generally true for fishes. However, prior to the recent comprehensive survey by LINDSEY (1966), rather more credulity had been accorded to this notion than published analyses should have allowed. Reiteration of the early work of MÖBIUS and HEINCKE (1883) by several authors had been substituted for extended research and appraisal of the subject. LINDSEY provides a compilation of the maximum recorded lengths available to him, of more than 9300 species of fish from a broad range of ecoclimatic zones: 'arctic', 'cool temperate north', 'warm temperate north', 'tropical', 'warm temperate south' and 'antarctic'. The fishes are divided among three categories: 'freshwater', 'marine' and 'deep-sea' and data are presented as percentages of the total number of species lying within arbitrarily established lengths. In marine arctic species almost 30% have been recorded at lengths exceeding 80 cm whereas among tropical species the modal class of slightly more than 30% reached maximum length between 20 and 40 cm. Size distributions for species inhabiting intermediate latitudes are also intermediate. Abyssal species frequenting depths below 2000 m have even more pronounced latitudinal trends than neritic species. While the occurrence of larger body size in higher latitudes is established for marine fishes, the relation is even more pronounced in freshwater fishes of the four major continental masses. Approximately 60% of the maxima exceeded 40 cm for species collected above 60° N while 60% of the tropical forms were less than 20 cm. LINDSEY states emphatically that these data do not indicate the existence of more, larger species in cooler waters but rather, that a greater proportion of those

present has evolved in the direction of increased sizes, while those of the low latitudes have tended toward smaller body sizes, even though there has been more structural diversity.

The trends of global distribution of body sizes among fishes present further grounds for consideration of the role of temperature in the biogeographic 'size-rules' of BERGMANN and of ALLEN, cited frequently in survey texts of animal ecology. The rules were established for homeotherms from empirical studies. The rule of BERGMANN states that adult body size of individuals or races of a species increases with increasing level of latitude or in the cooler parts of its range. ALLEN's rule states that there are reductions in the proportional sizes of distal structures such as pinnae, tails and beaks in individuals or races of a species in the cooler regions of its range. Both sets of relations have been interpreted commonly as being adaptations favouring the retention of heat because of the relative reduction of radiating surfaces. SCHOLANDER (1955) has offered arguments against those relations as a mechanism sufficient to enhance an animal's survival in a cold habitat and he proposes, instead, circulatory control and insulation as the important adaptations. These rules, whatever their functional and structural bases, have only intraspecific importance and have little or no foundation among species or higher taxa of homeotherms.

Among poikilotherms, and fishes in particular, evidence suggesting that these rules have universal application is scant: thus they should be viewed with reservation. However, RAY (1960) attempts by some experimental evidence to support the extension of these rules. Unfortunately, his use of data from quite immature subjects, such as newly hatched alevins from HALL's (1925) study of *Coregonus* incubated at higher and lower temperatures, is hardly in keeping with the central notion of BERGMANN's rule. The valid approach, within a species of fish, would seem to be the comparison of samples of a chosen year-class, which had passed the stage of growth inflection, collected simultaneously from cooler and warmer areas of its range. Except in species having determinate growth, the expectation is that such a sample from the warmer locale would be larger if no density-dependent factors such as food competition were operative to prevent growth from reaching its thermally controlled maximum.

Perhaps, in the search for physiological adaptations to explain such trends, the emphasis of LINDSEY's (1966) findings should be shifted to reflect not the relative abundance of larger species but the relative and absolute scarcity of smaller species in cooler marine waters. From his data it is obvious that the number of tropical species exceeding a length of 80 cm is more than twice the total of arctic species examined. Many of the largest species habituate tropical latitudes. For example, elasmobranchs reach their greatest size in lower latitudes as do many teleosts including tunas (family Scombridae), billfishes (families Istiophoridae, Xiphiidae), sea basses (family Serranidae) and sunfishes (family Molidae). Thus, with numerous large species in both arctic and tropical waters, no particular benefit is obvious from the acquisition of large size as has been suggested in references concerning surface and volume relations. However, such relations might have some physiological importance toward the smaller end of the size scale. LINDSEY has suggested that, although confirmatory evidence is largely lacking, conservation of body heat may have some importance; quite small species,

therefore, would be at greatest disadvantage in cold waters. The subject invites considerable study.

Evidence from relative growth studies suggests that ALLEN's rule does not apply to fishes since lower temperature has induced the formation of both larger and smaller body parts. Also, the equivalence of the extremities of homeotherms and those of fishes as radiating surfaces has not been established. Fish are not liable to frost-bite!

A critical assessment of the available information, then, indicates that there is no justification for suggestions that BERGMANN's rule obtains among fishes. The rule was formulated to describe a phenomenon within species of homeotherms; it has not been established interspecifically for homeotherms nor intraspecifically for fishes. Therefore, any similarity in the latitudinal patterns of size distributions among fishes and mammals should be viewed as unrelated coincidence even though both phenomena are probably significant structural responses of positive adaptive value. Finally, while BERGMANN's rule holds equivocally through the geographic range for homeotherms, use of the rule could be attempted for marine fishes only poleward since many large species are also prevalent in lower latitudes.

(*b*) *External Structures*

Form is the consequence of the relative sizes of the various anatomic units which contribute to the marginal configuration in any plane. When rates of growth determined from linear measure of the various structural aspects such as body depth, girth, fins, eyes, head and its several parts, remain in constant ratio to the increase in total length the animal continues to have the same configuration. This uncommon situation is termed 'isometry' or 'isauxesis' (HUXLEY and co-authors, 1941). Generally, however, growth of any part changes at least once relative to the growth of the whole animal, a condition termed 'heterauxesis'. The accessory terms 'tachyauxesis' and 'bradyauxesis' signify respectively accelerated or retarded relative growth of a part or a dimension. Since growth of poikilotherms is controlled by temperature when other variables are optimal, the possibility exists then that relative growth of structures could be affected in such a manner that body form could be altered also.

Environmental influence on the form of fishes has been studied by MARTIN (1949), who employed logarithmic regressions of size of part on total size. MARTIN analyzed a broad range of marine, diadromous and freshwater species and found by graphic examinations that there were pronounced inflections in the regressions indicating changes in growth constants. Four inflections occur in the salmon *Salmo salar*, creating five growth stanzas. Data for other fishes, although less complete, suggest that this is a general phenomenon. These changes occur approximately at the 'eyed' embryo stage, hatching, onset of ossification and sexual maturity, respectively. He confirmed an earlier but not well documented idea which suggested that more slowly growing individuals have relatively smaller parts, within a species. However, MARTIN also found exceptions to this pattern in which slowly growing individuals had larger parts. The important finding in his study is that, in intraspecific groups, differences between more slowly growing and more rapidly growing 'populations' are among the intercepts rather than the

slopes of regressions. Therefore, the major control of body form is body size attained at the various growth inflections. Thus, growth rates during embryogeny and early post-hatching life have profound effects on the values of these intercepts. Hence temperature influences body form through its effects on the growth rate; although the relation is indirect it is of greatest importance in determining such form.

The expectation that form could be altered by variations in number of body segments probably can be dismissed. In various species of salmonids, for example, a reduction of 3 vertebrae (more or less equivalent to segments) can be expected from the slowest to the most rapidly developed embryos, which is a shift of approximately 5%. However, the concomitant reduction in length would be 30%. This suggests that segments are larger in the larger more slowly growing individuals, at least at hatching.

(c) *Internal Structures*

Both qualitative and quantitative phases of differentiation are labile and subject to the controlling influence of temperature on developmental metabolism. In fishes, the best known aspect of such plasticity is the modification of the number of parts in several of the organ systems. However, other developmental responses occur at various levels of structural organization. Those which can be considered to be deleterious are classified as teratologic conditions or 'terata'. Still other histologic and cytologic responses occur either during embryogeny or in later life, which appear to be innocuous or even essential.

Structural responses at the cellular level of organization to gradients of temperature are divisible into those which fall within the normal range of variation and those which are dysplastic anomalies.

Very little information is available on either qualitative or quantitative changes in tissues and cells within normal limits. Cellular responses probably are documented best for gonads where, in the great majority of fishes, there are repeated cycles of oogenesis and spermatogenesis (Hoar, 1957). However, in many species the influence of the cycle of natural light either confounds the analysis of causation or appears to be the prime stimulus. Seasonal increase in water temperature causes spermatogenetic changes in seminiferous tubules, and hypertrophy of interstitial cells, in the stickleback *Gasterosteus aculeatus* (Craig-Bennet, 1930) and in *Fundulus heteroclitus* (Burger, 1939). Merriman and Schedl (1941) found in the stickleback *Apeltes quadracus* that higher temperature is required for the maturation of spermatozoa while lower temperature is essential for the completion of oogenesis. In contrast, in the killifish *Fundulus confluentus* lower temperature is required during the early stages of oogenesis while higher temperature is essential for its completion (Harrington, 1959). In the unique, self-fertilizing euryhaline cyprinodont *Rivulus marmoratus* a large percentage of males can be induced by exposing embryos to low incubation temperatures. Ovarial tissue of the ovotestis degenerates (Harrington, 1967).

The possible effects of temperature acclimation on histologic changes in the thyroid gland of three teleosts, including the eel *Anguilla anguilla* produced no drastic cellular alterations except for a slight reduction in thickness of the

epithelium at the higher temperature (OLIVEREAU, 1955). The pancreas of elvers of *Anguilla anguilla* held for extended acclimations at 10° or 20° C responded more positively (PALAYER, 1963); the mass was greater, relative to either gross volume or cube of body length, for those held at 10° C, and the same was true for the surface area of the islets of Langerhans. Investigations of hepatocytes of mature rainbow trout *Salmo gairdneri* acclimated to 5° C and to 18° C by BERLIN and DEAN (1967), revealed an increase in size of the Golgi apparatus in trout acclimated to the lower temperature. Also, there were higher concentrations of particulate inclusions in the Golgi cisternae. This investigation, in which nearly all literature citations are drawn from studies of mammals, points to the great need for detailed research to elucidate structural alterations as the basis for the interpretation of physiologic processes in fishes.

The term meristic structure was established for bilaterally formed anatomic units situated serially about the longitudinal axis. Ordinarily, these are myomeres, vertebral elements, basalia and rays of the mesial fins, dermal bony scales and scutes. This definition has been extended gradually to include almost any set of similar structures such as gill-rakers, pyloric caeca and rays of the appendicular fins.

Numerical variability of gill-rakers has not been studied thoroughly and the meagre information available on the possible influence of temperature on their formation is conflicting. Latitudinal clines have been observed for anchovy *Engraulis mordax* by MCHUGH (1951) and for seven species of greenlings (family Hexagrammidae) by QUAST (1964). However, studies of various salmonids in lakes in Sweden (SVÄRDSON, 1965) and in Canada (VERNON, 1957) failed to show differences which could be related to developmental temperatures. Differentiation of rakers continues for some time during the postembryonal growth phase, and this poses a source of error when smaller specimens are included.

Apparently, the possibility that branchial filaments and their lamellae respond numerically to developmental temperatures during their differentiation has not been studied. This might prove to be an important ecological consideration, since the relative extent of respiratory surface has a pronounced influence on the activity and hence the niche assumed by a particular species. This was shown by GRAY (1954) for a representative array of marine fishes.

Variation in the number of pyloric caeca, although considerable among individuals of a species, has not been associated with developmental conditions in the few studies reported (VERNON, 1957; NORTHCOTE and PATERSON, 1960; MARTIN and SANDERCOCK, 1967). The formation of caeca parallels that of gill-rakers, increasing in number during early growth.

Reviews of meristic variability or ecogeographic 'rules' of structural clines regularly cite the inverse relation of the number of scale-rows to temperature or the direct relation to latitude. However, well-documented records which associate temperatures with scale variations are few and mostly concern freshwater species. HUBBS (1922) demonstrated that certain cyprinids of the North American Great Lakes produce more lateral-line scales when early development occurs in cooler waters. MOTTLEY (1934) produced the same trend experimentally in the trout *Salmo gairdneri*. QUAST (1964) studied latitudinal clines in lateral-line scales in Pacific hexagrammids and found direct relations between scale number and

latitude in half of the species (those which were studied through broader latitudinal ranges).

The only available study of variation in other dermal structures is that by HEUTS (1947), who investigated numbers of lateral scutes in the stickleback *Gasterosteus aculeatus*. His study was concerned with influence of salinity; but labile structures generally respond to a variety of factors, so further investigations seem desirable.

A study of the symmetry of form and of the numerical modification of branchiostegal rays which support the ventral opercular folds has been presented by CROSSMAN (1960) for several species of pike (family Esocidae) but without reference to conditions of developmental environments. The fact of variation, however, suggests the need for further study to determine whether trends occur in relation to environmental gradients.

Appendicular fins of fishes, while having no demonstrable relation to metamerism, except in Chondrichthyes, have serially differentiated rays which are subject to intraspecific numerical variation and considered to be meristic elements. Studies in natural populations of several species have yielded variable results. While MCHUGH (1954) reports a decline in the number of pectoral rays of the Pacific herring *Clupea pallasi* southward through a broad range of latitude, TESTER (1937) has been unable to find a trend in herring along the Pacific coast of Canada. The investigation of hexagrammids by QUAST (1964) revealed declines with decreasing latitude in several species. Laboratory studies employing controlled temperatures also give variable results. TÅNING (1944, 1952) found the highest counts at intermediate temperatures in *Salmo trutta*. LINDSEY (1954) an inverse trend to that of temperature in paradise fish *Macropodus opercularis*, and GARSIDE (1960) no trends in two salmonids. The ventral or pelvic fins have received little attention. GARSIDE (1960) was unable to show trends in ventral rays through a large range of developmental temperatures.

Intraspecific alterations in the number of rays in the mesial fins have been demonstrated in both laboratory and field studies but not without instances of contradictory results. The number of dorsal rays increases with increasing developmental temperatures in *Clupea pallasi* (HUBBS, 1925) and, with considerable variability, in the anchovy (MCHUGH, 1951). However, in eight hexagrammids QUAST (1964) found declines in numbers of both spinous and soft rays from northern to southern latitudes in the Pacific Ocean. Among the several laboratory investigations, LINDSEY (1954) reported the lowest number at an intermediate temperature in *Macropodus opercularis* and a reduction with increasing temperatures in *Gasterosteus aculeatus*. The number increased with increasing temperature in plaice *Pleuronectes platessa* (MOLANDER and MOLANDER-SWEDMARK, 1957). Trends having the highest counts at intermediate temperatures of development have been reported in several salmonids by TÅNING (1952), SEYMOUR (1956) and GARSIDE (1960). Rays of the anal fin are equally plastic but the direction of the trend sometimes opposes that for dorsal rays, even in the same samples, as shown by HUBBS (1925) for *Clupea pallasi* and by HEUTS (1949) for *Gasterosteus aculeatus*. Experimentally, the highest number occurs at an intermediate temperature in several salmonids (TÅNING, 1952; SEYMOUR, 1959; GARSIDE, 1960). Numerical determination of rays in the homocercal caudal fin apparently has been studied

only by LINDSEY (1954, 1962) in *Macropodus opercularis* and *Gasterosteus aculeatus*. Some *M. opercularis* produced an additional group of proximal segmented rays in the dorsal lobe at lower incubation temperatures. In both species there was a reduction in the number of rays with increasing temperature. Apparently, the possible environmental control of segmentation of rays has not been investigated.

Series of cartilaginous or bony elements, the basalia or pterygiophores, are situated midsagittally, distal to the vertebral column, and subtend the rays of the mesial fins. LINDSEY (1954, 1962), studying the influence of temperature on their plasticity, found the lowest number at an intermediate temperature in *Macropodus opercularis* but a decided reduction through the series of increasing temperatures in *Gasterosteus aculeatus*.

The aspects of structural plasticity which have been considered to this point concern those which might be termed the 'lesser' meristic structures since the primary motivation for the majority of these studies has been the attempt to elucidate the relation between environmental variables, principally temperature, and the more primary differentiation of mesoderm in the formation of axial segments and vertebrae. Historically, recognition of numerical variation in meristic structures, which are used widely as systematic characters, is credited to GÜNTHER (1861)[1] who observed that, within the wrasses (family Labridae), genera in seas of temperate latitudes had higher numbers of both abdominal and caudal vertebrae than those in tropical waters. Subsequently, GILL (1863) and JORDAN (1891) reported similar trends in vertebral number in many families having broad ranges of latitudinal distribution.

HEINCKE (1898) provided the first insight into intraspecific variation in meristic series of fishes in relation to geographic localization by statistical analysis of frequency distributions in his definitive racial studies on *Clupea harengus*.

The experimental approach to the study of meristic variability was introduced by SCHMIDT (1919, 1920). He incubated groups of embryos of the trout *Salmo trutta* at several constant temperatures, and subsequently observed that for any of the lots, each the progeny of a single pair, the lowest mean vertebral counts were produced at the intermediate temperature and the highest numbers were at the lowest temperatures. Thus, when these data were displayed graphically, the curves were of an asymmetrical V shape. SCHMIDT also performed experiments using the blenny *Zoarces viviparus* and found reduced vertebral counts associated with increasing temperature of development.

Since these beginnings a considerable body of information pertaining to meristic variation has accumulated, mostly concerning vertebrae. Extensive general reviews have been prepared by TÅNING (1952) and GARSIDE (1966); MOLANDER and MOLANDER-SWEDMARK (1957) reviewed meristic studies on *Pleuronectes* and BLAXTER and HOLLIDAY (1963) have listed the available studies on clupeids.

Most laboratory investigations have been performed on species which spawn in fresh water while most field studies have been conducted on marine forms. The findings of many of the laboratory studies are in agreement with those of the field studies, that vertebral number varies inversely with the temperature of development. When data on vertebral counts from field studies, for which adequate

[1] GILL (1863), JORDAN (1891) and authors of several subsequent reviews cite this date as 1862 but the date given in the title page of the Catalogue is 1859 to 1861.

records of temperature are available, are assembled graphically there is a single trend, that of decreasing number with increasing temperature. Broadly speaking, there is also an inverse relation between the temperature of superficial oceanic waters and latitude so that a direct correlation generally exists between latitude and vertebral number within species.

In considerable contrast have been results of some generally carefully controlled laboratory tests which, beginning with the experiment with embryos of *Salmo* by SCHMIDT (1919), have produced V-shaped curves indicating that, while vertebral number declines with increasing temperature, there is an inflection beyond which the number increases with further elevation of temperature. The V-shaped relation, because it differs from the observed natural situation should be treated as an anomalous occurrence. However, various investigators have attempted to formulate explanations from the opposite stand. SCHMIDT suggested that particular vertebral numbers were manifestations of the selective effect of temperature on various genotypes. Later, MARCKMANN (1954) found in *Salmo trutta* a remarkable parallel between the V curve for vertebral number and a plot of day-degrees calculated from an arbitrarily selected threshold temperature and the numbers of days of incubation at each temperature. He considered these products to be proper measures of metabolism and so the metabolic aspect of differentiation was most economical, requiring the least number of day-degrees at the intermediate temperature which produced the lowest number of vertebrae. BARLOW (1961) stripped this interpretation of plausibility by showing that the form of the second curve was controlled by the selected level of the threshold. He also argued that computation of day-degrees should be based on the absolute or Kelvin scale and by making this transformation with MARCKMANN's data, he found a simple decline in day-degrees with increasing temperature rather than a V curve.

Because of the absence of V curves in data for natural clines and because this configuration is not universal in results of laboratory studies, GARSIDE (1960, 1966) scrutinized experimental techniques for an explanation of this phenomenon. SCHMIDT (1919, 1920), TÅNING (1944, 1952), MARCKMANN (1954), and MOLANDER and MOLANDER-SWEDMARK (1957) have determined vertebral numbers by criteria involving vertebral arches rather than centra; they have assigned values greater than 1 to any complex vertebra, that is, a centrum bearing replicate neural and/or haemal arches. Complex vertebrae generally occur with much greater frequency at the extreme temperatures of incubation (MOLANDER and MOLANDER-SWEDMARK, 1957; SEYMOUR, 1959) so that additional counts would elevate the means at the terminal temperatures, and V curves would be created inadvertently. This could explain the discrepancy between the curves presented by TÅNING (1944) and those in his later study (1952). In the former, he showed V curves but with the highest mean counts at the lowest temperature while in the later study the highest counts were recorded at the upper incubation temperature, indicating, probably, the location of the greatest frequency of abnormality in each instance.

If the view is held that V curves are anomalous and that the norm is a decline in vertebral number through a series of increasing temperatures, then there is no problem of interpretation for results obtained in the transfer experiments in which embryos at various earlier stages are transferred temporarily either to higher or to lower temperatures for periods ranging from a few hours to a week, depending

on the species used and the embryonal stage initially involved (TÅNING, 1952; LINDSEY, 1954; ORSKA, 1962). These experiments invariably produce lower mean counts when the transfer is made to a higher temperature, relative to those of the corresponding control lots.

The observation of LINDSEY and ALI (1965) and others that the standard practice in experimental meristic studies of subjecting embryos to constant temperatures does not simulate natural conditions is open to some objection. They employed fluctuating temperatures to gain the desired effect for medaka *Oryzias latipes*, but failed to induce significant changes. However, most commonly used in such experiments are species from cool-temperate latitudes which produce demersal ova. Only such ova if resting in quiet shallow water, free of ice-cover, could be expected to be subject to fluctuating temperatures. In most of these species spawning occurs in massive bodies of water, either during the progressive warming of spring or the progressive cooling of autumn, so that significant fluctuations would be unusual. In fact, many species pass all but an early segment of their embryogeny in water having its temperature of maximum density. Even marine pelagic ova would be subject to rather limited thermal fluctuations in their relatively brief developmental period. Diel fluctuations on the other hand could be expected more frequently in lower latitudes where there is intense insolation and much re-radiation during the long nights. If significant temperature fluctuations were the general case and if differentiation in medaka was representative, then rather less natural meristic variation could be expected in fishes than is actually the case.

A more plausible explanation of changes in meristic series, based on developmental processes rather than direct elimination of rigidly determined phenotypes by selective effects, was advanced first by HUBBS (1926). He viewed the determination of vertebral and other meristic numbers as a phenomenon produced by the interplay of differentiation and growth responding to regulation by developmental metabolism. HUBBS offered the hypothesis that, relative to growth, differentiation would terminate under retarding conditions rather more slowly than under accelerating conditions so that more units would be formed. Subsequently, HUBBS and HUBBS (1945) predicted that the number of segments or vertebrae would be proportional to the space available, assuming units of similar size. Such space need not be available before differentiation of structures occurs, as is the case for somites and vertebrae, since the potential for differentiation must terminate ultimately and this provides the same effect. Support for HUBBS' interpretation was provided by GABRIEL (1944) who found in experimental studies on *Fundulus* that not only was vertebral number inversely related to developmental temperature, but that within any group at any temperature the more slowly developed embryos produced more vertebrae than those which developed more rapidly.

To reconcile the two basic trends in meristic elements, BARLOW (1961) proposed a model in which a relatively longer period for differentiation is derived from the assumption that growth has a high coefficient of temperature and thus will be retarded relatively more by decreasing temperature than will be the 'rate of formation of vertebrae' (apparently meaning 'differentiation'), which is assumed to have a lower temperature coefficient. This model is applied to the V relations

by the supposition that the apex of such a curve coincides with inflections in curves of the pertinent series of temperature coefficients.

The original proposition was investigated by GARSIDE (1966) who was able to demonstrate in salmonids an inverse relation between vertebral number and measure of the rate of development during an assumed period of numerical determination, a finding which is in keeping with HUBBS' (1926) hypothesis. This hypothesis and associated findings convey the notion that numerical variation in vertebrae is confined to terminal alterations of the peduncular region. This must be abandoned in the light of several other investigations since much or all of the change frequently occurs in the abdominal region. Also, results of temporary transfer experiments at various embryonal stages indicate that the formation of additional vertebrae can occur at any site along the serially developing column. The next step required in the attempt to elucidate this phenomenon is an exhaustive histologic evaluation of the nature and progress of embryonal differentiation produced by various developmental rates.

Numerical shifts in meristic series are not peculiar to the controlling effect of temperature on developmental metabolism. Such other prime environmental variables as dissolved oxygen, quantity and quality of light and salinity, can alter the metabolic rate of developing embryos. Levels of any of these entities which retard the observed pace of embryogeny are associated invariably with increased average values of such series (TÅNING, 1952; GARSIDE, 1966). Thus there can be little doubt about the central role of the rate of developmental metabolism in the extent to which differentiation of structural series can proceed.

Latitudinal clines in meristic series, vertebrae particularly, are observed not only within species but also among species and this situation has phylogenetic implications. JORDAN (1891) recognized the predominance of malacopterygian species in higher latitudes and a preponderance of the more highly evolved acanthopterygians in tropical latitudes. The latter group is characterized, with relatively few exceptions, by having fewer than 40 and mostly less than 30 vertebrae while the more primitive malacopterygians have more than 40 with a broad spectrum ranging to 70 in salmonids and to more than 100 in various eels. JORDAN reasoned that the phylogenetic decrease in vertebral number is a manifestation of increasing specialization which he termed, "ichthyization, the intensification of fish-like characters". He viewed the trend as the consequence of differential intensity of 'natural selection' between the relatively uniform conditions in the waters of high latitudes or depths in tropical seas and, on the other hand, the highly variable circumstances of tropical pelagic and littoral environments which promote many adjustments of structure and function. Such an interpretation of the differences between these regions obviously does not include thermal conditions, which are generally more variable, polewards. FISCHER (1960) makes a diametrically opposite interpretation, suggesting that the physical aspects of the tropical environment are relatively constant and that those of higher latitudes are most variable and hazardous. His explanation of the more rapid and more extensive speciation in the tropics is based on the premise that environmental temperatures approximate thermal optima of animals and so permit the preservation of a wider range of structural and functional variation. FISCHER also suggests that conditions in lower latitudes have been free of significant alterations

for a considerable span of time during which mutation and selection have proceeded and have produced the diversity now evident.

The parallel between the phylogenetic trend of vertebral number and the latitudinal and vertical patterns of water temperature in the great seas implies that reduction has selective survival value in warmer conditions or, perhaps more indirectly, with other circumstances accruing in warmer waters of low latitudes. The phenomenon, whatever might be its explanation, is not related to size trends in fishes since both very large and very small species of acanthopterygians have low vertebral number.

Teratologic formations occur rather infrequently in samples of wild fishes because of their negative survival value. For instance, MANION (1967) reported several instances of abnormal structure of the trunk in a few thousand silt-bound ammocoetes of four species of lamprey (family Petromyzontidae) collected in the North American Great Lakes, but none was detected in the trunks of more than 250,000 adult specimens from the same locale. However, abnormal individuals of many species occur with some frequency in cultures and they can be induced in the laboratory by exposing embryos, in various stages of development, to unusual levels of natural physical agents such as temperature, or to unusual chemicals. Resulting structural alterations often form more or less continuous series, deviating progressively from the accepted normal condition to that which is judged to be gross deformity.

Aberrant structural conditions cannot be organized readily into a simple classification because of their diversity and also because of the problem of appreciating the limits of normality. The latter difficulty is especially obvious in the 'normally' plastic characters, proportional dimensions and meristic series, in which relatively broad ranges rather than precise singular values must be accepted.

The definitive laboratory study of terata in fishes was conducted by STOCKARD (1921) on embryos of *Fundulus heteroclitus* and a trout, presumably *Salvelinus fontinalis*. He induced a variety of anomalies by the application of temporary but sudden and drastic reductions in temperature. STOCKARD grouped deformities as '*monstra in defectu*' with structural deficiencies, or '*monstra in excessu*' with supranormal differentiations. In the former category are anomalies of the eye (anophthalmia, microphthalmia, monophthalmia and cyclopia), bilateral asymmetry of the brain and numerous dysplastic developments of the dermocranial elements, the mandibles and branchial arches. Reduction of abdominal and peduncular regions also were reported. Supranormal monsters are twinned forms in which there are separate heads and varying degrees of anteroposterior duplication of the trunk region which are determined by the angle of arc separating the anlage of the embryonic shields. When the angle reaches the maximum of 180° the embryonal axes are totally separate, the shared yolksac forming the only union. Another important contribution to knowledge of teratologic formation in marine fishes is the comprehensive study by BATTLE (1929) of the rockling *Enchelyopus cimbrius* (family Gadidae). Exposure of rockling embryos to extreme temperatures of the biokinetic range produced deformities of the eyes, inner ears, brain, mandibles, pericardium, notochord, myotomes and fins. BATTLE also presents an extensive review of earlier studies of the occurrence and induction of terata.

Anomalies of vertebral centra and their arches have been discussed by KÄNDLER (1935), GABRIEL (1944), ORSKA (1956) and GARSIDE (1959, 1960). They include serial fusions of centra, accessory arches on centra and asymmetric alignment of bilateral elements of centra and arches. Vertebral columns also develop various gross derangements including permanent bends directed either laterally or ventrally, about the level of the anus; others are coiled permanently.

The central role of developmental rate in the initiation of anomalous structures and gross deformations was recognized first by STOCKARD (1921). He concluded that temporary suppression of developmental processes would induce various deformities, the type being controlled as well, by the stage of development which is involved. He also observed that the same anomaly is induced by various inhibiting agents when applied at the same developmental stage. This has been confirmed more recently by ALDERDICE and co-authors (1958) and GARSIDE (1959). Since their experimental treatments were conducted at levels which are plausible natural conditions, one can speculate with some assurance that such structural disturbances do occur in nature but that those which are afflicted generally succumb in early life so that the incidence is apparently extremely rare.

(*d*) *Conclusions—Structural Responses*

There is a growing body of information which indicates that in fishes there are structural responses to gradients of ambient conditions which are particularly active during embryogeny. Rigid genotypic control, which casual students of classical genetics expect, frequently is not operative in some aspects of development. Thus the phenotype is also a product, even more subtly perhaps, of the tonic and the limiting variables of the environment, particularly temperature, regulating the rates of differentiation and growth.

The nature of phenotypic expression is related to the degree of stress imposed by the level of the variable. Drastic but sublethal retardation or acceleration of developmental rates generally produces acute dysplasia of the several organ systems, rendering such individuals inadequate to survive beyond the alevin stage. Within the normal range of developmental rates the interaction of differentiation and growth produces a variety of morphologic and anatomic responses. Slower rates produce larger final size in fishes having determinate growth but this probably is not applicable to most species in which growth is indeterminate. Form is influenced indirectly by the regulation of body size at growth inflections. Usually, constituent regions or structures tend to be relatively smaller in more slowly developed individuals.

Information concerning structural responses during development, at cellular and intracellular levels, is lacking. However, even brief temperature shifts can alter cells and tissues in the viscera, endocrines and gonads of mature fishes. Patterns of change in temperature are sometimes important for the maturation of gametes.

Meristic structures have the most widely demonstrated developmental plasticity. The general, but not invariable, trend is the reduction in number of such structures with increasing developmental rate. Although studies of this phenomenon point strongly to the interaction of differentiation and growth rather than selective action by various environmental conditions, a complete explanation is lacking.

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