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.

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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

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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

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VOLUME II

Physiological Mechanisms

Part 2

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FOREWORD

to

VOLUME II: PHYSIOLOGICAL MECHANISMS

'Physiological Mechanisms' deals with synthesis and transversion of organic material, regulation, evolution and population genetics, and orientation to environmental components in space and time. It is subdivided into 2 parts which contain the following chapters:

Part 1

Chapter 1 : Introduction to Volume II
Chapter 2 : Mechanisms of Chemo-autotrophy
Chapter 3 : Mechanisms of Heterotrophy
Chapter 4 : Mechanisms of Thermoregulation
Chapter 5 : Mechanisms of Ion and Osmoregulation
Chapter 6 : Mechanisms of Evolution and Population Genetics

Part 2

Chapter 7 : Orientation in Space: Plants
Chapter 8 : Orientation in Space: Animals
    8.0 General Introduction
    8.1 Invertebrates
    8.2 Fishes
    8.3 Mammals
Chapter 9 : Orientation in Time : Endogenous Clocks

Why a volume on **Physiological Mechanisms** in a treatise on **Marine Ecology**? Because ecology comprises more than the description of organismic assemblages and food-chain interrelationships. Because studies on functions and structures of living systems and their relation to the environment are based on knowledge of the essential mechanisms effective at the individual level. Because proper synthesis requires pertinent analytical detail. We cannot assess, comprehend and forecast the ecological dynamics of life in oceans and coastal waters without taking into account the physiological mechanisms involved in biotransformation of energy and matter, in metabolic regulation, in population genetics and in orientational behaviour.

The term 'ecology' has been coined by the German biologist E. HAECKEL, and defined as the science investigating the natural relationships of organisms, both to their inorganic and organic environment. HAECKEL's original definition has subsequently been enlarged to encompass life as a whole and practically all earth sciences ('Gesamthaushalt der Natur'), and it has been reduced, e.g. to population dynamics, community structure, biogeography, or to flow charts of energy and matter through living systems. Between these extremes, a variety of definitions has been offered, based on prevailing concepts and perspectives in different countries, schools of thought and individual investigators. We adhere to the original definition: ecology comprises studies of organisms in relation to their environment, abiotic and biotic.

Based on many disciplines, ecology is a primarily synthetical science. Ultimately, ecology attempts nothing less than to provide the key for comprehending history, present and future of life–environment correlations. Present-day organisms and ecosystems are the result of thousands or millions of years of interaction between living systems and their environment. There is every reason to assume that comparable interrelations will also control and determine the future of such systems. Can there be anything more important on this earth than to know and to apply the principles which support and maintain healthy communities of life? Can there be a better rationale for man's existence than to preserve and to sustain, rather than to misuse and degrade life on earth?

The difficulties involved in organizing and completing the Treatise on Marine Ecology are formidable—more so than we have anticipated. The seemingly inexhaustible body of information available increases exponentially, sometimes competing acutely with the reviewer's 'digestion rate'. There is progressive specialization in the three basic areas of marine ecology—microbiology, botany and zoology—and new subfields with narrow perspectives and specific terminology develop like grain in the summer sun after a warm rain. While such specialization affords advantages, it also leads to fragmentation and loss of synthetic potential. Insufficient integration and lack of comprehensive, critical assessments of the 'state of the art' begin to hinder effective scientific progress and often lead to endless repetitions of studies, ultimately insufficient for comprehending the functions and structures of complex living systems. We have experienced these difficulties in numerous discussions concerning volume scope and detailed chapter outlines.

Fortunately, encouraging support has come from many sources: all contributors, numerous colleagues and several institutions. Most of the work concerning organization and editorial preparation of Volumes II and III was completed while on a 'Senior Foreign Scientist Fellowship'—supported by the National Science Foundation of the United States of America—at the Department of Zoology of Arizona State University, Tempe, Arizona. It is with great pleasure that I gratefully acknowledge this assistance, and the help and kindness received from the Chairman Dr. S. D. GERKING and the members of the Department of Zoology, as well as from my assistants Valerie CLARK and Helga WITT. Among the colleagues who offered advice and criticism regarding Volume II, the following deserve special mention: Drs. H.-P. BULNHEIM, M. S. GORDON, K. H. LÜNING, M. M. MULLIN, D. SIEBERS. Assistance regarding individual chapters is acknowledged at the end of the respective chapter.

O. K.

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PHYSIOLOGICAL MECHANISMS

7. ORIENTATION IN SPACE: PLANTS

K. SEITZ

(1) Introduction

(a) General Principles of Spatial Orientation in Plants

Spatial orientation of plants is controlled by environmental factors (Volume I). Orientation responses can be brought about by locomotion, by changes in growth direction or by induction of polarity in germinating cells. In addition, there are intracellular orientation movements of cell organelles (i.e. plastids). Accordingly, depending upon the plant, four response types can be distinguished which result in orientation relative to the environmental stimulus:

(i) In freely moving plants, such as planktonic flagellates and algae which glide on the ground (blue-greens, diatoms and desmids), orientation involves locomotion towards or away from the stimulus. Such orientation responses are known as **taxis** or **tactic responses**; with light as orienting stimulus the process is called phototaxis (pp. 458, 465).

(ii) In terrestrial plants and attached benthic marine algae, orientation responses involve a change in growth direction. This type of orientation is known as **tropism**, i.e. phototropism (stimulus: light) or geotropism (stimulus: gravity; p. 476).

(iii) In originally apolar germinating cells (spores or zygotes) which do not move freely and have not begun to grow, the polarity direction of future development can be determined by directional environmental stimuli (**induction of polarity**, p. 480).

(iv) Intracellular orientation **movement of chloroplasts** occurs between different walls of the cell as a function of light conditions (p. 483).

Nastic movements will not be discussed here, since their directive components are determined by the anatomy of the plant organ concerned and bear no direct relationship to the inducing environmental factors.

All orientation responses of plants are initiated by an external stimulus, which must be perceived by the cell. The stimulus induces a reaction sequence of biochemical and physiological processes which bring about the response. Accordingly, we can distinguish several elements in an orientation response: (i) The effective stimulus; (ii) the perception of this stimulus; (iii) the perception of the direction of the stimulus; (iv) the primary molecular and secondary physiological processes of the action mechanism; (v) the orientation response itself. In addition to this reaction sequence there are (vi), the tonic processes controlling amount and direction of the response (HAUPT, 1965a). The orientation response may be directed towards the source of the stimulus (positive response); or it may be directed away from the stimulus (negative response).

In this review only well-analysed responses are described in detail. These are mainly positive responses. Wherever possible, marine or freshwater plants have been selected as examples. Since plant physiologists have devoted, thus far, little attention to orientation of marine plants the responses must be described and discussed mainly on the basis of available knowledge from limnic and terrestrial forms. It is hoped, however, that this chapter will stimulate the investigation of orientation responses and their ecological significance in marine plants.

(b) Effective Stimuli

Practically all physical or chemical parameters of the environment can be effective as orienting stimuli if they act in a unilateral direction upon the plant. The best investigated and apparently most important stimulus is light; it controls phototaxis, phototropism, induction of polarity and orientation movement of chloroplasts. Consequently, the elements of orientation responses will be discussed in greater detail for light.

Water movement, chemical gradients (ions or other dissolved substances) and gravity are also effective stimuli, controlling rheo-, chemo- or georesponses. Much less is known about the importance of temperature, pressure, electric or magnetic fields, and mechanical contact (thigmoresponses) as orientation stimuli.

Most of these factors act not only as inducing and orienting stimuli; they are also effective via tonic processes, which control the disposition of the plant to respond to an orienting stimulus. Tonic effects operate via a different reaction sequence and interact with the orientation responses.

Light especially can influence orientation responses; this is known from geo- and phototropism (AUDUS, 1969; CURRY, 1969) and also from phototaxis of flagellates (NULTSCH, 1970; FEINLEIB and CURRY, 1971a). Light is effective in these cases mainly by photomorphogenic responses through the phytochrome system or by supplying energy or substrates for the response via photosynthetic processes.

(c) Perception of Light as Orientation Stimulus

Incident light quanta are absorbed by a photoreceptor. This is a pigment molecule or chromophoric group, usually bound to a protein *in vivo*. The chemical nature of the photoreceptor can be determined from an action spectrum of the response, since only light absorbed by the photoreceptor can induce the response (SHROPSHIRE, 1972). Action spectra generally agree in their form with the absorption spectrum of the responsible photoreceptor pigment (e.g. Figs 7-9 and 7-15). This agreement can be disturbed by the presence of shadowing pigments or by interference of other light-dependent reactions. As a consequence, action spectra sometimes yield no information about the photoreceptor (e.g. *Nitzschia*, Fig. 7-6). Some variations in action spectra may also be caused by differences in experimental conditions (e.g. Fig. 7-9) and by use of different objects (e.g. Fig. 7-15).

Effective photoreceptors in plant orientation are chlorophylls, biliproteins, phytochrome, and riboflavin. Chlorophylls and biliproteins can supply energy, redox equivalents or carbohydrates via photosynthetic processes. Phytochrome is the red–far-red reversible pigment system controlling photo-morphogenesis of plants (Briggs and Rice, 1972; Mohr, 1972). Instead of riboflavin, carotinoids are often considered as photoreceptor in the responses induced by blue light. Such alternative is still an open question (Thimann, 1967; Bergman and co-authors, 1969; Curry, 1969). Photochemical data are, perhaps, more in support of flavin as photoreceptor.

Light is radiant energy in the form of electromagnetic waves (Volume I: Jerlov, 1970); in linearly polarized light, the vibration is restricted to one plane. Polarized light can be absorbed only if the vibrational direction of its electric vector is oriented parallel to the direction of the electron transition moment in the photoreceptor. Accordingly, experiments with polarized light can provide information about the orientation and, indirectly, about the location of a photoreceptor in the cell. From such experiments, which reveal an action dichroism of linearly polarized light, it is known that the photoreceptor is often localized in the peripheral, non-moving cytoplasm in or near the plasmalemma and oriented preferentially parallel to the cell surface.

With increasing irradiance more photoreceptors are excited and thus a higher rate of primary reactions is induced. This conveys to the plant a measure of the intensity of the incident light. In addition to the absorption of light and the registration of its intensity, the perception of its direction is essential for an orientation response.

(d) Perception of Light Direction

The basis for the perception of light direction is unequal absorption of light in relation to its direction at different sites of the plant. Such absorption gradient can be realised by different mechanisms or principles in a plant cell or organ, depending upon the specific anatomical structure (Haupt, 1965b; Haupt and Schönbohm, 1970; Feinleib and Curry, 1971a).

The first of these mechanisms is the shadow principle (Fig. 7-1). As light passes through the cell, it is attenuated by absorption; for instance, in a shadow pigment. In a multicellular plant, scattering at cell walls can also effect an attenuation. Due to attenuation, a reduced irradiance is transmitted to the rear part: less light is absorbed by the photoreceptor in the rear than in the front, resulting in a front-rear gradient of effective light absorption. This gradient provides the plant with information on the light direction.

Two other principles—the lens principle and the by-passing principle—are based on light refraction. In the case of the lens principle, the plant cell functions as a converging lens, concentrating the light in a focus at the rear of the cell (Fig. 7-1). This makes it possible for more light to be effectively absorbed in the photoreceptor at the rear part of the cell than in the front. Thus a gradient of light absorption is established. The direction of this gradient relative to the external light direction is inverse in comparison to that established by the shadow principle. The lens principle can be demonstrated experimentally by placing the cell in a medium with a refractive index higher than that of the cell (e.g. paraffin oil, $n = 1{\cdot}57$). The cell then functions as a diverging lens and the direction of the orientation response is reversed. As a consequence of the converging light path caused by the refraction of light, there is a range at the flanks, where no direct light reaches the peripheral

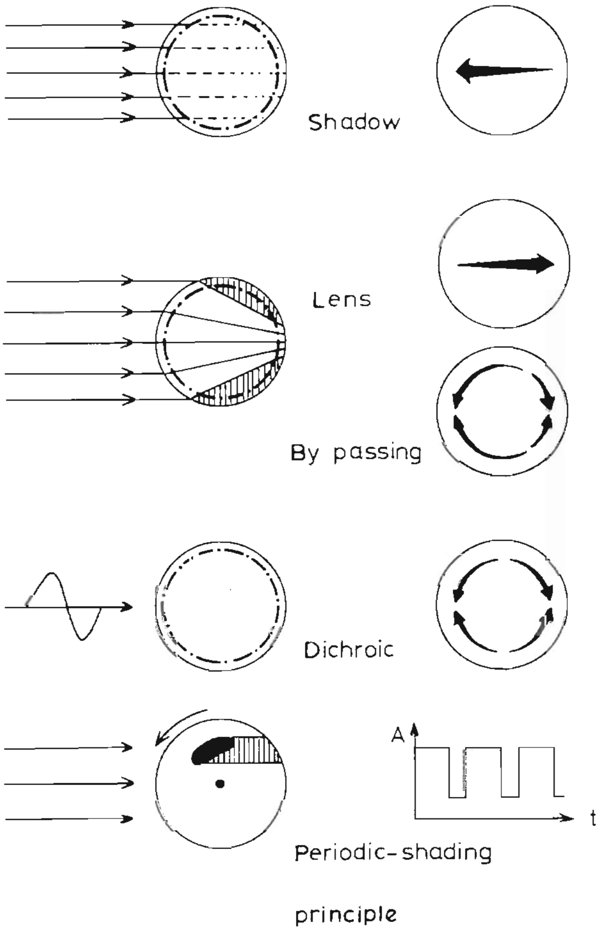

Fig. 7-1: Principles effective in the perception of light direction in plants. Schematic illustration of light path and resulting absorption gradient in cells. Dots or dashes: photoreceptor molecules. Heavy arrows: absorption gradients (pointing from low to high absorption). A: absorption; t: time. (After HAUPT 1965b and HAUPT and SCHÖNBOHM 1970; modified; reproduced by permission of John Wiley & Sons Ltd., London and Wissenschaftliche Verlagsgesellschaft, Stuttgart.)

cytoplasm. This peripheral by-passed zone receives no light, except that scattered from other cell parts. Hence the flanks receive much less light than the front and rear parts of the cell. So this by-passing principle establishes an absorption gradient between front or rear parts and the flanks of the cell (Fig. 7-1).

One prerequisite for these two principles is that the cells must be sufficiently transparent so that no antagonistic shadow gradient is established. Another prerequisite is that there must be a sufficiently great difference in the refractive index between cell interior and ambient medium. Since the refractive index of the cell is on average about 1·4, the difference will be greatest in air ($n = 1{\cdot}0$) and much reduced in fresh water ($n = 1{\cdot}33$) or sea water ($n = 1{\cdot}34$).

Besides shading and light refraction, a fourth mechanism can be effective in the perception of light direction: the **dichroic principle.** This principle is based upon the differential action of linearly polarized light. The photoreceptor must be oriented parallel to the cell surface in the peripheral cytoplasm; then polarized light, vibrating with its electrical vector parallel to the cell surface, will be absorbed. Light vibrating perpendicularly to the cell wall will not be absorbed. In-between orientations can be divided vectorially into two components, oriented either parallel or perpendicular. In a more or less transparent cell, polarized light oriented parallel to the longitudinal direction of the cell will be absorbed equally at all sites on the cell's cross-section. Hence there will be no gradient of absorption. Light vibrating perpendicularly to the cell axis, on the other hand, will be absorbed only at the front and rear side of the cell—not at the flanks. Thus an absorption gradient results between front or rear parts and the flanks of the cell (Fig. 7-1). In the natural environment, usually only unpolarized light is effective. Yet this unpolarized light can be thought to consist of one half polarized parallel and the other half normal to the longitudinal cell axis. The portion vibrating parallel will again be absorbed equally well all around the cell. The part oriented normal to the cell axis, on the other hand, will be absorbed only at the front and rear walls of the cell. Thus also unpolarized light can establish an absorption gradient by the dichroic principle.

In many cases, more than one of these principles is effective in the perception of light direction. The dichroic principle, especially, may be involved in most cases, since the photoreceptors (except photosynthetic pigments and carotinoids) are located in the peripheral cytoplasm or in the plasmalemma in a surface-parallel orientation.

In all four principles described above, the plant is not moving. Hence there is a constant spatial relationship between the cell and the light source during the perception of light direction.

In freely moving plants, with continuously changing spatial orientation, the direction of light cannot easily be detected by such a spatial absorption gradient in the cell. A different mechanism can be effective here—the dynamic **principle of periodic shading.** In this principle, the light direction is not measured instantaneously by a spatial intensity gradient in the cell, but serially by comparing the change of light absorption in the photoreceptor in two different positions of the cell during the movement. In unicellular plants which rotate during locomotion, the photoreceptor can be located inside the cell. In unilateral light a shading device (stigma), located on one side of the cell, then casts its shadow once per rotation upon the photoreceptor. This periodic shading causes a periodic change of absorption by the photoreceptor and thus provides the cell with information on the direction of light in relation to its longitudinal axis (Fig. 7-1). If the plant is oriented symmetrically to the light source (light coming from the front or the rear) no periodic shading will occur.

(e) Physiological Mechanisms of the Orientation Response

The first step in the reaction chain leading to a light-induced response is the absorption of a quantum (photon) which results in excitation of the photoreceptor. The photoreceptor then initiates a photochemical reaction. This primary photochemical process can be a redox reaction (electron transfer) or a conformational change in a protein. The latter may be an enzyme or a structural protein in a membrane. So the primary effect can be a change in the activity of an enzyme or in the permeability of a membrane. Analogous primary effects can be considered for other stimuli. In many cases, the stimulus is perceived in the cell membrane (plasmalemma) which transforms the external signal into intracellular processes. Details about the molecular mechanism of the primary processes are not yet available for most of the orientation responses to be described. Some speculative considerations are presented to stimulate further investigations.

Regarding the physiological mechanism of orientation responses, no general concept can be offered; the reactions involved will be described individually in the different sections. In each case the orientation response depends upon the metabolism of the cell. This may involve mainly the energy supply in case of movements; or the availability of substrates and the rate of protein- or cell-wall synthesis in case of growth reactions. Changes in metabolism often document themselves as tonic effects.

(f) Orientation as a Cybernetic Control Mechanism

The ecological significance of orientation responses lies primarily in keeping the plant in an environment optimal for growth and reproduction. Since homeostatic mechanisms are involved in these responses, control of orientation can be compared with a cybernetic control system (Fig. 7-2). The effective external stimulus acts as a signal, turning cellular processes on or off, usually without supplying the energy or motive force for the response. The deviation of the direction of the signal from the desired optimal orientation (the set point) is measured (perception of direction)

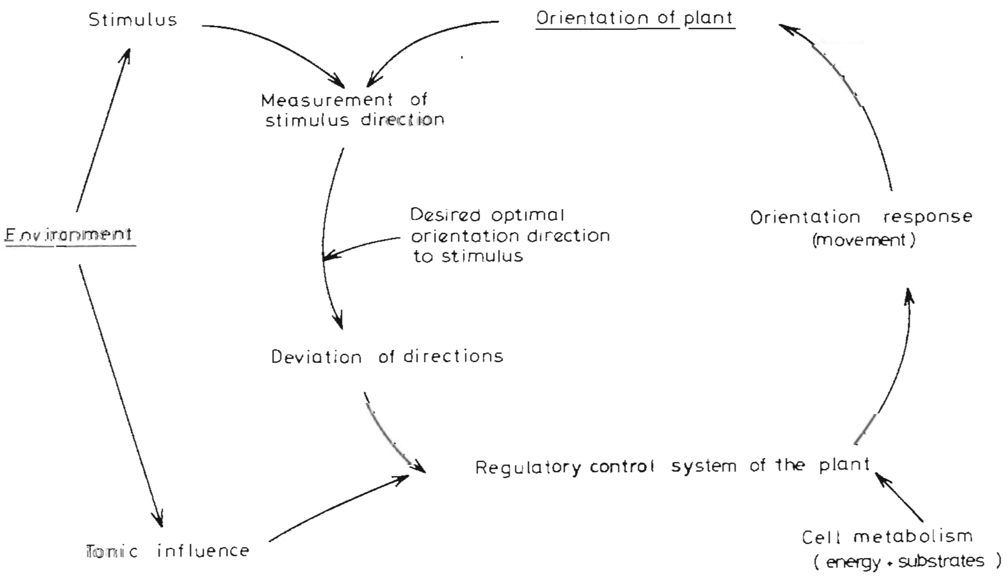

Fig. 7-2: Reaction scheme for control of spatial orientation in plants. (Original.)

and is effective as an error signal. The orientation response is then initiated as a regulating mechanism, which proceeds until the optimal orientation is attained again.

The optimal orientation may be variable, that is, it may be set to different values due to tonic effects, depending upon metabolic and environmental conditions. In some cases the control system can be effective only during a short period of sensitivity; for instance, in the induction of polarity. If orientation responses of plants operate like a cybernetic control system, it should be possible to entrain oscillations of the response under special conditions. This has indeed been observed in the geotropism of *Helianthus annuus* (ANDERSEN and JOHNSSON, 1972).

Orientation responses of plants are, like those of animals (Chapter 8), controlled by a complex interaction of various processes. The stimulus light, for instance, can be effective in the control of orientation in 3 different ways: Light can act as inducing stimulus; it can tonically control the amount and direction of the response; and it can supply energy or substrates via photosynthetic reactions.

(2) Orientation via Locomotion

(a) General Aspects

Orientation of freely moving plants to light involves 3 different light-dependent movement responses or photomotions: **phototaxis, photophobic response and photokinesis** (NULTSCH, 1970).

Phototaxis, or phototopotaxis, is a directed movement towards (positive phototaxis), or away from (negative phototaxis), the light source. It is related strictly to the direction of the incident light.

The photophobic response, also called photophobotaxis (for definitions consult HAND and DAVENPORT, 1970; CHECCUCCI, 1973; NULTSCH, 1973), is a brief change of movement, usually a sudden stop and resumption of movement combined with a change in the direction (reversal response). The photophobic response is induced by sudden temporal changes in the intensity of light. It is independent of the direction of incident light. The phobic response can be easily demonstrated in a light trap—a bright light field surrounded by a field of reduced light intensity. In a light trap, phobic responses can occur upon crossing of the border. Such crossing, being a movement through a steep gradient of irradiance, causes a sudden change in irradiance perceived by the organism. A positive phobic response, which is induced by a sudden decrease in irradiance, results in aggregation of freely moving plants in the light trap.

A negative photophobic response, which is induced by a sudden increase in irradiance, results in a depletion of the light trap. Experimental errors can be caused by the fact that, besides the phobic response, also phototaxis and photokinesis can be involved in the aggregation of organisms in a light trap (NULTSCH, 1970).

Photokinesis is an effect of light on the speed of movement leading to a steady level in dependence upon irradiance. In positive photokinesis the speed of the movement is increased in comparison to the dark rate; in negative photokinesis it is decreased.

Photophobic response and photokinesis do not depend upon the direction of light; but these responses can interact with, and contribute to phototaxis. In some cases (*Euglena gracilis* and *Volvox aureus*), the photophobic response constitutes an essential part of the phototactic orientation mechanism; in other cases (species of *Phormidium*), it has no obvious relation to orientation.

Positive or negative responses generally occur within a certain range of irradiance. Positive photophobic response and positive phototaxis are usually observed under medium irradiance, and negative phobic response and phototaxis under high irradiance. Since the direction of the response depends upon tonic conditions (p. 451), the response can be positive or negative under identical irradiance, depending upon the experimental conditions, and it can change quickly from one direction to the other. This variability in the response complicates the experimental investigation of photomotions. Another complication can arise from interactions of chemotaxis with the photomotion responses.

Photomotions have been observed in bacteria, flagellates, gliding algae and motile, propagative forms (gametes or zoospores) of sessile algae and fungi. Reviews on these responses have been provided by HAUPT (1959, 1966), BENDIX (1960), HALLDAL (1962) and NULTSCH (1970). Methods and problems regarding the measurement of photomotions have been reviewed by HAND and DAVENPORT (1970) and by CHECCUCCI (1973).

(b) Phototaxis in Flagellates

Phototaxis of Volvox aureus

General characteristics

In the multicellular colonies of *Volvox aureus*, the cells are located at the periphery of a hollow sphere. Each cell has two flagella. The active beat of these flagella is directed obliquely backwards in a constant relation to the main axis of the colony. This results in forward movement and rotation of the whole colony around its main axis. About 8 secs are required for 1 rotation around the axis and the speed of forward movement is about 1 mm sec^{-1} (HUTH, 1970). *V. aureus* colonies normally exhibit positive phototaxis; but negative phototaxis can also be observed. About photokinesis of the colony movement no details are known.

In the induction of positive phototaxis in species of *Volvox*, blue light is most effective, with a maximum in the action spectrum around 490 nm. Hence a yellow pigment is the photoreceptor, the chemical nature of which is still unknown. Since a movement response of the *V. aureus* colony depends upon reactions of the single cells, the analysis of the colony's orientation must begin with an investigation of the photomotion response of the single cells.

The photophobic response

In a single cell of *Volvox aureus*, a sudden increase in illuminance induces a stop response of the flagella in the range of medium illuminance (about 1500 lux—considered to be 100% in this section). This stop response is a typical phobic response; since it occurs upon an increase in light intensity, it is a negative photophobic response. The flagella stop in a characteristic position ('Sperrstellung') and remain in this position for several seconds. A return of the light intensity to the original level immediately terminates the stop response and causes resumption of flagellar activity in the original direction. The duration of the stop response depends upon the degree of the intensity change. It lasts about 3 or 9 secs, e.g. if the illuminance is changed from 50 to 100% or from 0 to 100%, respectively. Even an illuminance change of 60 to 100% is sufficient to elicit a response. This difference in light intensity agrees well with the change a single cell experiences during its movement from the shaded to the lighted side of a unilaterally illuminated colony, since the transmission of the colony in the blue range of the spectrum is about 50 to 60% (HUTH, 1970)

Phototaxis

Due to the rotational movement of the *Volvox aureus* colony the single cells pass, in unilateral light, alternately from the light to the shadow side of the colony. Upon transition from the shaded to the lighted side, which effects an intensity increase from about 55 to 100%, a stop response is induced. The flagella on the shaded side remain active so that the colony moves on, and the cells from the lighted side are moved again to the shaded side, where the flagellar activity is resumed (HUTH, 1970). In other words, all flagella on the shaded side beat, whilst those on the lighted side rest. This results in a mechanical turning impulse, as in a rowing boat, causing the colony to orient toward the light. Accordingly, the direction of light is perceived in *V. aureus* by the dynamic principle of periodic shading, and phototactic orientation of the colony is caused by the sum of phobic responses of the single cells.

In case of negative phototaxis in the high irradiance range, on the other hand, the stop response would have to be induced by a decrease in irradiance in order to bring about an orientation away from the light source.

In the colony there is a gradient in the sensitivity of the cells to irradiance changes and in the characteristics of the stop response: the front cells are more sensitive than the rear ones (HAND and HAUPT, 1971). Hence the most effective response regarding the orientation is induced in the front region of the colony. In addition to shading by the colony a specific shading by the stigma in the single cells may be involved in the perception of small angle variations in light direction (HUTH, 1970). Nothing is known about the light-induced secondary reactions leading to the stop response.

Phototaxis of Euglena gracilis

General characteristics

The unicellular flagellate *Euglena gracilis* has one long emerging flagellum which is inserted in an open vacuole on the ventral side in the front end of the cell (Fig. 7-3). A second, non-emerging flagellum joins the long flagellum at the paraflagellar swelling. Near this swelling, on the dorsal side of the cell, is the stigma—a conglomerate of about 20 to 50 globules containing yellow and orange pigments (xanthophylls and carotenes) with a broad absorption maximum between 400 and 500 nm (TOLLIN, 1969). The cell also contains several (about 12) chloroplasts.

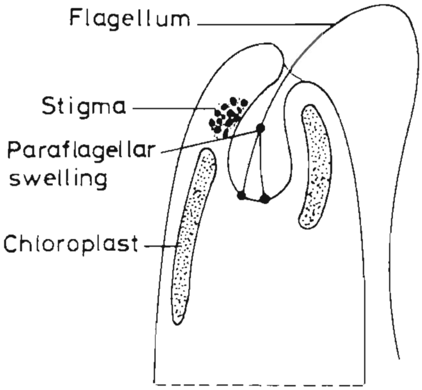

Fig. 7-3: *Euglena gracilis.* Schematic cross-section through front end. (Original.)

Studies with mutants showed that for normal positive phototaxis the stigma, the paraflagellar swelling and the chloroplasts are necessary.

The flagellum curves ventrally backwards. The motive force of the flagellar undulations is generated by contractile, ATP-consuming filaments. The forward movement of the cell is combined with a rotation around its longitudinal axis. The speed of the forward movement is about 0·15 mm sec^{-1}, and the cell rotates 1 to 2 times per sec (JAHN and BOVEE, 1968). The photomotions induced by light comprise, besides photokinesis, a photophobic response and phototaxis. The responses are elicited by blue light and are intimately interrelated, as in *Volvox aureus.*

The photophobic response

In the range of medium irradiance, *Euglena gracilis* responds with positive phototaxis; upon sudden reduction of such irradiance falling upon a swimming *E. gracilis,* a phobic response is induced. In this response the flagellum reacts in a specific way with one single beat to the ventral side. Due to this side stroke, the front end of the cell is turned towards the dorsal side. As soon as the cell is adapted to the new incident irradiance, the flagellum resumes normal beating and *E. gracilis* swims in a different direction. As a result of such positive phobic responses to a sudden decrease in irradiance, *E. gracilis* individuals accumulate in a light trap.

The light-sensitive region lies in the front of the cell: only here can a flagellar response be induced. This agrees well with the assumption that the photoreceptor is most probably located in the paraflagellar swelling. The extent to which details of the phobic response of *Euglena gracilis* can be compared with the stop response in *Volvox aureus* remains to be analysed. The physiological mechanism in the flagellum may be similar (p. 459) even if *Volvox* responds to an increase and *Euglena* to a decrease of irradiance in the medium intensity range.

Phototaxis

Because of the rotational movement in a unilaterally irradiated *Euglena gracilis,* the stigma casts its shadow on the photoreceptor once every turn. This induces a brief phobic response, i.e. beat of the flagellum to the ventral side. Hence, once per rotation the cell's movement is changed towards the stigma on the dorsal side, i.e. towards the light source. This phobic response is re-induced every turn until the cell is oriented towards the light source in such a way that there is no further periodic shading of the photoreceptor caused by the stigma (HAUPT, 1959, 1966; FEINLEIB and CURRY, 1971a). Accordingly, the phototactic orientation of *E. gracilis* is caused by a series of photophobic responses, and the direction of light is perceived by the principle of periodic shading.

Under high irradiance, which induces negative phototaxis, the phobic response must be assumed, in analogy to the above, to be induced by irradiance increase. The response should be elicited when the shadow of the stigma moves away from the photoreceptor.

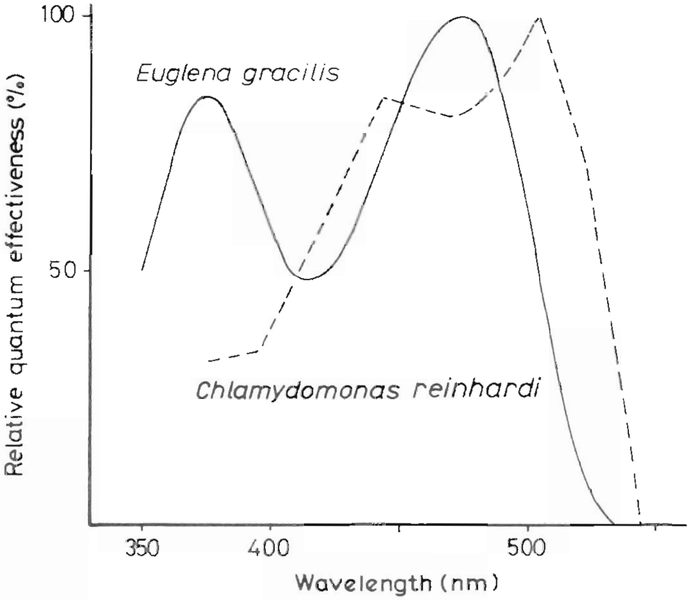

Fig. 7-4: *Euglena gracilis* and *Chlamydomonas reinhardi*. Action spectra of positive phototaxis. (After DIEHN, 1969a, and NULTSCH and co-authors, 1971; modified; reproduced by permission of Elsevier Publishing Co., Amsterdam and Springer-Verlag, Heidelberg.)

Action spectra of phototaxis have peaks in the blue range of the spectrum, mainly at about 375 and 475 nm (Fig. 7-4). This indicates that a yellow pigment, most probably a flavin, absorbs the light (DIEHN, 1969a). Action spectra from other investigations show peaks around 490 and 420 nm (HAUPT, 1959); in one case also red light has been found to be effective (WOLKEN and SHIN, 1958). In the phototaxis of *Euglena gracilis* the effective range of irradiance is broad. The threshold for phototactic responses lies around 0·5 erg cm^{-2} sec^{-1} of blue light (DIEHN and TOLLIN, 1966). The transition from positive to negative phototaxis occurs at about 10^4 to 10^5 erg cm^{-2} sec^{-1} in white light (DIEHN, 1969b); but dose-response curves covering the whole range of effective intensities have not been published so far.

Very high intensities ($> 3 \cdot 10^5$ erg cm^{-2} sec) of blue light suppress all phototactic movement (TOLLIN and ROBINSON, 1969).

Photokinesis

Positive photokinesis has been observed in *Euglena gracilis*. Light increases the speed of movement by about 50%. The effect reaches this maximal level at an illuminance of about 300 lux. Blue (465 nm) and red (630 nm) light are most effective (WOLKEN and SHIN, 1958).

Mechanism of light action

Experiments with inhibitors yielded the following results: Uncouplers of oxidative phosphorylation, such as 2,4 dinitrophenol or azide, inhibit motility and phototaxis in *Euglena gracilis*. On the other hand, DCMU (3-[3,4-Dichlorophenyl]1-1-dimethyl urea), which inhibits photosynthetic electron flow, inhibits only phototaxis without affecting cell motility. This indicates that the photosynthetic electron flow and/or the accompanying photophosphorylation are essential for the orientation response. Such assumption agrees with the observation that only cells which contain chlorophyll are capable of a positive phototactic response.

In one hypothetical mechanism suggested, light controls the supply of ATP from photosynthetic phosphorylation. A sudden change in the irradiance is assumed to induce a pulse of ATP, which would then cause the flagellar reaction in the phobic response (DIEHN and TOLLIN, 1966; TOLLIN, 1969; FEINLEIB and CURRY, 1971a). Further speculation about this mechanism is presented on p. 492. Some difficulty in this model arises from the question how pulses in ATP supply can be transmitted fast enough from the chloroplast to the flagellum to elicit the phobic response and from the fact that most of the action spectra do not imply chlorophylls as effective photoreceptors.

In another suggested mechanism, light induces a change in electric membrane potential, which, being propagated as an action potential, could control flagellar activity in the photophobic response. The change in membrane potential could be induced either by a sudden change in the photosynthetic electron flow (NULTSCH, 1970, 1973) or, more directly, by the photoreceptor in the paraflagellar swelling (JAHN and BOVEE, 1968; BOVEE and JAHN, 1972).

Phototaxis in Chlamydomonas reinhardi *and* Gyrodinium dorsum

Two other flagellates, *Chlamydomonas reinhardi* and *Gyrodinium dorsum*, differ in some respects from *Euglena gracilis*. *G. dorsum* has no stigma which could serve as a specific shading organelle, and in *C. reinhardi* the stigma is located far from the flagellar basis in the chloroplast (FEINLEIB and CURRY, 1971a). But the plastids could function as a shading device, at least in *G. dorsum*. Both organisms have two flagella. *G. dorsum* rotates around its axis during the movement like *E. gracilis*. But *C. reinhardi* probably moves without rotation (NULTSCH and co-authors, 1971); hence there can be no periodic shading of the flagellar basis, which in this flagellate even bears no structure comparable to the paraflagellar swelling in *E. gracilis*. Accordingly, both flagellates probably differ from *E. gracilis* in the mechanism of perception of light direction and in the reaction leading to phototactic orientation.

Gyrodinium dorsum responds to increase in irradiance, for instance to a transition from dark to blue light of medium irradiance, by cessation of locomotory movement: it turns and resumes swimming in the direction towards the light source. This reaction takes only about 0·5 sec. Hence in the sequence of events there is first a phobic stop response, then phototactic orientation. *G. dorsum* must perceive the direction of light by a spatial gradient of absorption in the cell; a mechanism of orientation based on repetitive shading and phobic responses, as in *Euglena gracilis*, would require much more time (HAND, 1970).

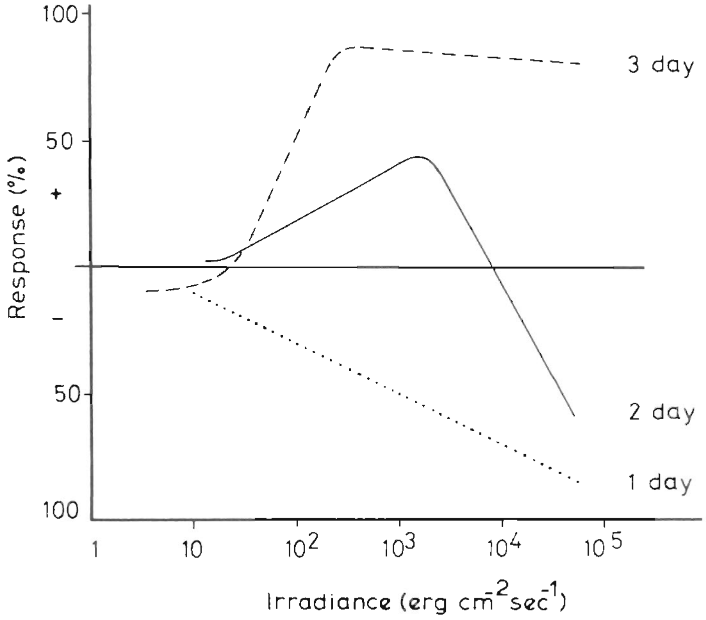

Fig. 7-5: *Chlamydomonas reinhardi*. Dose-response curves of phototaxis. 1-, 2-, and 3-day-old cultures. Irradiation with broad band blue-green light. (After FEINLEIB and CURRY, 1971b; modified; reproduced by permission of Scandinavian Society for Plant Physiology, Copenhagen.)

In *Chlamydomonas reinhardi*, the onset of light also induces a stop response within 0·1 sec. The cells remain motionless for a short time, then they resume swimming in a new direction. If the direction of unilateral light is changed, the cells swim in the new direction after a lag period of about 0·2 to 0·5 sec only. In *C. reinhardi* orientation can also be induced by very short light flashes in the μsec range (FEINLEIB, 1972). Such flashes are too brief to allow a change in position of the organism whilst the light is on.

According to these experimental results, the principle of periodic shading cannot be effective in the perception of light direction, neither in *Chlamydomonas reinhardi* nor in *Gyrodinium dorsum*. Among unicellular flagellates, *Euglena gracilis* is apparently rather unique with its stigma and with the periodic shading of the photoreceptor. However, also in *E. gracilis* an orientation response (in this case measured as density change of the population in a light trap) can be induced by light flashes of only 0·001 sec duration. This effect was explained on the basis of phobic responses (DIEHN, 1969b).

In *Chlamydomonas reinhardi* and *Gyrodinium dorsum* the effective intensity ranges and the wavelength dependence of photomotions are very similar to those in *Euglena gracilis*. Dose-response curves for phototaxis in *C. reinhardi* are presented in Fig. 7-5. The negative response of the 3-day culture at low irradiance—if significant—may be of interest for further research. Action spectra reveal highest effectiveness in the blue region (Fig. 7-4), but give no specific information regarding the photoreceptor. In *G. dorsum*, also the phytochrome system is involved in the control of phototaxis (FORWARD and DAVENPORT, 1968).

Control of Phototactic Sensitivity and Transition from Positive to Negative Response

Most plants tested exhibit positive phototaxis at low to medium, and negative phototaxis at high, irradiance. But the tendency for the plant to respond positively or negatively at a given irradiance is not only a function of this irradiance. The phototactic sensitivity and the direction of the response are controlled by internal and external factors via tonic processes (HAUPT, 1966; NULTSCH, 1970).

Internal factors are the age of the individual or culture and diurnal changes in motility or in phototactic sensitivity. Young cultures of *Chlamydomonas reinhardi* respond negatively, older ones positively to the same range of irradiance (Fig. 7-5; FEINLEIB and CURRY, 1971b). Diurnal rhythms in movement and in sensitivity to light are known from many organisms (see also Chapter 9). In *Euglena gracilis* general motility of cells is high during the day and low during the night (BRINKMANN, 1966). In *Gyrodinium dorsum* and in *E. gracilis*, phototactic sensitivity is high during the day—with maximum response early in the morning—and low during the night (DIEHN and TOLLIN, 1966; FORWARD and DAVENPORT, 1970).

Environmental factors which control phototactic responses are light, temperature, CO_2 supply, and ionic composition of the medium. For example, phototaxis depends strongly upon the light conditions effective during pretreatment and upon the relative concentrations of Mg^{++} and Ca^{++} (HAUPT, 1959; HALLDAL, 1962; NULTSCH, 1970).

The control of phototactic sensitivity by all these factors is rather complex and this may be the cause of some contradictory results reported in the literature. The degree of response variability due to environmental factors and age can be reduced by standardized pretreatment conditions and by the use of homocontinuous cultures (NULTSCH and co-authors, 1971; see also Volume III, Chapter 4).

Ecological Significance of Phototaxis in Planktonic Flagellates

Phototaxis may be involved in diurnal vertical migrations of marine planktonic flagellates (Chapter 9). Many of these organisms move up towards the surface during the day and sink downwards at night. The migrations can be related to the diurnal rhythm of phototactic sensitivity (FORWARD and DAVENPORT, 1970). In the vertical migration of the phytoplankton, 3 components are effective: active movement of the organisms, changes in their buoyancy, and turbulence of the surrounding water. Non-moving organisms, like centric diatoms, can migrate only by changing their density and thus their buoyancy relative to that of the water, for instance by accumulation of oil. Such 'passive' movement can also be present in motile organisms. The rate of sedimentation of actively moving unicellular phytoplankters is dependent upon their general motility and upon phototactic migration (Brinkmann, 1966; Forward and Davenport, 1970). The main question is whether the active phototactic movement is sufficient to bring about effective vertical migration. The speed of phototactic organisms such as *Chlamydomonas reinhardi*, *Euglena gracilis* and *Gyrodinium dorsum* is 0·1 to 0·3 mm sec^{-1}, which makes about 0·7 m hr^{-1} if the movement proceeds along a straight line. Accordingly, the cells could cover a considerable distance during the day and could thus compensate their daily sedimentation.

The irradiance is highest at the water surface, and the flagellates respond here with negative phototaxis; they move downwards and leave the brightest zone; by doing this, they may possibly avoid photochemical damage. With increasing depth, irradiance decreases and the range is approached at which the phototactic response changes from negative to positive. The flagellates then begin to move upwards again. Ultimately, they will tend to aggregate in a depth zone of medium irradiance with optimum conditions of irradiation for photosynthetic CO_2 fixation. The actual depth of this zone naturally depends upon environmental factors such as temperature, salinity, CO_2 supply and brightness of the sky. Presumably, the zone of medium irradiance coincides with the zone of maximum organic-matter production (Steemann Nielsen, 1960). In great depths with prevailing blue and blue-green light, the high phototactic sensitivity of flagellates to blue light appears to facilitate survival.

(c) Phototaxis in Gliding Algae (Blue-Greens, Diatoms and Desmids)

Phototaxis in Phormidium *species*

Characteristics of the movement

Species of the filamentous blue-green alga genus *Phormidium* (Oscillatoriaceae) glide on solid ground. In the movement, continuous secretion of mucilage results in the formation of a sheath, which surrounds the filament and assures good contact to the ground. Contractional waves on the cell surface, passing along the filament from end to end and acting upon the sheath, are considered to generate the motive force. The filaments thus glide in their sheath, displacing it backwards; associated with the movement is a rotation of the filament around its longitudinal axis (Drews and Nultsch, 1962; Halfen and Castenholz, 1970). Due to this locomotory mechanism, movement and changes in direction are rather slow in comparison to the flagellates. The actual speed of forward movement is about 0·1 mm min^{-1}.

Normally, under conditions of diffuse light, the direction of the movement changes autonomously; the filaments move at intervals of about 10 mins, alternating directions. There is no morphologic polarity in the filaments; both ends are equivalent, and the reversal of the direction in this shuttle movement occurs without a preference for one direction. Photomotions of blue-green algae have been investigated mainly by NULTSCH (1970, 1973).

The photophobic response

As response to a sudden decrease in irradiance, a decrease in movement rate and movement stop are induced (positive photophobic response). After a brief rest, the movement is resumed in the opposite direction. Under special conditions, a negative photophobic response can also be induced, i.e. response to increase in irradiance. The most sensitive region is the momentary front region, but all cells can respond independently. This implies some co-ordinative mechanism in the response.

The photophobic response has been investigated in *Phormidium uncinatum*. In white light, the threshold of the positive phobic response is near 1 to 20 lux. An optimum in the response is reached at 5000 lux; still higher illuminance again reduces the accumulation of individuals in the light trap. *P. uncinatum* filaments are very sensitive to changes in intensity; the discrimination threshold is reached at an intensity change of 5% (NULTSCH, 1970).

Action spectra of the positive photophobic response show peaks at 550–560, 610 and 670–680 nm; this suggests that the photosynthetic pigments phycocyanin, phycoerythrin and chlorophyll *a*—even if there is only a small response in blue light—are effective as photoreceptors. The action spectrum closely parallels the action spectrum of CO_2 fixation.

The photophobic response can be suppressed by inhibitors of the photosynthetic electron flow. This indicates that a change in the rate of photosynthetic electron flow causes the phobic response. Changes in the photosynthetic electron flow could be effective as changes in the redox state of the cell; and this, in turn may cause a change in a membrane potential. But, as in *Euglena gracilis*, changes in the rate of ATP supply from non-cyclic photophosphorylation—which is coupled to the electron flow—have also been discussed as possible action mechanism in the photophobic response (NULTSCH, 1970).

Phototaxis

In unilateral light, a phototactic movement of *Phormidium* sp. filaments towards the light source can be observed. This phototaxis is based on the following mechanism of orientation: There is no active steering; orientation is brought about by a trial and error system. Unilateral light changes the rhythm of the autonomous shuttle movement by controlling the reversal system. In filaments, which by chance are oriented more or less parallel to the direction of the incident light, reversal is retarded when moving towards the light source, and when moving away from the light, reversal is promoted. Filaments oriented perpendicularly to the light direction are not affected by the light. But they are bound to change the direction of their movement accidentally due to unevenness of the ground, and thus will orient parallel to the light direction.

The perception of light direction is presumably caused by an absorption gradient in the cells. In the filament the momentary front region is most sensitive, but all cells can respond to the light. Consequently, there must be some coordination between perception of light and movement direction (HAUPT, 1966; TOLLIN, 1969).

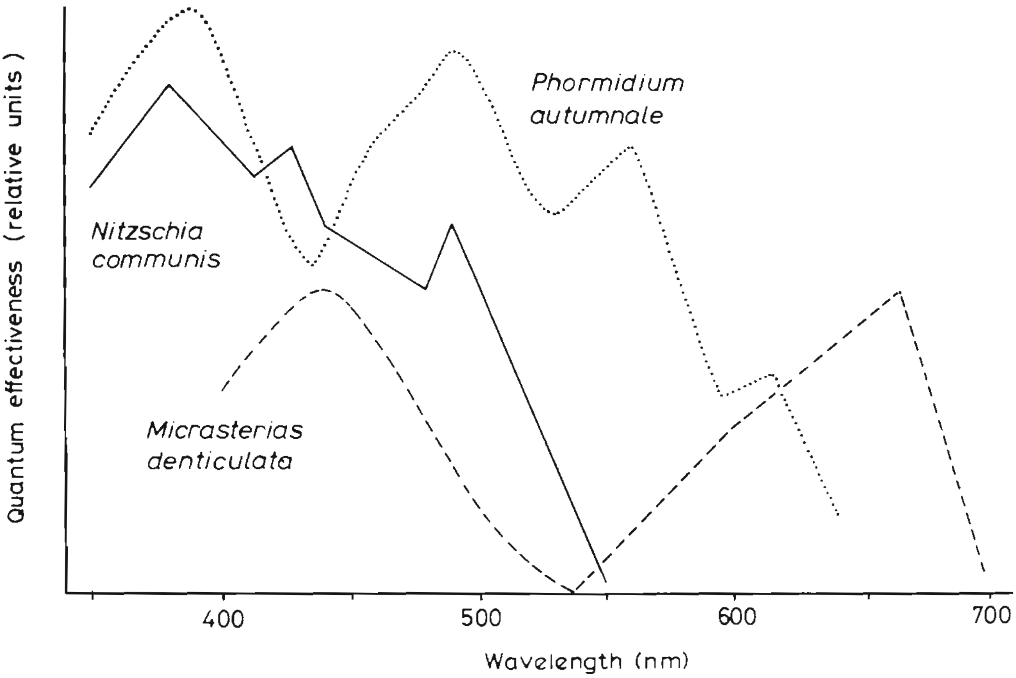

Fig. 7-6: Action spectra of positive phototaxis in gliding algae. The curves are shifted along the ordinate. (*Phormidium autumnale*; after NULTSCH, 1961, 1962; reproduced by permission of John Wiley & Sons Ltd.; *Nitzschia communis*; after NULTSCH, 1971; reproduced by permission of Microforms International Marketing Corporation; *Micrasterias denticulata*; after NEUSCHELER, 1967; reproduced by permission of G. Fischer, Stuttgart.)

In white light, the illuminance threshold of positive phototaxis of *Phormidium autumnale* and *P. uncinatum* lies at about 5 lux. The response reaches an optimal level around 200 lux; it then decreases until, at 10^4 lux, no phototactic movement can be induced. Other species of *Phormidium* show negative phototaxis at an illuminance above 10^4 lux. Action spectra of positive phototaxis have maxima in the near-u.v. range at 380, in the blue at 490, and in the green at 560 to 570 nm (Fig. 7-6). This indicates that a flavin and the biliprotein phycoerythrin are the photoreceptors.

In blue-green algae, the relation between phototaxis and the phobic response is not as clear as in *Euglena gracilis* or *Volvox aureus*. Both positive responses are similar as far as movement towards the direction of the more illuminated half of the filament is favoured. This could suggest a similar mechanism; but the different peaks of the action spectra contradict this possibility.

Photokinesis

In *Phormidium autumnale* and *P. uncinatum*, photokinesis has been investigated as the rate of spreading of filaments from a spot of inoculation. This rate is about 3 to 4 mm hr^{-1}. Filaments of *P. autumnale* and *P. uncinatum* are mobile in darkness. Irradiation changes the rate of movement. The threshold for the increase in rate (positive kinesis) is at about 0·02 lux. The speed of movement then increases with illuminance and reaches a maximum at 2000 lux. At higher illuminance, the rate of movement decreases again, until at about 30,000 lux the movement is retarded by light in comparison to the dark rate.

The action spectrum of positive photokinesis has peaks in the blue at 430 to 440 nm and in the red at 670 to 680 nm and shows good effectiveness at still longer wavelengths. These peaks suggest chlorophyll as photoreceptor. Accordingly, light is effective in photokinesis most probably by supplying additional ATP from photophosphorylation (NULTSCH, 1970).

Phototaxis in Anabaena variabilis

In the blue-green alga *Anabaena variabilis* (Nostocaceae), the mechanism of phototactic orientation is different from that in *Phormidium* species. In *A. variabilis*, orientation is achieved by active change in movement direction. In unilateral light, the filaments form a U. The bent portion of the U is oriented towards the light source, and its branches are symmetrically oriented parallel to the light beam. Both halves of the U glide at the same speed. The filament does not rotate around its axis during the movement. Upon a change in light direction, bending occurs towards the light until the U is again oriented symmetrically to the light. The bending is caused by a different behaviour of the lighted and shaded side. During bending, the lighted side is retarded in its movement (NULTSCH, 1970).

The action spectrum of photokinesis shows only one broad peak in the red range (600–670 nm); this corresponds to the absorption of phycocyanin and chlorophyll *a*. Blue light has no effect here; this is in contrast to results obtained from *Phormidium*, but it agrees with the action spectra of photosynthesis in these algae (NULTSCH and HELLMAN, 1972). Action spectra of phototaxis and of the photophobic response have, so far, not been investigated in *Anabaena variabilis*.

Phototaxis in Nitzschia communis

Diatoms of the order Pennales exhibit gliding movement due to secretion of mucilage and a motive shearing force generated along the raphe (DREWS and NULTSCH, 1962). As in the blue-green alga genus *Phormidium* there is no morphologically defined polar differentiation into front and rear end of the cell. The diatoms also perform autonomous reversals in the direction of their movement. Orientation is achieved by a mechanism similar to the trial and error method employed by *Phormidium* species. The rate of movement is about 10 μm sec^{-1}.

Photomotions have been investigated in greater detail in the earth-living diatom *Nitzschia communis*, but they are also known from marine diatoms. In *N. communis* positive phototaxis occurs in white light between 2 and 10,000 lux, with a maximum in the response at 200 lux. Action spectra of phototaxis and of the photophobic response show one broad maximum near u.v. or blue range with peaks at 380 (Fig. 7-6) or 450 nm, respectively. Conclusions regarding the photoreceptor cannot be derived from these spectra. In contrast, the action spectrum of photokinesis has maxima in the blue (at 430 nm) and in the red (at 680 nm); this suggests chlorophyll to be the photoreceptor (NULTSCH, 1971).

Phototaxis in Micrasterias denticulata

Desmids like *Micrasterias denticulata* glide on the ground. The locomotory mechanism secretes mucilage from two pores at the rear end of the cell. Orientation of the movement is effected by an active mechanism: differential rates of mucilage secretion from the right or left pore force the cell to turn into a new direction. The speed of movement amounts to only 1 to 2 mm hr^{-1}.

In white light, positive phototaxis has an extremely low threshold illuminance of about 10^{-4} lux; over a broad intensity range it extends to 10^3 lux. Higher illuminance elicits a negative response. The action spectrum has peaks in the blue (at 450 nm) and red (at 660 nm; Fig. 7-6). These peaks are attributed to different photoreceptors, which may also induce different primary processes (NEUSCHELER, 1967).

In *Micrasterias denticulata*, photokinesis exhibits an interesting dose response curve. In blue and red light, the threshold of the positive response is around 0·1 erg cm^{-2} sec^{-1}; positive photokinesis reaches a first maximum at 30 erg cm^{-2} sec^{-1}. At higher irradiances, the response decreases again, until at 10^3 to 10^4 erg cm^{-2} sec^{-1} a minimum (under special conditions also a negative response) is reached; at still higher irradiance a second increase of positive response is caused. The minimum in the dose-response curve of photokinesis occurs in that intensity range, where in phototaxis the transition from positive to negative response is observed. As in *Euglena gracilis*, photosynthetic inhibitors block phototactic orientation but do not reduce motility of *M. denticulata* cells (NEUSCHELER, 1967).

(3) Orientation via Growth Processes

(a) Phototropism

General Aspects

Phototropism is a differential growth response of sessile plants and their organs to light. Phototropism results in the well-known orientation of the main shoot axis towards the light (**positive phototropism**) and of the roots away from the light (**negative phototropism**). The leaves, on the other hand, are brought into a position oriented perpendicularly to the direction of light. Phototropism has been investigated mainly in the coleoptile of *Avena sativa* (THIMANN, 1967; CURRY, 1969) and in the transparent cell of the *Phycomyces* sporangiophore (BERGMAN and co-authors, 1969). But phototropic responses can also be observed in the protonema of mosses and ferns, and in algae.

Phototropism in the Avena sativa *Coleoptile*

Perception of light

The phototropic response of the coleoptile is a curvature in the direction of light (Fig. 7-7). It can be induced by short irradiations; the curvature begins to develop about 15 mins thereafter. The threshold intensity of the response lies, in white light, at an illuminance of about 1 to 10 lux. The dose-response curve shows a characteristic

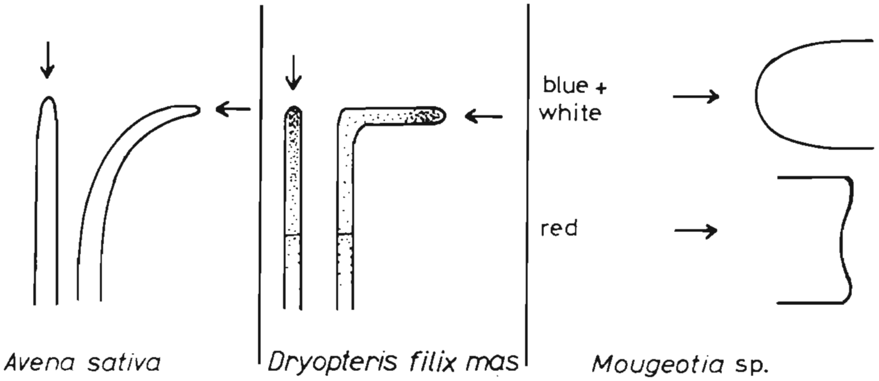

Fig. 7-7: Phototropic response in a higher plant organ (coleoptile of *Avena sativa*), a cryptogamic protonema (*Dryopteris filix mas*), and a filamentous alga (*Mougeotia* sp.). Arrows indicate the direction of incident light. (*D. filix mas* and *M.* sp. schematized after MOHR, 1956 and NEUSCHELER-WIRTH, 1970; reproduced by permission of Springer-Verlag, Heidelberg and G. Fischer, Stuttgart.)

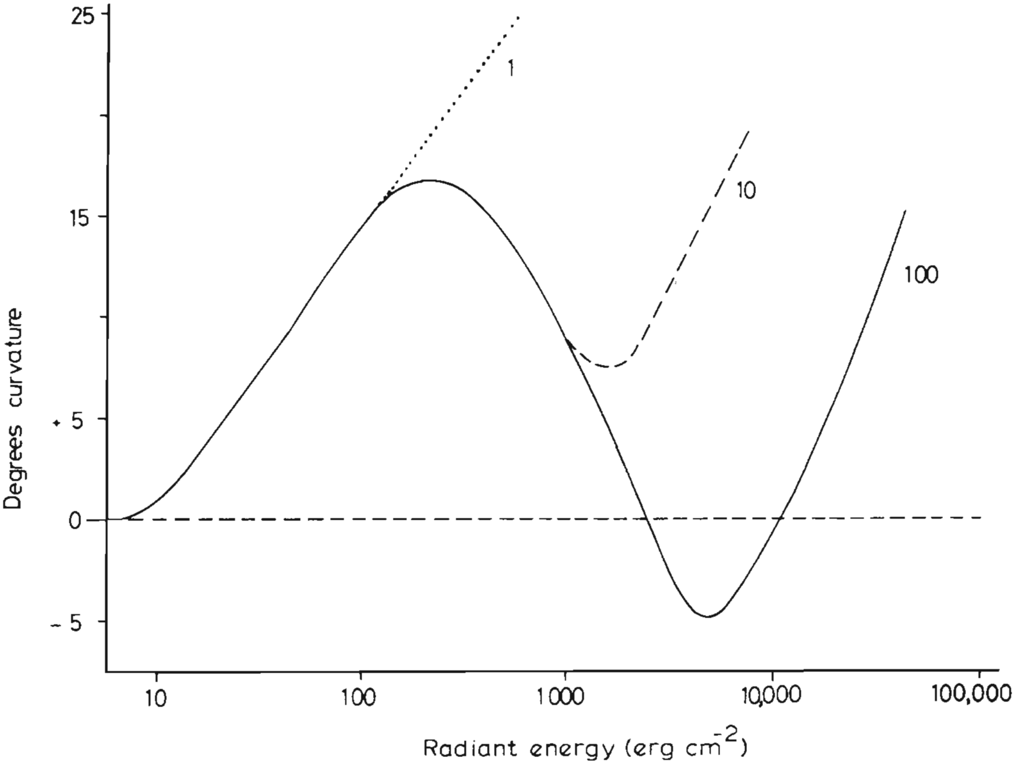

Fig. 7-8: *Avena sativa*. Dose-response curve of coleoptile phototropism, obtained after irradiation with 3 different irradiance levels of blue light (430–480 nm); 100 corresponds to about 50 erg cm^{-2} sec^{-1}. (After EVERETT and THIMANN, 1968; modified according to data from BLAAUW and BLAAUW-JANSEN, 1970, and CURRY, 1969; reproduced by permission of American Society of Plant Physiologists.)

course. Upon short irradiation (up to about 2 mins) there occurs first a positive response, then a range of negative response and at high irradiance, again, a second range of positive response (Fig. 7-8). The dose-response curve is even more complex, since a second depression to a minimum and a third increase in the response can be observed at high irradiance levels (BLAAUW and BLAAUW-JANSEN, 1970). This intensity dependence of the phototropic curvature, involving first positive, negative and second positive responses, indicates that there are at least 2 different primary processes effective in the control of the response. With increasing irradiation time, at constant energy, there is a shift of the range of second positive curvature in the dose-response curve to lower energy values. Due to this shift, the negative response and the minimum in the curve disappear until, at an irradiance time longer than about 3 mins, only positive responses can be induced (EVERETT and THIMANN, 1968). Such long-lasting irradiation is comparable to the conditions usually effective in the natural environment.

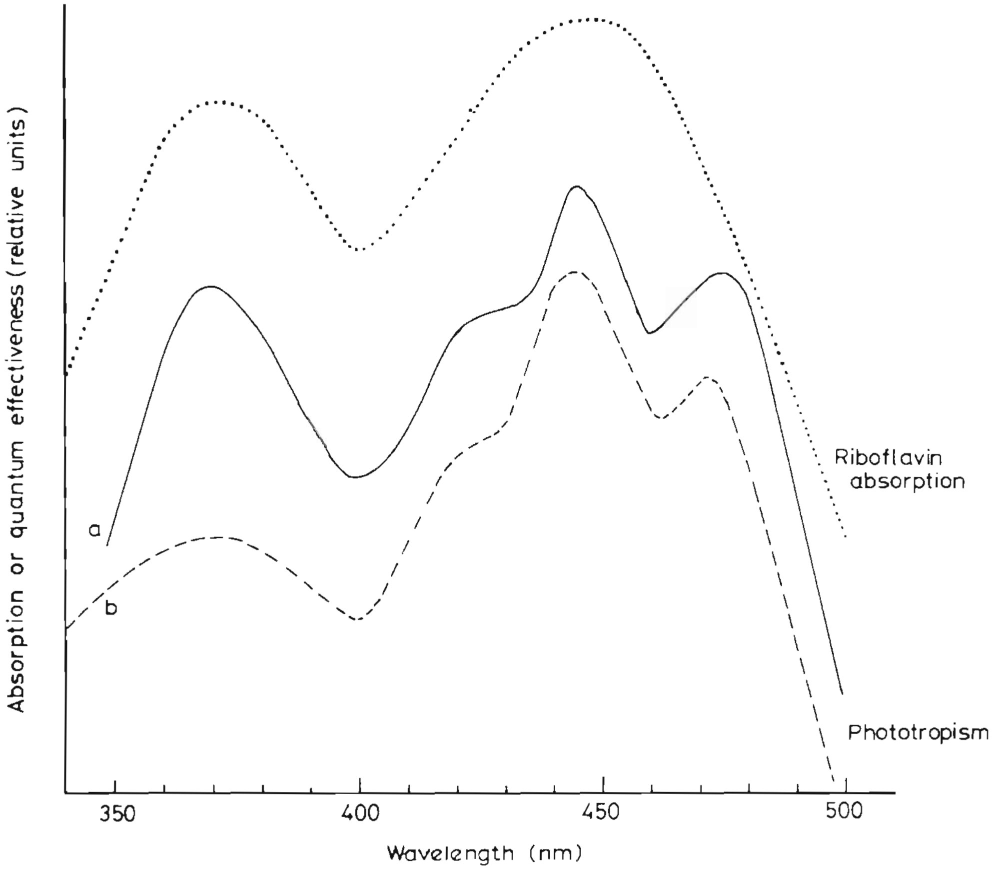

Fig. 7-9: *Avena sativa.* Action spectra of phototropism in the coleoptile. The absorption spectrum of riboflavin is presented for comparison. The curves are shifted along the ordinate. (a: After SHROPSHIRE and WITHROW, 1958; reproduced by permission of American Society of Plant Physiologists. b: After CURRY, 1969; reproduced by permission of McGraw-Hill Book Company (UK) Ltd.)

Action spectra of phototropism have been investigated mainly in the range of the first positive response (Fig. 7-9). They have peaks in the near ultra-violet at 370 nm and in the blue at 450 nm, with shoulders at 425 and 475 nm. Two spectra from different investigations are given in Fig. 7-9 as an example for variations in action spectra of the same response in one object. The spectra agree very well, except in the relative height of the u.v. peak. This difference may be caused by small variations in plant material or experimental procedures. Red light has no effect. The general form of the action spectrum parallels the absorption spectrum of riboflavin. The fine structure in the blue peak could be caused by a location of the flavin photoreceptor in a hydrophobic intramolecular environment (THIMANN, 1967). But the shoulders at 425 and 475 nm can also be taken as an indication of a carotinoid as photoreceptor. The negative phototropic response is also induced most effectively by blue light, but an action spectrum has not been determined so far.

The coleoptile tip is the region most sensitive to light. The absorption gradient across the coleoptile for the perception of light direction is most probably caused by the shadow principle. But the response can be inverted if the coleoptile is submerged in paraffin oil. This indicates that the principles of light refraction may also be involved, if the inversion is not caused by secondary metabolic processes or by a membrane effect (MEYER, 1969).

Physiological mechanism of light action

In the coleoptile the growth (cell enlargement) is controlled by auxin (IAA), which is transported polarly through the coleoptile cells from the apex to the basal region. The active process is a preferential secretion of IAA at the basal end of the cells. In positive phototropic responses, irradiation from the side induces a lateral transport of IAA from the lighted to the shaded side of the coleoptile. Hence more auxin is available on this side and less on the lighted side. Since the growth rate is limited by the available concentration of IAA, the result is an increased rate of growth on the shaded side and a decreased rate on the lighted side. This difference in growth rate on the two sides of the coleoptile leads to the phototropic curvature. The curvature proceeds until the axis of the coleoptile is directed towards the light source, i.e. until equilibrium in light absorption between the two flanks at the tip is attained. In the case of negative curvatures, the situation is inverse—IAA is transported laterally to the lighted side.

The primary process which causes the lateral secretion of IAA is still unknown. In positive curvatures, the IAA secretion through the plasmalemma could be inhibited on the lighted side or it could be activated on the shaded side of the cells. In both cases, the result is an asymmetric transport of IAA towards the shaded side; this is schematically illustrated in Fig. 7-10. The asymmetric IAA-transport activity of the cells may be caused by photo-oxidation products of IAA, which would be formed to a higher extent on the lighted side and which can inhibit the IAA-transport system of the cell membrane on this side (HAGER and SCHMIDT, 1968). A more plausible cause of asymmetric transport of IAA is the intracellular light-induced orientation movement of cytoplasm and chloroplasts (p. 483; CURRY, 1969); this is indicated in Fig. 7-10. The rate of transport indeed depends strongly upon the amount of cytoplasm present at the respective basal side of the cell (GOLDSMITH

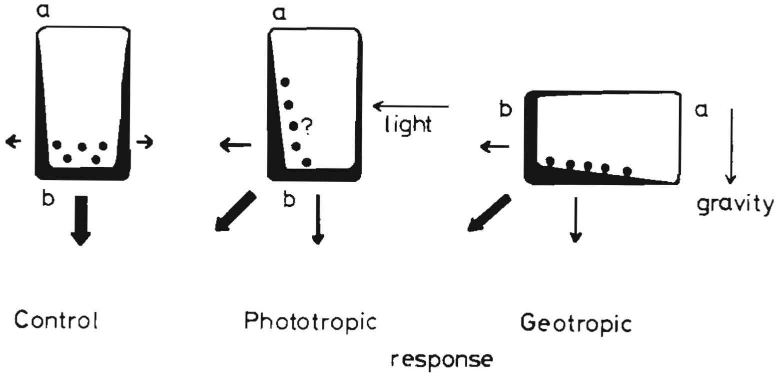

Fig. 7-10: *Avena sativa.* Direction of IAA-transport in coleoptile tip cells in relation to photo- and geotropism. a: apical, b: basal end of the cell. The capacity of the cell membrane to secrete IAA is indicated by differences in wall thickness. Arrows indicate main direction and amount of IAA transport through the cells. Dots represent plastids. (After Hager and Schmidt, 1968, and Hertel and Leopold, 1963; modified; reproduced by permission of Springer-Verlag, Heidelberg.)

and Ray, 1973). The latter mechanism would be applicable to negative as well as to positive curvatures and would offer some analogy to the geotropic response.

Tonic effects of light

The phototropic sensitivity of coleoptiles depends upon environmental factors; the most prominent effect is, again, induced by light. Pre-irradiation with red light (about 1–2 hrs before the blue stimulus) induces decreased sensitivity in the first positive part of the dose-response curve which, accordingly, is shifted to higher energy values. The sensitivity in the range of the second positive response, on the other hand, increases. Hence this part of the curve shifts to lower energy values and a more pronounced curvature is observed. Consequently, the negative response is considerably reduced and may disappear completely (Curry, 1969). The red light is effective via the phytochrome system, which controls the growth rate of coleoptiles and other plant organs, but which—surprisingly—cannot induce a phototropic curvature (Mohr, 1972). Since the phytochrome system also absorbs blue light, the tonic effect of light can interact with the orienting stimulus in case of long-term irradiations with blue light (Blaauw and Blaauw-Jansen, 1970).

Phototropic Responses in the Protonema of Dryopteris filix mas

Phototropism

The spores of mosses and ferns germinate with their rhizoid oriented away from, and their chloronema towards, the light source. This polarity can be induced by light (Bünning and Etzold, 1958). During further development, the rhizoids grow with negative phototropism and the chloronema with positive phototropism. The phototropism of the chloronema has been investigated in detail in *Dryopteris filix mas* (Etzold, 1965; Steiner, 1969).

The growth of the chloronema is restricted to a narrow region of the tip. In this apical growth zone also the highest sensitivity to light is located. A change in the direction of unilateral light induces a phototropic curvature of the chloronema tip. In this response, a new growth centre is formed at the site of highest light absorption in the growing region of the tip. The result of this shift of the growth centre is a very sharp curvature at the chloronema tip (Fig. 7-7). This response is quite different from the curvature in the *Avena* coleoptile, where the cause is a difference in the rate of intercalary growth at the two sides of the organ.

The intensity dependence and the action spectrum of the response have been analysed mainly in polarotropism, which is the phototropic response to polarized light.

Polarotropism

For the investigation of polarotropism the protonema of *Dryopteris* are grown in agar under a glass plate. This method prohibits phototropic curvature towards the light and keeps the chloronema in the plane of the glass plate. When irradiated with polarized light, the chloronema grow perpendicularly to the vibration plane of the electric vector. The rhizoids, on the other hand, grow parallel to this direction. This observation can be extended to a more general rule: an organ with positively phototropic response grows perpendicular, but a negatively phototropic organ parallel to the direction of the electric vector of polarized light (BÜNNING and ETZOLD, 1958). Polarotropism as such is more or less a laboratory response; it cannot be observed in the natural environment. But the results obtained are important for an understanding of the mechanism of phototropism in the chloronema.

Upon a change in the orientation of the vibration plane of polarized light the chloronema grows perpendicularly to the new direction of the electric vector. In the case of phototropism, a new growth centre forms at the site of highest light absorption. Polarized light can be absorbed only if its electric vector vibrates parallel to the photoreceptor. Hence the photoreceptor must be oriented parallel to the cell surface in the peripheral part of the chloronema. If the electric vector is oriented perpendicularly to the chloronema, maximum absorption and growth activity occur in the very tip. Accordingly, the perception of light direction in the phototropic response is mediated by the dichroic and shadow principle in the tip of the chloronema, which is full of dense cytoplasm and chloroplasts.

The dose-response curve of the polarotropic response has a complex and variable form which depends upon irradiation time, wavelength and temperature (STEINER, 1969). If a rather short irradiation time is used (15 mins) the dose-response curve has two maxima and in between a minimum, but no negative response can be observed. In the case of a long irradiation time (240 mins), only one increase in the response occurs, which leads to a level of saturation. Hence the general character of the dose-response curve is similar to that in the phototropism of the *Avena* coleoptile. The complex dependence of the response upon time and intensity of irradiation indicates that more than one photoreceptor is involved in the primary process induced by light. This can also be deduced from the action spectra. Both in blue and in red light chloronema grow perpendicularly to the plane of the electric vector. Blue light is about 100 times more effective than red. The action spectra of polarotropism in chloronemata of *Dryopteris* show peaks around 370, 450 and

660 nm. In the blue and near-ultra-violet, a flavin could be the photoreceptor. In the red, which is partly reversible by far-red, the phytochrome system is effectively absorbing the light (ETZOLD, 1965; STEINER, 1969).

Phototropism in the Alga Mougeotia *sp.*

Phototropic responses of algae are known from species of *Acetabularia, Bryopsis, Spirogyra* and other algae (BANBURY, 1959). In algae growing attached to the substratum, usually the thallus responds positively phototropic towards, and the rhizoid negatively away from, the light.

Phototropism has been investigated in more detail in the filamentous alga *Mougeotia* sp. (NEUSCHELER-WIRTH, 1970). The growth of *Mougeotia* filaments can be restricted to one plane, if they are cultivated on a wet agar surface. The filaments then respond phototropically in a different way to red and blue light.

In unilateral red light of about 1600 erg cm^{-2} sec^{-1} the end cells of filaments, as well as single cells, respond to a change in light direction with a sharp curvature of the tip towards the light (Fig. 7-7). Unilateral light induces the formation of a new growth centre as in the chloronema of *Dryopteris*. In long filaments, in addition, a difference in the growth rate between the two sides of the filament is caused. The cells grow more actively on their lighted side. This results in a curvature of the filaments towards the light (Fig. 7-7). Under polarized red light a polarotropic growth of filaments perpendicular to the direction of the electric vector is induced as in chloronema of *Dryopteris*.

In unilateral blue and white light (intensity 1000 erg cm^{-2} sec^{-1} or 2000 lux), on the other hand, there is no sharp curvature of the end cells towards the light. Here only a bending of the filaments due to increased growth along the whole length of the lighted side of the cells is observed. This leads to a U-like curvature of the filaments with the end cells directed away from the light (Fig. 7-7). Under polarized blue or white light, growth of cells parallel to the electric vector is promoted, the filaments thus grow preferentially in this direction—unlike the chloronemata of *Dryopteris*.

These characteristic differences in the responses to blue and red light in photo- and polarotropism of *Mougeotia* filaments indicate that two different photoreceptors (possibly flavin and phytochrome) are effective, which may also induce different secondary processes. Both photoreceptors apparently are located in a dichroic orientation parallel to the surface of the cell.

Ecological Significance of Phototropism

Phototropism is of great ecological significance in sessile, rigid land plants, where it brings about symmetrical orientation towards the light and thus enables even illumination of all plant organs, especially leaves. This is essential for optimal utilization of the light available for photosynthetic processes. Phototropism is also of ecological significance in sessile, more or less rigid algae, such as species of *Acetabularia* and *Bryopsis*. But in flexible algae, which float in the turbulence of the surrounding water, phototropism can hardly be of any ecological importance. Here, the only effect may be an orientation of rhizoid growth.

(b) Geotropism

General Aspects

Geotropism comprises oriented growth movements relative to the earth's gravitational field. In general, plant shoots grow in an upward direction by bending away from the centre of gravity (negative geotropic response). Roots and rhizoids grow downwards towards the centre of gravity (positive geotropic response). This pertains to the main axis of shoots and roots, but the lateral branches often grow transverse to the direction of gravity (AUDUS, 1969).

Together with phototropism, geotropism controls the direction of shoot growth and, together with an endogenous downward growth tendency (epinasty), the orientation of the branches and leaves in terrestrial plants. Geotropism is less important in flexible, buoyant marine algae. Here its only significance seems to be the directional control of rhizoid growth which in addition may also be influenced by chemotropism. Geotropism has been investigated mainly in the coleoptiles of *Avena sativa* and in rhizoids of *Chara foetida*.

In geotropism the mechanism of perception of the stimulus direction is different from the principles effective in light-induced responses. Since there is no attenuation of gravity in the organism, gravity is equally effective at all sites in the cell or the organ. Hence there is no gradient of the effectiveness of the stimulus in relation to its direction. The direction of gravity can be perceived by a change in the position of a cell organelle under the influence of gravity, if this organelle is heavier—or lighter—than the surrounding cytoplasm. Such organelles are the statoliths.

Geotropism in the Rhizoid of Chara foetida

The geotropic response of *Chara foetida* rhizoids has been analysed by SIEVERS and SCHRÖTER (1971). The rhizoids grow at their tip. Cell-wall expansion growth in the tip is supported by polysaccharide-containing golgi vesicles, which are transported along the cell's periphery from a more basal region to the tip. Just behind the apical growth zone in the tip are the statoliths—highly refractive and heavy bodies of unknown chemical composition. They are gathered in a plate-like arrangement in the centre of the rhizoid's cross section (Fig. 7-11). As long as the rhizoid is oriented vertically, the statoliths do not inhibit the transport of golgi vesicles. Hence the golgi vesicles can reach the tip at all sites of the cell's cross section equally well, and the tip grows symmetrically. If the rhizoid is placed in a horizontal position, the statoliths, following gravity, are displaced in about 3 to 6 mins to the lower side. Here they block the path of golgi vesicles to the tip (Fig. 7-11). So less vesicles can reach the lower part of the tip and more will be diverted to the upper part. Thus more golgi vesicles can be incorporated into the growing wall here. This leads to an increase in growth rate at the upper side and to a decrease at the lower side in the subapical growth region of the tip. Consequently, about 10 to 15 mins following

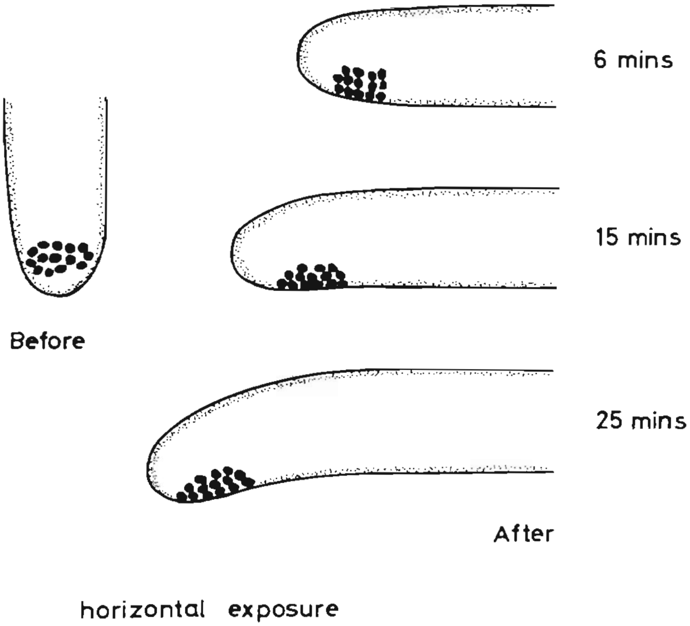

Fig. 7-11: *Chara foetida.* Function of rhizoid statoliths in the geotropic response: Statolith position before and after geotropic stimulation. Increasing length indicates growth. (After SIEVERS and SCHRÖTER, 1971; redrawn; reproduced by permission of Springer-Verlag, Heidelberg.)

horizontal exposure, the tip begins to bend downwards in a positive geotropic response; apparently the statoliths are effective just by their presence, i.e. without inducing physico-chemical secondary processes.

Geotropism in the Coleoptile of Avena sativa

Avena sativa coleoptiles respond to a gravitational stimulus with a negative geotropic curvature. The response can be induced by short (ca. 5 mins) horizontal exposure. The curvature begins to develop after about 15 mins. As in phototropism, the region of maximum sensitivity lies in the tip of the coleoptile. In a horizontally oriented coleoptile, the polar transport of IAA is diverted laterally to the lower side. Increased IAA supply at the lower side induces a higher growth rate, whilst the reduced concentration at the upper side retards growth there. Due to the differential growth between the upper and lower side, the coleoptile bends upwards in a negative geotropic response.

How can gravity induce the lateral transport of IAA? The cells of the coleoptile contain plastids. These amyloplasts can function as statoliths. During horizontal exposure, the plastids fall to the lower side of the cell, exerting pressure upon the plasmalemma (Fig. 7-10). Possibly, this pressure induces a conformational change in a protein of the membrane. Thus the membrane's enzymatic IAA-transport system could be activated. This would result in increased IAA secretion towards the lower cell side (FILNER and co-authors, 1970). Accordingly, the statoliths induce secondary processes and are not effective just by their presence as in the *Chara* rhizoid.

(4) Orientation via Induction of Polarity

(a) General Aspects

During its growth, a plant develops from an apparently apolar germ cell (egg or spore) to the adult stage, which is grossly differentiated into shoot and root in the case of higher plants, or into thallus and rhizoid in the case of most algae. The axis of this polar differentiation can be determined by external stimuli. The process of orientation of the polarity axis in a previously apolar cell is called induction of polarity. It documents itself in propagative cells of lower plants usually by the direction of the germination of the rhizoid. A fundamental question here is: does the external stimulus induce polarity or does it only re-orient an already existing, endogenous polarity axis? In the absence of an external orienting stimulus, the rhizoid forms at a site determined by some endogenous factor or by a developmental circumstance, like the orientation of the spore in the sporangium (e.g. species of *Equisetum*) or the site of entry of the sperm (e.g. fucacean eggs). These facts seem to indicate that the external stimuli only orient a pre-existing but labile axis of polarity (HAUPT, 1962).

The polarity axis can be oriented by light, gravity, electric fields and concentration gradients of chemical substances (established either by local diffusion or by a flow in the medium). The most prominent and best investigated of these factors is light. Light has been shown to orient polarity in germ cells of species of *Fucus* and *Pelvetia* (JAFFE, 1969), and of *Ceramium*, *Codium*, *Polysiphonia* and other marine algae (WEBER, 1969). Light is also effective on spores of other cryptogams such as *Botrytis*, *Equisetum*, *Funaria* and *Osmunda* (HAUPT, 1962; JAFFE and ETZOLD, 1965; VON WETTSTEIN, 1965). The induction of polarity has been investigated most thoroughly in zygotes of the brown algae *Fucus furcatus*. *F. serratus*, *F. vesiculosus* and *Pelvetia fastigiata*; hence the responses of fucacean zygotes will be discussed in more detail.

(b) Induction of Polarity in Zygotes of *Fucus* species by Light

Time Course of Photopolarizability

Soon after fertilization, the *Fucus* zygote begins to secrete an adhesive wall mucilage, by which it becomes firmly stuck to the ground. About 12 hrs after fertilization, germination begins: the rhizoid emerges. Before or after this, depending upon the environmental conditions, there is a polar, unequal division of the zygote, resulting in a rhizoid and a thallus cell (HAUPT, 1962).

During development from the fertilized egg to the embryo with its stabile axis of polarity, there is a phase in which the pre-existing endogenous polarity is still labile.

This is the sensitive phase of the cell during which an external stimulus can determine polarity; that is, the external stimulus can re-orient the pre-existing labile polarity axis of the cell. During the phase of polarizability, the sensitivity (per cent response to a given stimulus) increases to a maximum and then decreases again. Photopolarizability reaches its highest value 12 hrs after fertilization (Fig. 7-13); a second maximum at about 15 hrs has also been observed (BENTRUP, 1968; FEUCHT and BENTRUP, 1972). Following the maximum, the sensitivity decreases again.

The Response to Light

The rhizoid of the *Fucus* zygote germinates at the site of lowest irradiation, i.e. the site of lowest absorption in the photoreceptor. In unilateral light this is the shaded side pointing away from the light source (Fig. 7-12a). Under unilateral polarized light, the rhizoid germinates in the direction of the electric vector, at one of the two sides of the cell, where the cell's surface is oriented normal to the electric vector (Fig. 7-12b). Usually, the response is slightly subequatorial (in a direction pointing about 110° away from the light source) and in some *Fucus* species twin forms with two rhizoids are induced (JAFFE, 1958). A sub-equatorial response can also be observed in unilateral unpolarized light at lower irradiance. The effect of polarized light, together with the subequatorial response, indicates that the photoreceptor must be localized in the periphery of the cell, oriented in a dichroic way parallel to the surface. Hence the photoreceptor is possibly localized in the plasmalemma. According to these results, dichroic, shading and by-passing principles must be involved in the perception of light direction.

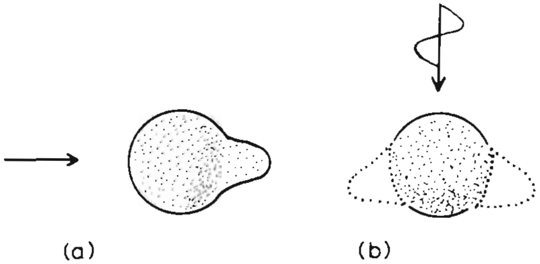

Fig. 7-12: *Fucus* sp. Induction of polarity by light in the zygote. Formation of rhizoid in unilateral (a) and linear polarized light (b). (Original.)

A few seconds of irradiation are sufficient to induce the response, which is measured as percent orientation of rhizoids away from the light. In blue light, the energy threshold of the response in *Fucus serratus* lies at about 5000 erg cm^{-2}. The dose-response curve for the orientation of polarity by light shows a first increase to a maximum then a decrease to a minimum and, finally, a second increase. Similar to the phototropic curvature of the *Avena sativa* coleoptile (p. 477) with increasing time but equal irradiation energy, the second increase in the dose-response curve shifts towards the first increase (until it coincides with it) so that the minimum in the curve disappears. In contrast to the *Avena* phototropism, however, the minimum does not extend into the range of negative responses—i.e. in *F. serratus*: rhizoid orientation towards the light—(BENTRUP, 1963).

The dose-response curve with its two peaks, separated by a minimum, indicates that two photoreceptors are involved. The action spectrum of the first increase in the dose-response curve has a maximum at 455 nm; it is flanked by a sharp decrease towards 530 nm, a minimum at 380 nm and, towards shorter wavelengths, by a continuous increase in effectiveness until 250 nm. A photoreceptor with a comparable absorption spectrum is not known; possibly, it may be a carotene, bound in a special chromoprotein complex. The action spectrum of the second increase has maxima at 370 and 440 nm, which are separated by a minimum at 400 nm; here a flavin could be the effective photoreceptor (BENTRUP, 1963).

Mechanism of Light Action

The first effect of light in the induction of polarity is a labile gradient in the cell; this can be demonstrated experimentally by a second antagonizing irradiation, which, during the period of photopolarizability, can easily re-orient the polarity axis induced by the first irradiation. The labile polar gradient in the cell, the nature of which is not known, is then stabilized to a structurally fixed polarity which must be located in the peripheral stationary cytoplasm of the cell (HAUPT, 1962).

Light is absorbed in the periphery of the cell, the photoreceptor probably being located in the plasmalemma. Hence the primary effect of light must be localized here as well. Via a conformational change in proteins light could alter the permeability pattern of the plasma membrane and thus could effect a change in the electric potential at the plasmalemma. This in turn would result in an electric gradient across the cell, determining the polarity axis. Such an assumption is supported by the effect of chemical stimuli as well as by the following experimental finding: After induction of polarity by light, in serially aligned zygotes an electric potential can be measured along the cell axis, the rhizoid end becoming negative. This potential increases parallel to the germination process and continues to increase thereafter parallel to the germling's growth rate (JAFFE, 1966). The electric potential may be a consequence or a cause of the rhizoid's growth (SCOTT, 1967; JAFFE, 1969). It can certainly help to stabilize the cell's polarity by an electrophoretic redistribution of molecules in the cell.

(c) Induction of Polarity in *Fucus* by Chemical Substances and Related Stimuli

Induction by Ionic Gradients

If a steady concentration gradient of potassium ions is established across *Fucus furcatus* zygotes the rhizoid will be oriented in dependence upon the potassium concentration. At concentration differences higher than about 7 mM across the zygote, the rhizoid forms towards the higher potassium concentration reaching 35% orientation at a concentration difference of 20 to 40 mM. The average concentration (i.e. mean of low and high) of potassium outside the cell in these experiments was between 20 and 80 mM. Exposure to concentration differences of 5 mM and lower across the zygote, at an average outside concentration of 5 to 10 mM, induces rhizoid formation towards the lower potassium concentration. In a hydrogen-ion gradient the rhizoid forms towards the higher H^+ concentration, i.e., towards the acid end. In the case of the potassium and the hydrogen ion gradient the percent orientation is directly proportional to the percent difference in concentration across the cell. The ionic gradients probably induce the orientation of the polarity axis of the cell by a transcytoplasmic electric gradient across the cell, which may be caused by a differential depolarisation of the membrane potential at the 2 sides of the cell (BENTRUP and co-authors, 1967).

Induction by Electric Fields

External electric fields, applied across the zygote of *Fucus serratus,* also induce polarity. The rhizoid forms either towards the anode or towards the cathode. The direction of rhizoid orientation depends upon the potassium-ion concentration of the surrounding medium. In normal sea water, with a potassium-ion concentration of about 10 mM, the response is towards the cathode. The percent orientation is proportional to the strength of the electric field in the range from 0·1 to 2 V cm^{-1}, which corresponds to a transcellular potential difference of about 1 to 20 mV.

The response to a constant electric potential is proportional to the potassium-ion concentration. In low potassium concentrations, the rhizoids orient strongly towards the cathode. This orientation decreases linearly with increasing potassium-ion concentration, and at concentrations above about 20 mM the rhizoids orient towards the anode.

As an action mechanism, the external electric field could, like ionic gradients, induce a differential change in the cell membrane potential; this, in turn, might lead to orientation of the polarity axis: the rhizoid germinating on that side of the cell where the membrane potential is shifted farthest off its normal value (BENTRUP, 1968).

Induction by Water Movement and the Group Effect

Orientation of the polarity axis by a flow in the surrounding medium (water movement) is referred to as **rheotropic response**. The response depends upon pH and speed of the movement. At pH 6·5, rhizoids form in downstream direction at flow speeds between 0·01 and 10 μm sec^{-1}. The percent orientation increases proportionally to the speed of water movement, reaching an optimum between 1 and 10 μm sec^{-1}. At higher rates the percent orientation decreases again. At about 100 μm sec^{-1}, rhizoids grow in the opposite (upward) direction. At pH 8, no downstream orientation can be observed; the rhizoids grow upstream at flow speeds exceeding 1 μm sec^{-1} (BENTRUP and JAFFE, 1968).

If *Fucus* eggs are located close together in groups or pairs, the distance from egg to egg not exceeding 3 egg diameters, the polarity axis orients in such a way that the rhizoids germinate towards or away from the neighbouring cell. Such group-effect orientation occurs also towards eggs and pieces of other algae and towards non-living diffusion barriers. The response in *F. furcatus* depends upon the pH of the ambient sea water: At low pH values around pH 6, rhizoids form towards the neighbouring cell; at higher pH values above pH 7·5, rhizoids form away from each other.

The conditions causing orientation of the polarity axis in the group effect are similar to those in the rheotropic response. Movement of water establishes in the rheotropic response a concentration gradient of diffusible substances across the cell, which is established by local diffusion in case of the group effect. The group effect is thus related to the rheotropic response. In both responses, diffusible substances are involved which are emitted by the egg and which are locally effective in it or in neighbouring eggs. One of these substances is the hypothetical rhizin, a labile, small molecular substance, which stimulates the formation of rhizoids (JAFFE and NEUSCHELER, 1969).

(d) Comparison of the Different Responses

In the action mechanism of all stimuli which induce polarity in the *Fucus* zygote, perception of the stimulus and response occur at the periphery of the cell, probably in the plasmalemma. In all cases a change in the electric potential at the plasmalemma may be involved (BENTRUP, 1968; JAFFE, 1969). The cell's sensitivity to different stimuli changes during its development (Fig. 7-13). About 2 hrs after fertilization, the rheotropic response—and presumably also the group effect—is most sensitive. After 5 hrs, electropolarizability reaches its peak of sensitivity.

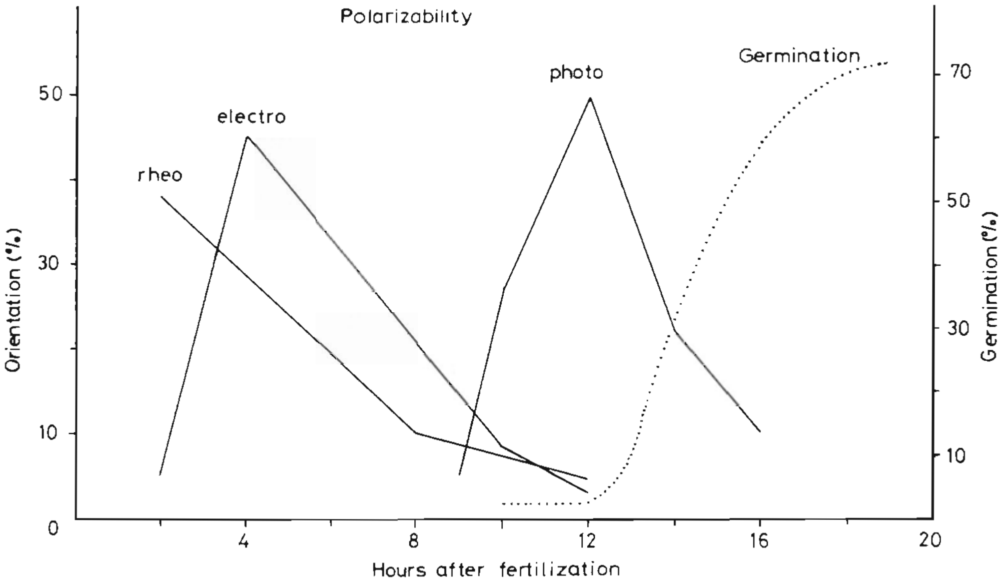

Fig. 7-13: *Fucus serratus*. Time course of polarizability and germination. Orientation response (%) to rheo-, electro- or photostimulus at different times after fertilization; rheoresponse is from *F. furcatus*. Right ordinate: percent germination. (After BENTRUP, 1968 and FEUCHT and BENTRUP, 1972; modified; reproduced by permission of G. Fischer, Stuttgart.)

Polarizability by these stimuli then decreases in a parallel manner, probably depending upon the same cellular processes. After about 12 hrs, photopolarizability attains maximum values; photopolarizability decreases again in correspondence to the beginning germination, which signals stabilization of the polarity axis (BENTRUP, 1968; FEUCHT and BENTRUP, 1972).

The different time course of polarizability by the different stimuli indicates differences in the primary physiological mechanisms of the responses. The time course also indicates that, under natural conditions, light is the most important stimulus in the orientation of the polarity axis. Since light is the last in the time sequence of effectiveness, it can re-orient a polarity gradient induced by any of the other stimuli. Photopolarizability is effective until the final structural stabilization of the polarity axis and the germination of the rhizoid begins.

The intracellular parameters controlling polarizability by the different stimuli are unknown. An interesting correlation in the time course of polarizability is the fact that, during the phase of electropolarizability, a maximum in the activity of RNA synthesis has been observed, whereas, during the phase of photopolarizability, a maximum in the rate of protein synthesis has been found in *Fucus vesiculosus* (QUATRANO, 1968; FEUCHT and BENTRUP, 1972).

(5) Intracellular Orientation Responses

(a) Orientation Movement of Chloroplasts

General Aspects

The intracellular arrangement of the chloroplasts of most plants depends upon environmental light conditions (see reviews by HAUPT, 1968; HAUPT and SCHÖNBOHM, 1970). Light-induced orientation movements of chloroplasts have been investigated in a variety of freshwater plants and algae (species of *Elodea*, *Lemna*, *Hormidium*, *Mougeotia*, *Vallisneria* and *Vaucheria*) and in terrestrial plants (species of *Funaria*, *Selaginella*), but they can also be observed in the plastids of marine algae, such as *Dictyota dichotoma* and red algae.

In darkness (i.e. in absence of an orienting light stimulus) the chloroplasts are usually more or less evenly distributed over all walls of the cell in a random position. At low or medium light intensity, the chloroplasts move to the pericline walls in cells of leaves and thalli or to the front and rear parts of cells in filamentous algae (Fig. 7-14). At high intensity, the chloroplasts move to the anticline walls in leaf cells or to the flanks in cells of filamentous algae (Fig. 7-14). In the filamentous alga *Mougeotia* sp., the single plate-like chloroplast turns inside the cell, exposing its face towards the light under low intensity and turning to profile position under high intensity (Fig. 7-14).

The orientation movement of chloroplasts into the high intensity arrangement represents the high-intensity movement, and in analogy the movement into the low-intensity arrangement, represents the low-intensity movement. Originally, orientation movements of chloroplasts were described as phototaxis of chloroplasts, the low-intensity movement being the positive and the high-intensity movement the negative phototactic response. But chloroplasts are transported passively by

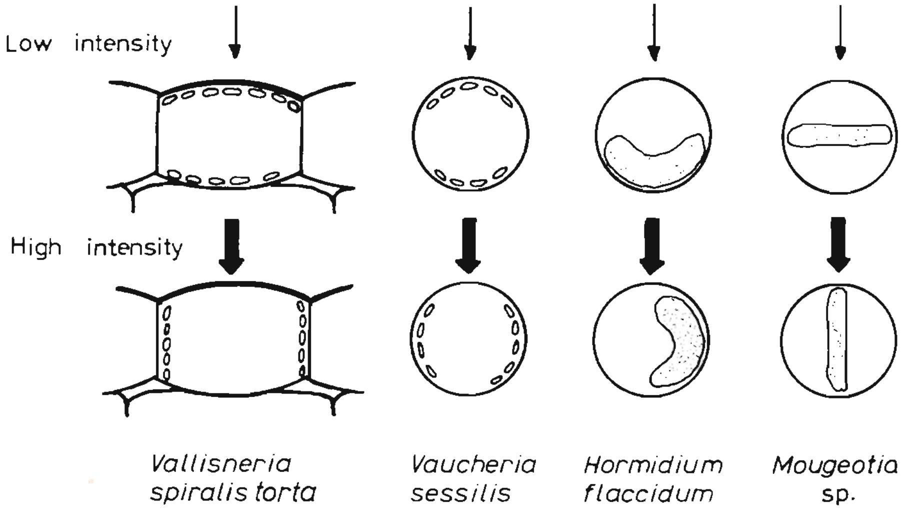

Fig. 7-14: *Vallisneria spiralis torta*, *Vaucheria sessilis*, *Hormidium flaccidum*, and *Mougeotia* sp. Arrangement of chloroplasts under low and high light-intensity. Schematized cross-section of different cell types. (After HAUPT, 1964; modified; reproduced by permission of Deutsche Botanische Gesellschaft, Göttingen.)

the cytoplasm, and the perception of light and the active mechanism are located in the cytoplasm. Hence analogy to the phototaxis of free-moving organisms is not fully justified (HAUPT, 1965a).

Other light-dependent movement responses of chloroplasts are cyclosis and the passive mobility in a centrifuge. Though these responses are not oriented by light, they are intimately related to the orientation movement and hence must also be considered here.

The Perception of Light

Action spectra of light-induced orientation movements of chloroplasts have peaks in the blue around 450 nm and in the near-ultra-violet region at 370 nm. This suggests a flavoprotein as active photoreceptor. The action spectra are very similar in different plants and they agree also in regard to the induction of low and high intensity movements (Fig. 7-15). This indicates that both responses are mediated by the same photoreceptor system and, possibly, by the same primary process.

In *Mougeotia* sp. and *Selaginella martensii* the position of the peak in the blue range is shifted to longer wavelengths (ca. 470 nm); this may be caused by a modified chromoprotein configuration in the photoreceptor. In addition, for *Mougeotia* sp. an action spectrum of the high-intensity movement in polarized light is presented in Fig. 7-15. This spectrum reveals a peak at 370 nm comparable to the spectra of the other plants. The difference in the action spectrum between unpolarized and polarized light indicates complications, which may be caused by interaction of several photoreceptors or by differences in the dichroic orientation in the two absorption bands of the photoreceptor (SCHÖNBOHM, 1971). In the orientation

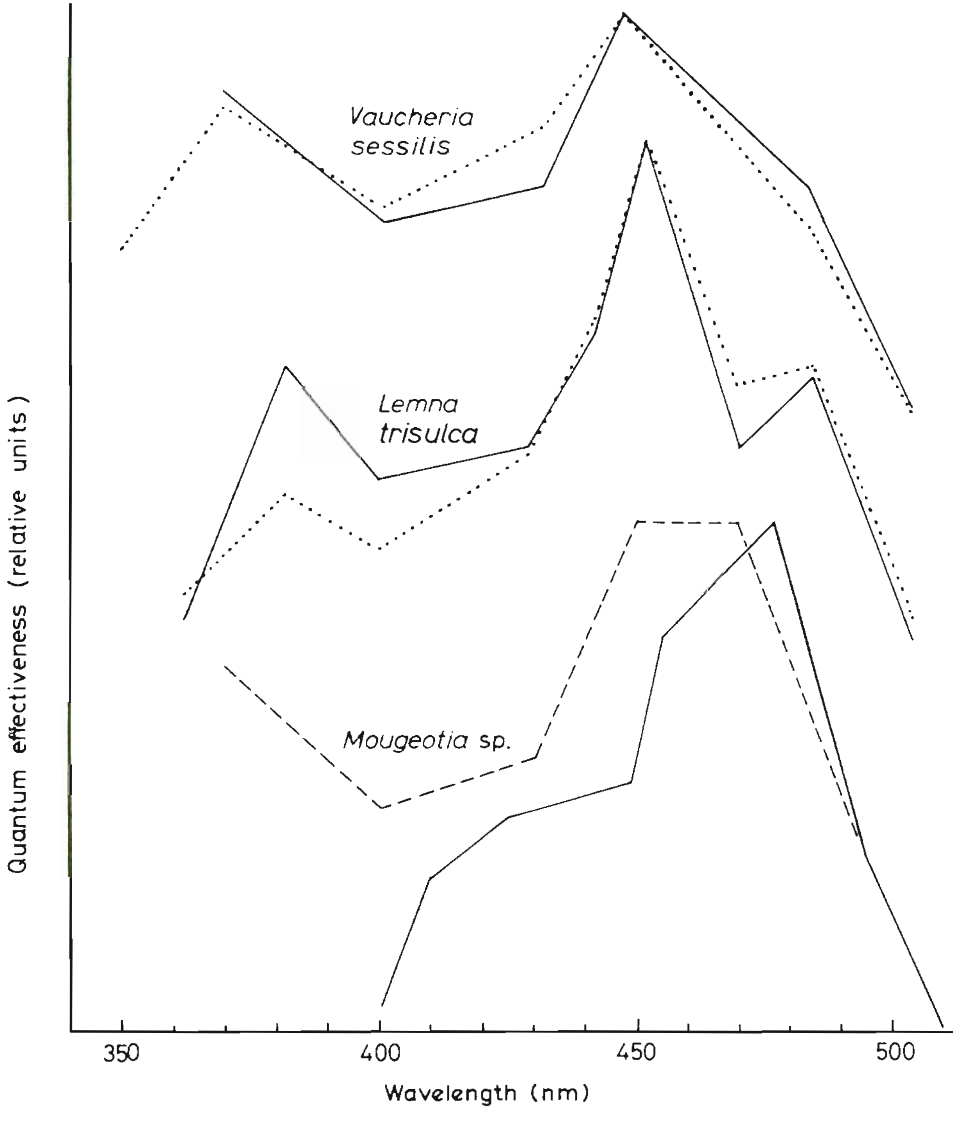

Fig. 7-15: *Vaucheria sessilis*, *Lemna trisulca* and *Mougeotia* sp. Action spectra of orientation movement of chloroplasts. Dotted lines: low-intensity movement; solid lines: high-intensity movement; broken lines: high-intensity movement in linearly polarized light, i.e. electric vector perpendicular to cell axis. The curves are shifted along the ordinate. (After HAUPT, 1964, and SCHÖNBOHM, 1963; redrawn; reproduced by permission of Deutsche Botanische Gesellschaft, Göttingen and G. Fischer, Stuttgart.)

movement of the *Mougeotia* chloroplast, only the action spectrum of the high-intensity movement has a form comparable to the other objects with a maximum in the blue range. In contrast to this, the low-intensity movement is induced most effectively by red light (660 nm). This effect of red can be reversed by far-red (730 nm); hence in the low-intensity movement of the chloroplast the phytochrome system is operating.

In the high-intensity movement of *Lemna trisulca*, *Selaginella martensii*, *Vallisneria spiralis torta*, and some other plants also red light is effective; but in comparison to blue light, red-light effectiveness is only about one tenth. The action peak at 680 nm indicates that chlorophyll absorbs the light (Fig. 7-17). Accordingly, in the primary process of chloroplast orientation movements two photoreceptor systems are involved (HAUPT, 1964; SEITZ, 1967), a flavoprotein and phytochrome in *Mougeotia* and a flavoprotein and chlorophyll in the other plants.

The localization of the photoreceptor in the cell can be derived from microbeam irradiations and from the effect of polarized light. Polarized light is most effective if its electric vector is oriented parallel to the plane of the cell wall. This is the case for the high- and low-irradiance effect of blue light in all plants investigated and also for the phytochrome-mediated effect of red light in *Mougeotia* sp. These experiments indicate that the flavin-photoreceptor as well as the red-absorbing form of phytochrome in *Mougeotia* sp. are localized in the cytoplasm and are oriented preferentially parallel to the cell wall. The latter fact implies that these photoreceptors must be localized in the non-moving peripheral ectoplasm or in the plasmalemma (HAUPT and SCHÖNBOHM, 1970).

The direction of light is perceived in most cases by the by-passing principle. Light refraction leads to a much-reduced intensity at the anticline walls of cells in leaves (e.g. of *Lemma trisulca* or *Vallisneria spiralis torta*) or at the flanks of filamentous algae, such as *Vaucheria sessilis* and *Hormidium flaccidum* (ZURZYCKI, 1962). In the *Mougeotia* cell, the principle of dichroic orientation of the photoreceptor is used to establish a gradient of light absorption between front and rear and flanks of the cell (Figs 7-1, 7-14; HAUPT and SCHÖNBOHM, 1970). The dichroic principle may, in part, also be effective in the other plants; this is indicated by the effect of polarized light.

Physiological Mechanism of Light-induced Movement

During their movement in the cell, the chloroplasts are transported passively by cytoplasmic streaming. Hence the orientation movement of chloroplasts is accompanied by a re-arrangement of portions of cytoplasm and cytoplasmic organelles including the nucleus (ZURZYCKI, 1962; HAUPT and SCHÖNBOHM, 1970). The motive mechanism of cytoplasmic streaming is localized at the boundary between the stationary peripheral ectoplasm and the moving endoplasm containing the chloroplasts. In the generation of the motive force contractile protein filaments are involved which generate a gliding movement of the endoplasm along the ectoplasm (KAMIYA, 1962). The activity of these contractile elements depends, like the actomyosin system of muscle cells, upon the availability of ATP as energy source.

Experimental data for the relation between cytoplasmic streaming and chloroplast movement come from an investigation of the light-induced increase in rate of cytoplasmic streaming and induction of cyclosis of chloroplasts in *Elodea canadensis*. High irradiance first induces, in about 1 to 5 mins, an increase in the rate of rotational cytoplasmic streaming. Chloroplasts then start to move and to participate in the cyclosis of cytoplasm as soon as the rate of cytoplasmic streaming has reached its maximal level (SEITZ, 1964). Accordingly, chloroplast movement in cyclosis is initiated by light as a consequence of an activation of cytoplasmic streaming. This permits the further conclusion that the start of chloroplast orientation movements is also induced via activation of cytoplasmic streaming.

For the orientation movement a gradient between the anticline and the pericline wall of the cell is necessary. Hence there must be a difference in chloroplast mobility between these walls. A measure for the mobility of chloroplasts is their centrifugability. The centrifugability depends upon the strength of the 'anchoring bonds' in the contact layer between chloroplasts and ectoplasm at the site where the motive mechanism of cytoplasmic streaming is located (ZURZYCKI, 1962). An increase in centrifugability corresponds to increased mobility of the chloroplasts and can be taken as a parameter for the activity of cytoplasmic streaming and for the start of chloroplast movement (SEITZ, 1971).

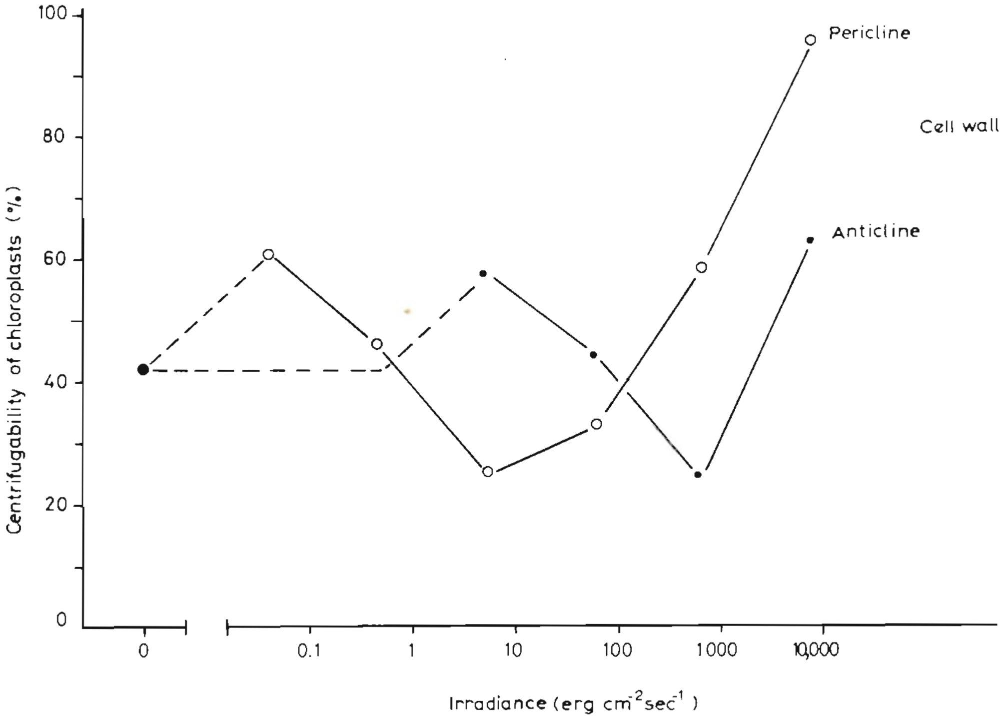

Fig. 7-16: *Vallisneria spiralis torta*. Centrifugability of chloroplasts at the pericline and anticline cell wall as a function of irradiance. 20-min irradiation at 454 nm. (After SEITZ, 1971; modified; reproduced by permission of G. Fischer, Stuttgart.)

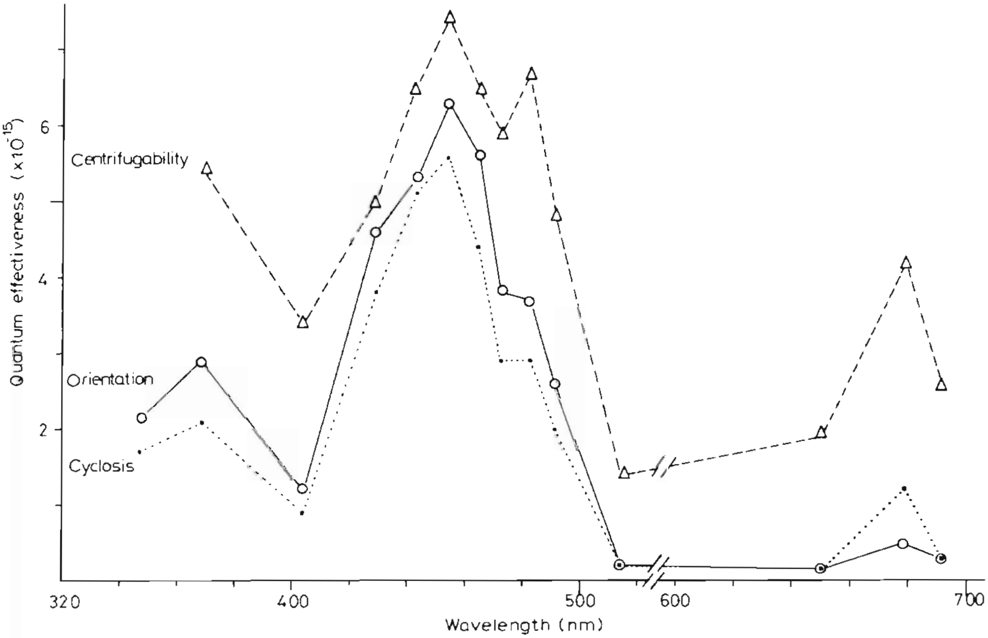

Fig. 7-17: *Vallisneria spiralis torta*. Action spectra of light-induced movement responses of chloroplasts. Ordinate: reciprocal of the quanta cm^{-2} sec^{-1} required for a 10% response. Irradiation time 20 mins. (After SEITZ, 1967; modified; reproduced by permission of G. Fischer, Stuttgart.)

The irradiance dependence of the light effect upon chloroplast centrifugability shows a characteristic pattern. For cells of *Vallisneria spiralis torta*, the dose-response curve for blue-light irradiation is given in Fig. 7-16. It shows a separate evaluation of centrifugability at the anticline and pericline cell walls. In comparison to an unirradiated dark control, low irradiance induces at the pericline wall an increase, medium irradiance a decrease, and high irradiance again an increase in centrifugability. Accordingly, the dose-response curve exhibits a sequence of first positive, negative, and second positive responses. At the anticline wall, the curve shifts towards values of higher irradiance, due to the lower incident irradiance at this wall. The results indicate that the ratio of incident irradiance between pericline and anticline wall is between 10:1 and 100:1.

As can be seen in Fig. 7-16, high irradiance induces increased centrifugability of chloroplasts at the pericline walls and decreased centrifugability at the anticline walls. The resulting gradient in chloroplast mobility controls the high-intensity movement. Medium irradiance, on the other hand, induces increased centrifugability at the anticline wall and decreased centrifugability at the pericline wall. Following this gradient, the chloroplasts exhibit low-intensity movement.

For *Vallisneria spiralis torta* the action spectra of the light-induced increase in centrifugability in the high-irradiance range and for the induction of cyclosis of chloroplasts are shown in Fig. 7-17, together with the action spectrum of the high-intensity orientation movement. These spectra agree very well with the spectra of low and high-intensity movement in other plants (Fig. 7-15). Location of peaks and amount of incident quanta necessary to induce the responses agree in the spectra of Fig. 7-17. This indicates that light induces the three movement responses of chloroplasts by means of the same photoreceptor system and the same primary reaction which comprises, most probably, activation of the motive mechanism of cytoplasmic streaming (SEITZ, 1971).

The Primary Process of Light Action

From experiments with metabolic inhibitors it is known that inhibitors of photosynthesis reduce the effect of red light. Uncouplers of oxidative phosphorylation inhibit the increase in centrifugability and the movement reactions of chloroplasts induced by blue and near-ultra-violet light. This indicates that these responses are dependent upon an unimpaired supply of ATP from oxidative phosphorylation. The importance of ATP for the movement reactions of chloroplasts is stressed, furthermore, by the fact that also exogenous ATP can induce or sustain movement reactions of chloroplasts (HAUPT and SCHÖNBOHM, 1970; SEITZ, 1971).

On the basis of such experimental evidence, the following action mechanism of light has been suggested for chloroplast movement in *Vallisneria spiralis* (SEITZ, 1971): Light could control the intracellular availability of ATP for the motion responses of chloroplasts via two different processes; in this control, the two photoreceptor systems—flavin and chlorophylls—would be effective.

A response which may cause an increase in ATP availability is the light-induced increase in the rate of oxygen uptake. This effect is known from species of *Chlorella* (KOWALLIK, 1969); it has been found also in *Lemna trisulca*, where it is related to the orientation movement of chloroplasts (ZURZYCKI, 1970). The increase in the rate of oxygen uptake is induced by low irradiance. The action spectrum of this response agrees with the spectra of chloroplast movement reactions and suggests a flavin as active photoreceptor. The light-induced increase in the rate of oxygen uptake corresponds to an increased rate of respiration (KOWALLIK, 1970) and, presumably, also to an increase in the rate of oxidative phosphorylation.

Accordingly, irradiation with blue light may cause an increase in the availability of ATP from oxidative phosphorylation. This ATP could induce, via the motive mechanism of cytoplasmic streaming, the increase in centrifugability of chloroplasts in the range of low and high irradiance.

The decrease in centrifugability of chloroplasts, induced by medium irradiance, depends upon a different primary process. It is induced by blue and red light with a similar relative effectiveness as in photosynthesis, and it can be inhibited by DCMU (SEITZ, 1974). This demonstrates that the photosynthetic electron flow is essential for this response.

In addition to photosynthetic electron flow and concurrent non-cyclic photophosphorylation, cyclic or pseudocyclic photophosphorylation can be activated by light in photosynthesis. The relative activity of the two systems competing for electrons may be controlled by the availability of NADP (nicotinamide adenine dinucleotide phosphate) as a function of irradiance (METZNER, 1967; AVRON and NEUMANN, 1968; HEBER, 1973). In the range of medium irradiance, electrons of the photosynthetic electron-transport chain will flow preferentially to NADP because of its great electron affinity. Thus, as long as NADP is available, all electrons will join the processes of NADP reduction and CO_2 fixation. In CO_2 fixation, more ATP is consumed than is synthesized in the concurrent non-cyclic photophosphorylation, which is coupled to electron flow and to CO_2 fixation. At high irradiance (high rate of electron flow), and especially when CO_2 fixation approaches saturation, the availability of NADP becomes limiting. Under this condition, electrons will be diverted to cyclic or pseudocyclic photophosphorylation and will support synthesis of ATP in these processes.

According to these considerations, medium irradiance could result in ATP shortage, forcing chloroplasts to take up ATP from the surrounding cytoplasm. This, in turn, would lead to a reduction of ATP available to the motive mechanism of cytoplasmic streaming, and thus could cause the decrease in centrifugability of chloroplasts. High irradiance, on the other hand, causes again a surplus of ATP, which can induce increased centrifugability and initiate chloroplast movement. On the basis of this hypothesis, chloroplast movement could be controlled by light via an intensity-dependent regulation of the availability of ATP from oxidative and photosynthetic phosphorylation (SEITZ, 1971). The intracellular gradient of light action would be maintained by increased synthesis at one, and by simultaneously increased consumption of ATP at the other, wall.

Ecological Significance of Chloroplast Movement

The primary ecological significance of the light-induced orientation movement of chloroplasts seems to lie in a quantitative control of photosynthetic processes. In addition, there may be a physiological significance in the action mechanism of other orientation responses, e.g. phototropism (p. 469).

In the low-intensity arrangement, chloroplasts can absorb the incident light very well for photosynthesis. This arrangement is realized under natural light conditions in the absence of direct sunlight. In the high-intensity arrangement, realized under direct sunlight, chloroplasts accumulate at a site of reduced irradiance in the cell. This may protect them from photochemical damage, or may bring them into a position where the irradiance is more favourable for photosynthesis. This consideration is supported by the fact that orientation movements can be observed only with photosynthetically active plastids.

The intracellular orientation movement assures exposure of chloroplasts to medium irradiance which is optimal for photosynthetic CO_2 fixation. Orientation movement of chloroplasts allows the plant to adjust its photosynthetic processes to changes of the environmental factor light. The movement apparently has some analogy to the vertical migration of planktonic flagellates.

(b) Light-induced Changes in Chloroplast Shape

In addition to the activity of the motive mechanism of cytoplasmic streaming a structural response is of significance for the movement of chloroplasts: the light-dependent change in the outer shape and size of chloroplasts. In darkness, and under high irradiance, the chloroplasts acquire a more or less rounded shape and a reduced diameter; in medium irradiance, they flatten, increasing their surface of contact with the ectoplasm and reducing their cross-section and mechanical resistance to cytoplasmic streaming. The flattening of chloroplasts (shrinkage response) is intimately connected with photosynthetic processes (PACKER and DEAMER, 1968). Greater roundness and contraction, on the other hand, is induced by blue light, most probably via a flavin photoreceptor (ZURZYCKI, 1966).

In the chloroplast of *Mougeotia* sp., the dose-response curve of light-induced changes in chloroplast shape has been investigated over a wider irradiance range (SCHORER-MÖRTEL, 1972). Blue light of high and low intensity induces chloroplast contraction (corresponding to greater roundness in normal chloroplasts); medium intensity induces flattening of the chloroplast. The dose-response curve of the changes in chloroplast shape has thus a similar form to that of centrifugability of chloroplasts (Fig. 7-16), with two ranges of 'positive' response separated by a range of 'negative' response.

(6) Conclusions

In the ecology of plants, spatial orientation to light is of basic importance. Most orientation responses are controlled by blue light; action spectra are generally similar in form and suggest that a flavin acts as photoreceptor. Some hypothetical considerations regarding the primary process of these blue-light-induced responses are discussed below.

The dose-response curve of blue-light-induced responses often has a characteristic form with two peaks separated by a minimum (which may extend to negative responses in some cases). Such dose-response curves are known from phototropism in *Avena sativa* coleoptiles (Fig. 7-8), polarity induction in *Fucus serratus*, centrifugability of chloroplasts in *Vallisneria spiralis torta* (Fig. 7-16), change of chloroplast shape in *Mougeotia* sp., photokinesis in *Micrasterias denticulata* and, less pronounced, also from polarotropism of *Dryopteris filix mas* chloronema.

The great similarity in the action spectra and in the form of the dose-response curves in this group of responses indicates that light may be effective in all cases via the same photoreceptor and the same primary processes. Two other response groups, in which either positive and negative or only positive reactions can be distinguished (e.g. phototaxis of algae or phototropism of the *Phycomyces blakesleeanus* sporangiophore), may be special forms of the first group.

If the environmental factor light is effective via the same primary action mechanism in all the responses, the question arises: which physiological processes are involved? A dose-response curve with two peaks of response, separated by a minimum, can be explained on the basis of at least two primary processes, which are independent and antagonistic in their effects. Models involving more than two processes have been suggested as well (CURRY, 1969). It is also possible to assume one primary process, which induces, and a second reaction, which tonically controls the direction (positive or negative) or the level of adaptation of the orientation response (FEINLEIB and CURRY, 1971a, b; SCHÖNBOHM, 1971).

Let us consider a model with two independent and antagonistic primary processes. This comprises the mechanism described in detail for the orientation movement of chloroplasts (p. 493). A blue-light-dependent response which could be involved in the primary process is the light-induced increase in the rate of oxygen uptake. By a still unknown mechanism, light induces here an increase in the rate of substrate supply to the respiratory chain or renders new substrates available for respiration (KOWALLIK, 1970). An increased respiratory rate could result in increased ATP availability or in a change of the redox state of the cell. As alternative mechanism one could also consider a light-induced change in the rate of some other process consuming ATP and thus stimulating respiration.

The primary process of orientation responses will be discussed on the basis of one of these mechanisms, assuming that the blue-light-induced increase in oxygen uptake causes an increase in ATP availability. This increase is induced by blue light of low irradiance in the case of continuous irradiation. It can also be induced by short light flashes (5 secs) of higher irradiance; in a subsequent dark period the effect reaches a maximum after about 6 mins and then slowly decreases again (KOWALLIK, 1970).

The other photoresponse, which could antagonize the increase in ATP availability in blue light is photosynthetic CO_2 fixation. Under medium irradiance, photosynthesis can, via CO_2-fixation, cause a shortage of ATP (p. 490). At high irradiance, on the other hand, photosynthetic phosphorylation can supply a surplus of ATP. Accordingly, light could control the availability of ATP for cellular processes as a function of irradiance. In this control, light would be effective via increase in respiration and via photosynthetic processes. The two systems are mutually interrelated via cell metabolism and they differ in the kinetic dependence upon irradiation. Oxygen uptake increases rather slowly to its higher level in light and slowly decreases again in darkness, thus showing an after-effect in darkness. Photosynthetic phosphorylation, on the other hand, responds rather fast to changes in light and shows no longlasting after-effect in darkness. Due to these characteristics a change in irradiance may result in temporary pulsatory change of ATP supply (LEWENSTEIN and BACHOFEN, 1972) and in a change in the steady level of ATP availability. The expected dependence of ATP availability in relation to respiration and photosynthesis is schematically summarized in Fig. 7-18. Instead of ATP, changes in redox state or other parameters could also be considered. The general form of the curve agrees with the dose-response curves of blue light responses (e.g. Figs 7-8, 7-16). Comparable experimental data for the irradiance dependence of oxygen uptake and oxygen production are known from leaves of *Lemna trisulca* (ZURZYCKI, 1970).

Irradiance-dependent control of ATP availability has been proposed as the mechanism involved in photophobic responses of flagellates, which can be induced either by a sudden increase or by a decrease in irradiance. The photophobic response may be caused by a sudden change in ATP supply (TOLLIN, 1969; NULTSCH, 1970; FEINLEIB and CURRY, 1971a). In the range of medium irradiance (Fig. 7-18) an increase in irradiance would result in a decrease of ATP availability, and a decrease in irradiance would cause an increase in ATP. In the range of low and high irradiance, in contrast, increase in irradiance would cause an increase in ATP availability. In the case of *Euglena gracilis*, the equilibrium intensity between positive and negative photophobic response—and phototaxis—is close to the saturation intensity of photosynthesis (DIEHN, 1969b). This intensity range agrees with the minimum in the ATP curve in Fig. 7-18. A phobic shock response is induced only if the direction of the intensity change is away from the equilibrium intensity,

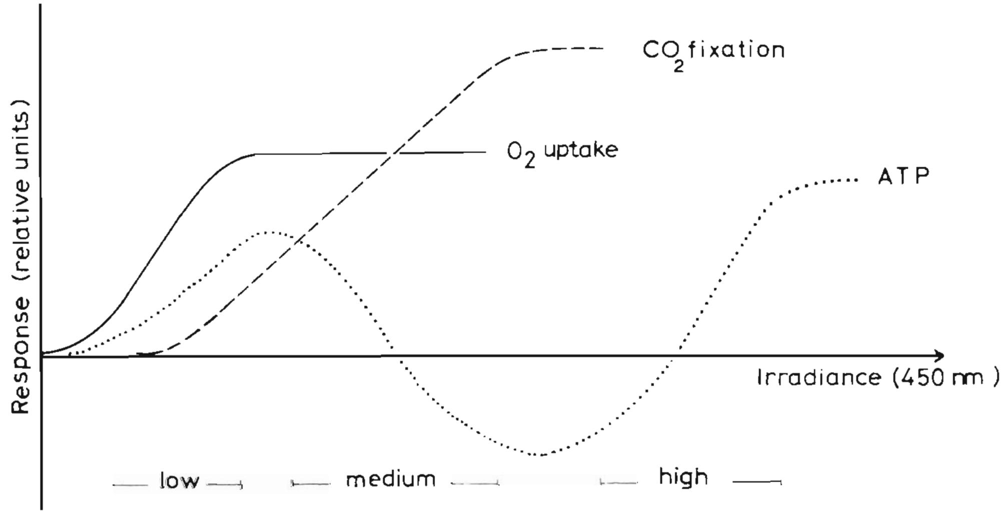

Fig. 7-18: Expected ATP availability and its relation to respiration and CO_2 fixation as function of irradiance. Hypothetical scheme according to experimental data from O_2-exchange in *Lemna trisulca* (ZURZYCKI, 1970). Relative values in comparison to a dark control are given on the ordinate. (Original.)

corresponding to increased ATP availability in Fig. 7-18. A comparable correlation apparently is also present in the photomotions of *Micrasterias denticulata*. Here a minimum of photokinesis occurs at the transition intensity from positive to negative phototaxis.

Of course, these considerations are highly speculative and require experimental verification. Whether they can be applied to all plant groups and to all responses is open to debate. In agreement with the above considerations is that in all responses of the first group photosynthetically active plastids are present. However, red light exerts only a small or no effect. This ineffectiveness of red light seems to exclude a participation of photosynthetic processes (NULTSCH, 1971). Nevertheless, experiments with inhibitors support the view that photosynthetic processes are involved in several responses. An explanation for the low effectiveness of red light could be that the physiological response is initiated only by co-operation of the blue-light system with photosynthetic processes. Such co-operation, resulting in a gradient of light action inside the cell, can only be effective in blue light.

The functions and structures involved in the perception of environmental stimuli are of great importance for ecological considerations. The numerous unsolved basic problems regarding the physiological mechanisms of plant orientation deserve concerted attention.

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8. ORIENTATION IN SPACE: ANIMALS

8.0 GENERAL INTRODUCTION

H. Schöne*

(1) General Aspects

(a) What is Orientation?

'To orient oneself' means to place oneself into a particular relation to known facts (or principles). For example, lions orient their hunting behaviour to the daily schedules of their prey animals; or an attacking lion orients his run with respect to the location of his target, e.g. a buffalo; or the lion orients his final attack with respect to the size and strength of the buffalo. These three examples refer to (i) temporal, (ii) spatial and (iii) physical (intrinsic) properties, which represent the three basic attributes of matter.

We shall be concerned primarily with the second form of orientation phenomena, spatial orientation or orientation in space. This, however, is often coupled with the first, orientation in time (p. 547, Chapter 9). Such coupling may, for example, consist of modulation of the spatial orientation by a daily periodicity: orientation may begin at certain times of the day, or direction may change according to the time of day (e.g. sun-compass orientation, p. 548). Spatial orientation is also related to the third form of orientation, involving physical characteristics of the object such as size, shape, colour, etc. That is, an animal 'recognizes' the orientation stimulus by these objective properties (p. 506).

Of the many mechanisms of spatial orientation which an organism may employ, only orientations involving behaviour are discussed. 'Behaviour' is taken to comprise all active and externally visible, i.e. overt, movements of the animal. Orientation processes within the organism, such as internal transport of substances, are not covered here. The term 'spatial orientation' thus refers to the ability of animals (and man) to relate position and positional changes of body or body parts (or other objects, p. 500) to spatial cues (Schöne, 1973a). This definition refers to the motor performance of orientation movements (motoric orientation). It also includes the oriented state, characterized by sensory control of the spatial situation (perceptive orientation, cf. Bischof, 1966a). Correspondingly, spatial orientation mechanisms may be defined as functions or structures which facilitate active arrangements of behavioural events in space.

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(b) Environment, Behaviour and Orientation

Orientation is of paramount importance in ecology and comprises an indispensable part of behaviour. For example, animals turn towards their partners or away from their enemies; they find and capture food; they migrate to their breeding grounds.

LORENZ and TINBERGEN (1938) consider behaviour to be composed of a specific movement pattern of basically constant form ('fixed action pattern'), and of orientation or 'taxis' components. The orientation components link the movements to the spatial demands of external and internal circumstances.

The apparatus and mechanisms used by an animal for orientation are adapted to the structure of its specific environment. Orienting stimuli of importance to plankters are different from those used by coral fishes, or whelks on the substrate, or worms in the mud.

Different orientations interlaced with, or replacing, one another are frequently required for the performance of complex action patterns (p. 543). Young salmon migrating towards the ocean orient by the sun compass as well as by the direction of the water current; they also position with respect to the vertical by reference to gravity and light.

(c) Terminology

First of all, the object of orientation may be considered: What is oriented? Secondly, events and arrangements may be described in terms of the geometric relations of movements with respect to space and to spatial cues; the orientation mechanisms will be related to these geometrical aspects. Thirdly, orientation terms may be classified by means of functional and other characteristics. Functional characteristics refer to the function in the biologic-ecological context.

Object of Orientation

Orientation is often considered only in terms of the whole animal. The animal is orienting itself, it is the object of orientation (i). But an animal may only move parts of its body in an oriented manner, i.e. in relation to spatial cues. In this case the body parts are the objects (ii). Finally, an animal may orient other objects, distinct from its body (iii).

As already discussed, orientation might be restricted to mere registration of spatial relations. This holds especially for type (iii). Animals (as well as humans) are capable, for instance, of evaluating the orientation of visually perceived objects with respect to the direction of gravity. Birds fly preferentially to horizontal branches; fishes, octopuses and bees can be trained not to take food unless a vertically oriented figure is presented next to them (WELLS, 1962; WEHNER, 1967; INGLE, 1971). A human being can judge whether a picture is hanging 'straight' (Fig. 8-17).

Type (iii) can be linked to type (ii). We can, for instance, orient an arm with respect to gravity: we stretch it upwards in a vertical position. This can be compared to the orientation of other objects: instead of the arm we may adjust the picture on the wall to the vertical position. In both cases the objects have been oriented in regard to exogenous spatial cues. But they may also be oriented with respect to the (main) body; orientation refers to endogenous spatial cues. These orientation forms may be distinguished as **body related** versus **space related** (for the relevant spatial cues see p. 506).

Geometry of Orientation

All spatial movements consist of one or both of two basic components, as has been discussed also by JANDER (1970): rotation and translation. A **rotatory** (or angular) **movement** changes the position (viz. direction) of the axes of the body with respect to (surrounding) space. It can be quantitatively defined in terms of angular measures. A **translatory movement** changes the locus (locality) of the body in space. It transfers the body from one place to another. The translation can be represented by the parameters of a co-ordinate system. The locus of the body may change for instance from point X_1, Y_1 to point X_2, Y_2. The co-ordinate system must be three dimensional (X, Y, Z) if the spatial alteration can be described only with respect to the three planes of space.

A translatory change may be expressed also in terms of distance and direction (polar co-ordinate system). The transfer of the body produces **distances**. Furthermore, the transfer is directed in space, i.e., it has a **rotatory** component.

According to these geometrical considerations different orientation types can be classified as follows (Fig. 8-1): Orientation of a rotatory movement is called **rotatory orientation or angle orientation or directional orientation.** Orientation of a transfer from one point to another may be named **co-ordinate orientation.** If an

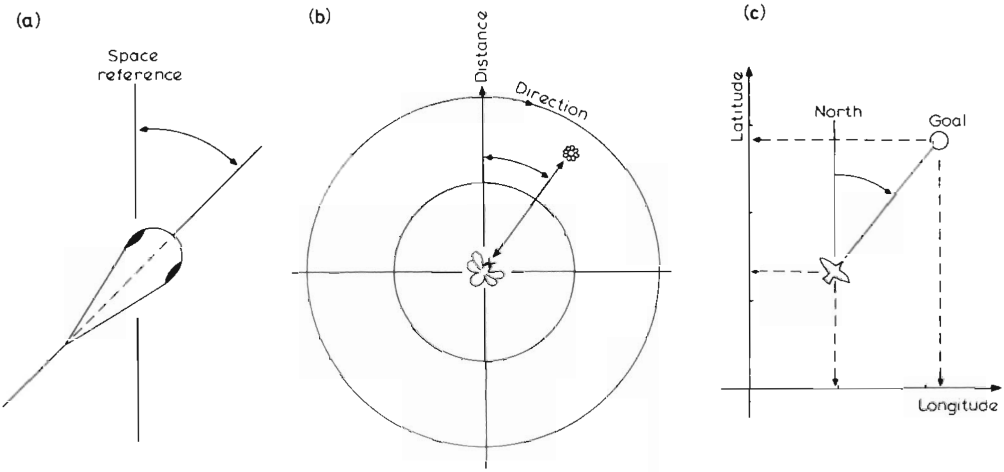

Fig. 8-1: Geometry of orientation. (a) Rotatory, directional or angle orientation. (b) Translatory orientation referring to directional and distance parameters, presented in an (animal-fixed) polar-co-ordinate system. (c) Translatory orientation, referring to bi-co-ordinate and directional cues ('map and compass'), presented in a (space-fixed) cartesian co-ordinate system. (Original.)

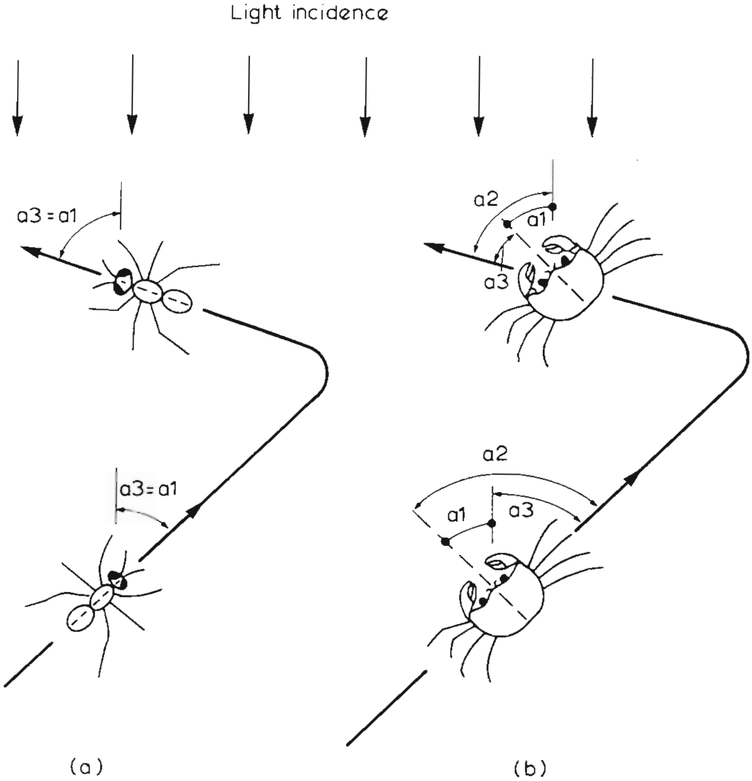

Fig. 8-2: Course orientation. (a) Coincident body orientation (a3 = a1; a2 = 0); (b) space-constant body orientation (a1 = const.; a3 = a2 − a1). (Original.)

orienting mechanism refers only to the distance of a translatory movement one may call it **distance orientation.** If, on the other hand, only the directional component is concerned, the term **course orientation** may be used, i.e. the object follows a course in space.

Directional orientations of translations and/or body axes are also called **compass orientations**, if the direction of the orienting object is related to exogenous spatial cues such as gravity or (sun) light.

Course orientations can be of two types, which differ with respect to the rotatory behaviour of the body axes (Fig. 8-2): (a) The body axes alter in coincidence with the changes of the course. The animal rotates its body in order to achieve a new course of locomotion. This type may be called course orientation with **coincident body orientation**. Insects seem to orient only according to this type. (b) The animal shows space constancy of body orientation, notwithstanding alterations of its locomotory course. This type involves course orientation with **space-constant body orientation**; it is known from crabs which may run forward, sideways or backwards without changing their body axes with respect to the reference direction (e.g. sun direction). The control of the course, however, depends on the sensory input about the sun direction, although this input remains constant (p. 543).

Translatory orientation as determined by distance and direction may be called also **vector orientation** because these parameters constitute the definition points of a vector.

In **co-ordinate orientation** the animal may represent the centre for measuring the spatial cues and for controlling the spatial changes. A bee, for instance, flying towards a distant food source controls its travel with respect to two spatial parameters: (i) the angle between flight direction (i.e. body axis) and the sun, and (ii) the distance, in terms of energy consumption (VON FRISCH, 1965). In all cases, the measures refer to the position of the animal. That is, the animal represents the origin of the co-ordinate lattice which, consequently, moves with the translation of the animal.

In contrast to this, **navigation** refers to another type of co-ordinate orientation: The co-ordinate system is fixed in space and the animal is capable of localizing its position in this system by determining characteristics of the locus, for instance by recording $x\,y$-values (**bico-ordinate orientation**). This information and a direction reference is needed to steer a particular course in order to find another locus in the co-ordinate system, the destination point of the orientation manoeuvre. A model of the navigation system of migrating birds assumes the interaction of a mechanism of bico-ordinate control of the geographical position and a compass mechanism ('map and compass' hypothesis of KRAMER, 1957). For the determination of the compass direction, a sun-compass mechanism is present in birds. Orientation by means of the earth's magnetic field has also been detected (KEETON, 1971; WILTSCHKO and WILTSCHKO, 1972; Chapters 8.1, 8.2). Almost nothing is known about the mechanism delivering information about the geographical position.

In classifications of mechanisms of homing and migration in birds (GRIFFIN, 1952; SCHMIDT-KÖNIG, 1965), directional (and distance) control by means of reference to landmarks is called **piloting** (orientation type I); compass orientation and navigation constitutes types II and III, respectively.

Functional and Other Aspects

Animals occupy a **normal or preference position** in space. Often their body is maintained with its dorsal side up, and the orientation mechanism obtains its reference from gravity and/or light incidence. In many cases, the reference basis for the normal position is the substratum, the positional data being mediated by tactile cues. For instance, walking and creeping animals orient their ventral side towards the substratum. Regarded from the geometrical point of view these are rotatory orientations.

The normal position will be maintained also when the animal performs orientation movements in other planes. Thus, during oriented translations along horizontal paths many animals tend to keep their dorso-ventral body axis vertical. FRAENKEL and GUNN (1961) have termed normal-position orientation **primary orientation**; superimposed orientation forms of translations, **secondary orientation**.

A special type of normal-position orientation is **equilibrium orientation**. This orientation serves to maintain the physical state of body equilibrium with respect to the force of gravity, which continuously acts on the body mass and endangers posture stability. Equilibrium orientation is of particular significance in animals which carry the body high above a relatively small-standing base on the substratum, e.g. long-legged land dwellers. An important reference cue for this mechanism is gravity itself. However, visual cues may also play a role; this has been demonstrated in humans: apart from gravity, the equilibrium mechanism depends on the 'visual vertical'. This reference direction may be defined as the resultant computed in the visual system from the main directions of (all) elongated figures of the visual surroundings (see BISCHOF, 1966a).

A large group of orientation types is characterized by the common feature of aiming at a particular area, place or object: **goal, target or object orientation.** If the goal is at a distance able to be bridged by sense organs, the orientation mechanism may use cues released from the target: **direct ('unmittelbare') orientation** of BRUN (1914), **proximate orientation** of WATSON and LASHLEY (*in*: CHMURZINSKI, 1964). If the goal is reached by means of other 'intervening' cues, for instance landmarks or celestial cues (sun compass), the terms **indirect ('mittelbare') orientation** or **distant orientation** have been employed by the respective authors. The 'intervening' cues must be known to the system as leading to the goal, i.e. often they have to be experienced first.

Many beach-dwelling animals, such as species of *Talitrus*, orient by means of the sun compass. By this means they find their way back, if placed outside of their habitat zone on the beach (PARDI and GRASSI, 1955). Here the goal is an area, characterized by a main elongation in one direction. Planktonic forms orient towards a particular zone, elongating in two (horizontal) directions which is defined by the vertical distance from the sea-level (e.g. vertical migration into a particular depth). The mechanism depends on cues of gravity and light as well as of hydrostatic pressure (p. 547).

The **goal areas** can be circumscribed locally, for instance in the orienting system of salmon which head towards their upstream breeding areas. At fall or spring migration, birds aim at their winter areas or at their homeplaces, respectively.

Target size can be even more restricted, for instance, to the entrance of a nest, a hole, or a particular hiding place. This may be called **locus orientation.** The name **immediate orientation** has been proposed by CHMURZINSKI (1964) as a specification of proximate orientation which defines the finding of the nest surroundings in landmark orientation.

All orientation types mentioned involve more or less extended locomotory activities in order to bridge the distance from start to goal. The situation is different in orientations controlling object hitting: **object orientation.** The animal reaches and hits its target in a single motoric action. Type (1) involves striking at the target with body appendages. Toads, frogs, and chameleons make use of their tongue; crabs, mantids, and primates grasp with claws, legs or arms; birds peck with their bill. Type (2) comprises throwing the whole body at the object in a quick jump, e.g. fishes and carnivores jump at their prey object.

(2) Physiology of Orientation

(a) Presuppositions Regarding the Orientation Process

Orientation movements are components of complex behavioural events. The very first step is the initiation of the oriented behaviour, the release. The **releasing** factors are to be distinguished from the **orienting cues**, i.e. the cues needed for spatial arrangements of the behaviour (TINBERGEN, 1969, p. 81). A perch resting by the entrance of its hole, or a lobster loitering about in search of food, is alarmed by a shadow. The animals flee into their respective hiding places. The shadow releases the flight, the characteristics of the hiding place direct it.

Irrespective of release, orientation depends not only on **spatial cues**, but also on other (endogenous and/or exogenous) presuppositions as determined by the behavioural context. These factors affect the endogenous disposition (SCHÖNE, 1973b). The resulting **specific disposition** is responsible for the particular value of the orientation to be performed. Cybernetic terms for this 'prefixed' or 'preset' value are **set point** or **index value**. From the ethological point of view 'specific disposition' has a meaning similar to the terms 'motivation', 'readiness to react', and 'mood'.

An example of the effect of **external** factors on the central disposition is demonstrated by crustacean plankton. Animals which swim towards a light source, will change their direction and swim away if irradiance intensity increases (MAST, 1911; PARDI and PAPI, 1961). The direction of the light and the overall irradiance can be considered as independent stimulus variables. Overall irradiance intensity affects the index value of orientation; light direction serves as the reference base for the orienting process.

Endogenous control of the specific disposition prevails in caterpillars. The course with respect to light changes as the individuals grow: The first stages move towards the light source. Later on, when the caterpillars approach the pupal stage, they move away from light. This reversal is related to an increase in the concentration of ecdyson in their body fluid (BEETSMA and co-authors, 1962).

The larvae of dytiscid waterbeetles (*Dytiscus marginalis*, *Acilius sulcatus*) also alter their swimming course 'spontaneously' with respect to light direction when submerged for a certain time. They turn upwards from the horizontal path, towards the light (Fig. 8-16). At the surface, they expose the caudal end of their body—which bears the stigmata—to the air and exchange respiratory gases. Thus the index value of the swimming course is controlled by a mechanism linked to the physiology of respiration.

The last event of the orientation process involves interaction with spatial cues, i.e. the **reaction to the stimulus**. This may be defined as the motor action by which the input data about spatial cues are changed until they fit the index values of the central disposition.

Thus orientation presupposes (i) the specific endogenous disposition and (ii) the relevant spatial cues.

Orientation reactions in general have been extensively analysed in terms of the concepts of tropisms and taxes (p. 526). These concepts do not refer to the alternations of orientation caused by a change in specific disposition. Orientation changes of this kind, however, have been taken into account in the conceptual models of the re-afference principle, the related considerations of 'corollary discharges', and in the cybernetic approach (pp. 530, 534).

(b) Information About Spatial Cues

The procedure of orientation is based on information about the spatial cues. The acquisition of this information may be called 'localization'.

Spatial Cues

With respect to the geometrical aspect of orientation, three types of spatial cues may be distinguished: (i) directions in space, (ii) distances, (iii) relations between different directions which may concern different modalities (p. 540).

Another characteristic for classifying spatial cues concerns their origin. The information may stem from external sources, such as light, gravity or chemical stimuli. Orientation based on this type of spatial information is called **allothetic** (MITTELSTAEDT and MITTELSTAEDT, 1973). The information is mediated along the sensory path, i.e. by means of stimulation of sense organs.

On the other hand, information which—in the last analysis—is produced by the organism itself is called **idiothetic.** This group includes (i) proprioceptive cues not dependent on external factors, (ii) cues relevant for 'correcting behaviour', e.g. of a milliped which returns to its former moving direction after a forced turn; (iii) (other) cues responsible for 'kinaesthetic' orientation. In types (ii) and (iii) of idiothetic orientation, information of a **non-sensory** origin may be of importance. Information regarding directional changes of motor activity is already existent in central nervous activities initiating and steering the motor processes in question. This information might be stored and used later for repeating or reversing the orientation, or for changing it in another way.

External spatial cues can be subdivided further on the basis of their physical and spatial structure into three types: (i) Practically **parallel stimulating agents** (sunlight, gravity, earth's magnetic field), (ii) **gradient structures**, and (iii) stimuli emanating from locally restricted sources, such as **landmarks.** Parallel agents are used, for instance, as reference directions for rotatory orientation; the source is—from the viewpoint of ecological significance—not directly relevant for the orientation (it is never the goal of an orientation). Orientation in gradients (e.g. chemical) leads the animal towards the origin or away from it. Landmarks assign a particular spot in space as a reference mark for 'direct' orientation. A trail comprises marks which are arranged in a line, one mark closely following the other; the orienting animal follows this trail.

In general, spatial cues are characterized by two kinds of properties (p. 499): (i) physical parameters used for identification of the cues, and (ii) spatial parameters used for their localization.

Identification and Localization of Spatial Cues

A bee may head for a yellow flower. The flower is the orientation mark; its yellow colour constitutes the specific sign. Irrespective of this, it is the spatial data of this mark regarding location and directional cues which are required for the orienting procedure itself.

Not only complex cues, such as landmarks, must be identified. Rather 'simple' spatial references as, for instance, directed light may be used in different orientation systems. Consequently, the sources must be distinguished by identification characteristics. Many animals show compass orientation with respect to directed light under normal daylight conditions. In the dark, however, animals head towards a bright light source, a behaviour which is exploited for catching fishes and other aquatic animals. This 'trapping effect' (Verheijen, 1958) of light demonstrates the importance of identification mechanisms. Another example: Males of minnows recognize and locate conspecific females by their sounds (Delco *in*: Erulkar, 1972).

Identification parameters of an orientation stimulus have been determined quantitatively in experiments on prey orientation of toads (Ewert, 1970, 1973). Objects of various sizes, configurations, etc., were moved around a toad, which followed with an orienting turn, stopped, and turned again. The number of turns performed changed as a function of the input variable (Fig. 8-3). A round disc, for instance, elicited a maximum turning rate if subtending a visual angle of about 5°. When the disc size was increased above 16°, the toad tended to turn away from the model. These data indicate that the identification mechanism operates not in an 'all or nothing' fashion, but according to continuous scales of stimulus parameters. The experiments indicate also, that localization is a different process: independent of the rate of turns, every turn ended with fixation of the object.

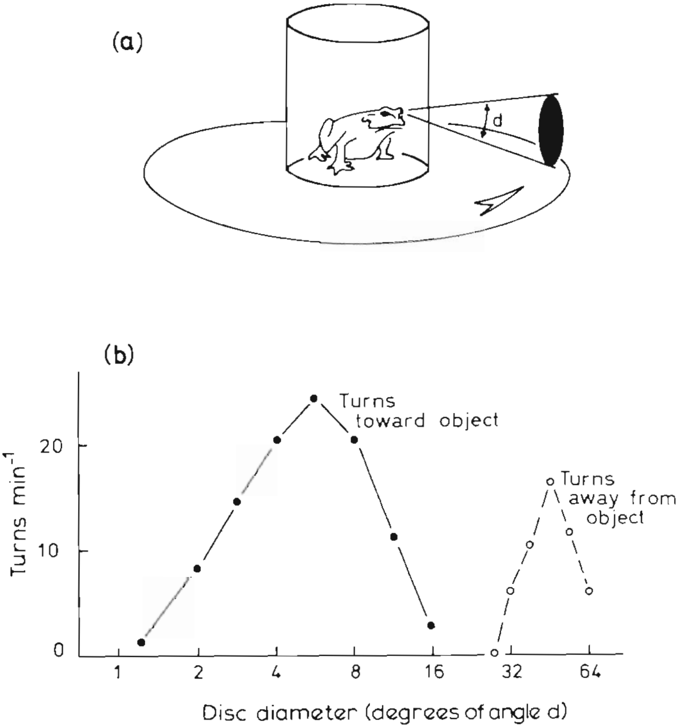

Fig. 8-3: *Bufo bufo*. Identification of orientation stimulus. (a) Moving a black disc around the toad releases orientation turns. (b) Rate of turns as a function of disc diameter (i.e. of identification parameter). (After Ewert, 1970; modified; reproduced by permission of S. Karger, Basel.)

Differentiation into identification and localization is not merely a terminological play. In many cases it has been shown that the central nervous mechanisms corresponding to these capabilities are different (p. 549).

Thus orientation cues are characterized by two kinds of properties, physical (identification) and spatial (localization): The cues which release a behaviour (releasing stimuli) are defined only by physical properties (SCHÖNE, 1973b).

Stimulus and Receptor

The term 'stimulus' may be considered from two aspects: it refers (i) to the stimulating agent, originating at the stimulus source; (ii) to the effect on the receptor, i.e. the production of excitation. Excitation which proceeds centrally from the receptor is called **afference**, that which flows from the centre to the periphery, **efference**.

A **stimulating agent** may have properties which may be altered independently (independent variables, parameters). In regard to orientation, properties are significant which allow the determination of spatial characteristics. Such properties are, for example, direction and velocity of propagation of the agent and intensity gradient.

The properties of receptors especially suited to localization are (i) sensitivity to intensity, (ii) sensitivity to time differences, (iii) directional sensitivity, and (iv) 'local sign'.

With regard to sensitivity to intensity of a stimulus agent, excitation is a function of the 'quantity' of the stimulating agent (irradiance intensity, sound loudness, concentration of chemical substance, magnitude of gravity). Sensitivity to differences in arrival time of stimuli requires receptors and CNS mechanisms which can record and evaluate temporal intervals.

Directional sensitivity involves changes in the amount of excitation in proportion to the angle of stimulus incidence. The quantity of the afference (for instance, nerve impulses $\sec^{-1}$) is a function of stimulus direction. This is often achieved by means of shielding or absorbing structures which modulate the stimulus intensity according to incidence direction, e.g. in eyes or ears.

Labelling according to the 'local sign' of the receptor on the body is a property inherent in the structure of the sensory-CNS connections. It relates sensory data on spatial cues to the body and thus provides means for locomotor-orienting body activity. In animals with two symmetrically arranged chemoreceptors, for example, the central mechanism is organized in such a way that the spatial information extracted from the system of right and left receptors results in appropriately directed orientation reactions. Here the local body sign refers to the topographical site of the receptor (right versus left). In directionally sensitive receptors, however, the 'local sign' links the directional response characteristics of the receptor to body reference axes; it is to be understood as 'body directional sign' (see p. 543). For details of sensory-central structures see GAZE (1970).

Localization of Directional Cues

This section classifies mechanisms which ascertain data regarding directional cues. The information required often results from sensory-central activity alone.

In some cases, however, interaction with the motor system occurs, e.g. in sequential sampling of stimulations in a gradient or in scanning methods. Thus localization may be the result of sensory-motor interactions. In that case it cannot be regarded as an event separated from the orientation process as such.

The following classification is based mainly on the type of input depending on the above-mentioned receptor characteristics. An 'input unit' comprises receptors which transfer the stimulus quantity (or quantity changes) according to the same direction-excitation function. Thus the input unit may consist of several receptors mediating the same information. The conformity may be based on the equality of structure and of local sign of the receptors.

With respect to the number of input units involved in localization of direction, we shall distinguish three types: systems with (i) one input unit, (ii) two input units, and (iii) multiple input units (rasters; Fig. 8-6).

With respect to receptor sensitivities the types may be characterized as operating on the basis of (a) sensitivity (only) to intensity, (b) sensitivity to time differences and (c) sensitivity to stimulus direction.

(i) **One-input unit systems** may be subdivided into systems reacting only to intensities (ia) and systems responding to incidence direction of stimulus (ic). Type (ia) can be further differentiated: (ia_1), reactions to instantaneously recorded stimulus change; (ia_2), reactions to differences of sequentially sampled intensity data, which assumes storage of data. The systems will be discussed below, except type (ia_1). This type includes, for instance, 'kinesis' mechanisms (p. 527) and phobotactic 'trial and error' methods (p. 526). The excitation of the input system affects the quantity of locomotor activity, by changing velocity of locomotion or number or magnitude of turns; this results in orientation with respect to a gradient.

(ii) In **two-input unit systems** the data of two, often 'antagonistically' arranged, inputs are compared. These systems may be of three kinds: (a) Comparison of data of two stimulus intensities as recorded by the two inputs. (b) Recording and evaluating the differences in stimulation time of two inputs (delay time) dependent on propagation velocity of the agent. (c) Comparison of the excitation of two direction-sensitive inputs.

(iii) **Multiple-input unit systems**, rasters, are composed of directional sensitive units; they are used for determining incidence direction to the stimulus.

Those of the systems (i, ii, iii) which are based on sensitivity to intensity (a) are employed preferably in determination of gradients, those sensitive to time difference or incidence direction (b, c) in determination of incidence direction of stimuli.

Determination of gradient direction involves measurement of the stimulus magnitude at different positions along the gradient. The method comprises differential measuring based on comparison of measurements at two points in space, recorded at one point or at two points in time. That is, the stimulus magnitudes are recorded either with one unit (ia_2) by sequential sampling or with two units (iia) operating simultaneously. The gradient direction is determined from data on the intensity differences and on the relative positions of the measurement sites.

An example for (iia) is given first: A bee might sense two odour intensities simultaneously with the chemoreceptors on its two antennae. Providing the odour has attractive qualities, the bee turns to the right, if the right antennal receptors are excited more strongly (local sign). Information regarding the direction of the gradient, is gained from the difference in excitation between right and left receptors. If both sides are excited equally, the bee moves straight ahead; it is adjusted to the gradient direction, i.e. the system has localized the direction of the gradient.

This kind of gradient registration presupposes certain characteristics of the gradient and certain properties of the receptor system. The gradient must be steep enough so that the receptors are excited differentially. This, in turn, depends firstly upon the sensitivity of each receptor to intensity differences (discrimination threshold), and secondly upon the spatial separation of the two receptors. The more sensitive the receptors are and the greater the distance between them, the higher is their capacity for detecting gradients by simultaneous measurement.

If the gradient is too slight to be determined by simultaneous sampling, a sequential sampling method is used (ia_2). Measurements are taken at various sites along the gradient—at points more distant from one another than can be spanned simultaneously by the animal's two receptor systems. Measurements follow each other. The animal moves between two measurements, and data concerning this change of location must be taken into account by the mechanism, as must the local signs of the receptors in the simultaneous procedure.

These types of orientation involve detection and tracing of graded intensities. It implies that the animal can only find a stimulus source which lies along the line of the gradient. Gradients, however, could be oriented transverse to incidence. A light gradient, for instance, might be caused by translucent substances of graded absorbency, arrayed across a light beam. By means of type (a) systems an animal can find, of course, only the region of greatest brightness or darkness across the beam; it is not capable of orienting with respect to the light beam, since it cannot detect the direction of light radiation.

Direction finding by evaluation of delay time (iib). As in the previously described systems, delay-time measurement requires stimulation at multiple sites. The mechanism, however, analyses differences in arrival time, not differences in intensity. If, for instance, a man is oriented with his right ear towards a sound source, the distance source to his right ear is smaller than that to his left ear; the sound thus reaches the left ear later. From this time difference (delay-time) the central mechanism calculates the directional cue of the sound source. This calculation is based upon the (inherent) knowledge of two constants: propagation velocity of the stimulating agent and spatial disparity of the receptor locations, both of which affect delay-time.

Direction finding with one or two direction sensitive input units (ic, iic). The remaining methods of determination of incidence direction have one attribute in common: the directional sensitivity of the input units (c). Each unit is excited differentially by stimuli from different directions. The directional response characteristics can be represented diagrammatically by a plot of response magnitude versus incidence angle of the stimulus (Figs 8-4, 8-5). A change in stimulus direction causes a change in response of the unit.

Type (ic) systems rely on sequential measurement of input data. Present measurements are compared with previous ones stored. Considerations of this kind have been put forward by KRAMER (personal communication). Klinotactic mechanisms (p. 527) may be included here.

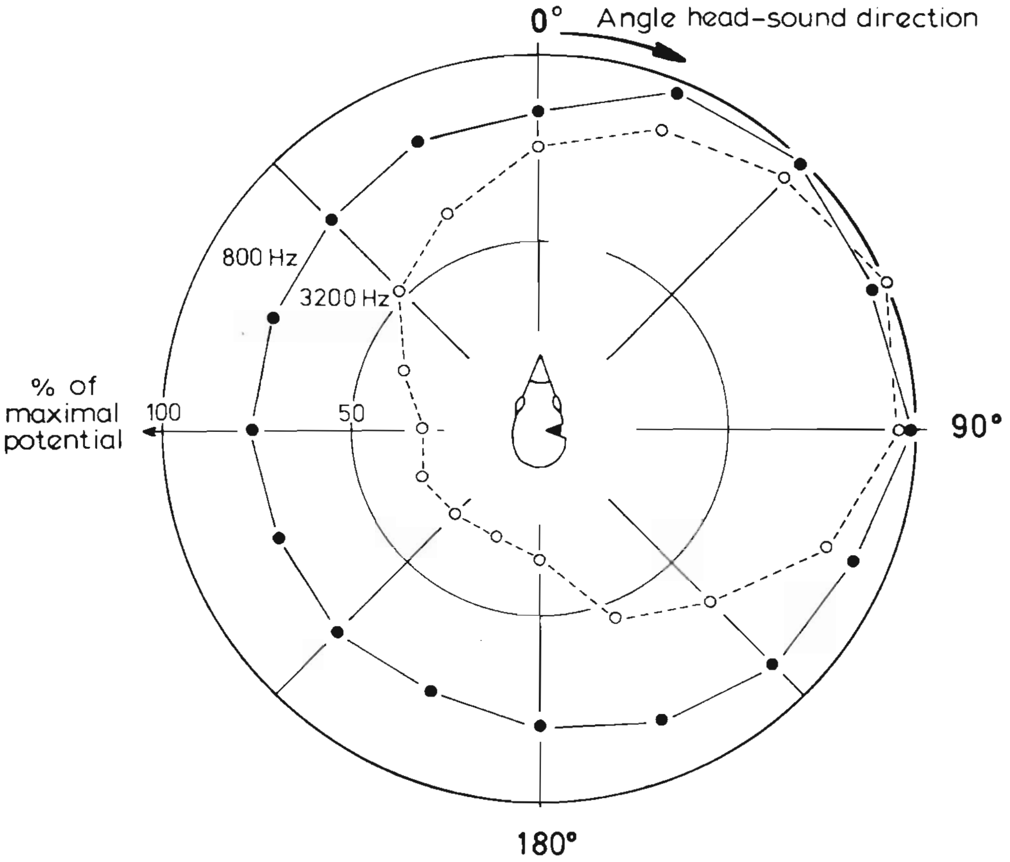

Fig. 8-4: *Pyrrhula europaea.* Direction characteristics of the right bullfinch ear representing an input unit. Cochlea potentials (% of maximum) as a function of sound direction with respect to head at two frequencies of sound. (After SCHWARTZKOPFF, 1962; modified; reproduced by permission of Springer-Verlag, Berlin.)

Systems operating with two units (iic)—arranged symmetrically or in another topological order (e.g. front versus back sites)—are capable of determining stimulus direction simultaneously. A change in stimulus direction alters the excitation of each unit according to its characteristics. Because (per definition) the local signs of two units are different, their excitations change differentially. It is this difference, the **ratio** of the excitation quantities of the two units, which forms the basis for the directional information in this type of system.

Comparison between type (iic) and type (iia, e.g. in gradient measurement) reveals a similarity: in both, the excitation difference of two units is important. However, in (iia) it is caused by external differences in stimulus intensity (gradient), whereas in (iic) it is a function of incidence direction of the agent.

Two-input unit systems may also employ the method (ic) of consecutive

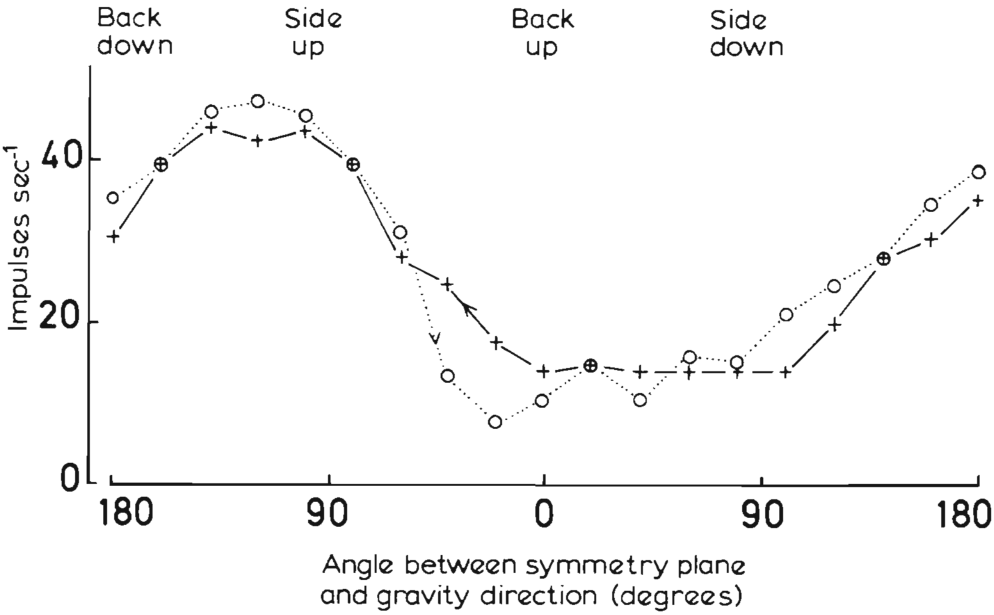

Fig. 8-5: *Raja clavata*. Direction characteristics of a single fibre of the utricle. Impulse frequency as a function of position with respect to gravity in a ray fish rotated around its longitudinal axis. (After LOWENSTEIN and ROBERTS, 1949; modified; reproduced by permission of Cambridge University Press.)

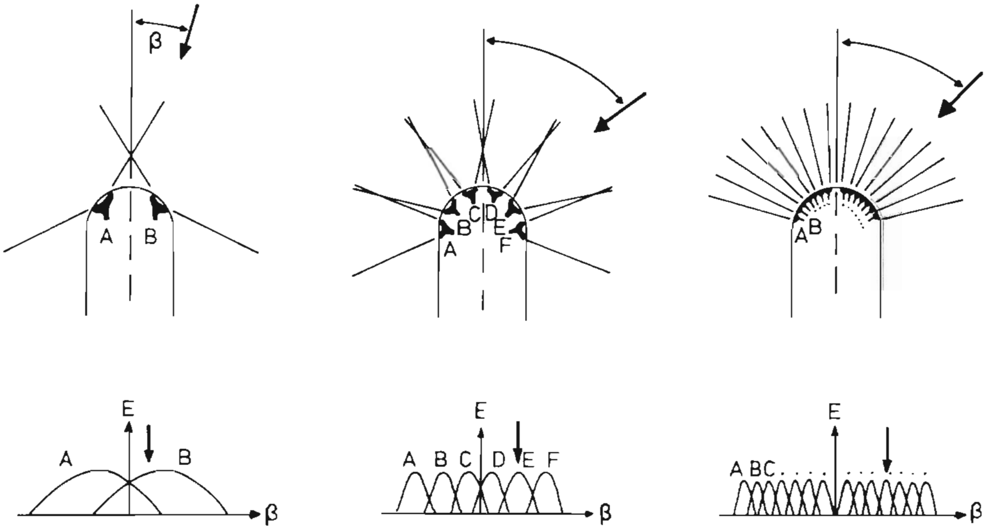

Fig. 8-6: Models of localization of stimulus direction with different numbers of input units. Upper: Front part of body with opening sectors of units. Lower: Direction characteristics of input units. Excitation (E) as a function of β; β: angle of stimulus incidence; A, B, . . . : input units. (After SCHÖNE, 1973a; reproduced by permission of G. Fischer Verlag, Stuttgart.)

sampling, evaluating the difference of actually to previously recorded excitations. Thus the direction of the strongest excitation may be determined by means of scanning movements. These may involve the whole body or the receptor organ, or only the shielding structures (e.g. the pinnae of the ears).

Direction finding with rasters (iii). A raster is composed of many direction-sensitive input units. In (ic) or (iic) systems each unit is capable of receiving stimuli from a rather large sector, in some cases over 360°. A two-unit system (iic) operates on only two local signs; accurate determination of a stimulus direction depends on the difference of the excitations of the units. Each unit of a raster, however, is open to a relatively small sector of stimulus directions. The whole field is divided into (many) sectors. The signals produced are assessed in relation to a local body sign (i.e. a directional label), which is based on the local signs of the units. It is the local sign, i.e. the site of the response, which provides the main cue to stimulus direction. But, of course, also in rasters the topographical relations of the units are of importance; they provide the basis for calculating the site of maximal excitation. Determination of stimulus direction, however, is a matter of localizing the peak of excitation (local sign of maximum), not of evaluating the differences of two excitatory quantities. Directional information supplied by a raster may thus be said to be coded in terms of quality (local sign); that supplied by two units, in terms of quantity. As demonstrated in Fig. 8-6, these two types are, in principle, not different; they might be considered extremes of a range of possibilities.

Raster organs frequently possess fixation areas (foveae). The animal turns in such a way that the stimulus strikes this spot and then maintains this position, fixating the stimulus. In the foveal region the density of the units is often rather high.

When different stimuli strike different units of a raster simultaneously, image formation becomes possible. For example, compound eyes have retinae, the units of which can respond independently to simultaneously arriving stimuli. Thus a pattern of stimuli may be recorded. In other kinds of rasters, this is not possible: At any given time, gravity-sensing systems of the raster type are excited only at one site in the raster, since there is only one stimulus. Several forces, e.g. gravity and centrifugal force, act as vector quantities, acting on the statolith masses which transmit the resultant force (only one force) to the receptor.

Raster mechanisms are often correlated with particular central nervous structures. In centres associated with visual rasters, areas are found which represent the spatial arrangement of the units of the retina in a topological array; they form a point-to-point projection of the visual field (p. 550; for insects consult BRAITENBERG, 1972; WEHNER 1973). A kind of mould of the visual surroundings permits localization of a point stimulus as well as detection of stimuli configurations (pattern recognition). This template of sensory representation forms the basis for exact spatial control of motor activity.

The mechanisms of central representation of space directions in two-unit systems are hardly known. Possibly, there exists a kind of spatially ordered representation of the auditory space field in the auditory centres of higher vertebrates (JEFFRESS, 1948; COLEMAN, 1959; ERULKAR, 1972, p. 344). This would imply that directional cues, expressed in terms of ratio values from two units, may be transformed centrally into an array with space characteristics.

Determination of Distance

Distance determination is of importance in many mechanisms of goal or object localization. The quick jump of a prey-catching fish must take into account the distance; while prey animals, on the other hand, must pay careful attention to the striking range of potential attackers. Taking into consideration the modality of distance determination, sensory and non-sensory mechanisms can be distinguished.

An example of the non-sensory mechanism is found in bees. Collecting bees begin to fly in 'search' circles as soon as they have reached the distance from the hive at which they had found food previously, even in cases in which the food source was removed and placed at a greater distance from the hive. This mechanism refers to the amount of energy expended during the preceding flight, thus predicting the location of the food source (VON FRISCH, 1965). This procedure may be classified under idiothetic orientation because the spatial cue stems from an endogenous source. It represents a third type of idiothetic information in addition to the proprioceptive and the efference copy types, discussed on p. 506.

Most mechanisms of distance determination are based upon sensory processes. We will consider 7 types:

(i) Measurement of stimulus direction from two loci. Both directions converge at the stimulus source. The two measurements, therefore, allow the calculation of the convergence angle and thus of the distance to the source. Measurements may be performed simultaneously with two receptor organs, as in the visual system of many predatory fishes, carnivores and primates, as well as of predatory insects, e.g. dragonflies and their larvae, or the praying mantids. Successive determinations of direction with considerable distances between loci (e.g. scanning), give a greater angle of convergence allowing more precise evaluation of distance.

(ii) Visual mechanisms using dioptric properties as parameters; e.g., focal distance as controlled by accommodation of lenses or by variation of lens-retina distance.

(iii) Visual mechanisms employing the deviation of the retinal image from corresponding points on the two retinae (lateral disparity, 'Querdisparation'). An object located in the plane of focus is perceived as one object, although it stimulates two retinal sites, i.e. one in each eye. These sites are called 'corresponding loci'. Objects deviating from the focal plane stimulate loci distinct ('disparate') from the corresponding loci. Disparity increases with object distance from the focal plane.

(iv) Displacements of the retinal image. Lateral dislocation of the object results in a shift of the image on the retina. The shift is a function of distance: shift magnitude increases as the distance to the object decreases. Another displacement phenomenon corresponds to the relative dislocation of the object with respect to the overall (visual) background. This also helps to evaluate distance cues.

(v) Mechanisms of stereoscopic vision. The difference between the images recorded by two eyes is distance-dependent. Objects seen at a great distance offer almost the same aspect to both eyes, whereas in nearer objects, differences are more pronounced.

(vi) Acoustic mechanisms of distance evaluation in bats and delphinids involve the echo rebounds of self-produced sound pulses. The active-biosonar system determines the time elapsed between emittance and reception of sound pulses (e.g. SIMMONS, 1971; ERULKAR, 1972, p. 295; Chapter 8.3).

(vii) Distance evaluation based on the intensity of the received stimulus presupposes that the determining mechanism is informed about stimulus intensity at the source. For instance, we can estimate our distance from a running motor vehicle if we know how much noise its engine produces.

Peculiarities of Modality

In addition to the general aspects of spatial cue determination, the diverse modalities show specific characteristics corresponding, for instance, to physicochemical specialities of the agents, or to usefulness for the species. As far as acoustical events and chemical agents are concerned, the propagation velocity is a quantity which is accessible to organisms; in regard to light and gravity this parameter is beyond organismic capabilities.

Mechanisms depending on allothetic cues (p. 506)

Visual cues are often analysed by means of rasters capable of image formation (lens eyes of vertebrates, cephalopods, spiders; compound eyes of arthropods; pit eyes of snails). Many protozoans (flagellates) with eye spots (stigmata) can be classified under system (ic) (p. 509; see also Chapter 7). Attached to one side of the light-sensitive area is a 'shield' of pigment granules constituting directional sensitivity of the unit (MAST, 1911; HAND and DAVENPORT, 1970). Control of direction depends on successive registrations of directional data. Some flagellates, e.g. species of *Gyrodinium* (HAND and DAVENPORT, 1970), are suspected of simultaneous orientation by a two-unit system (iic). Type (iic) comprises also systems of two primitive eyes (ocelli) of multicellular animals, such as planarians and larvae of *Arenicola marina* (MAST, 1911). In planarians, reactions of type (ia_1) have been reported (FRAENKEL and GUNN, 1961).

Thermal cues serve to find sites, e.g. water bodies of preferred temperature, and to locate heat-radiating prey animals. Snakes of the family Crotalidae receive thermal cues with their pit organs. These thermoreceptive sensors respond to the rather weak infra-red radiation emitted by small warm-blooded animals such as mice (BULLOCK and DIECKE, 1956). The morphological and topographical features of the pit organs are suited for operating on the two-unit principle or on the raster principle (iic, iii, p. 509). The known physiological and behavioural data, however, are insufficient for adequate description of this localization mechanism.

Electrical cues play the major role in the orientation mechanism of electric fishes (particularly of the families Gymnotidae and Mormyridae) some of which live in the very turbid waters of African rivers (BENNETT, 1971a, b; SZABO, 1973). These fishes have organs which produce electric pulses at short intervals (up to several hundreds sec^{-1}). An oscillating electrostatic field is built up around the fish between its rostral and caudal end. Objects with a conductivity differing from that of the water alter the pattern of the field lines. This is recorded by the electroreceptors distributed all over the body. The response pattern of the electroreceptors delivers the cues for locating the object.

Non-electric fishes, such as sharks or *Petromyzon marinus*, are reported to react to electrical stimuli produced by muscular activity (for instance of the heart or respiratory basket) of prey animals (DIJKGRAAF and KALMIJN, 1966; KLEEREKOPER, 1969, p. 136).

The electroreceptors of electric fishes, distributed over the body, form a raster. A topographically ordered 'map' of this raster has been found in the torus region (inferior colliculus) of the midbrain (SCHEICH and BULLOCK, 1973).

The electric organs of some strongly electric fishes, for instance the electric eel *Electrophorus electricus*, are probably not involved in orientation. The system is capable of producing discharges of high voltage (several hundred volts), which are used to anaesthetize and kill prey.

Many aquatic animals respond to strong artificial electric currents. Their neuromuscular system is forced by the current to adjust to its direction. Biological function and ecological significance of this phenomenon are open to debate.

Magnetic cues. Magnetic fields may affect light orientation of invertebrates. This has been documented in planarians and snails (*Nassarius obsoletus*; BROWN and co-authors, 1959; BROWN, 1962; see also Chapter 8.1). Orientation of migrating robins is affected by the horizontal component as well as by the inclination and by the intensity of the magnetic field (WILTSCHKO and WILTSCHKO, 1972). Homing pigeons may use a sun compass as well as the magnet compass which is based on the magnetic field of the earth (KEETON, 1971). Nothing is known about receptor mechanisms.

Chemical cues. In a stationary medium a chemical agent disperses only by the rather slow process of diffusion, forming a circular gradient around the source. The gradient is transformed into an elongated field if the medium moves into one direction. The gradient direction is often localized by one- or two-unit mechanisms (ia, iia, p. 509). *Porcellio scaber* orients in humidity gradients on the basis of type (ia_1) (orthokinesis; FRAENKEL and GUNN, 1961).

Bees sample intensities simultaneously or successively (iia_1, ia_2; LINDAUER and MARTIN, 1963). Fishes may orient in chemical gradients on the basis of simultaneous measurements with two units or of sequential sampling with one unit (KLEEREKOPER, 1969, p. 148; HARA, 1971).

In the presence of water movement, chemoreception is often integrated with current reception in a composite mechanism of goal orientation. Potentially, there are two ways of detecting an odour source by this combined mechanism. (i) Odour marks the current, and the animal orients with respect to this current. Direction finding depends upon receptors responding to the mechanical stimuli of the current, whilst chemosensors operate 'only' as releasers which activate current orientation, e.g. in *Diplodus sargus* (KLEEREKOPER, 1969, p. 154). Experiments on bees (KRAMER, personal communication) may also be interpreted in this way. (ii) Chemoreceptors serve as direction sensors, either in combination with current receptors or without. The direction of incidence of the chemical substance is detected by the chemoreceptor system which, of course, must be direction sensitive.

Chemical cues may also be important as landmarks. Some territorial animals mark their areas by urinating or deposing specific odour substances (e.g. EIBL-EIBESFELDT, 1967).

Bees of the genus *Meliponini* mark paths leading to food sources by secreting a substance which they deposit along the path at short intervals (LINDAUER, 1963).

They thus lay a trail which is followed by companions from the nest. Trail orientation is very common in ants and termites, but is also a well-known element of prey pursuit in vertebrates, e.g. in snakes and dogs. This orientation mechanism may be included under direction determination of type ia_2 or iia (p. 509).

A trail consists of a line of maximal odour concentration attenuating at both sides. Snakes take samples with their forked tongue and test the adhering substance with the chemoreceptors of Jacobson's organ. Dogs, by sniffing, sample odour successively. Snakes and dogs both aim for maximum odour concentration. However, the characteristic of trail orientation is that the animals do not remain at the first point of maximum concentration reached, but continue to follow the line of highest concentration.

Employing a similar mechanism, sharks follow the three-dimensional scent trail produced in water, for instance, by a prey animal losing blood.

Humans lateralize an odour source by means of the time delay in reception at the two nostrils (type iib on p. 509; VON BÉKÉSY, 1964).

Gravitational cues are involved in equilibrium orientation, compass orientation, orientation of normal position, and directional orientation of body parts as well as of other objects.

Gravity receptors of some mussels and snails are of the raster type (iii, p. 509) (DIJKGRAAF and HESSELS, 1969; WOLFF, 1970, 1973). The walls of the statocysts are covered with sensory hairs. The statolith stimulates maximally those sensory cells that are located at the lowest part of the cyst. The directional cues are evaluated on the basis of the local signs of these cells: the locus of maximal excitation is the decisive cue.

Crustacean statocysts are discussed in some more detail because they appear to comprise a combination of two types of localization. The experimental data obtained have been interpreted as follows (Fig. 8-7; SCHÖNE, 1971, 1973a; STEIN, 1974): Directional cues are analysed by a combination of type (iic) and (iii), i.e. two input units and raster. In Fig. 8-7c the crayfish rolls (e.g. is inclined towards right side), the hairs of one statocyst can be regarded as one input unit, since the amount of excitation from all hairs alters proportionally. The difference between the two statocysts thus is changed. In Fig. 8-7d the animal pitches, inclining with head down: the differences between caudal and rostral groups of hairs is changed. The crustacean, however, may alter from a roll position directly into a pitch position, without going back to normal positioning, i.e. the plane of tilt changes. A positional change of this kind is demonstrated by a crayfish which walks on a vertically oriented plane and alters its walking direction with respect to gravity. It changes its posture from roll tilt to pitch tilt or vice versa (Fig. 8-7e); the site of maximal stimulation in the groups of sensory hairs is altered. With respect to this change, the maculae resemble a raster. In the crayfish, therefore, alterations of the planes of tilt are differentiated on the basis of the raster principle, whereas the degree of tilt (in a given plane) is evaluated by means of the two-unit principle.

In vertebrates, a similar combined mechanism operates; this can be concluded from morphological and physiological findings (VON HOLST, 1950a; TRINCKER, 1962; FLOCK, 1964; FLUUR and MELLSTRÖM, 1970). The sensory hairs of the macula of the utriculi show a fan-like pattern in their direction of polarisation (i.e. direction of maximal response), thus forming a raster which is capable of discriminating between tilt planes (Fig. 8-8). If, on the other hand, an animal stays in one plane

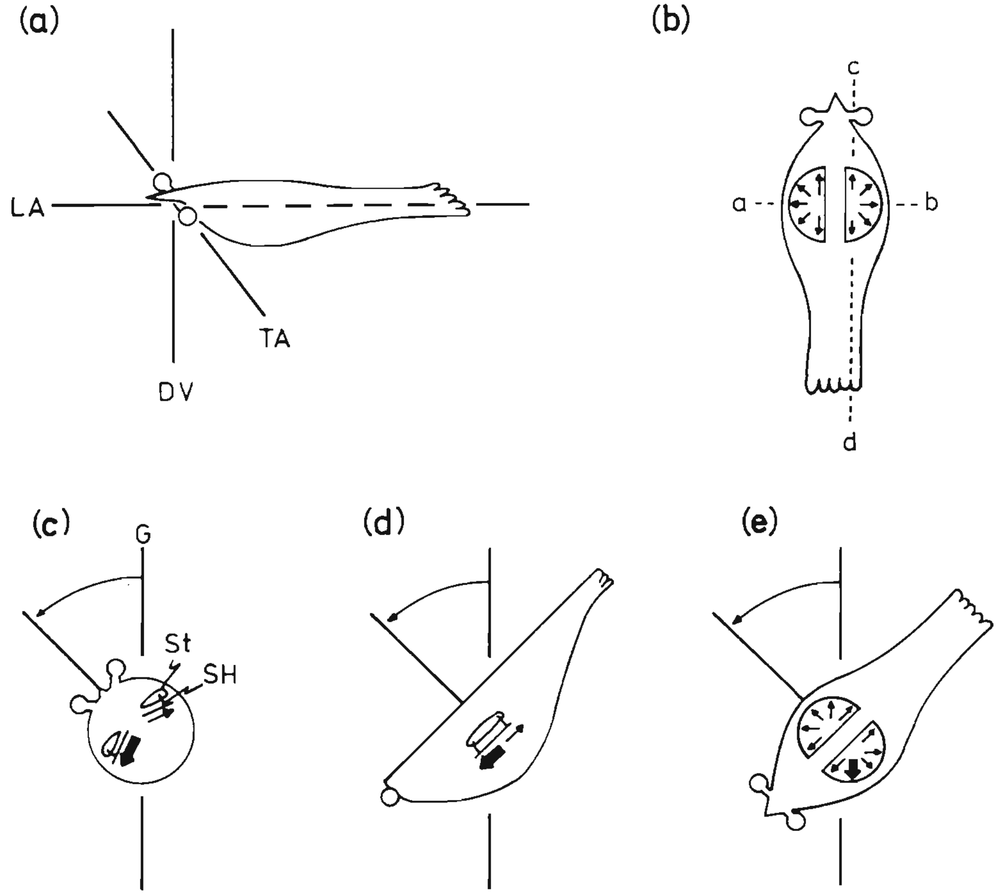

Fig. 8-7: Model of gravity localization in a decapod crustacean. (a) Body axes; LA: longitudinal, TA: transversal, DV: dorsoventral. (b) Dorsal aspect with statocyst symbols; arrows correspond to directions of polarization, i.e. of maximum stimulation of sensory hairs; a–b: section plane of (c), c–d: section plane of (d) (schematic, in reality statocysts are in antennules). (c) to (e) Excitation of sensory hairs as a function of positional change around different body axes. (c) Roll around horizontal LA; magnitudes of excitation (symbolized by arrow thickness) of right and left sensory hairs change. (d) Pitch around horizontal TA; excitation of front and back sensory hairs changes. (e) Movement around horizontal DV (yaw in vertical plane); location of maximally stimulated sensory hairs changes. G: gravity direction, St: statolith, SH: group of sensory hairs similarly stimulated. (After SCHÖNE, 1973a; reproduced by permission of G. Fischer Verlag, Stuttgart.)

and inclines more and more, for instance, rolling to one side, the information regarding gravity direction depends upon the difference between the right and left receptor groups.

In octopus the maculae of the statocysts show a radial array of sensory hairs (BARBER, 1968), again representing a kind of raster. Gravity direction is determined by analysing the response pattern of the raster units (BUDELMANN, 1970).

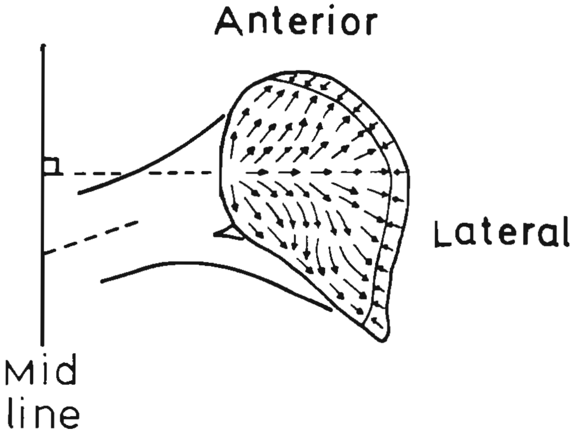

Fig. 8-8: *Lota vulgaris*. Pattern of morphological polarization of (groups of) sensory elements on right macula utriculi. (After Flock, 1964; reproduced by permission of Rockefeller University Press.)

Some water insects (species of *Nepa*, *Ranatra*) make use of the lifting effect of air, which adheres to their seta-covered body (Baunacke *in*: von Buddenbrock, 1952, p. 276). Sensory hairs attached to the air bolsters are stimulated differentially as a function of body position in relation to gravity. In the genus *Ranatra*, right and left groups of hairs seem to co-operate in a two-unit fashion in side tilting, front–back groups in forward–backward tilting.

Land insects do not have special gravity receptors. Patches of sensory hairs, located at the joints of appendages or movable body parts are stimulated by positional changes which correspond to alterations in the animal's position with respect to gravity (Markl, 1963, 1971; Wendler, 1971). Experiments on *Dixippus morosus* (Wendler, 1972) revealed that position may be evaluated also by the muscular effort needed to maintain the body posture against the force of gravity. Appropriate receptors could be the sensillae campaniformes of the cuticle, but the mechanism recording force and direction of muscular activity is not yet known.

Auditory cues require mention of the difference between orientation towards sounds produced by external sources and echo-orientation. An owl finds a mouse by locating the mouse's rustling sounds. Bats and odontocete cetaceans detect prey with their active biosonar (Chapter 8.3). They emit high frequency calls and analyse the parameters of the echo. This mechanism is also used in landmark orientation: the animals orient with respect to an object or a configuration of objects, thus taking auditory 'pictures' of their surroundings.

Blind people may use echo-orientation in a similar way, analysing reverberation parameters produced by the sound of their own steps or movements (e.g. Cotzin and Dallenbach, 1950; Erulkar, 1972, p. 246).

In mosquitoes the locating mechanism can be classified as raster mechanism (type iii; p. 509). The oscillations of the sound waves, for instance of wing movements of flying females, displace the antennae. The direction of displacement is analysed by means of Johnston's organ, a circular arrangement of scolopidial receptors in the antennae. Excitation attains a maximum at receptors of the circle located in the direction of antennal displacement (SCHWARTZKOPFF, 1962; ERULKAR, 1972). Males of *Aedes* have been shown to be capable of locating females even if one antenna has been removed (ERULKAR, 1972, p. 272).

In fishes, the experimental results obtained may be interpreted in terms of location mechanism type (ia) (p. 509: one unit, only intensity sensitive). Minnows follow apparent gradients of sound intensity (ERULKAR, 1972, p. 275). Frequency and size of turns seem to be affected by intensity changes (ia_1, 'klinokinesis'). It has been suggested that the swimbladder of teleosts might be involved in direction finding of pressure waves (ERULKAR, 1972, p. 277). Sharks can discriminate between two sound sources which are 10 degrees apart from each other (NELSON, 1967). It has been suggested, that the lateral-line system may be involved in the process of directional analysis of sound in fishes (DIJKGRAAF 1963c, 1967). For a detailed account of spatial orientation in fishes consult Chapter 8.2.

The ears of birds and mammals respond to frequency and intensity (pressure) of sound. Each ear may be regarded as a direction-sensitive input unit. The central mechanism evaluates differences in time (delay time) and intensity between the units (types iib and iic); it also includes aspects of frequency analysis. Low frequencies are refracted around the head to a greater extent than are higher ones. Therefore, the ear nearer a sound source receives a higher percentage of high-frequency components than does the averted one. Hence there is a difference in pitch. Monaural (and binaural) localization with directional sensitive systems may be based also on scanning, i.e. on sequential measuring (type ic; ERULKAR, 1972, pp. 284, 307).

Mechanical cues. This category comprises also gravity and auditory cues which have already been discussed separately. There is no sharp borderline between auditory and vibratory cues from a physical point of view. Auditory stimuli are characterized by relatively high frequencies and the fact that they stimulate specialized sense organs (ears). Vibratory stimuli are of low frequency. Fishes, amphibians (e.g. the aquatic toad *Xenopus laevis*; ERULKAR 1972, p. 274), as well as some aquatic insects (e.g. *Notonecta glauca*; MARKL and WIESE, 1969) and crustaceans (*Cyclops* sp.; SCHRÖDER, 1960) are capable of locating objects which produce vibratory stimuli, or which reflect the oscillations emitted by the movements of the locating animal itself.

In fishes and amphibians, low frequency oscillations, i.e. near water displacements are received supposedly by the lateral line organs (KRAMER, 1933; DIJKGRAAF, 1967; ERULKAR, 1972, p. 274). Their distribution over the body seems to be well suited to localize a source of low-frequency sound; analysis is based on the pattern of stimulus intensities or on time differences in the array (raster type).

Tactile cues recorded with antennae or bristles are often used to orient with respect to edges, surfaces or crevices. Some dragonfly larvae catch prey which they have localized with respect to direction and distance by touching with the tips of both antennae (BUCHHOLTZ, 1962).

Current cues. Two types of current, e.g. water movement relative to the animal, can be distinguished: (i) the animal propels itself through the medium and thus causes it to stream along its body. Current receptors respond to the flow of the medium and serve to control locomotory parameters, e.g. speed and direction of locomotion with respect to medium. (ii) A medium moves with respect to a reference basis (e.g. bed or banks of a river, geographical marks in ocean currents). This movement can be related to an animal only if the animal is part of the reference, i.e. if it is connected in some way to the reference. This obviously is the case in animals which are in physical contact with a solid substrate (reference). An animal, however, may also have connection to the reference by distance, e.g. visually. As has been shown, the reaction to currents depends on the relative movement of the (visual) background (HARDEN-JONES, 1963). The mechanism of current perception employs an optomotor system which records the apparent visual movement of the reference pattern.

Thus in free-floating animals, orientation with respect to current direction requires two types of spatial information: (i) Data about the spatial relation to the reference. In a homogenously flowing water body, no animal can perceive the movement of the medium if it is without this information, simply because the movement of the medium (i.e. current) exists only with respect to the reference base. Neither fishes in the ocean nor birds high up in the air can orient with respect to the direction of the respective currents (ocean current, wind), if they lack relation to the reference, in birds, for example, visual contact to the ground. If spatial relation to the reference is available, the animal can detect information (ii): i.e. it can relate its body or its course to the current direction. The situation might be different in turbulent zones of a current. Theoretically, turbulences might contain information about the direction of the current, but little is known about mechanisms detecting and using this information in swimming or flying animals. Blinded minnows *Phoxinus laevis*, for instance, drift helplessly with the streaming water (DIJKGRAAF, 1967).

Current receptors of fishes and amphibians are assumed to be represented by the free end-organs of the lateral line system (neuromasts). The mechanism of current detection is not yet known, but the topographical arrangement of the receptors indicates a raster-like function.

Wind receptors, which record the wind direction in walking insects, are situated in the antennae (LINSENMAIR, 1969, 1973). They consist of circularly arranged scolopidia (Johnston's organ) in the pedicellus, and are stimulated by the flagellum, which moves with respect to the scolopidia circle. The site of maximally responding scolopidia in the circular raster seems to mediate the directional cues.

Mechanisms depending on idiothetic cues

Idiothetic cues (p. 506) participate in a variety of orientation mechanisms.

Sensory cues are involved in mechanisms of directional stabilization which are based on cues originating in the semicircular canals and in other organs responding in a similar way to inertial forces. An example of the last is the 'pendulating' head of dragonflies (MITTELSTAEDT, 1950), the thread hairs in crab statocysts (DIJKGRAAF, 1956b), and the cristae in the octopus statocyst (DIKJGRAAF, 1961). Proprioceptive information might be involved in orientation of appendages or parts of body with respect to other parts (p. 502).

But this orientation may also depend on non-sensory cues, corresponding, for example, to correlates of efferent commands (efference copy cues; p. 530). This may be regarded as a direct source of information about the spatial structure of the own movement. Comparatively, the proprioceptive way seems a 'detour'.

The term 'kinesthesia' (movement sensation) applies to the perception of one's own movements. Kinesthetic cues may be of both types, proprioceptive or efference copy. In kinesthetic orientation the cues must have been experienced first. During primary movement events, cues are collected, ordered and stored. The subsequent orientation process depends upon repetition of the sequence of movements (or their inverse) by reference to memory-stored spatial data.

Distance orientation may depend upon non-sensory cues, e.g. in bees (p. 514); migratory birds are another example. Experiments with *Phylloscopus* species (GWINNER, 1972b) evidenced that the end of the migration is determined by the end of the migratory restlessness ('Zugunruhe'). The distances covered by the birds are the product of the velocity of migration and of the duration of restlessness, both of which are species-specific parameters. Time and length of migratory restlessness seem to be controlled by an endogenous rhythm with a periodicity of about one year (circannual rhythm); this fact justifies classification as an idiothetic clue.

(c) Orientation as Reaction

Orientation reaction has been defined as a motor action released by spatial cues which do not fit the central disposition (p. 505). The motor action changes the position of the animal (with respect to the cues) until the cue values coincide with the index value of the central disposition. The action is an expression of the mechanism's tendency to attain this coincidence. Consequently, the tendency arises only if spatial-cue values deviate from the index value of the central disposition.

Since we are dealing mainly with rotatory orientation, the terms 'rotatory' or 'turning movement' and 'turning tendency' are used.

Orientation as a Function of Stimulus Parameters

The turning tendency can be related quantitatively to the spatial cues, e.g. to the values of the reference stimuli. Shrimp *Palaemonetes varians* were forced to deviate from their preferred orientation (index value), i.e. back towards the light. The tendency to return was measured directly in terms of the torque which a shrimp produced by its swimmerets in its effort to turn against the tension of a spiral spring (Fig. 8-9). The tendency was found to be a function of the sine of the shrimp's angle to the direction of light incidence; it changed also in proportion to the logarithm of irradiance intensity (within a limited range of intensities).

If more than one reference stimulus is involved the respective turning tendencies may interact. The animal adopts an intermediate position between the stimuli directions. The quantitative relationships may be demonstrated by vector diagrams (Fig. 8-10a). If, for instance, two light sources interfere, the vector directions represent the two light directions impinging on the animal; the vector lengths correspond to the irradiance intensities, the resultant to the orientation of the animal. The representation in terms of vector diagrams implies that directional responses occur corresponding to functions of sine or cosine of stimulus angle.

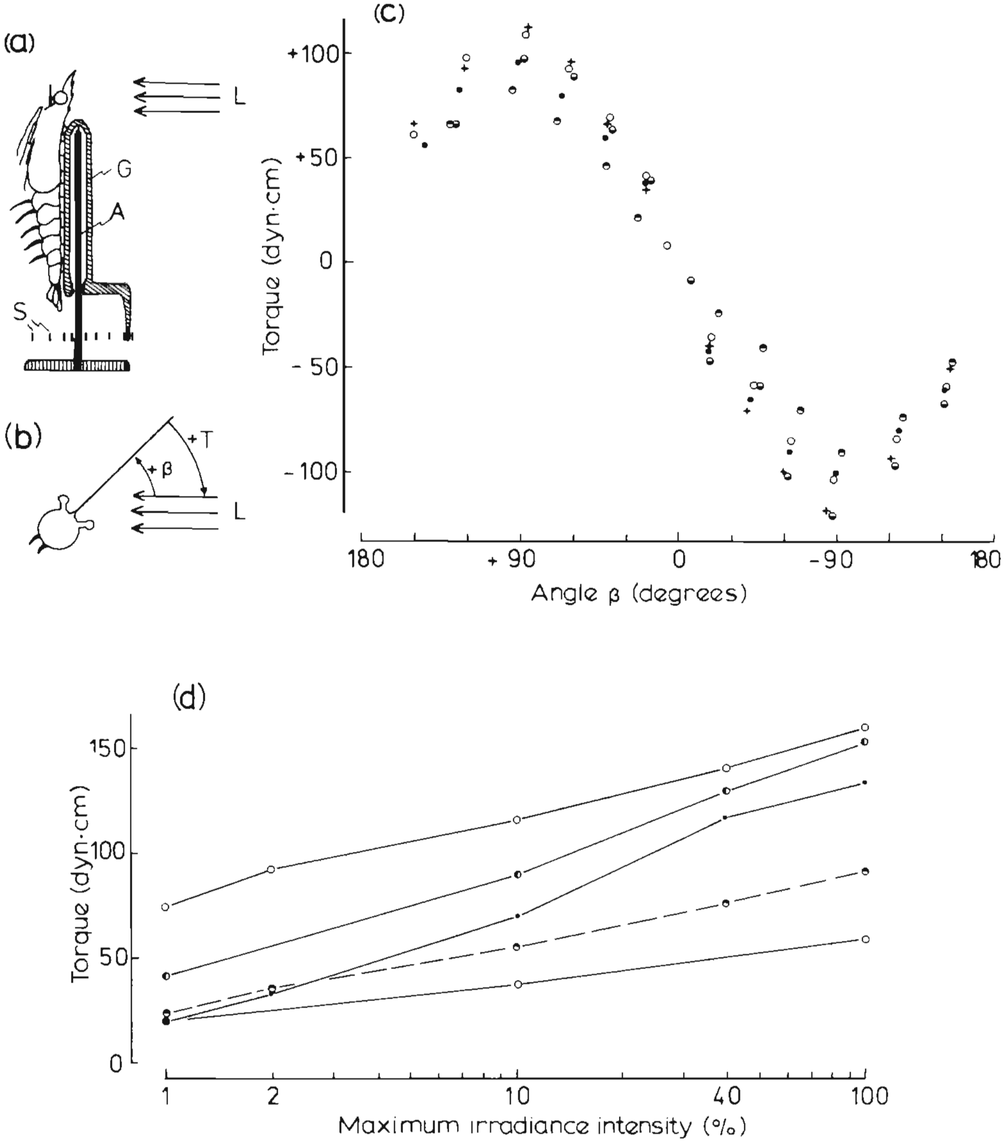

Fig. 8-9: *Palaemonetes varians*. Measurement of turning tendency. (a) Shrimp attached to glass tube (G) connected to spiral spring (S) is capable of rotating around axis (A). (b) Shrimp from above: deviating by β from light incidence (L); shrimp produces torque of spring (T). (c) Torque values as function of β; data from 5 individuals. (d) Maximal torque (i.e. torque at $\beta = 90°$) as function of irradiance intensity L, data from 5 individuals. (Original.)

That is, the turning tendencies alter in proportion to the sine of the angle of light incidence.

In a number of animals, e.g. in shrimp *Palaemonetes varians*, larvae of the water-beetle *Acilius sulcatus*, larvae of *Calliphora* sp. (SCHÖNE, unpublished), the copepod *Phyllothalestris mysis* (FRAENKEL and GUNN, 1961), it has been found,

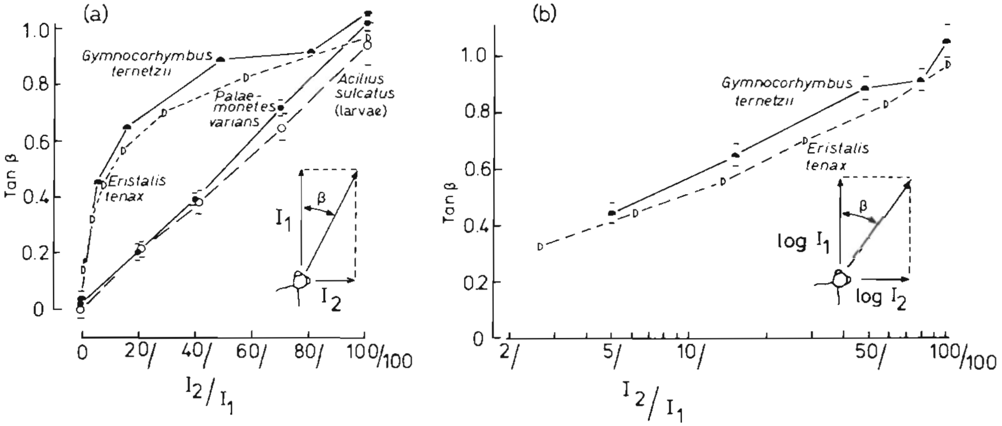

Fig. 8-10: Orientation with respect to two lights in shrimp *Palaemonetes varians*, larvae of water beetle *Acilius sulcatus*, flies *Eristalis tenax* and fish *Gymnocorhymbus ternetzii*. Tangent of β is plotted as function of the proportion of irradiance intensities I_2/I_1 (insets). (a) Linearly, (b) logarithmically plotted light values. I_1: irradiance of standard intensity; I_2: irradiance of reduced intensity (in parts of I_1); β: angle between direction of animal and I_1; vertical delimitations indicate 3-fold standard deviation. (Data for fish, shrimp and beetle larvae, original; for *E. tenax* from DOLLEY and WIERDA, 1929, reproduced by permission of the Wistar Institute.)

that a vector diagram matches the data best if the vector length is in linear proportion to irradiance intensity (Fig. 8-10a). The same has been discovered in crayfish *Astacus fluviatilis*, which has been exposed to two lights of varying intensities and intersection angles (60° to 150°; SCHÖNE and SEYDEL, unpublished). This orientation behaviour, called 'resultant law' (FRAENKEL and GUNN, 1961), implies that the two lights are evaluated in linear proportion to their intensities. This is in contrast to findings that the response to irradiance intensities, successively presented, is a function of the logarithm of the intensity, even in the same animals. In other cases, two-light experiments revealed that the responses may correspond to the vector resultant as calculated on the basis of the logarithms of the two intensities (Fig. 8-10b), e.g. in the fly *Eristalis tenax* (DOLLEY and WIERDA, 1929) and the fish *Gymnocorhymbus ternetzii* (WELLER, 1973).

Many animals orient simultaneously to stimuli of different modalities, for instance, to gravity and light. This orientation can also be expressed in terms of vector calculations and vector diagrams, as has been shown in fishes (VON HOLST, 1950a). The vector relations have been exemplified by the model of a mechanical balance (Fig. 8-11). The relations, i.e. the behaviour of the fish, are represented by the function:

$$F \times \sin a = L \times \sin \beta^{*} \tag{1}$$

where F = gravitational force (magnitude), L = light (irradiance intensity), a = angle of fish to gravity direction, β = angle of fish to light direction. The terms

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[*] For the sake of clarity, proportionality constants have been omitted from this and the following equations.

$F \times \sin a$ and $L \times \sin \beta$ represent the turning tendencies initiated by the gravity and light stimuli, respectively. In the resultant orientation the two turning tendencies are in balance (Equation 1). If one of the four variables is altered, the fish alters its orientation, i.e. its position between light and gravity, in order to attain balance again. Equation (1) may be transformed into

$$\frac{F \times \sin a}{L \times \sin \beta} = 1 \tag{2}$$

or

$$\frac{F}{L} = \frac{\sin \beta}{\sin a} \tag{3}$$

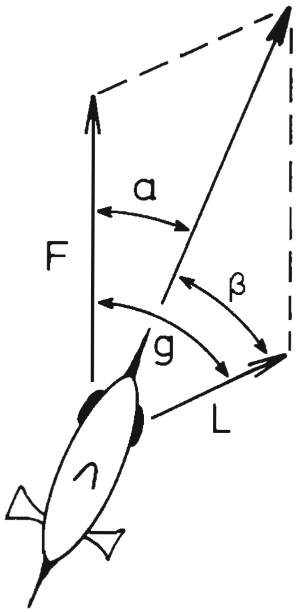

Fig. 8-11: Orientation to gravity and light in a fish. Fish position corresponds to resultant of vector diagram as calculated from direction (a) and magnitude (F) of gravity stimulus, and direction (β) and irradiance intensity (L) of light stimulus. If g (intersecting angle of gravity and light), or F or L are changed, the fish responds according to $F \times \sin \alpha = L \times \sin \beta$. (Original.)

The relationship is called 'proportion of response to light and gravity' or 'proportion of evaluation' of light and gravity; its quantity, 'number of static-optic response proportion'. As Equation (3) indicates, the static-optic proportion number is a function of F and L. Regarding L (irradiance magnitude), it changes according to a logarithmic proportion for a certain range of intensities (BRAEMER, 1957).

The proportion number depends also on the fish's central disposition. It may alter, i.e. the fish may change its orientation, without any (preceding) changes in light and gravity. Increase of hydrostatic pressure, for instance, may cause the fish to turn more towards the gravity direction. On the other hand, the fish inclines more towards the light direction, if exposed to strong water movements which affect its position. As demonstrated by VON HOLST (1950b) the static-optic proportion number in fishes is also affected by internal states such as appetite.

A response proportion of two stimuli has also been investigated in mechanisms of successive responses to different stimuli, e.g. in the transposition of light orientation into gravity orientation in bees (VON FRISCH, 1965). The angle of the sun compass is translated into an angle of the same quantity with respect to gravity, which implies a proportion of 1 : 1.

Sine-like functions of turning tendency curves have been found also in light orientation of swimming insect larvae (Fig. 8-16), and in light/gravity orientation of walking insects (JANDER, 1963). Evidence is increasing, however, that the mathematical descriptions of the turning tendency curves do not correspond to true sine functions in all cases. The maxima of the curves are found at angular positions between 0° and 90° instead of exactly at 90° (EDRICH, personal communication).

Experiments on insects walking on oblique planes and responding simultaneously to light and gravity revealed different effects of stimulus magnitude. The direction of the walking course was either affected by changes of light intensity or inclination of plane respectively ('prophoto-' or 'progeotaxis', JANDER, 1963) or the animals did not react to changes of stimulus magnitude ('metaphoto-' or 'metageotaxis').

Tropisms, Taxes and Kineses

Early terminology

Orientation movements have been investigated formerly mainly with respect to the relationship between stimulus and reaction. The underlying physiological mechanisms have been described in terms of conceptual models of tropisms, taxes and kineses; they refer to rotatory orientations. In analogy to the term 'taxis' used for description of rotatory orientation reactions, the specification 'elasis' has been proposed for distance orientation (CHMURZINSKI *in*: JANDER, 1970).

The terms 'tropism' and 'taxis' were coined by PFEFFER (1888) who investigated, on a broad experimental basis, the locomotory behaviour of unicells, such as protozoans and gametes of primitive plants, as a function of the physico-chemical properties of the medium.

LOEB (1900, 1913) developed an elaborate concept, the tropism theory. He applied the term 'tropism' to the orienting behaviour of motile organisms, when these respond to stimuli with a sequence of physico-chemical events in sense organs and CNS which result in a distinct motor action. The basic property of this system is a tendency to balance physico-chemical states and events on the right and left body sides. The essence of Loeb's concept is the 'tonus hypothesis': The morphological plane of symmetry corresponds to a plane of symmetry with respect to physiology and dynamics of function. That is, the chemical constitution, and the velocity of chemical reaction are equal in the symmetrical sense organs, as is the tension of symmetrical muscular systems. Light stimulation from one side accelerates the velocity of chemo-reactions in the exposed eye, the tonus of the connected CNS side increases, the physiological symmetry of the two sides and, consequently, of the symmetrical muscles is disturbed. The muscular tension of the more stimulated side increases, thus causing a stronger reaction of the muscles which turns head and body towards the light source.

Kühn's (1919) conception is based on Loeb's (1900, 1913) ideas: The orientation reactions (taxes) of multicellular animals are reflex movements. The reaction depends upon the linking of particular sites of stimulus reception to particular elements of the motor apparatus by the nervous system (Kühn, 1919, p. 9). Kühn's classification system is summarized in Table 8-1. The term 'tropism' designates the directed response only of sessile forms, including plants (Chapter 7), while 'taxis' refers to directed behaviour of motile organisms.

Kühn's (1919) conception has been elaborated and modified by Fraenkel and Gunn (1961), based on a wide range of analytical investigations of orientation (Table 8-2).

Some of the terms used in these classifications are phenomenological; they refer to exterior characteristics of the orientation: light-compass reaction, dorsal or ventral light or gravity reaction; prefixes of modality: photo-, geo-, chemo-; or directional notations: positive, negative, transversal. The basic terms, however, refer to physiological properties of the mechanism involved. Kinesis and phobotaxis correspond to mechanisms of response to stimulus intensity, not to stimulus direction. The direction of a stimulus constitutes the reference characteristic of tropo-, telo- and menotaxes.

Table 8-1

Orientation reactions classified in accordance with Kühn (1919; reproduced by permission of Dover Publications, Inc.)

1 **Tropism:** stimulus-directed reaction of sessile organisms.

2 **Taxis:** orientation reaction of motile organisms; photo-, geo-, chemo-, galvanotaxis.

  2.1 **Phobotaxis:** undirected fright reaction following a change of stimulus intensity; final orientation is the result of 'trial and error' (e.g. protozoans).

  2.2 **Topotaxis:** directed orientation with respect to stimulus direction.

    2.2.1 **Tropotaxis:** turning as a result of unequal stimulation of right and left sensors, until equal excitation ('balance') is achieved, corresponding to symmetrical orientation with respect to the stimulus.

    2.2.2 **Telotaxis:** stimulation of a site in the sensory area releases a turn, resulting in 'fixation' of the stimulus.

    2.2.3 **Menotaxis:** the animal maintains an 'accidental' pattern of excitations, corresponding to asymmetrical orientation with respect to the stimulus.

    2.2.4 **Mnemotaxis:** orientation from memory, i.e. according to previously learned and memory-stored values of direction.

Table 8-2

Orientation reactions classified in accordance with FRAENKEL and GUNN (1961; reproduced by permission of Dover Publications, Inc.)

1 **Kineses:** reactions to changes in intensity of stimulus without relation to stimulus direction but with orientation effect.
  1.1 **Orthokinesis:** change in speed or amount of movement; e.g. woodlice congregate in places because activity is reduced in high humidity.
  1.2 **Klinokinesis:** change in the frequency of turning or in size of angles turned; e.g., an animal moves away from a stimulus which increases turning frequency, because movements directed away from the stimulus contain fewer turns and thus bring the animal away faster.

2 **Taxes:** reactions to stimulus direction; orientation of the longitudinal body axis (and of movement) in, or against, the direction of stimulus incidence.
  2.1 **Klinotaxis:** indirect orientation; each turn of an alternating right-left sequence results in receptor stimulation; the excitation affects the turning angle (successive comparison of stimuli); e.g. maggots crawl away from a light, whilst turning the front part of the body from side to side.
  2.2 **Tropotaxis:** direct orientation; turning as a result of unequal stimulation on right and left sensors, until balance of excitations is achieved (simultaneous comparison of stimuli).
  2.3 **Telotaxis:** turning as a result of stimulation of a sensory location until the stimulus is received at the fixation area.

3 **Transverse orientation reactions:** orientation of the longitudinal body axis is transverse or oblique to the stimulus direction.
  3.1 **Light compass reaction:** adoption of an asymmetrical orientation with respect to stimulus; mechanism similar to telotactic fixation.
  3.2 **Dorsal- (ventral-) light reaction:** orientation transverse to light direction; a telotactic mechanism is suggested in orientation about the transverse body axis, a tropotactic one in orientation about the longitudinal axis.
  3.3 **Ventral-gravity reaction:** orientation transverse to gravity direction; a telotactic mechanism is suggested in orientation about the transverse body axis, a tropotactic one in orientation about the longitudinal axis.

In a **telotactic mechanism**, the receptor elements first stimulated elicit a turning movement, which orients the animal so that a particular, frontal site of the receptor organ will be exposed to the stimulus, the 'fixation area'.

A **tropotactic mechanism**, on the other hand, resembles the tropism apparatus of LOEB. Differences in excitation of receptors and corresponding centres of right and left body side induce asymmetrical motor actions, i.e. turning movements, until both sides are equally affected and a state of symmetry is reached. KÜHN (1919) included turning reactions around other body axes. For instance, rostral and caudal receptors may interact tropotactically as a pair in orientation about the transverse axis. Thus the tropotactic reaction is the result of the integration of excitations of all sensory elements of antagonistically paired receptors. The symmetry state has been designated by KÜHN as 'balance of excitations'. Orientation symmetrical to the stimulus field is an expression of a symmetry of excitations in the nervous system and thus of a symmetrical tension of musculature (KÜHN, 1919, p. 13).

The symmetry state must be maintained actively: Equal excitations are continuously fed into the CNS, where they preserve the balance. This process has been compared by KÜHN with controlling a team of horses by means of two reins kept under tension.

The interlacing of orientation elements with the basic pattern of a co-ordinated movement has been studied by LORENZ and TINBERGEN (1938) who analysed the egg-rolling behaviour of the graylag goose. When a brooding goose perceives an egg outside the nest, it extends its neck, lowers head and bill beyond the egg, and retracts them smoothly, thus rolling the egg back into the nest. The egg is balanced with its centre of mass just behind the ventral edge of the bill by means of adjusting lateral movements. These adjustments can be regarded as orienting reactions (taxes) which are elicited by tactile stimuli from the egg. The basic movement pattern of neck-head retraction is, therefore, adjusted to the demands of environmental factors (e.g. the particular movement of the egg).

Orientation has been defined by LORENZ and TINBERGEN (1938) as a taxis in the sense of KÜHN (1919). According to TINBERGEN (1969) and KOEHLER (1950), taxis comprises only the turning action—for instance of a frog which aims at, i.e. turns toward, a fly. This concept of taxis does not include the oriented state: the frog fixating its prey. Thus it narrows KÜHN's definition, who included the oriented state, as illustrated by his example of controlling a horse team with tense reins.

From the causal, i.e. physiological, definitions of tropotaxis and telotaxis (interaction of excitations of two antagonistical groups of receptors versus fixation of the stimulus), operational characteristics have been developed. One criterion for tropotaxis was: the animal orients into the resultant direction of two impinging stimuli; another, it shows circular locomotion after 'switching off' one of the two organs. The respective alternatives indicating telotaxis are: decision for one of the two stimuli, no circular movements, but almost straight orientation.

Critical evaluation of early terminology

Close examination of sensory mechanisms reveals difficulties in applying the early terminology. If, in fishes or decapod crustaceans, one statocyst has been removed, the animals first rotate. Later on, however, they demonstrate almost normal orientation with respect to gravity, thus fulfilling the operational criteria for both tropo- and telotaxis.

According to electrophysiological and behavioural analyses, gravity receptors produce 'basic' excitations ('resting discharge') without specific stimulation (VON HOLST, 1950a; SCHÖNE, 1954; COHEN, 1955). The basic excitation of one organ releases a turning reaction, if the other has been disconnected. Turning tendencies resulting from unilateral removal of receptors have been interpreted as an effect of loss of balance of stimulus-induced central states of excitation, i.e. tropotaxis (KÜHN, 1919). Basic excitation, however, is not the result of stimulation. It is only modified by the gravity stimulus as mediated by the statoliths. It is these modifications, i.e. the variations of the basic excitations, which correspond to the directional cues. They are produced also if one organ has been put out of function. It is open to debate, if at this state of affairs the discussion tropo- versus telotaxis contributes very much to a better understanding of the physiological mechanism involved.

Similar difficulties of interpretation may arise with respect to the second operational criterion. If, for instance, an animal changes its direction between two light sources quickly in short sequences, this results in an almost straight path coinciding with the vector resultant: Telo- or tropotaxis?

It is questionable, if in 'good' tropotactic systems the illustrative metaphors of 'balance of excitations', and 'team reins under tension' are suited for characterizing the central nervous events involved. Unfortunately, we do not know very much about the neurophysiological machinery. Some of the most important elementary processes governing the evaluation and transformation of nervous excitation in neurophysiological systems are facilitation, inhibition and lateral inhibition. A model describing 'tropotactic' reactions using these elementary processes cannot easily be described in terms of the metaphors mentioned.

Central mechanisms which may be compatible with the concept of telotaxis mechanisms will be discussed later (p. 549).

In considering the relations of taxis mechanisms to the types of localization as discussed above (p. 509), one may postulate that telotaxis demands a sensory apparatus of the raster type. For a tropotaxis, on the other hand, a two-unit system would be sufficient. It does not appear very likely that raster systems operate on the basis of central balancing in the sense of KÜHN (1919).

In conclusion, the early taxis terminology has been found insufficient for a detailed description of mechanisms which have been thoroughly analysed. This is one of the reasons why the taxis terms still used today are mostly employed in a phenomenological sense, describing the overt form of the response, e.g. a positive phototactic or chemotactic reaction. Taxis specifications are seldom intended to indicate characteristics of the physiological causation.

There is, however, one more fundamental objection which is as old as LOEB's (1913) basic conception. In postulating his 'tropism theory', LOEB neglected the knowledge of his time regarding the complexity and plasticity of the CNS as, for instance, formulated by MAST (1911, p. 287):

> '. . . all reactions are directly controlled by internal factors which are in turn influenced by external factors, . . .we may have movements and changes of movements without immediate changes in the environment.'

The concepts of tropisms and taxes refer only to those aspects of orientation which deal with its dependence on the reference stimuli (reactions). The orientation mechanisms have been regarded as a complicated automaton which transfers input data into output data (MITTELSTAEDT, 1971).

(d) Taxis and Re-afference Principle (Orientation as 'Action')

The aspect of the specific central disposition has already been taken into consideration by KÜHN (1919). Each taxis presupposes a defined central-nervous state (mood). Consequently, if the animal alters a taxis direction, one can assume that the central disposition has altered. The 'changeable' geotaxis of a ctenophore, for instance, has been interpreted as reflex reversal; according to HORRIDGE (1965), this 'change of mood' can be released by vibration stimuli: the ctenophore turns from an upward directed course into a downward one.

The specific disposition predisposes a specific value for the orientation, the index value or set point (p. 536). In this terminology reflex reversal would be called change of index value. It is unlikely that, during the change, the sensory contact with the stimulus is inhibited or interrupted. Many investigations indicate a continuous sensory control of active orientation changes (re-orientation). In larvae of the waterbeetle *Acilius sulcatus*, for instance, re-orientation is performed by means of continuous visual monitoring of the light direction (SCHÖNE, 1962). If the light impinges from below instead of from above, the larvae reverse their orientation behaviour, swimming again up or down or horizontally, but related to the new light incidence, i.e. upside down and with reference to the floor instead of to the water surface. These positions must be actively maintained because the stable buoyancy position is the normal, i.e. dorsal-side-up position.

MITTELSTAEDT (1949) conducted the first experiments on optomotor behaviour of flies to support the hypothesis of sensory control of active changes in orientation.

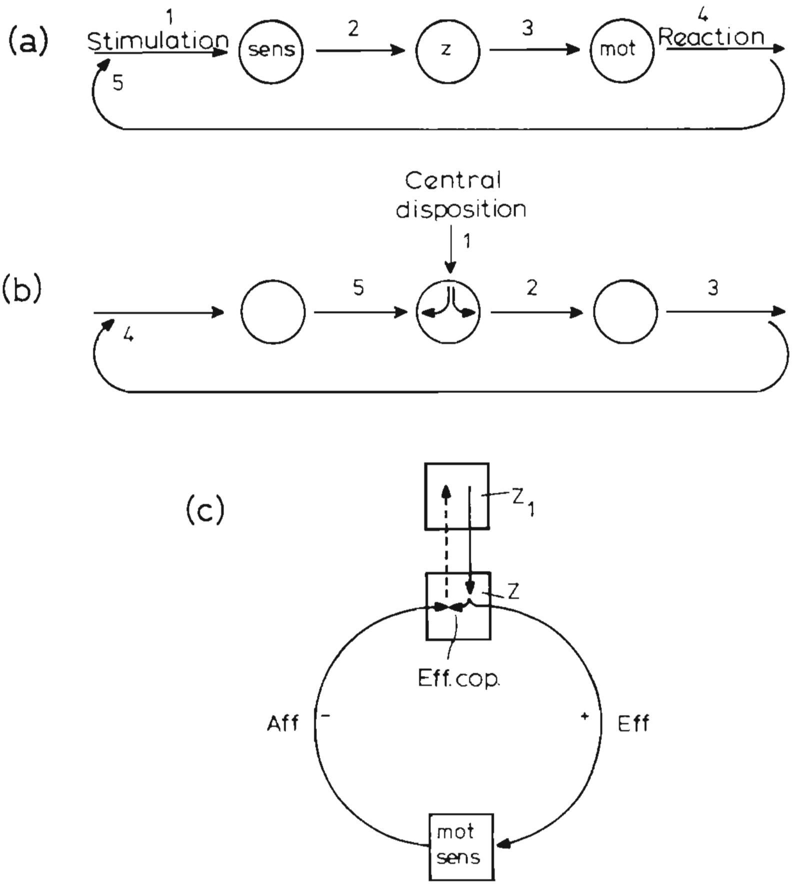

Fig. 8-12: Graphical description of orientation processes. (a) Orientation reaction. (b) Re-orientation. (c) Re-afference principle; note that (c) can be derived from (b). (After VON HOLST and MITTELSTAEDT, 1950; reproduced by permission of Springer-Verlag, Berlin.)

The results indicated that the optomotor mechanism operates not only when the animal reacts to changes in its visual surroundings, i.e. to optomotor stimulation, but also when it initiates a movement and by this movement causes optomotor stimulation (re-orientation). In this case, the sensory input controls the movement.

The two situations, reaction and re-orientation, are illustrated in Fig. 8-12: (a) represents a reaction, (b) an active change of orientation (re-orientation). In (a), the stimulation (1), caused, for instance, by alteration of stimulus direction, affects the sensory apparatus (sens); the afference (2) releases in the centre (z) an efference (3), which initiates the motor apparatus (mot) to perform the reaction (4). This in turn changes the animal's position with respect to the stimulus, thus compensating for the stimulation (5). In (b) the same graph is used to illustrate re-orientation, by adding an input to (z). This input represents the effect of the change of the specific central disposition (1), initiating an efference (2), which causes the following events: motor action (3), change of position to stimulus, i.e. stimulation (4). The resulting afference (5), however, does not initiate a (new) efference in the centre and thus a reaction, in contrast to the normal reaction procedure.

This discrepancy attracted the attention of VON HOLST and MITTELSTAEDT (1950). They attempted an explanation called the **re-afference principle**. MITTELSTAEDT's (1949) findings in the flies were one of the arguments in favour of putting forward this principle. The authors postulated a causal linkage between the initial alteration of the central state and the lack of efficacy of the afference. The central change causing the efference remains effective, and compensates for the returning afference, thus preventing the reaction. The linkage of the central state and the afference has been conceptualized by VON HOLST and MITTELSTAEDT (1950) as a branching-off component of the efferent motor command, named 'efference copy'.

The graphical illustration of this system (Fig. 8-12c) can be linked to the graph in Fig. 8-12b. The components (sens) and (mot) are combined and presented as a functional unit. A change in state of a superior centre (z_1) releases in (z) an efference, which via mot/sens causes an afference. This afference 'meets' the efference copy, a relict or branched-off part of the efference. By this the afference is blocked, its reaction-releasing effect is prevented.

VON HOLST and MITTELSTAEDT (1950) called this type of afference 're-afference', because it is caused by the animal's movements and thus can be regarded as a retro-action. Simultaneously with the re-afference principle, a similar concept was published by SPERRY (1950) who had experimented with fish. After operative change of eye position, the fish exhibited disturbances in orientation, comparable to those shown by MITTELSTAEDT's flies. SPERRY concluded that from the central excitation patterns, causing the muscular actions of a movement, 'corollary discharges' branch off into the visual centres where they compensate for retinal excitations caused by the shift of visual stimuli as induced by the movements. Recently, neurons have been detected in the central visual pathways (tectal commissures) of fish, which are interpreted as efference copy neurons (JOHNSTONE and MARK, 1969, 1971).

The concepts of tropisms and taxes regarded the CNS from two rather contrasting viewpoints: (i) as a simple link between sense organs and motor organs, transforming the sensory excitation more or less directly into muscular excitations; (ii) as a complex organ affecting, in a rather unpredictable manner, the behavioural

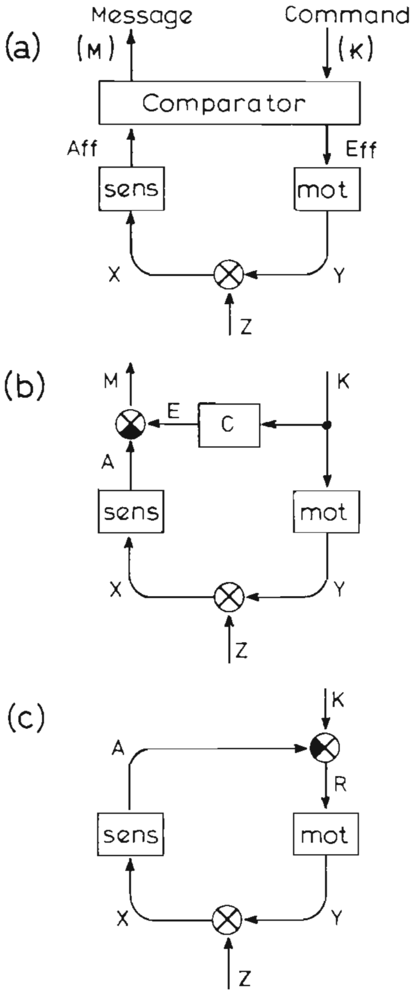

Fig. 8-13: Re-afference principle. (a) Modern presentation of re-afference diagram (see also Fig. 8-12c). (b) Efference copy version of (a). (c) Feedback-loop version of (a). (After MITTELSTAEDT, 1970; modified; reproduced by permission of Springer-Verlag, Berlin.)

(orientational) events. VON HOLST and MITTELSTAEDT (1950) as well as SPERRY (1950) treated the particular central processes involved in re-orientation as a variable quantity intervening in the causal chain of the orientation mechanism which connects sensory inputs and motor outputs.

JANDER (1957) developed a 'compensation theory' of orientation. He presented a model of a central taxis mechanism, related to the re-afference principle. The model hypothesizes a basic state of tropotactic symmetry of excitations, responsible for the 'basic orientation' and corresponding to a symmetrical orientation of the animal with respect to the stimulus. Non-symmetrical stimuli, i.e. deviations from the basic orientation, cause afferences and thus central excitations, which are called 'turning excitations' ('Dreherregungen'), because they induce reactions turning the animal back to the basic orientation. Re-orientation on the other hand is caused by a 'turning command' ('Drehkommando'), which may be understood as a central excitation compensating for the turning excitation. JANDER's hypothesis relates and restricts the general considerations of the re-afference principle to the symmetry mechanism of KÜHN's (1919) tropotaxis concept.

The efference copy hypothesis is only one of the possible mechanisms of afference compensation included within the re-afference principle (Fig. 8-13a–c). As MITTELSTAEDT (1971) explains, another type is the regulating or feedback-loop hypothesis. The afference is linked directly to the efferent command. This process may be explained best in terms of control engineering or cybernetics.

(e) Systems Analysis of Orientation (Cybernetics)

This aspect refers only to operational relations of a (functional) system (MITTELSTAEDT, 1958, 1961; HASSENSTEIN, 1966). It does not take into consideration details of function and morphological construction, such as sensory structures, nervous connections, sensory centres, or motor apparatus.

In cybernetics, the operational connections within the organism and via outside linkages are investigated. Inside, for instance, the sensory apparatus affects central links and these act on the motor apparatus. The motor apparatus, in turn, affects the animal's relation to environmental factors and this, in turn, influences the sensory system.

The functional relations of a system may be depicted in block diagrams. These are composed of blocks or black boxes connected by arrowed lines. A line indicates that an effect (i.e. a quantity), e.g. the angular relations of stimulus direction to a body axis, is conveyed to a box or from one box to another. The line represents the transmission of variations in the quantity; it thus represents a variable quantity (in short, a variable). The block represents the transformation from one variable (input variable) into another (output variable). If, for instance, the angle of stimulus direction is transformed into (corresponding) nervous information, a block may represent the sensory apparatus, which is stimulated by the angular change (input) and responds with nervous excitation (output). The mathematical function, with respect to which the transformation occurs, may be written in the block. The function $0 = \sin I$, for example, indicates, that the output variable 0 alters in proportion to the sine of the angle of the input variable I.

Variables may interact without transformation. If, for instance, the interaction consists of a simple superimposition, corresponding to an addition (or subtraction), a circle is drawn at the junction of the lines with a diagonal cross inside. Blackening of one of the sectors indicates subtraction, i.e. reversal of sign of the variable connected to this sector. One variable may effect more than one other variable, i.e. enter more than one box. The line bifurcates, the branches running to the diverse boxes.

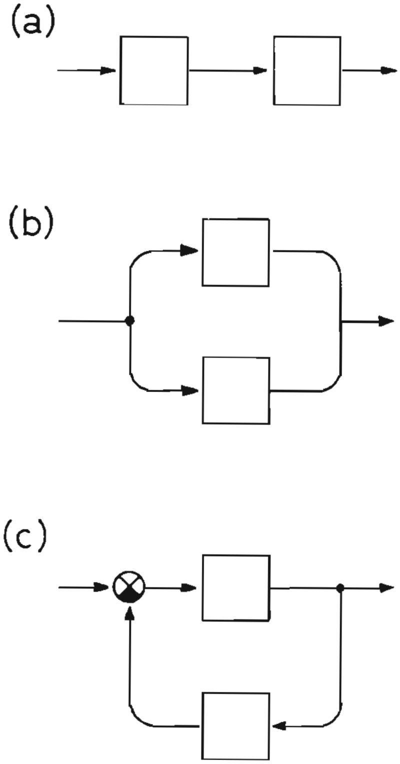

Fig. 8-14: Basic system processes. (a) Chain; (b) mesh; (c) (feedback) loop. (After MITTELSTAEDT, 1964; reproduced by permission of Society for Experimental Biology.)

It is possible to analyse one variable according to several components. For instance, the angle of a fish's swimming direction with respect to the sun may be regarded from three points of view: The first concerns, for instance, what the fish does, i.e. the output of a locomotor box contributing to compass angle; the second is related to possible effects on the compass angle from outside, e.g. disturbing water movements; the third, what the fish's eyes perceive, i.e. the input into a sense box. These three aspects may be regarded as three variables, two of them (motor output and disturbance) adding up and resulting in the third (sensory input), as will be discussed in the following.

The aims of system analysis are (i) to reveal the network of linkages between the variables involved, (ii) to determine the transformation functions. This is accomplished experimentally by varying the input quantities and measuring the output quantities.

We may distinguish three types of basic control patterns: **chain**, **mesh** (or feed-forward loop) and (feedback) **loop** (Fig. 8-14; MITTELSTAEDT, 1964). The control pattern chain may be exemplified by a toad (EWERT, 1969) or a jumping spider

(LAND, 1972) turning at prey objects, or by males and females of fireflies responding to the flashes of females or males, respectively (MAST, 1912). If the stimulus has been localized the system releases an orienting motor action, which then runs 'blindly', i.e. without any further visual control, without feedback. The feedback loop will be considered in more detail.

Feedback Control Systems

A feedback control mechanism regulates a defined variable state of a system, the controlled condition (corresponding to X in Fig. 8-13c). The controlled condition may be, for instance, the compass course which a fish maintains with respect to the sun. It is affected by the output of the system, the turning movement changing the fish's direction (regulating variable Y). The actual state (X) of the controlled condition is recorded by the sensors (input into the box sens). This constitutes a feedback which serves to maintain the controlled condition at a certain value. This is done by checking the controlled condition: The visual afference A of the actual value X, as recorded by (sens), is compared to the value of a reference quantity (controlling variable). This reference value is called index value or set point (K), it coincides with the index value or set point as predetermined by the central disposition. The comparison of the sensed actual value A and the index value K may correspond to a simple addition (with reversal of sign, i.e. subtraction), the result corresponding to the deviation of the actual value from the index value, called error (R). This variable is fed into the box (mot), and transformed into a motor action, the regulating variable Y. This action changes the fish's position (X), it reduces the difference K–A and thus the error R. When A coincides with K the error is zero and the system maintains the respective value X of controlled condition.

Errors, i.e. deviations of A from K, may arise from either of two sources: (i) The actual value of the controlled condition, i.e. A, is changed by a disturbance (Z). A force, for instance, affecting the system from outside, may alter the fish's direction with respect to the sun. (ii) The index value (K) of the controlling variable is altered, corresponding to a change in central disposition. In both cases the mechanism reduces the deviation $K - A$ by means of changing A and adjusting it to K. This means that either the system compensates for the Z-induced change and thus re-establishes the old X of controlled condition (i) or that it adjusts X to the new K (ii), this being a process of re-orientation.

Obviously, this mechanism depends upon the process of subtraction of A from K, which implies a reversal of sign somewhere in the loop. A shrimp, for instance, may swim in an oblique path from the surface downwards, e.g. $-20°$. A local disturbing water movement causes a deviation further down, e.g. $-25°$. The deviation of $-5°$ is corrected by an upward turn of $+5°$ resulting in the old direction $-20°$. The reversal of sign characterizes these systems as loops with negative feedback.

Taxes and control systems. The term taxis may be applied to non-regulatable orientation processes, such as chains, as well as to feedback systems. In feedback orientation, the term taxis (or orientation reaction) corresponds to the correction of errors of both originations: (i) To call a correction of a disturbance (Z), i.e. of a forced stimulus change, 'taxis' is in accordance with the usual meaning of that term.

(ii) However, also the compensation of an error caused by a change in the index value (K) deserves the name 'taxis'. As **KÜHN**'s (1919) conception of taxis presupposes a specific central disposition, a new taxis is regarded as the effect of an alteration of the central disposition, resulting in a reaction to a previously ineffective stimulus.

In conclusion, a taxis is not a function of the stimulus, i.e. of the stimulus afference as such, but of the divergence of the afference from the specific central disposition.

Introduction of Index Value, Re-orientation

The following analysis is not concerned with the circumstances producing the disposition for an index value (K), but with the way the controlling variable (and thus K) is introduced into a control system of orientation. Hence we do not ask 'why' does the system change a direction, but 'how'. This is a matter of the integration of the controlling variable, i.e. of the mechanism of re-orientation.

The error (R) may be regarded as equivalent to the turning tendency ($T = R$). A change of K implies a change of the functional relations of turning tendency to stimulus direction. Several ways of modelling this relation by K have been proposed. One model (Fig. 8-15a) corresponds to the simple feedback loop described in the

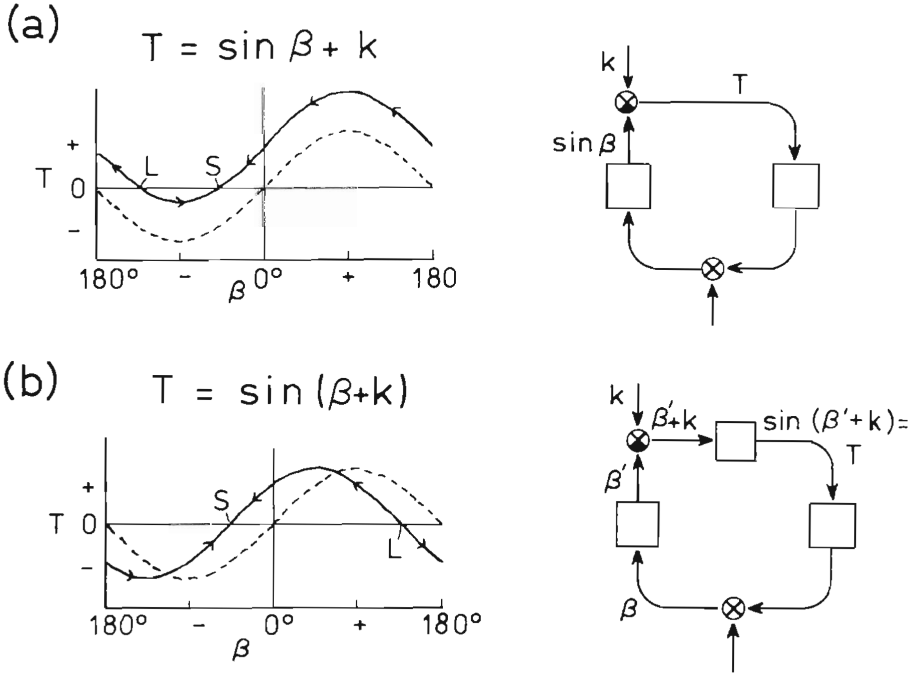

Fig. 8-15: Models of re-orientation: Variations of introducing the controlling variable (k) into a feedback loop of orientation. Each model is represented by formula, by plot of turning tendency (T) as function of incidence angle of stimulus (β) and by block diagram. (a) Addition of k to $\sin\beta$: change of k results in vertical shift of T-curve (solid curve with respect to dotted curve, which refers to k corresponding to $\beta = 0°$). (b) Addition of k to β, transformation of the sum into sine: change of k results in horizontal shift of T-curve. (Original.)

previous section, where T is a function of the difference between A and K ($T = K - A$). As has been discussed already (Fig. 8-9) the turning tendency T is very often a function of the sine of the angle of stimulus incidence, which shall be called β ($X = \beta$). According to model A, introduction of K results in $T = (-) \sin \beta + K$. That is, a change of K remodels the relation between T and $\sin \beta$ in such a way that all T-values change by the same amount, i.e. the amount of the K-change. This alteration corresponds to a vertical shift of the turning tendency sine curve.

This model matches the experimental results obtained on vertical light-compass orientation in larvae of the dytiscids *Acilius sulcatus* and *Dytiscus marginalis* (SCHÖNE, 1962). The turning tendency has been measured at different angles of light incidence (β) and at different index values of direction.

By a special technique of blinding, β was fixed with respect to the animal, i.e. the larva received light only from one incidence direction, irrespective of its movements. The incidence direction could be changed between experiments. Several kinds of reactions could be observed in one experimental situation depending on the central disposition (index value). A larva receiving light only from dorso-rostral, for instance, swam (i) straight ahead, or (ii) in somersault-like circles (with its ventral side towards the centre). A straight path resulted if the central disposition was to swim forward–upwards (*fu*) towards the surface (Fig. 8-16, $\beta =$ ca. 45° in lower curve, and in right illustration). If the larvae intended, however, to steer its course downwards (*d*), circles appeared ($\beta =$ ca. 45° in upper curve).

The central disposition could be manipulated: preventing a larva from reaching the surface for some time resulted in upwards, i.e. 'towards light' intention. Frightening a larva away from the surface caused the intention downwards ('away from light'). Only in the first case did the intention ('towards light') correspond to the incidence direction of light (dorso-rostral) forced upon the larva, resulting in maintenance of swimming direction, i.e. in straight course. In the second experiment (frightened, i.e. downward-tending larva), however, the incidence direction of light diverged constantly from the larva's intention, resulting in a constant turning tendency.

In these experiments the feedback loop has been opened by interrupting the line Y (Fig. 8-13c). That is, the motor output (regulating variable Y) could no longer affect the controlled condition X, i.e. the input into (sens). Thus the deviation $A - K$ was not corrected, as in the normal situation. Consequently, the turning tendency R persisted, and was thus available for measurement. It was measured in terms of the diameters of the circles. Measurements along the whole range of incidence directions resulted in sine-like curves of R, if arranged according to central disposition, i.e. to downward or upward intention, respectively (Fig. 8-16). One curve is shifted with respect to the other in vertical direction, thus matching model a.

Swimming courses forwards–downwards (*d*) and backwards–upwards (*bu*) have almost identical orientations with respect to light, and consequently the same index values (Fig. 8-16, right). This is an example of (change of) course orientation with space-constant body orientations (p. 502).

This model of addition of the index value to the sine of β has a drawback. The sine curve has two crossing points (L, S) with the T-zero-line (Fig. 8-15a). Point S refers to the stable orientation, i.e. orientation according to index value. All

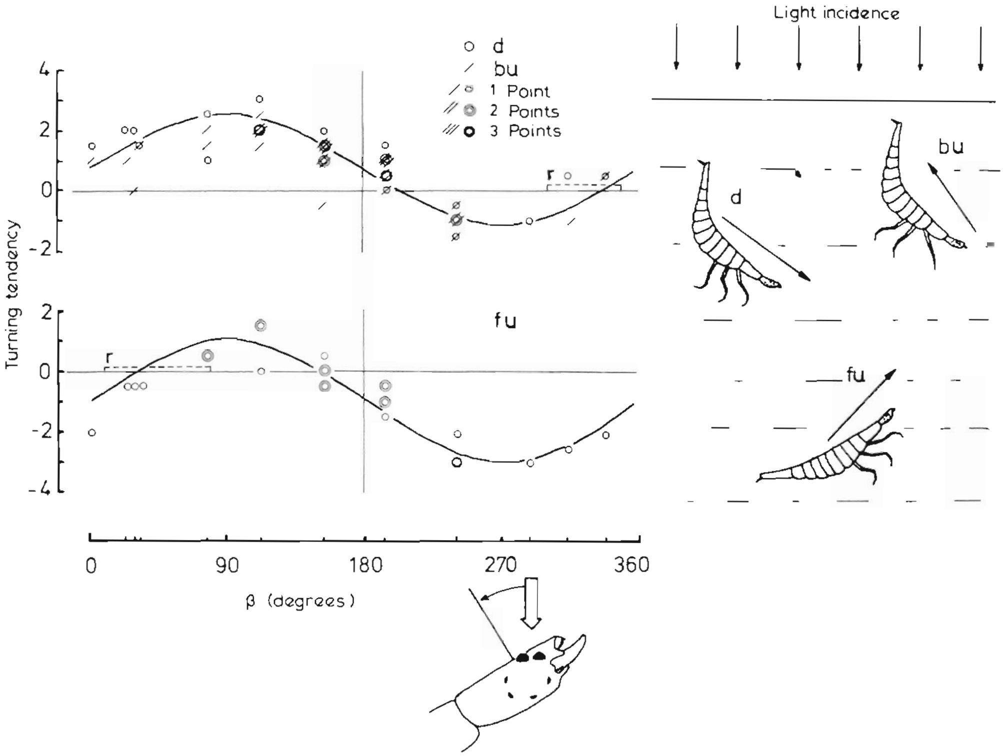

Fig. 8-16: *Acilius sulcatus*. Light-compass orientation in larvae. Diagrams of turning tendency (T) as function of light incidence β, corresponding to the directional intentions indicated (right). Upper: Data from larvae intending a downward (d) or a backward–upward (bu) swimming course. Lower: Data from larvae intending a forward–upward (fu) course. The arbitrary units of T correspond to diameter of circles, which experimental animals swam with ventral side towards centre (+), or dorsal side towards centre (–); r: β range of normal larvae swimming up- or downwards under normal light conditions. (After SCHÖNE, 1962; modified; reproduced by permission of Springer-Verlag, Berlin.)

corrections (turning tendencies) intend to reach this orientation. The other point (L), called labile point, corresponds to the stimulus direction of labile orientation. That is the one stimulus direction of no-turning, where the turning tendency to the one side changes into the opposite turning tendency. All tendencies turn the animal away from this direction and towards the stable orientation. The vertical shift of the T-curve, corresponding to increase of index value from $\beta = 0°$ to $\beta = 90°$, results in approaching S and L. This implies loss of stability of the orientation process, since slight disturbances of stable orientation may displace the animal beyond the labile direction, which would release a full turn of the animal.

Three other models avoid this problem. The second one is a derivate of model A. It assumes a reversal of sign at angles of $\beta = 90°$. The effect is, that the vertical shift corresponding to a change in the index value is opposite in the ranges of $\beta = 0°–90°$ and $\beta = 90°–180°$. The result is that stable and labile points remain at equal distance. Corresponding models have been proposed by BUTENANDT

(1968) and LINSENMAIR (1973). The model may be applied also to JANDER's (1957) results on sun-compass orientation in ants.

In the two last models, integration of the controlling variable results in a horizontal shift of the T-curve if the index value changes. This is accomplished by adding the index value not to the sine of the angle β, but to a quantity of input which is a linear function of the angle β. That is, β and K are added first, followed by transformation into the sine. Model b is the simplest kind of this computation, $T = \sin\ (\beta + K)$ (Fig. 8-15b). Another version postulates a transformation of the term $\sin\ (\beta + K)$ into $\sin\beta \times \cos \mathrm{K} + \cos\beta \times \sin K$. This implies that each of the two variables β and K is transformed in the first step into a sine and a cosine value. The components are multiplied crosswise and the products added. The resulting T-curve is identical with that of model b. On account of its two main components, this model has been named by its author (MITTELSTAEDT, 1958, 1961) 'bicomponent model'. Some experimental results can be interpreted according to this model. Other data do not fit, e.g. those on shrimp orientation with respect to gravity (SCHÖNE, 1971) and the above-mentioned results on dytiscid larvae.

These models should not be related to specific conceptions of central nervous mechanisms, such as tropotaxis-like central shifting of excitation blocks. They may be applied to all kinds of mechanisms including, for example, raster mechanisms.

(f) Mechanisms of Space Constancy

Change of orientation implies an alteration of the spatial relations between the orienting subject and the reference cues. What does the subject perceive? Does it perceive (i) stimulus direction as moving with respect to itself; (ii) itself turning, but the stimulus direction remaining stationary; (iii) only a relative change of the angle between stimulus and itself?

Re-orientation, i.e. active change of orientation, will be discussed first. The stimulus direction changes with respect to the animal, but the animal does not react. Provided that 'normally' a change in stimulus direction releases a reaction, alternative (ii) appears most likely: The animal perceives the cues as stationary entities in space; it perceives space constancy of reference stimuli. This must be related to the preceeding change of central disposition, which compensates for the stimulus shift (p. 532). A forced change of orientation, however, may also result in perception type (ii), if additional information regarding the stimulus shift is available for compensation. (For a detailed discussion of the concepts of constancy phenomena see BISCHOF, 1966a.)

The perception of space constancy presupposes a system that compensates for the relative shift of stimuli. The mechanisms of compensation may be grouped in two classes: (i) The relative shift of stimuli is recorded by the receptors, but the information about this shift is nullified in the CNS by means of additional information about the subject's movement ('nervous' compensation). (ii) The shift is not recorded, since the receptors themselves are moved in counteraction to compensate physically for the change of stimulus direction ('physical' compensation). As in (i), additional information is needed regarding the moving action in order to control the countermovement of the receptor.

(i) **Nervous compensation.** One model of the nervous compensation mechanisms corresponds to the efference copy hypothesis (VON HOLST and MITTELSTAEDT, 1950; TEUBER, 1960, p. 1648; BISCHOF, 1966a, p. 404). Fig. 8-13b may be applied, for instance, to the perception of space constancy of visual surroundings in man. When turning our eyes we do not perceive movement of visual configurations, although the image on the retina shifts. However, if the same retina stimulation is caused by actual movement of the visual surroundings, we perceive this as a movement phenomenon; an optomotor reaction of the eyes may occur as a consequence. The efference-copy explanation implies the following: From the efferent command K, which causes the eye turning (Y) via the eye muscle system (mot), the efference copy E branches off (via box C). E is united with the retinal afference A. If both correspond to each other, full compensation occurs, resulting in a message M that indicates space constancy of visual objects. If, however, M indicates a difference between E and A, a movement of the surroundings is perceived. This might be caused by (i) a change in A without change in E, or (ii) change in E without change in A. In (i), A-changes may be caused by real dislocation of surroundings or by forced movements of the eyeball (little pushes with the fingertips on the side of the eyeball). In the latter case, the surroundings appear to 'jump' in accordance with the pushes. A crucial experiment attempted to initiate an efference K, and thus a copy E, but to prevent the motor action of the eye Y, for instance, by anaesthetizing the eye muscles (KORNMÜLLER *in*: BISCHOF, 1966a, p. 404). Every time the test person intended to 'look around', he reported an apparent shift of the surroundings. In terms of the model, E had been changed because of the eye-moving intentions; the change of Y, however, was blocked and thus A remained constant. Hence M changed and an apparent dislocation of the surroundings was perceived (loss of space constancy).

Another method employed for gaining additional information about the subjects turning uses a (second) sensory system, for instance in perception of other objects with respect to vertical orientation. If a subject changes position with respect to the vertical (Fig. 8-17), two position variables are affected: (i) relation to gravity (angle a_2) and (ii) relation to the visual objects (angle a_1). Thus both sensory systems are stimulated, the gravity sensors (sens a_2) and the visual sensor (sens a_1). The output of the sensors, i.e. the afferent informations, Sa_2 and Sa_1, are integrated to result in Sa_3, which corresponds to the message on object to gravity relation (a_3). This message indicates the state of space constancy, i.e. constancy of visual objects with respect to gravity. If Sa_2 and Sa_1 indicate equality of positional changes to gravity (a_2) and to the object (a_1), respectively, they compensate fully, i.e. the resulting Sa_3 indicates constancy.*

This, however, is not the case when the transformations in sens a_1 and sens a_2 (Fig. 8-17) follow different functions. If, for instance, a human subject surpasses the positions of the normal range of about 30° from the upright position, the gravity sensors indicate inclinations smaller than the true positional changes, i.e. Sa_2 increases at a lower rate than a_2. Information a_2 appears to be transformed into Sa_2 according to a non-linear function (SCHÖNE and UDO DE HAAS, 1971). Information Sa_1, however, i.e. that of the visually perceived relation object–body, seems

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* For further discussion of the block diagram consult next section.

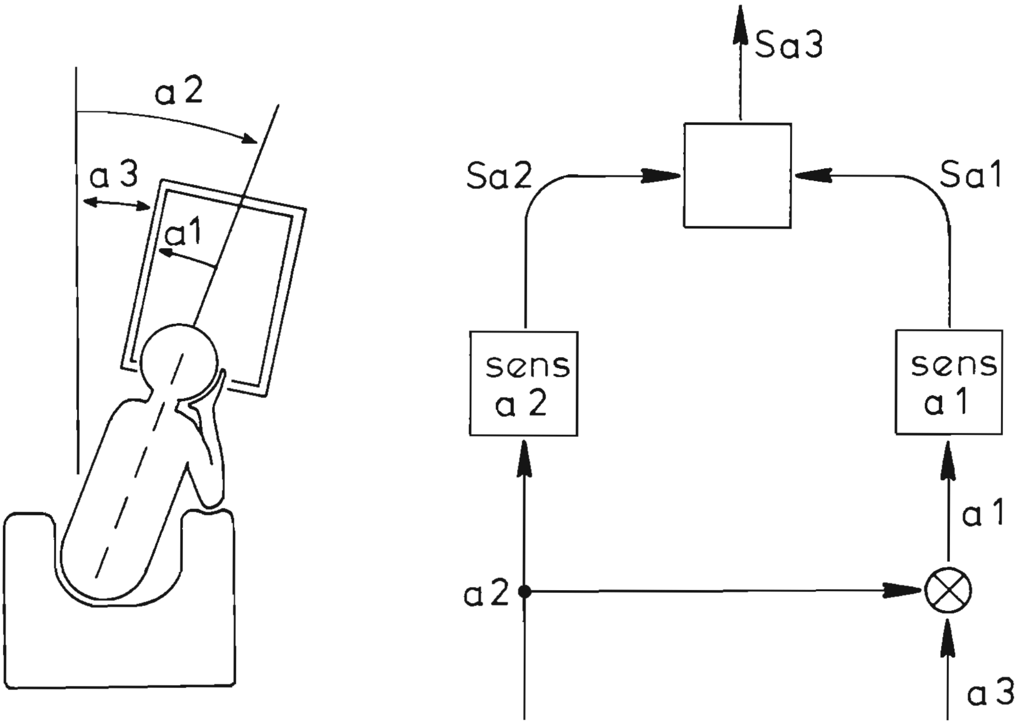

Fig. 8-17: Perception by man of orientation of a figure with respect to gravity. Sensory data on a2 (angle subject–gravity) and a1 (angle figure–subject) are integrated in a message about a3 (angle figure–gravity), which is not accessible by direct sensory input. For further explanation see Fig. 8-18. (Original.)

to coincide with the actual change in a_2 (linear transformation function). The resulting discrepancy between Sa_2 and Sa_1 corresponds to a change in Sa_3. The subject perceives a positional change of the object in space, although in reality the object's position does not change. A phenomenon of this kind may be experienced, for instance, if one looks at a hanging lamp or at the edges of a window, and inclines head and body sideways: the object appears to deviate from the vertical. These perceptual phenomena of deviation of the perceived from the true vertical are known in psychology as **Aubert**, and **Müller phenomenon**, respectively (TEUBER, 1960; BISCHOF, 1966a, b). A similar system is involved in tactile-kinesthetic perception of horizontality of objects (FITGER, personal communication).

In neurophysiological experiments with decapod crustaceans 'space-constancy neurons' have been found (WIERSMA, 1967; WIERSMA and YANAGISAWA, 1971). The neurons responded only to visual stimuli if the corresponding retinal area was 'up' with respect to gravity; the effect appeared to be a function of the statocyst input. From units in the visual cortex of cats, receptive fields have been recorded which changed their orientation in opposite direction to tilt of the animal (HORN and co-authors, 1972).

(ii) **Physical compensation.** The second class of mechanisms maintaining the stimulus perception constant in space employs physical compensation, for instance compensatory or counteracting movements of the sense organs or of the sensor-carrying body appendages.

In many animals (crustaceans, cephalopods, vertebrates), the eyes or the head show compensatory movements when the body is tilted with respect to gravity. These movements are released by the gravity sensors. They act to maintain the visual field constant. Another example refers to bees; hovering in front of a visual target, bees have been found to maintain the head position stable with respect to horizontal reference, whereas trunk position varied (WEHNER, 1972, 1973). The stabilizing mechanism is not yet known.

Physical compensation mechanisms also include the systems of course orientation with space-constant body orientation (p. 502, Fig. 8-2): The visual input is maintained constant, whereas the course direction, i.e. the locomotory direction of the legs may vary. Leg action is linked to the visual input by means of idiothetic cues. Both types of data, i.e. visual and idiothetic, result in the information regarding the course of the leg action with respect to a visual reference.

Mechanisms of visual-field stabilization expressed in nystagmus movements of eyes are well known. The sensory input controlling the compensatory eye movement may be the semicircular canals or the visual system itself. Movements of the head stimulate, for instance, the canals; this releases nystagmic eye movements, i.e. back-and-forth oscillations of the eyeballs. The single movement consists of a slow phase, which compensates for the head movement, and a quick returning flick.

There is evidence that some animals are capable of maintaining their auditory field stable in space. Rabbits demonstrate ear nystagmus which depends on semicircular canal or optomotor stimulation (SCHAEFER and co-authors, 1971).

(g) Composed Systems

Composed systems may be defined as systems combining several inputs or data records of spatial (or temporal) cues, as for instance some space constancy systems (p. 540). The first of the following systems may be regarded also from the viewpoint of space constancy.

In spiny lobsters, the compensatory eye movement is a function of gravity input on the one hand and of a proprioceptive input on the other. The statocysts are located in the antennules. These can be moved actively in all directions, including up-down, e.g during chemoreceptive exploration of the environment. Although the statocysts are stimulated by these movements, no gravity reactions occur, e.g. no compensatory eye movements can be observed. They are 'counteracted' by the input from a proprioceptor in the basal joint of the antennules which has been found in *Panulirus argus* (SCHÖNE, 1971).

The functioning of this system may be presented by a block diagram (central portion of Fig. 8-18; see also Fig. 8-19a). Two input variables a_1 (angle statocyst–gravity) and a_2 (angle antennules–trunk) enter the boxes sens a_1 (statocysts) and sens a_2 (stretch receptor), respectively. Variable a_1 is the result of the addition of a_2 and a_3, i.e. angle antennules–trunk is superimposed on angle trunk–gravity resulting in angle antennules–gravity. The input variables a_1 and a_2 are transformed in the sens-boxes into the variables Sa_1 and Sa_2, respectively. These are integrated to provide the message Sa_3 on the position of trunk to gravity. By this computation

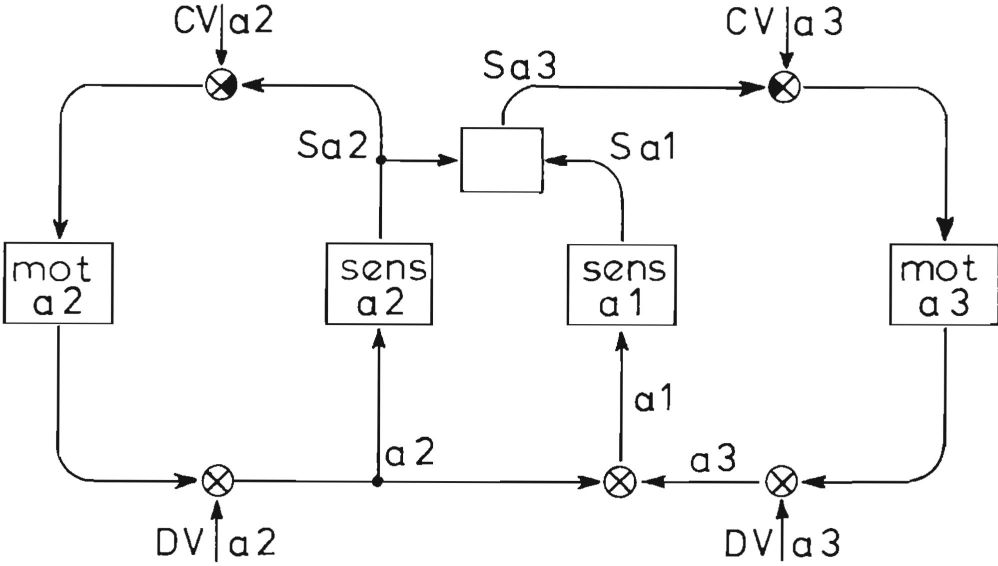

Fig. 8-18: Model of operational systems: Orientation related to gravity in man and spiny lobsters (see also Figs 8-17 and 8-19). Central part: recording of a2 and a1 by sensory inputs sens a2 and sens a1 respectively, resulting in sensory data Sa2 and Sa1, which are integrated in Sa3. Right: Sa3 is used in a feedback loop to regulate a3, via actions of a motor apparatus (mot a3). Left: A branch of Sa2 is fed into a loop regulating a2, via a motor link (mot a2). CV and DV refer to controlling and disturbing variables respectively. (Original.)

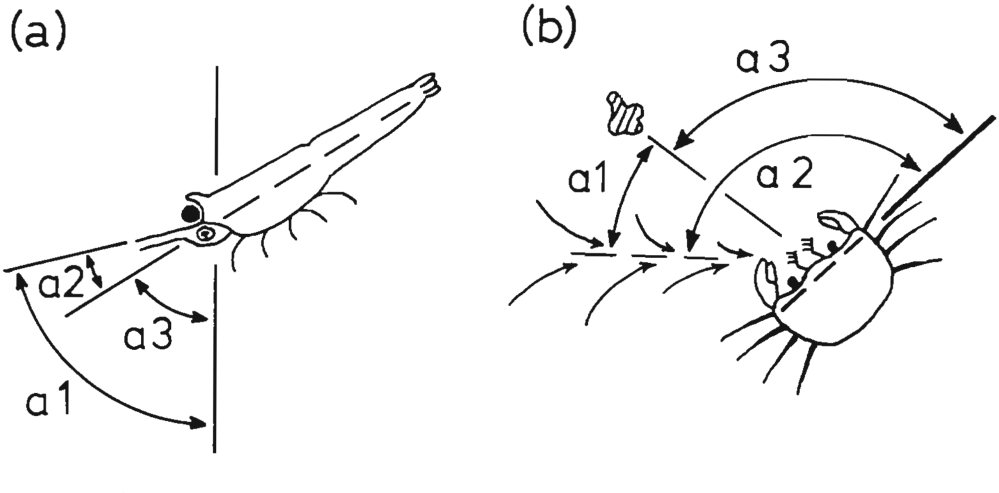

Fig. 8-19: Composed orientations. (a) Gravity orientation in spiny lobsters; a1: angle antennules–gravity, recorded by statocysts; a2: angle antennules–trunk, recorded by proprioceptors; a3: angle trunk–gravity. (b) Chemocurrent orientation in crabs; a1: angle food direction–'replacing current'; a2: angle 'replacing current'–body; a3: angle food direction–body. (Original.)

the system gains information regarding a_3 which is not directly available to it. This information is fed into the motor system of the eyestalks and thus controls the compensatory eye movements (not shown in the block-diagram), which serve to stabilize the visual field (space constancy).

This system contains a mesh (p. 535). The variable a_2 bifurcates and affects both sens-boxes, sens a_1 and sens a_2. The outgoing variables Sa_1 and Sa_2 join again in the link box, thus completing the mesh.

The diagram is extended to a model enclosing two feedback loops, one controlling trunk position with respect to gravity (right side of Fig. 8-18), the other controlling antennule position with respect to trunk (left side). As for the first loop, Sa_3 is fed into the motor system of the legs. A controlling variable (CV a_3) is added to this, introducing the index value of gravity position into the loop. The output from the motor system affects, in addition to the disturbance variable (DV a_3), the position of the animal to gravity (a_3, controlled condition). This, in turn, influences the input a_1, as already discussed.

The control of antennule position (left loop) may be carried out by a branch of Sa_2 which is also combined with a controlling variable (CV a_2). The resulting variable acts on the muscular system (mot a_2) changing the position of the antennules (a_2); this, in turn, is fed back to sens a_2 and thus completes the loop.

A system similar to that of the central and right side part of the diagram is found in gravity-position control of higher vertebrates which have a movable head containing the gravity receptors.

In general (irrespective of the aspect of space constancy), systems of this kind are often found where a sense organ is not firmly fixed to the body but is attached to a movable appendage. The position of the appendage is recorded idiothetically. This information, regarding the local sign (p. 508), is used to relate the spatial data recorded by the mobile sensor to the body.

The same model (Fig. 8-18) may be applied to the system of orientation (or perception) of other objects in space, which has been discussed already from the viewpoint of space constancy (p. 542). The central portion of the model (which is identical with the diagram of Fig. 8-17) represents the mesh of the computation of the two sensory inputs a_1 (visually recorded angle between subject and object's position) and a_2 (angle between subject's position and gravity) resulting in the message Sa_3 on the position of the object with respect to gravity (a_3). a_1 changes if a_2 is changed as well as if a_3 is altered, i.e. it results from the physical addition of a_2 and a_3(see left drawing of Fig. 8-17). Two feedback loops may also be attached here. The loop on the right-hand side (Fig. 8-18) permits the system to regulate the position of the object (a_3), the left side loop to control the position of the body with respect to gravity (a_2).

The common characteristic of all of these systems is the gaining of information (Sa_3) on spatial cues which cannot be recorded directly, but is computed from (two) other input data (second order information). This seems to be valid also for the orientation system of brachyurans and hermit crabs towards food by means of chemical and current stimuli. These crustaceans investigate their surroundings by drawing fingers of current towards them (BROCK, 1930). The water jets leaving the frontal openings of the branchial chambers can be deflected by quick flicking movements of the maxilliped flagellae. The water dragged along with the exhalent current is replaced by water coming from the opposite direction (replacing current). The crab orients its antennules towards the replacing current (Fig. 8-19b). It can change the direction of the replacing-current finger by altering the flagellae movements. The angle between food direction and current finger a_1 is minimized by searching manoeuvres with the current finger, which are controlled by the chemoreceptors on the antennules. The direction of the current finger (i.e. of maxillae movement) with respect to walking direction (angle a_2) is known to the system in terms of idiothetical cues. The data on a_1 and a_2 are integrated to result in data on a_3, the angle between food direction and walking direction which is brought to zero, i.e. the crab moves in that direction and thus approaches the food.

Similar components seem to be involved in the food finding mechanism of marine gastropods (BROCK *in*: TINBERGEN, 1969, p. 23). The gastropod 'inhales' water via a siphon into the branchial chamber. The siphon is movable and can thus scan the surrounding environment. The direction of maximal food-odour intake can be found this way. When the gastropod is in a current, the direction opposite to the current flow is the direction of maximum stimulation.

The **orientation systems of vertical migration** are of particular importance for plankters. Many planktonic animals maintain themselves at a specific depth below the water surface, or migrate vertically in the water column, exhibiting a diurnal rhythm: they move down during the day and up at night. Three sensory inputs appear to be involved: stimulation by light, gravity and hydrostatic pressure. Other inputs, for instance temperature and water chemistry, may also affect the system.

Many plankton forms, such as mysids, decapod larvae, small molluscs and fish larvae respond to changes of hydrostatic pressure (RICE, 1961, 1964; Volume I, Chapter 8). The plankters move upwards if pressure increases, and downwards if it decreases. Experiments in which light and gravity inputs were altered indicate that the vertical movements are oriented with respect to gravity and to light direction, i.e. by means of statocysts and eyes. It may be assumed that the pressure gradient is not used as an orientation stimulus, in the strict sense of directing the upwards and downwards locomotions, because the gradient is rather small with respect to body dimensions. Even a pressure sensitivity equivalent to a few centimetres of depth would imply a trial-and-error mechanism, which appears unlikely.

Fig. 8-20 proposes a hypothetical model of the operational system controlling the orientation of vertical migration. The two central boxes mot a and mot v represent the motor system controlling the two parameters of locomotion, (i) the angle of inclination of body axis, i.e. of locomotory course with respect to surface (a), and (ii) the velocity of locomotion (v). These two can vary independently; therefore, the motor system is split into two boxes. Both variables contribute to vertical displacement and hence to the change in pressure. The pressure change (p) is a function of the product of the sine of a and the velocity ($p = v \times \sin a$). p is added to the disturbance variable of $p(DVp)$, to give the total amount of pressure change. DVp changes, for instance, if the animal is carried up or down by currents; p is recorded by the pressure sensor (sens p) and there transformed into the information Sp, which is fed back to the motor system, after being combined with the controlling variables CVp, CVa and CVv. These are postulated since other environmental and physiological factors may intervene and alter the index values of

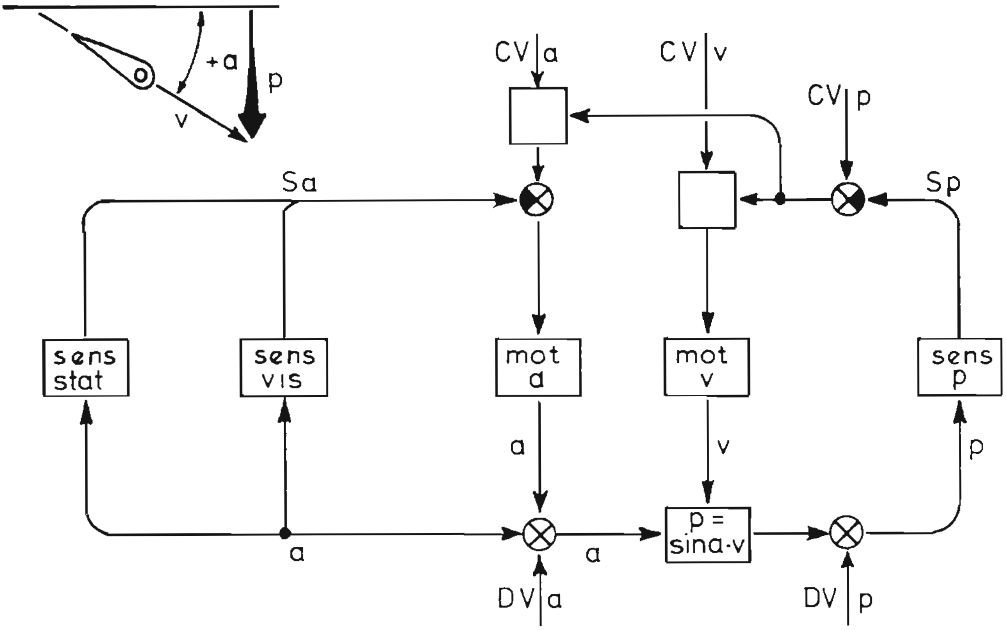

Fig. 8-20: Model of operational system: Vertical 'migration' of plankton animals responding to gravity and light direction (a), and hydrostatic pressure (p). Pressure (depth) varies as a function of swimming velocity (v) times sin a. Sens stat and sens vis: sensors of gravity and light direction (a), respectively; for further explanation consult text. (Original.)

swimming direction, velocity and pressure, respectively. For example, the depth preference, i.e. the CVp index value, may be altered; or food requirements, overcast weather conditions, temperature, and the presence of predators may influence the response of the system via the index values of CVa and CVv.

The locomotory direction (a) is monitored by the feedback loop on the left side containing the boxes sens *vis* and sens *stat* (visual and gravity sensors, respectively).

The whole system is elaborately integrated: the regulation of depth by means of pressure sensitivity (Fig. 8-20, right) cannot function normally without interaction with the systems controlling direction in space. This model, if subjected to experimental investigation, may have to be altered or supplemented. Eventually further variables may be integrated, for instance, irradiance intensity or water properties (e.g., CO_2-content).

In systems of vertical migration it is likely that timing mechanisms are also involved, for instance in control of onset or end of migration by manipulation of CVa, CVv and CVp.

(h) Temporal Control of Orientation

Many orientation procedures occur with temporal regularity and may be described in terms of biological rhythms (Chapter 9). In the sun-compass orientation the compass direction of the animal is a function of the time of the day. The index value is altered continuously by about 15° hr^{-1} (counter-clockwise in the northern hemisphere), thus compensating for the azimuth component of the sun's apparent motion. 15° hr^{-1}, however, is the mean over the whole day. Around noon, for instance, when the sun moves along the zenith region, its azimuth velocity is faster than earlier or later in the day, the difference being a function of the latitude. In some fishes, the shift of the index value of compass direction follows these variations exactly (Fig. 8-21; BRAEMER and SCHWASSMANN, 1963).

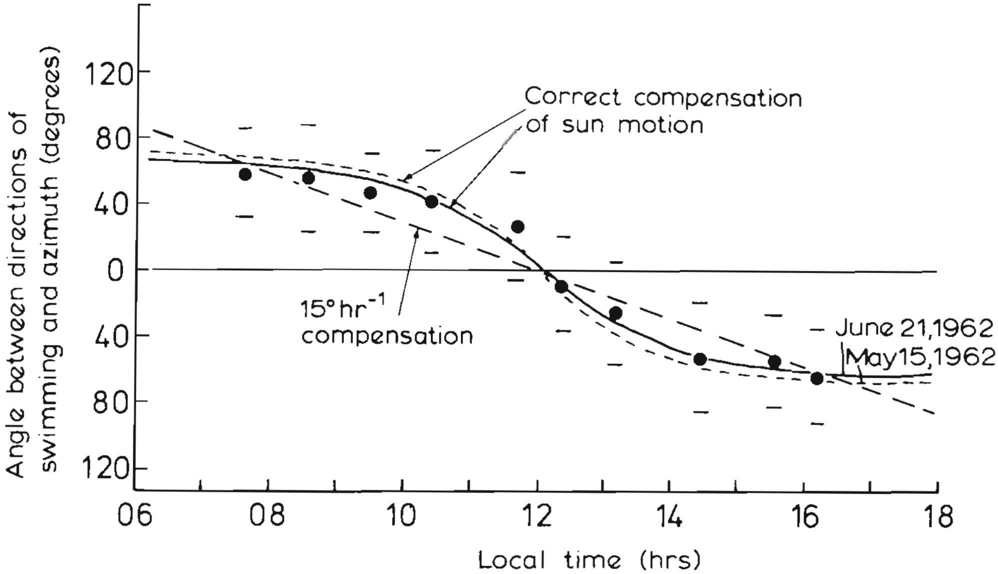

Fig. 8-21: *Crenicichla saxatilis.* Sun compass orientation in a cichlid at a location close to the equator. The fish had been trained to find a cover after swimming in southern direction; they were tested without cover. Swimming direction, with respect to sun's azimuth direction, is plotted as a function of local time of day. Dashed straight line refers to mean compensation of the sun's motion (15° hr^{-1}); dotted and solid curves refer to correct compensation as calculated from the real azimuth motion of sun on the days indicated (data from astronomical tables). Experimental time: May 31 to July 7, 1962. Vertical delimitations indicate standard deviation. (After BRAEMER and SCHWASSMANN, 1963; modified; reproduced by permission of Springer-Verlag, Berlin.)

The time compensation is based on an endogenous timing mechanism, often called internal clock (HOFFMANN, 1972). Best known is the diurnal clock. If an animal is kept under constant light conditions, i.e. without the time indications of natural day (dark–light change), in many cases the biological activities show cycles of a period not exactly of 24 hrs, but close to it (circadian rhythms). The internal clock, however, is sensitive to environmental cycles, e.g. to the dark–light change corresponding to the daily dawn and dusk periods. These influences act as 'Zeitgeber' (pacemakers), adjusting the internal rhythm to the 24-hr day (Chapter 9).

In some animals, time controls of orientation of longer than daily periods have been found, e.g. circalunar, circatidal rhythm (Chapter 9). Cycle ranges of a year seem to be involved in the orientation system of young salmon migrating downstream to the ocean and in migrating birds. The salmon on the one hand change sun-compass direction daily in the normal way. In addition, they show an alteration of the overall orientation which corresponds to the geographical directions of the river's course (GROOT, 1965). Experiments indicate that these changes are a function also of time. Some salmon were caught and kept in tanks. Exposed to the natural light conditions they showed a shifting of direction preference with time which was in accordance with the locomotory direction of their normal migrating conspecifics, as was observed in samples caught at consecutive stations down the river at the respective time intervals.

The migratory restlessness of the warblers *Phylloscopus trochilus*, *P. collybita*, *Sylvia borin*, and *S. atricapilla* appears to be a function of an internally controlled circannual rhythm (GWINNER 1972a, b; Chapter 9). Experimental results support the hypothesis that during the migratory course the index values of direction change as a function of this timing mechanism (GWINNER and WILTSCHKO, personal communication). As has already been mentioned, also distance determination depends on this clock system (p. 514).

(i) Neurophysiological Mechanisms

Orientation procedure is the result of interaction of many parts of the neurophysiological complex. The components such as sensory reception, identification, localization and control of motor system can often be distinguished experimentally.

The neurophysiological basis of the input side of the system shall be exemplified on the basis of vertebrate vision (GRÜSSER and GRÜSSER-CORNEHLS, 1969; EWERT, 1973; STONE and FREEMAN, 1973).

The functional pathway begins at the sensory elements of the retina; it continues via corpus geniculatum to the thalamus, pretectum, tectum of the midbrain, and, in higher vertebrates, to the visual cortex. The retinal elements (rods and cones) are arranged in groups converging in higher order neurons, first at the ganglionic cells of the retina. The neurons of these cells have been grouped in classes corresponding to the response capability with respect to stimulus parameters, such as size of stimulus, contrast, or angular velocity.

The superficial layers of the tectum represent topologically ordered projection areas of the visual field; this has been established in mapping experiments: localized stimuli in the visual field cause excitation of a corresponding site of the tectal 'map', detectable by electrophysiological recording (Fig. 8-22; for fish see SCHWASSMANN and KRUGER, 1965).

A similar organization has been found in the visual area of the cortex (area 17). In addition to this large-scale representation of the visual field, cortex cells respond to specific configurations of stimuli, e.g. lines of a particular orientation with respect to body axes. Other cells are stimulated by simple shapes or by moving figures.

The tectum area seems to play an essential role in the process of space-direction localization (BERLUCCHI and co-authors, 1973; EWERT, 1973). Application of electric stimuli to tectal loci effected toads to turn towards the fictitious visual stimulus (EWERT, 1967, 1973). Stimulation of a site in the projection area of the lower left

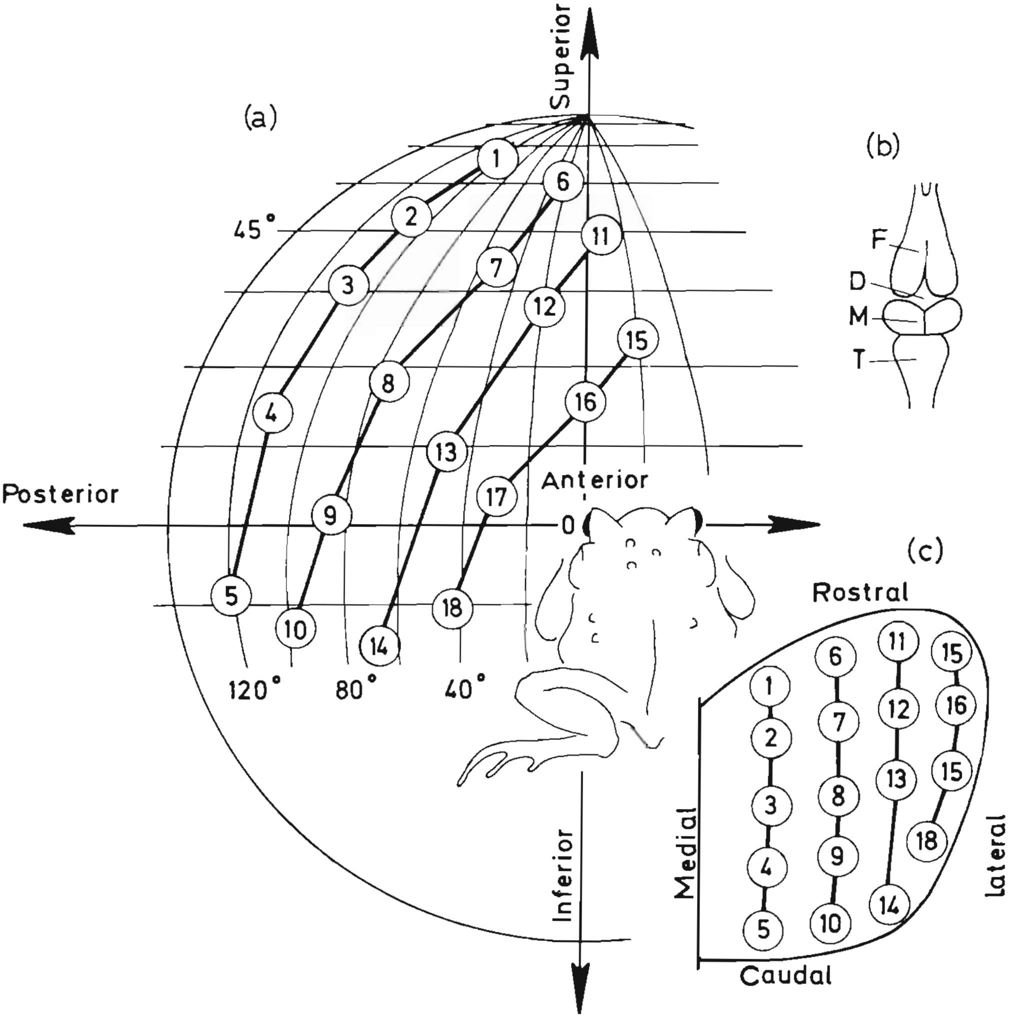

Fig. 8-22: *Bufo bufo*. Stimuli at loci in the left visual field (a) of a toad release maximal excitation in corresponding loci of the right tectum (c). (b) Brain from dorsal; F: forebrain; D: diencephalon; M: midbrain (upper layers: tectum), T: telencephalon. (a, c after EWERT and BORCHERS, 1971; reproduced by permission of Springer-Verlag, Berlin.)

visual field, for instance, caused a toad to turn to the lower left and to 'look' at an imaginary object. From these findings it can be concluded that turning is accomplished on the basis of preprogrammed patterns of co-ordinated motor actions, released in the tectal sites. This implies that the performance of the action, once started, needs no further visual control. This corresponds to some observations that toads finish an orienting turn even if the stimulating object had been removed in the meantime.

Evidence is increasing that the visual process of identification differs from the localization mechanism. In golden hamsters the two processes seem to take place at different loci of the brain. The visual cortex is essential for identification, the tectum for localization (SCHNEIDER, 1969). After removal of the visual cortex the hamsters could still orient with respect to moving objects, but they were unable to differentiate between different visual patterns. If, on the other hand, the tectum had been eliminated, no visual orientation could be observed. Visual patterns, however, could still be distinguished by the hamsters. Similar conclusions on the function of visual cortex and tectum in identification and localization of objects have been drawn from experiments on monkeys (TREVARTHEN, 1967; HUMPHREY, 1970).

Investigations on the auditory system of cetaceans indicate that different central structures are involved in discrimination (of social sounds) and localization (of echo sounds). For further details consult BULLOCK and RIDGWAY (1972) and Chapter 8.3.

(3) Orientation and Learning (Influence of Experience)

A hamster orienting in a choice box learns, on the one hand, the identification marks characterizing 'right' and 'wrong' alleys, and on the other, 'where' these marks are to be found (SCHNEIDER, 1967). These two aspects refer to learning on the input side of the orientation. Other questions are concerned with the effect of experience on co-ordination between internal components of the mechanism, such as the linkage between timing mechanism and setting of the orientation-index value, or the integration of input information and motor output.

In general, the necessary extent of potential experience is adapted to the requirements, which are biological and ecological characteristics of the species.

(a) Acquisition of Identification Parameters of Reference Stimuli

Identification of the characteristics of fundamental reference stimuli, such as light or gravity, seem to be genetically fixed; this may be concluded, for example, from light and gravity reactions of newly hatched fish larvae and nauplii of crustaceans. In stellar orientation of birds, however, experience plays a role in recognition of the reference pattern (WALLRAFF, 1972).

If orientation concerns environmental cues of not very permanent existence, the importance of learning is obvious. Thus experience is necessary in territorial orientation, e.g. of coral fish, lobster or octopus.

In object or goal orientation, e.g. finding of food or home places, the characteristics also often vary; that is, the signs have to be learned. This has been demonstrated in young toads (EIBL-EIBESFELDT, 1967), chickens (HESS, 1964), and goslings (WÜRDINGER, 1974). Cephalopods may be trained to associate new visual or tactile parameters with the stimulus complex marking the target of its orientation (WELLS, 1962).

In landmark orientation, digger wasps show 'locality studies' (TINBERGEN, 1969, p. 147). In *Bembex rostrata* the characteristics of the nest spot are acquired during a short circling orienting flight of the wasp before leaving the nest site. The duration of this 'pre-leaving' flight is a function of the discrepancy between the sign pattern expected and that actually seen when the wasp did return (VAN IERSEL and VAN DEN ASSEM, 1965).

Many examples may be found among 'releasing mechanisms' of ethology referring to orientation processes. The red spot at the tip of a gull's beak, for instance (TINBERGEN, 1969, p. 76), or the sexual attractant scent of the female silkworm (KAISSLING, 1971; PRIESSNER, 1973) are reference signs for object orientation of the gull chick and the male silkworm, respectively. As is often found in social behaviour, in which orientation in relation to conspecifics is observed, the identification of the reference signs (releasing stimuli) has a genetically fixed basis. However, experience may also play a role, e.g. in cases of individual recognition of the conspecifics, which has been demonstrated even in invertebrates, e.g. in the rank order behaviour of crayfish (BOVBJERG and LOWE *in*: SCHÖNE, 1965).

A genetic basis may also be expected in orientation of species adapted to a rather extraordinary habitat. Thus, the shrimp *Tuleariocaris sansibarica* or the fish *Siphamia permutata* living on and between the spines of the sea-urchins *Diadema setosum* swim back in a straight line to specific configurations of spines, if they have been dislocated (FRICKE and HENTSCHEL, 1971; FRICKE, 1973). Avoidance of vertical depth (visual cliff) has been found in unexperienced rats and cats at first exposure (TEUBER, 1960, p. 1633). The reaction is based on visual perception of a perspective pattern.

(b) Learning of Spatial Parameters of Reference Stimuli

Bees orienting their foraging flights with respect to the sun may have acquired the values of flight direction from other workers during the waggle dance in the hive (VON FRISCH, 1965). BRAEMER and SCHWASSMANN (1963) trained fishes to swim in a particular sun-compass direction by presenting a refuge in that direction during training.

Amphipods (*Talitrus saltator*), however, do not seem to be open to experience with respect to sun-compass orientation (PARDI, 1960). These intertidal sandhoppers live in the wet zone of beaches. If displaced they return in a direction perpendicular to the water's edge of their home beach, irrespective of the true beach orientation. If placed close to a strange beach, they move in the compass direction corresponding to their home beach orientation. PARDI hatched young sandhoppers in the laboratory from mothers collected from different beaches. When the juveniles were exposed to sunlight they preferred directions corresponding to their respective mother's home beach.

(c) Experience and Internal Linkage of Components

The mechanism of **time compensation** of the sun's motion may be influenced by experience. The sun's apparent motion is opposite in the northern and southern hemisphere. BRAEMER and SCHWASSMANN (1963) have shown that some tropical fishes can learn to compensate according to both alternatives, but that some northern hemisphere fishes cannot.

Sensory-motor integration. Very often reactions to light, gravity and other stimuli are performed in the 'correct' way at the very first exposure to the stimuli. This implies that the functional system from sensors to effectors is linked together in a genetically determined manner. This linkage may be examined experimentally.

Fishes and amphibians with artificially inverted eyes suffered persistent disturbance of orientation. Experience had no effect on performance (SPERRY, 1950; TEUBER, 1960, p. 1647). Similarly, chickens looking through prism spectacles did not learn to peck correctly at grains (HESS, 1956). They missed consistently by the disparity corresponding to the prism's refraction. Improvement with time was related only to the scattering of the pecks. As in normal chickens, the group of pecks of a trial was less scattered after practice, the disparity of aiming, however, did not change.

Monkeys and man, on the other hand, seem to be able to compensate for the inverting and distorting effects of prisms on vision by experience. The orientation of subjects wearing a prism is first grossly disorganized, but after some weeks the system adapts, the central co-ordination being re-arranged, perception and orientation appear to return almost to normal (KOHLER *in*: TEUBER, 1960, pp. 1634, 1647). In this context the findings of HELD (1967) in cats and man are of importance. The experience of the visual feedback in (self-produced) movements is necessary for establishing the correct sensory-motor interaction of visually guided behaviour.

Experimental changes have also been made to examine the role of experience on the motor side. The insertions of flexor and extensor muscles of a rat's limb were exchanged. The animals did not learn to orient the limb correctly (SPERRY, 1958). A small improvement was observed, however, in monkeys on which similar operations were performed: The tendons of antagonistic muscles of one arm were rearranged. After a great deal of experience and with visual control of the arm's movements, the monkeys increased their capability to reach for food.

8. ORIENTATION IN SPACE: ANIMALS

8.1 INVERTEBRATES

F. CREUTZBERG

(1) Introduction

There can be little doubt that locomotory activity is one of the most characteristic features of animal life. However, it is not easy to assess the ecological significance of a specific locomotion pattern. This requires identification and comparison of different locomotion patterns and analysis of the physiological mechanisms involved in spatial orientation.

In its normal everyday life an animal continually exhibits locomotory activities —e.g. exploratory movements, feeding excursions, courtship behaviour, escape reactions and withdrawal to shelter—which require an ability to respond adequately to certain stimuli from the outside world for maintaining proper orientation. Other locomotory movements involve habitat selection. These movements bring or keep the animal within a particular environment whose physical, chemical and biological conditions suit its morphological and physiological characteristics. Since both physiological state and environmental conditions are subject to changes, migratory movements are in many cases basic to existence. In a number of species, on the other hand, a fixed position somewhere in the environment, a so-called 'home', provides the animal with a more or less permanent setting to which it may show habituation and which promotes its survival.

There is a considerable diversity among locomotory and positioning responses of organisms to environmental stimuli. Several workers have endeavoured to rationalize them into a single system of classification. The classic scheme of orientation reactions was advanced by KÜHN (1919) and modified by GUNN and co-authors (1937) and FRAENKEL and GUNN (1940, 1961). Their classification in terms of kineses and taxes is based on the mechanisms of orientation processes. This concept has been considered critically in Chapter 8.0. The present chapter concentrates on physiological and ecological aspects of orientation. Orientation responses of invertebrates depend largely upon the nature of the stimuli and the functional and structural ability of the corresponding sense organs. In the following pages orientation processes, including migration and homing, in marine invertebrates will be discussed on the basis of the various stimulus modalities.

(a) Migratory Movements

In terms of active long-distance displacement, migratory movements in marine invertebrates are not very spectacular, although there are a few examples of long-range movements reminiscent of what is known of bird and fish migrations. For example, several lobsters (species of *Panulirus*, *Homarus*, *Jasus*) and crabs

(*Callinectes*) migrate over distances of 8 to 50 km or even more (BAINBRIDGE, 1961). Apart from well-established migrations to deep water in winter and from moulting or feeding movements to favourable areas, occasionally observed migrations against the prevailing currents by mature females are tentatively interpreted as a mechanism enabling the young to return with the aid of the current to the adult habitat (GRAHAM, 1949). This principle, comparable with the spawning migration of plaice *Pleuronectes platessa* in the North Sea (see also HARDEN-JONES, 1968), deserves further study because of its paramount ecological significance.

Striking underwater observations off the west coast of Bimini, Bahamas, have been made on the manner in which the autumnal mass migrations of the spiny lobster *Panulirus argus* take place (HERRNKIND and CUMMINGS, 1964). The lobsters were seen moving in southerly directions in single file queues of 3 to 30 individuals walking in physical contact with each other. Separate queues moved in parallel directions at an estimated speed of 40 to 50 cm sec^{-1}. HERRNKIND (1969) has questioned whether these mass migrations have a reproductive function. Attempts to clarify the mechanism whereby directionality is maintained suggest that the orientation is based on multiple cues (HERRNKIND and MCLEAN, 1971).

Other examples of extensive migrations are found in cephalopods. The squid *Loligo vulgaris* (TINBERGEN and VERWEY, 1945) and the cuttlefish *Sepia officinalis* (VERWEY, 1949a) are reported to migrate in spring and summer—presumably through the Straits of Dover—from the eastern Atlantic Ocean into the North Sea, where they spawn, and to leave the North Sea again in autumn and winter. Numerous parallels with bird migration are emphasized by the authors. Comparable long-range migrations are mentioned by SUMMERS (1969) for *Loligo pealei* in the western Atlantic Ocean off the American coast, where the northernmost range limit of this species in winter is reported to be 600 km south of the range limit in summer. *L. pealei* is assumed to avoid water temperatures below 8° C. By means of a tagging programme in the Sea of Japan, TASHIRO and co-authors (1972) demonstrated migratory movements of the squid *Todarodes pacificus* over distances of more than 1000 km (see also MURATA and co-authors, 1973).

Apart from these long-distance migrations, passive transport of planktonic organisms, including larvae of benthic invertebrates, by ocean currents is a well-known feature in the marine environment. The extent of the dispersal of larvae of bottom-dwelling animals is largely determined by the duration of the planktonic phase, which may range from a few hours to several months. SCHELTEMA (1971, 1972) reports trans-Atlantic transport of larvae of the invertebrate shelf fauna, which apparently facilitates reciprocal trans-oceanic genetic exchange.

While the horizontal displacement of planktonic organisms must be regarded as a passive process, the duration, and in some cases also the direction, of the transport is controlled by biological processes and adaptive responses. In other words, vertical movements through different water layers which may move in different directions or withdrawal from the moving water masses (e.g. by settlement) are closely related to the physiological state of the animals and dependent on a variety of responses to environmental factors. A considerable body of information on this subject is available. Some orientational aspects are treated in the following pages. For more information on the mechanisms involved in the vertical migration of planktonic invertebrates consult Volume I: SEGAL (1970, e.g. pp. 169, 194).

Another very important category of migratory movements is the on-shore and off-shore movements of coastal and intertidal animals, which either may be induced by the tides or will be the result of a variety of activities such as feeding, reproduction and seasonal migration. Essential characteristics of any coast, where the ecological conditions vary basically only in directions transverse to the shore line, are reflected in a variety of adaptive responses that guide the animals in directions perpendicular to the coast line and which are responsible for the shift or maintenance of certain zonation patterns. For extensive information on the ecological implications, the recently revised book of NEWELL (1972) on the biology of intertidal animals should be consulted.

Somewhat more complex are the conditions in estuarine areas whose inhabitants, like shrimps and crabs, migrate inward and outward according to the seasons and in which temperature and salinity gradients and tidal currents play a dominant role. Problems concerning the ecology of animals living in this type of environment, especially in the Waddensea, have been treated by VERWEY (1949b, 1960, 1966).

(b) Homing

In several cases 'homing' has been reported in marine invertebrates. In molluscs homing behaviour is known in the intertidal naked pulmonate *Onchidium floridanum* and some species of *Chiton*; most work has been done on limpets (review by THORPE, 1956, pp. 186 ff). Limpets live on rocks in shallow depressions into which they fit exactly and which are caused by the wearing effect of their shell. After feeding excursions, the limpets return to their scars. Recent attempts to clarify the return mechanism have led to the hypothesis that retracing of mucous trails which the limpets have laid previously is involved in home finding by *Patella vulgata*, *P. depressa* and *P. aspera* (COOK and co-authors, 1969) and the pulmonate limpet *Siphonaria alternata* (COOK, 1971). The results of these experiments have ruled out several alternative hypothesized cues such as orientation to gravity or the sun—as established in the feeding excursions of *Littorina littorea* (NEWELL, 1958a, b) or a form of orientation based on memory of past movements (kinaesthetic memory), which apparently is involved in the homing of fiddler crabs *Uca tangeri* (ALTEVOGT and VON HAGEN, 1964) and *Uca rapax* (VON HAGEN, 1967a).

In recent years, with sonic tracking techniques, good evidence of homing behaviour has been obtained in the spiny lobster *Panulirus argus*. Out of 10 individuals released about 200 m from the capture site, 8 returned to within 30 m of their 'home' even when blinded; but there is little information on the mechanism of directional orientation (HERRNKIND and MCLEAN, 1971).

(c) Releasing Factors

In studies concerning oriented movements of animals, a clear differentiation of releasing and orienting stimuli should be made, as pointed out for instance by STIEVE (1961) and VERWEY (1966). The particular condition searched for in its migratory movements is not necessarily the factor to which the animal responds for orientation. For instance, when the sandhopper *Talitrus saltator* is placed on dry sand, low humidity merely releases migration, but celestial cues are utilized in directing it to wetter areas of the beach (PARDI and PAPI, 1953). On the other hand, the effect of releasing factors alone may be sufficient to cause a displacement towards areas with more favourable conditions. This type of migration is found in cases where selective transport by currents is involved. When, for instance, in an estuarine area during ebb the salinity drops too far, the crab *Macropipus holsatus* responds by swimming, which automatically carries it on the ebb tide to more saline areas (VENEMA and CREUTZBERG, 1973).

In general, non-directional stimuli like temperature, salinity, hydrostatic pressure (Volume I, Chapters 3, 4, 8), and chemical stimuli act as releasing factors, while directional stimuli such as light (Volume I, Chapter 2), gravity, water movement (Volume I, Chapter 5) and presumably vibrations can be utilized by marine invertebrates as orientation cues. Light and sound or vibrations are also found to act as releasing stimuli. In several cases the interaction between releasing and orienting stimuli is extremely close. The frequently used term 'chemotaxis' (orientation to chemical stimuli), for example, should in most cases be read as 'orientation to currents released by chemical stimuli'.

It is a common observation that environmental changes, as well as changes of the physiological state of the animal, can induce reversals of the sign of orientation. This highly adaptive mechanism was already recognized by LOEB (1893), who demonstrated that planktonic animals respond photonegatively (or geopositively) to temperature increase or salinity decrease and vice versa. ROSE (1925) found the same effect and emphasized its biological significance in relation to the stratification of water in terms of temperature and salinity. Salinity discontinuity layers—such as occur frequently in estuaries—indeed appear to act as a barrier to a number of copepod species and the larvae of a decapod crustacean attempting to swim to the surface in an experimental water column (LANCE, 1962; see also Volume I: KINNE, 1971, p. 969). In diurnal vertical migration of plankters, however, changes in irradiance are considered to be the primary initiating factor in controlling the sign of orientation (Volume I: SEGAL, 1970, p. 194).

The influence of the physiological state of planktonic animals on the sign of phototaxis has been demonstrated, for instance, by SINGARAJAH and co-authors (1967), who found that more nauplii of *Balanus balanoides* and *Elminius modestus* become photonegative when fed than when starved. Well-fed nauplii apparently leave the surface water rich in phytoplankton for darker regions where, presumably, they are less exposed to visually directed predation.

The development of benthic animals through various pelagic larval stages yields numerous examples of adaptive-sign reversals in vertical orientation. The early stages generally move upward, which promotes dispersal by currents, whereas just before metamorphosis and settlement the larvae move downward. This general principle finds expression in a wide variety of specially adapted modifications. For extensive information, the review of THORSON (1964) should be consulted (see also Volume I: SEGAL, 1970, p. 169).

(2) Light

The visual environment of an animal may be regarded as a complex of interrelated properties of light (Volume I, Chapter 2). In almost all natural conditions the sun alone acts as the primary source of radiant energy. During the night, the moon (as a reflector of sunlight) provides a secondary irradiance source of much lower intensity. In addition the stars and bioluminescence (see review by TETT and KELLY, 1973) function as natural light sources.

For a proper analysis and understanding of the responses of organisms to photic stimuli, the fundamental aspects of light have to be taken into account:

(i) The rectilinear propagation of light determines its definitely directional character.

(ii) The intensity of irradiance is a rather complicated aspect. In the first place it is related to the strength of the light source. The important physical principle that irradiance decreases proportionally with the square of the distance from the light source does not apply to the practically parallel rays of sun or moon, but only to the divergent rays of a nearby light source. Under natural conditions, reflecting objects or entrances of caves through which scattered light penetrates are, in this respect, comparable with artificial light sources. Another factor which produces a gradual decrease (gradient) of irradiance is the absorbing and scattering properties of the aquatic media.

(iii) The spectral composition of light does not seem to have received much attention in problems related to the orientation of marine invertebrates.

(iv) Another fundamental property of light is polarization. Direct sunlight is not polarized. Polarization, however, occurs as the result of scattering by particles in the atmosphere as well as in water. According to WATERMAN (1955), polarization is a permanent aspect of underwater illumination.

The photic environment of a marine animal, however, is determined not only by the properties of light. Any differentiation between biotopes according to irradiance distribution will be based on the physical properties of the biotopes. Two extreme cases of irradiance distribution, for instance, are represented by the simple and regular conditions in the open sea as opposed to the complex conditions in shallow parts along rocky coasts and coral reefs.

(a) Photokinesis

Kineses as opposed to taxes or oriented movements are defined as non-directional changes in random movements due to changes in the intensity of the stimulus, not to its direction. The responses may involve a change of the velocity or frequency of locomotory movements (**orthokinesis**) or a change of the rate of random turning (**klinokinesis**). Animals commonly show a combination of the two reactions in their activities. In normal conditions these responses are maximal to unfavourable stimuli, resulting in a longer stay in areas with more favourable conditions. Thus if the locomotor activity of a photonegative organism within an irradiance gradient is increased by light and diminished in darkness, the individuals will aggregate in the shaded region.

It appears far from easy, however, to produce clear evidence of the occurrence of purely photokinetic responses since under almost any conditions the directional character of light can play a role in orientation.

Since the latter part of the 19th century it has been a controversial issue whether animals are guided by the directional properties of light or by successive changes in irradiance perceived during the course of their random movements. In the early years a dominating position was occupied by LOEB (1890, 1905), who propounded a very mechanical theory of light orientation. According to this theory, an animal is impelled to move either towards or away from a light source through compensatory movements which continuously correct any deviation from equal stimulation by light on both sides of its symmetrical plane. By means of certain experimental arrangements, LOEB demonstrated that photopositive organisms move towards the light source even when this reaction takes them into a darker region and that the reverse applies to photonegative organisms. Among LOEB's opponents, a number of authors attempted to demonstrate that aggregations occur in an 'optimal zone' of a light gradient through the action of non-oriented kinetic responses (older terms: phobotactic or photopathic responses).

Planktonic Invertebrates

Planktonic organisms would appear to be our prime interest in this context because they live in an environment in which the spatial relations are dominated by a vertical irradiance gradient. There are, however, surprisingly few workers who claim to have demonstrated non-oriented kinetic responses in planktonic animals. YERKES (1899) and DITLEVSEN (1907) worked with freshwater crustaceans (Cladocera and Copepoda). GOLDSMITH (1921) used a number of marine planktonic crustaceans such as *Mysis chamaelaeon*, *Centropages hamatus*, *Acartia clausi*, nauplii of *Balanus* species and zoeae of *Maja squinado*. These authors introduced their animals into an irradiance gradient crossing the path of the light rays. The gradients were produced, for instance, by triangular glass dishes filled with an absorbing liquid (e.g. indian ink solution) or some kind of graded filter (smoked glass). From aggregation of the invertebrates in a particular area of the irradiance gradient they concluded that they are guided by the intensity, not the direction, of irradiance.

The 'intensity theory', however, has been criticized by several authors. With reference to YERKES' (1899) work, TOWLE (1900) made a remark which is worth recalling because of its general applicability. YERKES used a long and narrow experimental trough set at right angles to the direction of the light source, thus preventing the animals from moving towards the light. By means of an indian ink prism placed in front of the trough an intensity gradient was produced in its long axis. TOWLE, however, comments that to an individual animal placed in a darker part of the trough (in the conditions created by YERKES) the lighter part of the gradient actually acts as the light source. In other words, locomotory movements in so-called 'non-directional gradients of light' may still be oriented movements.

The problem of phototaxis (oriented movements towards or away from a light source) as opposed to photokinesis (aggregations in regions of a particular illumination intensity) has been studied by a number of workers on marine zooplankton. GROOM and LOEB (1890), using the classic 'window-arrangement', concluded that nauplii of *Balanus perforatus* orient by the direction of the light rays. In this arrangement a long trough or test tube is placed perpendicularly to the plane of a window. The room side of the trough is illuminated by direct sunlight, while the window side is illuminated by more or less diffuse light from the sky by means of screens. Positively 'heliotropic' (= phototactic) nauplii moved straight to the window side even when this reaction took them into a darker region. Negatively heliotropic nauplii moved away from the window and accumulated in the brightest part of the trough. Although LOEB (1893, 1905) recognized the possible existence of photokinetic responses ('Unterschiedsempfindlichkeit') in freshwater Planaria, he never found photokinesis in the marine planktonic organisms studied by him: larvae of the horseshoe crab *Limulus polyphemus*, larvae of the archiannelid *Polygordius* sp., copepods, and larvae of crustaceans, worms and molluscs.

LOEB (1890) was the first to apply convergent light to demonstrate that photopositive invertebrates swim towards the light source instead of accumulating at the point of highest irradiance, the focus. This type of experiment with convergent and divergent light has been carried out by other authors as well. MOORE (1909), working with nauplii of *Balanus* species, used focused light in cylindrical museum jars. According to his description, photopositive nauplii, introduced within the divergent part of the light field, move through the focal point (region of highest irradiance) towards the source of light (region of lower irradiance). Photonegative nauplii move away from the source of light towards the focal point and on to the distal part of the jar. In photonegative larvae of the polychaete *Sabellaria spinulosa* KALMUS (1931), using a convergent beam and a light gradient produced by a wedge-shaped filter, found oriented movements away from the light source towards the brightest region.

In an extensive study, SPOONER (1933) reviewed the problem of the 'direction-intensity controversy' in marine planktonic invertebrates and carried out detailed experiments. He paid special attention to the angular-radiance distribution in different light-gradient devices used by some previous workers and carefully observed the paths followed by individuals. Like TOWLE (1900) and HOLT and LEE (1901), he concluded that irradiance coming from all directions has to be taken into account in any interpretation of this kind of experiment. A wide variety of planktonic animals were tested such as copepods, *Sagitta*, larvae of *Balanus*, annelids, molluscs and fishes. The results of his experiments showed that in no case did photopositive animals aggregate in the brightest region when this was away from the light source. The animals tested were able to maintain their normal movement in the direction of the incidence of the light, whatever changes in total irradiance were encountered during their progress. The reverse situation obtained with photonegative animals. According to SPOONER, the phototactic response of an invertebrate is explicable on the basis of the specialized distribution of light sensitivity over its surface, which, however, makes the invertebrate lose the ability to record the changes of irradiance that occur in its surroundings, unless it is capable of allowing for its direction of orientation. This, he comments, by no means implies that changes in irradiance have no influence at all. They may activate or inhibit the locomotory movements. They are, however, of no significance for the pathways followed by a wide range of plankters which are able to orient to the direction of the incident light.

Regarding the responses of the trachymedusa *Gonionemus murbachi*, YERKES (1903, 1906), MORSE (1906, 1907) and MURBACH (1909) agree that illumination elicits swimming activity; in shaded regions the medusae slow down and settle on the bottom. According to YERKES, however, *G. murbachi* is oriented by the directional property of the incident light. In his view, this is accomplished by the earlier and more forceful contraction of that side of the bell farthest away from the shade. This conclusion has been criticized by MURBACH. Comparable results were obtained by ROSE (1925) with the hydromedusa *Phialidium hemisphericum* and the ctenophore *Pleurobrachia pileus*. Under the influence of direct sunlight dark-adapted individuals start swimming in all directions without any sign of orientation to photic stimuli. ROSE did not, however, investigate the mechanism of aggregation in any particular area of irradiance. Observations made by HYMAN (1940) on the medusae *Aequorea aequorea*, *Halistaura cellularia*, *Phialidium gregarium*, *Stomotoca atra* and *Sarsia mirabilis* did not provide any indication of a response when the medusae moved from a sunlit region into the shadow of the dock, nor was any tendency seen towards accumulation in either shaded or sunlit areas.

In general it may be concluded that, apart from a not yet clarified photic orientation mechanism in medusae and ctenophores, a proper photokinetic mechanism of aggregation in certain areas of irradiance, i.e. random exploratory movements, has not yet been clearly demonstrated in plankton invertebrates. Nevertheless, a photokinetic component may be incorporated in phototactic responses in the sense that locomotory activity is initiated (released) by 'unfavourable' changes of irradiance, resulting in oriented movements towards more 'favourable' conditions.

In free-swimming larvae of the ascidian *Diplosoma listerianum*, CRISP and GHOBASHY (1971) found positive phototactic behaviour in a parallel light beam. In a light gradient perpendicular to the light path, on the other hand, the swimming larvae were more or less evenly distributed along the experimental trough with no obvious preference for high or low illumination, which is in agreement with the results mentioned before. Metamorphosing larvae, however, showed a totally different behaviour. They respond negative-phototactically to a parallel light beam but when introduced into a light gradient, they clearly aggregate in the less illuminated sections of the trough, having a preferendum of the order of 300 lux. Apparently, the metamorphosing larvae show photokinetic responses at settlement. But they are then no longer planktonic.

Littoral and Benthic Invertebrates

As has been pointed out before (p. 559), littoral and benthic invertebrates live in optic fields far more complex and irregular than do their planktonic and pelagic counterparts. Apart from the neritic invertebrates swimming close to the sandy bottom or among rocks, corals and seaweed, most of them are restricted in their movements to crawling about on these more or less irregular surfaces. This biotope is predominantly characterized by dark–light boundaries.

For several littoral, benthic and neritic animals a photokinetic behaviour (orthokinesis as well as klinokinesis) has been described in the literature. The klinokinetic component, however, needs some attention here. Originally **klinokinesis** was defined by KÜHN (1919) as **phobotaxis** (other terms: avoiding reaction, trial-and-error reaction, 'Schreckreaktion', 'Unterschiedsempfindlichkeit'). This concept derived from observations of animals turning away at abrupt intensity boundaries. The question is whether these responses involve directionality (which is expressed in the word 'taxis') or may be regarded as random turning movements.

ULLYOTT (1936) worked on light responses of the limnic planarian *Dendrocoelum lacteum*, and investigated the problem of 'phobotaxis'. Using a uniform, non-directional light field, he claimed to have demonstrated the relationship between the rate of random turning or the 'rate of change of direction' and irradiance. In the dark, the rate of random turning is low. When light is switched on, it increases immediately. Under constant stimulation, however, the rate of turning decreases considerably owing to sensory adaptation. In a horizontal smooth light gradient (illumination from above through graded filter), the combined effect of intensity changes and adaptation—according to ULLYOTT—leads presumably to aggregation in regions of lower intensity. This has been theoretically confirmed by ROHLF and DAVENPORT (1969) in simulating experiments with a mathematical model using a digital computer.

In order to stress the non-oriented character of this type of response, GUNN and co-authors (1937) decided to classify it as kinesis; they proposed to divide kineses into (i) orthokinesis (variations in linear velocity), and (ii) klinokinesis (variations in angular velocity). Further, they designated the classical avoiding reaction (phobotaxis) as a special case of klinokinesis.

PRECHT (1942), however, criticized ULLYOTT's (1936) interpretation of the mechanism of aggregation, and EWER and BURSELL (1950) objected to all 'shock' reactions being designated as an extreme case of klinokinesis. They adduced observations of animals stopping at a boundary, making some exploratory movements and then taking a new course, not random but spatially related to the stimulus. Similar 'shock' reactions have been described by HARDEN-JONES (1971) in *Dendrocoelum lacteum* exposed to high intensities of illumination. A comparable type of reaction is frequently shown by wire-worms (Coleoptera) in steep humidity gradients, which LEES (1943) interpreted as a directed reaction of the 'klinotaxis' type of behaviour (p. 566).

In a recent study STASKO and SULLIVAN (1971) have questioned the validity of the klinokinesis concept, which actually was based solely on ULLYOTT's (1936) hypothesis about the possible mechanism of accumulation at the darkest end of a light gradient by planarians, but which has so far not been supported by experimental evidence. In an extensive series of experiments with planarians, STASKO and SULLIVAN did not find any indication of klinokinesis being operative in the selection of dark areas; rather, their observations suggested that the planarians were in fact oriented by scattered lateral light.

A common feature in littoral, benthic and neritic invertebrates is their movements along tortuous pathways, which give the impression of being completely random and are thus likely to be explained in terms of kinesis. An interesting case was described by BLUM (1934a, 1954) concerning the responses to light of tide-pool-inhabiting littoral copepods *Harpacticus fulvus*. When placed in a rectangular dish in direct sunlight, the copepods, racing about in all directions, assembled at the end away from the sun. Every time the dish was reversed, the entire flock 'drifted' rapidly away from the sun. Their individual movements were seemingly not oriented at all but gave the impression of being purely kinetic. In fact, the parallel rays of the sun illuminated the entire dish evenly, so that there was no light gradient and the aggregation could not, therefore, be explained in terms of photokinesis.

According to BLUM, the copepods were subject to the directive influence of the light, but changed their pathways so frequently that this orientation was effectively masked.

Actually, kinetic movements are very difficult to evaluate properly when related to photic stimuli. In many cases of reported photokinesis the animal in question is perfectly capable of orienting to the directional property of the light. However, photokinetic responses on the basis of irradiance may be responses to releasing stimuli within the mechanism of photic orientation as a whole. Several publications on photokinetic behaviour should be considered from this point of view.

FRANZ (1911b) analysed the characteristic to and fro movements of the underwater-cave inhabiting mysid *Hemimysis larmornae*. He found an inverse relationship between the frequency of turning and the distance from the light source, the movements, however, being directed in relation to the light source. The locomotory activity of the polychaete *Nereis diversicolor* is stimulated by illumination, which results in an aggregation of individuals in shaded areas, where they come to rest. The orientational capacities of these polychaetes are fairly well developed (HERTER, 1926; AMELN, 1930). In the polychaete *Nephtys cirrosa* photo-orthokinetic behaviour seems to be more distinct. The frequency of locomotion tends to increase linearly with irradiance, resulting in a marked accumulation in dark areas (CLARK, 1956).

Another case where photo-orthokinesis appears to play an important role was demonstrated by EVANS (1951). At low tide the intertidal chiton *Lepidochitona cinereus* is almost invariably found on the undersurfaces of stones. If such a stone is overturned in sunlight, the chitons on top of the stone will be observed to begin moving and to aggregate again on its new lower surface. Under these conditions the chitons have been shown to orient to the force of gravity; but photokinetic responses appear to contribute to the rapid finding of the sheltered areas. From experiments in shallow dishes it was clearly demonstrated that the velocity of the randomly moving chitons increased with irradiance. In half-shaded dishes the chitons moved randomly along tortuous pathways within the illuminated part and slowed down and finally came to rest in the shaded area.

OHBA (1957) studied the photo-orthokinetic activity of the photo-negative littoral snail *Monodonta labio*, which he expressed as the percentage of moving animals. In dark-adapted snails he found a linear correlation with the logarithm of irradiance. With exposure to constant stimulation the activity decreased considerably due to sensory adaptation. The removal of the stalked eyes has no influence on the photokinetic activity nor on the process of light adaptation.

NEWELL (1958a, b) reports an increase of the rate of crawling in *Littorina littorea* with increasing irradiance. He suggests that this 'orthokinetic' response may have some importance in stimulating the snails to crawl and feed. Broadly similar results were obtained by NEWELL (1962) with the gastropod *Peringia ulvae*. It is doubtful, however, whether these two cases can properly be interpreted in terms of photo-orthokinesis.

In his study of the behaviour of the interstitial archiannelid *Trilobodrilus heideri*, BOADEN (1963) made a short note on the influence of light. When archiannelids were placed in a half-shaded dish, they gradually accumulated in the shaded area following extremely convoluted pathways. Once an individual had moved

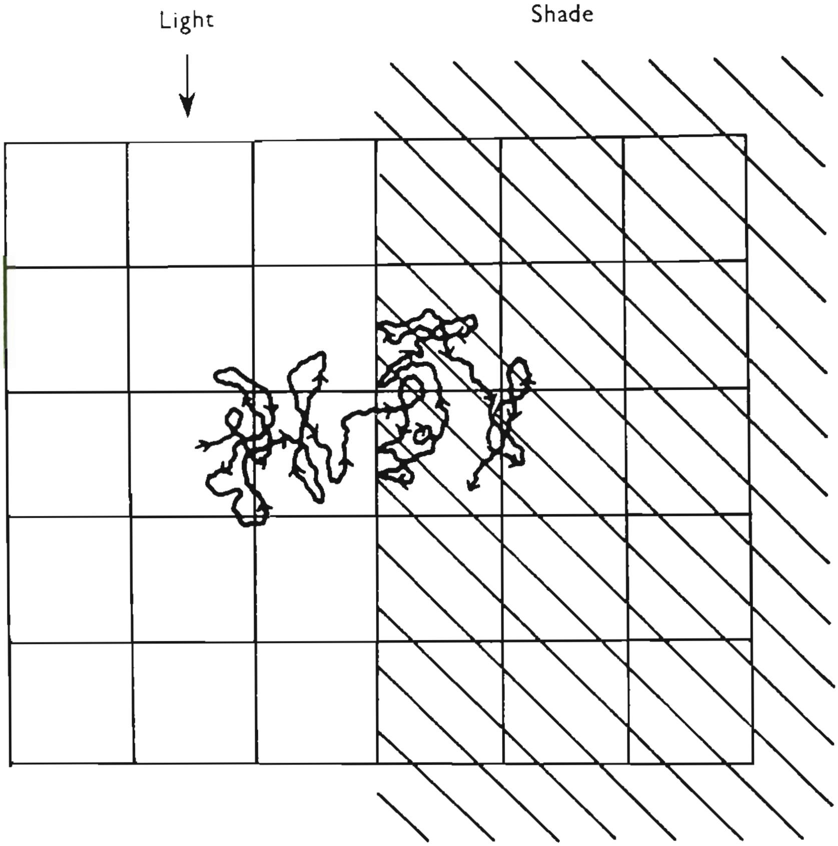

Fig. 8-23: *Trilobodrilus heideri*. Orientational response to light. Movement trace of an individual to illustrate reaction to a light/shade boundary. Barbs indicate half-minute intervals. Graticule in 1 cm squares. (After BOADEN, 1963; reproduced by permission of Marine Biological Association of the U.K.)

into the shaded part, it turned sharply back into the shade whenever it encountered the light-dark boundary again. However, judging from the movement trace of an individual (Fig. 8-23), neither the linear nor the angular velocity shows any differences between the illuminated and the shaded areas. The aggregation of *T. heideri* in shaded areas seems to be effected purely by 'shock' reactions at the light–dark boundary.

The holothurian *Opheodesoma spectabilis* in daytime normally lives in aggregations in beds of the brown alga *Sargassum echinocarpus*, where it finds protection against sunlight (BERRILL, 1966). When placed on a sand flat, the holothurians move rapidly away from the direction of the sun until they encounter a bed of *S. echinocarpus*, where they come to rest. They show no orientation in relation to the position of the alga. When released under an overcast sky, their movements not only are slower, but also lack any orientation. They show a relatively high rate of random turning. When *O. spectabilis* in which the 15 pairs of ocelli have been removed are placed on a sand flat in sunlight, their behaviour is fairly similar to that of intact individuals under an overcast sky. This would imply that the ocelli of *O. spectabilis* are involved in directional light orientation under sunlight conditions. The light sensitivity, however, persists in the absence of ocelli and may be responsible for the photokinetic behaviour.

According to EDWARDS (1969), zonation of the gastropod *Olivella biplicata* in the intertidal zone, segregated by body size, would be the result of photo-orthokinetic responses.

(b) Phototaxis

The term **phototaxis** is used for directed orientation either towards or away from a light source. It may also be defined as longitudinal orientation, as opposed to transversal orientation. Locomotion towards a light source is called **positive phototaxis** and away from a light source **negative phototaxis** (Chapter 8.0).

It has always been a matter of debate whether or not the phenomenon phototaxis should be considered a functional orientation mechanism. This problem is discussed on p. 574. In the literature, a considerable amount of information can be found as to whether particular animals are photopositive or photonegative. For some groups synopses are available (PARDI and PAPI, 1961: crustaceans; YOSHIDA, 1966: echinoderms).

In the present context, phototaxis will be discussed as a phenomenon which, in its different manifestations, may reveal some of the principles of the physiological mechanisms of orientation. According to the classification of FRAENKEL and GUNN (1940), phototaxis can be subdivided into three types: photoklinotaxis, phototropotaxis, and phototelotaxis.

Photoklinotaxis

In photoklinotaxis regular deviations or rotating movements are necessary for orientation. This response is observed in organisms with poorly developed photosensitivity or with a single eye, not known to be more than a simple irradiance receptor. In many cases the receptor is exposed asymmetrically on one side and masked by pigment on the other side, so that its angle of light acceptance is limited. In swimming along a longitudinal spiral the receptor points successively in different directions. The mechanism is supposed to be based on the comparison of irradiances, successive in time, from different directions.

Klinotactic responses are well known from some Protista, species of *Euglena* being a classic example in this respect (JENNINGS, 1906; MAST, 1938; DIEHN, 1969; Chapter 7).

In marine invertebrates photoklinotaxis is an uncommon type of reaction. It occurs in tadpole larvae of the ascidians *Amaroucium constellatum* and *A. pellucidum* (MAST, 1921). These larvae possess a single asymmetrically placed eye with pigment cup and lens. At each rotation the tail responds to irradiance fluctuations received by the eye in such a way that the larva, during its initial photopositive phase, moves towards the light source but after it has become photonegative, at the time of settlement, away from the light source. In ectoproctan (bryozoan) larvae, RYLAND (1960) observed a response to directional illumination which appears to be photoklinotactic. The larvae follow a spiral course, either towards or away from the light source by means of ciliary movements. FRAENKEL and GUNN (1940, 1961) also include the behaviour of the swimming post-trochophore larvae of *Arenicola*, described by MAST (1938), among photoklinotactic responses, although they are provided with two symmetrical photoreceptors. In this stage the larvae are highly photopositive; locomotion is the result of ciliary action, while orientation is brought about by muscular contraction. When swimming, the larvae rotate longitudinally so that, on lateral illumination, each eye is alternately illuminated and shaded. The muscles on the side where illumination increases contract violently, forcing the head towards the light. This process occurs twice during each rotation, thus effecting rapid orientation.

The other type of photoklinotaxis, in which the invertebrate, when crawling, turns alternately to the right and to the left, has been observed in the mobile bivalve *Lasaea rubra* by MORTON (1960). By comparing successively the irradiance on either side of its path, the mollusc presumably finds small crevices or other places of refuge.

Phototropotaxis

Phototropotaxis, as opposed to phototelotaxis, is based on simultaneous comparison of intensities on both sides of the body.

This mechanism of orientation is the starting point of LOEB's 'tropism theory', which he considered to be the basis of all orientation processes in animals. According to LOEB (1890), the bilaterally symmetrical structure of animals underlies the principle of balance of processes in the two body sides. The processes inducing locomotion are equal in both halves of the central nervous system, causing an equal 'tension' of the symmetrical muscles so long as the animal moves straight towards or away from a light source, and the photochemical processes in the photoreceptors are equal. If, however, the animal deviates from its course, the illumination of the photoreceptors and the photochemical processes will be different, the physiological symmetry no longer exists and the muscles will no longer produce an equal response. As a consequence the animal will, in a 'forced movement', correct its course until the symmetrical stimulation is re-established.

An important criterion for defining a reaction as phototropotaxis is the behaviour of the invertebrate in a light field illuminated from two different directions. The strength of the light sources may be either equal or different. In phototropotactic behaviour, which is based on equal stimulation of the photoreceptors on both sides, the pathways followed by the invertebrate at each point in the light field will be determined by the proportional intensity of the light sources or, in other words, by the resultant as given by the triangle of forces rule. This principle has been elaborated for various marine invertebrates by LOEB and NORTHROP (1917) in photopositive barnacle larvae; by NORTHROP and LOEB (1923) in the photonegative horseshoe crab (*Limulus*); and by FRAENKEL (1927a) in the copepod *Phyllothalestris mysis*, the amphipod *Corophium longicorne*, the polychaetes *Nereis dumerili* and *Polyophtalmus pictus*, and caprelids. In their experiments on orientation in animals showing a tropotactic response in a 'two light' situation, these authors also confirmed the validity of Bunsen and Roscoe's photochemical law, which says that the photochemical effect is proportional to the product of the intensity and the duration of illumination. They effected variations in the duration of the illumination by placing a rapidly rotating opaque disc between one of the light sources and the aquarium, with a greater or smaller sector cut out of the disc. In the case, for instance, that a sector of 180° had been removed the duration of illumination was reduced to one half. From pathways followed by the invertebrates under these circumstances it could be concluded that the effect of a light source reduced in duration of illumination is equivalent to that of a light source which, to the same degree, is reduced in intensity.

Another frequently employed method for testing whether the mechanism of orientation employed is phototropotactic, comprises unilateral blinding of an animal, either by painting over or by removal of one of its eyes. If one eye is rendered unfunctional, the balance of stimulation is disturbed. With lateral illumination, photopositive animals tend to deviate towards their intact side. In uniform or overhead illumination, they perform **circus movements**. Photonegative animals deviate towards the blinded side.

The behaviour of unilaterally blinded horseshoe crabs (*Limulus*) has, for instance, been studied by COLE (1923). In his experiments clear circus movements were observed, with the crabs turning towards the side of their functional eye. Furthermore, it was found that the rate of turning depends on the intensity of the illumination. The diameter of the circles decreases with increasing photic stimulation, at a rate inversely proportional to the logarithm of the illumination intensity. COLE considered these results as satisfactorily explained by the tropism theory of LOEB. In *Limulus polyphemus* the lateral eyes as well as the dorsal ocelli mediate positive phototaxis, the latter, however, responding only to near-u.v. light (LALL and CHAPMAN, 1973).

For circus movements by unilaterally blinded animals to be adopted as a criterion for a phototropotactic mechanism, however, some difficulties exist, which are extensively discussed by FRAENKEL and GUNN (1940, 1961). Especially in overhead or uniform illumination, animals which behave telotactically likewise perform circus movements when unilaterally blinded. One of the reasons is the absence of a light source which can be fixed and used as a guide, so that telotaxis cannot come into action.

Phototelotaxis

Phototelotaxis comprises direct orientation towards (or away from) a light source without a balance of stimulation of the two sides of a bilaterally symmetrical body. In this mechanism it is essential that the eyes (or single eye) have a number of separate receptor elements, each of which can be stimulated from a particular direction. These elements may be retina cells acting in conjunction with a lens or ommatidia of a compound eye. Essential, also, is a central nervous organization which can inhibit all stimuli except those from one direction. This enables animals to move straight in the direction of a source of stimulation towards which these particular elements of the eye, forming a **fixation region**, are directed, other light sources being disregarded. This process can be demonstrated in two-light experiments. When the animals are placed in front of two lights they move directly towards one of them, ignoring the other. It may occur, however, that during their progress they switch over to the other light or even follow a zig-zag course, alternately moving towards each of the two light sources before making a final decision. This type of reaction in marine invertebrates has been demonstrated clearly by VON BUDDENBROCK (1923) in the decapod crustaceans *Eupagurus bernhardus*, *Carcinus maenas* and *Galathea intermedia*, the mysid crustacean *Mysis ornata*, the gastropod *Buccinum undatum* and the nemertine *Oerstedia dorsalis*, and to a certain degree also in the gastropod *Nassa incrassata*, the opisthobranch *Aeolis landsburgi*, the cephalopod *Allotheutis subulata* and the echinoderm *Asterias rubens*; by ALVERDES (1930) in the decapod *Eupagurus bernhardus*; by FRAENKEL (1931) in the isopod *Aëga* sp.; and by FRIEDRICH (1931) in the copepods *Calanus helgolandicus* and *Corycaeus anglicus*. As a striking example of telotactic behaviour, FRAENKEL and GUNN (1940) advanced the observations made by FRANZ (1911b) and FRAENKEL (1931) on *Hemimysis lamornei*. When a number of these mysids are placed in an aquarium and illuminated laterally, they continually swim towards and away from the light source, always keeping in line with the light beam. After each turn of 180° they cover a distance of about 10 cm. If a second light source is placed at right angles to the first, some of the mysids persist in their characteristic movements, keeping in line with the first light beam, but others start moving in line with the second beam, ignoring the first light source; this results in two crossing streams of mysids.

Another method frequently used to demonstrate phototelotactic behaviour, as opposed to phototropotaxis, is unilateral blinding (p. 568). Because of the complex structure of the eyes, with several photosensitive elements pointing in different directions, each of the two eyes is supposed to be endowed with directional sensitivity. Unilateral blinding then should hardly affect the telotactic orienting ability of the animals, and since symmetrical balance of stimulation is not consistent with telotaxis, unilateral deviations or circus movements should not occur. In marine invertebrates, results of this kind have been obtained by ALVERDES (1930) in the decapod crustaceans *Eupagurus bernhardus* and *Carcinus maenas*. In his experiments, however, photonegative unilaterally blinded crabs would sometimes spontaneously shift to tropotactic behaviour either by deviating towards the blinded side (*E. bernhardus*, *C. maenas*) or by performing circus movements (*E. bernhardus*). Unilaterally blinded shrimps (*Leander xiphias* and *Processa canaliculata*), in a number of cases, also show locomotion straight towards or away from a light source (ALVERDES, 1926). Differences in muscle tonus resulting from unilateral blinding, however, appear to interfere in such a way that generally a deviation towards the blinded side occurs in photonegative as well as in photopositive shrimps. In phototropotaxis a deviation towards the blinded side is only observed in photonegative individuals.

The distinction between phototropotaxis and phototelotaxis on the basis of two-light experiments and unilateral blinding has given rise to a good deal of controversy. The point at issue is not so much the occurrence of phototelotaxis but rather whether a pure phototropotactic mechanism of orientation occurs. Extreme positions have been taken by VON BUDDENBROCK (1915a, 1923), who criticized the 'resultant law' and 'balance of stimulation' theories, and FRAENKEL (1927a), who based his analysis of the tracks of a number of marine invertebrates on the 'resultant law' theory and concluded that, apart from telotaxis, tropotaxis exists as an effective mechanism.

The contradictory results obtained by several other workers in this field have hardly settled the issue. Unlike von Buddenbrock (1923), Just (1927) concluded from his two-light experiments that the sea-star *Asterias rubens* behaves phototropotactically, while Diebschlag (1938) observed an entirely different behaviour in the same species. The phototropotactic behaviour of *Littorina rudis*—described by Bohn (1904a, 1909) in experiments showing an orientation towards darkness (skototaxis, p. 575)—has been denied by Bierens de Haan (1921), while Charles (1966) observed both kinds of reactions toward black screens. In experiments with two lights, Newell (1958b) found in *Littorina littorea* a behaviour suggesting phototelotaxis. Similar results were obtained by Newell (1962) with the littoral gastropod *Peringia ulvae*. In experiments using either two lights or unilateral blinding, Herter (1926) found phototropotactic orientation in the polychaete *Nereis diversicolor*, in which only the posterior eyes were reported to be involved. Ameln (1930) came to approximately the same conclusion, but found that the anterior as well as the posterior eyes play a role. Working with the same species, Brand (1933), however, obtained results more readily interpretable in terms of phototelotaxis. With decapod larvae in two-light experiments, von Buddenbrock (1923) as well as Wojtusiak (1931) obtained results explicable either way.

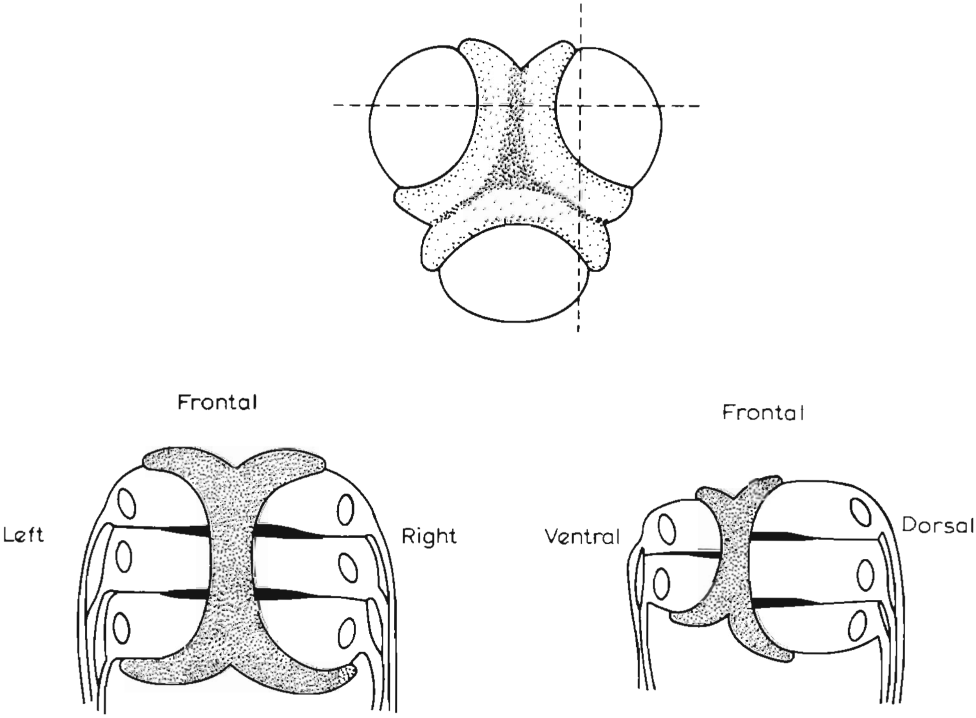

Fig. 8-24: Nauplius eye. Scheme of typical arrangement of 3 pigment cups containing the retina cells. Top: frontal view; bottom: frontal cross-section (left) and parasagittal cross-section (right) in the planes marked in top figure. (After Jander, 1965; reproduced by permission of Akademische Verlagsgesellschaft Geest & Portig, Leipzig.)

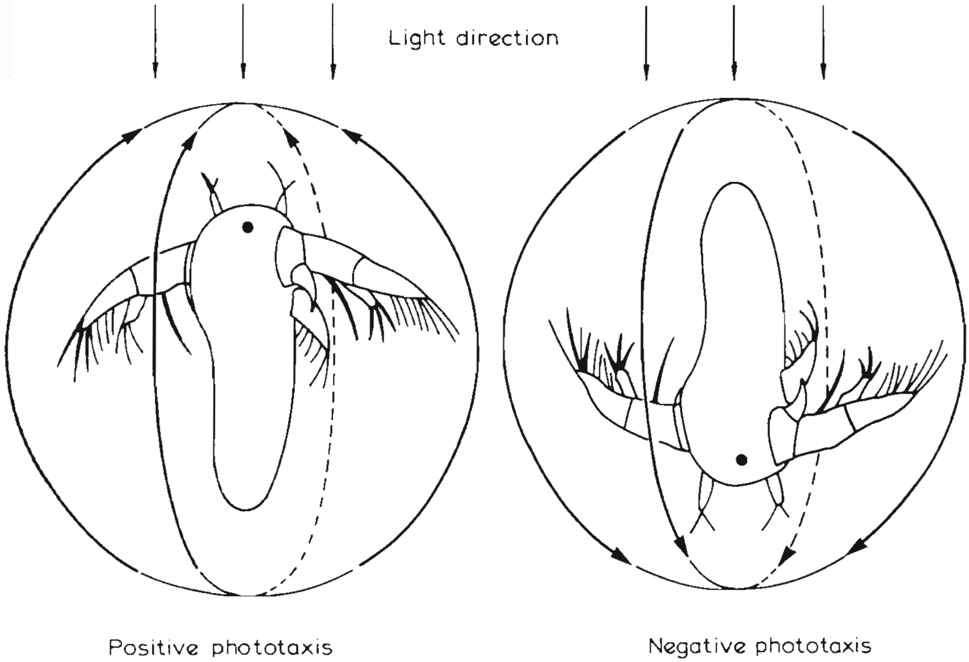

Fig. 8-25: *Artemia salina*, metanauplius. Scheme of rotation responses about dorso-ventral and transverse axes in positive (left) and negative (right) phototaxis. (After JANDER, 1965; reproduced by permission of Akademische Verlagsgesellschaft Geest & Portig, Leipzig.)

Much attention has been paid to the general problem by FRAENKEL and GUNN (1940), PRECHT (1942) and JANDER (1965). To a certain extent these authors agree that both phototropotaxis and phototelotaxis may be functional mechanisms in different species, within one species or even in a single individual. According to circumstances, one of the mechanisms will dominate. Undoubtedly, photonegatively reacting animals will, when exposed to one or more light sources, find themselves in a fundamentally different situation than do photopositively reacting animals (PRECHT, 1942). In the former case there is no target which can be fixed during progression, and tropotaxis will most probably come into action.

Interesting phylogenetic considerations with regard to phototropotaxis, phototelotaxis and transversal orientation in relation to the anatomy of the single nauplius eye and the compound eye in crustaceans are found in JANDER (1965). The median eye of nauplii consists of one ventro-median and two dorso-lateral pigment cups containing retina cells exposed in corresponding directions (Fig. 8-24). This triangular configuration enables the nauplii to respond phototropotactically in two planes by turning along the dorso-ventral axis as well as along the transverse axis (Fig. 8-25). The same primitive mechanism is found in adult planktonic copepods (e.g. species of *Calanus*). According to JANDER, this mechanism and the absence of compound eyes in recent as opposed to fossil copepods are a secondary adaptation to open-sea conditions dominated by vertical light incidence.

(c) Spatial Orientation and Direction of Locomotion

The normal mode of locomotion in most animals is forward, the longitudinal axis being kept in line with the direction of locomotion. In phototropotaxis (symmetrical balance of stimulation) this type of movement is regarded as axiomatic. In phototelotactically reacting animals it has likewise been shown that, in a number of cases, locomotion in line with the longitudinal axis is closely related to the functional differentiation in the structured eye where, for instance, a specialized fixation region is only operative in the forward direction. In general terms, in the majority of animals the spatial orientation of the body axes and the direction of locomotion show a more or less constant geometrical relation.

In some groups of marine invertebrates (e.g. echinoderms and crustaceans), however, there seems to be no stable relation between the animal's spatial orientation and the direction of locomotion. Is there a morphological or a functional anterior end in echinoderms? Except in holothurians and irregular echinoids there seems to be, broadly speaking, no preference as to which part of the body moves in advance during locomotion. A pertinent review has been given by REESE (1966, p. 168); YOSHIDA (1966) has reviewed photosensitivity in echinoderms. The most detailed information exists in the literature on asteroids. These echinoderms can move with any arm foremost, the particular arm which at any given moment is forward being defined as the 'leading arm'. It may also occur that two arms (or an interradius) are leading. A common observation is that when an asteroid reverses its direction of locomotion it does so without changing the orientation of the body axes. That is, in its new course the asteroid moves with another arm foremost (JUST, 1927: *Asterias rubens*; KALMUS, 1929: *Asterina gibbosa*).

Locomotion in asteroids is accomplished by the tube feet of all five arms. The tube feet perform co-ordinated stepping movements in the line of progression. In the leading arm, these movements are directed towards its distal end. The works of HOPKINS (1926), DIEBSCHLAG (1938), SMITH (1945, 1950) and KERKUT (1954, 1955) suggest that the central nervous co-ordination of the unidirectional stepping of the tube feet of the five arms is controlled by the dominant activity of one of the five neuron systems, each of which is situated at a junction of the radial nerve cord and the circum-oral nerve ring. A change of direction of locomotion is brought about when the dominant role of one of these centres is taken over by another. The case of an interradius (or two arms) moving in advance is explained by SMITH (1950) as the resultant of the activity of two adjacent centres. YOSHIDA and OHTSUKI (1968) made an attempt to find a relation between the part played by these centres and phototaxis. Working with photopositive sea-stars *Asterias amurensis*, they found that an illuminated arm (while the others are shaded) takes the 'leadership' in locomotion. An extensive series of experimental combinations, however, also revealed that an individual with ocelli removed from 2, 3 or 4 arms and totally shaded, moves in a direction away from the intact side. Apart from the positive effect of light on an intact arm as described in the former experiment, the authors conclude tentatively from the latter experiments that, in addition, an intact arm can actively perceive shading; information is conducted to the eyeless arms with the result that their tube feet step in a direction opposite to that of the 'seeing' arm when shaded. According to YOSHIDA and OHTSUKI, their results can only be explained if the neuron-system dominance theory is somehow reconciled with the idea of an organisation based on co-ordinated interaction of the five arms.

Comparable problems arise when the locomotion of certain crustaceans is considered. The most remarkable movements are performed by crabs. HOLMES (1908), discussing the side-wise locomotion of the photopositive fiddler crab *Uca pugnax* towards a light source, pointed out the inconsistency of this lateral orientation with the tropism theory of LOEB (1890, 1905), at the time regarded as the only possible orientation mechanism. The same arguments were advanced by VON BUDDENBROCK (1915a) with respect to the locomotion of the crab *Carcinus maenas*.

VON BUDDENBROCK (1923) and ALVERDES (1930) clearly demonstrated photo-telotaxis in *Galathea intermedia*, *Eupagurus bernhardus* and *Carcinus maenas*; this implies that these crabs must be able to fix an object (e.g. a light source) towards which they move. While in progress, however, the crabs sometimes change the orientation of their body axis without altering the general direction of locomotion or, on the other hand, change the direction of locomotion without altering the orientation of the body. This behaviour does not fit readily into the scheme described for some insects that have eyes with differentiated fixing regions. Apparently any part of the crab's eye can act as a fixing region (FRAENKEL and GUNN, 1940, 1961).

In *Eupagurus bernhardus* and *Carcinus maenas* there is, according to ALVERDES (1930), a close connection between the direction in which the antennules (known as chemoreceptors) are pointed and the direction of locomotion (see also BROCK, 1930). The locomotory direction may even be predictable from the position of the antennules. In the uncommon cases where a crab moves in a direction exactly between two lights (apparently tropotactically) the antennules have been observed pointing alternately to each of the lights; from this ALVERDES concluded that the lights were continually perceived and central nervously registered as two separate sources of stimulation.

The concept of a crab's flexible fixing region, however, needs to be qualified: it must be assumed that once an area of the crab's eye is acting as a fixing region it will persist in doing so for a longer or shorter period. This may be deduced from the ability of crabs to turn their eyestalks in following moving objects (optokinetic responses), or even from the 'optokinetic memory' displayed by the correcting movement of the eyes after the visual field has moved a little during a short period of darkness (HORRIDGE, 1966a). Striking observations were made by WOLTER (1936, p. 591) in *Carcinus maenas* which, during locomotion in the presence of a stationary light source, keeps its eyestalks at a constant angle to the light source, apparently fixing this object with a particular group of ommatidia. When, however, the crab has progressed so far that the eyestalks touch the edge of the orbita, it performs a nystagmys, with the result that the light source is now fixed with a new group of ommatidia and the compensatory eyestalk movements can be continued.

Some authors have paid attention to the relation between body posture and direction of locomotion in crustacean larvae (LYON, 1906, larvae of *Palaemonetes*; FOXON, 1934, larvae of Caridea, Astacura, Anomura, Thalassinidea and Brachyura; BLUM, 1934b, larvae of *Homarus vulgaris*). JANDER (1965) considered phylogenetic aspects. More recently, JANDER (1970) has proposed a basic distinction between two types of redirection of oriented progression: (i) Resetting of the afferent system or change of taxis; this is the common type of progression, where directional changes of locomotion are accomplished by aligning the longitudinal body axis to the new pathway. (ii) Resetting of the efferent system or change of kinesis; in this case the locomotory direction can change without any change in body orientation.

(d) Non-natural Aspects of Phototaxis

For years phototaxis has dominated the field of photo-orientation as a supposedly fundamental aspect of animal behaviour. However, under non-natural conditions (e.g. in experiments with artificial light sources) positive phototaxis is an extremely common feature, which, in many animals, is far from consistent with their normal behaviour in nature. LOEB (1905, p. 267) was probably already aware of this problem when he noticed that in his experiments animals were rarely negatively heliotropic (= phototactic)—much more rarely than he had formerly assumed. FRANZ (1913) made a special study of the biological significance of phototaxis for free-living animals. While working with planktonic larvae of benthic invertebrates, he was struck by the inherence of their phototactic responses, which he considered a valuable asset for these larvae enabling them to stay in open water after hatching. This view is supported by observations of GIESBRECHT (1910) on the phototactic behaviour of stomatopod larvae (*Squilla mantis, Lysiosquilla eusebia*); directly after hatching, these larvae pass through two bottom-dwelling stages in which they show photonegative responses; thereafter they start a planktonic life and correspondingly become positive phototactic. Similar observations were made by DINGLE (1969) in the stomatopod *Gonodactylus bredini.*

In general, however, FRANZ (1911a, 1913) regarded positive phototaxis in experimental devices as an attempt to escape from unusual conditions. He demonstrated, for example, that with lateral illumination several species (e.g. tadpoles of Amphibia and shrimps of the genera *Leander* and *Palaemon*) become positive phototactic if they are confined in a small glass dish, whereas these animals move about at random when kept in a large container. Likewise, he explained negative phototaxis as an escape reaction of animals usually finding protection in burrows, in crevices or under stones. The phototaxis concept has also been sharply criticized by RUSSELL (1934, p. 35):

> 'bright and localized sources of light are practically unknown in nature and the apparently forced phototaxis which many nocturnal insects exhibit towards a bright lamp has something abnormal, meaningless and pathological about it.'

This, of course, would also apply to the aggregation of marine invertebrates and fishes (Chapter 8.2) around an underwater lamp. Further, RUSSELL stresses that tropisms (= phototaxis) represent 'in fact very largely laboratory products—the outcome of exposure to artificial and unnatural stimuli.'

SCHALLEK (1942, 1943) paid attention to the phenomenon—reported by several authors—that planktonic organisms which, under natural illumination, show a photonegative response become positive phototactic when an artificial light source is used. In his experiments the copepod *Acartia tonsa*, under highly directional illumination, moved towards the light but did not when the illumination was more diffuse. SCHALLEK explained this result as the effect of an abnormal angular light distribution with an extreme 'concentration' in the direction of the light source in relation to other directions. This problem has been studied extensively by Verheijen (1958), who bases his discussion on nocturnal insects flying towards bright lamps, birds crashing against lighthouse lanterns and marine invertebrates and fishes gathering at night around light sources placed either above or below the water surface. Like Schallek, Verheijen came to the conclusion that an unnatural angular light distribution is responsible for this 'trapping' effect. Apart from lamps, the light distribution in a room with windows may be an abnormal condition too. On the basis of an extensive literature review and his own experiments, Verheijen deals at length with the physiological mechanism of disorientation in animals under these conditions. His study casts serious doubts on the prolific literature on phototaxis, especially where lamps in dark surroundings are involved. One even begins to question the validity of the phototaxis concept as a natural process. However, according to Verheijen, not all animals are subject to the trapping effect of artificial light. Animals from environments dominated by distinct light–dark boundaries (e.g. rocky coasts) are frequently reported to move away from a lamp in laboratory experiments. As has been mentioned on p. 559, in this environment sun-reflecting objects in shadowed surroundings or cave entrances are comparable to artificial light sources in regard to angular light distribution.

Undoubtedly, non-natural trapping effects under artificial conditions will frequently have led to misinterpretations of experimental results. However, there is no ground for dropping phototaxis as a useful concept in evaluating some natural forms of photo-orientation. For instance, all investigated forms of nauplii have only two possible responses to illumination, either towards or away from the light (Jander, 1965); together they constitute 'longitudinal phototaxis' (as opposed to 'transversal phototaxis'). No other types of photo-orientation have been observed in these plankters. Because of the predominantly vertical direction of incident light in the open sea, all orientation of pelagic nauplii in natural conditions is supposedly along the vertical, either upward or, head first, downward. Upward orientation (towards the light) has been observed far more frequently; Jander explains this as a compensation of downward sinking. For a large number of copepod species equipped with nauplius eyes the same principles hold; but, according to Jander, also crustaceans with two eyes will, under natural conditions, be capable of longitudinal phototaxis besides other types of photo-orientation. It has to be borne in mind that in the open sea environmental factors such as light, temperature, salinity, and food availability vary mainly in the vertical plane; in this plane, light incidence and gravity (p. 642) provide the only directional cues.

(e) Skototaxis and Contour-related Orientation (Form Vision)

Only negative phototaxis has been mentioned thus far as the reverse of positive phototaxis. However, several photonegative animals move towards black areas, objects or screens, even if they have to deviate from their course away from the light source. The term skototaxis (orientation towards darkness) has been introduced by Alverdes (1930). Most work on skototaxis has been carried out on terrestrial animals, especially insects (Jander, 1965). The ecological significance of skototaxis is commonly recognized as an orientation towards a hiding-place. In marine invertebrates skototaxis has been observed in littoral gastropods of the genus *Littorina* (BOHN, 1905; BIERENS DE HAAN, 1921), the polychaete *Nereis diversicolor* (AMELN, 1930; BRAND, 1933), the crab *Carcinus maenas* (ALVERDES, 1930) and the stomatopod *Gonodactylus glabrous* (BOLWIG, 1954). The results of ALVERDES (1930) deserve special attention. They show a distinct telotactic orientation towards black screens by photonegative crabs (*Carcinus maenas*). A characteristic case is illustrated in Fig. 8-26, which demonstrates the interplay between negative phototaxis and 'positive skototaxis'.

Some authors doubt whether skototaxis is a separate form of photo-orientation. In regard to orientation towards black surfaces.ULLYOTT (1936, p. 254) argues

> 'the correct interpretation is almost certainly that the diffused light from the rest of the surroundings is acting as an orienting stimulus'.

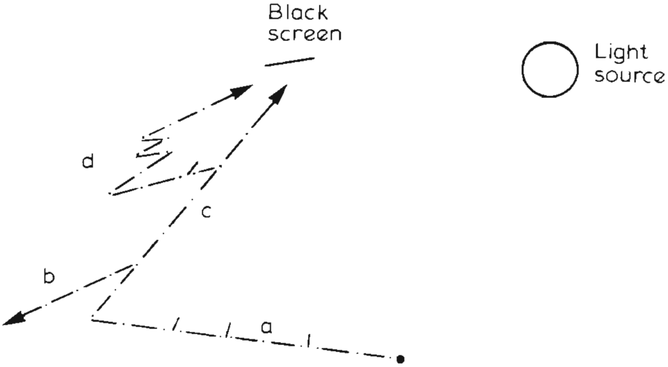

Fig. 8-26: *Carcinus maenas*. Experiment with one light source and one black screen. a: interplay of negative phototaxis and positive skototaxis (barbs represent position of antennules), b: negative phototaxis, c: positive skototaxis, d: zig-zag course resulting from alternating negative phototaxis and positive skototaxis. (After ALVERDES, 1930; modified; reproduced by permission of Akademische Verlagsgesellschaft Geest & Portig, Leipzig.)

This means that he regards skototaxis as a form of negative phototaxis. FRAENKEL and GUNN (1940, 1961) raise the question whether the absence of any photic stimulus (darkness) can act as a stimulus. The answer might be found in research conducted by HARTLINE (1938): Oscillographic records of action potentials of separate optic fibres in the eyes of the scallop *Pecten irradians* revealed that part of the fibres discharge impulses only at cessation of the illumination or upon a reduction of its intensity. This so-called 'off reaction' is supposed to be responsible for the vigorous 'shadow reactions' exhibited by several benthic and littoral invertebrates. From the interesting study by LAND (1968) it may even be concluded that scallops can perceive ambient moving dark objects via the 'off'-reaction system. Work in this field, however, has not yet advanced sufficiently to allow comparison between this mechanism and skototaxis.

Can skototaxis be distinguished from the mechanism of contrast perception or form vision? This question was raised by FRAENKEL and GUNN (1940) and may yield the most acceptable interpretation of the phenomenon 'skototaxis'. MICHIELI (1963) worked with 50 different species of arthropods and showed that, for example, in *Carcinus maenas* in many cases of so-called skototaxis, orientation was mainly directed towards the edges of the black screens—a behaviour already known from insects. Similar observations were made by HORRIDGE (1966b) in his studies on the optokinetic responses of *C. maenas* in a striped drum. Depending on experimental conditions, the crabs see either edges or areas of black and white stripes. According to these results, perception of contours and shapes may play an important role in the orientation of invertebrates with adequately developed eyes. WILLIAMSON (1951b, 1954) investigated the movements of the sandhopper *Talitrus saltator* and found indications that landward orientation is directed towards objects beyond the high-water mark, probably to some feature of the skyline; this implies some degree of form vision in *T. saltator*. Laboratory experiments support this assumption. *T. saltator* were released in front of a screen on which various shapes and configurations, painted on lantern slides, were projected; the sandhoppers react very distinctly to slopes projected with light above and dark below, always moving towards the foot of the incline; if the slope was projected as dark over light, they did not show any directional orientation (WILLIAMSON, 1954).

Comparable results were obtained by EVANS (1961) with *Littorina punctata* on the Ghana coast. These littoral gastropods orientate not only to the sun and to gravity but, when moving shoreward, also to terrestrial beacons. In laboratory experiments EVANS (1965) found that *L. saxatilis* and *Melarapha* (= *Littorina*) *neritoides*, which live above high-water neaps, are never, when moving upward, trapped by half-tide rocks; he tentatively suggested that the snails 'see' the water surface from below. A morphological study of the eye of *L. littorea* by NEWELL (1965) provides good evidence that these littoral gastropods are capable of a certain degree of form vision. Through the converging system of cornea and lens, sharp images of distant objects can be focused on the retina when the snail is above the water. The acuity, however, is limited by the spacing of the cones of the visual cells subtending an angle of about 7° at the centre of the lens. Below the water, on the other hand, distant objects form sharp images behind the retina. It seems, therefore, that in water acuity is limited by the dioptrics rather than by the structure of the retinal mosaic. However, a system of accommodation may possibly exist (NEWELL, 1965).

Fiddler crabs, which inhabit sandy or muddy intertidal flats, show clear directional seaward and landward orientation based on celestial cues (menotaxis, p. 582). In *Uca pugilator*, however, HERRNKIND (1968) demonstrated that orientation towards prominent landmarks (e.g. mangroves or rows of beach grass) comes into action under conditions such as dense overcast or disorientation resulting from transportation to another shore. HERRNKIND emphasizes the adaptive value of modifiability of responsiveness to different visual guidance cues, since neither celestial stimuli alone nor landmarks alone (e.g. underwater or amidst shore grass) always provide appropriate directional information.

A remarkable form of orientation to contrasts is exhibited by vertically migrating *Daphnia magna*. The same principle may also be applicable to vertical orientation in a number of marine planktonic animals. Due to refraction, any organism underwater receives light through the water surface only within an inverted cone of rays with an angle of 49° to the perpendicular (Fig. 8-27; HARRIS, 1953). Rays falling on the eye outside this cone are reflected at the water surface and originate from deeper water layers with much lower irradiance. An aquatic animal, therefore, will 'see' the surface as a brilliantly lit circle right overhead, contrasting with a dark background. Irrespective of depth, the circle will always subtend an angle of 98°, and the exact overhead position is independent of the sun's altitude and azimuth. In a marine environment, where the water surface is mostly disturbed, the boundary of the circle will be broken up by irregularly moving light and dark patches but the contour will still be recognizable and serve as a means of orientation. In an interesting series of experiments, RINGELBERG (1964) was able to demonstrate that photopositive *D. magna* orient to the light–dark boundary of the circle rather than to the light area overhead. His experimental device consisted of a small circular perspex box placed in the centre of a circular fluorescent tube. A *D. magna* was pinned down through its broodpouch in the centre of the box, allowing free movement round the pin as the animal's transverse axis. The fluorescent tube provided homogeneous illumination in the animal's median plane. Screening off a sector of 270° left a contrasting light sector of 90°, simulating—in the median plane only—the bright overhead circle in the pelagic environment (Fig. 8-28). With a few beats of the antennae, *D. magna* is immediately oriented under these circumstances. Using a binocular microscope the orientation of body axis and eye axis were measured. The results (RINGELBERG, 1964; SIEBECK and RINGELBERG, 1969) showed that usually the body axis is directed more or less to the centre of the light

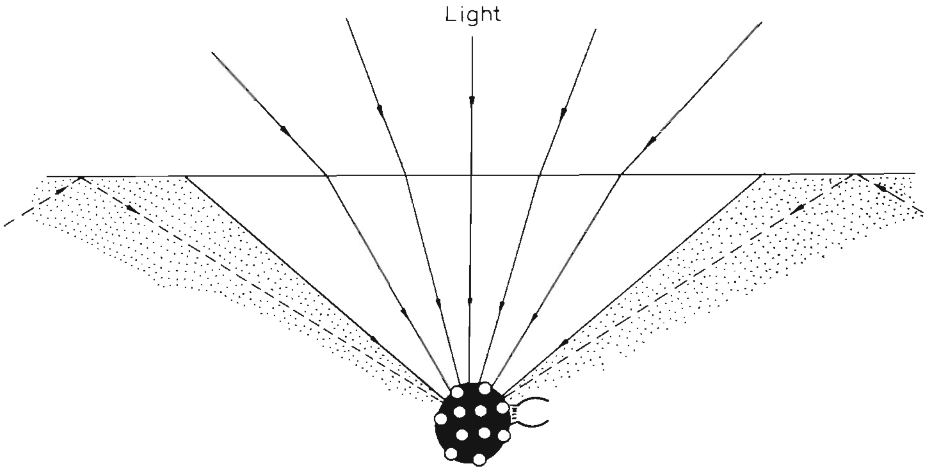

Fig. 8-27: *Daphnia pulex*. Critical cone of illumination in relation to eye. Rays entering eye at an angle greater than 49° to the vertical (indicated by dashes) are reflected at water surface and originate from deeper water layers. (After HARRIS, 1953; reproduced by permission of Company of Biologists Ltd.)

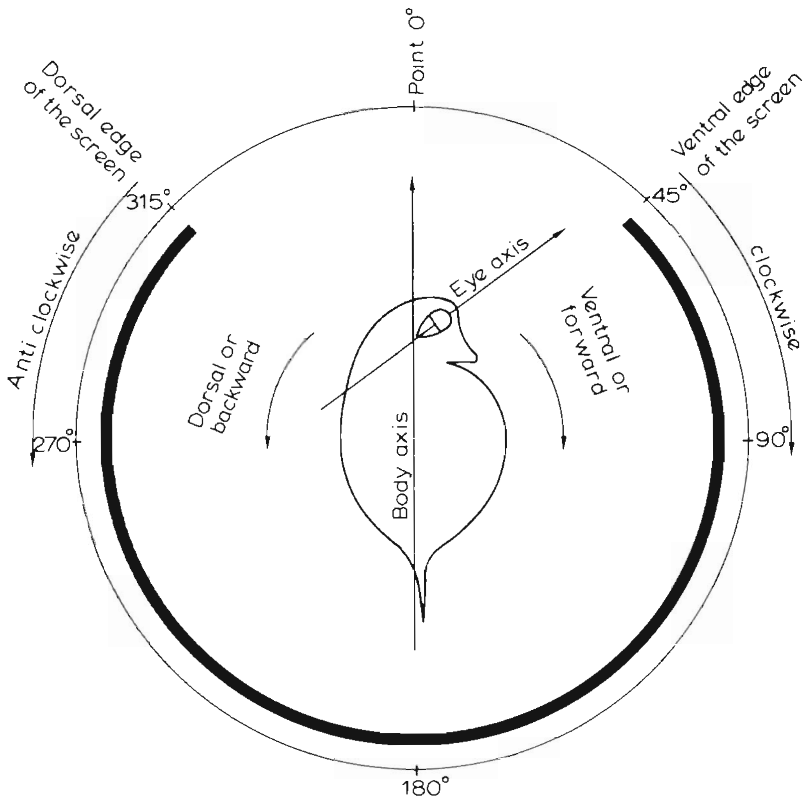

Fig. 8-28: *Daphnia magna.* Orientation experiment. The test individual is pinned through its broodpouch in the centre of a box, allowing free movement about the pin acting as transverse axis. An illuminated sector of 90° simulates—in the median plane only—the bright overhead area in the pelagic environment. (After RINGELBERG, 1964; modified; reproduced by permission of Netherlands Institute for Sea Research.)

area. The eye axis, being rather mobile, is mostly kept at a constant angle of about 70° to the body axis in the ventral direction. The actual orienting cue was found by shifting the dark–light boundaries of the light sector. In most cases only corresponding corrections were performed when the dorsally situated edge was moved (e.g. through 30°) either clockwise or anticlockwise. Shifting of the ventrally situated contrast did not affect body-axis orientation. This implies that in most cases only the dorsal ommatidia of the compound eye are concerned in fixing the dorsally situated boundary of the light circle. A number of observations were related to photonegative individuals. Their body axis pitched forward at an angle of about 140° to the vertical. In this position apparently the opposite boundary (the ventrally situated contrast) is fixed and again with the dorsal ommatidia of the eye.

Important for contrast perception are spontaneous tremor-like eye movements causing a constant shifting of the image projected on the retina. Using a special device, DITCHBURN (1963) demonstrated in experiments with man that if an image on the retina does not move, the contrasts fade away within a few seconds and the visual field becomes grey. This effect is attributed to rapid sensory adaptation of the photoreceptive cells. HARRIS (1953) reported tremor-like movements of the eye of *Daphnia pulex* and suggested that their function is scanning in form vision by eyes of low visual acuity. RINGELBERG (1964) likewise pointed out the significance of these movements in contrast perception. An extraordinary scanning mechanism exists in *Copilia quadrata* (GREGORY and co-authors, 1964). In this copepod, which has paired eyes, the lenses are rigidly fixed at the anterior edge of the carapace. Behind these lenses a long 'crystalline cone', a second pair of lenses and the photosensitive elements are suspended in a dynamic system of ligaments and muscles producing oscillatory movements, apparently across the image plane of the anterior lenses.

Interesting observations on tremor-like eye movements in *Carcinus maenas* have been made by HORRIDGE (1966b). A crab was clamped down within a striped drum. During a short period of darkness (e.g. 15 secs or 1 min) the drum is moved through a small angle. On re-illumination the eye stalks perform a correcting movement in the same direction ('optokinetic memory'). If, however, the movement of the drum has gone beyond a half period of black and white stripes, the correction on re-illumination is the reverse, as if the drum had been moved in the opposite direction; this suggests that the crab 'sees' the areas of the black and white stripes. In a number of cases, however, reversed corrections have been observed at about $\frac{1}{4}$, $\frac{1}{2}$ and $\frac{3}{4}$ period, which suggests that the crab only 'sees' the edges of the black and white stripes. The difference between the two types of response can be accentuated artificially by controlling the tremor of the eye. When the right eye is clamped to the carapace in order to prevent tremor and the left eye is painted over and allowed to move freely and to perform the above-mentioned corrections (open loop condition), the responses suggest that the crab 'sees' the stripes as black and white areas. When in the same arrangement a controlled amount of tremor is imposed on the seeing eye by oscillation of the drum the perception of the edges is enhanced.

Another physiological adaptation promoting contrast perception was demonstrated by HARTLINE and co-authors (1956) in the lateral compound eyes of the horseshoe crab *Limulus polyphemus*. This mechanism is based on lateral inhibition of photoreceptive units. When a receptor unit is excited it inhibits its neighbours and, in turn, is inhibited by them. The strength of the inhibition depends on the level of excitation of the interacting units and the distance between them. As a result, differences in illumination of receptor units are experienced as being larger; thus contrast vision is enhanced. VON CAMPENHAUSEN (1967) demonstrated in *L. polyphemus* the existence of an optokinetic response to a striped drum, but the reaction is very weak. It seems likely that in the horseshoe crab perception of forms or motion is poorly developed.

The ability of marine invertebrates with well-developed eyes to distinguish shapes makes possible a vast range of ecologically significant activities in which both intra- and interspecific orientation is involved. Newly hatched predating cuttlefish *Sepia* are exceptionally selective and will only attack moving objects closely resembling small crustaceans (*Mysis*) on which they normally feed (WELLS, 1958).

(For a detailed study of visual-attack orientation in *Sepia officinalis* consult MESSENGER, 1968.) Untrained, full-grown *Octopus vulgaris*, which mainly feed on crabs, preferably attack elongate objects moving along their longitudinal axes (SUTHERLAND and MUNTZ, 1959). Working with the same species, YOUNG (1959) found that responses to crabs are particularly difficult to eliminate by unrewarded training. During courtship, male *Sepia officinalis* normally show a 'zebra' pattern, which is intensified when approaching, or being approached by, another cuttlefish (TINBERGEN, 1939). In addition, the male displays the brightly striped lateral surface of the fourth arm extended towards the other individual. This action probably serves to identify the sex of the cuttlefish approached, since males return the display and females do not. A comparable display of a striped pattern has been reported by YOUNG (1962) during the courtship of the reef octopus *O. horridus*. A large amount of information on the physiology and organization of form vision and learning in cephalopods has been summarized by WELLS (1966).

According to VON HAGEN (1962), form vision plays a role in sex discrimination by the male fiddler crab *Uca tangeri*. The white claw of another male elicits threatening responses whereas certain leg patterns (e.g. an M-shaped model) release courtship waving. In *U. pugnax* and *U. pugilator*, ASPEY (1971) found interspecific sexual discrimination mediated by visual cues. HAZLETT (1972) analysed the essential visual characteristics of models eliciting agonistic display when presented to specimens of the hermit crab *Calcinus tibicen*. A comparable study has been carried out by JENSEN (1972) with *Carcinus maenas*.

A striking case of visual recognition of its specific habitat by the shrimp *Tuleariocaris sansibarica* was demonstrated by FRICKE and HENTSCHEL (1971). The shrimps (recently discovered) are usually observed in head-down vertical position among the black spines of the sea-urchin *Diadema setosum*. When released in front of a *D. setosum* they immediately swim towards the spines. In a series of experiments, the authors determined the crucial features of the optical stimulus provided by the sea-urchin. Primarily, a 'skototactic' orientation towards any dark object or area was observed. Habitat selection, however, appeared to be more complex: When the shrimps were presented with alternatives, they selected dark as against light spines, vertical as against oblique or horizontal spines and many spines as against few. The most effective configuration appeared to consist of many dark and vertical spines.

The possibility of visual cues being involved in the recognition of the giant red sea-urchin *Strongylocentrotus franciscanus* by its homochromous commensal shrimp *Betaeus macginitieae* has been studied by ACHE and DAVENPORT (1972).

(f) Transverse Orientation

So far, only mechanisms of orientation towards or away from a source of stimulation (e.g. light source or object) have been discussed. In addition, several animals are able to orient at an angle to the source of stimulation or, in other words, to use a source of stimulation as a reference point either for positioning their body axes in space (dorsal light reaction) or for maintaining a straight course (light-compass reaction).

Light-Compass Reaction or Menotaxis

The original discovery of light-compass orientation and the most advanced results have been obtained in terrestrial animals. Orientation in relation to the sun's azimuth was first described by SANTSCHI (1911) in migrating ants. VON FRISCH (1948, 1949) was the first to recognize the role of the polarization pattern of the blue sky in the orientation of honey bees, while KRAMER (1950, 1952) initiated the vast amount of work done on time-compensated sun-compass orientation in birds.

In marine invertebrates, light-compass orientation likewise seems to be a widespread phenomenon; it was first described by FRAENKEL (1927d) in the Mediterranean opisthobranch *Elysia viridis*. In a dark room with horizontal light incidence, the mollusc appears to crawl along a more or less straight course, maintaining a constant angle to the parallel rays of the light source (in these experiments the light incidence was artificially kept parallel by moving the light source along with the animal's progress). When the light is shifted to another position, a new course is taken up, but at the same angle to the light rays as before. When illuminated from above, the course becomes irregular. If the light source is stationary and near by, the path is curved. Orientation at an angle of nearly 90° to the light source results in a crawling movement in regular circles around the light source. If the orientation angle is smaller or greater than 90°, the path is a spiral respectively towards or away from the light source. Remarkably, in *E. viridis* the observed orientation angles appeared to be restricted to a range between 45° and 135° to the long axis of the snail, on both sides, with a prevalent value of about 90°. This feature is attributed to the anatomy of the eyes, in which light can only enter from an angle between 35° and 130° to the long axis. The snail cannot see directly ahead or behind. Apparently, the compass reaction can only be mediated by either one of the eyes. As in telotaxis, central inhibition in menotactic orientation has likewise been observed. In two-light exposure, only one light is used as reference point irrespective of differences in irradiance.

Another case of orientation with a light source for reference point was described by ALVERDES (1930). In his experiments on skototactic responses of *Carcinus maenas* the crabs were presented with a configuration of one or more light sources and black screens; the latter represent the preferred target. After some training, the target screen was removed. The crabs, however, maintained their course toward the place where the screen had been, the light-source configuration most probably serving as reference. This case involves no constant orientation angle to the light source(s), but landmark orientation in which the lights act as beacons in the neighbourhood of the object searched for.

A puzzling question has arisen through the work of WOLTER (1936), who studied menotaxis in *Carcinus maenas*. The pathways of the crabs were observed on a square platform (120 × 120 cm^2) on which 12 × 12 plots had been marked. In total darkness the paths were irregularly curved; in diffuse light, however, they were straight or slightly curved in all directions. In lateral illumination the paths likewise were straight or slightly curved in all directions, but the crabs always kept facing the light source with the eyestalks oriented towards the lamp. If the lamp was switched 180°, the crabs also turned their bodies through 180°, with the result that the light source was retained at the same angle to the eyes as before. Remarkably, however, the crabs maintained their original direction of locomotion. It is clear that *C. maenas*, although continuously fixing the light source, took their bearing from something else (the checkered pattern?) for maintaining their locomotory direction. WOLTER's conclusion that he had demonstrated light-compass orientation in *C. maenas*, therefore, does not seem justified.

Light-compass orientation has also been reported by AMELN (1930) in *Nereis diversicolor* on the basis of observed circular movements around a light source. In this process only the posterior eyes are reportedly involved. Field experiments carried out by NEWELL (1958a, b) showed that the littoral gastropod *Littorina littorea*, when crawling on wet sand, takes its bearing from the sun for maintaining its course. An analysis of the tracks revealed that they are roughly U-shaped and can often be seen to radiate out from, and back to, stones on which the snails have settled. At first, the direction of crawling is mainly towards the sun, but later, mainly away from it—although there is a good deal of variation. These looping movements are considered as feeding excursions ending with a return, approximately, to the starting point. The supposition that the sun acts as a visual cue during progress has been tested by shading these winkles from the sun. If the sun was then reflected from the opposite direction by means of a mirror, the snails responded by changing their direction and crawling back on a track parallel to their original course. Experiments by EVANS (1961) on a shore in Ghana provide strong indications that *L. punctata* likewise makes use of the sun as an orientation cue. In NEWELL's extensive study (1962) on the ecology of the small prosobranch *Peringia* (= *Hydrobia*) *ulvae*, living on mud flats, the same type of loop-shaped tracks as made by *L. littorea* are described. Similar observations have been reported by BRAFIELD and NEWELL (1961) in the bivalve *Macoma balthica*. This mollusc, usually living below the surface of mud flats, is known to be a deposit feeder using its long inhalant siphon as a kind of vacuum cleaner. Several times these molluscs have been observed to move about on the flats. According to BRAFIELD and NEWELL, these movements are to be considered feeding excursions. They describe U-shaped tracks which are oriented in relation to the sun's position. SWENNEN (1969), however, found that macomas crawling on the surface of the flats are without exception infected by the sporocysts of a trematode of the family Gymnophallidae. Crawling during air exposure in *M. balthica*, therefore, should rather be considered a pathological response, which exposes the host of the parasite to the risk of predation by birds, this being an essential condition for the life cycle of the parasite. In the mud snail *Nassarius obsoletus*, CRISP (1969) reported the existence of a light-compass reaction, which may account for the persistence of orientation when other stimuli seem inconstant or lacking. For a possible solar orientation in the littoral snail *Nerita plicata* see WARBURTON (1973).

The most detailed results on light-compass orientation in marine invertebrates have been obtained with littoral amphipods by PARDI and PAPI (1952, 1953) and PAPI and PARDI (1953). The littoral amphipods studied are obligate inhabitants of the intertidal region of sandy beaches, where environmental conditions vary predominantly in directions at right angles to the shore line. Orientation in this seaward–landward direction, therefore, is a basic ecological prerequisite for their existence. The sandhopper *Talitrus saltator* immediately returns to the wet sand of the beach when transported landward and released in dry sand. It moves at approximately right angles to the shore line. In an experimental dry glass jar the sandhoppers tend to escape in the same direction, directly seaward. When released in water they move landward. By shading the sandhoppers from the sun, and reflecting the sun from other directions, corresponding changes of orientation can be obtained. *T. saltator* from the Tyrrhenian Sea shore, released on dry sand on an Adriatic beach, move landward to the west. The polarization pattern of the blue sky is used in orientation when the sun is not visible. Under completely overcast conditions the sandhoppers are deprived of orientation cues and tend to turn towards the brighter parts of the sky. Since *T. saltator* show a correct orientation by the sun at any time of the day, even after a period of captivity, a time-compensating mechanism—to allow for the sun's motion—has to be assumed (Chapter 9). Night-time observations suggest the existence of lunar orientation. When the moon is not visible, even though the sky is clear, directional orientation fails.

In later years, sun-compass orientation has been reported for several other species of sand-beach amphipods: *Talorchestia deshayesei* (PARDI and GRASSI, 1955), *T. megalophthalma* and *T. longicornis* (MENAKER, 1958), *Orchestia mediterranea* (PARDI, 1960), *Orchestoidea corniculata* and *Orchestoidea benedicti* (ENRIGHT, 1961a), *T. martensii* (ERCOLINI, 1964), *Orchestia platensis* (JANKOWSKY, 1969) and the sand-beach isopod *Tylos latreillii* (PARDI, 1954).

A time-compensating mechanism in sand-beach amphipods, essential for celestial orientation, has been established (Chapter 9). PAPI (1955) transported *Talitrus saltator* through 71° to a different longitude and demonstrated that the angle of orientation to the sun at the new site was based on an 'internal clock' regulated in synchrony with the hour prevailing in the place from which they came. PARDI and GRASSI (1955) subjected *T. saltator* and *Talorchestia deshayesei* for several days to an artificial day–night rhythm retarded by 6 hrs with respect to the normal day (illumination from noon to midnight). When next exposed to the sun, the orientation of these beach amphipods was found shifted through 90°. They moved to the north instead of facing the sea in the west. Apparently, the endogenous rhythm can easily be adapted to a new situation; this implies that the 'internal clock' can be adjusted from day to day to the natural rhythm. Furthermore, there are indications that the 'internal clock' is influenced by temperature. Individuals kept at high temperatures (35°–37° C) for 18 hrs preceding the experiment orient at an angle to the sun in a way which would be correct some hours later (PARDI and GRASSI, 1955).

JANKOWSKY (1969) demonstrated in *Orchestia platensis* that temperature affects the 'internal clock' after sudden transitions. However, *O. platensis* is able to compensate temperature-induced variations of the endogenous clock; however, this is apparently not controlled by metabolic acclimation. BREGAZZI and NAYLOR (1972) found comparable effects of temperature in *Talitrus saltator* (see also Chapter 9).

Unlike the rather flexible 'internal clock', the geographic direction of orientation seems to be more or less fixed, presumably genetically. In experiments with laboratory-reared individuals of *Talitrus saltator* and *Talorchestia deshayesei*, kept under artificial day and night conditions (they never saw the sun), PARDI (1960) found that their orientational behaviour to a certain extent corresponds with the natural direction of orientation of the different populations from which they originate. Evidently, there exists an innate direction-finding tendency that differs from population to population; however, according to PARDI, this does not rule out the possibility of an acquired sense of escape direction, superimposed on the innate 'sense' of direction.

Lunar orientation in sand-beach amphipods and isopods is still a controversial issue. PAPI and PARDI (1959) and PAPI (1960) confirmed their earlier statement (PAPI and PARDI, 1953) that at night *Talitrus saltator* is able to orient 'correctly' by means of a time-compensated lunar-compass mechanism. Persistence of the appropriate orientation was even observed after the amphipods had been kept in darkness for a prolonged period. The authors tentatively advanced the hypothesis that two independently operating physiological rhythms are responsible for the solar and the lunar orientation. ENRIGHT (1961a) investigated the lunar orientation of another sandbeach amphipod, *Orchestoidea corniculata*. He likewise demonstrated that the moon's azimuth is the dominant orienting cue for this species under experimental conditions. However, if the amphipods are kept in constant darkness until just prior to observation they tend to maintain a fixed angle relative to the moon without any compensation for the changes of the moon's azimuth. This result does not support the hypothesis of a continuously operating lunar physiological rhythm as is claimed for *T. saltator*. If, on the other hand, the amphipods were exposed to sunset and moonrise on the night of observations, results were obtained that indicate the existence of time-compensated lunar orientation (Chapter 9). ENRIGHT (1961a) suggests that lunar orientation is based on re-phasing of the compensation mechanisms each night, initiated by appropriate stimuli. PAPI and PARDI (1963) confirmed their own statement on the basis of new experiments and suggested that the discrepancies may be caused either by species differences or by the fact that ENRIGHT made no special provisions regarding the humidity in his observation chamber. According to PAPI and PARDI, only extremely dry conditions release a correct lunar orientation. CRAIG (1971) has recently repeated the experiments of PAPI and PARDI and ENRIGHT. He used *O. corniculata* and followed the procedures used by PAPI and PARDI (e.g. humidity control) closely. The results obtained did not support any form of lunar-orientation theory (see CRAIG, 1973). For lunar and semilunar rhythms consult Chapter 9.

Discussing the 'dubious ecological value' of this type of orientation for *Orchestoidea corniculata*, CRAIG suggested that other orientation mechanisms may be involved under natural conditions. Experiments with the nocturnal sand-beach isopod *Tylos punctatus* have been carried out by HAMNER and co-authors (1968). This species is closely related to *T. latreillii*, which is known to be able to orient by the sun and the moon (PARDI, 1954). The authors, however, were unable to show any consistent celestial orientation in *T. punctatus*. On the other hand, it could be clearly demonstrated that this isopod can orient to slopes as small as 1°. It moves uphill when the substrate is wet, downhill when it is dry.

VAN DEN BERCKEN and co-authors (1967) investigated the orientation of *Talitrus saltator* and confirmed the existence of astronomical orientation. In addition, however, they found indications of a residual non-visual orientation mechanism directing the sandhoppers either seaward or landward depending on humidity, even in complete darkness and despite almost total elimination of the terrestrial magnetic field. ERCOLINI and SCAPINI (1972) repeated these experiments with the same species and with *Talorchestia martensii* (SCAPINI and ERCOLINI 1973) but did not find any directional orientation in complete darkness.

ERCOLINI (1964) and PARDI and ERCOLINI (1965, 1966) investigated the orienting ability of the intertropical beach amphipod *Talorchestia martensii*, which, periodically, is subjected to southern (clockwise) and northern (counterclockwise) culmination of the sun. In both periods the amphipods mostly show a correct time-compensated solar orientation. In an attempt to explain their ability to maintain a correct direction of orientation to quite different angular values according to whether the sun culminates north or south, the authors refer to the postulation of HORRIDGE (1966c, d) that crustaceans (*Carcinus maenas*) may directly perceive the apparent motion of sun and moon (see also BARNES and HORRIDGE, 1969). HORRIDGE demonstrated that a crab follows with its eyes a slowly moving light source with angular velocities in the range of 10 to 20° hr^{-1} as well as the movement of the sun itself. A hypothesis of celestial orientation—based on the perception of the rate of change in solar or lunar altitude—as outlined by PENNYCUICK (1960) for birds, would in HORRIDGE's view prove a rewarding subject for further investigation. The rate of rise or descent of celestial bodies is directly related to the azimuth, and the directional orientation would be independent of an 'internal clock'. Regarding HORRIDGE's work, however, it still remains doubtful whether the crab, though following the sun's movement with its eyes, really perceives the sun's motion as such.

Like littoral amphipods, a number of semiterrestrial decapod crustaceans are confined to the intertidal region. A variety of typical activities, such as feeding behaviour, flight responses and releasing of zoeae in the sea by females, require directional orientation perpendicular to the shoreline (HERRNKIND, 1968). Some workers were able to demonstrate the existence of a time-compensated solar orientation seaward or landward in littoral crabs such as the mangrove crab *Goniopsis cruentata* (SCHÖNE, 1963), the fiddler crab *Uca tangeri* (ALTEVOGT and VON HAGEN, 1964; ALTEVOGT, 1965) and *U. pugilator* (HERRNKIND, 1968). In comparison to the sand-beach amphipods, these crabs exhibit a great modifiability of responsiveness to guidance cues, which may be related to their more extensive wandering. The landward compass bearing of fleeing movements, for instance, can rapidly be modified by learning, while landmark orientation comes into action if celestial cues do not provide appropriate directional information. Like *Talitrus saltator*, these decapods show menotactic orientation to the polarization pattern of the blue sky when the sun is not visible. In SCHÖNE's (1963) experiments, the crabs were found to change their orientation to an artificial pattern of polarized light throughout the 24-hr day by amounts roughly compensating for the sun's azimuth changes. An artificial light source, acting as experimental 'sun', did not release menotactic responses.

In training experiments, the ghost-crab *Ocypode ceratophthalmus* (belonging to the same family as the fiddler crabs) showed menotactic orientation toward its home, presumably guided by the polarization pattern of the blue sky (DAUMER and co-authors, 1963).

A detailed review on orientation of shore-living arthropods has recently been presented by HERRNKIND (1972).

Sensitivity to Polarized Light

The ability to perceive the polarization plane of light (the so-called *e*-vector) seems to be widespread in terrestrial as well as in marine arthropods. It has also been reported in a number of cephalopods and marine gastropods (Table 8-3). Polarization is a fundamental property of light; it occurs as the result of scattering by particles in the atmosphere as well as in water. The blue sky provides polarized light; underwater light, down to any depth, is polarized; also certain types of light reflections are polarized. Basic information on this point and on the perception of polarized light in general has been provided by Waterman (1954, 1955, 1961) and Stockhammer (1959).

Table 8-3

Occurrence of polarized-light sensitivity in marine invertebrates. Studies supporting or demonstrating intra-ocular perception are indicated by an asterisk. (Compiled from the sources indicated)

Taxonomic group	Species	Author
Crustacea		
Anostraca	*Artemia salina*	Stockhammer (1959)
Copepoda	*Labidocera aestiva*	*Umminger (1968)
	Pontella meadii	*Umminger (1968)
	Centropages hamatus	*Umminger (1968)
	Tisbe furcata	*Umminger (1968)
	Caligus rapax	*Umminger (1968)
Mysidacea	*Mysidium gracile*	Bainbridge and Waterman (1957, 1958), *Waterman (1960), *Jander and Waterman (1960)
Isopoda	*Tylos latreillii*	Pardi (1954)
Amphipoda	*Talitrus saltator*	Pardi and Papi (1953)
Decapoda	*Ocypode quadrata*	*Schöne and Schöne (1961)
	Ocypode ceratophthalmus	*Daumer and co-authors (1963)
	Uca pugilator	Herrnkind (1968)
	Uca tangeri	Altevogt and von Hagen (1964), Altevogt (1965)
	Goniopsis cruentata	*Schöne (1963)
	Carcinus maenas	*Shaw (1966), *Horridge (1967)
	Cardisoma sp.	*Waterman and Horch (1966)
	Libinia emarginata	*Eguchi and Waterman (1968)
	Eupagurus bernhardus	Kerz (1950)
	Palaemon northropi	Bainbridge and Waterman (1957)
Chelicerata		
Xiphosura	*Limulus polyphemus*	Waterman (1950, 1954)
Mollusca		
Cephalopoda	*Octopus vulgaris*	*Moody and Parriss (1960, 1961) *Moody (1962) *Rowell and Wells (1961) *Tasaki and Karita (1966)
	Euprymna morsei	*Jander and co-authors (1963)
	Sepioteuthis lessoniana	*Jander and co-authors (1963)
Gastropoda	*Littorina littoralis* (= *obtusata*)	Burdon-Jones and Charles (1958) Charles (1961a, b, c)
	Littorina littorea	Charles (1961a, c)
	Littorina neritoides	Charles (1961a, c)
	Littorina saxatilis	Charles (1961a, c)
	Nassa obsoleta	Baylor (1959)

The physiological mechanisms involved in polarized-light perception present interesting problems. Detection of the plane of polarization requires a second polarizer, a so-called analyser. Where is this analyser located? Orientation to polarized light is not necessarily dependent upon the ability of the animal's eye to analyse the polarized light but may be due to brightness patterns in the environment. When light is reflected by a substrate or scattered in water by suspended particles, it becomes polarized. When incident light is already polarized (e.g. from the blue sky), the reflecting and scattering process may operate as an 'extra-ocular' analyser causing intensity patterns with quadrants of maximal and minimal brightness, the position of which depends on the direction of the *e*-vector. On this basis, BAYLOR (1959) explained the oriented responses to polarized light of the marine gastropod *Nassa obsoleta*, which were only observed when the snail was allowed to see the substrate. Comparable arguments were advanced by BAINBRIDGE and WATERMAN (1958) to explain the orientation of the marine mysid *Mysidium gracile* in turbid water, illuminated by polarized light.

In the experiments of CHARLES (1961a, b, c) with different species of *Littorina*, the polarized-light orientation most likely seems to depend on differential refraction/reflection phenomena at the eye surface according to the plane of vibration of the incident light as defined by Fresnel's laws (Fig. 8-29). Light vibrating parallel to

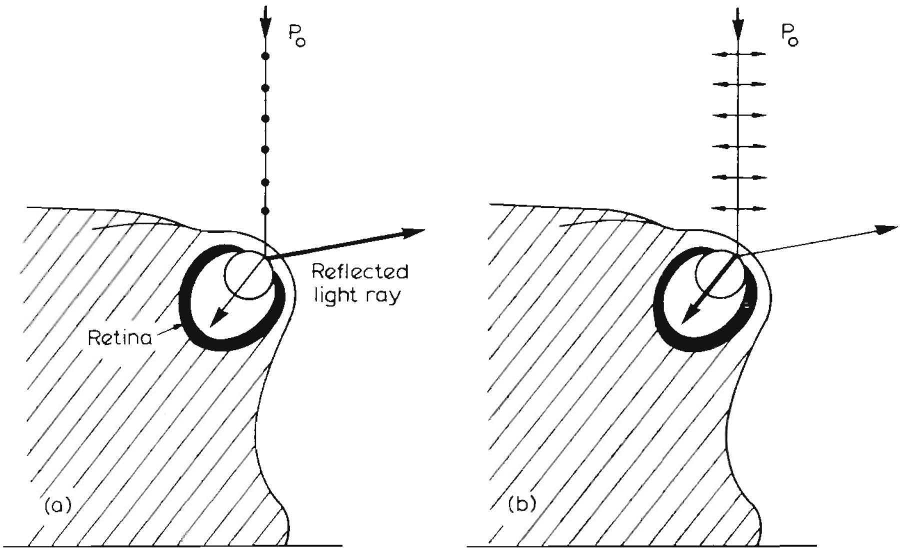

Fig. 8-29: *Littorina* sp. Anterior views of transverse sections of left side of a winkle head, showing the left optic cup. Po: Vertical ray of plane-polarized light incident upon lens aperture. (a) Winkle is crawling parallel with the plane of vibration of incident light; less light is refracted on to the retina. (b) Winkle is crawling at right angles to the plane of vibration of the incident light; more light is refracted on to the retina. (After CHARLES, 1961a; modified; reproduced by permission of Company of Biologists Ltd.)

the reflecting surface tends to be reflected while light vibrating at right angles to the surface tends to be transmitted.

There is no evidence yet that snails perceive polarized light as such. In arthropods and cephalopods, however, evidence of intra-ocular perception of polarized light has grown considerably.

Can the dioptric system in arthropods act as analyser? This question has been discussed by STOCKHAMMER (1959). Since the structures which compose the dioptric apparatus of the ommatidia do not reveal any polarizing effect, the analysing ability of the eye must be located in the photoreceptive cells themselves; this would be in accordance with the hypothesis of AUTRUM and STUMPF (1950). Several studies on marine invertebrates support the view of direct intra-ocular perception of polarized light independent of any irradiance-intensity cues that may be present. In Table 8-3 these studies are marked by an asterisk.

In the arthropod eye, the ability to perceive the plane of vibration is supposed to be correlated to the fine structure of the rhabdomeres of the retinula cells. Cephalopod eyes, although anatomically very different, show a striking similarity to arthropod eyes at the cellular and microstructure levels, through the occurrence in both, of regularly arranged retinula cells with similar rhabdom-like structures. The subject has been discussed by JANDER and WATERMAN (1960), MOODY and PARRISS (1960, 1961), JANDER and co-authors (1963) and UMMINGER (1968). Arthropods as well as cephalopods frequently show preferential orientation in 4 basic directions at angles of 0°, 45°, 90° and 135° to the *e*-vector. This raises the question as to whether there is some relation between this behaviour pattern and the (sub)microstructures in the receptor layers. The ecological significance of four preferential directions of orientation in polarized light is not yet completely understood either. According to JANDER and WATERMAN (1960), they may be basic reference directions from which menotactic orientation can be derived.

In an electrophysiological study, SHAW (1966), using intracellular micro-electrode techniques, demonstrated in the eye of *Carcinus maenas* the existence of two groups of retinula cells with maximal polarization sensitivities at right angles to one another. Comparable results were obtained by TASAKI and KARITA (1966) in the cephalopod *Octopus vulgaris* by a slightly different method. Electroretinograms revealed a selective adaptation to polarized light only in the vertical and the horizontal direction. No such adaptation effect was observed when the *e*-vector of the light was at 45° or 135°. Likewise, these results provide evidence that in the octopus retina there are two types of analyser operating at right angles to one another.

Further research by WATERMAN and HORCH (1966) with the crab *Cardisoma* sp., by EGUCHI and WATERMAN (1968) with the spider crab *Libinia emarginata*, and by WATERMAN and FERNANDEZ (1970) with the crayfish *Procambarus clarkii* has provided strong evidence for the existence of two intraretinal analysers, differentially sensitive to polarized light in directions perpendicular to each other and both occurring in each ommatidium. The analysing mechanism appears to be localized in the rhabdomeres and to be closely associated with their fine-structural organization, consisting of closely packed parallel microvilli, which are oriented perpendicular to each other in alternate layers.

Dorsal-light Reaction

Locomotion-associated orientation, with which we have been concerned so far, mainly involves turning movements along the dorso-ventral axis. However, in general, an animal maintains a certain position in space, which requires continuous correction along the longitudinal and transverse axes. Most animals hold the dorsal surface uppermost, and frequently they maintain this position by responding to the brightest sector of the visual environment, which is usually overhead. Since the terms 'up' and 'down' are by definition related to the earth's gravity, maintenance of a certain body position is first of all related to gravity force, with which visual reference stimuli may interact. For this reason, dorsal-light reaction and responses to gravity will be discussed as a complex orientation mechanism in the section on *Maintenance of Spatial Positioning* (p. 624).

(g) Control of Oriented Movements and Positioning

Oriented movements or positioning, far from being completely balanced or rectilinear, mostly show irregularities and deviations from the intended course or position, either due to external factors such as water movements or to locomotory inconsistencies. In orientation, therefore, a permanently operating correction mechanism is indispensable. For an extensive discussion see Chapter 8.0. Correcting mechanisms based on visual clues and controlled by the central nervous system have received comparatively little attention in marine invertebrates. Most work has been done on optomotoric reactions of crabs. When placed in a striped drum, which is then rotated, the crab's eyes follow the pattern and show nystagmus. If the stimulus is strong enough, redirection of the whole body will occur (VON BUDDENBROCK, 1952). If, however, the striped drum is stationary and the animal moves spontaneously, no such compensatory movements are observed although the striped pattern causes a similar shift of the retinal image. The crab's ability to distinguish between a shift of its visual environment produced by its own locomotory activity and an environmental shift caused by external conditions—such as passive displacement by water currents—has been brilliantly explained by VON HOLST and MITTELSTAEDT (1950), who advanced the physiological model generally known as the 're-afference principle'. According to this principle, within the CNS 're-afferent' stimuli (i.e., stimuli caused by the animal's own locomotion) are cancelled by a so-called 'efferent copy'—an equal but opposite stimulus—which is thought to accompany the command from the CNS to perform locomotory activity. For a comprehensive discussion of the re-afference principle consult Chapter 8.0.

Referring to WOLTER's (1936) observations, VON BUDDENBROCK (1952) pointed out that *Carcinus maenas*, when spontaneously walking along the inner wall of a stationary striped drum, actually performs optomotoric responses, and would therefore not be able to distinguish between real movement and apparent movement caused by its own locomotion. On the other hand, DIJKGRAAF (1953) maintains that this special case is precisely one in which the re-afference principle finds strong support. A crab moving along the inner wall of a cylinder is actually intent on taking a straight course, but through the curvature of the wall it is displaced in a lateral direction, which causes a non-'anticipated' shift of the retinal image. Crabs allowed to move unhampered along a striped pattern do not show compensatory eye movements. Incidentally, a similar principle finds application in nautical practice where the relative shift of two beacons provides information on the lateral displacement of the ship, for instance, by water currents.

A case of disturbance of visual feedback has been described by HORRIDGE (1966a). In his 'optokinetic memory' experiments with *Carcinus maenas*, in which immobilized crabs were exposed to a shift of the striped drum during a short period of total darkness, the eyes, on re-illumination, responded with angular corrections of maximally 70% relative to the angular shift of the pattern. If the right eye was clamped to the carapax and the left eye painted over, the latter (the blinded eye) performed correcting movements in response to a shift of the pattern perceived by the right (clamped) eye (open loop condition). In these conditions, the response of the blinded eye is surprisingly large—in the range from 12° to 20° with drum movements in the region of 0·125° to 1·0°—thus reflecting a situation in which the visual system is prevented from perceiving the effect of its own correcting movements.

How are, in 'voluntary' movements of either one of the eyecups, the effects of the visual feedback overcome? In order to answer this question HORRIDGE and BURROWS (1968) placed a *Carcinus maenas* with one seeing eye and the other painted over in a striped drum which performed oscillating movements. Since both eyes respond to the oscillations of the drum, the blinded eye apparently responds to the movements registered by the seeing eye. A forced movement imposed on the seeing eye by pushing it with a small probe either towards or away from the crab's midline, thereby causing a movement of the visual field in the opposite direction across the seeing eye, results in a movement of the blinded eye opposite to that of the seeing eye. If, however, the seeing eye moves voluntarily, the blinded eye does not respond, although a similar movement of the visual field across the seeing eye takes place. Since likewise no response of the blinded eye is observed when the 're-afferent' stimuli are suppressed either by mechanically preventing voluntary eyecup movements or by blinding the seeing eye, HORRIDGE and BURROWS were not able to fit these results into a single simple model based upon the action of a central 'efferent copy'. Proprioception was assumed not to be involved.

A totally different response to a moving striped pattern has been reported by DAVIS and AYERS (1972), e.g., in the lobster *Homarus americanus*. Specimens were restrained in place and exposed to a striped pattern moving backward, from which the lobster was separated by a transparent platform, through which it could see the moving stripes but not feel any movement of the surface mechanically. This visual movement of the striped pattern from front to rear appeared to induce forward locomotory movements in *H. americanus*, which DAVIS and AYERS considered a 'new class of optokinetic responses' controlled by 'positive visual feedback'. They discuss the stabilization of such positive-feedback control systems, which are inherently unstable.

(3) Temperature

In the marine environment, temperature changes primarily reflect seasonal fluctuations; they control a variety of physiological, ecological and behavioural aspects. Seasonal migratory movements, as reported for a number of marine invertebrates, may be regarded as a conspicuous example of such cyclic processes. However, the question whether these movements are primarily temperature controlled has, in many cases, still not been definitely answered. A number of other environmental factors such as illumination, day length, food availability, rainfall and river discharges, vary either parallel with, or inversely to, the seasonal temperature changes; endogenous cycles, entrained by one or a complex of these factors, play a part in the causal relations. For an extensive review of the functional and structural responses of aquatic invertebrates to temperature variations consult Volume I: KINNE (1970b; in that review distribution and migration are dealt with on pp. 502–511).

In coastal and estuarine environments the circumstance that air-temperature fluctuations are far more pronounced than water-temperature fluctuations will—at extreme temperatures—generally induce migratory movements from exposed areas (e.g. rock faces, mudflats, shallow waters) to areas with more stabilized thermal conditions (e.g. open sea or deep waters). Whether temperature gradients act as orientation cues under natural conditions is questionable. When *Convoluta roscoffensis* are placed in a trough filled with water, which is gradually heated at one end, the turbellarians tend to escape to the cooler part only at temperatures as high as 35° C, but many individuals die before they succeed in escaping from the heated end (GAMBLE and KEEBLE, 1903). Aggregation in areas of a particular temperature in special types of alternative chamber apparatus was more pronounced in the interstitial archiannelid *Protodrilus symbioticus* (GRAY, 1965), in the harpactoid *Nitocra spinipes* (GANNING and WULFF, 1966) and the cladoceran *Podon polyphemoides* (ACKEFORS and ROSEN, 1970).

In general, however, there are strong indications that temperature changes merely induce orientational behaviour to other cues such as gravity, water currents and light, which guide the invertebrates to more favourable conditions. *Littorina obtusata*, when placed on a vertical plane under water, usually move upward (negative geotaxis), but become positive geotactic when the temperature drops below 2° C (JANSSEN, 1960). WERNER (1956) reported mass emigration of *Arenicola marina* from tidal flats during severe cold. The lugworms apparently emerged from the tidal flat to be transported on the tide to deeper water once the temperature dropped below a critical value.

Carcinus maenas exhibits migrations up and down the intertidal zone, in which the majority of the larger individuals take part, and which appear to be controlled by seasonal temperature variations (EDWARDS, 1958; CROTHERS, 1968). These onshore and offshore movements have been studied extensively by NAYLOR (1962) and ATKINSON and PARSONS (1973) throughout the year. These authors sampled between the tide marks and related their findings to seasonal changes in spontaneous tidal locomotor rhythmicity. Their main conclusions may be summarized as follows: During the coldest winter months (January, February) crabs of more than 30 to 35 mm carapace width remain below the intertidal zone all the time and do not migrate onshore, not even at high tide. In the laboratory, such crabs do not show spontaneous tidal locomotor rhythmicity. Before the onset of spring (March), these crabs start moving up and down the intertidal zone with the tide, but still do not display endogenous rhythmicity; this suggests that their tidal migrations are controlled by exogenous factors. In late spring and summer, with rising temperatures, increasing numbers of crabs remain onshore at low tide, while an endogenous rhythmic pattern of locomotor activity (maximum activity with high tide and with hours of darkness) becomes apparent. Presumably, this rhythmicity enables *C. maenas*, which forages at high tide, to return to sheltered places before the ebb. With the onset of winter (November, December) a gradually increasing number of individuals lose their rhythmicity; they move offshore at low tide, at first returning onshore with high tide until, in the coldest months, they again remain offshore all the time. Migration, as well as onset of tidal rhythmicity, appear to be temperature controlled, the lower threshold being about 8° C. The juveniles (less than 30–35 mm carapace width) and the oldest crabs do not take part in these tidal and seasonal migrations. The former remain onshore throughout the year and display endogenous tidal rhythmicity during the warmer months; in winter they merely show circadian rhythmicity with nightly activities. The oldest crabs, on the other hand, remain offshore throughout the year and show no spontaneous tidal locomotor rhythmicity.

The tidal activity rhythm of *Carcinus maenas* is, apparently, entrained by a combination of tidal variables. Tidal temperature changes combined with immersion/emersion cycles and hydrostatic-pressure changes appear to act as synchronizers, being additive in effect (WILLIAMS and NAYLOR, 1969; NAYLOR and ATKINSON, 1972).

Onshore and offshore migrations on intertidal flats—in summer—have also been reported for the shrimp *Crangon crangon* (HARTSUYKER, 1966). Unlike *Carcinus maenas*, however, virtually the entire population leaves the tidal flats at low tide, except for a number of the smallest specimens, which have penetrated too far into the intertidal zone and which survive in stagnant pools left behind by the receding tide (BEUKEMA, personal communication). In winter, the shrimp remain in the subtidal areas and even show a marked seaward migration, followed by a return in spring. These seasonal migrations, extensively described by HAVINGA (1930) and LLOYD and YONGE (1947), are performed by both males and females, young as well as old, with differences of degree in their respective migratory patterns. For a review as well as for comparisons with migratory movements of other shrimp species consult ALLEN (1966).

According to HAVINGA (1930), the migratory movements of *Crangon crangon* may be initiated by the reversal of the temperature difference between inshore and offshore waters, since in late autumn as well as in spring the shrimp move from colder to relatively warmer water. For a possible interaction between temperature and salinity in shrimp migration consult p. 596. Temperature-dependent offshore migrations at the onset of cold waves have been reported for juvenile pink shrimp *Penaeus duorarum* (TABB and co-authors, 1962).

Temperature sensitivity in marine invertebrates appears to be mediated through responsiveness of the nervous tissue as, for instance, demonstrated in *Carcinus maenas* and *Maja squinado* (DORAI RAJ and MURRAY, 1962). No specific thermoreceptors are known so far (LAVERACK, 1968).

(4) Salinity

(a) General Aspects

Functional and structural responses of aquatic invertebrates to variations in salinity have been reviewed in Volume I: KINNE (1971). The responses of invertebrates to adverse salinities may be classified as (i) escape, (ii) reduction of contact, (iii) regulation, and (iv) adaptation (KINNE, 1964a, b, 1966). In this chapter, category (i), escape, which involves migratory movements to more suitable conditions, will be our main concern; category (ii), reduction of contact, comprises a number of responses which may reveal some additional sensory aspects. Orientational responses of invertebrates to salinity variations are largely restricted to coastal forms. We shall consider the intertidal residents and coastal migrators.

(b) Intertidal Residents

Intertidal residents are alternately submerged by sea water and exposed to air. During air exposure they face extreme temperatures in summer and winter, desiccation, sun irradiance, and rainfall.

A number of intertidal gastropods display differential responses to salinity. ARNOLD (1957, 1959) studied the behaviour of the limpet *Patella vulgata* which, at low tide, is exposed to air. When splashed with sea water, the limpet exhibits a positive response: it lifts the front edge of its shell, advances its head and extends the cephalic tentacles. Splashing with fresh water results in withdrawal of the head and clamping down of the shell (negative response). Different dilutions of sea water elicit graded responses, while an isotonic NaCl solution produces a reaction equivalent to that caused by sea water, apparently due to the concentration of chloride ions. Local stimulation revealed that mantle fringe and cephalic tentacles (the most exposed body parts) are responsible for salinity perception; foot and body wall appear to be insensitive.

Comparable results were obtained in the littorinid *Nodolittorina granularis* (OHSAWA and TSUKUDA, 1955). Salinity perception seems to be mediated through chemoreception rather than osmoreception, since solutions of non-electrolytes failed to elicit a response at any tonicity.

Remarkable observations were made by KRISTENSEN (1965) regarding the zonation of the intertidal Caribbean littorinids *Echininus nodulosus*, *Nodolittorina tuberculata* and *Tectarius muricatus*. *E. nodulosus* inhabits a zone within the reach of fine sea-water spray; *N. tuberculata* lives somewhat lower down and *T. muricatus* occurs higher up beyond the reach of the mist of spray. Under dry conditions none of the three snails leave their locations; but upon rainfall or when splashed with fresh water, they move about and browse. When sprayed with sea water in the form of fine mist, *N. tuberculata* and *E. nodulosus* browse, but *T. muricatus* move to an even higher point. When, however, sea water is splashed on them, *E. nodulosus* also move upward. On a coast exposed to heavy surf, *E. nodulosus* will be found 8 m above sea level, whereas on sheltered coasts it lives 0·5 m above the water.

The distribution of intertidal and semiterrestrial crustaceans is likewise determined by behavioural responses to salinity. The semiterrestrial crab *Pachygrapsus crassipes*, which spends approximately half its time in sea water, in the laboratory shows a clear preference for 100% sea water over 50%, 75%, 125% or 150% sea water (GROSS, 1957). Through this response the crab will avoid brackish or hypersaline areas even though it possesses a strong osmoregulatory capacity. BARNES (1967) investigated the effect of salinity upon five Australian grapsoid crabs exhibiting differential penetration into an estuarine system. Additional examples have been reviewed in Volume I: KINNE (1971, p. 925).

Escape responses are less obvious in highly potent osmoregulators. The harpactoid crustacean *Nitocra spinipes*, for example, inhabits Baltic Sea rock pools with salinities ranging from 3‰ to 35‰, and survives and reproduces in the laboratory well beyond this range (WULFF, 1972). In salinity-preference experiments, the harpactoid responds only to considerable salinity differences in the order of 9·5‰ to 18·5‰. When offered the choice between 11·5‰ and 7·5‰ S or 7·5‰ and 3·5‰ S (difference = 4‰) *N. spinipes* reveals no preference.

(c) Coastal Migrators

Coastal areas are characterized by tidal currents and augmented fluctuations of temperature and salinity. Salinity variations are primarily caused by tidal movements; the isohalines shift regularly in and out of the estuary. Salinity differences also result from different degrees of rainfall and river discharge according to seasons and wet and dry years. Since inshore and shallow water follow the changes of air temperature more closely than open waters, there is a parallel correlation between temperature and salinity in periods of cooling (late autumn and winter) and an inverse correlation in periods of warming (late spring and summer; POSTMA, 1954, p. 420).

Several species of penaeid shrimp exhibit extensive migratory movements in the course of their life cycle. The larval and postlarval stages move from offshore spawning sites to inshore nursery areas; here they remain until they return to offshore waters as juveniles or subadults. These migrations have been shown to be facilitated by selective use of the tidal currents as transporting media (p. 600). Arriving postlarvae of *Penaeus duorarum* (TABB and co-authors, 1962) and *P. aztecus* (ST. AMANT and co-authors, 1966) are predominantly found in samples taken during night flood tides, while the juveniles of *P. duorarum*, returning to the offshore waters, are taken on the night ebb tides. In laboratory experiments HUGHES (1969a) demonstrated that salinity decrease during ebb induces the pelagic postlarvae of *P. duorarum* to sink to the bottom where they withstand transport back to the sea. The juveniles, on the other hand, are positively rheotactic in a current of sea water; but they reverse the sign of rheotaxis or are passively transported towards the sea when the salinity decreases during ebb. According to HUGHES, offshore migrations would be facilitated by an increased freshwater runoff, whereas TABB and co-authors (1962) recorded large juvenile *P. duorarum* remaining in inshore waters when the salinity rose up to 30‰.

The shore crab *Carcinus maenas*, a characteristic inhabitant of shallow coastal and estuarine waters, is found in a wide range of salinities varying from 31‰ down to 10‰ or, occasionally, even lower (BROEKHUYSEN, 1936). BROEKHUYSEN, as well as CROTHERS (1969), believes that *C. maenas* is restricted to shallow coastal and inshore waters due to its preference for slightly reduced salinities (below 31‰) rather than by depth preferences. The salinities near the upper limit of occurrence appear to be the most favourable for egg development, especially when water temperatures are low (BROEKHUYSEN, 1936); apparently, this is in line with RASMUSSEN's (1959) observation that berried females tend to migrate to deep and more saline water until the larvae hatch. *Sacculina*-infested crabs—females as well as males—display the same behaviour in this respect. In the upper estuaries of the rivers Rhine, Meuse and Scheldt (Delta area, Netherlands), where the 10‰ S isohaline shifts seasonally with the larger or smaller discharges of the rivers, WOLFF and SANDEE (1971) observed corresponding migratory movements of *C. maenas*. Apart from these salinity-dependent migrations, *C. maenas* also exhibits temperature-controlled movements up and down the intertidal zone (p. 592).

BROEKHUYSEN's (1936) finding that egg development in the shore crab *Carcinus maenas* requires a minimum salinity of 20‰ at a temperature of 16° C as against a salinity of at least 26‰ at 8° C raised the question whether, in general, interaction between temperature and salinity is involved in seasonal migrations. In experiments initiated by CAUDRI (1937) and continued by BROEKEMA (1941), in which *Crangon crangon* were subjected to different combinations of temperature and salinity, indications were obtained that survival at low temperatures (about 4° C) is better in higher salinities (30‰–35‰), while survival at high temperatures (19°–22° C) is supported in lower salinities (25‰–30‰). In 1-year-old shrimp, which usually penetrate farther into the estuaries in summer, the optimal survival at high temperatures (about 20° C) was found to range as low as between 15‰ and 20‰ S. These results seem to bear out the hypothesis that at the onset of low winter temperatures the shrimp need higher salinities and move offshore. This view may find additional support in MEREDITH's (1952) observations in the Dee River estuary (near Liverpool, England), with high salinities throughout the year, that *C. crangon* does not leave the estuary under the influence of low temperatures. However, survival experiments by FLÜGEL (1960) with *C. crangon* from the Baltic Sea, and by HAEFNER (1969) with *C. septemspinosa* from the American west coast, revealed no such temperature–salinity interaction. Their results suggest that, at lower temperatures (5°–15° C for *C. crangon* and 10°–14° C for *C. septemspinosa*), the shrimp are able to tolerate a wider range of salinities than at higher temperatures. For further details on the combined effects of temperature and salinity on tolerance and on metabolism and activity consult WEBER and SPAARGAREN (1970), Volume I: KINNE (1971), ALDERDICE (1972). Although a general functional relationship between the osmoregulatory pattern of different estuarine crustaceans and their migratory behaviour is recognized, it is not known whether these physiological conditions play a role in migratory activities and spatial orientation.

(d) Responses to Changed Ion Ratios

Spatial orientation of aquatic invertebrates may also be affected by changes in the composition or ratio of inorganic solutes. Of particular importance seem to be changes in ion ratios. Unfortunately, the information available to date is exceedingly scanty.

Critical disturbances of ionic ratios may have detrimental consequences (Volume I, Chapter 4). Whether behavioural responses to such disturbances occur under natural conditions is not known. In laboratory experiments responses of invertebrates to a wide variety of acids, bases and salts have been recorded. KOHN (1961) has summarized the pertinent information available on gastropods. Apart from varying threshold values specific to different cations and anions, also qualitatively different effects have been found. In the littorinid *Nodolittorina granularis*—which, on being splashed with sea water, protrudes its head—salinity perception seems to be based on the detection of $NaCl + MgCl_2$, where Mg^{++} ions presumably act as the primary stimulus (OHSAWA and TSUKUDA, 1955). NH_4Cl and KCl were ineffective or even inhibitory when supplied in combination with $MgCl_2$ and NaCl; $CaCl_2$ caused a negative response (withdrawal into the shell). Likewise, the littoral isopod *Ligia baudiniana* can apparently distinguish isotonic solutions of $CaCl_2$ from NaCl when allowed to walk across filter papers soaked in the test solutions (BARNES, 1939, 1940). The holothurian *Caudina chilensis* exhibits contraction of its body wall at specific threshold values which vary for different cations (YAMANOUCHI, 1929a). Comparable responses to ionic ratios have been reported from numerous other aquatic invertebrates. The information available is, however, insufficient for critical assessment and does not allow conclusions regarding possible orientation mechanisms (see also Volume I, Chapter 4).

(5) Atmospheric Humidity (Desiccation)

Semiterrestrial amphipods such as sandhoppers are poorly adapted to low humidities. In laboratory experiments, survival times of *Talitrus saltator*, *Orchestia gammarella* and *Talorchestia deshayesii* range between 9 and 16 hrs at a relative humidity of 95%, decreasing to 1 to $1\frac{3}{4}$ hrs at 36% relative humidity (WILLIAMSON, 1951a). Remarkably, survival times greatly increase when the sandhoppers feed on wrack. The wrack (moist food) eaten is likely to meet the amphipod's water rather than energy requirements, since the faeces are rather dry. In an experimental humidity gradient all sandhopper species tested spent most of their time in moist air, orienting by means of kinesis. In very steep humidity gradients, the talitrids occasionally stop when moving into the dry air; they then move backward a little and turn—a process which WILLIAMSON (after FRAENKEL and GUNN, 1940) defined as 'klinokinesis'. A similar type of response shown by wireworms in steep humidity gradients has been interpreted as a directed reaction and therefore classified as 'klinotaxis' (LEES *in*: WILLIAMSON, 1951a, see also p. 562 and p. 618). Attempts to locate specialized humidity receptors in talitrids have not been successful. They are, therefore, thought to respond to differences in rates of evaporation.

Comparable investigations have been carried out with the isopods *Asellus aquaticus* and *Idotea baltica*; both occur in the Baltic Sea but the former inhabits also fresh water (LAGERSPETZ and LEHTONEN, 1961). While *I. baltica* did not show definite reactions to humidity, *Asellus aquaticus* exhibited responses similar to those observed in talitrids by WILLIAMSON (1951a). In subsequent experiments with aquatic amphipods LAGERSPETZ (1963) found that *Gammarus duebeni* and *G. oceanicus* are able to select the higher of two different air humidities. On the other hand, *Pontoporeia affinis*, which is never exposed to air, does not respond to differences in atmospheric humidity.

The terrestrial hermit crabs *Coenobita clypeatus*, which normally live in sheltered places in the daytime, likewise aggregate in areas of highest air humidity when placed in an experimental atmospheric humidity gradient (DE WILDE, 1973). Similar responses are known from other semiterrestrial crabs. They are able to select suitable humidities and to aid osmoregulation by specific behavioural patterns which have been reviewed in Volume I: KINNE (1971, p. 925, see also pp. 846–862).

(6) Water Movement

(a) General Aspects

Marine invertebrates cannot exist without water movement (Volume I, Chapter 5). In a sense, a marine invertebrate's basic environment can be differentiated into a fluid medium (the water) and a solid medium (the substrate). These two media are continually shifting their spatial relation to one another. While an invertebrate settled on the substrate perceives these shifts as water movements, a free-swimming specimen experiences water movement only if it has contact (visual, tactile) with the substrate: Apart from suggestions that fishes may orient to weak electric fields caused by water currents (Chapter 8.2), no evidence is available so far that aquatic animals are equipped with a mechanism by which they can detect their displacement by water currents when swimming freely as purely pelagic organisms.

Any discussion of the role of water movement in the life of marine invertebrates must take into account both benthic and planktonic forms, as well as intermediate cases in which benthic or semi-benthic animals selectively utilize water currents for transport.

(b) Intertidal and Benthic Invertebrates

A number of free-swimming invertebrates live close to the sea bottom and stay in certain places for some time. Schools of mysids, for instance, swimming among particular rocks or corals, would inevitably be swept away if they did not respond rheotactically. In these cases, however, it is not the current as such which is perceived, but the shift of the visual field, which the mysids compensate for by locomotory activity, comparable to optokinetic responses. Experiments with the lobster *Homarus americanus* (HADLEY, 1906), mysids (FRAENKEL and GUNN, 1961, p. 253) and *Daphnia longispina* (SIEBECK and FARWICK, 1971), in which rheotaxis is controlled by experimental shifts of the visual field, support this view.

Perception of Water Movement

Invertebrates which live in close contact with the substrate and in some way resist transport by water movement are subjected directly to the forces exerted by the current. Little work has been done so far on the mechanism of water-movement detection, but judging from the commonly reported current-oriented movements, such a mechanism must be of widespread occurrence in marine invertebrates. Discussing the positive rheotaxis displayed by the snail *Urosalpinx cinerea*, FEDERIGHI (1929) suggested that unequal tension on the parietal muscles produced by the pull of the shell—which tends to straighten in a water current—brings about orientation. In more recent work, comparable interpretations have been suggested (NEALE, 1965; DUCH, 1971). CROZIER and AREY (1919) found that the nudibranch *Chromodoris zebra*, which usually responds negative-rheotactically, is disoriented after removal of the rhinophores, while upon stimulation of the rhinophores with a localized current the nudibranch orients within 3 to 5 mins. BROCK (1930) demonstrated that outer and inner flagella of the antennules of the shore crab *Carcinus maenas* are sensitive to water movement. Probably, proprioception is involved (LAVERACK, 1964). However, according to BROCK, even after elimination of antennae and eyestalks, the crab responds—to a certain extent—to fairly strong currents, suggesting that a 'general body sensitivity' is responsible.

LUTHER and MAIER (1963) found that rheotactic orientation in the decapod crustaceans *Carcinus maenas*, *Clibanarius misanthropus* and *Crangon crangon* abruptly disappears upon antennule removal; but in the American freshwater crayfish *Cambarus affinis* rheotaxis persists after such an operation, suggesting that its water-movement receptors are not restricted to the antennules. *Eupagurus bernhardus*, *Palaemon serratus* and *P. xiphias* did not respond rheotactically in the experimental current channel.

In the lobster *Homarus vulgaris*, LAVERACK (1962a) described cuticular sense organs, widely distributed over the anterior part of the body, the so-called 'hair-peg organs', which respond to deflections caused by water currents as small as 0·30 cm sec^{-1}. Unlike the rapidly adapting hair-fan organs, mentioned on p. 652 as vibration receptors, the hair-peg organs adapt slowly, thus facilitating continuous monitoring of the water current. Hair-peg organs likewise have greater freedom of movement in one plane than in another, and the large number of such units, variously oriented, may make possible—through central integration—detection of the current's direction.

The sea-star *Asterias rubens* can perceive a minimum current velocity in the order of 0·15 cm sec^{-1} (CASTILLA and CRISP, 1973). Calculations of the forces acting on the sea-star justify the assumption that water-movement receptors are involved rather than proprioceptors detecting the lateral pull of the individual as a whole—as demonstrated in geotaxis by KALMUS (1929; see p. 646).

Functional Responses

A great variety of sedentary and semi-sedentary invertebrates depend on water currents for food supply (Volume I: RIEDL, 1971). The orientation of growth forms or food collecting appendages is frequently related to prevailing water movements. In addition to the review by RIEDL (1971), the following pertinent papers may be consulted: CRISP and STUBBINGS (1957) and BOWERS (1968) on orientation of barnacles; ZIEGELMEIER (1969) on tube construction by the polychaete *Lanice conchilega*; EMIG and BECHERINI (1970) on lophophore orientation in the phoronid *Phoronis psammophila*; REES (1972) on growth forms of the octocoral *Telesto riisei*; VELIMIROV (1973) on orientation of the sea fan *Eunicella cavolinii;* VELIMIROV (1974) on the oriented growth of *Millepora dichotoma.* In his study on orientation and growth forms of fan-shaped gorgonians (*Muricea californica*, *M. fruticosa*, *Adelogorgia phyllosclera* and *Eugorgia rubens*), GRIGG (1972) considered fan orientation—at right angles to the dominant current direction—a useful indicator of the prevailing direction of local water movements.

To mobile benthic invertebrates water currents are important for several reasons, not the least because they provide information on distant ecological conditions.

Invertebrates living in tidal areas may derive information over several kilometres—reaching them with alternating tides from two opposite directions. Responses to temperature, salinity and chemical stimuli are, therefore, commonly associated with orientation to water movement.

The most readily observable behaviour is upstream movement (positive rheotaxis) in the presence of attractive dissolved substances. Positive rheotaxis in feeding behaviour has been reported, for instance, in the gastropods *Nassarius obsoletus* (COPELAND, 1918, CRISP, 1969), *N. fossatus* (MACGINITIE and MACGINITIE, 1968, p. 368) and *Buccinum undatum* (BROCK, 1933); in the nudibranchs *Aeolidia papillosa* and *Trinchesia aurantia* (VAN HAAFTEN and VERWEY, 1960); in the decapod *Carcinus maenas* (LUTHER, 1930; LUTHER and MAIER, 1963); and in the echinoderm *Asterias rubens* (CASTILLA and CRISP, 1970). Chemical stimuli associated with a preferred substrate elicit positive rheotaxis in the mud snail *N. obsoletus*. When exposed to flowing water which has been in contact with muddy deposits the snails move upstream. This effect can be cancelled by filtering the water through charcoal or by boiling the mud (CRISP, 1969). Symbiotic invertebrates may exhibit host-oriented behaviour, based on the perception of specific substances, presumably involving positive rheotaxis. An example has been provided by ACHE and DAVENPORT (1972) in a study on host recognition by the shrimp *Betaeus harfordi* which lives in symbiosis with abalones of the genus *Haliotes*.

There are few examples of active downstream movements (negative rheotaxis). LUTHER and MAIER (1963) demonstrated that frightened *Carcinus maenas* and *Clibanarius misanthropus* escape downstream; removal of their antennules, which act as current detectors, causes disorientation. CRISP (1969) found negative rheotaxis in *Nassarius obsoletus* in clean sea water (apparently deprived of ecologically significant substances); the upstreaming response to olfactory stimuli can be abolished when unfavourable stimuli such as hypo- and hypersalinity are present simultaneously. CASTILLA and CRISP (1970, 1973) found reversal of the normal positive rheotactic response in *Asterias rubens* to be normally associated with unfavourable conditions. In experiments, the sea-stars moved downstream in the presence of their predator *Solaster papposus*, of damaged prey, or of lowered salinity, oxygen tension, and pH.

In general, it may be concluded that the most effective response of an invertebrate to a chemical stimulus is either positive or negative current orientation. For more detailed information on the mechanisms involved in orientation to chemical stimuli consult p. 618.

While positive rheotaxis may guide an invertebrate to favourable conditions, and negative rheotaxis is involved in avoidance reactions, the situation is entirely different when large-scale currents and seasonal migrations (encountered in extensive tidal areas) are considered. The tidal streams in these areas are commonly so strong that effective upstream movements can hardly be accomplished. Positive rheotaxis then takes the form of swimming to resist transport, often changing to clinging to the bottom or burrowing; downstream movements, on the other hand, often give way to passive drifting.

These processes have been exemplified by TABB and co-authors (1962) and HUGHES (1969a, b, c, 1972): The pink shrimp *Penaeus duorarum* hatch in the open sea and as postlarvae (approximately 1 cm long) move into estuarine areas (i.e. the

Everglades in Florida, USA). After a stay of 4 to 7 months in inshore nursery areas the juveniles (6–10 cm long) again move out into deeper waters where they will eventually spawn. Experimental evidence has been obtained that the postlarvae move inshore on the flood and respond to a decrease in salinity during ebb by dropping to the substrate; this prevents them from being transported back to the sea. When the salinity increases again during flood they swim and are transported further inshore. The juveniles, on the other hand, are positive rheotactic in sea water (flood tide), but when the salinity decreases (ebb tide) they swim downstream or let themselves be passively transported. In addition to external stimuli, an endogenous rhythm may control the tide-associated movements, although in HUGHES' experiments (1972) proper phasing with tidal cycles was not very clear. Undoubtedly, endogenous tidal and lunar rhythms (Chapter 9) will be involved in many other cases of tidal migration as, for example, in the swimming rhythm of the intertidal isopod *Eurydice pulchra* (FISH and FISH, 1972).

Selective use of tidal currents by marine invertebrates was already recognized by PETERS and PANNING (1933). They suggested that megalopa of the Chinese crab *Eriocheir sinensis* move inshore on the flood and stay on the bottom during ebb tide to avoid being carried back towards the sea. When adult *E. sinensis* return down the rivers to their spawning areas in the sea and encounter the estuary again, they supposedly burrow during flood and continue their journey on the ebb tide (PETERS, 1933).

A similar mechanism has been postulated by VERWEY (1949b, 1958, 1960, 1966) for estuarine invertebrates such as the shrimp *Crangon crangon* and the swimming crab *Macropipus holsatus*. The extent to which *M. holsatus* penetrates into brackish areas appears to be controlled by decreasing salinity. It has been demonstrated experimentally that when during ebb the salinity drops too far, the crabs begin to swim and thus are automatically carried on the ebb tide towards the sea (VENEMA and CREUTZBERG, 1973). These responses permit avoidance of adverse salinity conditions as soon as they occur. Comparable reactions have been observed in semi-sedentary invertebrates such as *Arenicola marina*: WERNER (1956) reported mass emigration from tidal flats during severe cold. The lug worms apparently emerged from the flats to be transported to deeper water when the temperature dropped below a critical value.

Emigration from Waddensea flats has recently been discovered by BEUKEMA (1973) in the bivalve *Macoma balthica*. Spatfall in summer concentrates in the highest, muddiest and most sheltered parts of the flats. In the ensuing winter and early spring, however, the bivalves (4–8 mm long) emerge from the substrate and are transported in great numbers on the ebb current towards the sea. In spring a secondary spatfall occurs on the more exposed sandy tidal flats and subtidal areas in the North Sea where they reach their final habitat.

Transport by tides towards the highest parts of mud flats has also been reported for the small prosobranch *Peringia* (= *Hydrobia*) *ulvae* (NEWELL, 1962). When these snails become submerged by the incoming tide, they launch themselves afloat upside down on the surface film of the water. They are then swept shoreward and, later, offshore again by the ebb; finally, they are redeposited on the mud. In an estuary, floating *H. ulvae* have also been observed by ANDERSON (1971). He considered whether the snails, floating on the tides, may drift either too far into the estuary or to the open sea. Laboratory experiments, indicating that the snails do not float when the salinity decreases below a certain value (see also NEWELL, 1964), led ANDERSON to suggest that their distribution is limited towards the sea as well as upstream by a salinity-controlled floating responsiveness. In the interstitial archiannelid *Trilobodrilus heideri*, loss of positive rheotaxis in lowered salinities has been suggested as the mechanism which keeps the worms within a restricted beach zone (BOADEN, 1963).

Selective transport of invertebrates by the uprush or backwash on surf-swept beaches, effecting a proper zonation, has been found to be controlled by pressure changes (amphipods, p. 606) or by vibrations due to breakers (bivalves, p. 650).

(c) Planktonic Invertebrates

Oceanic plankton organisms which do not perform vertical migration will be transported along in the one water mass they happen to be in (HARDY, 1935). However, their counterparts which conduct vertical movements undergo horizontal displacements differing in direction and speed, dependent on the water layers they inhabit at different times of the day (see also HARDY, 1956).

Vertical migration has significant ecological consequences in estuaries with respect to the dispersal of planktonic larvae of the benthic fauna. In his extensive and thorough study on the occurrence of barnacles in an estuary, BOUSFIELD (1955) stressed the precarious existence of estuarine bottom invertebrates with their planktonic larval stages (lasting from 1 to 5 weeks) being rapidly dispersed by tidal currents resulting in a residual flow towards the sea. Thus in the Miramichi estuary (New Brunswick, Canada), the tidal exchange of water masses over a period of 18 days (the estimated duration of the larval stage of *Balanus improvisus*) would deplete the population below the level necessary to maintain the estuarine adult population if the larvae displayed a uniform vertical distribution throughout the period. However, BOUSFIELD estimated the actual retention of *B. improvisus* larvae at 10%; this is sufficient to maintain the observed estuarine population. The mechanism by which the larvae are retained is in the main attributed to a changing vertical distribution of the larvae at their successive stages and the net circulation of the water in a stratified estuary, superimposed on the tidal movements. The residual drift transports the early larval stages (found near the surface) to the mouth of the estuary, whereas the later stages swimming near the bottom are carried back to, or even beyond, the original spawning sites. This mechanism is presumably re-inforced by the response to tidal currents of the cyprids, which swim higher during flood than during ebb.

A comparable retention mechanism in the two-layered circulation system of the Chesapeake Bay has been reported as—to some extent—responsible for retaining populations of the marine cladoceran *Podon polyphemoides* within the estuary (BOSCH and TAYLOR, 1973). Through diurnal vertical migration the cladocerans are alternately transported seaward and landward by the two opposing residual flows.

There is an extensive literature on the horizontal transport associated with the vertical migration of larvae of bivalves and barnacles in estuarine areas. For references and discussions consult KORRINGA (1941, 1952), VERWEY (1966), CARRIKER (1967), WOOD and HARGIS (1971), and DE WOLF (1973). Apart from the irregular, patchy occurrence of barnacle larvae (DE WOLF, 1973), a variety of environmental factors such as light, salinity, water movement, turbidity, and pressure are supposed to control the vertical distribution during the tidal cycles; most of the assumptions, however, are rather speculative. The question has even been raised whether the process is controlled by selective swimming through particular responses to environmental factors or whether the purely mechanical forces of strong currents and turbulences at the mid tides keep the invertebrates in suspension. WOOD and HARGIS (1971) compared transport rates of the larvae of the bivalve *Crassostrea virginica* during the tides with transport rates of coal particles; the particles were present in nearly all their samples and had a density almost identical to that of the larvae. WOOD and HARGIS found a different temporal pattern in the concentration maxima, and concluded that selective swimming must be involved. DE WOLF (1973), on the other hand, believes that the retention of barnacle larvae in estuaries can be explained purely mechanically along the same lines as demonstrated for suspended material by POSTMA (1961). In his proposed model the larvae are swirled up by strong currents and turbulences during both tides, followed by sinking during slack tide. The rate of sinking increases with larval age, resulting in a vertical distribution in which early stages are found higher than cyprids. The residual drift of the water near the bottom presumably promotes an inward transport of the larvae approaching settlement.

(7) Pressure

(a) General Aspects

Changes in hydrostatic pressure may significantly affect life in oceans and coastal waters (Volume I, Chapter 8). This environmental factor shares with gravity its permanent presence and constancy, but acts in all directions with the same intensity. It changes linearly with water depth, thereby providing reliable information on the distance between animal and water surface.

Not so long ago, pressure sensitivity was supposed to occur only in animals with gas-filled body spaces such as fishes (swim bladders) and some aquatic insects. Pressure sensitivity in marine invertebrates without gas-filled organs has been discovered surprisingly late. Field experiments with *Calanus finmarchicus*, lowered in vertical cylinders to various sea depths, demonstrated that the copepods increasingly tended to move upward with depth but irrespective of illumination intensity (HARDY and PATON, 1947). The experimenters postulated a 'sense of depth' supposedly based on pressure sensitivity. A few years later, laboratory experiments demonstrated definitely that decapod larvae (zoea and megalopa stages of *Portunus* sp. and *Carcinus* sp.) respond to increases in pressure of 500 to 2000 mb (equivalent to depths of 5 to 20 m) with upward movements (HARDY and BAINBRIDGE, 1951). Subsequent work proved that pressure sensitivity is a common and widespread feature in plankters (KNIGHT-JONES and QASIM, 1955; MOORE and CORWIN, 1956; RICE, 1961, 1962, 1964; BAYNE, 1963; SINGARAJAH, 1966;

LINCOLN, 1971) as well as in intertidal and benthic invertebrates (ENRIGHT, 1961b, 1962; MOULTON, 1962; MORGAN and co-authors, 1964; MORGAN, 1965, 1969a; see also Volume I: FLÜGEL, 1972).

In these two invertebrate groups, pressure changes are perceived under two basically different ecological conditions. On the one hand, free-swimming invertebrates can—under natural conditions—only be exposed to pressure changes as the result of their own, either active or passive, vertical movements. Intertidal and benthic invertebrates, on the other hand, are exposed to pressure changes by tides and wave action. The orientational aspects involved in these two cases are briefly reviewed below. Detailed reviews on the responses to pressure by marine invertebrates and the possible mechanisms of pressure perception have been presented by KNIGHT-JONES and MORGAN (1966), FLÜGEL (1972), KINNE (1972) and MORGAN (1972).

(b) Free-swimming Invertebrates

Hydrostatic pressure manifests itself as a vertical intensity gradient of a marked constancy. Hence plankters may, at least theoretically, derive solely pressure-based orientation from non-directional random locomotory movements, i.e. through a mechanism which may be called **barokinesis**. This possibility, however, which VERWEY (1966) did not wish to rule out, hardly finds support in the literature. Although increased locomotory activity is commonly observed with experimental pressure increase, and passive sinking with pressure reduction ('high barokinesis'), or the reverse ('low barokinesis'), as for instance in *Pleurobrachia pileus* which is usually buoyant when inactive (KNIGHT-JONES and QASIM, 1955), responses to pressure changes are in almost all cases linked to gravity or light-oriented movements. In other words, pressure changes actually induce geotaxis or phototaxis.

These responses have been studied by RICE (1961, 1962, 1964). Mysids, for instance, move geotactically upward (in vertical light above or below) when pressure increases; but in horizontal light they move horizontally toward the light source. After statocyst removal, orientation under pressure changes is almost purely phototactic (RICE, 1961). Pressure changes trigger purely phototactic responses in the copepod *Calanus finmarchicus*; in illumination from below it swims downward when pressure is increased, thus actually moving towards still higher pressures (RICE, 1962).

Of a total of 53 planktonic marine invertebrates—coelenterates, ctenophores, larvae of cephalopods and crustaceans—41 respond to pressure changes (RICE, 1964). Three main types of responses can be distinguished: Type I: Orientation entirely with respect to gravity (ephyrae of *Aurelia aurita*, ctenophores, megalopae of *Carcinus maenas* and larvae of *Loligo forbesi*). Type II: Orientation to gravity and (secondarily) light (mysids). Type III: Orientation entirely to light. In this last type pressure decrease leads to (i) passive sinking (e.g. zoea larvae), (ii) active photonegative swimming (e.g. nauplii of *Balanus* species), and (iii) either sinking or photonegative orientation (copepods). The ecological significance of these pressure-change induced movements is **compensatory depth regulation**. Such regulation may prevent plankters from sinking too deep and keep them within a certain depth range.

The threshold values, which in some cases are as low as 10 mb (megalopae of *Carcinus maenas*, and comparable stage of *Galathea* sp.; KNIGHT-JONES and QASIM, 1955) have been listed by KNIGHT-JONES and MORGAN (1966) and FLÜGEL (1972) for different taxonomic groups. BAYLOR and SMITH (1957) recorded compensating vertical movements of planktonic animals equivalent to the apparent displacement by a pressure change of 15 mb (15 cm depth) while, on the other hand, KNIGHT-JONES and QASIM (1967) found that the parasitic planktonic copepod *Caligus rapax* and megalopae of *Carcinus maenas* subjected to pressure increases of 700 to 800 mb (7–8 m) in a 6-m long glass tube compensate to a far less extent. Similar differences of behaviour can also be observed between successive planktonic larval stages of some decapod crustaceans. Depth-regulatory responsiveness to pressure changes is most obvious in young zoea stages but weakens with age. The last zoea stage of the xanthid crab *Leptodius floridanus* hardly responds to pressure changes in the order of 1 atm (SULKIN, 1973). In *Homarus gammarus* the megalopa stage is still responsive but this is no longer the case with the first juvenile stage (ENNIS, 1973).

Since under natural conditions pressure changes will only be experienced by invertebrates when they move vertically, they are not likely to initiate vertical migration. Diurnal changes in submarine illumination are undoubtedly the main factor releasing diurnal vertical migrations. Pressure changes during such migrations are presumably largely disregarded; but they may limit vertical movements (MORGAN, 1972). Presumably rapid accommodation to great increases or decreases of pressure plays a part in vertical migrations, allowing the invertebrates to occupy widely different depth levels in response to changes in daylight (KNIGHT-JONES and MORGAN, 1966; KNIGHT-JONES and QASIM, 1967; LINCOLN, 1970, 1971). The experimental evidence presently available is insufficient for an adequate understanding of the compensatory depth regulation mechanism.

(c) Intertidal and Benthic Invertebrates

The conditions under which intertidal and benthic invertebrates live are basically different from those obtaining for free-swimming organisms. Intertidal and benthic species are subjected to pressure cycles of tidal amplitude and frequency as well as to rapid pressure changes associated with wave action.

The tropical intertidal gastropod *Cerithium* sp. clusters at low tide and disperses upon submersion at high tide—a response which has been considered an adaptation to desiccation (MOULTON, 1962). Field observations and experiments in which a cluster of *Cerithium* sp., placed in a shallow pan, was lowered into a pool of sea water indicate that these snails respond to increase in hydrostatic pressure by the gradual breaking up of the cluster for feeding excursions; pressure decrease induces re-aggregation, presumably to withstand desiccation.

Inhabitants of tidal flats, such as *Nereis diversicolor* and *Hydrobia ulvae*, respond to experimental fluctuations of the water level by vertical movements in the sediment or by leaving their burrows (VADER, 1964). It is not known whether pressure sensitivity is involved.

In recent years attention has increasingly been devoted to pressure-related behaviour of invertebrates that spend most of their time close to the sea bottom or burrow in the sediment, but which periodically emerge for excursions in the overlying water ('hyperbenthic exploration and navigation'; KNIGHT-JONES and MORGAN, 1966). According to RICE (1961), *Schistomysis spiritus* respond to stepwise pressure changes at an overall rate similar to tidal changes; RICE pointed out that by day (many are planktonic at night) the mysids spend most of their time close to the bottom and presumably respond to the rise and fall of the tides. Referring to evidence produced by earlier workers that the mysids perform shoreward migrations with the incoming tide, he suggested that both pressure and irradiance intensity may control activity and distribution of mysids.

It should be borne in mind that burrowing intertidal invertebrates, on leaving the sediment, are usually subjected to horizontal transport by tidal currents or by waves up and down surf-swept beaches. Since these horizontal water movements are associated with hydrostatic-pressure changes, the ecological significance of proper swimming-activity timing controlled by pressure sensitivity is evident. Striking results have been obtained by ENRIGHT (1961b, 1962), who studied responses to slow and rapid pressure changes in the intertidal beach amphipod *Synchelidium* n.sp. Sharp activity bursts, lasting a few seconds, occurred as the result of either increase or decrease in pressure, the response to increased pressure being more clearly marked. The response threshold lies between 5 and 15 mb with rapid changes, and between 25 and 50 mb with slow pressure increases (2.8 mb sec^{-1}). The activity consists of fast scrambling and occasionally of upward swimming over a distance of only 2 to 4 cm, regardless of the extent of the pressure increase. This indicates that the responses involve no depth regulation. Activity bursts last 5 to 10 secs during flood and 15 to 25 secs during ebb; they vary with the degree of pressure change and the phase of tide. According to ENRIGHT (1962), the brief response during rising tide probably results in landward transport by the advancing wave front in the uprush zone of the beach; the amphipods burrow at about the peak of uprush. The prolonged duration of activity during falling tide will—after the uprush—allow the amphipods to follow the backwash and to re-burrow at a lower level; in this way they avoid becoming stranded during the receding tide (see also Chapter 9).

In the pycnogonid *Nymphon gracile* and the amphipod *Caprella acanthifera* RICE (1964) found a response opposite in sense to that usually associated with depth compensation; both species are active and swim upward with rapid pressure decrease. Apart from reactions to rapid changes, *N. gracile* also responds to cyclical pressure changes of approximately tidal range (8 m) and tidal frequency by swimming during artificial ebb (MORGAN and co-authors, 1964). Swimming activity alternates with visits to the bottom, apparently to monitor and analyse (by comparison with a time sense) the extreme slow pressure changes encountered (KNIGHT-JONES and MORGAN, 1966). This mechanism, seemingly not controlled by an endogenous rhythm, would promote seaward transport on the ebb tide.

A similar ebb-transport response to pressure changes of tidal amplitude and frequency occurs in intertidal *Corophium volutator*, opposite in sense to depth compensation, whereas *C. volutator* collected from non-tidal pools show responses consistent with the depth-regulating mechanism (MORGAN, 1965). According to field observations, more individuals swim during the ebb tide than during flood tide.

Additional attempts have been made in recent years to secure experimental evidence in support of pressure-change induced activities which subject invertebrates to properly timed horizontal tidal transport or wave transport. The response of *Macropipus holsatus* to rapid pressure changes (50 mb) within the range of tidal pressure changes led MORGAN (1967) to suppose that this swimming crab may be able to differentiate between ebb and flood tide during its tidal migrations (see also p. 601). The responses of the polychaete *Nephtys incisa* to changes in pressure (MORGAN, 1969a) are reminiscent of the responses of the beach amphipod *Synchelidium* n.sp. described by ENRIGHT (1962); but the ecological significance is difficult to evaluate since there is little information available on the behaviour of *N. incisa* under natural conditions.

Several studies of pressure sensitivity in intertidal invertebrates like the amphipod *Synchelidium* n.sp. (ENRIGHT, 1963), the shore crab *Carcinus maenas* (WILLIAMS and NAYLOR, 1969) and the isopod *Eurydice pulchra* (JONES and NAYLOR, 1970; FISH and FISH, 1972) deal with endogenous rhythms in which pressure fluctuations seem to operate as synchronizers. For details consult Chapter 9. In general, it may be postulated that hydrostatic pressure as such does not provide orientation cues for intertidal and benthic invertebrates; but pressure is apparently important in triggering mechanisms controlling adequate transport by tidal currents and wave action.

Mechanisms of pressure sensitivity in invertebrates without gas-filled organs are still obscure and exceed the scope of the present chapter. The interested reader is referred to DIGBY (1961, 1967), ENRIGHT (1962), KNIGHT-JONES and MORGAN (1966), MORGAN (1969b, 1972), SOMMER (1972) and Volume I, Chapter 8.

(8) Dissolved Gases

Orientation of aquatic invertebrates to changes in, or gradients of, dissolved gases has received little attention. While a number of papers indicate the ability of various invertebrates to perceive critical levels in oxygen and carbon dioxide concentration, the mechanisms of perception and directional evaluation are largely unknown. The same holds for hydrogen sulphide and other natural, as well as pollution-induced gases. For general functional and structural responses of marine organisms to dissolved gases consult Volume I, Chapter 9.

The ability of some marine invertebrates to avoid anoxic environments has been studied by means of preference experiments. *Gammarus oceanicus* actively avoids de-oxygenated water and spends more time on the aerated side of the experimental apparatus (COOK and BOYD, 1965). GAMBLE (1971) found a significant preference for oxygenated water in *Corophium arenarium*, whereas *C. volutator* appeared to be indifferent. This different behaviour may be correlated to the different oxygen regimes in the habitats. *C. arenarium* occupies areas with higher oxygen levels (see also p. 612). *Gammarus oceanicus* and *C. arenarium* exhibited orthokinesis in the dissolved-oxygen gradients offered. The investigators suggest that the responses were mediated through a chemoreceptor or an oxygen-receptor organ.

The ostracod *Heterocypris salinus* inhabits Baltic rockpools, which are subject to extreme oxygen fluctuations. According to GANNING (1967), they survive better in hypo-oxygenated than in hyperoxygenated or 100% saturated waters. However, the ostracods did not reveal a particular preference when offered a choice between hypo- and hyper-saturated water.

Avoidance of lowered oxygen tension (below $4{\cdot}18$ ml O_2 l^{-1}) by means of negative rheotaxis has been reported for the sea-star *Asterias rubens* (CASTILLA and CRISP, 1973). The interstitial archiannelid *Protodrilus symbioticus* was found to move to interstitial water with the highest oxygen tension, which under natural conditions will keep the worm at the sand surface (GRAY, 1966a). High temperatures, dry sand, and strong irradiance, however, force *P. symbioticus* to move deeper into the sand. Under conditions of hypoxia, the burrowing shrimps *Callianassa californiensis* and *C. affinis* exhibit pronounced ventilative activity of their pleopods; FARLEY and CASE (1968) suggested that these shrimps may be useful objects for studying oxygen-sensing mechanisms. PAGE (1973) identified the external sites of oxygen sensitivity in the horseshoe crab *Limulus polyphemus*.

(9) Organic Substances

(a) General Aspects

The ecological significance of organic substances in oceans and coastal waters has been reviewed in Volume I, Chapter 10. General information on chemoreception in marine invertebrates, including structural and physiological aspects of the chemoreceptors, has been presented by BARBER (1961) for crustaceans, KOHN (1961) for gastropods, CHARLES (1966) for gastropods and bivalves and LAVERACK (1968) for marine invertebrates in general. LAVERACK's review provides good evidence that the location, structure and physiology of the widely different chemoreceptors found in various marine invertebrates constitute a vast field of study about which increasing information has become available in recent years.

A distinction between taste or gustation and smell or olfaction is not easy to substantiate where chemoreceptors of marine invertebrates are involved. Although there are no absolute criteria, a distinction is usually made on the basis of receptor sensitivity. In general, two kinds of chemoreceptors are distinguished (KOHN, 1961; LAVERACK, 1968): (i) distance chemoreceptors with a low threshold (p. 618), (ii) contact chemoreceptors with a high threshold (p. 622).

(b) Behavioural Responses

A great variety of behavioural activities—such as food detection, sexual relationships, avoidance of enemies, spatial relations in symbiosis and parasitism, substrate selection and gregariousness—are mediated through chemoreception, almost invariably involving organic substances.

Food Detection

Scavengers, predatory carnivores and herbivores respond to specific organic substances associated with their habitual food. Carrion-eating snails like *Nassarius obsoletus* move upstream in a current which has passed over dead fish (COPELAND, 1918). The predatory oyster-drill *Urosalpinx cinerea*, on the other hand, is more responsive to living than to freshly killed oysters (FEDERIGHI, 1935). Strong indications that metabolic products secreted by the oysters mediate the predator's choice have been found by BLAKE (1960). For an extensive study of prey selection by *U. cinerea* consult WOOD (1968). Predatory sea-stars *Asterias rubens* exhibit positive responses to living *Mytilus edulis* in a *Y*-maze choice apparatus; but they avoid organic substances associated with carrion such as homogenates of their prey, solutions of bacteriological peptone and a number of selected amino-acid combinations (CASTILLA, 1972b). The responses of *A. rubens* to living *M. edulis* appeared to be fairly selective, since the sea-stars used in the experiments did not move upstream towards spat of the oyster *Ostrea edulis* unless they had been conditioned to oysters for about a month (CASTILLA, 1972a).

Such species-specific selectivity in food preference has also been demonstrated in the nudibranch *Aeolidia papillosa*, which feeds on the sea anemones *Metridium senile* and *Actinia equina*, and in the nudibranch *Cratena aurantia*, which lives on the hydroids *Tubularia larynx* and *T. indivisa*. The slugs select flowing water that had been in contact with their favourite prey. They are not responsive to each other's habitual prey nor (or to a lesser extent) to other sea anemones or hydroids tested (STEHOUWER, 1952; BRAAMS and GEELEN, 1953). Comparable results have been obtained by COOK (1962) in a study on food detection in two opisthobranchs, *Rostanga pulchra* and *Archidoris montereyensis*, each of which feeds on a different sponge.

Food selectivity has also been documented in herbivores that feed on specific algae, for instance, in *Aplysia juliana*, which responded to water to which fresh (not decaying) *Ulva lactuca* had been added (FRINGS and FRINGS, 1965) and in *Littorina obtusata*, which showed different levels of response to different species of *Fucus* and *Ascophyllum*. In the latter case, however, it could not be definitely established whether the selective responses were based on the quality or the quantity of the emanating substances (VAN DONGEN, 1956; BAKKER, 1959).

In feeding responses contact chemoreception also is involved, especially in cases where this form of chemoreception merely acts as a 'confirmatory' sense in invertebrates that predominantly use other means (e.g. visual stimuli or mechanical disturbances) for detecting and capturing food (LAVERACK, 1968; Chapter 3).

Sexual Relationships

The degree of species-specificity in regard to chemically mediated responses will undoubtedly be the most pronounced in sexual relationships. Responsiveness to organic substances acting as sexual chemical stimuli is ecologically significant for (i) synchronizing gamete release, e.g. in sea-stars (CHAET, 1966), and (ii) attraction of sexual partners when copulation is involved.

Substances effecting sexual attraction have been reported for the hermaphroditic nudibranch *Chromodoris zebra* (CROZIER and AREY, 1919) and the slipper limpets *Crepidula nivea* and *C. williamsi* (COE, 1953). In the latter case they control settlement of sexless juveniles on adult females, upon which they develop into functional males. In these two closely related species the juveniles are attracted only to the adult females of their own species. In the gastropod *Fasciolaria tulipa*, copulation, as well as intraspecific predation (cannibalism) and escape responses, may be elicited by the odour of conspecifics. Apparently, the intensity of the chemical stimulus—which depends on the size of the stimulating snail—determines whether the responding snail will attack (or copulate when meeting a sexual partner) or escape (SNYDER and SNYDER, 1971). For the possible occurrence of (sex?) attracting substances in *Littorina littorea* see DINTER and MANOS (1972).

In recent years sex attractants (pheromones) have also been demonstrated in decapod crustaceans such as *Portunus sanguinolentus* (RYAN, 1966), *Homarus americanus* (McLEESE, 1970; ATEMA and ENGSTROM, 1971) and *Pachygrapsus crassipes*, *Cancer antennarius* and *C. anthonyi* (KITTREDGE and co-authors, 1971). The occurrence of pheromones appears to be associated with the moulting processes in the females. The moulting hormone (crustecdysone) of female *P. crassipes* releases pre-copulatory behaviour in males of the same species, at higher thresholds also in males of *C. antennarius* and *C. anthonyi*. Additional information on chemically mediated social communication in the lobster *Homarus americanus* is to be found in McLEESE (1973a).

Evidence for the occurrence of sex pheromones in planktonic copepods *Eurytemora affinis*, *E. herdmani* and *Pseudodiaptomus coronatus* has been presented by KATONA (1973).

Avoidance of Enemies

Chemoreception is also involved in escape reactions from predatory enemies. When sea-stars *Pisaster brevispinus*, which feed on sand dollars *Dendraster excentricus*, are placed in a sand bed occupied by its prey, the latter—within a radius of at least 60 cm—immediately burrow into the sand (MACGINITIE and MACGINITIE, 1968, p. 226). Apparently, the escape response is induced by a substance emanating from the sea-star, since burrowing occurs predominantly downstream (TINBERGEN, 1969, p. 163). *Asterias rubens*, which usually moves upstream, reverses its rheotactic sign in the presence of its predator *Solaster papposus* (CASTILLA and CRISP, 1970).

Most of the information available on the importance of chemical stimuli for spatial relationships between predator and prey pertains to sea-star–mollusc interactions. Many cases of violent escapes by gastropods and bivalves, when touched by a sea-star, have been documented. They are not based on the sucking effect of the tube feet, as suggested by WEBER (1924), but rather on contact chemoreception, as demonstrated by HOFFMANN (1930) in *Nassa mutabilis* and by BULLOCK (1953) in various gastropods brought into contact with different species of asteroids. Although actual contact between the tube feet and gastropod is usually necessary to release an escape reaction, responses have also been observed when the sea-star was still at some distance (a few mm up to some cm). Mechanical stimulation with a glass rod is effective only if the rod has previously been rubbed against a sea-star.

There exists a considerable body of literature on these avoidance reactions, extensively reviewed by KOHN (1961), FEDER and CHRISTENSEN (1966) and ANSELL (1969). In recent studies, MACKIE and co-authors (1968) and MACKIE (1970) identified the substances operative in extracts from the sea-stars *Asterias rubens* and *Marthasterias glacialis*—which in very low concentrations induce escape reactions in the gastropod *Buccinum undatum*—as steroid glycosides with surface-active properties. Similar responses have been demonstrated when synthetic non-ionic surface-active agents (detergents!) were applied in equally low concentrations. For additional information consult MACKIE (1972).

THOMAS and GRUFFYDD (1971), like earlier workers quoted by them, found a correlation between the feeding habits of the sea-stars and the intensity of the escape responses they provoke in molluscs. The bivalve *Pecten maximus* exhibits the most intense responses to *Asterias rubens, Astropecten irregularis* and *Marthasterias glacialis*, which are all known to feed on molluscs. Less violent escape reactions were observed upon contact with *Luidia ciliaris* and *Solaster papposus*, which are carnivorous only on other echinoderms; the non-predatory sea-star *Porania pulvillus* induced the least marked reactions in *Pecten maximus*. There are also records of gastropods (genus *Acmaea*) responding only to those predatory sea-stars which they normally encounter in their natural habitat (MARGOLIN, 1964).

The release of escape reactions through contact chemoreception is not restricted to predatory asteroids. Carnivorous gastropods, too, may induce violent avoidance reactions in herbivorous gastropods and bivalves. CLARK (1958) observed rapid flight reactions of several herbivorous gastropods away from carnivorous gastropods as soon as contact was made between the soft parts. Mutual contact between two herbivorous or two carnivorous snails, however, did not induce escape reactions. Escape responses have also been reported in *Nassarius luteostoma*—elicited by *Natica unifasciata* (GONOR, 1965)—and in the Indo-Pacific strombid gastropods *Strombus gibberulus, S. luhuanus* and *Lambis lambis*—provoked by the carnivorous gastropods *Conus marmoreus* and *Aulica vespertilio* (GONOR, 1966). The responses, however, were mediated not only through contact chemoreception but also by water which had been in contact with the carnivorous gastropods.

A remarkable form of escape reaction has been reported by LAWS and LAWS (1972) in the bivalve *Donacilla angusta*, which pops out of the sand immediately ahead of an approaching burrowing predatory naticid *Polinices conicus*, ploughing along 1 cm below the sand surface. The authors refrain from discussing the possible mechanism of predator detection, but their description and drawing suggest not so much chemoreception as some other cue, for instance vibration (p. 650) of the substrate caused by the oncoming naticid.

Symbiosis

There are numerous examples of symbiotic relationships among marine invertebrates (DALES, 1966). Chemical stimuli play an important part in mediating such associations, and chemoreceptive specificity will be of great significance. DAVENPORT (1966) reviewed several types of chemically mediated host-oriented behaviour. Host detection may be brought about either by distance chemoreception as in the polynoid *Arctonoë fragilis* responding to water in which its host, the sea-star *Evasterias troschelii*, had been placed, or by contact chemoreception as for instance in the scale worm *Acholoë astericola* associated with the sea-star *Astropecten irregularis*.

Apparently, responses of symbiotic invertebrates may be influenced by the physical condition of the host: *Arctonoë fragilis*, for example, does not respond to, or may even be repelled by, water which has been in contact with damaged sea-stars *Evasterias troschelii*. Species-specific responses may conceivably be based on the quantity rather than on the quality of the substances emanating from the host. In experiments with the shrimp *Betaeus harfordi*, a symbiont of gastropods of the genus *Haliotis*, ACHE and DAVENPORT (1972) found a marked genus-specific response to the host but could not rule out a possible quantitative effect.

'Olfactory conditioning' has been demonstrated by DIMOCK and DAVENPORT (1971) in the polychaete *Arctonoë pulchra*, which is associated with at least 9 species (representing 5 classes and 3 phyla). Recognition of water associated with a particular host species, from which an individual had been collected, can be modified into a preference for water passed over an alternative host, if the test individual is placed on the latter species for some weeks.

Parasitism

Parasite–host relations are often characterized by highly specific responses based on chemical cues. A remarkable degree of specificity has been reported by CARTON (1968) for the parasitic copepod *Sabelliphilus sarsi*, which can distinguish—through chemoreception—its host polychaete *Spirographis spallanzani* from two closely related non-host polychaetes, *S. pavonina* and *S. spallanzani* var. *brevispira* (see also Volume III: LAUCKNER, in press).

Substrate Selection

As mentioned before (p. 600), the gastropod *Nassarius obsoletus* moves downstream in pure sea water, but when exposed to flowing water which has been in contact with muddy deposits—the snail's natural substrate—it moves upstream. This effect is cancelled if the water is filtered previously through charcoal or if the mud is boiled beforehand (CRISP, 1969). Several invertebrates, such as cumaceans and amphipods, inhabit a particular type of sand but also make short excursions in the overlying water, during which they may be displaced by water movements. These invertebrates must be able to return to their original habitat. WIESER (1956) made a study of the factors which control the choice of substrate in the cumacean *Cumella vulgaris*. From the cumaceans' distribution in different types of sand contained in shallow dishes, he concluded that, apart from a particular grain size, also the presence of organic material is of significance. Dried sand returned to the water proved less attractive; but it regained its attractiveness with the time of immersion. The organic material, essential as food, may be present either as a deposit in the sand or as a film on the surface of individual sand grains. Whether chemoreception is involved in this case has not been reported.

Comparable results were obtained by MEADOWS (1964) in a study on the differential preference for different substrate types in *Corophium arenarium* and *C. volutator*, suggesting that these amphipods respond to specific bacterial floras—present as a film on the sand grains under different conditions of oxygenation. The amphipods, however, showed no sign of being attracted from a distance. *C. volutator* prefers a substrate previously maintained under anaerobic conditions, whereas *C. arenarium* preferably burrows in aerobic sand. These results parallel those of GAMBLE (1971), who found in *C. arenarium* a clear preference for water with high oxygen concentration, whereas *C. volutator* is indifferent or even prefers hypoxic conditions.

In addition to burrowing cumaceans and amphipods which occasionally emerge from the substrate, also permanently burrowing invertebrates, like the interstitial archiannelid *Protodrilus symbioticus* (a species without planktonic larval stage) are capable of substrate selection; the worms respond to surface films on sand grains formed by micro-organisms (GRAY, 1966b). Comparable results have been obtained in the polychaete *Scolelepis fuliginosa* (GRAY, 1971). Acid-cleaned sand is highly unattractive but inoculation of naturally occurring sand bacteria readily restores attractiveness. Remarkably, the presence of *Protodriloides symbioticus* itself may render the sand in which it lives unattractive to other interstitial inhabitants, such as the gastrotrich *Turbanella hyalina*, by producing a heat-labile substance. Even when *P. symbioticus* and *T. hyalina* are abundant on the same beach, the two species have rarely been taken in the same sample (BOADEN and ERWIN, 1971).

The afore-mentioned studies were concerned with substrate selection by adults capable of making a new choice at any time (see also MEADOWS, 1967). Ecologically, substrate selection by planktonic larvae during settlement may be of even greater significance since most of them make an irrevocable choice. The planktonic larvae of most benthic and sedentary marine invertebrates are able to delay metamorphosis until a suitable substrate is encountered. This phenomenon was first reported by MORTENSEN (1921, pp. 105–106) in larvae of the echinoid *Mellita sexies-perforata*, which appeared to metamorphose only in the presence of their natural sandy substrate. In subsequent studies it became clear that postponement of metamorphosis in the absence of a suitable substrate is of widespread occurrence (DAY and WILSON, 1934; WILSON, 1937; THORSON, 1946). An extreme case of long postponement of metamorphosis (over one year) has been reported in the sea-star *Mediaster aequalis* by BIRKELAND and co-authors (1971). The properties which influence the choice of a substrate by settling larvae—summarized by WILLIAMS (1964)—may be of a physical nature such as texture or light-reflecting properties of the surface, but chemical or biotic factors have also been shown to play an important role. JÄGERSTEN (1940) demonstrated that the planktonic larvae of the interstitial archiannelid *Protodrilus rubropharyngeus* do not metamorphose until they are placed in a dish containing the natural substrate or water which had been in contact with this substrate. JÄGERSTEN believed that the metamorphosis-inducing substance is of an inorganic nature because of its resistance to chemico-physical destruction. Other properties, however, appear hardly compatible with an inorganic nature of the substance, and this led GRAY (1966b) to suggest that the work needs repeating (see also GRAY, 1967).

Larvae of the shipworm *Teredo norvegica* were, according to HARRINGTON (1921), attracted by a substance, presumably malic acid, extracted from wood. WILSON (1952) showed that metamorphosis of the shipworm only takes place in the presence of wood. Metamorphosis and settlement of the anthozoan *Alcyonium coralloïdes* is promoted in the presence of a water-soluble substance originating especially from gorgonids and the periostracum of *Mytilus galloprovincialis*, on which this anthozoan normally settles (BOURDILLON, 1954).

Postponement of metamorphosis and prolonged exploration or transport of larvae by currents in the absence of appropriate chemical or biotic stimuli has been demonstrated also in several other cases. The factor inducing maximum settlement of larvae of the polychaete *Ophelia bicornis* is the presence of sand grains coated with a film of particular micro-organism species occurring in a certain relative abundance (WILSON, 1955). A comparable effect has been reported for the settlement of larvae of the serpulid *Spirorbis borealis*; these settle more readily on films of diatoms and their associated bacteria than on those developed in the presence of a green flagellate (MEADOWS and WILLIAMS, 1963).

Veliger larvae of the gastropod *Nassarius obsoletus*, having attained the creeping-swimming stage, postpone metamorphosis and settlement as long as about 20 days until they encounter their natural substrate (SCHELTEMA, 1961). There are strong indications that the metamorphosis-inducing factor in the substrate is a water-soluble substance.

A number of organisms, such as serpulids and polyzoans, are normally found on the fronds of certain species of seaweeds. Experiments in which the larvae of these invertebrates were placed in a glass vessel and offered pieces of inert material either untreated or treated with extracts from the seaweed, provide good evidence that settlement is greatly promoted by organic substances. Larvae of the polyzoans *Alcyonidium polyoum* and *Flustrellidra hispida*, which normally occur on *Fucus serratus*, are attracted by filmed surfaces treated with extracts from *F. serratus*, *F. vesiculosus* and *Ascophyllum nodosum* (CRISP and WILLIAMS, 1960). Surfaces treated with extracts from *F. serratus* induce settlement of larvae of the serpulid *Spirorbis borealis* (WILLIAMS, 1964). GEE (1965) found a specific preference of *Spirorbis rupestris* (= *umbilicatus*) for surfaces soaked in aqueous extracts from the coralline alga *Lithothamnion polymorphum* on which they normally live. The larvae of the lined chiton *Tonicella lineata* likewise settle only on encrusting coralline algae or on pieces of roofing tile previously soaked in a coralline algal extract (BARNES and GONOR, 1973). For larval settlement on algae also KNIGHT-JONES and co-authors (1971) and STEBBING (1972) should be consulted. Detailed information on substrate selection by marine invertebrates has recently been provided in reviews by MEADOWS and CAMPBELL (1972) and NEWELL (1972).

Gregariousness

In a number of invertebrates the larvae settle in the close neighbourhood of, or even on, adult conspecifics. This gregariousness has especially been noted in barnacles, which sometimes form large aggregations. KNIGHT-JONES and STEVENSON (1950) demonstrated that cyprids of *Elminius modestus* settle in greater numbers on panels initially bearing barnacles than on bare panels. In subsequent investigations it even became clear that the settling reactions thus induced are to a certain extent species-specific. Larvae of *Balanus balanoides*, when offered a choice between stones bearing adult barnacles of different species, settle more readily on surfaces bearing conspecifics than on those bearing other species (KNIGHT-JONES, 1953, 1955). KNIGHT-JONES suggested that the cyprids may respond to a quinone-tanned protein which also occurs in the epicuticle of the barnacles and in the cement of their basis.

Chemically mediated reactiveness has been confirmed by CRISP and MEADOWS (1962, 1963): cypris larvae of barnacles settle in larger numbers on surfaces treated with aqueous extracts of barnacles than on untreated surfaces. When attached to a surface as an adsorbed layer, the effective substance appears to be resistant to severe physical and chemical treatments—a feature also observed by COOK and co-authors (1969), who found that homing limpets (p. 557) were able to follow trails they had previously laid down on the rocks, even after various chemico-physical treatments.

CRISP and MEADOWS (1962, 1963) advanced the hypothesis that, during exploration of the surfaces with its antennular attachment disc, the balanid cyprid must respond—through a 'tactile chemical sense'—to a specific molecular configuration of a sclerotized form of the protein 'arthropodin', which occurs in the cuticle of arthropods. Since the amino-acid composition of different arthropodins is slightly different, a specific recognition of the molecular arrangement, as also presented towards the surrounding water by the outer surface of barnacles, might be possible. The results obtained cannot be explained as due to a response to outward diffusion of dissolved protein from the substrate (see also CRISP, 1965). In recent studies on the fine structure of the antennular attachment disc of *Balanus balanoides*, by means of scanning electron microscopy, however, NOTT (1969) and NOTT and FOSTER (1969) found structures (e.g. of the axial sense organ) which, they think, function as normal chemoreceptors for the detection of soluble organic compounds. These compounds (e.g. amino acids derived from the integument of adult barnacles) may be released by enzymatic action of the attachment disc—a suggestion already advanced by KNIGHT-JONES (1953). For a detailed survey of attachment and settlement in barnacle cyprids the recent review by BARNES (1970) should be consulted.

Gregariousness induced by chemical stimuli has also been reported by CRISP (1967a) in settling oysters *Crassostrea virginica* and by BAYNE (1969) in *Ostrea edulis*. In almost every detail BAYNE's findings parallel the processes described for barnacles by CRISP and MEADOWS (1962, 1963) and CRISP (1965). The question as to whether enzymatic action mediates the perception of the adsorbed—apparently species-specific—protein layers had not been raised at the time, but BAYNE (1969) demonstrated that an extract of settlement-promoting protein from *Ostrea edulis*, while resistant to diverse chemical and physical treatments, is inactivated by treating it with pronase, a proteolytic enzyme.

WILSON (1968) described gregarious behaviour in the polychaete *Sabellaria alveolata*. After their pelagic stage the larvae crawl actively over solid surfaces and postpone metamorphosis for weeks if no suitable substrate is encountered. Physical factors and bacterial films seem to be of only minor influence. Contact with the sand tubes of adults of the same species, however, is a strong stimulus for metamorphosis and settlement. Metamorphosis is induced by cement secreted by adults for the construction of their sand tubes. The cement differs from the quinone-tanned protein of barnacles in that it is not resistant to severe chemical treatment; at the same time it is not very species-specific, since the larvae of *S. alveolata* hardly, if at all, discriminate between tubes of their own species and those of *S. spinulosa*. However, larvae of *S. spinulosa* almost unfailingly distinguish the cement of conspecifics from that of *S. alveolata* (WILSON, 1970). In settling larvae of *Spirorbis spirorbis* (= *S. borealis*) the mechanical detection of temporary attachment threads left on a surface by other larvae may stimulate gregarious settlement (NOTT, 1973).

Chemically mediated gregariousness has also been reported in the interstitial archiannelid *Protodrilus rubropharyngeus* (GRAY, 1967), the interstitial gastrotrich *Turbanella hyalina* (BOADEN and ERWIN, 1971), and the polychaete *Scolelepis fuliginosa* (GRAY, 1971).

Gregariousness is mitigated by a mechanism which prevents overcrowding. When, for instance, in barnacles a heavy settlement has taken place, spatial distribution reveals some regular pattern: the distance between individuals is more or less uniform (e.g. 2 mm). This 'spacing out' mechanism has been studied by CRISP (1961) in barnacles and reviewed for some additional groups of invertebrates by KNIGHT-JONES and MOYSE (1961).

(c) Chemical Basis of Orientational Responses to Organic Substances

The dissolved organic compounds resulting from excretion, secretion and decomposition processes unendingly going on in the sea, would seem to make the marine environment a baffling, continuously and randomly changing complex of countless chemical substances. However, the invertebrates moving through this environment respond specifically only to those chemical signals which have some bearing on conditions related to their own ecological requirements. Attempts to analyse the chemical basis of orientational and behavioural responses have led to a number of investigations—mostly related to feeding behaviour (LINDSTEDT, 1971a; Chapter 3) —in which known extracts and single compounds have been tested for their ability to evoke characteristic responses. KOHN (1961) summarized the responses of gastropods to a variety of organic compounds. CASE and GWILLIAM (1963) gave a survey of marine invertebrates known to be sensitive to amino acids. CARR (1967a, b) identified and measured the stimulatory capacity of individual compounds in shrimp-tissue extract which induces feeding behaviour in the gastropod *Nassarius obsoletus*. CRISP (1967b) studied feeding responses of the cirripede *Lepas anatifera* to a variety of amino acids, and MANGUM and COX (1971) conducted parallel investigations on the polychaete *Diopatra cuprea*. In asteroids, comparable work has been done with *Asterias vulgaris* (ZAFIRIOU, 1972; ZAFIRIOU and co-authors, 1972), *A. rubens* (CASTILLA, 1972b), and *Marthasterias glacialis* (VALENTINČIČ, 1973). Remarkably, the results obtained on the closely related species (often considered to be conspecifics) *Asterias vulgaris* from Woods Hole (USA) and *A. rubens* from British waters are totally different: the former exhibits scavenger behaviour by approaching tissue homogenates of bivalves (ZAFIRIOU and co-authors, 1972); the latter avoids substances associated with damaged prey or carrion (CASTILLA, 1972b). A number of compounds—mainly amino acids—have been found effective in controlling feeding behaviour in the sea anemone *Diadumene luciae* (WILLIAMS, 1972), in the reef-building coral *Montastrea cavernosa* (LEHMAN and PORTER, 1973) and in polyps of *Chrysaora quinquecirrha* (LOEB and BLANQUET, 1973). Possibly these coelenterates possess several types of chemoreceptor sensitive to different groups of compounds.

These behavioural studies have proved a number of compounds to be effective stimulants, viz. lactic acid, urea, succinic acid, betaine trimethylamine oxide and, especially, a number of amino acids like glutamic acid, ornithine, proline, valine, cysteine, taurine, etc. Reactiveness to these compounds varies widely, depending on the species.

Sensitivity to a variety of these compounds has also been demonstrated with electro-physiological techniques in chemoreceptors on legs of crabs and lobsters

(CASE and GWILLIAM, 1961; LAVERACK, 1963; CASE, 1964) and on the antennules of *Panulirus argus* (LAVERACK, 1964) and *Homarus americanus* (ACHE, 1972). It has been shown that some chemoreceptive units respond specifically to one substance or one class of substances whereas others are non-specific, responding to a number of substances (see also LAVERACK, 1968).

CASE (1964) found that the dactyl chemoreceptors of *Cancer antennarius* and *C. productus* are not sensitive to peptides and proteins. He argues that in feeding responses of virtually omnivorous crabs there is no particular advantage in perceiving proteins because—unlike amino-acid perception—that would introduce an 'unwarranted' species-specificity in the gustatory sense of the crabs.

To what extent are omnivorous invertebrates able to distinguish between the quality of different kinds of food? In the lobster *Homarus gammarus*, MACKIE and SHELTON (1972) found a definite preference for squid mantle tissue (*Loligo vulgaris*) over cod myotome tissue (*Gadus morhua*). The specific composition of mixtures of amino acids emanating from different types of food may for instance account for a certain degree of specificity. In recent years, remarkable results have been obtained when specially prepared mixtures of amino acids were presented to experimental animals. Studying the feeding behaviour in *Nassarius obsoletus*, CARR (1967b) tested the response-inducing capacity of a combination of 12 compounds occurring in shrimp extracts. To the effective compounds glycine and lactate less active substances as betaine, alanine, asparagine, aspartic acid, glutamic acid, glutamine, proline, serine, taurine and threonine were added. The stimulatory capacity of this mixture was found to be greater than could be attributed to the effectiveness of the individual compounds. The mixture of these isolated substances, however, did not attain the stimulatory capacity of the original shrimp extract (see also Chapter 3 and Volume III: KINNE, in press a, b).

In feeding responses of *Homarus americanus*, MCLEESE (1970) found indications that amino acids in a number of mixtures potentiated each other, whereas in others the effectiveness was less than expected on the strength of their individual stimulatory capacity, suggesting a possible antagonism. None of the mixtures, however, was as effective as the original cod extract. Such a synergistic effect has also been demonstrated by SHELTON and MACKIE (1971) in the crab *Carcinus maenas*. An entirely synthetic mixture of chemicals based on the composition of the clam *Tapes japonica* is more attractive than any one of its major components. *Homarus gammarus* shows clear feeding responses to an extract of squid mantle tissue (*Loligo vulgaris*). After fractionation of this extract into amphoteric and basic components, on the one hand, and neutral and acid components, on the other, the single components were found to be less attractive to the lobster than the whole extract; but recombination of the components yielded a solution which was as attractive as the original extract (MACKIE and SHELTON, 1972). A synthetic mixture of chemicals based on the composition of squid-muscle extract is far more attractive to *H. gammarus* than any of the components (MACKIE, 1973). The authors suggested that initiation of feeding responses in decapod crustaceans requires simultaneous stimulation of different classes of chemoreceptor cell which, as said before, may specifically respond to different substances. MACKIE and SHELTON, however, do not rule out the possibility of some interaction at the membrane of individual cells. In addition, it has been found that substitution of D-amino acids for natural L-forms reduces attractiveness, which indicates a stereospecificity of the receptors (MACKIE, 1973). A synergistic effect has also been found in the feeding responses of the zoanthid *Palythoa psammophilia* to combinations, in particular proportions, of the tripeptide glutathione and the α-imino acid proline (REIMER, 1971, 1972). LINDSTEDT (1971b) demonstrated that in the different phases of feeding behaviour of the sea anemone *Anthopleura elegantissima* contraction and bending of the tentacles is controlled by asparagine, while reduced glutathione controls ingestion once the food has contacted the mouth. The induction of successive feeding motions by different amino acids has likewise been demonstrated by NAGAI and NAGAI (1973) in *A. midorii*. In these sea anemones, performance of the entire feeding sequence apparently requires stimulation by a mixture of substances.

In negative responses to amino acids—as shown by CASTILLA (1972b) in *Asterias rubens* which apparently avoids substances associated with carrion—synergism likewise appears to play a role. If L-glutamic acid, the most effective repellant among the amino acids, is mixed with one or more of 9 other amino acids used in the experiments, its effectiveness is significantly increased.

The general view that substances of low molecular weight such as amino acids, betaines and amines—either single or synergistically potentiated in mixtures—are essential in (discriminatory) chemoreception still requires critical consideration. In a recent study, GURIN and CARR (1971) have found that *Nassarius obsoletus* show strong feeding responses to proteins occurring in human plasma and oyster tissue (*Crassostrea virginica*). They demonstrated that, after ultrafiltration of samples through membranes retaining substances of molecular weight greater than 10,000 or 1000 respectively, the major stimulatory activity of these fluids resided in the macromolecular fraction. In human plasma, purified serum albumin was found highly active; in oyster fluid, a glycoprotein with a molecular weight of approximately 120,000 accounted for almost all of the stimulatory effectiveness. Other proteins were found to be stimulatory only at relatively high concentrations.

There is an obvious need here for further work to clarify the true significance in chemoreception of either specific stimulatory proteins or certain mixtures of substances of low molecular weight. For a review of feeding mechanisms in marine animals consult Chapter 3.

Distance Orientation to Substances Dissolved in the Aquatic Medium

Dissolved substances have no immediate directional properties but usually constitute gradients. Unlike irradiance and pressure gradients, chemical gradients are subject to changes by diffusion or drift. Under natural conditions, static gradients of chemical substances seem next to impossible, since they are easily modified or destroyed by the slightest convexion. Consequently, orientation to chemical stimuli by means of random locomotory movements hardly appears to be an effective mechanism.

In some experimental studies, however, food or host finding by means of kinetic movements has been described. In an attempt to determine the effect of chemical gradients in the host-oriented behaviour of symbiotic invertebrates DAVENPORT and co-authors (1960; see also DAVENPORT, 1966) devised a trough olfactometer in which the test animals are presented with 3 streams moving slowly at the same rate, the central one of which could be host-labelled. The very convoluted tracks of the polychaete *Podarke pugettensis*—living in symbiosis with the sea-star *Patiria miniata*—(Fig. 8-30) were analysed and defined as 'tropotactic' as well as 'orthokinetic'.

The 'orthokinetic' designation was based on the fact that as soon as the polychaete enters the labelled stream it markedly increases its locomotory velocity. According to the definition of orthokinesis given by FRAENKEL and GUNN (1940, p. 11), however, the polychaetes would on the contrary accumulate in the unlabelled water, which was not the case in the experiments. FRAENKEL and GUNN themselves (1940, p. 273) elsewhere argued that 'the occurrence of an "excited" condition is typical of reactions to chemical stimuli; it represents an ortho-kinetic response'. If in such cases the movements were really non-directional—a premise in orthokinesis—the organisms would not reach the bait, but would, according to the former interpretation, accumulate in areas where reduced locomotory velocity prevails (see also KENNEDY, 1945). It has frequently been observed, however, that the test animals, in spite of their tortuous pathways, do reach the bait or host, which implies that either some directional mechanism is involved or that the orthokinetic

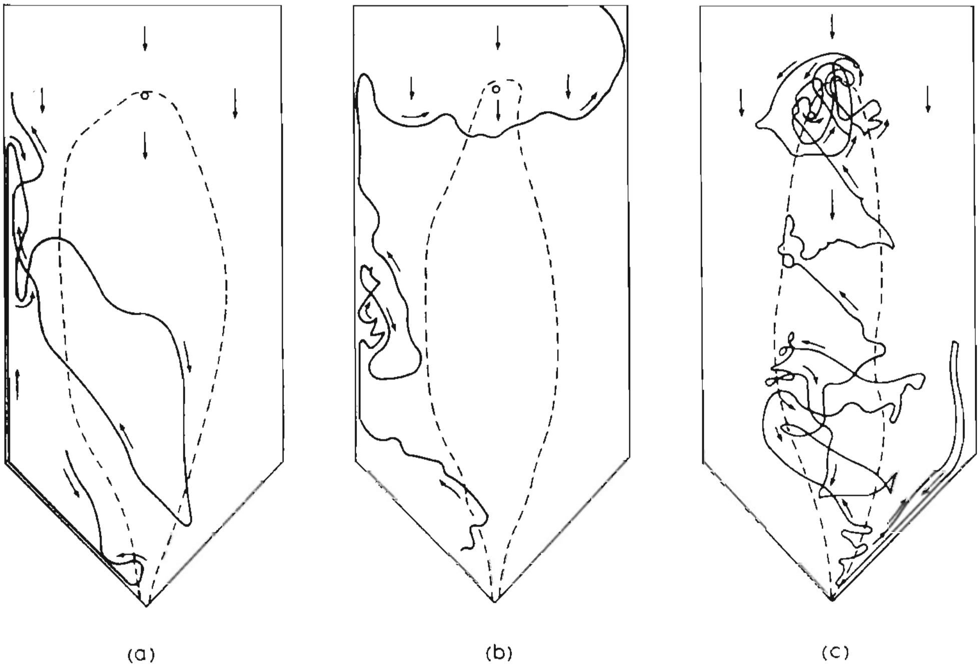

Fig. 8-30: *Podarke pugettensis*. Tracks in the trough olfactometer. (a) A free-living worm, central area containing host-labelled water and fluorescein; (b) commensal worm, fluorescein only; (c) commensal worm, host-labelled water with fluorescein. (After DAVENPORT and co-authors, 1960; reproduced by permission of Association for the Study of Animal Behaviour.)

processes are not yet fully understood. An attempt to analyse kinetic and tropotactic mechanisms has been undertaken by ROHLF and DAVENPORT (1969) in simulating experiments with a mathematical model using a digital computer. Hypothetical organisms were submitted to different systems of arbitrary rules simulating orthokinesis, klinokinesis, tropotaxis, sensory adaptation and combinations of them. One of the surprising outcomes was that 'orthokinesis' combined with 'sensory adaptation' drastically shifts the mean distribution of the organisms towards areas where increased locomotory velocity prevails.

Klinotaxis in some form or other (successive sampling of the environment) combined with rheotaxis in the form of a weak response to the very slow current may provide an equally, if not more, plausible explanation for the polychaete being 'physiologically trapped' in the host-factor stream and 'climbing up' towards the source. The conditions of the experimental design, however, do not permit definite conclusions.

The concept of 'klinokinesis'—whether or not constituting an effective mechanism (p. 562)—may likewise give rise to confusion. A questionable interpretation of the term—comparable to that of orthokinesis mentioned above—is observed in the use of 'klinokinesis' by DAVENPORT and co-authors (1960) in their study on the behaviour of the commensal crab *Pinnixia chaetopterana* collected from the tubes of the polychaete *Chaetopterus pergamentaceus*, and by MORTON (1962) in the host-finding behaviour of the mobile bivalve *Montacuta ferruginosa*, which lives in symbiosis with *Echinocardium cordatum*.

It has to be borne in mind that, in general, an odour-bearing fluid emanating from food or other objects will not immediately be diluted in the ambient water, but will rather move along with the stream as a clearly delimited flow whose concentration gradients are steeper transversely than longitudinally. An invertebrate encountering such a flow will undoubtedly be activated, but mere acceleration of random locomotory movements would rapidly result in loss of contact with the odour-bearing flow.

In several marine invertebrates a behavioural mechanism is found which is based on successive sampling within the environment with a single chemoreceptor or a group of chemoreceptors—a mechanism which FRAENKEL and GUNN (1940) defined as klinotaxis. The classic description originates from COPELAND (1918) in the channeled whelk *Busycon canaliculatum*. While crawling along, this gastropod performs swinging movements to right and left with its long siphon, a tube-shaped extrusion of the mantle edge through which water is conducted to the gills and the olfactory receptor, the osphradium. The significance for orientation to chemical stimuli of these siphon movements has been demonstrated by COPELAND: when the siphon enters odour-bearing water the position of the siphon at that moment determines the direction of the whelk's subsequent locomotory movement. Comparable observations have been made by BROCK (1933) in the whelk *Buccinum undatum*. In stagnant water the whelk has been found able to reach, by a tortuous pathway, a piece of fish at a distance of 21 cm.

In general, however, distance orientation to chemical stimuli is most effective when currents lend directionality to the stimulus. While in stagnant water, for example, *Nassa reticulata* was not able, in HENSCHEL's (1932) experiments, to find its food if located farther than 20 cm away, MACGINITIE and MACGINITIE (1968,

p. 369) reported that *Nassarius fossatus* moved upcurrent in a flow of water which had passed over a dead fish lying at least 30 m upstream. LAXTON (1971), in his experiments on the feeding behaviour of cymatiid gastropods, found that prey location by means of chemoreception is effective only when the stimulus is carried by a current. For the significance of currents in chemoreception see also p. 600.

In a current of pure sea water the whelk *Buccinum undatum* points its siphon upstream (BROCK, 1933); as soon as an odour-bearing current is encountered, the whole body follows the direction of the siphon. BROCK does not say whether the whelk waves its siphon when crawling upstream in the presence of a current-borne odour. CARR (1967a), however, briefly mentions siphon-waving in *Nassarius obsoletus* during upcurrent locomotion in the presence of substances leached from freshly killed crabs, fish, oysters and other animals. This behaviour must be of importance for the gastropods in maintaining contact with the odour-bearing flow. Scanning of the concentration gradient (klinotaxis) across the current, by waving the head from side to side, is also mentioned briefly by DAVENPORT (1950), who studied the commensal polynoid *Arctonoë fragilis* swimming upcurrent in host-labelled water in a Y-maze choice apparatus. MORTON (1962) likewise reported side-to-side deflections of the whole body as well as the siphon in the commensal bivalve *Montacuta ferruginosa* moving upstream in the presence of its host.

GAGE (1966), working with *Montacuta ferruginosa* and *M. substriata*, both commensals with spatangoid echinoids, also recognized this phenomenon and called it '**rheoklinotaxis**'. However, like DAVENPORT and co-authors (1960) and MORTON (1962), GAGE used the term 'chemokinesis' in cases where the animals increased their locomotory activity, in the presence of the host factor, along seemingly random, tortuous pathways. As argued before, that might precisely cause the bivalves to aggregate outside the host-labelled flow. In the experiments of the above-mentioned workers the current velocities are very low, probably far lower than those usually occurring in a normal marine environment. The suggestion is advanced here that what has been defined as 'chemokinesis' in these cases actually represents a poor reflection of 'rheoklinotaxis'—amounting to virtual disorientation—due to the deficient impact of directional cues in the experimental flow whose velocity is a fraction of the current velocities encountered in nature, even in the most sheltered places.

Invertebrates with paired chemoreceptors or a number of chemoreceptors located some distance apart may be capable of orienting chemotropotactically; sampling and comparing simultaneously different places across the current. Such a mechanism is thought by DAVENPORT (1950) to guide the polynoid *Arctonoë fragilis* at the point-of-choice in a Y-maze apparatus (Fig. 8-31). CASTILLA and CRISP (1970) likewise suggest that *Asterias rubens*, moving upcurrent to its prey, is able to respond to a gradient between two currents of a Y-maze and to orient to the odour-bearing stream.

The exclusive role of water currents in lending directionality to chemical stimuli has been questioned by SNYDER and SNYDER (1970). In the sea-urchin *Diadema antillarum* they observed alarm responses to juices emanating from damaged conspecifics—a behavioural adaptation to predation. Individuals located downstream of a crushed conspecific were seen moving rapidly further downstream. In stagnant water, however, they moved in any direction taking them away from a

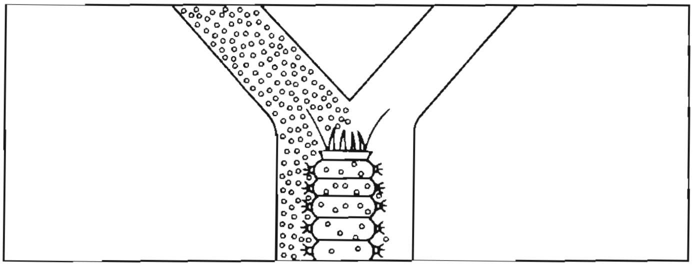

Fig. 8-31: *Arctonoë fragilis*. Commensal polynoid in a Y-maze apparatus. Flow characteristics as indicated by borax carmine, showing asymmetrical stimulation of tentacles at point of choice. (After DAVENPORT, 1950; reproduced by permission of *Biological Bulletin*.)

damaged specimen. When, in a current, *D. antillarum* were stimulated on their downcurrent side with intraspecific juice, they even moved upcurrent away from the stimulated side. Comparable doubts about the dominant orienting role of currents have been expressed by MCLEESE (1973b) in a study on chemo-orientation of the lobster *Homarus americanus*.

Apart from upcurrent attack by large individuals and downcurrent escape by small individuals in the cannibalistic gastropod *Fasciolaria tulipa*, SNYDER and SNYDER (1971) speculated on the possible ecological significance of cross-current locomotory movements. In a foraging individual cross-current orientation might seem an efficient way of encountering a maximum number of odour areas of potential prey per unit of time. For a smaller individual, however, it would increase its vulnerability by advertising its presence to other odour-responding predators (especially larger conspecifics).

Another mechanism of chemical orientation has been suggested by BROCK (1926) in the hermit crab *Pagurus arrosor*. Through the action of its respiratory plates (scaphognathites) the crab may attract respiratory water from some distance (up to 40 cm), thus creating a very slow water movement directed towards its body. If this flow is odour bearing, the crab will be able to locate its food. No evidence is available so far of whether this kind of mechanism is effective under natural conditions.

Orientation Through Contact Chemoreception

Unlike perception of dissolved substances, contact chemoreception may, under certain conditions, provide invertebrates with immediate directional information. In the chemically mediated escape responses of herbivorous gastropods coming into contact with a carnivorous gastropod, the most common reaction is an abrupt turning away from the point of stimulation, followed by rapid crawling away from the carnivore. When stimulated on the right side they turn left, and vice versa (CLARK, 1958). Although rarely mentioned explicitly, directional responses of this kind will undoubtedly be of common occurrence in many prey–predator relationships, e.g. between gastropods and predatory asteroids (p. 610). Contact chemoreception in *Octopus vulgaris* has been studied by WELLS (1963b).

Contact chemoreception also enables invertebrates to follow trails laid down on the substrate. BROCK (1933) described a case in which *Buccinum undatum*, scanning the substrate with its tentacles, readily followed a scent trail laid down with a piece of meat. The opisthobranch *Navanax inermis* locates other opisthobranchs, on which it feeds, by following their mucus-impregnated trails in the sand (PAINE, 1963; BLAIR and SEAPY, 1972). Apparently, *N. inermis* ignores trails laid down by prosobranchs. During pursuit two so-called 'inner folds' of the head shield—presumably the chemoreceptors—are kept in contact with the mucous trail; if one of these organs loses contact, appropriate corrections are made (tropotaxis). When *N. inermis* encounters a new trail, however, it is just as likely to follow the trail away from its prey as towards it. In general, no successful corrections are made and contact with the prey may eventually be lost. A similar pursuit by the predatory gastropod *Natica unifasciata*, when coming upon the mucous trail of *Nassarius luteostoma*, has been reported by GONOR (1965).

In more recent studies it has been shown that a mucous trail laid down by a snail may provide information on the direction in which the snail has been moving. When a *Nassarius obsoletus* is placed in a glass dish filled with sea water, it crawls to the edge and moves round it in a clockwise or anticlockwise direction. When a number of *N. obsoletus* (2–10) are placed in the dish simultaneously, they all move in the same direction, displaying schooling behaviour. After removal of these snails and the introduction of a single individual into the dish, the latter will, upon arrival at the edge, mostly move in the same direction as the 'convoy' did previously; this indicates that the mucous trails laid down by the group are polarized in some way (CRISP, 1969). The freshwater pulmonate *Physa acuta* likewise not only responds to its own trail and that of other individuals, but is able to determine the direction in which the trail-laying snail has been moving (WELLS and BUCKLEY, 1972). The polarized trail of *P. acuta* appears to persist for about 30 mins. This trail-following behaviour is most likely of widespread occurrence in gastropods. It has, for instance, also been demonstrated in the marine gastropods *Littorina saxatilis* and *Monodonta lineata* (WELLS and BUCKLEY, 1972), and *L. irrorata* (HALL, 1973). Presumably, the same principle is operative in homing limpets, which are supposed to retrace the mucous trails they have left previously (COOK and co-authors, 1969; COOK, 1971).

There are also situations in which orientation through contact chemoreception is mediated by no more than random search or orthokinesis. Substrate selection by *Corophium volutator* and *C. arenarium*, for instance, greatly depends on the presence of sand grains coated with organic material (MEADOWS, 1964). The amphipods show no sign of being attracted from a distance by some dissolved substance but rather, after alighting, explore the substrate by manipulating particles on its surface. They will then either burrow or swim off, depending on the nature of the substrate. Through this mechanism, already observed by WIESER (1956) in the burrowing cumacean *Cumella vulgaris*, aggregations will occur in suitable substrate areas.

This orthokinetic mechanism undoubtedly constitutes a dominant factor in the settlement of planktonic larvae of sedentary invertebrates. Extensive pertinent information is available from the gregarious settlement of barnacles (p. 614). The cyprids are thought to encounter suitable surfaces for settlement merely as a matter of chance. After alighting they explore the surface and may either metamorphose or not, depending on the presence of an adsorbed layer of protein, arthropodin, deposited by previously settled conspecifics (CRISP and MEADOWS, 1962, 1963). Arthropodin, extracted from freshly moulted crustaceans or living barnacles, does not induce settlement when offered in a low concentration in the ambient water. CRISP and MEADOWS therefore suggested a 'tactile chemical sense' responding through the antennular attachment disc to the molecular arrangement of the adsorbed and sclerotized proteins. The suggestion of NOTT (1969) and NOTT and FOSTER (1969) that the attachment disc may, through enzymatic action, release amino acids from the adsorbed protein layer and perceive them as dissolved substances, does not fundamentally affect the principle of orthokinetic orientation mediated through contact chemoreception. The products released from the protein film will be present in high concentration between the disc and the surface. The absence of a response to protein dissolved in the surrounding water can be explained in that the products of any enzyme activity would become too diluted and rapidly disperse away from the chemoreceptors.

In contrast to increased locomotory activity upon detection of an attractive substance emanating, for instance, from host or carrion, these examples of substrate selection mediated through contact chemoreception—as well as the experiments with oxygen or humidity gradients (p. 607 and p. 597)—can justifiably be labelled as involving orthokinesis, since in these cases unattractive conditions—which may comprise either presence or absence of a stimulus—promote purely random locomotion, resulting in aggregations in areas with favourable conditions, where the invertebrates settle or come to rest (KENNEDY, 1945).

(10) Gravity

The earth's gravity provides an orientation cue that is the most permanent and stable of all known stimuli. It is always present, it has definite vertical directionality and its intensity is almost invariable. There are two basically different types of orientation to the gravitational force: (i) Maintenance of spatial positioning, or equilibrium and (ii) oriented locomotory movements along the vertical, either towards the centre of the earth (positive geotaxis) or away from it (negative geotaxis). In a sense, orientation to the earth's gravity may be regarded as menotaxis or compass orientation in the vertical plane, with positive and negative geotaxis representing special—frequently occurring—cases.

(a) Maintenance of Spatial Positioning

General Aspects

For most animals the force of gravity is the basic frame of reference for the maintenance of a positional equilibrium. For a large number of invertebrates, however, light distribution provides additional information enabling the animal to distinguish up from down. This was already recognized by DELAGE (1887) in crustaceans (species of *Mysis* and *Palaemon*), which continue to maintain their position in spite of the removal of either the statocysts alone or the eyes alone. Further, proprioception and contact stimulation are reported by several authors to have a share in equilibrium reactions.

Thus a variety of mechanisms exist for position maintenance. The actual gravity receptors, however, in almost all taxonomic groups, are based on the same principle. An object, the **statolith** (e.g. loosely cemented sand grains or a solid structure of relatively high specific gravity, produced by the invertebrate itself) is enclosed in a fluid-filled cavity, the **statocyst**, which generally is an ectodermal invagination.

The statolith is supported by the ciliated sensory epithelium with which the inner surface of the statocyst is lined. A change of the invertebrate's position will alter the shearing force or pressure exerted by the statolith on the sensory hairs, thereby providing information for readjustment of the body position.

In former times the statocyst was called otocyst, because in vertebrates this organ is located in the ear, while HENSEN (1863) associated statocysts with sound perception in some crustaceans. Subsequently, through the work of DELAGE (1887) on 'otocysts' in the genera *Mysis*, *Palaemon* and *Octopus*, it became clear that these organs are involved in equilibrium orientation. Regarding the physiological mechanism, DELAGE made a comparison with the mechanism of the semicircular canals of vertebrates and tentatively suggested that the movements of either the statocyst fluid or the statolith releases compensatory movements during locomotion.

The important role of the statolith in gravity detection was conclusively demonstrated by KREIDL (1893) in his famous 'iron-filings' experiment. He offered newly moulted shrimps *Palaemon xiphios* and *P. squilla* iron-filings, instead of the sand grains which the shrimps normally introduce into their statocysts. The shrimps were then subjected to a magnetic field with the result that they became oriented to the resultant of both gravitational and magnetic forces.

Gravity perception by means of statocysts and statoliths appears to be widespread in the different taxonomic groups of marine invertebrates. It has been reported in Scyphomedusae (FRAENKEL, 1925; BOZLER, 1926a, b; HORSTMANN, 1934a, b), in ctenophores (VERWORN, 1891; BAUER, 1910), in turbellarians (FRAENKEL, 1929), in polychaetes (VON BUDDENBROCK, 1912, 1913), within the class Crustacea only in the Malacostraca, especially in decapods and mysids (see COHEN and DIJKGRAAF, 1961), in gastropods and bivalve molluscs (see CHARLES, 1966), in cephalopods (see WELLS, 1966) and within the phylum of Echinodermata in holothurians and supposedly in some groups of echinoids (see REESE, 1966).

Positioning by Means of Statocysts

Normally the mechanism of equilibrium orientation aims at keeping the longitudinal and transverse body axes horizontal, that is perpendicular to the force of gravity. FRAENKEL and GUNN (1940) therefore used the term **transverse gravity orientation**. There are, however, a number of radially symmetrical planktonic organisms like ctenophores and medusae which usually keep their axis of symmetry vertical and which, accordingly, move either upward or downward. As a consequence of their terminology FRAENKEL and GUNN preferred to classify this type of equilibrium movements as 'geotaxis'.

In ctenophores there is a single statocyst located at the aboral pole. Eight rows of beating comb-plates, arranged in meridian lines, accomplish their locomotion. The mouth is located at the opposite (oral) pole. Within the statocyst the statolith is supported by four pillars of fused cilia. The statocyst's role as a balance-organ in ctenophores was suggested by ENGELMANN (1887) and demonstrated experimentally by VERWORN (1891) in *Beroë ovata.* When the ctenophore is tilted, the statolith exerts an unequal pressure on the fused cilia, which causes a differential propulsory effectivity of the rows of beating comb-plates, thus restoring the individual to its original position. The normal vertical position of *B. ovata* will—depending on ecological conditions—be with the oral pole either upward (resting position) or downward (excited stage). When the ctenophore is tilted from the former position, the statocyst supposedly inhibits the beat of the upper rows of comb-plates, while the lower rows continue to beat normally, thereby restoring the individual to its oral-pole-up position. If the ctenophore is tilted from the excited position (oral-pole downward), readjustment is achieved by the upper rows beating more vigorously than the lower (BAUER, 1910). According to FRAENKEL and GUNN (1940) and VON BUDDENBROCK (1952), comparable results have been obtained with *Pleurobrachia pileus,* confirming the role of the single aboral statocyst in ctenophores as an equilibrium organ. Detailed studies of the mechanism of neural transmission and comb-plate coordination in ctenophores can be found in, for instance, DE CECCATTY and HERNANDEZ (1965), HORRIDGE (1965) and TAMM (1973).

In scyphomedusae there are 8 statocysts arranged around the margin of the umbrella. The representative studied by FRAENKEL (1925), *Cotylorhiza tuberculata,* normally keeps its axis of symmetry vertical. Locomotion is achieved by alternating contraction and relaxation of the umbrella, comparable with the pulsation of the heart. If the scyphomedusa is tilted over to one side, the uppermost statocyst apparently releases a greater excitation with the result that the upper part of the umbrella is contracted for a longer time and relaxes only to a certain extent. Consequently, the beat of the lower side becomes more effective; this restores the individual to its normal position. In subsequent detailed studies dealing with the organization of the pulsory movements of scyphomedusae, BOZLER (1926a, b), who worked on species of *Cotylorhiza* and *Pelagia,* and HORSTMANN (1934a, b), who worked on species of *Aurelia* and *Cyanea,* confirmed the equilibrium function of the statocysts in scyphomedusae. The ecological significance of orientation and locomotion in vertical migration of scyphomedusae was discussed by VERWEY (1942) in his extensive study of these organisms.

In bivalve molluscs an asymmetrical type of equilibrium reaction has been described for *Chlamys opercularis* (VON BUDDENBROCK, 1911, 1915b). Characteristically, this mollusc swims by vigorously flapping its shell valves, which produces propulsory ejections of water, controlled by the position of the mantle curtains. *C. opercularis* mostly move obliquely upward with the free edge of their shell in front. If the mollusc is suspended from a thread in a symmetrical position with the hinge either upward or downward, it veers away from either position until it is oriented obliquely upward and then swims away (Fig. 8-32). VON BUDDENBROCK found strong indications that this oriented position is mediated by gravity perception. *Chlamys* species have asymmetrical statocysts, the left one being well developed whereas the right one is less differentiated. Elimination of the left statocyst

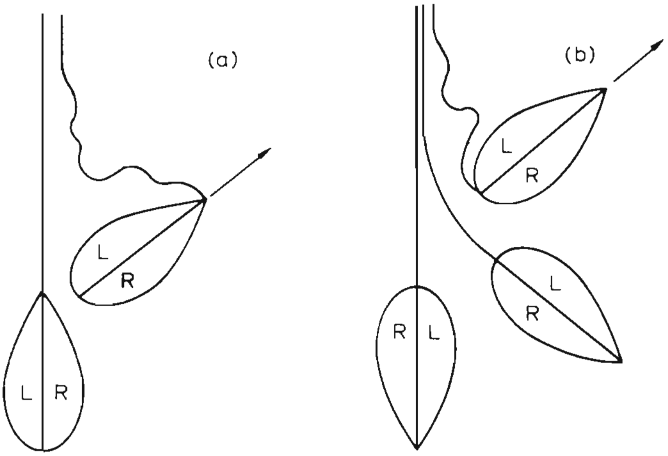

Fig. 8-32: *Chlamys opercularis*. Scheme of oblique upward movement of individual suspended from a thread, with the hinge either downward (a) or upward (b). (After VON BUDDENBROCK, 1911; reproduced by permission of Heidelberger Akademie der Wissenschaften.)

upsets orientation, whereas elimination of the less-developed right statocyst does not affect the swimming posture.

In most invertebrates the statocysts are symmetrically paired organs. This raises the question whether each of the two organs responds to angular displacements along the longitudinal axis in either direction (two-way action) or whether bilaterally symmetrical stimulation of the receptors is required for equilibrium maintenance (one-way action of the statocysts). This problem is somewhat reminiscent of the telotaxis–tropotaxis problem in visual orientation (p. 569), but there are fundamental differences (FRAENKEL and GUNN, 1961).

Earlier work in this field yielded some conflicting results. Examples are the statocysts of the heteropod prosobranch *Pterotrachea mutica*, a predaceous planktonic mollusc, which normally swims with its morphological ventral side uppermost, using its foot as a fin. TSCHACHOTIN (1908) extensively described the statocysts and demonstrated their role as equilibrium organ. After removal of one of the two statocysts he reported a persistent rolling about the longitudinal axis, providing an example of one-way action of statocysts. FRIEDRICH (1932), working on the same prosobranch, however, came to the conclusion that rolling after removal of one of the statocysts is merely an immediate effect of the operation and that in time (e.g. 5 mins) an operated individual regains its original ability to maintain its balance. Through unilateral section of the statocyst nerve, DIJKGRAAF and HESSELS (1969) likewise demonstrated two-way action in the statocysts of *Aplysia limacina*. Upon further analysis they found indications of neural transmission from each of the statocysts to the locomotory systems of both sides of the body. For details on the structure of mollusc statocysts consult the review by BARBER (1968).

In the literature on Crustacea, a group on which the most detailed information is available (consult COHEN and DIJKGRAAF, 1961), it is generally assumed that the statocysts show two-way action and that one of them is sufficient to control equilibrium. The action of the two statocysts is regarded as mutually reinforcing rather than counteracting. DELAGE (1887) already recognized this principle. He demonstrated in *Mysis* sp. and *Palaemon* sp. that in blinded individuals a perfect equilibrium orientation persists after removal of one of the statocysts. Other workers in this field (e.g. PRENTISS, 1901; VON BUDDENBROCK, 1914; ALVERDES, 1926) came to the same conclusion.

A remarkable exception to this generally assumed mechanism has been reported by KÜHN (1914) in the freshwater crayfish *Astacus fluviatilis*. After removal of one of the statocysts, this crayfish persistently exhibits compensatory movements independently of its position. These compensatory movements consist of eyestalk deflections towards the operated side, while the legs on the intact side make rowing movements, and the legs on the operated side are held up. These movements are identical to those made by an intact individual which is rotated along its longitudinal axis towards the side corresponding with the intact side of an operated crayfish.

In his extensive studies on equilibrium orientation in decapod crustaceans SCHÖNE (1951a) used the compensatory movements to obtain specific measures of the gravitational stimulus under experimental conditions. His work greatly contributed to a better understanding of the functional mechanism of the statocysts. The main results may be summarized as follows.

In *Astacus fluviatilis* with both statoliths removed from the intact statocysts, compensatory movements can be released by directly deflecting the sensory hairs of one statocyst with a fine jet of water (Fig. 8-33). Depending on the direction of the deflection in this one statocyst—either laterally or medially—the crayfish exhibits compensatory movements either to the right side or to the left side, which

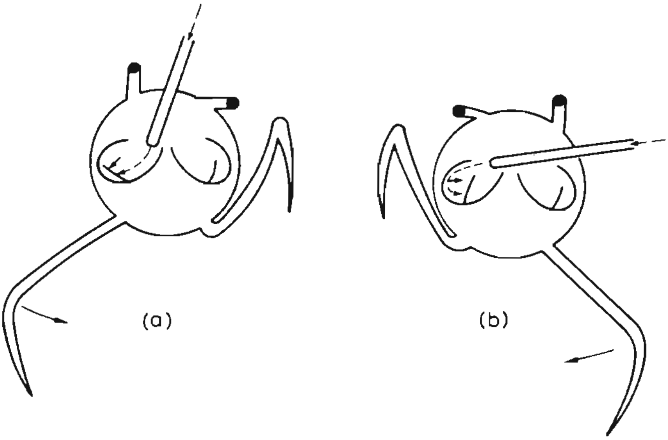

Fig. 8-33: *Astacus fluviatilis*. After statolith removal compensatory movements of eyestalks and limbs can be evoked by deflecting statocyst hairs laterally (a) or medially (b) with a fine water jet. (After SCHÖNE, 1951a; reproduced by permission of Akademische Verlagsgesellschaft Geest & Portig, Leipzig.)

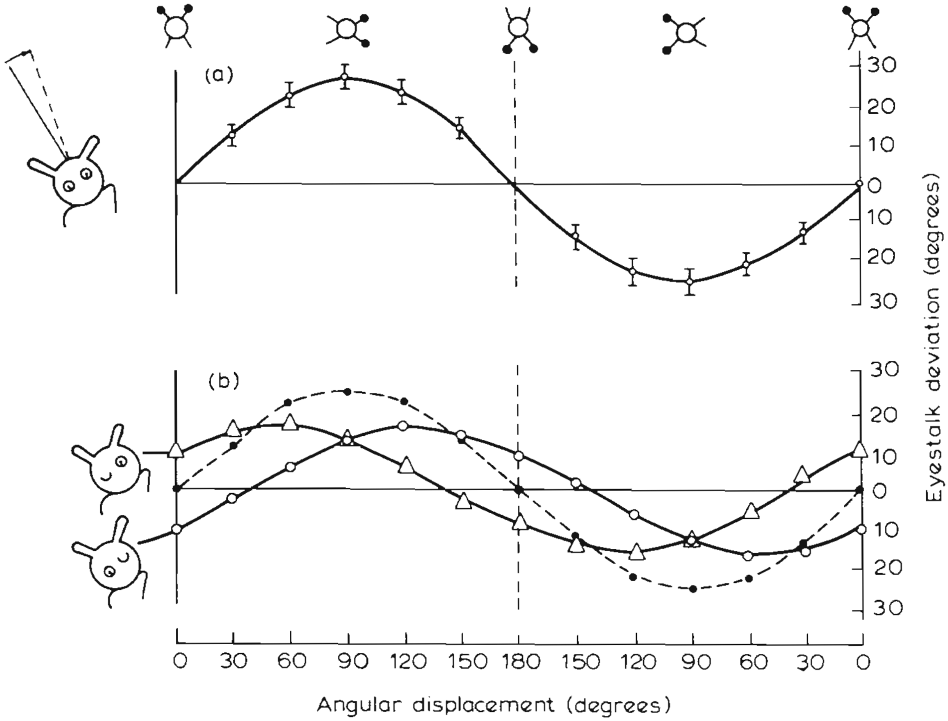

Fig. 8-34: *Palaemonetes varians.* Compensatory eyestalk movements (measured as angle between shrimp's dorso-ventral axis and the line bisecting angle between eyestalks; see top symbol on the left) of blinded individual rotated about its longitudinal axis. (a) Normal shrimp, (b) unilaterally deprived of statolith (left and right respectively) and the sum of the responses (dashed line) reproducing the original curve of normal shrimp. (After SCHÖNE, 1954; modified; reproduced by permission of Springer-Verlag, Berlin.)

provides definite evidence for a two-way action of each statocyst in *A. fluviatilis* (SCHÖNE, 1951a). Comparable results were obtained with *Crangon crangon*, *Homarus vulgaris* and *Palaemonetes varians* (SCHÖNE, 1954).

When intact decapods (species of *Astacus*, *Crangon*, *Palaemonetes* and *Homarus*) are rotated 360° about their longitudinal axis, the eyestalks exhibit compensatory deviations which are maximal at an angular displacement of 90° to the left side and the right side, while no deflection is observed in the resting position (0°) or when the animal is held upside down (180°) (Fig. 8-34a). This, apparently, reflects maximal and minimal shearing forces exerted by the statoliths on the statocyst hairs. The response curve, however, is a composite produced by the effects of each of the two statocysts separately. *Palaemonetes varians*, unilaterally deprived of the statolith, showed approximately the same curve when rotated, but the resting position shifted about 30° toward the operated side. The same shift occurred in the maximal response, now found at 120° to the operated side and at 60° to the intact side

(Fig. 8-34b). According to SCHÖNE (1954), this reactivity of an individual with a single statocyst is closely related to the fact that the statocyst floor shows a lateral inclination of about 30° (Fig. 8-35). In the resting position, which is inclined 30° towards the operated side (Fig. 8-36d), the floor of the intact statocyst is horizontal while at 120° to the operated side and at 60° to the intact side the floor is vertical, the shearing force of the statolith then being maximal. The response curves are sinusoidal; this indicates that the rate of deviation of the eyestalks is linearly related to the shearing force of the statolith. When the curves of the left and right statocysts are summed, they reproduce the original curve found in the intact individual in which, when in balance, the two statocysts work against each other to a certain extent (30° to each side; Fig. 8-36f). When the inclination exceeds this value, the statocysts work in the same direction (Fig. 8-36g).

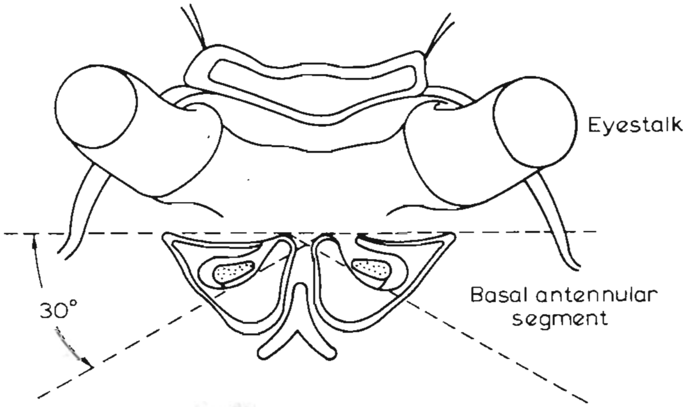

Fig. 8-35: *Astacus fluviatilis*. Front view with cross-section through basal antennular segments showing lateral inclination of statocyst floor by about 30° from horizontal. (After SCHÖNE, 1951a; modified; reproduced by permission of Akademische Verlagsgesellschaft Geest & Portig, Leipzig.)

Further investigations by SCHÖNE (1951a, 1954) provided strong indications that the sensory epithelium of the statocysts continuously generates impulses which cause a turning tendency to the contralateral side (Fig. 8-36a). If in an individual deprived of both statoliths one of the empty statocysts is removed, the animal exhibits rotation toward the operated side, which, through the lack of gravitational stimuli (absence of statoliths), is persistent and independent of the animal's position (Fig. 8-36b). The presence of statoliths, which bend the sensory hairs in either direction, causes impulses which promote proper compensatory responses and which are superimposed on the spontaneous activity of the sensory cells. This view, based on behavioural results, has been confirmed by COHEN and co-authors (1953) and COHEN (1955), who, by means of action potential recordings from primary afferent neurons in the statocysts of *Panulirus interruptus* and *Homarus americanus*, found continuous discharge of pulses in the resting position. When the statolith hairs are bent in either direction, the impulse frequency will increase or decrease;

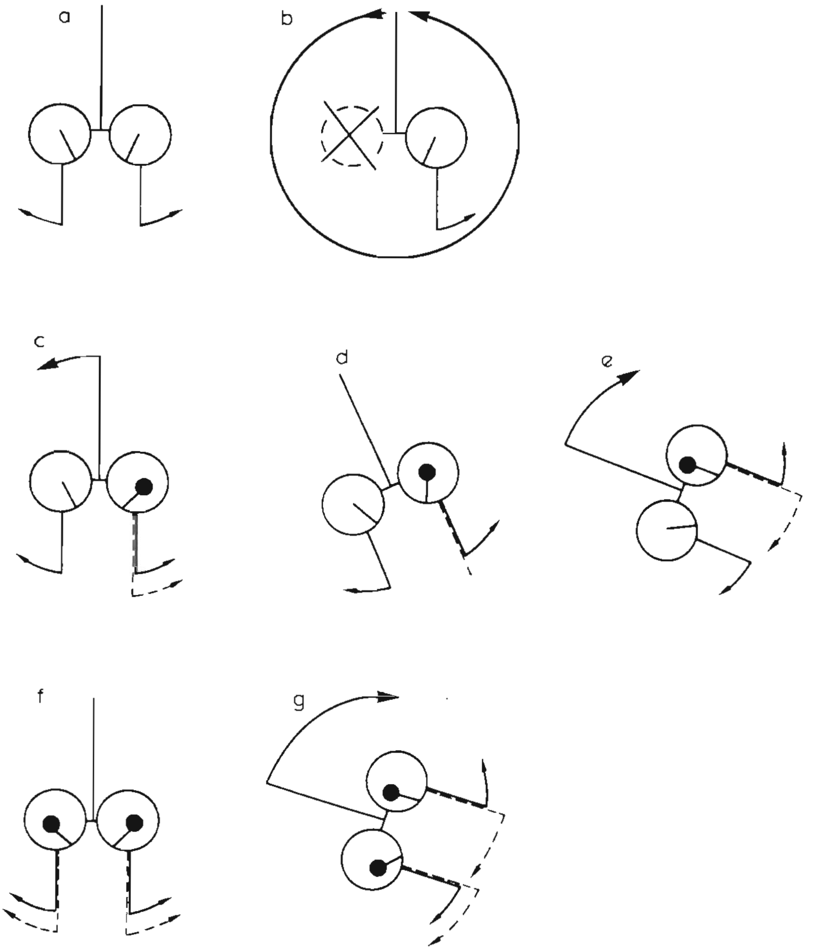

Fig. 8-36: Decapod crustaceans. Rotational tendencies about longitudinal axis (heavy arrows at top on b, c, e and g) caused by spontaneous antagonistic activity of statocyst hair receptor cells (small lower arrows in a–g) and by lateral or medial pull of statoliths (dashed arrows in c–g). (After SCHÖNE, 1951a; reproduced by permission of Akademische Verlagsgesellschaft Geest & Portig, Leipzig.)

this is consistent with the mechanism of bi-directionality of sensory hairs first established by LOWENSTEIN and SAND (1936) in electrophysiological experiments on the elasmobranch labyrinth.

Adaptational processes have also been described by SCHÖNE. If an animal is subjected to asymmetrical conditions—for instance by unilateral removal of the statolith or statocyst—the oblique posture or the compensatory movements do not persist at the same level for long. They may even disappear in the course of some days. If an asymmetric decapod, for example with one statolith, is made symmetrical again by removal of the other statolith, it even performs compensatory movements in the opposite direction (SCHÖNE, 1951a, 1954). This restoration to normal postures is due to central nervous compensation and may be regarded as biologically significant especially to those decapods whose statoliths, being made up of sand grains, are rarely balanced exactly.

In SCHÖNE's (1954) experiments *Carcinus maenas* showed the same behaviour in almost every detail; but the question arose as to how to interpret the mechanism in a crab which was known to be completely devoid of statoliths. A few years later, DIJKGRAAF (1956b) discovered in adult *Carcinus maenas* and *Maja verrucosa* a typical cluster of very small statoliths (small sand grains) in the ventrocaudal corner of the statocyst.

The principles of the statocyst function in decapod crustaceans rotating about their longitudinal axis, as revealed by SCHÖNE, appear to apply equally to angular displacement about the transverse axis (pitch). This has been demonstrated in free-swimming shrimps (*Crangon vulgaris* and *Palaemonetes varians*) which, after being released at the water surface of an aquarium, swim obliquely downward at a fairly constant angle (SCHÖNE, 1957). This is an obvious example of compass orientation in the vertical plane. When the gravitational force (g) is increased artificially in a large centrifuge—comprising the aquarium and the observer—the pathway of the downward-swimming shrimp is less steep. The shearing force (S) exerted by the statoliths, however, appears to be maintained at a constant level according to

$$S = g.\ \sin \alpha = \text{constant},$$

where α represents the angle between the water surface and the long axis of the statocyst floor. If, on the other hand, the joint effect of the statoliths is reduced by removing one of them, the pathway is much steeper (SCHÖNE, 1954). The mechanism by which a certain inclined position is maintained during downward swimming has been interpreted by SCHÖNE in the light of the 're-afference principle' advanced by VON HOLST and MITTELSTAEDT (1950; see also p. 590).

If the spiny lobster *Panulirus argus* is rotated about its transverse axis (pitch), the eyestalks exhibit compensatory movements in the dorso-ventral plane. When, however, the antennules—which in their basic segment contain the statocyst—move in the dorso-ventral plane, no such compensatory eyestalk movements take place, although the statoliths will effect similar changes of the shearing force on the sensory epithelium of the statocysts. SCHÖNE and SCHÖNE (1967; see also SCHÖNE, 1971) demonstrated that an antennular proprioceptor, located in the joint between the basic segment and the trunk of the lobster, is involved, acting antagonistically to the stimulus of the statocysts. Experiments in which either statocysts alone or the antennular proprioceptors alone were operative provided good evidence that the statocysts and proprioceptors are integrated in a system responsible for the maintenance of equilibrium of the main body of the lobster. This mechanism must be considered essential to invertebrates, such as decapod crustaceans, which have their gravity receptors located in movable appendages.

Recently, equilibrium orientation has also been analysed in *Octopus vulgaris* by BUDELMANN (1970) and SCHÖNE and BUDELMANN (1970). In the normal body position the sensory epithelium (macula) of the statocysts of the octopus is oriented vertically, while the macula planes of the left and right statocysts subtend an angle of 90° open to the front (Fig. 8-37a). Compensatory eye movements were

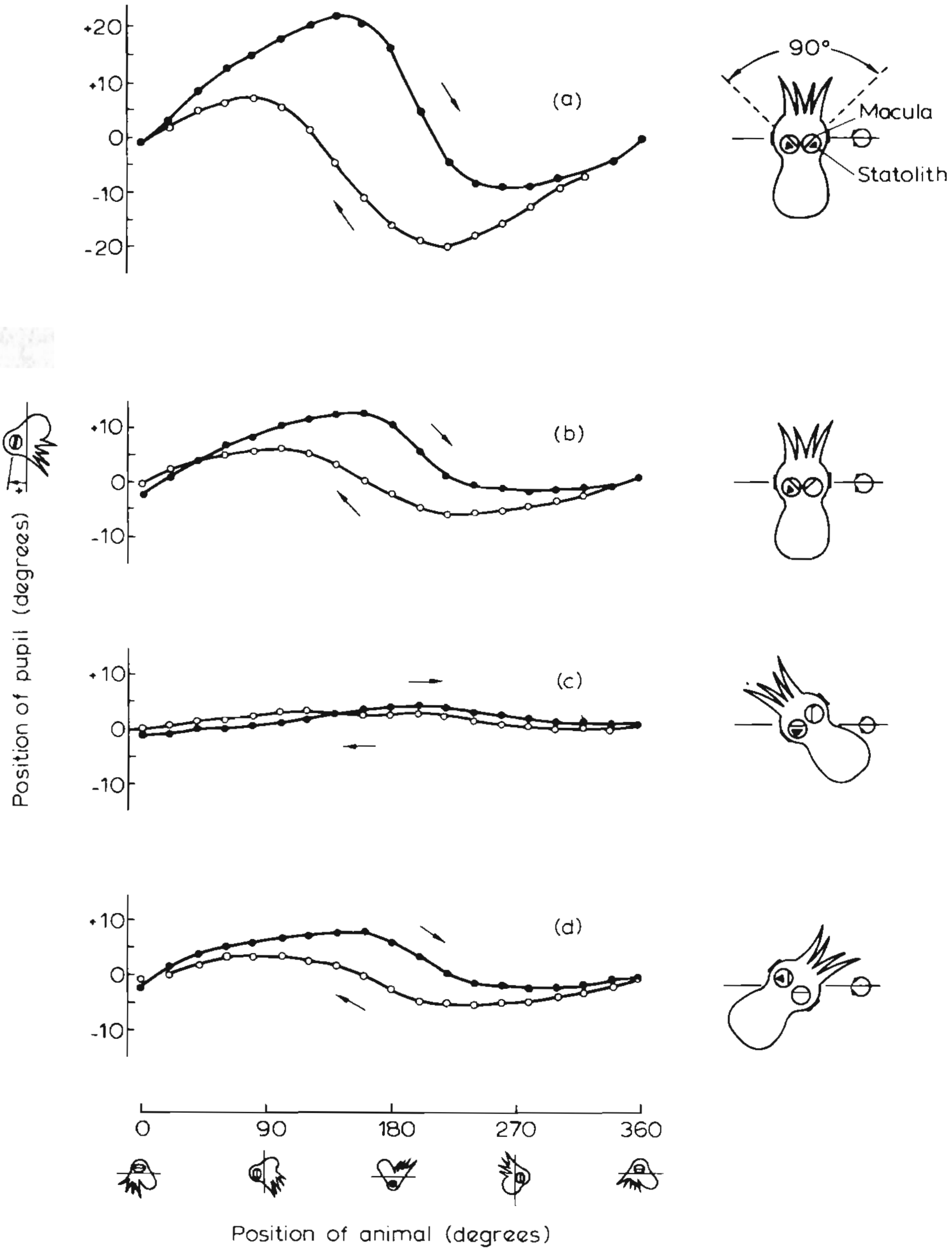

Fig. 8-37: *Octopus vulgaris*. Compensatory cyclorotational eye movements (measured as angle between octopus' longitudinal axis and pupil slit) as a function of body position. Arrows refer to direction of tilt. (a) Normal individual rotated about transverse axis; (b) individual unilaterally deprived of statolith, rotated about transverse axis; (c) ditto, rotated about axis parallel to intact macula plane; (d) ditto, rotated about axis perpendicular to intact macula plane. (After BUDELMANN, 1970; modified; reproduced by permission of Springer-Verlag, Berlin.)

recorded during rotation of the octopus about its transverse and longitudinal body axes. Remarkably, the extent of the compensatory eye movements, as well as the body position at which a maximal deviation occurred, appeared to be dependent on the direction from which a particular position was approached, in the sense of a delayed responsiveness or 'hysteresis effect' (Fig. 8-37). A comparable hysteresis effect has been demonstrated in the crayfish *Procambarus clarkii* by HISADA and co-authors (1969).

Unlike decapod crustaceans, *Octopus vulgaris*—in whatever body position—appeared not to respond to an increase in gravitational force in a centrifuge. Absence of compensatory eye movements has also been found when an octopus, unilaterally deprived of the statolith, is rotated about an axis parallel to the macula plane of the intact statocyst (Fig. 8-37 c). In normal position the shearing force of the statolith is directed vertically; during this rotation the shearing force merely decreases and then increases again, but it does not change its direction relative to the macula. If, however, the octopus is rotated about the axis perpendicular to the macula plane, the direction of the shearing force moves relative to the macula like the hands of a clock (Fig. 8-37d). During this rotation almost normal compensatory eye movements—compared with the situation illustrated in Fig. 8-37b—are observed. Angular changes, rather than quantitative changes, of the shearing force exerted by the statoliths on the sensory epithelium apparently control equilibrium orientation in *O. vulgaris* (BUDELMANN, 1970; SCHÖNE and BUDELMANN, 1970). For statocyst function in terrestrial pulmonate gastropods consult WOLFF (1970).

In a detailed electro-physiological study of the hair-receptors of the statocyst in the lobster *Homarus americanus*, COHEN (1955) found differentiated abilities and functions of individual receptors. He distinguished two main types: **Type I** position receptor shows a non-adapting specific discharge frequency for each position about the transverse axis, being maximal at about 90° and minimal at about 0° and 180° degrees of inclination. The frequency is (more or less) independent of the direction from which a given position is approached. Since the response curve is dome-shaped, the information derived from a single receptor is ambiguous in that it does not discriminate between two comparable positions on either side of the maximum response. The presence of various receptors with slightly different response curves, however, provides the CNS with a composite input pattern characteristic of each position. This type of position receptor is found to respond only to positional changes about the transverse axis. **Type II** position receptor responds to angular displacements either about the transverse axis or about the longitudinal axis, but any individual receptor never responds in both planes. Type II likewise signals absolute positions by specific discharge frequencies, but in addition supplies information on the direction from which a certain position is approached. During movements towards a position of higher discharge frequency an excessive frequency increase takes place, whereas movements away from such a position are accompanied by a markedly abrupt decrease of the discharge frequency. Within an adaptation period of a very few seconds the frequency levels out to a value specific for a given position and no longer dependent on the direction of approach.

In recent electrophysiological work, WOOD and BAUMGARTEN (1972) have found in statocysts of the opistobranch gastropod *Pleurobranchaea californica* only one type of receptor cell, functionally resembling the lobster's Type II position receptor.

Rotation Perception

Apart from a purely static function of the statocyst and its ability to respond to the direction from which a certain position is approached, the decapod's statocyst also appears to be sensitive to angular acceleration or deceleration about the vertical, transverse and longitudinal body axes. The work of COHEN (1953, 1955) on *Homarus americanus* and DIJKGRAAF (1955b, 1956b) on *Carcinus maenas* and *Maja verrucosa* provides good evidence that the response to angular accelerations or decelerations is due to the flow of the statocyst fluid deflecting rows of implanted long thread hairs which extend freely into the cyst fluid (see also the review by COHEN and DIJKGRAAF, 1961).

A blinded crab exposed to rotation exhibits compensatory eyestalk movements in the opposite direction, mostly alternating with nystagmus movements. Continuous rotation at constant velocity causes the eyestalks to return to their symmetrical position. Upon abrupt cessation of the rotation, the crab shows after-effects consisting of eyestalk deviation in the direction of the previously imposed rotation and after-nystagmus. These effects are closely related to the deflections of the thread hairs. If the latter are bilaterally eliminated by denervation or cauterization, rotation sensitivity is abolished. Elimination of the thread hairs, however, does not affect equilibrium orientation, whereas elimination of the statolith function alone does not affect the crab's reactions to angular acceleration or deceleration. After unilateral elimination of the thread hairs both eyes still respond to angular acceleration, though to a somewhat reduced extent.

Besides **statolith hairs** and **thread hairs** also **free hook hairs** and **group hairs** have been described. The free hook hairs are shaped like statolith hairs but do not have contact with the statolith. They are supposed to be auxiliary rotation receptors but with higher threshold values. The function of the group hairs is unknown.

The sensitivity of thread hairs, like that of statolith hairs, is based on a continuous impulse discharge which either decreases or increases depending on the direction of the deflection (COHEN, 1955). In the absence of specific grouping of the hairs this mechanism does not supply selective information on rotations about the different body axes. Nevertheless it has been demonstrated that crabs respond selectively to angular accelerations about any of the body axes (vertical, longitudinal or transverse). This mechanism has always been associated with the characteristically vertebrate arrangement of three semi-circular canals perpendicular to each other, in contrast to the open-structure statocysts of invertebrates. Recently, however, SANDEMAN and OKAJIMA (1972) have published a description of the statocyst of the Australian mud crab *Scylla serrata* in which a horizontally oriented canal and a vertical one can be distinguished. In the horizontal canal the fluid flow results from rotations about the vertical axis. The circumference of the vertical canal, however, does not lie in the plane of the longitudinal axis nor in that of the transverse axis, but in an intermediate position at an angle of about 45°; this is important for the sensitivity of the system with respect to all three body axes. In addition, two groups of thread hairs—an upper one and a lower one—and a group of free hook hairs are

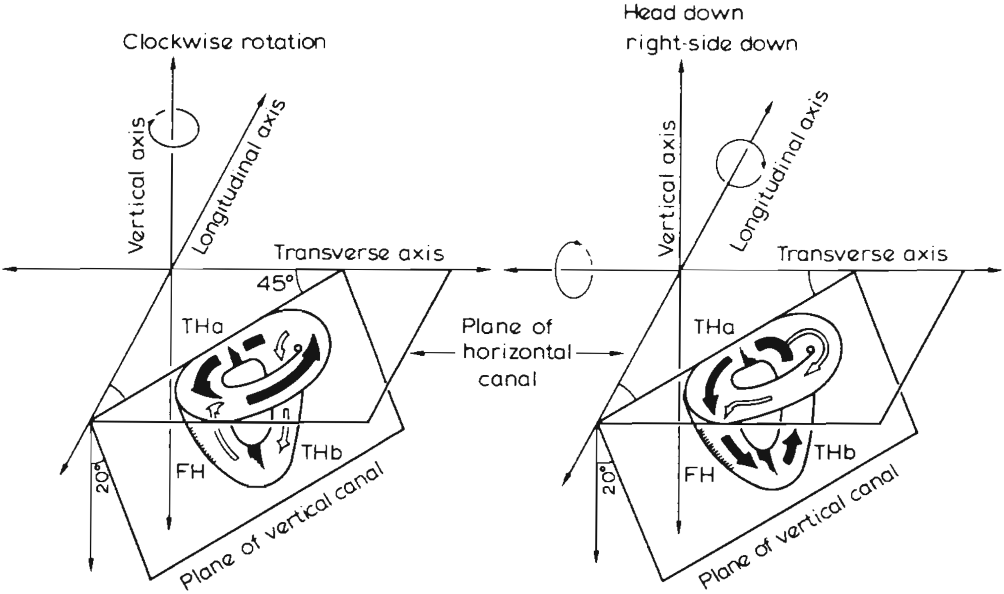

Fig. 8-38: *Scylla serrata.* Scheme of right statocyst showing its orientation to vertical and horizontal body axes and resultant fluid movements upon rotation about these axes. Heavy arrows indicate dominant direction of flow. THa: upper groups of long thread hairs, THb: lower groups of long thread hairs, FH, freehook hairs. In this case the right statocyst cannot separate head-down rotation from right-side-down rotation. In the left statocyst, however, the fluid moves in the opposite direction during right-side-down rotation and in the same direction in head-down rotation. 'Right side down' and 'head up' cannot be separated by the left statocyst. (After SANDEMAN and OKAJIMA, 1972; reproduced by permission of Company of Biologists Ltd.)

involved in the receptory system. On the basis of records of impulse frequency and of observed fluid movements in the statocysts, SANDEMAN and OKAJIMA have advanced a model of a receptor system which, through a composite input pattern, is able to discriminate between angular rotations about all the body axes, but in which signals from both statocysts are required for separating rotations about the two horizontal axes (Fig. 8-38). For additional information consult SANDEMAN and OKAJIMA (1973a, b).

Sensitivity to rotation has also been found in cephalopods. DIJKGRAAF (1961) demonstrated compensatory reflexes of *Octopus vulgaris* on a horizontal turntable and their disappearance after removal of the statocysts, while MATURANA and SPERLING (1963) presented electrophysiological evidence. The presence of three crista sections with hairs embedded in 'cupulae' arranged in three planes at right angles—reminiscent of the vertebrate semicircular canals—suggests that each statocyst is sensitive to angular acceleration in any direction (YOUNG, 1960). This has recently been confirmed by BUDELMANN and WOLFF (1973), using electrophysiological techniques. In addition, BUDELMANN and WOLFF demonstrated that the angular acceleration receptors (cristae) are also sensitive to gravity. In the receptor system of *O. vulgaris*, rotated about its longitudinal axis, they found

(i) different responses to identical angular acceleration (deceleration) stimuli dependent on the system's position with respect to gravity at the time of acceleration (deceleration) onset, (ii) different resting discharge rates dependent on position with respect to gravity and (iii) changes of discharge rate during constant velocity rotation. Sensitivity to acceleration has likewise been demonstrated in *Sepia officinalis* (DIJKGRAAF, 1963a; COLLEWIJN, 1970; MESSENGER, 1970). For details on the structure of maculae and cristae of the statocysts of *O. vulgaris*, *S. officinalis* and *Loligo vulgaris*, BUDELMANN and co-authors (1973) should be consulted.

Gravity and Dorsal Light Reaction

Apart from statocysts, other mechanisms are instrumental in body position maintenance. The role played by visual stimuli in equilibrium orientation was already reported by DELAGE (1887) in the crustacean genera *Mysis* and *Palaemon* and subsequently confirmed by several workers in this field. In *Hemimysis lamornae* and several other crustaceans, VON BUDDENBROCK (1914) demonstrated that after bilateral statocyst removal the animals invariably swim with their dorsal surface towards the light independently of their position relative to the gravitational field. He introduced the term **dorsal light reaction** ('Lichtrückenreflex') but pointed out that some crustaceans which usually swim upside down, like *Penaeus* sp. larvae and *Euphausia* sp., show **ventral light reaction.** Ventral light reaction is also found in the brine shrimp *Artemia salina*, which has been extensively studied by SEIFERT (1932). The extent to which either the gravitational force or dorsal light reaction participates in equilibrium orientation of decapod crustaceans varies considerably from one species to another. The shrimp *Penaeus membranaceus*, for instance, does not respond to light at all and is completely disoriented after bilateral statocyst removal, whereas decapods without statocysts (e.g. species of *Virbius* and *Hippolyte*) show the same reactions to light as *Hemimysis lamornae* from which the statocysts have been removed. Brachyuran zoeae respond to light; but megalopae with developed statocysts maintain their body position independently of light incidence.

In marine invertebrates positioning by means of photic stimuli occurs in several groups; it is sometimes very obvious in animals without statocysts. Positioning by photic stimuli has been reported in the hydromedusae *Leuckartiara* sp. and *Charybdaea* sp. (FRAENKEL, 1931), in the pelagic polychaetes *Tomopteris* sp. (FRAENKEL, 1931) and *Alciope* sp. (VON BUDDENBROCK, cf. 1952), in the heteropods *Pterotrachea mutica* and *P. coronata* through interaction with statocysts (FRIEDRICH, 1932), in the echinoderms *Asterias rubens*, species of the genus *Astropecten*, and *Psammechinus miliaris* (DIEBSCHLAG, 1938) and, as mentioned before, in several crustaceans (VON BUDDENBROCK, 1914). VON BUDDENBROCK suggested that dorsal light reaction prevails in pelagic animals whereas in benthic animals equilibrium orientation by means of statocysts dominates.

Extensive studies on the interaction between the statocysts and the eyes in equilibrium orientation in decapod crustaceans have been carried out by ALVERDES (1926, 1928) and SCHÖNE (1952, 1959). ALVERDES worked with the shrimps *Leander xiphias*, which has statocysts, and *Processa canaliculata*, which has no statocysts. In *L. xiphias* the action of the statocysts dominates over the dorsal light reaction.

Intact individuals exposed to unilateral illumination only react with eyestalk deviation. In *P. canaliculata* equilibrium orientation is based entirely on dorsal light reaction as is the case in *L. xiphias* after statocyst removal. Regarding the question of whether the dorsal light reaction is based on balanced stimulation of the two eyes, conflicting results have been obtained. Unilateral blinding by removal of one of the eyes may produce different effects. *L. xiphias* (deprived of statocysts) exhibits compensatory movements about the longitudinal axis toward the operated side until it finds a new resting position in which it is tilted over at an angle of about 45°. *P. canaliculata*, on the other hand, behaves like an intact individual. SCHÖNE (1952) likewise found after operative elimination (by cutting through the optical ganglion) of one of the two eyes in *Palaemonetes varians* (deprived of statocysts) a tendency to rotate towards the blinded side. Remarkably, the rotation is more intensive in complete darkness than in an illuminated environment. Unilateral blinding by covering one of the eyes, however, results in a rotation towards the seeing side. The physiological mechanism has not yet been clarified (SCHÖNE, 1959).

When *Palaemonetes varians* is exposed to two lights 90° apart, of either equal or different intensity, the shrimp orient according to the triangle of forces rule (SCHÖNE, 1959). This indicates balanced stimulation of the two eyes, comparable to phototropotaxis.

An interesting aspect of dorsal light reaction is the angular displacement about the transverse axis (pitching) where no balance of stimulation mechanism of the two eyes can be involved. SCHÖNE (1952), however, demonstrated that blackening the posterior or anterior zone of the two eyes causes *Palaemonetes varians* (deprived of statocysts) to somersault in the ventral or dorsal direction, respectively. These results are reminiscent of observations by SCHÖNE (1951b) on aquatic beetle larvae —possessing 6 ocelli on each side of the head—which exhibit a balanced action between anterior and posterior visual receptors.

To what extent does light contribute to equilibrium orientation in different angular positions? The actual extent appears to vary with the shearing force exerted by the statoliths (SCHÖNE, 1961). *Palaemonetes varians* with one statolith removed were exposed to unilateral illumination at a constant angle to the eye. When the floor of the intact statocyst is horizontal (statolith not exerting any shearing force), eyestalk deviation is maximal; but when the statocyst floor is vertical (maximal shearing force), eyestalk deviation is minimal. The difference between the two extremes of eyestalk deviation becomes more accentuated when the shearing force of the statolith is increased in a centrifuge.

Comparatively little attention has been paid to the interaction between eyes and statocysts in mysids. FOXON (1940) described dorsal light reaction in *Hemimysis lamornae* with the statoliths removed. He found that dorsal light reaction coincides with either negative or positive phototaxis; these cause, irrespective of the direction of the incident light, a movement away from the light source with the ventral surface foremost or a movement towards the light source with the dorsal surface forwards.

JANDER (1962) pointed out that *Mysidium gracile* usually swim in a horizontal plane, performing extensive spontaneous turnings to the right and to the left about the vertical axis, but that rotations about the longitudinal and transverse axes are restricted. The equilibrium orientation appears to be the result of the joint action of responsiveness to gravity and dorsal light reaction. When free-swimming intact individuals are subjected to horizontal illumination they swim in a slanted position reflecting a compromise between two conflicting stimuli. The dorsal light reaction component increases with irradiance, causing a more pronounced tilt. The effect of light is greater in rotations about the transverse axis than about the longitudinal axis. JANDER (1965) reviewed phylogenetic aspects of the dorsal light reaction in arthropods and listed extensive references.

There is clear evidence of a close interaction between gravitational and photic receptors in many invertebrates. A comparison of the physical properties of the stimuli involved reveals some interesting aspects. Light (intensity of radiant energy, directionality, contrast) provides the invertebrate with a multitude of sensory tools for orientation in space. Gravity, on the other hand, is characterized by its invariability; it provides the invertebrate with the most reliable plane of reference. There are several instances of stabilization of the visual field on the basis of gravity in invertebrates that can move their eyes, e.g. in a number of crustaceans and cephalopods. This is discussed by MILNE and MILNE (1965), who argue that these animals 'move their eyes in relation to the body to prevent their eyes from moving in space' (p. 285). Electrophysiological evidence for the relationship between eyes and statocysts in crustaceans has been provided by WIERSMA and OBERJAT (1968), WIERSMA and FOIRE (1971) and YORK and co-authors (1972).

A striking example is the shrimp *Tuleariocaris sansibarica*, which usually maintains a head-down vertical position on the long vertical spines of the sea-urchin *Diadema setosum* (FRICKE and HENTSCHEL, 1971). When released in a vertical position in front of vertical and horizontal spines, the shrimps invariably swim towards the vertical spines. When released in a horizontal position, most individuals (76%) at first approach the horizontal spines, but after about 3 secs move towards the vertical spines. Apparently, the shrimps primarily orient their long body axis to the visual field, but then re-adjust their position to bring it in line with the gravitational field.

Control of the visual field by gravitational force is displayed by *Octopus vulgaris*; as appears from the constant horizontal position of the slit pupil irrespective of the body position, they keep their eyes stabilized by cyclorotational correction. This ability disappears upon statocyst removal. Furthermore, a trained octopus loses its ability to discriminate between horizontal and vertical objects when its statocysts are removed; but it continues to discriminate successfully between, for instance, a black and a white disc (WELLS, 1960).

On the other hand, the statocyst system may be controlled by visual stimuli. In central-nervous compensation of an equilibrium-receptor system whose balance has been upset (e.g. by removal of one statolith in a decapod crustacean) visual or proprioceptive frames of reference will undoubtedly be involved.

Other Mechanisms Controlling Positioning

Body orientation may be controlled by systems other than statocyst action and/or dorsal light reaction alone.

This was first reported by VON BUDDENBROCK (1914), who found that after statocyst removal invertebrates like *Leptomysis mediterranea*, *Hemimysis lamornae* and *Palaemon serratus* are still sensitive to gravity, as is *Squilla mantis*, which has no statocysts at all. He named this phenomenon 'general position reflex' ('allgemeiner Lagereflex') and suggested that this orientation mechanism results from gravitational force acting upon internal organs supported by mesenteries. RICE (1961) likewise came to the conclusion that swimming mysids lacking statocysts are able, even in complete darkness, to orient in relation to gravity—presumably through the 'general position reflex', the actual operation of which is still not understood. The idea of internal organs hanging from mesenteries and acting as gravity receptors in righting reactions of asteroids was also advanced by WOLF (1926), who worked with *Asterina gibbosa*, *Astropecten auranciacus* and *Marthasterias glacialis*.

As the result of equilibrium studies on the heteropod prosobranchs *Pterotrachea mutica* and *P. coronata*, FRIEDRICH (1932) suggested that, apart from statocysts and eyes, also paired organs described as skin projections ('Hauthügel') contribute to equilibrium orientation. The mechanism, however, is not known.

Far more conspicuous are the responses evoked by tactile and proprioceptive stimuli. KÜHN (1914) experimented with the freshwater crayfish *Astacus fluviatilis*. An intact individual was suspended in a slanted position. It performed compensatory movements to right itself, immediately rotating in the opposite direction (towards a more tilted position) when the legs on its elevated side touched a solid substrate. The same response occurs in an asymmetrical individual (one statocyst removed) performing compensatory movements towards the operated side. As soon as the legs on the operated side come into contact with the substrate, the crayfish exhibits compensatory movements towards the intact side. The marked difference between the behaviour of suspended shrimps *Leander xiphias* and *Processa canaliculata* and of shrimps allowed to rest freely on a substrate emphasizes the importance of a symmetrical contact stimulus and proprioception in the legs (ALVERDES, 1926). Completely disoriented, statocystless and blinded lobsters *Palinurus vulgaris* regain their oriented posture as soon as the legs make contact with a solid substrate (DIJKGRAAF, 1956a). Apparently, this reaction is superimposed on the statocyst-evoked responses; this would seem understandable in view of the natural positioning of crabs, lobsters and shrimps in a rocky environment. Irrespective of the inclination of the substrate, the crustaceans tend to keep their dorso-ventral axis perpendicular to the plane of the substrate. In *Astacus leptodactylus* STEIN and SCHÖNE (1972) demonstrated that the effect of leg contact—recorded quantitatively from compensatory eyestalk movements—is stronger after statolith removal; conversely, compensatory eyestalk movements—caused by imposed rotation of a crayfish about its longitudinal axis—are reduced when the legs are in contact with the base plane.

There is an extensive literature on the positioning of echinoderms, especially asteroids, comprehensively reviewed by REESE (1966). Most authors agree that, after overturning, righting is generally released by absence of podia contact; in upside-down position, stimulation of the podia is reported to prevent righting. The same holds true for marine gastropods in which absence of contact stimulation of the foot releases righting reactions initiated by search movements of the foot (WEBER, 1926). In rock-dwelling gastropods (e.g. species of *Haliotes* and *Trochus*), the direction of search movements is not related to gravity; but in gastropods which live on sand (e.g. species of *Nassa*, *Natica*, *Conus*, *Murex* and *Chenopus*), search movements are gravity oriented.

The integrative orientation mechanisms of *Octopus vulgaris* have been discussed by WELLS (1963a). Surprisingly, interactions between contact receptors and proprioception on the one hand, and positioning on the other, are poorly developed; WELLS regards this as a consequence of the pelagic ancestry of the Octopoda.

(b) Geotaxis

The term geotaxis refers to locomotory movements with a vertical component controlled by gravity perception. Movements toward the earth's centre are called **positive geotaxis**; those away from it, **negative geotaxis**.

Burrowing Invertebrates

Statocysts are involved in geotactical responses in a number of cases. Especially in burrowing marine invertebrates gravity appears to be of paramount significance and to represent the most important frame of reference. VON BUDDENBROCK (1912, 1913) studied the two burrowing polychaetes *Arenicola grubei* and *Branchiomma vesiculosum*. He observed the worms in sand-filled glass jars or dishes which could be tilted. *A. grubei* burrows head-first vertically downward. When the container is tilted 90° or 180°, the worm changes its direction in the sand by 90° or 180° respectively, continuing to burrow straight downward. Upon removal of the paired statocysts (located in the head region), positive geotaxis is completely abolished and the worms move in any direction. A worm with one statocyst removed behaves like an intact individual.

Branchiomma vesiculosum has its statocysts also in the head region, but it burrows tail first. When the container is tilted, directional changes are initiated by the tail, while the head region (containing the statocysts) inevitably remains in the tilted position until it reaches the new vertical section of the burrow initiated by the tail. In an extensive series of experiments VON BUDDENBROCK (1913) demonstrated that irrespective of the position of the head, and regardless of the curves of the intermediate part of the body, the tail invariably points downward. Removal of one statocyst does not affect this behaviour but removal of both statocysts causes complete disorientation. The remote control of the tail in response to the angular displacements of the statocysts in the head region has been explained by VON BUDDENBROCK as due to an integrated proprioceptive system which tends to keep the tail parallel to the position the head attempts to attain. Remarkably, the upward movements of these invertebrates to the surface do not seem to be controlled by the statocysts, a feature which has also been reported by JÄGER (1932) in the sand-dwelling turbellarian *Otoplana* sp.

Statocyst-controlled movements of burrowing invertebrates are found in different taxonomic groups. They may be regarded as an ecological adaptation to a habitat which provides no visual cues. Burrowing bivalve molluscs (e.g. species of *Solen*, *Cardium* and *Venus*) have statocysts in that part of their foot which leads the burrowing movements (VON BUDDENBROCK, 1952; CHARLES, 1966). In a rotating trough filled with wet sand *Solen ensis* burrows in a direction which corresponds to the resultant of the centrifugal and gravitational forces (FRAENKEL, 1927c). Statocyst extirpation in burrowing bivalves has not yet been performed.

The burrowing turbellarian *Convoluta roscoffensis*, when placed on a rotating vertical glass plate (covered with gelatine to provide a foothold), likewise moves according to the resultant of the centrifugal and gravitational forces (FRAENKEL, 1929). *C. roscoffensis* has a single statocyst, located in its brain and inaccessible to operation. Occasionally, however, GAMBLE and KEEBLE (1903) found individuals which lacked the statocyst; these individuals did not respond geotactically.

The holothurian *Synapta digitata* normally burrows vertically, head first; it has 5 statocysts close to its nerve-ring (VON BUDDENBROCK, 1912). In the burrowing holothurian *Caudina chilensis*, the 5 pairs of statocysts located close to the nerve-ring may likewise account for the positive geotactic response of the oral end but, remarkably, not for the negative geotaxis of its anal end. The tail end persists in responding negative-geotactically, even when isolated from the nerve-ring (YAMANOUCHI, 1929a, b). The burrowing isopod *Cyathura carinata* also possesses statocysts; after statocyst extirpation it is no longer able to dig burrows effectively (LANGENBUCH, 1928). The statocysts do not seem to be involved in upward movements towards the surface.

Burrowing invertebrates, while orienting to gravity, need not necessarily move vertically. The fiddler crab *Uca pugilator*, for instance, digs burrows in different directions, vertical as well as slanted. Burrowing *U. pugilator* were observed by DEMBOWSKI (1926) in a sand-filled container consisting of two glass plates 2 cm apart. When the container is tilted 90°, the crabs change the direction of their burrows by 90° irrespective of the initial direction of the burrow but maintain a constant angle relative to the direction of gravity (SCHÖNE, 1961). This example again fits in well with the interpretation of orientation to gravity as compass orientation in the vertical plane.

Vertical Migrations of Zooplankton

Vertical movements of planktonic invertebrates sometimes extend over several hundred metres (e.g. RUSSELL, 1927; CUSHING, 1951; BAYLOR and SMITH, 1957; BAINBRIDGE, 1961; BANSE, 1964; RINGELBERG, 1964; THORSON, 1964; VERWEY, 1966; Volume I: KINNE, 1970b, 1971, and SEGAL, 1970). While effects of light, temperature, salinity, pressure and gravity have been reported, or suggested, to affect vertical zooplankton migrations, the main orientation mechanisms seem to be related to light distribution. Orientational responses to light (phototaxis) are fairly well established; but notwithstanding the prolific literature, orientation based on gravity perception (first mentioned by PARKER, 1902) is still a debatable issue.

In surprisingly few cases has gravity perception by statocysts been shown to be involved in vertical migrations of zooplankters. In scyphomedusae and ctenophores (p. 625) statocyst action controls the positioning of the symmetry axis in a vertical direction and determines vertical locomotory movements (cf. FRAENKEL and GUNN, 1961). In mysids, vertical migration controlled by statocysts has been demonstrated by FOXON (1940) and RICE (1961); in intact individuals gravity dominates over light, but after statocyst removal the influence of light increases. Strong indications for statocyst-controlled vertical movements have also been obtained in the ephyrae of *Aurelia aurita*, the ctenophores *Pleurobrachia pileus* and *Bolinopsis infundi-*

bulum, the megalopae of *Carcinus maenas* and larvae of the cephalopod *Loligo forbesi* (RICE, 1964).

In a large number of plankters (e.g. various nauplii and zoeae, copepods, cladocerans, euphausiids, anthomedusae, and a variety of larvae of benthic invertebrates) special gravity receptors have not been found. VERWEY (1966) postulated gravity-controlled vertical migration as of widespread occurrence in planktonic organisms on the basis of numerous literature references. However, actual use of gravity as a plane of reference has, he argued, never been proved conclusively. The usual method of demonstrating geotaxis in vertical movements is to eliminate the influence of light, but this only proves that light is not involved. VERWEY (1966) did not rule out an alternative mechanism acting on the hydrostatic-pressure gradient.

By and large, the mechanism controlling vertical orientation without the aid of statocysts and light perception is still obscure. The demonstration by RICE (1961) that mysids deprived of statocysts are still able to perform oriented vertical movements in complete darkness indicates that such a mechanism is likely to exist. The 'general position reflex' suggested by VON BUDDENBROCK (1914), or the functioning of the antennae suggested by BIDDER (1929) as auxiliary gravity receptor systems, deserve consideration in this context.

Some authors have advanced the idea that a specific mechanism of gravity orientation is not necessarily required if stable equilibrium is achieved through the position of the centre of gravity. Supposedly, the invertebrate then only needs to swim or sink in order to perform vertical movements (EWALD, 1910, in *Daphnia* sp.). In gastropod larvae the weight of the shell determines the vertical position, while locomotion is linked to feeding since the apparatus used for both activities (the velum) is the same (RICHTER, 1973).

Another remarkable feature of vertical movements of planktonic invertebrates is the close interaction between phototaxis and geotaxis (whether or not mediated by statocysts). In some invertebrates, like larvae of the horseshoe crab *Limulus polyphemus*, larvae of the polychaete *Polygordius* and larvae of *Loligo* sp., LOEB (1893) observed in photopositive specimens a tendency to move upward, while photonegative individuals tended to move downward or to crawl along the bottom. In other words, positive phototaxis seems to be associated with negative geotaxis, and negative phototaxis with positive geotaxis. Further, LOEB found that the reversal of the signs of phototaxis and geotaxis can be induced by the same conditions. For a critical discussion of this linkage of taxes consult KALMUS (1931). The same type of interaction between phototaxis and geotaxis was found by CLARKE (1930) in *Daphnia magna* and *D. pulex*. Reversals of the signs of phototaxis as well as geotaxis were induced by changes in irradiance intensity. The phenomenon seems to be rather widespread and may be considered a complex of two mechanisms reinforcing each other in keeping the invertebrates in the proper water layers, also during the night.

The linkage of positive phototaxis to negative geotaxis and vice versa, however, appears not to be so strict in all cases. The phototaxis-geotaxis interaction may show adaptive modifications according to the prevailing conditions. BAYNE (1964) demonstrated in the larvae of the bivalve *Mytilus edulis* a variety of geotaxis-phototaxis combinations, dependent upon the particular larval stage and environmental conditions. During the greater part of their pelagic life, the larvae do not respond to light but show strong negative geotaxis. Once the eye spots develop, the larvae become photopositive and geonegative; but at the time of settlement the signs of both taxes are reversed. In the subsequent phase, when they crawl about on the substrate, they remain photonegative but become geonegative; this apparently facilitates selection of a more elevated position for final attachment.

A comparable process has been described by CRISP and GHOBASHY (1971) in larvae of the ascidian *Diplosoma listerianum*, which in the swimming stage are photopositive and geonegative. However, when the larvae approach settlement they become photonegative but remain geonegative, apparently to prevent settlement in a fully illuminated region while precluding descent to excessive depths. Under natural conditions the larvae preferably settle on the shaded underside of objects like overhanging rocks.

Crawling Invertebrates on Sloping or Vertical Substrates

The locomotory movements of crawling invertebrates, unlike those of burrowing and free-swimming organisms, are confined to a two-dimensional plane which need not be flat or horizontal. Several workers have paid special attention to the ecology and behaviour of intertidal invertebrates crawling on inclined or vertical substrates (e.g. rock faces); the ecological implications have been extensively reviewed in NEWELL (1972). Most work concerning the mechanism controlling vertical movements has been done on littorinids. Negative geotaxis and negative phototaxis appear to dominate over positive geotaxis and positive phototaxis. This would facilitate finding darker rock areas for resettlement after displacement, e.g. by wave action. Cessation of climbing towards the upper level of zonation is reported to be caused by dryness of substrate, as observed in *Littorina littorea* (KANDA, 1916; GOWANLOCH and HAYES, 1926), in *L. neritoides* (FRAENKEL, 1927b) and *L. littoralis* (= *obtusata*) (BARKMAN, 1955). There are further indications that the upward movement of *L. littoralis* is halted by the occurrence of fucoid seaweeds, among which they preferably settle (BARKMAN, 1955). According to KANDA (1916), downward movement in *L. littorea* is the result of strong solar illumination or desiccation. FRAENKEL (1927b), however, never observed active downward crawling in *L. neritoides*. Under adverse conditions like desiccation or strong overhead illumination the snails, after closing their shells, attach themselves firmly to the substrate or drop down. According to BARKMAN (1955), *L. littoralis*, upon finding itself too high in the tidal zone, likewise attaches itself firmly or moves downward. A marked reversal of negative geotaxis into positive geotaxis in *L. littoralis* (= *obtusata*) as the result of severe cold (below 2° C) was observed by JANSSEN (1960).

An interesting interpretation of the complex phototactic-geotactical reactions of immersed littorinids climbing a rock face with crevices has been presented by BOHN (1904b, 1905) and FRAENKEL (1927b). Being geonegative, the snails crawl up the rock. When they encounter a crevice, they crawl into it more or less horizontally as the result of negative phototaxis, until they reach the far end of the crevice where, being geonegative, they move upward to the ceiling. When a snail finds itself in an upside-down position on the ceiling it becomes photopositive. Due to this reversal of the sign of phototaxis the snail moves out again. A littorinid, therefore, will not

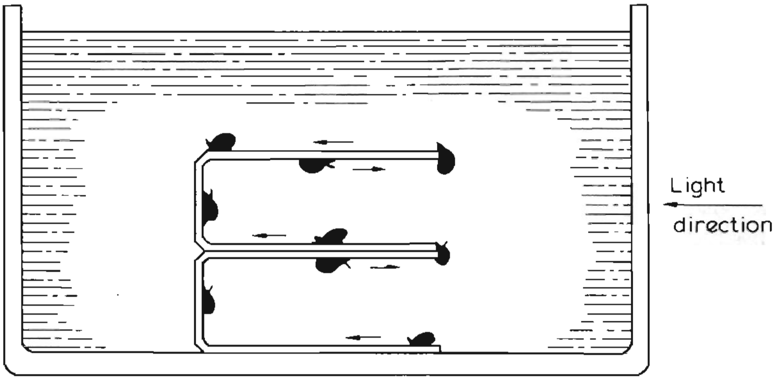

Fig. 8-39: *Littorina neritoides*. Oriented movements are determined by negative phototaxis while on the floor of container, by negative geotaxis while on the vertical wall and by positive phototaxis while hanging on the ceiling in upside down position. (After FRAENKEL, 1972b; reproduced by permission of Springer-Verlag, Berlin.)

be trapped in an immersed rock crevice (Fig. 8-39). This process continues until the snail encounters a crevice which is not immersed; here it will settle since, in air, its reaction is photonegative even in an upside-down position.

In his extensive ecological study on *Littorina littorea*, NEWELL (1958a, b) has given an account of the widely different habitats in which these periwinkles occur and the great variety of adaptive behavioural responses which cannot be adequately explained in terms of simple taxes. In feeding excursions, winkles settled on vertical or sloping surfaces will as a rule first move downward, then horizontally and then up again, to regain approximately their original position. Further, NEWELL demonstrated that—for a period varying from a few hours to 10 days—snails collected from horizontal surfaces are, as a result of habituation, indifferent to gravitational stimuli; this effect gradually diminishes when the snails are presented with vertical surfaces.

There are some other intertidal molluscs living on rocky coasts, in which, as in littorinids, adaptive responses to gravity have been demonstrated. The mobile bivalve *Lasaea rubra*, which can crawl about as freely as a gastropod, normally lives attached by temporary byssus threads, nestling in small crevices (e.g. empty shells of the barnacle *Chthalamus stellatus*) in the upper tidal zone. MORTON (1960) demonstrated that these bivalves, when removed from their site, exhibit primarily negative geotaxis. At the same time, their negative photoklinotaxis enables them to find darker crevices or refuges in which, finally, lateral contact (thigmotaxis) gives the bivalves an increasing precision in securing shelter against wave action, sunlight and desiccation.

The chiton *Lepidochitona cinereus*, on the other hand, when uncovered during low tide, is found on the underside of stones. If such a stone is overturned, the chitons start moving downward: they aggregate again under the new lower surface of the stone. *L. cinereus* are very sensitive to desiccation. In laboratory experiments EVANS (1951) showed that the chitons exhibit strong positive geotaxis when in air; but when in water they are indifferent to gravity. The effect of the positive geotaxis is reinforced by photokinesis, which induces faster movement when illuminated.

Is gravity perception involved in the vertical migration of *Littorina neritoides*? This question has been investigated by FRAENKEL (1927b). When placed on a horizontal rotating dish, the snails, being negatively geotactic, move towards the axis of rotation. Referring to KANDA (1916)—who considered the gravitational pull of the heavy shell or the action of statocysts as releasers of upward crawling —FRAENKEL demonstrated that when an upward pull was exerted on the shell of an immersed individual (by affixing a piece of wax of very low specific gravity) negative geotaxis persisted. This experiment indicates that the well-developed statocysts may be involved in gravity perception, as already suggested by KANDA; because of the small size of littorinids FRAENKEL refrained from operating. In the freshwater snail *Lymnaea stagnalis*, GEUZE (1968) succeeded in removing the statocysts. While intact snails, when placed in air, move straight downward on a plane inclined by 30° or 15°, and straight upward when immersed in oxygen-poor water, operated individuals are disoriented. Unilateral removal of the statocyst causes deviation towards the intact side when the snail is geopositive, and towards the operated side when it is geonegative.

Several invertebrates without statocysts have been reported to respond to gravity on inclined or vertical substrates. OTTAWAY and THOMAS (1971) studied the intertidal anemone *Actinia tenebrosa*. Zonation at midtide level is brought about by negative geotaxis when *A. tenebrosa* are submerged for a prolonged period; positive geotaxis can be induced by a period of prolonged emergence. It is suggested that the differential muscle tensions due to gravity in air and under water might represent the effective stimulus. Several pertinent studies have been conducted on echinoderms (cf. REESE, 1966). The strong negative geotaxis of the long-spined sea urchin *Centrechinus* (= *Diadema*) *antillarum* has been discussed by PARKER (1922), who suggested that the pull of the spines, with their relatively high specific gravity, may be perceived at their supports. According to WOLF (1926), the weight of the gut, suspended by mesenteries, is perceived by asteroids and ophiuroids. He introduced iron-filings into the gut and demonstrated that natural righting reactions can be interfered with by means of a magnet. In the holothurian *Thyone briareus* the negative gravity response is supposed to be controlled by the sensitivity of the body wall to displacements (STIER, 1933).

In an extensive study KALMUS (1929) demonstrated that the pull of the body on the podia—when on a vertical surface—induces *Asterina gibbosa* to move upward. If an upward pull is exerted on *A. gibbosa* (by attaching a cork float by a thread to its dorsal side) the echinoderm moves downward. On a horizontal plane a lateral pull evokes locomotion in the opposite direction. These results have been confirmed by CROZIER (1935) in the same species.

The twenties and thirties witnessed a debate on a theory advanced by CROZIER and his associates concerning the orientation of animals, including some marine invertebrates, on an inclined plane (Fig. 8-40). On a slanted surface, the angle (θ) of ascent or descent relative to a horizontal in that plane is related to the slope of the plane (α). When the plane slopes steeply (over 70° relative to the horizontal), the

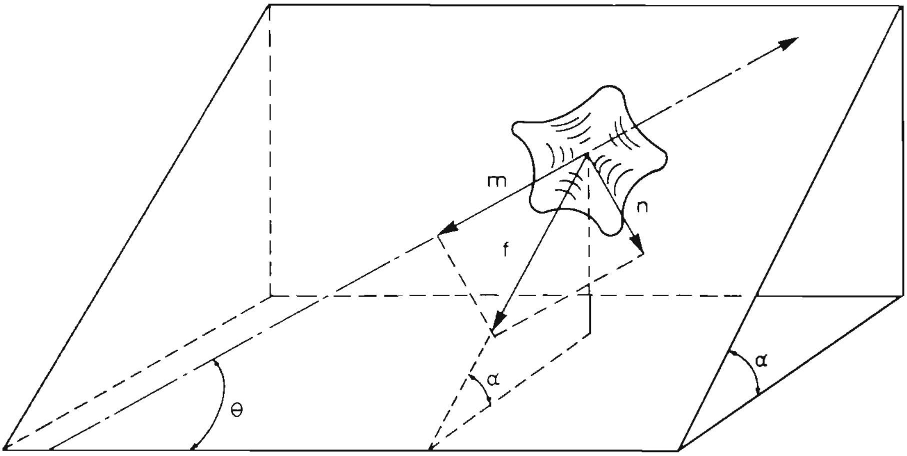

Fig. 8-40: *Asterina gibbosa.* Oriented movements of test animal on slanted surface. m: line of progression at angle θ relative to the horizontal in the plane, f: effective gravitational pull, n: lateral pull, α: inclination of the plane. (After CROZIER, 1935; modified; reproduced by permission of the Rockefeller University Press, New York.)

animals move along the steepest way (θ = about 90°), but when the plane is less steep they tend to move more horizontally. This 'geotactic orientation' (θ) has been expressed mathematically as a logarithmic, rectilinear or other function of sin α, while the mechanism is seen as controlled by the difference—due to the tilt—in muscle tension ('muscle tension theory') of the limbs on either side of the body, which should not exceed a certain critical value. For marine invertebrates such behaviour has been demonstrated in the fiddler crab *Uca pugnax* (KROPP and CROZIER, 1928) and in the sea-star *Asterina gibbosa* (CROZIER, 1935).

JÄGER (1932) carried out a series of experiments with invertebrates—including some marine representatives, such as the polychaete *Arenicola marina,* the turbellarian *Otoplana* sp. and the echinoderm *Asterias rubens*—and critically surveyed the problems encountered on an inclined surface. JÄGER found two types of response: (i) Invertebrates which, at any inclination of the surface, take the shortest and steepest way upward or downward; an example is *Arenicola marina* which has statocysts and exhibits genuine positive geotactic orientation. (ii) Invertebrates which more or less obey the principle advanced by CROZIER; i.e., where the angle of ascent increases or decreases with the slope of the inclined plane. An example of the second type is *Asterias rubens,* which shows little variation in direction when the slope is steep, but a great variety of locomotory directions on a less steep slope, indicating that the sea-stars do not respond geotactically at all, but actually tend to move in any direction except that along which the lateral pull or the amount of rolling exceeds a certain value. In other words, the steeper the surface, the less freedom the sea-star has to move horizontally. CROZIER's principle is more accurately reflected by invertebrates which attempt to move as horizontally as possible but are prevented from doing so due to increasing surface inclination.

An extreme type of orientation on an inclined surface has been reported by HAMNER and co-authors (1968) for the nocturnal sandbeach isopod *Tylos punctatus*. Like the sandhopper *Talitrus saltator* the isopod moves up and down the beach; but instead of using solar-compass orientation it appears to be sensitive to the inclination of the beach, responding to slopes as small as 1°. It is not known whether gravity perception or geotaxis is involved.

(11) Sound and Vibration

Very little is known yet of the role played by sound and vibration in the orientation of marine invertebrates. Unlike visual cues, however, conditions for transmission of acoustic energy and other mechanical waves through water are better than in air and may be utilized far more effectively for long-range detection of the source of stimulation than light (PUMPHREY, 1950; HORRIDGE, 1966e; Chapter 8.3).

While in marine fishes (Chapter 8.2) and especially in odontocete cetaceans (Chapter 8.3) information on sound perception is increasing rapidly, knowledge regarding perception of acoustic energy by marine invertebrates is still fragmentary and largely speculative. In his review FRINGS (1964) emphasized the technical problems in marine acoustic research and stressed the present lack of uniform terminology. While PUMPHREY (1950) defines **hearing** as the reception of vibratory stimuli of any nature, provided the source of stimulation is not in contact with the body of the perceiving animal, VON BUDDENBROCK (1952) maintains that hearing comprises the functioning of a specialized hearing organ, which, as far as we know, would confine this sensory ability largely to insects and vertebrates. According to COHEN and DIJKGRAAF (1961), hearing occurs only in animals which (i) are sensitive to air-borne or water-borne sound and (ii) detect these stimuli with specialized sound receptors. If the second condition is not fulfilled, these authors speak of **sound reception**, whereas perception of sound or vibrations transmitted through a solid substrate (e.g. vibrations caused by tapping an aquarium wall) is called **vibration reception**. Since so little is known yet of the mechanism of sound or vibration sensitivity in marine invertebrates, FRINGS and FRINGS (1967) suggested that the term **phonoreception** be used for reception of sound irrespective of the nature of the stimulation and regardless of the medium through which it is transmitted.

Although at one time the otocyst (= statocyst) was supposed to act as an auditory organ in crustaceans (HENSEN, 1863), no evidence is so far available for the existence of specialized phonoreceptors in marine invertebrates. From observations by PRENTISS (1901) in crustaceans (*Palaemonetes vulgaris*) it appeared that the perception of water-borne vibrations is most likely mediated through tactile receptors, while COHEN and co-authors (1953) and COHEN (1955, 1960) demonstrated in *Panulirus interruptus* and *Homarus americanus*, by means of action-potential recordings, that the statocyst nerve does not respond to water-borne or air-borne pressure waves but only to vibrations conducted through the solid substrate. The latter stimulus appears to be received by the same receptors (thread hairs) which respond to accelerations, but apparently with a different input pattern.

Even *Octopus vulgaris*, which has well-developed statocysts (YOUNG, 1960), did not respond—in training experiments—to hydrodynamic sound waves (HUB-

BARD, 1960; DIJKGRAAF, 1963b); but it appeared to be sensitive to very low-frequency vibrations when the side of the aquarium was jarred (WELLS, 1966). In DIJKGRAAF's experiments, however, *Sepia officinalis* responded to strong underwater sounds of 180 Hz.

While the existence of hearing in the commonly accepted usage of the term has hitherto been doubted in marine invertebrates, responsiveness to solid-borne or water-borne vibrations has frequently been reported. In field observations PRENTISS (1901) showed that a variety of air-borne sounds did not affect the feeding behaviour of fiddler crabs *Uca pugilator* but, on the ground being struck with a heavy stone, all crabs within a radius of 4 m appeared startled. Apart from waving displays and sound production, observed in their natural courtship behaviour, several fiddler crabs of the genus *Uca* have been found to produce signals via solid-borne vibrations by rapping on the ground with their cheliped or by vibratory movements of their ambulatory legs (CRANE, 1943; VON HAGEN, 1961, 1962; SALMON and STOUT, 1962; SALMON, 1965, 1967; SALMON and ATSAIDES, 1968; WALKER, 1972; SALMON and HORCH, 1973). This behaviour, characteristic of many burrow-inhabiting semi-terrestrial crabs, is not restricted to fiddler crabs. It has also been reported for other ocypodid crabs like *Dotilla* sp. and *Ocypode quadrata*, in grapsid crabs like *Sesarma curacaoensis* and *S. rectum* (VON HAGEN, 1967b), and in the almost terrestrial crab *Gecarcinus lateralis* (KLAASZEN, 1973). The male of *S. rectum* has been seen rapping its own cheliped—laid down on the substrate as an anvil—with the other cheliped, acting as a hammer (VON HAGEN, 1967b). *Gecarcinus lateralis*, which has specialized stridulatory organs, has been observed inducing vibrations in the substrate, by pressing its body to the ground during stridulation (KLAASZEN, 1973).

In experiments with *Uca pugilator* the results of sound play backs—recorded with a microphone sensitive to substrate vibrations and relatively insensitive to air-borne sounds—have shown that conspecific males, as well as females, respond to these signals (SALMON, 1965; SALMON and ATSAIDES, 1969).

Most experiments carried out with fiddler crabs strongly suggest that the acoustic energy transmitted through the substrate is the primary stimulus in sound reception. In some fiddler crabs, however, such as *Uca rapax*, *U. mordax* and *U. pugnax*, the sound-producing mechanism, operating through vibratory movements of the ambulatories rather than by rapping the chelipeds against the substrate, suggests that the air-borne component of the acoustic energy may be of importance in sound reception, but no experimental evidence is available yet (SALMON, 1967). Only in the ghost crabs *Ocypode ceratophthalmus* and *O. quadrata* has the perception of air-borne sounds, in the order of 1 to 2 kHz, been demonstrated neurophysiologically (HORCH, 1971). These crabs are sensitive to substrate vibrations as well. The sensitivity to high-frequency substrate vibrations and air-borne sounds has been localized in the myochordotonal organ (Barth's organ) in the merus of each walking leg. According to HORCH's hypothesis, hearing in *Ocypode* species involves the induction of vibrations in the exoskeleton of the merus and the transmission of these vibrations to Barth's organ; this implies that the crabs cannot distinguish sounds from substrate vibration.

In the field, females of *Uca pugilator* have been observed to orient and move towards rapping males at night from distances of up to 25 cm, but nothing is known about the orientation mechanism involved (SALMON and ATSAIDES, 1969). Discussing vibration sensitivity in *Ocypode ceratophthalmus*, HORCH (1971)—and in *Uca minax*, SALMON and HORCH (1973)—speculated on how the sensory system might enable female crabs to localize sound-producing males. Theoretically, differential arrival times at different legs of sound pulses caused by rapping on the one hand, and phasic comparison of more prolonged vibratory sounds on the other hand, may provide adequate clues. Detailed information on acoustic behaviour in semi-terrestrial crabs has been presented by SALMON and HORCH (1972).

Sensitivity to substrate vibration has also been reported to be operative in the symbiotic relationship between the commensal polychaete *Nereis fucata* and the hermit crab *Eupagurus bernhardus* (GILPIN-BROWN, 1969). When a hermit crab was introduced in a finger bowl containing young *N. fucata*, the worms protruded from their tubes about two-thirds of their body length and made searching movements. These specific sweeping responses have been found to be initiated by vibrations in the substrate caused by the host's shell when it is dragged along the sandy substrate. Similar responses could be evoked when an empty shell was made to bounce gently on the bottom. These results have been confirmed by GOERKE (1971) in adult *N. fucata*.

A striking adaptive response to vibrations transmitted through the substrate has been described in the tidal migration of different beach clams of the genus *Donax* (MORI, 1938, 1950 *in*: TURNER and BELDING, 1957; LOESCH, 1957; WADE, 1967; ANSELL and TREVALLION, 1969; TIFFANY, 1971). These clams live in the sand of the water-saturated part of the wash zone of beaches and move up and down the beach with the tidal shift of the saturated zone by surf transport; this is made possible by the strong mobility of their siphons and foot. When, with the rising tide, the environment becomes too wet, they react to the acoustic shock of the breakers by jumping up in advance of the uprushing water and, after being transported, dig in—within a few seconds—at a higher level of the beach. The clams can be made to jump if the observer generates shocks with his foot (TURNER and BELDING, 1957) or by running a jeep about 20 m from the population (LOESCH, 1957). When the zone in which the beach clams burrow becomes unsaturated during the receding tide, they no longer respond to the acoustic shock and finally emerge to be carried by backwash to the saturated areas again. TIFFANY (1971) believes that clams in unsaturated sand fail to react to the acoustic shock of breakers, because interstitial water is absent and hence cannot carry the shock waves to the clams. In *Donax gouldii*, which apparently maintains a preferred position on the beach through the tides, no such jumping response to the breakers has been observed (IRWIN, 1973).

Apart from these adaptive responses to solid-borne vibrations, fright reactions of aquatic invertebrates are well known, for instance, when the aquarium wall is tapped.

On the basis of experiments and an extensive literature study FRINGS (1964) and FRINGS and FRINGS (1967) attempted to analyse the possible sensory bases of underwater sound receptions in which tactile stimuli, pressure changes, microcurrents or gross movements of the medium may be involved. They paid much attention to the possible role of innervated projections of the body wall such as cilia, setae, bristles and hairs, or appendages with associated proprioceptors and other mechanoreceptors, which may all be potential phonoreceptors. Detailed analyses of the functional significance of proprioceptors in crustacean limbs for detecting solid-borne disturbances have been presented by BURKE (1954) for *Carcinus maenas* and by ALEXANDER (1970) for *Ligia oceanica*.

In recent years, some evidence has been obtained for the existence of orientation to acoustic stimuli in marine invertebrates. HORRIDGE (1966e) listed some examples of adaptive responses and pointed out the possible sensory mechanism involved: tiny non-motile cilia sprouting from sensory cells in the body wall. In some cases, phonoreception seems to be involved in avoiding adverse disturbances of the water surface. The ctenophore *Pleurobrachia pileus*, for instance, commonly swims upward, but when the water surface is disturbed it responds by turning over and swimming downward. The first sign of the response is a contraction of the two long tentacles. This contraction can also be induced in either of the tentacles separately by means of a vibrating needle—attached to a loud-speaker diaphragm—brought close to it. Presumably the non-motile cilia described by early workers are involved in the perception. HORRIDGE postulates that the statocyst cannot be very effective as a vibration receptor.

A comparable avoidance of surface ripples has been demonstrated in the hydromedusa *Eutonia indicans*; it can likewise be elicited by a vibrating needle. The medusae turn over in a direction away from the stimulus.

In other cases the vibration sense is used for locating prey. JOSEPHSON (1961) demonstrated that polyps of the hydroid *Syncoryne mirabilis* bend rapidly towards a nearby vibrating object. The response threshold justifies the assumption that a small copepod moving a few millimetres from the polyp creates sufficient disturbance to evoke the reaction. The ctenophore *Leucothea multicornis* locates its prey acoustically. If, for instance, a copepod swims in its immediate vicinity, *L. multicornis* shoots out finger-like organs towards the prey. The effective sense organs have been identified as non-motile cilia responding to vibrations of 10 cycles sec^{-1} (HORRIDGE, 1966e).

Comparable studies have been carried out on acoustic prey detection in the benthic chaetognath *Spadella cephaloptera* (HORRIDGE, 1966e; HORRIDGE and BOULTON, 1967). When the tip of a wire is vibrated within a distance of 1 to 3 mm from a hungry specimen, it performs an oriented attack. The attack only takes place when the vibration of the wire tip has a certain amplitude (100–500 μ) and a frequency ranging between 9 and 20 Hz, with maximal responsiveness at about 12 Hz. Other vibrations and disturbances of the surrounding water have no effect or induce an escape response. This narrow range of effective frequencies provoking an attack in *S. cephaloptera* led NEWBURY (1972) to suppose that the chaetognath selects specific copepods by the vibration rates which their appendages produce during filter feeding and swimming. Hence *S. cephaloptera* would be specialized on *Calanus finmarchicus*, whose vibration rate is estimated at 10 Hz (up to 20 Hz). Attempts to elicit attacks in the planktonic chaetognath *Sagitta elegans* in similar experiments have not been successful (FRASER, 1969).

There are strong indications that the receptors for minor disturbances (small movements rather than pressure changes) in *Spadella cephaloptera* consist of fan-shaped groups of stiff, non-motile cilia borne by sensory nerve cells arranged around the body's margin, alternating with tufts of setae which presumably have no receptor function (HORRIDGE, 1966e; HORRIDGE and BOULTON, 1967). The fan-shaped tufts of cilia are oriented in various directions in different parts of the chaetognath, and as stimulation of a single cilia group does not evoke feeding responses, the integrated action of several groups is believed to be essential for the specific oriented response.

For the lobster *Homarus americanus*, LAVERACK (1962b) has described comparable fan-shaped and variously oriented structures, distributed over the anterior part of the body, which likewise may provide information concerning the location of disturbances. These hair-fan organs are presumed to detect disturbances since they adapt rapidly to steady water currents (see also p. 599), but show a continuous discharge of pulses when the water nearby is agitated.

Although it may be concluded that orientation to acoustic stimuli is part of the sensory equipment of marine invertebrates, the examples mentioned here relate to cases in which disturbances are detected from close by. The detection of sounds at somewhat longer ranges and the orientation to these stimuli are still *terra incognita*.

A great variety of underwater sounds, produced by marine invertebrates, is known (FISH, 1964). A number of decapod crustaceans even appear to have specialized structures (stridulation organs) to produce specific sounds; this suggests that these sounds may have some ecological significance (for references consult FRINGS, 1964 and FRINGS and FRINGS, 1967). However, indications that these specific noises are actually perceived by conspecifics are still rare. Intraspecific responses to stridulation have been observed in the spiny lobster *Panulirus interruptus*, but only when the stridulating and the responding individuals are within a range of 60 cm (LINDBERG, 1955). On one occasion, intraspecific responses to stridulation were also observed in *Palinurus vulgaris*; but the possibility of tactile perception of the vibrations could not be ruled out (DIJKGRAAF, 1955a). Evidence that crabs respond 'phonotactically', since they can be lured by underwater sounds in the range of 700 to 900 Hz, has been claimed by KIM and YANG (1970). A technique which may be rewarding in investigating sound perception by crustaceans is that of conditioning the heart rate, by applying, for instance sound combined with an unconditional stimulus such as AC current. Using this technique, OFFUTT (1970) demonstrated sensitivity to water-borne sound in *Homarus americanus* with lowest threshold for pressure (about −13 dB) at 37·5 Hz and for particle velocity (about 19 dB) at 75 Hz.

(12) Electrical and Magnetic Fields

(a) Electrical Fields

In the marine environment weak electrical fields are generated by flowing water masses which, as conductors, move in the earth's magnetic field. No attempts to establish whether these weak electrical fields are possibly utilized by marine invertebrates in orientation to ocean currents—as recently suggested in regard to the orientation of pelagic fishes (Chapter 8.2)—have come to the reviewer's attention.

Responses to stronger electrical fields, however, have engaged several early workers. An extensive review on 'galvanotropism' of unicellular organisms, invertebrates, fishes and amphibians has been presented by ROSE (1929). Animals may be directed either to the cathode or the anode, or exhibit transverse orientation. Although the strong electrical fields employed in these experiments have no immediate relevance to the conditions prevailing in oceans and coastal waters, it is evident that the locomotory system is affected in some way. The receptive physiological mechanism involved is still unknown.

Possible application of electrical fields in shrimp fisheries has been investigated by HIGMAN (1956). In an experimental tank, the best results with pink shrimp *Penaeus duorarum* were obtained with a current density of $2\frac{1}{2}$ milliamps DC cm^{-2}, a pulse rate of about 5 sec^{-1} and a current on/off ratio of 1:2. The shrimp moved to the anode either head foremost propelled by their swimmerettes or rapidly backward by contractions of their telson. HIGMAN considered the amount of power required for this type of electro-fishing too large for practical use in commercial shrimp fisheries. Substantial improvement of catches by means of electrified fishing gear appears to result mainly from hopping responses of the shrimp ahead of the oncoming net (KESSLER, 1965; KLIMA, 1968). Commercial fishing of *Penaeus duorarum* and *P. aztecus*, which forage at night and burrow during daylight, is normally restricted to night trawling; daytime application of an electro-shrimp trawl yields results similar to night-time non-electric catches (PEASE and SEIDEL, 1967).

When *Penaeus duorarum* face the negative electrode, the threshold voltages for hopping are twice as high as when they face the positive electrode (KESSLER, 1965). He also demonstrated that threshold voltages depend on the size of the shrimp, i.e. larger shrimp respond to lower voltages than smaller shrimp. This feature may be essential for improvement of the ratio commercial-sized/under-sized shrimp in catches. In experimental *Crangon crangon* beam-trawl fishing, electrified gear yielded 116% more commercial-sized shrimp and 81% more under-sized shrimp (BOONSTRA and DE GROOT, 1974). Attempts to apply electro-fishing have also been reported for *Nephrops norvegicus* (STEWART, 1972) and krill *Euphausia superba* (STASENKO, 1967; PETUSHKO, 1969). Since the conditions created by these artificial electrical fields do not occur in the marine environment, this discussion must remain restricted to the few examples provided.

(b) Magnetic Fields

Recent attempts to establish and analyse effects on orientation of electromagnetic forces in the order of magnitude which invertebrates actually encounter in their natural environment deserve more attention than hitherto received. Apart from a large number of well-established cases of orientation to generally accepted stimuli such as light, gravity and organic substances, which are perceived by recognizable receptor areas, invertebrates are apparently also able to perceive and to use such subtle stimuli as the earth's magnetic field, electrostatic fields and gamma radiation (Volume I, Chapter 11) for identifying geographical directions. They appear to be sensitive to geophysical cycles as well.

In an extensive series of publications (only a few are mentioned here) BROWN and his colleagues, working with species of *Paramecium*, *Volvox*, *Drosophila* and especially with the freshwater planarian *Dugesia dorotocephala* and the marine gastropod *Nassarius obsoletus*, developed a complex picture of these effects, which—with particular reference to *N. obsoletus*—will be briefly summarized below. More detailed information is found in the reviews by BARNWELL and BROWN (1964) and BROWN (1971); for some interesting comments LAVERACK (1968, p. 315) should be consulted.

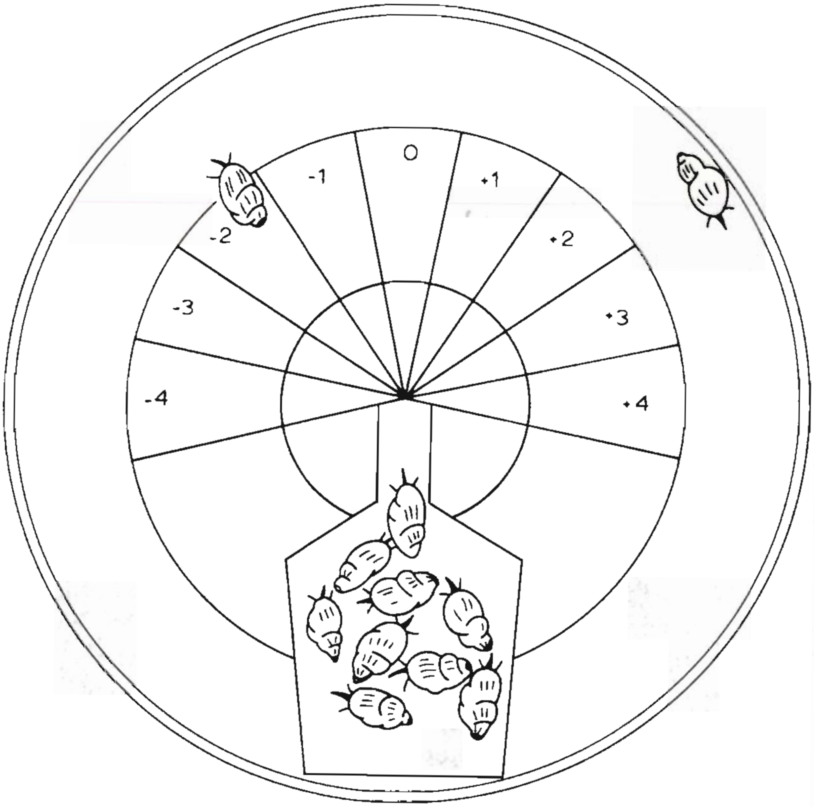

Fig. 8-41: *Nassarius obsoletus*. Orientation apparatus viewed from above. Snails are allowed to emerge from an aluminium 'corral' and orientation is quantified by means of a broadly calibrated arc. (After BROWN and co-authors, 1960a; modified; reproduced by permission of *Biological Bulletin*.)

In a basically simple device (Fig. 8-41) *Nassarius obsoletus* were allowed to leave an aluminium 'corral' through a narrow corridor (BROWN and co-authors, 1960a). The spontaneous orientation responses—in symmetrical illumination—upon emergence from the corridor were quantified by means of a broadly calibrated arc. The experiments were carried out either in the natural magnetic field (0·17 Gauss) or in an imposed magnetic field varying from 0·04 to 10·0 Gauss. Although there may be some doubt as to the precision of the measurements of the snails' pathways relative to the small total effects (BROWN, 1971, p. 241), there appear to be grounds for concluding that the snails are sensitive to the geographical direction in which the experimental apparatus is placed (BROWN and co-authors, 1964b).

Further experiments demonstrated that differing imposed magnetic fields, either parallel or transverse to the natural field, produced different deviations from the mean pathway. To determine the optimum effective strength of the magnetic field in inducing these deviations, a series of 8 strengths (0·04, 0·1, 0·2, 0·4, 0·8, 2·0, 4·0, and 10·0 Gauss) was presented (BROWN and co-authors, 1964a). Remarkably, the strength of 0·2 Gauss, which is closest to the natural magnetic field strength (0·17 Gauss), appeared to be the most effective. The orientational responses of the mud snails apparently also fluctuated with the diurnal cycle (BROWN and co-authors, 1960b), the lunar cycle (BROWN and WEBB, 1960), and the seasons (WEBB and BROWN, 1962).

Weak electrostatic fields and gamma radiation, of the order of strength occurring in the natural environment, have been shown to affect orientation in the planarian *Dugesia dorotocephala* (BROWN, 1971). Orientational responses to electrostatic fields and to gamma radiation appeared to be influenced by the geographic orientation of the experimental apparatus, i.e. its orientation with respect to the earth's magnetic field. Also, the influence of the electrostatic field seemed to vary with the time of day, while the effect of gamma radiation was apparently dependent on the phase of the moon and the time of year. Finally, the strength of the various fields imposed also appeared to effect deviations from the mean paths in planarians and mud snails, and in some cases even to bring about reversals (BROWN, 1971).

We are still a long way from understanding adequately the nature and the ecological significance of these electromagnetic effects on invertebrate orientation. The multiplicity, and apparent interdependence, of the variables involved underscore the need for caution in interpreting the results of future work in this field of research.

Acknowledgements. I am grateful to Mr. J. A. A. SPIEKERMAN (The Hague) for help given with the English version of this subchapter. Further I owe gratitude for criticism and advice to Drs. D. DAVENPORT, A. D. G. DRAL, H. SCHÖNE and F. J. VERHEIJEN.

8. ORIENTATION IN SPACE: ANIMALS

8.2 FISHES

F.-W. Tesch

(1) Introduction

(a) General Aspects

Fishes orient in space and time. This subchapter is concerned with spatial orientation; orientation in time (temporal orientation) is covered in Chapter 9. In fishes, long-distance orientation, e.g. long-range migration, seems to require more complex mechanisms than short-distance orientation. Hence long-distance orientation is of major concern to the ecologist and ethologist. However, current knowledge on long-distance orientation is scarce. In this subchapter it is necessary, therefore, to allocate much attention to experiments and observations on short-range movements. The restricted amount of information available on spatial orientation in marine fishes requires, furthermore, inclusion of knowledge on freshwater fishes.

The difficulties to investigate mechanisms of orientation in marine fishes are formidable. With a few exceptions, proper recording of fish migration in oceans and coastal waters has been practically impossible. The primary method of gaining information has been conventional tagging of fishes. But this method yields, in essence, only indirect evidence. Moreover, tagging experiments have been mostly restricted to commercially valuable fish species, and hence to shore areas.

While tagging has its methodological shortcomings, both number and extent of the tagging studies conducted are considerable. Far more information is available on tagging of fishes than on tagging of birds. A substantial number of fish-tagging operations have contributed to our present knowledge on the orientation mechanism involved. In addition, large-scale investigations on the ecology and distribution of adult and, especially, juvenile commercial fishes has yielded a wealth of data on migratory activities and possible orientation cues. For this reason, the last section of this chapter is devoted to reviewing, assessing and interpreting the results obtained from such investigations.

Laboratory experiments on orientation of marine fishes are difficult. Most oceanic fishes cannot yet be cultivated (Volume III: Kinne, in press, a, b). In fact, it is difficult to imagine that fishes such as the herring *Clupea harengus* will ever lend themselves to laboratory experiments on orientation. How could we provide adequate laboratory conditions for deep-sea fishes, which are of particular interest to the student of orientation mechanisms? No doubt, laboratory experiments on orientation of marine fishes will remain restricted to a small number of species. The same is true of a new method of field experiments on fish orientation: telemetric tracking. While this technique opens up new possibilities for research on orientation mechanisms, it requires the capture or cultivation of fishes exhibiting normal vitality. It confines the experiments to individuals of a suitable size, usually excluding small juvenile stages, and does not always allow control or manipulation of important environmental factors.

(b) Prerequisites for Orientation and Migration

Fishes require a stimulus not only for the directional control of their movement, but also for initiation and continuation of movement. The stimulus which initiates migration, the so-called releasing factor (Chapter 8.0), is provided by endogenous and/or exogenous conditions. For example, the drive to feed, which is endogenously released, causes the fish to move in order to find food; the resulting locomotory activity becomes oriented via a directional stimulus. A certain maturity stage of the gonads acts as internal releaser for the onset of the spawning migration which, in turn, needs another stimulus in order to direct the fish to the spawning site. High irradiance as external releaser may stimulate the fish to move downward, with directional cues provided by the vertical irradiance gradient and gravity. Seasonal migration may be initiated by the onset of winter (reduced temperatures and/or daylengths). Reduced temperatures may stimulate the fish to leave shallow areas and to migrate to warmer deep waters. Temperature gradients provide also directional cues, as do gradients in salinity and hydrostatic pressure. In fact, all environmental factors which act as releasing stimuli can also be used by fishes as directional stimuli for short- and long-range orientation.

In many cases, several releasing factors may act in concert. This is especially true for initial spawning-place migrations. When a certain temperature is reached, the herring *Clupea harengus* begins to migrate toward its spawning area. Important prerequisites for such migration are, in addition to the external releaser temperature, developmental characteristics such as the state of pituitary gland and of gonads. Similarly, the eel *Anguilla anguilla* begins its migration towards the Sargasso Sea in the autumn, when the temperature falls to about 14° C. But only ripe individuals—the so-called silver eels with advanced gonadotropic pituitary cells, silvery pigmentation, long pectoral fins and enlarged eyes—are seen to move seaward. Releasing of orientational responses may be induced by temperature; it is a function of growth stage and body size. On the other hand, even ontogenetic condition does not act as releasing factor at temperatures below about 6° C (TESCH, 1972, 1974). At 14° C eels may not start to migrate until their body has attained the migratory stage. This might be the case later and at still lower temperatures. However, if the temperature drops to 6° C, the eel interrupts its migration for the whole winter.

In addition to the releasing factors which initiate migration, other releasers are effective during migration. Knowledge on the effectiveness of such mid-migration factors is essential for planning and interpretation of orientation experiments. Otherwise directional swimming activities could easily be misinterpreted. An example is provided by young Pacific salmon (smolts of *Oncorhynchus nerka*) which leave their native lake system, a chain of lakes with different directions in their longitudinal extension (GROOT, 1965). The smolts pursue a preference direction in accordance with the main geographical direction of each individual lake; this helps to cross the lake to its outlet. If the next lake is entered, with a longitudinal direction different from that of the preceding lake, the smolts change their direction in accordance with the new longitudinal lake extension. Obviously, this change must be initiated by a releasing factor. The prevailing swimming direction changes as the season proceeds and with increasing age of the fish. Hence the release to change the fish's compass course seems to be endogenous. Usually, more than one successive releasing stimulation is necessary.

Apparently, similar conditions prevail in regard to the spawning migration of the eel *Anguilla anguilla* through North Sea and Atlantic Ocean. To reach the northern opening of the North Sea, eels from the German Bight must swim northwest (TESCH, 1972, 1974a); to reach their spawning areas in the Sargasso Sea from the North Atlantic Ocean they must turn southwest. The releasing factor for this change in direction is unknown. It might be endogenous, depending on the developmental stage; but it could also be an exogenous releaser, based on changing hydrographical conditions, e.g. increasing light penetration and greater water depth.

In order to analyze the release as well as directional changes of migrations, deportation and homing experiments have often been carried out. The stress suffered from transplantation (deportation from the home area to a foreign environment) appears to release activities which ultimately result in the return to the home area. Homing of deported fishes depends far less on natural releasing factors than normal migration and is not as restricted to brief developmental stages or difficult to define environmental conditions. Homing migrations are possible through most months of the year.

(2) Light

(a) Constitutional Capacities and Environmental Conditions

Functional and structural responses of aquatic organisms to light have been reviewed in Volume I, Chapter 2. Even pure water attenuates radiant energy to a considerable degree, more at higher, less at shorter wavelengths (Volume I: JERLOV, 1970). Hence, the deeper fishes live in the water column, the more the spectral sensitivity of their eye changes towards shorter wavelengths (Volume I: BLAXTER, 1970, p. 222; MUNZ, 1971). Through the clearest oceanic waters, sunlight of 10^5 μW cm^{-2} penetrates only into depths of about 1000 m resulting in a local irradiance of only 10^{-9} μW cm^{-2}; in comparatively clear coastal waters this penetration intensity is found in 200 m (CLARKE and DENTON, 1962). Sea areas with higher trophic levels, especially lagoons and estuarine waters, have much higher attenuations. Turbid waters are less penetrable to shorter wavelengths. For these reasons the suitability of visual organs for orientation is limited in waters of high turbidity (Volume I, Chapter 6).

The quantitative and qualitative differences of light in waters inhabited by different species may cause adaptive specialization, i.e. genetic adjustments to prevailing light conditions (KOBAYASHI, 1962). In numerous species, different ontogenetic stages exhibit different spectral sensitivities of their eye. Examples are the stationary and migratory stages of the eel *Anguilla anguilla* which live in quite different environments (CARLISLE and DENTON, 1959), and of the salmon

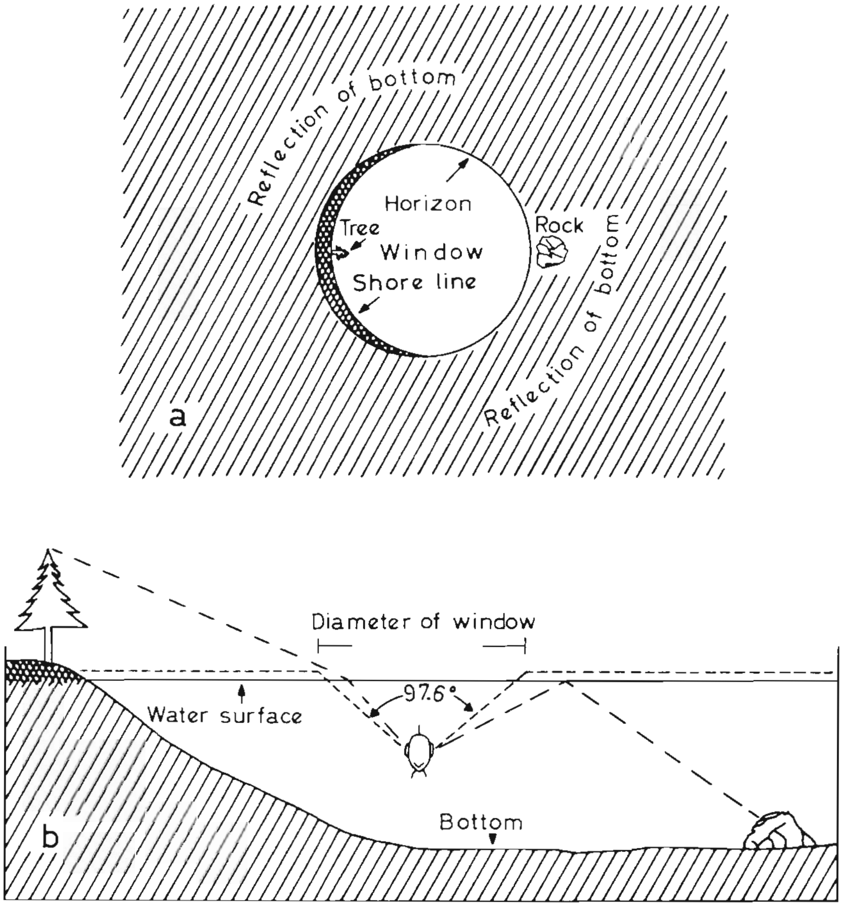

Fig. 8-42: Fish-eye perspective of water surface and 'visual window'. (a) Water surface and visual window as seen from below. (b) Sideview. Light rays striking the surface within the window are refracted to the eyes of the fish. Within an angle of 97·6° the fish sees out into an aerial hemisphere; but outside this angle it sees objects on the bottom, reflected at a silvery surface. In order to obtain a clear picture, the surface must be completely calm. (After WALLS, 1963; modified; reproduced by permission of Cranbrook Institute of Science.)

spawning-migration phase (BEATTY, 1966; for ontogenetic development of retinal pigment consult BRIDGES and YOSHIKAMI, 1970). In the guppy *Poecilia reticulata*, the ability to perceive colours depends on lunar periodicity (LANG, 1969, 1970). Conceivably, lunar periodicity may also affect the migratory behaviour of the eel *Anguilla anguilla* (TESCH, 1973).

Apart from the narrow optical range, light refraction above the surface causes further difficulties. An eye underwater perceives celestial and coastal objects under a different angle (Fig. 8-42 and Volume I: JERLOV, 1970). If the sun is in the zenith the apparent angle is 90°, the same as from a point in the air. But if the sun is at the horizon, the apparent angle of altitude perceived underwater is not 0° but 41·5°. When the sun's position is at a true angle of 20°, underwater it shines at an altitude of 45·5°, not very different from the actual horizontal position. The relationship is more favourable if the sun's true altitude is 60°; it then seems to shine underwater at 68° (ÅNGSTRÖM, 1925). Except when the sun is in the zenith, it always appears at a higher elevation underwater than above the water. From this, it follows that near an underwater altitude of 41·5° all objects appear considerably compressed and in particular coastal objects near the horizon are distorted. It is still an open question whether the acuity (Volume I: BLAXTER, 1970, p. 672) of the fish eye can discriminate shore-line characteristics and use them as orientation cues. JAHN (1969) took some underwater pictures near the bank of a lake. He writes (p. 1258):

> 'No land features were visible on underwater pictures taken from depths of 0·5, 1·0 and 2·0 m. . . . Clouds were visible on several of these pictures. Tops of trees were distinguishable on a few pictures taken from depths of 1·0 and 2·0 m 20–80 m from shore. Clouds and trees were visible only on pictures taken when the lake surface was very calm.'

With respect to shape discrimination, the fish eye's abilities are also restricted (HERTER, 1953; Volume I: BLAXTER, 1970; INGLE, 1971). In addition, an increasing reflection of light, which amounts to 35% at an altitude of 10° and to 100% at 0°, diminishes the visibility of objects above the water surface.

This not only limits measurements of altitude but also of the azimuth. The perception of the azimuth becomes even more difficult as the fish swims deeper (Volume I: BLAXTER, 1970). Underwater, the apparent direction of the sun moves towards the zenith with increasing water depth. Hence, the apparent altitude of the sun increases as the fish enters greater depths, and simultaneously, the amount of information obtainable from irradiance distribution decreases. In addition, the radiance distribution depends on the optical properties of the water. The radiance distribution in the Sargasso Sea and in the Baltic Sea is illustrated in Fig. 2-4 of Volume I. Theoretically, information on altitude and azimuth of the sun can no longer be obtained in 400 m depth in the Sargasso Sea and in 100 m in the Baltic Sea. Since the accuracy of angle discrimination in fishes may be 10° or less, the actual limiting depth might be far less: in the Sargasso Sea below 200 m, and in the Baltic Sea below 50 m.

As just mentioned, even in smaller depths wave action reduces the capacity for directional discrimination of the sun. In the North Atlantic and North Pacific Oceans storms are quite common (not to speak of long periods of overcast skies in these regions: p. 701). However, fishes such as the eel *Anguilla anguilla* and salmonids are known to conduct long-range migrations in these oceans. Indeed, the difficulties of exact location of the sun and other celestial bodies, as well as of landmarks, are enormous and there is no reason to assume marine fishes could make much use of them as orientation cues. GROOT's (1965) assumption that polarized light may be of importance for spatial orientation of fishes has been supported by experimental evidence (DILL, 1971; FORWARD and co-authors, 1972; WATERMAN and FORWARD, 1972). The surface-living teleost *Zenarchopterus dispar* exhibits menotactic azimuth preference under experimental conditions and responses to natural polarized light may be involved also in normal direction finding. Whether polarized underwater light or other light sources could be of ecological significance to *Z. dispar* is still uncertain. It should be taken into consideration that the degree of polarization in horizontal lines of sight is maximal near the surface and ±90° from the bearing of the sun. All factors which decrease the directionality of underwater light also decrease the percentage of polarization. Consequently, the proportion of polarized underwater light diminishes as a function of cloudiness of the sky, turbidity of the water, depth and, to some extent, also wavelength of greatest penetration (WATERMAN, 1959).

In addition to qualitative aspects, quantitative capacities of light perception are of importance. In Volume I, Tables 2-17 and 2-18, and Fig. 2-31 provide a measure of the brightness increment discernible by fishes. The most insensitive fishes are the dogfish *Mustelus manazo*, *Trachurus japonicus* and the loach *Misgurnus anguillicaudatus*. More sensitive are the cod *Gadus morhua*, the coalfish *Pollachius virens* and, especially, the capelin *Mallotus villosus*. The table reveals also that one of the best known migratory fish, the eel *Anguilla anguilla*, is rather insensitive to underwater light. But the values presented might have been obtained from non-migratory stages. Additional evidence of the limited optical efficiency of the eel was provided by investigations on its ability to perceive moving objects. Comparing *Salmo gairdnerii*, a thunnid fish and *Anguilla* sp. (modified flicker-ERG), the highest values at a given temperature and irradiance were exhibited by trout, the lowest values by eel (YONEZAWA and TAMURA, 1971). A further criterion for optical abilities is the size of the nucleus of the nervus oculomotorius (KIRSCHE, 1966). Here again, the eel exhibits one of the lowest values, comparable to that of other bottom fishes like the burbot *Lota lota*; the highest values were shown again by the rainbow trout *Salmo gairdnerii* and by the piscivorous freshwater fishes such as *Esox lucius*, *Lucioperca lucioperca* and *Perca fluviatilis*.

A comparison of the total sense area of retina and olfactory organ in different fishes is provided in Fig. 8-43. This illustration underlines the importance of the sense of vision for migratory or semi-migratory fishes like *Salmo irideus* and *Gasterosteus aculeatus*. On the other hand, the small extension of the retinal area of the migratory *Anguilla anguilla* and *Lota lota* is remarkable. The different optical abilities of fishes regarded as migratory indicates that vision might not be used for orientation in long-range migrations, but for short-distance movements involving, for example, search for food, avoidance of obstacles or social contact.

Are fishes assisted by other photosensitive organs in directional orientation towards light? With the exception of larvae of lamprey and of eyeless fishes, the photosensitivity of the pineal organ is of restricted importance. Experiments with blinded and with pinealectomized goldfishes *Carassius auratus* showed that phototactic responses depend only in part upon the presence of the pineal organ. In any case, photic information received by the pineal cannot be translated into a directional response (FENWICK, 1970). Also from other investigations, especially on migratory salmonids (HOAR, 1955; HAFEEZ and QUAY, 1970), photosensitive control of the pineal is known but other light-sensitive parts of the fish body are even less competent for spatial orientation. However, upon light exposure the migratory eel *Anguilla anguilla* exhibits phobic reactions not only when the pineal region is stimulated but also when the anal part of its body is illuminated (MOTTE, 1963, 1964; see also Volume I: BLAXTER, 1970, pp. 217–218).

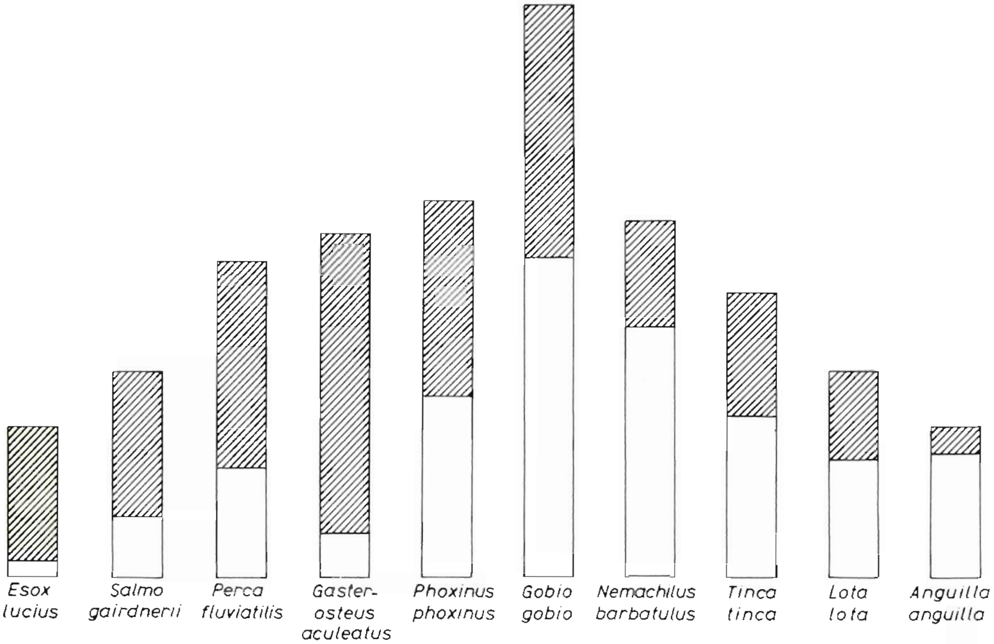

Fig. 8-43: Total sense areas of retina (hatched) and olfactory mucosa (white) in various fishes. (After TEICHMANN, 1955; modified; reproduced by permission of Springer-Verlag, Heidelberg.)

(b) Vertical Migration

Vertical movements of shore and deep-sea fishes have been discussed extensively in Volume I (BLAXTER, 1970). Nearly all marine animals perform vertical migrations, mainly correlated with the diurnal light cycle or with seasonal temperature changes. Parallel changes between irradiance and resident depth of deep-sea fishes were observed by CLARKE and BACKUS (1964), CLARKE (1966), and BODEN and KAMPA (1967). Light-dependent vertical movements of clupeids follow a preferendum or are triggered by sudden changes in irradiance. These *in situ* observations have been supported by field experiments employing artificial light (BLAXTER and CURRIE, 1967). Aquaria experiments with freshwater fishes provided evidence that light, not pressure, acts as orienting stimulus for vertical movements (GIRSA, 1971).

However, pressure perception may stop the downward movement during vertical migration over several hundred metres. In greater depths, differences in irradiance are no longer perceived, and hence pressure effects may override light effects. Pressure effects receive detailed attention on p. 676. The integrating mechanism effective during vertical migration—comprising visual, pressure and gravitational inputs—is considered on p. 688.

As in invertebrates (Volume I: SEGAL, 1970), light acts as main orienting stimulus in the vertical migration of many fishes. The ecological significance of vertical migration appears to be: more variety in food supply, protection against predators during night feeding in most trophic zones in the surface layer and shelter during daytime in the darker depths, reduction of interspecific competition. In some cases, vertical migration might facilitate more effective horizontal migration (VERWEY, 1966). Thus it is known that the elvers of *Anguilla anguilla* maintain higher positions in the water column during night-time than during daylight. The negative phototactic elvers use the night for drifting with the higher-speed tidal current in the upper water layers (DEELDER, 1960; CREUTZBERG, 1961). Restriction to greater depth and lower current velocity during the day may also reduce losses due to predation. Adult eels may benefit from vertical migration during their spawning migration. Although this is still speculative, it seems that light forces the eel to avoid the upper oceanic layers and to swim at depths greater than those in the turbid, light-absorbing coastal waters. In this way, the American eel *Anguilla rostrata*, for example, would travel below the maximum speed of the Gulf Stream (RICHARDSON and KNAUSS, 1971; for further literature consult TESCH, 1973). The sole *Solea solea* swims near the surface during the night (DE VEEN, 1967); this negative phototactic and bottom-living flatfish may make use of the strongest tidal current for faster movement at the surface during the night if the current is directed towards its spawning grounds. The plaice *Pleuronectes platessa* exhibits movements in upper water layers during the night which seem to have an ecological significance similar to that mentioned for *S. solea* (WALKER and co-authors, 1971).

(c) Short-Distance Horizontal Migration

Detection of Food

Most short-distance horizontal migrations of fishes are initiated by search for food, more suitable hydrographic conditions (e.g. temperature, salinity, water movement), shelter, or spawning places. Very common in fishes are visually directed short-range horizontal migrations for obtaining food. They are often combined with vertical migrations and frequently assisted by chemical cues. The importance of optical abilities in searching for and taking up food is evident from the influence of light on feeding activity (Volume I: BLAXTER, 1970, pp. 233–238). Out of 20 fish species, only 5 fed in darkness. GIRSA (1962), who studied salt and freshwater fishes, reports that of 7 predatory species 4 fed in darkness (Volume I, Fig. 2-40). WUNDER (1936) compared 12 fresh- and brackish-water fishes in regard to the importance of different sense organs for food finding. His table reveals that the eye is the most important organ for detecting food: 6 species employ definitely, and 4 probably, their visual sense. ARONOV (1965) investigated the food-detecting abilities of 5 Black Sea fishes by impairing different sense organs. In 3 species the visual sense proved to be the most important one. That vision is necessary for most shore fishes to detect food has also been proved by bait offered in water of different light transmittance. MURPHY (1959) demonstrated, by trolling, in water of different turbidity, that the success of capturing thunnid fishes increased with decreasing turbidity.

Visual food acquisition prevails not only in fishes with good optical capabilities; the visual sense may induce feeding also in fishes with pronounced olfactory capacities. While sharks of the family Carcharhinidae employ olfaction as the most effective sense in long-range prey detection, the final approach towards a motionless prey is normally guided by vision, even though acuity and discrimination ability are low (Hobson, 1963).

Detection of Obstacles

Careful analysis of the physiological mechanisms which allow fishes to avoid a net has provided important information for developing more effective fishing gear. The interest of commercial fisheries in gear avoidance has prompted a large number of studies on visibility and responses to fishing gear (Volume I, Table 2-20). The investigations show that (i) transparent monofilament gill nets capture more effectively than multifilament nets; (ii) nets are less effective in clear water than in turbid water; (iii) nylon nets catch more successfully (are less transparent) than cotton nets; (iv) the effectiveness of nets as guidance barriers decreases in the order red > yellow > green.

More recently, experiments have been carried out with ultrasonic tagged bream *Abramis brama* and pike *Esox lucius* to explore the behaviour of fishes encountering a net (Malinin, 1970b). During the day, the fishes perceived the net at a distance of 1 m. During the night, the nets were detected only upon contact. Similar experiments with the American shad *Alosa sapidissima* gave less unequivocal results (Leggett, 1971): During the day the shad also perceived the gill net at a distance of 1 to 2 m; however, a number of avoidance reactions were observed when light intensities were inadequate to allow visual detection; mechanical sense mechanisms such as the lateral line may have been involved. From Leggett's experiments it is obvious that in daylight obstacles in rivers and lakes can be detected at a distance of at least 1 m. In clear coastal waters this distance may be greater. For this reason, gill-net efficiency is higher in rivers than in the sea during the day, and about the same in both habitats at night.

In most fishes the major organ for detection of obstacles is the eye. Some experiments demonstrate that also other sense organs may be involved. Pronounced light gradients can act as barriers (Volume I: Blaxter, 1970, pp. 242–243). But the effects of such light curtains can be substantially enforced by combination with, e.g., air bubbles, mechanical chains, cables or sounds; that means mechanical stimuli such as water movement, sound or contact are involved.

In commercial fisheries and experimental ecology light curtains are installed for fishes with negative phototactic behaviour. Pure light barriers ending in a trap net for registration have been used to catch migrating silver eels *Anguilla anguilla* (Lowe, 1952; Bräutigam, 1961a, b, 1962; Frost, 1961; Hölke, 1964; Swierzowski, 1964; consult Tesch, 1973 for a detailed review). Unfortunately, none of these papers provide information on irradiance. The papers do contain important information on orientation behaviour however: (i) On their nightly spawning migration silver eels, in rivers and in the sea, are repulsed by sudden high irradiance (to prevent high irradiance during the day, they normally seek deeper water; in the waters examined they do not migrate in daylight). (ii) Non-migrating yellow eels are not disturbed by nightly light curtains. (iii) Fishes like herring *Clupea harengus*, roach *Rutilus rutilus*, pike *Esox lucius*, perch *Perca fluviatilis*, and zander *Lucioperca lucioperca*, react positively phototactically; they swim toward the light and aggregate near the light curtain. (iv) If attempts to detour the bright light fail, some silver eels may ultimately adapt to the high irradiance and cross the curtain. This is favoured by an inadequate angle of the barrier relative to the direction of migration, by too long barriers and too wide interspaces between the single light sources of the curtain.

Detection of Spawning Sites

The spawning migration terminates at the spawning sites (non-migratory fishes do not leave the neighbourhood of their spawning grounds). The orientation mechanism employed in the vicinity of the spawning sites changes more often than the orientation mechanism used during long-range movements (p. 694). Whereas long-range migration in oceanic waters does not seem to depend on visual and olfactory cues, orientation in the vicinity of the spawning places is usually based primarily on vision. The eyes are important for locating the spawning sites (LABAR, 1971). Similarly a fish which often leaves the spawning site and returns with nest-building material, or which takes care of the earlier deposited eggs, often orients itself visually. The stickleback *Gasterosteus aculeatus*, for example, first uses the distribution of light as orienting stimulus; in the immediate vicinity of the nest it uses local landmarks such as stones or plants (TSCHANZ and SCHARF, 1971), i.e., it discriminates forms and, perhaps, also colours.

(d) Social Contact

Schooling of fishes requires visual orientation to the neighbours. It is based on the maintenance of a defined distance to school members and on avoiding loss of contact. The limiting effect of light on schooling has been discussed in Volume I (BLAXTER, 1970, p. 228). A large number of laboratory studies demonstrate that, if irradiance is sufficiently reduced, fishes no longer maintain schools (reviews *in*: ATZ, 1953; SHAW, 1961). However, some field observations show that schooling contact is maintained in 'darkness' (HATANAKA and co-authors, 1957; RADAKOV, 1960; HARDEN-JONES, 1962; WHITNEY, 1969). But it is not certain whether these field studies have been conducted under conditions of total darkness. Moonlight, starlight, skylight and bioluminescence may yield sufficient irradiance for the fishes to maintain their schools by visual orientation (WHITNEY, 1969).

Visual contact by different individuals of a school has been demonstrated in experiments with the zebrafish *Brachydanio rerio* by MCCANN and co-authors (1971): Body shape and stripe pattern of the neighbour constitute the stimuli. Optomotor reactions also facilitate communication and orientation within a school, e.g. in *Mugil* sp. (HORSTMANN, 1959). Turning of one fish may initiate a correspondent turn of its neighbours. This reaction often spreads almost like an explosion among all members of the school and leads to immediate turning of the whole school. The fish do not lose contact, because each individual orients its own position relative to another moving object in such a way that the picture on its retina moves from the caudal to the oral part. In experiments on *Leucaspius delineatus*, SIEGMUND and co-authors (1969) found that the optomotor amplifying effect of one individual is limited to a maximum of 23 other individuals of a school.

In numerous other cases, perception of odour or mechanical properties provide the most effective stimuli. For rheotactic behaviour and vision see p. 673.

(e) Long-Distance Horizontal Migration

Orientation to cues above the water is difficult and more complicated than to underwater cues. Two major categories of directional stimuli may be received from above the water: landmarks, and celestial cues. Orientation to landmarks is either direct (telotaxis), or involves compass-course stimuli (menotaxis). Orientation to celestial cues always involves a compass course.

Orientation to Landmarks

Gobies *Bathygobius soporator* exhibit topographic memory (ARONSON, 1951); they can jump out of their tide pool in such a way that they always land in a neighbouring pool or in the open water. Such memory of the local topography can be retained for at least two weeks. Laboratory tests on *Phoxinus laevis* revealed that directional stimuli for finding food were obtained from small marks on wall and floor of the experimental tank (HASLER, 1956). To the reviewer's knowledge, these experiments are the only ones which prove the existence of landmark orientation in fishes. The term 'landmark' is often used in the literature. It conveys the connotation of long-distance courses which are maintained or re-inforced by topographical features, such as coastal mountains, trees or coastlines. The studies cited were conducted in small water bodies (pools of about 20 m diameter and experimental tanks of 1·2 m). In the open ocean and in large lakes, landmark orientation seems far more difficult and, if present, restricted to special cases. The observations reported by JAHN (1969), cited on p. 661, suggest possibilities to discriminate optical stimuli of special shape characteristics above the water.

Landmark orientation via visible bottom characteristics seems less difficult and more likely to be employed by fishes. Immature parrot fishes, for example, obtain directional cues from bottom landmarks; adult stages, however, use the sun as reference point (see below). But the bottom marks can hardly deliver guideposts for far-distant orientation.

Orientation to Celestial Cues

In fishes, capacities for compass-course orientation by the sun seem to be restricted (p. 659). Field experiments suggest that they are limited to areas along the coast and to small lakes. However, they are necessary to provide hints for the existence of, or evidence for, the ecological significance of laboratory results on celestial orientation. In the marine environment, the most convincing experiment has been conducted by WINN and co-authors (1964) who worked on the shores of Bermuda on two perciform fishes, *Scarus guacamaia* and *S. coelestinus*. These parrot fishes live in offshore caves at night and feed during the day along the shore line. Caught over their feeding grounds, deported and released again, adult individuals always attempt to escape in a southeasterly direction, pointing towards their home caves. They maintain this direction regardless of bottom topography and hydrographic conditions. Tracking of the parrot fishes was possible by marking them with small floats. Orientation is lost under cloud cover, in darkness during the

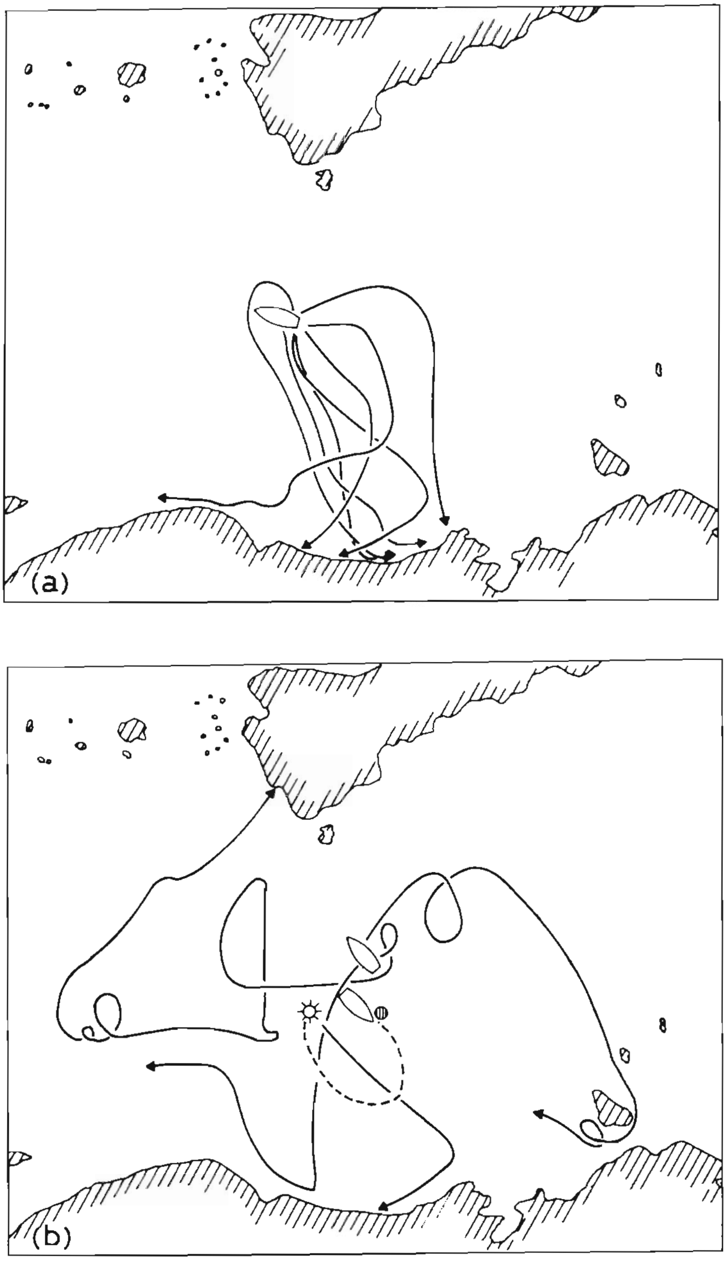

Fig. 8-44: *Scarus guacamaia* and *S. coelestinus*. Paths of adult parrotfishes released during the afternoon (July/August) in Bailey's Bay (Bermuda). (a) Seven individuals during bright sunshine. (b) Three individuals (upper release point) under complete cloud cover, one individual (lower release point; dotted line) under cloud cover during release. As the circled point was attained the sun came into full view and the fish oriented immediately southeasterly. (After WINN and co-authors, 1964; modified; reproduced by permission of Verlag Paul Parey, Hamburg-Berlin.)

night, or when the eyes are covered with opaque cups (Fig. 8-44). In parrot fishes, in which the daily light cycle was retarded experimentally, orientation to the sun azimuth shifted 190° clockwise from the southeasterly direction. The experiments suggest that the fish compensate for actual hourly changes in sun azimuth. Presumably, directional stimuli are obtained directly from the sun's position, not from the polarization pattern of underwater light. For some time, the observer could see the sun as an intensely lighted spot through a cumulus cloud; this was accompanied by a strong polarization pattern; but the fishes appeared disoriented. They were able to orient again only after the sun was fully visible. Immature parrot fish do not orient to the sun; WINN and co-authors (1964) assumed that the horizontal narrow water band towards shallow water, and the wide dark band towards deeper water represent the most likely orientational stimuli to immature individuals.

Further pertinent experiments, both in the field and in the laboratory, have been performed on freshwater fishes (HASLER and co-authors, 1958; HASLER and SCHWASSMANN, 1960; BRAEMER and SCHWASSMANN, 1963) and migratory fishes during the freshwater phase (JOHNSON and GROOT, 1963; GROOT, 1965); an earlier comprehensive review has been presented by BRAEMER (1960). These studies have also been referred to extensively in Volume I by BLAXTER (1970).

The information at hand provides evidence of the ability of fishes to maintain a compass course:

(i) The movement of the sun can be calculated continuously through 24 hrs. Compensation is accomplished either as if the sun moved in a clockwise direction throughout the 24 hrs, or as if it moved only during daytime and between sunset and sunrise (accompanied by behaviour as if the sun moved counterclockwise).

(ii) The capacity to calculate the sun's azimuth may be innate. Differences in the innate direction of compensation were found which are related to the different geographical distributions of the fishes tested.

(iii) Quantitative computation of the sun's movement is effected by the length of the day in which the fish lives and by the sun's altitude, or by a correlated factor.

(iv) Displacement along the same degree of latitude, simulated by shifting the phase of the light–dark cycle, resets the internal clock involved in direction finding in a predictable way.

Subsequent experiments confirmed the earlier results. In test arenas the mosquitofish *Gambusia affinis* move on a compass course perpendicular to its home shore, provided either the real sun or an artificial sun is visible to them. Overcast skies, diffuse light, or a preceding 72-hr period of total darkness prevent orientation. *G. affinis* are able to time compensate (GOODYEAR and FERGUSON, 1969). Similar results were obtained on the starhead-top minnow *Fundulus notti* which uses the sun in small woodland ponds for direction finding of the land–water interface. Underwater, the movement is directed shoreward; but *F. notti* succeeds in orienting visually also on land on a compass course: it moves in a direction that leads it back to the pond (GOODYEAR, 1970). Less unequivocal results are available on the seaward migration of young salmon *Oncorhynchus nerka* (GROOT, 1965; see p. 699). The salmon were probably guided by polarized light. Laboratory investigations on orientation of salmon fry in estuarine waters supported the assumption that the sun could possibly deliver cues for the seaward migration of juvenile salmonids (HEALY, 1967).

In field investigations, in a large artificial lake, ABROSIMOVA and co-authors (1968) displaced the cyprinid fish *Rutilus rutilus* over distances of 15 to 5 km. Captured fish were tagged with floats, released and tracked. When the sky was blue and the sun visible, 30% homed; with overcast sky only 10% of the fish were able to find their home area. Most of the failing individuals swam southward. Field experiments by MADISON and co-authors (1972) provided some evidence that in coastal waters, vision may be significant for homing *Oncorhynchus nerka*. Ultrasonically tracked salmon exhibited a higher cruising speed during daytime than at night. The angular swimming pattern of the salmon revealed diurnal differences which might be related to visual orientation.

But even these experiments cannot convince that vision plays a major role in the long distance orientation of Anguillidae, Salmonidae, Thunidae and other migratory fishes. While earlier laboratory and field experiments by HASLER and co-authors (1958) seemed to show that, after deportation, the white bass *Roccus chryops* used the sun for homing to its spawning place, more recent and technically more sophisticated experiments (telemetric trackings) on the same species and in the same lake remained inconclusive if water currents, wind-generated surface waves or the sun could deliver cues to swim towards the spawning places (HASLER and co-authors, 1969). Tagging investigations with adult salmon *Oncorhynchus keta* in coastal areas of Japan demonstrated that the fish found their home river even when blinded (HIYAMA and co-authors, 1967). Lake-bound cutthroat trout *Salmo clarkii* provide an excellent example of the possibility to design a model of the orientation mechanism which may hold also for other salmonids in the sea. So far, all field experiments with homing cutthroat trout, which in laboratory experiments employed the sun as reference point for orientation (JAHN, 1969), gave no evidence of the presence of compass orientation directed by celestial stimuli. Other senses had to participate (MCCLEAVE, 1967; MCCLEAVE and HORRALL, 1970; MCCLEAVE and LABAR, 1972). The experiments were carried out on trout displaced from their home stream during spawning migration over a distance of up to 22 km. Homing was studied by the tagging–release–recapture method, float-, and ultrasonic-tracking. Only in one experiment was the number of tagged, blind, trout returned significantly smaller than in the controls. Apparently, the fish returned to the home river but, due to their blindness, did not find the trap. Vision is involved, but only in close-range orientation.

Tagging of blinded bream *Abramis brama* in a large artificial lake over distances of up to 135 km resulted in recapture at the place of their first capture (PODDUBNYI, 1966). The fact that yellow eel *Anguilla anguilla* homed in the North Sea when displaced 100 km and more can hardly be attributed to visual performance (DEELDER and TESCH, 1970; TESCH, 1970). The ability of migrating silver eels to maintain a surprisingly exact compass course in turbid North Sea waters, unaffected by darkness during the night and heavy overcast during the day, again seems to exclude visual stimulation as a mechanism responsible for compass-course navigation (TESCH, 1972, 1974a).

(3) Temperature

Functional and structural responses of fishes to temperature have been reviewed in Volume I: BRETT (1970), GARSIDE (1970). Temperature is likely to represent an important orienting stimulus. However, pertinent knowledge is very sparse (MURRAY, 1971). In fishes, thermoreception seems to be based on cutaneous segmental innervation, but not on lateral-line organs. Teleost thermal receptors are scattered over the whole body surface and depend on spinal nerves. In the freshwater fish *Rutilus rutilus*, mechanoreceptors of the head and spinal nerves record temperature stimuli provided these are accompanied by simultaneous mechanical stimulation (SPÄTH, 1967). Some marine fishes have been shown to respond to minute temperature changes: in conditioning experiments, species of *Blennius*, *Centronotus*, *Cottus*, *Gadus*, *Onos*, *Zoarces*, *Crenilabrus*, *Cyclopterus*, *Gobius*, *Raniceps*, *Spinachia*, *Nerophis*, *Platichthys* and *Pleuronectes* have revealed threshold values as low as 0·03 C° to 0·07 C° (BULL, 1936). Temperature increase or decrease of 1 C° has been perceived by freshwater fishes (DIJKGRAAF, 1940).

Is such pronounced thermosensitivity used for orientation? Preference experiments show that fishes are capable of selecting waters of specific temperatures within a given water body. The earlier pertinent literature has been reviewed by SULLIVAN (1954). In a temperature gradient, moving fishes appear to select a particular temperature; when fish move through the gradient, the frequency of their movements is least at the preferred temperature; but maximum cruising speed is greatest at the selected temperature. Hence the mode of orientation within a temperature gradient seems to be klinokinetic and not very different from that in a salinity gradient (p. 672).

HARDEN-JONES (1968) assumes that a fish with an observed threshold sensitivity of 0·03° C—or with a sensitivity of 0·001° C if the temperature changes within 1 sec (BARDACH and BJORKLAND, 1957)—is able to detect the temperature gradient between polar and Atlantic water near East Greenland. In this area the water temperature falls 4·5° C within a distance of 400 m (0·01° C m^{-1}). In that way, thermal gradients in estuaries could be detected. Comparable information may also be obtained from a halocline, detected by a similar mechanism, and guide the fish into a river or from the river to the open ocean.

Another response initiated through temperature is the release of positive or negative rheotaxis (NORTHCOTE, 1962). In recently emerged fry of the rainbow trout *Salmo gairdnerii*, low experimental temperatures evoke negative rheotaxis: in darkness the fry exhibit reduced tactile bottom contact, they lose visual contact and move downstream. The reverse is the case at high temperatures: these induce bottom contact in darkness; a sharp temperature rise leads to 'upstream' movement. Corresponding movements of *S. gairdnerii* have also been observed in the natural environment. Further evidence of downstream movement during temperature decrease has been obtained for *S. gairdnerii* and *Salvelinus fontinalis* by COOPER (1953).

Temperature may also act as releaser of upstream migration in certain fishes at the beginning of their spring migration into brackish water of tidal areas. In spring, coastal and inland water temperatures rise earlier and faster than those of the sea. Mugilids and related forms presumably depend on thermal stimuli for initiation of positive rheotactical behaviour which leads them into inland waters. In summer, open-sea fishes may be stimulated by the warmer ebb water to react rheotactically—similar to the swimming crabs *Macropipus holsatus* which leave their bottom hiding places and, on flood tide, enter medium water layers to be transported shoreward (VENEMA and CREUTZBERG 1973; Chapter 8.1). Tide-related vertical movements may be released by changes in salinity and, perhaps, in temperature. Shoreward movements in spring and seaward migrations in autumn seem to be stimulated primarily by temperature.

(4) Salinity

Responses of fishes to salinity have received detailed attention in Volume I (HOLLIDAY, 1971) and in Chapter 5 of the present volume. Gradients in total salinity and ion composition may provide stimuli for spatial orientation. Unfortunately, detailed critical experiments are largely lacking.

Although fishes possess external chemoreceptors (e.g. TATEDA, 1964) the mechanism of salinity perception is unknown. External receptors such as the 'common chemical sense' are likely to be involved in chemotactical movements in salinity gradients. VERNEY (1949) has suggested the possibility that in higher vertebrates 'osmoreceptors' in the hypothalamus may perceive changes of osmolarity in blood. This suggestion has received some support from anatomical and electrophysiological observations (JOYNT, 1966). Still, it is difficult to imagine how such information could provide cues for directional orientation; it could possibly act as releaser.

Juvenile salmon *Oncorhynchus* sp. can perceive changes in salinity during their seaward migration (MCINERNEY, 1964): with increasing age, representatives of 5 species gradually changed their salinity preferences towards increasing salt concentrations. These changes parallel the salinity gradients typical of estuaries passed by young salmon on their way to the ocean: the terminal patterns indicate a preference for open-ocean water. How does the salmon orient within the exceedingly small local salinity gradients of an estuary (approximately 0·0000035‰ salinity cm^{-1})? We do not know. A taxis type of orientation seems very unlikely. MCINERNEY rather assumes that a kinesis might be involved. Successful search for preferred salinities could result from trial and error movements; this would involve klinokinetical orientation. These considerations seem to favour VERNEY's (1949) hypothesis proposing 'osmoreceptors' in the hypothalamus and perception of blood osmolarity.

The seasonal migrations into, or away from tidal areas have been considered on p. 671 in connection with temperature stimuli and in Chapter 8.1. Salinity preferences of *Oncorhynchus* sp. and *Gasterosteus aculeatus* have been treated in Volume I (HOLLIDAY, 1971).

(5) Water Movement

The ecological importance of water movement for aquatic organisms has been reviewed in Volume I, Chapter 5. In regard to fishes, stimuli generated by currents or turbulence are perceived by the lateral-line organ. Accounts on functional, morphological and neurophysiological aspects of this organ have been provided by WUNDER (1936) and FLOCK (1971). WUNDER speaks of 'Strömungssinn' (sense of current).

HOFER (1908) presumed that fishes direct their head against the water current and that the lateral line receives the stimuli responsible for correcting their position in relation to the current. If HOFER directed a weak water jet against the lateral line of a resting pike *Esox lucius* the fish responded by a certain change in the positioning of its dorsal fin. If the water jet stimulated only one canal organ, the pike did not respond; the same was true if nerves of the canal organs were eliminated. These observations were confirmed by electrophysical experiments on spinal dogfishes *Scyliorhinus* sp. (ROBERTS, 1972). When the part of the body overlying the receptor was flexed, the electric impulses of the non-active fish were either enhanced or depressed depending on the direction of water movement. In swimming spinal dogfish, sense organs discharge in bursts in a frequency coinciding with the swimming rhythm. Hence the lateral-line receptors may not only provide information useful for locomotory coordination, but also perceive minor changes in the movement of ambient water.

(a) Rheotactic Behaviour

Orientational responses to water movement (Volume I, Chapter 5) are known as rheotaxis. Rheotactic reactions require visual, mechanical or, for release, chemical stimuli. Rheotaxis is not possible if the fish swims in a large drifting water mass (Chapter 8.0). Without reference stimuli it cannot perceive the displacement.

Moving-background experiments revealed the following threshold values for evoking rheotactic responses: 3 to 9 cm sec^{-1} in *Clupea harengus* (BRAWN, 1960); 2 to 5 cm sec^{-1} in *Gadus morhua*, *Merlangius merlangus*, *Micromesistius poutassou* and *Clupea harengus* (HARDEN-JONES, 1963). Rheotaxis was initiated in young salmon *Oncorhynchus* sp. by threshold values of only 0·4 to 0·5 cm sec^{-1} (GREGORY and FIELDS, 1962).

Rheotactic behaviour has been investigated and discussed by KLEEREKOPER (1967). Beside other fishes, he investigated sharks, such as *Scyliorhinus stellaris*, *Mustelus mustelus*, *Ginglymostoma cirratum* and the sparid fish *Diplodus sargus*. KLEEREKOPER used a circular tank with 16 compartments for directional choice and introduced odorous substances. Without increasing the water flow in the respective compartment, introduction of odour changed the locomotory pattern resulting in smaller or larger turns, compared with the controls, and in a decrease of the radius of the turns. But the source of the odour could not be located unless the odour was associated with a differential flow rate from the respective compartment. Presumably, the presence of the odorous attractant releases rheotaxis.

The significance of the stream flow has just been indicated by the experiments with carcharhinid sharks in the search of odour traces (HOBSON, 1963) and described on p. 680. KLEEREKOPER's (1967) results indicate that a water current may be an indispensable prerequisite for proper release of directed swimming, and that water movement is of considerably greater importance for finding a food source than orientation cues provided in an odour gradient. Such current-based orientation may also characterize the main orientation mechanism of homing salmon during their river migration (p. 683). Further evidence for the existence of a current-dependent mechanism of orientation has been provided by CREUTZBERG (1959, 1961) whose results have been confirmed by MILES (1968a). Elvers of *Anguilla* sp., during inland-water migrations, swim against an experimental water current only if unfiltered natural inland water is offered. The attractiveness of the fresh water is due to dissolved and particulate organic matter which is biodegradable, heat stable and non-volatile. It is suggested that these substances are perceived by the olfactory organ. A possible stimulation of the gustatory sense is not excluded because the olfactory abilities of the elvers might be less pronounced than those of the adults (see also LAIBACH, 1937). For further examples on the release of rheotaxis see p. 671.

Displacement is not perceived by olfactory stimuli, but mostly by visual perception of the moving background. In young eels *Anguilla anguilla* vision is necessary for directed swimming movements (SCHIEMENZ, 1952). Some examples of visual dependence of rheotaxis in marine fishes have been presented in Volume I (BLAXTER, 1970, p. 262). JONES (1963), who investigated several fish species, concluded that flatfishes exhibit no rheotactic responses. But ARNOLD (1969) demonstrated rheotactic behaviour in the first ontogenetic stages of *Pleuronectes platessa*. As the larvae metamorphose, rheotactic behaviour mediated through visual stimuli decreases. Adult flatfishes, such as *Solea solea*, are known to drift without swimming at the surface (DE VEEN, 1967, p. 235): 'they only move and dive when actually touched by a stick or dip net'. In migratory Salmonidae visual rheotaxis is released when they begin to ascend the river during spawning migration perceiving the odour of their home stream (p. 683). In the Mugilidae rheotaxis seems to be released during feeding migrations in spring, which lead them into brackish waters and into rivers; the releasing factor and the reference stimuli for rheotactic migration used by Mugilidae is unknown. The development of rheotaxis in early stages of some cyprinids, percids, *Atherina mochon* and *Mugil* sp. has been investigated by PAVLOV (1966): At early developmental stages, the main mechanism of rheotaxis in running water is based on visual stimuli and related to the optomotor reaction; at later stages, physiomechanical mechanisms of orientation become relevant.

Negative rheotaxis exists in species of *Mugil* and *Anguilla* (FROST, 1950; MEDCOF, 1966; TESCH, 1973) during seaward migration to their spawning grounds, and in *Salmo* sp. during migration to the feeding grounds (HASLER, 1966). Elvers of *Anguilla* sp. may lose visual contact with the bottom during flood phases, during which they drift into the estuaries. At later ontogenetic stages they may use bottom contact as reference stimuli for rheotactic migration.

Adult burbot *Lota lota* migrate mainly during the night (TESCH, 1967) and are known to seek contact with the bottom substratum which provides reference stimuli for rheotactic orientation; they have poorly developed optical senses (WUNDER, 1936; KIRSCHE, 1966). A similar situation prevails during the spawning migration of the lamprey *Lampetra fluviatilis* (RYAPOLOVA, 1964; TESCH, 1967; for earlier references consult TESCH, 1960).

(b) Detection of Food

In addition to orientational responses to environmental factors, food detection is of vital importance. According to WUNDER (1936), fishes can locate prey via canal organs in their head region. WUNDER used blinded pikes *Esox lucius*, and offered them dead prey fish. Only if the prey fish's movements were simulated did the pike snap at it. Apparently, the resulting turbulence stimulated the canal organs and thus enabled the pike to locate its prey, at distances less than 5 to 10 cm. In normal pike the lateral organ seems to be unimportant for prey location: visual perception dominates food detection. In the sturgeon, vision is far less important; *Huso huso* in particular sometimes uses the lateral line for food detection (PAVLOV and co-authors, 1970). In electric catfish, *Malapterurus electricus*, which exhibit high sensitivity to gustatory stimuli (p. 679), prey-capture behaviour is released also by small water disturbances produced in the vicinity of the head (BAUER, 1968).

(c) Avoidance Reactions

Avoidance reactions of fishes depend mainly on visual stimuli (p. 665) except in darkness. Avoidance of nets by the shad *Alosa sapidissima* at night—established through field observations by ultrasonic tracking—was attributed to the lateral-line organ (LEGGETT, 1971). HEMMINGS (1973) conducted diving studies on the behaviour of haddock *Melanogrammus aeglefinus* during the operation of a seine net. The haddock kept station with the moving net, suggesting that optomotor responses might be involved. Apparently, the moving background delivered the visual stimuli for a co-ordinated rheotactic response.

(d) Social Contact

Social contact of fishes sometimes depends on the perception of hydrodynamical effects which are produced by a neighbouring fish. CAHN (1972) carried out experiments with tunas *Euthynnus affinis* on the side-to-side spacing of schooling specimens. The individuals tested had visual contact with one another, but hydrodynamic contact was blocked by transparent partitions between them. CAHN concluded that hydrodynamic contact was apparently essential for typical spacing and positional orientation and that the lateral line should play a primary role as pertinent sensory mechanism.

(6) Substratum

Contact with the bottom substrate presumably provides orientation stimuli for bottom fishes (see also Volume I, Chapter 7). Especially in the search for resting places, e.g. of flatfishes, gobiids and eels, tactile stimuli are important. Sensory cells perceiving tactile stimuli are distributed over the whole body; but they are more concentrated in body parts which usually maintain contact with the bottom, such as the barbels, ventral and pectoral fins. WUNDER (1936) quotes investigations by SCHICHE on the catfish *Ameiurus nebulosus* searching for a comfortable place in an aquarium. In complete darkness, the catfish prefers a sandy bottom to stony substrates as a resting place. If the substratum is uneven and the light is switched off, it selects a hollow which provides maximum contact between body and substrate.

Flatfishes rely on their tactile sense to select proper substrates, suitable for resting and protection. On sandy substrates they tend to burrow themselves; on gravel or solid substrates they rest on the substrate surface. Substrate selection might involve kinetically oriented movement. Locomotory activity is reduced if contact with sandy bottom is attained.

(7) Pressure

Hydrostatic pressure (Volume I, Chapter 8) acts in all directions with the same intensity. Hence it cannot provide directional cues, except for vertical gradients. Pressure is a continuously acting force and, like sound waves, may be perceived by intervention of the swimbladder. According to WUNDER (1936), pressure perception might be the most important task of the swimbladder. It is still unknown which sense organs of fishes perceive changes in pressure (STEEN, 1970). The simplest method would be transfer of the pressure stimulus by Weber's ossicles from the swimbladder to the inner ear; but this would be possible only in the Ostariophysi, a fish group known to possess this connecting organ and which exhibits the highest capacities for sound perception (p. 689). Since pressure can also be perceived by non-ostariophysians, e.g. the Gadidae (TYTLER and BLAXTER, 1973), receptors in the swimbladder may well be involved (QUTOB, 1960; HARDER, 1964). Other groups without Weber apparatus, like *Cichlasoma*, *Macropodus*, two Percidae and *Esox*, have also been shown to be sensitive to pressure changes. They perceive differences in water-column height of 0·4 to 2·0 cm at a pressure-change speed of 10 cm water column per second (TSVETKOV, 1969). This threshold value is similar to that recorded for the ostariophysian *Misgurnus fossilis* which is sensitive to a change in water-column height of 4 to 14 mm at 10 mm min^{-1} (TSVETKOV, 1972).

These experiments document a high sensitivity of fishes to pressure changes. Fishes are even capable of perceiving pressure changes of atmospheric origin (TSVETKOV, 1972); this conveys to them the ability to avoid detrimental weather conditions, and may provide orientational cues. Minor topographical changes involving water-depth changes of only a few centimetres can possibly also be perceived by certain fishes. In fishes travelling on, or close to the bottom, this ability may facilitate the perception of shorelines or of tidal channels. However, no proof is available as yet for the dependence on the pressure sense during migration in shallow shelf areas. KUHNE and STROTKOETTER (1967) conducted training experiments with Cyprinidae, Siluridae and Cyprinodontiformes in order to examine their pressure sensitivity. If displaced, the experimental fishes were able to locate a distinct place in their aquarium without assistance of optical and chemical senses. KUHNE and STROTKOETTER presume that distance estimation and in some cases also pressure perception are significant for locating the places.

In the Baltic Sea, migrating eels *Anguilla anguilla* exhibit a westward trend (TESCH, 1973). When encountering the Swedish or Danish shorelines, they change their course. It seems difficult to imagine that they perceive these coasts by vision, especially since migration continues also at night. Possibly, course corrections are induced by stimulation of their pressure sense or by turbulence. Decreasing water depth may release a change in swimming direction and subsequent direction finding may depend on trial and error. Possibly, turbulence due to upwelling water may support orientation. Field experiments with ultrasonically tracked eels in coastal waters of the North Sea revealed that silver eels during their spawning migration did not leave deep channels in areas with water depths less than 6 m (TESCH, 1972). Similarly silver eels, marked by surface floats, exhibited movements along the 4·5 to 5 m isobath in Kursk' lagoon (USSR) of the Baltic Sea (OVCHINNI-

KOV, 1971). In areas with very gentle bottom slopes, free from obvious tactile or visual orientation cues, the fish may have to rely on their pressure sense. An example of such a situation is the Kursk' lagoon which has no steep bottom gradients and provides no or little turbulence cue.

Control of the vertical position depends not only on pressure stimuli. Irradiance may assist in depth-preference orientation (p. 663). Depth-preference movements involving changes in body positioning require integration of pressure and gravity perception (p. 688). For integration of different types of orientation stimuli consult Chapter 8.0.

(8) Dissolved Gases

Dissolved gases (Volume I, Chapter 9), especially oxygen, exert pronounced effects on physiochemical processes in fishes and—similar to temperature and salinity—can evoke behavioural and orientational responses. It is unknown whether dissolved gases stimulate a fish via direct influences on its receptors.

Investigations on postlarvae of the flounder *Paralichthys lethostigma* indicate that escape from water of low oxygen is not accomplished by random movement. No flounder remained in the region of de-oxygenated water longer than 3 secs. All postlarvae responded by turning and swimming directly upward towards water areas containing sufficient oxygen (DEUBLER and POSNER, 1963). Possibly, klinotaxis is involved; this would require at least two receptors located in different areas of the body.

Orientational stimulation due to low oxygen concentration helps to avoid, or escape from, conditions that may soon cause death and hence are of considerable ecological significance. Salmon *Oncorhynchus tshawytscha* ascending the Sacramento River system (USA) were tagged by ultrasonic transmitters and traced during upstream migration. Practically no salmon passed barriers characterized by dissolved-oxygen concentrations below 4·5 ppm (HALLOCK and co-authors, 1970). However, additional stress due to high temperature may also have been involved. The salmon may, furthermore, have suffered from dypnoea and thus may have been physically unable to continue migration. Such behaviour might be considered a kind of passive orientation (non-sensory) which prevents the fish from entering dangerous environmental conditions.

(9) Organic Substances

Organic substances (Volume I, Chapter 10) are of considerable importance for organismic activities in oceans and coastal waters. A number of substances, perceived by various fishes in very low concentrations, serves as guideposts for migration and social contacts. Most fishes have considerable capacities for discriminating specific organic substances.

(a) Perception of Organic Substances

In many fishes, perception of organic substances functions more effectively than visual perception. In fact, the olfactory and gustatory organs of many fishes are as effective as those of land vertebrates (Table 8-4; TEICHMANN, 1962; PFEIFFER, 1969). Since fishes smell and taste in an aquatic medium, distinction between these two senses is difficult; definite specialization of the two senses is often doubted.

In general, the taste organ analyzes gross quality and quantity of organic substances and examines substances which the olfactory organ has discovered. Early experiments by STRIECK (1924) indicate that the olfactory organ of fishes is specialized to some degree for perceiving odour. Removal of olfactory lobes in minnows *Phoxinus phoxinus* resulted in no decrease in gustatory capacity if typical taste substances, like sucrose and sodium chloride, were offered (KRINNER, 1935; see also WUNDER, 1927).

Table 8-4

Sensitivity of olfaction in fishes, amphibians and mammals (After various authors, compiled by PFEIFFER, 1971; reproduced by permission of Wissenschaftliche Verlagsgesellschaft, Stuttgart)

Animal	Chemical cue	Lower critical concentration detected	
		Dilution	Number of molecules in 1 cm^3
Fishes			
Phoxinus phoxinus	β-phenyl-alcohol	$1:10^{7}$	10^{14}
Salmo sp.	β-phenyl-alcohol	$1:10^{10}$	10^{11}
Anguilla sp.	β-phenyl-alcohol	$1:10^{18}$	10^{1}
Anguilla sp.	Extract from *Tubifex* sp.	$1:10^{17}$	—
Phoxinus phoxinus	Extract from fish skin	$1:10^{7}$	—
Phoxinus phoxinus	Extract from heart of horned cattle	$1:10^{7}$	—
Calamoichthys calabricus	Extract from heart of horned cattle	$1:10^{11}$	—
Polypterus sp.	Extract from heart of horned cattle	$1:10^{14}$	—
Amphibians			
Frog (in water)	β-phenyl-alcohol	$1:10^{6}$	10^{13}
Salamander (in air)	Butyric acid	—	10^{10}
Mammals			
Rat	Isovalerian acid	—	10^{10}
Man	Mercaptan	—	10^{7}
Dog	Butyric acid	—	10^{4}

The olfactory organ of fishes is of special importance for spatial orientation. If the usually very sensitive olfactory organ is eliminated, dissolved substances can no longer be located, e.g. in sharks of the genus *Scyliorhinus* (VON UEXKÜLL, 1895), catfish *Ameiurus* sp. (PARKER, 1910), dogfish *Mustelus canis* (SHELDON, 1911; PARKER, 1914), Polypteridae (PFEIFFER, 1969). Investigations on trained goldfish, *Carassius auratus*, however, showed that perception of chemicals, such as coumarin and amylacetate, in operated individuals (cutting of filia olfactoria; extirpation of bulbus olfactorius) is possible if the concentration of the chemical is 5 to 8 times higher than the critical level detected by intact individuals (ZIPPEL and co-authors, 1970). The authors argue that coumarin, which yielded no 'gustatory' response in earlier experiments, has a pronounced bitter taste; hence some earlier results (PARKER, 1910; STRIECK, 1924; SANDERS, 1940; NEURATH, 1949) are questionable because gustatory components may have participated.

Additional chemical receptors are located on exposed body surfaces of fishes, the so-called 'chemical sense' (PARKER, 1912). This sense is assumed to be concerned in the perception of chemical substances, including some which cause man-made pollution. In contrast to the other chemoreceptors, the chemical sense has free nerve endings in the epidermis connected to spinal nerves. The common chemical sense can be stimulated also by odour of prey animals (SCHARRER, 1935; SCHARRER and co-authors, 1947). But numerous orientation experiments document that the most important sense for orientation to odorous substance is located in the olfactory organ and that the sense of smell primarily or exclusively operates on orienting stimuli. SUTTERLIN and SUTTERLIN (1970) identified external receptors located in the snout region of *Salmo salar*. These receptors do not function as taste buds but perhaps represent the so called 'naked' type of pit organs. They are sensitive to several chloride salts as well as mineral and organic acids, but insensitive to neutral amino acids and simple sugars. Their electrophysiological susceptibility and character of discharge is quite different from that of the taste buds. They are possibly involved in the detection of osmotic gradients in the ambient water (p. 672).

The gustatory sense of fishes is not restricted to mouth and lips. Taste buds also occur on gill rakers and gill arches, on fin and barbels, and in some fishes on the entire body surface. The concentration of taste buds in branchial regions is more pronounced in limnic than in marine fishes (IWAI, 1964). Catfishes (Siluridae) can perceive a bitter taste within their mouth, whereas sweet, sour and salty tastes are perceived outside the mouth (VON LUKOWICZ, 1966).

A comparison of the size of the sense areas devoted to vision and to smell reveals pronounced differences in *Anguilla anguilla* (Fig. 8-43): its sense-of-smell area is much more developed than that of vision. In other migratory or semi-migratory fishes the proportions may be similar or quite different: *Lota lota*, for example, has similar-sized olfactory and optic organs; *Salmo gairdnerii* and *Gasterosteus aculeatus*, on the other hand, have far smaller smell than visual organs. Similar differences exist in regard to the number of folds in the olfactory rosette: *G. aculeatus*, a fish with excellent visual capacities, has 2 folds, *S. gairdnerii* 13 to 18, *Lota lota* 30 to 32 and *A. anguilla* 68 to 93 (TEICHMANN, 1955). In addition, *A. anguilla* has a much larger bulbus olfactorius than most other fishes examined.

Structural differences among sense organs may also exist in different ontogenetical stages. One would expect, for example, that the leptocephalus stage of *Anguilla anguilla* with only 9 folds in its olfactory rosette (LAIBACH, 1937) is less able to perceive odorous substances than the adult with 68 to 93 folds. The leptocephalus is a bathypelagic organism which, like many other pelagic fishes seems to make little use of its sense of smell, whereas the adult eel during its continental period is demersal; this requires, in general, stronger olfactory capacities.

(b) Search for Food

Many fishes orient towards a food source primarily by employing the olfactory sense. Gustatory receptors are presumably used only exceptionally. Electrophysiological investigations on the participation of either sense of smell or sense of taste by stimulation of the olfactory area in *Carassius carassius* resulted in activities similar to normally induced feeding behaviour; stimulation of vagal lobes, on the other hand, produced no feeding activity (GRIMM, 1960). This finding indicates that the peripheral gustatory system normally plays no essential role in the arousal of feeding activity. Later investigations on young *Salmo salar* revealed that the relations can be more complicated (SUTTERLIN and SUTTERLIN, 1970). In addition to good olfactory abilities, the salmon also has excellent visual abilities (Fig. 8-43); after visual food perception and prey seizure, the gustatory sense (but not the sense of smell) seems to become involved immediately in further stimulation of feeding behaviour, especially if carriers (simulatory food pellets) with aliphatic acid of comparatively high chain length as well as with valeric and caproic acids are offered. Olfactory-inhibited fish are also stimulated. Electrophysiological controls revealed that the receptors in these experiments are the taste buds on the palatin organ of the upper jaw.

The following migratory and sea fishes are known to use their sense of smell in the search for food: *Scyliorhinus canicula* (VON UEXKÜLL, 1895), *Mustelus laevis* (SHELDON, 1911), *Anguilla anguilla* (VON HESS, 1913; HARTMANN, 1935), *Gobius niger*, *Platichthys flesus*, *Lota lota*, *Ctenolabrus suillus*, *Gadus merlangus*, *G. morhua*, *Labrus mixtus*, *Raja clavata*, *Raniceps raninus* (PIPPING, 1926, 1927); *Salmo trutta*, *S. gairdnerii* (WUNDER, 1927), *Blennius pholis*, *Pleuronectes platessa* (VAN DEN BERGHE, 1929). The results concerning *Anguilla anguilla* have been confirmed recently (Fig. 8-45) by field experiments off the southern North Sea coast (TESCH, 1970). These investigations were originally designed to ascertain the effect of impaired olfaction upon the eel's homing ability.

STEVEN (1959) conducted aquaria experiments with two shoaling fishes, *Hepsetia stipes* and *Bathystoma rimator*, from the coasts of Jamaica and the Western Atlantic Ocean. He found that aqueous extracts of tissues from terrestrial mammals and various marine animals, as well as different waters in which live plankton had been kept, release exploratory feeding activities. In stimulated fishes, the average swimming speed was about twice as high as in their unactivated counterparts. Blinded *B. rimator* respond to extracts of *Arca zebra* muscle and are able to locate the food pieces.

In addition to the sharks, others also mentioned, e.g. the Carcharhinidae, are guided by their sense of smell (HOBSON, 1963). They can detect by olfaction both injured and uninjured fish in a state of stress. The prey can be detected over a considerable distance, providing the olfactory stimulus has had sufficient time and means for dispersal, e.g. an olfactory trail has been drawn out by a current or the source of the olfactory stimulus is moving. When the gustatory stimulus has been perceived and the substance detected does not permit acceptable stimulation, *Carcharhinus menisorrah* rejects the potential food. In other sharks—*Negaprion* sp., *Sphyrna* sp. and *Ginglymostoma* sp.—electrical potentials were recorded from the olfactory sac in the presence of extracts from crabs and tuna. Both amplitude and

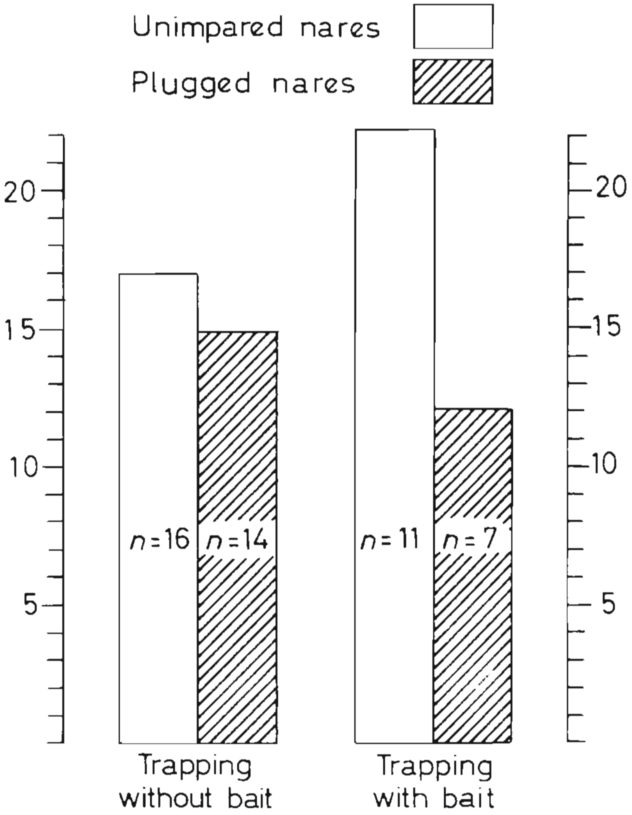

Fig. 8-45: *Anguilla anguilla*. Percentage of trap recaptures yielding yellow eels with unimpaired or plugged nares. Traps without bait: fike nets with wings blocking up the entrance of a sluice in the dyke of the Isle of Föhr (North Sea); traps with bait (mostly smelt); baskets placed in the Elbe estuary east of Cuxhaven. (Based on findings by Tesch, 1970; original.)

frequency of the potentials clearly increased during stimulation (Gilbert and co-authors, 1964). Aronov (1965) investigated the significance of the different sensory organs in 5 species from the Black Sea and presumed that several fish species of this area find their food by their olfactory sense.

The sturgeons *Acipenser baeri*, *A. güldenstädti* and *Huso Huso* provide examples of food search aided by taste organs (Pavlov and co-authors, 1970). The juveniles of these species control wide sea-bottom areas with their sense of touch and taste. Similarly, catfishes of the genus *Ictalurus* locate chemical traces by their taste organs (Bardach and co-authors, 1967). They compare organic substances in terms of concentrations in time and space. Gradients are perceived without assistance of water currents (p. 673).

Bauer (1968) reports that prey-capturing behaviour is released in the electric catfish *Malapterus electricus* by stimulation of its gustatory receptors. If a catfish is touched at its tail (which is provided with taste receptors) with a glass-rod, covered with mucus of other fishes, it emits at once strong electric pulses. If all sensory pathways going from the tail to the cranium are eliminated, except that providing the caudal gustatory receptors, the fish also reacts with emission of pulses; it does not react if this nerve is cut. Stimulation of prey-capturing behaviour is also possible by water currents (p. 673); visual stimuli are ineffective.

(c) Social Contact

Schooling

Minnows, *Phoxinus phoxinus*, recognize conspecifics as well as heterospecific fishes by their sense of smell (WREDE, 1932; GÖZ, 1941). Bullheads *Ictalurus notatus*, are stimulated by interspecific odours (TODD and co-authors, 1967). Bullheads are capable of discriminating between conspecifics of a given population. Possibly, contact between the different individuals of a school is maintained by olfactory stimuli. Blinded rudds *Scardinius erythrophthalmus* detect and prefer water which has contained other rudds (KEENLEYSIDE, 1955). This ability disappears after destruction of the olfactory epithelium. Similar effects on salmon *Oncorhynchus tshawytscha* evoked by the smell of other individuals of the same species were found by OSHIMA and co-authors (1969a).

Experiments on roaches *Rutilus rutilus* with 'two-fish schools' suggest that school structure is maintained by a balance of attractive and repulsive forces. The attraction modalities involved are olfaction at night and vision during the day (p. 666). The repulsion modality is delivered by a mechanical sense (p. 672), the lateral-line sense (HEMMINGS, 1966). In the cyprinid *Abramis brama* schooling effects could be maintained only if the different vessels containing single individuals were connected with one another allowing for water exchange between the jars. Visual stimuli alone were not sufficient to maintain social contact (RYŽKOV, 1970).

KÜHME (1963) reported a schooling effect in *Hemichromis bimaculatus* and *H. fasciatus* which is released by chemical stimuli. One-day-old individuals were separated from their school and placed singly in a special aquarium. If water was added to this aquarium from the school-containing aquarium, the single fish preferred those areas which contained water conditioned by the school. Water from schools of other fishes did not have this effect.

The observations of STEVEN (1959) on schooling fishes led to the conclusion that light facilitates contact between individuals. But STEVEN also found that the fishes can detect the odour of plankton and of mammalian tissue; this finding suggests the additional possibilities that fishes may aggregate along concentration gradients of organic substances released by their food organisms, and that schools of the same species may find each other by this means. It is probably due to this effect that herring *Clupea harengus* aggregate in the North Sea near areas where their principal food organism, *Calanus finmarchicus*, is abundant and that they tend to be absent from areas where *C. finmarchicus* is scarce. Similar relations may exist between mackerel *Scomber scomber* and *C. finmarchicus* in the western English Channel and in the Celtic Sea.

Spawning aggregations are a special case of schooling. In this case, too, organic substances may act as stimuli providing cues to individuals which search for schools of their own species or race, or individuals of the opposite sex. NIKOLSKY (1963) quotes cases in which steroid hormones may stimulate the opposite sex (KIRSHENBLAT, 1952; PUCHKOV, 1954). The stimulant may be absorbed through the gills and thus attain admission to blood and endocrine glands evoking hormonal activities. This leads to the release of behavioural changes required for spawning. The stimulant may also act on chemical receptors to release orientation activities and/or to provide directional stimuli. A similar type of chemoreception is involved if the organic substances in question are released from the skin (pheromones).

Homing salmonids (see below) and *Anguilla anguilla* elvers may derive cues from organic substances for discriminating inland water during up-stream migration (NORDENG, 1971). Especially experiments with transplanted, seaward migrating, and landlocked char *Salmo alpinus* show that the homing ability may depend on the presence of the brood-stock conspecifics in the home stream. NORDENG quotes a transplantation experiment with salmon which documents the dependence of homing activities on pheromones: In 1957, Soviet Russian scientists began to introduce pink salmon *Oncorhynchus gorbuscha* into four rivers of the Kola Peninsula. As a consequence of transplanting this Far-East species into European waters, in 1960 thousands of mature individuals were caught on the coasts of Norway, Iceland and Scotland; the absence of brood stock in the streams of these coasts is considered to be the cause of the wide-range random migration recorded. Coincident with natural spawning and continued release of pink fry in the Kola rivers, the catches of mature pink salmon in Norwegian waters decreased to zero in 1961 to 1962: a local population had built itself up in the Kola rivers and the migrating salmon were now able to recognize these streams as their home areas.

Avoidance Reactions

In a way, avoidance reactions represent a behaviour opposite to that involved in social contacts. Substances released by an organism into the water repel a fish or evoke fright reactions. Avoidance reactions are known from five species of Salmonidae during upstream migration. Of various organic substances tested, diluted water rinses of mammalian skins caused excitation and resulted in initiating alarm effects (ALDERDICE and co-authors, 1954; BRETT and MACKINNON, 1954). It is not known whether these substances have, in addition to releasing effects, also a directional effect. The same pertains to alarm reactions of prey fishes released by skin substances of predatory fishes (VON FRISCH, 1941; REED, 1969). Alarm substances released by the injured skin of conspecifics are found in many fishes (detailed references *in*: REED, 1969 and PFEIFFER, 1971).

(d) Homing

The orientational behaviour of salmonids suggests the possibility that olfactory perception plays an important role in spatial orientation of fishes. Already BUCKLAND (1880) hypothesized that landward-migrating salmon may be able to recognize the scents of their home river. This hypothesis has since received support from

HASLER and associates in the early 1950's (for references see HASLER, 1966). Since then, a considerable number of field and laboratory investigations have been conducted in order to explore the physiological mechanisms involved in salmon homing. For details consult the reviews by HASLER (1966) and HARA (1970, 1971).

Other fishes also have been found to depend on the olfactory sense for detecting their home area. A landlocked population of the alewife *Alosa pseudoharengus* was shown to exhibit, like marine populations, upstream migration to its spawning places (THUNBERG, 1971). In experiments, specimens with unimpaired olfactory sense selected tank compartments filled with home water. *A. pseudoharengus* which had their nares plugged by cotton were not able to make such selection, but regained their ability to recognize the home water upon removal of the cotton.

Another experiment which demonstrated dependence of homing ability on the olfactory sense was conducted with longear sunfish *Lepomis megalotis* (GUNNING, 1959), a non-migratory stream fish with a very limited territory. Specimens with impaired olfactory sense exhibited reduced homing capacities after displacement. Blinded sunfishes, as well as controls, however, exhibited good homing abilities. Involvement of the olfactory sense in homing is also obvious from displacements of intact individuals transported upstream, and compared with those transported downstream. Downstream-released sunfishes homed more successfully. This finding is consistent with the hypothesis that the fish home on an odorous substance carried downstream with the water current.

While most investigators now agree that olfaction is of major importance for spatial orientation in salmon, trout and several other fishes during migration from the estuary to upstream spawning grounds, the mechanism involved is still being discussed. As pointed out above (p. 673), olfaction alone can hardly account for orientation towards the source of smell. Chemotropotaxis requires the presence of a steep odour gradient. Considering the long distance between estuary and spawning grounds, the gradient seems too weak. Hence also 'rheotaxis', released by olfactory stimuli, appears to be involved. While stimulation of the sense of smell increases the swimming speed (IDLER and co-authors, 1961)—a kind of ortho- or klinokinesis—rheotaxis (p. 683) requires reference stimuli, visual or mechanical, for assessing movements relative to bottom or banks of the river. In salmonids, the comparatively well-developed visual abilities are probably important. In the sea, visual orientation fails because of lack of reference points. Odorous cues of the home water seem to become perceptible only in the vicinity of the estuary. It is not clear how the first chemical stimuli perceived in coastal regions facilitate directional orientation.

Pacific Salmonidae of the Fraser River (USA) travel forward in salt water always on the flood tide, close to the surface, and commonly display their presence by leaping and breaking the surface of the water. They disappear on ebb tide and their movements are unknown. On the return of the flood they re-appear at the surface, close to the location where they disappeared, and continue their migration to the Fraser River. They passively enter the Fraser River with the flood, but when the tide ebbs they do not turn with it or disappear from the surface; they continue on actively upstream (BABCOCK *in*: HARDEN-JONES, 1968). This behaviour is similar to that of the elvers of *Anguilla anguilla* on their migration in tidal areas directed towards inland waters (p. 664). Modern techniques, such as have been used for migrating silver eels *A. anguilla* in the North Sea (TESCH, 1972, 1974a), provide the means to critically test the field observations at hand. However, investigations with *Oncorhynchus nerka* near Dundas Island (British Columbia) did not give conclusive results, apparently because the home-river destination of the individuals tested was not clear (MADISON and co-authors, 1972). In addition, the local morphology of coastlines and estuaries seemed to be rather complex. Further tracking results obtained in the vicinity of river outlets support the view that olfactory mechanisms of orientation are used (SCHOLZ and co-authors, 1972).

How do elvers (and perhaps also salmon) perceive the end of the flood tide in tidal areas with no turbulence to indicate the tidal phase? This question has been discussed by CREUTZBERG (1961) and TESCH (1965). TESCH suggested that an internal rhythm could time the beginning ebb and commencing flood tide. In areas without tidal water movement, it should be easier to discover if or how the fish traces the river water outside the estuary, where open-ocean orientation (p. 699) ends and where coastal orientation begins to depend on olfactory cues for upstream migration.

In a more restricted area, investigations have been conducted with a landlocked salmon, the kokanee *Oncorhynchus nerka* (LORZ and NORTHCOTE, 1965). Salmon with impaired olfaction were released 150 m off the inlet into the lake of a very small spawning stream. In the trap near the stream inlet nearly all the individuals recaptured were without impairment (controls). This result was confirmed in threefold repeated experiments. Gill-net catches and echo-sounder traces indicated that entry into the inlet occurred preferentially on days with strong onshore winds; i.e. on days during which small odour traces of the little creek were presumably widely distributed along the shore. On calm days the river's water discharged into the lake in the form of a small band. Regarding the behaviour of the salmon on calm days, LORZ and NORTHCOTE write:

> 'Small groups of Kokanee swimming more or less parallel to the shoreline, were repeatedly observed to turn abruptly upon reaching the influence of the creek and move up it to the shallow delta at its mouth where they usually stopped briefly before entering the creek itself. Occasionally individuals which veered out of the path of creek water within the lake appeared to circle about until they had relocated its influence' (p. 672).

While LORZ and NORTHCOTE (1965) provide much evidence that, in the vicinity of the estuary, olfaction enables orientation, sense and cues employed by salmon farther away from the shoreline are unknown. Results received by ultrasonic or float tracking and by the marking and recapture method of MCCLEAVE (1967), JAHN (1969) and MCCLEAVE and LABAR (1972) indicate that far away from the estuary, olfactory orientation is unimportant. As mentioned above (p. 670), *Salmo clarkii*, released up to 22 km from the river inlet in Yellowstone Lake (USA), exhibited no distinct deviation if their sense of smell was impaired. However, in some cases the influence of river water mixed with sea water is stronger, especially in the case of greater river discharges. That river water spreading in the estuary is likely to provide cues to homing fishes has been shown by HELLE (1966) who investigated the homing of pink salmon *Oncorhynchus gorbuscha* along the coasts of Alaska. HELLE found that displaced salmon did not return to their original spawning area under conditions of extremely low river discharge. However, when the river discharge was normal or higher, the salmon homed successfully. Japanese investigations on *O.*

keta with impaired olfaction revealed that near the river mouth the sense of smell is important for the homing success (MIYAMA and co-authors, 1967). Similar results have been obtained for *Salmo salar* in the Baltic Sea. At a distance of 35 to 40 km from the estuary *S. salar* could not locate the mouth of the River Indalsälven if their nares were closed (BERTMAR and TOFT, 1969). Water of the Columbia River (USA) marked by isotopes originating from effluents of a reactor was identifiable even 115 km seaward of the estuary (GROSS and co-authors, 1965). Conceivably, odorous substances, distributed as far as the isotopes, might still be able to stimulate the olfactory sense of homing salmon.

A question still unsolved is whether anadromous fishes are stimulated by odours only of their home water or from the whole water passage to their spawning ground. The first possibility would require one odour to be followed during upstream migration (single-odour hypothesis). The second possibility would necessitate continuous learning of the odour sequence encountered during downstream migration (sequential-odour hypothesis).

Social contact (p. 682) seems to be based on pheromones (NORDENG, 1971). A similar situation may prevail in migrating fishes, i.e. young fish are conditioned to attractants of the local resident fish population with which they were associated before the onset of their seaward migration. This would support the **single-odour hypothesis**. While NORDENG's (1971) arguments fail to support that hypothesis convincingly, there are other observations which support it: OSHIMA and co-authors (1969a) investigated electrical olfactory bulbar responses of salmon. They placed two adult chinook salmon *Oncorhynchus tshawytscha* overnight in a small tank with creek water (non-home water); this water stimulated young chinook salmon very strongly. Water from the same creek which was not conditioned by adult chinook salmon evoked only a weak response. The same was true if it was conditioned by silver salmon, *O. kisutch*.

HARDEN-JONES (1968) and HARA (1970) advanced the hypothesis that odour imprinting occurs along the whole odour chain from upstream spawning places to the estuary. This **sequential-odour hypothesis** requires further qualification (see also HARA, 1971). The main point which led HARDEN-JONES and HARA to prefer the sequential hypothesis in favour of other assumptions is the tremendous dilution of the home water once it reaches the estuary; the resulting reduction in the intensity can hardly be assumed to be perceivable by the salmon. Data presented by IDLER and co-authors (1961) suggest that the lower threshold concentration for home-stream water recognition is close to 10 ppt. This concentration is far below that in the estuary of the Fraser River system (mostly below 1 part home water per thousand parts river water).

Another argument in favour of the sequential-odour hypothesis has been presented by UEDA and co-authors (1967) and OSHIMA and co-authors (1969b). Water samples downstream of the home water evokes electroencephalographic (EEG) responses of the olfactory bulb of a lower magnitude than home water. These responses, however, showed no substantial decrease with increasing distance from the spawning ground. Subsequent samples downstream of the Issaquah home water showed EEGs of 90%, 93%, 55%, 74%, 74% of the home water response (100%), the last value having been obtained near the estuary of the river. Fig. 8-46 shows silver salmon EEGs recorded in home water diluted with different amounts of

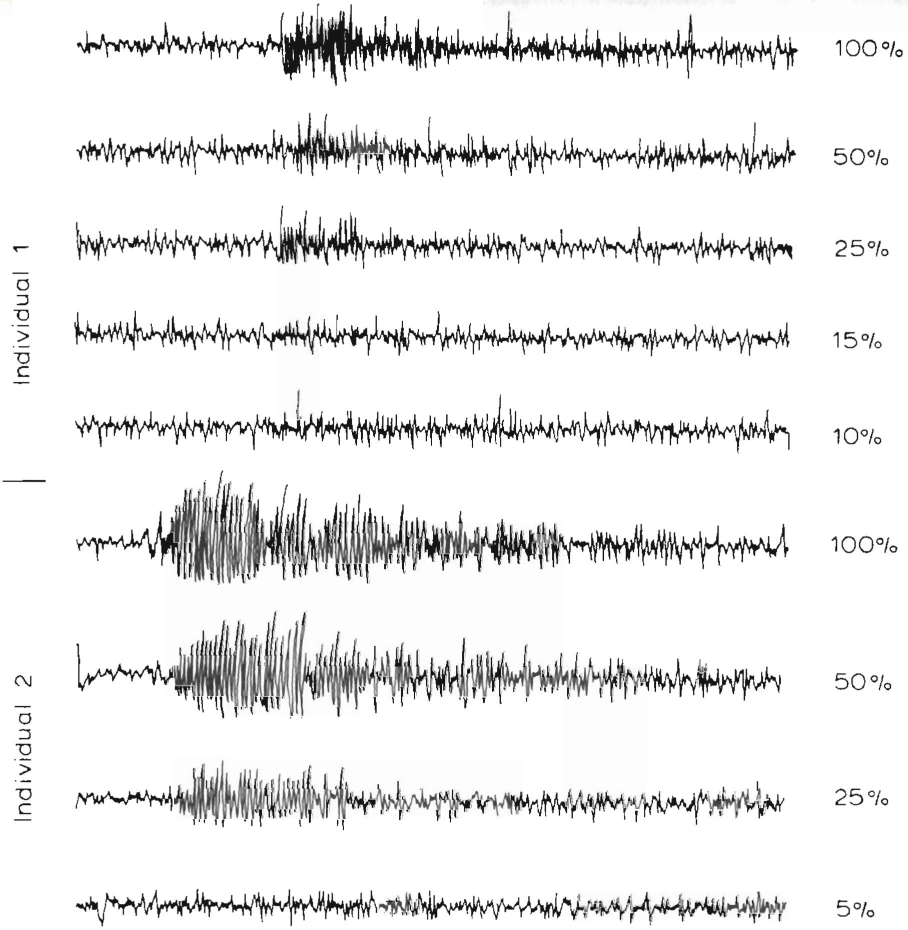

Fig. 8-46: *Oncorhynchus kisutch.* Electroencephalogram, recorded from olfactory bulb, showing effect of infusion of nasal cavity with home water (100%) and home water diluted to different percentages with distilled water. Individual 1: from a pond watering into Lake Washington Canal, USA. (After Ueda and co-authors, 1967; modified; reproduced by permission of Microforms International Marketing Corp.) Individual 2: from Soos Creek, near Auburn, USA. (After Oshima and co-authors, 1969b; modified; reproduced by permission of the *Journal of the Fisheries Research Board of Canada.*)

distilled water after the results of two different publications (Ueda and co-authors, 1967; Oshima and co-authors, 1969b). Criticism of conclusions drawn from EEG studies has been presented by Cooper and Hasler (1972).

Whatever the source of odour or the location and mechanism of scent imprinting may be, the period necessary for imprinting the stimulating substance is short (Carlin *in*: Hasler, 1966; Skrochowska, 1969). EEG techniques revealed that two-year-old *Oncorhynchus tshawytscha* acclimated to the odour of a new environment within about 70 hrs (Oshima and co-authors, 1969a). In a field experiment

(JENSEN and DUNCAN, 1971), 36 to 48 hrs sojourn after transplantation into a new water was sufficient for causing homing in salmon smolts *O. kisutch* to this new environment; there was no evidence for return to the old environment, to which they had been accustomed until the experimental separation.

The short duration of the imprinting process provides no evidence in favour of or against the two hypotheses proposed. Further analysis requires knowledge of the chemical composition of the odour substances involved. While such information is still lacking, some pertinent circumstantial evidence is at hand. FAGERLUND and co-authors (1963) claim that volatile material is important for stimulating migration. However, IDLER and co-authors (1961) and MCBRIDE and co-authors (1962) obtained stimulation also by the non-volatile fraction. MILES (1968a) investigated the attractive compounds involved in elver (*Anguilla anguilla*) invasion (p. 664) and demonstrated that dissolved and particulate organic substances which are biodegradable, heat stable, and non-volatile act as stimulator.

SUTTERLIN and SUTTERLIN (1971) measured electrical responses of the olfactory epithelium of the Atlantic salmon *Salmo salar* and compared the effects of different chemicals. Highly stimulatory compounds were amino acids; in contrast, several sugars, n-aliphatic acids, alcohols or amino-substituted alcohols gave only weak or no reactions. In *Anguilla anguilla* the attractiveness of one of its major food organisms is mainly produced by synergistic or additive effect of some amino acids (HASHIMOTO and co-authors, 1968; KONOSU and co-authors, 1968). Investigations on alarm-substance cells of cyprinids led PFEIFFER and co-authors (1971) to conclude that small molecular proteins excreted by these cells are probably the organic substances eliciting the responses (p. 683). Hence both the single-odour hypothesis (e.g. involvement of pheromones) and the sequential-odour hypothesis may be applicable to fish orientation by odour.

(10) Gravity and Inertia

In fishes, gravity and inertia are perceived by the labyrinth: within this organ the otolith provides the gravity stimuli. The semicircular canals comprise the sense of inertia and recept stimuli if angular acceleration is involved. Structure and function of the labyrinth has been described by LOWENSTEIN (1971).

Gravity is important in many kinds of orientation; proper locomotory performance is possible only if the sense of gravity is integrated. The dependence of positioning in space on gravity and light has been demonstrated by VON HOLST (1950a) and SCHÖNE (1959) (see also Chapter 8.0, Fig. 8-11). Fig. 8-47 illustrates the position in space of a guppy *Poecilia reticulatus* influenced by gravity and light (dorsal light reaction). The fish's 'upright' position depends on gravity and light; if a light source above the organism is lowered into a more horizontal position, the fish's dorso-ventral axis assumes a direction intermediate between the directions of the two forces, depending on stimulus strength and physiological sensitivity to light and gravity.

The importance of inertia and perception of angular acceleration for spatial orientation is underlined by results of KLEEREKOPER and co-authors (1969). *Carassius auratus* maintains during thousands of turns of varying magnitude, direction and sequence, a nearly constant relationship between left and right

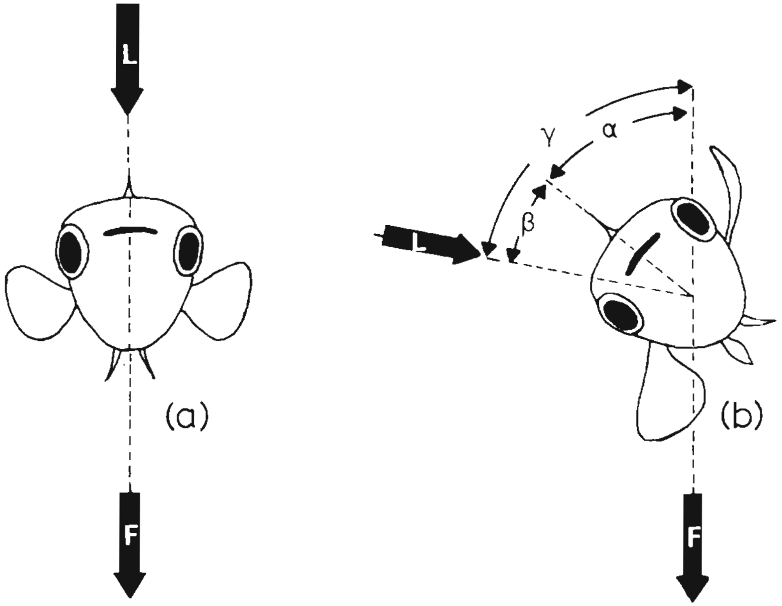

Fig. 8-47: *Poecilia reticulatus*. Dorsal-light reaction. (a) Light entering from above, (b) from side. F: strength and direction of earth-gravity field; L: irradiance at light-emitting slit and direction of light rays entering the swimming cage. α: Depositioning angle of fish, β: angle of light rays entering the fish' eye; γ: angle of light entering the swimming cage. (After LANG, 1967; modified; reproduced by permission of Springer-Verlag, Heidelberg.)

turns, i.e. the cumulated angles of consecutive left and consecutive right turns are symmetric. Continuous compensation of angle of turn demonstrates that a direction of progression, once established, can be maintained by *C. auratus* in the absence of directional cues. KLEEREKOPER and co-authors suggest that this ability may be important in long-range orientation, if the general swimming direction has been established by other cues. But frequent control of the swimming direction by other cues seems necessary in order to avoid deviation from the original compass course.

If, for example, a fish is swimming within an ocean current which has gyral character or within a frequently changing tidal current, the fish's position and hence course is altered very slowly. This slow directional change is certainly below the perception threshold of angular acceleration and soon the fish would be carried into a different swimming course. Hence a fish, which has perceived stimuli from the sun to adjust to a compass course, but which cannot obtain such visual cues during the night or during a subsequent period of prolonged cloud cover, would be misled by its inertial guidance system.

(11) Sound and Vibration

Sound and vibration provide essential cues for orientation in space of fishes, e.g. for locating the site of breakers on the coast, a rock, or floating obstacles.

Sounds are also used for social interrelations, for locating individuals of the opposite sex or for joining a school. Noise can also elicit avoidance reactions: fishes withdraw from specific sounds of their predators, or from operations of man such as fishing.

The senses involved in sound and vibration perception are the stato-acoustical organ and the lateral-line system. Functional and structural properties of these organs have been described by MOULTON (1963), FLOCK (1971), LOWENSTEIN (1971), TAVOLGA (1971), ERULKAR (1972) and others. Fishes with a swimbladder seem to possess better hearing capabilities; the swimbladder perceives the pressure waves. Fishes with a Weber apparatus, the Ostariophysi, exhibit the best acoustic-energy discrimination capacities; this includes frequency range and auditory threshold. Frequency discrimination of Ostariophysi (*Phoxinus phoxinus* and *Carassius auratus*) amounts to a quarter tone to a half tone (WOHLFAHRT, 1939; DIJKGRAAF and VERHEIJEN, 1950; JACOBS and TAVOLGA, 1968). Non-Ostariophysi can discriminate only between two tones, octaves or more, depending on the frequency level (literature *in*: TAVOLGA, 1971). In general, freshwater fishes have the highest capacities for hearing; sea-water fishes most often rely on stimuli other than sound and vibration.

In fishes without a swimbladder, perception of sound and vibration may be restricted to the lateral-line system; this causes further restriction in acoustical abilities. The lateral line responds only to frequencies below 500 Hz (KLEEREKOPER and ROGGENKAMP, 1959). Many fishes with a swimbladder can perceive frequencies of 2000 Hz and more. In general, the lateral line perceives water displacements and is regarded as 'near-field' detector. The inner ear, assisted by the swimbladder, is considered a 'far-field' detector which perceives pressure waves (for details consult VAN BERGEIJK, 1964).

Since the inner ear of fishes cannot have bipolar receptive capabilities (ERULKAR, 1972), the bipolar, or better raster-like (p. 509), stimulation may be restricted to the lateral-line system. This reduces frequency range and discriminatory possibilities for localization of the sound source. Perception of sound direction thus might be restricted to the near field and very short distances (HARRIS and VAN BERGEIJK, 1962; VAN BERGEIJK, 1964). An effective near field can exist only at a distance of about one-sixth of a wavelength. But sharks, which lack a swimbladder, can detect low-frequency sounds at a distance of 200 m (NELSON and GRUBER, 1963; see also ENGER, 1969). Hence this problem requires further investigation.

Sharks seem to be attracted towards the direction of the sound source; this indicates possible involvement of bipolar reception. Also the cyprinid fish *Semotilus*, which has good auditory capabilities, is able to detect the direction of a sound (KLEEREKOPER and CHANGON, 1954); however, experimental distance was low and near-field effects could have been involved. Later investigations revealed that the carp *Cyprinum carpio* orients toward the direction of a sound by means of turning movements indicating klinotaxis (KLEEREKOPER and MALAR, 1968) and demonstrating that no raster-like receptors are necessary.

MOULTON (1963) studied sound location in the clupeid *Brevoortia tyrannus* and the gadid *Poronotus tricanthus*, which has no linkage between swimbladder and ear. Both species orient toward the highest sound-intensity source. However, the intensity of the sound was sufficiently high to have activated receptors other than those of the ear.

There are more indications that fishes are able to perceive the direction of sound. Field experiments in a Norwegian fjord on *Labrus bergylta* revealed that the fish can perceive a change in sound direction. The experiments were carried out at depths over 3 m with signals of 115 Hz, and the kinetic variables (motion) exceeded the far-field ratios to the sound pressure in the training (conditioning) experiments by about 35% (3 dB) (SCHUIJF and co-authors, 1972).

Lemon sharks *Negaprion brevirostris* were attracted to pulsed broad-band noise presented from a loudspeaker (BANNER, 1968, 1972). The sharks approached as close as 15 m and, in some cases, actually hit the transducer. Moreover, MYRBERG and co-authors (1969) showed that sharks could locate in the far-field, within seconds, a sound source, characterized by relatively short wavelengths and low amplitudes. Pulsed sounds (WISBY and co-authors, 1964) or irregular pulsed signals, either containing harmonics or consisting of octave band of noise (MYRBERG and co-authors, 1969), are most attractive to sharks.

Field observations are less conclusive with respect to the possible mechanisms of acoustic orientation. PROTASOV (1965) described the reactions of clupeid schools influenced by high-intensity sound sources. He established by echo-sounders that the fishes dived. When air-guns were fired, shoals of whiting *Merlangius merlangus* withdrew to greater depth (CHAPMAN and HAWKINS, 1969). If the firing was continued for a longer time they became adapted. It is doubtful whether these movements represent a type of negative acoustical tropotaxis. It could also be negative orthokinesis, a fright reaction which released downward movement controlled by other stimuli, such as light or gravity.

Investigations into the problem whether sound could be of significance for homing of salmonids have been carried out by STOBER (1969). Since *Salmo clarkii* of the Yellowstone Lake did not provide much evidence that vision or olfaction is essential to locate the entrance of a creek into a lake (pp. 671, 685), STOBER analyzed the noise spectrum of the creek and studied the auditory-frequency spectrum of *S. clarkii*. He concluded that the sound source must be audible to the fish, but could not decide whether this was important for their homing ability.

(12) Electrical and Magnetic Fields

Orientation by means of electric and magnetic stimuli seems not to be as restricted as supposed until a few years ago. Many skates (Rajidae) and sharks possess electroreceptors. Perhaps all elasmobranchs have ampullae of Lorenzini, i.e. tonic electroreceptors (BENNETT, 1971c). Possibly, also other fishes are sensitive to low voltages perceived via their lateral-line system. In addition to locating objects by disturbance of their own electric field and sensing low voltages emitted by other animals (see also Chapter 8.1), navigation or better control of a compass course may be involved. Simultaneous perception of geomagnetism could deliver directional stimuli. Comprehensive treatments of the function and structure of electric organs and of electroreceptors including aspects of orientation have been presented by BENNETT (1971a, b) and SZABO (1973). A review on the orientation of animals in the geomagnetic field has been published by MARTIN and LINDAUER (1973).

(a) Active Electrolocation

From experiments of LISSMANN and MACHIN (1958) we know that *Gymnarchus niloticus* can distinguish between externally identical objects which cause a different degree of distortion of its own electric field in the water; but *G. niloticus* cannot distinguish between objects of different structure which similarly distort its electric field. The mechanism involved is comparable to that of echolocation where the faint echo returning after a loud sound pulse is evaluated (Chapter 8.3). But there is some difference: in electrolocation the fish acts as a multiple ohmmeter; it does not detect reflected waves. In other words, the fish acts as a dipole generator and its field decreases as the cube of distance. Therefore, the effect of a disturbance produced by an object, which can in special cases be considered to be an equivalent dipole, will similarly decrease as the cube of distance. Contrarily, sound can be beamed when emitted, and only the returning echo will decrease as the square of distance. Hence, electrolocation is a comparatively short-range detector (BENNETT, 1971c), serving short-distance orientations (localization of food, predators, schooling individuals), and providing information on the nature of the nearby physical environment, e.g. sea bottom or obstacles.

Active electroreception comprises the perception of conductance changes for which electric organ discharge is necessary (BENNETT, 1971b). Many electrically active gymnotids move away from a metal rod that is brought close to them, whereas they tend to ignore visually similar insulators. More aggressive species attack metal objects and stimulation is much stronger than to objects of low conductivity.

(b) Passive Electrolocation

Although various marine fishes have electric organs (e.g. *Torpedo* sp.) there is little evidence of active electrolocation. Perhaps in sea water it would cost too much energy to keep the electric organ going all the time; no marine fish continually emits electric pulses. But also marine fishes with electric organs have a possibility for spatial orientation by an electric sensory mechanism. In elasmobranchs such a mechanism comprises the ampullae of Lorenzini; these are able to perceive electric stimuli; the openings of the receptor canals are distributed over many parts of the body surface, e.g. of *Raja* sp. (MURRAY, 1962). These receptors are tonic, in contrast to the phasic receptors of electric freshwater fishes. They are very sensitive—even more so than the tonic receptors of limnic relatives. Their discharge frequency is perceivably accelerated by stimuli of a few microvolts.

According to KALMIJN (1971) the shark *Scyliorhinus canicula* and the skate *Raja clavata* are extremely sensitive to electrical stimulation. Most marine and limnic fishes generate electrical discharges without possessing electrical organs (see below). The flatfish *Pleuronectes platessa*, for example, emits bio-electrical fields into its surroundings. In his experiments KALMIJN found that flatfish buried in the ground were perceived by predatory elasmobranchs (Fig. 8-48). Dead flatfishes or individuals insulated electrically did not evoke the typical prey-locating behaviour of sharks or skates. But if the bio-electric field of the flatfish was simulated by a pair of electrodes buried in the sand, the elasmobranchs reacted positively. This documents that these predatory marine fishes use their electric sense for food

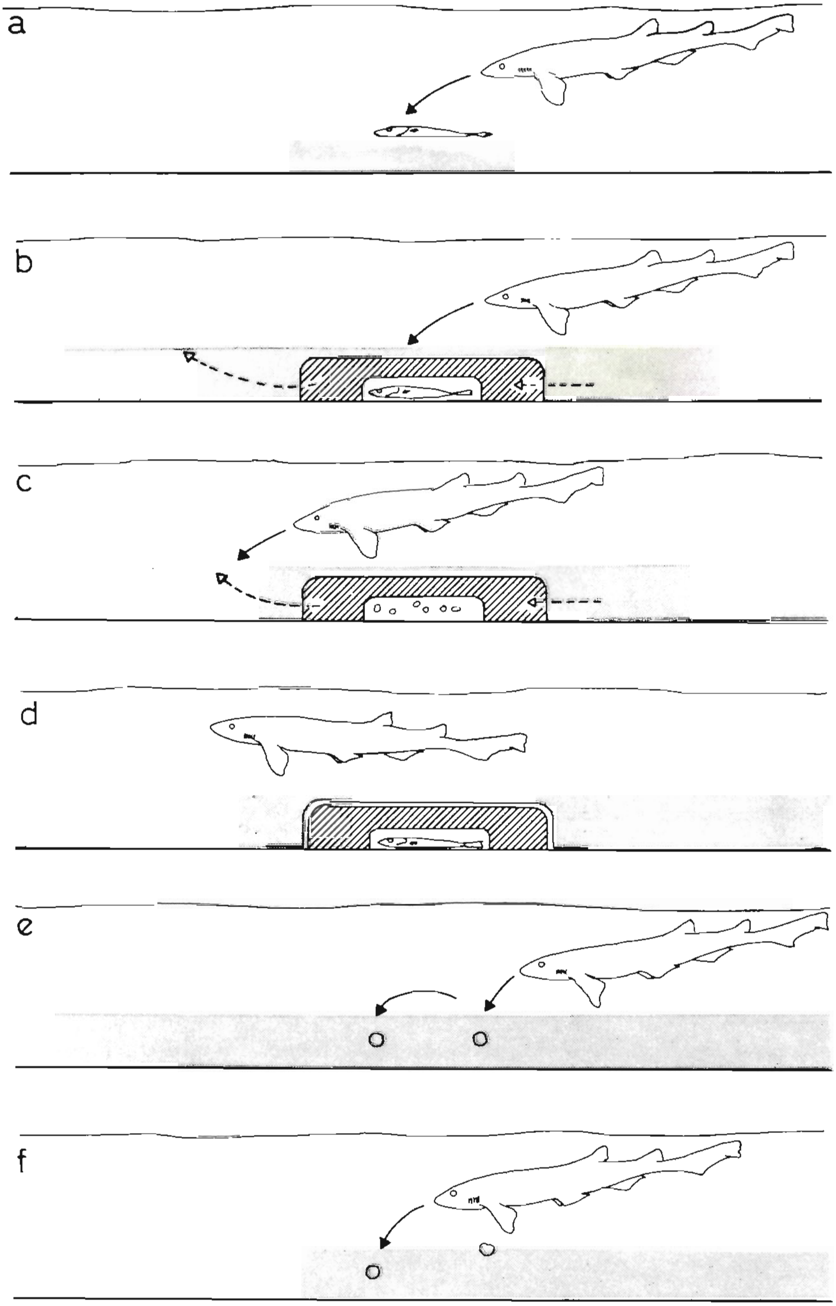

Fig. 8-48: *Scyliorhinus canicula.* Feeding responses to a: plaice under sand; b: plaice in agar chamber; c: pieces of whiting in agar chamber; d: plaice in agar chamber covered with plastic film; e: electrodes producing electric dipole field; f: piece of whiting and electrodes (only 1 electrode shown). Agar chamber not to scale. Solid arrows: responses of shark; broken arrows: flow of sea water through agar chamber. (After KALMIJN, 1971; modified; reproduced by permission of Company of Biologists Ltd.)

detection. A similar sensitivity mediated by the small pit organs seems to exist in freshwater fishes such as *Ameiurus nebulosus* (DIJKGRAAF, 1968) and *Ictalurus nebulosus* (PETERS and MEEK, 1973).

What is the ecological significance of the electrical discharges recorded in a variety of non-electric fishes (e.g. by BARHAM and co-authors, 1969; IWATA and co-authors, 1969; PROTASOV, 1969; PROTASOV and co-authors, 1970, 1971; CHEPURNOV and co-authors, 1971)? BARHAM and co-authors (1969) found amplitudes of 0·01 to 40 μV in several freshwater fishes; while very weak, these amplitudes are still perceptible by the predatory fishes mentioned. BARHAM and co-authors presume that many fishes are electric to some degree because all nerve firings and most muscle contractions produce measurable potentials (see also IWATA and co-authors, 1969). Presumably, evolutionary intermediates exist between non-electric and electric fishes.

PROTASOV (1969) observed weak electric discharges in 13 species of Black Sea fishes. In shoals these discharges accumulate and form an electric field characteristic of a school. PROTASOV suggests that this electric field facilitates orientation. In small schools of the freshwater fish *Leucaspius delineatus* two groups of potentials could be observed: One, with an amplitude of 5 to 20 mV is attributed to respiration and occurs during phases of resting inactivity; the other with an amplitude of 150 mV is connected with movement. Voltage and frequency increase with excitement. The bio-electrical currents of single individuals are correlated in such a way that breathing movements, for example, become synchronized (PROTASOV and co-authors, 1971).

These findings suggest that electrical perception aids in establishing social contacts and in co-ordinating school activities. Similar conclusions may be derived from observations on young eels *Anguilla anguilla* (CHEPURNOV and co-authors, 1971). The eels generate pulses of electrical current of 120-msecs duration at a frequency of 80 to 800 Hz; the voltage of one impulse ranges from 0·5 to 14 mV. In schools the voltage increases up to 5 times above the performance of a single individual; it seems that the electrical activity increases during daylight. The young eels were 7 to 10 cm long and hence in the stage of anadromic migration (TESCH, 1973). During upstream migration they exhibit specific schooling behaviour in the upper tidal area of the river (TESCH, 1965): they form a narrow shoal band along the river bank during a quite distinct time of the day or of the tide; this could be accounted for by electrical location of the school neighbour and of the bank. Similar interpretations may be applicable to behavioural activities of other schooling fishes which have been treated in the preceding sections and are primarily related to other senses.

(c) Compass-Course Movements

The presumptive significance of electrical cues for long-distance migration is even more speculative than that for short-range orientation. The difficulties of visual or olfactory orientation in long-range migrations have been discussed under the respective subheadings. In the sea, geomagnetic and the dependent electrical forces are less diminished than light and chemical cues and hence may represent better reference points for menotactic orientation. The suggestion that the geomagnetic field of the earth could provide reference points for long-range orientation has received support from experiments on birds (MERKEL and WILTSCHKO, 1965; MERKEL, 1971; WILTSCHKO and WILTSCHKO, 1972).

Experimental evidence that fishes can be guided by forces dependent on the earth's magnetic field has been provided by BRANOVER and co-authors (1971) and GLEISER and KHODORKOVSKII (1971). *Anguilla anguilla* of 10 to 15 cm length aligned their movements in a strong artificial magnetic field in the direction of the lines of forces; in a gradient field they move in the direction of decreasing potentials. It is hypothesized that the eels recognize the different electrical potentials and the electric current generated by their motion in a magnetic field. This would imply that the perception of the field depends upon magnetohydrodynamic phenomena. VASILIEV and GLEISER (1973) claim that the level of activity of *A. anguilla* also depends upon the existence of a magnetic field, especially in increased salinities.

Similar arguments have been put forward by MCCLEAVE and co-authors (1971; see also ROMMEL and MCCLEAVE, 1971) who found, in an experimental freshwater tank, that *Anguilla rostrata* and *Salmo salar* change their heart rate when an electric field of 0·167 μ amp cm^{-2} is applied perpendicularly to their body axis. Neither *A. rostrata* nor *S. salar* appear to respond when the field is applied parallel to their body. There was no change in heart rate when the responsiveness to the magnetic field was tested. It was concluded that *A. rostrata* and probably also *S. salar* can detect weak direct-current electric fields of the strength mentioned, which corresponds to a potential gradient of about 670 μV cm^{-1}. This is about one or two orders of magnitude greater than in the case of the limnic catfish. Perhaps the method used did not reveal the lowest possible sensitivity. Hence orientation assisted by the geomagnetic field in a way proposed by ROYCE and co-authors (1968) seems practicable. These authors follow an idea originating from DEELDER (1952): The intensity and polarity of the comparatively uniform electric fields generated by water currents could enable migrating fishes to maintain a menotactic course. Current speeds of 0·12 m sec^{-1} to 0·5 m sec^{-1}, e.g. in the Pacific Ocean, can result in gradients of 0·06 μV sec^{-1} to 0·25 μV cm^{-1}. If half the voltage were lost in the water-current system and half outside by various return paths, then electric-current densities between 0·001 and 0·004 μ amp cm^{-2} would be available to the fishes, swimming perpendicularly to the horizontal component of the geomagnetic field. In the Gulf Stream near Florida, MCCLEAVE and co-authors (1971) predicted a current density of up to a maximum of 0·16 μ amp cm^{-2} at the surface. The electric currents calculated for Pacific Ocean and Gulf Stream are only one to two orders of magnitude smaller than the sensitivities recorded for *A. rostrata* and *S. salar*.

The concept advanced by American scientists differs from that of the Russian authors mentioned: the former ascribe the generation of the electric potential to the movement of the water current, the latter to that of the fish. There are arguments for and against both of these hypotheses. BENNETT (1971a) discusses the possibility of current-induced electricity with a view on elasmobranchs and apparently comes to a positive conclusion. Larger fishes should be more sensitive than smaller ones, and their behavioural threshold may not be far below the strength of the geophysical stimuli expected. But although the calculations suggest that electric sensitivity may suffice for orientational purposes, the noise of swimming due to electromyograms, as well as mechanical effects on the receptors and streaming potentials, might make orientation more difficult than assumed. Especially in freshwater fishes, orientation assisted by electrical cues seems, for several reasons, to be more problematic; but HATAI and co-authors (1932) report that catfish are influenced by earth currents.

Support for the hypothesis, that the fish's movement generates the electric potentials seems to come from investigations by TESCH and LELEK (1973a, b). They studied directional choice in silver, yellow and glass eels (*Anguilla anguilla*) in a circular tank without water currents, light, chemical or other measurable influences. The tank contained sea or brackish water. Glass eels (elvers) obviously exhibited no directional preferences (Fig. 8-49). However, eels on their spawning migration (silver eels) preferred north or northwest directions; this agrees with the main swimming direction in the sea of ultrasonically tracked individuals (Fig. 8-50). Displaced stationary eels (yellow eels) or pre-migratory individuals preferred northerly and southerly directions. These results are in accordance with behaviour exhibited by other displaced stationary fishes (e.g. *Abramis brama*), examined during field experiments by the float-tracking method (PODDUBNYI, 1965). Of the

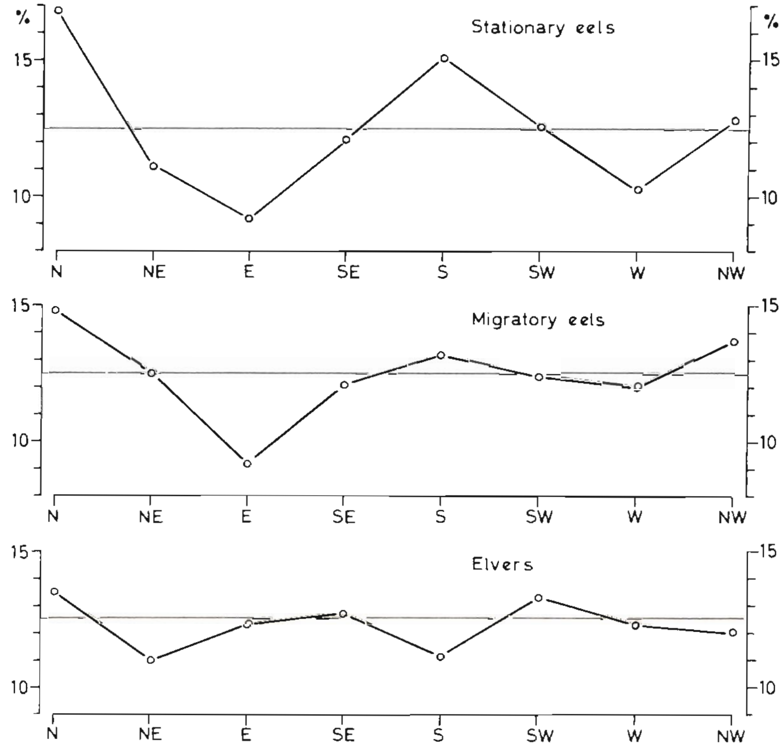

Fig. 8-49: *Anguilla anguilla.* Directional choices (%) of stationary eels, migratory eels and elvers. (After TESCH and LELEK, 1973b; reproduced by permission of the Bundesforschungsanstalt für Fischerei, Hamburg.)

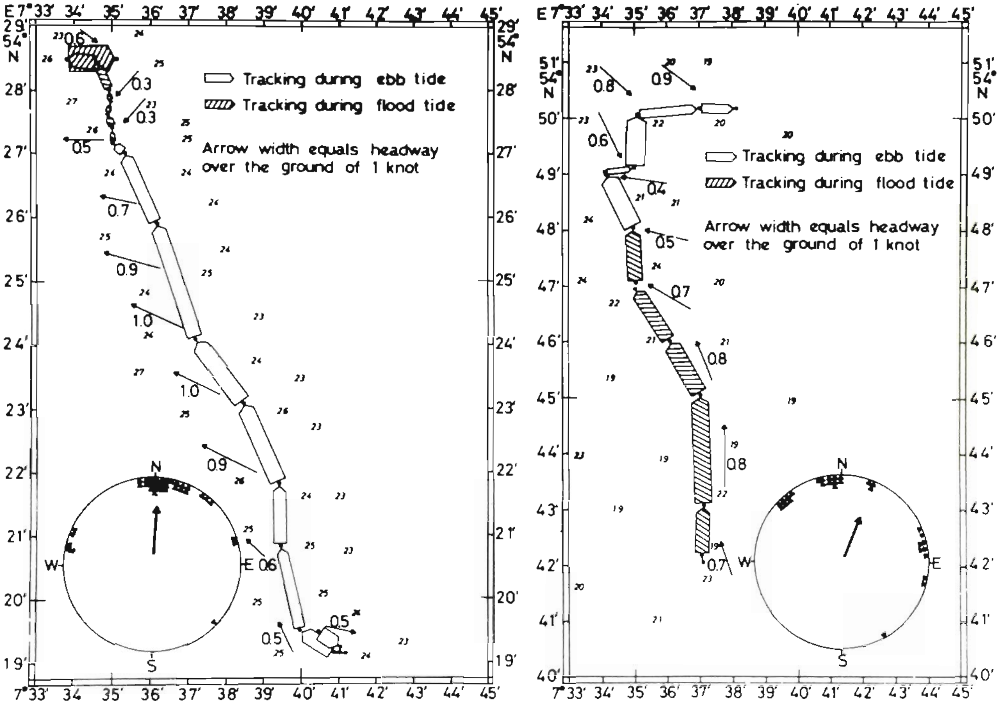

Fig. 8-50: *Anguilla anguilla.* Northern swimming course displayed by two silver eels tracked ultrasonically in the North Sea north of Helgoland; small arrows indicate current directions, their numbers current speed (knots). The smallest numbers designate water depth. Triangles in compass circle: swimming direction of eel through the water, calculated every 15 mins; arrow in centre of compass circle: mean compass direction. (After TESCH, 1974a; reproduced by permission of Verlag Paul Parey, Hamburg-Berlin.)

displaced breams 87·5% moved along the magnetic meridian, of the non-displaced individuals only 50%. Electric and magnetic fields may have been involved as potential cues in the experiments of TESCH and LELEK (1973a, b), in which nearly all other known factors had been excluded from affecting the eels tested. Except for the eels' own movements there was also no source that could have induced voltage gradients; but in view of the limited movements, eel-induced voltage gradients seem also a rather restricted possibility. Perhaps the slight preferences shown for the directions mentioned could be considered to have been caused by the low swimming activities. Since it is uncertain whether the locomotory activities of the eels in the tank were sufficient to cause electrical stimulation due to magneto-hydrodynamic effects, stimulation by magnetism cannot be ruled out. TESCH (1974b) examined directional choices of silver eels (*Anguilla anguilla*) in the presence of a compensated or reversed geomagnetic field, using a method similar to that mentioned above (TESCH and LELEK, 1973b). Experimental changes in the earth's magnetic field are paralleled by alterations in the directional choices indicated by the test eels. In view of the apparently rather limited own swimming activity (as evidenced by photographic controls) it seems unlikely that the movement of

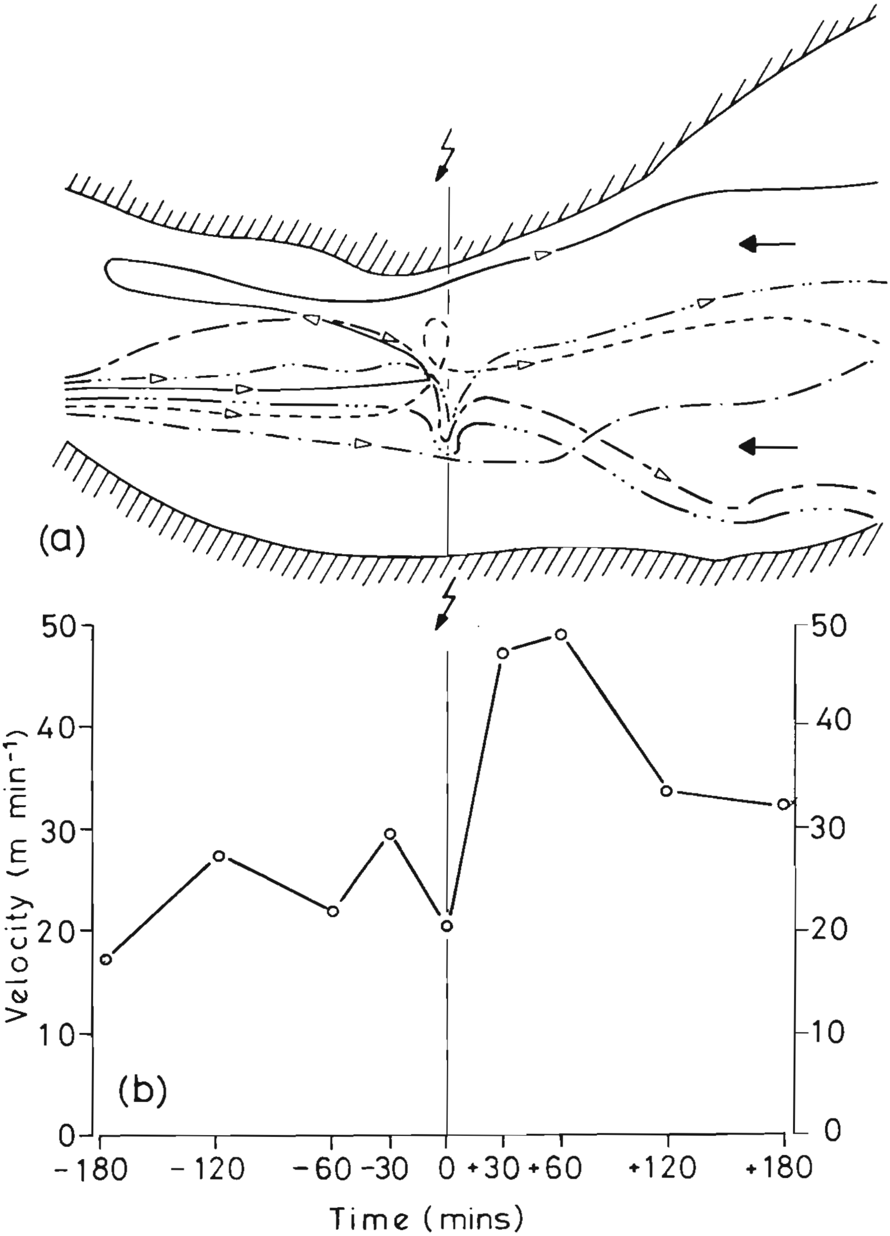

Fig. 8-51: *Acipenser güldenstädti.* (a) Traces of 6 passages of sturgeons under a high-voltage electrotransmission. (b) Swimming speed (m min^{-1}) recorded over a period of 6 hrs. (After PODDUBNYI, 1969; modified.)

experimental eels produced electromagnetic fields. It seems likely, that the course maintained by silver eels during their long-distance migration—at least while on the continental shelf—relies on stimuli provided by the geomagnetic field.

KHOLODOV (1958) and KHOLODOV and VEREVKINA (1962) claimed that a homogenous magnetic field can influence fishes of the Black Sea; they used conditioned reflexes as criteria. However, MALININ (1970a) could not detect any responses to the magnetic field in juvenile *Abramis brama*. This finding seems to be in accordance with the behaviour of juvenile eels (TESCH and LELEK, 1973b). Discussing the manifold physiological influences of weak magnetic fields on fishes, amphibians, birds and mammals, KHOLODOV (1965) concluded that the physiological mechanism of the primary effect of the magnetic field may consist of changes in the chemical affinity of glial cells. CHAGNEUX and CHALAZONITIS (1972) studied the anisotropic responses of cell fragments (external segments) in the rods of the frog eye. Placed in a physiological suspension these fragments align themselves along the lines of a constant homogenous magnetic field. This sensitivity of the segments is explained by magnetic anisotropy of the rhodopsin molecules.

A critical examination of the important question whether or not magnetism can supply directional cues requires experiments on unconditioned fishes in which potential electrical forces or magnetic fields must be eliminated or changed. In addition, field experiments are necessary in order to test whether electricity or magnetism are of ecological significance for providing essential cues during migrations. Such experiments pose many methodological difficulties. However, a chance field experiment by PODDUBNYI (1969) shows that an assessment of the ecological meaning of electric or magnetic fields is possible (Fig. 8-51). During his ultrasonic telemetric trackings, sturgeons *Acipenser güldenstädti* passed along a high-voltage transmission line which created an electromagnetic field with horizontal strength of about 0·6 electromagnetic units (Oersted) in the water; 63% of the passages revealed sharp reflections in swimming direction. In addition, all sturgeons reduced their swimming speed when approaching the passage, and increased it sharply when passing the overhead wires. Since no other barriers intervened it seems quite clear that electrical or magnetical forces provided stimuli for this behaviour.

(13) Migratory Cycles as a Function of Environmental Factors

In the preceding sections, we have considered different elements of orientation such as receptors, stimuli and environmental prerequisites. In the present section we shall attempt to analyze the dependence of migration cycles on different environmental factors. This intention restricts the discussion to a few major migratory fishes and to long-distance orientation; at the same time, it stresses the fact that orientation of fishes in their natural environment does not depend on a single cue but comprises a complex cue hierachy with 'built-in' alternatives.

(a) Salmon

A comparison between the migration route of the pink salmon *Oncorhynchus gorbuscha* as observed by ROYCE and co-authors (1968) and the North-Pacific currents is illustrated in Figs 8-52 and 8-53. From coastal areas young salmon enter the ocean in July to September. They travel rapidly westward along the coast, following the Alaskan Stream north of the Alaskan Gyre. Later, by December, they turn southward—in accordance with the prevailing current. In January and

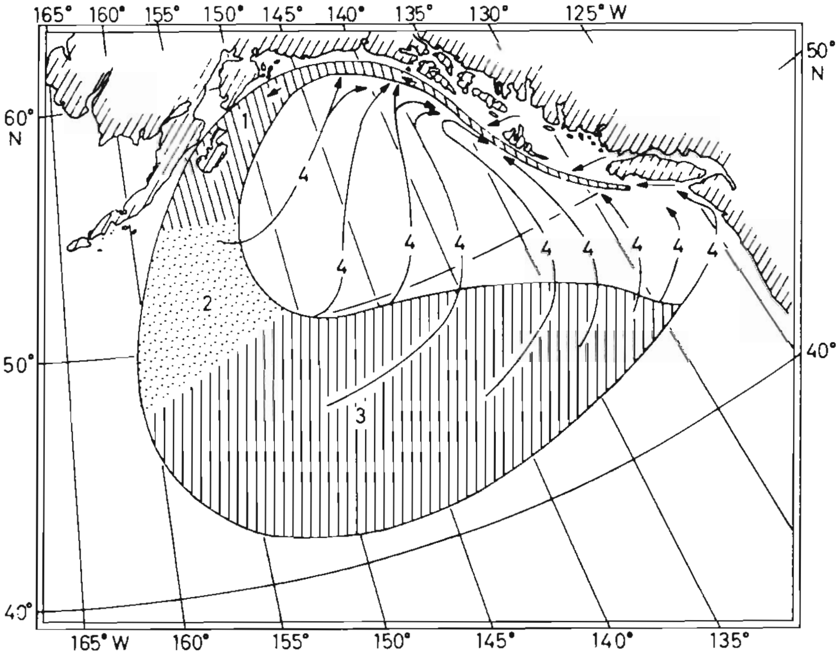

Fig. 8-52: *Oncorhynchus gorbuscha*. Oceanic migration cycle of pink-salmon stocks from southeastern Alaska and British Columbia. 1: Salmon of 10 to 25 cm length, in July and September; 2: 20 to 30 cm length, October to December; 3: 25 to 40 cm length, January and February; 4: 35 to 60 cm length, March to August. (After ROYCE and co-authors, 1968; modified.)

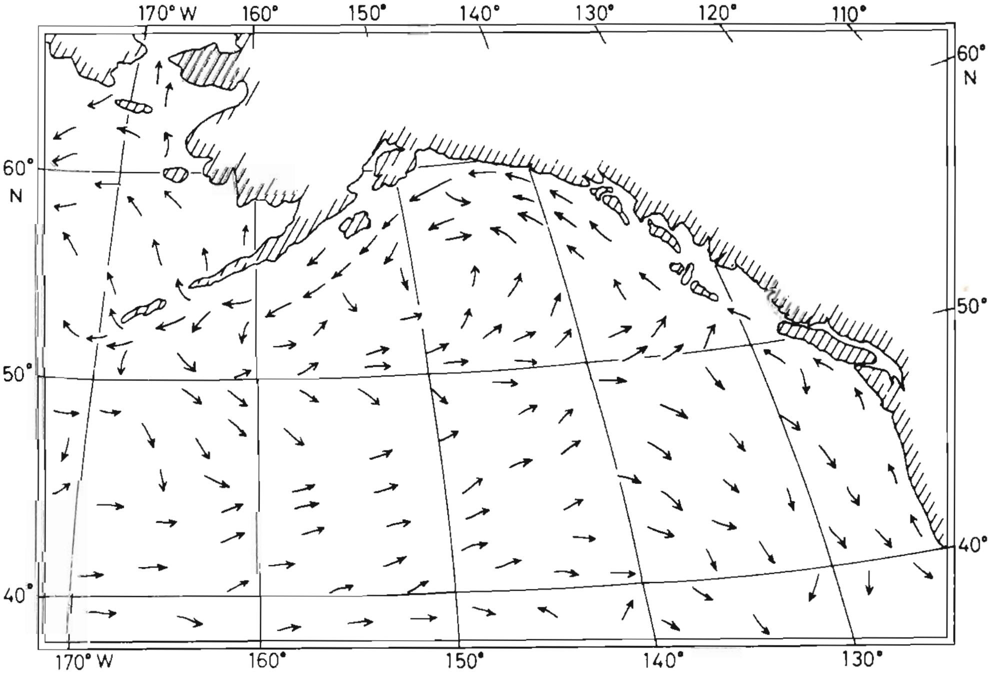

Fig. 8-53: Water currents in the North Pacific Ocean during winter. (After MORSKOI ATLAS, 1953; modified.)

February they dissipate widely but with a general tendency to migrate eastward, proceeding in the direction of the eastward Sub-Arctic Current south of the Alaskan Gyre. In spring and summer they finally turn northward and then coastward to their respective destination (Canadian and Alaskan estuaries). The northward movement also seems to be somewhat in the direction of the Gyre of that respective area.

The most interesting aspect of this migration pattern is that the long-range movements do not follow a linear but a circular route. The same is true for other salmon species and for other areas. Further examples have been provided by ROYCE and co-authors (1968); they include the sockeye salmon *O. nerka* from the Bristol Bay which performs not only one but multiple circles (loops). All these gyre-connected migrations are directed 'downstream' and, possibly, primarily due to passive drifting. Maturing salmon travel on average 46 to 56 km per day and ocsionally may average more than 83 km daily over long distances. These speeds clearly exceed those of the ocean currents carrying the salmon. The captures in nets of both adults and juveniles also indicate that their migration speed is faster than that of the current. There can be no doubt: migrating mature salmon actively pursue their course to a certain degree.

The facts at hand demonstrate that most parts of the migratory cycle are connected with prevailing water currents. In river-bound mature migrators, counter-currents, as well as olfactory and/or visual stimuli provide the major reference points for spatial orientation (pp. 674, 683). In oceanic migrators currents may also be involved, but not via induction of positive or negative rheotaxis; this is not conceivable because of the lack of reference stimuli (p. 673). A menotactic course depending on visual stimuli is not very likely (p. 661), especially not in the North Pacific Ocean:

> 'The weather of the Aleutians area is characterized by persistently overcast skies, highwinds, and violent storms. . . . Even in the milder summer periods, the sky is obscured by fog, mist, haze, or clouds most of the time. In the outer parts of Bristol Bay the average weather in June (the month when most salmon are homeward bound) is 44 percent fog, mist or haze and mean cloud cover is 8/10. In the central Gulf of Alaska the average June weather is 25 percent fog, mist, or haze; the mean cloud cover is 9/10' (ROYCE and co-authors, 1968, p. 457).

It should be added here that salmon also migrate during the night.

Other potential stimuli have been discussed (p. 694) which depend on magnetohydrodynamical effects, i.e. on electric potential gradients generated by ocean currents. Experimental evidence that salmon might be sensitive to these electric forces has been presented by MCCLEAVE and co-authors (1971). Possibly, an inherited electrical sense, effective during open-sea migration, is involved. Generation of electrical potentials could also be due to the fish's own movement; this phenomenon may not necessarily exclude the magnetohydrodynamical effect of ocean currents. Dependence on geomagnetism itself is also imaginable (p. 697). But the last-mentioned two mechanisms are not bound to be supplied by the ocean current of the gyre which seems so strikingly connected with the migration cycle of the salmon. A problem which concerns all types of potential electrical or magnetical cues for sensing the migration route would be differential polarization within the different sections of the cycle. A succession of genetically fixed sensitivity patterns, integrated in migration timing, might be a necessary prerequisite.

The presumably current-dependent migration of Pacific salmon finds—according to present knowledge—no counterpart in the Atlantic salmon, *Salmo salar*. This is especially true for the Baltic salmon, because in the Baltic Sea a uniform current cycle (as in the North Pacific) does not exist. Frequently, changing winds continuously induce changes in current directions (DEUTSCHES Hydrographisches Institut, 1967). Only short-distance migrations are connected with these wind-generated currents. This is indicated by salmon catches which often increase suddenly during one- to two-day periods (THUROW, 1966). A definite, perhaps current-dependent movement has been observed only in the young salmon (smolts) which entered the Gulf of Bothnia (Baltic Sea). The smolts seem to follow the southerly directed currents along the Swedish east coast.

Some North Atlantic salmon migrate nearly as far as the Pacific salmon (THUROW, 1966; recent reports of the International Commission for Exploration of the Sea, Anadromous and Catadromous Fish Committee). This concerns especially salmon from the Greenland coasts originating from European and North American rivers. Almost nothing is known on the migration patterns of these stocks.

(b) Eels

Migratory cycles of members of the genus *Anguilla* first received attention by SCHMIDT (1923). His papers have been discussed in various reviews (e.g. BERTIN, 1956; BRUUN, 1963; TESCH, 1973). Eels migrate in directions opposite to those of salmon, i.e. they are catadromous. The initial phase of the spawning migrations is well known. It begins in the rivers as a downstream ('catadromous') movement. While the term 'catadromous' is correct if applied to this migration phase, it can hardly be used to characterize movements of eels in coastal regions. The difference between migrational aspects of salmon and eel is that the former spawns in fresh water, the latter in the ocean. Adult coastal eels might temporarily perform upstream (anadromous) migration if swimming against tidal currents or, later, if swimming against the Gulf Stream.

The mechanism of orientation employed during catadromous migration seems quite simple: if ripeness is attained, internal factors release negative rheotaxis and the eel is carried seaward. But this release does not function if the eel starts from the coast or even from an inland lake. In that case active movement must be released and this movement must be directed. Involvement of a menotactic course is documented by migration patterns of *Anguilla anguilla* in the Baltic Sea (Fig. 8-54). All tagged eels were recaptured in a western direction (in the southern Baltic Sea even northwestern). The barrier of the Swedish coast forces them to swim more southerly. Field experiments in the Baltic Sea with eels tracked by the floating technique (EDELSTAM, 1965) have confirmed this westward compass-course swimming. In the open North Sea with its even bottom topography the eels swim northwest (Fig. 8-50; TESCH, 1972, 1973, 1974a). As TESCH's field experiment has shown, the swimming direction remains the same no matter in which compass direction the tidal stream was directed. Under these conditions, the often very strong current (up to 2 km hr^{-1}) could at most result in sideways drifting. The

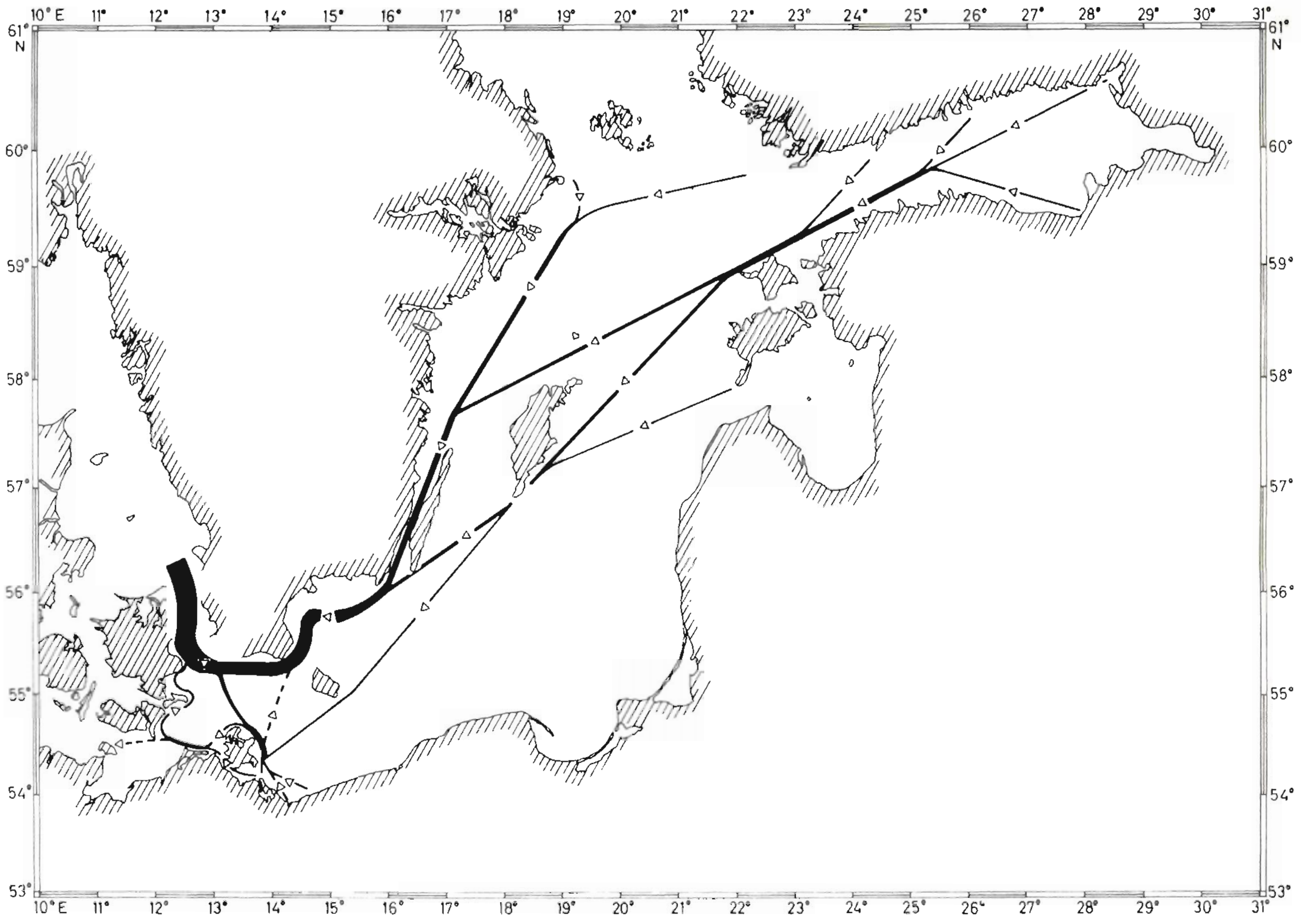

Fig. 8-54: *Anguilla anguilla*. Migration pattern in the Baltic Sea based on tagging experiments. (After TESCH, 1973; modified; reproduced by permission of Verlag Paul Parey, Hamburg-Berlin.)

unaffected swimming in no way supports the idea that current-generated potentials could guide the eels—a mechanism proposed for the salmon (p. 701). Also the laboratory experiments with migratory eels (p. 696) do not favour such a possibility. Sun-compass orientation appears entirely impossible because (i) several of the field experiments were conducted during the night, and (ii) during long periods, heavy cloud cover obscured the sun during the day.

Laboratory experiments by MILES (1968b) exploring the directional choice of American silver eels *Anguilla rostrata* seem doubtful as far as light stimuli of celestial origin are concerned (TESCH and LELEK, 1973b). Similarly doubtful is the possibility of olfactory orientation (pp. 680, 683). Topography or gradients of temperature and salinity proved insignificant in ultrasonic tracking experiments (TESCH, 1974a) or not strong or linear enough to evoke a straight swimming course.

Results of field and laboratory experiments indicate that influences of the geomagnetical field may guide the eel. The course maintained during the experiments was northwesterly; this preferred direction, of course, could only be maintained until the open Atlantic Ocean was reached. Perhaps a subsequent stimulus would then release a turn towards a more southerly course. This release could originate from (i) endogenous factors such as the degree of sexual maturity, (ii) exogenous factors such as reduced turbidity in open Atlantic areas or increasing temperature (Gulf Stream). For the final part of the migration, perhaps temperature gradients could enable the eels to find the high temperature trough in the Sargasso Sea.

Considering the return of the eel larvae to the continent, SCHMIDT (1923) supposed that they are carried by the Gulf Stream without the need for active movement. This assumption has received support from drift calculations (HARDEN-JONES, 1968); however, there are reservations concerning the southern component of the larval population. Upon metamorphosis, active movements assist to attain continental waters. Upon entering the estuaries, transportation by tidal currents, orientation via olfactory stimuli (natural fresh water) and rheotactic behaviour (at least during ebb tides) guide the young eels (p. 673).

Among the Anguillidae only the migration cycle of the Atlantic eel is known. Indo-Pacific eel species presumably display similar patterns, but very few data are available. Also other families or species of the Anguilliformes perform long-distance migrations. The North Atlantic deep-sea eel *Synaphobranchus kaupi* seems to use the same migration routes as *Anguilla anguilla* as far as geographical position and route to the spawning place are concerned (BRUUN, 1937).

(c) Herring

Perhaps the most intensively investigated migratory fish is the Atlantic herring *Clupea harengus*, especially the North Sea populations. But nearly all information on migratory cycles comes from synoptical field data such as catch statistics, or investigations on growth, recruitment and mortality. Detailed studies have been conducted on differences in meristic characters including vertebral and gill raker counts (Volume I, Chapters 3 and 4). The most important character for identification of the different spawning communities is the time of spawning, which each year on any one ground is very regular. Experiments on herring—both in the field and in the laboratory—are difficult; however, some experiments with conventional tagging have been performed. Consequently, the information at hand on migration patterns is hypothetical. Although adults of, for example, the Downs herring substock appear to return year after year to the same spawning place, it is unknown whether the fixed spawning areas of other populations are identical with the native spawning grounds. Reviews on herring migration have been written by CUSHING (1968) and HARDEN-JONES (1968).

The migration cycle of three North Sea stocks, compared with prevailing currents, is illustrated in Figs 8-55 and 8-56. The similarities between migratory cycle of adolescent herring and the current system are obvious. Perhaps the cycle is completed once each year. For example, the Downs herring live in the main North Sea swirl in summer, but in the English Channel in winter. Very similar is the drift

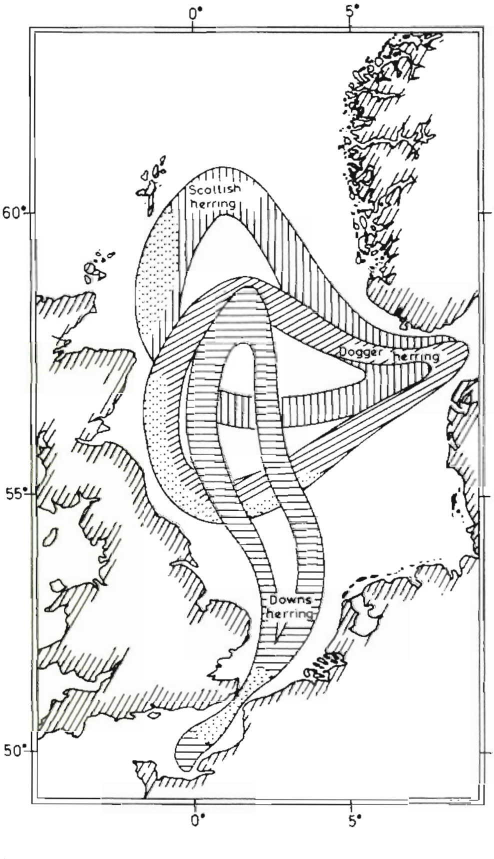

Fig. 8-55: *Clupea harengus*. Migration pattern of three spawning stocks in the North Sea: Scottish, Dogger Bank and Downs herring; dotted areas: spawning places. (After CUSHING, 1968; modified; reproduced by permission of the University of Wisconsin Press.)

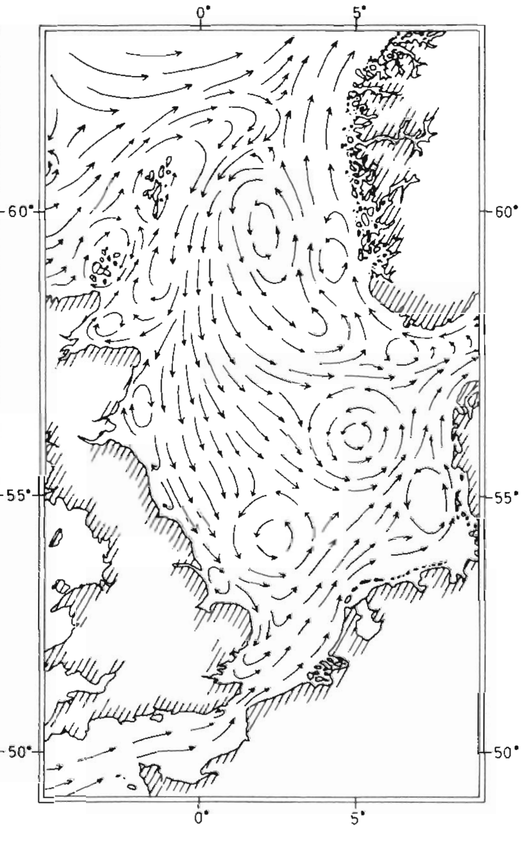

Fig. 8-56: Residual currents of surface water in the North Sea. (After HARDEN-JONES, 1968; reproduced by permission of H.M. Stationery Office, Crown Copyright and Edward Arnold (Publisher) Ltd.)

of their larvae, although they first drift nearer to the shore and only later enter the central regions of the North Sea.

The progress made by migrating adult herring seems to be rather small, it amounts to only 5 km per day. Passive drifting (shown for larvae) of adults cannot be excluded. Deviations from prevailing current patterns may be induced by the search for food and, in the vicinity of the spawning grounds, by search for depths and bottom properties adequate for reproduction. Nevertheless, the overall congruity of herring movements and currents resembles the situation reported for Pacific salmon (p. 699). 'Downstream' movements similar to those shown by the Downs herring, are exhibited by the Norwegian spring spawning herring, the stock appears to be contained within the Norwegian Sea gyral. Of the many different stocks of the Atlantic herring, several may behave similarly.

(d) Other Species

A most striking orientation is performed by tunas *Thunnus thynnus*: large specimens of over 125 kg as well as small individuals of 10 kg (2 years) and 16 kg (3 years of age) migrate 8000 km from the Straits of Florida to Norwegian waters, or 5500 km from the Long Island area to the Bay of Biscay (MATHER, 1962; TIEWS, 1963; MATHER and co-authors, 1967). Some large tunas were free for less than 3 months; the speed of migration amounted to 3 km hr^{-1}, assuming that straight courses were followed and the date of recapture was the actual time of arrival; most likely, the real swimming speed was faster. Random movement can be excluded and maintenance of a compass course is probable. Visual orientation seems possible at least during the southwestern part of the journey which is generally favoured by good weather. But the northeast Atlantic Ocean section rarely offers sufficiently good weather conditions for a menotactic sun course. The difficulties are similar to those discussed in regard to other fishes (pp. 701, 704), compass-course orientation, assisted by magnetical or electromagnetical cues, is more probable. Assistance of ocean currents (hydrodynamical effects) seems unlikely because in the northeastern parts of the Atlantic Ocean, current velocities are very low.

Compass-course orientation seems also to be employed by skipjack tuna *Katsuwonus pelamis*. These fish perform nightly journeys of 25 to 106 km away from a bank near Hawaii, returning every morning. This fact has been ascertained by telemetric ultrasonic tracking (YUEN, 1970). The mechanism of orientation is unknown. During the night the tunas swim close to the surface which might facilitate celestial orientation in this area, characterized by good weather conditions. However, no experimental evidence for celestial orientation has yet been produced, except for sun-compass orientation. Hence in *K. pelamis*, similar orientation mechanisms may be involved as in the *Thunnus thynnus*. Certainly this species is a favourable subject for field experiments. The obvious dependence of the migratory cycle of young *K. pelamis* on hydrographical factors has been discussed by WILLIAMS (1972).

Several fish species exhibit circular migration cycles similar to those described for Pacific salmonids (p. 699). An example is the Arcto-Norwegian cod *Gadus morhua* (HARDEN-JONES, 1968). Throughout its life cycle the spawning community seems to be assisted by ocean currents, at least during part of the journey. Spent and feeding fish move essentially downstream, and without doubt eggs, larvae and juveniles are transported northward over long distances. Current velocities of 0·4 km hr^{-1} carry a young cod about 1000 km in 5 months; this period equals the duration of the pelagical stage. It is unknown whether certain sections of the migration cycle depend upon active, directed movements. Hence this species provides no support to the hypothesis that orientational cues may be obtained from ocean-generated electric currents (p. 695). Passive rheotaxis, or rather downstream drifting, with loss of visual contact seems to be the most probable migration method.

Comparable passive movements are exhibited by another gadid fish, the Lowestoft whiting *Merlangius merlangus*. The majority of the population follows an anticlockwise cyclic movement in the southern North Sea. *M. merlangus* returns to Lowestoft again having circulated within the southern North Sea for a year (ROUT, 1962). A corresponding gyre is known for currents in the southern North Sea (Fig. 8-51). The migration patterns of the whiting can be compared with those of the herring (p. 704).

Migratory cycles in plaice *Pleuronectes platessa* (HARDEN-JONES, 1968) and the sole *Solea solea* (KOTTHAUS, 1967) seem to be related to water movement in coastal areas. As in many other species, eggs and larvae are presumably transported by residual water currents. In the North Sea, the anticlockwise gyral provides the means of transportation. After settlement on the sea bottom, the young *P. platessa* begin to migrate shorewards; this migration is later followed by an offshore movement. Considering the small initial size of the young *P. platessa*, onshore migration presumably depends on making differential use of tidal currents, rather than on (continuous) active movements. Perhaps a mechanism is involved similar to that described for elvers of *Anguilla anguilla* (p. 673) and for swimming crabs *Macropipus holsatus* (p. 671): onshore migration during flood tides and offshore migration during ebb tides. The stimuli which release upward swimming into the carrying water layers may be related to temperature or salinity variations. As *P. platessa* attain sexual maturity they migrate to their spawning grounds; there is some indication that they spawn in the parents' spawning area (HARDEN-JONES, 1968).

Statistical evaluations of tagging-recapture data indicate the presence in *Pleuronectes platessa* of a certain tendency for homing (DE VEEN, 1970). During homing, apparently both swimming against or with the current may be involved, and even movements across the current. No information on the possible mechanisms of orientation during spawning migrations has come to the reviewer's attention. In this connection, observations on temporary surface swimming of *Solea solea* (p.674) may be of interest. *P. platessa* lends itself for field and laboratory experiments and may prove a valuable test organism for exploring details on near-shore migratory patterns and on the physiological mechanisms involved in spatial orientation.

8. ORIENTATION IN SPACE: ANIMALS

8.3 MAMMALS

O. KINNE

(1) Introduction

Orientation involves active relating to spatial and temporal components of the environment; it is based on intrinsic properties of the organism concerned. This subchapter concentrates on spatial and intrinsic aspects. Temporal aspects receive attention in Chapter 9. Dynamically, orientation involves feedback processes: environmental cues cause directed responses (e.g. positioning, locomotion) which tend to alter the stimulus patterns perceived; the new stimulus patterns, in turn, represent the basis for the next orientation response. The drive to orient continues until a temporary equilibrium is attained during which the stimulus remains ineffective (Chapter 8.0).

Orientation in space is a multifactorial phenomenon: a variety of different cues are perceived and interpreted by several different physiological mechanisms. Marine mammals obtain cues, for example, from light, temperature, salinity, water movement, substratum, pressure, organic substances, gravity, sound and vibration, and mechanical stimuli, as well as from nutritive, reproductive and social conditions. The principal physiological mechanisms involve visual, auditory, tactile and chemical senses. Exclusive reliance on a single cue type does not seem to occur, although a certain class of stimuli may predominate: delphinids in muddy waters or in darkness, for example, rely heavily on acoustic cues.

Studies on spatial orientation of marine mammals encounter considerable difficulties: (i) Field work, due to methodological problems, is usually below the standard of field studies conducted on terrestrial mammals. Much of our present knowledge is based on questionable, incomplete and insufficiently documented observations. (ii) Laboratory experiments involve considerable costs (test animals, buildings and maintenance). Until recently, they have been restricted largely to commercially operated zoos and oceanaria. Since these serve profit purposes, the suitability of facilities and the design of experiments have often been characterized by suboptimal compromises. Among the cetaceans, only small odontocetes have become available for experimentation. (iii) Semi-natural or wholly artificial environments tend to reduce environmental and social complexity and hence to falsify performances involved in behavioural orientation. (iv) Some forms, especially odontocetes, are known for their imitative behaviour (e.g. TAYLER and SAAYMAN, 1973). Both in captivity and at sea, and without apparent external reinforcement, complex behavioural sequences (previously unfamiliar phonations or motor patterns) are performed, both in the presence and in the absence of the stimulus which originally evoked the imitation. This behaviour complicates the differentiation between 'normal' performance at sea and secondary modifications due to imitation and learning. Only in the last few years has it become possible to improve the reliability of field work due to radio-tracking techniques used in combination with aerial observations, and to conduct adequate experiments as a result of the establishment of special facilities (e.g. Oceanic Institute, Hawaii; Marine Mammal Facility at Scripps Institution of Oceanography, La Jolla; Navy Marine Mammal Research Facility, San Diego, USA).

Substandard methodological accuracy at sea, insufficient accessibility and potential falsification of performance in laboratory studies: how can we obtain ecologically meaningful results? This question comprises a unique challenge to any behavioural ecologist working with these intelligent creatures of the sea. Obviously, we must rely on well-designed parallel investigations at sea and in experimental pools, lest we produce data utterly inadequate for the comprehension of life as it exists in oceans and coastal waters.

The importance of behaviour for solving orientational problems increases with increasing organismic complexity and differentiation (e.g. KINNE, 1957a, b). While plants (Chapter 7) and lower invertebrates (Chapter 8.1) respond primarily via basic physiological and morphological processes (e.g. changes in metabolic performance, or in directional growth of body parts), 'higher' forms of life tend to depend increasingly on integrated complex neurophysiological responses. As evolution proceeds, 'passive' tolerance of environmental stress becomes accompanied by active search for, and interpretation of, information on the environment. At the same time, the progressive need to orient actively to environmental components constitutes a major driving force of behavioural evolution, ultimately providing additional possibilities for effective exploitation of ecological niches and for avoiding, or counteracting, potentially detrimental conditions.

Active relating to the environment includes communication. In marine mammals, communication involves transmission of information between two or more individuals. Some authors have inferred intention to such exchange of information. However, experimental evidence does not support such a view (BASTIAN, 1967; EVANS and BASTIAN, 1969): A male and a female bottle-nosed (or bottlenose) dolphin *Tursiops truncatus* (the famous 'Flipper' of television shows) were separated in two adjacent enclosures with no visual contact between them. The male was required to press one of two paddles in order for either to receive food; but the visual signal indicating which of the two paddles had to be activated was presented only to the female. Hence the female had to communicate this information acoustically to the male in order to obtain food. These two dolphins were successful over thousands of trials. But when the visual barrier between the dolphins was removed, and even when the male was removed from his enclosure, the female continued to emit the acoustic signals as usual. Such behaviour does not justify the assumption of intention:

> 'This rather complex performance is very much what might have been expected had the female been trained by herself to emit signals differentially in the presence of the different visual signals and if the male had been separately trained to press his paddles differentially with respect to these acoustic signals' (EVANS and BASTIAN, 1969, p. 433).

This experimental result and comparable information on related species create no need to assign a special status to communications between delphinids. Anthropomorphisms are unjustified.

Odontocete whales, especially the delphinids, exhibit unusual learning and problem-solving capabilities, and their abilities for spatial orientation are very high. The brilliant performances of captive *Tursiops truncatus* have led many observers to infer a considerable degree of intelligence to these playful and contact-eager whales. McBride and Hebb (1948) suggested that this dolphin surpasses dogs in motivation and in man–animal communication, and Kellogg (1961) has placed *T. truncatus* above the chimpanzee. Learning efficiency of *T. truncatus*, evaluated on the basis of auditory discrimination learning-set tasks, has been reported to rival that established for individual rhesus monkeys in visual discrimination learning-set tasks (Herman and Arbeit, 1973). Other small odontocetes (*Phocoena phocoena, Delphinus delphis, Stenella caeruleoalba*) have been claimed to rank between the genera *Homo* and *Simia* (Gihr and Pilleri, 1969; Pilleri, 1971a; see also: Lilly, 1961, 1964; Ridgway and co-authors, 1966; Kraus and Pilleri, 1969a, b; Gruenberger, 1970; Pilleri and Gihr, 1970a, b). In contrast, Voronin (1970) doubts whether *T. truncatus* and related odontocetes can be placed on the same high level as the anthropoid monkeys. Of course, such ranking invites criticism. In a letter to the reviewer (1973), K. S. Norris says—and I agree with him—

> 'This lining animals up in hierarchies leaves me cold. There are many different varieties of intelligence or mental capability, each adaptive to its own environment.'

In cetaceans, size and complexity of neural structures (brain, cortex, higher brain centres) are extraordinary. The sense organs are characterized by a strange mixture of highly differentiated and greatly reduced structures (Jansen and Jansen, 1969). The cetacean brain features brachyencephaly and a high degree of telencephalization. The cerebellum is very large and unique in the relative development of its subdivisions: small anterior lobe, large paramedian lobule, enormous paraflocculus, rudimentary flocculonodular lobe, and extraordinarily developed nuclei (dominating size of posterior interpositus nucleus, very small lateral nucleus). The relative extension of general surface areas of the cortex in the common dolphin *Delphinus delphis*, some other mammals and man reveals both considerable interspecific differences, and surprising similarities between man and dolphin (Table 8-5). No satisfactory explanation is currently available for the extraordinary development of the delphinid neocortex. Acoustic centres are hypertrophied. In the river dolphins *Pontoporia blainvillei, Platanista gangetica* and *P. indi*, considerably less-developed brains are found (Pilleri and Gihr, 1971b); the same is true for Sirenia, Pinnipedia and Mysticeti. More data are required on functional and structural details (number and distribution of cortical neurons, their dendritic fields, synapses, etc.), before we can embark on meaningful, detailed discussions regarding the intellectual capacity of marine mammals (Jansen and Jansen, 1969).

General accounts on classification and distribution of marine mammals have been compiled by Matsuura (1943), Scheffer and Rice (1963), de Lattin (1967) and Rice and Scheffer (1968). Taxonomic and zoogeographical contributions on

Table 8-5

Relative general surface areas of cortex in the common dolphin *Delphinus delphis*, some other mammals and man. All areas expressed as relations of the surface area of the whole cortex (=100) (After FILIMONOFF, 1966; modified; reproduced by permission of Akademie-Verlag, Berlin)

Neocortex		Allocortical complex		Paleocortex		Archicortex		Periarchicortex	
Dolphin	*97·8*	Hedgehog	67·6	Hedgehog	29·8	Rabbit	23·8	Hedgehog	17·6
Man	95·9	Rabbit	44·0	Anteater	19·3	Hedgehog	20·2	Kangaroo	7·1
Seal	94·4	Anteater	42·8	Rabbit	14·0	Anteater	17·9	Rabbit	6·2
Dog	84·2	Kangaroo	30·8	Kangaroo	9·3	Kangaroo	14·4	Anteater	5·6
Kangaroo	69·2	Dog	15·8	Dog	8·6	Dog	6·3	Dog	2·7
Anteater	57·2	Seal	5·6	Seal	1·8	Seal	2·2	Seal	1·6
Rabbit	56·0	Man	4·1	Dolphin	*0·9*	Man	2·2	Man	1·3
Hedgehog	32·4	Dolphin	*2·2*	Man	0·6	Dolphin	*0·8*	Dolphin	*0·4*

groups of marine mammals have been provided by: KING (1964), REPENNING and co-authors (1969, 1971): seals; SCHEFFER (1958): seals, sea lions and walruses; NISHIWAKI (1965): pinnipeds and whales; MATSUURA (1944), BOURDELLE and GRASSE (1955), NORMAN and FRASER (1963), HERSHKOVITZ (1966) and MARCUZZI and PILLERI (1971): whales; D. W. RICE (1967): synopsis of cetacean families; SLIJPER (1962), MACKINTOSH (1965, 1966): mysticetes; FRASER (1966): Delphinoidea.

Marine mammals in restricted areas have been reviewed by TAKASHIMA (1933): marine mammals of Japan; KLEINENBERG (1956): mammals of the Black and Azov Seas; DAUGHERTY (1965): mammals of California; NISHIWAKI (1966, 1967): mammals of the North Pacific area; WILKE (1954): seals of northern Hokkaido; KENYON and SCHEFFER (1955): seals, sea lions and sea otter of the Pacific coast; KING (1956): seals of the Pacific coast of America; NISHIWAKI and NAGASAKI (1960): seals of Japanese waters; HIRASAKA (1933): Pacific sirenians; GASKIN (1972): whales, dolphins and seals of the New Zealand region; JONSGÅRD (1966): Balaenopteridae in the North Atlantic Ocean; SCHEFFER and SLIPP (1948): cetaceans of the west coast of North America; GIBSON-HILL (1949): cetaceans in Malayan waters; GIBSON-HILL (1950): cetaceans in Sarawak waters; TOMILIN (1951b, 1957, 1962, 1967): cetaceans of the USSR; TAGO (1922): whales of Japanese waters; MOORE (1966): beaked whales in North American waters; OGAWA (1937): odontocetes near Japan; MERCER (1973): odontocetes in the western North Atlantic; KLUMOV (1959): commercial dolphins of the Far East. SOKOLOV (1971) has discussed taxonomical, distributional and other studies devoted to cetaceans by scientists in the USSR.

This seemingly impressive, long list of papers does not provide very much solid information. Several papers lack accuracy and thoroughness. Admittedly, definite information on taxonomy and zoogeography is difficult to come by: work at sea and specimen collection is expensive; occasionally found carcasses often decompose before they can be examined; the large dimensions of cetaceans defy normal dissection methods; several marine mammals live in remote areas; close-range observations and proper tracking experiments require equipment which has only recently become available; cultivation is still restricted to a few representatives (Volume III: KINNE, in press a).

A recent list of marine mammals of the world (RICE and SCHEFFER, 1968) comprises 118 species, including limnic representatives of predominantly marine groups. The number of species varies significantly in the five orders of marine mammals: Carnivora: 1 species, Pinnipedia: 33, Sirenia: 5, Mysticeti: 10, Odontoceti: 69.

(2) Light

(a) General Aspects

In mammals, the light-perceiving eye tends to be the most effective sense organ yielding information on spatial properties of the environment. Simultaneous, detailed panoramic point-to-point representation of the surroundings, immediate directionality and distance evaluation over considerable ranges by binocular stereoscopic vision cannot be matched by any other spatial-orientation mechanism.

However, for marine mammals which live predominantly underwater, optical cues and the sense of vision often appear to be of somewhat less importance than for many of their land-living counterparts. In greater water depths, in turbid waters and at night, low visibility prevails, and in the open oceans, visual 'landmarks' are restricted to the light emitted by sun, moon or stars. While bioluminescence is of some importance, diving mammals are often forced to employ, additionally or primarily, non-visual orientation mechanisms. In particular, they must rely on auditory cues (p. 792).

Seeing involves (i) focusing, i.e. adjustments of each eye to produce the sharpest possible retinal image; (ii) movements relating the two eyes to each other and to the objects viewed; (iii) image formation on the retina; (iv) photoreception; (v) neural transmission; (vi) central interpretation. In mammals, 4 types of eye movements may be distinguished: spontaneous (not looking at anything in particular), exploratory (searching for something), pursuit (following a moving object, or a static object during own movements), idle (resting motions). Phylogenetically, the oldest visual response is reaction to object movement. Additional aspects of orientation seeing involve object location (assessment of direction and distance), object recognition (perception of size, shape and other properties), and visual object memory (a basic prerequisite for visual re-orientation).

Visual abilities may be assessed on the basis of irradiance thresholds for vision, brightness discrimination, colour vision, acuity, directional perception, and shape and movement discrimination (Volume I: BLAXTER, 1970).

(b) Terminology

Visual acuity is the power to resolve spatial detail by optical means (e.g. PIRENNE, 1962; RIGGS, 1965).

The term **emmetropia** characterizes the normal refractive condition of the (mammal) eye: with relaxed accommodation, parallel light rays are brought accurately to a focus upon the retina (**emmetropic**: having normal light refraction). Non-adjusted lens refraction, changes in the refractive media of the eye, and abnormal length or shortness of the eyeball result in defective vision. The consequences are: short-sightedness (seeing distinctly at short distances only) or long-sightedness (seeing distinctly at long distances only).

Myopia describes the condition of the eye in which the visual images are brought to a focus in front of the retina (because of non-adjusted refraction, a defective optical system, or abnormal eyeball length), resulting in defective vision of distant objects: i.e. short-sightedness (**myopic**: having abnormal light refraction; affected by or exhibiting myopia).

Hyperopia (hypermetropia) characterizes a condition in which the visual images come to a focus behind the retina, resulting in defective vision of near objects (long-sightedness).

Ametropia and **astigmatism** refer to a defect of vision (failure of the light rays to meet in a single retinal focus point).

(c) Carnivora

Carnivora are represented in marine habitats by only 1 species: the sea otter *Enhydra lutris* (Family Mystelidae). Formerly, this small mammal ranged from

Baja California (US west coast) to the coast of the Alaska Peninsula, along the coast of Kamchatka, and through the Kuril Islands to northern Hokkaido. Hunted commercially, *E. lutris* became almost extinct. The sea otter is now protected through international agreements; only a few pelts per year are allowed to be taken in Alaskan areas of maximum abundance. *E. lutris* breeds mainly in central California, Prince William Sound, Shumagin Islands, south side of Alaska Peninsula, and in the Aleutian, Commander and Kuril Islands. It does not seem to migrate and often establishes large local groups of loose social structure. *E. lutris* feeds on a variety of bottom organisms, especially abalone, sea-urchins and bivalves, visiting water depths in excess of 9 m with diving times between 7 and 94 secs (VANDEVERE, 1972).

In *Enhydra lutris*, the sense of vision seems to be of primary importance for spatial orientation, e.g. for location and capture of food, for reproduction (courtship, mating, brood care) and for other interindividual contacts. In air, mother–pup relations also depend on acoustical signals. To LIMBAUGH (1961) the visual capacities appeared to be good, hearing exceptionally fine. As in other organisms (e.g. MARLER and HAMILTON, 1966), combinations of different orientation modalities are required for maximum orientational efficiency.

According to GENTRY and PETERSON (1967), the visual abilities of *Enhydra lutris* are inferior to those of the sea lion *Zalophus californianus* (p. 719). GENTRY and PETERSON did not examine the vision of *E. lutris* in air, but suggest that the eye of this otter is emmetropic in air (WALLS, 1963) and shows adaptations for underwater vision; in contrast, they claim that the eye of *Z. californianus* is emmetropic underwater with adaptations for aerial vision. BALLIET and SCHUSTERMAN (1971) criticized this interpretation because it emphasizes the different dioptric mechanisms but ignores the neutral structure and organization at the retinal and cortical-projection levels. The latter authors attribute the superior underwater visual acuity of *Z. californianus* to the higher resolving power of its retina. In the ferrets *Mustela* f. *renata* and *M. corninea*—close relatives of the sea otter *E. lutris*—maximum visual acuity in air is about one-third that of *Z. californianus* (NEUMANN and SCHMIDT, 1959; p. 719). The type of stimulus configuration employed in 1965 by SCHUSTERMAN and co-authors (*Z. californianus*) and 1967 by GENTRY and PETERSON (*E. lutris*) were later found to have been inappropriate for measuring visual acuity uncontaminated by intensity discrimination (SCHUSTERMAN and BALLIET, 1970b; BALLIET and SCHUSTERMAN, 1971).

In order to re-assess the visual abilities of otters, BALLIET and SCHUSTERMAN (1971) examined the aerial and underwater visual acuity of 2 mature male Asian 'clawless' otters *Amblonyx cinerea cinerea*. These mustelids are widely distributed throughout southeast Asia; they are used by Malays for fishing; their food consists of a variety of animals including fishes, crabs, frogs and birds (HARRIS, 1968). Acuity targets were produced from 12·7 cm^2 photos of Ronchi rulings with black and white stripes of equal width. The standard grating consisted of 300 lines 2·54 cm^{-1}, the variable grating of lines varying in width from 12·7 to 4·8 mm. For further methodological details consult p. 717. All targets were presented simultaneously and the otters were maintained at a fixed distance (1·9 or 3 m). Testing in air and underwater alternated daily. The otter's task was to approach the stimulus with the variable grating in order to obtain a piece of chicken neck.

The visual acuities obtained in air and underwater are illustrated in Fig. 8-57.

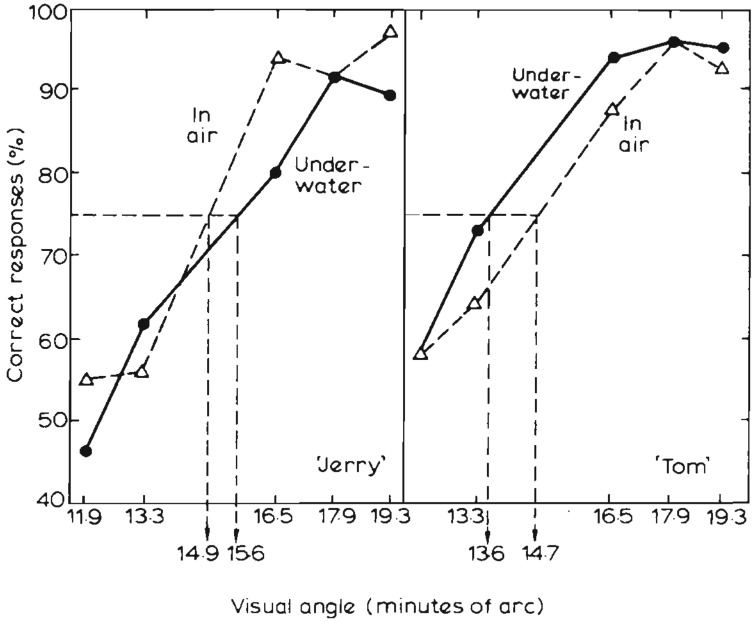

Fig. 8-57: *Amblonyx cinerea cinerea*. Aerial and underwater visual acuity of two individuals ('Jerry' and 'Tom'). Threshold estimates measured in minutes of visual angle over the 16 test days were 14·9 and 14·7 for aerial and 15·6 and 13·6 for underwater acuity. Daylight conditions in outdoor pool. (After Balliet and Schusterman, 1971; modified; reproduced by permission of Macmillan (Journals) Ltd.)

Visual angles associated with 75% correct responses reveal the threshold values. These indicate: aerial and underwater visual acuity are about the same; both are similar to the values obtained on aerial visual acuity of other mustelids (Neumann and Schmidt, 1959). Balliet and Schusterman (1971) conclude that the dioptric mechanism of otters is presumably such that it (i) allows the eye to function normally in air without special accommodation, and (ii) is capable of producing sufficient accommodation underwater. Controlling ambient irradiation levels, Schusterman and Barrett (1973) produced data that indicate faster decrease in visual acuity underwater than in air. They consider two reasons for this: (i) pupillary dilation resulting in insufficient squeezing of the anterior portion of the lens by the iris sphincter muscles; (ii) insufficient pupillary dilation in the dark. Comparing the effectiveness of visual orientation mechanisms of aquatic mammals, Schusterman and Barrett conclude that a correlation between the degree of genetic adaptation of different amphibious species to aquatic or terrestrial habitats can only be established when the tests are conducted over a wide range of irradiance conditions.

A study on visual size discrimination of *Amblonyx cinerea* has also been presented by Nachtigall (1969). However, the methods employed determine the sensitivity to reflected light from the background and its relationship to the black targets (Schusterman *in:* discussion to Nachtigall, 1969) rather than visual acuity *per se*.

(d) Pinnipedia

The amphibious Pinnipedia have external ears (pinnae) and large front flippers—their primary means of locomotion. Although feeding underwater, they spend much time on land, resting and exercising social interactions (BARTHOLOMEW, 1959; PETERSON, 1961; PETERSON and BARTHOLOMEW, 1967; EVANS and BASTIAN, 1969; LEBOEUF and PETERSON, 1969a; CALLOWAY, 1972; GENTRY, 1972; ONO, 1972; SANDEGREN, 1972; STIRLING, 1972). The amphibious qualities of the visual mechanism of pinnipeds have recently attracted increased attention. Underwater, the pinniped eye is essentially emmetropic; in air, it exhibits dioptric adaptations which provide sufficient resolving power for perceiving optical details. Compared to terrestrial relatives, the curvature of the pinniped lens is modified. In contrast to pinnipeds, man cannot sufficiently compensate the loss in underwater light refraction in his eye (WALLS, 1963) without wearing goggles: at a distance of 0·7 m, man's visual underwater acuity is reduced 8-fold, compared with that in air, and at a distance of 5 m his visual resolving power fails to reveal adequate detail (SCHUSTERMAN and BALLIET, 1970a).

While visual abilities seem of basic importance for food localization, hunting, migrations and for maintaining social structures, visual acuity of pinnipeds has been assumed to be poor (PETERSON and BARTHOLOMEW, 1967). The relative significance of visual, auditory, tactile and olfactory cues for food catching, reproduction and social contacts remains uncertain.

Preliminary experiments on shape discrimination and transfer in *Zalophus californianus* (SCHUSTERMAN and THOMAS, 1966) indicate appreciable abilities of transfer from original stimuli patterns. Experiments designed to determine the minimum areas of circles and rectangles detectable by *Z. californianus*, Steller sea lion *Eumetopias jubatus* and harbour seal *Phoca vitulina* revealed that these pinnipeds are capable of discriminating between area differences as small as 6 to 9% (SCHUSTERMAN, 1968; see also FEINSTEIN and RICE, 1966). However, the stimuli presented were presumably inadequate: the test animals may have responded to the total amount of irradiance reflected and thus revealed abilities of brightness discrimination rather than of acuity.

In a subsequent study on visual acuity, SCHUSTERMAN (1972) improved his methods and presented the first visual-acuity threshold estimates for pinnipeds (see also SCHUSTERMAN, 1969; SCHUSTERMAN and BALLIET, 1970a, b, 1971). He offered grating patterns (in which the widths of parallel lines vary from coarse to fine) and determined acuity in terms of angular width of the finest grating pattern (threshold) that can be resolved (e.g. PIRENNE, 1962; RIGGS, 1965). Acuity targets were produced from 12·7 cm^2 photos of Ronchi rulings with black and white stripes of equal width (standard grating: 300 lines 2·54 cm^{-1}; without a lens, these lines are invisible to the human eye and the stimulus display appears as a flat grey square). The variable gratings consisted of lines changing in width from 25·4 to 0·96 mm. All gratings were surrounded by a large black border and, in underwater tests, were presented 30 cm below the water level. A perpendicular divider of mesh wire (projecting down to the floor of the experimental tank and 68·6 cm outward) separated the two targets offered thus preventing the test individuals from swimming laterally from one target to the other. All test animals had been trained previously to remain at a position about 6 m in front of the stimulus display until signalled to approach (by the sound of the display being lowered into the water). Their task was to push the target with variable grating in order to obtain a fish reward. Following a 10-trial 'warm-up' period with a supra-threshold target, each of the 6 variable gratings was paired randomly with the standard for 10 successive trials. The total number of trials was 70 per session, and each individual totalled 15 sessions. During the first experiments, ambient irradiance was 130 millilamberts (mL) on clear days, and 85 mL on overcast days.

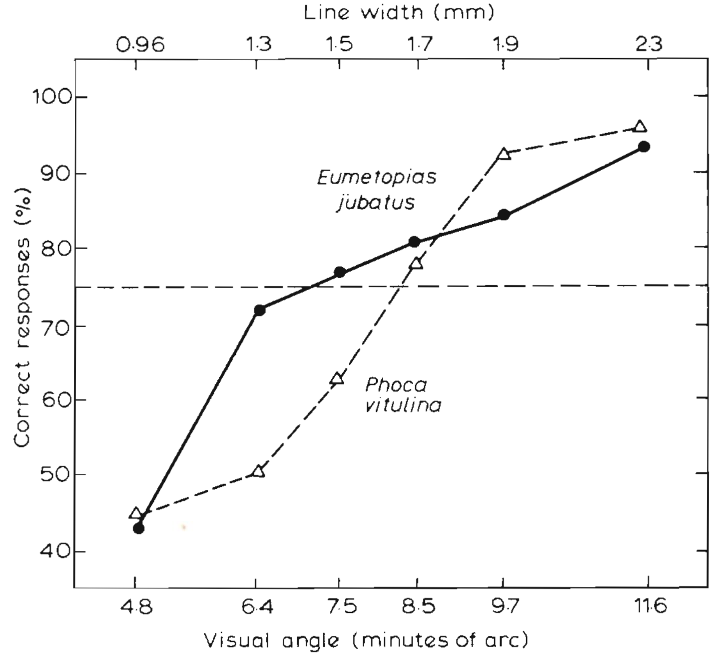

Fig. 8-58: *Eumetopias jubatus* and *Phoca vitulina*. Underwater acuity test on adult males. Percentage of correct responses as a function of visual angle (line width) calculated for a target distance of 68–6 cm. Illuminance: 130 mL on clear, 85 mL on overcast days. (After SCHUSTERMAN, 1972; modified; reproduced by permission of Plenum Publishing Corp.)

Average threshold estimates, expressed in minutes of visual angle, were 7·1 for *Eumetopias jubatus* and 8·3 for *Phoca vitulina* (Fig. 8-58). Despite slightly 'milky' eyes, *E. jubatus* exhibited significantly better underwater visual acuity at line widths subtending a visual angle of 6·4′ of arc; both pinnipeds resolved stripes that subtended an angle of 8·5′ of arc with relatively high accuracy. In *E. jubatus* and *P. vitulina* the number of orienting responses of head and eyes (SCHUSTERMAN, 1965a, b, 1966a) increases as a function of discrimination difficulty (Fig. 8-59); this increase in orientation responses is paralleled by the length of response-latency periods (SCHUSTERMAN, 1972). Fig. 8-60 illustrates visual acuity-threshold curves

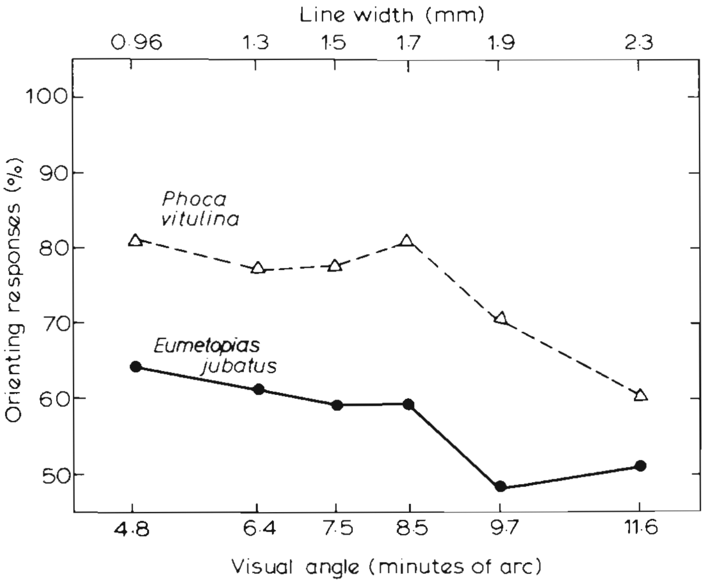

Fig. 8-59: *Eumetopias jubatus* and *Phoca vitulina*. Underwater orienting responses (%) of adult males as a function of visual angle. The number of responses increases with the difficulty of discrimination. Illuminance: 130 mL on clear, 85 mL on overcast days. (After SCHUSTERMAN, 1972; modified; reproduced by permission of Plenum Publishing Corp.)

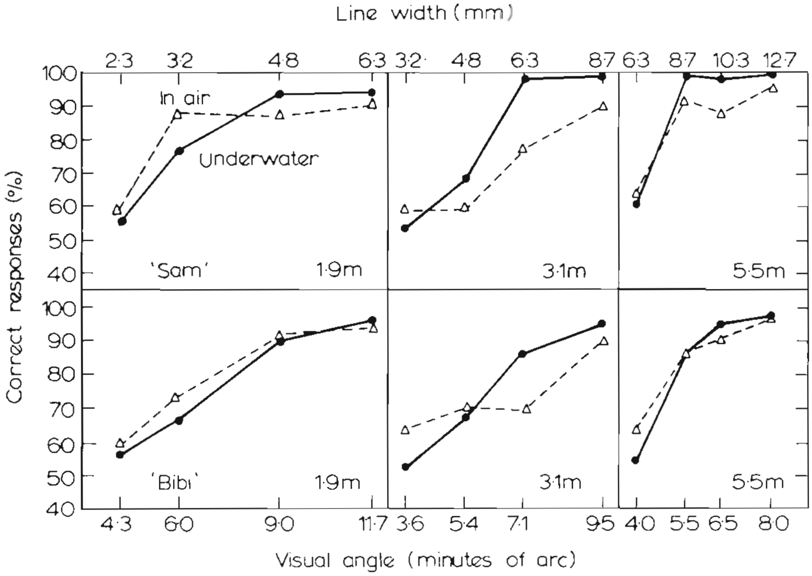

Fig. 8-60: *Zalophus californianus*. Visual acuity thresholds in air and underwater. 'Sam': adult male; 'Bibi': adult female. Target distances: 1·9, 3·1, or 5·5 m. Day-light conditions. (After SCHUSTERMAN, 1972; modified; reproduced by permission of Plenum Publishing Corp.)

obtained for two adult *Zalophus californianus* ('Sam' and 'Bibi') in air and underwater, at 3 different target distances. Differences in air and underwater are small, except at 3·1 m where underwater performance tends to be superior in both individuals.

What do we know about visual acuity of pinnipeds at low levels of irradiance? Ecologically, this question is of considerable importance since some, if not most, pinnipeds of the families Phocidae and Otariidae hunt and feed nocturnally (e.g. SCHEFFER, 1958; HOBSON, 1966; ICHIHARA and YOSHIDA, 1972). In addition to the above-mentioned high-luminance studies, SCHUSTERMAN (1972) exposed a 4-year-old male *Zalophus californianus* to 6 different levels of background luminance (light-tight tank; acuity targets illuminated, at known levels, from behind). His results are presented in Fig. 8-61 and Table 8-6: Both aerial and aquatic acuities decrease with decreasing luminance, but the decrease is less pronounced underwater. This finding seems in agreement with observations that *Z. californianus* hunts in dim underwater light (HOBSON, 1966), and with anatomical evidence (WALLS, 1963) according to which seals have a better light-reflecting tapetum lucidum (more cells, larger area) than some nocturnal land mammals. *Z. californianus* may also be quite active at night while on land, especially during the breeding season (PETERSON and BARTHOLOMEW, 1967); however, under such conditions, acoustic cues (p. 758) seem to be more important for orientation than visual stimuli (PETERSON and BARTHOLOMEW, 1969).

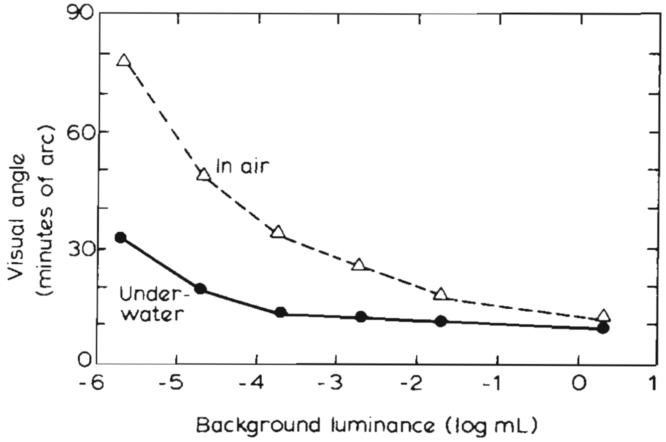

Fig. 8-61: *Zalophus californianus*. Visual acuity in air and underwater as a function of background luminance. 4-year-old male. Minimum target distance: 61 cm. (After SCHUSTERMAN, 1972; modified; reproduced by permission of Plenum Publishing Corp.)

With 5′ to 9′ visual angles, the underwater visual acuity of the 3 pinnipeds examined—*Eumetopias jubatus*, *Phoca vitulina*, *Zalophus californianus*—is, at

Table 8-6

Zalophus californianus. Percent correct orientation responses to visual stimuli as a function of visual angle (calculated for a distance of 61 cm) and luminance. 4-year-old male (After SCHUSTERMAN, 1972; modified; reproduced by permission of Plenum Publishing Corp)

Visual angle at 61 cm	Line width (mm)	Luminance (mL)											
		3		3 × 10^{-2}		3 × 10^{-3}		3 × 10^{-4}		3 × 10^{-5}		3 × 10^{-6}	
		No. trials	Percent correct	No. trials	Percent correct	No. trials	Percent correct	No. trials	Percent correct	No. trials	Percent correct	No. trials	Percent correct
						In air							
2°23·0′	25·4											60	97
1°47·5′	19·1									40	95	110	89
1°11·5′	12·7									70	87	100	72
58·2′	10·3									110	84	60	67
47·8′	8·7					10	100	50	94	110	75	20	50
36·3′	6·3			20	100	90	94	140	84	40	60		
26·5′	4·8			80	88	130	80	90	61				
18·0′	3·2	70	97	110	80	60	55	10	50				
13·0′	2·3	90	83	60	45								
11·0′	1·9	100	77										
9·6′	1·7	50	60										
8·6′	1·5	10	40										
						Underwater							
58·2′	10·3											10	100
47·8′	8·7											60	90
36·3′	6·3									60	97	120	83
26·5′	4·8					20	100	20	100	150	92	70	66
18·0′	3·2			40	98	50	96	100	95	150	73	20	45
13·0′	2·3			80	93	110	92	110	75	50	50		
11·0′	1·9	20	100	90	77	80	58	40	58				
9·6′	1·7	100	93	50	66	30	67						
8·6′	1·5	90	60	10	50	10	50						
7·2′	1·3	30	53										
6·7′	0·96	10	50										

high illuminance, considerably inferior to the in-air acuity of primates (man: 26″; chimpanzee: 28″; rhesus monkey: 34″), but comparable to elephant (10′), antelope (11′), red deer (9·5′) and domestic cat (5·5′) (RAHMANN, 1967). Low illuminance decreases underwater acuity of *Z. californianus* only slightly, but reduces acuity in air considerably. Low-illuminance underwater acuity of *Z. californianus* is comparable to that of the rhesus monkey and baboon in air at 10^{-4} to 10^{-5} mL (8–13′; BEHAR, 1968). According to SCHUSTERMAN (1972), his results are consistent with current histological knowledge on retinas of pinnipeds (LANDAU and DAWSON, 1970); they do not support the view that the eyes of pinnipeds reveal special adaptations to underwater vision.

In a note comparing the visual acuity of *Tursiops truncatus* and *Zalophus californianus*, SCHUSTERMAN (1973) corrects a misinterpretation of his research by DAWSON and co-authors (1972): although pupillary constriction in the *T. truncatus* eye may be as important for seeing details in air as it is for *Z. californianus*, at approximately 100 mL there is an air–water equivalence; at 3 mL, pupillary changes in *Z. californianus* reduce acuity in air more than in water. This effect increases as luminance is decreased further.

The eyes of pinnipeds seem to be able to collect more underwater light than the human eye, and the tendency of sea lions and seals to approach their prey from below (e.g. BONNOT, 1932; HOBSON, 1966)—silhouetting it against the illuminated water surface—may considerably increase their ultimate visual capabilities available for practical use. HOBSON mentions also the possible importance of bioluminescence for successful prey location by visual means. The diet of the northern fur seal *Callorhinus ursinus*, during its high-sea migrations, is composed largely of lantern fish and squid (WILKE, *in*: HOBSON, 1966). The lantern fish is well known for its luminescence, and other prey organisms may reveal themselves by swimming in water with plankton organisms which bioluminate when disturbed, thus betraying the prey's location.

In the pinnipeds studied, vision is of basic importance for spatial orientation, both underwater and in air. Visual orientation participates essentially in target discrimination, food finding, navigation, social contacts and communication.

(e) Sirenia

The holo-aquatic Sirenia inhabit coastal waters and rivers. The order comprises four species: the dugong *Dugong dugon* (tropical bays and estuaries of the Indian and western Pacific Oceans; Red Sea; Solomon Islands; northern Australia) and three manatees: the Caribbean manatee *Trichechus manatus* with two races (*T. m. manatus:* Mexico, Columbia, Bahamas, Greater Antilles; *T. m. latirostris* along the coast of Florida, USA); the West African manatee *T. senegalensis* (from Dakar, Senegal to Luanda, Angola); and the Amazon manatee *T. inunguis* (Amazon and Orinoco river systems and rivers of the northeastern part of South America). A fifth species, the Steller sea cow *Hydrodamalis gigas* lived near the Bering and Copper Islands; it was exterminated about 1768 (MOORE, 1951a, b, 1953).

No detailed information is at hand on visual capacities of sirenians. The remaining populations are small and chances for close-range observations have been rare. WALLS (1942, 1963) suggested that the eyes of most sirenians are less well adapted to underwater vision than those of cetaceans, and that the vision of sirenians is 'wretched'. Poor vision has been credited to sirenians also by BERTRAM (1963).

In the Everglades National Park (Florida, USA), the manatee *Trichechus manatus latirostris* inhabits turbid waters in remote inland bays and the labyrinthine waterways of the vast mangrove area (MOORE, 1956). The animals are difficult to observe; they breath only briefly at intervals of about 10 mins (5–15 mins), exposing not much more than their muzzles. Only active, swimming manatees surface more often (about once a minute). The turbid waters occupied and the totally aquatic way of life suggest that non-visual cues participate significantly in orientation related to feeding, reproduction and navigation.

A detailed beneath-the-surface study on Florida's manatees has been conducted by HARTMAN (1969) in the clear waters of Crystal River, north of Tampa. Snorkling and skin diving in close contact with the manatees—who exhibited 'the disposition of contented cows'—HARTMAN (p. 343) suggests that the vision of the herbivorous *Trichechus manatus latirostris* is relatively unspecialized and probably myopic. In the silt-laden rivers normally occupied, visibility may be 30 cm or less. Since maximum speed is about 20 miles per hour, orientation mechanisms other than vision must dominate, presumably hearing.

(f) Mysticeti

Most cetaceans have well-developed, though modified, eyes (JANSEN and JANSEN, 1969). The relative number of fibres in the optic nerve suggests better vision in Mysticeti than in Odontoceti. For a critical evaluation of inter-taxa differences in visual orientation additional and more reliable data are needed. No definite information is available on visual acuity thresholds of mysticetes and on the importance of their sense of vision for spatial orientation. MATTHIESSEN (1891, 1893) claimed emmetropic vision underwater and strongly myopic vision in air. However, indirect evidence suggests that aerial vision of mysticetes is also reasonably good (e.g. SLIJPER, 1962; ANONYMOUS, 1973). Possibly, a visual mechanism may be available to mysticetes comparable to that found in the delphinid *Tursiops truncatus* by DRAL (1972; p. 725).

The ontogeny and functional morphology of the eye of the fin whale *Balaenoptera physalus* has been studied by PILLERI and WANDELER (1970). In the youngest stages, the eyeball is spherical; later it gradually becomes oval with a flattened anterior surface. In adults the cornea is flattened, the iris has very little stroma, and the ligamentum pectinatum is barely represented; the spongium iridocornealis contains lamellary receptors (discovered in *Megaptera novaeangliae*); the choroid is thick and has a tapetum lucidum fibrosum.

The timing of feeding and reproductive migrations of grey whales *Eschrichtius robustus* and of humpback whales *Megaptera novaeangliae* seems to depend on daylength (PIKE, 1962; see also p. 840; DAWBIN, 1966). DAWBIN has suggested that pregnant females of *M. novaeangliae* are least sensitive, and lactating females most sensitive to decreasing daylengths, while resting females exhibit intermediate sensitivity. Daylength-controlled reproductive (hormonal) activities may also act as migratory releaser in other marine mammals.

(g) Odontoceti

Use and Development of Visual Mechanisms

Most marine odontocetes make effective use of their sense of vision for orientation, both in water and in air. This statement is supported by anatomical, neurophysiological and behavioural evidence. However, some limnic muddy-river odontocetes have a greatly reduced visual apparatus: *Inia geoffrensis*, *Platanista gangetica* and *P. indi*, for example, possess much less pronounced optical mechanisms (e.g. PILLERI and GIHR, 1971a, b; PILLERI, 1972; PURVES and PILLERI, 1973) than the marine *Tursiops truncatus*, *Phocoena phocoena* and related forms (e.g. WALLS, 1942, 1963; BREATHNACH, 1960; KRUGER, 1966; JANSEN and JANSEN, 1969).

Even the most thoroughly investigated odontocete, the bottle-nosed dolphin *Tursiops truncatus*, does not yet yield much information on the use of its visual mechanisms under ecological conditions. *T. truncatus* inhabits coastal areas in temperate and tropical zones, and feeds predominantly on fishes. Anatomical and neurophysiological information indicates that its mechanism of visual perception and interpretation—although inferior to acoustic brain centres—is quite well established (e.g. BREATHNACH, 1960).

Platanista gangetica and *P. indi* have vesicular, purely direction-finding eyes, based on the principle of a pinhole camera (PURVES and PILLERI, 1973). Vision is improved by a contractile iris, but the cornea contains vessels that are assumed to reduce its transmitting power and to preclude contour vision and focusing. Presumably the eyes of *P. gangetica* and *P. indi* perceive the direction of incident light or of pronounced light–dark gradients. During the day, these side-swimming inhabitants of muddy river waters seem to orient their body positioning to the light gradient between water surface and river bed. Since the eyeball is embedded deeply in the head, only a narrow light beam can reach the retina. During swimming, one eye is directed to the surface, the other to the river bed (Fig. 8-128).

Making use of whatever orientational cues are available, odontocetes employ their eyes whenever possible or necessary. As in other animals, combined use of different sensory modalities seems to prevail during difficult orientation tasks. While light and sound appear to dominate as cues for spatial orientation, other environmental stimuli and social factors may be of importance.

Visual Acuity and Problem Solving

The visual acuity of delphinids is assumed to be inferior to that of man (e.g. REYSENBACH DE HAAN, 1957; KELLOGG, 1961; LILLY, 1961), and the optic colliculus of *Tursiops truncatus* is less than one quarter as large as the acoustic one (KELLOGG, 1928). On the other hand, captive dolphins display remarkable abilities of target localization and recognition, and on shape and movement discrimination when jumping out of the water. They can be directed easily by their trainer via hand signals and are able to recognize a cigar-sized fish, held 5 to 6 m above the water surface, seizing it with impressive accuracy. How could they do all this without perfect eyesight?

According to Dawson and co-authors (1972), the eye of *Tursiops truncatus* is emmetropic in water and myopic or ametropic in air. Dral (1972) investigated the aquatic and aerial visual capacities of *T. truncatus* employing ophthalmoscope and keratoscope measurements. He established that underwater the whole field of vision is emmetropic, but that in air emmetropia is restricted to the eye's naso-ventral part: *T. truncatus* can use the whole range of its eyes for underwater vision, but only its naso-ventral part for aerial vision. This finding explains why, in many cases, *T. truncatus* looks at underwater objects sideways with one eye at a time, and in air with its two eyes simultaneously. Such behaviour was observed in the Dolphinarium at Harderwijk (Netherlands) and in other oceanaria: underwater, the dolphins focus targets which catch their attention (e.g. food or other dolphins) with either one eye or both eyes. However, as soon as they lift their heads into air, some convergence of the eyes occurs 'and it is a striking experience to be looked at by the animals with both eyes simultaneously' (Dral, 1972, p. 510). Dral suggests that *T. truncatus* may possibly accommodate by changing the shape and/or the position of the lens due to muscular action of the operculum. Possible changes of the lens cannot be affected by the ciliary body because it does not contain even a trace of musculature. The mechanism suggested by Dral would confer on *T. truncatus* considerable visual abilities also in air (see also Langworthy, 1931, 1932; Slijper, 1962; Kellogg and Rice, 1966; Herman and co-authors, 1969).

Few experiments have been conducted thus far on visual performance in odontocetes. This is in marked contrast to the considerable attention which has been paid to acoustic orientation in this whale group.

Using the method of constant stimuli, Pepper and co-authors (1972) presented, in air, horizontal black-line gratings to a *Tursiops truncatus* (ca 11-year-old female

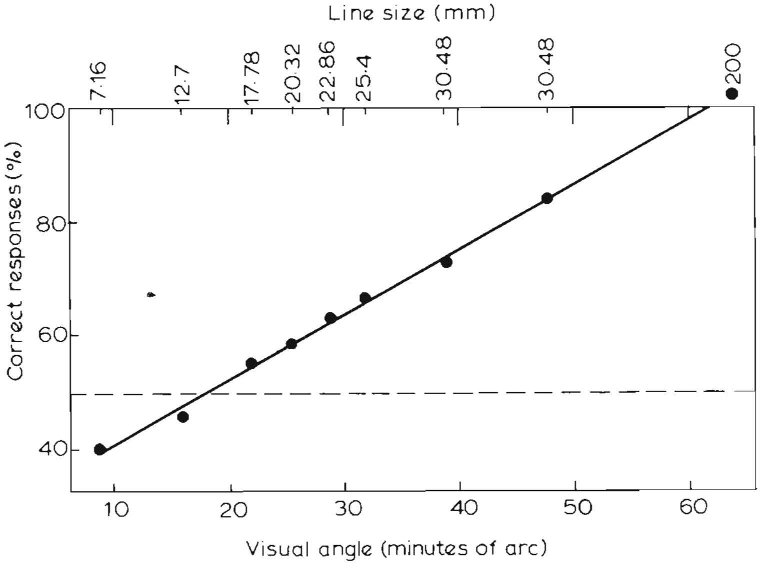

Fig. 8-62: *Tursiops truncatus*. Visual-acuity threshold curve in air. (After Pepper and co-authors, 1972; modified; reproduced by permission of Biological Sonar Laboratory, Fremont, California.)

of about 120 kg) in a discrimination task. Over a constant viewing distance of 276 cm and at a detection threshold of 50% mean correct responses to the variable target, the minimal angle of resolution was calculated to be 18′ of arc (Fig. 8-62). This value of in-air visual acuity is inferior to that of pinnipeds (5′ to 9′; p. 720). The results of PEPPER and co-authors correct WALLS' (1942) original suggestion (poor aerial vision of delphinids) and credit *T. truncatus* with a visual mechanism which allows them to see comparatively well in air.

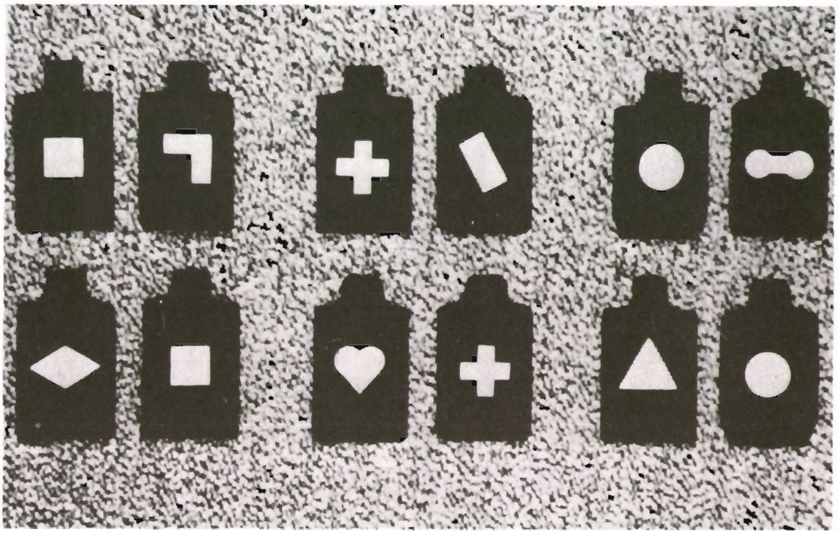

Fig. 8-63: *Tursiops truncatus*. Six of the 21 visual stimuli pairs (stimulus area: 12·9 cm^2) discriminated by 'Paddy'. In each pair one is the positive (left), the other the negative stimulus. The same symbol can serve as positive and negative stimulus: for example, the cross is positive when paired with the bar, but negative when paired with the heart. 'Paddy' had little trouble with such reversals and could differentiate between them at any subsequent time without confusion. (After KELLOGG and RICE, 1966; originally published by the University of California Press; reprinted by permission of The Regents of the University of California.)

The experiments conducted by KELLOGG and RICE (1964, 1966) on visual discrimination and problem solving in *Tursiops truncatus* deserve detailed attention. These two authors have studied the responses of a captive 136-kg, 8-year-old individual ('Paddy') well adapted to human handling (7 years of intimate, almost 24-hr contact with human beings). Out of a total of 25 pairs of stimuli, Paddy discriminated 21 (84%) pairs successfully (Fig. 8-63). The stimuli pairs were offered to the dolphin above the water in air (Fig. 8-64) and below the water (Fig. 8-65). All choice-runs began after Paddy had returned to a defined starting point (about 6·1 m from the apparatus). Trial intervals were never less than 30 secs. After each group of 10 trials, rest periods of 2 mins were allowed, after approximately 50 trials of about 20 mins. One session consisted of about 100 trials and the total number of test trials exceeded 7000. Positive responses were reinforced by offering herring pieces on the appropriate side of the choice apparatus.

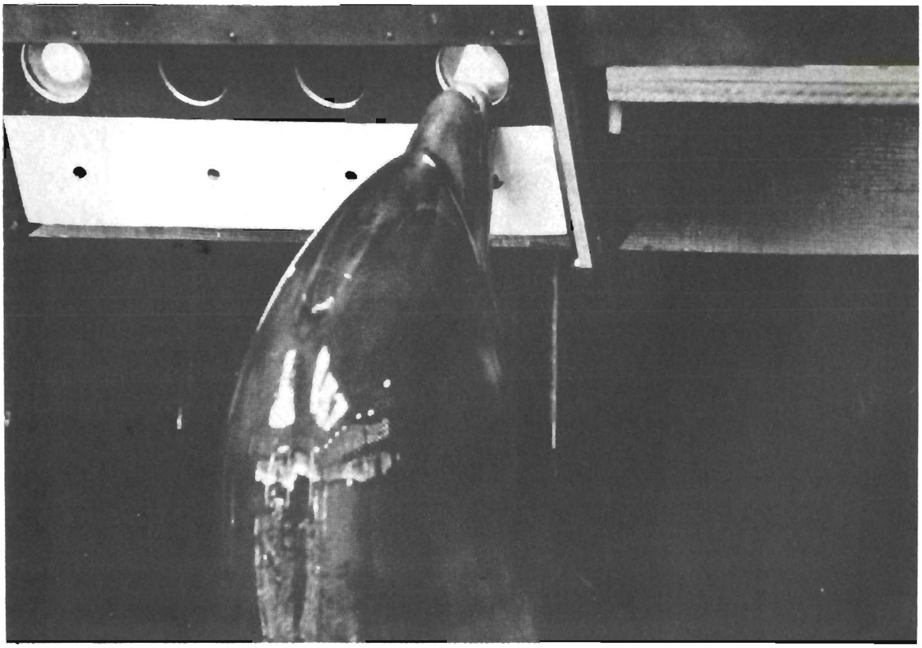

Fig. 8-64: *Tursiops truncatus*. Stimulus-choice apparatus above the water surface. The apparatus requires 'Paddy' to press positive stimulus. Here he is responding to a circle-triangle choice. Positive discrimination is rewarded by dropping a small piece of herring through the food slot on the appropriate side of the apparatus. (After KELLOGG and RICE, 1966; originally published by the University of California Press; reprinted by permission of The Regents of the University of California.)

KELLOGG and RICE (1966) stress the sharp difference in discrimination ability between stimuli presented in air, but seen from beneath the water, and the same pattern viewed underwater: all discriminations were made by underwater vision, and none could be made from water to air, unless the stimuli had been previously differentiated successfully underwater. Such poor water–air vision is in contrast to the general experience that dolphins perceive forms and movements above the water. In fact KELLOGG and RICE could get Paddy to respond to slight postural changes of a human attendant, such as slight motions of head or hand. However, accurate discrimination of shapes and motions from water to air does not necessarily mean that visual images of geometric figures can be differentiated equally well. KELLOGG and RICE report that skin divers, who went in the experimental pool and observed the stimuli from the same position as Paddy, saw the figure images often distorted to such a degree that identification was very difficult. Only after he had learned what to look for could Paddy apply this knowledge to the water-to-air situation. Apparently, a distance of 2·4 m or more is necessary for visual perception from water to air. Of course, also the angles of vision and of refraction are important (Chapter 8.2, p. 660).

Discriminating acoustic targets, *Tursiops truncatus* often performs head movements from side to side (scanning) subtending angles of 10° or more (p. 803).

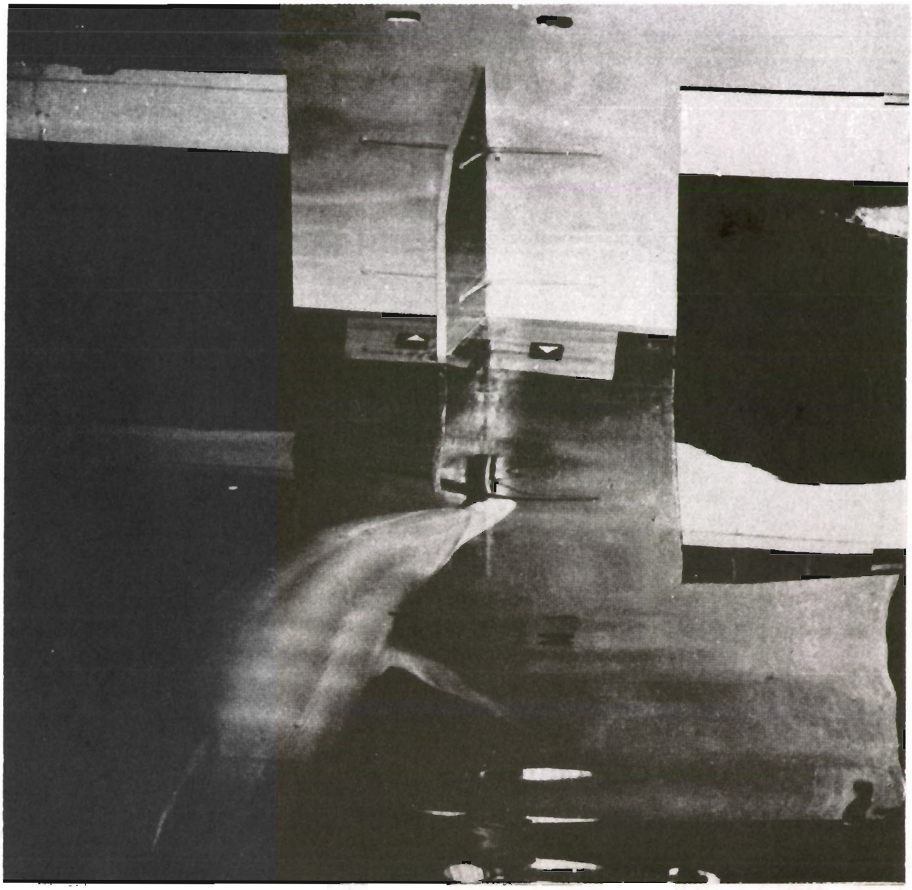

Fig. 8-65: *Tursiops truncatus*. Stimulus-choice apparatus below the water surface. Approaching the apparatus, 'Paddy' oscillates his head from left to right, apparently looking at the stimuli first with one then with the other eye. Here 'Paddy' has turned his head far to the right and seems to examine the stimuli (triangles) with his left eye. (After KELLOGG and RICE, 1966; originally published by the University of California Press; reprinted by permission of The Regents of the University of California.)

Similar head movements were made by Paddy as he was swimming toward submerged visual targets (Fig. 8-65). Yet KELLOGG and RICE (1966) never detected any active-biosonar clicks under these conditions (clicks could not reach the visual stimuli since they were placed behind a 32 mm window). No head scanning was noted during visual discrimination in air.

Underwater visual acuity of an adult female Pacific white-sided dolphin *Lagenorhynchus obliquidens* has been assessed by SPONG and WHITE (1971). The female was required to discriminate between one and two vertical lines presented simultaneously in a two-choice apparatus. Visual discrimination learning was unexpectedly slow during the training phase. During the testing phase, 8 two-line versus one-line problems (differing only in two-line gap widths) were presented in a random sequence 100 times each during 10 daily sessions, at a minimum viewing distance of

45 cm. Underwater visual acuity is approximately 6′ of arc—a value roughly comparable with that for the cat in air (Fig. 8-66). Similar data have been produced by SPONG and WHITE in a study with the killer whale *Orcinus orca* (unpublished Technical Report, 1969).

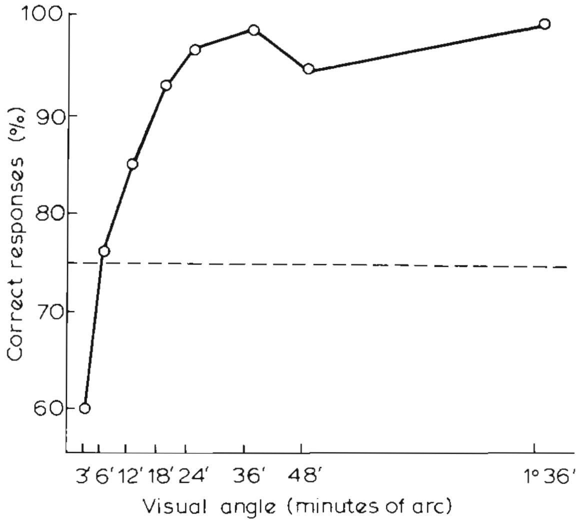

Fig. 8-66: *Lagenorhynchus obliquidens*. Performance during a visual-acuity test. Points represent mean scores over 100 trials. Applying the standard psychophysical criterion to these data (difference threshold defined as the visual angle corresponding to the 75% performance level), underwater visual acuity was estimated to be approximately 6′ of arc. (After SPONG and WHITE, 1971; reproduced by permission of Academic Press, Inc.)

In the freshwater-living Amazon dolphin *Inia geoffrensis* the eye openings are rather small. Some authors have doubted that the eyes are functional. However, LAYNE (1958), LAYNE and CALDWELL (1964) and M. C. CALDWELL and co-authors (1966) assume, on the basis of gross behavioural evidence, that visual acuity is adequate and that vision is the preferred or primary mechanism for environmental investigation and orientation. Circumstantial evidence suggested to M. C. CALDWELL and co-authors that night vision is excellent; the eye itself is comparatively large and well enervated. Critical experiments on visual acuity of *I. geoffrensis* have not yet been performed. The river dolphins *Platanista gangetica* and *P. indi* live in low visibility, muddy waters (p. 800). According to PURVES and PILLERI (1973), the function of their eyes appears to be restricted to direction finding (p. 724).

In summary, it may be stated that the experiments hitherto conducted confer considerable visual capabilities to the delphinids examined. Visual acuity and discrimination should be sufficient to allow significant participation of vision in spatial orientation.

Sun-Compass Navigation

In the western Mediterranean Sea, sun-compass orientation has been claimed for the common dolphin *Delphinus delphis* (PILLERI and KNUCKEY, 1968; see also PILLERI, 1970a). Depending on the time of day, the *D. delphis* herds are reported to head always in a definite direction, either west to east or east to west. Although detailed information is lacking, PILLERI and KNUCKEY assume that their observations—made during 2 expeditions in July—demonstrate the ability of *D. delphis* to navigate by the sun. During daily herd movements, the dolphins swim towards the sun (Fig. 8-67). As the sun direction changes from east to west the herds travel eastward until about 12·00 hours and then westward. The dolphins do not seem to feed at any particular time of day. Sometimes small groups have been seen to separate from the main herd, but to rejoin it in the evening. Apparently, specific herds occupy a certain territory (e.g. along the Spanish coast between Gibraltar and Malaga).

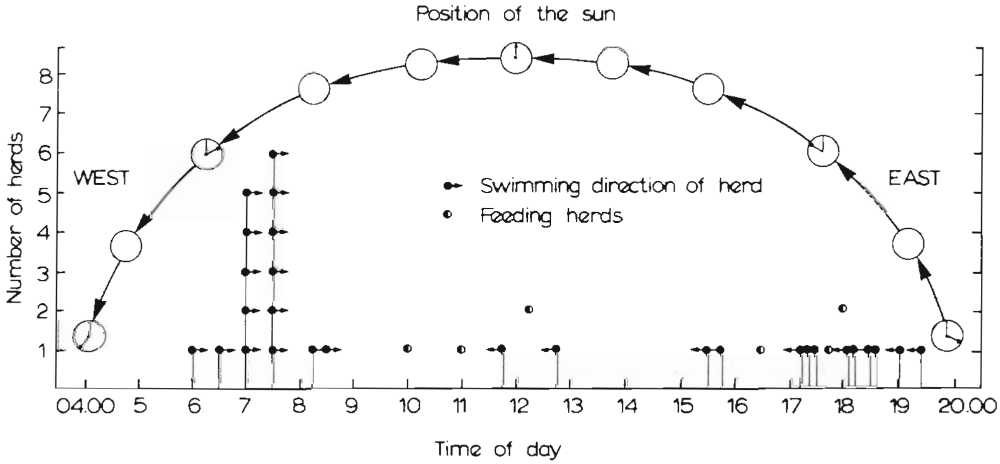

Fig. 8-67: *Delphinus delphis*. Directions of herds in the western Mediterranean Sea (July, 1967). The dolphins are reported to swim always towards the sun. As the sun direction changes from east to west (from right to left in the diagram), swimming direction reverses at about 12·00 hours. (After PILLERI and KNUCKEY, 1968; modified; reproduced by permission of Birkhäuser Verlag, Basel.)

These observations agree with earlier reports by BUSNEL and DZIEDZIC (1966a) and are essentially in line with observations by EVANS (1971). On various cruises, BUSNEL and DZIEDZIC met *Delphinus delphis* herds of 50 to 100 individuals in the western Mediterranean Sea, swimming at high speed in a straight line, 2 to 3 m apart, in the direction of the sun. Such behaviour was always noticed between 15·00 and 17·00 hours with good weather and clear water (visibility down to water depths of 70 to 80 m). On these occasions, no acoustic signals were emitted, not even active-biosonar clicks. BUSNEL and DZIEDZIC (p. 637) refer to this behaviour as 'silent navigating'.

Before we can accept sun-compass orientation in *Delphinus delphis* as a fact, additional information is required. In any case, rigid sun-navigation would seem to be restricted to special situations rather than to represent the basic orientation pattern. Other populations of *D. delphis* have been seen to pursue hunting and migration routes, apparently not directly related to the position of the sun.

(3) Temperature

(a) General Aspects

Next to light, temperature is the most important environmental factor affecting life on earth (Volume I: KINNE, 1970a, p. 322). In contrast to poikilotherms, which depend strongly on ambient thermal energy (Volume I: BRETT, 1970, KINNE, 1970b; Chapter 4 of this Volume), homeotherm animals have increased the degree of independence of their central body functions from environmental temperature conditions. Internal temperature regulation has made it possible for marine mammals to inhabit areas with extreme thermal climates—polar ice and tropical waters. Several species migrate freely between such extremes (p. 829). Even over short distances, steep thermal gradients may be encountered during deep dives, especially in temperate or tropical areas.

Marine mammals possess effective mechanisms of thermoregulation. Metabolic heat production, insulation, vascular heat exchange and peripheral heat loss are adjusted to life in aquatic habitats with widely varying temperature conditions. The mechanisms of thermoregulation employed by marine mammals have been discussed or reviewed by SCHOLANDER and co-authors (1950), TOMILIN (1951a, 1960), SCHOLANDER and SCHEVILL (1955), IRVING and HART (1957), KANWISHER and LEIVESTAD (1957), BELKOVICH (1961, 1965), KANWISHER and SUNDNES (1966), IRVING (1969), BABENKO and co-authors (1970), SOKOLOV (1971) and WHITTOW and co-authors (1972). In sea otters and several seals, resting heat production proved to be higher than predicted from the mammalian standard curve, presumably due to the considerable heat loss to the aquatic environment (IVERSEN and KROG, 1973).

While the temperature differences between body surface and ambient water are small—in delphinids, gradients between body surface and water do not exceed 1 C°, those between fins and water never 4 C° (KOZLOV, *in*: SOKOLOV, 1971)—steep thermal gradients exist between central and peripheral body parts, especially in polar mammals. Control and maintenance of such gradients are the key to survival under extreme temperature conditions. These internal gradients deserve more attention in analytical studies concerned with thermoregulation. They also pose interesting problems of adaptive differences in nerves and muscles operating along the gradient axis. A study on freshly excised nerves under controlled conditions aboard ship revealed that the nerves in the appendages of seals (*Phoca vitulina*, *Pusa hispida*, *Histriophoca fasciata* and *Erignathus barbatus*) can still conduct at temperatures as low as −5° C (L. K. MILLER, 1972; see also 1967, 1970); even the proximal tibial nerve sections function at low temperatures (ca 0° to 5° C).

The distribution of marine mammals in thermally different environments has been reviewed by IRVING (1969) and by MARCUZZI and PILLERI (1971). However, the importance of environmental temperature as a controlling factor in marine-mammal distributions remains uncertain. Distribution patterns may often depend more on food availability. In fact, in many cases, the evidence at hand supports such an assumption. Other key aspects to be considered are breeding behaviour and specific seasonal temperature requirements of mating adults, pregnant females, and newly borns.

(b) Pinnipedia

Definite information on the importance of temperature for spatial orientation in pinnipeds is not available. As in mysticetes, seasonal temperature changes may act as releasers of migratory activities.

Northern fur seals *Callorhinus ursinus* are nocturnal hunters (e.g. ICHIHARA and YOSHIDA, 1972) which dive to considerable depths and may thus encounter significant temperature gradients. Earlier estimates of diving depths (SCHEFFER, 1946: 7–73 m; KENYON, 1952: 55 m) have been superseded by echosounder measurements of ICHIHARA and YOSHIDA (1972) which testify to maximum diving depths in the Japan Sea exceeding 100 m. Water temperature was 10·1° C at the water surface, 9·7° C in 10 m, 8·6° C in 25 m, 5·3° C in 50 m, and 2·8° C in 100 m. Such a thermal gradient could conceivably provide, in addition to gravity and pressure, vertical orientation cues.

(c) Sirenia

The coastal and riverine manatee genus *Trichechus* inhabits tropical areas on both sides of the Atlantic Ocean.

Usually not gregarious and without defined social structures (except temporary mother–young relations), the Florida manatee *Trichechus manatus latirostris* aggregates during cold spells. At temperatures below 5° to 10° C, groups of 10 to 60 individuals may be found in warm-water sanctuaries, e.g. springs of suitable, fairly constant temperatures (MOORE, 1956; HARTMAN, 1969). In cold-spell congregations, *T. m. latirostris* establishes even more body contact than usually: muzzle-to-muzzle contact, nuzzling, nibbling, nudging, butting, and embracing. HARTMAN speaks of a serene ballet, an intimate slow-motion ritual of lazy posturings, twistings and turnings. Whether very close body contacts may help to reduce heat loss during cold spells is not known.

(d) Mysticeti

Distributions, migrations and summer and/or winter aggregations of several mysticetes appear to be influenced decisively by seasonal temperature changes. In most cases, temperature appears to act as releaser of migratory activities rather than as provider of directional cues. Temperature effects may also manifest themselves indirectly through the distribution of prey organisms.

Evidence of seasonal influences on whale distributions has been presented in numerous papers, e.g. KCHUZIN (1960), NORRIS (1966), ANDERSEN (1969). and SOKOLOV (1971). Grey whales *Eschrichtius robustus* and humpback whales *Megaptera novaeangliae* migrate seasonally between warm breeding areas (about 25° C water temperature in the case of *M. novaeangliae*) and cold feeding areas (p. 836). Assemblages occur near continental or island shores with suitable water temperatures.

Reviewing the evidence at hand, KLUMOV (1955) concludes that oceanic whale herds of the northern and southern hemispheres do not, as a rule, exchange members. Body measurements, and endo- and ectoparasite occurrence support this view. High surface temperatures are assumed to render difficult or to prevent crossing of the equatorial-tropical belt.

Whale-marking investigations (IVASHIN, 1962) seem to indicate that there exist a few local schools of *Megaptera novaeangliae* with separate wintering localities, where most individuals remain, and separate feeding areas (see also DAWBIN, 1966). Some individuals may pass from one feeding area to another. Temperature seems to be of ecological significance in regard to the selection of wintering localities. The possible importance for whale distributions of areas where cold and warm ocean currents meet has been discussed by SLEPTSOV (1961d). According to TOMILIN (1953, 1960), most whale herds tend to remain associated with a certain ocean area.

In the North Pacific area, distribution and migration routes of mysticetes seem to have been influenced by the overall climatic temperature increase recorded for that region (NISHIWAKI, 1967). Mysticetes which have migrated to the south in the past are now reported to migrate to areas of high latitudes; others have extended their distributional area northward into waters near Japan. Northward-migrating mysticetes encounter their 'first boundary line' in the Aleutian Island Chain, the 'second boundary' in the Bering Strait (NISHIWAKI, p. 48); they are assumed to be influenced by the Kuroshio Current, the Oyashio Current and the warm Alaska Current.

The comprehensive review on the zoogeography of Cetacea by MARCUZZI and PILLERI (1971) has been criticized by several experts. It deserves critical reevaluation.

(e) Odontoceti

No detailed accounts have been published on orientational responses of odontocetes to environmental temperature. The information at hand pertains largely to distributions; it is heavily descriptive and often inconclusive.

The lowest temperature recorded in waters occupied by Risso's dolphin *Grampus griseus* is 7·5° C. In captivity, this odontocete loses its appetite and dies when the water temperature drops below 5° C (NISHIWAKI, 1967). Females of the sperm whale *Physeter catodon* do not enter into sea areas with surface-water temperatures below 10° C (about 50° N latitude; TOWNSEND, 1935; NISHIWAKI, 1966). *P. catodon* often accumulate and feed at the boundary line between cold and warm waters. This fact has caused some sperm-whale hunters to locate their prey with a thermometer (BENNETT, 1932). According to CLARKE, (1953, 1954a), *P. catodon* aggregate in areas of upwelling cold, high-productivity waters or near countercurrents (e.g. near the equatorial divergence; literature *in*: D. K. CALDWELL and co-authors, 1966a). While the male exhibits an almost cosmopolitan distribution (SCHEVILL, 1961), females and subadults appear to be limited largely to the areas between 50° N and 50° S (SALVESON, 1915; GILMORE, 1959; SLIJPER, 1962). In general, the distribution of females is restricted by the 20° C isotherm, but in the eastern North Pacific Ocean they occur regularly at temperatures below 17° C (GILMORE, 1959). According to SCHUBERT (1951, 1955), off Chile and Peru *P. catodon* exhibits segregation from the coast westward: females occupy waters of 17° C and warmer, bachelor herds range from 16° to 18° C, and solitary males inhabit waters between 15° and 17° C. However, such segregation could only be confirmed in part by CLARKE (1962).

Near Japan, the bottle-nosed dolphin *Tursiops truncatus* is mainly found in waters of 18° to 23° C (NISHIWAKI, 1967). In other areas, *T. truncatus* inhabits both temperate and tropical coastal waters. This dolphin ranges in the north up to southern Baffin Island, southern Greenland, Norway, Japan and California (USA), and in the south down to Argentina, South Africa, southern Australia, New Zealand and Chile.

Information on temperature sensitivity and thermal gradient discrimination of odontocetes is not available. TOMILIN (1960) has suggested that the common dolphin *Delphinus delphis*, which is widely distributed in warm-temperate and tropical waters, is able to respond to short-range gradients of less than 1 C°. The fins are particularly sensitive to ambient temperature; they have been claimed to act as thermoreceptors and to assist in thermoregulation (TOMILIN, 1950, 1951a; KANWISHER and SUNDNES, 1966; IRVING, 1969).

The distributions of several cetaceans correlate well with thermal patterns in oceans and coastal waters (e.g. TOMLIN, 1960; NORRIS, 1967a). In coastal waters of southern California (USA), the distribution of the Dall porpoise *Phocoenoides dalli* is closely related to water temperatures of 11° to 12° C (NORRIS and PRESCOTT, 1961). A similar congruence between surface temperature and whale distribution has been reported for other delphinids off eastern and southern New Zealand (GASKIN, 1968). Irregularities in the patterns of thermal energy in the sea (e.g. steep gradients, discontinuity layers) are often paralleled by topographic sea-bottom peculiarities or organismic aggregations. Conceivably, all three—bottom topography, food aggregation and thermal pattern—could serve as cues for spatial orientation. If so, parallelism between temperature and odontocete distributions would often indicate indirect, rather than direct, relationships.

In summary, the extent to which temperature patterns may provide primary orientation cues to marine mammals remains uncertain. Indirect evidence suggests that the local thermal regime may act as a releaser of orientational behaviour. Once in migratory mood, the mammals seem to be guided by directional cues such as light (sun direction, visual landmarks, p. 713), water movement (p. 735), sound and vibration (p. 739), food organisms and sea-bottom morphology.

(4) Salinity

Salinity is of considerable ecological significance for potential food organisms of marine mammals: benthic plants (Volume I: GESSNER and SCHRAMM, 1971), invertebrates (Volume I: KINNE, 1971), and fishes (Volume I: HOLLIDAY, 1971).

Salinity affects orientational responses of invertebrates (Chapter 8.1) and fishes (Chapter 8.2); but no conclusive information is available regarding the importance of salinity for orientation of marine mammals.

Major differences in salinity affect the well-being of marine mammals. Marine forms may contract a variety of (skin) diseases when kept in freshwater tanks and limnic representatives may suffer when exposed to sea water.

It is not known whether marine mammals are capable of perceiving small differences in salinities or salinity gradients. While chemoreception may be sufficiently developed in pinnipeds, sirenians and mysticetes, it seems poor in odontocetes. The latter are claimed to be anosmatic (have no sense of olfaction), and a gustatory sense has been reported to be presumably absent in most whales (SLIJPER, 1962; see also p. 738). Even though lack of detailed knowledge does not permit general statements, the anatomical information at hand indicates poor prerequisites for salinity discrimination.

(5) Water Movement

Functional and structural responses of marine organisms to variations in water movement have been reviewed in Volume I, Chapter 5. Water currents generate weak electrical fields which may be used as orientational cues by invertebrates (Chapter 8.1) and fishes (Chapter 8.2). Very little information is available on the potential importance of water movement for orientation of marine mammals.

In the open ocean, an organism swimming in moving water cannot detect its overall displacement unless reference stimuli are available. In the absence of pertinent external stimuli (e.g. visual or auditory cues), asymmetrical muscle tension, general sensitivity of the body surface to local variations in water movement and inertial navigation may be involved. At the borders of neighbouring water bodies, when tracing the course of a specific water current, or in the presence of recognizable environmental gradients, water movement could, conceivably, also be detected indirectly via changes in physico-chemical water properties, especially in forms with adequate olfactory or gustatory discrimination capabilities.

In the killer whale *Orcinus orca*, SPONG and co-authors (1972a) noticed close relationships between pod movements and patterns of tidal water movement. Typically, the pods hunt in one direction with the flow of the tidal current until the tide changes. Perhaps resting during slack tide, they become active again to hunt with the flow of the new tide. This orientation to water movement of hunting *O. orca* may be determined by the behaviour of their major local prey organism: salmon. According to SPONG and co-authors, the salmon schools are strongly influenced by tide and current. Apparently *O. orca* exhibits a variety of hunting strategies, some of which involve movements against the water current.

The sperm whale *Physeter catodon* is found in greatest numbers in or near powerful water currents or where neighbouring currents flow in opposite directions (BENNETT, 1840, *in*: D. K. CALDWELL and co-authors, 1966a). Such areas are usually characterized by high food abundance. *P. catodon* feeds on deeper-dwelling, large squids and fishes, occasionally also on seals, crustaceans, jellyfish, sponges, etc.

Orientation to water movement by marine mammals may often be indirect—such factors as temperature, water quality and water contents representing the primary cues. Swimming performance and hydrodynamic properties of cetaceans have been reviewed by LANG (1966), HERTEL (1969) and SOKOLOV (1971).

(6) Substratum

No definite information is available on the importance of bottom-substratum properties for spatial orientation in marine mammals. A number of authors have suggested that bottom topography, i.e. significant changes in depth or contour, may assist cetaceans in direction finding (e.g. EVANS, 1971); but proof of such assumptions has not been provided.

Responses of micro-organisms, plants and non-mammalian marine animals to substrates have been discussed in Volume I, Chapter 7.

(7) Pressure

The significance of hydrostatic pressure as an environmental variable has been reviewed in Volume I, Chapter 8. Pronounced pressure increase may affect metabolic performances and anatomical structures. But even very slight pressure gradients—equivalent to a few centimetres of water depth—can provide cues for orientation in invertebrates and fishes (Volume I: FLÜGEL, 1972; see also Chapters 8.1, 8.2 of this volume). While acting in all directions with the same intensity, vertical pressure gradients—by virtue of their omnipresence and permanence—provide reliable stimuli for vertical orientation. However, in invertebrates, orientation to pressure is usually linked to gravity or light effects, and pressure changes are assumed to serve primarily as releasers of geotaxis or phototaxis in plankters and for controlling adequate transport by currents (Chapters 8.0, 8.1, p. 604).

Can pressure gradients be perceived with sufficient accuracy by marine mammals to facilitate discrimination of their exact vertical position in the water column? We do not know. During up and down movements, pressure perception may be expected to provide a definite source of orientational information. The common dolphin *Delphinus delphis* has been reported to be able to discriminate hydrostatic-pressure gradients corresponding to differences of 10 to 40 mm of water column (KOLCHIN and BELKOVICH, 1973).

Physiological problems encountered by Pinnipedia and Cetacea during deep diving have been considered by KOOYMAN and ANDERSEN (1969). These two authors discussed also hypotheses regarding the avoidance of 'bends' due to prolonged pressure exposure and rapid decompression; but experimental verification of the assumptions made is not yet available.

The sperm whale *Physeter catodon* is a deep-water species, rarely entering shallow coastal waters (minimum water depth about 100 m). Its dives are among the longest and deepest of all cetaceans and are possibly exceeded only by the bottle-nose whale *Hyperoodon planifrons* (SCHOLANDER, 1940; MATSUURA, 1943; for a review consult D. K. CALDWELL and co-authors, 1966a). The length of a dive increases as a function of body length. Large *P. catodon* (15 to 18 m) have been reported to dive for periods ranging from 60 to 90 mins. It is an old whalemen's rule of thumb that for each minute spent diving, a large bull respires once: for example, an 18-m male weighing nearly 60 tons stayed down 60 mins and subsequently spouted 60 times

(ASHLEY, 1942). If the number of respirations is reduced for some reason, the following dive will have to be shortened. Each spout averages about 3 secs, and the first blow, an explosive blast, may be heard over several hundred metres (CLARKE, 1954b). Smaller specimens dive for periods up to 20 to 40 mins and must respire more frequently for each diving minute. The rate of breathing increases to once every 10 or 12 secs after strenuous diving work; it amounts to once per minute when swimming at high speed, and to once every 2 or 3 mins when travelling leisurely at the surface. Sperm whales have been recorded swimming at 2250 m depth (WHITNEY, *in*: NORRIS, unpublished). Presumably, maximum diving depths lie somewhere near 2500 to 3000 m. How can *P. catodon* manage to get along with its oxygen supply for 1 hr? How can it emerge from long and deep dives without signs of caisson disease? And how do these whales orient in the oceans' depths at pressures which may, at least theoretically, interfere with their mechanisms of sound generation and sound perception? We do not know. Some of the pertinent information has been reviewed by KELLOGG (1938), SLIJPER (1962) and D. K. CALDWELL and co-authors (1966a).

(8) Organic Substances

Responses of marine organisms—except mammals—to organic substances have been reviewed in Volume I, Chapter 10. Organic-substance discrimination involves the senses of taste (gustation) and smell (olfaction). In aquatic organisms, gustation and olfaction overlap in their functions and proper distinction is difficult or impossible. While both senses have been found to be well developed in some invertebrates (Chapter 8.1) and fishes (Chapter 8.2), little definite information is at hand in regard to marine mammals.

It would be surprising, however, if gustation and olfaction did not participate in orientational behaviour of sea otter and pinnipeds. Circumstantial evidence suggests that both senses assist in securing food, facilitating reproduction (female–male, mother–pup relations), avoiding enemies and, possibly, in detecting gradients of organic substances, both in water and in air, thus providing additional cues for medium or long-range orientation. Captive cetaceans are very selective about food. They reject spoiled food and will eat only representatives of certain species if fed in air (NORRIS, personal communication). This gives the impression of the presence of a taste sense.

The sea otter *Enhydra lutris* is assumed to possess an exceptionally keen sense of smell (KENYON, 1959); but exact data are not available. Crucial experiments are also lacking in pinnipeds. While SCHEFFER (1958) has assumed that most pinnipeds have a poor sense of smell, it has been claimed by trainers that sea lions are able to sense the presence of man by olfactory cues alone (EVANS and BASTIAN, 1969); sealers always approach seal herds down wind to avoid detection (SCAMMON, 1874); and HOWELL (1930) credits pinnipeds with a well-equipped olfactory mechanism. Both otariids and phocids display much nose-to-nose contact, inferring recognition by olfaction, especially between mother and pup (KING, 1964; PETERSON and BARTHOLOMEW, 1967). In Weddell seals *Leptonychotes weddelli*, final recognition between mother and pup appears to be by smell during nuzzling (KAUFMANN and co-authors, 1972), while medium-distance contacts are maintained by acoustic means. Smell during nose-to-nose contact seems also to be involved in the walrus *Odobenus rosmarus* (Fig. 8-127).

In sirenians, the sense of smell is assumed to be rudimentary, if not altogether absent (HARTMAN, 1969). During submersion, their nostrils are tightly closed by valves; they open only during the few seconds of surface breathing. Nose-to-nose contacts among manatees seem to involve tactile cues and gustation rather than olfaction.

In cetaceans, the potential importance of organic substances for gaining orientational cues has been considered mainly on the basis of anatomical structures. According to JANSEN and JANSEN (1969), there are no typical taste buds in cetaceans. But ARVY and PILLERI (1970) described vestigial taste buds, in the form of papillae, at the base of the tongue of the Ganges dolphin *Platanista gangetica* and other odontocetes. Anatomical evidence implies a sense of smell in mysticetes which is (at least) as well developed as that of man, but lack of a sense of smell in odontocetes (JANSEN and JANSEN, 1969). Since ambient-water circulation past the site of the olfactory organ is limited in air-breathing whales, JANSEN and JANSEN find the existence of a well-developed olfactory sense in mysticetes more surprising than the lack of it in odontocetes. Although present in some odontocete embryos (KELLOGG, 1938), neither olfactory nerves nor olfactory brain lobes are present after birth (TOMILIN, 1955).

However, the conclusion that odontocetes are completely anosmatic may be premature: YABLOKOV (1958) refers to 'olfactory pits' at the root of the odontocete tongue which could possibly perceive odorous substances and, conceivably, transmit the information obtained to the quite normally developed olfactory region of the cerebral cortex. In males of the sperm whale *Physter catodon* and the white whale *Delphinapterus leucas,* YABLOKOV calls attention to a preanal gland which opens directly into the water, and to the frequent urination of cetaceans, indicating possible orientation and communication functions. Similarly, LILLY (1961) has suggested the possibility of communication via olfaction–gustation by means of excreta in the bottle-nosed dolphin *Tursiops truncatus.*

> Mysticetes possess both olfactory conchae and olfactory lobes in the brain. 'When it is remembered that the Mysticeti are plankton feeders, and that plankton-rich sea water frequently has a distinctive odour, it is not difficult to imagine that these large animals may "sniff the winds" in search of their food' (PURVES, 1967, p. 263).

PURVES doubts, however, that there exists any intranarial directionality in the olfactory sense of mysticetes. He considers it possible that the tactile vibrissae on the surface of the head can act as long-range wind-direction perceptors and, underwater, as close-range environmental receptors. While a function of the odontocete tongue in gustation–olfaction cannot be ruled out entirely, its main functions are: (i) directing the prey caught in the mouth cavity; (ii) pushing it down the pharynx; (iii) preventing water from entering the digestive tract and expelling it from the mouth cavity (YABLOKOV, 1958).

In summary, gustatory–olfactory cues seem to be important for orientation in sea otter and pinnipeds and cannot be ruled out in cetaceans. Nothing pertinent is known in sirenians. Mechanisms of perception, thresholds, orientational interpretation and ecological significance remain to be investigated.

(9) Gravity

The importance of gravity for orientation has been reviewed in invertebrates (Chapter 8.1) and fishes (Chapter 8.2). Marine mammals employ mechanisms for gravity perception which are homologous and similar to those used by terrestrial animals. The importance of gravity perception for orientation of marine mammals has received no specific attention.

In cetaceans, the organs of equilibrium appear to be moderately developed. No exact data are available concerning proprioceptive sensitivity; but the elegance with which cetaceans perform leaves 'a definite impression of a refined proprioceptive apparatus' (JANSEN and JANSEN, 1969, p. 176). In view of the special role of motor control in an aquatic environment, proprioceptive mechanisms are of considerable interest for evaluating mechanisms of body orientation.

(10) Sound and Vibration

Orientation by sound and vibration tends to be of more general importance in oceans and coastal waters than in aerial environments. Beneath the sea, visual cues are less readily available, irradiance decreases rapidly with depth, visibility diminishes in turbid areas, and landmarks are often less pronounced or absent. In contrast, most terrestrial habitats feature conditions ideal for visual orientation except in special cases (e.g. night-active forms, cave or substrate dwellers, endoparasites).

Underwater sound fields depend significantly on physico-chemical and biological characteristics of a given water body and are affected by the boundary layers sea–atmosphere and sea–bottom. Consequently, underwater orientation by acoustic energy is a function of a variety of hydrographical, meteorological, biological and sedimentological properties. These, in turn, may vary in different sea areas, with prevailing weather conditions, and with season. While the major factors involved are known, their quantification remains difficult. Reflection, refraction, selective absorption and interference phenomena often result in complex acoustic conditions.

In terms of human technology, object finding, navigation and communication are more difficult underwater than in air: Radar (radio detection and ranging), based on electromagnetic waves, facilitates more efficient orientation than Sonar (sound navigation and ranging) based on underwater sound waves. Do comparable differences in the difficulties encountered exist in biological systems? Perhaps. But they have been mastered: to our knowledge, the acoustico-orientational performance of delphinids is quite similar to that of bats.

In sea water, the propagation velocity of sound is equal to the square root of elasticity divided by the density (Volume I: COLLIER, 1970): sound travels here about 4·5 times faster than in air (34·4 cm $msec^{-1}$). The high speed of underwater sound requires considerable abilities of temporal resolution on the part of the sound-perceiving mechanism.

(a) General Aspects

In marine mammals, acoustical cues have attracted more attention than in invertebrates (Chapter 8.1) or fishes (Chapter 8.2). The fact that many marine mammals employ acoustic energy for relating to spatial properties of their environment, and man's interest in technological aspects of underwater object location have produced an impressive body of literature and thus grossly unbalanced the information available on different environmental cues for spatial orientation. While acoustic energy is undoubtedly of considerable importance for marine-mammal orientation, the relative lengths of the sections in this chapter devoted to different environmental stimuli do not automatically mirror their respective ecological significance.

All marine mammals are capable of producing acoustic energy perceptible to con- and heterospecifics. About 20 marine mammal species have undergone or are currently undergoing detailed acoustical analyses (SCHUSTERMAN and co-authors, 1972). In most species, this acoustic energy is of importance for obtaining orientation cues including communication. Some bats, odontocete cetaceans and swiftlets have been shown to navigate by self-produced sounds (active biosonar, p. 794). The use of self-generated acoustic energy as orientation cue is presently the subject of intensive studies. In the last 10 years, more information has become available on the importance of sound and vibration for marine-mammal orientation than in the preceding 50. New concepts and hypotheses have often become outdated before they have been published.

Phylogenetically, improvements in acoustic orientation require first of all elaborations of the mechanisms involved in the generation and perception of sounds. These mechanisms, in turn, presumably developed in close context with behavioural arousal and increasing need for communication. Food search, courtship, mating, mother–calf relations, and competition—frequently involving considerable migrations (p. 829)—may have been the primary driving forces for the progressive use of acoustic energy in organism–environment and organism–organism relationships. Sounds are often employed simultaneously for spatial orientation and for communication. Both aspects assist the individual concerned to evaluate, and to relate to, components of its environment.

Acoustic activities of marine mammals underlie temporal variations (diurnal, annual, seasonal). In *Tursiops aduncus*, for example, SAAYMAN and co-authors (1973) report diurnal activity cycles—both in captivity and at sea—of sound emission and frequency of social interactions. Whistle emission rarely occurred at night and was still infrequent in the very early morning. Feeding and co-ordinated herd hunting attained maximum intensities in the early morning and in the late afternoon. Mating was first seen after the initial feeding peak; still apparent in the early afternoon, it declined near the secondary peak of feeding activities at 17·00 hours.

(b) Terminology

Sound is acoustic energy, manifesting itself as propagating rapid variations in the density of a medium (e.g. air, water, elastic solid). Underwater sounds cause

(i) pressure change, i.e. compression and rarefaction of water particles, (ii) displacement of water particles. While the amplitude of pressure decreases linearly with sound-source distance, the amplitude of displacement decreases to the second or third power. Hence, with increasing distance from the sound source, pressure amplitude decreases more slowly than that of displacement until a point of equal amplitude is attained. Distances within the equal-amplitude point have been referred to as 'near field', those beyond that point as 'far field' (VAN BERGEIJK, 1964, 1967). Near-field sounds comprise a propagated pressure wave plus displacement; far-field sounds, only a propagated pressure wave. A pressure wave is a scalar quantity with magnitude only, but a displacement wave is a vector quantity with magnitude and direction. Since a far-field pressure wave comprises no directional components, it cannot provide locational cues.

The science dealing with sounds is known as **acoustics**. Physically, acoustic phenomena can be characterized by velocity, frequency, intensity and impedance. The **velocity** depends primarily on the density of the medium. At 20° C the speed of sound is about 344 m sec^{-1} in air and about 1500 m sec^{-1} in fresh water. In pure water (20° C, atmospheric pressure) sound speed is 1482 m sec^{-1} (DEL GROSSO and MADER, 1972b). In sea water of 35‰ S (20° C, atmospheric pressure) the speed of sound is 1521 m sec^{-1} (DEL GROSSO and MADER, 1972a). These values were obtained in quiescent media. However, sound propagation may vary in fast-moving water (WENZEL, 1971). Sound **frequency** designates the rapidity of recurrence of repetitive sound-wave pattern and is expressed in Hertz* (Hz). A sound with a sinusoidal wave is called a pure tone. The **intensity** of acoustic radiation characterizes the loudness of a sound (at a defined distance from the sound source), usually relative to a standard density (corresponding to an average excess pressure of 1 dyne cm^{-2} in air, which is close to the normal level of conversational speech), and is expressed in decibels (dB). The minimum sound intensity audible to the human ear lies about 70 dB below this level, the maximum intensity (at which hearing becomes painful) about 50 dB above it; both figures are approximations and depend on frequency. The **impedance** is the ratio acoustic pressure: acoustic volume current (in analogy with electric current).

Vibration comprises rapid rhythmic motions. In the present context, we consider propagating acoustic energy waves which are primarily heard (perceived mainly by the ear) as sound, those primarily felt (perceived by the sense of touch) as vibration.

Sound waves are subject to **reflection** (echo phenomena), **refraction** (directional bending of sound paths by discontinuities in medium density), **diffraction** (bending of sound paths around solid obstacles), and **scattering** (multidirectional diffraction by numerous small objects). Sound reflection and refraction are of basic importance for orientation by sound, including object discrimination (direction, distance, properties). Orientation by sound is complicated in a moving medium, especially in fast-moving air (heavy winds).

Acoustic orientation characterizes the ability of an organism to place itself, by means of (air-borne, water-borne or solid-borne) acoustic energy, into a specific relation to its environment The term **bio-acoustics** designates the whole field of

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* After Heinrich Rudolph HERTZ (1857–1894), German professor of physics. 1 Hertz = 1 cycle sec^{-1}.

sound generation, perception and interpretation by organisms. **Biosonar** involves the use of sounds to obtain information on the environment including conspecifics. **Passive biosonar** (orientational hearing) comprises perception and interpretation of ambient sounds for object localization and recognition; the acoustic cues may be sounds generated by the object itself or environmental noises reflected by it. **Active biosonar** is based on the reflection of specific self-generated acoustic energy by foreign objects; the echo received informs the sound producer about presence, direction, distance, size, shape and other characteristics of an object. **Echolocation** or **echoranging** are synonymous terms, referring to the ability of an organism to generate, perceive and interpret own acoustic signals, thereby obtaining information on object direction and distance. The terms echolocation and echoranging are similar in connotation to active biosonar, but relate primarily to direction and distance, while active biosonar includes navigation and information on object properties. Since the information obtained during acoustic orientation often, if not usually, contains also details on physical target characteristics, the terms echolocation and echoranging are somewhat misleading.

Sounds produced by marine mammals are coherent patterns of acoustic energy. **Hearing** or **phonoreception** refers to the reception of acoustic energy by an organism.

(c) Mechanisms of Sound Generation

Life beneath the sea has modified the basic mammal plan. In the holo-aquatic mammals, mechanisms of sound generation tend to differ significantly from those employed by terrestrial relatives. Sound exchange between body and sea, and sound transmission inside the body are significantly affected by discontinuities in the media encountered. Sounds leaving or entering the body pass through a variety of density interfaces which may modify their direction and properties. Within the body, interphases exist, for example, between different adjacent tissues (muscle, fat, bone), between air spaces and tissues, or between fluids (e.g. oil) and tissues. Interphases between body and sea occur between blubber and skin, and between skin and sea water. Since these interphases involve gradients in medium density, they affect sound velocity. Depending on their quality, shape and location, medium interphases may reflect, refract, diffract, scatter or focus sounds.

The mechanisms employed by marine mammals for generating sounds have attracted considerable attention. In the last two decades, numerous papers have been published, especially on pinnipeds and odontocetes. However, the situation is more complex than expected; unequivocal results are rare and a solid fundament begins to emerge only hesitatingly. Despite numerous discussions, experiments, morphological descriptions and considerations of functional anatomy, uncertainty prevails and many details have remained in the dark. Exact site, muscular or mechanical processes, air dynamics and acoustic properties of the anatomical structures involved are insufficiently known in most of the species.

There is no lack of speculation. In fact, there are about as many assumptions, hypotheses or theories on how marine mammals—especially odontocetes—generate sounds as there are investigators concerned with the problem. Of course, the difficulties are formidable. Most of the mechanisms seem to be quite complex and the methods to study them are largely based on indirect evidence. In recent years, however, careful studies on functional anatomy (for reviews consult HARRISON, 1972 and EVANS and MADERSON, 1973), analytical acoustic measurements near presumptive sound-production sites, and X-ray cinematography have begun to add up to a conceptual framework.

Pinnipedia

Pinnipeds generate sounds in air and underwater. Their vocal cords are well developed (ODEND'HAL, 1966). Vocal-cord section (surgical excision of the medial two-thirds of the cords) in a sea lion resulted in devocalization of one or two specimens operated (EISEMAN and co-authors, 1965). In general, polygamous (harem-forming or polygynous) pinnipeds are more vocal than monogamous species. This fact underlines the importance of acoustic cues for maintaining and controlling structured social aggregations.

The sounds produced by pinnipeds may be grossly divided into clicks and burst pulses, e.g. barks, growls, buzzing, bangs, cracks (p. 758). Since these different

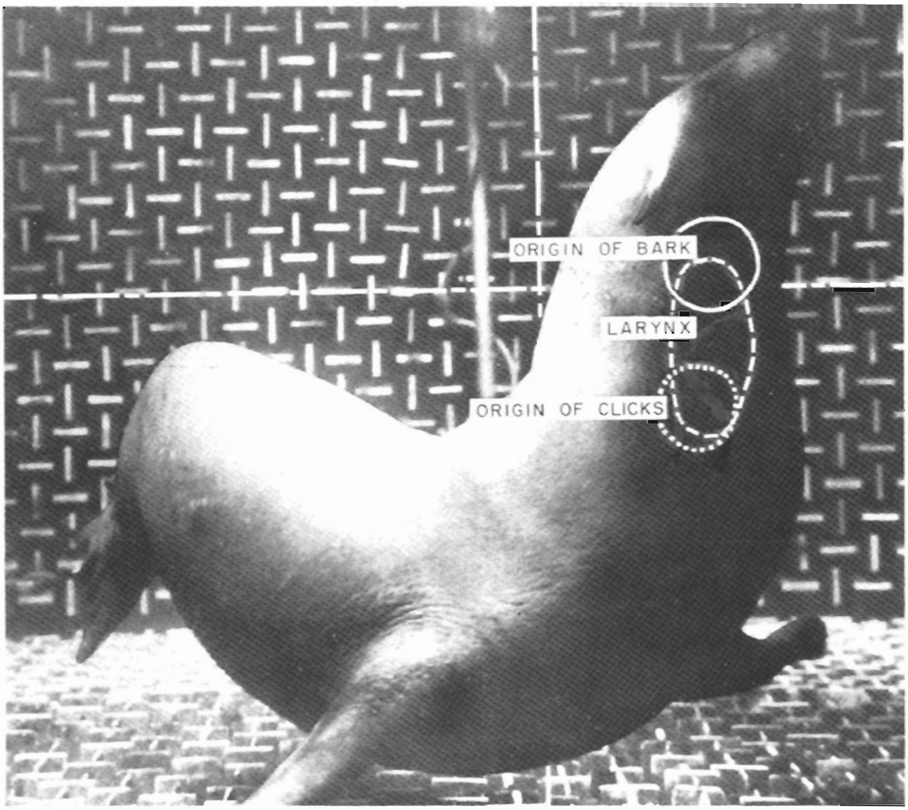

Fig. 8-68: *Zalophus californianus*. Areas of bark and click origin. Right-angle photograph. Straight lines mark horizontal and vertical centres of the experimental tank. The tank is lined with sound absorbing structures. (Reproduced by permission of Dr. T. C. POULTER.)

types of signals can be emitted simultaneously, at least two different mechanisms of sound generation seem to exist. For the California sea lion *Zalophus californianus*, POULTER (1965) suggested that clicks are produced posterior to the larynx, and barks in the region of the anterior larynx (Fig. 8-68). He employed a triangulation system: 2 photographs of the sea lion were taken simultaneously from 2 right-angle positions and at the same time sound signals were recorded from 4 hydrophones. Both clicks and barks can be produced with mouth and nostrils closed and hence without air-bubble emission, or with mouth and nostrils partially opened and with bubble release. ODEND'HAL (1966) implied that the clicks may originate from the dorsomedial pouch of the larynx. This proposal is consistent with an increase in the frequency of click harmonics by about one octave, observed in *Z. californianus* forced to breathe a mixture of 80% helium and 20% oxygen for a short time (BRAUER and co-authors, 1966).

Sirenia

Nothing definite is known on mechanisms of sound generation in sirenians. The Caribbean manatee *Trichechus manatus latirostris*—originally known from coasts and coastal rivers (Beaufort to Florida Keys, USA; Gulf of Mexico) and now extinct in many parts of its former distributional area (RICE and SCHEFFER, 1968)—produces sounds underwater (SCHEVILL and WATKINS, 1965a; see also p. 761).

Mysticeti

Mysticetes emit mostly narrow-band, low-frequency calls (p. 762). Their sound-generation mechanisms have not yet been studied critically. But there are obvious differences in the structure of nasal area and larynx in mysticetes and odontocetes. Presumably, these differences parallel the different properties of sounds produced by these two groups of whales. The larynx is well developed and may constitute the major vocalization organ.

Odontoceti

In contrast to pinnipeds, odontocetes have no or very reduced vocal cords. The main site of sound generation is the anterior part of the head; the mechanisms suggested comprise muscle or air-driven vibrators, mechanical friction and air-filled resonators. Two regions qualify as primary sites of sound production: the laryngeal area (arytenoepiglottic tube) and the nasal area, i.e. the region near the blowhole (nasal plugs, nasal sacs, pneumatic chambers). Internal sound often seems to be emitted into the ambient water via specific routes, e.g. tissues rich in sound-conducting components (such as special lipids; p. 752) and fat or liquid (oil) filled channels or compartments. In some cases, passage of acoustic energy through such transmission areas facilitates sound focusing.

The methods employed for investigating mechanisms of sound generation in odontocetes include (i) extrapolation of presumptive functions from anatomy; (ii) artificial production of sounds in dead individuals, severed heads or excised body parts, e.g. by forced air; (iii) analytical acoustic measurements (e.g. via hydrophones held on defined body parts) during phonation; (iv) X-ray cinematography recording the activity of internal structures—assumed to be involved in sound production—during phonation. Too much speculation has been based on descriptive anatomy. Several investigators have produced sounds by forcing air through isolated body parts (e.g. larynx). Certainly, this makes sounds, but what does it prove? Even if the resulting sounds resemble those emitted by living, intact dolphins, they should be viewed with critical reservation. Most promising and reliable seem experiments on normally phonating individuals, involving a combination of acoustic measurements, behavioural analysis and X-ray cinematography—if necessary also surgery. Recent reviews on sound-producing mechanisms in odontocetes have been written by NORRIS (1969), BELKOVICH and NESTERENKO (1972), and EVANS (1973).

NORRIS (1969) lists 7 sites or methods of sound generation in odontocetes: (i) larynx (PURVES, 1966); (ii) lips of the arytenoid extension of the larynx; (iii) diagonal membrane; (iv) lateral lips of the nasal plugs (EVANS and PRESCOTT, 1962); (v) lip of the blowhole (NORRIS and PRESCOTT, 1961); (vi) movement of the jaws (TAVOLGA, 1966); (vii) slaps of the body, flippers or flukes against the water. Except for the last three cases, most sounds produced by odontocetes appear to be generated via tissue vibrations due to muscle-controlled air movements and/or mechanical friction. Since many underwater sounds are emitted without air release and since several species perform long and deep dives, most air movements must involve internal air recycling.

The larynx of odontocetes is located in the lower throat region and is separated by tissue layers from the ambient water. In most odontocetes, the larynx is complexly folded and well muscled but contains no vocal cords (LAWRENCE and SCHEVILL, 1965). In delphinids, the larynx has greatly elongated anterior cartilages crossing the esophagus and entering the palate through a muscular sphincter just ventral to the bony nares. Air and food passages are thus effectively separated. This allows simultaneous underwater feeding and sound emission (e.g. NORRIS, 1969).

In *Pontoporia blainvillei*, which do not possess accessory air sacs, SCHENKKAN (1972) assumes that the three slits present at the apex of the larynx are of great importance for sound generation. Larynx width can be controlled by muscles, and the whole larynx, according to PURVES (1967), is suitable for producing high-pitched sounds requiring only very small amounts of air which can be stored easily, e.g. in premaxillary or, in *Phocoena phocoena*, in caudal nasofrontal sacs. In both cases, sound generation would not interfere with the tight sealing of the blowhole.

Based on comparative anatomical and functional evidence regarding the upper respiratory tract, SCHENKKAN (1973) arranged odontocete species in a series of phylogenetic stages. A gradual diminution in relative size of the more superficial air chambers was found and an increase in the relative volume of the deeper premaxillary diverticula. SCHENKKAN concluded that the size of sound generation seems to be located in the lower posterior narial tract, and that the sound is transmitted by the bones forming the rostrum. The most favourable internal sound paths were examined by radiography. Active-biosonar pulses are assumed to be produced by the larynx, which does not vary greatly in structure throughout the suborder.

In *Platanista indi*, active-biosonar pulses are apparently generated by epiglottic spout and larynx (PURVES and PILLERI, 1973). Nasal plugs are retained in position by cartilage; their shape precludes sound generation. During phonation, *P. indi* prevents loss of air by inflating a pair of nasofrontal sacs. As in other odontocetes, the reservoir for phonatory air is provided by the premaxillary sacs.

PURVES (1967) experimented with living and dead *Phocoena phocoena*, *Lagenorhynchus cruciger* and *Tursiops truncatus*. Locating a sound source (Galton whistle) in the larynx of individuals which had recently died and measuring sound intensity at various points on the head's surface, the highest acoustic energy was found to distribute along the central axis of the skull, notably along the vomer and particularly at the tip of the snout. The similarity of these findings with comparable measurements obtained on living sound-emitting dolphins led PURVES to conclude that the sound source is probably laryngeal. Studies on larynx, palatopharyngeous muscles, basicranial air sinuses and skull bones indicated to PURVES that the larynx acts as a triple sound source which produces (through interference phenomena) highly directional near-field sound beams. Examination of the upper narial region suggests that the accessory pneumatic chambers are necessary for air recirculation and occlusion of the blowhole during phonation, but are not directly involved in echolocation.

LAWRENCE and SCHEVILL (1956, 1965) investigated the functional anatomy of the nose and gular musculature of delphinids. Based on this study, EVANS and PRESCOTT (1962) examined phonations of living, intact *Tursiops truncatus* and *Stenella graffmani*, and simulated natural sounds by forcing air at controlled pressures and flow rates through the excised larynx and severed head. The sounds obtained show an asymmetrical sound-radiation pattern with the stronger signal output on the right, corresponding to the asymmetry of the cranial structures (LAWRENCE and SCHEVILL, 1956; see also HOSOKAWA, 1950). Air forced through an excised larynx, depending on air pressure and larynx position, generates sounds rich in harmonics, ranging from whistles to barks. Air forced through the nasal-sac system produces short-duration pulse-type clicks, similar to those employed during echolocation. Accordingly, EVANS and PRESCOTT postulated a dual sound source involving the larynx (arytenoepiglottic tube) for the production of whistles and barks, and the nasal plugs and associated sacs for click generation.

ROMANENKO and co-authors (1965) investigated mechanisms of sound generation in *Delphinus delphis* using the head of a recently killed individual. They stress the role of its soft tissues and of the cranium in sound generation and in directional sound emission. The soft tissues are assumed to assist in narrowing the sonagram obtained at high frequencies; the cranium is postulated to be of principal importance for directing the sound beam emitted. The air sacs of *D. delphis* do not immediately participate in respiration; neither during air intake nor during respiratory pauses do the air sacs fill with air, except for a partial filling of the tubular sacs (GUREVICH and KOROLKOV, 1973).

The anatomy of the external passages and facial complex of delphinids has been reviewed by MEAD (1972; see also LAWRENCE and SCHEVILL, 1956; EVANS and PRESCOTT, 1962; SCHENKKAN, 1971, 1972). Summarizing the information available, MEAD concludes that the most likely structures engaged in sound generation are those in the vicinity of the nasal plugs. Considering the anatomy of the nasal-sac system, Evans and Maderson (1973) find this statement supported by anatomical specializations as well as by recent experimental studies (e.g. Evans and Prescott, 1962; Diercks and co-authors, 1971; Evans, 1973).

In excised larynges and severed heads of *Tursiops truncatus* and *Stenella graffmani*, Evans and Prescott (1962) found active-biosonar clicks to be generated in the nasal-sac system. This system defies detailed verbal description (Evans and Maderson, in press). It comprises an interconnecting pneumatic tract with several cul-de-sacs, valves and lips. Tubular sacs combined with nasal-plug nodes appear to be the site of sound generation. Only tubular and connecting sacs allow continuous air passage; vestibular and premaxillary sacs are 'blind alleys'. Since blubber and fatty tissue are acoustically transparent (Reysenbach de Haan, 1957) due to impedance match for water, the spatial arrangement of nasal sacs, pneumatic valves and melon causes little energy loss of air-produced sound when transmitted into the ambient water. When Evans and Prescott (1962) forced air into a severed head, the blowhole became closed and the pressure was allowed to build up to 2 psi (pounds per square inch); the air sacs (especially the vestibular ones) became inflated—a prerequisite for click production. Clicks were achieved with an air pressure of 1·5 psi in *T. truncatus* and 1 psi in *S. graffmani* and at an air-flow rate of 10 l min^{-1} for both. The sacs can be collapsed by applying pressure, e.g. by a hand pressed across the forehead. Deflation of the upper or distal nasal tract stops the active-biosonar clicks.

Diercks and co-authors (1971) measured acoustic energy produced by *Tursiops truncatus*, *Inia geoffrensis* and *Orcinus orca*, using small hydrophones held on forehead and jaw tip of a discriminating individual. They report sound-emission sites on forehead and snout tip, with the most intensive sounds emanating from the snout tip. Similar results have been obtained by Norris and Harvey (*in*: Norris and co-authors, 1971) who pressed a microphone pair against the heads of a *T. truncatus* and a *Globicephala scammoni*. However, while Diercks and co-authors assume the nasal plugs to be the sound source, Norris and Harvey do not reject the possibility that the sounds were produced deeper in the respiratory system (e.g. in the laryngeal apparatus) and then transmitted to a beaming site in the region of the nasal plugs.

Investigations by Norris and co-authors (1971) on an adult male spinner dolphin *Stenella longirostris*, employing cineradiography (X-ray cinematography) provide direct evidence of sound generation by nasal plugs. While clicks were not emitted during the tests, their concurrent production with squeals (whistles) in other recordings and the presence of a larger lip on the right than on the left plug suggested to Norris and co-authors that clicks might be produced by the right plug, using the same air-pressure system employed to generate the squeals or chirps. Norris and co-authors saw that the upper sacs receive the air that passes the nasal plugs during phonation and that they play a part in moving the air back to the nasopharynx. The epiglottic spout seems to function as a stop-check valve, preventing air loss into larynx, trachea and lungs during air recycling. In this way, phonation due to air recycling can continue during deep dives, when little air is available, using air bled into nasopharynx, nares and sacs from the probably collapsed trachea and lungs. This mechanism is similar to that postulated by Norris (1964) except that air from below rather than from above actuates chirp generation.

Sound generation without complete dependence on air flow would be advantageous both in terms of energy efficiency and in independence of water-depth differences. EVANS (1973) assumes that the paired, muscular nasal plugs can be moved mechanically or pneumatically against the hard edge of the external bony nares (see also EVANS and MADERSON, 1973). In this way, 'relaxation oscillations' are set up by alternate resistance and plug release. Such a mechanism is comparable to chalk scratching across a blackboard. The acoustic energy thus produced would radiate into the ambient water via the melon, and along the premaxillary bones via the rostrum tip (Fig. 8-69). Since several odontocetes do not possess accessory air sacs (e.g. *Inia geoffrensis*, *Pontoporia blainvillei*, *Physeter catodon* and the species of *Phocoena* and *Kogia*), SCHENKKAN (1972)—who studied the nasal tract of *P. blainvillei*—has questioned the general importance of accessory air sacs in sound generation.

In delphinids, sounds emitted from the forehead are characterized by enforced directionality and are often emitted in form of high-frequency sound beams suitable for selective 'palpation' of the environment ahead. EVANS and co-authors (1964), for example, measured the directionality of sounds emitted from a miniature

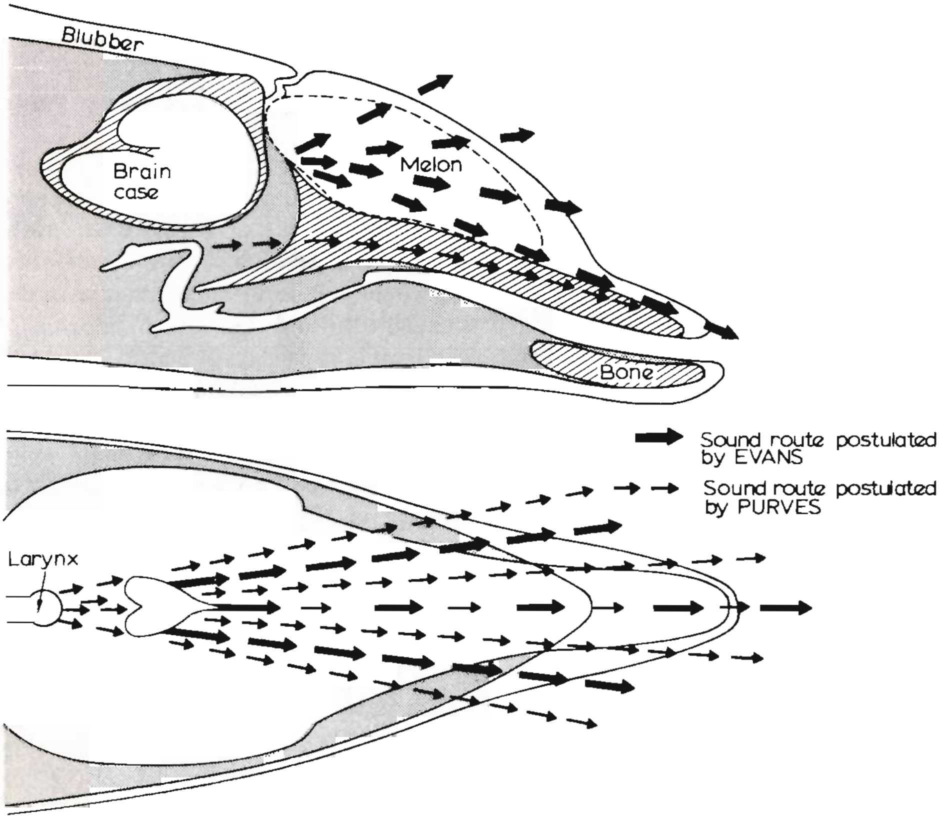

Fig. 8-69: *Tursiops truncatus*. Sites of sound generation and routes of sound transmission suggested by PURVES (1967) and EVANS (1973). (After EVANS, 1973; modified; reproduced by permission of Acoustical Society of America.)

projector, implanted at different locations in the head of a dead subadult *Stenella longirostris* or attached to the skull of an adult *Tursiops truncatus*. Placement of the dead dolphin in the desired angular positions relative to the receiving microphone was accomplished by attaching the specimen to a rotatable float suspended in a lagoon. The data obtained indicate that sounds generated above the skull in the area of the nasal sacs are reflected outward and upward in a beam. The upward angle of maximum sound radiation is 15° above the rostrum; in the horizontal plane, the angle is 30° to 40° right or left of the rostrum. When the sound source is located below the level of the premaxillae—in the area of the larynx—the point of maximum sound radiation is 90° below the level of the rostrum, directly under the dolphin; little acoustic energy is projected out in front of the rostrum. In all experiments, beam width proved to be strongly dependent upon the frequency of the signal, becoming increasingly narrower with increasing frequency.

What are the mechanisms responsible for such directionality of emitted sounds? There are two main possibilities: (i) Reflection by head bones and associated structures; (ii) focusing by the melon or comparable 'acoustic lenses'.

Reflection by a specifically adapted skull has been claimed by EVANS and PRESCOTT (1962). These two authors have considered that the premaxillae, maxillae and frontal bones act as an asymmetrical, somewhat parabolically shaped, sound reflector which aids some delphinids in the focusing of active-biosonar signals (p. 764). ROMANENKO and co-authors (1965) and BELKOVICH and NESTERENKO (1971, 1972) have rejected this consideration, pointing to the fact that delphinid head bones permit considerable sound penetration (even the very dense elephant tusks reflect not more than 35% of the acoustic energy received). However, the point is that the head bones shape the form of overlying air sacs which are excellent sound reflectors. More serious criticism results from the fact that (i) head bones are quite differently shaped in different delphinids possessing active biosonar, and (ii) head bones change size and shape during ontogeny. Since parabolic reflectors must be accurately designed in order to allow efficient sound focusing, significant changes will interfere with their presumptive function as directional sound reflectors. In young delphinids, maxillary bones are often almost flat structures lying more or less horizontally at nearly right angles to the nasal canal (SCHENKKAN, 1972).

The cavity of the middle ear of *Platanista indi* is continuous with a complicated system of air sinuses which extend over the forehead in large crests (Fig. 8-70). Experiments indicated to PURVES and PILLERI (1973) that the crests impart directional properties to active-biosonar pulses. There is evidence that sounds are prevented from passing directly to the middle ear by (i) isolation of the tympanic cavity from the air sinus system by the corpus cavernosum pterygoideus; (ii) peribullary air sinuses; (iii) envelopment of epiglottic spout by nasopharyngeal air sacs.

The melon, a fat body in the forehead of delphinids, has long been suspected to function as an acoustic lens (WOOD, 1957, personal communication *in*: SCHEVILL, 1964, p. 309). In recent years, evidence has accumulated which testifies to the melon's sound focusing capacities—even though measurements by contact transducers accommodated on both, melon and rostrum (EVANS, 1973), indicate that active-biosonar pulses are projected with equal efficiency from both areas (Fig. 8-71). Echoranging *Tursiops truncatus* scan with their head, apparently

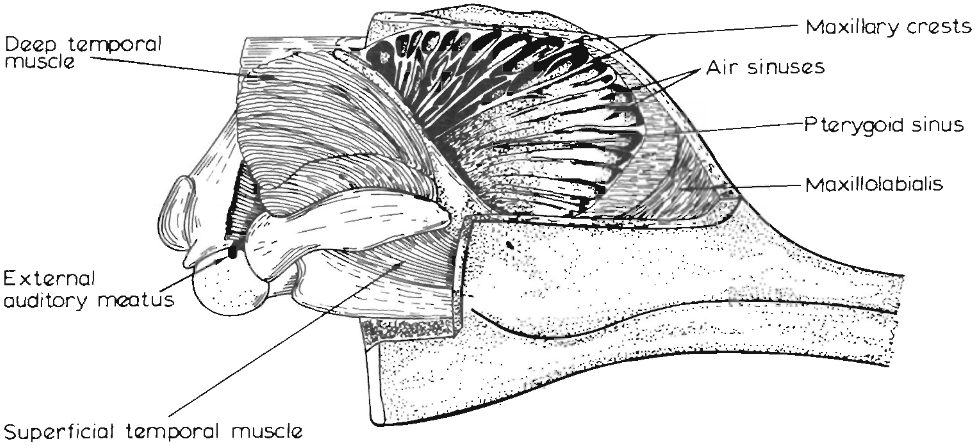

Fig. 8-70: *Platanista indi*. Right aspect of head dissection after removal of external osseous wall, showing maxillary crests and air sinuses. (After PURVES and PILLERI, 1973; modified; reproduced by permission of Professor G. Pilleri.)

pointing their melon in the direction of search; a blindfolded *T. truncatus* was unable to locate drifting targets moved below the level of its melon (NORRIS and co-authors, 1961).

The functional principle of an acoustic lens is based on differential sound velocities due to density gradients. According to BELKOVICH and NESTERENKO (1971, 1972), the acoustic lens of delphinids consists of fat tissue surrounded by supporting collagen fibres. The lens nucleus has an ellipsoid shape with the major axis pointing down (angle to main body axis: 60°). It reveals precise limits, but outwardly its histological structure gradually approaches that of the embedding tissue: the number of fat cells decreases while the abundance of connective tissue increases. Dorsally and ventrally, the lens complex is separated from the upper jaw bone by a layer of connective and muscle tissues. Slower propagation of acoustic energy in fat than in sea water and reduced sound reflection from the lens border due to gradual histological changes support the assumed functioning of the delphinid melon as transparent, inhomogenous, acoustic retardation lens. In addition to the melon, all muscles and bones of the rostral area seem to co-operate in acoustic beam formation.

Physico-chemical changes in the ambient sea water require lens adjustments. According to BELKOVICH and NESTERENKO (1971, 1972), appropriate gauging could be achieved by the muscle layers dorsal and ventral to the lens complex. They suggest that the differences in rostrum shape and anatomy among odontocetes may be related to habitat-water characteristics: species regularly exposed to pronounced fluctuations in temperature, salinity and hydrostatic pressure are claimed to possess an enlarged rostrum area. The validity of this correlation is questionable; it requires critical examination. Active changes in lens shape are assumed to facilitate specific focusing of active-biosonar and specific communication signals. Alternative use of different sound sources and acoustic-lens focusing are postulated to allow the generation of sound beams of different direction and frequency content.

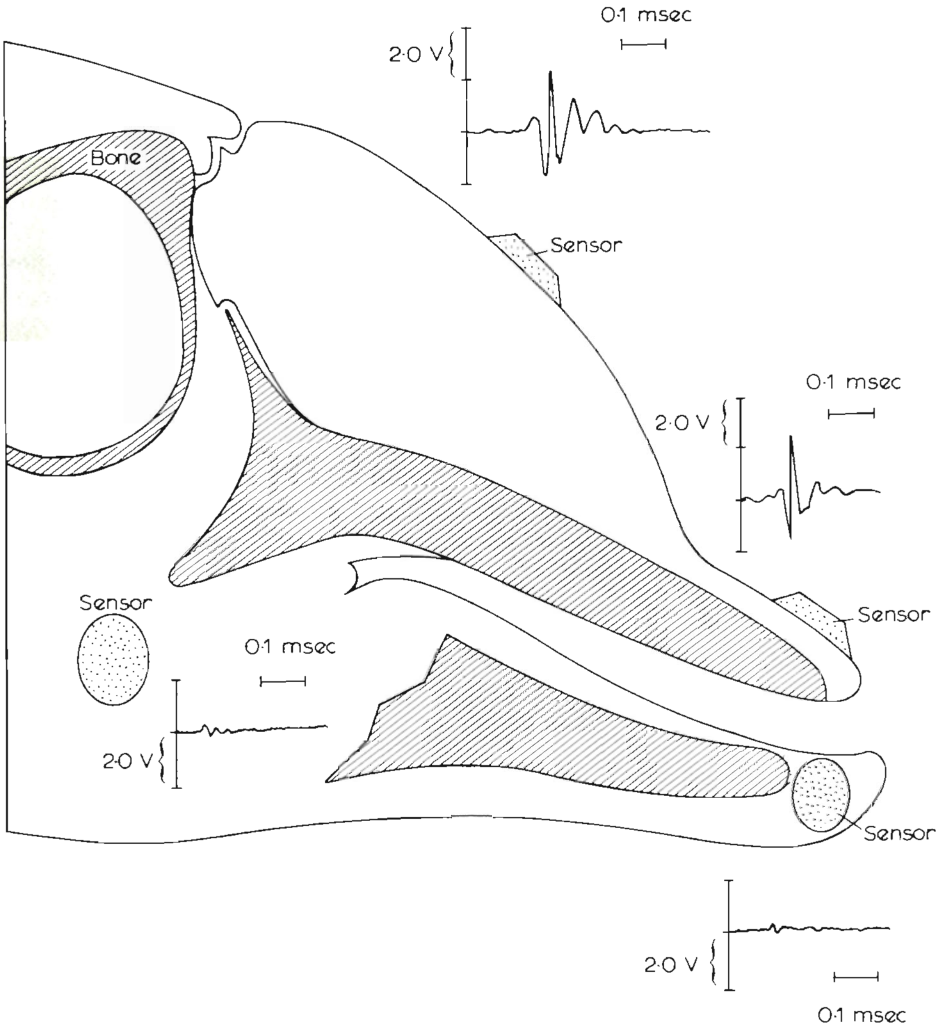

Fig. 8-71: *Tursiops truncatus*. Active-biosonar clicks recorded via attached sensors *in* a free-swimming, blindfolded, discriminating individual. Clicks are projected with equal efficiency from melon and rostrum. (After Evans, 1973; modified; reproduced by permission of Acoustical Society of America.)

In physical acoustics, liquid-filled, single-element ultrasonic lenses exhibit considerable beam-forming capacities (e.g. Folds, 1973; see also Jones, 1973; Mason, 1973; Tanaka and Koshikawa, 1973); they are limited though by spherical aberration to approximately 0·5°, and focal length is dependent upon temperature. Using established optical design methods and solid materials (common plastics), Folds succeeded in fabricating ultrasonic acoustic lenses with good performance characteristics and little sensitivity to temperature changes. Why should not the otherwise so sophisticated sound-navigation mechanisms of odontocetes be able to meet similar requirements?

Sound velocity measurements (NORRIS and HARVEY, in press) on a freshly dead adult *Tursiops truncatus* provide additional evidence that the melon is capable of (i) forming sounds produced behind it into a forwardly projected beam; (ii) matching these sounds reasonably well in terms of propagation velocity to sea water at the dolphin's body surface. Melon dissection reveals that the oily fat of the central melon corresponds to the area of low transmission velocity, and that the denser blubber surrounding it, which is heavily invaded by connective tissue fibres, facilitates high sound velocities. The low-velocity core surrounded by a high-velocity shell refracts sounds inwardly. NORRIS and HARVEY suggest that the sound beam focused by the low velocity core gradually increases in speed until it reaches the dolphin's body surface where it is less reflected by the transition from body to water than in the presence of a greater discontinuity in propagation velocity. These results and suggestions, and the observation by RAY (*in*: NORRIS and HARVEY, in press) that the shape of the *Delphinapterus leucas* melon can be significantly changed during phonation support the concepts presented by BELKOVICH and NESTERENKO (1971, 1972).

There is growing evidence that sound focusing is associated with the distribution of certain unique lipids in delphinid head tissues (VARANASI and MALINS, 1970a, b, 1971, 1972; MALINS and VARANASI, in press). Saturated branched lipids are deposited primarily in tissues related to active-biosonar functions. LITCHFIELD and co-authors (1973) reported significant variations in lipid composition of the melon tissue in *Tursiops truncatus*. Topographical analyses indicate 4 distinctive regions: a central 'inner melon' core surrounded by 'outer melon', 'under melon' and blubber tissues. It is assumed that this compositional topography of melon lipids aids in collimation of the ultrasonic pulses emitted during echolocation (see also WEDMID and co-authors, 1971; BLOMBERG, 1972; LITCHFIELD and GREENBERG, 1973).

In *Stenella longirostris*, evidence has been obtained that the premaxillary sacs assist in focusing sound or in blocking sound transmission deeper into the head (NORRIS and co-authors, 1971). This assumption is supported by the slight inflation of the sacs throughout phonation.

In the family Physeteridae, with the two genera *Kogia* and *Physeter*, the nasal anatomy differs from that of other odontocetes. The blowhole area of *Kogia breviceps* has been studied by BENHAM (1901), DANOIS (1910) and especially by KERNAN and VON SCHULTE (1918). The nasal anatomy of *Physeter catodon* has received attention by POUCHET and BEAUREGARD (1885), BEDDARD (1915, 1919), and especially by RAVEN and GREGORY (1933). CLARKE (1970), NORRIS and HARVEY (1972) and SCHENKKAN and PURVES (1973) have considered aspects of functional anatomy and presented theories on the importance of the spermaceti organ. According to SCHENKKAN and PURVES, the nasal complexes of *K. breviceps* and of *P. catodon* are homologous with those of less specialized odontocetes. However, in its relationship to the other head structures, the spermaceti organ is not homologous with the melon of other odontocetes. The spermaceti organ (Figs 8-72, 8-73) is unique to the Physeteridae and forms a part of the functional morphology of the right naris; it is not a bilaterally symmetrical structure like the melon. In adult *P. catodon*, the right nasal passage seems to be involved in sound generation (NORRIS, 1969).

In *Physeter catodon*, the spermaceti organ occupies up to 40% (NISHIWAKI and co-authors, 1963) of the entire length of the whale (Figs 8-72, 8-73, 8-74). This huge organ is covered dorsally and laterally by a thick wall of intermeshing ligaments. It may contain as much as 1900 l of waxy oil: the spermaceti, once used for candles and illuminating oil. At each end and below the spermaceti lie air sacs, constituting part of a complex series of asymmetrical nasal passages, valves and associated

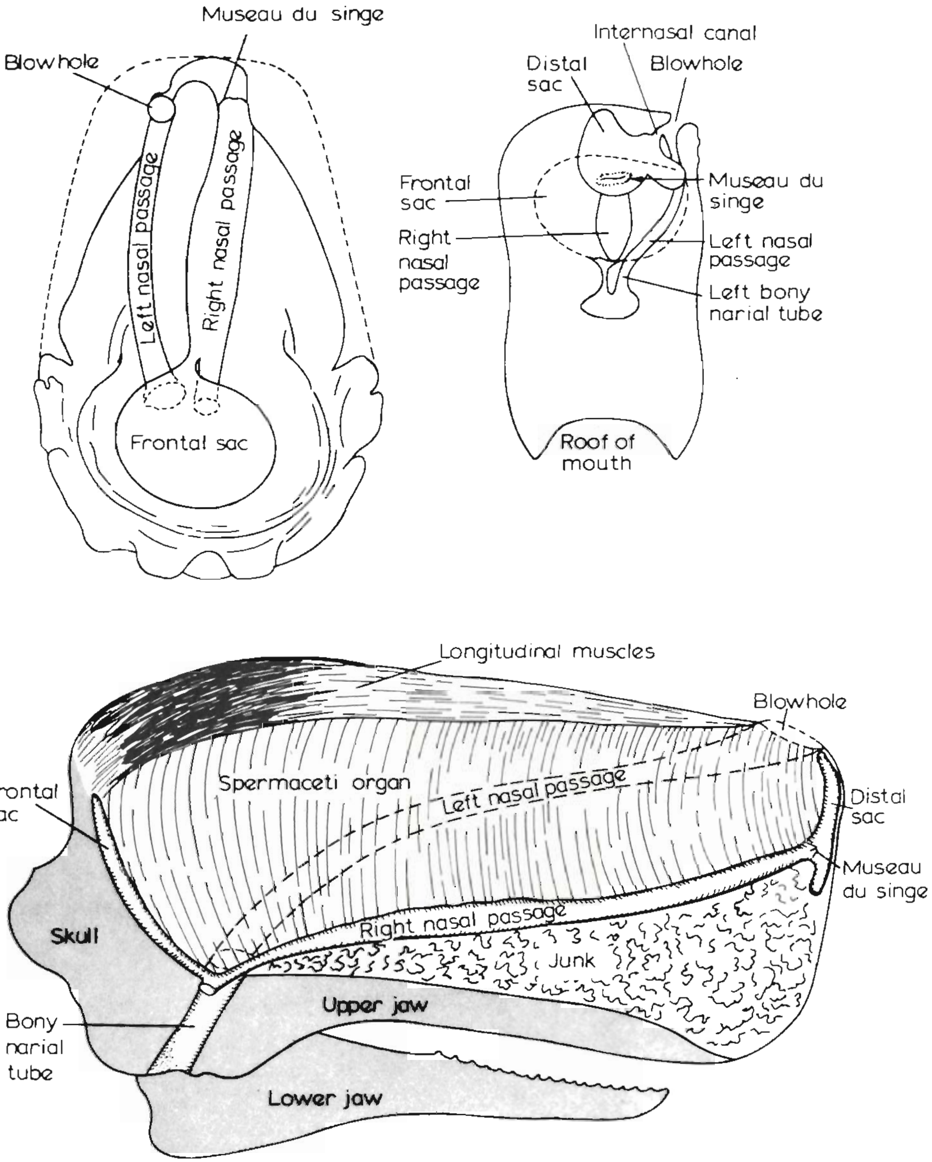

Fig. 8-72: *Physeter catodon*. Spermaceti organ and its structural relations to nasal passages and junk in a young male. (After RAVEN and GREGORY, 1933; redrawn; reproduced by permission of American Museum of Natural History.)

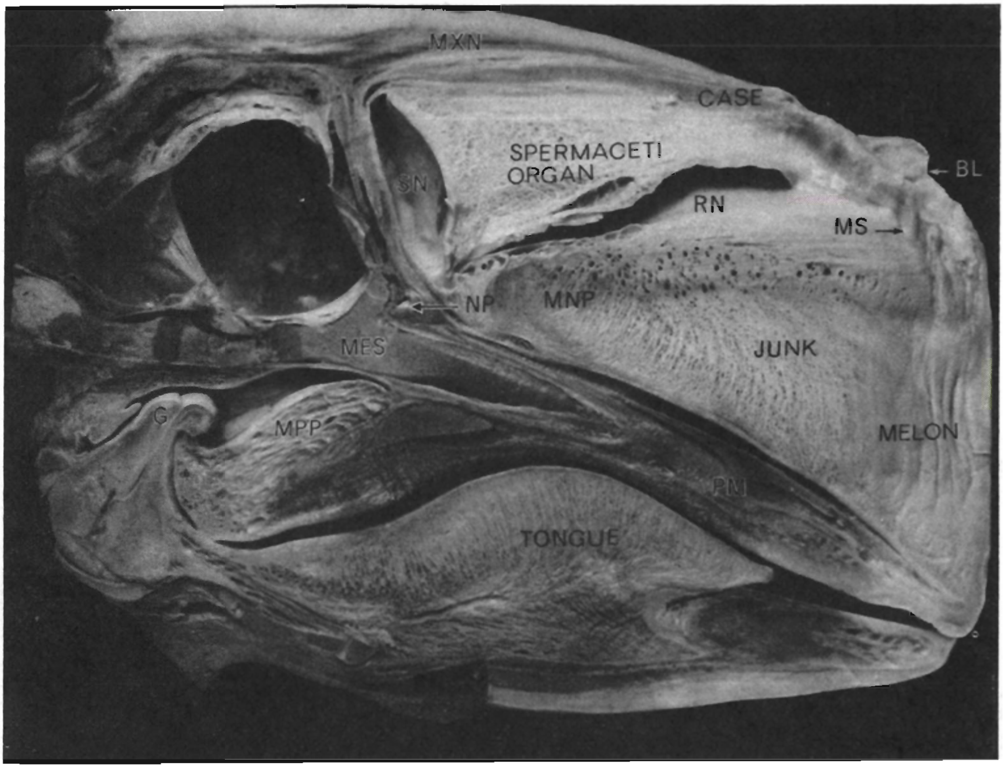

Fig. 8-73: *Physeter catodon*. Photograph of sagittal section through the head of a 150-cm foetus. BL: blowhole; G: glottis; MES: mesethmoid; MNP: nasal plug muscle; MPP: palatopharyngeal muscle; MS: 'museau du singe'; MXN: maxillonasalis muscle; NP: nasal plug; PM: premaxillary bone; RN: right naris; SN: nasofrontal sac. (After SCHENKKAN and PURVES, 1973; modified; reproduced by permission of Artis Library, Amsterdam.)

structures. Four theories have been presented regarding the possible function of the spermaceti organ: (i) According to RAVEN and GREGORY (1933), the spermaceti organ and its surrounding muscular sheath—besides assisting in the closure of the nasal passages after inhalation—may also (a) open the spiracular sacs; (b) admit small quantities of air under high pressure from the lungs to the distensible right

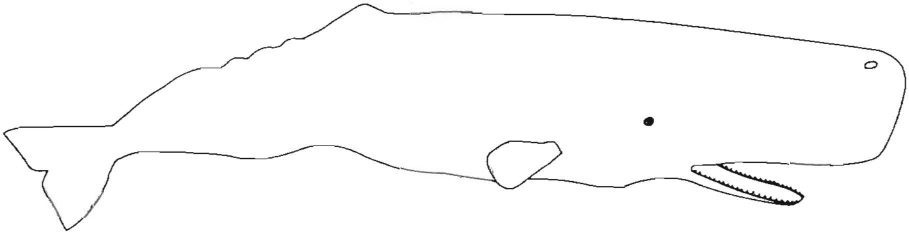

Fig. 8-74: *Physeter catodon*. Body shape of adult male. (Original.)

nasal passage and frontal sac; (c) shift the centre of gravity of the snout by suitable movements of air, oil and blood contained in the several reservoirs. The left nasal passage may be used primarily in quick exhalation and inhalation, while the right passage, with its expanded sacs and its small openings may be used in gradual pressure adjustments. (ii) Clarke (1970) suggests that the spermaceti organ assists in maintaining neutral buoyancy at different water depths. At great depths, neutral buoyancy is assumed to be achieved by cooling (local control of blood circulation; inhalation of cold sea water into right naris) the spermaceti oil, thus increasing its density in accordance with that of the ambient sea water. (iii) Norris and Harvey (1972) believe the spermaceti organ to be involved in the production of the unique burst-pulsed sounds of *P. catodon*. They suggest: (a) The spermaceti organ represents an acoustic resonating and sound-focusing chamber used to form burst-pulsed clicks. Presumably, the sounds are generated at the valvular lips of the anterior end of the spermaceti organ, the 'museau du singe', and the lips are actuated by air pressure within the right nasal passage. (b) The nasal passages of the forehead allow repeated recycling of air for phonation during dives and provide sound reflectors. (c) The entire mechanism produces sounds which are useful for long-range echolocation in the deep sea. (iv) Schenkkan and Purves (1973) propose that (a) the spermaceti organ assists in evacuation of the lungs prior to a deep dive; (b) the fat depots of the spermaceti organ in *Physeter* species, and the spermaceti organ and adipose cushion in *Kogia breviceps* absorb nitrogen at extreme hydrostatic pressures. All four hypotheses contain highly speculative elements. A critical evaluation must wait until more solid ground can be provided.

Considering the possible mechanisms of sound generation in *Physeter catodon*, Norris and Harvey (1972) propose that air is recycled from the right naris through the right nasal passages and the 'museau du singe' into the left nasal passage under the blowhole and back down the left nasal passage into the left bony naris, and from there back again in a complete cycle. Furthermore, the suggestion has been made that peristaltic pumps may exist within the bony nares themselves. However, this is now doubted and considered unnecessary:

> 'We no longer feel that a peristaltic pump is involved in air recycling. It's simpler than that—pressure from below in the basicranial space caused by the forward movement of the larynx is released into the upper nasal tract. It flows the opposite way as the larynx is retracted and the nasal plugs open' (Norris, in a letter to the reviewer, 1973).

The two vertically oriented air sacs bounding the ends of the spermaceti organ may act as sound reflectors. The frontal sac possesses a knob-covered posterior wall—probably an adaptation which allows maintenance of the sound reflector in any body orientation and during deep dives.

Schenkkan and Purves (1973) recall that, in common with their terrestrial relatives, cetaceans have a well-developed larynx; they believe that most of the sounds are generated by this organ. Sonic beams are assumed to be formed via interference phenomena. The necessary, large air volume required for larynx-produced sounds (especially at high hydrostatic pressures) is obtained, according to Schenkkan and Purves, from the non-respiratory cavities in the nasal tract. The right naris is not used in external respiration but forms the air reservoir required for phonation at extreme depths. The evidence at hand is insufficient for a well-founded evaluation of the different views presented by NORRIS and HARVEY on the one hand and by SCHENKKAN and PURVES on the other.

(d) The Sounds Generated and Their Properties

General Aspects

Marine mammals generate sounds that can most easily be described—in terms of man's hearing abilities, and in analogy to sounds produced by other animals—as clicks, whistles, hisses, chirps, buzzings, screams, snappings, squeals, grunts, moans, bangs, barks, cracks, etc. Clicks emitted at high repetition rates have been compared to the noise produced by a creaking door or rusty gate. The variety of sounds produced is myriad, the sound structure often complex.

Analogous verbal descriptions of sounds produced by marine mammals are useful for preliminary classification. They are insufficient, however, for analysis. Man's hearing capacity is different from, and in several cases inferior to, that of marine mammals. We cannot perceive some of the acoustic energy produced, e.g. the uppermost high-frequency sounds of delphinids.

The sounds generated by marine mammals have been recorded at sea and under laboratory conditions. Since ship noises (propeller; engine; passage of hull through water) may significantly disturb *in situ* recordings, boats have been developed which operate at very low noise levels (e.g. SCHEVILL, 1968b). For methodological reasons, many sound analyses have been restricted to artificial environments: small containers, anechoic tanks, experimental pools or oceanaria. Such restrictions facilitate experimental design, recording under known—or at least reproducible—acoustic conditions, localization of sound-generating and sound-perceiving sites, etc. However, they also affect the results obtained and their potential ecological significance. Acoustic analyses on captive marine mammals may suffer from (i) inadequately reduced complexity of environment and social structures (certain abilities may not show up, others may degenerate or become modified); (ii) artificially enhanced playfulness, especially in the most vocal forms such as *Tursiops truncatus* (certain sounds may result simply from a play with vocalizations); (iii) tendency toward vocal mimicry (some individuals are devoted mimics and may increase their natural vocabulary by imitated sounds specific to their captive environment);* (iv) special problems created by the acoustics of small tanks (e.g. PARVULESCU, 1967).

Unless the exact position of the sound-emitting animal is known, accurate description of sound properties is not possible (e.g. NORRIS and EVANS, 1967). Reliable instrumentation capable of pinpointing a sound source (of an individual in a community tank or in a herd at sea) is not yet available. However, several workers are concentrating on this important aspect (e.g. WATKINS and SCHEVILL, 1971, 1972). Significant progress would greatly facilitate ecological work on sound

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* According to SCHEVILL (personal communication) much of the alleged mimicry by captive odontocetes is better interpreted as effort to relieve the tedium of imprisonment; he believes that parrot or mocking bird talents have 'a very short baseline'.

production in marine mammals. Adequate evaluation of the ecological significance of acoustic energy for marine mammals requires comparative parallel studies in the field and in the laboratory.

A basic prerequisite for sound-property studies is appropriate wide-range equipment for recording and analysis. In many studies, it has not been possible to ensure that the total frequency content of the acoustic signals has been faithfully recorded. This fact adds further uncertainty to our present knowledge on sound properties. Sound analyses are based on tape recordings, sonagrams (sound spectrographs) and oscillograph tracings. The suitability of hydrophones, and of equipment for storage and analysis of sounds has been discussed by DIERCKS and co-authors (1973).

On the basis of their properties, the sounds generated by marine mammals may be subdivided into three general categories: (i) **Respiratory noises** (blow sounds); (ii) **percussion noises**, created by rapid collision of body parts, e.g. jaw clapping, fin clapping, etc; (iii) **phonations** (active-biosonar signals, screams, grunts, moans, barks, etc.). All three sound categories may serve orientational, including communication, ends.

Respiratory noises may contribute to maintaining social contact and to synchronizing respiratory patterns (p. 842). They are usually among the least audible (shortest range) underwater sounds, but are most apparent to a listener in air. Percussion noises are produced primarily in emotional contexts; they seem to signal, for example, danger, food or partnership. Phonations have received most attention and will be dealt with primarily in this section. While pure-tone phonations could conceivably serve acoustic orientation, there is little evidence at hand to support this. The vast majority of sounds used for orientation have a broad frequency band.

The importance of sounds for spatial orientation has been documented or implied in numerous papers. In general, low-frequency sounds facilitate long-distance orientation, since the penetrating power of a sound decreases with the square of its frequency. At the same time, however, the long wavelengths of low-frequency sounds cause considerable scattering. Consequently, low-frequency sounds contain little specific orientational information. They provide, at the most, vague, non-detailed overall cues for gross orientation and gross navigation. Low-frequency sound may, however, be of importance for long-range communication among con- and heterospecifics. High-frequency sounds, on the other hand, facilitate short-distance orientation, potentially providing detailed information on object direction, distance, size, shape and other properties. In situations of poor visibility, self-produced high-frequency sounds are essential for hunting, close-range navigation and obstacle avoidance.

The sounds generated and their acoustic properties vary in different taxonomic groups and in different species; in some cases, different populations of a given species and even different individuals have been shown to produce their own signature sounds (p. 824).

We shall briefly consider here a few examples of sounds generated by marine Carnivora, Pinnipedia, Sirenia, Mysticeti and Odontoceti. Reviews on sounds of marine animals have been presented by SCHEVILL (1964), TAVOLGA (1965), M. C. CALDWELL and CALDWELL (1967), EVANS (1967, 1973), and NORRIS (1969).

Carnivora

The sea otter *Enhydra lutris* (p. 715) generates sounds in air (e.g. LIMBAUGH, 1961). Acoustic mother–pup contacts increase markedly upon separation. As in other marine mammals, the sounds emitted seem to function as acoustico-orientational stimuli. Research to support such view and acoustic analyses of the sounds produced are not available.

Underwater phonations by *Enhydra lutris* have not been reported.

Pinnipedia

The capacity of pinnipeds to generate sounds has been documented in a considerable number of papers. Of the 33 pinniped species known, most seem to be able to produce some kind of underwater phonation. Some species have been shown to possess directional hearing and all appear to be capable of using acoustic cues for spatial orientation.

Typical phonations of the few pinnipeds studied are loud barks and faint clicks, usually composed of low frequencies. The clicks tend to have pronounced frequency bands (SCHEVILL and co-authors, 1963) and sometimes are frequency modulated (EVANS, 1967). The sounds are variable in intensity and structure: the California sea lion *Zalophus californianus*, for example, produces clicks, barks, whining sounds, buzzing, bangs or cracks (SCHUSTERMAN, 1967); the Weddell seal *Leptonychotes weddelli*, long (to 42 secs) trains of resonant pulses (SCHEVILL and WATKINS, 1965b); the walrus *Odobenus rosmarus*, 'church-bell-like' ringing (SCHEVILL and co-authors, 1966).

Zalophus californianus has received detailed attention: there are 5 different sound groups which are all associated with investigative and social responsiveness and related to a high level of arousal (SCHUSTERMAN, 1967; see also SCHUSTERMAN and co-authors, 1966; SCHUSTERMAN and DAWSON, 1968):

(i) Clicks are emitted in an almost infinite variety, especially in a 'novel' situation. Clicking habituates and recovers from habituation. It may be performed underwater or in air with the mouth closed or open. Most click trains last 2 secs or less, but many as long as 23 secs with pauses of less than 0·5 sec. The dominant frequencies range from below 500 Hz to 1200 Hz with components slightly above 4 kHz. Click-repetition rate varies from less than 5 $\sec^{-1}$ to 70 or 80 $\sec^{-1}$, all within a given click train (separation between successive clicks of 0·5 sec or less). A particularly interesting click series is illustrated in Fig. 8-75; the sonagrams show a sample of a continuous series. The 3-year-old female *Zalophus californianus* tested produced this series while apparently searching for food (live mudsuckers *Gillichthys mirabilis*) at extremely poor underwater visibility. The figure illustrates the beginning of the click series (a) with very low frequency components at a repetition rate of about 50 clicks $\sec^{-1}$. A short pause during the middle of the series (b) is followed by two high-energy cracks or bangs. Subsequently, another short pause occurs (c) and clicking resumes at a dominant frequency of 1250 Hz and a pulse rate as low as 10 $\sec^{-1}$. (ii) Barks display most energy below 3500 Hz. There is little variation in duration of an individual bark (200 to 300 msecs). (iii) Whinny sounds, produced during aggressive encounters, last for about 1·5 secs and may be repeated 3 or 4

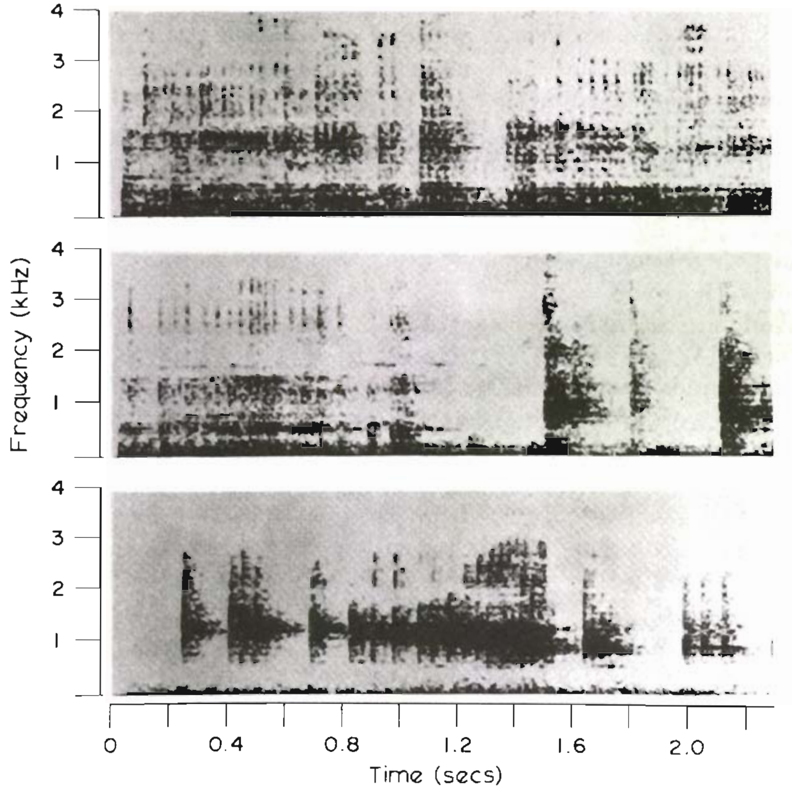

Fig. 8-75: *Zalophus californianus* (captive). Sonagrams obtained from a continuous series of clicks emitted by a 3-year-old female while apparently searching for food in turbid water. (After SCHUSTERMAN, 1967; modified; reproduced by permission of Professor R.-G. Busnel.)

times in succession (fundamental at 500 Hz with harmonics to 3 kHz). (iv) **Buzzing** may actually be a series of discrete pulses which occur so rapidly that, to the human ear, they assume a buzzing quality. (v) **Bangs** or '**cracks**', associated with very rapid swimming, appear loud and mechanical to the human ear; they are broad-band pulses with a rapid onset. SCHUSTERMAN (1967) heard comparable sounds produced by the Steller sea lion *Eumetopias jubatus* while performing an underwater visual discrimination task. It is not clear whether *Z. californianus* produces the 'bang' via its vocal apparatus, jaw clapping, front flippers, or by other means.

The frequencies recorded of *Zalophus californianus* clicks vary considerably: EVANS and HAUGEN (1963), POULTER (1963b), SCHEVILL and co-authors (1963), SCHUSTERMAN (1966b). Occasionally, click doublets occur, with the two clicks of a doublet usually having about the same frequency (SCHEVILL and co-authors, 1963); however, POULTER (1963b) reported a low-amplitude precursor click of high frequencies (13·4 kHz), followed by a silent pause and then a stronger, second click of lower frequencies (2–11 kHz). Underwater barking by male *Z. californianus* has been studied by SCHUSTERMAN and BALLIET (1969).

Sounds generated by the Guadalupe (Juan Fernández) fur seal *Arctocephalus philipii* at Isla Róbinson Crusoe included stereotyped low-frequency pulse series underwater and moans and snarls in air (NORRIS and WATKINS, 1971). Analyses of the underwater sounds show that the individual pulses started at 150 to 200 Hz and then decreased in frequency (5–50 Hz). These series were composed of 17 to 43 pulses and were generated at a rate of about 3 sec^{-1}. The results obtained were interpreted by NORRIS and WATKINS as indicating (i) some control over production of harmonics, (ii) individual acoustic characteristics (signature) of different seals, or (iii) that the harmonics may have been due simply to sound reflected off water surface or sea bottom.

The Weddell seal *Leptonychotes weddelli* emits unusual, persistent phonations (SCHEVILL and WATKINS, 1965b, 1971; see also RAY, 1967; WATKINS and SCHEVILL, 1968). The sounds received at 3 different hydrophone depths (McMurdo Sound, Ross Sea) were often 'puzzlingly very different' (SCHEVILL and WATKINS, 1971, p. 164). The maximum distance at which the top hydrophone could receive seal sounds was about 14,000 m. The impulsive calls start at repetition rates exceeding 140 sec^{-1} with usual frequencies between 1000 and 2000 Hz (maximum range: 1000–10,000 Hz); subsequently, the repetition rate decreases and the pitch descends. Individual-pulse duration varies from 0·005 to 1·5 sec, with the pulse length increasing as repetition rate slows. A pulse train may last up to 42 secs. Apparently, the calls are made with the mouth closed; there is no evidence of acoustic orientation other than maintenance of social contacts; but certain acoustic anomalies in the sounds recorded indicate a marked forward and downward sound projection (emission directionality). Underwater sounds of *L. weddelli*, played back to seals at McMurdo Sound, initiated normal vocal responses if the playback was of good fidelity. Poor-quality playback, however, elicited only silent interest (WATKINS and SCHEVILL, 1968).

Breeding herds of harp seals *Pagophilus groenlandicus* emit a variety of underwater sounds (MØHL and co-authors, 1972): (i) clicks (1 basic pattern with many variations and major energy components of 30 kHz); (ii) whistles and barks (15 types with major energy components from 0·1 to 10 kHz).

Captive mature males of the Atlantic walrus *Odobenus rosmarus* generate church-bell-like sounds (SCHEVILL and co-authors, 1966) which may be related to sexual encounter or aggression. More common sounds are clicks and rasps; they are produced especially during swimming, suggesting involvement in echolocation (the test individual generating clicks and rasps had impaired vision and often swam with its eyes closed). According to SCHEVILL and co-authors (1963), clicks have a base frequency of about 400 Hz (some harmonics reach 10 kHz); they last 0·015 to 0·020 sec and are separated by considerable pauses. Rasps emphasize frequencies between 400 and 600 Hz and have base frequencies between 200 and 300 Hz; they last 0·1 to 0·2 sec. A rasp begins with 10 to 14 pulses, separated by about 0·01 sec; as the call proceeds, both intensity and repetition rate increase, resulting in a nearly continuous sound with harmonic structure.

Field observations (San Nicolas Island, California, USA) and spectrographic analyses of tape-recorded sounds of the northern elephant seal *Mirounga angustirostris* reveal two main classes of in-air sounds: attraction calls and threat calls (BARTHOLOMEW and COLLIAS, 1962). Attraction calls (mother to pup) are unpulsed, of high and variable pitch, and show clear harmonic structure. In contrast, the harsh threat calls (both female and male) are highly pulsed, of low and steady pitch, and lack clear-cut harmonics. In general, pulse intervals between successive threat calls tend to increase with body size of the vocalizer. Yearlings use hissing as threat signals, and some yearling threat sounds are structurally intermediate between a hiss and a common roaring-type threat. Hissing occurs in many tetrapods; BARTHOLOMEW and COLLIAS point out that, phylogenetically, hissing probably has preceded and facilitated the evolution of vocal cords and patterned sounds. The importance of sounds for orientation to conspecifics (communication) has been documented for most pinnipeds; some recent examples relate to the New Zealand fur seal *Arctocephalus forsteri* (E. H. MILLER, 1972); Northern elephant seal *M. angustirostris* (LEBOEUF and PETRINOVICH, 1972); South American sea lion *Otaria flavescens* (VAZ-FERREIRA, 1972); and walrus *Odobenus rosmarus* (RAY and WATKINS, 1972).

Hooded seals *Cystophora cristata* generate sounds which seem to be variations of a low-frequency pulsed call—except for signals associated with the male proboscis (TERHUNE and RONALD, 1973). On the pupping areas in the Gulf of St. Lawrence, the male emits both underwater and air calls. In air, inflation and deflation of the adult male proboscis results in low-intensity sounds. Adult female and pup emit an in-air call.

Additional information on sounds emitted by pinnipeds has been presented by SCHEVILL and co-authors (1963), e.g. for ringed seal *Pusa hispida*, harbour seal *Phoca vitulina*, harp seal *Pagophilus groenlandicus*, grey seal *Halichoerus grypus* and hooded seal *Cystophora cristata*; by POULTER (1963b, 1966c, 1968a, b, c) for northern elephant seal *Mirounga angustirostris*, leopard seal *Hydrurga leptonyx*, ringed seal *P. hispida*, bearded seal *Erignathus barbatus*, harbour seal *P. vitulina*, Steller sea lion *Eumetopias jubatus*, *Neophoca hookeri*, ribbon seal *Histriophoca fasciata*, crabeater seal *Lobodon carcinophagus*, walrus *Odobenus rosmarus*, northern fur seal *Callorhinus ursinus*, *Otaria byronia*, *N. cinerea*; and by SCHUSTERMAN and co-authors (1970) for *Halichoerus grypus*, *Phoca vitulina* and *Eumetopias jubatus*.

Sirenia

Underwater, the Florida manatee *Trichechus manatus latirostris* generates weak, ragged squeaky chirps of 600 to 5000 Hz frequency composition and 0·15 to 0·5 sec duration (SCHEVILL and WATKINS, 1965a). The sounds consist of a series of emphasized but not necessarily harmonically related bands. These first sounds recorded of manatees seem to represent communication rather than active-biosonar signals. Subsequent investigations (HARTMAN, 1969), conducted in the natural underwater habitat of *T. manatus latirostris*, revealed a highly variable vocabulary including chirp-squeaks, squeals and screams—all produced in a variety of unrelated circumstances and indicating emotional involvement, especially alarm. A predictable vocal relation is the alarm duet between a mother and her calf as she calls it to her side before fleeing.

Underwater sounds generated by the Amazon manatee *Trichechus inunguis* have been recorded by EVANS and HERALD (1970). The majority of sounds emitted by a young male, kept in a cement display tank, were louder than (but otherwise similar to) those of *T. manatus latirostris*: the fundamental frequencies ranged from 6000 to 8000 Hz (2500 to 5000 Hz in the Florida manatee) the call duration from 0·15 to 0·22 sec. There is no evidence that any of the sounds produced are associated with echolocation or navigation.

Mysticeti

Mysticeti (baleen whales) usually generate low-frequency calls (moans and screams) of a much narrower band character and much longer duration than the average odontocete sound (SCHEVILL, 1964; NORRIS, 1969; PAYNE and MCVAY, 1971). While less complex and variable than odontocete phonations (p. 764), Mysticeti sounds are of impressive diversity. All or some of these sounds may serve spatial orientation; but conclusive evidence is not available.

The grey whale *Eschrichtius robustus* is one of the more vocal Mysticeti, particularly in regard to mother–calf relationships. Reports on grey whales generating underwater sounds have been published by EBERHART and EVANS (1962), PAINTER (1963), WENZ (1964), CUMMINGS (1967), and CUMMINGS and co-authors (1967). These investigators heard clicks, croak-like grunts of low-frequency rumbles, crunching and scratching, and low-pitched, undulating grunting. According to POULTER (1968d), the most unusual and loudest grey-whale sound resembles the 'bong' of a huge Chinese gong and is apparently used as alarm signal: usually preceded by a loud rasp, the bong is claimed to cause immediate cessation of all other whale sounds. Click, rasp and bong are not limited to the usual frequency range below 2000 or 3000 Hz but may go up to 12 kHz. Not heard by any other worker, the bong requires confirmation. *E. robustus* has been assumed to emit clicks resembling those of odontocetes (p. 764); however, definite proof is lacking.

Minke whales *Balaenoptera acutorostrata*, in the Ross Sea (Antarctica), emit intense, low-frequency underwater sounds (SCHEVILL and WATKINS, 1972). The loudest sounds in undistorted recording are estimated at about 65 dB re 1 dyne cm^{-2} at 1 m. The sounds were composed of a single downward sweep starting at 130 to 115 Hz and sweeping to about 60 Hz. Sounds recorded at a level low enough to be free from distortion had no harmonic structure. Individual sounds last from 0·2 to 0·3 sec.

The fin whale *Balaenoptera physalus* generates very low moans that are repeated monotonously in regular pattern (PATTERSON and HAMILTON, 1964; SCHEVILL and co-authors, 1964); it produces a 75 to 40-Hz sound (SCHEVILL and WATKINS, 1962), a 20-Hz (23 to 18 Hz) sound (SCHEVILL and co-authors, 1964) or a 20 to 100-Hz sound (THOMPSON and CUMMINGS, 1969). The 20-Hz pulses are very low (some human ears cannot perceive them) and may be emitted with monotonous regularity over many hours (PATTERSON and HAMILTON, 1964); they are narrow band (usually ±2–3 Hz) and of high intensity (70–76 dB re 1 μbar at 0·9 m). According to THOMPSON and CUMMINGS (1969), the most common type of signal consists of a 1·8-sec component at 68 Hz, followed by another 1·8-sec component at 34 Hz. *B. edeni* sounds last on average 0·4 sec and have an average frequency of about 124 Hz. Sounds of *B. musculus* have most energy below 50 Hz (CUMMINGS and THOMPSON, 1971). The intensity of most of these mysticete calls presumably lies near or above 60 dB re 1 dyne cm^{-2} at 1 m. The loudest biological sound ever recorded in the sea is a 20 Hz signal of *B. musculus*: 88 dB re 1 μbar at the source (CUMMINGS and

THOMPSON, 1971). *B. musculus* also has been claimed to produce pulses at about 25 kHz (BEAMISH and MITCHELL, 1971), and *B. physalus* to emit chirps and whistles at 1500 to 2000 Hz (PERKINS, 1966). These latter two observations require confirmation.

Spectrograms of non-blow sounds made by right whales *Eubalaena glacialis* (SCHEVILL and WATKINS, 1962; SCHEVILL and co-authors, 1962; D. K. CALDWELL and CALDWELL, 1971: in-air calls of a stranded moribund juvenile) reveal pulsed calls of fundamental frequencies between 100 and 750 Hz; some components ranged up to 4000 Hz with some energy as high as 7500 Hz. A variety of underwater sounds, recorded by PAYNE and PAYNE (1972) near several groups of *E. australis*, contained frequencies principally in the range 50 Hz to 500 Hz, but included some as high as 1500 Hz, not previously reported for this species. The frequency range of each sound was narrow, but the harmonic structure of some was complex. The irregular and non-repetitive sound pattern indicates that these are not 'songs', and different intensities in adjacent sounds suggest that more than one individual was involved in sound production. Vocal activity was greater at night than during the day. Both single sounds and sound groups lasted up to 1 min.

The humpback whale *Megaptera novaeangliae* generates a variety of frequency-modulated moans and screams (SCHREIBER, 1952; SCHEVILL, 1964), presumably related with spring time (SCHEVILL and WATKINS, 1962). Apparently, the cosmopolitan *M. novaeangliae* is the most vocal mysticete studied thus far. Travelling herds of *M. novaeangliae* emit series of 'surprisingly beautiful' (PAYNE and MCVAY, 1971, p. 585) and varied sounds for periods of 7 to 30 mins. They repeat such series with considerable precision. Although the social function of these sound patterns is not known, PAYNE and MCVAY refer to each sound series as a 'song' (i.e. a stereotyped, repeated phonation associated with courtship or territorial display, as in birds). Thus defined, 'singing' has not yet been proved for marine mammals, but evidence is mounting that forms such as *Leptonychotes weddelli*, *Erignathus barbatus*, *Odobenus rosmarus* and *M. novaeangliae* do, in fact, sing.

All prolonged sound patterns recorded for *Megaptera novaeangliae* are in song form and each individual adheres to its own song type. Songs are repeated without any obvious pause, and coherent song sessions may last several hours. According to PAYNE and MCVAY (1971), there seem to exist several basic song types around which the humpback whales 'construct' their songs, but individual variations are pronounced. In successive songs, the sequence of themes produced by the same individual remains the same. Although the number of phrases per theme varies, no theme is ever omitted completely. Surprisingly, even loud ambient sounds, such as dynamite blasts, do not seem to affect the whale's songs. According to NORRIS (personal communication), humpbacks sing only 'at the warm end' of their migration paths, e.g. off Bermuda or Hawaii, but not in colder areas, e.g. off Cape Cod.

Regarding the potential ecological importance of the sounds generated by mysticetes, it is tempting to interpret them in terms of social contact and spatial orientation (gathering of basic gross information on the environment ahead). At least some of the sounds seem to be involved in acoustic long-range (up to tens of miles) orientation. However, no definite proof has been obtained as yet of such an assumption, and no strong evidence is available for active biosonar capabilities in this group of whales (p. 796).

Odontoceti

Odontocete cetaceans are well known for their vocalness. At sea and in captivity, most species exhibit an impressive repertoire of sounds. Three basic groups of sounds can be distinguished: clicks, burst pulses and pure tones. A few species emit active-biosonar clicks and have been shown experimentally to orientate by active biosonar (p. 796). The properties of odontocete sounds have received much attention, especially in the last decade. It is neither possible nor desirable to document and to evaluate here all pertinent contributions in detail.

Despite considerable differences at the species level and variations even at the population or individual levels, the basic characteristics (waveform) of the delphinid active-biosonar signal are similar in *Tursiops truncatus, Inia geoffrensis* and other odontocetes of similar size (DIERCKS and co-authors, 1973; Fig. 8-76).

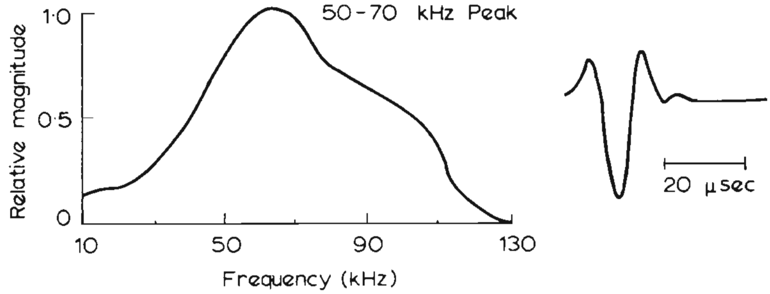

Fig. 8-76: Typical waveform and power spectrum of the delphinid active-biosonar signal. (After DIERCKS and co-authors, 1973; modified; reproduced by permission of Acoustical Society of America.)

Reviewing results obtained by Soviet Russian scientists, BELKOVICH and NESTERENKO (1971, 1972) conclude that most delphinids emit active-biosonar sounds within a broad frequency spectrum ranging up to 256 kHz, with maximum energy between 20 and 60 kHz. Signal duration varies usually from 0·1 to 1 msec, and the signals are repeated 1 to several hundred times per second. Below a target distance of 0·4 m, repetition rate increases suddenly from 50 to more than 200 sec^{-1} for about 0·3 sec. In contrast to the situation in bats, this indicates target recognition: numerous experiments by RESNIKOV and associates (*in*: BELKOVICH and NESTERENKO, 1971, 1972) have shown that dolphins can echolocate objects of sizes between 10 and 15 cm at a distance of at least 10 m (p. 707). Presumably, the increase in repetition rate indicates a shifting from rough to fine discrimination. The characteristics of delphinid active-biosonar sounds do not seem to depend on target properties (BELKOVICH and NESTERENKO, 1971, 1972).

Summarizing the information available on the properties of active-biosonar sounds emitted by odontocetes, EVANS (1973) distinguishes 4 categories: (i) Narrow band, about 400 Hz to 20 kHz; peak energy at 2 to 4 kHz; source level 25 to 30 dB re 1 μbar at 1 m (*Phocoena phocoena*). (ii) Broad band, 100 Hz to 30 kHz; peak energy at 16 to 20 kHz; source level 78 dB re 1 μbar at 1 m (*Orcinus orca*). (iii) Broad band, 16 kHz to 150 kHz; peak energy at 60 to 80 kHz; source level 66 dB re 1

μbar at 1 m (*Inia geoffrensis, Platanista gangetica*; **Herald** and co-authors, 1969). (iv) Broad band, 200 Hz to 150 kHz; peak energy at 30 to 60 kHz; range of source level 40 to 80 dB re 1 μbar at 1 m (*Tursiops truncatus, Lagenorhynchus obliquidens, Delphinus delphis*).

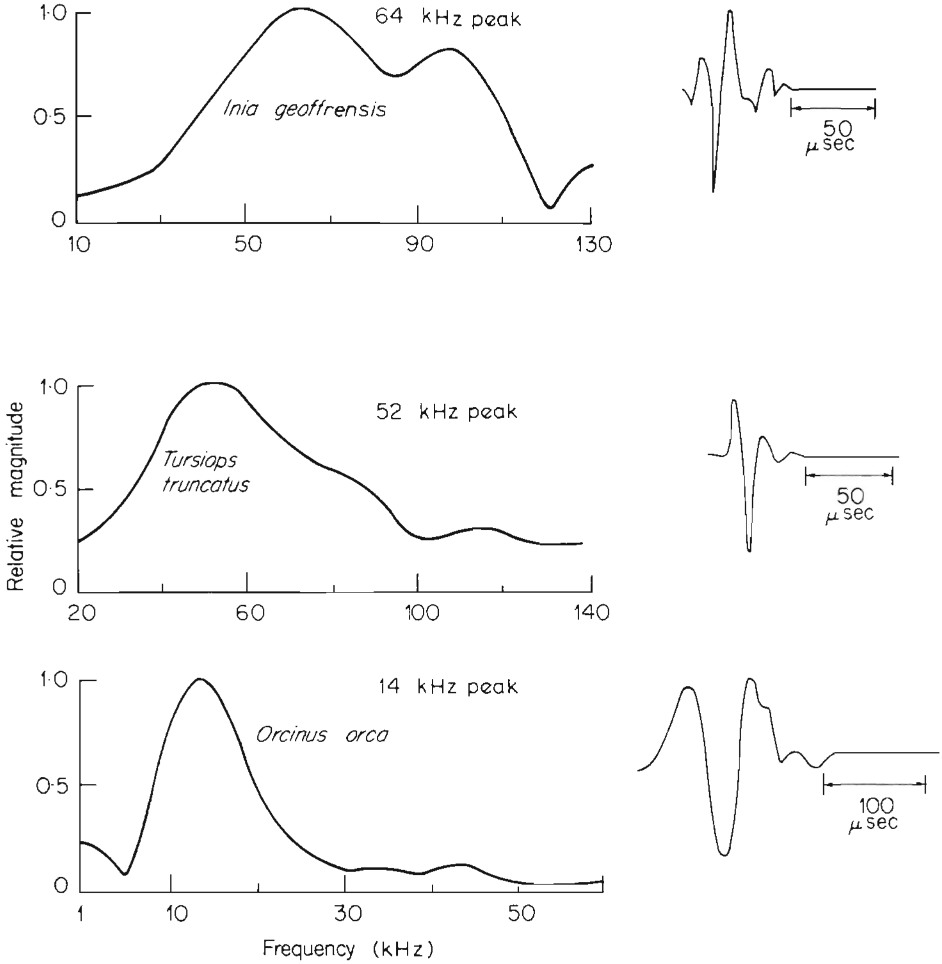

Fig. 8-77: Active-biosonar signals of 3 odontocete cetaceans: typical waveforms and associated power spectra. (After **Evans**, 1973; modified; reproduced by permission of Acoustical Society of America.)

For three species—*Inia geoffrensis, Tursiops truncatus* and *Orcinus orca*—typical wave forms and associated power spectra are illustrated in Fig. 8-77.

Captive *Tursiops truncatus* generate clicks, burst pulses and pure tones (e.g. M. C. **Caldwell** and **Caldwell**, 1967; **Norris**, 1969). Phonatory activities depend on social structure and environmental conditions (M. C. **Caldwell** and **Caldwell**, 1967). As the size of the dolphin group increases, the number of phonations per individual per hour tends to increase; an isolated individual's sound emission usually ceases quickly. Stable communities of long duration are less vocal than newly established communities. A constant environment without introduction of stimuli decreases phonation activities; but a group may suddenly become very vocal without apparent reason (in a tank in Florida, USA, CALDWELL and CALDWELL could eventually correlate this behaviour with occasionally occurring high wind velocities). In general, phonation decreases with increasing time in captivity. This seems to be due to environmental uniformity, lack of appropriate social stimuli, and predominance of essentially visual over acoustic cues. The number of sound emissions may be a function of diurnal periodicity (e.g. REYSENBACH DE HAAN, 1966).

EVANS and PRESCOTT (1962) differentiate 3 categories of sounds produced by *Tursiops truncatus*: (i) Clicks: active-biosonar pulses of 0·001 to 0·1 sec duration; frequency range: 100 Hz to 35 kHz and beyond; greatest intensity in the 20 to 35 kHz range, with considerable energy from 3 kHz to 20 kHz. (ii) **Whistles**: very narrow band, with one or two overtones; 0·10 to 3·6 secs duration; frequency range: 4000 Hz to 20 kHz. (iii) **Bark sounds**: rich in overtones; about 0·10 sec duration; frequency range: 200 Hz to 16 kHz (fundamental frequency 200 to 300 Hz). Clicks were the most frequently generated sounds. The dolphins were constantly echoranging the experimental tank, apparently checking for possible environmental changes, e.g. addition of food. Repetition rates of clicks varied from 1 or 2 sec^{-1} to 525 sec^{-1}. Whistles, the next most frequent sounds, were usually associated with movements of one or more individuals. A total of 18 basically different whistles were observed. The rarely heard barks were usually in context with some stationary activity rather than swimming.

Experiments on a captive adult female *Tursiops truncatus* (p. 801) and subsequent data analyses revealed important details on duration of click trains, repetition rate, click duration, intraclick interval and frequency (TURNER and NORRIS, 1966; NORRIS and co-authors, 1967):

Duration of click trains averaged 2·0 secs, ranging from 1·2 to 2·9 secs. More difficult discriminations resulted in a marked increase in variability of click-train length (p. 802). **Repetition rate** during discrimination runs averaged 65 clicks sec^{-1} (3·18 cm vs reference sphere), 74 clicks sec^{-1} (4·45 cm vs reference), and 78 clicks sec^{-1} (5·18 cm vs reference). These rates are very low compared to other published data (NORRIS and co-authors, 1961: 416 clicks sec^{-1}; EVANS and PRESCOTT, 1962: 525 clicks sec^{-1}; LILLY, 1962: 1200 clicks sec^{-1}). According to NORRIS and co-authors (1967), this difference seems to be related to the distance between dolphin and object. The changes in repetition rate recorded might serve proper placement of the echo in the interclick interval or superposition of the echo upon the next following click (Figs 8-78, 8-79). **Click duration** was difficult to measure because of the highly reverberant conditions in the pool. The clicks are paired emissions whose peaks can be clearly recognized against the background-noise level. Similar paired clicks have also been recorded at sea (Fig. 8-80), where reverberation is often insignificant and more detail can be noted. The **intraclick interval** (time between the prominent spikes of a double click) varies from 0·4 to 0·7 msec during a single run. The **frequencies** examined document considerable control of *T. truncatus* over the frequency composition of its acoustic signals, especially when switching from 'discrimination clicks' (absence of frequencies below the 2400–4800 Hz octave

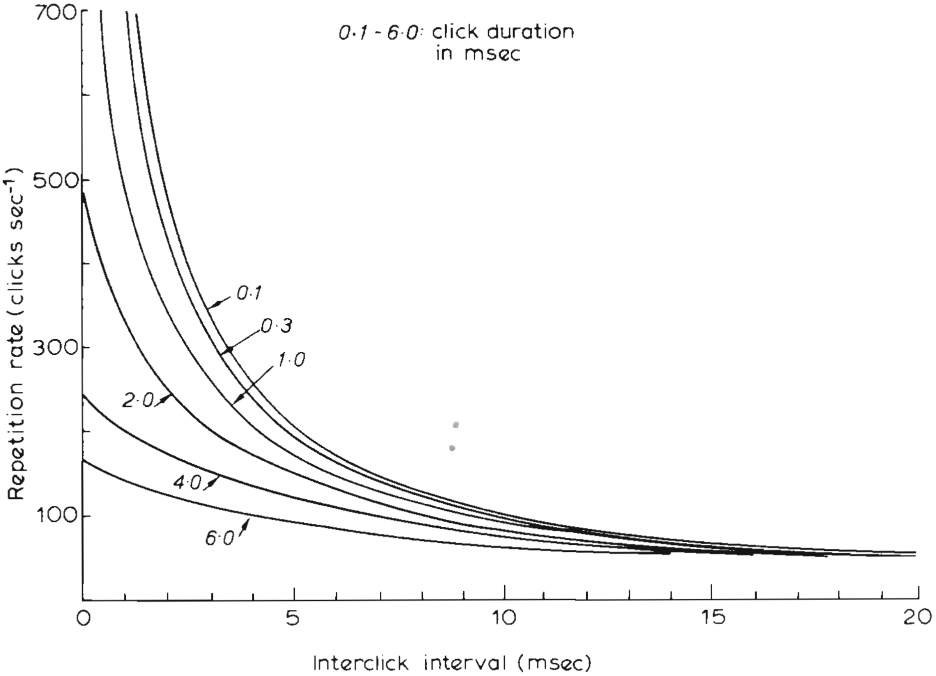

Fig. 8-78: *Tursiops truncatus* (captive). Relation between repetition rate and interclick interval for clicks of 0·1 to 6·0 msecs duration. 20° C; 35‰ S. (After NORRIS and co-authors, 1967; modified; reproduced by permission of Professor R.-G. Busnel.)

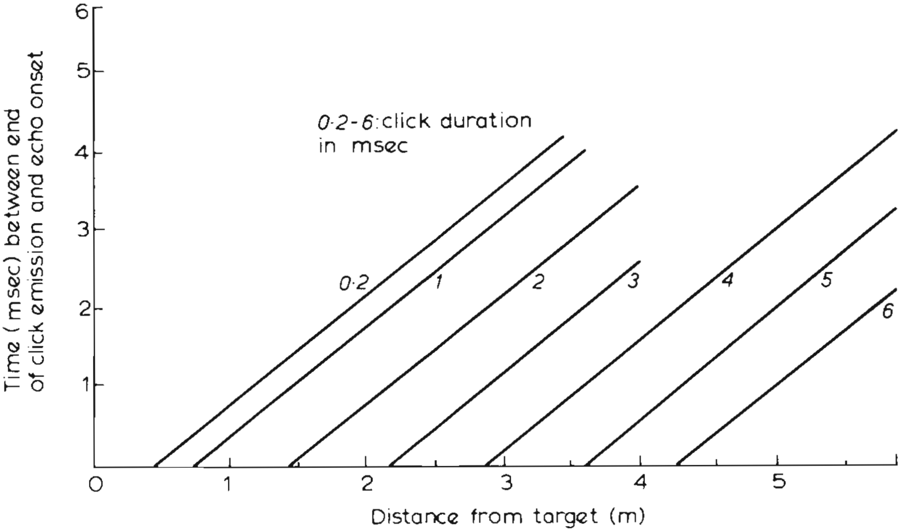

Fig. 8-79: *Tursiops truncatus* (captive). Circuit time for a click hitting the test target as a function of click duration. 20° C; 35‰ S. (After NORRIS and co-authors, 1967; modified; reproduced by permission of Professor R.-G. Busnel.)

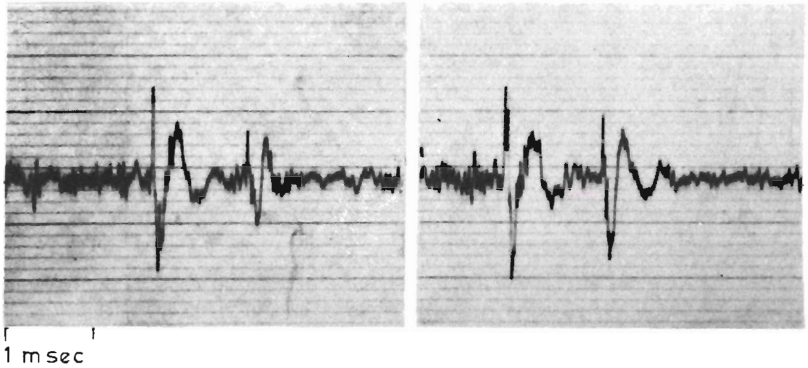

Fig. 8-80: *Tursiops truncatus* (at sea). Two recordings of paired clicks obtained off Santa Catalina Island, California, USA. Repetition rate: 40 to 50 sec^{-1}. (After NORRIS and co-authors, 1967; reproduced by permission of Professor R.-G. Busnel.)

band) to 'orientation clicks' (presence of frequencies down to the 300–600 Hz octave band; Fig. 8-81). Gear with high-frequency capability, used in additional tests with the same individual, revealed, during blindfolded discriminations, an approximate upper frequency level near 80 kHz with most of the acoustic energy concentrated between 16 and 30 kHz.

Tursiops truncatus is able to mimic a variety of sounds—man-made, electronically produced, and others (LILLY, 1961, 1962, 1965, 1967; EVANS, 1967, M. C. CALDWELL and CALDWELL, 1972). LILLY (1965) tested the ability of a captive, isolated *T.*

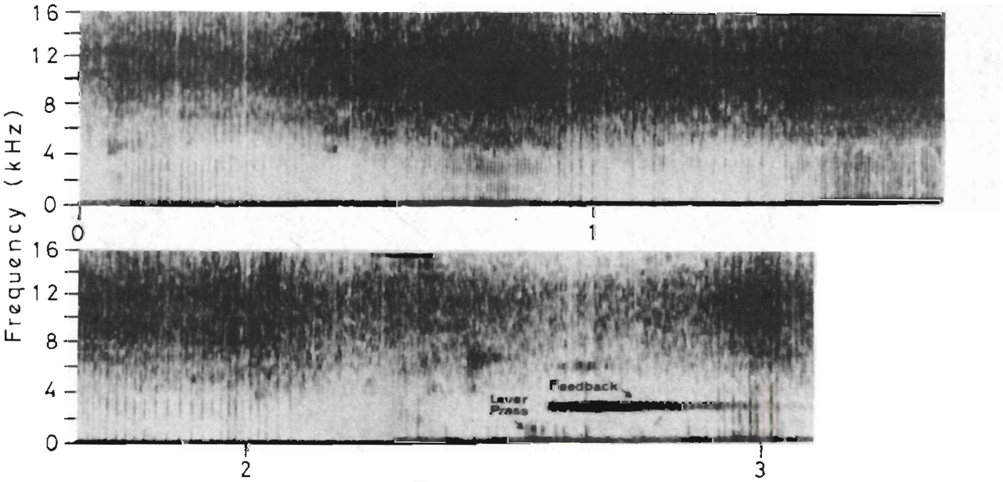

Fig. 8-81: *Tursiops truncatus* (captive). Sound emission during discrimination (target sphere disparity: 2 versus 2½, correct response). Note periodic increases in repetition rate and blank period (above 2-second marker); this is followed by the sounds of lever press and trainer's whistle (feedback), and then a series of directional orientation clicks (above 3-second marker). (After NORRIS and co-authors, 1967; reproduced by permission of Professor R.-G. Busnel.)

truncatus to match numbers and durations of human vocal bursts. By reinforcement (rewarding) and by evocative techniques, Lilly succeeded to change and augment natural in-air emissions from the open blowhole and to obtain sound aspects which may be interpreted as vocal mimicry. In 92% of the vocal exchanges between the trainer and *T. truncatus*, the number of dolphin bursts equalled, ±1, the number previously emitted by a man in sequences of 1 to 10 bursts. Evans (1967) refers to studies by R. Penner who was able to train *T. truncatus* to mimic fairly accurately an electronically produced whistle-like tone structurally similar to natural dolphin emissions. According to M. C. Caldwell and Caldwell (1972), a captive *T. truncatus*, at 'Ocean World', Ft. Lauderdale, Florida (USA), mimicked the phrase 'happy birthday!' (the effect was particularly obvious after the trainer had 'cued' the audience to expect this phrase), bird trills, human laughter, or human singing. M. C. Caldwell and Caldwell exposed a captive, isolated juvenile *T. truncatus* several times daily to a 10-kHz signal. After about 2 or 3 weeks, the dolphin began (without reinforcement by the trainer) to mimic this electronically produced signal, using his own whistle.

Vocal mimicry occurs also in other marine mammals. Especially captive, isolated individuals tend to become devoted mimics and may fool investigators who intend to record 'natural' sounds and to analyze their potential ecological significance. The evolution of vocal mimicking has been discussed by Andrew (1962); inheritance and learning of animal phonations have been reviewed by Marler (1963).

Busnel and Dziedzic (1966a) studied sound production in the common dolphin *Delphinus delphis* under the same circumstances as described in context with *Globicephala melaena* (p. 773), but at night. The squeaking heard at night was not the same as during the day; it is mixed with high-frequency echoranging clicks (Fig. 8-82; duration: ca 0·5 sec; maximum energy: between 4 and 9 kHz, with several harmonics; interharmonic intervals usually about 1000 Hz). Squeaking is emitted rather frequently in short series of 2 or 3. Approximately 80 night signals were analyzed, and 5 signal types were distinguished:

Type 1 signal (Fig. 8-83): long, strong-intensity whistle with sharp frequency drop in the first part and without harmonics. It lasts about 1·1 sec and starts at about 16 kHz. The signal was often repeated several times, especially when the ship was

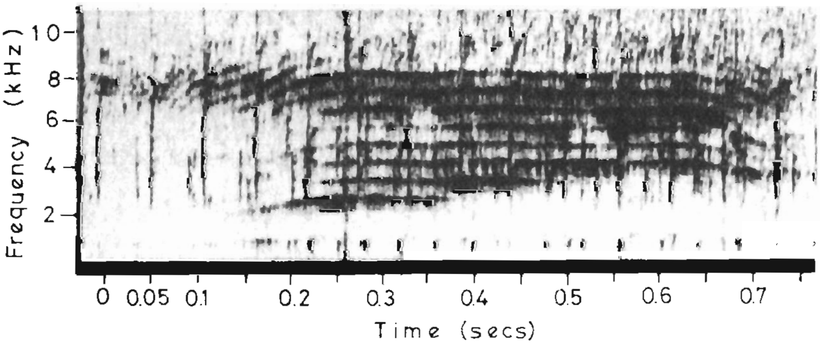

Fig. 8-82: *Delphinus delphis* (at sea). Sonagram of nightly squeaking. (After Busnel and Dziedzic, 1966a; originally published by the University of California Press; reprinted by permission of The Regents of the University of California.)

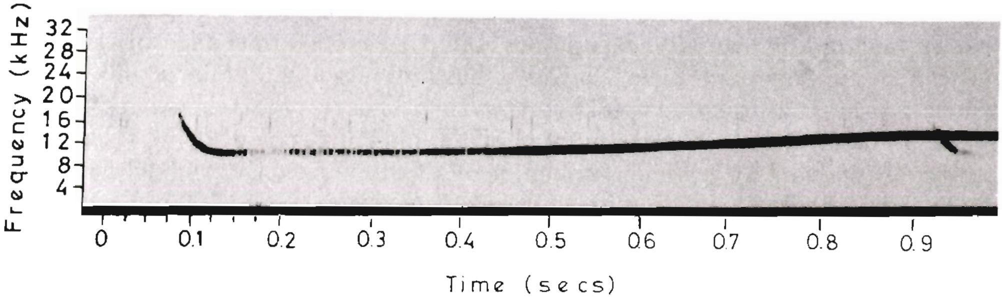

Fig. 8-83: *Delphinus delphis* (at sea). Sonagram of type 1 signal. (After BUSNEL and DZIEDZIC, 1966a; originally published by the University of California Press; reprinted by permission of The Regents of the University of California.)

drifting; but it was also heard when the engine was running. It is emitted by schools, almost never by isolated individuals.

Type 2 signal (Fig. 8-84): long whistle with short periods of frequency modulation. The signal was heard almost exclusively when the dolphins were swimming ahead of the ship.

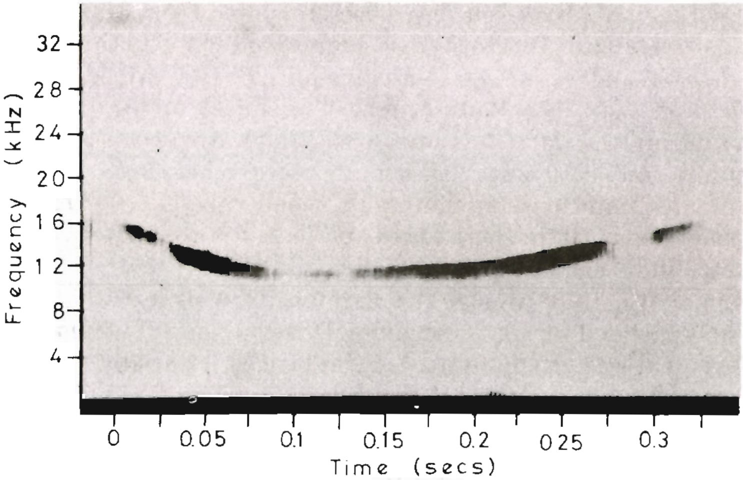

Fig. 8-84: *Delphinus delphis* (at sea). Sonagram of type 2 signal. (After BUSNEL and DZIEDZIC, 1966a; originally published by the University of California Press; reprinted by permission of The Regents of the University of California.)

Type 3 signal (Fig. 8-85): complex, regularly emitted, consisting of simultaneous whistle and active-biosonar emissions (the latter being similar to the type 3 signal of *Globicephala melaena*, p. 774). The whistle comprises 2 parts; the first has a fast frequency variation ending in a decrescendo; the second has an average frequency of 10 kHz. The signal was recorded when the dolphins were hunting.

Type 4 signal (Fig. 8-86): a short concave whistle, emitted by isolated individuals and repeated fairly regularly.

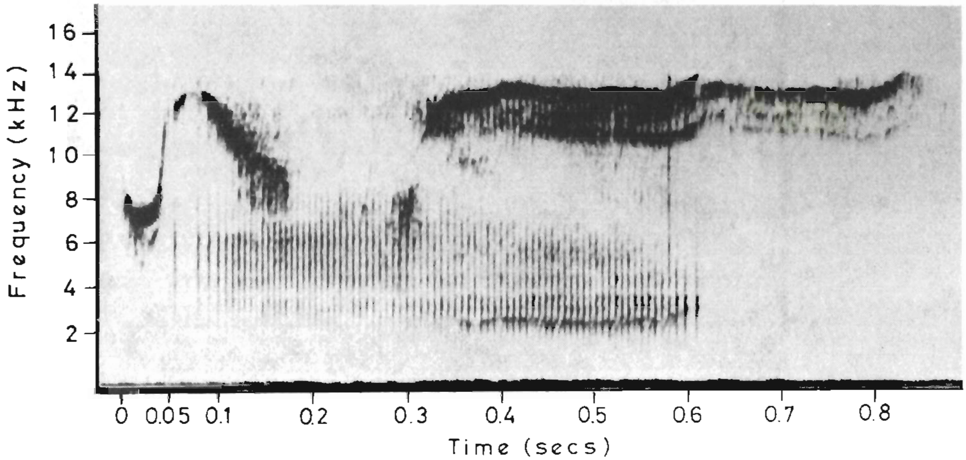

Fig. 8-85: *Delphinus delphis* (at sea). Sonagram of type 3 signal. (After BUSNEL and DZIEDZIC, 1966a; originally published by the University of California Press; reprinted by permission of The Regents of the University of California.)

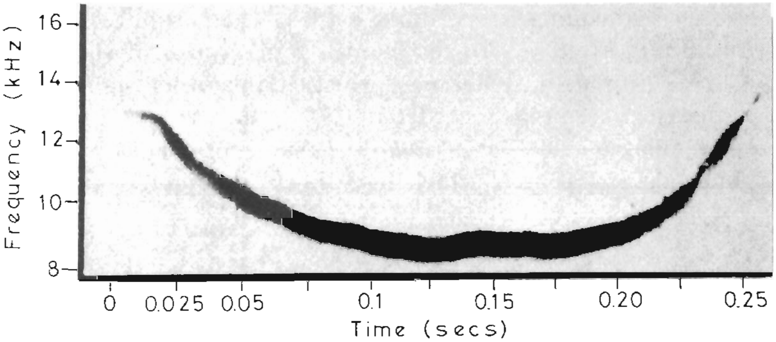

Fig. 8-86: *Delphinus delphis* (at sea). Sonagram of type 4 signal. (After BUSNEL and DZIEDZIC, 1966a; originally published by the University of California Press; reprinted by permission of The Regents of the University of California.)

Type 5 signal (Fig. 8-87): a very short whistle, concave in general form and not always regular. Produced after attempts to capture a dolphin (tail grabber or harpoon gun), that is, after the individual had been surprised (e.g. touched by an unknown object). The signal is repeated 4 or 5 times after each incident. It functions perhaps as a fright or distress call; in any case, it approaches the form of the distress call produced by *Tursiops truncatus* (p. 812). When type 5 signals were emitted from a transmitter (EDO transducer of the R.V. 'Calypso's' sonar sounding device) the nearby school of *Delphinus delphis* dived immediately after the first signal, remained underwater abnormally long (30 to 40 secs) and then changed direction. The dolphins swam rapidly in a front-line formation (they had previously been in single file). The school returned to its usual formation and direction after 10 mins but avoided the ship.

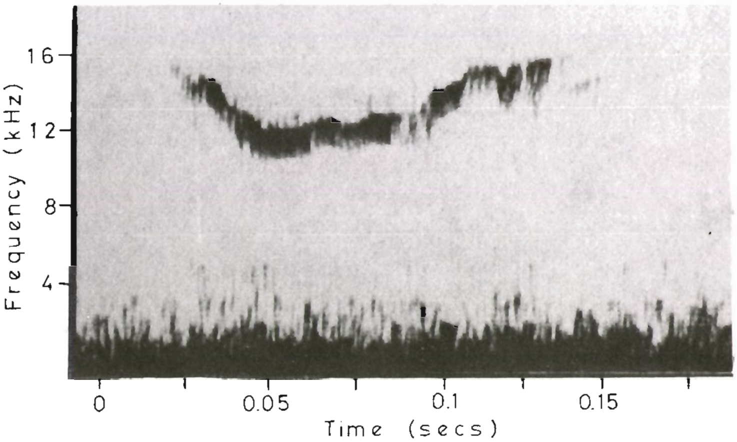

Fig. 8-87: *Delphinus delphis* (at sea). Sonagram of type 5 signal. (After BUSNEL and DZIEDZIC, 1966a; originally published by the University of California Press; reprinted by permission of The Regents of the University of California.)

BUSNEL and DZIEDZIC (1966a) describe 3 additional types of special whistles from *in situ* recordings and compare recordings made at sea and in captivity (VINCENT, 1960). TITOV and TOMILIN (1970) distinguish four groups of signals emitted by *Delphinus delphis* (impulses, quackings, whistles and other signals) and provide acoustical indices of the sounds recorded.

The common pilot whale *Globicephala melaena* emits short pulses, sometimes paired, at intervals of 0·01 sec, which have been interpreted as active-biosonar

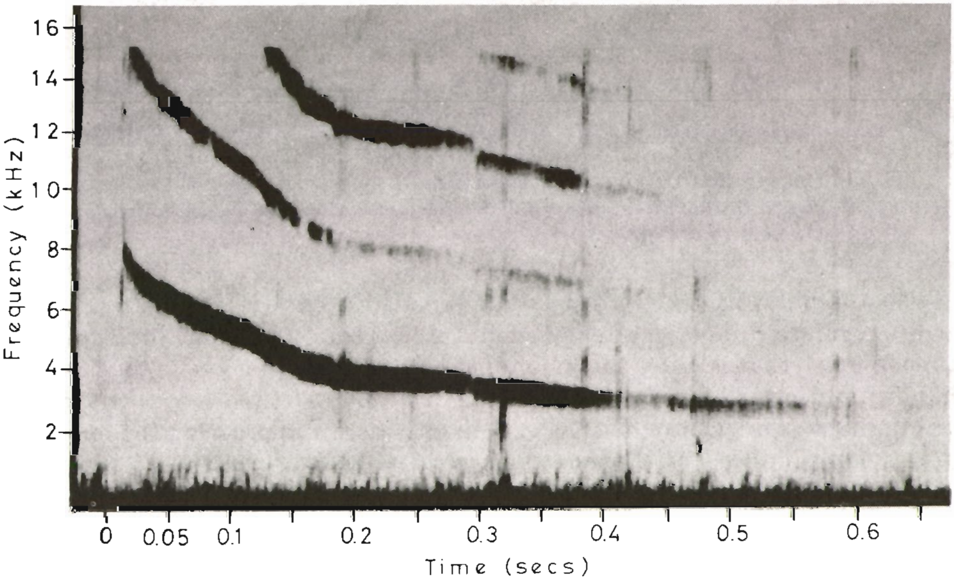

Fig. 8-88: *Globicephala melaena* (at sea). Sonagram of type 1 signal. (After BUSNEL and DZIEDZIC, 1966a; originally published by the University of California Press; reprinted by permission of The Regents of the University of California.)

signals. Busnel and Dziedzic (1966a) studied sound generation of *G. melaena* at sea from a school of 11 individuals. It was possible to approach close to the school; then an individual was harpooned; it was followed by a boat, but finally escaped. Of 423 signals identified, Busnel and Dziedzic analyzed 185 sounds. Five major signal types can be distinguished:

(i) Type 1 signal (Fig. 8-88) is the most abundant emission; it comprises whistles, sometimes accompanied by echoranging clicks and creakings. The signal is repeated fairly regularly at intervals of 3 to 5 secs, sometimes in series at 10- to 15-sec intervals; it lasts from 0·39 to 0·87 sec and consists of 1 fundamental and 3 or 4 harmonics decreasing in strength, either after a rapid rising tone or a rising and then falling tone.

(ii) Type 2 signal (Figs 8-89, 8-90, 8-91, 8-92) consists of three variations which sound similar to the human ear: creaking (Figs 8-89, 8-90), blast (Fig. 8-91) and squeaking (Fig. 8-92). All three seem to derive from a common basic form, corresponding to increased repetition rates of echoranging pulses, and are similar in physical structure. The creaking corresponds to rapidly repeated active-biosonar pulses of 0·1 to 0·2 sec duration.

(iii) Type 3 signal (Fig. 8-93) is frequently heard; it consists of the simultaneous production of a long whistle and a creaking. The whistle lasts 2 to 3 times as long as the creaking. Fig. 8-93 is an example of such bitonal emission. Total duration varies from 1·4 to 2·7 secs; the fundamental usually begins at 8·8 kHz and produces

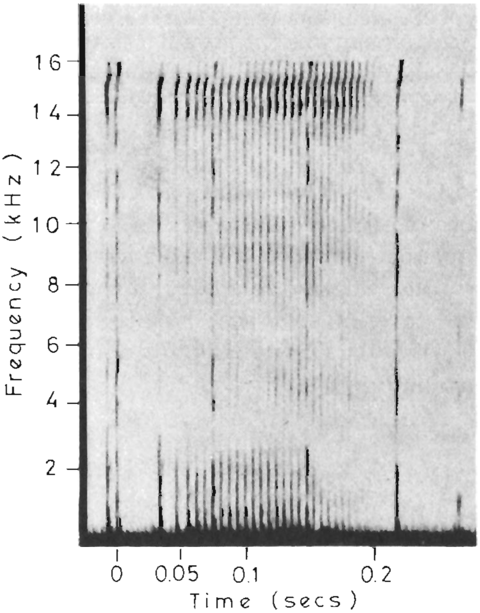

Fig. 8-89: *Globicephala malaena* (at sea). Sonagram of type 2 signal, creaking. (After Busnel and Dziedzic, 1966a; originally published by the University of California Press; reprinted by permission of The Regents of the University of California.)

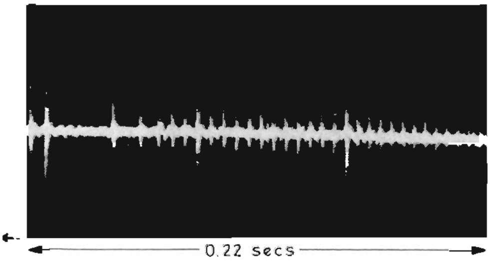

Fig. 8-90: *Globicephala melaena* (at sea). Oscillogram of type 2 signal, creaking. Total length in time: 0·22 sec. The sonagram of this signal is shown in Fig. 8-89. (After Busnel and Dziedzic, 1966a; originally published by the University of California Press; reprinted by permission of The Regents of the University of California.)

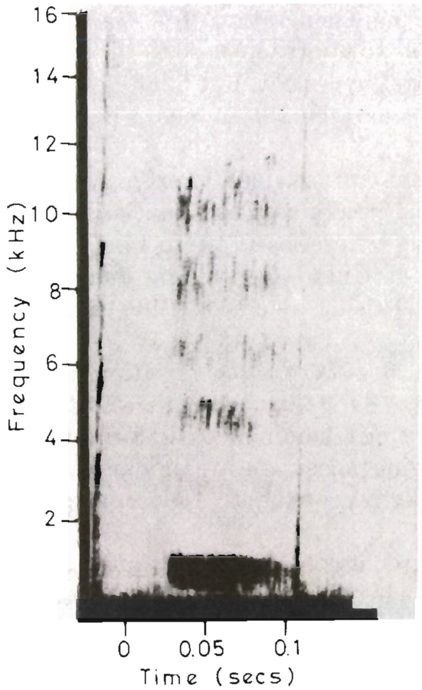

Fig. 8-91: *Globicephala melaena* (at sea). Sonagram of type 2 signal, blast. (After Busnel and Dziedzic, 1966a; originally published by the University of California Press; reprinted by permission of The Regents of the University of California.)

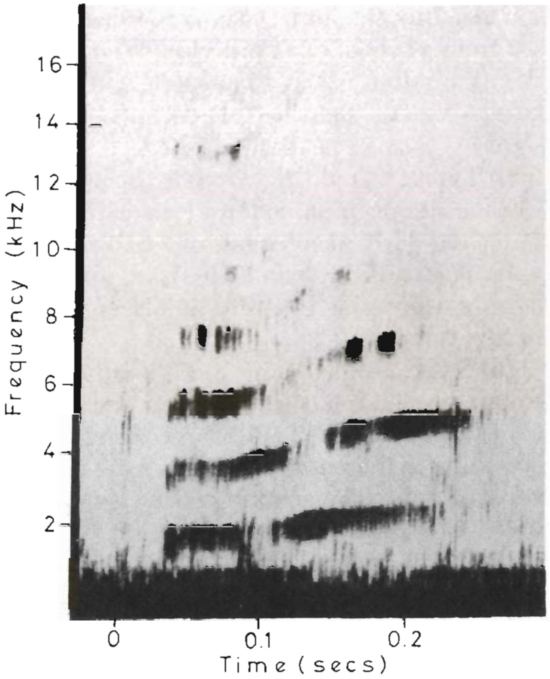

Fig. 8-92: *Globicephala melaena* (at sea). Sonagram of type 2 signal, squeaking. (After Busnel and Dziedzic, 1966a; originally published by the University of California Press; reprinted by permission of The Regents of the University of California.)

subharmonics, sometimes of low frequency (500 Hz). The initial flat part of the signal corresponds to a whistle which then goes over into a decrescendo, occasionally producing modulations, and ends at frequencies between 3 and 5·5 kHz.

(iv) Type 4 signal (Fig. 8-94) is characteristic and repeated regularly; it comprises two parts: creaking followed by a whistle. Total duration: 0·55 sec; main frequency: about 3 kHz. A variation of the signal has, in the first part, a fundamental above that of the whistle, 2 subharmonics and 4 to 5 harmonics.

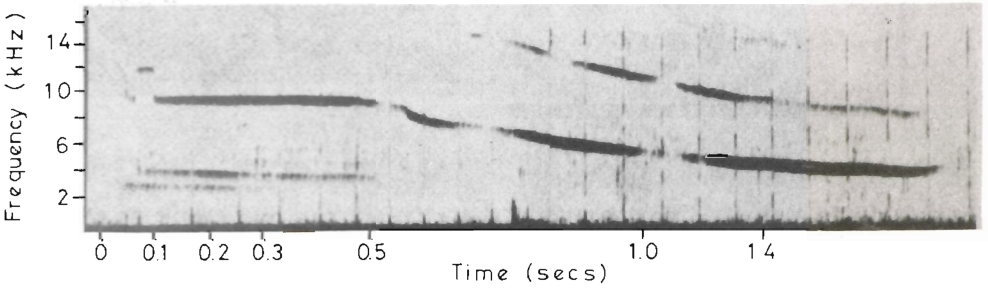

Fig. 8-93: *Globicephala melaena* (at sea). Sonagram of type 3 signal. (After Busnel and Dziedzic, 1966a; originally published by the University of California Press; reprinted by permission of The Regents of the University of California.)

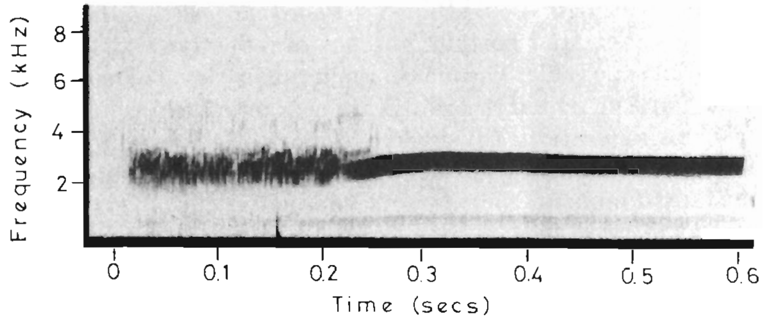

Fig. 8-94: *Globicephala melaena* (at sea). Sonagram of type 4 signal. (After Busnel and Dziedzic, 1966a; originally published by the University of California Press; reprinted by permission of The Regents of the University of California.)

(v) Type 5 signal (Fig. 8-95) is a long whistle (0·7–0·9 sec) starting and ending at 3 kHz with a peak at 4 kHz and revealing 1 or 2 superior harmonics.

Possibly, the 5 signal types can be given special characteristics and 'meanings' by variations in frequency or intensity and by breaks in the continuity of the signal. The signals obtained differ in frequency and general pattern from those recorded by Schevill and Watkins (1962) in *Globicephala melaena* and *G. macrorhyncha*. However, this difference reflects, according to Schevill and co-authors (1969), a difference in analytical techniques, especially in filter bandwidth. Additional, but less detailed information on properties of sounds emitted by *Globicephala* species has been presented by Kritler (1952), Brown (1960), Dreher and Evans (1962), M. C. Caldwell and Caldwell (1969a) and Busnel and co-authors (1971).

Underwater sounds of the harbour porpoise *Phocoena phocoena* have been studied by Busnel and co-authors (1963), Busnel and Dziedzic (1966a), Schevill and co-authors (1969), Titov and Tomilin (1970) and Dubrovsky and co-authors (1970b). They comprise predominantly low-intensity, narrow-band clicks, usually near 2000 Hz, produced singly or in bursts at repetition rates of up to 1000 sec^{-1}. However, Dubrovsky and co-authors (1970b) report the emission of occasional active-biosonar clicks of up to 100 kHz.

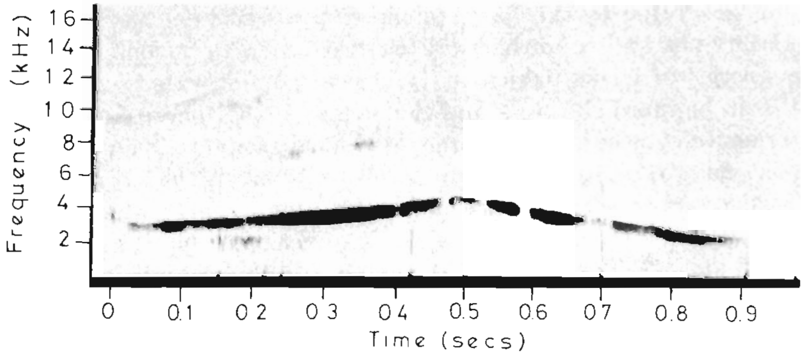

Fig. 8-95: *Globicephala melaena* (at sea). Sonagram of type 5 signal. (After Busnel and Dziedzic, 1966a; originally published by the University of California Press; reprinted by permission of The Regents of the University of California.)

SCHEVILL and co-authors (1969) studied 4 *Phocoena phocoena* held in a fish weir in 4·6 to 9·2 m of water. Mud bottom, absence of reflective walls and of shipping made quiet recordings possible. The maximum intensity level of the sounds emitted was ~1 dyne cm^{-2} at 1 m. Sound recordings are characterized by: (i) clicks or pulses, of 0·5 to over 5 msecs duration; (ii) single clicks or click bursts, up to 2 secs long; (iii) a dominant single frequency in each click (with little harmonic content); (iv) a relatively constant dominant click tone in successive clicks; (v) additional low-level overtones at discrete high frequencies not necessarily harmonically related. Despite shorter recordings the results parallel those obtained by BUSNEL and DZIEDZIC (1966a).

While WOOD (1952; see also WOOD and co-authors, 1970) reported loud barks, most of the pulsed sounds of captive *Stenella plagiodon* recorded by D. K. CALDWELL and CALDWELL (1971a) were of very low intensity. In marked contrast to these quiet pulsed sounds, *S. plagiodon* generates also loud narrow-band whistles. D. K. CALDWELL and CALDWELL (1971a) distinguish: sounds emitted during swimming, when feeding and during conditions suggesting excitement.

False killer whales *Pseudorca crassidens*, in the Mediterranean Sea, emitted sounds which resemble those produced by other delphinids during echolocation. The sounds are of short duration (~0·8 msec) with main energy between 8 and 12 kHz (BUSNEL and DZIEDZIC, 1968b).

Pelagic-oceanic rough-toothed dolphins *Steno bredanensis* generate highly directional echolocation signals; the sound pressure fields are directed sharply forward (NORRIS and EVANS, 1967). The highest frequencies (about 208 kHz) are emitted in a narrow beam. To each side of the beam frequency falls off rapidly (100 kHz at 10° and 60 kHz at 15° to either side of the midline). Maximum sound pressures relative to 0·0002 dyne cm^{-2} are reduced −6 dB between 11° and 17° from the midline and fall to about −17 dB at 45°. *S. bredanensis* exerts considerable control over the properties of the sounds emitted. Physical characteristics of signals emitted by *S. bredanensis* have been analyzed by BUSNEL and DZIEDZIC (1966b).

The finless porpoise *Neophocaena phocaenoides* emits clicks with repetition rates between 80 and 800 sec^{-1} and main energy between 0 and 4 kHz. In contrast to *Tursiops truncatus*, little energy content was found at higher frequencies (MIZUE and co-authors, 1967, 1968).

The sounds generated by the sperm whale *Physeter catodon* have been reviewed by D. K. CALDWELL and co-authors (1966a). At sea, *P. catodon* produce unique, monotonous series of clicks, which may be heard underwater over distances of 3000 to 6000 m or more (BACKUS and SCHEVILL, 1966). These burst-pulse clicks (Fig. 8-96) seem to be used for long-range food localization in open deep-sea water. Typical clicks have repetition rates up to 60 to 80 sec^{-1}. The highest repetition rates occur when a *P. catodon* is apparently examining a nearby object (NORRIS and HARVEY, 1972). The intensity of the clicks is sometimes very high (74 to 100 dB re 1 dyne cm^{-2} at 1 m). The burst pulses consist of 6 to 8 complex transients, each 0·5 to 1 msec in length; the entire click lasts usually close to 25 msecs, and click trains may sometimes continue for up to 1 min or longer (NORRIS and HARVEY, 1972). Compared to delphinid burst pulses, those of *P. catodon* are much lower in repetition rate. While the continuous delphinid click trains consist of single clicks repeated in a rather constant sequence, *P. catodon* emits bursts (clusters) of rapidly

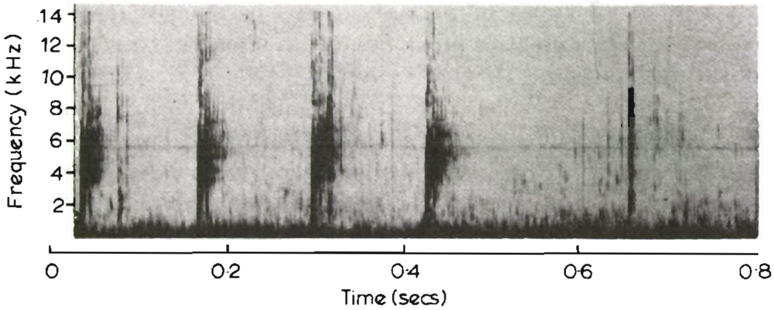

Fig. 8-96: *Physeter catodon* (at sea). Burst-pulse clicks. The broad frequency band of the first pulses decreases as the pulses are dampened. The horizontal band near 6 kHz is an artifact. Filter band width: 600 kHz. (After BACKUS and SCHEVILL, 1966; originally published by the University of California Press; reprinted by permission of The Regents of the University of California.)

damped clicks separated by relatively long silent periods. Further studies on *P. catodon* sounds have been published by WORTHINGTON and SCHEVILL (1957), BUSNEL and DZIEDZIC (1967a), and PERKINS and co-authors (*in*: BUSNEL and DZIEDZIC, 1967a).

A stranded subadult dense-beaked whale *Mesoplodon densirostris* emitted in-air sounds of fundamental frequencies from about 1000 to almost 6000 Hz (D. K. CALDWELL and CALDWELL, 1967). The fragmented information available on phonations of Risso's dolphin *Grampus griseus* have been summarized by D. K. CALDWELL and co-authors (1969), who recorded and described the sounds made by a stranded subadult male. A pygmy sperm whale *Kogia breviceps*, stranded and surviving for 48 hrs, emitted low-intensity and low-frequency (mostly below 1 to 2 kHz) sounds (D. K. CALDWELL and co-authors, 1966b).

Captive Ganges dolphins *Platanista gangetica* exhibit considerable, almost continuous phonations (HERALD and co-authors, 1969). They generate three different types of sounds (ANDERSEN and PILLERI, 1970): (i) Faint, high-pitched, regularly produced clicks of low intensity emitted during undisturbed swimming: most energy above 10 kHz, repetition rate about 80 sec^{-1}. (ii) Series of low-pitched clicks of much higher intensity, and with a regular repetition rate of ca 50 sec^{-1}; according to ANDERSEN and PILLERI, the concurrent behaviour suggests the use of these sounds in context with active biosonar. (iii) Very short, intense clicks noted at long, irregular intervals. These sounds resemble jaw snapping, but were not observed in connection with feeding. Whistles and bursts of pulses, typical of other odontocetes, were not heard.

For *Platanista indi*, PILLERI and co-authors (1970b) determined pulse repetition rates of 90 sec^{-1} in captivity and of 124 sec^{-1} in the natural river habitat. Intervals between repetition rates were about 1 to 60 secs. Frequencies ranged from 800 Hz to 16 kHz (some physical, but mostly biological sounds) and 20 to 100 kHz (biosonar pulses). The biological sounds are assumed to have communicative functions.

In captive Amazon dolphins *Inia geoffrensis*, PENNER and MURCHISON (1970) recorded high-frequency sounds between 25 kHz and 200 kHz and demonstrated echolocation capabilities (p. 804). Previously, M. C. CALDWELL and co-authors

(1966) had recorded 12 types of phonation in this species (crack, click (snap) whimper, bark, screech, squeak, squeaky squawk, squawk, squeal, grate, creaking door, echolocation-like run). M. C. CALDWELL and CALDWELL (1970) presented evidence for the absence of quasi-pure tone whistle in *I. geoffrensis*. The Amazon River dolphin *Sotalia fluviatilis* emits echolocation broad-band clicks, many with energy above 20 kHz (upper limit of the equipment used) with an apparent dominance range from 8 to 15 kHz (D. K. CALDWELL and CALDWELL, 1970b). Echolocation-type click trains were emitted especially during feeding. Click onset correlated directly with the approach to the food fish and ceased when the fish had been caught.

(e) Mechanisms of Sound Perception

Sound perception is a prerequisite for obtaining acoustic information on the environment, and hence for acoustic orientation. As in their terrestrial relatives, the inner ear is the most important sound-perceiving organ in marine mammals. But in forms fully adapted to aquatic life, other body parts co-operate significantly in sound uptake and sound conduction. Peripheral areas, especially sensitive to sound and vibration, act as general aerials and fat, oil or soft tissue may serve as major sound routes to the inner ear. Together with vision, hearing constitutes the most important mechanism of orientation in marine mammals.

The normal mammalian ear perceives sound in air; it is poorly adapted for underwater hearing. The ear of marine mammals had to adjust to acoustic conditions quite different from those encountered in air. The characteristic acoustic impedance of water is nearly 4000 times the characteristic impedance of air; hence, in air, a pressure wave of −74 dB re 1 μbar has the same acoustic intensity as a pressure wave of −38·5 dB re 1 μbar in water (SCHUSTERMAN and co-authors, 1972). In order to produce the same sound intensity, sound pressure in sea water must be 60 times as high as in air (REYSENBACH DE HAAN, 1957). Since, however, in a water sound wave, the maximum amplitude of particles displaced from their equilibrium position is only 1/60 of that in air, a much heavier and more rigid middle-ear mechanism is required. Moreover, the marine-mammal ear must be able to perceive much higher frequencies: for equal acoustic resolving power, the frequencies must be 4 to 5 times higher underwater than in air (REYSENBACH DE HAAN, 1957, 1966).

Studies on sound perception are concerned with anatomical and functional considerations of sound uptake, sound routes to the inner ear, and central auditory mechanisms. Auditory sensitivity and directional hearing have been studied in some detail only in a few representatives.

Anatomical and Functional Considerations

Anatomical and functional studies on mechanisms of sound perception in marine mammals are rare and often of a preliminary character. The ear of the sea otter *Enhydra lutris* and that of pinnipeds and sirenians differ less from the general anatomy of the terrestrial mammal ear than the ear of cetaceans. However, compared to terrestrial mammals, seals and sea lions have over-sized ossicles (MØHL, 1968b). In fact, progressive increase in weight of the auditory ossicula chain from otariids over phocids to sirenians is assumed to reflect the degree of genetic adaptation of these mammals to aquatic life. The external ear is reduced to a small pinna in otariids and is missing entirely in phocids. In the ringed seal *Pusa hispida*, the ear bones are markedly separated from the skull by enlargements of the lacerate foramen and the fissura petrosoccipitalis (Møhl, 1964). The hearing organ of cetaceans has been suggested to possess properties of a pendulum (Reysenbach de Haan, 1957): a suspension system is supposed to allow the ear to move differently relative to the skull, thus augmenting directional hearing (p. 790), since both ears are acoustically isolated from each other and from the skull. This suggestion has received support from Fleischer (1972). According to Reysenbach de Haan (1957, 1960), the pendulum consists of the mass of the heavy os petrotympanicum, connected by a rigid ligament to the large mass of the skull (suspension point). The properties of this system depend on the magnitude of the suspended mass (os petrotympanicum) and the stiffness of the suspension (ligament). The larger the mass for a given rigidity of suspension, the lower is the frequency of the system itself; the greater the rigidity for a given mass, the higher is its own frequency. The relations between the frequencies that are imposed on this mechanism and its own specific frequency, which is low, are such that the os petrotympanicum stands still with respect to ecologically significant sound frequencies.

Preliminary experiments on the common river otter *Lutra canadensis* indicate that the upper frequency limits, both in air and in water, do not differ significantly from those determined for ears of terrestrial carnivores (Evans and Bastian, 1969).

In pinnipeds, high-frequency sound perception occurs in *Phoca vitulina* and *Zalophus californianus* (Møhl, 1964, 1967). According to Norris (1969), this high-frequency hearing may be expected to be paralleled by anatomical modifications of the middle and inner ear. The cavity of the middle ear of *Z. californianus* and *Eumetopias jubatus* is lined by a mucosa containing a complex network of venou-channels and sinuses. Odend'hal and Poulter (1966) have suggested that, during dives, the hydrostatic pressure within the middle ear may be kept equal to the pressure in the external auditory meatus either by distension or depression of the mucosa due to the presence or absence of blood in the sinuses. Schusterman and co-authors (1972) assume that *Z. californianus* depends on different mechanisms for perceiving sonic and ultrasonic frequencies of underwater sounds. Only after several changes between sound frequencies above and below 36 kHz did the sea lion learn to shift readily from one mechanism of detection to the other.

In regard to sirenians, Bertram (1963) has suggested—without presenting precise data—high capacities for sound perception. The middle ear of sirenians contains large, extremely dense ossicles; but, as in cetaceans, the external auditory meatus is greatly reduced (1–3 mm in diameter; Evans and Bastian, 1969); more than 90% of the volume of the periotic bone consists solely of dense bone with no parts of the labyrinth or the acoustic nerve in it (Fleischer, 1971). A heavy perioticum facilitates movements of the stirrup relative to the periotic bone and hence effective hearing.

The fundament of our current anatomical knowledge on the cetacean ear has been laid by Boenninghaus (1903), Yamada (1953), Fraser and Purves (1954, 1959, 1960), Reysenbach de Haan (1957, 1960), Dudok van Heel (1962), Purves and van Utrecht (1963) and Purves (1966). Hearing in cetaceans is based on a mechanism homologous, and quite similar, to that operative in terrestrial mammals. Sound is transmitted via the ossicular mechanism of the middle ear by way of the tympanic annulus. Sound transmission involves displacement amplification (PURVES, 1966). In odontocetes, each ear is isolated acoustically from its immediate surroundings by air cavities. As the dolphin dives, this sound barrier adjusts to ambient hydrostatic pressure (FRASER, 1959; PURVES, 1966). Comparable acoustic barriers appear to exist around the ears of other marine mammals. The foam in the ear-surrounding air cavities of odontocetes—reported by PURVES and other authors—is not always present. According to NORRIS (personal communication), the foam represents 'almost certainly' a post-mortem artefact. Shrapnell's membrane is well developed in odontocetes, presumably resulting from atavistic conversion of the terrestrial mammal's tympanic membrane into a ligament. The ability to transmit high-frequency vibrations is due to the bony fusion of the manubrium to the tympanic annulus (PURVES, 1966).

On the basis of anatomical evidence, a number of theories have been advanced regarding the functioning of the cetacean ear (Table 8-7). Some of these theories

Table 8-7

Theories on sound perception in cetaceans (After PURVES, 1966; originally published by the University of California Press; reprinted by permission of The Regents of the University of California)

Theory	Author
1. Hearing occurs above water only, with air vibrations entering by the Eustachian tube.	CAMPER (1777), BUCHANAN (1828)
2. Tympanic bulla acts as resonance chamber. Auditory ossicles functional. Tympanic membrane and meatus functionless.	HUNTER (1787), HOME (1812), DENKER (1902), LILLIE (1910), KELLOG (1938)
3. Sound conducted through bones of skull, thence through air sinuses to middle ear. Periotic acoustically isolated. Chief vibrator, fenestra rotundum. Ossicles secondary. Meatus and tympanic membrane functionless.	CLAUDIUS (1858), BEAUREGARD (1894), TURNER (1913)
4. Sound enters anterior opening of bulla from periosteal lining of pterygoid sinus. Periotic acoustically isolated. Molecular vibration of ossicles only. Meatus and tympanic membrane functionless.	BOENNINGHAUS (1903)
5. 'Seismographic' principle. Periotic not acoustically isolated. Body vibrates as a whole while bulla remains stationary. Meatus and tympanic membrane functionless.	YAMADA (1953)
6. Sound enters by proximal end of external meatus. Tympanic membrane and ossicles functional. Amplification phenomenon. Periotic acoustically isolated. Distal end of meatus and muscles functionless.	REYSENBACH DE HAAN (1957)
7. As in item no. 6, except that meatal muscles produce tension of tympanic membrane	DUDOK VAN HEEL (1962)
8. Longitudinal waves conducted by external meatus.	HYRTL (1845)
9. Longitudinal waves conducted by external meatus, modified by extrinsic muscles. Tympanic membrane and ossicles functional. Amplification phenomenon and acoustic isolation.	FRASER and PURVES (1954, 1960), PURVES and VAN UTRECHT (1963)

have been re-evaluated and discussed in detail by **Purves** (1966).

While the principal structures of cetacean sound perception conform with those of other mammals, several special features exist (**Jansen** and **Jansen**, 1969): (i) The basilar membrane of the cochlea is very long (in *Balaenoptera physalus* at least 3 times as long as in man: **Hall**, 1967) and narrow (the narrowness seems to facilitate perception of high-frequency sounds). (ii) The cochlear nerve contains 3 to 4 times as many fibres as that of man. (iii) The ventral cochlear nucleus is strongly developed while the dorsal nucleus is small, as in man. (iv) The estimated total number of cells in the cochlear nuclei varies considerably from species to species; but even in *Phocoena phocoena* (fewest nuclei cells observed thus far) total cell number is about 5 to 6 times that of man. (v) The ratio of primary to secondary auditory neurons appears to be approximately 1:6; this suggests a considerable capacity for impulse processing at the level of the second-order neurons. (vi) Additional indications of an exceptionally high development of the auditory system are provided by the trapezoid body, the superior olive, the nuclei of the lateral lemniscus, the inferior colliculus, the medial geniculate body, and the temporal lobe. The large secondary acoustic nuclei (trapezoid-body nucleus, lateral superior olivary nucleus) and the small or non-existent medial superior olivary nucleus parallel the differential development of these structures in bats and seem to be related to active-biosonar capabilities.

Further anatomical and functional features of the acoustic perception apparatus of cetaceans have been discussed by **Dailly** (1971) and compared to his own findings on the primary cochlear nuclei of the Amazon dolphin *Inia geoffrensis*. Focusing attention on the river-inhabiting *I. geoffrensis* and the marine *Delphinus delphis* (**Zvorykin**, 1963) and *Phocoena phocoena* (**Osen** and **Jansen**, 1965), **Dailly** concludes that no significant differences exist. *I. geoffrensis* and *P. phocoena* possess anatomically equally well-developed acoustic nuclear structures. However, the marine forms are superior in regard to their optical capabilities (p. 724).

Sound perception may suffer from masking: the 'drowning' of faint sounds in the presence of loud ambient noises. The masking effect is greatest for sounds whose frequencies are close to the disturbing background noise. Hence high frequencies of echoranging signals reduce or avoid masking. In addition, they enhance information on acoustic detail; their pulse character is important in solving signal/noise problems.

Sound Routes to the Inner Ear

In air, and possibly also underwater, the amphibious marine mammals—sea otter and pinnipeds—perceive ambient sounds primarily via their external auditory canals. While nothing pertinent is known on sirenians, the most effective sound routes to the inner ear of cetaceans are still a matter of dispute.

In odontocetes, ambient sounds are first perceived by skin and blubber coat. Subsequent channelling of the acoustic energy absorbed occurs by tissue discontinuities such as interphases between blubber, muscle, fat, bone or between tissues and internal liquids (e.g. oil). Three major routes to the inner ear have been suggested: (i) fat body in the lower jaws; (ii) soft body tissues, especially in the head region; (iii) external auditory canal.

The importance of skin and blubber coat for sound uptake has been stressed by Belkovich and Nesterenko (1971, 1972). Sokolov and Kalashnikova (1971) found various ultrastructural features in the epidermis of *Phocoena phocoena*, but could not ascertain their definite functions. Belkovich and Nesterenko have suggested that the whole, well-innervated, external skin surface, especially in the head region, serves as receiving area for acoustic as well as other environmental cues. This suggestion is supported by recent experiments (Norris, in press): Small hydrophones implanted in the head of freshly dead adult *Tursiops truncatus* indicate that pulsed sounds are channelled by the blubber coat and reflected by blubber–muscle interfaces. Sea-borne sound entering the body of an odontocete first encounters a water–blubber interface. Thus the blubber may act as general sound perceiver. Once inside the body, the sound will hit on various tissue layers which may channel and modify the acoustic energy perceived.

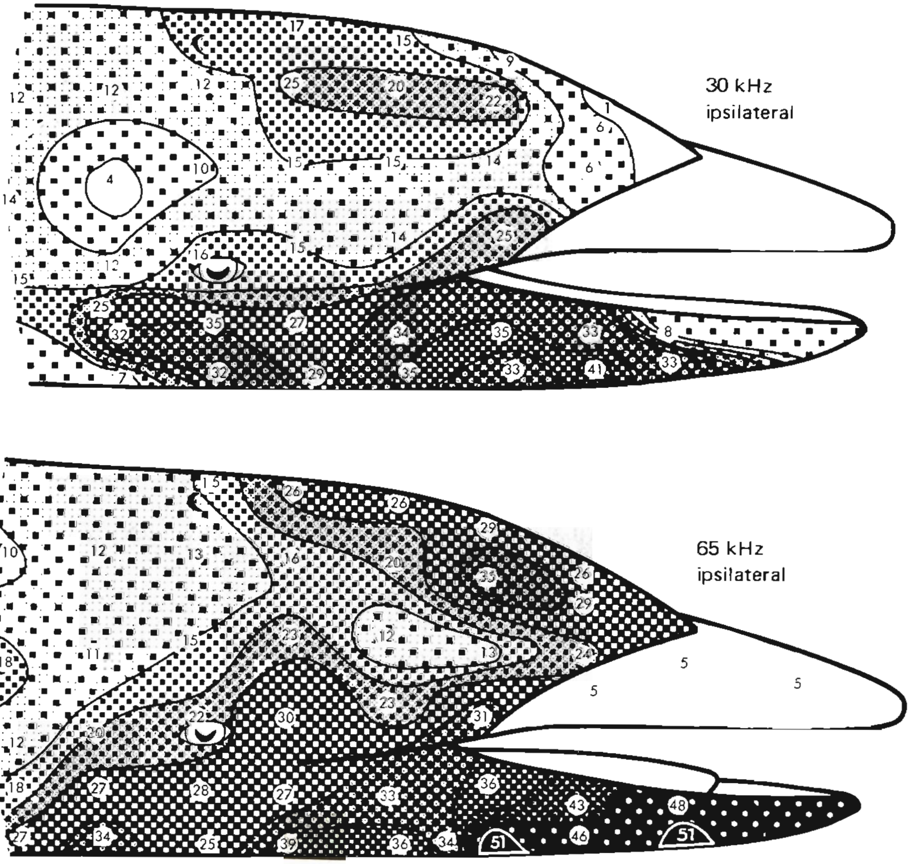

Fig. 8-97: *Stenella caeruleoalba*. Ipsilateral pattern of sensitivity to sound cues, produced by a hydrophone pressed against the head surface at the points indicated. Numerical values represent attenuation at threshold: highest numbers indicate greatest sensitivity. Contour lines are drawn at intervals of 5 dB. Recording was from the inferior colliculus. (After Bullock and co-authors, 1968; reproduced by permission of Springer-Verlag, Berlin.)

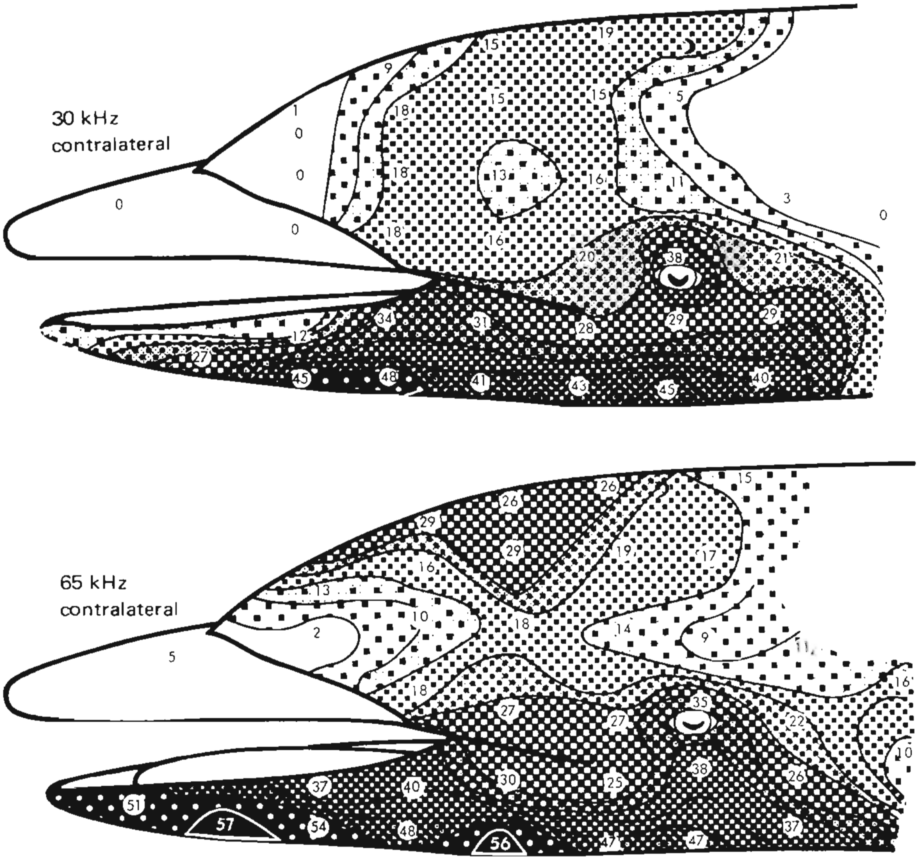

Fig. 8-98: *Stenella caeruleoalba*. Contralateral pattern of sensitivity to sound cues. Conditions as described in legend to Fig. 8-97. (After Bullock and co-authors, 1968; reproduced by permission of Springer-Verlag, Berlin.)

The fat body inside the lower jaws of some delphinids has been credited with the function of a major sound route. Postulated by Norris (1964), facilitation of sound transmission by intra-mandibular fat has received support from experiments conducted by Yanagisawa and co-authors (1966) and Bullock and co-authors (1968). In *Stenella caeruleoalba*, Bullock and co-authors found sensitivity to ambient sound to be maximum over the side of the contralateral lower jaw, nearly as high over the ipsilateral side of the melon, markedly lower over the side of the head (including the external ear orifice), and almost nil at the rostrum (Figs 8-97, 8-98). A cone of best sound reception is directed forward and downward, some 5 to 30° from the midline in the horizontal plane (the higher the frequency the closer to the midline), and 5 to 20° below the horizontal. At more lateral angles, sensitivity decreases sharply (up to 1·5 dB degree^{-1}). Perception of sound coming from above the horizontal is presumably much reduced.

In a variety of delphinids, the skin surfaces of posterior mandibles and melon form angles relative to the longitudinal body axis that allow near-maximum

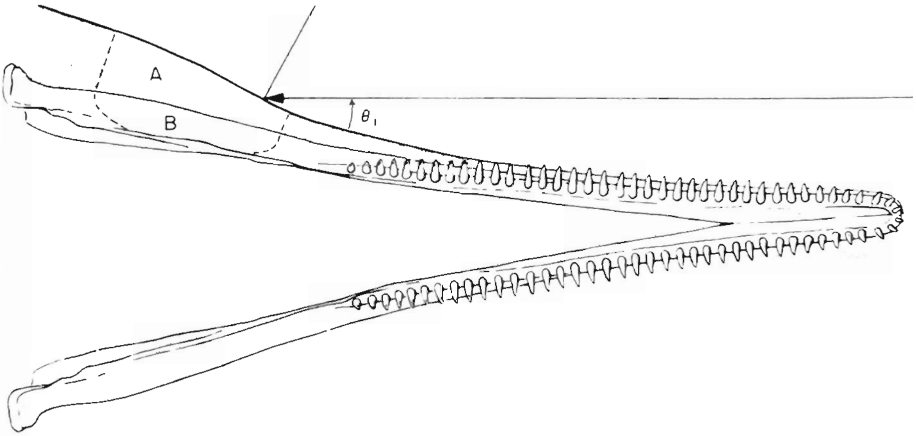

Fig. 8-99: Delphinid lower jaw, showing tissue overlying the jaw (upper part of figure) with its fatty 'acoustic window' (A, B) and angle of incidence (θ_i) of sound (arrow) received from ahead. (After NORRIS, 1969; reproduced by permission of Academic Press, Inc.)

transmission of echoes from own clicks into the head tissue (Fig. 8-99); by rotating movements of the snout (scanning) large transmission changes are produced (NORRIS, 1968, 1969). In some species, perception angles differ on jaw and melon and may serve to allow both sensitive hearing and fine angular discrimination. Scanning moves the echo received from a given object relative to the position of jaw and melon surfaces, 'hence the intensity of reception can be varied in a very refined way' (NORRIS, 1969, p. 414). According to BULLOCK and co-authors (1968), sound may also reach the mandibular fat body from the melon via local soft tissues.

Soft body tissues, especially in the head region, have been suggested to act as main sound routes to the inner ear by several workers, e.g. MCCORMICK and co-authors (1970) and FLEISCHER (1972). MCCORMICK and co-authors studied *Tursiops truncatus* and *Lagenorhynchus obliquidens*. They report that the external auditory meatus has become vestigial and no longer serves for sound conduction. The tympanic membrane lacks a direct connection with the ossicular chain; it is connected only by a ligament and is also non-functional. The ossicular chain retains its acoustic function, although the malleus can be lost without serious effects. Ambient sounds enter, and are assumed to be conducted by, soft tissues. Cochlear stimulation occurs by bone conduction similar to this situation in other mammals. FLEISCHER examined 4 heads of *T. truncatus*, frozen shortly after the dolphins had died. He found that the outside of the tympanicum (vibration receiver) is situated underneath the skin surface shown to be most sensitive to ambient sound by BULLOCK and co-authors (1968). FLEISCHER assumes that the vibrations travel through soft head tissues to the hearing organ, and that the tympanic ligament acts as receiver and conductor of vibrations, especially at high frequencies. Stimulation of the outside of the tympanic bone results in movements of the stirrup relative to the periotic bone. This could be measured up to 240 kHz, with a maximum sensitivity at 46 kHz. Fusion of the goniale to both malleus and tympanicum is essential for hearing: fracture causes inability of the middle ear to transport sound (at least its high frequencies). The connection between the vibrating, thin part of the tympanicum and the perioticum is weak and FLEISCHER's tests indicated to him that this structure functions as a decoupling device, especially for high frequencies.

The external auditory canal has been claimed to act as primary sound route in *Platanista indi* by PURVES and PILLERI (1973; see also PURVES, 1966). These authors insist that sound conduction is not the major function of the fat body inside the lower jaws of odontocetes. They stress the great disparity of fat-body dimensions throughout the order, the difficulty in avoiding jamming by self-produced sounds, and the danger of damage to the sound-conducting mechanism when the lower jaws are used as a weapon (e.g. when attacking sharks, sometimes with such force as to lift them clear out of the water). Anatomical studies on a head of *P. indi*, perfused with formaldehyde, indicated to PURVES and PILLERI that the external auditory canal seems to be fully functional; it is much wider than in other odontocetes and contained in a thick cartilage throughout its length. The shape of the tympanic membrane is intermediate between that of terrestrial mammals and of higher delphinids; but the ossicular chain of the middle ear and the cochlea resemble their equivalents in the higher delphinids.

BELKOVICH and NESTERENKO (1971, 1972) assume that passive-biosonar signals enter through the external auditory canal of delphinids, while active-biosonar signals are perceived via the lower jaw, assisted by the skin of the rostrum.

In summary, the evidence at hand suggests general sound uptake by the external skin surface (aerial function) and subsequent sound channelling in accordance with the patterns of continuities and discontinuities in medium density encountered. Size, direction and shape of the sound-conducting media (e.g. fat, oil, soft tissues, muscles, bones) and the interphases between them affect sound distribution and sound properties. Accordingly, details of sound routes are likely to differ in different species and during ontogeny. While the external auditory canal may be functional in some of the more primitive species, its importance in odontocetes is reduced in comparison to the situation met in pinnipeds or terrestrial mammals. Fat bodies, soft tissues and fluid (oil) compartments which facilitate short-route sound conduction to the inner ear qualify as primary internal sound paths.

Central Auditory Mechanisms

In order to serve as orientational cue, sound energy must be made available to central processing organs: energy of elastic medium deformation must be transformed into an energy form acceptable to neurophysiological transfer, computation and evaluation.

In cetaceans, especially odontocetes, anatomical evidence testifies to extraordinarily well-developed central auditory structures (e.g. LANGWORTHY, 1932; OGAWA and ARIFUKU, 1948; KRUGER, 1959, 1966; BREATHNACH, 1960; JACOBS and JENSEN, 1964; HALL, 1967; JANSEN and JANSEN, 1969). However, our present knowledge on central auditory mechanisms in marine mammals is quite limited and restricted largely to odontocetes. Only a few aspects, immediately pertinent to orientation in space, are reviewed here.

Twelve sea lions *Zalophus californianus* and one harbour seal *Phoca vitulina* were examined by BULLOCK and co-authors (1971) by recording acoustically evoked potentials from the inferior colliculus and adjacent structures. Electrical recording from electrodes inserted into the brain stem (either under barbiturate anaesthesia, acutely, or without anaesthesia, after implanting the electrodes some days before recording) produced similar results in air and underwater. The properties found do not seem to differ greatly from those in the human auditory system. But BULLOCK and co-authors imply, by extrapolation from the physiological properties of the potentials evoked, that *Z. californianus* and *P. vitulina* are much less skilful with respect to 'fine grained' acoustical discrimination than delphinids. The averaged response evoked by a sharply rising tone consists of early brief peaks and later slow waves. The latency of the earliest deflection is 3·5 to 4·8 msecs from the moment of arrival to a sound pip at the ear. The potential increases in size with sound intensity over a range of 60 to 70 dB. Both pinnipeds tested are less well specialized than delphinids for perceiving and evaluating sounds of extremely short duration and fast rise time, for rapid recovery, or for ultrasonic frequencies (best frequency is about 4 to 6 kHz).

Employing gross-electrode electrophysiological techniques, BULLOCK and co-authors (1968) investigated the central auditory mechanisms of 29 specimens of 4 species of dolphins (mostly striped dolphin *Stenella caeruleoalba*). Under N_2O and Fluothane anaesthesia, supplemented by succinylcholine chloride, the test individuals were stimulated with air-borne sound, water-borne sound and by hydrophone pressed against the head. None of the response parameters studied was found to be affected by the anaesthetics used. The responses recorded (chiefly from the inferior colliculi, but also from medullary auditory centres and the medial geniculate body) are onset responses of complicated waveform, usually consisting of components with latencies of 2 to 4 msecs. The longer latency responses probably represent heterogenous input to the inferior colliculi and, in a few cases, activity of collicular cells or input into the medial geniculate body; the shorter latency responses presumably are output of the cochlear nuclei and activity of medullary auditory nuclei. Response thresholds and waveforms are sensitive to changes in rise time between 0·1 and 0·2 msec. Evoked potential responses, in certain locations and intensity ranges, vary with sound intensity changes as small as 1 dB; in other intensity ranges, even changes of up to 10 dB cause little alteration. Gentle stroking of the side of the jaw or splashing of water on the jaw masks the response to sounds. The effective input of such stimuli is acoustic and the effective area is identical to that for sound. But electrical stimulation of the skin of the jaw neither elicits response in auditory centres nor masks the responses to sound.

According to BULLOCK and co-authors (1968), there are heterogenous populations of neurons from which recordings can be obtained; some of these appear to be especially adapted to active-biosonar functions. Possibly, significant populations of cells exist that are specifically responsive to sounds with certain characteristics of frequency modulation. Temporal resolution of successive sounds is extremely rapid: recovery of responsiveness takes a minimum of 0·8 to 1·0 msec between clicks; some initial recovery is often recognizable at ca 0·5 msec; more typical recordings show complete recovery after 3 to 5 msecs. The effective interaural distance (between the most sound sensitive areas on both lower jaws) represents a binaural time difference of about 60 to 90 msecs. In humans, arrival times are about 4 or 5 times this value; hence the authors suggest that it would require resolution of arrival-time differences of 2 to 3 msecs for dolphins to localize as well as man in the horizontal plane. However, there is no evidence for this, and the theory does not provide for a central mechanism of vertical localization. Consequently, BULLOCK and co-authors propose that orientation may be primarily based on intensity measurements assisted by head scanning.

The auditory zone of the brain cortex of *Phocoena phocoena* has been determined by recording the potentials induced by clicks (LADYGINA and SUPIN, 1970). The focus of the maximum amplitude of primary responses is located 1·5 to 3 cm laterally of the sagittal suture and 5·5 to 6 cm caudally of the coronary suture. In the auditory zone, the primary response occurs with a latent period of 6 msecs, the secondary response with a latent period of 15 to 20 msecs.

An unusual sensory area in the cerebral neocortex of *Tursiops truncatus* has been described by LENDE and WALKER (1972). Multiple-unit responses were elicited from a cortical area located on the broad frontal pole of the right hemisphere of the brain by (i) air-borne auditory stimuli; (ii) underwater auditory stimuli; (iii) cutaneous mechanical stimuli; and (iv) other mechanical stimuli (tapping teeth, skull, or wooden headrest). The authors discuss the possibilities that the area is auditory, activated by acutely sensitive cutaneous mechanoreceptors, or activated by either somatosensory or auditory inputs. Since cetacean neural functions are exceptionally specialized and only few data are available, no final conclusions are drawn regarding the nature of this neocortical sensory area.

A more definite picture regarding the computation and evaluation of acoustic energy by central auditory mechanisms of marine animals may be expected from future detailed electrophysiological studies employing micro-electrodes.

Auditory Sensitivity

Only a few accounts exist on auditory sensitivity of marine mammals. For individuals of *Zalophus californianus*, *Phoca vitulina*, *Inia geoffrensis*, *Tursiops truncatus*, *Phocoena phocoena* and *Orcinus orca*, underwater audiograms (lower sound-detection thresholds over a wide range of pure-tone frequencies) have been obtained (Fig. 8-100). Prior to testing their auditory sensitivity, the test animals were conditioned (e.g. encouragement through feeding, discouragement through non-feeding or gentle punishment) to indicate the presence of a tone (e.g. by pressing a lever or emitting a sound). They were also trained to maintain their head at a certain distance and in a defined position relative to the sound source immediately before being offered the test signal (e.g. Fig. 8-101).

In the California sea lion *Zalophus californianus*, the frequencies tested ranged from 250 Hz to 64 kHz (SCHUSTERMAN and co-authors, 1972). The audiogram obtained (Fig. 8-100) reveals high sensitivities from 1 to 28 kHz with a sensitivity maximum near 16 kHz. Between 28 and 36 kHz auditory sensitivity decreases rapidly. With relatively intense signals (>38 dB re 1 μbar), *Z. californianus* is claimed to respond to frequencies at least as high as 192 kHz.

In the harbour seal *Phoca vitulina*, MØHL (1968a) used frequencies ranging from 1 to 180 kHz. The audiogram obtained (Fig. 8-100) reveals that sensitivity to

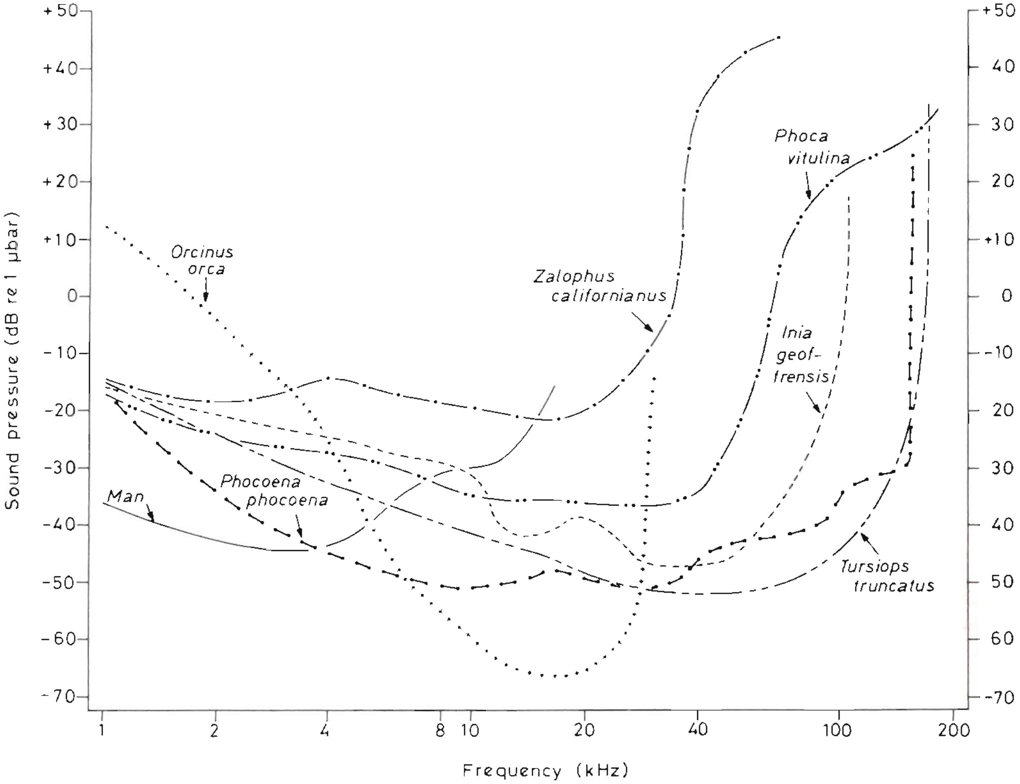

Fig. 8-100: Underwater audiograms of 5 marine mammals and man. Compiled from sources quoted in the text.

high frequencies falls rapidly above 50 kHz. Maximum underwater auditory sensitivity lies near 32 kHz (see also Møhl, 1967); in contrast to man, auditory sensitivity and frequency range are greater underwater than in air.

The Amazon dolphin *Inia geoffrensis* was tested at frequencies between 1·0 and 105 kHz. Highest sensitivities were recorded between 75 and 90 kHz (Jacobs and Hall, 1972); in this range the lower auditory threshold lies near –50 dB re 1μbar. The effective upper frequency threshold is 105 kHz.

The bottle-nosed dolphin *Tursiops truncatus* has been tested by Kellogg and Kohler (1952), Schevill and Lawrence (1953), Johnson (1966, 1967a, 1968) and Bullock and co-authors (1968). While early behavioural experiments by Kellogg and Kohler suggested auditory sensitivities up to about 80 kHz, the tests by Schevill and Lawrence—during which a trained dolphin was required to return for a food reward upon hearing a tone of random frequency—indicated hearing up to about 153 kHz. Johnson's audiogram (Fig. 8-100) confirms this higher value. Johnson required a *T. truncatus* to push a lever-operated switch upon hearing a pure-tone signal of random frequency (75 Hz–150 kHz). He recorded high sensitivities between 10 and 75 kHz, and maximum sensitivity between 50 and 70 kHz. The latter values have been confirmed by Bullock and co-authors, who reported maximum auditory sensitivity of about 60 kHz. Below 50 kHz, Johnson found the lower sensitivity threshold to increase continuously with decreasing frequency to about 37 dB at 75 Hz (not shown in figure). BELKOVICH and SOLNTZEVA (1970) report, with certain reservations, that sound perception in *T. truncatus* and *Delphinus delphis* is possible up to 280 kHz. Working on dead *T. truncatus*, FLEISCHER (1972) reports a maximum sensitivity near 46 kHz. However, auditory sensitivities obtained on fixed preparations suffer from a number of drawbacks and certainly must be expected to represent sub-optimal conditions, e.g. due to the absence of muscular tuning effects. JACOBS (1972) determined the range of maximum frequency-discrimination sensitivity of *T. truncatus* to lie between 2 and 20 kHz. Measurements by HERMAN and ARBEIT (1971), however, suggest that maximum frequency sensitivity may extend considerably beyond 20 kHz.

The harbour porpoise *Phocoena phocoena* was tested by ANDERSEN (1970a) at frequencies ranging from 1 to 150 kHz. Maximum auditory sensitivity was obtained between 8 and 32 kHz. Between 140 and 150 kHz the sensitivity falls off rapidly. The audiogram for *P. phocoena* (Fig. 8-100) is similar to that obtained for *Tursiops truncatus*. Using the method of skin-galvanic responses, SUPIN and SUKCHORUCHENKO (1970) report auditory perception of pure tones in *P. phocoena* from 4 to 180 kHz with a sensitivity maximum between 64 and 128 kHz. For sounds with a bandwidth of about 1 octave (total range offered: 3–100 kHz), auditory thresholds resemble those obtained for pure tones (SOKOLOV, 1971).

In the killer whale *Orcinus orca* an audiogram was obtained by HALL and JOHNSON (1971) for frequencies between 500 Hz and 31 kHz. Maximum signal sensitivity was recorded at 15 kHz (-70 dB re 1 dyne cm^{-2}). The observed upper limit of hearing was 32 kHz. Frequencies below 500 Hz were not tested.

An air audiogram has been obtained for the harp seal *Pagophilus groenlandicus* by TERHUNE and RONALD (1971). Using frequencies from 1 to 32 kHz, the maximum auditory in-air sensitivity was 4 kHz (at 29 dB re 0·0002 dyne cm^{-2}). The authors believe that the outer and (or) middle-ear structures and their acoustic impedance mismatch with the air, are responsible for the comparatively irregular and slightly insensitive hearing of the seal in air, and that the lumen of the external auditory canal is acoustically blocked.

Experiments by MCCORMICK and co-authors (1970) on the *Tursiops truncatus* ear involved making a hole in the outside of the tympanic bone. According to FLEISCHER (1972), such procedure would almost inevitably break the goniale; this would explain why the maximum auditory sensitivity found by MCCORMICK and co-authors lies at much lower frequencies than in other studies, and why the malleus and the tympanic ligament could be removed without significantly reducing the effectiveness of the ears as examined by means of cochlear microphonics.

A detailed evaluation of the audiograms obtained is not possible. Lower and upper hearing thresholds, maximum sensitivities and curve shapes have been obtained, in most cases, from single individuals. In order to be representative of a population or of the species, statistically valid data must be presented for both sexes and for different age groups. The validity and comparability of the audiograms obtained is further restricted by the different conditional techniques employed, discrepancies in recording equipment and tank properties, and failures to provide exact data on water quality (e.g. temperature and salinity) as well as on distance between sound source and test animal.

Directional (Binaural) Hearing

Directional hearing requires binaural perception: unless the head is moved, a single ear cannot discern the direction of a sound source. Directional hearing is based on (i) the time difference in sound perception by both ears, which depends upon the distance between the peripheral most sensitive sound receiving areas and the velocity of internal sound conduction; (ii) differential sound intensity; (iii) differences in phase and complexity of the sounds; (iv) central nervous interpretation of such differences. A sound source located to the right of a listener is perceived earlier and with a higher intensity by the right ear because the sound path is shorter and because, in air, the left ear is 'shadowed' by the head. This shadow effect is practically absent in water. Differences in phase occur in simple tones, since the longer travel time to the farther ear allows the sound waves to get out of phase. Sound complexity can provide directional cues because the farther ear receives the high-frequency components attenuated. The acoustic energy perceived by both ears is computed and evaluated by central nervous processes which then initiate the orientational response.

In the human ear, binaural hearing in air is based mainly on intensity in the case of high tones, on phase in low tones, and on intensity, time and timbre* in complex tones and noises. For divers, minimum audible angles (MAA) were determined underwater (3·5 kHz, 6 kHz, and broad-band white-noise pulses of 100 msecs duration with a rise-decay time of 10 secs, and a repetition rate of 1 $\sec^{-1}$). After training, the mean MAAs obtained were 11·3° at 3·5 kHz, 11·5° at 6·5 kHz, and 7·3° with white noise (FEINSTEIN, 1973). Assuming that the MAAs reflect the general level at which the binaural system operates, it seems likely that man can be an effective underwater sound navigator.

In the marine mammals tested thus far, the capacity for directional hearing is high. It differs in different species, and even in individuals, and depends on the properties of the sounds perceived, and on the angle and distance of the sound source. In cetaceans—presumably also in other forms—the inner ears are acoustically isolated to a considerable extent from ambient tissues. In the cetaceans examined this isolation is accomplished by air cavities (p. 780). Maximum efficiency of evaluating small differences in sound intensity and sound spectrum requires that echolocators employ beamed high-frequency components and that they use wavelengths comparable to the total dimensions of their air cavities.

Acoustic energy does not necessarily propagate along straight lines. It bends around obstacles and its direction may be modified by discontinuities in the conducting media, as well as by rapid media movements (in air: heavy winds; underwater: pronounced water currents). Consequently, the terminal sound path may not always be indicative of the true direction of the sound source.

In the California sea lion *Zalophus californianus*, directional hearing has been documented by GENTRY (1967). A young male was trained to approach one of two underwater transducers in a partially anechoic tank. The minimum audible angle was 10° at 6 kHz, and 15° at 3·5 kHz. At an angle of 25°, a generally linear improve-

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* Sounds with a different distribution of energy among the overtones seem different to the human ear, even though they may have the same fundamental frequency and contain the same overtones. This difference, arising from the relative magnitude of the components, is called the 'timbre'.

ment in auditory localization was found from 1·5 to 6·5 kHz; the performance was conspicuously poor at 2·5 kHz. GENTRY concludes from his experiments that *Z. californianus* can probably locate sound direction as well as the harbour porpoise *Phocoena phocoena*. Directional hearing has also been reported for the harbour seal *Phoca vitulina* (MØHL, 1964): for a single seal, a minimum azimuth angle of about 3·1° was obtained at 2 kHz.

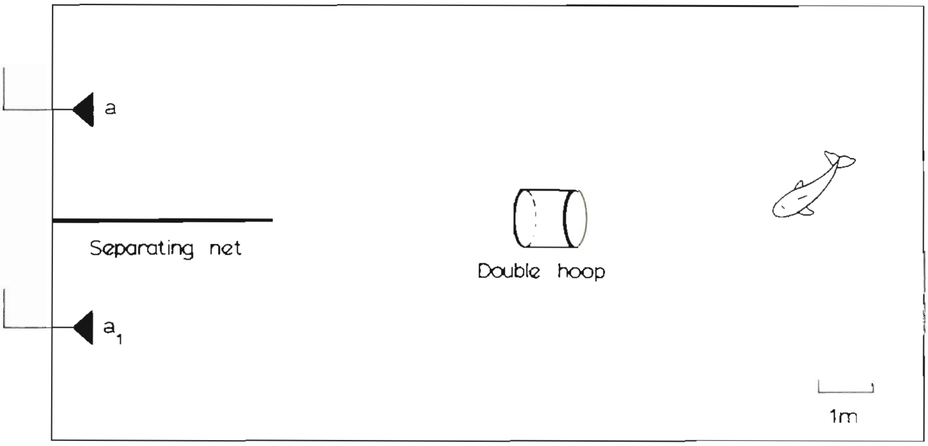


Fig. 8-101: *Phocoena phocoena*. Experimental design for testing directional hearing. a, a_1: transducers. (After ANDERSEN, 1970b; modified; reproduced by permission of Professor G. Pilleri.)

Directional hearing in the harbour porpoise *Phocoena phocoena* has been studied by DUDOK VAN HEEL (1959) and ANDERSEN (1970b). ANDERSEN analyzed angular discrimination at 2 kHz in a captive 3-year-old female tested in an enclosure (16 × 8 × 3 m) which was installed in a non-used harbour. Three sides of the enclosure consisted of wire mesh, the fourth was formed by a stone pier. In order to bring the porpoise into a defined position, it was taught to swim through a double hoop (Fig. 8-101). When entering the first hoop, it released a sound signal by shading a photoresistor, and when passing the second hoop (placed 85 cm from the first) a second photoresistor terminated the signal. A separating net forced the porpoise to choose between a left and a right transducer (a, a_1). The test animal was requested to select the transducer, suspended 50 cm below the water surface, which had emitted the signal. A positive response was rewarded with a fish. Sound pressure in the double hoops was kept at about 20 dB re μbar. The duration of the signal was determined by the porpoise's speed, usually about 12 km hr^{-1}. The distribution of signals in the left and right transducer was semi-random and the position of the transducers was changed 3 to 4 times each session (30 trials). At 2 kHz, the minimum audible angle was about 3° deviation from the median plane. To the right side, the porpoise responded 100% positively to angles equal or larger than 5°; the 50% level was reached at 0°6′ (Fig. 8-102). To the left, the porpoise seemed to have trouble in indicating sound direction at small angles. This may have been due to disturbances, although ANDERSEN failed to measure any.

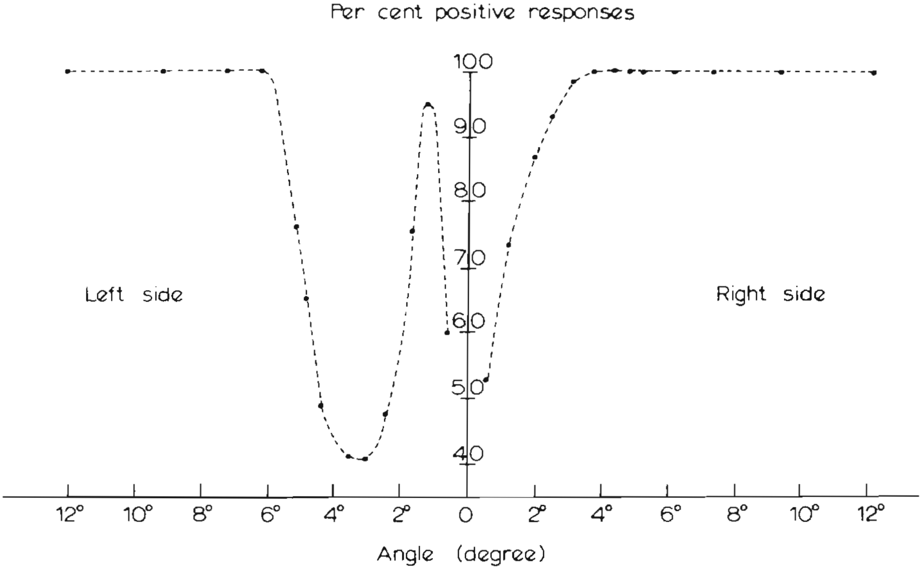


Fig. 8-102: *Phocoena phocoena*. Capacity for directional hearing: psychometric function of angular discrimination at 2 kHz. (After ANDERSEN, 1970b; modified; reproduced by permission of Professor G. Pilleri.)

The areas most sensitive to sound perception on the lower jaw of *Stenella caeruleoalba* (Figs 8-97, 8-98) are only about 10 to 15 cm apart, compared with a separation of 25 cm of the external meatuses (BULLOCK and co-authors, 1968). The maximal effective interaural distance of 15 cm allows a maximum differential sound arrival time of only 60 to 90 msecs. This difference is 4 to 5 times shorter than the arrival-time difference used by humans to localize sound sources. However, BULLOCK and co-authors assume, on the basis of neurophysiological and behavioural responses, that directional hearing of delphinids is based on binaural sound-intensity measurement rather than on binaural timing.

Comparative evidence on sound perception and sound interpretation in different groups of animals (Chapters 8.1, 8.2, 8.3) suggests that directional hearing evolved very early and preceded other discrimination capacities of the hearing mechanism.

(f) Use of Sound and Vibration Cues for Orientation

General Aspects

For a marine mammal travelling or feeding in the vast marine environment sounds constitute the most efficient 'messenger energy', offering a variety of cues for orientation in space and time. Caused by a multiplicity of living organisms—including the marine mammals themselves—water movement, or man's maritime activities, the countless sounds of the sea and their manifold echoes must have special meanings to the experienced traveller or hunter. Especially in situations in which other cues (e.g. visual) are diminished or absent, marine mammals tend to rely on acoustic energy for obtaining information on their living and non-living environment. Sounds are of equal importance for orientation toward conspecifics: in addition to visual and tactile (in some pinnipeds also odorous) cues, auditory stimuli provide a major avenue for social contact and communication.

Recent reviews on the use of sound and vibration cues for orientation by marine mammals have been written by NORRIS (1969), AIRAPETIANTZ and KONSTANTINOV (1970), ERULKAR (1972) and EVANS (1973). A review by EVANS and BASTIAN (1969) concentrates on communication between marine mammals, stressing such aspects as social structures and signalling systems.

Passive versus Active Biosonar

Passive biosonar (orientational hearing) involves the perception and evaluation of ambient sounds for object localization and recognition. Active biosonar comprises the use of self-generated sounds to obtain, via echoes, information on object direction, distance and properties. Both mechanisms are characterized by differences in degree rather than in principle. In all probability, active biosonar comprises phylogenetic elaborations of passive biosonar—adjustments of pre-existing functions and structures rather than developments *de novo*. The elaborations involve the systematic emission of beamed clicks, directional perception of their echoes, as well as increased capabilities for acoustic-signal resolution and interpretation.

Passive and active biosonar may be operative in one and the same individual. The preferential use of these mechanisms depends on (i) the environmental situation, (ii) motivation, and (iii) personal experience (imprinting, conditioning, learning). Passive and active biosonar are of importance for orientation in space as well as for social functions.

Passive Biosonar

A detailed critical evaluation of the importance of passive biosonar for spatial orientation of marine mammals is not yet possible. Exact data on acoustic acuity (hearing thresholds, directional hearing, resolving power, sound interpretation) have still to be produced for the majority of marine mammals. While numerous papers witness the importance of sounds for social contact and communication, few attempts have been made to analyse the relationships suggested in depth.

As has been shown, Sirenia, Pinnipedia, Mysticeti and Odontoceti produce a large variety of underwater sounds (p. 756). There can be hardly any doubt that they obtain orientational information both from foreign ambient sounds (biogenous and non-biogenous) and from reverberations of their own sounds. Why should a mysticete whale, migrating over vast distances, obtain acoustic orientation cues only from ambient sounds and exclude reverberations of its own signals? There is no reason not to postulate that passive biosonar represents an important mechanism of acoustic orientation in all marine mammals.

In the California sea lion *Zalophus californianus*, CONBOY (1972) has conducted experiments which demonstrate the sea lion's ability to navigate by foreign sounds.

A *Z. californianus* was trained to swim to underwater objects identified by 9-kHz acoustic beacons. This ability was then used for practical object recovery from the sea floor (55 m depth): the sea lion carries a grabber device, with recovery line attached, down to the object by means of a fitted nose cup; it then activates the spring-loaded arms of the grabber by pressing it against the target. Subsequently, the object is lifted from the sea floor by the recovery line without diver assistance.

Active Biosonar

Active biosonar (echolocation, echoranging) is of special significance for object localization and recognition, hunting, close-range navigation, and obstacle avoidance—especially under conditions of poor visibility (turbid water, great depth, at night). Active biosonar constitutes the most sophisticated acoustic orientation mechanism evolved by marine mammals. In the absence—or during insufficient availability—of other orientational cues, the self-produced and object-reflected acoustical cues may assume primary importance for relating to the environment.

Among marine mammals, so far only several odontocetes have been shown to possess active biosonar. No experimental evidence is available to suggest the presence of echolocation systems in marine carnivores and sirenians. In pinnipeds and mysticetes, neither the presence nor the absence of active biosonar has been demonstrated unequivocally. The importance of active biosonar for long-range movements of herds or individuals has often been over-estimated. We have no proof that active biosonar represents an essential mechanism for long-distance migrations.

Among other animals, active-biosonar capabilities may be present more often than hitherto expected, especially in forms which hunt at night or which inhabit environments where visual cues are not readily available. In individuals normally relying primarily on non-acoustic cues, latent active-biosonar abilities may be enhanced upon incapacitation of other (e.g. visual) orientation mechanisms. Such individual adjustments can be expected to be more successful in young than in old individuals. Active biosonar is well developed in some bats (e.g. GALAMBOS, 1942; GRIFFIN, 1958; PYE, 1961; GRINNELL, 1962, 1963a, b, c, d, 1967; SCHWARTZKOPFF, 1962; SUGA, 1964a, b, 1965a, b; AIRAPETIANTZ and KONSTANTINOV, 1965, 1970; GRIFFIN and co-authors, 1965; GRINNELL and GRINNELL, 1965; HENSON, 1965, 1967; FRIEND and co-authors, 1966; MARLER and HAMILTON, 1966; BUSNEL, 1967a, b; NEUWEILER and MÖHRES, 1967; SCHNITZLER, 1968, 1971; ERULKAR, 1972; EVANS, 1973). Active biosonar has also been shown to be used in 'total darkness' by some night-active birds (oil bird *Steatornis caripensis*: GRIFFIN, 1953, 1958; swiftlet *Collocalia brevirostris unicolor*: MEDWAY, 1959; NOVICK, 1959). GOULD and co-authors (1964) and GOULD (1965) have presented evidence for echolocation in insectivore shrews and tenrecids (tenrecs). Latent echolocation capacities have been reported to exist in (blind) man ('facial vision', 'obstacle sense of the blind'; e.g. KOHLER, 1967; C. E. RICE, 1967a, b, 1969; see also SEASHORE and LING, 1918; AXELROD, 1959).

Comparing the active-biosonar capabilities of delphinids and bats, ROMANENKO (1964) first postulated significantly higher abilities in the latter. However, later (personal communication *in*: SOKOLOV, 1971) he concluded that both delphinids and bats possess comparably well-developed direction-finding mechanisms. Other experts have come to similar conclusions (e.g. DZIEDZIC, 1968).

Pinnipedia

As has been pointed out on p. 720, orienting sea lions *Zalophus californianus* rely heavily on visual cues. It was surprising, therefore, when POULTER (1963a, b) reported that 'totally blind' *Z. californianus* apparently remained in as good a physical condition over a period of 2 years as their companions with normal vision. This observation was made on a population inhabiting a small island, 800 m offshore and about 70 km south of San Francisco (California, USA); it stimulated a series of subsequent studies and produced controversies. POULTER began to record the underwater sounds emitted by *Z. californianus* and those of related sea lions and seals. Some of the signals obtained from these pinnipeds are—according to POULTER (1963a)—suitable for purposes of echolocation. When approaching pieces of fish thrown into the experimental pool at night, *Z. californianus* emitted trains of clicks and quickly learned to discriminate between pieces of fish and horse meat of identical size, or between pieces from different species of fish (POULTER, 1963b, 1966a, b, 1972; see also SHAVER and POULTER, 1967, 1968; POULTER and JENNINGS, 1969). According to POULTER (1963a, 1972) and SHAVER and POULTER (1967), *Z. californianus* use a double click containing a silent (listening) period of less than 10 msecs duration and receive echoes from targets over a distance of up to 7·6 m with an accuracy of ±4 cm. The seals have been claimed to be able to discriminate between targets of different texture (POULTER and JENNINGS, 1969) and to possess active biosonar as an innate, not a learned, ability (POULTER, 1969a, b), possibly employing the vibrissae in some manner in conjunction with their sonar (POULTER, 1972); however, the methods applied and the conclusions arrived at deserve severe criticism and necessitate re-investigation.

While POULTER reports echoranging capabilities, EVANS and HAUGEN (1963), SCHUSTERMAN and FEINSTEIN (1965), HOBSON (1966), SCHUSTERMAN (1966b, 1967) and SCHEVILL (1968a) stressed the fact that in their experiments, *Zalophus californianus* failed to demonstrate active biosonar capabilities under conditions that should motivate its use. SCHUSTERMAN (1967) concludes that if a mechanism of echolocation is operational, it must be inferior to that of odontocetes, and DYKES (1972) found it unlikely that the vibrissae of the harbour seal *Phoca vitulina* can serve as sensors in a biosonar system. In addition, SCHUSTERMAN (1968) criticizes POULTER's experiments because they were poorly controlled. Acoustically evoked potentials recorded from midbrain auditory structures of *Z. californianus* and *P. vitulina* (BULLOCK and co-authors, 1971) could not settle the question whether echolocation is employed; but these studies indicate the lack of high specialization for active-biosonar sounds used by bats and delphinids.

However, why should visually incapacitated sea lions not benefit from self-generated acoustic cues, and—under the pressure of starvation—'train' themselves to elaborate passive biosonar to an extent at which sound-based spatial orientation, including location and acquisition of food, becomes possible? Of course, not all *Zalophus californianus* may be able to do this. We should expect significant genetic variation in individual capacities and larger ultimate adjustments in young than in older individuals. Experimental and field data obtained on other marine mammals seem to indicate that acoustic orientation often prevails only when other cues are unavailable or insufficient. A shift in emphasis of the orientation mechanism primarily relied on—induced by endogenous or environmental conditions—is known from numerous organisms (Chapters 8.0, 8.1, 8.2). According to KENSHALO (discussion to SCHUSTERMAN, 1967), some birds (cave swiftlets, South American oilbird) and a mammal (flying fox *Rosettus* sp.) employ echolocation as a primary means of orientation only if other cues (e.g. visual or olfactorial) are inadequate.

Shifting emphasis from one type of orientational cue (e.g. visual) to another (e.g. acoustic) involves non-genetic adaptations including adjustments of complex central processes and modifications in concomitant behaviour. Just as invertebrates require a preceding period of stabilization (i.e. adjustment to defined environmental and nutritive conditions for maximum performance; Volume I: KINNE, 1970b, p. 414), conditioning to a specific environment and to given orientational tasks are a basic prerequisite for proper assessment of the ultimate capacity for acoustic orientation in marine mammals.

Mysticeti

Do Mysticeti possess active biosonar? No definite evidence in favour of such a possibility has come to the reviewer's attention. Neither of the two baleen whales maintained for brief periods in captivity has been examined for possible echolocation abilities. However, BEAMISH and MITCHELL (1973) have recorded narrowband pulses (4 to 7·5 kHz; repetition rate 6·75 sec^{-1}) in the presence of a Minke whale *Balaenoptera acutorostrata* which might be suitable as active-biosonar clicks. The whale was circling within tens of metres of a quiet ship.

While active biosonar has been claimed for mysticetes by WENZ (1964) and PERKINS (1966), circumstantial evidence against echolocating capabilities in the coastal-water grey whale *Eschrichtius robustus* has been presented by EBERHART and EVANS (1962): A grey whale blundered through an acoustic barrier consisting of air-filled aluminium tubes stretched in his path. The whale struggled free and traversed the barrier without emitting any sounds. At the same time, a herd of *Tursiops gilli* apparently detected the barrier from a considerable distance, inspected it and retreated from it—continually emitting click trains (EVANS and DREHER, 1962). Nevertheless, it seems safe to assume that mysticetes listen to their sometimes loud sounds and their reverberations. In this way, they may obtain general cues on their aquatic environment. The cues may be of restricted or no value for locating discrete objects, but they may be superior to the delphinid sonar for long-distance navigation (location of large food-organism aggregations and breeding places, gross assessment of water properties) and long-distance communication among conspecifics.

Odontoceti

Our present knowledge on active biosonar employed by odontocete cetaceans is based on experimental evidence obtained from captive individuals. In most cases, pool-cultivated specimens were trained to perform orientation tasks in darkness or while blindfolded. Orientation targets were food (e.g. pieces of fish), wires, spheres, rings, cylinders, discs, vitamin capsules, etc. The odontocetes were required to avoid, detect or discriminate between these targets. The targets were almost exclusively static. There is a deplorable lack of information concerning active biosonar capabilities of odontocetes in regard to target speed and target quality.

Efficient active-biosonar capabilities require low auditory thresholds, high auditory resolving power, fast temporal resolution, detailed classification and memorizing of target properties, computation of direction and distance of non-moving and moving targets, and compensation for interferences (p. 809). Different active-biosonar capabilities obviously mirror differences in the ecology of the species concerned. Size, movement, and distribution of food organisms and their availability as visual orientation cues seem to represent primary determinants of the evolutionary divergencies observed today.

Although suspected, suggested or claimed for a variety of marine mammals, active biosonar has been demonstrated experimentally in only 8 species: the Atlantic and Pacific bottle-nosed dolphins *Tursiops truncatus* and *T. gilli*, the harbour porpoise *Phocoena phocoena*, the common dolphin *Delphinus delphis*, the North Pacific white-sided dolphin *Lagenorhynchus obliquidens*, the Amazon dolphin *Inia geoffrensis*, the Ganges dolphin *Platanista gangetica* and the Indian river dolphin *P. indi*. A number of other odontocete cetaceans qualify (on the basis of anatomy and pulse signalling) for the possession of active biosonar, notably the pilot whales *Globicephala melaena* and *G. macrorhyncha*, the killer whale *Orcinus orca*, the La Plata dolphin *Pontoporia blainvillei*, and the finless porpoise *Neophocaena phocaenoides*.

The first evidence that delphinids use sound for underwater orientation was provided in 1947 by A. F. MCBRIDE (*in*: SCHEVILL and MCBRIDE, 1956), the Curator of Marine Studies, Marineland (Florida, USA). Based on reports of the fisherman R. V. CAPO and on his own observations, MCBRIDE compared the responses of bottle-nosed dolphins *Tursiops truncatus* towards nets to the obstacle-avoiding behaviour of echolocating bats. Without knowledge of MCBRIDE's conclusions, the first experiments which indicated the possession of an active-biosonar mechanism by *T. truncatus* were conducted by KELLOGG and co-authors (1953; see also KELLOGG and KOHLER, 1952) and SCHEVILL and LAWRENCE (1956). The latter two workers demonstrated that captive *T. truncatus* are capable of finding food via navigation by sound (click emission). KELLOGG (1958, 1959, 1960, 1961) supported and extended these findings, showing that the active-biosonar of *T. truncatus* can differentiate between fishes of different size and shape, and that a blindfolded individual can navigate rapidly through metal pole mazes. Discrimination between a water-filled 2-cm gelatin capsule and a piece of fish flesh of about the same size, as well as location of a steel rod-supported disc at distances of 6 to 7 m by a blindfolded *T. truncatus* has been demonstrated by NORRIS and co-authors (1961).

These pioneering studies have been extended by TURNER and NORRIS (1966) and NORRIS and co-authors (1967). Comparable investigations demonstrated active-biosonar capabilities also in the harbour porpoise *Phocoena phocoena* (DUDOK VAN HEEL, 1959; BUSNEL and co-authors, 1965a, b; BUSNEL and DZIEDZIC, 1967b; GOLUBKOV and co-authors, 1969; ZASLAVSKY and co-authors, 1969; see also KONSTANTINOV and co-authors, 1968; AIRAPETIANTZ and co-authors, 1969). The common dolphin *Delphinus delphis* can discriminate by auditory means between geometric figures (BELKOVICH and co-authors, 1969; GUREVICH, 1969). *D. delphis* is also able to detect temporal shiftings of its active-biosonar signals and to distinguish targets made of different materials.

Proper quantitative assessments of active-biosonar capabilities require exact knowledge on the acoustic radiation properties of the targets offered. Such knowledge was available only in a few recent studies (e.g. NORRIS and co-authors, 1967; PENNER and MURCHISON, 1970). Hence most data at hand are insufficient for a critical, detailed evaluation of the resolving power of delphinid biosonar mechanisms.

As pointed out by EVANS (1973), a partial solution to this limitation was the use of metallic discs with known percent reflectivity. *Tursiops truncatus* and *Lagenorhynchus obliquidens* were tested on such a target series. Further refinement of test targets was facilitated by a set of precision cylinders (Naval Undersea Center, San Diego, USA). According to EVANS (1973), these cylinders are 18 cm long and consist of a cork-neoprene compound, Armstrong chloroprene type—DC 100. Target strength varies in 1 dB increments as a function of cylinder radius only (DIERCKS and co-authors, 1971). The ability of blindfolded *T. truncatus* and *Inia geoffrensis* to detect a standard target of –19 dB strength, paired with a target of different strength, is illustrated in Fig. 8-103. A fish of about 19 cm total length has a target strength of approximately –33 dB in side aspect, providing it possesses a swimbladder (ANDREEVA, 1964). Removal of the swimbladder reduces target strength to approximately –45 dB. In the Black Sea, *T. truncatus* can detect fishes of such

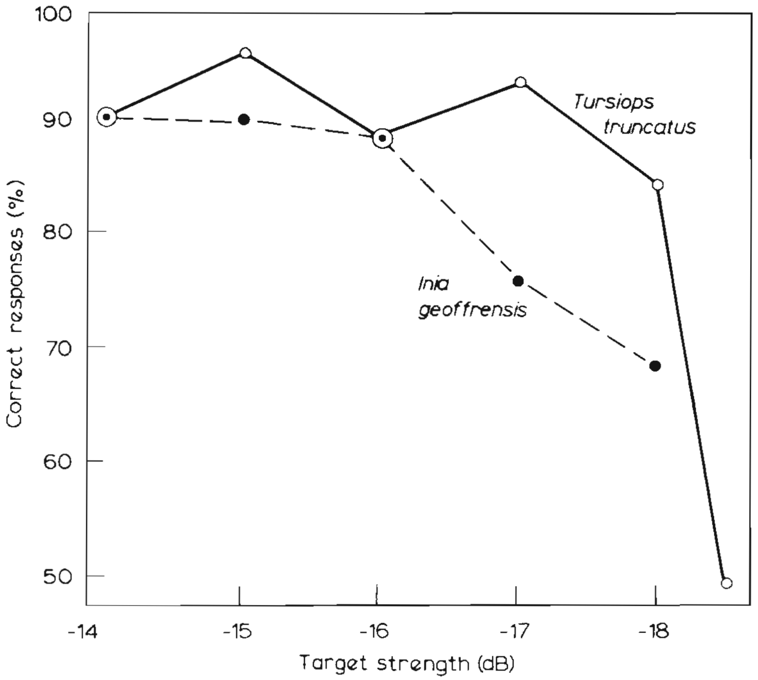


Fig. 8-103: *Tursiops truncatus* and *Inia geoffrensis*. Abilities to discriminate targets (chloroprene cylinders) of different strength; 50% or less is chance performance. (After EVANS, 1973; modified; reproduced by permission of Acoustical Society of America.)

Table 8-8

Capability of odontocete active biosonar for detection and classification of underwater targets. Δ dB: detectable difference in target strength (After Evans, 1973; modified; reproduced by permission of Acoustical Society of America)

Species	Target detection		Target classification			Author
	Min. size	Max. distance	Strength	Shape	Material	
Phocoena phocoena	0·35 mm wire (79% successful avoidance)	At 1 km: fish school (possibly involving passive biosonar)	—	—	—	Busnel and Dziedzic (1967b)
Orcinus orca	25 cm diameter plastic ring, air-filled	3 m				Evans (1973)
Inia geoffrensis	1·3 mm wires (70% successful detection)	2 m	Δ2 dB chloroprene cylinders	—	—	Penner and Murchison (1970)
Tursiops truncatus	3 mm sphere (at 3 m)	At 400 m: 6 cm × 3 m air-filled cylinder	Δ1 dB chloroprene cylinders	Different shapes of equal target strength	Copper disc 30 cm ϕ, from aluminium disc, 30 cm (equal target strength)	Evans and Dreher (1962), Turner and Norris (1966), Evans and Powell (1967), Johnson (1967b), Norris and co-authors (1967), Airapetiantz and co-authors (1969)
	10 cm diameter celtite disc	At 5–10 m: 5–15 cm fish	Nickel-steel spheres, diff. 0·64 cm; celtite disc, diff. 0·5–0·9 cm			
Lagenorhynchus obliquidens	25 cm diameter plastic ring, air-filled	2 m	Δ1 dB		Copper disc, 30 cm ϕ, from aluminium disc 30 cm (equal target strength)	Evans (1973)
Delphinus delphis	100 cm^2 styrofoam 12 mm thick pyramid	6–7 m	100 cm^2 and 50 cm^2 styrofoam pyramids	100 cm^2 styrofoam pyramids	Styrofoam from ebonite (same area)	Gurevich (1969)

target strengths at a distance of 5 to 10 m (AIRAPETIANTZ and co-authors, 1969). Data on odontocete capacities for target detection and target classification are listed in Table 8-8.

For the Ganges dolphin (susu) *Platanista gangetica* and the Indian river dolphin *P. indi*, active biosonar has been claimed by PILLERI (1970b) and PILLERI and co-authors (1971a). The two limnic dolphins inhabit muddy rivers (Ganges, Brahmaputra, Indus) and their tributaries. Their brain morphology, the thick auditory nerve and the advanced degree of atrophy of optic nerve and eye suggest a sensory predominance of the acoustic system. The active biosonar of *P. gangetica* and *P. indi* seems to function equally well in the highly turbid waters of their home rivers and in the crystal-clear water of a swimming pool (Fig. 8-104). According to PURVES and PILLERI (1973), a blind *P. gangetica* could manipulate with its snout a ball of lead-shot suspended from a nylon filament. The authors conclude that this performance indicates a very high degree of discrimination ability. *P. gangetica* swims generally on its (right) side (HERALD and co-authors, 1969; PILLERI, 1970b) and in this position enters water as shallow as 20 cm. Occurring singly or in schools of 5 to 10 individuals, *P. gangetica* feeds on fishes, shrimps and crabs, being particularly active at night (see also ANDERSEN and PILLERI, 1970; PILLERI and co-

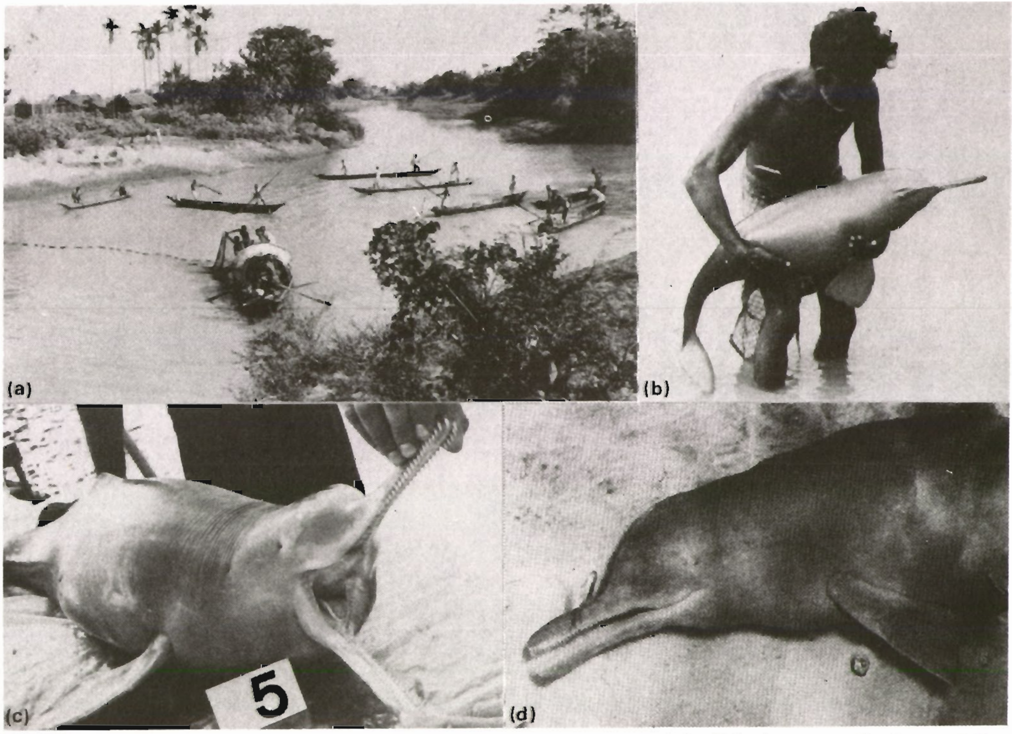


Fig. 8-104: *Platanista gangetica*. (a) Catching dolphins in the Gela Bil river, a tributary of the Brahmaputra (India); (b) captured dolphin; (c) female showing tongue (apparently lacking gustatory papillae) and rudimentary eye; (d) dolphin catching fish in experimental pool. (a: after PILLERI, 1970b; b: PILLERI, 1970c; c: PILLERI and co-authors, 1970a; d: ARVY and PILLERI, 1970; reproduced by permission of Professor G. Pilleri.)

authors, 1970a, 1971b). Its gustatory sense seems poorly developed (Arvy and Pilleri, 1970). Active biosonar has also been claimed for the La Plata dolphin *Pontoporia blainvillei* (Pilleri, 1971b). The finless porpoise *Neophocaena phocaenoides* emits clicks which seem to indicate active-biosonar capabilities (Mizue and co-authors, 1968), and so do, in fact, most other odontocetes examined.

Experiments on active biosonar. It is not possible here to cover all studies conducted on active biosonar. The major results obtained are considered and evaluated in other sections of this subchapter. It must suffice to review a few of the most revealing experiments. We shall concentrate our attention on *Tursiops truncatus* and briefly refer to some related delphinids.

Turner and Norris (1966) experimented with a captive adult female *Tursiops truncatus* (2·1 m, 135 kg), housed in a plastic pool (7·3 m diameter × 1·2 m deep). The female was blindfolded (cast RTV silicone rubber suction cups, pressed lightly over her eyes), required to circle the pool counterclockwise, and then to home on an underwater stimulus display. The display consisted of an inverted T-shaped rod, at each end of which was mounted a nickel-steel sphere. One sphere (reference sphere) was 6·35 cm in diameter, while the diameter of the other spheres varied from 3·18 to 5·71 cm. The side on which the reference sphere appeared was varied randomly, and the two spheres to be compared were 12·7 cm apart. The female was required to press a lever on the side where the reference sphere appeared. During all experiments, the pool contained water of 20° C and 35‰S.

The orientational performance of the *Tursiops truncatus* female was perfect (100% success) at sphere-size disparities of 5·40 versus 6·35 cm or greater; it decreased to 77% successful responses for the sphere pair of 5·71 versus 6·35 cm. Later analysis (Norris and co-authors, 1967) revealed that three kinds of echoes reflected from the sphere might provide the key cues for this orientational performance: (i) Differences in sound intensity, ranging from 1 to 6 dB for the sphere disparities used. (ii) Loss in low frequencies parallel to reductions in sphere diameter; for the minimum sphere disparity the breakpoints are about 2·5 kHz apart and should be easily recognizable by the dolphin. (iii) Secondary echoes should contain information about sphere properties (e.g. hardness and evenness of the material). During the test, the blindfolded female circled in the tank, respired once at about midtank, and began to emit a continuous series of clicks (often composed of 2 parts,

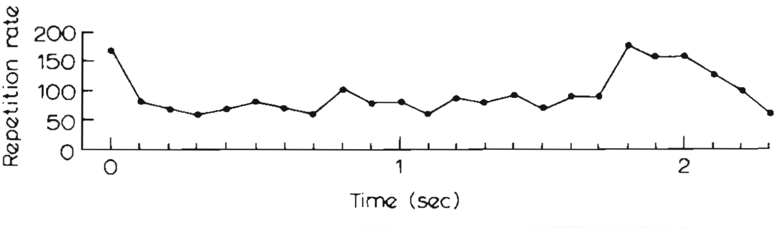


Fig. 8-105: *Tursiops truncatus*. Changes in click repetition rate of an adult female during a successful 2·3 sec discrimination run at sphere disparity 5·08 versus 6·35 cm. The initial high rate subsides to a rather uniform level and then increases suddenly just before the lever is pressed. (After Norris and co-authors, 1967; modified; reproduced by permission of Professor R.-G. Busnel.)

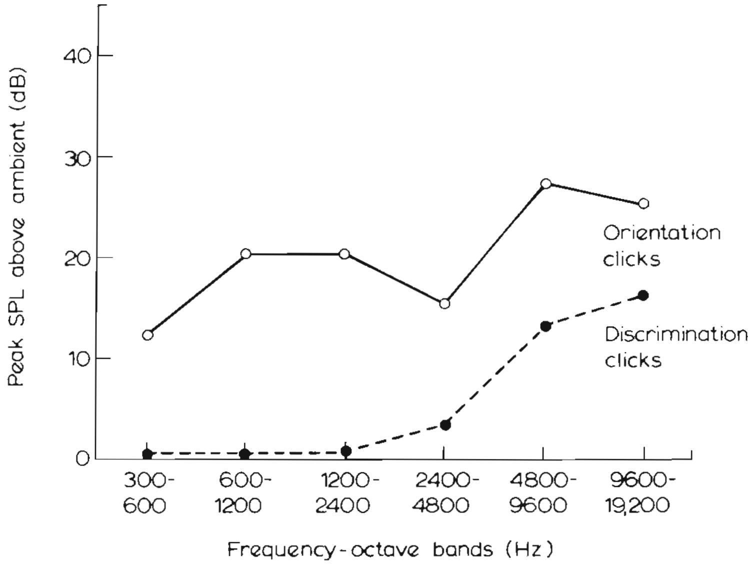


Fig. 8-106: *Tursiops truncatus*. Orientation and discrimination clicks generated during discrimination test. Octave band analysis of low-frequency click portions. (After NORRIS and co-authors, 1967; modified; reproduced by permission of Professor R.-G. Busnel.)

characterized by almost instantaneous rise time) as she approached the choice levers. The click trains usually started with a high repetition rate and quickly descended to levels between 50 and 70 $\sec^{-1}$; just before the lever was pressed repetition rate increased again to 130 to 180 $\sec^{-1}$ (Fig. 8-105); a silent period often just preceded lever press. Following the press, the female emitted about 12 very intense clicks, rich in low frequencies. Such 'orientation clicks' (NORRIS and co-authors, 1967) are produced when the dolphin is apparently orienting to general features of its environment; low frequencies are more emphasized than in discrimination clicks (Fig. 8-106). Echoes almost always fell in the interclick interval (time between the end of one single or double click and the onset of the following one).

NORRIS and co-authors (1967) further conclude from the experiments just described that the *Tursiops truncatus* female exerts considerable control over several features of her signal output. She can regulate repetition rate, intensity and frequency content and, possibly, click-doubling. The usual click duration of about 1 msec allows the dolphin to approach a target within about 75 cm and still place the echo after the last portion of the outgoing click. Repetition rate seems to be adjusted so as to accommodate the echo in the interval following the previously emitted click (NORRIS and co-authors, 1967). This may be the reason for the observed tendency for repetition rates to increase with decreasing target distance.

When inspecting its environment for information on location and properties of objects ensonified by its clicks, much or all of the echo produced may be important for the dolphin, including the maintenance of adequate interspace between successive clicks; either click duration or repetition rate may be manipulated for this purpose. Discrimination clicks are short, directional, have very rapid rise-times and little energy at low frequencies. Hence they generate only minimal reverberation, and switching from a discrimination click train to an orientation click train would allow the dolphin to control reverberation to some degree, and to ensonify a discrete target or much of the immediate environment (Norris and co-authors, 1967).

Reznik and co-authors (1970) required *Tursiops truncatus* to echolocate targets with different shapes of reflecting surfaces, made of different materials (parallelepipeds, triangles and discs made of Duralumin and organic glass). They concluded that sequential frequency and duration of echolocation signals in most of the cases examined did not change significantly and hence should not be regarded as classification indices for signal types. Dubrovsky and co-authors (1970a) offered to *T. truncatus* spherical targets made of different materials. They report that discrimination capacity depends largely on spectrum changes in the secondary echosignal. Targets of different materials (different speed of transverse waves) differentially affect the secondary echo perceived by the dolphin.

During navigation, reverberations produced by *Tursiops truncatus* are likely to allow a quick general appraisal of location and size of large objects: Energy-rich low frequencies enlarge the functional range (distant schools of fish, general topography of the sea bottom). Norris and co-authors (1967) suggest that many of the acoustic signals recorded at sea from odontocetes are of this type.

While echolocating, *Tursiops truncatus* often scans with its head (10° to 30°) from left to right (Norris and co-authors, 1961); similar scanning movements may occur in other delphinids. However, anatomical differences (*T. truncatus* has 5 free cervical vertebrae; *Inia geoffrensis* 7; many pelagic delphinids have fused cervical vertebrae) infer concomitant differences in manoeuvrability, and some odontocetes (e.g. species of *Lagenorhynchus* and *Orcinus orca*) seem to scan more by rolling than by head movements (Evans, 1973). The immediate importance of head scanning for echolocation has been challenged by Belkovich and Nesterenko (1972), and Resnikow and associates (*in*: Belkovich and Nesterenko) who insist that, within a tolerance range of 10° to 20°, head movements have nothing to do with acoustic scanning: without any head movements, the dolphins can shift their sound beams and, at the same time, can significantly modify the degree of directionality from signal to signal ('internal' scanning; see also Evans, 1973). The resulting sound beam can be rotated at a speed of about $3{\cdot}5\,.\,10^{5^\circ}\ \mathrm{sec}^{-1}$, thus ensonifying a small target for very brief periods only. The 'acoustic eye' of the dolphin is assumed by Belkovich and Nesterenko to be able to obtain, with a high degree of acuity, detailed information even on very small sound-reflecting objects and to provide rapid overall information on the environment ahead.

According to Evans (1973) *Tursiops truncatus* may be equipped with a multiple element transmitting array. Measurements of the radiated field reveal a pattern that varies several dB at the same angle from pulse to pulse. Fig. 8-107 illustrates recordings from three transducers. Directly ahead of the sound source, two distinct pulse waveforms can be distinguished (1 and 2); 20° to the right, only pulse 1 (maximum energy at 30 kHz) is evident; 20° to the left, only pulse 2 (maximum energy at ca 60 kHz) is seen. As the dolphin approaches and scans across the targets, successive changes in pulse waveforms occur. Fig. 8-108 shows the variability of beam patterns in the vertical plane as recorded from a 10-element hydrophone array at 5° incre-

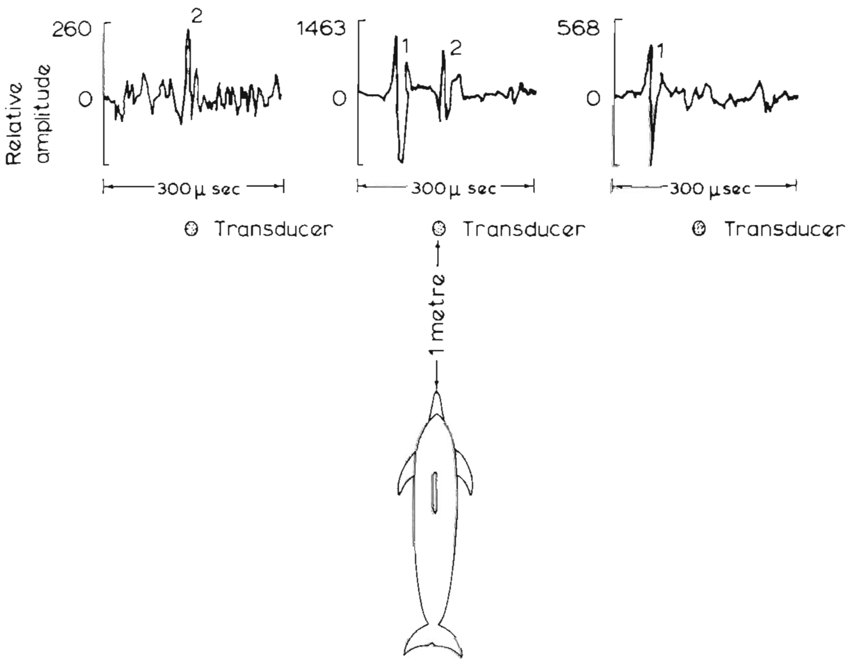


Fig. 8-107: *Tursiops truncatus*. Measurement of active-biosonar signals using a three-hydrophone array at a distance of 1 m from the dolphin's rostrum tip (20° separations between the left and right transducer). (After EVANS, 1973; modified; reproduced by permission of Acoustical Society of America.)

ments. A similar degree of variability has been reported for *T. truncatus* from the Black Sea. Some of this variability seems to be due to effects of the medium; but internal manipulation by the sound producing mechanism is still evident (see also YABLOKOV and co-authors, 1972).

BUSNEL and co-authors (1965a) and BUSNEL and DZIEDZIC (1967b) experimented with a captive *Phocoena phocoena* required to navigate blindfolded through a maze of wires (steel, iron, copper or nylon) suspended in the water of a sea-water pool. The investigators reduced the diameter of the wires until the cruising porpoise was no longer able to avoid them. Metal wires were avoided down to a diameter of 0·2 mm; monofilament nylon wires, to about 1 mm diameter. This difference was attributed to the greater acoustic mismatch between sea water and metal than between sea water and nylon.

In comparable experiments with *Inia geoffrensis*, the minimum metal-wire diameter recognized was 1·4 mm (PENNER and MURCHISON, 1970). The seemingly less sophisticated performance of *I. geoffrensis* may have been due to target contamination: During experiments with *I. geoffrensis*, small air bubbles formed on the wires within 1 min after immersion. These bubbles increase sound reflection and, if allowed to remain, augment the apparent wire discrimination capability to 0·6 mm wire diameter in 93·3% of the trials. BUSNEL and DZIEDZIC (1967b) did not comment on possible bubble formation; they may have overestimated the acoustical resolving power of *Phocoena phocoena*.

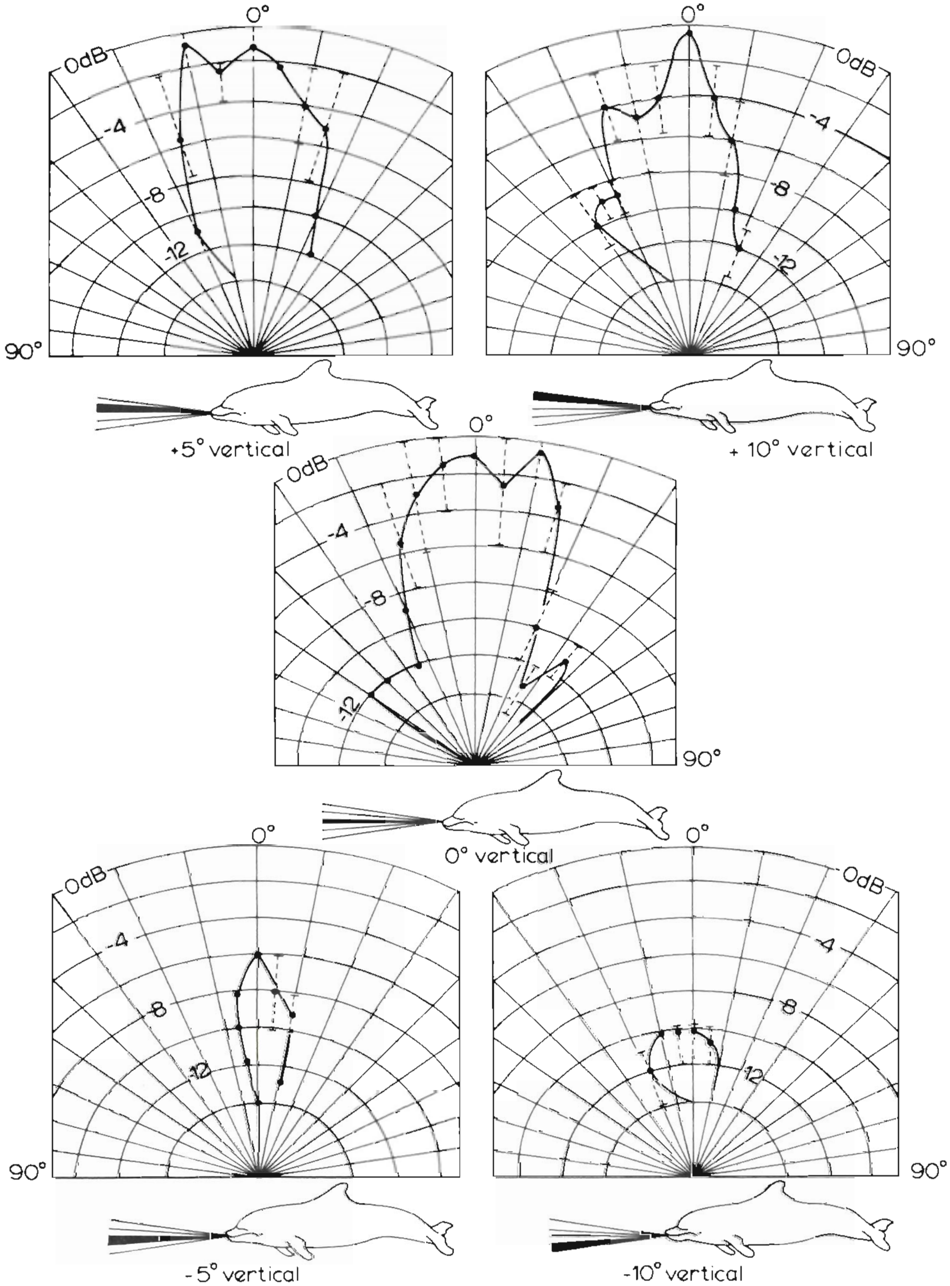


Fig. 8-108: *Tursiops truncatus.* Variation in horizontal beam patterns of the emitted echoranging signal, measured by 5° increments in the vertical access. (After EVANS, 1973; modified; reproduced by permission of Acoustical Society of America.)

Although a considerable number of papers has been devoted to sound production in *Phocoena phocoena*, the exact acoustic properties of the pulses used for echolocation are not known. Several analyses relied on recorded systems that were limited in response. According to ANDERSEN (1970a), the auditory sensitivity of *P. phocoena* is similar to that of *Tursiops truncatus*, with an upper limit of 150 kHz (p. 789). Limited equipment response has also resulted in the false conclusion that *Inia geoffrensis* produces a low-frequency pulse (DIERCKS and co-authors, 1973).

Experiments on *Delphinus delphis* have revealed that this dolphin can distinguish between geometrical differences in target shape and is able to discriminate by echolocation between flat figures which differ by 9·75% in area (BELKOVICH and co-authors, 1969; GUREVICH, 1969).

Captive *Platanista indi* continuously emit pulses with a signal duration of 12 to 33 μsecs (PILLERI and GIHR, 1971a). Interestingly, the frequency of the acoustical signal of a captive male is about 10 kHz higher than that of the female. Sound properties vary considerably, depending on (i) the number of dolphins per tank, (ii) tank or field conditions (PILLERI and co-authors, 1971a). The authors summarize their findings as follows: The pulses lie in the 800 Hz to 16 kHz and 20 to 100 kHz (possibly even higher) frequency ranges, the latter being 'distinctly sonar'; some of the low-frequency signals (800 Hz to 16 kHz) are water noises (surfacing, blowing, swimming); most are biological signals of yet undetermined nature. Repetition rates of about 90 $\sec^{-1}$ have been recorded in captivity, of 124 $\sec^{-1}$ in the field. Transmission intermissions between each individual pulse vary from about 1 to 60 secs (see also HERALD and co-authors, 1969).

Use and efficiency of active-biosonar depend on the experience of the individual involved and on its emotional state: A *Tursiops gilli* caught in clear offshore Hawaiian waters and taught to press a lever on command failed utterly when blindfolded; it missed the lever even though it was 20 cm in diameter and covered with acoustically reflective foam neoprene. Only when the pool water was made turbid with mud did the dolphin emit click trains (NORRIS, 1969). *Delphinus delphis* became disoriented when newly introduced into a pool filled with turbid water; it hit the pool walls frantically and some individuals drowned. When a trained *Lagenorhynchus obliquidens* was blindfolded, it promptly ran into the tank wall; only after several days did it learn to navigate by acoustic cues.

Effective Ranges of Biosonar

Assessments regarding the range of passive and active biosonar under *in situ* conditions remain speculative. The ranges depend primarily on intensity, frequency and directionality of the sounds, and on the auditory sensitivity of the mammal concerned. Low-intensity sounds attenuate rapidly. Low-frequency sounds carry farther and are more omnidirectional than high-frequency sounds; they may provide gross information from distant environmental areas. High-frequency sounds facilitate information input on discrete objects in the near field.

Passive biosonar based on a high capacity for sound detection and directional discrimination can provide long-range cues. e.g. during food search or migration. Low-frequency sounds tend to reverberate from discontinuity layers in the sea, from distant coasts, reefs and food-organism aggregations. Their effective range may measure up to several kilometres, possibly beyond that; definite information is not available.

Active biosonar constitutes a mechanism for short-range orientation. It is used primarily for detection and catching of food organisms, close-range navigation and obstacle avoidance—especially under conditions of poor visibility. In delphinids, the normal active-biosonar range appears to be between 1 and 20 m, the maximum range between a few centimetres and 300 to 500 m. Very high repetition-rate clicks (500–800 sec^{-1}) are used over distances of 1 m or less. Sporadic clicks (1–4 sec^{-1}) are sometimes emitted by migrating delphinids. Assuming a constant click-echo relation, 2 clicks sec^{-1} would allow about 375 m maximum range (NORRIS, 1969). A comparable range has been suggested for the low-repetition clicks of the sperm whale *Physeter catodon* (BACKUS and SCHEVILL, 1966), although these clicks are recordable over many kilometres (maximum: about 15 nautical miles).

Can migrating delphinids recognize details of sea-bottom topography by means of their active biosonar? Although capable of high resolution, the delphinid's active biosonar seems to be insufficient for orienting to differences in sea-bottom morphology over distances exceeding ca 70 to 90 m (e.g. GUREVICH, 1969; AIRAPETIANTZ and KONSTANTINOV, 1970). AIRAPETIANTZ and KONSTANTINOV (1970) assume that the maximum range of delphinid active-biosonar mechanisms is close to discriminating a 15-cm fish at a distance of 5 to 10 m. However, their passive biosonar may be capable of locating noise sources over considerable distances (several km). The common dolphin *Delphinus delphis*, for example, seems to be able to discriminate fish schools over a distance of 3 km (TOMILIN, 1970). Most of these data involve much speculation and are insufficiently backed by experimental results.

Measurement of Direction and Range

How do delphinids measure direction and range of underwater objects? This important question is still a matter of discussion. Five basic possibilities have been considered: (i) assessment of sound (echo) intensity; (ii) determination of the time interval between sound emission and echo return; (iii) perception of the time-difference tone; (iv) measurement of the Doppler shift; (v) application of the principle of 'sound division'.

(i) Assessment of echo intensity would seem most useful over medium and long distances. It involves the perception of attenuation gradients over the frequency range of the sound. Since the highest frequencies attenuate first, this method would allow measurement of range, providing the original frequency composition of the sound is known or the gradients are perceptible as the delphinid moves (see also *Directional Hearing*, p. 790). Neurophysiological and behavioural evidence suggested to BULLOCK and co-authors (1968) that delphinid target location is based on binaural intensity measurement rather than on binaural timing.

(ii) Determination of the time interval between sound and echo provides information on sound-travel time and hence on object distance. It is particularly useful for short-range orientation. Comparison of minimum or maximum intervals could provide directional cues. Since delphinids are capable of resolving tone pips only 1 msec apart (BULLOCK and co-authors, 1968) they should be able to determine sound-travel times at repetition rates up to some 400 clicks sec^{-1}. Such repetition rates are typical of echolocation signals emitted during nearby (10–20 cm) target discrimination. Knowing the sound-travel time and its own cruising speed, the delphinid could gain information on the relative speed of its target by assessment of the rate of change of echo placement.

> 'This very likely takes place not as an individual assessment of one click in relation to its echo, in rapid click trains at least, but as a psychoacoustical sensation produced by many clicks and echoes. . . . In this scheme the frequency of the tone would indicate distance, and the change in frequency the change of relative position between porpoise and target' (NORRIS and co-authors, 1967, p. 433).

(iii) Time-difference tones occur in human auditory perception (THURLOW and SMALL, 1955): two pulse trains of identical repetition rate but slightly separated in time give rise to a tone, the pitch of which corresponds to the magnitude of time separation. If, for example, one pulse train has a repetition rate of 100 sec^{-1}, and a second identical pulse train follows in 1/400th of a second, the time separation pitch perceived is that of a 400-Hz tone. Decreasing time separation causes the tone to sweep upwards; increasing time separation, downwards—until the difference is half the pulse interval (time-difference tone = octave of pulse repetition frequency). Further increase of time separation beyond this point causes the tone to sweep upwards again. Thus the time-difference pitch always corresponds to the shorter time separation. NORDMARK (1960) suggested that this mechanism may also be operative in bats and delphinids, and that the time difference between the peaks of the sound pressure determines the pitch. To an echolocator, tones in a certain frequency range would have a meaning of distance, and a rising pitch would signify shrinking distance. Taking into account the slightly earlier echo return in a moving target locator, the relations involved are expressed by the following equation:

$$f = \frac{c + v}{2s}$$

where f = frequency of the tone perceived (Hz), c = sound velocity (cm sec^{-1}) in the medium, v = velocity of the echolocator (cm sec^{-1}), s = distance between echolocator and echo source at the moment of sound emission (cm). As the target is approached, location accuracy increases, since pitch change is augmented. According to NORDMARK, maximum range of this mechanism would be 9 to 15 m in water-borne and 2 to 3 m in air-borne echolocators.

The time-difference tone can presumably be heard only as a result of a recurrent or a gradually changing pattern (NORDMARK, 1960). Approaching a target, the time-difference tone changes gradually. Focusing attention on this change, the echolocator should be able to sort out its echo from those of conspecifics and from a multitude of background noises (see next section).

(iv) Measurement of Doppler shift as the delphinid moves in on an object could assess closure rate; however, no pertinent evidence appears to exist (NORRIS, 1969).

(v) According to a hypothesis advanced by RESNIKOV (1970), orientational interpretation of acoustic cues by delphinids is based on the principle of 'sound division'.

The information at hand is insufficient for evaluating the potential merits of the five principles mentioned. While sound intensity and sound-travel time obviously provide essential cues, the time-difference tone mechanism appears attractive because of its simplicity and interference resistance. Its validity requires examination.

Considering some technical principles of sonars and radars, CHAPMAN (1971) points out that if measurements are made at more than a single angle (aspect angle) and at more than a single frequency, direction, distance, size and shape of a discrete target can be determined. In contrast to general opinion of sonar and radar engineers, CHAPMAN shows in his experiments that little bandwidth is needed to obtain measurements on target dimensions if data as a function of aspect angle are available. Phase measurements were not needed or used. But 'remarkable things can be done by interpreting interference effects from multiple sources' (p. 1189). Each pair of scatterers on the target creates a Fourier component in the intensity pattern in space. Fourier-type wave analyses of the pattern—observed (i) over about half a radian of known aspect angles at two closely spaced frequencies, or (ii) over about half an octave of frequencies at two closely spaced aspects—yield amplitude and phase for each wave number. These two methods are quite independent of each other. For pairs of scatterers, in method (i) width (lateral separation) between the two scatterers comes from wave numbers of amplitude peaks, depth (radial separation) from phase shift with frequency change. In method (ii), depth comes from peaks, width from phase shift with change of aspect angle. Combining the $n\ (n - 1)/2$ oriented separations from n scatterers, a unique outline drawing is obtained. CHAPMAN (1971) demonstrated both methods experimentally at about 14 kHz. He assumes that delphinids use these two physical principles. Since delphinids move about, they can perceive and interpret different aspects of a target.

But nature provides only few narrow-band sounds and all odontocetes examined employ broad-band signals, often of considerable complexity. They exhibit high resolutions in regard to intensity, frequency and temporal patterns. These capacities suggest that active biosonar mechanisms are based on the analysis of the sounds perceived by simultaneous comparison of intensity, frequency range, phase and arrival time of signal components at the two ears. The signal is compared with, and separated from, other environmental sounds by the central nervous system.

Counteracting Sonic Interferences

We may think of a migrating whale herd as being submerged in an acoustic field of high complexity and vast dimensions—a gigantic symphony of sounds providing a continuous flow of acoustic information on space and time, on food and water properties, on friend and foe. How can whales employing active biosonar sort out their own signals among the echoranging sounds of up to hundreds of nearby con- and heterospecifics, and in the presence of countless other sea noises? How can they detect and capture a small fish by active biosonar when myriads of additional echoes are returned from other organisms, hydrographical discontinuities (thermoclines, haloclines), sea bottom, or water surface? In other words: how can a high degree of orientational precision be achieved in a seemingly sonic chaos?

Attempts to jam the active-biosonar of bats by means of intense noise covering all frequencies of their pulses have failed. This failure initiated discussions of the means of active-biosonar mechanisms for counteracting sonic interferences. Early discussions centred around the little brown bat *Myotis lucifugus* and the long-eared bat *Plecotus townsendii*. While the sophisticated timing mechanism, which enables bats to perceive and to interpret sounds arriving within 0·1 to 0·2 msec, is a basic prerequisite for fast evaluation of sounds, it is by no means a specific neurophysiological property restricted to bats. GRINNELL (1967) assumes that a specific genetic adaptation lies in the central enhancement of recovery: the recruitment of 'larger and larger populations of units in progressively more central nuclei' (p. 476) for processing second-stimulus information. The bats' response to echoes is postulated to result from short-term, frequency-specific facilitation of large populations of auditory neurons. Facilitation is probably specific also for frequency change and signal duration. This provides knowledge of the signal characteristics which the bat is attempting to detect. Further assistance in counteracting sonic interferences is obtained from sharp directional hearing: high frequencies and large motile external ears reduce the effectiveness of sound coming from angles other than the one to which attention is being paid.

A comparable situation exists in regard to overcoming sonic interferences in echolocating odontocetes. Directionality of sound emission and perception—enhanced by specific head structures (e.g. acoustic lens, p. 749; ear isolation, p. 780; sound routes to the inner ear, p. 781) and body movements (scanning, p. 803)—counteract and reduce sonic interferences. In addition, interference due to own pulses could conceivably be cancelled by control systems such as are assumed to be operative in the re-afference principle (p. 530) and the compensation theory (p. 533).

Among the multitude of sounds emitted by marine mammals, the short, sharp-onset clicks qualify as most accurate acoustic cues. In this sound type, the echo can be made to fall in the interval between successive clicks, either by regulating click duration or repetition rate. Hence even slight variations in repetition rate are reflected faithfully in the echo train and provide means for identifying self-generated signals (NORRIS, 1969). The sharp onset of echoranging clicks imparts great instantaneous high-frequency energy to the signal, thus contrasting it well against the majority of sea noises which carry little high-frequency energy. According to NORRIS, it is the autocorrelation of emitted click and returned echo in a pulse fashion that allows discrimination between signal and background noise. Remarkable contrast against ambient sea noise prevails even in the intense low-frequency clicks of the open-ocean sperm whale *Physeter catodon*, which seems to exemplify an adaptation to long-distance, deep-water conditions. POULTER (1963a, 1972) claims that the hearing of *Zalophus californianus* is cut off whenever an acoustic signal is produced; thus the sound producer would not have been listening to the loud click just before perceiving the weak echo. This suggestion requires experimental verification.

While all these phenomena may, singly or in combination, assist in counteracting sonic interferences, even the most elaborate mechanisms of generation, perception and evaluation of sounds seem of limited use for acoustic orientation if the individual concerned is inexperienced. Take a cocktail party attended by 6 couples, each using a different language and chatting happily in one room—how could a blindfolded listener differentiate between their sonic messages if he knew neither the languages nor the persons involved? But give him a chance to learn the languages and to familiarize himself with each person, and he will—with the same auditory mechanisms at his disposal—be able to identify individual messages, differentiate between individual speakers and counteract what he considers sonic interferences during each task of auditory discrimination. More than that: sufficient learning will enable him to recognize one speaker out of thousands. In fact, he may be able to recognize a person by the sound of his footsteps generated by a large variety of shoes on a large variety of bottom materials and against a large variety of background noises. Physiological mechanisms of acoustic orientation are one thing, their conditioned use another. The mechanisms are the result of genetic adaptation to specific ecological conditions; their efficient and specific use is a matter of personal experience.

Progress in the analysis of mechanisms of acoustic orientation and critical evaluation of their ecological significance requires more emphasis to be placed on such general processes as imprinting, learning, memorizing, and focusing of attention on 'acoustic key parameters'.

(g) Communicative Importance of Sounds

Many authors have stressed the communicative function of sounds emitted by marine mammals (e.g. TOMILIN, 1955; LILLY, 1958, 1961, 1962, 1963, 1966, 1967; LILLY and MILLER, 1961a, b; DREHER and EVANS, 1964; LANG and SMITH, 1965; BATESON, 1966; BUSNEL, 1966, 1968; DREHER, 1966; TAVOLGA, 1966; M. C. CALDWELL and CALDWELL, 1967; EVANS, 1969; EVANS and BASTIAN, 1969; M. C. CALDWELL and co-authors, 1971a, b, 1973).

Auditory communication requires acoustic contact between individuals and involves transmission of information by acoustical means. Presumably, basic properties of communicative sounds are related to the message conveyed: A male sea lion attracting a female, or a dolphin mother calling for her lost calf are likely to use sounds with directional components that facilitate location of the sound source. In contrast, alarm signals conveying the presence of a predator are likely to contain much acoustic energy but little directionality. In both cases, sounds would be most effective if they differed significantly from the environmental background noise. The main components in the evolution of communicative sounds may have been (i) behaviour (hunting, mating, migrating, escape); (ii) structures and functions available (mechanisms of sound generation, perception and interpretation); (iii) acoustic properties of the environment; (iv) intra- and interspecific selection pressures. Highly emotional correlated sounds reveal interspecific similarities even when produced by non-homologous organs (COLLIAS, 1960).

Comparative studies on sound production and concurrent behaviour have led some authors to infer intention or semantic meaning to acoustic signals. However, such terms as 'distress call', 'sex yelp', 'chase squawk', etc.—while useful for a brief characterization of the situation observed—must be viewed with critical reservation. They should not imply an intent on the part of the sound emitter unless such intent can be documented objectively:

> 'we must regard all sub-human signals as non-purposeful on the part of the animal giving the signal. Social signals are actions elicited by an emotional

> state and are meaningful only in that another animal is able to receive them' (M. C. CALDWELL and CALDWELL, 1967, p. 879).

There is no experimental proof of the validity of the semantics of an acoustic signal:

> 'Même en observant un animal blessé, attaché encore à ligne d'un harpon, et émettant sans cesse, ce que nous avons appelé des signaux de "détresse", nous n'avons pas observé une modification quelconque du comportement de ses partenaires sociaux du groupe dans lequel nous l'avions attrapé. Nous savons cependant qu'il y a des comportements épimélétiques dans certain cas; toutefois, à ma connaissance, personne n'a pu encore les déclencher par la reproduction de signaux acoustiques. C'est pourquoi je suis d'ailleurs toujours des plus réservé quand j'entend parler du "langage" des dauphins, alors que nous ne savons rien de la sémantique de leurs signaux' (R.-G. BUSNEL, in a letter to the reviewer, 1973).

Sounds and their Potential Behavioural Correlates

LILLY and MILLER (1961b) studied vocal exchanges between two individuals of *Tursiops truncatus*. The tentative meanings of the sounds emitted have been interpreted as 'attention', 'irritation', 'distress', etc. A distress call which is repeated many times until an appropriate response is elicited has been described by LILLY (1963). The distress call consists of two whistles: the first with a rising, the second with a decreasing tendency; the lowest fundamental frequencies vary between 3 and 5 kHz, the highest between 8 and 20 kHz. The duration of each of the two whistles is 0·2 to 0·6 secs with a short pause in between. Distress calls are emitted underwater or in air and reveal individual differences (signature, p. 824). The most frequent situations which elicited distress calls were: (i) impeding or prevention of surfacing to breathe; (ii) removal from the water; (iii) pain; (iv) isolation of infants from their mother; (v) electrical stimuli in specific brain areas. Typically, the first response to the call of other individuals was to stop the emission of all sounds and to start a search for the porpoise expressing distress. When the distressed individual was found, the finder placed its own head under that of the distressed companion and lifted it to the water surface allowing it to take one or several breaths. After this 'rescue', the two individuals exchanged whistles. Subsequently, actions to assist the disabled individual in breathing were continued (up to weeks) until recovery. Distress calls have also been reported from other odontocetes (e.g. *Stenella styx*: BUSNEL and co-authors, 1968).

Do distress calls elicit comparable responses under *in situ* conditions? We do not yet know. Recording and playback of acoustic signals still suffer from lack in fidelity. Personal acquaintance, individual differences in sound quality, and specific social relationships seem to represent some of the aspects which require specific attention in future analyses of communicative acoustic field behaviour. In a study at sea, BUSNEL and DZIEDZIC (1968a) submitted representatives of the following species to acoustic signals emitted by wounded or frightened individuals: *Tursiops truncatus*, *Delphinus delphis*, *Stenella styx*, *Globicephala melaena* and *Physeter catodon*. Apparently, herd members were indifferent to the signals emitted by harpooned

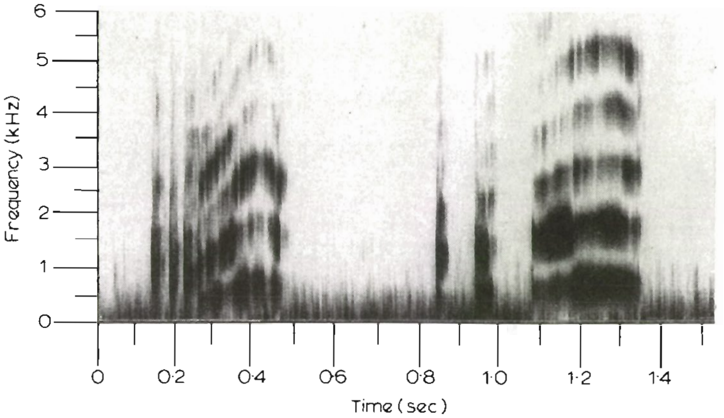


Fig. 8-109: *Tursiops truncatus* (captive). Sonagram of 'sex yelp' produced by an adult male during sexual advances towards an adult female. (After M. C. CALDWELL and CALDWELL, 1967; reproduced by permission of Professor R.-G. Busnel.)

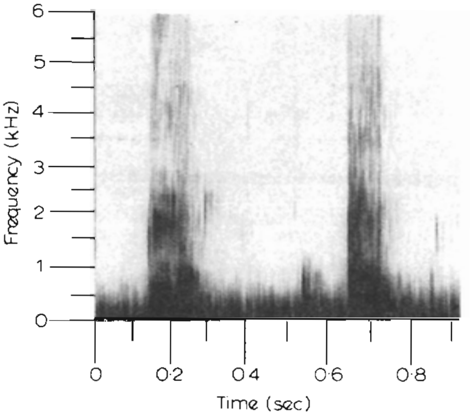


Fig. 8-110: *Tursiops truncatus* (captive). Sonagram of 'sex yelp' generated by a 9-month-old juvenile male just prior to intromission with his mother (see Fig. 8-111 for concurrent behaviour). (After M. C. CALDWELL and CALDWELL, 1967; reproduced by permission of Professor R.-G. Busnel.)

specimens. BUSNEL and DZIEDZIC assume that one reason for such indifference was due to the fact that all harpooned individuals were either males or immature females. The ambiguous results obtained from playback experiments could have been due to technical difficulties. Proper assessment of the communicative function of distress calls and related acoustical signals under ecological conditions requires: (i) Knowledge on social dynamics; (ii) high-fidelity, broad-range acoustic equip-

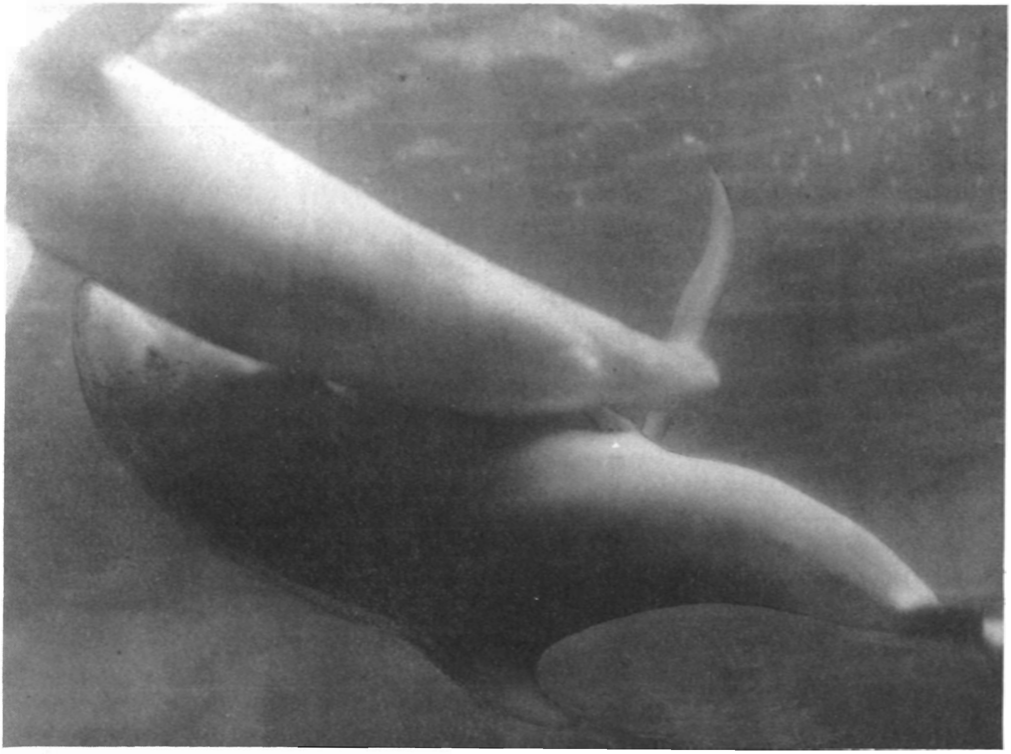


Fig. 8-111: *Tursiops truncatus* (captive). Juvenile male (lower) initiating intromission with his mother; this behaviour is often preceded by the male 'sex yelp' (see Figs 8-109, 8-110). (After M. C. CALDWELL and CALDWELL, 1967; reproduced by permission of Professor R.-G. Busnel.)

ment; (iii) long-term *in situ* experimentation after conditioning the mammals to human presence.

M. C. CALDWELL and CALDWELL (1967) studied and interpreted sounds of *Tursiops truncatus*. The authors distinguished:

(i) Sounds produced prior to and during copulation: The male 'sex yelp' (TAVOLGA and ESSAPIAN, 1957) was the only sound in the burst-pulse group that was not heard in any other orientational context; but it was no integral part of copulation (Figs 8-109, 8-110, 8-111). Ontogenetically, the sound develops from a more indeterminate but recognizable yelp of a juvenile male to the well-defined yelp of a mature bull.

(ii) Sounds produced during play chase: Captive *Tursiops truncatus* spend much time at play, especially chasing, often accompanied by the 'chase squawk' (Figs 8-112, 8-113).

(iii) Sounds produced during fight chase. Definite distinction between 'chase squawks' and 'fight squawks' has not yet been possible. Fights often result in physical injury (scratches, gashes). The recipient of an aggressive action may be pinned to the bottom of the tank by one or more dominant companions (Fig. 8-114).

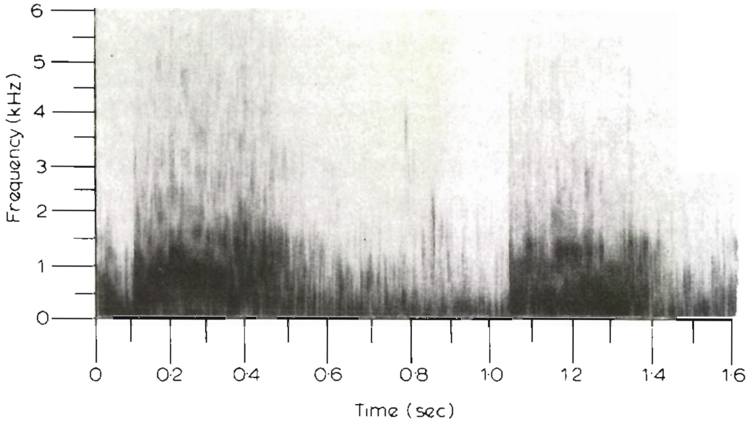


Fig. 8-112: *Tursiops truncatus* (captive). Sonagram of 'chase squawks' produced during play chase between an adult female and her juvenile male calf (see Fig. 8-113 for concurrent behaviour). (After M. C. Caldwell and Caldwell, 1967; reproduced by permission of Professor R.-G. Busnel.)

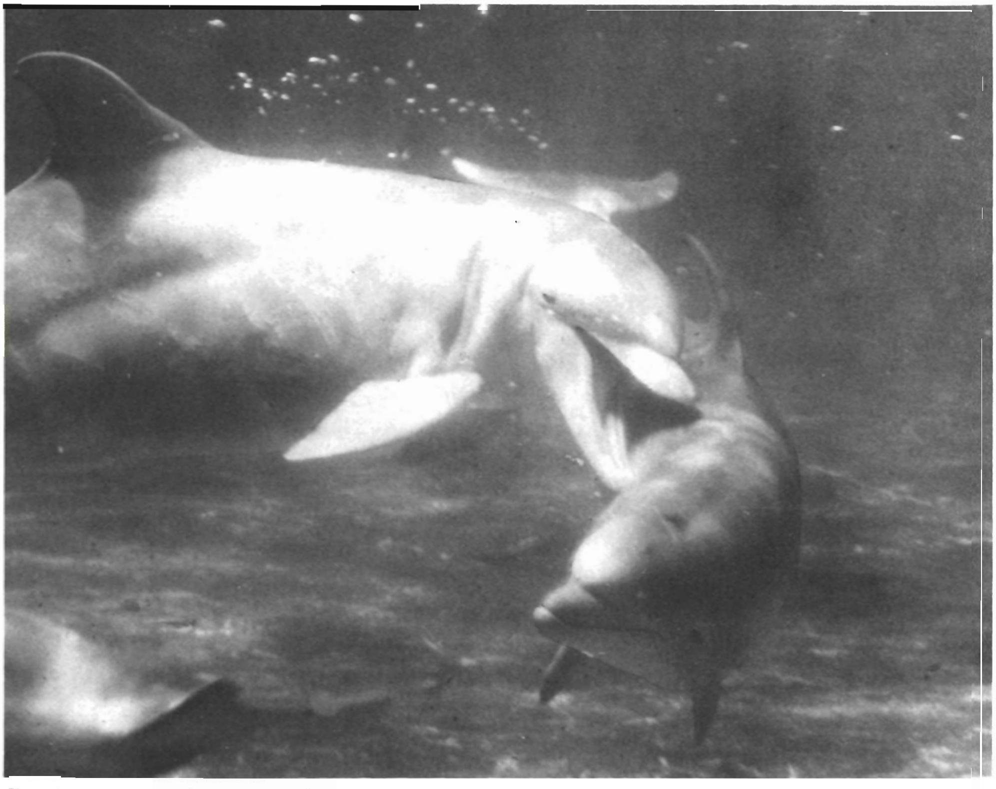


Fig. 8-113: *Tursiops truncatus* (captive). Play chase: an adult female (left) affectionately 'mouths' her juvenile male calf; this behaviour is often accompanied by loud 'chase squawks' (see Fig. 8-112). (After M. C. Caldwell and Caldwell, 1967; reproduced by permission of Professor R.-G. Busnel.)

Fig. 8-114: *Tursiops truncatus* (captive). Fight in which 2 females pin a subadult male to the tank floor; this behaviour is often accompanied by loud 'fight squawks' and frequently results in scratches or gashes. (After M. C. CALDWELL and CALDWELL, 1967; reproduced by permission of Professor R.-G. Busnel.)

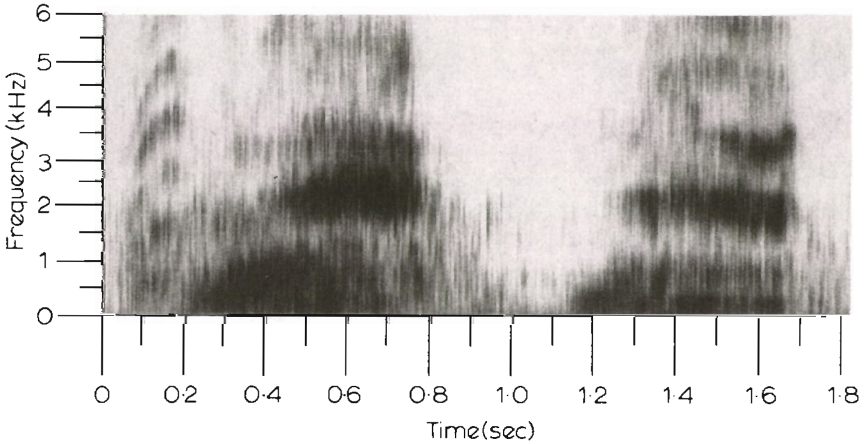


Fig. 8-115: *Tursiops truncatus* (captive). Sonagram of low-frequency squawks generated by an adult female carrying her stillborn calf (see Fig. 8-116 for concurrent behaviour). (After M. C. CALDWELL and CALDWELL, 1967; reproduced by permission of Professor R.-G. Busnel.)

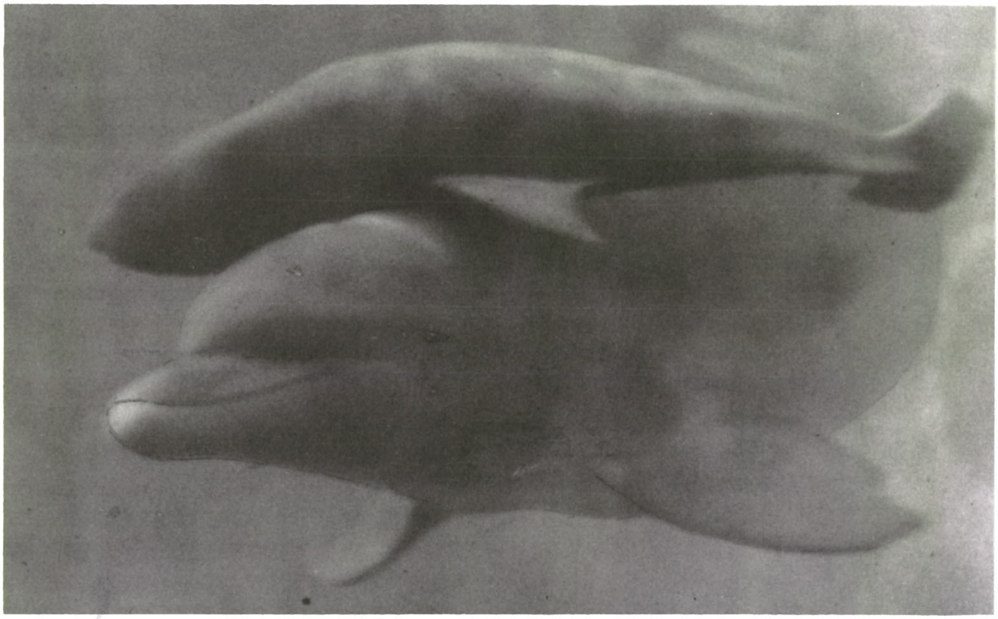


Fig. 8-116: *Tursiops truncatus* (captive). Adult female carrying her stillborn young over her melon; this behaviour was accompanied by repeated low-frequency squawks (see Fig. 8-115) until the dead calf was removed from the tank. (After M. C. CALDWELL and CALDWELL, 1967; reproduced by permission of Professor R.-G. Busnel.)

(iv) Sounds produced when lifting or carrying a dead infant are low-frequency squawks emitted repeatedly during the difficult task (Figs 8-115, 8-116).

(v) Concurrent emission of whistles and squawks (Fig. 8-117) reveals a tendency towards individually characteristic patterns. In some cases, porpoises whistling and

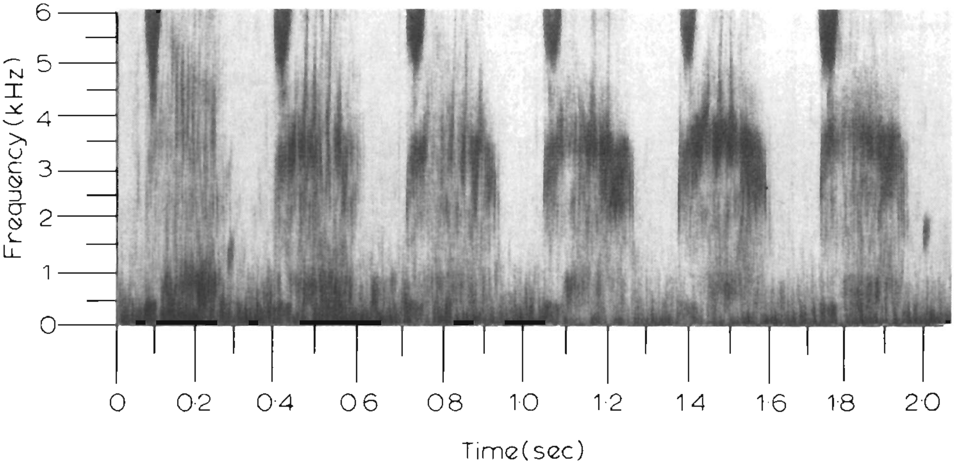


Fig. 8-117: *Tursiops truncatus* (captive). Sonagram of 'whistle squawks' produced by an adult female out of water. (After M. C. CALDWELL and CALDWELL, 1967: reproduced by permission of Professor R.-G. Busnel.)

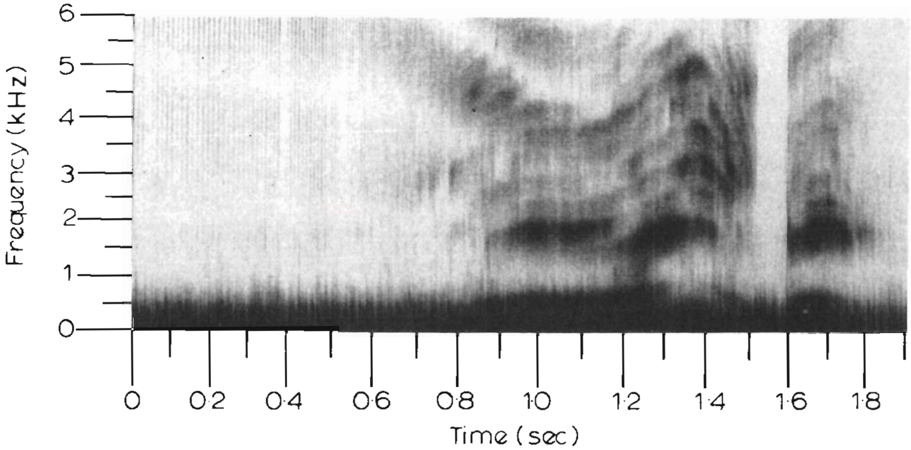


Fig. 8-118: *Tursiops truncatus* (captive). Sonagram of fine-discrimination active-biosonar clicks produced by a juvenile male in search of a tiny rock. (After M. C. CALDWELL and CALDWELL, 1967; reproduced by permission of Professor R.-G. Busnel.)

squawking at the same time seemed to convey protest (e.g. when lifted from a tank and placed on a stretcher).

(vi) Sounds produced while performing a difficult task: characteristic soft mewing, emitted while attempting to pick up small objects such as pebbles or coins

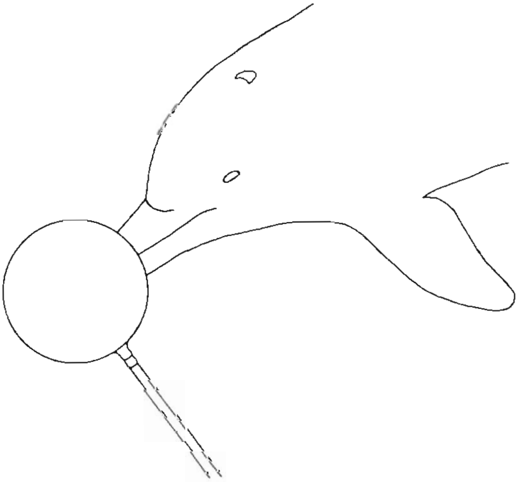


Fig. 8-119: *Tursiops truncatus*. Juvenile male pushing tether ball toward the bottom of his tank. This manoeuvre is accompanied by the production of fine-discrimination clicks similar to those in Fig. 8-118. (Based on a photo by M. C. CALDWELL and CALDWELL, 1967; reproduced by permission of Professor R.-G. Busnel.)

(Fig. 8-118). These extremely fast pulses seem to be associated with fine discrimination. They are also emitted when a dolphin is performing a difficult manoeuvre. In 'Marineland of the Pacific', M. C. Caldwell and Caldwell (1967) attached a tether-ball to a line which in turn was fixed to the floor of the community tank. The dolphins playfully attempted to push the ball (which contained sufficient air to put a strain on the holding line) forward with their snout (Fig. 8-119) until the ball touched the bottom of the tank. This involved difficult manoeuvring since the ball would immediately swing back to a position vertical above the fix point of the restraining line if the snout's tip pushed it the slightest bit off centre. Rapidly pulsed mewing sounds similar to those shown in Fig. 8-118 accompanied this performance. Caldwell and Caldwell find it reasonable to assume that other individuals in the community learn to associate this mewing sound with a harmless object in the vicinity.

(vii) Sounds associated with feeding are characterized by active-biosonar signals varying from loud, slow-pulsed clicks to the mewing produced during fine discriminations. Some of these signals are almost identical to the sounds shown in Fig. 8-118 and to the feeding sounds generated by *Phocoena phocoena* (Fig. 8-124). Other sounds are louder and more slowly pulsed, similar to those shown in the first section of Fig. 8-118. In the sea, such sounds may serve as cue indicating the presence of a fish school.

(viii) Sounds produced in a conflict situation have been observed in a captive mature bull offered fish in such a way that he would have to pass a narrow gate. *Tursiops truncatus* is afraid of narrow spaces. Even this bull, although in captivity most of his life and familiar with the pool, obviously found himself in a difficult conflict situation. The sonagram (Fig. 8-120) shows a typical phonation segment: loud active-biosonar clicks are followed by the rapid clicks associated with fine discrimination and finally by two loud cracks (at 1·55 and 1·95 secs, respectively).

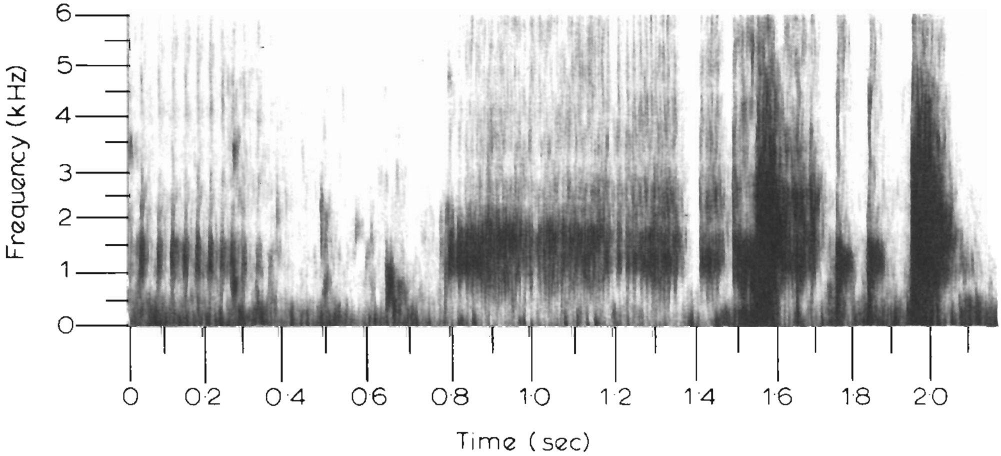


Fig. 8-120: *Tursiops truncatus* (captive). Sonagram of conflict-situation sounds produced by a mature bull which had to choose between passing through a narrow gateway or losing a fish reward on the other side. (After M. C. Caldwell and Caldwell, 1967; reproduced by permission of Professor R.-G. Busnel.)

After initial conflict confrontation, the intensity of the phonations and the concurrent fright behaviour decreased to some degree and loud squawks and barks were produced.

(ix) Sounds produced upon encounter of a new individual with an established group: When a large bull was introduced into a pool with an established community, a sound was recorded never heard on any other occasion: a puppy-like whimper (Fig. 8-121a). Because of the seemingly infantile nature of this signal, M. C. CALDWELL and CALDWELL (1967, p. 901) found it 'tempting to speculate that it is one of appeasement'.

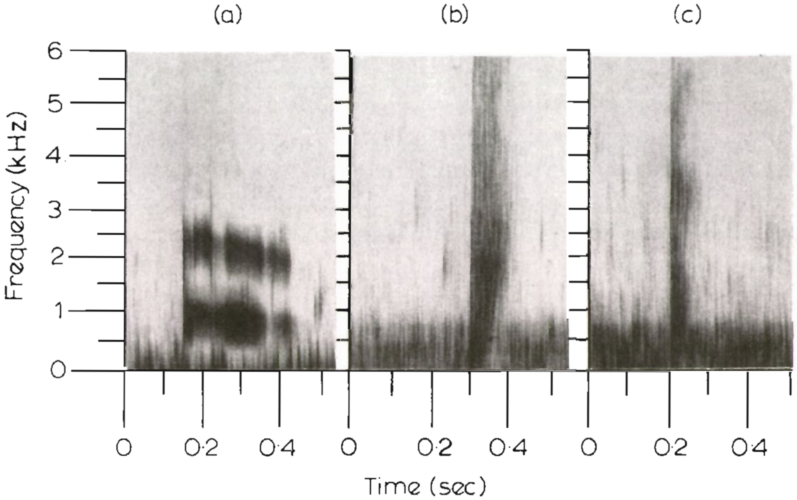


Fig. 8-121: *Tursiops truncatus* (captive). Sonagrams of adults: (a) whimper produced when a male was introduced into a pool with 4 newly captured individuals; (b) loud crack; (c) pop, both produced in response to novel stimuli. (After M. C. CALDWELL and CALDWELL, 1967; reproduced by permission of Professor R.-G. Busnel.)

(x) Sounds produced in response to novel stimuli: New stimuli or strange objects readily induce fear in *Tursiops truncatus*. When a new object is introduced, high-energy, broad-band cracks or pops may be elicited momentarily (Fig. 8-121b, c). A pop represents basically the same sound as a crack, but is of lower intensity. Both sounds are usually associated with a startle response and sudden flight; they are followed by quietness, interrupted only by an occasional chirp (a brief pure-tone emission) and then by soft active-biosonar sounds which may progress (after about 30 mins) to squeaks or high-pitched barks.

Complete absence of pulsed sounds has been observed occasionally by M. C. CALDWELL and CALDWELL (1967), even in groups of 10 or more individuals, both in captivity and in the sea. Often the sounds taper off gradually. Abrupt cessation of sound emission is common to *in situ* captures and captivity situations in which the potential danger can be seen coming on or in the presence of a frightening stimulus. Sudden cessation of sound production is considered as meaningful an alarm signal as a specific vocalization.

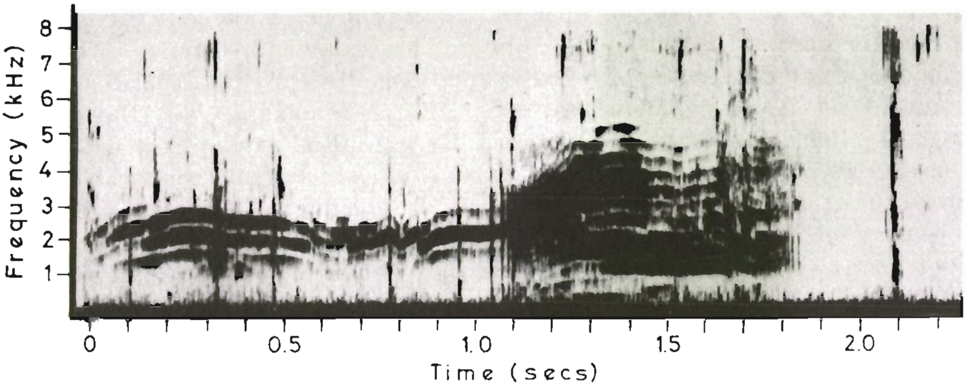
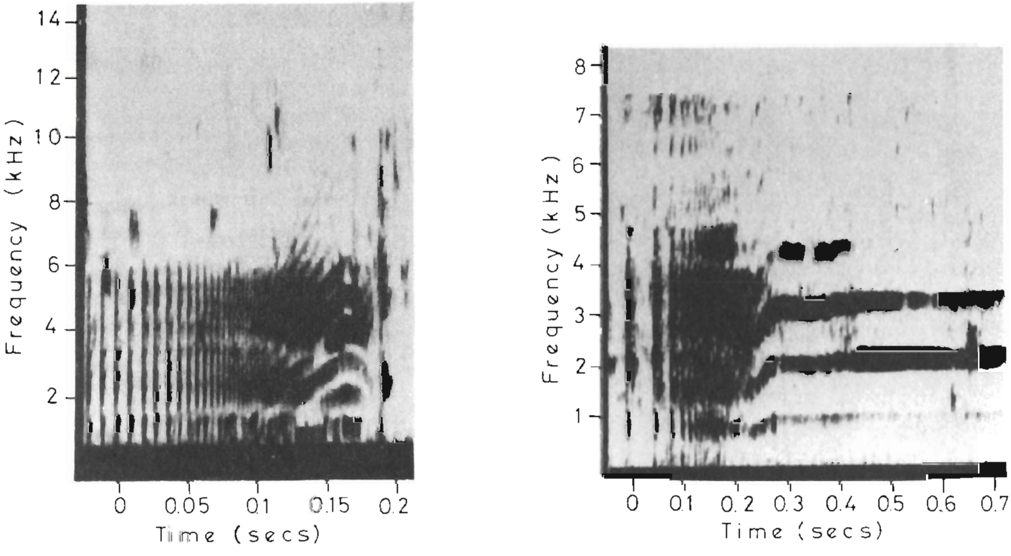


Fig. 8-122: *Phocoena phocoena* (captive). Sonagram of sound emitted during first attempts at courtship. (After Busnel and Dziedzic, 1966a; originally published by the University of California Press; reprinted by permission of The Regents of the University of California.)

Busnel and Dziedzic (1966a) experimented at sea (R.V. 'Calypso'; coast of Spain, western Mediterranean Sea) and in the laboratory (large tanks on Jutland, Baltic Sea). The sounds mentioned below were obtained from 3 females and 2 males, living in a plastic tank (10 m long, 6 m wide, 1·20 m deep). A total of 103 signals were recorded; at night the acoustic activity was sometimes rather weak. Five types of sound have been distinguished:

(i) Sounds produced during courtship: Courting *Phocoena phocoena* swim briskly around in pairs, maintaining close contact and approaching each other while moving. The male presents his abdomen, touches and rubs the female's dorsal



Figs 8-123 and 8-124: *Phocoena phocoena* (captive). Sonagrams of sounds preceding food intake (Fig. 8-123), and sounds emitted during feeding (Fig. 8-124). (After Busnel and Dziedzic, 1966a; originally published by the University of California Press; reprinted by permission of The Regents of the University of California.)

fin and sides with his tail, and passes underneath her abdomen; each partner touches the sides of the other with its head. This behaviour is similar to that described for *Tursiops truncatus* (McBRIDE and HEBB, 1948; WOOD, 1953; BROWN and NORRIS, 1956; TAVOLGA and ESSAPIAN, 1957), *Delphinus delphis* (BUSNEL and DZIEDZIC, 1966a) and other odontocetes. During initial attempts at copulation, acoustic signals are emitted, like that illustrated in Fig. 8-122, perceptible to the human ear as a squeaking of about 1 sec duration, and consisting of fast impulses (appearing on Fig. 8-122 as a succession of harmonics) with maximum energy at about 2 kHz. The interval between harmonics is 500 Hz but the total spectrum rises to 5 kHz. The signal may be strong (100 dB) or weak (60 dB). Another short signal emitted in this emotional context is a grinding (consisting of up to 7 harmonics) accompanied by a 'blast'.

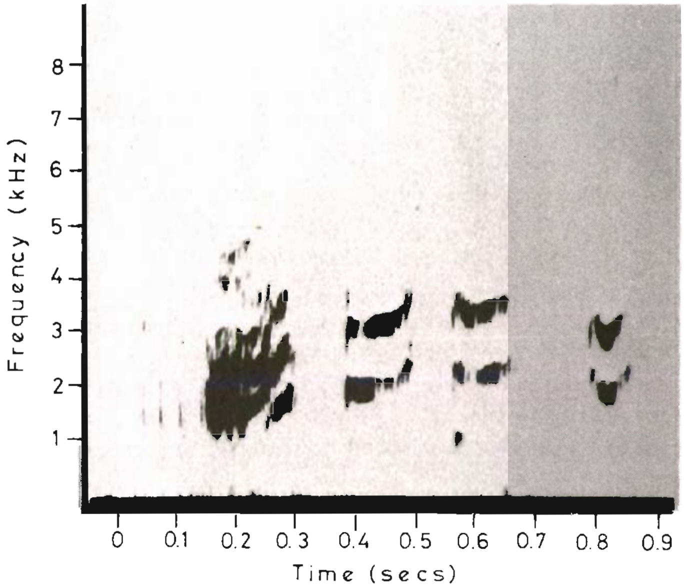


Fig. 8-125: *Phocoena phocoena* (captive). Sonagram of dominance signal. (After BUSNEL and DZIEDZIC, 1966a; originally published by the University of California Press; reprinted by permission of The Regents of the University of California.)

(ii) Sounds associated with feeding: The captive individuals took food from the hand, some on the day of capture, others after 24 to 72 hrs. When locating potential food, they began to emit echoranging clicks at a target distance of about 1 m. Closing in on the prey, repetition rate increases until the signal goes over into a characteristic creaking (Figs 8-123, 8-124). Average total signal duration is 0·27 sec; the first part consists only of individual clicks (about 0·14 sec duration); the second part, the creaking, lasts about 0·13 sec; it includes 4 to 10 progressively produced harmonics.

(iii) Dominance signals were produced especially at feeding time, and particularly from one of the females towards a young male: when this male approached a fish, the female left her routine circuit course and emitted the dominance signal, whereupon the male immediately left his prey to that female. The signal was heard under similar conditions from other dominating individuals and accompanied by rapid approaches and, sometimes, pushing with the rostrum. Dominance signals consist of 2 or 3 successive cries. The first part of the signal resembles the sounds emitted during feeding; but the pulses are much closer together. The second and third parts of the signal have a higher pulse repetition rate and rising frequencies, usually with 3 to 5 harmonics (Fig. 8-125). Intervals between harmonics, though variable, are in the range of 1 kHz.

(iv) Alarm or fright signal (sounds produced by newly introduced individuals): Placed together in a tank, two newly captured female *Phocoena phocoena* began to produce sounds immediately after they had been lowered into the water. The increased vocal activity lasted for the next 2 or 3 days. The signals were repeated at a quick rate (a few per minute) in the beginning and slowed down to a few per hour as the porpoises calmed down. Additional signals of the same type were emitted when a person approached the tank. The signal (Fig. 8-126) has been compared by BUSNEL and DZIEDZIC (1966a) to the complaining bleat of a sheep separated from the flock and brought into new surroundings; it expresses alarm or fright. The signal lasts from 0·4 to 1·55 secs. With maximum energy centring approximately at 2 kHz, the sounds comprise a dense succession of active-biosonar clicks (ca 200 sec^{-1}).

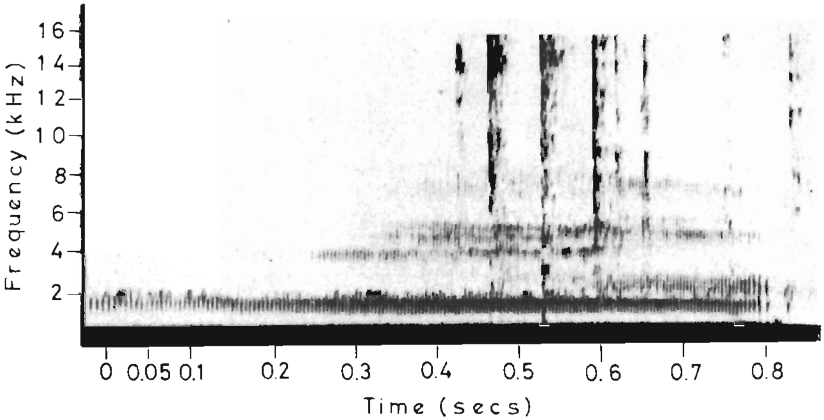


Fig. 8-126: *Phocoena phocoena* (captive). Sonagram of alarm or fright signal. (After BUSNEL and DZIEDZIC, 1966a; originally published by the University of California Press; reprinted by permission of The Regents of the University of California.)

(v) Other sounds: BUSNEL and DZIEDZIC (1966a) analyzed 56 additional 'anomalous' sounds with an average duration of 0·65 sec; for example, a rough squeaking comprising a substantial number of harmonics. The fundamentals are approximately 2 kHz, and the frequency spectrum rises up to 12 kHz.

DREHER and EVANS (1964) have considered contours of whistles recorded in *Tursiops truncatus*, *T. gilli*, *Delphinus delphis* and *Globicephala macrorhyncha* observed in 5 different situations (captive *T. truncatus* while feeding; ditto before and after presentation of a model of a baby dolphin or of a dead infant of *Stenella* sp.; a herd of *T. gilli* approaching and examining a sound-reflecting barrier placed across a lagoon; a migratory herd of *D. delphis* feeding in calm sea; a herd of *G. macrorhyncha* playing at sea). Some basic contours are listed in Table 8-9. Out of a total of 32 different contours, 5 are used by all species examined, 3 by all but *G. macrorhyncha*, 2 are shared by two species, and the remainder seem to constitute species-specific vocabularies.

Table 8-9

Some basic contours of odontocete whistles and their presumptive behavioural correlates (After Dreher and Evans, 1964; modified; reproduced by permission of Pergamon Press)

Contour	Presumptive behavioural correlate
	search
	feeding, disturbance
	fright, violent disturbance
	'baby talk'

Two isolated captive *Tursiops truncatus*, whose tanks were connected with an electronic acoustic link during alternate periods of about 2 mins, repeatedly communicated in a tight sequence. Their vocal interactions changed as the experiment progressed and was of considerable complexity (Lang and Smith, 1965).

Lilly (1962) kept an individual *Tursiops truncatus* ('Elvar') in constant daily contact with human observers who encouraged this young male dolphin to shape definite and distinctive 'words'. Lilly concluded that Elvar could be induced to emit 'humanoid emissions' in air. Analysis by sound-spectrograph and oscillograph methods demonstrated that these sounds are basically white-noise hissings and/or high-pitched buzzings, modulated in selective frequency bands. According to Lilly, some of these emissions appear to be attempts to reproduce words spoken by the investigators.

Analysis of sounds emitted by the false killer whale *Pseudorca crassidens* in the western Mediterranean Sea revealed 5 signal categories (types 1 to 5). The behaviour of the herd and the configuration of the signals (3 to 11 kHz) suggest to Busnel and Dziedzic (1968b) that the sounds are used for interindividual communication. Some signals resemble those recorded from *Globicephala melaena*.

Individual Sound Signature

Sounds may contain properties which are specific to the sound-generating individual. Such individual sound signature may be of importance for individual recognition and for establishing and maintaining social contacts and social structures. However, experimental evidence is rare and more information is needed before we can draw detailed conclusions.

Northern elephant seals *Mirounga angustirostris* recognize each other individually from phonations (threat calls) alone (LeBoeuf and Peterson, 1969a, b; LeBoeuf and Petrinovich, 1972). This ability appears to enable the males to identify companions from different populations, and might enhance reproductive isolation in breeding subunits of the population. The cows of various pinniped species seem to recognize their pups by voice, and the pups often appear to recognize their mother's voice. Such and other individual recognition by sound seems to function even in the presence of hundreds of con- or heterospecifics (e.g. Bartholomew, 1959; Kenyon and Rice, 1959; Eibl-Eibesfeldt, 1961; Bartholomew and Collias, 1962; Sergeant, 1965; Evans, 1967; Orr and Poulter, 1967; Peterson and Bartholomew, 1967; LeBoeuf and Petrinovich, 1972).

Bottle-nosed dolphins *Tursiops truncatus* may produce whistles and other sounds with individual characteristics (e.g. Essapian, 1953; Lilly, 1962, 1963; Busnel, 1963; M. C. Caldwell and Caldwell, 1965, 1967; M. C. Caldwell and co-authors, 1970, 1971a, b). The first conclusive experiments demonstrating that the whistles of *T. truncatus* contain sufficiently constant differences to allow individual identification have been conducted by M. C. Caldwell and co-authors (1970). Their results document that a dolphin can easily learn to discriminate between, and react differently towards, playbacks of whistles recorded from conspecifics. A single whistle is all that is needed, and even heavy masking seems to affect recognition but little. According to M. C. Caldwell and co-authors (1971b), *T. truncatus* is able to discriminate between the whistles of 8 conspecifics. This ability may play an effective role in communication among herd members and between different herds.

Tursiops truncatus can also discriminate between, and potentially identify to individual, the whistles of other odontocete species, for example *Stenella plagiodon* (M. C. Caldwell and co-authors, 1971a) or *Delphinus delphis* (M. C. Caldwell and co-authors, 1973). *T. truncatus* quickly learned to respond differentially to randomly assorted whistles of 2 *S. plagiodon* and 4 *D. delphis* individuals. Such performance 'opens the possibility for an intergeneric social ordering' (M. C. Caldwell and co-authors, 1973, p. 1). Statistical evidence for individual signature whistles has also been presented for the North Pacific white-sided dolphin *Lagenorhynchus obliquidens* (M. C. Caldwell and Caldwell, 1971).

Backus and Schevill (1966) report individual signature for clicks recorded at sea from sperm whales *Physeter catodon*. The structure of the single pulses that compose each burst pulse appears to be typical of each individual sperm whale. The spacing of pulses (interpulse interval) varies from individual to individual. Norris and Harvey (1972) propose that this variation may be due to the different lengths of the spermaceti organs (p. 752), but call for experimentation with living sperm whales.

Local Accents and Dialects

Since marine mammals (i) maintain social units (pods, harems, herds), (ii) often exercise appreciable separation between such units, and (iii) are capable of producing signature sounds, geographic gradients or local differences in phonation may be expected. The properties of certain sounds may vary as a function of the area inhabited or of the social unit belonged to. Such variation could, conceivably, lead to local accents and dialects.

Geographic variation in sound properties has been considered or suggested by several authors (e.g. ESSAPIAN, 1962). Northern elephant seals *Mirounga angustirostris* exhibit a local accent in regard to the threat call of adult bulls (LEBOEUF and PETRINOVICH, 1972). It is often difficult, however, to detect and to critically evaluate intraspecific variations in sound properties.

'Local accents' may reflect differences in analytical techniques, especially filter bandwidths: SCHEVILL and co-authors (1969) did not note real differences in '*Globicephala* signals' recorded in the Mediterranean and in the western North Atlantic and eastern North Pacific Oceans.

> 'Similarly, we find no significant differences of this sort between the *Delphinus delphis* signals reported by these authors and VINCENT (1960) from the Mediterranean and those from the east and west coasts of North America (SCHEVILL and WATKINS, 1962; CALDWELL and CALDWELL, 1968). Likewise, we find that *Megaptera novaeangliae* sound alike in the Atlantic (Bermuda, Gulf of Maine) and Pacific (California, Hawaii, New Zealand), and the same may be said of *Physeter catodon*. Recordings of *Orcinus orca* sound alike whether made off British Columbia or in the Ross Sea' (SCHEVILL and co-authors, 1969, pp. 725–726).

A new approach to local accents and dialects, employing modern analytical techniques and including behavioural studies, seems desirable. Definite knowledge on presence or absence of intraspecific gradients regarding vocal control of social relationships is important for assessing population heterogeneity, reproductive barriers and gene-flow dynamics.

(11) Electrical and Magnetic Fields

Weak electrical fields—generated by flowing water masses moving in the earth's magnetic field—may provide orientational cues to marine organisms (Chapters 8.1, 8.2). However, pertinent studies are rare and frequently inconclusive. No investigations have been conducted yet regarding the possible importance of electrical fields in oceans and coastal waters for orientation of marine mammals.

Magnetic fields can interfere with, or guide, orientational responses in invertebrates (Chapter 8.1) and fishes (Chapter 8.2). Again, conclusive pertinent information on marine mammals is not available. According to POULTER (1972), the vibrissae of the California sea lion *Zalophus californianus* appear to respond to weak magnetic fields. This suggestion deserves further attention; it requires critical qualification.

(12) Mechanical Stimuli

While mechanical stimuli participate in spatial orientation of marine mammals, their ecological significance and the degree to which they may be relied on are open to debate. In general, mechanical stimuli appear to be of importance in establishing, maintaining and controlling social structures. In some cases, mechanoreception facilitates also close-range object discrimination. Mechanoreception is based on contact sensitivity of external or internal sensors; it overlaps functionally with mechanisms of equilibrium and hearing. We consider here (i) external mechanical stimuli which act upon the general skin area or specific skin receptors and (ii) internal stimuli which act upon sensors (proprioceptors) located within body structures such as digestive tract, muscles or circulatory system. Mechanical stimulation is assumed to affect primarily sensitive molecular configurations; it controls energy conversion by secondary processes (translation of information or sensory transduction based on amplifying mechanisms, rather than energy transformation in the sense of physics; SCHWARTZKOPFF, 1973).

According to KING (1964), most pinnipeds have a well-developed tactile sense. Their vibrissae may act as receiver of mechanical stimuli. This has been suggested on the basis of experimental evidence by DYKES (1972) and POULTER (1972) for the California sea lion *Zalophus californianus*. In this sea lion, the vibrissae seem to assist in the discrimination of shape and texture of objects in the immediate vicinity of the face. Presumably, nose-to-nose contacts—frequently observed among pinnipeds—serve as a gesture of greeting, as precopulatory play, and to facilitate

Fig. 8-127: *Odobenus rosmarus divergens*. Muzzle contact between two walruses serves inter-individual communication. Presumably, it represents a gesture of greeting, participates in precopulatory play, and facilitates individual recognition. (Reproduced by permission of 'Marineland of the Pacific'.)

individual recognition (Fig. 8-127). Nose-to-nose contacts probably comprise mechanical as well as chemical (gustatory and olfactory) stimuli.

Similarly, Sirenia often touch each others' bodies, especially with their nose (p. 732). Such muzzle contacts have also been referred to as 'kissing'. They seem to serve functions comparable to those suggested for pinnipeds. Presumably, tactual cues are of importance to sirenians for maintaining social inter-relationships. However, little is known yet about interindividual behaviour in this order (EVANS and BASTIAN, 1969; HARTMAN, 1969).

Physical body contact among mysticetes is less pronounced than in pinnipeds and sirenians. Body contact and aggressive behaviour (NORRIS, 1967b) of mysticetes—nearly all docile, timid creatures—appears to be restricted largely to mating and parental care. Odontocetes, however, are known to employ body contact as a means of communication and, according to NORRIS, may exhibit aggressive behaviour in courtship and when suppressing attempts of young males to enter a breeding group. Amazon dolphins *Inia geoffrensis*, kept in a tank at 'Marineland of Florida' (USA), exhibit a pronounced tendency towards body contact, both between adults and between juveniles and adults (M. C. CALDWELL and CALDWELL, 1969b).

The ease, elegance and perfection of cetacean locomotion implies a high skin sensitivity to mechanical stimuli. Cetacean dermis papillae (SLIJPER, 1962) and the presence of special organs with sinus hairs on the rostra of all cetaceans examined (OGAWA and SHIDA, 1950), suggest acute mechanoreception, at least in specific areas, especially the snout region. In *Delphinus delphis* the threshold of tactile perception (10 to 40 mg mm^{-2}) conveys to the skin considerable capacities for discriminating 'mechanical oscillations' in the ambient medium, including those caused by acoustic energy (KOLCHIN and BELKOVICH, 1973).

The side-swimming (HERALD and co-authors, 1969; PILLERI, 1970b), muddy-river living dolphin *Platanista gangetica* maintains mechanical contact between pectoral fin and river bottom during much of its locomotory activities (Fig. 8-128).

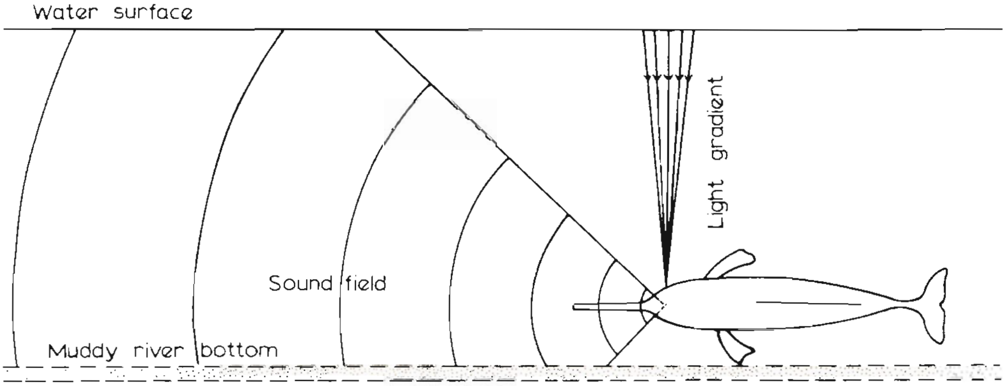


Fig. 8-128: *Platanista gangetica*. This side-swimming muddy-river dolphin navigates by sound, vertical light gradient and mechanical bottom contact (pectoral fin). (After PURVES and PILLERI, 1973; modified; reproduced by permission of Professor G. Pilleri.)

(13) Orientational Responses to Environmental Factors Acting in Concert

Most orientational responses seem to be based on several environmental factors acting in concert, rather than on the effect of a single cue. It is deplorable, therefore, that the studies hitherto conducted are concerned almost exclusively with single-cue analyses. Experiments on multi-cue effects open up important new avenues for assessing ecological aspects of orientation in space.

Interrelationships between underwater visual and acoustic cues and between the corresponding discrimination and evaluation mechanisms in *Delphinus delphis* have been investigated by BAGDONAS and co-authors (1970). The test dolphins were required to identify geometrical figures (square, triangles) made of materials with different optic and acoustic properties. The results obtained are not unequivocal; they invite further studies along similar lines.

The river dolphins *Platanista gangetica* and *P. indi* navigate in low-visibility, muddy waters at visual ranges of 2 to 3 cm (PILLERI, 1970b). Observations suggest that the sound field ahead, the echoes perceived, the vertical light gradient and the pectoral fin's mechanical bottom contact constitute the most important navigation cues used by these side-swimming odontocetes (Fig. 8-128). Obviously, water surface and river bed are two major aspects of spatial orientation in the dolphins' environment. The surface reflects most acoustic signals, while the muddy river bed acts as sound absorber (PURVES and PILLERI, 1973).

(14) Migratory Cycles

(a) General Aspects

Information on migratory cycles of marine mammals has been obtained by occasional observations, sealing and whaling data, and by tagging experiments. The present status of pertinent knowledge is characterized by scattered reports of varying reliability and detail. Hence the information at hand requires critical evaluation. We are badly in need of more objective and more comprehensive data. Even tagging experiments must be viewed with some reservation: Inadequate handling and significant disturbances may scare seals or whales away from their immediate home areas and may affect return rates of migrators. Modern techniques, such as intramuscular application of immobilizing and anaesthetizing drugs, may help to reduce negative catching and handling effects; ketamine, for example, has been used successfully in seals and sea lions (4·5 to 11 mg kg^{-1} of body weight) under laboratory and field conditions (GERACI, 1973). In addition, helicopter, aeroplane, and satellite surveys—in co-operation with ship studies—will greatly advance our present knowledge.

Evidence for the orientation mechanisms actually employed by migrating marine mammals is difficult to obtain. *In situ* experiments encounter a variety of problems. But transmitter attachment and radio-tracking of normal, displaced, or incapacitated (e.g. blindfolded, blinded, deafened, olfactosectomized, or drugged) individuals isolated from, or allowed to rejoin, their herds are likely to allow new insights.

Unless used to the presence of man, migrating marine mammals may change course and behaviour if followed too closely. Two principal avenues have been used in attempts to record behavioural details of migrating whale herds: (i) recording by transmitter attachment, and (ii) continuous close-distance observation by means apparently accepted by the herd.

(i) **Transmitter attachment** (e.g. STARKS, 1966; EVANS, 1971, 1972; EVANS and LEATHERWOOD, 1972; EVANS and co-authors, 1972) requires careful capture, tagging (e.g. EVANS and co-authors, 1972) and release. If a tagged individual rejoins the herd, it can provide data on migratory dynamics of its untagged conspecifics. In combination with long-range ship receivers or helicopter-borne receivers, possible disturbances of the migrating herd are kept to a minimum. A neutrally buoyant radio beacon was attached by EVANS (1971) to the dorsal fin of *Delphinus delphis* (Fig. 8-129), i.e. at a location that allows maximum exposure time of the instrument's antenna during air exchange and causes minimum hydrodynamic interference. The transmitter mount, lined with open cell-foam plastic, was designed so as to allow a free flow of water over the dorsal fin. A nylon pin—placed through the fin, spring-loaded on one end and fastened with a corrosive head on the opposite end—served for attachment. The pin had a holding life of ca 40 days and, apparently, did not adversely affect the fin. The transmitter was operated by a sea-water switch that was activated when the antenna broke water; it had an operational range of 10 nautical miles. A test individual (Fig. 8-130) indicated some difficulties in swimming during the first hour; but accommodation to the dorsal package was rapid.

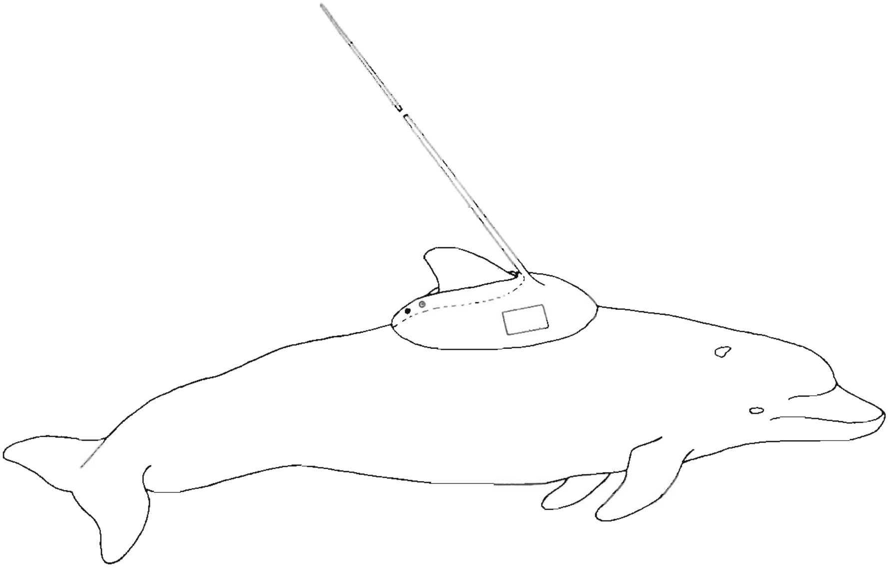


Fig. 8-129: *Delphinus delphis*. Radio beacon attached to dorsal fin in tank at 'Marineland of the Pacific', Palos Verdes, California, USA. (Based on a photo by EVANS, 1971; reproduced by permission of New York Academy of Sciences.)

At sea, EVANS (1971) tagged and released 8 newly captured *Delphinus delphis* during a 24-month period. All data transmitted from the instrumented individuals were received by an automatic direction finder, installed on a ship or a helicopter and capable of responding to less than 1 msec of signal. In general, herd movements reveal a close correlation with sea-bottom topography (Fig. 8-130). Just prior to and during sunset, the herd tended to swim in a circular pattern; after sunset, it began to spread again. This behaviour was repeated prior to sunrise, indicating a tendency towards cessation of unidirectional herd movement at sunrise and sunset. Breathing intervals reveal diurnal patterns; they are shorter during the day (midmorning, midafternoon) than near sunset or sunrise. Fishermen familiar with the coastal waters of California insist that delphinids—mainly *Delphinus delphis*—drastically change their behaviour at sunset and sunrise (Evans, 1971; see also Pilleri and Knuckey, 1968, and p. 730); large aggregations occurred primarily

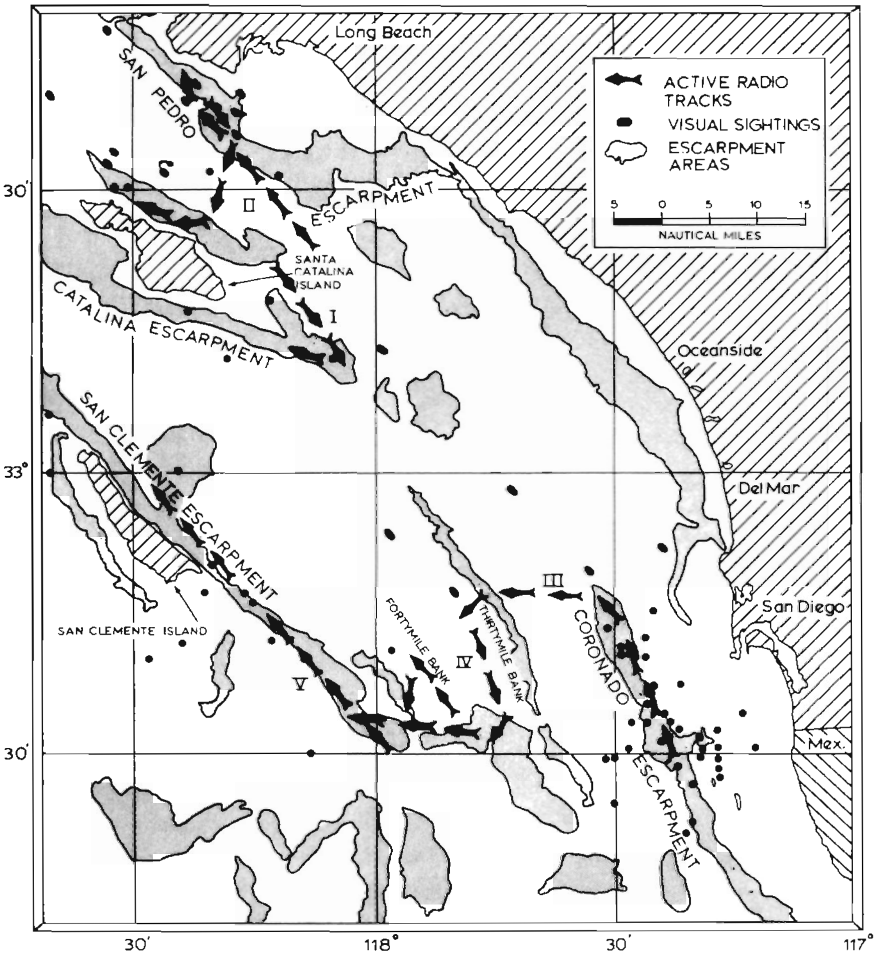


Fig. 8-130: *Delphinus delphis*. Radio tracks, supplemented by aerial sightings, of a school off the coast of Southern California, USA. Most herd movements are closely associated with prevailing bottom escarpments. (After Evans, 1971; modified; reproduced by permission of New York Academy of Sciences.)

between 06·00 and 09·00 hours and between 17·00 and 18·00 hours. Diving depths were 30 to 60 m (occasional excursions), 64 m (long periods of diving), 260 m (overall maximum depth). Maximum depths of single diving patterns exceeded the depth of the deep scattering layer in all cases. Although herd movements suggest that orientational cues—for example, on visual, acoustic or thermal features, or sea-bottom topography—are acquired during deep dives, there is no direct evidence available to support this.

In addition to revealing migration patterns, transmitter attachment to cetaceans can be used for measuring oceanographic data (e.g. light, temperature, salinity, dissolved gases, etc.) at various diving depths, for assessing the whales' environment, and for establishing relationships between these data and the seas' productivity. First experiments, using a captive yearling grey whale *Eschrichtius robustus*, released from 'Sea World' (San Diego, California, USA) during northbound migration of the California population (p. 836), showed that a large whale is a 'potentially invaluable platform' for collecting marine environmental data (EVANS, 1972, p. 18). The transmitter, mounted on the dorsal ridge, yielded details of migratory speed and direction, diving patterns, and thermal gradients.

(ii) **Continuous close-distance observations** via means apparently accepted by a herd have been made in several cases. An example regarding the killer whale *Orcinus orca* has been provided by SPONG and co-authors (1970, 1972a, b). They found that human presence (kayak, sailboat, motorboat, skin diver) was easily accepted by *O. orca*. Following consultations with local fishermen, SPONG and co-authors chose Hanson Island as site of a land-based field station and operated in the nearby waters of the Johnstone Straits (Canada). These waters are used each year as summer travelling route by *O. orca* herds. Acceptance of the observers by the herds facilitated a number of revealing observations: *O. orca* is an efficient hunter (p. 841), which tends to maintain long-term social structures (p. 842) and orients relative to tidal water changes (p. 735), apparently because the movements of salmon—its predominant local food source—are strongly influenced by water movement (tide and current). Hunting situations are characterized by frequent vocal exchanges between herd members, and by intermittent echolocation emission of active-biosonar clicks. During feeding, predominantly active-biosonar signals are emitted. Presumably, the hunting whales orient primarily to water movement, sound and visual cues. Individual phonations may convey information relating to the identification of the sound emitter, his position, prey data, and perhaps to the overall hunting strategy used by the herd (p. 842).

SPONG and co-authors (1972b) were thrilled by the many 'shows' presented by *Orcinus orca* during the field study. Interestingly, these performances (play behaviour) of wild animals comprise all essential elements of the shows presented in oceanaria: members of passing pods breach repeatedly, flip their flukes, stand on their heads with their flukes high in the air, rear out of the water vertically to the pectoral fins, spray water from their mouths, tail-lob furiously, upside down or on their sides, flap fins and flukes in the water creating explosion-like sounds, swim in circles forming giant O's and race at top speed over the water for 90 or 180 m, skimming the surface and spraying water in all directions.

Endogenous homeostasis—especially well-developed mechanisms of thermoregulation (p. 731)—convey to marine mammals a considerable degree of environmental independence and allow them to parallel the distributions of their major prey oranisms—except during reproduction, when the more limited tolerances of pregnant females and newly born calves, as well as the need for a suitable contact area where the adults can copulate, dictate additional dependencies on specific environmental conditions. During feeding migrations, abundance and behaviour of food organisms, grazing or hunting techniques and social structures seem to be important denominators of orientational activities. During reproduction, environmental factors such as daylength, overall water temperature, water depth and male–female as well as female–young relations tend to control orientational behaviour.

Evidence of close relationships between migrations of whales and food availability has been provided by numerous authors, e.g. SALNIKOV (1953), BETESHEVA (1954, 1955, 1960, 1961a, b), BETESHEVA and AKIMUSHKIN (1955), ARSENYEV (1957, 1961), BEKLEMISHEV (1959), BERZIN (1959), SLEPTSOV (1961a, b, c), GUDKOV (1962), D. K. CALDWELL and co-authors (1966a) and TARASEVICH (1968a, b). The literature on reproduction in marine mammals has been reviewed by HARRISON (1969); pertinent reviews on cetaceans have been written by SLIJPER (1966) and SOKOLOV (1971). While the latter author has restricted his sources to USSR contributions, he has provided an important document of cetacean research in the Soviet Union. Additional information on reproductive activities in cetaceans has been presented by SOKOLOV (1950, 1953, 1954, 1962), CHUZHAKINA (1955), TOMILIN (1967), KLEINENBERG and YABLOKOV (1960) and KCHUZIN (1963). Epimeletic (care-giving) behaviour has been reviewed by M. C. CALDWELL and CALDWELL (1966). The evidence at hand documents that mating, pregnancy, birth and lactation—as well as migratory patterns and social structures—are often related to seasonal dynamics.

In marine mammals, the major endogenous driving forces which control migratory activities are correlated to nutrition and reproduction. At the same time, nutrition and reproduction appear to constitute the basic evolutionary initiators for behavioural specificity. In many marine mammals, nutritive and reproductive activities alternate as a function of, or are significantly affected by, annual rhythms based on seasonal influences. In all cases in which the distribution of food organisms underlie pronounced seasonal variations or in which reproductive requirements differ essentially from those found near the feeding grounds, migrations become necessary. The release of migratory activities seem to depend on endogenous, nutritive and hormonal conditions, and these—in turn—appear to be based on, and co-ordinated by, environmental factors, especially light and temperature. Seasonal changes in daylength may control endogenous cycles and thus release migratory activities.

The extent of migrations varies considerably among species. And even within the same species, migrating and resident populations may exist—possibly based on genetic differences (interspecific gradients) and local nutritional or climatic conditions. In marine mammals which migrate over long distances, for example baleen whales, the onset of migration is characterized by a typical chronological sequence, and the migrating herds exhibit typical differences in composition. Both temporal and structural properties of migrating herds are closely correlated to endogenous properties (e.g. nutritional state, sexual maturity, pregnancy, lactation, age and sex) of the individuals concerned.

(b) Pinnipedia

Most pinnipeds migrate. They fan out over the sea for feeding and, at a given time, aggregate for breeding. Reproduction takes place on defined, usually small land or ice territories. Homing to the breeding places is, at first, often a matter of individual response. Later, migrating herds assemble, and finally breeding aggregations of hundreds or thousands of individuals crowd in restricted breeding areas. Even though territorial restriction and territorial reproduction facilitate observation, tagging and experimentation, little definite information is available on orientation cues and orientation mechanisms employed during migration.

Some pinnipeds conduct extensive migrations: Northern fur seals *Callorhinus ursinus* migrate several thousand miles and home to specific, very small territories for successive breeding seasons (PETERSON, 1968). Alaska- and Cape-fur-seal mothers leave their young, feed for more than 2 weeks at sea, and promptly return to their own pups (BARTHOLOMEW, 1959; RAND, 1967). Weddell seals *Leptonychotes weddelli* dive down to depths of 600 m for as long as 1 hr (KOOYMAN, 1966), exhibiting considerable orientational skills under the Antarctic ice (KOOYMAN and ANDERSEN, 1969). Northern sea lions *Eumetopias jubatus* and California sea lions *Zalophus californianus* conduct annual migrations along the coast of Oregon (USA): MATE (1972) observed well-ordered and co-ordinated seasonal migrations with directed movements of whole populations at uniform speed; the migrations are related to breeding, feeding and overwintering. Even pups may travel considerable distances (e.g. pups of the South African fur seal *Arctocephalus pusillus*: ca 1500 km in the first 10 months after tagging; BEST and RAND, 1972), although, in general, pups tend to remain in the vicinity of their birthplace for several months. Such extensive migrations require well-developed mechanisms of spatial orientation and considerable abilities for cue memorization.

In general, homing capacities increase with age (experience). While basic navigational abilities appear to be genetically fixed in most species, observation and tagging on rookeries point to the importance of imprinting and learning. In herds, directional 'decisions' made by older individuals dominate the responses of subadults. No exact data are at hand on the routes travelled, nor on the directional precision maintained during migration.

According to ONO (1972), nursing females of the Northern sea lion *Eumetopias jubatus*, returning from feeding excursions, orient to the same part of the island where they left their pup. The female then emits a loud, prolonged sound—distinct from all other rookery noises and easily located by an observer. She then continues to move towards her pup and to phonate while her pup responds by emitting sounds and by moving towards her. Upon contact, the pair usually go through a 'recognition' phase. This phase involves phonations by both, female and pup, and nosing prior to suckling—a process similar to that in the Northern fur seal *Callorhinus ursinus* and the California sea lion *Zalophus californianus*. It involves a sequence of acoustic, visual, and tactile–olfactorial cues.

Pinniped migration routes may differ in females and males. In *Zalophus californianus*, for example, some females remain either near the breeding grounds (Channel Island, Southern California, USA), or move southward to Baja California, while the males move northward as far as British Columbia (Canada; e.g. FRY, 1939). In

Odobenus rosmarus divergens, sexual and age segregations have been reported by FAY (1955) and BUCKLEY (1959). Observations on colour-marked individuals of *Mirounga angustirostris* on San Nicolas Island (California, USA) revealed that females of a harem tend to remain near a given spot (BARTHOLOMEW, 1952; BARTHOLOMEW and COLLIAS, 1962). Females of low dominance are often forced to move by the aggressive behaviour of more dominant females and their pups are likely to become lost and to be bitten by other females. Vocalizations play an important role in maintaining the highly polygynous social structure and the modified proboscis of the adult male appears to have no function other than to produce vocal threats.

JAMES and RENOUF (1972) observed that *Phoca vitulina*, during both pupping and moulting, frequently cross the 0·5 km of sand which separates the south coast of Sable Island (Canada) from the lakes in the island's interior. According to JAMES and RENOUF, this migration is unaffected by horizontal visibility, cloud opacity, wind direction or the apparent direction of the sound of the surf. Displacement of seals 1 to 1·5 km east or west of their normal crossing route does not reduce the considerable accuracy with which the shortest connection between sea or lake is found. Apparently, overland navigation of *P. vitulina* is independent of local landmarks and meteorological cues. JAMES and RENOUF found that the performance of displaced, newly weaned individuals of *P. vitulina* and of grey seals *Halichoerus grypus* is much less accurate than that of adult *P. vitulina*; but the subadults are generally able to find the sea from any point of the island, irrespective of prevailing weather conditions. Their mean track bearings may be deflected by the apparent direction of the surf sound; it seems clear, however, that they are not merely homing on an acoustic component of the surf which is audible to the human ear.

Lack of visual landmarks, long excursions under ice-covered waters with low visibility, and absence of odour cues or other tracks in snow-swept land areas provide little ground for many of the assumptions and theories offered in regard to possible orientation mechanisms. Radio-tracking of adult females and males should allow better insights into the migratory behaviour of these amphibious inhabitants of extreme, challenging and remote aquatic and terrestrial habitats.

(c) Sirenia

Scattered reports indicate that, in Florida (USA), sirenians migrate between coastal sea areas and river habitats. During the cold season, and especially during extreme cold spells, they move to warm-water refuges (e.g. warm springs; p. 732).

In order to determine the migration routes of the Florida manatee *Trichechus manatus latirostris*, HARTMAN (1969) interviewed local crabbers, mullet fishermen and park guides. From the information obtained and his own observations, HARTMAN concludes that the manatees avoid extremely shallow flats and waterways. Seeking open water, they travel along established corridors through a complex of sand bars, oyster beds and limestone shelves, characteristic of the coast areas inhabited.

(d) Mysticeti

Mysticetes undertake impressive migrations. In general, the giant whales feed in high latitudes during summer and reproduce in low latitudes during winter.

Such alternation between feeding and reproductive periods—separated by weeks or months of migratory activities—requires considerable capacities for navigation and for temporary storage of energy resources. Mostly stored in the form of thick blubber coats, the reserve materials often last for up to 6 months.

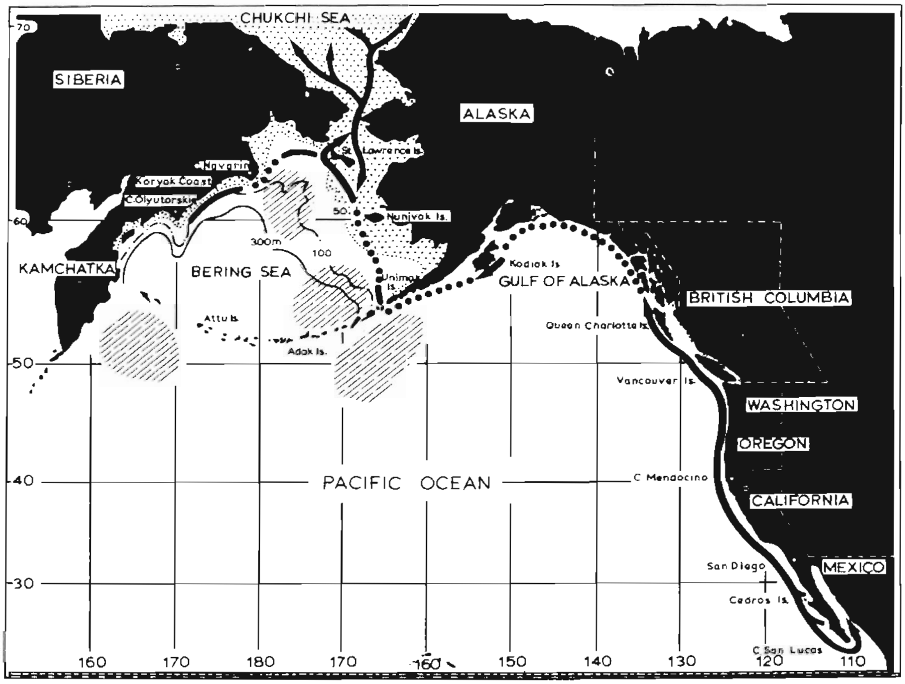


Fig. 8-131: *Eschrichtius robustus*. Migration routes of Northeast Pacific population. Solid lines: known routes; dotted lines: probable routes; hatched regions: whaling areas where *E. robustus* is not seen. (After PIKE, 1962; reproduced by permission of *Journal of the Fisheries Research Board of Canada.*)

The grey whale *Eschrichtius robustus*—the sole survivor of the Eschrichtiidae, the most primitive mysticete family—undertakes annual migrations which are assumed to be the longest performed by any mammal (Fig. 8-131). The Northeast Pacific population ('California population') covers some 9000 to 12,000 km between the warm breeding (calving) grounds in the bays and lagoons of northeastern Mexico and the cold feeding grounds in the highly productive arctic waters of the Bering and Chukchi Seas (ANDREWS, 1914; GILMORE, 1961; WILKE and FISCUS, 1961; PIKE, 1962; RICE and WOLMAN, 1971). Migrating in small groups, usually of 2 to 5 individuals, the herds require about 7 to 11 weeks for each route. The average daily distance travelled is estimated to be somewhere near 110 to 150 km at a speed of 5 to 7 km hr^{-1} for a daily 20-hr active period. The West Pacific population ('Korean population') migrates between breeding (calving) grounds near Korea and the cold, productive Okhotsk Sea. The migratory cycle of the Korean population is less well known than that of the California population.

The California population of *Eschrichtius robustus* begins its southward migration when the first pack ice forms in autumn. The feeding aggregations (50 to 150 individuals) break up into small subgroups, apparently headed by pregnant females; courting males and non-pregnant females follow somewhat later. Females mature sexually at a length of 12 m, males at 11 m (ZIMUSHKO, 1969). On their southward route, *E. robustus* probably pass through the Aleutian Chain in the vicinity of the Unimak Pass (ICHIHARA, 1958). In the Gulf of Alaska, the exact migratory route is not known. According to PIKE (1962), the grey whales appear to follow the Gulf's shore line; however, at least some whales cross open, deep water, approaching the coast again in British Columbia, Washington or Oregon (HUBBS, 1959; GILMORE, 1960a). The subsequent migration route closely follows the coastline until the Mexican breeding places (Baja California, Sonora–Sinaloa coast) are reached (Fig. 8-131).

During migration, *Eschrichtius robustus* usually keeps to water depths between 10 and 180 m; however, some individuals enter near-stranding depths (e.g. in kelp beds) or travel over depths of 1370 m (NORRIS, 1967a). Grey whales passing Cedros Island (off Baja California) or Clarion Island (Revillagigedo Islands) must have traversed water depths of 3660 m (GILMORE, 1960b). Most individuals travel on an empty stomach (SCAMMON, 1874) and whalers report that grey whales returning to the Arctic are 'dry', i.e. contain much less oil than the fat, southward-migrating individuals (PIKE, 1962). General fasting of these bottom feeders seems to prevail also on the calving grounds (RICE and WOLMAN, 1971).

In contrast to the details known on migration, timing, route, speed and water depth, the major cues and mechanisms used for orientation can only be guessed. Migration timing seems to depend primarily on light (daylength; PIKE, 1962) and temperature (ice formation). In addition to these two major exogenous releasing factors, physiological condition (e.g. pregnancy, hormonal activities) appear to act as endogenous releasers. Among the possible cues, light (aerial vision), sound, thermal gradients, water quality, substratum properties and sea-bottom topography seem to be important. Nothing is known about chemical cues, and the theory that *Eschrichtius robustus* follow certain ocean currents (GILMORE, 1955, 1960a, b) lacks support (PIKE, 1962).

Landmarks, celestial stimuli, water quality, bottom topography and coastal climate qualify as key cues for migratory orientation. SCAMMON (1874), GILMORE (1960a) and DAUGHERTY (1965) have called attention to the grey whale's habit of periodically raising its head out of the water, apparently looking around for visual cues. Subsequent movements suggest re-orientation (GILMORE, 1960a). It is not known whether visual abilities would allow long-distance landmark orientation, but circumstantial evidence seems to support such a possibility. According to PIKE (1962), landmarks 30, 150, 300, 600 and 1200 m high could be visible from ca 18, 45, 55, 90 or 135 km respectively. The high mountains along the west coast of North America would provide almost continuous landmarks for the grey whales between feeding and breeding areas. Since calves accompany their mothers on the first northward migration, orientational cues could be learned and memorized. During the brief off-coast migration phases, celestial navigation may replace landmark navigation, and periods of poor visibility (night, fog, high waves) may be bridged by gross directional memory (proprioceptive or inertial guidance). Of course, there is little danger of getting completely lost during coast-parallel migrations: all a traveller gone astray has to do is to turn left when southbound and to turn right when northbound; such course correction will always bring him to the coast, where specific orientational cues become available.

A few papers have been published on migrations of *Balaenoptera* species. The minke whale *B. acutorostrata* is widely distributed in all oceans, but rare in tropical waters. In antarctic waters, *B. acutorostrata* aggregate, as a rule, on the borders of water masses rich in phytoplankton; the same holds for subtropical waters in the Indian Ocean (DOLZHNIKOV, 1970). Fin whale *B. physalus* and blue whale *B. musculus* also inhabit all oceans, but the former has rarely been observed in tropical waters or among pack ice (RICE and SCHEFFER, 1968). Fin and blue whales exhibit a variety of migratory movements; nearly all have predominantly north–south components (NORRIS, 1967a). This is especially true in the Southern Hemisphere where open waters prevail and facilitate feeding and reproductive migrations more or less unblocked by land masses. While the time of arrival at, and departing from, the antarctic feeding grounds are known (MACKINTOSH, 1966), most of the migrational cycles remain in the dark. The migratory routes are farther offshore than in *Eschrichtius robustus* and (presumably) *Megaptera novaeangliae*. Possibly, southward routes vary more than northward routes, which may parallel to some extent the continental slopes (SLIJPER and co-authors, 1964).

In the Atlantic sector of the Arctic Ocean, *Balaenoptera physalus* exhibits a ratio of pregnant to non-pregnant females of 3:1. The females are assumed to bear 2 to 3 calves in 3 to 4 years (KULIKOV and IVASHIN, 1959). They attain sexual maturity and begin to breed at a total length of about 20 m (ZEMSKY, 1950a, b, 1960, 1961). Maximum mating activity occurs in August and September—large females mating earlier than small ones. The sex ratio at birth is 1:1. Herd structure in *B. physalus* is determined by similar factors as in the odontocete cetacean *Physeter catodon* (TARASEVICH, 1967a, b). But the resulting pattern is different: in *P. catodon* (p. 841), cows form the nucleus of the herd, and calves swim near them, small groups of females being widely distributed over the feeding area; in *B. physalus*, the herd nucleus is composed of sexually mature males surrounded by non-reproducing subadults; pregnant females occur in small, widely distributed groups. *P. catodon* herds are organized similar to those of delphinids. *B. physalus* schooling, on the other hand, appears to exhibit more species-specific characteristics. TARASEVICH (1967b) distinguishes four *B. physalus* herd types: (i) female herds composed mainly of large individuals breeding in the current season; (ii) male herds consisting of large sexually mature males; (iii) mixed herds, occurring mainly in spring; (iv) herds of sexually immature individuals. Grouping of whale herds (*B. physalus* and *B. borealis*) into breeders, immatures, or non-pregnant females has also been reported by ZEMSKY (1960, 1961). In the Antarctic Ocean, the sei whale *B. borealis* forms dense aggregations consisting mostly of females from the breeding ground (JUKCHOV, 1969).

The cosmopolitan humpback whale *Megaptera novaeangliae* migrates along the coasts from summer feeding grounds in high latitudes to breeding areas in low-latitude waters. Numerous populations have been recorded which seem to be largely independent of one another. North Pacific populations migrate southward on both sides of the Ocean (and also to Hawaii). Comparable migrations occur in the Atlantic

Ocean with a regular migration route passing near Bermuda. Southern-hemisphere populations migrate along both sides of Africa and on both sides of South America, Australia and New Zealand. While *M. novaeangliae* travel farther offshore than *Eschrichtius robustus*, they migrate mostly inshore of the continental slopes, except when traversing wide stretches of deep sea in order to reach islands such as Fiji, Tonga, New Zealand or Hawaii. Breeding occurs in shallow, warm waters (e.g. 25° C) near major land masses or small islands (DAWBIN, 1966; NORRIS, 1967a). Migrations of northern populations have been discussed by DOROSHENKO (1969): summer aggregations occur in the coastal waters of the Gulf of Alaska and the eastern Aleutian Islands; the northeastern Bristol Bay; the coastal waters of the Lisij Islands and the Anadyr Bay; the M. Serdtse-Kamen.

In the southern hemisphere, during northward migration, first the *Megaptera novaeangliae* females accompanied by weaning yearlings migrate towards lower latitudes. They are followed in succession by immature individuals, mature males with resting females, and finally by females in late pregnancy. During southward migration, females in early pregnancy travel first, followed by immature individuals, then by resting females with mature males, and finally by females in early lactation. After calving in the tropics, lactating females accompanied by their offspring enter cold waters last, and return first to warmer waters in the north with their weaning calves. Hence lactating females and their calves spend about 8 weeks less in the cold water of the antarctic feeding grounds than do pregnant females. All travel schedules appear to be fairly constant from season to season. Upon arrival at the feeding grounds, the differently composed travel herds seem to mix randomly (DAWBIN, 1966).

Reproducing humpback whales *Megaptera novaeangliae* have been observed in the Atlantic sector of the Antarctic (Southern) Ocean. The females may have up to 4 pregnancies over a period of 5 years (KULIKOV and IVASHIN, 1959). Marking experiments appear to indicate that humpbacks belong to a few herds with separate feeding areas and specific wintering localities, where the bulk of the whales remain (IVASHIN, 1962); apparently, some individuals may pass from one feeding area to another.

There is also a high degree of segregation between populations that breed off western and eastern Australia (DAWBIN, 1966). *Megaptera novaeangliae* which pass New Zealand and Norfolk Island and breed near Fiji and its adjacent island groups, segregate significantly from herds of eastern Australia, despite overlap in antarctic feeding areas. Nevertheless, the apparent genetic homogeneity of southern-hemisphere humpbacks indicates that the restricted exchange of members between adjacent whale groups may provide sufficient gene-flow interchange to maintain a racial continuum. However, interchange between southern and northern hemisphere humpbacks has never been observed. Calculated from data on maximum abundances at consecutive latitudes, the migration speed of *M. novaeangliae* averages about 1700 km per month. There is no evidence for consistent differences in migration speed of differently composed herds (age or breeding-condition differences).

HARDY and GUNTHER (1935) have claimed close relationships between the abundance of nutrient salts (nitrates and phosphates), plankton, and baleen whales. Since *Megaptera novaeangliae* feed extensively on plankton in antarctic waters, such correlation is not surprising. However, in subtropical and tropical waters, humpbacks feed rarely, if at all; this is witnessed by stomach contents of thousands of *M. novaeangliae* caught in warm waters (NEMOTO, 1959). At this migration phase there exists no definite relation to plankton distribution or to physico-chemical water properties.

According to DAWBIN's (1966) analysis, based on tagging and numerous whaling records, the migration routes of *Megaptera novaeangliae* cannot be consistently related to bottom topography, direction of ocean currents, or the nature of water masses. The rate of temperature change during the feeding period is considered too small to be an effective releaser of the different migration schedules for lactating as compared to pregnant females. Migrations of *M. novaeangliae*—just as those of *Eschrichtius robustus*—seem to be timed primarily by seasonal changes in the local light regime (DAWBIN, 1966; see also p. 723). As in some other mammals, seasonal shifts in daylength appear to affect the whale's hormonal dynamics and reproductive organs. Presumably, the resulting endogenous changes release migratory activities.

According to this hypothesis, the local daily light regime determines the onset of the migration. During the migration, directional cues seem to be obtained from celestial bodies (sun, moon, stars), visual landmarks, sound, water quality, thermal gradients, and sea-bottom properties. This assumption requires examination. At the end of the breeding period, return of hormonal levels and of reproductive organs to normal conditions, as well as hunger, may release the onset of the migration back towards the feeding grounds. Employing essentially the same navigational cues, the migrating herds may finally be guided by water-quality criteria indicative of plankton-rich waters.

(e) Odontoceti

Odontocete migrations are less spectacular in regard to distance and habitat diversity than those of mysticetes. Typically, odontocetes are hunters, almost continuously pursuing their prey. This makes their migratory travels more directly dependent upon prey movements or prey aggregations than is the case in baleen whales. Almost continuous contact between hunter and prey seems desirable because the capacities for storage of reserve materials are quite limited.

Some odontocetes do not undertake significant migrations. Under normal conditions, they find sufficient food in their local hunting districts. Examples of such non-migrators are the Hawaiian spinner dolphin *Stenella roseiventris* and most river dolphins.

The large, cosmopolitan (except polar ice fields) sperm whale *Physeter catodon* exhibits different migratory activities in different ranges of its distributional area: In low, equatorial latitudes, resident populations with little or no true migratory activities prevail; but in high latitudes, seasonal migration patterns occur, which are reminiscent of those exhibited by mysticetes. Larger males go farther north than the females, and subadults appear to stay preferentially in warm, tropical waters (NISHIWAKI, 1966). In the northern hemisphere, both sexes migrate southward as the northern winter season approaches. In the southern hemisphere a reverse movement occurs at the onset of the southern winter season. In the northern hemisphere on western grounds (20° to 40° N), almost all captures occur during the summer. In the southern summer, catches are more numerous on the coasts of

South America and around the Cape of Good Hope than in the tropics. In less numbers, *P. catodon* is also caught all the year round in the Pacific tropics. The pertinent literature has been reviewed by D. K. CALDWELL and co-authors (1966a).

According to BENNETT (1840, *in*: D. K. CALDWELL and co-authors, 1966a), *Physeter catodon* herds are composed of 20 to 50 cows and calves, and at least 1 adult bull. Pods (smaller associations) of half-grown males and pods of fully grown males may occur; but adult males usually prefer to hunt alone. Two or more herds may temporarily merge especially during migration. Recent evidence supports these early findings and adds more detail; in the waters off California, 3 rather distinct social organizations occur (RICE, *in* D. K. CALDWELL and co-authors, 1966a): (i) Large, often tightly packed herds of 12 to 50 individuals consisting of immature females, pregnant adult females, lactating females with calves, immature males, and puberal males up to 11 m in length. (ii) Loose aggregations of young adult males (10·5 to 14 m long); up to 12 individuals may be scattered over an area of 5 to 10 km^2, without gathering into a typical herd, and move from area to area more or less as a unit. (iii) Solitary old males (12–17 m long). There may be no, one or several large adult males with each female herd, as well as several smaller, but sexually mature bulls. Adult bulls sometimes withdraw a short distance from the herd composed of females and calves, and older bulls preferentially travel singly. In migrating adult males, the tendency towards solitude increases as arctic regions are approached (CLARKE, 1962). In the Azores, CLARKE (1956) saw two social structures, not reported from anywhere else: (i) herds consisting predominantly of pregnant females, and (ii) herds composed of juvenile males and females, weaned but still quite young. For further details, also on parental sexual behaviour, social facilitation and related matters consult D. K. CALDWELL and co-authors (1966a).

In the eastern seas of the USSR, *Physeter catodon* occur in herds of definite size and age composition (TARASEVICH, 1967a). Different possibilities and preferences for obtaining food (depending on morphological properties, i.e. age, of the whale) are assumed to promote formation and retention of groups of similar-sized individuals. In herds composed of small individuals, the whales are presumably of similar age; but in herds of larger individuals, the age structure varies. Age and size structure further varies in accordance with the season. In spring and early summer, small groups occur which consist of relatively small males; towards summer, when a greater number of large males leave the females, herds composed of large males occur and herd size increases.

The killer whale *Orcinus orca* inhabits primarily the near-coast waters of all oceans, particularly in temperate and cold regions. *O. orca* seems to conduct migrations in immediate contact with its primary prey. Possibly, the major prey varies to some extent in different areas of the killer whale's distributional range. The killer whale is an efficient, meticulous hunter (SPONG and co-authors, 1972a): one or several herds may co-operate for hours, systematically surrounding and aggregating schools of salmon—in certain regions their predominant or perhaps even sole food source—before feeding. Similar to hunting, feeding appears to be a co-operative process:

> 'When a school of salmon has been surrounded by a tight circle of whales, most of the whales maintain their stations on the perimeter of the circle, while

> a few dash in to feed. Effortlessness was perhaps the single most impressive characteristic of these food acquisition activities' (SPONG and co-authors, 1972a, p. 183).

Co-ordinated hunting and feeding activities dominate the daily routine of *O. orca* and are based on social structures both at the herd and population levels. Separate herds hunt in different areas, and within each herd, the whales hunt as a team. Two or more herds may combine and co-ordinate their efforts for half a day or so, and then re-organize and resume their separate ways. Although abundant, local food sources other than salmon were apparently not appreciated by the whales. SPONG and co-authors (1972a) never saw a herd pause while passing one of the cod assemblages (p. 183), nor did the *O. orca* herds pay any recognizable attention to other marine mammals: a solitary sei whale, Dalls porpoises, common porpoises, or pilot whales. Each summer, the arrival of *O. orca* herds corresponds closely with the onset of the annual salmon runs.

Orcinus orca herds seem to maintain a certain constancy in individual composition. SPONG and co-authors (1972b) have been able to identify numerous individuals—principally from gross variations in dorsal-fin contours, dorsal-fin cuts and deformities, and variations in size and shape of the white head patch. Senior bulls are most easily identifiable. The authors found it tempting to classify senior bulls as herd (pod) leaders, but there is no solid evidence to justify such presumption.

Orcinus orca gatherings may consist of several hundred individuals, and there is numerical and compositional variability among the herds comprising such a population. According to SPONG and co-authors (1972b), there was an apparent orderliness to the progression of herd arrivals in their study area (Johnstone Straits, Canada): the earlier herds were numerically dominated by adults, the later ones by juveniles (ca 1 to 5 years old). A few individuals may exhibit motility between herds, notably senior bulls, and different herds may interact behaviourally. Co-ordination of respiratory behaviour is common. Occasionally, the members of an entire herd may be seen to respire simultaneously. More typically, however, herds appear to be organized into 'respiratory subunits' (SPONG and co-authors, 1972b, p. 190), comprising at least a pair of whales. Thus a herd of 20 whales may be hunting and respiring co-ordinatedly in 5 subunits of 4 individuals each.

The widely distributed common dolphin *Delphinus delphis* prefers warm-temperate and tropical waters. Daily short-range migrations in limited, population-specific hunting territories seem to be characteristic of this and many other delphinid(s). Herds serve as hunting and reproductive units and often exhibit integrity through time, with a high degree of isolation from neighbouring schools (PERRIN, 1969a, b). On one occasion, PERRIN watched chaser skiffs try to drive two *Stenella graffmani* schools together:

> 'They could not do it; the schools ran side by side for half a mile or more and then split apart again' (p. 47).

D. delphis occupies waters on both sides of the Straits of Gibraltar, but the herds do not seem to cross the Straits into each other's territory; biometric studies indicate that the Atlantic specimens are larger than their counterparts in the Mediterranean (PILLERI and KNUCKEY, 1968).

Age–sex structures of *Delphinus delphis* herds in the Black Sea have been observed by TARASEVICH (1957): in winter, schools consist mainly of (i) mature and some immature males, or (ii) mature (pregnant and 'sterile') females plus immature individuals of both sexes. In spring and summer, schools are composed of (i) late-stage pregnant females plus a few immature individuals of both sexes; (ii) about equal numbers of mature males and females accompanied by a small number of young individuals; (iii) subadults from disintegrating winter female schools. In addition, there are herds of random composition as a result of reforming and mixing of the main type schools.

The beluga or white whale *Delphinapterus leucas* inhabits coastal waters of the Arctic Ocean and adjacent seas, and often ascends high up larger rivers of Siberia and Alaska. About 10,000 individuals have been recorded in the western Hudson Bay (SERGEANT, 1973). In July and August, herds of the Hudson Bay population concentrate in river estuaries at 57° to 60° N and migrate in mid-August through September to between 62° and 66° N. Wintering occurs in the western part of the Bay. SERGEANT assumes that the herds enter the estuaries and rivers for reproduction as much as for feeding (fish, crustaceans, squid, polychaetes). Gestation lasts 14, lactation about 20 months. Calving occurs about once every 3 years (see also PROVOROV, 1957; KLEINENBERG and YABLOKOV, 1960; SERGEANT, 1962; KCHUZIN, 1963; KLEINENBERG and co-authors, 1964; JONKEL, 1969; SERGEANT and BRODIE, 1969a, b).

Bottlenose whales *Hyperoodon ampullatus* avoid shallow waters such as the continental shelf, the Barents Sea and the North Sea during their feeding migrations. Most *H. ampullatus* migrate from the beginning of April to the end of July. Mating and calving activities attain a maximum in April (BENJAMINSEN, 1972). Details on orientational aspects of the migrations are not known.

In the tropical eastern Pacific Ocean, close correlations exist between the distributions of the delphinids *Stenella longirostris*, *S. graffmani* and *Delphinus* sp. on the one hand, and the tunas *Thunnus albacares* and *Eutunnus pelamis* on the other. While details on the orientational principles involved are not available, this association is so close and permanent that the tuna purse seine industry depends on it (PERRIN, 1969a, b). The fishermen locate the tuna by spotting the surfacing delphinids associated with them. They approach the herd, tighten it up with 2 or 3 speedboats and set a seine around the whole complex. Then they try to let as many delphinids as possible escape without losing the fish. They do this not for conservational aesthetics, but because they fear being unable to find the tuna should the delphinids disappear. Comparable delphinid–tuna associations have been reported for the west coast of Africa (SIMMONS, 1968), but not for Hawaiian waters (which differ markedly from those of the other two habitats mentioned; EVANS, 1971). Common food organisms, e.g. fishes, seem to be a major reason for the associations described. Movements of delphinid herds closely orientated to movements of their prey have been suggested by TOMILIN (1960), NORRIS (1967a) and EVANS (1971).

Although definite data are lacking, we may assume that food supply, water characteristics (patterns of acoustic and thermal energy), and topographic cues constitute important guideposts for delphinid migrations. Since organismic distributions in shelf areas tend to be associated with bottom topography (escarpments, sea mounts, banks, etc.) and since pronounced vertical bottom elevations are usually accompanied by hydrographic discontinuities, migrating marine cetaceans may recognize major characteristics in bottom topography by indirect cues: modifications in the ambient acoustic and hydrographical fields due to (i) self-produced or foreign sounds reflected by biological or physical discontinuities; (ii) thermal gradients; (iii) differences in water movement.

(15) Stranding of Whales

Despite apparently well-developed orientation mechanisms, whales have been reported time and again to strand. In mysticetes, most strandings refer to solitary, obviously sick and weak individuals; mass strandings are not known. This fact has restricted the investigation of circumstances and possible reasons of strandings to odontocetes.

Numerous reports on solitary and mass strandings of odontocetes have been documented and discussed, especially by GILMORE (1959) and DUDOK VAN HEEL (1962, 1966). On the basis of these three papers and the discussion following the last mentioned, a complex picture has emerged. There seem to be a number of different circumstances and reasons responsible for odontocete strandings. Regarding the circumstances, the following observations deserve consideration: (i) Most solitary and mass strandings of odontocetes have occurred on gently shelving beaches or on rocky shores with a shallow area in front. (ii) Weak, wounded or sick individuals may also strand on any other kind of shore. (iii) Whether alone or in a herd, stranding odontocetes often exhibit considerable directional determination. If transported back into deeper water, several stranded whales (e.g. *Stenella plagiodon*, *Globicephala melaena*, *G. macrorhyncha*, *Kogio breviceps*) have refused to accept their freedom. Invariably, they have turned around and come back to the shore in the same direction. Comparable behaviour has been reported for a stranded Cuvier's beaked whale *Ziphius cavirostris* (BACKUS and SCHEVILL, 1961).

Among the possible reasons for the strandings observed, the following rank highest: (i) Difficulties in the use of (active) biosonar due to local sea-floor peculiarities or water-body irregularities. The assumption of such difficulties gains support from the fact that in mysticetes mass strandings are unknown. (ii) Extreme emotional state (e.g. panic, hunger, cold, 'hunting fever'). (iii) Seemingly healthy odontocetes may strand because of virus of bacterial infections or parasitic infestations which cause disease to important (acoustic) orientation mechanisms or of the brain itself (see also Volume III: LAUCKNER, in press). (iv) Insufficient ability to counteract water movements due to extreme weakness and illness. (v) In cases of mass strandings, man's efforts to rescue single individuals by transporting them back into deeper water may fail because of herd instinct. But in solitary strandings, other factors must be effective to account for the apparent drive to maintain a direction which leads to disaster. In a letter to the reviewer (1973), NORRIS writes

> 'Solitary odontocetes that strand are, so far as my experience goes, invariably sick . . . I have recorded one with flukes in the foramen magnum and with pneumonia.'

Additional papers on odontocete strandings have been published by GUILER (1967), MITCHELL and HOUCK (1967), GRESSON (1969), D. K. CALDWELL and co-authors (1970) and ANONYMOUS (1972). Acoustic attenuation coefficients in shallow water have been discussed by INGENITO (1973).

NORRIS (1967a) recalls that certain beaches have been the site of repeated strandings and reports 'a text book example' of an acoustic situation in which active biosonar might be ineffective, and a combination of circumstances might serve to trap odontocetes (Fig. 8-132): A negative vertical thermal gradient, composed of several thermoclines, will tend to refract the sound beam of an approaching dolphin downward, perhaps not even reaching the very shallow part of the coastal water. The echo will also refract downward at each density interface and finally may pass under the advancing dolphin without being perceived. Assuming that the usual sounds signalling a coastline to a dolphin (e.g. surf, subtidal and intertidal animal noises) are ineffective, NORRIS goes on to suggest that the dolphin may suddenly find itself in dangerously shallow water and get frightened; shock, social cohesion and chaos finally complete the trapping. But how could all coastal noises be rendered ineffective for the approaching dolphin (unless serious disease prevails)? And why would other orientation mechanisms (e.g. vision) fail?

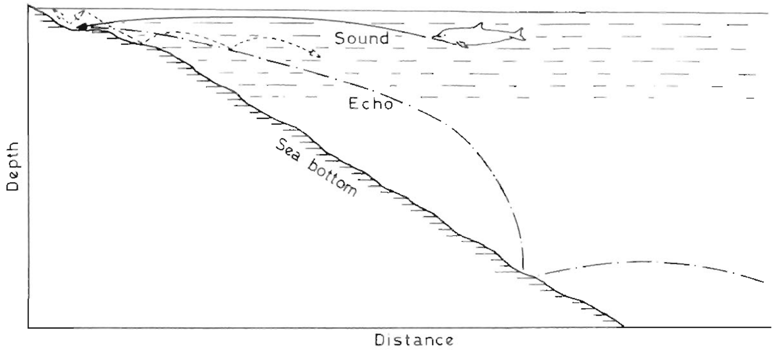


Fig. 8-132: Hypothetical acoustic odontocete trap. Successive vertical density-discontinuity steps in near-shore waters are assumed to refract the delphinid sound beam, the echo returned, and the paths of coastal noises (open arrows). (After NORRIS, 1967a; modified; reproduced by permission of Oregon State University Press.)

(16) Conclusions

As for other organisms, orientation in space is a basic prerequisite for successful existence of marine mammals. Spatial orientation to the environment involves sampling of cues by peripheral receptors and subsequent evaluation by central systems. Physiological mechanisms of orientation comprise both, peripheral and central components. The resulting orientation response usually leads to an increase in the chances for survival: it assists in finding food, in establishing and maintaining social contacts, in reproduction, and in avoiding or escaping danger. Both the environmental cues and the resulting response identify orientation as an important aspect of the ecology of the organism involved. The ability to obtain information on the environment over some distance and to respond by appropriate behaviour represents a significant augmentation of the ecological potential. Differences in the properties of long- and medium-distance orientation cues underwater and in air force considerable adjustments, both functional and structural, on any organism which transgresses—in the course of its evolution—the sea–air boundary. A comprehensive, critical review on spatial orientation in marine mammals must consider such functional and structural adjustments in detail in order to provide a sufficiently solid fundament for comprehending the physiological mechanisms involved.

Marine mammals possess well-developed mechanisms of spatial orientation. In odontocetes, the functions and structures devoted to orientation in space have received much attention. Numerous papers witness the extraordinary complexity of the subject and the difficulties in obtaining reliable information. In spite of considerable efforts, large white spots have remained on the map of our knowledge. An overwhelming amount of problems remain to be solved and much of what has been written is based on insufficiently founded speculation. This is no glamorous platform for drawing conclusions.

As far as we know, no marine mammal relies exclusively on a single orientation cue or a single orientation mechanism. A hierarchy of cues is obtained and evaluated by several different mechanisms (e.g. visual, auditory, tactile, chemical). While one cue type (e.g. visual or auditory) may be primarily relied on in a certain situation, additional input modalities are computed and act in concert in providing key signals for navigational manoeuvres or migratory activities. The orientational information obtained seems to be largely restricted to ecologically relevant details of the surrounding environment. However, uptake and evaluation of additional information may be within the intrinsic capacity of the mechanisms if adequate stimulation and subsequent reinforcement (conditioning, training, learning) are present. The information obtainable on spatial components of the environment depends on the properties of the cues available and the capacities for perceiving and interpreting them. The relative importance of the cues may change with the physiological state of the perceiver, i.e. its central disposition (hungry or satiated, migratory or non-migratory, reproductive or non-reproductive), personal experience, developmental stage (calf, subadult or adult), sex, and the environmental situation encountered.

Apparently, the central disposition can be affected directly by environmental factors such as light (daylength) or temperature (seasonal dynamics), resulting in changes in hormonal levels, and in functions and structures of specific organs (e.g. ovary or testes). No critical experiments have been conducted as yet on this important aspect of marine-mammal orientation. But it is here that the scene is being set for cyclic changes in social structures and in orientational activities (migrations). Alterations in central disposition can also be expected to modify the hierarchical sequence of the orientational cues relied on. The efficiency of orientation may be significantly affected by personal experience (imprinting, learning). Training experiments on odontocetes have shown that specific and selective improvement of visual or auditory discrimination abilities is possible. Incapacitation of one mechanism 'automatically' improves the use and performance of other mechanisms. For instance, blind individuals tend to rely more on auditory cues, and deaf individuals more on visual cues than normal, healthy conspecifics.

Navigation at night may shift cue emphasis and modify the hierarchy of information input. Delphinids in muddy waters rely more on auditory and tactile cues than their counterparts used to day-navigating in clear water.

We may summarize these points as follows: Orientation in space of marine mammals is characterized by: (i) multi-cue and multi-mechanism systems; (ii) built-in capacities for compensation in cases of incapacitation (e.g. blindness); (iii) adjustments to specific environmental circumstances due to variations in central disposition and in personal experience. These characteristics impart to the individual, herd or population concerned a considerable degree of both plasticity and specificity in their responses.

Most experiments on orientation in space of marine mammals have been restricted to examining responses to a single cue type, e.g. light or sound. Unequivocal demonstration of the primary dependence on the cue-type provided requires a rigid experimental design. The dominating importance of active biosonar, for example, can only be documented unequivocally by orientation to self-generated sounds in the absence of other cues (e.g. visual, thermal or rheotactic) or by orientation failure after impairment of the individual's active-biosonar mechanism. Not a single experiment conducted thus far meets such rigorous requirements. The only attempt to block sound emission during discrimination was inconclusive (NORRIS and co-authors, 1961): a blind-folded *Tursiops truncatus* was required to wear an acoustically opaque head cover. The dolphin refused to swim forward; it uniformly backed away and shook the head cover loose before performing further. However, even without 'perfect' experiments, we now know that several odontocetes are capable of sound navigation and of locating and evaluating small targets by means of acoustic energy. The most natural way of eliminating visual cues is to experiment in total darkness, using acoustical techniques to track the test animal in the experimental tank; however, such tracking is laborious and eliminates parallel observation on concurrent behaviour. Another technique employed is blindfolding by suction cups placed over each eye. Suction cups were successful in delphinids, but did not work on the hair cover of pinnipeds, where opaque contact lenses have been used instead. While hearing of bats can be blocked by ear plugs, submerged marine mammals perceive sounds via routes which defy blocking. Their sense of hearing can be eliminated only by destroying the ear; this may result in side effects and renders 'normal hearing' versus 'no-hearing' tests on one and the same individual impossible.

Orientation potentials demonstrated in 'trained-seal experiments' require careful consideration in regard to the actual performance delivered by normal individuals under field conditions. Are the potentials demonstrated in trained individuals really used at sea? And if so, to what extent? There is considerable need for experiments designed to simulate conditions actually met in the natural environment.

Observations at sea and in captivity, as well as experimental evidence, reveal significant differences in orientational performance in different taxa, species, populations and even individuals. Hence representative statements regarding the orientational capabilities of a given group of animals require performance tests on a statistical basis and analytical differentiation between genetic and non-genetic components. Our restricted potential to keep marine mammals in captivity and the non-availability of large numbers of test individuals has not allowed statistical data (e.g. on audiograms, sound properties or orientational responses) to be obtained. Conceivably, genetic differences may be considerable—especially in populations from different habitats with little or virtually no gene exchange. Non-genetic differences—due to the specific environment histories of the individuals involved—are likely to result in variations in the ultimate orientational potential. Consequently, proper conditioning to comparable environments and to comparable orientation tasks must precede the actual test. Such 'stabilization' of the test individuals prior to experimentation should become standard procedure.

Prolonged captivity may result in reduction or even loss of natural capacities for spatial orientation, as well as in acquiring capabilities not acutely present in the field. After years of captivity, an old individual, never required to use and develop a certain aspect of spatial orientation, is likely to perform significantly poorer than a conspecific which has been trained—or which trained itself—to use that aspect intensively. Also, isolated individuals may behave differently from those kept in groups. Close-to-natural behaviour may only be displayed in social groups of sufficient size and structure maintained under quasi-natural conditions.

These considerations may be summed up as follows: A critical evaluation of the physiological mechanisms involved in spatial orientation of marine mammals requires (i) studies under adequate environmental conditions. The mechanisms have evolved under specific ecological circumstances, and they can be expected to function properly and specifically only if examined under such circumstances. (ii) Presumably, the mechanisms have evolved in close context with social behaviour; hence maintenance of essential social structures appears necessary for the assessment of the ultimate efficiency and performance exhibited under field conditions.

As far as generalizations are permissible in regard to the orientational performance of different marine-mammal groups, it is the parallelism between habitat properties, behaviour and orientation mechanisms primarily employed that begin to emerge from the fragmented information available. The amphibious sea otter and the pinnipeds, for example, appear to rely more on visual cues than the holoaquatic sirenians, mysticetes and odontocetes. Muddy-river dolphins have reduced eyes and seem to depend largely on acoustic information. Difficult to support in detail and untestable by experiment, the causal congruence between habitat and orientation becomes all too obvious if we consider phylogeny as an ecological process (e.g. von Wahlert, 1973). Phylogenetically, the capacity for orientation in space must be considered in the light of its selective value: increasing orientation capacity results in decreasing randomness of activities in space and hence in increasing ecological efficiency (e.g. Adler, 1970).

Regarding the environmental factors which may provide essential cues for orientation of marine mammals, light, temperature, and sound and vibration have received most attention. While temperature may be important as releaser of orientational activities and for overall geographic distribution, light and sound qualify as dominating cue-types providing information on direction, distance and properties of targets and on the position of the orienting individual.

In principle, visual orientation is superior to acoustic orientation, since it can provide instantaneous, detailed panoramic replicas of environmental arrangements with a minimum of interference. However, underwater vision is limited due to turbidity and rapid decrease in irradiance with depth. As has been pointed out, the importance of visual orientation tends to decrease in the sequence carnivores, pinnipeds, sirenians, cetaceans; in the same sequence, vision is increasingly assisted by hearing, until—in muddy-river dolphins—the importance of acoustic orientation may exceed that of vision. Detailed assessments on the relative significance of vision and hearing require, in the first place, exact information on visual and auditory sensitivity thresholds and resolving powers. While adequate experimental methods have been worked out for determining visual and auditory acuities, few definite data are at hand. In regard to other mechanisms (e.g. olfaction, gustation, gravity perception) no acuity measurements have been made. In many cases, assessments on the presumptive importance of a mechanism have been inferred from the anatomy and histology of the organs concerned.

In most marine mammals, eyesight and hearing seem to co-operate closely and sometimes may be used alternatively. This is suggested by several laboratory experiments and supported by three field accounts: BEALE (1839) reported the catching of a blind *Physeter catodon* that was in excellent nutritive condition, and TARASOV (1960) captured a well-fed deaf individual. POULTER (1963a, b) observed a blind *Zalophus californianus* which remained in normal physical condition over 2 years. Unfortunately, none of the authors states how blindness or deafness had been established.

Acoustic orientation has received unusual attention and hence requires more detailed comment here than other orientation mechanisms. The most sophisticated mechanism of acoustic orientation evolved by marine mammals is active biosonar (echolocation, echoranging). So far, only some odontocetes have been shown to possess active-biosonar capabilities. No evidence is available in favour of active-biosonar abilities in the sea otter and in sirenians. In pinnipeds and mysticetes, neither the presence nor the absence of active biosonar has been conclusively demonstrated. Active biosonar involves the use of self-generated, beamed, high-frequency (up to about 200 kHz) sounds for obtaining, via echoes, information on object direction, distance and properties; it operates at close ranges (presumably up to some 10 m) and seems to be used primarily for hunting, navigation and obstacle avoidance, especially under conditions of poor visibility.

Cetaceans can perceive underwater sounds at threshold levels comparable to those perceived by terrestrial mammals and humans in air (JOHNSON, 1966). But, in humans, underwater-sound perception is considerably reduced: at a water depth of about 11 m, 18 dB re 0·0002 μbar at 125 Hz to 56 dB at 8000 Hz (BRANDT and HOLLIEN, 1967; see also WAINWRIGHT, 1958). How did the cetaceans adjust their acoustic mechanisms to life beneath the sea? How did they master the need to rely on acoustic information in order to orient successfully in their aquatic environment? Which are the functional and structural modifications, elaborations or reductions of pre-existing organs forced upon these mammals by their holoaquatic way of life?

Discussing the adaptations acquired by echolocating odontocete cetaceans, BULLOCK and co-authors (1968) list 5 essentials: (i) highly specialized, heterogeneous cell populations responsible for sound perception and sound interpretation; (ii) high-frequency range of active-biosonar signals; (iii) acute frequency and intensity discrimination; (iv) rapid frequency recognition by the cochlea; (v) high temporal resolution of outgoing pulses and returning echoes. High frequencies of active-biosonar signals are essential, since the intensity of an echo depends critically on the ratio between target dimensions and signal wavelength. Delphinids, like bats, use high frequencies. At any given frequency, wavelengths in water are nearly 5 times longer than in air. The larger size both of delphinids and of their prey, as compared to bats, seems to compensate for this disadvantage.

In general, delphinids seem to obtain less information from single echoes, or small numbers of echoes, than bats (BULLOCK and co-authors, 1968). Dolphins often employ pulse trains with hundreds of clicks at rates of 100 to 700 sec^{-1}, while bats can perform difficult discrimination tasks with as few as 3 to 5 echoes, and, at repetition rates of up to 200 sec^{-1}, rarely use more than 30 to 40 echoes during one pursuit or avoidance.

The methods applied by delphinids to measure direction and range of underwater objects and to obtain information on their properties are still being discussed (p. 807). In comparing the outgoing acoustic signal with the incoming echo, delphinids seem to rely on differences in sound intensity, time interval between sound emission and echo return, and differences in sound properties. Echoranging delphinids ensonify the environment ahead systematically and selectively with beamed active-biosonar clicks, and pick up the returning echoes at strategic skin areas, especially in the head region. Arrangement and chemical composition of specific body structures (e.g. fat or liquid compartments, tissue layers, air sacs) assist in conduction and focusing of sounds and in isolating each ear acoustically from its immediate surroundings. Evolutionary refinements of active-biosonar systems are characterized by increasing control over direction and properties of sounds emitted, increased capacities for sound perception and conductance in specialized head areas, and augmented resolution and evaluation of temporal, directional and physical properties of the sounds perceived. At the same time, behavioural correlates (e.g. capacities for learning and memorizing) tend to increase and greatly affect the ultimate potential for orientation in space. In experiments, bats (*Megaderma lyra*), for example, reveal considerable spatial memory (NEUWEILER and MÖHRES, 1967): when removed, even small obstacles are remembered for days and the bats continue to avoid the position of the no-longer-existent obstacles in flight. The position of a frequently used square is well remembered after a training pause of 6 weeks, but nearly forgotten after 12 weeks. According to NEUWEILER and MÖHRES, spatial memory is the most important component in re-orientation. Presumably this pertains also to delphinids.

Regarding the evaluation of sound-source localization by 'higher' animals, especially mammals, ERULKAR and co-authors (1968) and ERULKAR (1972) have presented and discussed several hypothetical models. Distinguishing between single-neuron models and models involving populations of neurons, ERULKAR (1972) points out that central analysis of sound localization depends on the interaction of excitatory and inhibitory events elicited by binaural stimulation. Summarizing the evidence at hand, he concludes that synaptic activation consists of a depolarizing input on one side and a hyperpolarizing input on the other. Myriad combinations of synaptic input are possible, but for accurate directional localization both excitation and inhibition must be involved, and, in order to be meaningful, a definite temporal sequence of these inputs must be present. Binaural interaction of neural impulses occurs at relatively low levels of the central nervous system. Responses to binaural interaction depend on interaural time relationships and on stimulus intensity. Upon binaural interaction, time preservation is maintained for some neurons, but as inhibitory inputs dominate, transformation of the information code seems to occur.

With respect to a delphinid pursuing a prey fish, two questions may be raised: (i) Is orientation assisted by cues produced by the fish? (ii) Can the fish hear the delphinid's active-biosonar clicks, and hence attempt to escape? While prey sounds and other prey-generated cues may assist in object orientation, active biosonar does not depend on these additional cues: it operates successfully also on static dead fish and, in fact, on a variety of non-living objects with a multitude of different properties, as long as these reflect sound, i.e. return an echo of the clicks emitted. The evidence at hand suggests that most fishes do not seem to be able to perceive active-biosonar clicks. But we cannot yet rule out the possibility that some fishes may have developed 'anti-sonar capabilities'. Pertinent studies remain to be conducted.

Despite a considerable amount of work performed under *in situ* conditions and in the laboratory, uncertainty prevails about the orientation cues actually relied upon in the unrestrained environment and about the extent to which acoustic orientation contributes to the ecological success of truly marine species. The importance of celestial bodies (sun, moon, stars), meteorological factors (weather), and electrical and magnetic fields for orienting marine mammals remains unclear. Inertial navigation, in the form of inertial guidance systems (BARLOW, 1964) similar to those used today in the navigation of aeroplanes, submarines and missiles, may possibly be involved in long-term, open-sea migrations. However, proof of the presence of such mechanisms—which compute position, relative velocity and heading from information on the initial position and from endogenous processes without recourse to exogenous cues—is not available.

Ontogenetic and phylogenetic aspects of orientation (ADLER, 1970) have received insufficient attention in marine mammals. Comparative evaluations of orientation mechanisms both as a function of different body plans and of geological time spans are likely to open up new perspectives. Ontogenetic and phylogenetic studies complement the information based on immediate correlations between organism and environment and add two essential dimensions to the general topic considered.

Marine-mammal distributions and migrations are restricted by environmental tolerances (e.g. to low or high ambient temperatures), water depth (coastal versus open-ocean areas), and food availability. Since environmental factors such as light, temperature or salinity are basic denominators in the life of many prey species, they may be expected to exert indirect influences on distributions and migratory activities.

The spectacular north–south migrations of large whales pose interesting problems. What makes them travel up to several thousand miles each year 'burning up' considerable energy? We do not know; but the little that is known invites speculation. Possibly, the original warm-water habitats have failed to provide sufficient food (adequate densities of specific food organisms) at a time when these large mammals were ecologically highly successful and increasing numerically. They had to leave their home areas for more and more extended feeding excursions. The highly significant combination of biological-fuel storage (blubber) and its properties as peripheral heat-loss reducer provided basic prerequisites for conquering the nutrient-rich temperate and near-polar waters. In the absence of concurrent adjustments in thermal tolerance of early ontogenetic stages (and in reproductive behaviour), periodic return to the warm home waters remained essential for continued existence. Within the limitations imposed by environmental tolerance and reproductive cycles, food availability seems to have primarily programmed the spatial and temporal aspects of the migration patterns observed today.

While we speculate, we may suggest that the drive for populational segregation, observed in several marine mammals with wide distributional areas, is related to (i) making maximum use of the food sources available and (ii) maintaining a social structure which facilitates 'personal acquaintance' among the members of the group. Differences in distribution and migration patterns of subunits (populations, herds) seem to result largely from adding individually acquired information to the species-specific, genetically fixed, orientational abilities.

The high capabilities for orientation, learning and problem solving of marine mammals, especially pinnipeds and delphinids, are being increasingly used by man to serve his purposes. Representatives of these mammals have been trained to locate, recover or transport objects underwater. Harmless in some cases, such abilities have also been used for purposes of military 'defence'. Reportedly, a trained dolphin has been sent by one country into a military harbour of another; it deposited special recording instruments and recovered these after a week, thus obtaining the information desired. Such misuse of intelligent animals may lead to their extermination during war: safety considerations will require that also untrained individuals be considered dangerous, and the need to surface for air exchange will make the mammals easy-to-hit targets. Even though military establishments contribute to financing research projects on orientation of marine mammals, they should discontinue training programmes that threaten the very existence of these innocent creatures.

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9. ORIENTATION IN TIME: ENDOGENOUS CLOCKS*

J. T. ENRIGHT

(1) Introduction

In its natural environment, an organism experiences fluctuations in a whole array of environmental factors to which adaptation must take place; the factors range from light conditions and temperature to food availability. It can be taken for granted, therefore, that organisms under field conditions will show temporal variation in their behaviour and physiology in response to environmental fluctuation. When, however, an organism is brought from the field into the relative constancy of a laboratory environment, both the ecological need and most potential external causes for temporal variation are removed—yet temporal variation persists.

Some of the changes observable under constant conditions are associated with phenomena which would not ordinarily be classified as 'timing' processes, phenomena including, for example, adaptation, hunger and learning. Far more intriguing, however, are the instances in which temporal variation is rhythmical: cases in which the organism's performance varies systematically with time of day, stage of the tide or phase of the moon, in the absence of any obvious environmental stimulus which might account directly for the changes. For such rhythms, the term timing process seems appropriate: certain aspects of the animal's performance recur at intervals approximating those of natural environmental cycles, and it seems probable that this kind of spontaneous repetition plays a role in the timing of activities in the normally fluctuating field environment.

The literature dealing with biological rhythms of this type is extensive, and the present chapter is not intended to provide complete coverage; a number of recent books and reviews are available (ASCHOFF, 1963, 1965; HARKER, 1964; BÜNNING, 1967; HALBERG, 1969; SWEENEY, 1969; MENAKER, 1971). Instead, attention will be focused on those few aspects of endogenous timing which may be of particular interest to the ecologist, and more specifically, the marine ecologist.

(2) Are the Rhythms Actually Endogenous?

A first suspicion, when confronted with data showing long-term persistence of a biological rhythm in an apparently constant environmental situation, is that the laboratory conditions may not be as constant for the organism as they appear to be to the investigator: that the organism may be responding directly to some unrecognized stimulus associated with the natural outdoor environmental cycles. The possibilities which could come to mind in this connection might include laboratory

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* Dedicated to Professor JÜRGEN ASCHOFF on the occasion of his sixtieth birthday.

disturbances associated with human activity as stimuli which might evoke daily rhythms; and vibrations from waves on the shore—if the laboratory is near the ocean—as stimuli which might lead to tidal rhythms. The careful study of 'biological clocks' has, however, produced several lines of evidence which are inconsistent with such an interpretation.

An animal's 24-hr rhythm can, for example, be shifted in its timing by an artificial lighting regime out of phase with the outdoor day–night changes, and the resynchronized rhythm will thereafter persist under constant light or darkness with a new induced time relationship with the natural day. This means, then, that no simple natural 'alarm clock' exists to which the animal reproducibly responds under constant light conditions. Furthermore, the period of a persistent biological rhythm under constant light conditions seldom if ever corresponds exactly with that of the natural environmental cycle (hence, the terms **circadian** and **circatidal**, to emphasize the approximate correspondence in period). No known environmental factor is available which could account, in a simple stimulus-response manner, for a long-persistent biological rhythm which has a period, for example, of 23 hrs 50 mins, or 25 hrs 30 mins. Beyond this, the period of a persistent biological rhythm can be predictably modified by temperature (e.g. SWEENEY and HASTINGS, 1960), by the genome of the organism (KONOPKE and BENZER, 1971; BRUCE, 1972), by chemical manipulation (e.g. FELDMAN, 1967; ENRIGHT, 1971a, b), and by the level of constant light intensity (ASCHOFF and co-authors, 1962; HOFFMANN, 1965). All these lines of evidence are consistent with the interpretation that the observed rhythms are endogenous: spontaneously generated periodicities involving a feedback loop, and, therefore, in the same general class of phenomena as heart beat and the human menstrual cycle.

In spite of such evidence, an aura of mystery has continued to surround 'biological clocks', based on the contention that the phenomena may, in spite of all evidence and all experimental precautions, be the direct result of some subtle, pervasive timing stimulus associated with natural environmental cycles. This interpretation is based upon the proposition that the persistence of the rhythm may require a periodic 'forcing cycle' which would, however, produce no correspondence, in phase or frequency, between the forcing environmental oscillation and the forced rhythm of the animal (BROWN, 1965, 1970, 1972; see, however, ENRIGHT, 1973). This hypothesis has been designated **autophasing**, another term for frequency transformation; to date, in spite of extensive discussion, no plausible physiological mechanism has been proposed which might produce such a transformation.

Careful consideration demonstrates that this proposition has only one unequivocally predictable consequence: that in an environment which is truly constant with regard to the relevant, subtle pervasive timing stimulus, persistent rhythmicity would disappear. As long as the relevant stimulus remains unspecified, the hypothesis must remain untestable. Similarly, one cannot exclude the hypothesis that the human menstrual cycle is driven by the revolution of the moon about the earth, mediated by an unspecified stimulus and the process of frequency transformation. The menstrual rhythm (under free-running conditions) shows inter-individual variability in period; it has no generally fixed phase or timing relationship with phase of the moon; and its period can be influenced by chemical (i.e., hormonal) manipulation. These are all properties which it shares with other biological clocks. But when the hypothesis of frequency transformation is invoked, these lines of evidence cannot, in themselves, exclude the possibility that the menstrual cycle is driven by some stimulus emanating from the moon.

If moonlight is the proposed forcing cycle, the hypothesis could be tested by maintaining experimental subjects in an environment where moonlight cannot enter, with the expectation, if the hypothesis is valid, that the menstrual cycle would then disappear; if gravitational influences of the moon on barometric pressure are the proposed forcing cycle, the subjects could be maintained at constant air pressure. But if 'some lunar influence' is invoked, the hypothesis is untestable, since the revolution of the moon cannot be brought to a halt. Even experimental subjects in a space ship, in independent solar orbit, could conceivably be responsive to lunar influences, since the threshold for response to an unspecified driving stimulus is, of course, also unspecified.

Viewed in this light, the extensive controversy about whether 'biological clocks' under constant light and temperature conditions are endogenous or exogenous is clearly a sterile discussion. The persistent rhythms, whether menstrual cycle or circadian 'clock', behave in all essential characteristics as though they were endogenous. There is no more reason to suspect that the revolution of the earth directly causes a persistent biological rhythm with a period of 24 hrs 30 mins, than to suspect that the revolution of the moon directly causes a persistent menstrual cycle with a 32-day period.

(3) Endogenous Rhythms and the Ecologist

The above emphasis on the internal or endogenous source of biological rhythms, as manifest under ordinary constant laboratory conditions, should not be taken to imply that similar rhythms, when observed under field conditions, are similarly due only to endogenous processes. In a natural, fluctuating environment, the situation is much more complex. Normal environmental cycles serve to synchronize those free-running rhythms which can be seen under constant conditions, so that a circadian rhythm becomes a daily rhythm, a circatidal rhythm becomes a tidal rhythm, with periods identical, on the average, with those of the relevant environmental cycles. Furthermore, the process of synchronization includes phase control, with the result that diurnal animals are active only during the daylight hours, nocturnal animals at night; that some intertidal organisms are active only at high tide, and other species only at low tide.

Beyond these influences of the environment, which assure that internally governed rhythmic processes are appropriately timed, the environment provides direct stimuli to which the organism responds on a moment-to-moment basis. But—to add further complexity—the intensity of a response, and sometimes the very nature of a response to concurrent stimuli can depend upon the time within the endogenous cycle at which the stimuli occur. At certain times of day or stages of the tide, there may be an endogenous 'readiness' to respond in one way to a stimulus, at other times in another way. This complex situation can be described in terms of endogenous timing processes which modify the response to concurrent stimuli, or in terms of external stimuli which modify the expression of endogenously evoked behaviour; but in either case, we must recognize that the performance of the organism under field conditions represents the non-additive resultant of internal and external variations (ENRIGHT, 1970).

Such complications are, of course, well recognized in the context of annual cycles: no one is surprised that a bird shows markedly different responses to nesting materials and to conspecifics during the breeding and non-breeding seasons. These differences arise because of changes in internal physiological conditions which are due to environmentally synchronized endogenous 'timing processes'. The full appreciation, however, that comparable cycles in readiness to respond can occur on the much shorter time scale of a few hours has developed only recently.

As we shall see in the subsequent consideration of specific cases, the extent to which internal rhythms contribute to the timing of biological events under field conditions varies greatly from one species to the next, from one situation to another. In some cases an internal rhythm plays a major role, and in others it may be of negligible significance. A well-balanced coverage of the present topic ought, therefore, to include considerable emphasis on cases in which endogenous timing plays no important role in determining behaviour. Unfortunately, however, that will be very difficult because biological 'non-rhythmicity' is a topic which has been neglected in the literature. This bias in the examples to be considered seems unavoidable and should be borne carefully in mind.

Endogenous rhythms, demonstrable under constant laboratory conditions, represent a subject of investigation which is of self-evident importance to the physiologist. It is, however, seldom if ever of direct ecological significance that an organism can continue to show a persistent rhythm under constant environmental conditions, a rhythm which may persist for many cycles; constant conditions represent an extreme departure from the natural situation. Experiments of this sort serve only to demonstrate that the organism has the potential to time certain of its activities by an environmentally independent system. The extent to which this capacity affects behaviour and physiology under the normally cyclic natural environment is the relevant problem to which the ecologist must address himself: how important (if at all) are internal timing processes for the interpretation of a given set of field observations? The purpose of this chapter is by no means to convince the ecologist that endogenous timing processes are generally of overriding importance in a natural environment. Instead, it is hoped to demonstrate that internal timing can, in some cases, be of importance for understanding certain aspects of field studies.

(4) Some Ecological Phenomena Involving Endogenous Rhythms

The cases of endogenous timing to be described below represent a small number of examples drawn from an extensive literature. These studies should, however, be sufficient to indicate to the ecologist the spectrum of phenomena that are, or may be, involved in 'biological clocks' in oceans and coastal waters.

(a) Daily Rhythms of Zooplankton

The surface waters of the world's oceans are the arena for that conspicuous manifestation of biological rhythmicity known as vertical migration. The participating organisms cover a broad spectrum of sizes and represent diverse taxonomic groups and feeding habits. The usual observation is an aggregation in the surface waters during the night of many species of both herbivores and carnivores, animals which during the daytime are found at greater depths. The most widely accepted ecological interpretation of the phenomenon is that herbivores, which must seek their food in the surface waters where primary production occurs, are able significantly to reduce the risk of predation by 'hiding' in the relative darkness at greater depth during the daylight hours; and that carnivores follow their prey to the surface at night, to take advantage of the feeding aggregations. Many other hypotheses, however, have also been proposed (see review by McLaren, 1963; McAllister, 1969).

Explanations of this sort deal, of course, with the selective advantage of the behaviour, and would represent causes only in an evolutionary sense rather than proximate mechanisms responsible for the migrations. The interpretation has long prevailed that the immediate, direct cause of vertical migration is a response to light conditions; but this is only part of the story. Experimental studies have demonstrated that endogenous timing processes can play a significant role in vertical migration (Enright and Hamner, 1967). Some species show a continuation of vertical migration under constant dim light conditions, demonstrating involvement of a biological clock in timing the movement, while other species seem to respond almost exclusively to prevailing light intensity, and still other species show intermediate behaviour (Fig. 9-1).

The experiments which led to the data in Fig. 9-1 also demonstrated that when endogenous rhythms underlie vertical migration, the rhythms can be synchronized easily by artificial lighting cycles, and are in this way comparable with the better known circadian rhythms of terrestrial animals. The amphipod *Nototropis* sp. showed a strong endogenous rhythm; the extent of cyclic changes in behaviour was nearly as great under constant conditions as during the prior lighting cycle. Peltidiad copepods exhibited a weak endogenous rhythm; cyclic changes in surface abundance, under constant conditions, were superimposed upon a general tendency for these animals to remain near the surface under dim light. Epicarid isopods showed apparent absence of cyclic behaviour under constant conditions, in spite of strong response to initial lighting cycle. The data for the amphipod *Tiron* sp. suggest the presence of an 'hour-glass' timing mechanism. Under constant conditions, these animals rose to the water surface and then disappeared some 8 to 12 hrs later in the absence of additional stimuli, but never returned to the surface: as though dusk triggered upward migration and set in motion a one-cycle timer leading to downward migration about 12 hrs later. (Consult Enright and Hamner (1967) for experimental details.) The broad spectrum of rhythmic capacities shown in Fig. 9-1, all of which resulted in comparable behaviour under light–dark cycles (first 2 days), leads to the question, 'Why should the ecologist care in the least whether internal timing is involved in vertical migration, since the resulting behaviour under field conditions would be so similar?' The answer is that for the large-scale consequences of vertical migration, the mechanism by which it is timed, whether response to exogenous or endogenous factors, is of peripheral interest at most. The important facts for most marine ecologists are simply that vertical migration occurs and that it has a variety of consequences for the interactions between populations. The presence of internal timing processes can ordinarily be expected to affect only minor details in

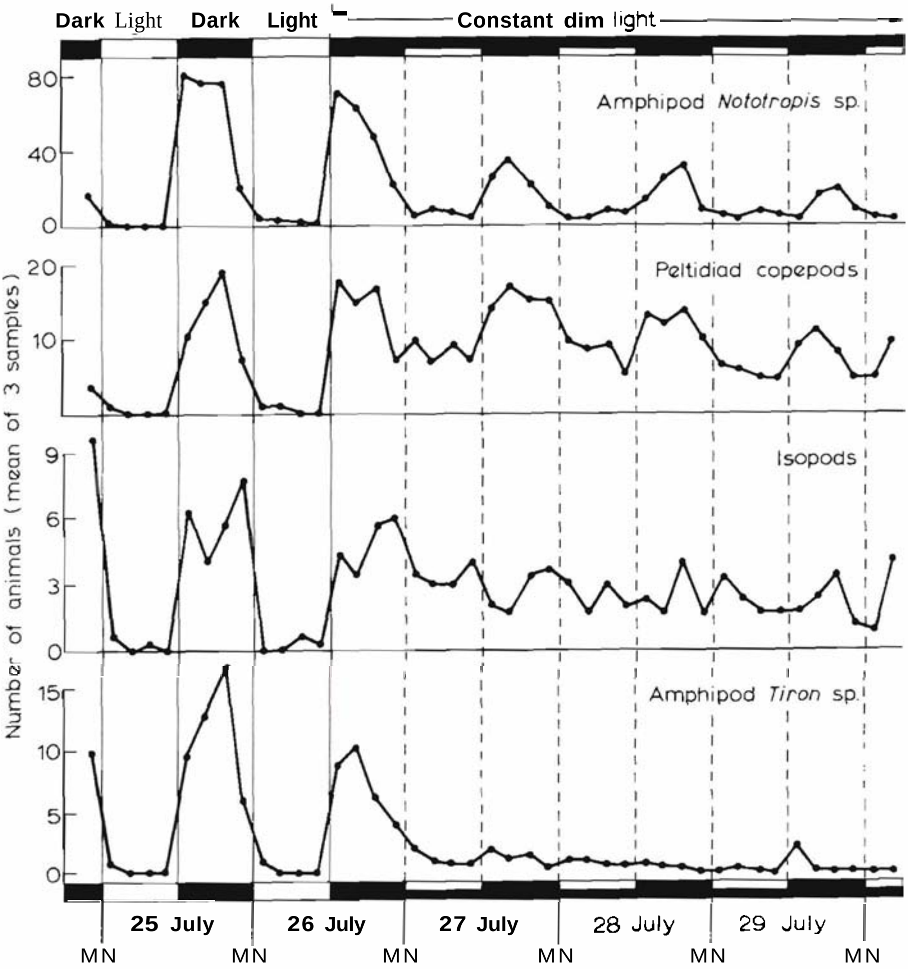

Fig. 9-1: Vertical migration of zooplankton under light–dark cycles (first 2 days) and under constant dim light (last 3 days). Migratory tendency persisted under constant conditions to different extents in different species. Plotted values are averages for triplicate samples taken at the surface every 4 hrs. The lighting cycle was shifted 6 hrs from outdoor conditions, with light from midnight to noon. MN: midnight. (Original.)

the timing of vertical movement: (i) the influence of cloud cover, or of moonlight, or of a solar eclipse; (ii) the question whether upward migration coincides perfectly with light-intensity changes associated with sunset, and downward migration with sunrise, or only approximately so.

(b) Daily Rhythms of Phytoplankton

One of the most striking demonstrations of daily rhythms in phytoplankton involves the luminescent alga *Gonyaulax polyedra*. Populations of these flagellates show a several-fold difference, from day to night, in the amount of light produced by a standard mechanical stimulus; and it has been shown that this change in luminescent capacity persists as a circadian rhythm under constant conditions (HASTINGS and SWEENEY, 1958, 1959; Fig. 9-2a and b). Nocturnal displays of this luminescence along the shore can be extremely impressive to both layman and ecologist; but, to date, no convincing ecological explanation has been offered to account for the evolution of algal luminescence. Nor, of course, is there any clear ecological consequence to the fact that circadian cycles in luminescent capacity can continue under constant conditions.

Other aspects of algal rhythms, however, will be of greater importance to the ecologist. It has been demonstrated, for example, that many species of phytoplankton tend to divide synchronously in the presence of normal light–dark cycles; furthermore, in some cases, cell division will continue as a coordinated rhythmic process in the population, with a period near 24 hrs, under constant conditions (SWEENEY and HASTINGS, 1958; Fig. 9-2c; see also, for example, EDMUNDS, 1971). The synchronization in cell division seen under field conditions cannot, then, be interpreted as due only to a direct response to environmental stimuli. Other studies have demonstrated that phytoplankton photosynthetic potential (energy fixed per unit light energy available) can vary markedly in certain algal species, depending upon time of day; and that this variation is also under the control of internal processes and will continue as a persistent rhythm under constant conditions (HASTINGS and co-authors, 1961; Fig. 9-2d).

Both synchronous cell division and circadian variations in photosynthetic potential have significant implications for the ecologist. Since dividing algal cells will be larger in cross-section than non-dividing cells, the synchronization in cell divisions will impose cyclic changes in food availability on filter-feeding grazers, depending upon the size of their filtering 'mesh' (Chapter 3). Daily variations in photosynthetic potential have direct relevance for field studies of photosynthesis, since single short-term measurements are often used as the basis for extensive extrapolation. Hence, the field relevance of rhythmic variation in these phenomena is clear, even though the long-term persistence of the rhythms under constant laboratory conditions is of little obvious ecological importance.

Every good ecologist recognizes, of course, the hazards of interpreting field data in terms only of the environmental conditions prevailing at the moment of observation. The state of a biological system at a given time is often strikingly dependent upon the history of the system. Synchronized endogenous biological rhythms, however, represent a history-dependence of a peculiar sort which can make the problems of interpreting field data particularly difficult.

The data of Fig. 9-2d suggest an example of the problems: careful measurements under field conditions may show a systematic increase in total photosynthesis from dawn until mid-morning hours, a phenomenon which is repeated day after day. Such an increase might readily be interpretable as due to the concurrent increase in illumination. The data of Fig. 9-2d indicate, however, that a major component of this phenomenon may well be due to inherent timing processes, that is, a biological clock. The effect, if any, of increased incident light may well be superimposed upon an endogenous increase in photosynthetic potential per unit light intensity; and under some circumstances, the importance of the endogenous contribution may

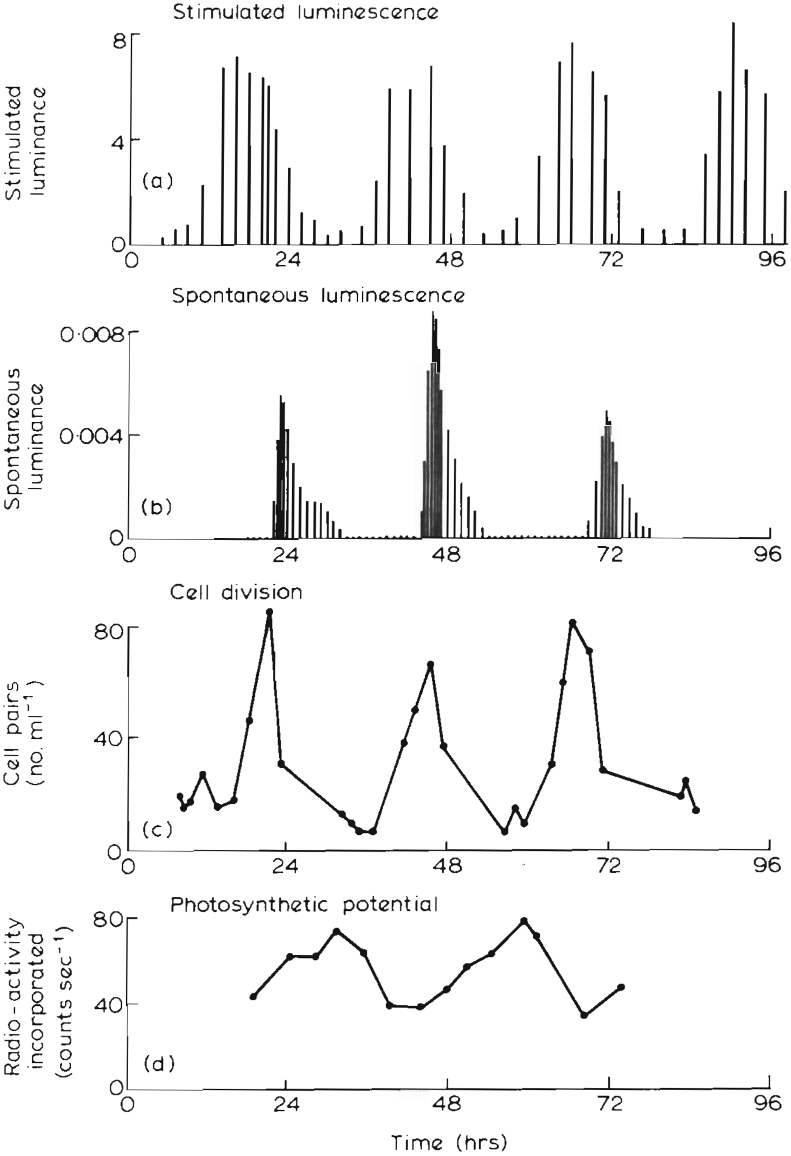

Fig. 9-2: *Gonyaulax polyedra*. Four endogenous rhythms shown by the alga. (a) Stimulated luminescence in response to mechanical disturbance; data from HASTINGS (1960, Fig. 4). (b) Spontaneous luminescence, the 'glow' rhythm of undisturbed cultures; data from SWEENEY and HASTINGS (1958, Fig. 6). (c) Cell division; data from SWEENEY and HASTINGS (1958, Fig. 4). (d) Photosynthetic potential, measured as rate of ^{14}C uptake under standard lighting conditions; data from HASTINGS and co-authors (1961, Fig. 2). Slight apparent differences in periods of the 4 rhythms are probably due to differences in experimental temperature and light intensity; experiments were not simultaneous. (After the sources indicated; reproduced by permission of the Long Island Biological Association, Inc.; the Society of Protozoologists; and the Rockefeller University Press.)

exceed the exogenous one. This is just one instance of the general problem: extensive series of field data may show an essentially perfect correlation between a given biological phenomenon and an environmental variable—a correlation of the sort that would strongly encourage the interpretation of a simple causal relationship. Such a correlation may, indeed, represent a direct causal link, but the possibility that endogenous rhythmicity is involved must impose severe restrictions on the acceptance of such conclusions (Volume IV).

(c) Daily Rhythms of Benthic Organisms

The most conspicuous form of daily rhythmicity in terrestrial animals is in cycles of locomotor activity: changes manifest in the waking–sleeping rhythms of higher vertebrates, and in superficially similar changes, from an 'active' to an 'inactive' state, in many lower animals as well. These gross changes in behaviour are, in the natural environment, usually synchronized with the day–night cycle, and have, of course, led to the ecological designation of certain animals as 'diurnal' and others as 'nocturnal'. It was, until recently, assumed by both layman and ecologist that the basis for such phenomena was to be sought primarily in the direct influences of light and temperature (Volume I); for example, because diurnal animals are visually and thermally adapted to daytime activity, the environmental conditions prevailing at night were thought to force these animals into inactivity. It is, however, now generally recognized that many species—perhaps most—can, when placed under appropriate constant conditions of light and temperature, continue to show an alternation of activity and rest, which represents a persistent rhythm with a period near 24 hrs. There is, then, an endogenous rhythmic mechanism which underlies the animals' daily cycles of activity in the natural environment.

Rhythms of locomotor activity prove to be particularly easy to monitor on an automatic basis in the laboratory, and an extensive literature dealing with such rhythms has accumulated. Most of the studies have dealt with terrestrial organisms, but there are a number of cases dealing also with marine species (MORI, 1943, 1960; Fig. 9-3). While the data of Fig. 9-1, dealing with vertical migration, may also have involved cyclic changes in phototaxis, it seems probable that cycles in total locomotor activity—alternations between an active and a resting phase—were also involved in a major way in the observed migrations (Chapter 7 and 8).

It is appropriate at this point to consider the studies of barnacle activity undertaken by SOMMER (1972). Working with a wide variety of light–dark cycles, he was unable to find any significant evidence in the cirral movements of *Balanus balanus* for endogenous timing processes related to either the day–night cycle or the tidal cycle. Nevertheless, the barnacles responded strongly to prevailing light intensity, being much more active in the dark than in the light. This species might, therefore, be expected to show a strong daily rhythm under field conditions, but a purely exogenous rhythm, caused by the natural day–night light cycle. In a subsequent section, we will consider the restrictions that must be placed on such an interpretation.

What, if anything, should these laboratory studies of activity, under constant conditions, mean to the ecologist? The answer varies from one case to another. If the ecologist is interested in the extent to which utilization of a habitat is temporally subdivided, or in the kind and extent of interactions that occur between species,

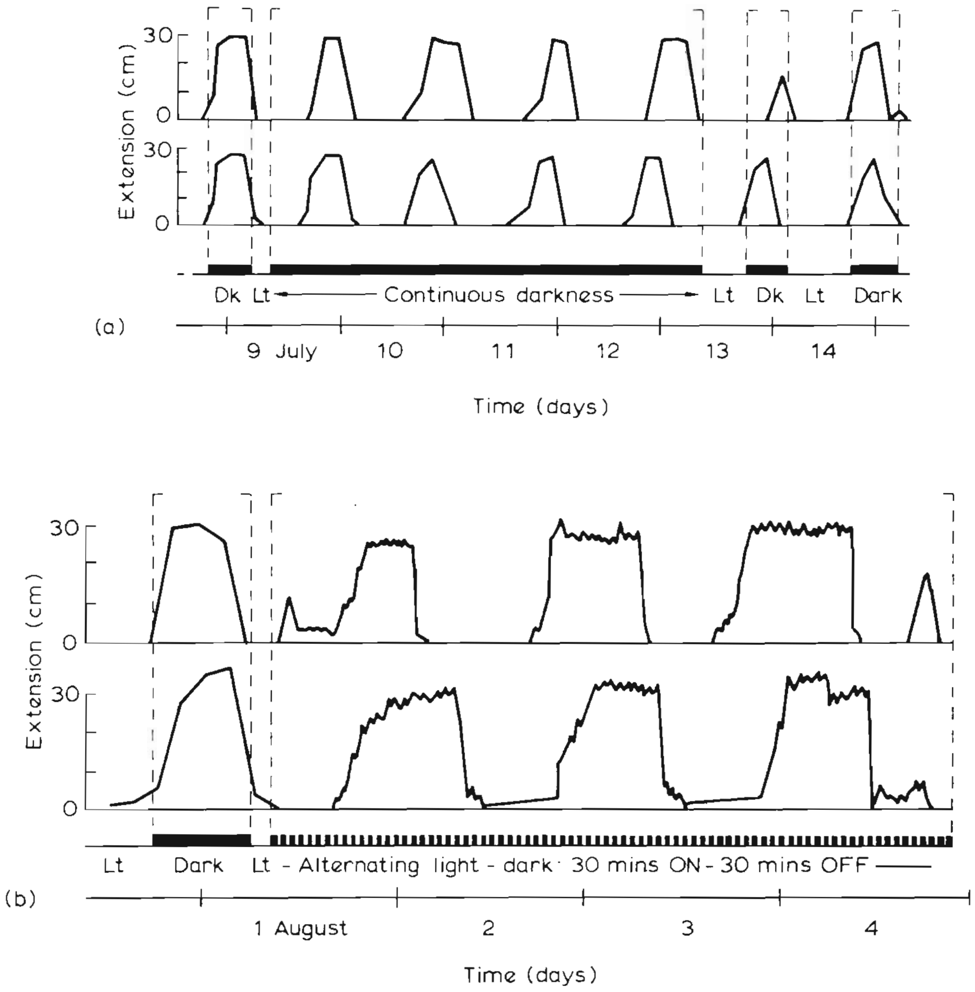

Fig. 9-3: *Cavernularia obesa.* Persistence of circadian activity rhythm in the sea-pen. (a) Persistence in constant darkness; data from MORI (1943, Fig. 1). (b) Persistence under alternating light-dark regime, with 30 mins light and 30 mins dark; data from MORI (1960, Fig. 1). Note slight superimposed effect of lighting in (b), indicating a weak exogenous effect of light. (After the sources indicated; reproduced by permission of the Long Island Biological Association, Inc.)

then he needs an accurate record of when each species is active, when it is seeking food, when it is dormant. But the ecologist need not, in general, concern himself about whether the observed timing of activity arises from endogenous mechanisms or is due to concurrent stimuli. On the other hand, if the ecologist is interested in accounting for details in the activity pattern of a particular species, data on endogenous activity rhythms can serve to indicate the limits within which responses to concurrent stimuli might modify endogenous potential.

> 'Endogenous rhythmicity provides the organism with a temporal inertia, a time-dependent readiness to respond to environmental stimuli in an appropriate manner. This temporal inertia can permit the organism to be relatively independent of concurrent environmental time cues' (ENRIGHT, 1970, p. 236).

Another well-known manifestation of daily rhythmicity which can be noted in the intertidal environment involves the colour changes of certain crustaceans, which tend to be darkly shaded in the daytime, due to extensive dispersion of pigment granules in the chromatophores, and to be much paler during the night. Colour changes of this sort are particularly conspicuous in fiddler crabs, and extensive laboratory investigation has demonstrated that internal timing processes, in the form of persistent circadian rhythmicity, underlie the phenomenon. Early studies of these crabs led to the interpretation that the animals showed a colour-change rhythm with a period which was exactly 24 hrs under constant conditions of light and temperature (e.g. BROWN and WEBB, 1948), and this result represented one of the cornerstones of the hypothesis, mentioned earlier, that unrecognized external timing cues may be responsible for the persistence of biological rhythms under apparently constant conditions in the laboratory. A careful re-examination of fiddler-crab colour-change rhythms, however, demonstrated that the exact 24-hr period observed in the earlier experiments was a technical artefact, a product of the observational procedure which included disturbance of the animals, coupled with light stimuli, at regular intervals of time (STEPHENS, 1962; STEPHENS and co-authors, 1964). When individual crabs were studied by observation at random times of day, the colour-change rhythm was found to have a circadian period, in some cases different by an hour or more from the 24-hr period of the natural day–night cycle.

While it is clear that the differences in pigmentation shown by fiddler crabs and other crustaceans may have significant ecological consequences, particularly in terms of susceptibility to predation, the fact that endogenous timing underlies the phenomenon is probably of peripheral interest to the ecologist.

The discovery of time-compensated celestial orientation by KRAMER (1950) and VON FRISCH (1950) gave strong impetus to the study of endogenous timing. Birds and bees were shown able to use the position of the sun to orient in a given, constant compass direction, regardless of time of day; this performance clearly implies that the animals have access to a timing process which permits them to compensate for hourly changes in the direction of the sun. A number of lines of evidence indicate that the timing process involved is basically the same kind as that responsible for other manifestations of daily timing: an internal rhythmic system which is ordinarily synchronized by environmental cycles, and can persist under constant conditions with a period near 24 hrs.

Shortly after the initial description of time-compensated sun orientation in birds and bees, PARDI and PAPI (1952) discovered that intertidal crustaceans, amphipods of the family Talitridae, have a similar capacity. In a dry environment, deprived of all directional cues except a view of the sun, these animals have a strong tendency to orient in a compass direction which would be toward the sea, i.e., perpendicular to the shore line, on the beach from which they were collected. Populations from different shorelines show differences in preferred direction (PARDI and PAPI, 1953) and evidence has been obtained which indicates that a major component of these differences is genetically determined (PARDI, 1960; Chapter 8).

Since the amphipods depend, for their survival, on environmental conditions prevailing on only a very narrow strip of the beach, near the preceding high-tide line, their ability to orient properly on the shore is of obvious ecological significance. Since the sun is a sufficient orientational reference and since phase-shifting the light regime produces predictable deviations in direction, it seems clear that in this case, as well, internal timing processes play a major role in the performance.

In principle, it appears that the animals would not need a persistent biological clock as the timing process underlying compensation for solar movement; a simple hour-glass mechanism, re-initiated with sunrise each day, ought to be adequate to permit proper orientation. The amphipods, however, show only slight decrease in their orientational capacity when maintained for several days under constant conditions, indicating that repetitive, rhythmic timing processes are involved.

The general question of how animals orient themselves in space, so as to find and remain in an optimal habitat, represents a major area of research at the interface between behavioural physiology and ecology (Chapter 8). The capacity of animals, in both the terrestrial and the marine world, to use celestial cues for this orientation represents one of the foundations for the interpretation of many puzzling phenomena seen under field conditions. And the contribution of endogenous timing processes to celestial orientation cannot be overlooked. Thus the ecologist concerned with orientation is one to whom internal timing is a problem of first-rate importance.

(d) Tidal Timing

For organisms which inhabit that narrow strip of land which lies between the extremes of high and low tide, environmental fluctuations associated with the tidal cycle are apt to be of even greater ecological significance than the day–night cycle. It should come as no surprise, then, that the behaviour of such animals is often associated with endogenous timing processes which are synchronized by the tidal regime. A recent review by PALMER (1973) summarizes the literature on this subject, with an excellent description and critique of experimental data and an extensive bibliography.

These endogenous timing processes have been shown to represent persistent internal rhythms, comparable, at least qualitatively, with the circadian rhythms of animals from the non-intertidal environment. Three examples of such tidal rhythms, involving changes in amount of locomotor activity of crustaceans, are given in Fig. 9-4. The data obtained for the amphipod *Synchelidium* sp. represent counts plotted at 15-min intervals; for juveniles of the anomuran sand-crab *Emerita analoga*, and for the isopod *Excirolana chiltoni*, counts are plotted at 20-min intervals. Arrows over tidal records represent times of estimated peaks in activity. The maximum of activity in a given peak is correlated with the height of high tide on that day, particularly in *Synchelidium* and *E. chiltoni*. Animals like those in Fig. 9-4, which come from marine sand beaches, seem to have particularly strong endogenous tidal rhythms; a plausible evolutionary explanation for this

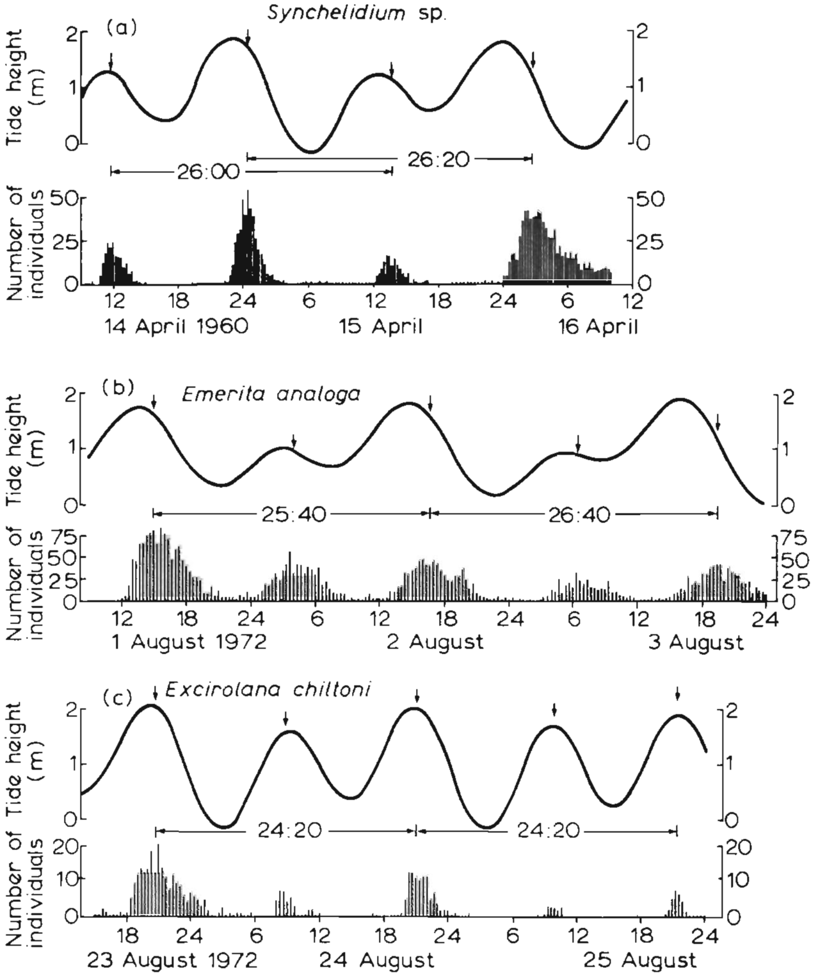

Fig. 9-4: Tidal rhythms of swimming activity exhibited by representatives of three species of sand-beach crustaceans, together with simultaneous tidal regime. Freshly collected animals were placed in aquaria together with sand and sea water, and photographs of the aquaria were taken at regular intervals of time. Plotted are the numbers of individuals visible, swimming in the sea water, as a function of time. (Original.)

importance of internal timing processes can be found in the nature of the habitat. For animals occupying sand beaches, the rhythmicity in locomotor activity plays a major role in determining the spatial distribution of the population, enabling them to take advantage of the abundance of food which accumulates at the washline on the shore, and to avoid being marooned, between tides, on the high beach, where they would suffer extremes of desiccation (ENRIGHT, 1963).

The data illustrated in Fig. 9-4 deal only with locomotor activity. Other kinds of experiments with one of the species, *Synchelidium* sp., indicate that spontaneous locomotor activity is only one of several behavioural characteristics of the species which are affected by an endogenous rhythm. Both the duration and the nature of the response of the animals to pressure-change stimuli vary markedly, depending upon whether the tide is high and the animals are in their active state, or the tide is low, and the animals are in their 'resting' state (ENRIGHT, 1962; see also FLÜGEL, 1972). Furthermore, the phototactic response of the animals to a steady light stimulus also depends upon endogenous factors which parallel the activity rhythm: a positive phototaxis prevails during the active phase of the rhythm, and a negative phototaxis during the resting phase (ENRIGHT, 1961; see also Chapters 7 and 8). Without an appreciation of the possible contribution of endogenous timing processes, the behaviour of these animals, in the laboratory as well as on the beach, would remain a confusion of contradictions.

As illustrated in Fig. 9-4 (particularly a and c), animals collected from a shoreline where they have experienced a complex tidal pattern show persistent activity rhythms which reflect this complexity, with greater activity occurring at times associated with the higher high tide, lesser activity at times of lower high tide. There are strong indications that the rhythmic system of these animals has a fundamental period of about 25 hrs, rather than 12·5 hrs: the pattern of activity, under constant conditions, repeats itself not at the average interval between successive high tides

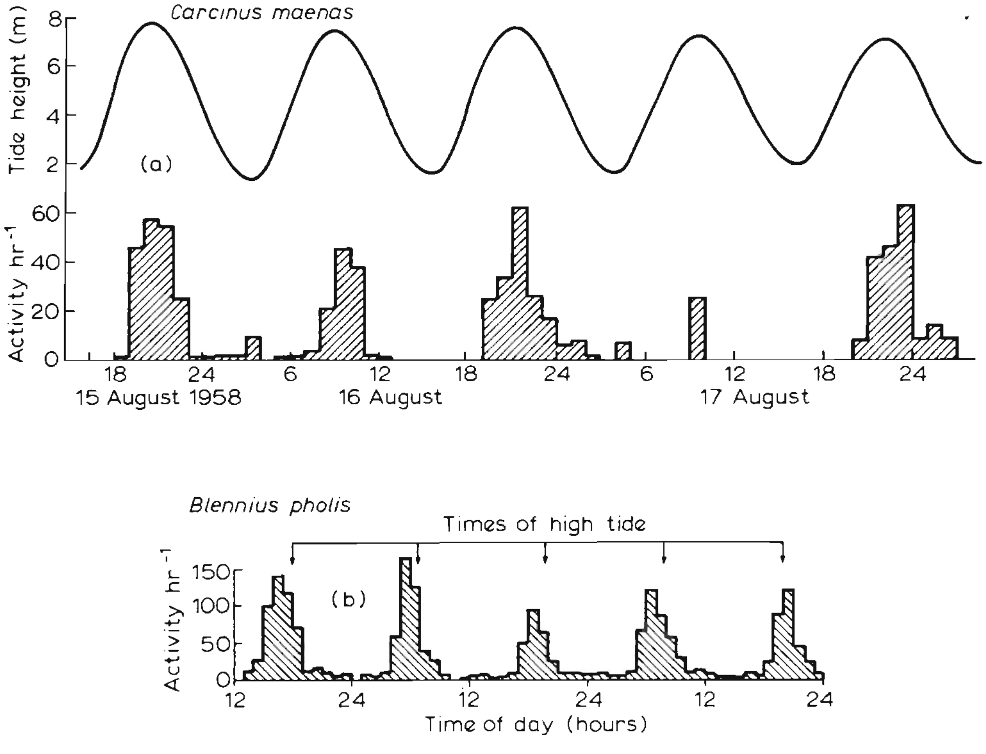

Fig. 9-5: Tidal rhythms of locomotor activity of animals from the rocky shoreline. (a) *Carcinus maenas*: Counts of movements per hour, together with concurrent tidal regime; data from NAYLOR (1958, Fig. 6). (b) *Blennius pholis*: Swimming activity with arrows to show times of high tide; data from GIBSON (1965, Fig. 1). (After the sources indicated; reproduced by permission of Company of Biologists, Ltd.; and Macmillan (Journals) Ltd.)

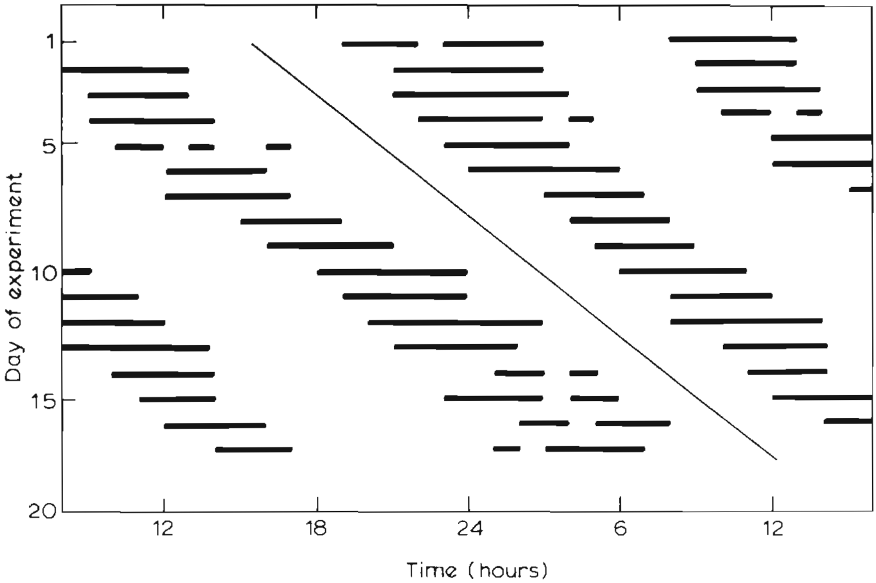

Fig. 9-6: *Uca minax*. Endogenous rhythm of locomotor activity of a fiddler crab. In this derived actogram, data from successive days are plotted beneath each other so that a 24-hr rhythm results in a vertical column of activity blocks. The diagonal line, which approximately parallels the activity pattern, has a slope of 1¼ hrs per day, indicating a free-running period of about 25¼ hrs. 8 hrs of each day's record have been plotted in duplicate to facilitate visual recognition of long-term patterns. Plotted are hours during which activity was equal to or greater than 50% per hour. (Data from BARNWELL, 1966, Fig. 4; reproduced by permission of *Biological Bulletin*.)

(12·4 hrs) but at about twice that interval. This suggests that the basic mechanisms involved may be similar to those responsible for better-known circadian rhythms. Tidal rhythms of this type have been observed to persist, in single individuals of *Excirolana chiltoni* (Fig. 9-4c), for more than 2 months, as do the circadian rhythms of activity of higher animals (ENRIGHT, 1972). As in the case of circadian rhythms, the long-term persistence of tidal rhythms under laboratory conditions has only peripheral interest for the ecologist, since constant conditions represent an extremely 'unecological' situation.

As shown in Figs 9-5 and 9-6, animals from other intertidal environments—the crab *Carcinus maenas* and the fish *Blennius pholis* from rocky intertidal habitats, and the fiddler crab *Uca minax* from estuaries—also exhibit tidal rhythms in their locomotor activity which persist under constant conditions. Fig. 9-7 presents data from an extensive study on the fiddler crab *Uca crenulata* (HONEGGER, unpublished; see also HONEGGER, 1973). In *U. crenulata* endogenous rhythmicity is expressed only very weakly. Data of this type are unusual in the literature; they serve to emphasize the bias, mentioned in the introduction to this chapter, which attends any discussion of endogenous rhythms: data which show clear rhythmicity will readily find their way into the literature and the memory of the reader; data which show weak rhythms or non-rhythmic behaviour tend to be easily lost from sight.

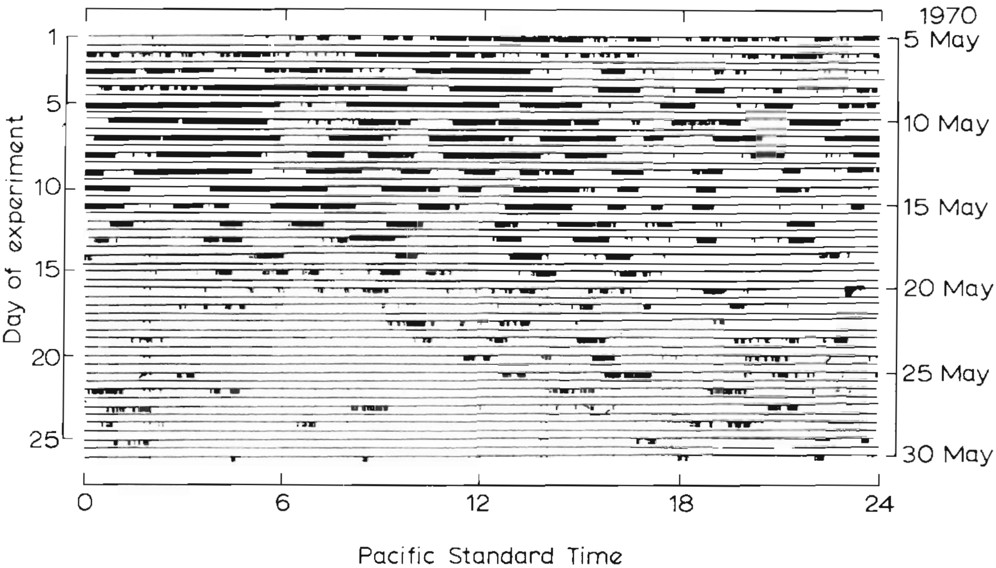

Fig. 9-7: *Uca crenulata*. Original activity record for a fiddler crab. Consult legend to Fig. 9-6 for method of data presentation. There is a weak suggestion of endogenous rhythmicity in portions of the record, with a period somewhat longer than 24 hrs. (Recording kindly supplied by Dr. H. W. HONEGGER.)

It appears to be an intuitively plausible conclusion that an organism which shows weak or negligible evidence of persistent rhythmicity, under constant conditions, such as seen in Fig. 9-7, will have its behaviour under field conditions primarily determined by concurrent stimuli on a moment-to-moment basis, but such a conclusion must be tempered with caution. The expression of endogenous rhythmicity in the laboratory depends very greatly upon the nature of the constant environmental conditions provided. For example, passerine birds generally show clear and strong endogenous circadian activity rhythms under constant dim light; when such a bird is placed in bright continuous light, however, all evidence for endogenous circadian timing processes will usually disappear; arrhythmic, essentially continuous activity results. Hence, the weak rhythmicity evident in Fig. 9-7 may be due to inappropriate choice of experimental conditions rather than to an unimportance of endogenous rhythmicity for this species. It should, however, be noted at this point that HONEGGER obtained similar diffuse patterns of activity from *U. crenulata* under a wide variety of light intensities, experimental temperatures and holding chambers for the animals.

Two other difficulties, which weaken any conclusion to be drawn from data like those of Fig. 9-7, are the possibility that endogenous timing processes exist which are important under field conditions but do not lead to persistent rhythmicity: the equivalent of hour-glass timing processes (Fig. 9-1: *Tiron* sp.); and the possibility that endogenous rhythmic timing processes may underlie some other physiological function of the organism such as respiration or colour change, without being expressed in locomotor activity. Hence, laboratory observations of arrhythmic behaviour under constant conditions provide the ecologist with no firm foothold for the interpretation of field behaviour; such observations lead to the suspicion—but do not demonstrate—that concurrent stimuli under field conditions are the primary determinant of behaviour.

(e) Lunar and Semilunar Rhythms

The tidal cycle on the shoreline is characterized by a fortnightly amplitude modulation, due to the phase of the moon, and expressed in the cyclic changes from spring to neap tides. These long-period variations in tidal height represent significant environmental fluctuations for many intertidal organisms. One of the most dramatic of the phenomena involved is the spawning of a small atherinid fish, the grunion *Leuresthes tenuis*, on the beaches of Southern California and Mexico. During the spring and summer months, on certain nights which are closely correlated with lunar phase, at times of night which are closely correlated with high tide, vast numbers of these fish swarm onto the moist upper beach where, between waves, they mate and bury their eggs into the sand, thereafter to return to the sea (Fig. 9-8). The fertilized eggs undergo development while buried in the sand, and the larvae then hatch some 8 to 12 days later, when the next series of high spring tides washes the upper beach (WALKER, 1949). The times of intense spawning, both day of month and time of night, are predictable with great reliability even years in advance, on the basis only of tide and moon tables. Fig. 9-9 presents data from an extended series of careful field observations, which demonstrate the astonishing regularity of the semilunar rhythm of the grunion.

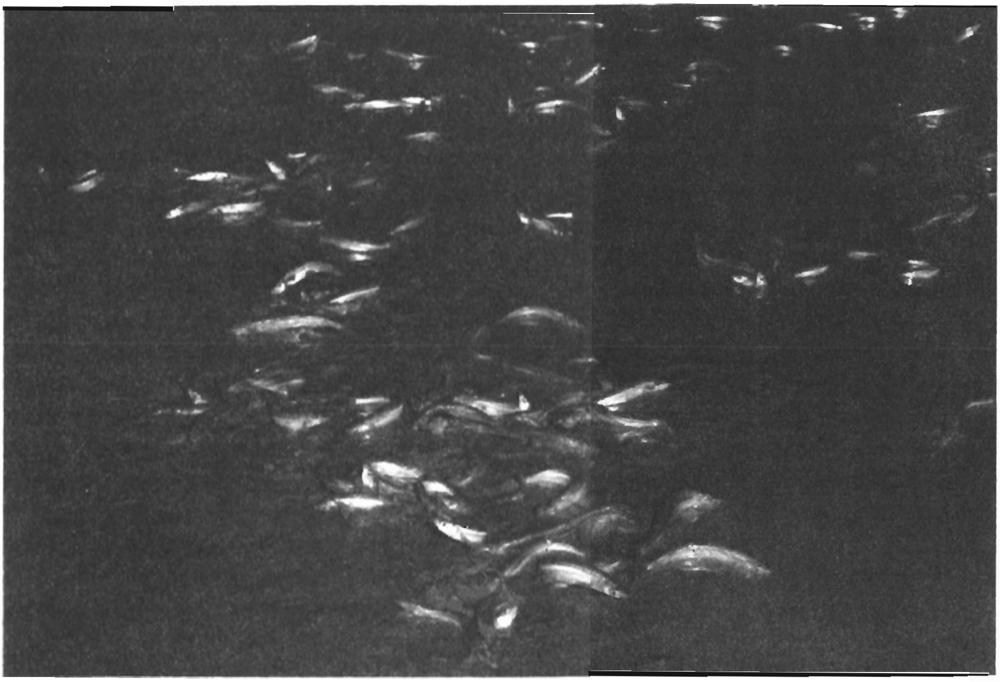

Fig. 9-8: *Leuresthes tenuis*. Masses of grunion spawning between waves on the intertidal beach. (Reproduced by permission of Academy Films, Hollywood, California, USA.)

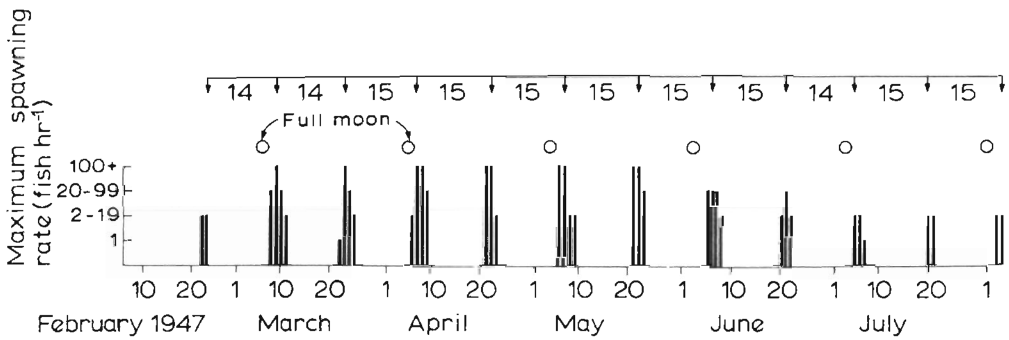

Fig. 9-9: *Leuresthes tenuis*. Field data on times of spawning of grunion on the beach in front of the Scripps Institution of Oceanography, La Jolla, California (USA), during 1947, based on systematic observation during the entire season. Plotted are maximum observed rates of spawning each night. Vertical arrows: nights of maximum integrated spawning (fish per night) for each series of spring tides; numbers are the days between these maxima. (Data from WALKER, 1949).

There have been no successful studies of grunion spawning behaviour under constant laboratory conditions, and so the full extent to which endogenous timing is responsible for the behaviour remains uncertain. Since, however, the ovarian cycle of the fish involves ripening of the eggs which takes several days before spawning, some kind of internal timing must be involved in order to account for the strong synchronization of the population.

Another well known instance of lunar rhythmicity in the spawning of marine organisms is that of the palolo worm *Eunice viridis* of the South Pacific Ocean. In this case it seems unlikely that the fortnightly and lunar changes in tidal amplitude are of importance to the worms, since their normal habitat is deep below the intertidal zone. The observed coincidence of spawning with the last quarter of the moon has been generally interpreted as a means of synchronizing population reproduction, so as to maximize the probability of fertilization; the fact that the spawning is at a given moon phase is presumed to be irrelevant to the survival or reproductive success of the animals. It appears probable in the palolo worm as in the grunion that endogenous timing processes participate in the observed synchronization, but laboratory studies have not yet clearly demonstrated this (e.g. HAUENSCHILD and coauthors, 1968).

For another species of marine polychaete, however, experimental studies have apparently demonstrated such an endogenous lunar rhythm in spawning. The reproductive behaviour of *Platynereis dumerili* can be synchronized in the laboratory by means of light given at night to mimic moonlight, and the population synchrony seems to persist thereafter for several cycles without further direct stimulation by artificial moonlight (HAUENSCHILD, 1960).

The most detailed laboratory studies of lunar and semilunar reproductive rhythms are those of NEUMANN (1966), who has explored in detail the physiological processes leading to reproductive synchrony in a species of intertidal insect, the midge *Clunio marinus*. At times of extreme low spring tides, i.e., at intervals of a fortnight, the adult males emerge from their pupal cases and search out the pupae of the unwinged females, which they assist in eclosion. Copulation follows immediately and the female is then deposited on the substrate, to lay her eggs before the tide rises again. The full life cycle of this species lasts several weeks; the adult insect, however, lives only a few hours, so synchronization within the population must be maintained to assure reproductive continuity. The synchrony of these insects under field conditions is probably as complete as that of the grunion.

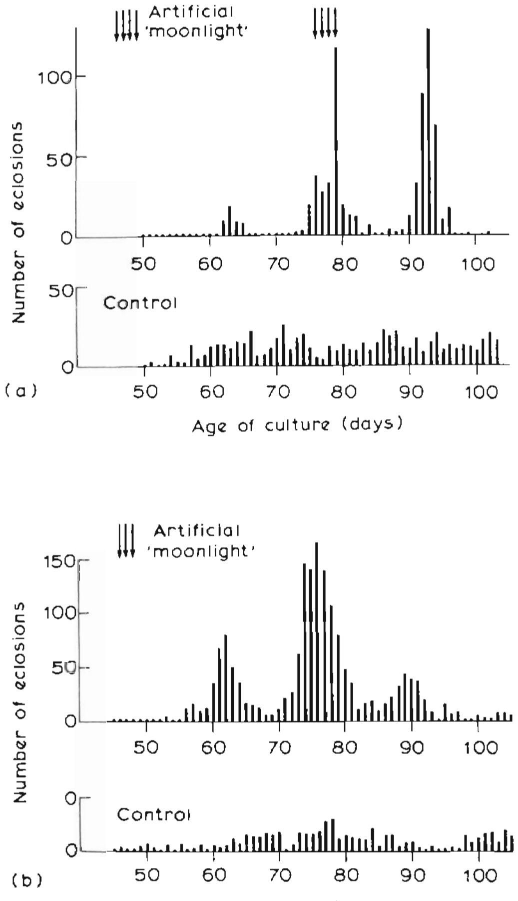

Fig. 9-10: *Clunio marinus.* Laboratory data showing semilunar rhythm of spawning induced by dim illumination at night, together with simultaneous data from control populations which did not receive synchronizing stimuli. (a) Artificial moonlight presented for 4 days (arrows), and then repeated at 1-month intervals; (b) artificial moonlight presented for 3 days (arrows), once only. (Data from NEUMANN, 1966, Figs 12 and 18; reproduced by permission of Springer-Verlag, Berlin.)

One of the primary processes leading to the synchrony of *Clunio marinus* populations is an endogenous semilunar rhythm, which is synchronizable by means of dim illumination at night, simulating moonlight (NEUMANN, 1966). Data demonstrating the endogenous nature of the semilunar rhythm, under laboratory conditions which exclude direct lunar influence, are shown in Fig. 9-10. The observation that the period of the rhythm is about 15 days, although the appropriate synchronizing stimulus, moonlight, is available only in a monthly cycle, indicates that this is an instance in which endogenous timing processes play a very important role in field behaviour. If the insects were to rely only on direct lunar stimuli for population synchrony, the series of spring tides associated with either new moon or full moon would be unavailable to them, although the tidal cycle is quite comparable at full and new moon. These data represent a unique case in the literature on endogenous rhythms, in which an internal rhythm with a given period (14–15 days) is naturally synchronized by an environmental stimulus which recurs at twice that period (29 days). It is entirely possible, in the laboratory, to synchronize the circadian rhythm of a finch, for example, to a 24-hr period by means of a light cycle with a period of 48 hrs, but only in an organism like *C. marinus* does this kind of potential have a clear ecological relevance.

The data of Fig. 9-10 demonstrate a physiological system which is sufficient to account for the fact that *Clunio marinus* ecloses and reproduces on the appropriate days of the month, but an additional process is necessary to provide synchrony with the times of low tides. NEUMANN has demonstrated for most populations of *C. marinus*, from various places along the European coast, that an endogenous circadian rhythm, synchronized by the light–dark regime, is responsible for the time of day at which eclosion takes place. Thus, this species has evolved a remarkably indirect means of coordinating its activities with the environment: in order to achieve synchrony with the extreme low tides, the insects rely upon an endogenous fortnightly rhythm synchronized by moonlight, to confine eclosion to the days of the month on which extreme low tides occur; and rely upon an endogenous daily rhythm, synchronized by sunlight, to confine eclosion to that time of day at which the substrate will be exposed by the low tide.

On different portions of the European coast, the extreme low tides occur at different times of day, and it has been found that populations of *Clunio marinus* from different areas, when brought into the laboratory, show differences in the time of day of eclosion which correspond with habitat differences in time of day of the low spring tides. By means of elaborate breeding experiments, NEUMANN (1966) has, furthermore, demonstrated that these population differences in timing are associated with a polygenic system of inheritance: not only do the animals inherit the capacity to synchronize their reproduction with the environment, but they also inherit a phasing of the activity measured relative to the day–night cycle, which is appropriate to the tidal cycle on the particular coastline on which they live.

Probably the most significant aspect, for the ecologist, of these studies on *Clunio marinus* is the demonstration that in a predictable environment, an animal can rely on very indirect timing cues. The relevant environmental time to which the animals coordinate their reproductive activity is extreme low tide; neither moonlight nor sunlight is of direct importance to the reproduction, but the endogenous rhythmic system of *C. marinus* permits the insects to utilize these reliable environmental time cues to produce synchrony with the appropriate tidal phase.

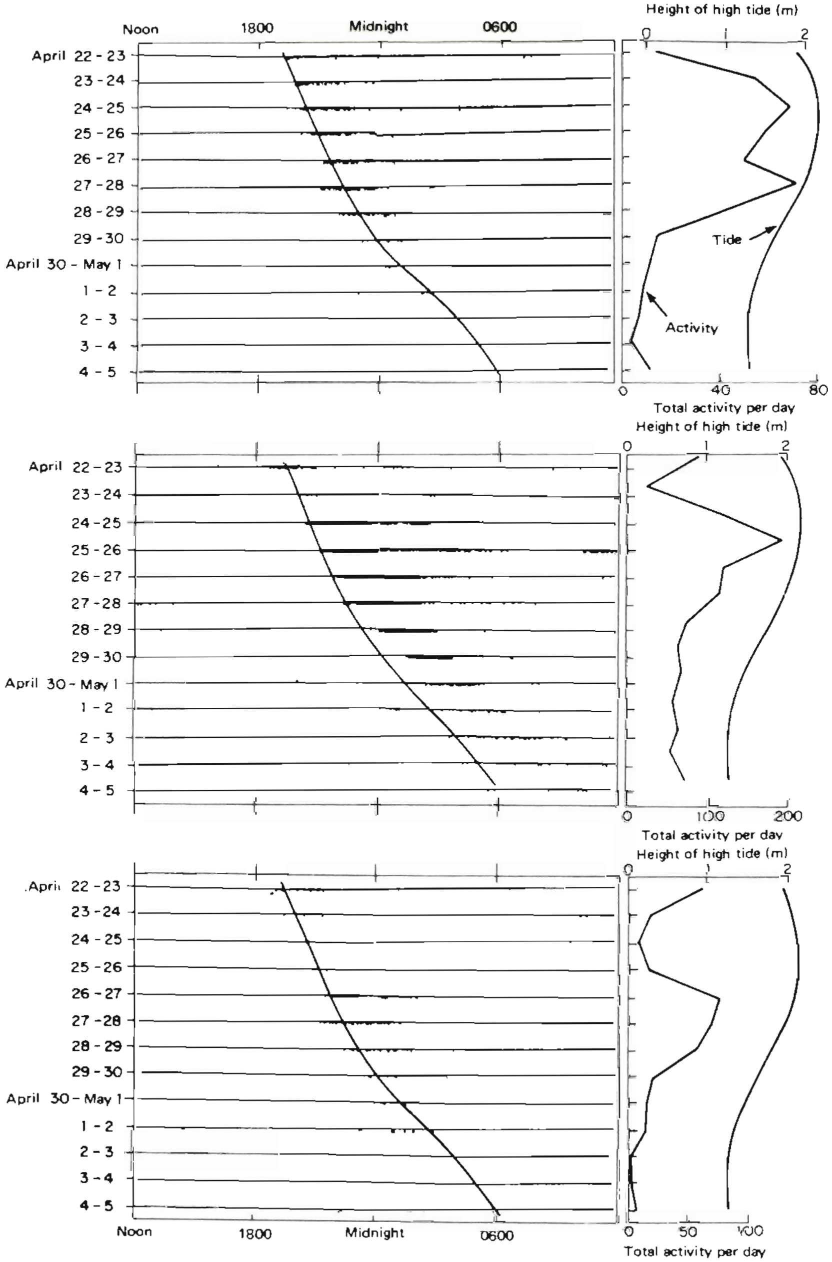

Fig. 9-11: *Excirolana chiltoni*. Three original activity records obtained simultaneously from individual isopods, April 22 to May 5, 1971. Diagonal lines drawn through times of high tide. Summed daily activity, together with height of evening high tide plotted to the right of each record. Maximum height of high tide occurred on the night of April 24; all three individuals exhibited activity peaks on days near tidal maxima. Activity peaks reflect an endogenous lunar rhythm which modulates the amplitude (i.e. intensity) of expression of the tidal rhythm. (Original; see ENRIGHT, 1972 for further experimental details.)

Although most of the literature on lunar rhythms deals with reproductive activities, like those of the grunion, of the palolo worm and of *Clunio marinus*, recent evidence has demonstrated lunar periodicity in several other functions of an intertidal invertebrate. As shown in Fig. 9-11, the level of locomotor activity of isolated individuals of the sand-beach isopod *Excirolana chiltoni* is maximal at the times of month of highest spring tides, when the isopods are kept in the laboratory (see also ENRIGHT, 1972); and, as shown in Fig. 9-12, these maxima recur at intervals of about 15 and/or 30 days.

Field data have also shown that moulting of *Excirolana chiltoni*—as well as feeding, distribution on the shore, and reproduction—vary with a fortnightly periodicity: moulting and birth of the young occur predominantly during the

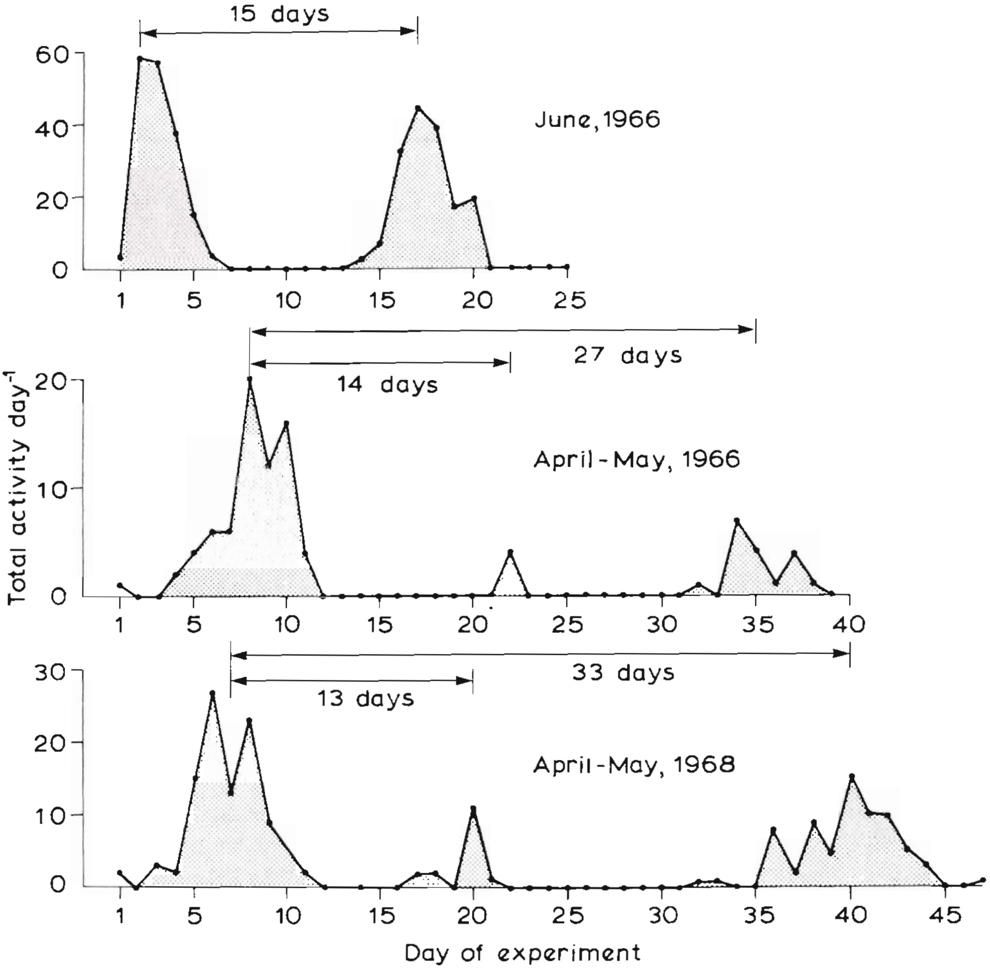

Fig. 9-12: *Excirolana chiltoni*. Lunar and semilunar rhythms of a sand-beach isopod. Plots of total activity per day of individual isopods, showing repetition of activity peaks at intervals of about 15 days and of about 30 days. (Original; see ENRIGHT, 1972 for further experimental details.)

week before highest high tides; these are times of minimal feeding activity, as well as lowest zonation of the isopods on the intertidal beach (KLAPOW, 1971).

Cycles of this sort would be particularly troublesome to the ecologist who attempts to interpret population biology on the basis of limited field data; samples of a field population taken to estimate parameters involved in reproduction, feeding rate and growth could be seriously biased, depending upon the time of month at which data were collected.

(f) Annual Cycles

Both in the terrestrial and the marine environment, annual variations in distribution, reproduction, feeding habits and basic physiology are conspicuous. The involvement of internal timing processes in the achievement of this environmental synchrony is clearly demonstrated in the array of phenomena designated as photoperiodic responses: dependence of growth and reproductive processes upon seasonal differences in daylength. It would be surprising indeed if marine organisms do not also show adaptation to season based upon photoperiodic timing processes. I am unaware of any convincing demonstration of such a dependence on daylength in a marine form, but it is a possibility which the ecologist, in attempting to interpret his field data, must keep in mind. Even if photoperiodism is of minor significance in oceans and coastal waters—and it may not be!—it seems very probable that marine organisms often synchronize their activities with season in a way that is relatively independent of concurrent conditions; for example, environmental temperature or food availability in February might be largely responsible for the timing of reproductive activity which begins in May. Once again, then, the ecologist must be on guard against the common prejudice that a given biological event now is associated primarily with conditions prevailing now.

Recently, evidence has been obtained for both rodents and birds that animals maintained under constant conditions can show an endogenous annual rhythm: that annual cycles in behaviour and physiology can persist in the absence of photoperiodic timing information. The suspicion therefore arises that endogenous annual rhythms may exist in marine organisms; however, the possibility of such a long-persistent oscillation under constant conditions is of less interest and concern to the ecologist than the possibility that on a shorter-term basis of several months, endogenous timing mechanisms may affect behaviour and physiology.

(5) The Physiology of Endogenous Timing

Since the present chapter is intended to emphasize ecological aspects of endogenous timing processes, no extensive treatment of the underlying physiological mechanism will be undertaken; the reader is referred to more general reviews. The physiologist must admit, however, that too little is known yet about details of the processes responsible for biological clocks to justify more than a speculative consideration of physiological mechanisms.

For most of the biological clocks which have been studied, light (Volume I, Chapter 2) is by far the most effective synchronizing stimulus; for plants and many poikilotherms, cycles of temperature (Volume I, Chapter 3) are also often able to synchronize endogenous rhythms. Because of the usual involvement of light in synchronization, there has been a widespread tendency to consider biological clocks as a component discipline in the general field of photobiology, with the implication that photochemical processes are intimately involved in the timing mechanism. This is, however, certainly an oversimplification. A wide variety of endogenous circadian rhythms will persist indefinitely when the animal is held in total darkness, demonstrating that light input is not essential to the proper functioning of the clock. Circadian rhythms of birds have been synchronized by cycles of noise—both by conspecific song (GWINNER, 1966; MENAKER and ESKIN, 1966) and by a simple mechanical buzzer (LOHMANN and ENRIGHT, 1967)—in an otherwise constant environment, demonstrating that light stimuli and temperature are not the only significant inputs to the synchronizing system. For the tidal rhythms of certain arthropods, cycles of mechanical stimuli associated with water turbulence can synchronize the endogenous rhythm when light cycles cannot (ENRIGHT, 1965; KLAPOW, 1972), demonstrating that the synchronizing system of biological clocks is not, of necessity, sensitive primarily to light. It appears that most organisms with biological rhythms rely upon light as a synchronizing stimulus because it is the most dependable environmental clue for timing events in the natural environment, and not because light is, in some fundamental way, directly involved in the endogenous rhythmic mechanism. Light is a stimulus which can, but need not, affect that peripheral aspect of biological clocks which leads to synchronization.

Another line of negative argument that can be made about the physiology of biological clocks is that the mechanisms are not comparable with those involved in learning. Many higher vertebrates can be trained to respond, in an experimental situation, at approximately constant intervals of time, ranging from a few seconds to a few minutes; and one of the earliest experiments with biological clocks involved 'training' bees to return to a particular feeding dish at the same time each day. There are certain formal similarities in the experimental procedures involved, which led to the use of the term 'Zeitgedächtnis' (time-memory) in the literature on bees, and led others to suggest that a process resembling learning or imprinting may be involved in daily rhythms (THORPE, 1963). Several different lines of evidence, however, indicate that this conclusion is mistaken. HOFFMANN (1957), for example, raised lizards in both 18-hr and 36-hr light cycles, and found that in subsequent exposure to constant conditions, both groups of animals had activity rhythms with free-running periods near 24 hrs: the animals had not 'learned' the period of the imposed cycle. As another example, PITTENDRIGH and BRUCE (1957) have demonstrated that fruit flies maintained from the egg in complete darkness show no rhythm in their eclosion; but that a single light treatment of, say, 4 hrs is sufficient to induce a clear circadian rhythm in the eclosion. Since the 4-hr treatment provides no information about the 24-hr length of the normal day, one must conclude that the period of the rhythm is inherited, not learned. Recent experiments have even led to the discovery of a single gene in *Drosophila melanogaster* which can change the free-running period of their rhythm, from near 24 hrs to near 19 hrs (KONOPKE and BENZER, 1971); comparable genetic control over period lengths has also recently been demonstrated in the alga *Chlamydomonas reinhardi* (BRUCE, 1972).

If, then, biological clocks should not be subsumed under the heading of photobiology (except, of course, in the sense that light affects, to a greater or lesser extent, nearly the whole spectrum of behaviour), nor should they be considered a special case of learning or 'imprinting', what can one say in a positive sense about the physiological mechanism? The answer is 'precious little'. Many workers suspect that protein synthesis may be intimately involved in circadian rhythms. One line of evidence supporting that interpretation is that cycloheximide, an inhibitor of protein synthesis, dramatically lengthens the period of the phototactic rhythm of *Euglena* (FELDMAN, 1967); but this exciting development has been deprived of broad significance by the subsequent observation that the effect can be seen only when the cell culture is growing logarithmically (BRINKMANN, personal communication); a stable cell culture of *Euglena* sp., which shows clear circadian rhythmicity, is unaffected by cycloheximide. Other speculation has involved the possible role of DNA and/or RNA synthesis in the timing processes underlying biological clocks, but the net weight of available evidence does not support this proposition as a generalization.

Most kinds of chemical and pharmacological treatment of the organism seem to be without any clear effect on the internal rhythm. In view of this usual immunity, one of the most interesting recent developments in the attempts to understand the biochemistry of biological clocks has been the discovery that heavy water (D_2O) lengthens the period of circadian (and circatidal) rhythms in a whole array of organisms, ranging from unicellular algae through arthropods to birds and mice (BRUCE and PITTENDRIGH, 1960; SUTER and RAWSON, 1968; ENRIGHT, 1971a and literature cited there). Heavy water is known to have many different effects in biological systems—from influences on ionic activity and hydrogen bonding to rates of enzyme synthesis—so an influence on the period of a biological rhythm provides, in itself, very little specific information about mechanisms. More surprising, however, is the observation that the dosage dependence of the effect (period lengthening per fraction D_2O) is quite comparable over the entire phyletic assemblage of organisms tested: a period lengthening of about 2% for each 10% D_2O in the tissue fluids. This uniformity of response suggests that heavy water may interfere with the same kind of rate-determining processes in plants, arthropods and vertebrates.

Other experiments have shown that heavy water slows a variety of biological rhythms in the high-frequency range, from the 500 sec^{-1} discharges of the electric fish, *Stenarchus albifrons*, to the respiratory rate of goldfish. In contrast with the rather uniform effect on circadian rhythms, however, there is great variability in the dosage dependence of the effect of D_2O on high-frequency rhythms. Hence, the uniformity of the effect of circadian rhythms is all the more surprising (ENRIGHT, 1971a).

Another recent experimental finding that may be of broad significance is the fact that ethyl alcohol slows the biological clock of the intertidal isopod, *Excirolana chiltoni*, in a simple dosage-dependent manner (ENRIGHT, 1971b), and has also been reported to have a similar effect on the bean plant *Phaseolus multiflorus* (KELLER, 1960). It is generally accepted that the majority of effects attributable to alcohols in biological systems are associated with solution of the alcohol molecule in cellular membranes, with a consequent effect upon the fluxes across membranes and the chemical processes within them. Hence the observed effects of alcohol on *E. chiltoni* and *P. multiflorus*—if they prove to be general—would strongly implicate membrane processes as rate-limiting factors in biological clocks. This interpretation is also consistent with the observed effects of heavy water, which, among its other influences, can be expected to affect cellular electrochemistry by altering ion mobility. The available data are, however, far too few to justify this interpretation as more than speculative. At present it seems fair to admit that although we have a great deal of data about the behavioural and physiological phenomena which vary due to endogenous timing processes, far more research will be required before we can legitimately discuss 'Mechanisms of Orientation in Time'.

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