

EXCELLENCE IN ECOLOGY

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O. Kinne, Editor

Tom Fenchel

Ecology - Potentials and Limitations



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EXCELLENCE IN ECOLOGY

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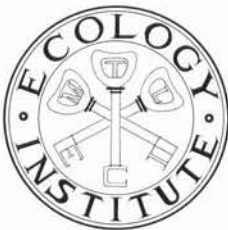
Tom Fenchel

ECOLOGY- POTENTIALS AND LIMITATIONS

Excellence in Ecology. An Introduction (Otto Kinne)

Tom Fenchel. A Laudatio (John Gray)

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Excellence in Ecology. An Introduction

O. Kinne

Ecology Institute, Nordbunte 23 and 30, D-2124 Oldendorf/Luhe, Federal Republic of Germany

It is with great pleasure and profound gratitude to all Staff members of the Ecology Institute (ECI) that I present here the first book of the annual series 'Excellence in Ecology'. The following pages briefly introduce the series; the first book 'Ecology – Potentials and Limitations'; its author Professor Tom Fenchel; and the aims and activities of ECI.

Excellence in Ecology

The series Excellence in Ecology publishes books authored by the best ecologists of our time: the recipients of the Ecology Institute Prize. Selected by a jury of the Ecology Institute (ECI) and taking into account ECI's aims (see below), the prize winners summarize and evaluate important aspects of the scientific knowledge available in their respective fields of expertise, and critically interpret them on the basis of their own experience and insight. ECI's aims are demanding. Hence each individual book can cover only a portion of them.

Never in history has humanity been more in need of ecological knowledge and its wise application for protecting nature and the very basis for man's own existence. Therefore, the books published in Excellence in Ecology – while authored by leaders in their fields and covering complex scientific facts and concepts – attempt to carry the word of acknowledged scholars beyond narrow professional borderlines and to bring first-hand ecological knowledge before a large, world-wide audience.

In an annually rotating pattern, a book will be published in the field of marine, terrestrial or limnetic (freshwater) ecology. Excellence in Ecology addresses researchers, teachers, students and interested laymen, as well as administrators and politicians professionally engaged in ecology-related decision making.

Published by the Ecology Institute on a nonprofit basis, Excellence in Ecology is distributed by ECI world-wide at cost price.

The Book

The first book in the series Excellence in Ecology has been written by the well-known Danish marine ecologist Professor Tom Fenchel. The book briefly traces the history of ecological research, and then focusses on the relation of ecology to other natural sciences; the significance of ecology for understanding the forces which control the dynamics of organismic assemblages in time and space; the central ideas, problems and results of contemporary ecology; our present knowledge on the properties of communities and ecosystems; and the significance of modern ecological research for assisting societies in facing and appropriately responding to major problems caused by man's detrimental effects on nature.

Offering and explaining his definition of ecology, Tom Fenchel delineates the scope of ecology relative to other biological disciplines and explores the potentials and limitations of ecology as a science and as a means of controlling man's unique impact on his environment.

The blending together of concepts and methodologies employed in different fields of research is considered a prime source of progress in science. While different disciplines mirror historical developments and heuristic classifications of natural phenomena, they must ultimately be combined for constructing the best possible picture of the world around us.

In order to attract money and attention, scientists have often promised rapid progress in return for substantial funding. Such opportunism has led to disappointment and doubt in the potential of science to help solve the many problems facing modern societies. A solid and less corruptible basis for sponsoring sciences is called for, along with more support for basic research – the very expression of man's learned curiosity and the very foundation of all his scientific efforts.

The Author

Professor Tom Fenchel is the recipient of the Ecology Institute Prize 1986 in marine ecology. The ECI Jury found Fenchel's contribution to ecological knowledge in a variety of research fields to be of the highest international class. In particular, the Jury cites his brilliant and uniquely important studies on the microbial loop which have opened up a fundamentally new research field. Professor Fenchel is, in addition, an excellent publicizer in his field of research with authorship of a number of standard works in marine ecology.

Tom Fenchel's achievements and the highlights in his professional career are outlined in a Laudatio (p. XV) by the Chairman of ECI's 1986 Marine Ecology Jury, Professor John Gray.

ECI Marine Ecology Jury 1986

Professor John Gray, Oslo, Norway (Chairman)
Professor Hans-Peter Bulnheim, Hamburg, FRG
Professor John D. Costlow, Jr., Beaufort, NC, USA
Dr. Nicholas S. Fisher, Upton, NY, USA
Professor Ernest Naylor, Bangor, UK
Dr. Trevor Platt, Dartmouth, N.S., Canada
Dr. T. S. S. Rao, Dona Paula, India

The Ecology Institute – its Aims, Prizes, Funding and Staff

Located some 55 km south of Hamburg (FRG), the Ecology Institute (ECI)* is an international nonprofit organization of research ecologists. Neither the director nor any member of the scientific staff receive remuneration.

Aims

ECI's aims are to honor and support excellence in ecological research, further the exchange between marine, terrestrial and limnetic ecologists, and to narrow the gap between ecological science and its application for the benefit of nature and society.

Recognizing

- the insufficient cooperation and interchange among marine, terrestrial and limnetic ecologists
- the overwhelming flood of analytical research papers and the general lack of support for efforts towards critical syntheses
- the need to provide keys for opening the doors to scientific ecological information so that it becomes accessible also to non-experts and society at large,

ECI strives to

- further the exchange of information between marine, terrestrial and limnetic ecology

* Ecology Institute, Nordbunte 23 and 30, D-2124 Oldendorf/Luhe, Federal Republic of Germany

- compensate for the lack of balance between analyzing and synthesizing research efforts and thus help to provide more feedback and critical overview for ecological science
- draw the attention of scientists, university teachers, students, administrators, politicians and the general public to important issues resulting from ecological research
- assist in finding a long-term compromise between the increasingly destructive potential of modern industrial societies and the need for defining and applying measures to protect nature, commensurate with achieving and sustaining the highest possible living standard for man.

Possible future activities of ECI, still being discussed among staff members, are:

(1) *Support of young ecologists.* Young colleagues from countries with very limited financial resources should be enabled to travel to, and to work in, centres of scientific excellence for extended periods of intensive study.

(2) *Support of high-risk research.* While there are a variety of financial resources available for conducting ecological research, there is little or no support for young, unusually talented researchers with bold new ideas who are able and willing to tackle venturesome projects entailing high probabilities of failure. Most conventional research sponsors tend to shy away from supporting such projects, and for many young scientists the risk of failure is not acceptable in terms of establishing a professional career and of meeting social and family responsibilities. Increasing both the financial basis and the length of time of an ECI stipend beyond average levels should compensate for the increased risk involved.

We believe that there is a need for leading scientists to be in control of independent sponsor bodies such as ECI. Providing we succeed in attracting appropriate financial resources, the diversity and excellence of talents represented in ECI's staff would seem to form a most suitable medium for selecting and supporting young ecologists from poor countries and/or highly innovative, creative and audacious research projects.

We welcome additional or alternative proposals for potential future ECI activities, in line with ECI's aims, from the international community of research ecologists.

Prizes

Every year, ECI selects and honors – in a rotating pattern – a marine, terrestrial or limnetic ecologist distinguished by outstanding scientific achievements. Two prizes are set out: The Ecology Institute Prize* and the

IRPE Prize (International Recognition of Professional Excellence). Prize winners are nominated by the international community of research ecologists and selected by an ECI Jury.

While there are several prizes offered these days in ecology, ECI prizes are unique for two reasons: (1) They were established and are financed by research ecologists; (2) the ECI Prize gives and takes: it both honors the recipient and also requires him/her to serve science and society by authoring a book to be made available world-wide on a nonprofit basis. The book must take into account ECI's aims. The IRPE Prize honors a young ecologist who has conducted and published uniquely independent, original and/or challenging research efforts representing an important scientific breakthrough. The winner of the IRPE Prize 1986 in marine ecology is Dr. Colleen Cavanaugh (The Marine Laboratories, Harvard University, 16 Divinity Avenue, Cambridge, Massachusetts 02138, USA). Colleen Cavanaugh was awarded the IRPE Prize for her highly original research on chemosynthesis in sulphide-rich habitats. Challenging established concepts, her hypothesis proved to be correct and significantly advanced our knowledge on chemosynthetic energy pathways.

I thank ECI's Marine Ecology Jury most sincerely for their judicious, impartial and successful work in selecting the Prize Winners 1986.

Procedure for selecting and awarding prizes

Nominations are welcome from all ecologists. They must be addressed to the Chairperson of the ECI Jury. ECI Prizes are announced world-wide in appropriate outlets (journals, society circulars, meetings, etc).

Eligible are all ecologists engaged in scientific research, including ECI Staff members, but excluding ECI's Director and the Chairperson of ECI's Jury. A Staff member nominated will be excluded automatically from the Jury's activities, and be replaced by another Staff member selected by the Jury's Chairperson.

The Jury is appointed by ECI's Director. It consists of – in an annually rotating pattern – 7 marine ecologists, 7 terrestrial ecologists, or 7 limnetic ecologists. Jury members elect among themselves a Chairperson, and then select the Prize Winner(s) using the nominations received, as well as their own professional judgement.

Selection. Nominations and opinions of Jury members are circulated by the Chairperson among all Jury members. The final decision, which must take into account ECI's aims (p. IX), is then made by majority vote of the Jury.

Prize awarding. The Chairperson of the Jury informs ECI's Director of the Jury's decision. The Director will then (a) organize procedural details for awarding the prize(s); (b) in his role as Editor, discuss with the recipient of the ECI prize concept, contents, title, etc. of the Prize Winner's book.

* The ECI Prize is endowed with a stipend of US \$ 5000

ECI's funding

ECI is funded by Inter-Research, the publisher of 'Marine Ecology Progress Series' (MEPS) and 'Diseases of Aquatic Organisms' (DAO). When I founded these two international journals I made arrangements for channeling part of the income into setting up an institute that would honor and support excellence in ecological research, and thus serve ecological science. It was possible to acquire small but modern and well-equipped facilities in Oldendorf/Luhe, Federal Republic of Germany, which now house both the editorial staff for the two journals and the technical staff of ECI.

We hope that individuals and/or agencies sympathetic to ECI's aims will support our non-profit-making activities financially and thus allow us to pursue with vigor the activities of ECI.

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Tom Fenchel: Recipient of the Ecology Institute Prize 1986 in Marine Ecology. A Laudatio

J. Gray

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Marine ecology (biology) is a relatively young science. Even up to the 1950's it was still fashionable to organise large expeditions to collect animals from the ocean depths. As an example the Danish 'Galathea' expedition returned from her voyage with many new and hitherto undescribed species. In the past decade the discovery of a unique fauna from deep-sea hot vents in many parts of the ocean is testament to the youth of marine ecology as a science. The hot vent fauna has excited science at large by the discovery that the fauna's primary energy source is chemosynthesis rather than photosynthesis. Thus much of marine biological research today remains descriptive with only a rudimentary theoretical base. Marine ecology therefore, affords the research worker with opportunities which few other disciplines have, that of making original observations, erecting hypotheses and by experimentation checking whether or not the hypothesis can be falsified.

The juxtaposition above of the Danish connection to deep-sea research and the discovery of chemosynthesis in hot-vent fauna relates discoveries in which Professor Tom Fenchel has been intimately involved. Danish marine biological research has a long tradition of excellence. At the beginning of this century C. Johannes Petersen laid the foundation for modern quantitative benthic ecology. Thorson's pioneering work on larval biology and Steeman-Nielsen's development of the classical method for measuring primary production continued the trend. Today the Aarhus University Department of Ecology and Genetics is a world-renowned centre of excellence in marine research. It was Tom Fenchel's vision and scientific excellence that has built up the Aarhus tradition in the mould of the earlier Danish pioneers.

Tom Fenchel, born in Copenhagen (Denmark) in 1940, obtained his D. Phil. degree from the University of Copenhagen in 1969. From 1970 he has been Full Professor in Ecology and Zoology at the University of Aarhus,

Denmark, and from March 1987 he has taken up the appointment of Full Professor of Marine Biology at the University of Copenhagen at the Helsingør Marine Biological Station.

Tom's doctoral thesis, on ciliate Protozoa, already showed the high international class that has become the hallmark of his research: it became a Citation Classic. Much of his early research concentrated on the role of the microfauna in marine ecosystems, particularly in sediments. In 1970, together with Rupert Riedl, he published a major paper (*Mar. Biol.* 7:255–268) on the sulphide system below oxidised layers in marine sandy sediments, suggested new evolutionary processes, and pointed to the potential importance of chemosynthesis in such systems. The recent discovery of the deep-sea hot-vent fauna has focussed much research effort on chemosynthesis and increasing attention is being given to chemosynthetic processes in shallow depths; a field of research that was suggested by Fenchel and Riedl some 17 years ago!

The Aarhus School has a deservedly high international reputation for their work on the microbiology of sediments. Tom Fenchel's research into the sulphide system culminated in a book 'Bacteria and Mineral Cycling' written together with Professor Henry Blackburn. Together with F. B. Christiansen he authored another book 'Theories of Populations in Biological Communities' which reflects another of his major interests, that of population biology. This interest can be traced back to a paper stemming from his doctoral thesis on the ecology of marine microbenthos, dealing with the reproductive potential of ciliates. Based largely on his own experimental research, it is a classical paper which is widely used in ecology in general wherever reproductive rates are compared.

The book with Freddy Bugge Christiansen also delves into evolutionary ecology, a field where Tom and his students have made important contributions particularly on competitive interactions. Tom's studies on character displacement in the snail genus *Hydrobia* are used as illustrations of the process in many new textbooks of ecology. It must be said, however, that there are recent papers which question the idea, but science only progresses by innovative research even if the idea later has to be modified.

Tom Fenchel's recent research on heterotrophic microflagellates in the water column is again a new and innovative contribution to our understanding of ecological processes in the sea. Since the first publications on this topic in 1983, Tom's research has already reached classical status. What characterises his research on microflagellates (and indeed all his research) is his unique ability to go back to first principles, examining the basic physics of the process, followed by careful studies of the fundamental aspects, construction of theoretical models of the process, and then verification of

the model by field studies. Few scientists possess his wide-ranging expertise, or his ability to be conversant in so many disparate fields – from mathematics, through physics, to microbiology and evolutionary biology. I for one will never forget the lecture I was privileged to hear at the University of Uppsala's field station at Klubban, Sweden, where Tom gave an illustrated talk on how bacteria and ciliates move in seawater. The illustrations included clockwork fishes in different fluid densities which graphically illustrated the physical processes he was demonstrating and gave us an overview from physics, through mathematics to biology.

His most recent publications are not in marine biology but in freshwater biology. Again his 1986 studies with B. J. Findlay (*J. Protozool.* 33: 139–145, 34:534–542) illustrate perfectly the breadth of his scientific competence.

Not surprisingly, Tom Fenchel is much sought after as a lecturer and has lectured extensively in Europe and North America. In addition, his critical faculties are widely used in editorial aspects of science where he sits on the editorial boards of no fewer than 11 journals.

The year 1986 will, I suspect, be long remembered by Tom. In addition to the Ecology Institute Prize he also received the Huntsmann Medal for Excellence in Oceanography 1986. He also had a new book published, 'The Ecology of Protozoa'.

Whilst 1987 cannot promise to be as eventful, Tom Fenchel has moved to be Full Professor of Marine Biology at the University of Copenhagen, his *alma mater*, where his talents will be warmly appreciated. We wish him well in his new position and expect that the University of Copenhagen soon will once again be a worldwide center of marine biological research.

Preface

A preface is supposed to explain the author's motives for writing a book. In my case this is simple: I won a prize with strings attached. However, this gave me opportunity and stimulus to contribute my views on the scope and delimitations of ecology within the context of other biological sciences. As such the book is written for other ecologists to engage them in a debate on the definition of ecology. Another purpose of the book is to present central problems and results of ecology to biologists at large and to other scientists. Many ecologists may disagree with my restricted delimitation of the realm of ecology and with my rather critical attitude towards ecology as a panacea for solving all problems pertaining to the relations between man and nature. However, I believe that all my colleagues will agree that a debate on the delimitation of ecology as a science is desirable; by writing this book I therefore also hope to serve some of the purposes of the Ecology Institute.

I take this opportunity to express my gratitude and happiness as a recipient of the Ecology Institute Prize. Next to making a scientific discovery, the greatest award for a scientist is the recognition by his or her peers.

I am grateful to Dr. Jørgen Hoffmann-Jørgensen (Department of Mathematics, University of Aarhus, Denmark) for references to and discussion on models of epidemics, and to Dr. Volker Loeschke (Department of Ecology and Genetics, University of Aarhus) for discussions on various aspects of evolutionary ecology. Hilary Adler Fenchel made many linguistic improvements. Dr. Freddy B. Christiansen (Department of Ecology and Genetics, University of Aarhus) also read the entire manuscript and suggested many improvements. The book, however, owes even more to Freddy's and my discussions and collaboration on various aspects of theoretical ecology during the last 16 years. This has in many ways influenced, shaped or modified my thinking about many ecological problems and how to approach them as reflected by this book.

Aarhus, February 1987

Tom Fenchel

I Introduction

Nearly 30 years ago my biology textbook used exactly one page to cover 'Ecology'. It briefly explained that ecology means the study of the relationships between organisms and their environments and illustrated this with a map of the world showing isotherms for the coldest month and the distribution of palm trees. It was not this revelation which inspired me to study biology at the University of Copenhagen after finishing school. Although the term ecology was still not generally known, things were not very much different with respect to the biology curriculum at the university. Ecology was regularly referred to in conjunction with the natural history parts of zoology and botany and in subjects such as marine biology, but no formal teaching of ecology was offered. (To be sure, a course referred to as 'botanical ecology' was given; its substance was to make students learn, by heart, a certain number of plant species characteristic of particular habitats.) Actually, a framework of theoretical biology had by then already been developed (to a large extent by non-biologists such as mathematicians) but this was not readily accessible to natural history oriented biologists who considered it irrelevant anyway in the face of a complex nature which was best approached descriptively. And the development of empirical ecology which had already established itself as an academic discipline in the USA and in Britain seemed for a long time to make little impact on the biology curricula at universities in continental European countries. Finally, certain topics which we today consider as ecology were treated only in applied fields such as soil biology, fisheries science, etc.

This situation changed rapidly during the sixties and seventies. Among the general public the term 'ecology' is in common usage today, although its present meaning has changed somewhat from the original one (and from that of this book) to cover environmental science in general and further to designate an attitude or ideology rather than a branch of natural science. Thus an 'ecologist' has in some contexts become to mean a follower of a variety of movements such as 'green parties' and the like with an (to me at least) unattractive puritan outlook on life and sometimes with scary politi-

cal undertones. This development is undoubtedly due to an increasing (and to a large extent justified) concern about the quality of natural and man made environments, first signalled perhaps, by the publication of Rachel Carson's 'Silent Spring' in 1962 [1].

During the same period ecology grew and flourished as an academic discipline and everywhere universities established departments, chairs and courses with ecology (or at least with the prefix 'eco-') in their names. Sometimes, it would seem, this went too far since biology is more than just ecology and in particular since the 'eco-' prefix was also adopted to obtain funds or as an allegation of not being 'old fashioned'. Thus comparative physiology has become 'ecophysiology', courses on ethology and evolutionary biology are bound to be entitled 'behavioural ecology' and 'evolutionary ecology' and a monograph on the natural history of some systematic group of organisms seems to sell better if the title reads: 'The Ecology of ...'. (Actually this trend has most recently tended to reverse: in order not to be associated with organic gardening, subsistence farming or the 'Greenpeace' movement, some university ecologists tend to avoid the term ecology and to offer courses in, e.g. 'population biology' instead.) The reason that ecology showed such an expansion (and in part became a bandwagon) among biological sciences reflects the above mentioned awareness of environmental quality in a broad sense, but it also reflects genuine growth in insight and knowledge regarding the core of ecological science. Ecology has also added perspective to adaptive physiology, ethology, palaeobiology, biogeochemistry and evolutionary biology.

This also explains why ecology today seems to be a 'diffuse' science and although the subject was given a name more than a century ago, it can perhaps still be referred to as an 'immature science'. If asked, a biologist is likely to have difficulties in giving an exact definition of ecology. If a practicing ecologist is asked, the answer is likely to be a rather narrow reflection of his or her particular interests. There are several journals dedicated to theoretical population biology and they are rarely read or understood by field or experimental ecologists and conversely the results of the latter are often blissfully ignored by theoreticians. Also, ecologists are split between aquatic and terrestrial ecologists and the old dichotomy of the animal and plant kingdoms is also reflected in contemporary ecology. Finally, many view ecology from the standpoint of related disciplines such as physiology or biogeochemistry.

In some respects, of course, this situation is not unique to ecology. All branches of natural science suffer from excessive specialisation (or narrowness) and fragmentation. This may be explained by the vast amount of papers (and the large, if somewhat more modest amount of new results and

insight) published every year and also by other aspects of the sociology of science. However, ecology differs from most other natural sciences in seemingly lacking a central core of ideas, concepts, methods and goals on which everyone can agree. Other disciplines have, like ecology, gathered a huge amount of observations and results, but while it is still possible to write a 100 to 200 page textbook on genetics, for example, which presents the basic concepts and ideas of that discipline, ecologists have been unsuccessful in this respect. Undergraduate textbooks in ecology therefore seem to fall into two categories: they are either bulky volumes containing an endless number of facts or they are shorter (possibly well-written and competent) treatments of some restricted part of ecology (e.g. 'population ecology', 'marine ecology', etc.).

This book attempts to delimit and characterise ecology as a natural science and to present what I believe is the core of that discipline. It is primarily written for scientists at large in order to explain what ecology is all about, but also for fellow ecologists in the hope that it will contribute to a synthesis of the field. More ambitiously, I hope that the book will find some non-scientist readers who are interested in ecology, although this is not a popular book and some chapters require elementary knowledge of exact sciences. I have written the book as a practising scientist which makes me acutely aware of my shortcomings when attempting to synthesise such a vast field as ecology. I have tried to avoid an excessive simplification of problems and results and perpetuation of already simplified textbook examples. Nevertheless it has been necessary to treat topics on which I have only second hand experience and so I apologise if guilty of misinterpreting or misunderstanding the work of colleagues cited in the following narrative. I believe in the value of the history of science and, although I am not very knowledgeable in that respect, I will refer to it here and there. The book is not, however, an attempt to contribute to the 'philosophy of science'. This metascience has recently found ecology worthy of study [2]. The results of this field of inquiry are sometimes interesting, but I must admit that as a practicing scientist I often cannot recognise my own or my colleagues methods and motives as they are described by philosophers of science.

The book is structured into four main sections. The first one (Section II) offers a brief historical background of contemporary ecology and my view on how ecology should be defined. I analyse the concept of explanation of ecological phenomena and in this context, I discuss different types of theoretical models used in ecology. I further attempt to delimit ecology relative to a number of other biological disciplines. It is my general attitude that the application of ideas and methods of one discipline to other ones, and the study of connections between different fields of inquiry, is of immense im-

portance. Indeed, it is one of the main sources of scientific progress and new insight. But it is at the same time important to keep different disciplines conceptually apart. Major scientific disciplines arose not only in order to get someone a chair or due to departmental vendettas, as is sometimes inferred. They also represent an heuristic classification of natural phenomena and the definition and delimitation of a discipline represents in itself an insight into the real world. Also, I warn against using 'interdisciplinary studies' as a camouflage for scientists who accomplish to be, e.g. pedestrian ecologists and pedestrian physiologists at the same time. The section also offers some considerations regarding the general view on the biological world emerging from ecological texts versus that emerging from the Darwinian theory of evolution. In particular it is shown how traditional ecological thinking may sometimes yield misleading interpretations. The section concludes with some general thoughts about ecology as an immature science.

Section III treats in a somewhat more detailed manner what I consider to be the core of ecology: the general mechanisms which govern patterns in time and space of assemblages of organisms as explained by the properties of individual species. As such, this section represents what should be the framework of the above mentioned elementary 100–200 page ecology textbook by synthesising the central ideas, problems and results in contemporary ecology. Section IV may then be considered to complement the preceding one by describing a few selected examples in more detail which illustrate some general principles.

Section V is concerned with applied ecology. As demonstrated elsewhere in the book, applied problems (including fisheries science, epidemiology, soil fertility, conservation, game management, the spread of pollutants) have often served as an inspiration for the development of ecology and ecology – as other natural sciences – should be used to serve society in solving immediate problems when applicable. The relationship between pure and applied sciences is complex and in my view it is important that scientists discuss it to a larger extent. In western Europe, science, and in particular research at universities, has during the last decade been subject to increasing pressure and criticism from the society at large. As a consequence, the growth of pure scientific research has recently tended to stagnate or even decline. This largely reflects an increasing amount of disappointed expectations. Thus, science has not so far eradicated cancer or ensured a sufficient technological and economic growth and (although this in part represents a paradox) it is at the same time held responsible for problems associated with industrial societies (such as toxic effluents from chemical industries or the risks involved in the use of nuclear power) and

also of, as it would seem, largely imaginary hazards (such as 'genetic engineering'). Regarding disappointed expectations, it cannot be denied that the scientific establishment itself has a share of the responsibility by promising rapid progress in return for large fundings and then later failing 'to bring home the bacon'.

The net result of all of this seems to be that governments tend now to transfer funds from pure research to the solution of applied problems and to short-term projects with a promise of immediate return. In this climate, entirely exotic fields (e.g. Egyptology) risk losing funding. Ecology, which is often viewed mainly as an applied field by society and by science managers and bureaucrats, runs additional risks: the disruption of fertile research environments and the temptation to carry out trivial work in the quest for funding. Even more serious is the risk that an increasing amount of studies within the field will serve to 'prove' or 'disprove' desired or undesired 'results', respectively. The section will conclude that applied research is necessary and desirable and often intellectually rewarding, but also that ecology for various reasons may be especially vulnerable to intellectual corruption.

II Delimitation and Characteristics of Ecology

1 What is Ecology?

Few, if any, natural sciences show such a complex genealogical chart as does ecology which stems from many independent scientific traditions. It may be argued that ecological knowledge has always been a part of human existence in relation to the exploitation of nature, farming practices or plagues of rodents, locusts or infectious diseases which all represent applied ecological problems. On a more philosophical level, speculations on the maintenance of the 'balance of nature' can be traced back to antiquity [3]. Here we will attempt to trace the roots of contemporary ecology during only the last three centuries. The term 'ecology' was coined by Ernst Haeckel in 1869 [4]. However, while Haeckel in fact never contributed to ecology himself, ecological problems were studied well before the term came into existence.

It is possible to trace two main lines of development in addition to some minor ones and to some extent these have still not entirely merged into one coherent science. The oldest source of modern ecology stems from considerations on human demography in England in the seventeenth century. The first, somewhat crude demographic data for the city of London (see also Chapter 3) led a Captain John Graunt to conclude that the population of that city doubled every 64 years. Contemporaries of John Graunt recognised the difficulty implicit in exponential growth (using the Biblical tradition for the age of the world and assuming two initial human beings, Graunt estimated that a doubling every 64 years would have led to a total human population of 10^{26}). It was held by some authors that the conditions of life had generally declined through history and so generation time would tend to increase. This pessimistic view was rationalised by Malthus (1798) who noted that whereas populations tend to grow exponentially their resources do not and so populations reach a level where they are controlled by famine and misery. Whereas Malthus took no particular interest in non-human populations, his contemporary Benjamin Franklin wrote: 'animal

and plant populations expand until limited by lack of food and space', which is a clear statement of 'density dependent population regulation'. However, although the interest of Malthus was one of national economy he did, through the work of Darwin, obtain a considerable influence on the development of biology [5].

In the following century interest in mathematical modelling of the growth of populations limited by their own density arose. Among various attempts, the 'logistic equation' (see Chapter 12) proposed by the Belgian mathematician Verhulst, plays a central role in theoretical population biology today since its rediscovery by Pearl and Reed in 1920.

An innovative approach in the attempt to model multi-species interactions was made by Ross in the first decade of this century. Ross was a co-discoverer of the lifecycle of malarial parasites. In an attempt to understand the equilibria between the protozoan parasite, its mosquito vector and man, he constructed and analysed dynamic models based on coupled differential equations. His approach was undoubtedly a source of inspiration for later theoretical ecologists; it is, however, strange that the theoretical study and role of infectious diseases in nature has otherwise been practically ignored by ecologists and is rarely even mentioned in ecology textbooks. Theoretical epidemiology remained an isolated and largely medical activity. Only quite recently has the significance of epidemiology been recognised by ecologists [6].

The twenties and thirties became what has been called the 'golden age of theoretical ecology' [7] and certainly much of the framework of theoretical population biology was developed then. The Italian mathematician Volterra and a school of mathematicians inspired by his work were especially important. Volterra seems to have taken interest in ecological problems through fisheries statistics and so constructed theoretical models of multi-species interactions such as prey-predator interactions, food chains with several trophic levels and competing species as well as considering stability properties of multi-species communities. These studies in part offered a profound and thorough analysis of many ecological problems; some of this work has only recently been re-discovered by ecologists. Alfred Lotka, an American contemporary, formulated, independently of Volterra, some of the same models. His book 'Elements of Physical Biology' of 1925 [8], is more accessible than some of Volterra's work and contains a large amount of ideas pertaining to other ecological phenomena such as energy flow and element cycling, but again it had a substantial impact on ecology only several decades after its publication.

Up to this period a quite independent development of ecology took place on the basis of the naturalist tradition. The foremost ecologist in this

tradition in the last century was beyond doubt Charles Darwin. Most of his arguments in favour of evolution by natural selection were based on ecological fact and observation and above all, of course, on the concepts of inter- and intraspecific competition. Moreover, his studies on the formation of coral reefs and on the biology of earthworms remain classics of ecology.

This tradition in ecology was based on an accumulating number of naturalist observations. In particular it became a goal for the still infant field of ecology, which in the early twentieth century began to evolve into an academic discipline, to explain the distribution and abundance of organisms in nature. Several schools of ecology arose from this. One stressed the physical environment of the organisms as an explanatory factor, and the goal of the ecologist would be to quantify physical and chemical factors in the field and to correlate these findings with the distribution of organisms. These investigations were expanded to laboratory experiments on the tolerance and adaptations to different environmental factors and this approach also contributed to what today is called physiological ecology.

A quite different approach was that of 'community ecology'. The idea of treating natural assemblages of organisms as a 'natural unit' with its own properties, the explanation of which was to be found among interactions between the component species populations, may first have been expressed by Möbius who coined the word 'biocenosis' to describe an oyster bed in the North Sea. Of greater impact were perhaps the studies on plant communities originated by the botanist Warming, and eventually a whole school of 'plant sociology' developed. This again was paralleled by the study of marine benthic invertebrate communities initiated by the fishery biologist C. G. J. Petersen, who divided the sea bottom of Danish waters into a restricted number of communities characterised by 'key species' and which correlated with the type of sediment and water depth. These schools accomplished a systematic description of faunal or floral assemblages; they also led to a longstanding controversy regarding the 'nature' of communities: that is, to what extent they are 'true' biological units held together by strong biological interactions as opposed to the view that they are statistical assemblages of organisms mainly living together because of common preferences for certain physical properties of the environment. The heated debate lasted for most of the first half of this century and although it seems to be a pseudoproblem when viewed from other angles, the controversy has re-opened during the last decade and seems to some extent to be old wine in new bottles [9].

A considerable impact on ecology was made by the work of Elton and his school in Britain. In particular his early book: 'Animal Ecology' (1927) was important [10]. It took a much more empirical and functional view on

the structure of organismic assemblages and on the explanation of abundance and distribution of species in nature. It also included bioenergetic considerations about the structure of food chains and altogether laid a foundation for a strong empirical tradition in British ecology.

A similar strong tradition for empirical ecology developed in America. The most influential ecologist here is undoubtedly G. E. Hutchinson who has played a substantial role with regards to two major trends in contemporary ecology. One of these is the study of 'ecosystems': that is to include the flow of materials and bioenergetics in the description of biotic communities and the formal description of communities in terms of trophic levels and also the inclusion of biogeochemistry into ecological considerations [11]. The other great contribution of Hutchinson (and his many students) has been to integrate and, as it were, to translate the results of theoretical population biology into empirical and field ecology. This tradition, although in many ways extended both as regards empirical and theoretical results, seems to be a dominating trend in ecology today [12]. The attempts to bridge theoretical and empirical population ecology did, however, have important forerunners. In particular F. G. Gause attempted in the thirties to illustrate the theoretical models of Lotka and Volterra by describing two-species interactions (competition for common resources, prey-predator relationships) using protozoa and other microorganisms. Similar experimental work, in particular on insects, was carried out in Australia, USA and Britain and played a considerable role in convincing field oriented ecologists of the relevance of theoretical ecology (although they also managed to antagonise others even more against a theoretical approach) [13].

There is no point in bringing this brief history of ecology up to date here since this would lead to an overlap with the contents of the rest of the book. It is, however, reasonable to mention a couple of other 'evolutionary lineages' of ecology which have also lived much of their life in splendid isolation. One of these stems from agricultural science whose results on productivity and nutrient demands of plants, nutrient cycling in soils and soil microbiology during the first part of this century could have had a considerably larger impact on the development of ecology than was actually the case. The study of insect pests and the control of their populations, however, did have a more immediate impact on population ecology. Also stemming in part from applied problems is the development of 'microbial ecology'. The pioneering work of Winogradsky at the beginning of this century not only disclosed a number of novel physiological types of bacteria, but also demonstrated the ecosystem concept experimentally as well as elucidat-

ing a number of principles pertaining to community structure [14]. Microbial ecology is even today an enterprise which is only slowly having an impact on 'main stream' ecology. Still, it provides the best examples of species interactions and the best experimental systems for studying a number of properties of communities and, as far as the impact on the chemistry of the biosphere goes, microbes are among the most important creatures on earth.

The above account shows that contemporary ecology has a complex and divided past. One reason is that ecology even in a restricted sense of the term has a wide and bewilderingly complex range of study objects and the emphasis on which phenomena were to be explained has varied. The basis of ecology must be natural history since, after all, the *raison d'être* of ecology is to explain what we observe in nature and without naturalists there would be no science of ecology. On the other hand, naturalists grew out of a tradition of observing and describing – and after all that was once the only possible approach to biology. They therefore felt (and to some extent still feel) that ecology should be exactly what they had been doing all along: largely to observe, describe and try to make some order out of an astonishing diversity of life. They were often repelled by an approach in which the whole thing was taken apart and substituted by sets of differential equations in an attempt to find general principles which were not only empirical generalisations. That the traditional training of naturalists has not included mathematics did not improve matters. Conversely, theoreticians without any intuition or knowledge of natural history have managed to produce models which possibly have some mathematical interest, but which are hardly of any ecological relevance. (This seems, if anything, to be an increasing problem as the premium on the rapid publication of short papers is increasing and the belief became widespread that a not too advanced course in mathematics is a sufficient condition for doing ecology.)

This dichotomy seems especially well developed for ecology when compared to other natural sciences. It can be contrasted with e.g. genetics. Once the Mendelian laws were rediscovered in 1900 and the concept of particulate heredity and the mathematically simple laws of Mendelian heredity were accepted, no serious investigation of heredity could be undertaken in disregard of these laws. Theoretical, experimental and practical genetics has since functioned together as a unified field of inquiry although genetics, just as ecology, includes a vast and diverse amount of observations of single phenomena the totality of which no single human being can keep in his head. While I do not believe that ecology will ever become a fully unified science with relative few basic principles and concepts, this book is an attempt toward such development.

This leads to the question as stated by the chapter heading: What is Ecology? Attempts to define ecology are, of course, far from new. Ernst Haeckel defined it as the study of all relationships between organisms and their surroundings. This definition is so broad as to contain nearly anything biologists are concerned with. Elton considered ecology as 'scientific natural history'. This, of course, expresses what ecology is supposed to explain. I would suppose that 'unscientific natural history' is simply bad natural history and anyway I find it more fruitful to search for a definition which explicitly distinguishes ecology from natural history.

Odum (1963) defined ecology as 'the study of the structure and function of nature' (which is indeed a very broad definition) and later (1971) that ecology is the study of biological systems at organisational levels above the species (viz. species populations, communities, ecosystems), a broad definition which does not, for example, exclude population genetics. Andrewartha (1961) suggested that ecology is the study of the distribution and abundance of organisms, a definition which is more concise, but excludes topics which one would normally include as ecology and it also has a certain ring of a mainly descriptive science to it. Krebs (1978) defined ecology as 'the scientific study of the interactions that determine the distribution and abundance of organisms' which is an improvement over Andrewartha's definition in that it stresses the functional aspect [15].

My own suggestion is that 'natural history' should be resurrected and respected as a natural science in its own right with the purpose of describing individual species of organisms in nature. The definition of ecology of this book then becomes considerably more restricted as *the study of the principles which govern temporal and spatial patterns for assemblages of organisms*. The emphasis is on principles, but the definition does not restrict ecology to theoretical ecology. It includes field observation and experiment in the quest for such general principles. Indeed, the most fruitful method will always be a combination of the three approaches. The definition does not defy its origin from natural history; it will always depend on the results of natural history and the ability of ecology to explain the findings of naturalists will remain a test of its success. The following chapters will attempt to further clarify this definition of ecology.

2 Explanations in Ecology

Biological systems are much more complex than are ordinary physical and chemical systems. Although everyone today agrees that organisms are built only from ordinary matter and that they obey the rules of physical and

chemical laws, their complexity modifies methods and approaches in their scientific study relative to those used in e.g. classical physics. The degree by which biological sciences differ in this respect from classical physical sciences varies again among biological disciplines. Molecular biology resembles 'hard sciences' most in that it has a single goal on which everyone agrees – to understand the heredity and function of cells in terms of chemistry and physics – and a limited number of established methods so that there is no disagreement with respect to what constitutes a valid explanation of an observed phenomenon. This also applies to physiologists who study organs or tissues in isolation from their normal context. Observations are to be explained in terms of the properties of the constituent tissue or cells. Any reference to the organism which harbours the organ may yield information about its significance for the organism in question, but this does not constitute an 'explanation' in the eyes of a physiologist.

Turning to ecology, there are several problems with respect to scientific methodology. Ecology has been termed a 'pluralistic' science [16]. By this is meant that it depends on a wide variety of methods and approaches rather than on a limited set of experimental techniques and concepts. This is in contrast, e.g. to organic chemistry or to the above-mentioned examples from other fields of biology. In part this is a question of scale. Organisms span a factor of more than 10^7 with respect to length and generation time (see Chapter 11) and the scales of ecological events vary accordingly. Thus ecological phenomena may be followed in a flask over a few days or may require a large forest and exceed a human lifespan. Small organisms can be manipulated conveniently in laboratory experiments, but rarely in the field. Conversely, convincing ecological experiments with large animals may be impossible to perform in the laboratory and are often difficult, illegal or unethical in the field and would often require a very long period in order to yield results. For this reason alone, ecologists cannot limit themselves to applying classical scientific experiments, but are often forced to infer mechanisms and events from observations on distribution patterns and correlates with respect to the occurrence of different organisms or between organisms and physical properties of the environment.

Another fundamental difficulty in ecology is that whatever we observe in nature is not only a function of laws and principles (which we may discover). It also is a function of singular historical events and chance. Thus, the presence or absence of a species may be explained by the presence or absence of, e.g. competitors or by some aspect of the physical environment, but it may also be a function of stochastic events in the past which determined whether the species happened to colonise the particular area or whether it became extinct due to demographic stochasticity (that is, the

element of chance in birth and death processes) or to some past environmental conditions on which we have no information.

Another dimension is added to this problem when we include evolutionary events. Organismic evolution takes place through natural selection on the basis of hereditary variation. There is a certain degree of predictability, or rather regularity, in evolution. Thus the independently evolved mammal faunas of Australia and of the Old World show many similar morphological types and ecological roles (each fauna including e.g. the ecological equivalents of a mole, a flying squirrel, large carnivores, etc.). But there are also differences; for example, no direct equivalent to hoofed mammals occur in Australia (although kangaroos have to some extent taken over this 'ecological niche'). Evolutionary history entails an element of necessity, but there are also elements of historically singular events and of stochastic events: whether a trait will evolve depends on the presence of genetical variance, on constraints in form and function in the ancestor and on past environmental conditions. Only in very few cases is it possible to make reproducible experiments on evolutionary events. Past evolutionary events can be analysed and understood, but the stochastic and opportunistic properties of evolution do not allow for a theory which is predictive in specific cases.

By all this I do not mean to suggest that ecologists should not attempt to subdivide complex systems into components which can be studied experimentally (or through analytically tractable theoretical models) rather like a physiologist would proceed. On the contrary, such an approach should always be used whenever applicable, but it will never be sufficient in ecology (or in evolutionary biology) which in part describes and attempts to explain systems whose properties are in part determined by historical and stochastic events.

These considerations also explain why ecology is often characterised by disputes about correct methodology; although such disputes may be useful, they will never be entirely resolved. They also explain why an analysis of ecological systems requires intuition and background in natural history. These characteristics of ecology render the discipline an 'immature' or 'soft' science in the eyes of philosophers of science who consider physics and chemistry as the paradigm of natural science. There are, however, some parallels among the 'hard sciences'. Thus astronomy (which cannot possibly be considered an 'immature' science) is totally barred from experimentation and must infer everything from observational data.

What constitutes a valid explanation of an ecological phenomenon? Ultimately, there are two fundamental and complementary types of explanations in biology. One is to explain the form and function of organisms

(and for that matter also of populations and ecosystems) in terms of their constituent molecules and in terms of physical and chemical laws. Immense progress has been made in this respect at the cellular level, but there is a long way (if it will ever happen) before this goal can be completely reached with respect to multicellular animals or to ecological systems. The other, fundamental type of explanation is an evolutionary one which always has a historical element to it. It is based on the principle of natural selection on hereditary variation which is a natural law of fundamental importance to living things.

The two complementary types of explanations are therefore both necessary in order to fully understand biological phenomena at all levels of organisation, although many biologists seem to be content with one type of explanation according to the tradition of their discipline. As an example, consider osmoregulation in fish. Marine bony fish have blood which is hypotonic relative to seawater and in order not to become dehydrated these fish possess salt-excreting glands. Sharks and rays also have blood with a lower concentration of inorganic ions relative to seawater, but their blood remains isotonic with seawater due to a high concentration of urea. Physiologists may analyse the mechanisms of osmoregulation in both types of animals and come to understand this in terms of cellular processes and eventually at a molecular level. But this does not explain why marine fish do not have an isotonic blood in the first place nor why selachians and teleosts 'chose' different solutions to the problem. This requires an evolutionary explanation. (Which in part seems to be that the ancestors of fish evolved in freshwater and that they had already diverged into the two groups which gave rise to selachians and teleosts, respectively before they colonised the sea. Why the two groups solved the problems in different ways is not, to my knowledge, understood; it could be a chance effect or it could be due to some functional constraints of the respective ancestral types of fish.)

Ecology is mostly thought of as a science which attempts to explain patterns in nature on the basis of the properties of organisms as they happen to be and with the assumption that the ecological time scale is much shorter than the evolutionary time scale; that is, the genotypes of organisms remain constant during the time-span within which ecological events take place. First of all, this last statement is certainly not always true. But even if this was the case, the complete understanding of ecological phenomena always has an evolutionary and historical dimension which, perhaps in contrast to some other biological disciplines, is not easy to escape. The evolutionary component of ecology is dealt with in more detail in Chapter 5.

Leaving the evolutionary and historical aspects of ecological systems aside for the moment, we may consider what a scientific explanation in

ecology is. This is perhaps best illustrated by Table 1, which shows different 'levels of organisation' of living things. The realm of ecology is represented by the two upper levels. While it is often stated that one goal of biology is to describe life in its totality in terms of physical and chemical laws, this is not yet feasible for higher integrative levels. A meaningful explanation of a phenomenon at any such level in biology is then to understand it in terms of the properties of a lower level. Thus, just like a scientifically valid explanation of the function of an organ is to understand it in terms of its constituent tissues or cells, properties of ecosystems and communities must be explained in terms of the properties of the constituent species populations and their relationships to one another and to the environment. The properties of species populations, in turn, must be understood from the properties of individual organisms. Only this can qualify as a true explanation in ecology. Such an hierarchical system of explanations is also found in the physical sciences; thus explanations in chemistry ultimately relate to the outer electron shells of atoms and molecules; at another level nuclear physics is concerned with phenomena which require an understanding of the internal structure of the atom.

Table 1. Organisational levels of biological systems. Original

Organisational level	Biological discipline
Communities, ecosystems	Ecology
Species populations	Ecology, population genetics
Individuals	Natural history, genetics, physiology, anatomy
Organs	Physiology, anatomy
Cells	Cell biology,
Organelles	Cell biology, molecular biology
Molecules	Biochemistry

I stress this point because it has been, and in part still is, fashionable among some ecologists to equate empirical generalisations about ecosystems and communities with a genuine explanation. Empirical generalisations are necessary and useful, in particular when a complete understanding in the above sense has not yet been possible. Even when such an understanding has been achieved it may not necessarily yield quantitatively accurate predictions which are sometimes desirable. Indeed, a number of useful generalisations about organisational levels of ecosystems and communities can be made (e.g. concerning patterns of successions following a dis-

turbance of particular communities or on properties of mineral cycling in ecosystems). However useful such empirical generalisations may be, they remain a descriptive approach.

A further step in the direction of making pseudo-explanations has been to rationalise them in terms of 'holistic' philosophy. Higher levels of organisation, so goes the argument, have properties which tend to be qualitatively different from the sum of the constituent components. From which should follow that an understanding can and should be obtained in terms of the properties of the intact system [17]. Personally, I find this philosophy a useless approach which detracts from the intellectual satisfaction of studying ecology and circumvents a true understanding of the phenomena and may in the end lead to false predictions. In fact, I find the entire argument as nonsensical as stating that an alarm clock is qualitatively different from its constituent wheels, bolts, and springs. A holistic approach to an alarm clock, I suppose, is to observe that when wound, it will run. To arrive at a real understanding of the device one must take it apart in order to see how it works (or to remain in the jargon, to take a 'reductionist' approach).

Other attempts to short-cut a genuine understanding of ecological systems have appeared and for a time been fashionable. They have generally been based on false analogies to other more or less complex systems. H. T. Odum's attempt [18] to describe ecosystems largely in terms of energy flow is at best a descriptive approach, but strongly deceptive if used as a predictive or analytical tool. The fundamental reason is that neither in an ecological nor in an evolutionary context is efficiency in terms of energy conversion necessarily maximised or in any way the most important factor. The developed models may therefore describe energy flow in a static ecosystem, but cannot predict how that system will change over an ecological or an evolutionary time scale, nor how other, not yet studied ecosystems may function. Another, it seems now extinct, approach was to make analogies between non-equilibrium thermodynamics and ecological systems, such as equating species diversity of communities with 'negative entropy' of chemical systems [19]. Again, this is a fundamentally false analogy and it had an appeal for some time, I suppose, only because it was sufficiently obscure and incomprehensible to appear profound.

The conclusion of this chapter then, is that a true understanding of ecological systems can only be achieved in terms of the properties of lower organisational levels. Thus ecosystems and communities must be understood through an understanding of the properties of species populations, and properties of species populations must be understood as a function of the properties of individual organism. In all ecological systems there is an element of historical singularity due to the process of evolution and to other

past events although this is a property which is really shared by biological systems at all organisational levels.

3 Models of Ecological Phenomena

*A model in its elegance
Is better than reality
Its graphical simplicity
Denotes a rare intelligence.*

*The simple graph incites the wrath
Of field men who, half undressed,
Go rushing out to start a test
Which culminates in aftermath [20]*

All sciences apply models in order to describe, understand or analyse real phenomena. Such models may be physical; an example is demonstrating the properties of light, such as interference, by a shallow tray with water in which waves are induced somehow. Models may also be expressed verbally or graphically or they may be expressed in the language of mathematics. Common to all such models is that they present an analogy to the real phenomenon they intend to describe and such analogies always have limitations; for example, the mechanical wave model mentioned above does not incorporate the quantum effect of electromagnetic radiation. Models may yield insight and lead to the prediction of new phenomena; they may also be misleading.

Verbal and graphical models are used extensively in ecology, but they are often not considered as such; by models, ecologists usually think of mathematical models. In fact, mathematical models are particularly useful in a field which is often concerned with numbers of individuals or quantities of materials and they may yield insight and results which could not have been obtained otherwise. Mathematical models also incur strong emotions among some ecologists who are unfamiliar with the approach. Conversely the general success in the use of such models has led others to produce versions with little ecological substance. To build a successful and meaningful model of an ecological system, it is necessary to carefully analyse the biological interpretation of the parameters which go into the model, to recognise that usually only a limited part of the system under study can be included into any one model (and so it is necessary to decide what the most important components are), and finally to recognise other limitations of the model. In the following I will discuss these properties of models by presenting different types with different limitations. This also allows me to present some real ecology at the same time.

The first example is usually considered to belong to epidemiology. It is, however, really highly relevant to ecological systems, in that infectious diseases play a considerable role in nature as well as among human beings and

among cultivated animals and plants. My example is that of a bacterial disease, plague.

Before discussing a model of a plague epidemic, a few words will be useful on the natural history of plague. The disease is caused by the bacterium *Yersinia pestis*. The organism can reside in rodents (rats were particularly significant as vectors) and from there transferred to humans via fleas. This causes a disease, bubonic plague, which is virulent and mostly lethal, but it is not very infectious. However, sometimes the lungs of the victims become infected and this leads to pneumonic plague which seems always to be lethal after a few days and which is extremely infectious as well. Plague did apparently not occur in Europe (in an epidemic form, at least) prior to 1343 when it came to Messina with a ship from the Middle East. It rapidly spread over Europe to reach Scandinavia a few years later and by that time it had killed about one third of the population of the continent. Recurrent epidemics occurred at roughly 30 year intervals and, interrupted by some longer periods of absence, until the beginning of the eighteenth century. Since then only isolated cases of plague have occurred in Europe, but the disease is still endemic in other parts of the world. It has been estimated that by 1400 the population of Europe was only about one half of that prior to the first appearance of the disease. The great epidemics of plague count among the most traumatic episodes in the history of Europe [21].

The example is appropriate in an ecological context for an additional reason. During the seventeenth century some towns collected data on mortality at regular intervals to serve as an early warning of the plague; when mortality was on a sudden increase it was time to leave town for those who could. In London such data served as the first inspiration for scientific demography and population biology, as already discussed in Chapter 1 [22].

Figure 1 shows the vital statistics of the city of Copenhagen for 1711, which was the year of the last plague epidemic in Denmark. The three columns list the weekly numbers for marriages, births and deaths, respectively. The sums at the bottom of the table indicate 22,535 deaths in the city during 1711; this should be compared with an estimate of a total of only about 60,000 inhabitants in the city at the time. Thus about one third of the population died that year, predominantly due to pneumonic plague. When the columns are examined more closely, it can be seen that mortality slowly increased during spring (this was the time to get out) and then during summer suddenly increased to about 2000 deaths per week. In September the epidemic declined about as rapidly as it started and by December everything was normal again. (Irrelevant here, but remarkable anyway, is the column listing weekly numbers of marriages. Understandably few felt like

Bortegnelse

Vaa dennem / som udi dend Kongelige
Residens = Stad Kjøbenhavn / fra den
I Januarij 1711 til Aars-Dagen 1712

Hver Uge
Ere

Anno 1711.				Anno 1711.				
	Copulerede.	Føde.	Døde.		Copul.	Føde.	Døde	
Til Januar. - 10	-	13	- 43	- 84	Til Juli - 4	- 18	- 33	- 126
- 17	-	6	- 35	- 86	- 11	- 20	- 34	- 228
- 24	-	10	- 24	- 61	- 16	- 16	- 36	- 342
- 31	-	14	- 34	- 80	- 25	- 17	- 29	- 748
Febr. - 7	-	20	- 39	- 61	Aug: - 1	- 9	- 32	- 1032
- 14	-	20	- 48	- 63	- 8	- 4	- 41	- 1951
- 21	-	15	- 44	- 63	- 15	-	- 38	- 1831
- 28	-	14	- 29	- 72	- 22	- 4	- 35	- 1949
Martii - 7	-	11	- 33	- 68	- 29	- 2	- 37	- 2393
- 14	-	9	- 31	- 68	Sept: - 5	- 4	- 27	- 2119
- 21	-	12	- 17	- 55	- 12	- 1	- 24	- 2326
- 28	-	16	- 29	- 46	- 19	- 1	- 20	- 1751
April - 4	-	5	- 32	- 49	- 26	- 1	- 21	- 1312
- 11	-	17	- 35	- 45	Octobr: - 3	- 5	- 10	- 974
- 18	-	17	- 39	- 52	- 10	- 2	- 13	- 613
- 25	-	30	- 36	- 65	- 17	- 5	- 15	- 369
Maji - 2	-	27	- 30	- 50	- 24	- 10	- 12	- 241
- 9	-	36	- 34	- 57	- 31	- 8	- 11	- 176
- 16	-	24	- 35	- 67	Novembr: 7	- 11	- 14	- 92
- 23	-	23	- 41	- 55	- 14	- 17	- 15	- 84
- 30	-	29	- 34	- 54	- 21	- 20	- 11	- 60
i - 6	-	25	- 27	- 50	- 28	- 30	- 20	- 64
- 13	-	17	- 40	- 54	Decembr: 5	- 25	- 22	- 51
- 20	-	16	- 27	- 65	- 12	- 34	- 19	- 47
- 27	-	25	- 36	- 95	- 19	- 39	- 12	- 41
					- 26	- 23	- 20	- 28
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Summa				800. 1464. 22535.				



Kjøbenhavn /
Trykt hos Jørgen Matthiøen Godiche.

Fig. 1. Contemporary account of the vital statistics for Copenhagen, 1711. In direct translation the caption reads: 'List of those who in the royal residential city of Copenhagen have every week' and the column headings read 'married', 'been born', and 'have died', respectively [21]

marrying during August and September, but already in mid-October life went on as usual as if the horrors of the summer had all been forgotten.)

From an ecological view-point we are dealing with a host-parasite system in which the parasite has a much higher population growth rate than the host and we may take advantage of this when modelling the system by ignoring host birth rate. Our primary goal is to understand the kinetics of the epidemic and in particular why the epidemic peaks at some time to decline long before all potential hosts are infected.

We denote the number of healthy (non-infected), the number of infected and the number of dead individuals by respectively, x , y , and z . At time zero we then have $x(0) = 60,000$, $y(0) = 1$ and $z(0) = 0$. Now, the rate of change of healthy individuals is likely to be proportional to the probability of a non-infected individual meeting an infected one, that is xy , so we write:

$$dx/dt = -axy$$

This means that the rate of disappearance of non-infected individuals is proportional to the number of non-infected individuals, the number of infectious individuals and a proportionality constant, a , which is a measure of the infectivity of the disease. This parameter is, of course, somewhat complex; it summarises properties of the disease with various environmental conditions and behavioural properties of a Copenhagener anno 1711, but this measure is likely to have remained relatively constant over the time span we consider. The rate of increase of dead individuals is described by:

$$dz/dt = by$$

Here the parameter b measures the rate at which infected individuals die, or to be more precise, the reciprocal value of the length of time during which an infected individual is capable of infecting other people and this is likely to be somewhat shorter than the time span between being infected and the moment of death. The rate of increase of infected (but living individuals) must be the rate of infection minus the rate of mortality or:

$$dy/dt = axy - by = y[ax - b]$$

Now the general behaviour of the epidemic can be inferred from this last equation. Initially, x is large and may be considered nearly constant and y is very small so the rate of increase in the number of infected individuals is nearly exponential. But as y (and hence the product, by) increases and x decreases the rate of new infections decelerates and at a critical point, when $x = b/a$, the bracketed becomes zero and the epidemic peaks. There-

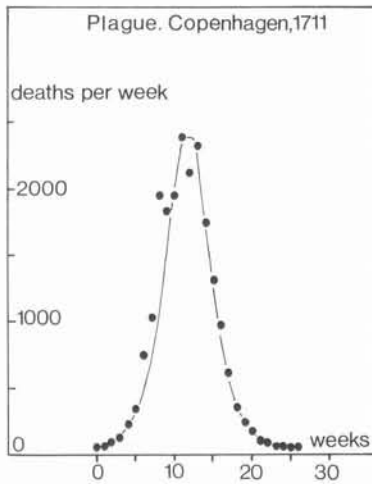


Fig. 2. Epidemiological model (discussed in text) fitted to the data shown in Fig. 1. Original

after as x keeps declining, the rate of new infections decline. We see that there is a critical population density of the host ($= b/a$) below which an epidemic cannot start.

In this case we have no independent estimates of the parameters a and b . So instead the solution of the model is fitted to the data (by methods we do not have to be concerned about here). Figure 2 shows that the model fits the data beautifully. The parameter values are estimated to be: $a = 5.6 \times 10^{-5}$ (per y per week), and $b = 2.96$ (per week) so that $b/a = 52,800$ individuals. The practical usefulness of this is clear; had some measure been taken at the time to keep the population within the narrow confines of the Copenhagen city wall below about 50,000 people, epidemics of plague could have been avoided. Alternatively even marginal improvements in hygienic standards could have lowered the value of the parameter a sufficiently to avoid the catastrophic event. The argument shows in a general way that even a partial immunity brought about by a vaccination programme may eradicate an infectious disease.

The model has some wider, more ecological and evolutionary implications. In nature, such parasites with a critical minimum host density may explain certain types of spatial and temporal heterogeneity of biotic communities and under some situations keep host species below the carrying capacity of their habitat allowing for the co-existence of more species competing for the same resources (provided the parasite is host specific). Seen from the 'view point of the parasite', the model shows that the high degree of virulence in fact limits its ability to spread in less dense host populations. The reason is, of course, that an infected host has a very short time (in this

case only about two days) in which it can infect other individuals. In pneumonic plague this is made up for by a high probability of infection. Diseases with a low infectiousness tend to develop slowly so as to increase the probability of transferring to a new host. An example is provided by leprosy. In general one may expect that natural selection tends to decrease virulence in parasites for that reason.

Let us finally consider the limitations of the model. It is obvious that it ignores a number of properties of the host-parasite system we are discussing. Since it ignores host growth rate, the model is incapable of telling us anything about the recurrent behaviour of the epidemic. Prior to 1711 the epidemics tended to occur at intervals of roughly 30 years and this, of course, reflects that the population had during that period recovered to the density it had prior to the previous epidemic. The above model also ignores other important aspects such as the geographical spreading of the disease and the complications of the rodent vector and the two forms in which the disease occur in man. All of these topics are interesting subjects worthy of study. However, little will be gained by attempting to build a single model which incorporates all aspects of the system. Such a model would be analytically intractable and yield little insight even if (by numerical solutions in a computer) it would be capable of fitting observational data.

I will discuss two additional models which in a sense represent extremes with respect to what models can be used for in ecology. The first one exemplifies the fact that a theoretical and possibly rather unrealistic model may sometimes yield qualitative and non-trivial results which allow new ways of looking at real data. Specifically I will discuss the properties of a simple model of density dependent growth (that is, a single species population, the growth of which declines with increasing population density as a result of intraspecific competition for limiting resources).

Consider an organism which reproduces once a year and each individual produces R eggs. Let us also initially assume that the population growth is unlimited (fertility is constant and there is no mortality). If the population size during the first year is denoted $x(0)$, then the following year there will be:

$$x(1) = x(0) + x(0)R = x(0)[1 + R] \text{ individuals}$$

The following year again there will be:

$$x(2) = x(1) + x(1)R = x(0)[1 + R]^2 \text{ individuals}$$

In general, the size of the population after n generations will be:

$$x(n) = x(0)[1 + R]^n$$

This, of course, represents exponential growth. Now suppose that growth rate declines as x increases due to a decreased fertility or an increased mortality resulting from a smaller per capita food ration. We could suggest the following equation (which is a kind of discrete generation time version of the logistic model, see Chapter 12):

$$x(1) = x(0) + x(0)R[1 - x(0)/K] \text{ where } K \text{ is a constant}$$

We see that as long as x is very small (so the value of the bracket is nearly unity) the model initially behaves as the exponential growth version. As x grows, however, the value of the bracket, and hence the annual increment of the population, declines. When $x = K$, growth is zero (the population remains constant) and if $x > K$, the population declines. If we start the population with a small value of x ($x \ll K$) and calculate the value for x successively from one generation to the next, we would *a priori* expect that x would approach K in some way and remain at that value.

This is also the case as long as R is small (< 1). When R is in the interval $1-2$ the population shows damped oscillations around the equilibrium (Fig. 3). When R is slightly larger than 2, the population shows stable oscillations (a 'stable limit cycle'). Finally, when R approaches 3, the population will show totally erratic or 'chaotic' fluctuations. It is this latter behaviour which is of interest here (quite besides it being surprising that such a simple, deterministic equation may show such a complicated behaviour). The point is, that when complex and violent fluctuations of populations are encountered in nature, one is likely to expect the cause to be some fluctuating environmental factor and possibly try to identify it. The model (which implicitly assumes a constant environment) shows, that such environmental fluctuations are not necessarily what drives the population fluctuations; these may also be due to the deterministic dynamics of the population itself. This general conclusion holds even if the model as described above is in some ways an unrealistic description of an annual population with density dependent growth regulation. As recently pointed out [23], there is some irony in this. During the forties and fifties, some ecologists, notably Andrewartha and Birch argued that populations in nature in general are limited by density independent factors (such as the vagaries of weather) rather than intraspecific competition. This again caused a heated controversy among ecologists at the time [24]. The irony is that the main argument of Andrewartha and Birch against the idea that populations are controlled by their resources was based on the erratic and strong population fluctuations they had found in some insect populations (Fig. 4). The above model shows how the dynamics of intraspecific competition may possibly generate exact-

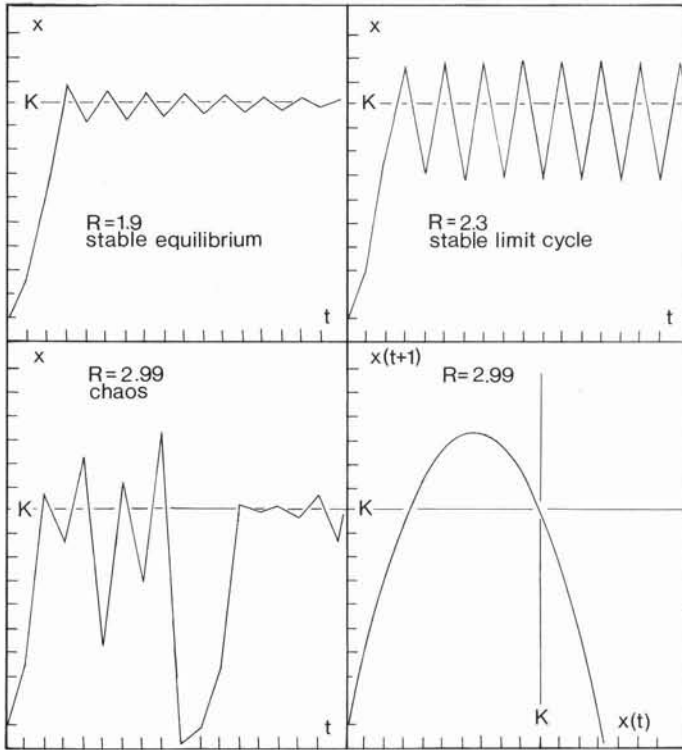


Fig. 3. Time dependent behaviour of the model of density dependent population growth (discussed in text) for three different values of R . When population size is plotted against population size of the following generation (below, right) the deterministic nature of the 'chaotic' behaviour shows. The graph was made by iterating the model for one thousand generations and can be used for generating the population sizes of successive generations. Original

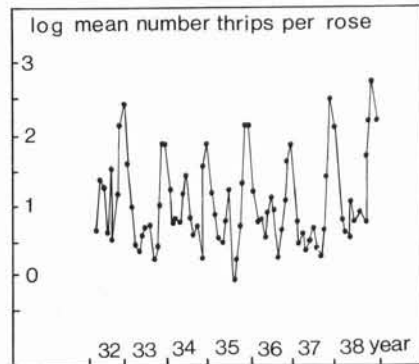


Fig. 4. Mean number of thrips per rose in an Australian garden over a seven year period (note logarithmic scale). After Davidson & Andrewartha [24]

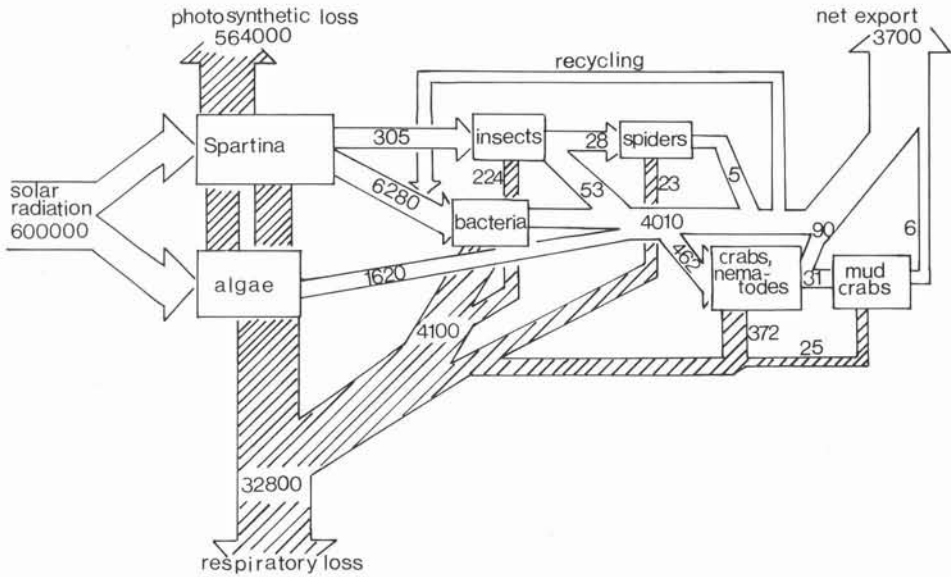


Fig. 5. Compartment model of the energy flow in a salt marsh in Georgia. Numbers are kilocalories per metre square per year. After Teal [25]

ly the kinds of population fluctuations studied by Andrewartha. Mathematical techniques allow the analysis of such data (see also Fig. 3) to show their deterministic nature. Some examples of such field data on population sizes which would seem to display stochastic fluctuations over time, including Andrewartha's data on an insect population (thrips), have recently been analysed in this way to suggest that they have a deterministic basis and are due to biological interactions.

Let me conclude this chapter with a third, entirely different kind of ecological model, which has been widely used to describe the flow of energy or materials in ecosystems. This type of model was originally developed for physiological research. Figure 5 shows such an example of a 'compartment model' for a salt marsh along the coast of Georgia [25]. The model includes the standing crops of the various 'compartments' (the sizes of which are here omitted for simplicity) and the flow of energy through the system. This energy flow has in practice (except for solar radiation) been quantified as rates of food intake and the respiratory rates of the various components. The diagram represents a considerable simplification relative to the real salt marsh, which contains many more species than suggested by the diagram and considerably more complex food interrelationships, e.g. not all insects feed on marsh grass. Also the accuracy of the individual estimates of

rates probably varies. Each living compartment in the system takes up energy. In the case of the photosynthetic organisms this is in the form of light; the other organisms are heterotrophic: they take up organic material, some of which is used for growth and reproduction and some of which is degraded into carbon dioxide, water and mineral salts in order to meet the energy requirements of the organisms. Note that most of the marsh grass production is degraded by bacteria many of which are subsequently washed off shore ('exports') together with various other debris. In principle, of course, it is possible to include much more detail into such a diagram.

In a sense this is an entirely descriptive model and its quality depends totally on the correctness of the qualitative observations (concerning who eats whom) and the quantitative measurements. In spite of the dynamic arrows, it is in a sense a static description. First of all the flows and compartment sizes of the real system are not likely to remain constant throughout the year. Also the model has no power to predict why the compartments or rates of flow have some given magnitude nor how the system will evolve in future. Even so it is a useful way to summarise the findings of such an investigation and to express ideas on how the system may function.

Compartment models such as this may also be used as an analytical tool. Suppose that the system is given a pulse of the radioactive C-14 isotope in the form of carbon dioxide. The model can then (after some mathematical exercise, but not requiring more field data) be converted into an analytical model which predicts where the radioactive material will be found at any time following the pulse. It is implicit that the system is in a steady over the time span followed. In a similar way the fate of some pollutant in the given ecosystem can be predicted. I apologise for the crude simplification in the following, but I wish only to present the principle of using this type of model: assume that the marsh is polluted with DDT. This compound is lipid-soluble and so organisms tend to retain whatever DDT they take up in their food. Assume that the marsh grass and algae take up a small amount of the insecticide from the water. This is then passed along the food chains and since each compartment respire some of the food, but retains the DDT, they become enriched by this compound relative to their food. Consider, for example the mud crabs in Figure 5. They are estimated to consume 31 units of food per unit area of which they respire 25 units. Assuming that the crabs retain all the DDT of their food, they will then concentrate DDT in their body tissues relative to their food by a factor of $31/(31-25)$ or about 5. Obviously, given sufficiently good data and knowledge on how individual organisms treat certain compounds, this type of model can be used to predict the fate of pollutants such as heavy metals, radioactive compounds and chlorinated hydrocarbons in nature.

4 Ecology and Natural History

This and the following four chapters will briefly discuss the delimitation and relationship of ecology relative to other fields of biology. While few biologists with a general overview of biology still exist, it is in general an unrealistic hope that practitioners of so relatively self-contained fields as physiology, molecular biology or genetics will acquire a deep insight into ecology. The intimate relationship between ecology and neighbouring fields is reflected by an overwhelming number of books with titles such as 'Ecological Physiology' and 'Genetical Ecology'. They often make for valuable reading for ecologists and other biologists, but their contents are rarely really ecology in the sense that they offer an integrated view on patterns in nature. Rather they tend to view ecological problems from some fixed angle and implicitly consider other approaches to be irrelevant or peripheral. Consequently, ecologists should at least attempt to maintain a generalist attitude towards biology at large.

'Natural history' has long had a Victorian ring to its name and been banished from the main stream of biology. Naturalists have been associated with amateur bird watchers and butterfly collectors and survived in academic institutions largely by disguising themselves as ecologists. While natural history represents the origin of ecology – and actually of all biology – it is something different. It is devoted to the study and description of the uniqueness of the individual species. The naturalist is supposed to identify organisms and to describe where they live, how they are specially adapted to their surroundings, and so on. And this is in contrast to other biologists who attempt to find principles of more or less generality. The naturalist and the ecologist (or the physiologist) may, of course, be one and the same person. One, among several, beautiful examples is provided by MacArthur's studies on American warblers: detailed studies on the biology and behaviour of several species of these birds (the natural history part) were carried out in order to arrive at general principles pertaining to interspecific competition and co-existence in closely related organisms (which is ecology) [26]. Both approaches have a value in their own right, but the discovery of general ecological principles or at least a test of their validity requires the detailed descriptions by the naturalist.

The fact that biology has this dual nature: one dealing with the uniqueness of each individual biological phenomenon and one dealing with general principles of living systems and that both must be studied has gained more acceptance in the last couple of years [27] after a long period where the largely descriptive activity of naturalists was looked down upon. In ecology one of the fashionable trends in the last decades has been to build

compartment models such as that discussed in the previous chapter (Fig. 5). This approach may be quite appropriate for some purposes, but it is often forgotten that it is not entirely irrelevant how individual species are partitioned among the abstractions called compartments. Failure to recognise the importance of the natural history and the identity of the species belonging to the system under study may lead to incorrect interpretations when attempting to describe it in a schematic and simplified form.

Other approaches to ecology have an obvious need for precise information on the natural history of individual species. One fundamental problem in ecology is to explain the species richness of different communities and what maintains the diversity in the face of competition, extinction and so on. The measurement of species diversity obviously requires the ability to identify species and a meaningful analysis of species interactions requires a detailed knowledge of the natural history of the species involved. Another important field of inquiry on the borderline of ecology and genetics is the adaptive significance of different types of 'reproductive strategies' which shows an astonishing diversity (Chapter 18). To approach this, a comparative method must be used (e.g. to look at variations in egg sizes or numbers in different related forms in relation to their biology and habitats) and this requires studies on many species; detailed knowledge on the laboratory rat or the intestinal bacterium *Escherichia coli* is not sufficient.

So far about 1.7 million multicellular animals and some 400,000 vascular plants have been given a name; to this must be added fungi, protists (unicellular or multicellular eukaryote lineages not belonging to any of the above mentioned groups) and prokaryotes (= bacteria). It is likely that a large number of organisms remain undiscovered, exactly how many is hard to say [28] (see also Fig. 6). The rising fear that many species (including undiscovered ones) will become extinct in the decades to come, mainly as a

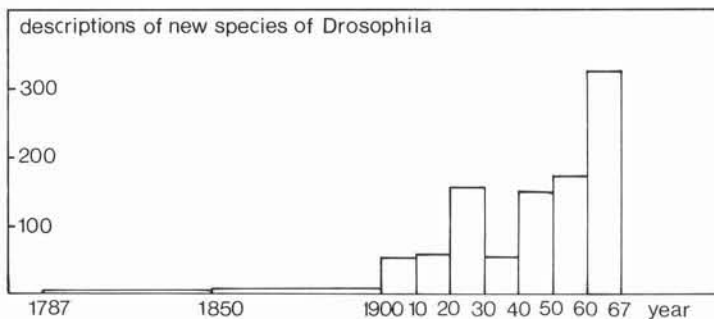


Fig. 6. Number of descriptions of new species of fruit flies in different time intervals between 1787 and 1967. Altered after Mayr [27]

result of the clearing of tropical forest, seems further to stimulate naturalist efforts especially in the tropics [29] and the contribution of ecology to the preservation of such organisms will depend on the accumulation of data provided by naturalists.

5 Ecology and Evolutionary Biology

The relationship between ecology and evolutionary biology (and genetics) is very complex. That there is a very close relation is obvious: evolution takes place in and as a response to the ecological context of organisms, as Darwin was already aware or as expressed by the title of Hutchinson's book: 'The Ecological Theater and the Evolutionary Play' [30].

To understand the adaptive significance of a trait is to understand the ecological context in which it developed. From the theoretical side this has led to a special discipline, 'evolutionary ecology' which allows for changes in genotypes in ecological models. In classical theoretical population genetics, genotypes are assigned a fitness and the relative frequencies of different genes in future generations are followed; possibly the considerations also include the effects of mutation rate and random genetic drift. In evolutionary ecology, genetic variation in the parameters of ecological population models is allowed for in order to study the evolutionary effects of ecological interactions. The approach has been successful in some respects, but it also has pitfalls. In particular, parameters which occur in ecological models may, in fact, be quite complex summaries of phenotypic properties and properties of the environments. While this may be acceptable in models which assume unalterable phenotypes, it may lead to false conclusions in models of evolutionary events if the biological interpretation and the effect of the parameters in the model have not been sufficiently analysed. Examples of such models are discussed in Chapters 17 and 18.

In a quite different context, genetical knowledge is relevant with respect to the preservation of large animals. So-called endangered, large mammals typically have small absolute population sizes, a substantial part of which may reside in zoos or breeding centres. While the immediate concern of the ecologist may be one of extinction due to demographic stochasticity, the risk of loss of genetical variation and inbreeding depression may set more demanding limits to the minimum population size which ensures a reasonably high probability of survival of a species [31].

Traditional theoretical population models in ecology (and the way ecologists in general think about the systems they study) imply that the phenotypes (and thus the genotypes) of the individuals of a species population

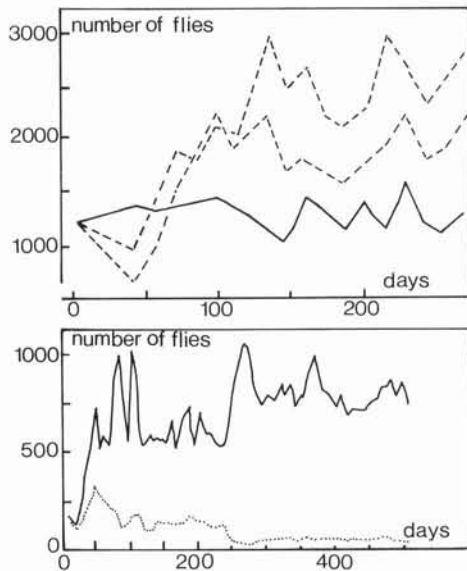


Fig. 7. Above: growth of three populations of the fruit fly *Drosophila birchi* in population cages. Two of the populations (dashed lines) were irradiated prior to the experiment. This introduced new genetic variation in the populations and through natural selection, their fitness increased during the experimental period relative to the wild type. Below: competition between populations of two species of fruit flies, *D. serrata* (dotted line) and *D. nebulosa* in a population cage. After about 200 days genetic change in the population of the latter species improves its competitive ability relative to the other species and its population increases accordingly at the expense of *D. serrata*. In none of the examples is the actual change in phenotype known, but both illustrate evolutionary change within the time span of a population ecological experiment. Redrawn from Ayala [32]

are identical and that they remain constant during the processes under study. It is therefore implied that the time-scale of evolutionary events is much longer than that of ecological events. This is not necessarily true. It is well known that bacterial strains may quickly evolve strains that are resistant to various antibiotics just as many insect pests, over a span of few years, become resistant to certain pesticides. A more direct evidence for evolutionary change within an 'ecological time-scale' is provided by the experiments shown in Figure 7 with fruit flies in population cages. Altogether, there is ample evidence that natural populations have a considerable genetic variance and that some phenotypic traits (such as body size) rapidly respond to artificial selection [32].

At another scale, evolutionary events of the past may render interpretation of present patterns difficult. Consider Fig. 8 which shows the distri-

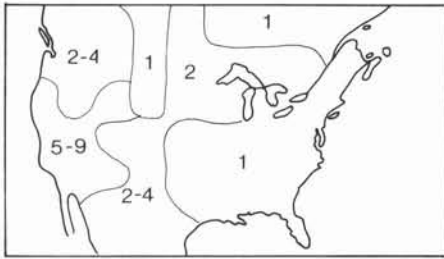


Fig. 8. Numbers of species of ground squirrels ('chipmunks') in different parts of North America. Redrawn from MacArthur [33]

bution in numbers of species of ground squirrels in North America [33]. Clearly there is a much richer fauna of these animals in the western part of the continent and this could have an ecological as well as an evolutionary explanation. The latter would suggest that the geologically recent or ongoing mountain formation in the west led to perpetual isolation of populations in valleys followed by allopatric speciation and that the number of species found represent an equilibrium between speciation and extinction. Conversely, the eastern part of the continent has been geologically stable for a very long period and there have been no isolation mechanisms which would allow such a high rate of speciation. An ecological interpretation would be that the diversity of habitats in the mountains allow for a higher number of regionally co-existing species. The untangling of evolutionary (historical) and ecological factors when explaining such patterns is often not trivial.

A methodological development of genetics is now having an impact on population ecology. In the sixties, enzyme electrophoresis was introduced in population genetics and it was found that most populations show a much higher degree of genetic polymorphism than hitherto believed — much more than current ideas about mutation rates, drift and selection immediately could explain. Many large scale investigations on isozyme variation of natural populations were initiated in an attempt to demonstrate selective forces which could maintain this variation and also to find ecological correlates with isozyme patterns. This quest has proved unsuccessful and it is now widely held that much of the variation is selectively neutral or nearly neutral and that strong selective forces only act at few loci at any one time and these are not likely to show up in a small random sample of the entire genome [34]. However, the developed methods have proved useful to trace genetic isolation of populations and to study speciation events. The methods can also be used for studying the structure of natural populations including migration patterns and for identifying and delimitating breeding populations. An example is provided in Figure 9. The data show that the eelpout (*Zoarces viviparus*) is indeed a stationary fish which forms appar-

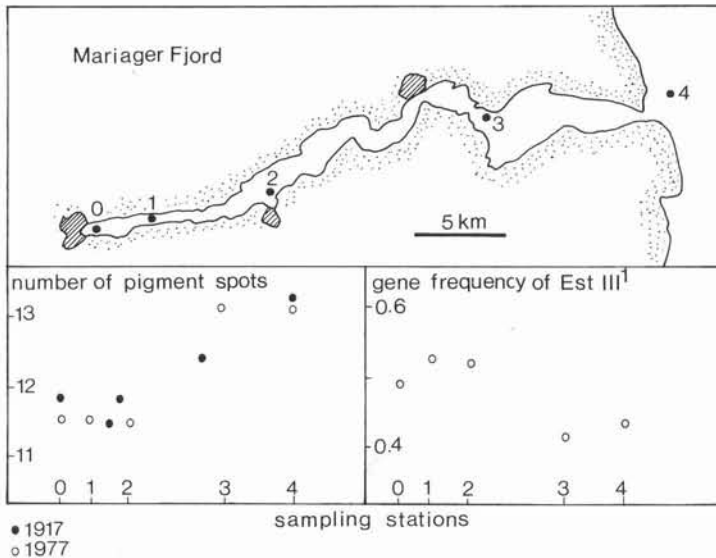


Fig. 9. A phenotypic trait and the gene frequency of a gene specifying an esterase of the fish *Zoarces viviparus* (eelpout) along a 25 km long fjord on the east coast of Jutland, Denmark. These (and other data) show that the genotypic and phenotypic differences correlate and that the fish in the innermost part of the fjord constitute an isolated breeding population and have done so for at least most of this century. Redrawn from Christiansen *et al.* [35]

ently totally isolated breeding populations over a fairly short distance in a Danish fjord. Data on the phenotypic variation in the fish were also collected some 60 years earlier and suggest that the small isolated population in the inner part of the fjord has persisted for at least that period [35].

6 Ecology and Physiology

The relation of an organism to its physical and chemical environment is always an important factor when its distribution in nature is studied. Connell's study on the vertical distribution of two species of barnacles on a rocky intertidal coast in Scotland provides an example of the combined effect of physical and biological factors [36]. One species, *Chthalamus stellatus*, is always found at a higher level on the coast than is *Balanus balanoides* and the two barnacle zones are sharply delimited from each other. Larvae of *Chthalamus* settle in the *Balanus* zone as well and if individuals of the latter species are removed artificially, the former thrives normally. The quicker growing *Balanus* is the superior competitor (it simply

overgrows or underslips its competitor) but is less resistant to desiccation at low tide and so cannot survive at the high level of the shore. The physiological aspect of this example is then to study how barnacles survive desiccation and why the two species are different in this respect. Barnacles avoid being desiccated at low tide by closing their tests. In so doing they have to contend with an anaerobic metabolism and this eventually kills them due to the accumulation of metabolic waste products if they are not submerged in water after some time.

There is a vast amount of literature pertaining to the tolerance and adaptive mechanisms with respect to salinity, desiccation, temperature, anoxia, etc.; about mechanisms of digestion (which are relevant when evaluating the nutritive value of food for animals, for example); about the physiology of photosynthesis and mineral uptake of plants; the physiology of hibernation in mammals, or the resistive stages of lower organisms; and so forth. Such studies are indispensable for ecological research. Conceptually, however, it is easy to keep the two approaches apart: physiologists study mechanisms within organisms while ecologists apply information on how the physiological properties of the organisms affect their performance in nature.

To a microbial ecologist, however, the relationship to (cell) physiology becomes far more intimate and integrated. A unicellular (prokaryote or eukaryote) organism is directly exposed to the vagaries of the environment. Although such an organism – in the eyes of the microbial ecologist or the naturalist – is a ‘complete’ organism comparable to a multicellular organism, its adaptations to the environment are to be found at the cellular level. An ecological understanding of microorganisms therefore includes an understanding of their cellular physiology and molecular biology.

A brilliant example of this is provided by Koch’s studies on the adaptations of *Escherichia coli* to a ‘feast and famine existence’ [37]; although concerned with cellular physiology, the work is highly recommended reading for ecologists. Koch observes that it is not a trivial thing that the organism is capable of displaying balanced growth over a wide span of rates as this implies complicated regulations of the synthesis rate of RNA and other macromolecules. Since the rate at which protein is synthesised per ribosome is invariant with the growth rate, the RNA contents per cell should be proportional to the growth rate constant and the rate of synthesis of RNA must then be proportional to the square of the growth rate constant. Koch also found that at very low growth rates, when the cells are starved, they contain an excess of RNA (relative to the above expectation) which could be considered a costly investment for the cell. *Escherichia coli* lives in the intestine of mammals such as man. Since the turnover of the intestinal con-

tents in the latter case is perhaps of the order of 24 hours and since the bacterial density may be assumed to be relatively constant over time, one could expect that the bacteria had a fixed generation time of around 24 hours.

Now, the habitat of the bacterium is, in fact, not such a 24-hour chemostat. During late night and long after the last meal of the host has been exploited by the bacteria, they are starving. When breakfast appears

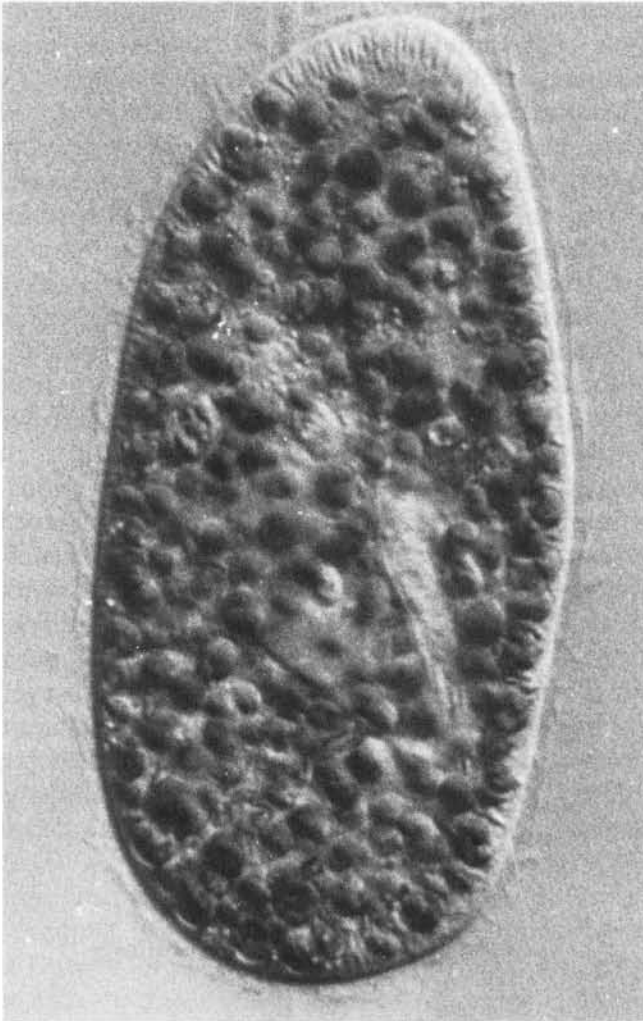


Fig. 10. A *Paramecium bursaria* cell. This 0.1 to 0.15 mm long ciliated protozoon typically harbours about 250 cells of the green alga, *Chlorella*. In some ways this cellular consortium can be considered as a self-contained ecosystem. Original

in the morning, the bacteria have a feast in an environment which allows for rapid growth. The selective premium for the cells is at this moment to resume rapid growth before their kin and so they synthesise excess RNA during starvation in order to minimise time before they can resume cell division. This cycle is then repeated (typically) twice more per day. The study is therefore not only an analysis of the molecular biology of a bacterium, but also an ecological analysis of a temporally heterogeneous environment and of the adaptations of its inhabitants.

A final example of the intimate relation between cell biology and microbial ecology is illustrated in Figure 10. It shows a very widespread phenomenon among protozoa (and some invertebrates), viz., intracellular symbionts. The example here is the freshwater ciliate *Paramecium bursaria* which in nature nearly always harbours cells of the green alga *Chlorella*. This case has been especially well studied [38]. The ciliate does feed on bacteria like its congeners, but in the light, and provided with some mineral nutrients, the ciliate-algal consortium can be grown without any external food resources. In a sense this represents a small self-contained ecosystem. The study of this system (which includes questions as how the ciliate recognises the symbiont which can re-infect their hosts via a feeding vacuole and how the growth rate of the algae is controlled to maintain a relative constant population in the cell, etc.) is then ecology and cell biology at the same time.

Indeed, it is now generally held that eukaryote cells originated as symbiotic consortia of prokaryote cells and that some cell organelles (chloroplasts, mitochondria) derive from endosymbiotic prokaryotes. There is now considerable support for this hypothesis including the presence of organelle chromosomes and the similarity in macromolecules between the organelles and extant, free-living prokaryotes believed to be related to the ancestors of the organelles. There is also much circumstantial evidence in form of a large number of such endocellular symbionts of extant protists which show different degrees of specialisation and integration with their host cells [39]. If this is so, cell biology and ecology of eukaryote unicellular organisms in a sense become nearly identical disciplines.

7 Ecology and Behavioural Biology

Great progress has been made in understanding animal behaviour and large amounts of observational data have accumulated. At the same time progress has been made in understanding the physiological background for

at least simple behavioural patterns in lower organisms in terms of neural anatomy and function, or, in the case of unicellular organisms, in terms of the properties of the cell membrane and effector organelles. Regarding the complex behaviour of higher animals (especially vertebrates and insects) progress has been made with respect to understanding the adaptative significance and evolution of these traits. This latter aspect is studied under the heading 'sociobiology' [40].

Even the 'lowest' organisms show some sort of motile responses to various sensory stimuli. In a wide sense the adaptative significance is nearly always associated with habitat selection. Photosynthetic aquatic organisms modify their swimming patterns in such a way as to accumulate in the light zone, and many protozoa use chemical clues so as to accumulate in patches of food. Such responses are extremely important for the understanding of microbial communities. This is in particular obvious when studying bacteria in chemical gradients of, for example, oxygen and hydrogen sulphide. Steep gradients may result in many different habitat niches for bacteria, so that zonation patterns with a size scale of perhaps 100 μm or so may be observed. In the absence of, albeit very simple, chemosensory responses, this would not be possible as the random motility of the bacteria would result in the cells 'diffusing' away from such small habitats with such a small spatial distribution (see Chapters 15 and 19).

All motile organisms (or motile stages of otherwise sessile organisms) show a number of responses which allow them to find food and avoid predators or obnoxious physical or chemical environmental factors, and such responses are important when interpreting ecological observations. When we consider vertebrates and some more highly evolved invertebrate groups, a much more complex behaviour including learning is found, in addition to the stereotypical behavioural patterns of lower organisms.

The ecological implications of such more complex behaviour must be taken into account and this is sometimes in principle straightforward. What is more questionable is to interpret such behaviour in a purely ecological context. The behavioural trait in question may well have ecological consequences, but these may be fortuitous by-products of behavioural patterns which evolved in a quite different context. One example is territorial behaviour among many species belonging to quite different taxonomic groups. For example, Strandgaard [41] studied the territorial behaviour of roe deer in a Danish forest. Males occupy a territory through much of the year together with a number of females, and excess males are driven out of the forest (and these days mainly fall victim to motor cars). The ecological effect of this is obvious: the total population is kept well below the level which the forest could otherwise sustain. From an evolutionary point, how-

ever, the behaviour must be seen as the outcome of competition for females among the males; that is, sexual selection has been the driving force and the behaviour cannot be understood in the light of 'saving resources' or similar mechanisms which anyway would imply group selection. The ecological effect of the behaviour is thus a secondary one.

Another example is provided by Hamilton's analysis of schooling or herding behaviour [42]. Such behaviour has often been considered in the light of predator avoidance and this is in a sense true (but not with quite the effect one could naively expect). Hamilton convincingly argues that the behaviour has evolved because it minimises the individual probability of being eaten when encountering a predator because individual prey can hide in the crowd. The larger the herd or school of fish the smaller the probability that one particular individual is taken when a predator turns up (and assuming that the probability of a predator finding such a herd is independent on its size). However, the predator will pick its prey anyhow so the predation rate on the population remains constant. There is even evidence to suggest that schooling or herding sometimes makes it easier for predators to detect and stalk their prey and so the anti-predatory behaviour brought about by selection on individual fitness may be dysgenic in terms of the prey population.

8 Ecology and Biogeochemistry

It is now believed that life originated early in the history of the earth, perhaps 4×10^9 years ago. Since then it has had a profound influence on the chemistry of the atmosphere and the hydrosphere. This is because living organisms transform chemical compounds in the process of assimilatory metabolism (in which chemical species from the surroundings are incorporated into cells) and in the process of dissimilatory metabolism (in which the organisms acquire free energy through chemical or photochemical processes). Oxygenic photosynthesis is believed to have originated around 3×10^9 years ago when blue-green bacteria appeared. This led to a steady increase in the oxygen tension of the atmosphere, which is believed to have been very low prior to this period [43].

The function of the biosphere is based on the creation of local chemical disequilibria by electromagnetic radiation from the sun and mediated by photosynthetic organisms (certain bacteria and plants). This process maintains a chemical disequilibrium of the entire atmosphere. Thus, the bulk of the oxygen in the atmosphere is produced and maintained by photosyn-

thesis and (together with sulphate in seawater and sediments) these oxidation equivalents are balanced by a corresponding number of reduction equivalents in the form of reduced carbon (and some other reducing compounds) in living organisms and in particular as fossil organic carbon in sedimentary rocks.

In particular, certain bacteria with more exotic metabolic pathways contribute qualitatively and quantitatively to the maintenance of the chemistry of the biosphere. One example is provided by the turnover of atmospheric nitrogen. Nitrogen is not stable in an oxidising atmosphere, but is slowly oxidised to nitrous oxides either directly or indirectly via nitrogen-fixing bacteria to reduced nitrogen and subsequently via oxidation to nitrate, a process carried out by nitrifying bacteria (and today, of course, via the fertilizer industry). The reason that nitrogen and oxygen are maintained in the atmosphere rather than changing the oceans into nitric acid, is that denitrifying bacteria, which use nitrate as an electron acceptor in a respiratory process produce nitrogen gas as a metabolic end product [44].

Biogeochemistry is the study of how organisms transform the chemistry of the surface of the earth. This includes not only global aspects, as exemplified above, but also the formation of certain deposits such as coal, lignite, mineral oil, certain sulphur deposits and guano on a more local scale. Many of the qualitatively unusual (but very important) processes (such as transformations of sulphur and nitrogen compounds) are mainly or exclusively mediated by prokaryotes. Regarding the reduction of carbon dioxide to organic carbon and the cycling of mineral nutrients, plants have an immense quantitative significance. The role of larger animals in transforming the chemistry of the environment, on the other hand, is exceedingly small. Of course, when studying the productivity of, e.g. fish, this is, per definition, important.

To the realm of biogeochemistry also belong ecosystems (such as a lake), the flow of reduced carbon through food chains and how it is partitioned among the different components, and how, together with other elements, it is eventually remineralised to become available to primary producers. Biogeochemistry is an integral part of ecology as are the microbial processes in soils, sediments and water. It is the part of ecology which interfaces most with applied aspects such as ecotoxicology, eutrophication of land-locked waters and the productivity of ecosystems from the view point of their exploitation. The methodology widely overlaps with that of the population ecologist in the field in that an increase in the numbers of individuals is a measure of production. Direct measurements of chemical fluxes are, of course, also involved.

9 Problems of Practising Ecological Research

The preceding chapters have attempted to delimit ecology as a natural science relative to other fields and to indicate some of its characteristics. This chapter should serve as an introduction to the following section which treats what I consider to be the core of ecological concepts and problems. At this point, however, I would like to summarise some of the problems which one is confronted with when doing ecological research and which emerge from the preceding chapters, and then add a few more!

I have defined ecology as the search for basic principles which govern patterns in nature (with respect to living organisms and their impact upon each other and on their environment). There is a multitude of such principles, not just a few simple ones (such as Mendelian heredity in the case of genetics).

One reason for the 'pluralistic' nature of ecology relative to that of other biological disciplines is the way in which life is structured as a hierarchy of organisational levels. At the lowest levels of biological organisation, that of heredity and the transcription of the hereditary code, few general principles pertain to all organisms. Cells also contain other units such as ribosomes, and eukaryote cells, for example, also mitochondria and centrioles, the function and structure of which is nearly invariant. At the cellular level, many general principles still apply, but there is also a wide variation in form and function when cells representing different unicellular organisms or constituting different types of tissues are compared. When comparing different multicellular organisms a tremendous variation is found although they are all built from units of cells for which the similarities are more evident than the differences. Further complexities arise when these organisms are combined and interact with the abiotic environment to form ecological systems.

One consequence of this is that ecology may never reduce to a few simple principles and another one is that ecologists to a larger degree than other biologists have to be generalists. This is also a consequence of the fact that not all ecological systems are amenable to experimental analysis.

A further complication arises because of the historical uniqueness of all ecological systems due to stochastic events in an ecological context and to evolutionary events which took place in the past in an often unknown ecological context, and which again have stochastic and opportunistic components. This really applies to all types of inquiries in biology, but it is most acutely felt in ecology and in natural history.

A real explanation of an ecological phenomenon is one which explains it in terms of the properties of its constituent parts, viz. the properties of

individuals and of species populations. General empirical principles pertaining to entire ecological systems (homeostatic properties, patterns of diversity or succession, and so forth) are not real explanations, but merely represent more or less successful descriptive attempts. Conversely, when generalisations are used to 'explain' properties of individuals (viz., as an evolutionary explanation) this represents teleological reasoning and often leads to false or misleading conclusions.

Another problem – in a purely academic context – has been the violent expansion of ecology during the recent decades. All types of natural sciences have shown an enormous growth during the last three decades, but ecology started from a relatively small base. It grew not only because of intrinsic reasons in terms of an increase in insight and in the generation of new, interesting problems to solve, but also because of external pressures in terms of man-made environmental problems and, as ecology became fashionable and lucrative, through immigration and intrusion from neighbouring fields. Today ecology has become a vast enterprise and subject to a high degree of specialisation to which meaningful ecological research is vulnerable.

One special aspect of this is the output of new journals. Looking only at international journals devoted to general ecology (thus excluding journals in for example marine biology, limnology, soil science or applied aspects) there were about ten of them about 30 years ago, and most of these had been established for several decades. In the year of writing this book (1986) not less than five such new journals appeared or have been announced; in addition, two of the long established ones have expanded their output [45]. If similar statistics were made for more specialised ecological journals (with titles like 'Journal of Plankton Research' and the like) the figures would be overwhelming.

During the last couple of years, numbers of staff and students of academic institutions have been stagnating in most countries and everyone complains about inadequate funding. So where do the authors of this ever increasing output of printed material come from? And where are the readers for all this? I cannot possibly believe that it really represents an increase in the amount of original work of quality, but must conclude that an increasing amount of trivial and sloppy work is being published. The problem is general, of course, and the reason seems to be the lack of an appropriate market mechanism (a few large libraries buy whatever is published, so publishers can still make a profit by starting new journals) and also the competition for funds and positions seem to be won through numbers of papers rather than by their contents.

This is an especially serious problem for a research discipline which is somewhat diffuse and soft and in which in particular the 'uniqueness' of each ecological system can be abused to produce a flood of trivial publications. And so I find it appropriate here to appeal to my colleagues to contribute to the reversal of the trend of ever increasing output of paper.

III Concepts, Ideas and Problems in Ecology

10 Scales of Size and Time among Living Things

One of the astonishing things about life is the tremendous variation in size of organisms; this is probably unchallenged by other categories of things. Figure 11 shows a logarithmic scale of length covering the span from the diameter of a hydrogen atom (0.1 nm) to large whales which measure more than 10 m. Things we recognise as organisms (from bacteria, the smallest of which measure less than $1\ \mu\text{m}$ to the above-mentioned whales) span a size factor of more than 10^7 and a weight factor of more than 10^{21} (and this even excludes giant redwood trees from consideration). During evolution, increase in body size has to a large extent taken place by increasing the number of rather uniform cells, and so it is perhaps not so astonishing that cell biologists can provide unifying characteristics of life. Thus it is nearly impossible to distinguish a microscopic section of some tissues of a mouse from those of an elephant. Yet, it should be noted that the unicellular eukaryotes ('Protozoa') span a size range nearly comparable to that of mul-

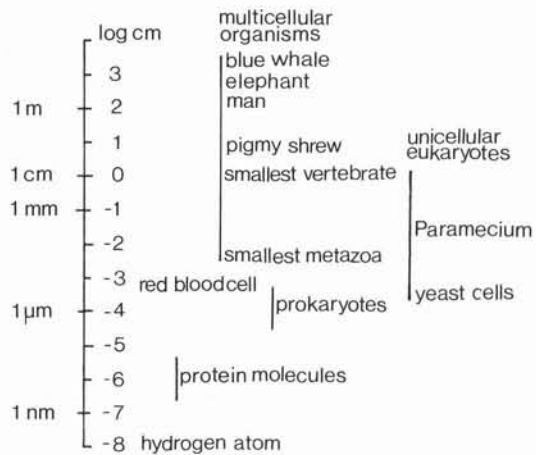


Fig. 11. Length scale of living things. Original

ticellular organisms (a factor of about 10^4). Large cells, however, seem also chiefly to have developed by duplication of organelles.

It is astonishing that biologists who study whole organisms and ecological systems can make generalisations which are valid for all organisms. Actually, there are many functional and structural constraints which pertain to size. Some of these are not intuitively obvious and their study is usually referred to as scaling [46]. It has been a favourite subject of fiction (from Gulliver's travels to Hollywood masterpieces which, e.g. describe a giant gorilla that climbs the Empire State Building) to imagine animals or men with sizes which deviate strongly from their normal ones. The physical realisation of such fantasies are impossible. The above mentioned gorilla, had it been real, would have had a boiling body surface because it could not have dissipated the metabolic heat produced per unit volume and the bones of the legs would have been crushed under its immense weight. More interesting, perhaps, are the problems of being very small; the physics of the surroundings is perceived quite differently by a bacterium than by a larger aquatic organism [47]. Some of the effects of size have important implications for the structure of ecological systems and will be discussed below.

It was recognised early that metabolic rate (usually measured as the rate of oxygen uptake which is an adequate measure of power generation in an aerobic organism metabolising organic matter) is not proportional to body weight, but rather that the metabolic rate per unit weight of tissue tends to decline with size. The earliest investigations considered only 'homeotherm' animals (i.e., animals which maintain a certain, elevated temperature relative to their surroundings, essentially include mammals and birds). It was thus suggested that metabolic rate should be proportional to body surface area rather than weight because the dissipation of excess heat would be directly proportional to surface area ('Rubner's law'). Thus metabolic rate was expected to vary with the $2/3$ power of weight (the weight specific metabolism should vary with the $-1/3$ power of weight, i.e. to be inversely proportional to length). It was later observed that a similar rule also applied to heterotherm organisms (lower vertebrates, invertebrates, unicellular organisms), but then again, it is reasonable to assume that biological processes are controlled by transport of substances through surfaces. Also the efficiency by which an organism can collect food or dissolved nutrients tend, everything else being equal, to be proportional to body surface or length rather than volume.

Extended analysis of a large body of data [48] has shown that metabolic rate tends to be proportional to the $3/4$, rather than $2/3$ power of weight (the weight-specific metabolism being proportional to $-1/4$ power of weight). In

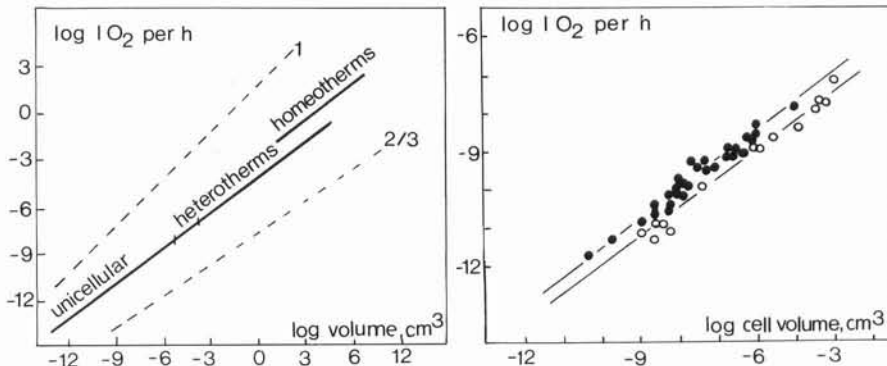


Fig. 12. Left: metabolic rate as a function of body volume. Right: a similar presentation for protozoan cells. The data show a considerable spread around the regression line; this may represent experimental error or it may reflect something real. The fact that metabolic rates of amoebae (open circles) seem to be consistently lower than those of flagellates and ciliates (filled circles) suggests that at least this difference is real. After Fenchel & Finlay [48]

spite of many attempts it has not yet been possible to rationalise this deviation from Rubner's law; Figure 12. It is seen that there is a discontinuity between heterotherm and homeotherm organisms; this reflects the additional metabolic costs of maintaining an elevated body temperature relative to the surroundings, but also the costs of maintaining a higher growth rate relative to similarly sized heterotherm animals (which again is made possible by the higher and controlled body temperature). The seemingly exact fit of this relationship applies only when organisms covering a wide span of sizes are compared. If parts of the graph in Figure 12 were to be magnified, this would show that many individual data points deviate strongly from the regression line. In part this reflects methodological difficulties. Thus no individual organism maintains a constant metabolic rate over time; rather it changes according to the physiological conditions and these cannot always be uniformly defined or reproduced under experimental conditions. Furthermore, some deviations from the regression lines reflect real differences between organisms of similar sizes. The relationship must therefore be considered as an empirical generalisation which holds when organisms covering a large span in size are compared. The relationship also shows the temporal aspect of size: small organisms have a higher 'rate of living'.

There are several correlates with size which may somehow be connected to the above described relationship in a causal way [49], but what is most interesting in this context is the relationship with productivity and growth. Metabolic rate is to a large extent coupled to growth. This is particularly evident in microorganisms where there is a nearly linear relation between

the rate of growth and metabolic rate (the production of cells or of biomass is linearly related to the consumption of resources). In microorganisms, by far the largest part of the power generation is involved in the synthesis of macromolecules and so directly coupled to growth. In larger animals, power generation is to a larger extent used for other purposes (such as motility) and the relation between growth and metabolic rate may also change considerably during the life of an individual. However, relative to the range in metabolic rates when a wide range of sizes of animals are compared, this becomes negligible (except when homeotherms and heterotherms are compared; the former are systematically less 'cost effective' as far as the rate of production per unit of power generated is concerned).

Another point is that the demographic concept of the exponential population growth rate constant is related to the production of biomass. Again this is most easily seen in the case of unicellular organisms: an individual cell grows until it has reached a certain size and then divides into two new cells of half the size of the mother cell. If one were to harvest an otherwise exponentially growing population so as to keep the population size constant, the yield of cells per unit time would be proportional to the growth rate constant and is at the same time a measure of the productivity of the population. This argument also pertains to an exponentially growing population of multicellular organisms with a more complex reproductive pattern (assuming that a stable age distribution of the population has been achieved so that the relative size composition of the organisms harvested remains constant). Of course, a species populations grows at different rates depending on environmental conditions, but again, reasonable estimates of the maximum growth rate of organisms can be obtained and the lack of precision of such estimates is modest relative to the range of growth rates with which we are concerned here. Another parameter to consider is generation time. In organisms which reproduce by binary fission, generation time is simply the reciprocal value of the growth rate constant times the logarithm of 2. This relation between growth rate constant and generation time does not quite hold in the case of organisms with a more complex mode of reproduction, but for the present purpose it is admissible to consider the reciprocal value of generation time as an adequate measure of growth rate.

We therefore expect that the growth rate constant should have the same functional relation to body size as weight specific metabolic rate (that is to be proportional to $-1/4$ power of weight) and consequently that generation times of organisms should increase with the $1/4$ power of weight or with a power of about $3/4$ with respect to length. Figure 13 shows that this seems to hold true. Again it must be stressed that this is only a real generality when

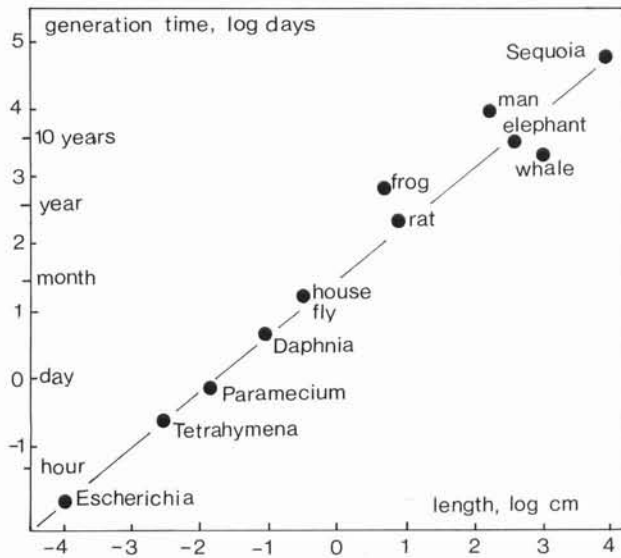


Fig. 13. Generation time as a function of body length for various organisms. Original

organisms covering a large size span are compared. When comparing organisms of roughly similar sizes, real deviations from the generalisation are apparent. These deviations are interesting in their own right, but this falls outside of our present discussion.

What I do want to stress by these considerations is that the scales of time and space are widely different for different organisms. What is a universe to a protozoon is a water drop to an elephant and what is a generation time to an elephant represents about 10^5 generations to the protozoon. (*Homo sapiens* evolved from some ancestral form during the Pleistocene period and has not yet lived through nearly as many generations.) Many people think of ecological systems as if every component interacts in a complex way so as to 'maintain the balance of nature'. In fact organisms of very different sizes do in general show only weak or indirect ecological interactions and in a sense live in 'different worlds'. This is the implicit rationale for carrying out studies on e.g. the microbial ecology of a lake or on the ecology of small mammals. In the former case, the fish have little direct effect on the ecology of the microbes and in the latter cases, mammals are not directly concerned with soil protozoa. But this is not to say that many similar principles do not pertain to the interactions among rodents and those among microbes. I might add that there are notable exceptions. An obvious example is provided by pathogenic microbial parasites of larger organisms such as the plague example in Chapter 3 which indeed represents a strong ecological interaction between a microbe and a mammal. Under all circum-

stances, the relation between body size and rate of living and also the fact that the strongest ecological interactions occur between organisms of comparable sizes have both a considerable influence on the structure of biotic communities. I will discuss some of these effects later.

First, however, I will discuss another size related aspect: that of the size ratio between predators and prey. The consumption of particulate matter is unique to eukaryote organisms and is considered a typical feature of animals, but the unicellular eukaryotes referred to as protozoa also make their living in this way. All such phagotrophic organisms have special adaptations which serve to concentrate or capture food particles. These adaptations show a tremendous diversity among animals and include the baleens of large whales, beaks and teeth, webs of spiders, gills of bivalves (which have developed into a filtering apparatus for catching suspended small algal cells), and the toxic or sticky tentacles of coelenterates or heliozoa. To which may be added sensory and behavioural traits which facilitate the finding of prey.

All such adaptations, however, show constraints in that they are only efficient for certain types or qualities of prey; obviously a killer whale with its huge teeth is not good at catching krill whereas a baleen whale cannot catch or kill a seal. This, of course, is one basic reason that animal life is so diverse: increased efficiency in utilizing one type of food render an animal inefficient with respect to other types of food. In particular there are mechanical constraints in that the mechanism of food capture and the metric dimensions of the mouth or other parts of the food-capture apparatus define a limited size spectrum of food particles which can be used. Some examples illustrating this are shown in Figure 14. Here the sizes of the food particles are shown as a fraction of the sizes of their consumers. This illustrates that the 'food niche width' with respect to particle size is not very different for animals of different sizes.

Certain consumers utilise organisms which are much larger than themselves; this applies, for example, to phytophagous insects, but in this context they are perhaps best considered as parasites of plants. Regarding typical predators there is a more or less fixed relation between the sizes of predator and prey. The prey rarely exceeds the predator in size, but there is also a minimum size of prey which can be efficiently utilised. In raptorial predators, which catch their prey individually, prey size usually exceeds the predator by one tenth and there is a clear linear size relation e.g. between different sized cats, or birds of prey and their respective prey species; see Figures 14 and 15, [50]. There are aquatic animals which are specialised to catch small suspended particles in bulk by sieving them from the water. Again, however, there is some relation between the sizes of the consumers

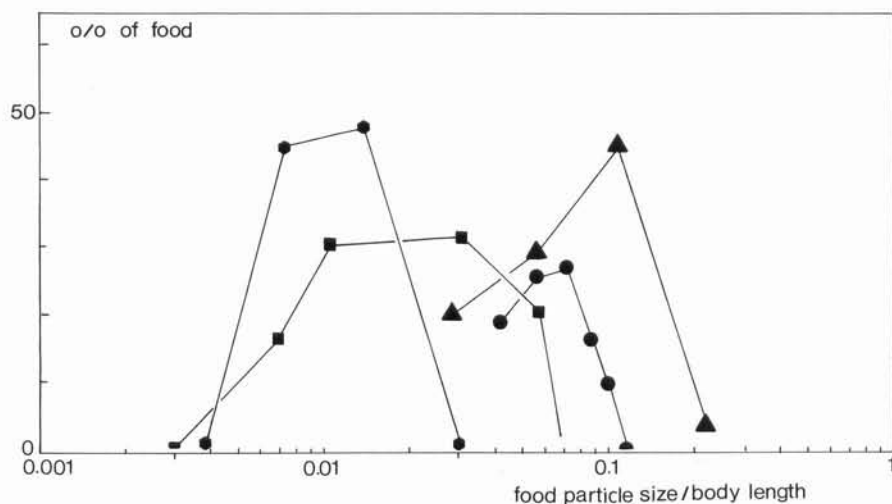


Fig. 14. Size spectrum of ingested food particles (as a fraction of the body length of the consumer) for different organisms. Hexagons: prosobranch snail *Hydrobia ventrosa*, which measures about 3 mm; squares: the ciliate, *Glaucoma scintillans*, which measures about 35 μm ; circles: ciliate *Euplotes vannus*, which measures about 70 μm ; triangles: lizard *Anolis marmoratus*, which measures about 10 cm. Some predators can engulf prey which approaches their own size. However, the examples shown, which cover body size ranging a factor of about 3000, do show that the size ratio of food particles: consumers varies by a factor less than 100. Data on which the graph is based derive from references in [50]

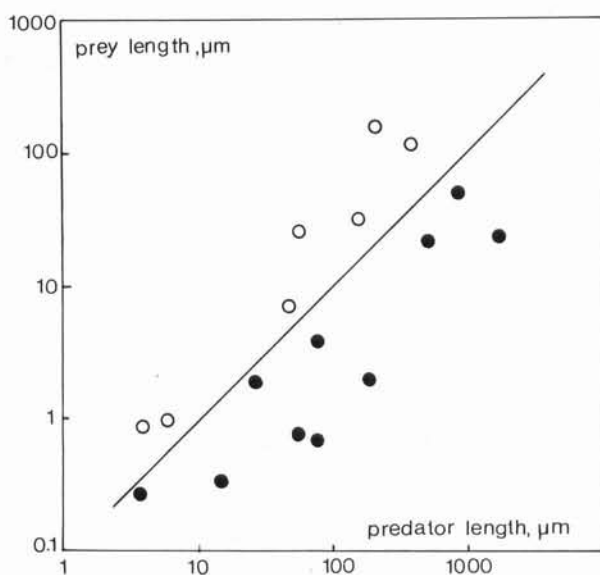


Fig. 15. Ratio between food particle size and cell length in ciliated protozoa. Filled circles are 'filter feeders' which sieve suspended particles from the water with specialised feeding organelles; open circles represent 'raptorial' species. The graph exemplifies that a food particle: body length ratio is typically around 10. Redrawn from Fenchel [50]

and their food particles. To take an extreme example: among ciliates, the about 50 μm long *Glaucoma scintillans* filters about 0.5 μm long bacteria while a 10 m long baleen whale filters about 10 cm long fish; in both cases the size ratio between consumer and prey is about 100:1. At the other extreme, the predatory ciliate *Didinium nasutum* which is specialized in feeding on another ciliate, *Paramecium caudatum* which is only slightly smaller than its enemy and a similar size relation exists between killer whales and their prey (see Fig. 16).

Therefore, even if the food particles of similarly sized phagotrophs may vary by a factor of about 100, a size relation between predators and their prey will be obvious when we compare a wide size range of organisms. Let us now consider a planktonic community. In the sea (or in lakes) the production of particulate living cells is primarily due to photosynthetic unicellular organisms (algae and flagellates) which measure anything from 3 to perhaps 50 μm in diameter, to photosynthetic prokaryotes, and to other bacteria which utilise dissolved organic matter and which typically measure around 1 μm . The smallest (protozoa) and the largest (whales) phagotrophs in the sea measure, let us say, 10 μm and 10 m, respectively. Let us further assume that the typical length ratio between prey and predator is 1:10 (a weight ratio of 1:1000); so in a food chain from primary producers to whales we expect about 6 or 7 'trophic levels'.

If we apply the considerations on the relationships between body weight and metabolic rate and population growth rate, respectively, we can now predict the relative biomass or numbers of individuals in each logarithmic size class of our plankton community provided it is in a steady state (that is, that each size class of organisms retains a constant number of individuals over time, which admittedly is not a quite realistic assumption). The basic way to proceed is to consider for each trophic level the size-dependent energetic requirements for growth and metabolism, and to equate these with the size-dependent productivity of the prey. This theoretical consideration can be carried out in different ways [51] among which the most elegant one considers the food chain as a continuum of sizes rather than the derivation for a compartmentalized food chain as offered in Appendix 1.

At any rate, such models suggest that in a pelagic food chain of the sort we have described, the total biomass of each logarithmic size class should be about equal or decline slightly with size. Thus the total biomass, for example of fish, in the size range 10 cm to 1 m should be about the same as that constituted, for example, by small invertebrates in the size class of 1 mm to 1 cm. The numbers of individuals in each size class should thus be inversely proportional to their weight. As seen in Figure 17 this prediction seems to hold when oceanic plankton communities are considered. The ab-

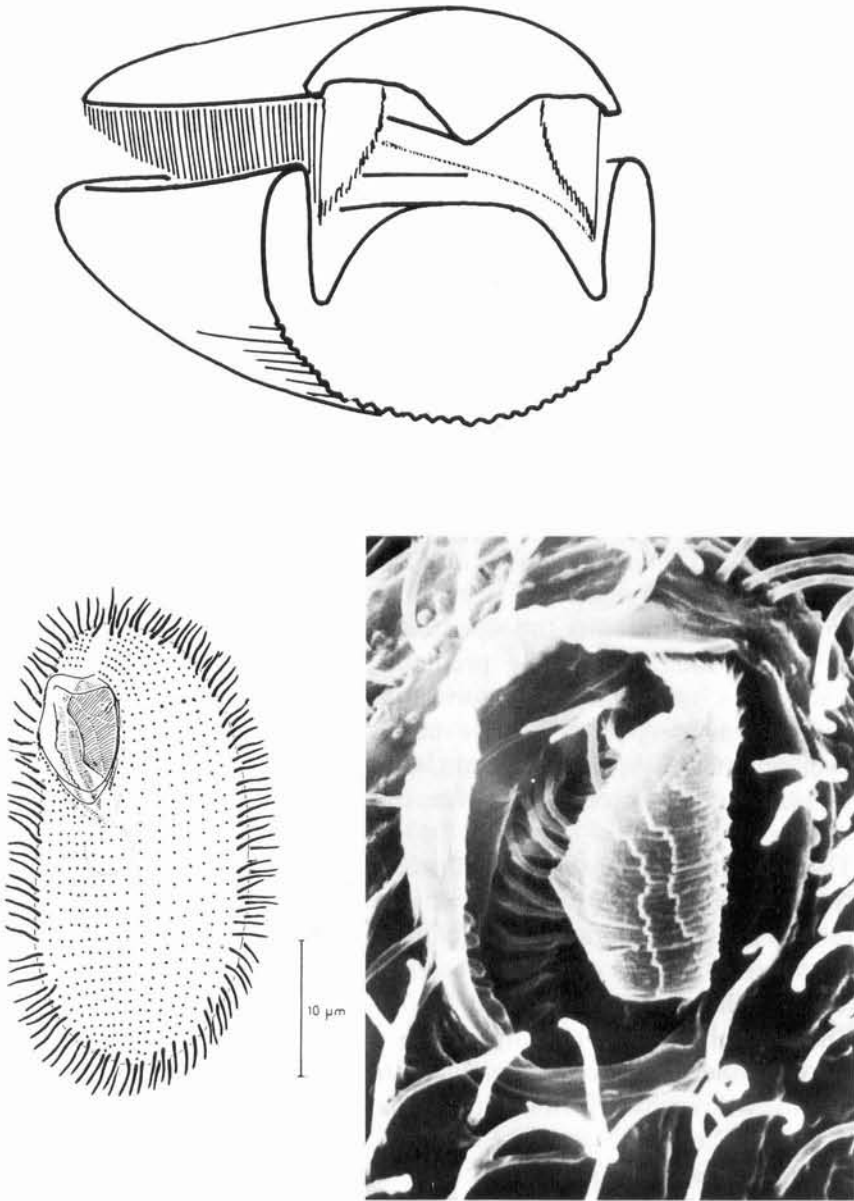


Fig. 16. Above: section through the head of a baleen whale showing the whale bones by which the animal sieves food particles from the water. Below a 'ciliate baleen whale', *Glaucoma scintillans* (whole cell) and a scanning electron micrograph of the mouth. The ciliate squeezes water through an array of cilia in its mouth, thus retaining suspended bacteria. Length ratios between the organisms and their food particle are about the same in the two cases. Original

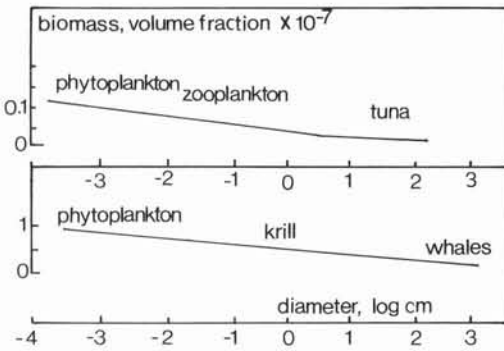


Fig. 17. Biomass of different size classes of pelagic organisms in the tropical Pacific Ocean (above) and in the Antarctic Sea. Redrawn from Sheldon *et al.* [51]

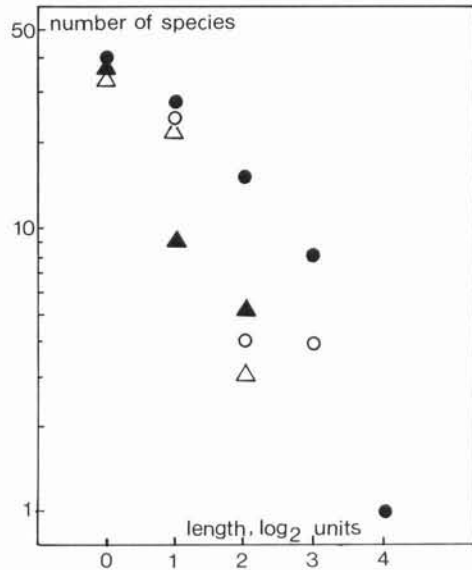
solute values of the biomass or number of individuals are, of course, determined by the primary production of algal cells and bacteria. In this food chain, when going from smaller to larger organisms, the turnover rate of organic carbon decreases. Since there are metabolic and other losses at each step in the food chain, the flow rate of organic material and thus productivity, declines strongly with size.

It is possible to predict the size structure of other types of biotic communities in which the simple predator-prey size relation assumed for plankton does not hold. In a terrestrial community like a forest, for example, the primary producers are mainly large organisms with a relatively lower productivity per unit weight. Consequently, and in contrast to the plankton, their total biomass far exceeds that of the other components of the system.

There are many other ecological problems which pertain to body size; I will return to some of them in later chapters. The present chapter will conclude with a quite different aspect of size which relates to species richness of communities. It is a common observation that there seems to be many more small than large organisms. Most people recognise the local large mammals or birds or even many exotic ones as well. When it comes to rodents and passerine birds this is not quite as easy and there are probably few, if any, who recognise all the insects of his or her neighbourhood.

It is a fundamental idea in ecology that species populations in nature persist in the face of competition from other species by having different 'ecological niches'. Organisms possess some specialisation in relation to their utilisation of their environment which render them superior relative to other species in this particular respect. One such aspect of ecological niches is choice of habitats. There are innumerable examples to show how otherwise relatively similar species differ with respect to their preferred environment in terms of, for example, salinity, humidity, soil pH, and so

Fig. 18. Species numbers for different size classes of some taxa. Open circles: Danish freshwater snails; filled circles: Danish beetles (family Scarabaeidae); open triangles: European freshwater fish (family Cyprinidae); filled triangles: European rodents. The size classes have been normalised so that the smallest species within each taxon has been assigned the length of unity. Data derive from various books on local faunistics. Original



forth; the case of the barnacles discussed in Chapter 6 also provides an example.

Now, the environment appears much more complex to a small than to a large animal. A large mammal may conceive an entire forest as a rather homogeneous area. To a small mammal such as a rodent the same forest constitutes a mosaic of habitats and to an insect it is extremely complex. Different habitats for different types of insects may include different plants, or even parts of plants such as leaves, the trunk or they may be associated with the roots; they may live in soil or in the litter layer or in a number of other places. Roughly speaking, the type of environment an animal may conceive as a habitat should be gauged in terms of its own body length so it could be suggested that the number of species in any size group is inversely proportional to their lengths.

Figure 18 shows that this seems to hold true for some different, arbitrarily chosen groups of animals; within each of these groups the overwhelming majority of the species are small. Does this relation hold for the entire animal kingdom? Apparently not; May [52] has made a similar comparison which includes all described terrestrial animals. For animals exceeding about half a centimetre, an inverse relationship between size and species numbers was evident, but when including even smaller animals there was a tendency of decreasing species numbers with decreasing body size. May explained this as a result of taxonomic inadequacy: the 'missing' small animals have simply not yet been described or the taxonomic resolu-

tion may be poorer when small animals are considered. This could be part of an explanation, but I do not believe it is the whole story. In part, it seems, the tremendous diversity of certain insect groups is due to the diversity of terrestrial vascular plants which offer a wide selection of habitat niches and these may in particular be exploited by certain medium-sized classes of terrestrial organisms. However, in aquatic environments a similar observation can be made; the very smallest organisms seem to present fewer species than would be expected. Thus extrapolating figures such as those compiled by May one would expect perhaps 10^7 species of protozoa to exist; thus far, however, at most some 50,000 species have been named.

There is no doubt, a large number of protozoa which remains to be discovered, but this alone cannot explain the discrepancy. One reason, perhaps, is the geographically wide distribution of individual species of protozoa (and of other very small organisms) which is due to the immense population sizes of the single species populations in conjunction with a high ability of dispersal. This might suggest that the rate of speciation due to geographical isolation is lower in the smallest organisms relative to larger ones where disjunct and isolated populations of single species may occur much more frequently over geological periods of time.

11 Flows of Energy and Materials

Organisms grow and reproduce, thus maximising their individual fitness. To do so they need free energy and materials from their surroundings so that the metabolic machinery of the cells can convert these into potential chemical energy and macromolecules. The metabolic machinery may be considered as consisting of two parts: a dissimilatory one and an assimilatory one. This distinction is rarely made when considering animals which obtain all their needs from the particulate organic material they eat, but it is useful when photosynthetic organisms and bacteria are considered.

The power generation of photosynthetic organisms is based entirely or partly on photophosphorylation and on the photochemical reduction of carbon dioxide to produce organic compounds which are then used either in the assimilatory or the dissimilatory metabolism. Eukaryotes and blue-green bacteria use water as a reductant in photosynthesis whereas other bacteria (including some blue-greens) use reduced sulphur compounds, hydrogen gas or organic compounds as reductants. In the extant biosphere these processes constitute the entire energetic base for life. To be sure, hydrogen sulphide and possibly other reduced inorganic compounds deriving from geothermal processes can support some rather exotic biotic communi-

ties in hot springs and geothermal vents. Communities based on the bacterial oxidation of, in particular, hydrogen sulphide are common elsewhere, but here the sulphide always derives from the anaerobic degradation of photosynthetically produced organic material. The assimilatory metabolism of photosynthetic organisms is in principle based on carbon dioxide (but organic compounds may also be used in some cases) and on the uptake of mineral salts which cover the need for different essential elements; in some cases this is associated with an assimilatory reduction, e.g. when nitrate is the source of nitrogen while, for example, phosphorus does not change oxidation state in biological processes.

All other organisms are chemotrophs which generate power through oxidation-reduction processes involving chemical species from the environment. Among prokaryotes there is a considerable variety of processes including fermentative ones with substrate phosphorylation and a variety of respiratory processes (electron transport phosphorylation) involving different electron acceptors (oxygen, sulphate, nitrate, carbon dioxide, organic compounds) and electron donors (organic compounds, reduced compounds of sulphur, nitrogen and iron, methane, hydrogen gas). In addition there is a great variety of assimilatory processes; bacteria may depend on the assimilatory reduction of carbon dioxide or the uptake of organic materials and their needs for other elements may be met in a variety of ways [53]; see also Chapter 19.

In comparison with prokaryotes, the metabolic processes of eukaryotes are stereotypical. They depend on organic material for their assimilatory and dissimilatory metabolism and power generation is predominantly due to oxidative phosphorylation (although very few animals, few protozoa and some fungi may be facultative or obligate anaerobes, depending on fermentative power generation).

In many ecological contexts, it is of interest to measure the relation between the uptake of resources and the resulting production; the previous chapter already used this concept. There are different measures of these efficiencies. It seems an invariant property of cells that they can produce about 10 g of dry weight of organic material from the generation of 1 mol of ATP (a compound which all organisms use for storing chemical energy). What this means in terms of the uptake of a certain quantity of substrate or food depends, of course, on its chemical composition and the dissimilatory processes involved. If an aerobic organism consumes organic compounds in which the carbon atoms have a reduction level such as in glucose (and this is the most common situation in animals and in plants) about 60% of the carbon turns up as cell material while the remainder is mineralised in dissimilatory processes: that is the 'net growth efficiency' is 60%. If the organ-

ism utilises the same substrate through some fermentative pathway, the power generation per mol substrate, and so the net growth efficiency, will only be about one tenth of that of aerobic respiration. These relations have been established in cultures of various prokaryotic and eukaryotic microorganisms. A net growth efficiency of 60% in terms of organic carbon, however, does not apply if the cells are starved with respect to some other nutrient such as nitrogen or phosphorus; in that case the growth efficiency may be much lower. Embryonic and juvenile tissues of animals (except for homeotherms which have a somewhat lower net growth efficiency) can also grow with a net growth efficiency of about 60%, but in most multicellular organisms growth efficiency declines with the age of the individual [54].

Under all circumstances, the actual 'yield coefficient' (microbiologist jargon) or 'gross growth efficiency' (animal ecologist jargon) tends to be somewhat less than the expected 60% (assuming oxidative phosphorylation) in terms of the amount of consumed material which turns up as the eventual production of cells. All organisms excrete some dissolved organic material which represents a loss (this may be a considerable fraction of the primary production of plants and algae). In the case of animals, food items are only incompletely digestible; for example, most animals cannot or can only partially digest certain structural polymers like lignin, cellulose or chitin and so, particularly in herbivores, may extract a limited amount of the organic material they consume.

The above considerations also apply to photosynthetic organisms as far as the biochemical processes go. The efficiency with which light is harvested, however, is relatively low. At most about 10% of the energy flux of the photosynthetically active electromagnetic radiation (which is again about half of the total solar radiation) is recovered in terms of the generation of reduced carbon. In terms of incident radiation the growth efficiency of plants is low.

These measures of conversion efficiencies have so far implicitly been considered to be properties of individual organisms and their actual values will vary according to the physiological state and the age of the individuals. The concept can also be applied for whole populations, but the conversion efficiencies may then vary over time. However, if we consider exponentially growing populations which have attained a 'stable age structure' or 'balanced growth', they will be time invariant. These two attributes are essentially identical and describe a state which all exponentially growing populations eventually will attain. The state is characterised by the property that in whatever way which we quantify growth (number of individuals, organic carbon, DNA, etc.), we will measure the same rate constant. Measures of efficiency can also be assigned to whole functional groups of communities,

such as the photosynthetic efficiency of the entire greenery within some specified area.

The processes outlined above are really those which mediate most species interactions such as competition for common resources, prey-predator relation, parasitism and many types of mutualistic interactions. In fact, the transfer of materials and competition for these materials are implicit in the theoretical models of populations we shall discuss in later chapters.

To see this, it is perhaps best first to observe that productivity is limited. Ultimately, solar radiation is the limiting factor and this situation is sometimes realised in, for example, very productive ponds or in forests where virtually all photosynthetically active light is absorbed by chlorophyll [55]. In terrestrial environments, the availability of water often sets a limit to plant biomass and production; otherwise the availability of mineral nutrients, in particular nitrogen and phosphorus, sets a limit to production. Most of the primary production is rapidly mineralised by heterotrophic microbes and animals. As regards some of this organic material, there is a time lag in its mineralisation; this material is represented by organic 'detritus' and leaf litter and especially polymeric and resilient material such as humic acids which in a dissolved form make up the bulk of organic matter in natural waters. Most of this is eventually degraded as well, and only a very slight fraction of the organic material is eventually fossilised under certain geochemical conditions in sediments as peat, lignite and other sedimentary organic material to be effectively removed from the biosphere. This argument — that all production eventually is consumed — shows that at least some components of ecological systems must be limited by food resources [56].

Let us next look at the concept of 'limiting resources'. The basic observation here is, of course, that while organisms require many things from their environments in order to survive and grow, the absence or scarce supply of just one such factor may limit growth. Plants (as all other organisms) have, for example, an absolute requirement for phosphorus which they can take up in the form of dissolved phosphate. If this is not available, the plants will not grow irrespectively of whether all other demands of the plant are met. In terms of mineral salts and also organic substrates for bacteria this is often discussed in terms of 'Liebig's law of the minimum' [57] which amounts to the statement that only one component is limiting at any one time.

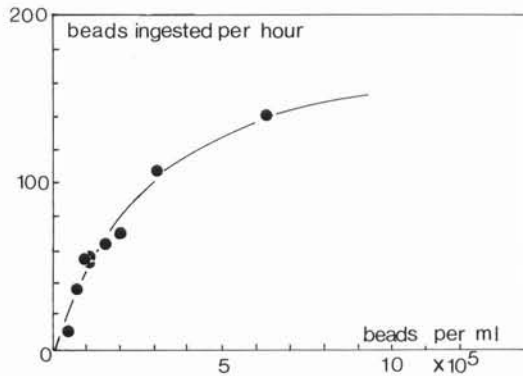
Liebig's law is often interpreted in an ambiguous way. To the extent it refers to the amount of biomass which can be generated on the basis of a given amount of a resource, Liebig's law represents a clear (and correct) statement. For example, the molar ratio of phosphorus to carbon of unicellular algae is 1:106. Consequently, an amount of algae which can be grown

in a flask with a given amount of dissolved phosphate can be calculated (provided other algal resources are present in excess). However, Liebig's law is often inferred when considering growth rates (in cultures or in the field). This, however, can be somewhat elusive in that a population which grows slowly due to, e.g. a low ambient phosphate concentration may, in fact, be stimulated by the addition of other nutrients. Also complications arise, because the uptake per cell of certain nutrients may not be proportional to growth rate and some cells take up an excess of certain nutrients under some growth conditions 'in anticipation' of a future shortage [53].

Animals may, of course, also be limited by their food resources; they may also be limited by a variety of other types of resources (such as nesting places, places to hide or attach to, etc.) but this is not a concern in this chapter. Under all circumstances, it would seem useful to consider the rate of consumption or uptake of a resource as a function of the concentration or abundance of that resource in the environment. It is obvious that such relationships must influence the dynamics of prey-predator or consumer-resource systems. They are also important when considering the competition for limiting resources between different phenotypes of a single species or between populations of two species which depend on the same resource. Such relationships are referred to as 'functional responses' by zoologists (that is the rate of food particle consumption per individual as a function of the abundance of food particles). Microbiologists and plant physiologists refer to the rate of uptake of a limiting dissolved nutrient as the 'uptake kinetics'.

Let us first discuss the functional responses of animals. Their study owes much to Holling with respect to a theoretical as well as an experimental treatment [58]. Holling distinguished between three types of responses. They all have a satiation effect in common; that is, at some level of prey density or food particle concentration, no further increase in consumption takes place. The 'Type II' functional response is probably the most general one and certainly the easiest to rationalise. Assume that a predator can search a certain area for prey per unit time and denote that with the symbol F . The magnitude of F depends on factors such as the velocity at which the predator moves, its sensory ability to detect the prey and perhaps other factors, but it is assumed to be invariant with prey density, x . With these assumptions, prey consumption per predator should simply be linear or $I(x) = Fx$. Now assume that when prey is detected, it takes a finite time period, T , to catch, kill and ingest the prey. Thus during a fraction of the time equal to $I(x) T$, it is incapable of searching for prey because it spends its time handling and eating prey already caught. The functional response

Fig. 19. Ingestion of 2 μm large plastic beads by the ciliated protozoon *Halteria grandinella*, as a function of the concentration of beads in the water. The functional response fits the Holling type II model (curve fitted to data). After Fenchel [50]



then becomes: $I(x) = Fx[1 - I(x)T]$, or rearranging the equation:

$$I(x) = I'x/[I'/F + x]$$

Here I' is the maximum rate at which prey can be consumed ($= 1/T$) as can be seen by letting x approach infinity. As x approaches zero, the consumption rate becomes $I(x) = Fx$. The model can equally well be applied, e.g. to a filter feeder: only in that case, F is the volume of water processed per unit time ('clearance'). An example of the functional response of a protozoan filter feeder is provided in Figure 19. Here the time constant is that needed for the ciliate to make a feeding vacuole and F the volume of water the cell can propel through its ciliary filter.

The equation is analogous to the Michaelis-Menten equation describing enzyme kinetics in which the 'half-saturation constant' corresponds to the ratio I'/F in the present model; in both cases this is an ad hoc parameter which measures the concentration corresponding to one half of the maximum sustainable uptake rate.

Another type of functional response (Holling's 'Type I') is one in which the rate of prey ingestion is nearly linear up to a certain threshold prey density at which the consumption becomes constant. This type of functional response is likely to occur, but has not to my knowledge been well documented. In fact, regarding much of the published data on functional responses, it is statistically impossible to distinguish between the two mentioned types of functional responses and also to distinguish these from some other, empirically derived equations which yield rather similar predictions. A third type of functional response is probably only found in higher animals (Fig. 20). It is sigmoid in shape and this reflects that at very low prey density, the search efficiency is relatively lower than at higher prey densities. There are various interpretations of this. One is that the predator simply 'doesn't bother'

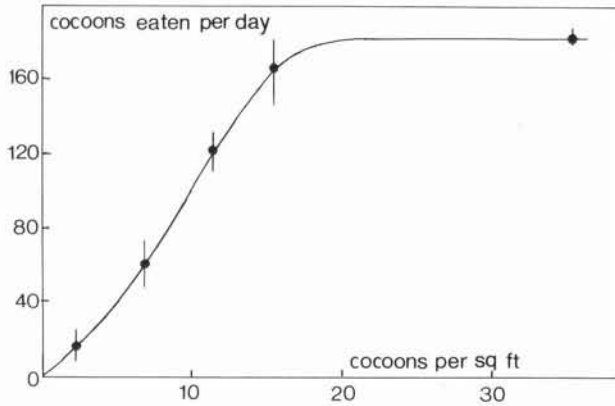


Fig. 20. Functional response of the small mammal, *Peromyscus*, feeding on insect cocoons. Redrawn from Holling [58]

at low prey densities; that is, the expenditure of searching does not give a reasonable pay-off. Another is that there is a certain learning process involved in catching a certain kind of prey in terms of recognising or handling it. This effect is particularly interesting when a predator has two alternative prey species, but tends to catch the more common one more efficiently (Fig. 21). This is interesting in that it represents a mechanism whereby two competing prey species can co-exist due to predation pressure and it has also been inferred in the maintenance of protected colour polymorphism in prey species [59].

Holling also introduced the term 'numerical response' to mean the response in population growth rate as a function of food density. In microorganisms the relation to the functional response is an easy one in that the yield coefficient or gross growth efficiency is nearly invariant with growth

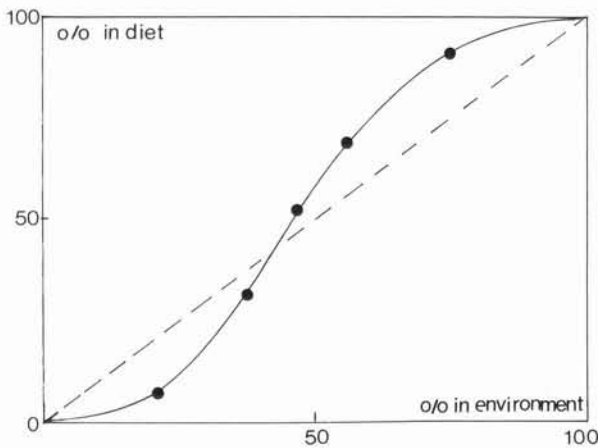


Fig. 21. Ingestion of mayflies by a species of the predatory water bug genus, *Notonecta*. The bug was presented to mixtures of mayflies and an alternative prey, the crustacean *Asellus*; the graph shows the relative importance of mayflies in the diet as a function of their relative abundance among the prey. Redrawn from Lawton *et al.* [59]

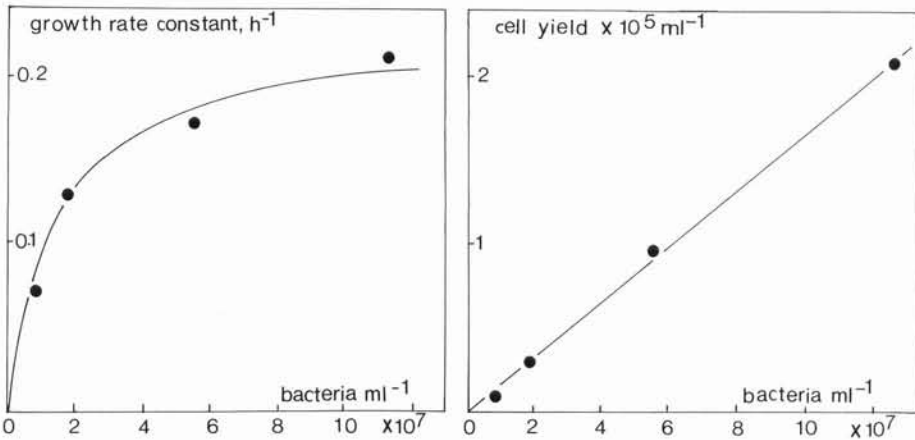


Fig. 22. Left: growth rate constant of the flagellate *Paraphysomonas* as a function of the concentration of its food particles: suspended bacteria. The relation is identical to the functional response since (right) the growth efficiency (yield coefficient) is invariant with growth rate. After Fenchel [58]

rate. The two functions then become identical except for a proportionality constant, which is the yield coefficient (Fig. 22). In multicellular organisms this relation is not for a variety of reasons quite as simple. Also there may be a considerable time lag in the numerical response to a changed food level.

Uptake kinetics (and numerical responses) of bacteria and microalgae have been described in terms of the Michaelis-Menten equation (that model is quite analogous to that of the Holling Type II functional response) since the studies by Monod on bacterial growth, and in most cases the model, closely fits experimental data [60]. A rationale for this can be obtained in a quite similar way. Two factors are believed to control the uptake of a dissolved nutrient. At very low concentrations it is the diffusion of the substrate towards the cell. In the extreme case, the concentration of the substrate is zero at the cell surface and the transport of the solute to the cell is due to the diffusion gradient surrounding it. This flux is determined by the diffusion coefficient of the substrate, its concentration in the bulk fluid and the geometry of the cell (being proportional to cell length see Appendix 2). It can in principle be calculated for a spherical cell, but this theoretical 'maximum clearance' seems to be higher than empirical results suggest for reasons which are only incompletely understood [61]. As the bulk concentration increases, the transport capacity of the cell membrane plays an increasing role and eventually sets the limit for the maximum uptake rate, which is then proportional to surface area (the derivation of this is given in

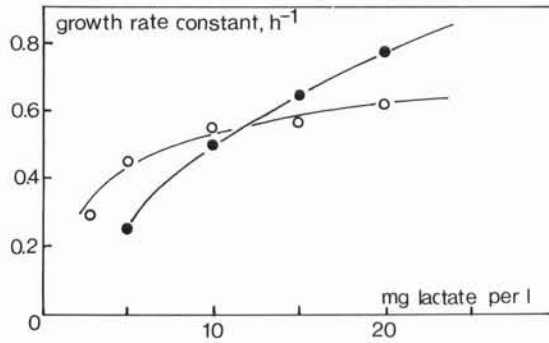
Appendix 2). One immediately interesting consequence is that since, at very low substrate concentrations, uptake is proportional to cell length (that is, inversely proportional to the $\frac{2}{3}$ power of cell volume) only the smallest organisms (bacteria) should be competitive in utilising dissolved organic material in natural waters where the concentration is usually exceedingly low, and this prediction seems to hold. On the other hand, at very high concentrations, when uptake becomes proportional to surface area (and thus roughly with metabolic demands) larger organisms should in principle also be competitive in the utilisation of this resource. This is mainly exemplified by certain protozoan and metazoan intestinal parasites.

Relations such as these allow us to infer properties of predator-prey systems (see Chapter 13). Knowing the parameter values for the uptake of solutes or for the capture of particulate food, we can — at least in principle — estimate actual uptake rates in nature if we know the densities of the organism and of its resources. It also allows us to predict the outcome of competition for limiting resources.

Competition is a complex concept which describes several kinds of interactions. In the type with which this chapter is concerned suspended or motile organisms compete for a dissolved nutrient (mineral or organic substrate) or for dispersed food particles of some sort. In a homogeneous universe, the consumer population will increase until the resource concentration has decreased to a level where the production rate of the resource can just sustain a constant consumer population size. Consequently, if two organisms compete for the same resource, the winner can be inferred from the functional response or the uptake kinetics. The species which is capable of growing at the lowest resource concentration will have the highest 'clearance' or, in terms of a graphical presentation of the functional response, the steepest slope at the origin. This organism will always be the winner in a resource competition because it can maintain growth at a resource level where its competitors cannot grow.

However, it is possible to isolate different bacteria which seem to utilise similar substrates, but in which the parameters of the uptake kinetics differ. An example is shown in Figure 23 [62]. Clearly, the *Spirillum* strain is the more efficient bacterium at low substrate concentrations and so it is not obvious how the *Pseudomonas* strain survive in a competitive world. However, at high substrate levels the latter obviously has a higher efficiency. Its survival could be based on the fact that the world is heterogeneous. If *Pseudomonas* colonises an isolated patch in soil or sediments with a local high concentration of resources (such as debris of a dead animal or plant or fecal material) it will there be able to grow faster than its competitor in this particular patch as long as there is a relatively high substrate concentration.

Fig. 23. Growth rate constant of two strains of bacteria (open circles: *Spirillum*; filled circles: *Pseudomonas*) as a function of the substrate concentration in the environment. Redrawn from Veldkamp & Jannasch [62]



It may eventually be outcompeted, but as long as some of its progeny will make it to another patch, the population will persist. Other explanations for such an isolated example could be given; for example, that their performance with respect to other organic substances differs. However, the example does under all circumstances illustrate the principle that a large capacity for uptake and growth can be an adaptive trait in a heterogeneous environment while at the same time sacrificing competitive ability at low substrate concentrations.

So far I have implied that the cycling of other elements follows that of carbon; that is to say that when a unit of organic material is produced or mineralised all its constituent elements are taken up or mineralised in the same proportion as they occur in the tissue of the organisms. This may also be the case for food chains consisting of animal prey and predator species because their elemental composition is nearly similar and animals cannot take up dissolved mineral nutrients from their environment. If we, for example, consider nitrogen, the fraction mineralised equals that of consumed organic carbon which is respired, divided by the carbon to nitrogen ratio of the tissue. However, in many cases this simple relation between the different elements in the flow of materials in ecosystems does not hold.

One reason for this is that larger photosynthetic organisms and in particular vascular plants have a relatively low concentration of essential elements (other than carbon, oxygen and hydrogen). For example while the carbon to nitrogen ratio of bacteria and of most animal cells is 5 to 6 and that of unicellular algae is 7 to 8, the C:N ratio of vascular plants is within the range of 16 to 68 and that of fresh wood may be around 1000. From an evolutionary point of view this may be seen as an adaptation to environments with an intense competition for available nitrogen (and other elements) and it reflects, of course, that the bulk of vascular plants is made up of supportive tissue which mainly consist of structural polysaccharides and other nutrient-poor polymers. It may also be considered as an adaptive

trait in that the low nitrogen contents of most types of plant tissue renders it useless as food for animals and inhibits its degradation by bacteria and fungi. The production of 'honey dew' by aphids exemplifies this; when aphids suck plant juices there is an excess of carbohydrates relative to organic nitrogen and so the insects excrete a large amount of the ingested organic material. It has been generalised that when the carbon to nitrogen ratio exceeds about 18, the material cannot be used as food by animals because their nitrogen demands cannot be met [63]. Herbivores which depend on microbial symbiosis for the degradation of their food, e.g. ruminant mammals and termites constitute an exception to this. Termites host nitrogen fixing, bacterial symbionts. Ruminants provide the rumen bacteria with mineral nutrients dissolved in saliva; these nutrients are re-absorbed and so re-cycled within the ruminant [64, 125].

These considerations in part explain why 'the world is green' (i.e. why herbivores do not graze larger plants much more efficiently and why slow-growing large plants represent by far the largest part of the living biomass in terrestrial environments), and also why litter and detritus derived from vascular plants is degraded so slowly. Herbivores simply cannot make direct use of much of the tissue of plants, and bacteria and fungi need external mineral nutrients in order to degrade it. It can be calculated that the organic substrate of aerobic bacteria must have a carbon to nitrogen ratio which does not exceed 10 in order for the bacteria to be net mineralisers of nitrogen. Otherwise the bacteria will have to assimilate dissolved nitrogen from the surroundings. Additional reasons for the limits to herbivore utilisation of plants and the slow degradation of dead plant material by microbes are (1) the presence of secondary plant compounds (such as phenols) which inhibit herbivory and microbial activity; (2) the fact that few animals can hydrolyse structural plant compounds; (3) a mechanical degradation of plant tissue is often a necessary prerequisite for rapid microbial degradation.

That bacteria often need external sources of nitrogen and phosphorus in order to build sufficiently large populations which can degrade plant detritus rapidly is exemplified in Figure 24 [65] which illustrates the degradation of barley hay by an aquatic microbial community. Thus, bacteria 'mineralising' plant tissue may in fact at the same time compete with the plants for mineral nutrients. This has some important implications for natural and man made ecological systems. A too large addition of organic material (such as straw) to soils may have an adverse effect on soil fertility in that the microbes which degrade this material compete with the crop plants for mineral nutrients. In many terrestrial ecosystems the mechanism has the effect that mineral nutrients are immobilised by microbes outside the grow-

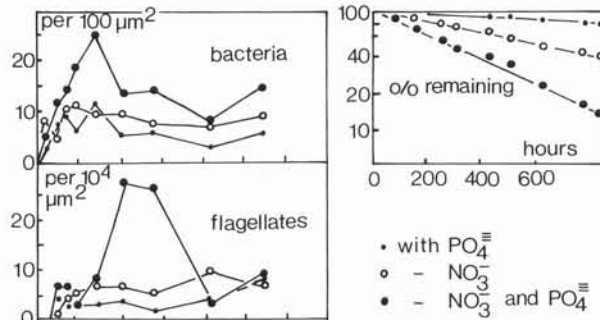


Fig. 24. Development of bacterial populations and of protozoa consuming bacteria (left), and the rate of degradation (right) of barley hay particles in seawater and enriched with different combinations of mineral nutrients. The experiment shows that the mineral nutrients enhance degradation rates and micobial population sizes; thus, in order to mineralise the nutrient-deficient organic material, bacteria assimilate mineral nutrients from the environment. Redrawn from Fenchel & Jørgensen [65]

ing season and so retain nutrients which otherwise tend to wash out of the soil [66].

There are other mechanisms which complicate the cycling of mineral nutrients. Different types of bacterial dissimilatory metabolism may interfere with the cycling of certain elements. If we stick to nitrogen as an example, we may first note that this element occurs with different oxidation levels in its biological cycle (Fig. 25). All forms (including atmospheric N₂) may be used in the assimilatory uptake of plants, fungi and bacteria. Each individual species or physiological type can only use a restricted number of nitrogen compounds; fixation of atmospheric nitrogen, for example, is carried out only by blue-green bacteria and by certain other, mainly anaerobic or microaerophilic bacteria. Reduced forms of nitrogen (but not atmospheric nitrogen) can also be oxidised in a dissimilatory metabolic process of 'nitrifying' bacteria in aerobic environments and so non-assimilated reduced nitrogen tends to become oxidised to nitrate. Nitrate in turn serves as an electron acceptor in a respiratory process carried out by many types of ('de-nitrifying') bacteria in anaerobic or microaerophilic environments. The main end product of this latter process is atmospheric nitrogen. All these microbial processes tend to complicate the nitrogen cycle [53].

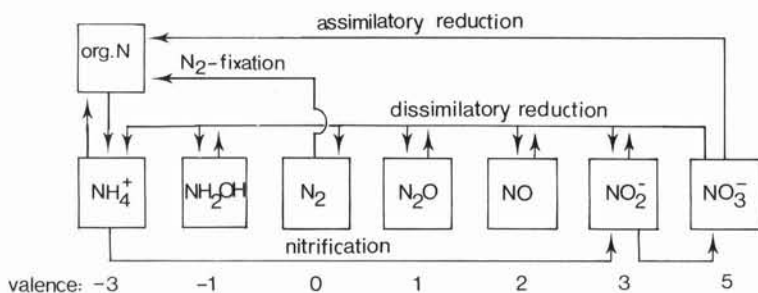


Fig. 25. Biological nitrogen cycle. Animals (and protozoa) utilise only organic N; plants may take up nitrogen in the form of ammonia or nitrate. Some prokaryotic organisms can utilise atmospheric nitrogen ('nitrogen fixation'). Various prokaryotic organisms may assimilate nitrogen in other forms; in addition, some forms utilise different nitrogen compounds in dissimilatory (energy yielding) processes (either using oxidised forms of nitrogen as a electron sink in a respiratory process or by oxidising reduced forms of nitrogen). After Fenchel & Blackburn [53]

Different element cycles also interact. One example of this is perhaps provided by the fact that the ratio of nitrogen to phosphorus of planktonic algae is similar to that of seawater (with local exceptions), that is, about 16:1 [67]. This could, of course, be fortuitous; or it could be that algae had adapted during their evolution their contents of these two elements to the ratio characteristic of seawater. Another hypothesis is that the ratio of these two elements in seawater is controlled by the composition of algae in conjunction with the microbial transformation of nitrogen compounds and with the chemical properties of phosphate. The concentration of dissolved, inorganic phosphate is controlled by precipitation with calcium and iron ions and by the subsequent dissolution of these phosphates which takes place in acid or reducing chemical environments. Thus phosphate controls algal growth in seawater; if there is an excess of nitrate this is lost to the biota through denitrification and conversely if there is an excess of phosphate relative to nitrate then nitrogen-fixing organisms (in the sea mainly cyanobacteria) are stimulated. This mechanism would explain why the relative concentrations of dissolved inorganic nitrogen and dissolved phosphate is maintained at the same level as found in living cells.

12 Limits to Growth: Competition for Resources

If the reproductive pattern of the individuals of a population remains invariant with time that population will grow exponentially. Growth and the probabilities of death and reproduction are, of course, age dependent for

any one individual, but as long as this age-dependent behaviour remains the same for the different individuals, exponential population growth will result. This amounts to saying that the growth of the population is at any time proportional to population size (irrespective of how we measure it). The proportionality constant is usually designated r (microbiologists favour μ) and it is also referred to as 'Malthusian parameter' or 'intrinsic rate of increase'. Exponential growth can thus be described by the differential equation: $dx/dt = rx$, the solution to which is $x(t) = x(0) \exp[rt]$, where $x(t)$ is the density or absolute size of the population at time t . When $r > 0$, the population will increase exponentially, if $r = 0$, it will remain constant, and if $r < 0$ it will decline exponentially. The value of the growth rate constant r depends on the species (or rather the genotype) and on environmental conditions. For any set of environmental conditions, r is a characteristic of the species (genotype). Actually, a population initiated by an arbitrary age structure and grown under constant environmental conditions may not at first grow exponentially, but rather approach this state asymptotically at the same time as the population approaches a stable, time invariant age structure.

The generalisation that all populations, given a constant environment, will grow exponentially was made by Malthus. The theory of exponentially growing populations which has been developed in this century is usually referred to as 'demography'. This includes the relation between the exponential growth rate constant and features which primarily determine population growth: individual death and birth events; relation of the stable age structure to the growth rate constant; and generation time. Demography is of immense importance in the description of human populations and also in applied ecology, such as game management and in theoretical studies, for example, concerning the evolution of life cycles [68].

The concept of exponential growth is also the reference and starting point for all theoretical population biology. This might seem strange because although this theory has been thoroughly studied and although it can often be applied when describing real populations it is fundamentally unrealistic and the reason for this is that populations alter their environment as they grow. With respect to microorganisms or small animals such as water fleas and the like, it is possible to grow cultures in the laboratory under conditions which allow for a close approximation to exponential growth over several generations, and continuous culture devices such as the chemostat can, in principle at least, maintain very close approximations to balanced, exponential growth.

Regarding nature, it is obvious that neither positive nor negative exponential growth can be maintained for a very long time; in the former case

the populations would increase to infinity and in the latter case the population would be driven to extinction. It follows that the growth rate constant of all non-extinct populations must, if a sufficiently long time span is considered, average exactly zero. A central question in ecology is how this is accomplished.

Much attention in population biology has been given to how environmental factors and their stochastic fluctuations influence population size over time and hence population growth rate. There is no doubt that all populations are to a varying degree affected by the stochasticity of the physical and chemical environment. Such regulatory mechanisms of populations are referred to as 'density independent' regulation implying that birth and death rates remain unaffected by the population size. However, even if the vagaries of the environment have a profound influence on how death and birth rates fluctuate over time they cannot solely be held responsible for maintaining finite population sizes. It is not conceivable that such environmental fluctuations could exactly balance, that is, that favourable and unfavourable conditions accomplish an average growth rate constant of exactly zero. Even an extremely small positive or negative deviation from zero would over time lead to the population taking over the world or to extinction, respectively [69]. Population control through predation and parasitism is indeed an important factor in controlling the sizes of populations in nature; again, as discussed in Chapter 13, control mechanisms which entirely rely on the predation of an otherwise exponentially growing population are not realistic. Therefore, even if we find for a given population that the majority of the deaths of individuals can be ascribed to periodically unfavourable physical conditions, we are forced to conclude that density-dependent factors which influence birth and death rates, however weak they may seem, play a decisive role in determining the sizes of populations in nature. The fundamental mechanism is the competition for limiting resources, the intensity of which increases with increasing population density. In the following I will briefly discuss some models which describe the effect of intraspecific competition for resources and then expand this discussion to cases where more species compete for common resources.

In so doing we will already in this relatively simple ecological situation experience that the complexity of real populations and their interactions with the environment do not allow for a complete and general description and that the biological interpretation of the models' parameters is not always simple. Practically all population models which describe situations other than exponential growth simplify, or even more frequently altogether ignore age structure. In real populations the density-dependent factors may mainly or exclusively affect certain age classes. There are likely to be dif-

ferent mechanisms involved in density-dependent population regulation. In sessile organisms, such as the barnacles discussed in Chapter 6, population size seems ultimately to be limited by the space available, and something similar may apply to species with territorial behaviour, or to birds competing for suitable nesting sites. In other cases populations may be limited by the density of some limiting resource such as prey species or dissolved phosphate. It is not likely that a single, simple model can adequately describe these different situations or, if this is accomplished, that the parameters of the model always can be interpreted in the same way. We will also see that a parameterisation of a model may be permissible and useful in some contexts (for example when describing the growth of a population in which it is assumed that no evolutionary change takes place) whereas the same parameters become meaningless or misleading in other contexts (such as describing evolutionary changes in that particular population).

There exists a whole family of models which attempt to describe the dynamics of density-dependent population growth. Many of these have the general form:

$$dx/dt = F(x)$$

Here F is a function which is positive for sufficiently small values of x and which, at least above certain values of x , decreases with increasing x . If x exceeds a certain value, K , then the function F becomes negative. The population size K is then supposed to represent the equilibrium size, or at least the average size around which the population will fluctuate. The magnitude of K , which is referred to as the 'carrying capacity' is obviously a function of the environment as well as of the phenotypes of the population.

The simplest of such models is usually referred to as the 'logistic model' or the 'Pearl-Verhulst model' after its two (independent) discoverers [70]. It assumes that the per capita reproductive rate of the population simply decreases linearly with population size. The model is usually parameterised in terms of the growth rate constant r , describing growth at low densities and the carrying capacity, K :

$$dx/dt = rx[1 - x/K]$$

Its properties are easily deduced. The per capita growth rate, dx/dt $1/x$, declines linearly with x and is zero for $x = K$. The population growth is zero for $x = 0$ and for $x = K$ and takes a maximum value for $x = K/2$. The integrated version of the model describes a sigmoid population growth which is nearly exponential for very small values of x , and x approaches K asymptotically with time.

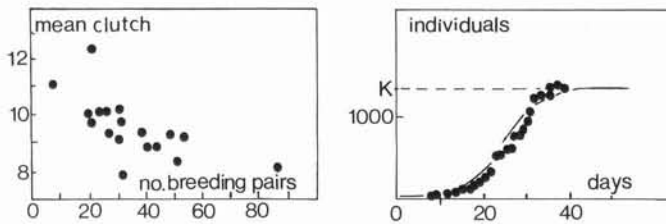


Fig. 26. Left: mean clutch size of a population of titmice, *Parus major*, as a function of the number of breeding pairs. Right: the growth of a population of the freshwater coelenterate, *Hydra* sp., in an experimental tank. Data were fitted to the logistic model. The data, in fact, deviate significantly from the predictions of the model (solid line). Based on Lack (left) and on Christiansen & Fenchel (right) [70]

The model is often presented without any attempt to rationalise its properties and in fact this may not be easy. It is a fact that empirically the model often describes real populations reasonably well; the per capita population growth rate does often decrease approximately linearly in real populations and it is often possible to obtain a reasonably good fit between the integrated version of the model and real populations (Fig. 26). One rationale for the model could be that in many further theoretical applications of the model, the situation around the equilibrium is the one of particular interest and so it is permissible to linearise the density-dependent effect within a small interval around $x = K$. Which is not necessarily to say that the logistic model actually describes the biological mechanisms in an adequate manner.

One way to rationalise the logistic model in the case of the competition for a resource is the following. Imagine a limiting resource, the density of which is denoted R (see also Fig. 27). When the resource is not utilised, $R = S$ (that is the carrying capacity of the resource is S). It is further assumed that the consumer population needs a minimum resource intake, T , in order to increase. The growth rate of the consumer population is then given by the expression:

$$dx/dt = x[iR e - T]$$

Here i is the efficiency by which x concentrates or captures its resource and e measures the conversion or growth efficiency. The resource level as a



Fig. 27. 'Resource axis'; the concentration of the resource R equals S when not exploited. The consumer can increase in numbers when $R > T/ie$. For further explanation see text. Original

function of x is:

$$R = S - ix$$

The equations show that x will increase until $R = T/(ie)$. The basic assumption of the model is that the resource itself has a logistic growth and that its growth rate is much higher than that of the consumer. It is further assumed that the growth rate of x is linearly related to resource concentration (which may be realistic only when the concentration is low, see Chapter 11). By substituting for R we have:

$$dx/dt = x[eSi - T - i^2 ex]$$

This is identical to the logistic equation when $r = eSi - T$ and $K = (eSi - T)/(i^2 e)$. Such derivation of the logistic equation is didactic in that it shows that the parameter K is, in fact, a compound parameter and in particular that the numerator in the expression is simply the Malthusian parameter r (while the denominator can be considered as a coefficient which measures the intensity of the intraspecific competition). Therefore, while the parameter K may be useful for describing population growth, it is entirely misleading in an evolutionary context. This is important to stress because the concept of 'r-versus K-selection' remains a popular one [71]. The idea holds that in populations which are mainly controlled by density-independent mechanisms, traits that increase r will be selected for whereas when intraspecific competition is intense, selection will favour an increase in K . Quite besides the fact that natural selection does not favour a maximum population size *per se* (and sometimes, such as in the case of territoriality, the converse is true) it is meaningless to consider K as a genotypic trait since it is an ad hoc parameter which even includes the Malthusian parameter as a component.

The logistic equation has been modified in many ways to describe some special situations. These include models in which the per capita growth does not decrease linearly with increasing population density (which in some cases makes biological sense) and those where time-lags are introduced (which is usually meant to model the fact that the intense resource competition is seasonal or associated with certain age classes). Such time-lag models tend to predict oscillatory behaviour of the populations and have been beautifully demonstrated in laboratory as well as natural populations [70]. A special type of logistic model attempts to describe the fact that many species have discrete generations; examples are provided by annual insects or plants with a single reproductive event which takes place during a restricted period of the year. An example of such models was given in

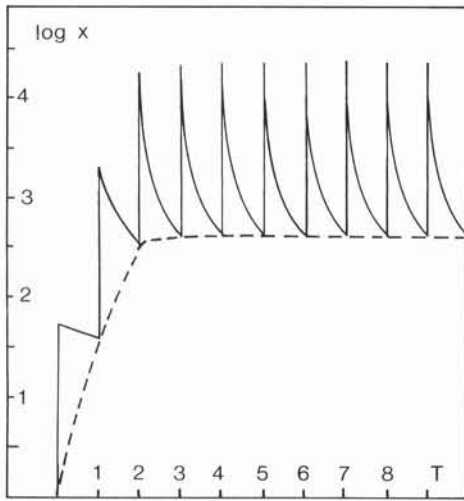


Fig. 28. Population with discrete generations growing according to the model described in the text. The population is initiated by one individual and B (number of eggs per individual) = 50. The dashed line connects the adult populations and is identical to a logistic curve. Original

Chapter 3, but this is unrealistic in that it assumes that not only the birth process, but also death is a discrete seasonal event.

In a more realistic version of populations with discrete, non-overlapping generations it must be assumed that density-dependent and density-independent death both occur throughout the life cycle, while birth takes place as a discrete event at time intervals of T . If the adult population is denoted x , and each individual produces B eggs (or seeds) the new generation will initially be represented by $u(0) = Bx$ individuals. These juveniles will then suffer density dependent and density independent death so their numbers decrease according to $du/dt = -u[d + mu]$, where d and m represent a density independent and a density dependent death rate, respectively. The number of adults resulting from this generation will be $x = u(T)$. It can be shown that a population growing according to these equations will over time reach a constant adult population size. The integrated version of the equations is shown in Figure 28; Figure 29 shows a natural population of the sort the model attempts to describe [72].

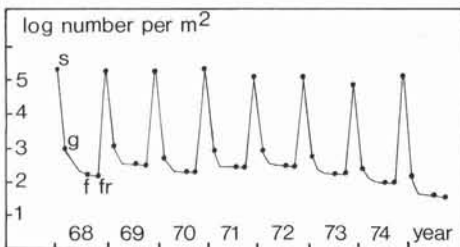


Fig. 29. Population size of the annual plant, *Androsace septentrionalis* through seven years; s: seeds, g: seedlings, f: flowering plants, fr: fruiting plants. Redrawn from Symonides [72]

Interspecific competition is usually treated apart from intraspecific competition, but one type of interspecific competition is naturally discussed in this context: that of competition for common resources. Although this represents one of the most important ecological mechanisms, its treatment is sometimes misleading. One reason for this is the failure to acknowledge that there are different types of competition. We may distinguish between three cases, the properties of which are different in important respects. Two of these cases represent competition for common resources. Among these, one is the competition for food resources between species in an environment in which both the food particles (or dissolved resource) and the competing consumer species are homogeneously distributed. The other one is competition for space between sessile organisms. A third type of interspecific competition is usually referred to as 'antagonistic competition'; it does not directly involve competition for resources, but includes cases where individuals of one species directly affect the individuals of other species. Interspecific aggression or antibiosis are examples. This latter type of competition will be treated in more detail in Chapter 13.

The other reason why the concept of interspecific competition is difficult is that the different types can all formally be described by a similar set of equations with similar parameters. But it is not simultaneously recognised that the biological mechanisms involved are different and that the parameters in the models have somewhat different meanings in the different cases.

I will start by discussing competition for resources. Consider first the model shown in Figure 27 for intraspecific competition. Assume first a Mendelian population which is genetically polymorphic so that the phenotypes varies with respect to their value of $T/(ie)$. Obviously the phenotypes which have the lowest values of $T/(ie)$ will be the most fit ones and the genes responsible for these phenotypes will increase. Now consider an asexual population with different phenotypes. Here the phenotype with the lowest value of $T/(ie)$ will eventually dominate and the other ones will be excluded because the most fit ones will equilibrate at resource levels below that which can sustain a population of the less fit phenotypes.

This latter case is, of course, interspecific competition for food resources. Excluding the unlikely event that the individuals of two species have exactly the same value of $T/(ie)$, which measures the minimum resource concentration at which they can sustain populations, then one of the species will be excluded. This represents the 'competitive exclusion principle' which states that if two (or more) species are forced to depend on one single type of resource, only one species will prevail (this argument was already presented in a different way in Chapter 11). If we now consider two

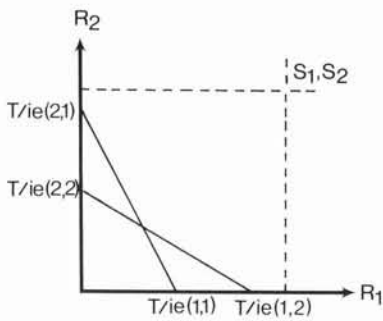


Fig. 30. Two-resource, two-consumer, competition model. $T/ie(n, m)$ is the threshold concentration for the m 'th species depending on resource n . In absence of consumers, resource concentrations equilibrate at S . The lines represent all the resource combinations which yield zero-growth for the respective consumer species. Points to the right and above these lines represent resource combinations allowing growth. Equilibrium resource levels is given by the intersection of the lines. Original

different types of resources (Fig. 30) we see that co-existence may be possible even if both consumer species can utilise both types of resources as long as the two resources are utilised in a differential way. Here $T/ie(n, m)$ represents the threshold concentration of the m 'th resource with respect to species n . In the presence of both species they will equilibrate at resource concentrations corresponding to the intersections of the lines.

The graphical model in Figure 30 can be used in a quite similar way as I used the model in Figure 27 to derive the 'Lotka-Volterra' equations for two competing species (which is simply a two-species extension of the logistic model):

$$dx_1/dt = r_1 x_1 [1 - x_1/K_1 - \beta_{12} x_2/K_1]$$

and

$$dx_2/dt = r_2 x_2 [1 - x_2/K_2 - \beta_{21} x_1/K_2]$$

In these coupled differential equations, r_i , x_i and K_i represent the Malthusian growth rate, the population size and the carrying capacity of species i and β_{ij} is the 'competition coefficient' which somehow quantifies the effect of species j on species i . In the case of competition for common resources the interpretation of the competition coefficients must be that they measure the 'overlap' in resource utilisation. In the case of the two-resource, two-species system shown in Figure 30 they measure the relative efficiency in the utilisation of the two resources by the two competitors. When interpreted in this way, the competition coefficients cannot exceed unity; this limiting case represents total identity between the two species with respect to the way in which they utilise their resources. If the competition coefficients are both zero, then there is no overlap in resource utilisation and the model degenerates into two (independent) logistic equations.

Analysis of the Lotka-Volterra equations (Appendix 3) shows that co-existence requires that $K_i < K_j/\beta_{ji}$ ($i, j = 1, 2$) and competition is revealed by lower equilibrium population sizes of both species than is found when each of the species grows alone. Given that the two species, and by implication their carrying capacities, are not very different, the condition for co-existence of the two-species system is not very demanding; that is, even a slight difference in the utilisation of the resources will permit co-existence; the particular type of competition we discuss can therefore be considered a 'soft' competition relative to the other types. However, the biological interpretation of the condition is not as straightforward as is often implied in elementary ecology texts. Thus, the parameters K , and r are both functions of the resource level in the absence of consumption; of the lowest food intake level which allows growth, the growth efficiency and the efficiency of food capture and the competition coefficients are functions of the two latter properties. Therefore, and to an even larger extent than when discussing the logistic equation, its two-species expansion may describe real competing populations well (as shown experimentally by Gause in the thirties and later by many other authors in laboratory experiments), but the biological interpretation may be elusive if it is not understood that the parameters are complex functions of the actual biological properties of the organisms.

The real basis for this type of resource exploitation competition is an indirect effect of one species population on another; that is, the presence of one species population changes the resource spectrum which will be available for another species. If one of the species is already established, then a competing species can invade the universe if it can increase given the available resource spectrum with which the first species equilibrates. If this also applies in the reciprocal case, the species can co-exist or otherwise one of the species will be excluded. This type of competition does not involve any direct interference between the two species beyond their indirect effect on the available resources. Other environmental conditions may influence the parameters which describe the competitive interaction and so the outcome of the competition. The competition between two species distributed along some environmental gradient may therefore have different outcomes in different parts of the gradient and this may be interpreted as habitat preferences of the two species.

It is clear that the treatment of the theory for species competing for food resources is not, so far, easy to apply to natural populations and it seems to be a rather abstract undertaking to extend the considerations to more than two species. A significant contribution in this respect was given by MacArthur and Levins [73] in their attempt to interpret models of resource competition in terms of ecological food niches. The considerations are

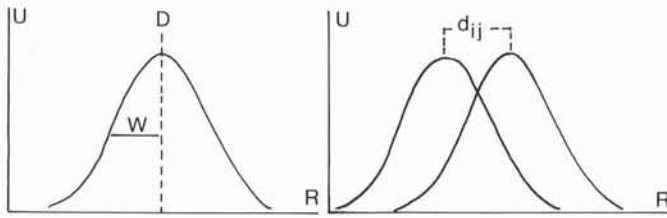


Fig. 31. Niche model; R = a gradient in a resource quality; U = rate of exploitation of the different resource qualities; D = niche position; W = is niche width and d is niche distance between the niches of two species exploiting the resources. Original

based not only on a few discrete types of resources, but rather on a 'resource spectrum' which represents a continuum of resource qualities. The resource spectrum may represent a gradient in, e.g. food-particle size and the food niche of a species is then a 'utilisation function' which describes the efficiency by which individuals of the species utilise different qualities of the food (Fig. 31). The 'niche position' is defined as the mode of the function and the niche width as the standard deviation of the niche. Basically the overlap of such food niches represent competition and a measure of this overlap is then defined as the competition coefficients of the Lotka-Volterra equations in a way entirely analogous to the two-resources, two-species situation. The basic result of all this is that for a higher number (> 2) of competing species, co-existence requires that the distance between neighbouring niche positions along the resource gradient axis is about one niche width (one standard deviation) apart. Although this result requires a number of assumptions and simplifications, extended analysis has shown that the result is quite robust regarding the details of these assumptions.

All this has in turn inspired many studies to test the predictions in nature. A quite large number of such studies seem to lend support to the theoretical results, especially regarding the size spectra of food particles consumed by co-existing, closely related forms [74, 75]; see also Figure 32. Since, as discussed in Chapter 10, there is a close relation between the metric properties of otherwise similar consumers and their preferred food particle sizes, this 'limiting similarity principle' is believed to be reflected in the discrete size ratios found between related, co-existing animals, e.g. in birds of prey. It has been generalised that a metric size ratio of 1.3 is typical [74]. Needless to say, this does not represent a 'proof' and counter-examples where co-existing species show a niche overlap which exceeds that permitted by the principle of limiting similarity are found. As discussed later in this book there are many mechanisms related to the heterogeneity of natural communities which may explain this.

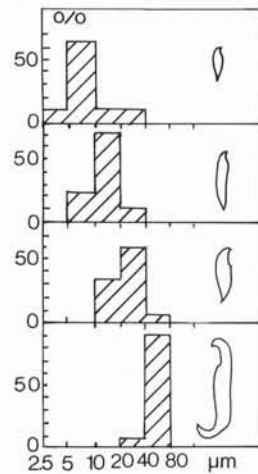


Fig. 32. Size spectra of diatoms ingested by four co-existing species of the ciliate genus *Remanella*. Data from Fenchel [75]

So far we have considered the competition for resources which are exploited; a different type of competition is one of the occupation of space between sessile organisms. In this case, at any point in space only one species will persist as the outcome of the competitive interaction. This is a 'harder' type of competition than the resource exploitation competition discussed above. The mechanisms involved may differ in different cases; in plants they usually imply shading of the competitor or competition for water or mineral salts and in many marine, sessile invertebrates (such as the barnacles discussed in Chapter 6) by over-growing. As discussed in the following chapter, in many, if not most groups of sessile organisms, special mechanisms of interference have evolved.

Competition for space may formally be described by the Lotka-Volterra equations, but the parameters involved must be interpreted in another way; in particular the competition coefficients cannot be interpreted as only a measure of resource overlap and the outcome of the competition is often given by the growth rate of the particular organisms under particular environmental conditions. In principle, regional co-existence is possible if different patches have different environmental conditions some of which favour one and some of which favour another competing species. Again, however, a mosaic of species may be found in a seemingly homogeneous area due to mechanisms related to temporal heterogeneity (Chapter 15).

13 Interactions between Species Populations

In addition to the competition for common resources a number of other types of species-pair interactions exist. Together these could be considered

as the units of which communities are built. Also, and in contrast to complex multispecies communities, the two-species systems are amenable to analytical treatment. Among such possible types of interactions, exploitative and antagonistic competition have one feature in common, *viz.* that the relation is dysgenic for both species populations involved and this can be denoted symbolically by $(-, -)$. In host-parasite and in prey-predator interactions, the relationship is dysgenic for the host or prey populations but favourable to the parasite or the predator populations: $(-, +)$. Parasites are usually much smaller than their hosts and have a much shorter generation time and the host may or may not be killed by the parasite. Prey and predator species are usually of comparable sizes and with comparable generation times and an encounter is lethal for the prey. There is no sharp delimitation between the two types of interactions. 'Parasitoid' hymenoptera who deposit their eggs in other insects provide an example of an intermediate between predators and parasites. Their eggs develop within and at the expense of the doomed host.

'Mutualism' is a type of interaction which benefits both components $(+, +)$ whereas commensalism is neutral to one of them: $(0, +)$. The small amoebae which seem to occur invariably in the oral cavity of man provides an example of the latter. There exists a vast number of parasitic, mutualistic and commensalistic associations in nature. In many cases the exact functional significance is not understood; the term 'symbiosis' is therefore often used to designate all such cases of 'living together' (although some authors use this term as a synonym of mutualism). The functional significance of symbiotic relations may also vary according to the genotype of the components or to environmental conditions.

'Amensalism' describes associations which are neutral to one component and dysgenic to the other $(0, -)$. Elephants stepping on terrestrial snails, I suppose, provides an example. Finally, and for the sake of completion, the trivial 'indifference' $(0, 0)$ should be mentioned.

In antagonistic or interference competition, and in contrast to exploitation competition, the individuals of one species population directly affect the individuals of another species population. Interspecific aggression is one such case. For a long time the classical competition experiments conducted by Park [76] on flour beetles of the genus *Tribolium* constituted the standard example of antagonistic competition in ecology texts. Since then, however, it has been found that interference competition is widely distributed among sedentary organisms, in particular those which build clonal colonies belonging to a wide variety of taxa.

Many vascular plants produce 'allelopathic' compounds which inhibit or kill neighbouring plants belonging to other species. In prokaryote and

fungal microorganisms, the production of antibiotics with the similar effect of inhibition of competitors is of common occurrence. Most recently it has been found that many groups of marine invertebrates (corals, sponges, tunicates) also are engaged in a 'chemical warfare' against their neighbours. Also, the destruction of settling larvae by adult benthic invertebrates belonging to other species has been seen [77]. Antagonistic competition has a profound effect on the structure and species richness of communities of sedentary organisms and I will return to this in conjunction with the role of patchiness in communities (Chapter 15). Here I concentrate on the formal description of the phenomenon and the dynamics of populations engaged in interference competition.

This can be described by the same set of Lotka-Volterra equations used for describing exploitation competition. However, the competition coefficients have another meaning in this case. In the case of exploitation competition, they measure the overlap in the utilisation of the available resources and they cannot exceed unity. In the case of antagonistic competition the (formally identical) parameters measure the direct inhibitory effect of species i on species j relative to the intensity of intraspecific competition of species j . Of course, species engaged in antagonistic competition may at the same time also compete for common resources in which case the competition coefficients also include this aspect. These parameters therefore become extremely complex as far as their explicit biological interpretation is concerned which is not to say that they cannot be used in order to study the general behaviour of populations engaged in such competition.

The fact that the competition coefficients can exceed unity renders the dynamic properties of the population qualitatively different. Although the analysis of such equations reveals a point of equilibrium with co-existence, this equilibrium is unstable and the practical outcome of the competition is always that one of the species is excluded and the other one wins. The actual outcome, however, depends on the ratio between the initial population sizes of the two species (see Appendix 3). I will return to the implications of this, but briefly mention here two obvious effects. In a succession, e.g. on a patch of bare soils, the particular species of plants which will eventually dominate the patch may be the consequence of a stochastic event, that is, which species initially happens to place most seeds on the patch. Another effect is that a sufficiently dense stand of plants may show a significant resilience against competitors which otherwise would be competitively superior under the given environmental conditions.

The simplest possible model of prey-predator systems state that the growth rate of the prey population equals its density-independent (exponential) growth minus the number of individuals consumed by the pred-

ator, and that the predator population grows as a function of the number of prey consumed minus the (starvation-induced) mortality of the predator. In terms of differential equations this becomes:

$$dx/dt = rx - axy$$

and

$$dy/dt = bxy - dy$$

Here x and y denote the population sizes of prey and predator, respectively; r is the Malthusian parameter of the prey; and d the starvation death rate of the predator. The expression ax is the functional response (Chapter 11), that is, the number of prey individuals captured per predator per unit time as a function prey density (which is considered here to be a linear function). Finally, b represents a conversion factor such that b/a is gross growth efficiency.

An analysis of this set of equations (Appendix 4) reveals that the system shows neutrally stable oscillations around an equilibrium with neutral stability. The oscillations will have a period of $2\pi(1/rd)^{1/2}$, with the phase of the predator population lagging $1/4$ cycle behind that of the prey population and (as indicated) the amplitude depends on the initial population sizes. These properties of neutral stability are definitely unattractive from a biological view-point. However, before I proceed with more realistic versions, it is worthwhile considering the properties of the equilibrium point because they are basically shared with that of more realistic models. Setting the equations equal to zero shows that the equilibrium is $x = d/b$ and $y = r/a$; that is, the prey population is proportional to the death rate of the predator and the predator population is proportional to the growth rate of the prey. If an additional mortality is imposed on the system which equally affects the prey and the predator, the paradoxical result is that the prey population increases and the predator population decreases. This effect was first noted in Italian fisheries statistics during World War I. During the war, fishing intensity decreased and the consequence was an increase in predatory fish species relative to prey fish. The effect is also important in the application of insecticides in that these may kill off not only the pest but also its natural predators, and so the result may be quite opposite of the desired one.

In order to transform the above model into something ecologically more palatable, it is only necessary to introduce density-dependent population regulation in the prey (e.g. letting it grow logistically) so that the prey equation becomes $dx/dt = rx - axy - cx^2$. The system will then show dampened oscillations and end up at a stable point of equilibrium (Appendix 4). (A

density-dependent term can, of course, also be added to the predator equation, but this is biologically speaking a less obvious thing to do in that the predators are already limited by competition for prey. If the predator has e.g. territorial behaviour this would be relevant. Under all circumstances this does not change the qualitative properties of the system.)

The models discussed above remain unattractive in that they imply a number of assumptions which may not be realistic or at least include details of the interactions which may not be general. One such assumption is that of a linear functional response of the predator. Extrapolated to high prey densities this is certainly an unrealistic detail. An entirely general prey-predator model was analysed by Kolmogoroff [78]:

$$dx/dt = xF(x, y)$$

and

$$dy/dt = yG(x, y)$$

It can be proved that for a wide range of qualitative and biologically reasonable assumptions this system has either a stable point of equilibrium or (and) a 'stable limit cycle' (that is, the system will oscillate with characteristic amplitudes and period and, if perturbed, will afterwards return to this state). The biologically perhaps most attractive model, which is somewhat more explicit than that of Kolmogoroff, was devised by Rosenzweig & MacArthur [79]:

$$dx/dt = x r(x) - y C(x)$$

and

$$dy/dt = y[-d(y) + e C(x)]$$

Here $r(x)$ is the density dependent growth rate of the prey (e.g. a logistic term); $C(x)$, the functional response of the predator (e.g. a Holling type II function); $d(y)$, the density-dependent death rate of the predator; and e , its growth efficiency. For reasonable assumptions about the components of the model it predicts stable limit cycles or a stable equilibrium point (Fig. A 4 in Appendix 4).

There are two fundamental properties of all these models which are of general interest to ecology. The first of these is: they suggest predator-prey systems (in contrast to competition) to be inherently stable; that is, they do not predict the prey or the predator to become extinct even after severe perturbations away from the equilibrium. This property can even be extended to food chains with more than two 'trophic levels'. The result is of

general significance, but some of the shortcomings of the models must be remembered in this context. First of all (and like all the models so far discussed in this book) they consider populations as a continuum rather than a collection of discrete individuals. When the models predict very low population sizes (during oscillatory cycles) this may for a moderately sized, real population correspond to a fraction of an individual. Also populations which are small in an absolute sense tend to become extinct due to demographic stochasticity (Chapter 14), and so these models do not guarantee the survival of prey-predator systems in the real world. Also, the models do not allow for time lags or discrete generations. Models which include these features are less stable and may lead to extinction or to chaotic behaviour ([80], see also Chapter 3).

The other fundamental property of the models is what has appropriately been termed the 'paradox of enrichment' [81]. This means that if the carrying capacity of the prey increases, the models predict an increased tendency of the system to oscillate and with increased amplitudes of the oscillations. Conversely, if the equilibrium population size of the prey is close to its carrying capacity the system tends to have one stable point of equilibrium. That this is so can be understood intuitively, since when the carrying capacity of the prey becomes very large the system approaches the neutral system discussed first (see also Appendix 4). Irrespective of the complexities of real systems this principle constitutes the basic explanation for some common observations. Thus in homogeneous stands of trees violent outbreaks of pest insects occur, while where their host plants are rare and spread out among other species, the insects occur in small, but relatively stable numbers. Inland waters which are 'eutrophied' by the addition of mineral salts show violent fluctuations in population sizes of algae and of their animal grazers whereas nutrient poor, 'oligotrophic' lakes with a low carrying capacity for algae harbour relatively stable population sizes. This effect is also easily demonstrated in prey-predator systems in the laboratory and is of importance in the context of environmental problems [82].

Gause demonstrated prey-predator oscillations in laboratory systems with protozoa and since then these have been demonstrated many times for various other prey-predator and host-parasite systems in the laboratory. Regarding natural populations the classical example is that of the hare-lynx populations in Canada which is depicted in most texts. It has generally been held that such oscillations are rare in nature and that this is because more complex food webs (each predator has several alternative prey species) would disguise such effects. However, coupled prey-predator oscillations may be more common than previously thought, as suggested by more re-

cent data for different types of communities and from more sophisticated means of analysing such data (Figs. 59–60 [23], [83]).

The last important type of species interaction to discuss is mutualism. In contrast to its wide occurrence and importance in nature, little is usually said about it in terms of theoretical population biology. This is perhaps so because one would *a priori* expect such associations to display stability (in contrast to competition and predation). Formally, mutualism can be modelled using competition equations with a change in the sign of the interaction coefficients. In realistic models these coefficients must not exceed unity; otherwise a *perpetuum mobile* is created (that is, the mutualistic consortium grows without bounds) and this is hardly a biological realistic situation.

Characteristic for all the two-species systems we have so far discussed is that they can be analysed with respect to their stability and other properties. This is mainly due to the graphical methods exemplified in Appendices 3 and 4. However, very few communities consist of only two species: on the contrary, even within a very restricted and seemingly homogeneous area or volume of the biosphere there may be hundreds or thousands of species. A central question then becomes: in how many and how strong interactions is each species population involved and how does this affect the properties of the communities and in particular how does this affect their 'stability'. In the context of the properties of the 'ecological universe' implicit in this chapter (which as discussed in following chapters are incomplete relative to the real world) this has mainly been studied by May [84].

The type of models we have discussed could be extended to a community of n species by looking at the behaviour of n coupled differential equations of the type $dx_i/dt = x_i F_i(x_1, x_2, \dots, x_i, \dots, x_n)$ which describes the growth of the i 'th species as a function of all the species in the community and where the functions F include all the coefficients which describe the interactions between them. However, there are two fundamental difficulties. First of all there are no mathematical techniques which allow for the analysis of the properties of a general system such as depicted in Figure 33 to give biologically meaningful, qualitative results. An analysis comparable to that of two-species systems can only be extended to a few special cases such as the many-species competition for resources with the ecological niches arranged along a resource axis (Chapter 12), for linear food chains or for, e.g. two competing species which are preyed upon by a predator species. Even here it is often not possible to make predictions about the 'global stability' of the system, but only on the 'local stability'; that is, on the behaviour of the system close to its state of equilibrium (if subject to a small perturba-

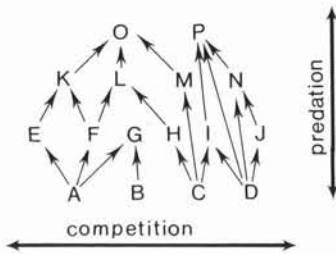


Fig. 33. 'Food web' depicting predator-prey and exploitation competition interactions in a hypothetical community. Original

tion, will the system return to the equilibrium or will it stray off towards another state, perhaps losing species?).

Another problem is, of course, to define what is meant by 'stability' since this term is used in a rather loose way among ecologists. To May this means the ability of an ecological system to return to a state of equilibrium following a small perturbation. We have seen that this is a property of most of the two-species systems discussed above. In the real world, stability of an ecological system would mean its ability to return to its original state in terms of species composition following some perturbation such as exploitation of populations, pollution, or whatever.

May's extensive analysis (which applied mathematical techniques beyond the scope of this book) does yield one substantial and robust result: The simpler an ecological system, the more stable it becomes. As a general rule, increasing the number and intensity of species interactions render ecological systems more vulnerable to perturbations. At the time of the publication of May's book, this was counter-intuitive to many ecologists who argued that an increasing complexity (in terms of an increasing number of alternative pathways for the energy flow) should render ecological systems more stable. Regarding the empirical evidence (one way or the other) this seems to be resolved as a semantic problem. It had been argued that tropical rain forests or coral reefs with their impressive richness of species also show the highest degree of 'stability' in the sense that population sizes remain relatively constant over time whereas temperate and arctic biotic communities, with a relatively lower richness in species, often show strong seasonal fluctuations. However, this argument may be turned around: the species rich tropical communities can exist exactly because they are not subject to strong environmental fluctuations towards which temperate and arctic communities are much more resilient. In a sense this view has been supported directly during the last decades: tropical forests with their richness in plant and animal species have proven extremely vulnerable to exploitation and environmental deterioration and to an extent not known for temperate forests.

I believe that May's analysis unambiguously shows that a description of ecological systems as a multitude of 'checks' and 'balances' in the form of ecological interactions which allows for a 'homeostatic' behaviour of the systems is not satisfactory. There is no doubt that strong ecological interactions (such as competition and predation) do occur and are important in nature, but each species population is at best only involved in few such interactions. Species richness found in nature cannot be explained by such interactions: rather, it is necessary to explain why there are so many species in spite of such interactions.

A comparison of these considerations with Figure 33 which does reflect some reality, seems paradoxical. It is resolved by the recognition that an increasing number of arrows means that the interactions become weaker. If a predator feeds on several prey species, the relation of each of these species to the predator 'degenerates' to an additional increment of the density independent death rate. Similarly, relative fluctuations of prey species populations will not affect the predator population much.

Finally, real communities do not conform to one basic assumption of classical theoretical population biology: homogeneity in time and space. Competition and predation do occur and are important within patches of space or within finite intervals of time, but they are insufficient for explaining all properties of natural ecological systems. This is the topic of the following chapters.

14 Extinction

It is generally accepted that extinction is an integral part of the evolutionary process. Past spectacular episodes of extinction such as the disappearance of dinosaurs towards the end of the Cretaceous period or the disappearance of many species of large mammals during the Pleistocene have been widely popularised. These are often considered to be singular events, but given the geological time scale and the limited time resolution of stratigraphical studies they may not have seemed so dramatic at the time. Extra-terrestrial interference (which is currently a popular theory) may not be necessary (nor does it meet the approval of all geologists) as an explanation of past extinctions of species or groups of species. In this chapter, the central theme will be local extinctions of species populations in order to draw this aspect into further consideration on the structure of biotic communities. But local extinctions are, of course, the basis of global extinction; in the case of some 'endangered species' local and global extinction are nearly synonymous. Extinction at different scales is also a central issue for conservationists.

Extensive analysis of the fossil record shows that some geological periods may have had an elevated rate of global species extinctions. However, the rate of extinction within most taxa seems to be roughly constant, and over evolutionary time it is balanced by the rate of speciation. Extinction is thus a 'normal' process in evolutionary terms [85].

Nevertheless, it is generally felt that extinction (like death in a detective novel) must have a 'cause'. Indeed this is frequently the case. Man-made and certainly also natural processes can lead to extinctions of species of plants and animals over smaller or larger areas. Ice scouring of rocky coasts of temperate seas at intervals removes the entire attached fauna and flora in many places. During warm summers anoxic conditions may develop at the surface of the sediments of shallow seas to kill virtually all invertebrate animals over extensive areas. Forest fires and volcanic eruptions (such as that of Krakatau which destroyed all life on that island) result in local extinctions. Direct or indirect effects of human activity have resulted in the extinction of large mammals and birds over extensive parts of most continents. On a larger scale the Pleistocene glaciations led to local as well as global extinctions; see also Figure 66.

However, the extinction of a species population does not necessarily have an extrinsic cause or at least this may only be part of the explanation. It is possible to show that all finite populations will eventually be doomed; the expected time for this to happen, however, depends strongly on the absolute size of the population.

The type of population models we have discussed so far cannot be applied to the study of extinction for two reasons. First of all, they treat population size as a continuum and while this may be a good approximation when describing large populations it is a poor one for small populations since these must be described as assemblages of discrete individuals. Also, the models discussed so far are deterministic so that given initial conditions they predict a precise outcome at any future time. To the extent such models predict 'extinction' (for example, in models of competing species), they describe this as if the population approaches zero asymptotically. In order to discuss what is called extinction due to 'demographic stochasticity' we must apply stochastic models which describe populations as an assemblage of discrete individuals and births and deaths as probabilistic events.

Extinction due to demographic stochasticity is based on the fact that each single individual does not produce an average number of offspring or enjoys an average life-span. Rather each individual has a certain probability of surviving to a certain age and a certain probability of producing a given number of offspring. Consider now a population initiated by one individual. The species is annual and reproduces at the end of its life. We as-

sume our population can grow unlimited and if the mean production of offspring is R then after T years our expected population size will be R^T individuals.

Our founder individual (like other individuals of the species) has a finite probability, p , of dying before it reproduces, so $p = q(1)$ is the probability of the (one-individual) population becoming extinct during the first year. Now, with the probability $1-p$, the individual will survive to reproduce. We find the number of offspring from some probability distribution with the mean, R so that $P(k)$ is the probability of a progeny of k and so that $\sum P(k) = 1$. Suppose the individual produces k offspring. The probability of all these animals dying before reproduction is p^k . The probability of the population going extinct during the second generation is therefore $q(2) = (1 - q(1))\sum P(k)p^k$ where $P(k)$ is the probability that the second generation is initiated by k offspring. The probability of the population going extinct during the first or the second generation is therefore $q(1) + q(2)$. This argument can be extended to the following generations. For a population initiated by one individual and under conditions which allow for exponential growth, the probability that it will be extinct some time in the future is $q = q(1) + q(2) + q(3) + \dots$. If the population is initiated by n individuals the probability of future extinction is q^n .

If our population has a mean number of offspring $R > 1$ (that is in a deterministic model the population will increase exponentially), then the probabilities of extinction decrease from generation to generation because the population size tends to increase. The above sum of extinction probabilities will therefore converge to q with $0 < q < 1$, that is, with a finite probability q the population will go extinct and with the probability $1 - q$ it will grow to infinity. If, however, $R = 1$ then the average population size is not expected to increase and the probability of extinction will on the average remain the same from generation to generation. The sum of these probabilities therefore cannot converge towards a probability < 1 , or in other words the population is bound to become extinct at some time.

Real populations cannot be expected to grow exponentially for ever, but are limited to some (average) size, K . From the above considerations it is clear that the extinction probability of a density limited population of size K must be at least q^K , that is, that of an exponentially growing population initiated with K individuals. However, the extinction probability must be larger, because if the population increases above K it is expected to return back to that size again. The extinction probability is therefore not decreasing from generation to generation and so the expectation that the population will at some future time become extinct is unity. In other words: all finite populations will eventually become extinct [86].

While this – perhaps sad – result is inevitable it must at the same time be said that the expected time for extinction increases strongly with increasing K . Another way to formulate this is to say that if we have a large collection of populations, all of size K , the rate of extinction of these populations will decrease strongly with increasing K .

In order to estimate, or at least to arrive at some feeling for, actual probabilities of extinction due to demographic stochasticity as a function of absolute population size, data on the demography of the particular species are necessary. Such estimates are relevant and are made in the case of endangered large mammals and birds [87]. The general considerations have a wider applicability. Many species occur in the form of numerous small ‘island populations’ with a restricted rate of migration between them. Such isolated and small populations are bound to become extinct at intervals and become re-colonised later by individuals from some other population. If the population was very isolated from other conspecific populations this may take a long time. In conservation practice it must be recognised that the preservation of some habitat may be insufficient if it is too small or too isolated from other similar habitats. The species population itself may be so small that relatively rapid extinction is inevitable even if the environmental conditions are satisfactory.

Extinction due to demographic stochasticity is often the final result of a number of other processes which have already reduced the population size. These may include the reduction of habitat size, environmental stochasticity, excessive human exploitation, predation or competition from other species. Whereas exploitation competition may not in a deterministic sense lead to extinction; it may lead to small absolute population sizes and so to an increased probability of extinction due to demographic stochasticity. Eventually, this process sets an ultimate limit to the number of species which can exist within a particular ecological system or on a global scale. Theories on competition and on ecological niches (Chapter 12) and ideas about ‘time niches’ in a temporally patchy world (Chapter 15) in principle allow for an infinite number of species as long as they are sufficiently specialised with respect to resources, habitats or life cycles. However, since resources are finite, an increasing number of species means decreasing average population sizes and hence an increase in the rate of extinction.

15 Heterogeneity in Time and Space

Animals have always coped with more or less patchy environments and cannot be held responsible for the fact that ecologists have not [88]

Adding spatial and temporal heterogeneity to our description of biotic communities allows for an astonishing degree of complexity. To include patchiness in ecological theory is not to negate the classical models of species interactions entirely; rather they are assumed to control the dynamics within individual patches. But migration barriers between patches, stochastic extinction of species populations within patches, and biologically or physically generated heterogeneity in time and space add new qualities to the overall system.

Early work by Hutchinson and by Skellam [89] suggested the importance of patchiness for understanding ecological communities and in a sense the 'theory of island biogeography' of MacArthur and Wilson also drew attention to this aspect (this theory will be discussed in the following chapter). More recently, interest in the effects of spatial and temporal heterogeneity has been steadily growing regarding theoretical as well as field ecology. Also, it seems likely that this topic for the time being represents the most fruitful interphase between theoretical ecology and field ecology and so merits some attention.

It is perhaps easiest to start the discussion with an example that shows how spatial heterogeneity can generate ecological complexity and more specifically explain co-existence of competing species which would not be possible in a homogeneous environment. The model, originally suggested by Levin [90], considers two species which are engaged in antagonistic competition. In its simplest and symmetrical form, a two species competition can be described by:

$$dx_1/dt = x_1[1 - x_1 - ax_2]$$

and

$$dx_2/dt = x_2[1 - x_2 - ax_1]$$

Here the two (identical) competition coefficients, $a > 1$. As shown in Appendix 3 and Chapter 13, this system does not allow stable co-existence, but the initially most numerous species will exclude the other one. Now consider two totally isolated habitat patches (Fig. 34) which harbour the two species. This allows for four stable equilibria: Species 1 is established in both patches, Species 2 is established in both patches, or Species 1 is established in either one or the other patch and Species 2 is then established in the other patch.

Consider one of the two last situations, that is, in which the two patches harbour different species. If we now allow for some migration between the patches for both species then it can be shown that co-existence will occur in

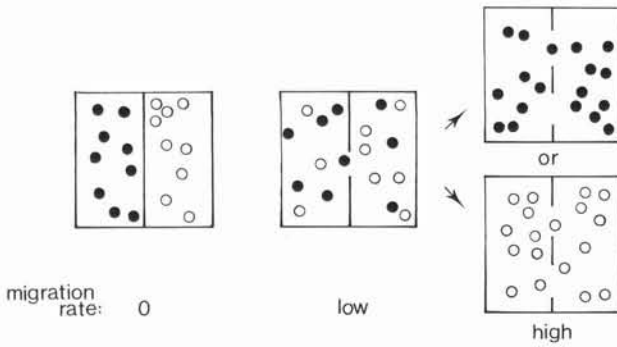


Fig. 34. Co-existence of two species engaged in antagonistic competition provided patchiness and a limited migration between patches. Original

both patches. Formally it can be proved that this happens if the inequality: $0 < m < 1/2[(a-1)(a+1)]$ is satisfied; if m (= migration rate) exceeds the requirement of the right hand side we are back in the homogeneous situation where only one of the species persists. The result can be understood intuitively; as long as each of the species remain quantitatively dominant in one of the patches, the dynamics of the competition will tend to increase their population size at the expense of the other species. However, this tendency is balanced by the net immigration from the other patch. The principle can be extended to n patches surrounded by migration barriers which can then maintain n species while among these n species only one would persist in a homogeneous environment.

This model may appear naive, but in fact the general principle is of great significance in communities consisting of sessile organisms and in particular those which produce clonal colonies. Such organisms seem more frequently than not to produce allelopathic compounds which inhibit or kill other species (see Chapter 13). Also these organisms, through their form of growth and colony formation, produce the spatial heterogeneity which makes the mechanism work. The effect has been thoroughly studied in coral reefs and other communities of sessile marine invertebrates. When colonies of different species meet (by growth, thus increasing the surface area they cover) the contact line shows that one of the species is inhibited by the other. Complex hierarchical systems regarding the dominance in competitive encounters have been described (the systems do not therefore necessarily have the symmetry of the model), but the same general principle applies and explains the maintenance of the species diversity of these communities.

The mechanism also seems to play a substantial role for the structure of plant communities in which patchy stands of single species (clones) cannot be conquered by other plants due to allelopathic compounds and in conjunction with an heterogeneous distribution. Clearing patches of forests can

lead to stands of shrubs which are very resilient to competition from trees and therefore persist for a long time apparently defying principles of succession [91].

The generation of patchiness has a multitude of causes. They include all kinds of heterogeneity of the physical environment and temporal aspects such as the diurnal or seasonal cycles. The organisms themselves create heterogeneity; on a spatial scale, plants in the terrestrial environment and sessile invertebrates such as corals in marine environments add physical complexity. The activity of microorganisms leads to chemical gradients which again account for habitat niches of other microorganisms (Chapter 19). On a temporal scale, prey-predator cycles create patchiness and seasonal cycles trigger successional patterns governed by biological interactions such as competition and predation. The rate constants of these interactions determine the characteristic time scales of events (see Fig. 24, 56 and 59). The importance of this last mechanism for explaining species richness in communities of planktonic algae in lakes was first emphasised in Hutchinson's paper: 'The Paradox of Plankton' [92]. Although these organisms are essentially limited by the same factors – light and a few types of mineral nutrients – a large number of such species seemingly co-exist in lake water. The seasonal cycle and the changes in water chemistry brought about by the organisms themselves in conjunction with small differences in physiology between species together result in that their relative competitive ability changes over the season. They therefore displace each other in some more or less predictable successional pattern during the summer. The whole thing then starts all over again the following spring so that an equilibrium is never reached.

When discussing heterogeneity, scales of size and time become important. If we consider a resource which fluctuates over time, it makes a difference whether organisms can trace these fluctuations in terms of population growth or whether their growth rates are low relative to the time scale of the resource fluctuations so that the organisms only experience the average resource concentration. In fluctuating environments growth rate becomes a niche parameter in itself and the co-existence of species exploiting the same fluctuating resource may be possible provided they have differential population growth rates (which again is a correlate of body size). A quite similar argument can, of course, be made for the size scale of spatial heterogeneity; obviously small habitats can only be used by small species [93].

A consideration which is relevant here and which couples scales of time and size is that of 'critical patch size'. It was originally formulated in conjunction with the occurrence of 'red tides'. A red tide is a term used to describe the mass occurrence of certain planktonic photosynthetic organisms

(mainly dinoflagellates) which occur in coastal seas; in temperate regions this usually happens in the summer. Some of the red tide species produce toxins; the organisms may in turn be consumed by bivalves which then prove to be toxic (or in rare cases even lethal) when consumed by humans. The phenomenon has therefore attracted attention and is of considerable concern wherever bivalves are popular as food.

Mass blooms of red tide organisms seem to occur in more or less isolated water masses in which conditions are especially favourable in terms of mineral nutrients and light. This probably explains the seasonal occurrence of red tides in that thermal stratification of water masses during the summer may create and stabilise lenses of water in which mass reproduction of the cells take place. The question then becomes: what is the critical minimum size of such a water mass which can sustain a bloom of dinoflagellates?

This problem can be considered for one, two or three dimensions. The first would apply, e.g. to a chemical gradient (and the problem would be how steep the gradient can be and still maintain a population of a species which requires some particular range of concentrations in order to survive). The two-dimensional case applies to organisms which live on or along surfaces, and the three-dimensional case applies, e.g. to the above mentioned red-tide plankton organisms.

Assume that there is a region in which some organism can grow at the rate r . Outside of this region the organism is incapable of growing and the surroundings are therefore considered to be a sink for all individuals which happen to venture outside the benign patch. Now, most organisms (such as the plankton flagellates) are motile. An appropriate description of the motility of flagellates (and of other primitive organisms) is that of a 'random walk' (like particles undergoing Brownian movement). The individuals swim in straight runs for a while and then 'tumble', that is, they stop and change their swimming direction (in a more or less random way) to continue with a new run. Such motility can be quantified as a diffusion coefficient (being proportional to the square of the average swimming velocity times the average time interval between tumbles).

There will therefore be a continuous loss (diffusion flux) away from the favourably patch and for this to be balanced by growth within the patch it has to be above a certain minimum size. The solution to this can be found analytically, but it can also be inferred from dimensional considerations to be $L = k(D/r)^{1/2}$, where L is the critical minimum diameter, D is the motility of the organism and k is a constant of the order of unity. This is so because the critical patch diameter must increase with increasing values of D and decreasing values of r . D has the dimension $L^2 T^{-1}$ and r has the

dimension T^{-1} and the answer has to come out with the dimension L . The magnitude of k depends on the dimensionality and geometry of the situation [94].

To get a feeling for predicted values of minimum habitat sizes we can try a few examples. Consider a bacterium with a generation time of 40 min ($r = 2.8 \times 10^{-4} \text{ s}^{-1}$). Bacteria typically swim with a velocity of about $30 \mu\text{m sec}^{-1}$ and tumble at intervals of 30 s which yields $D = 0.9 \text{ mm}^2 \text{ s}^{-1}$. The above model then suggests that a patch with favourable conditions in an otherwise hostile world should measure at least about 5 cm in diameter. A similar calculation for a protozoon (or creatures such as the red tide organisms) which may have a generation time of, say 12 h and a swimming velocity of 1 mm s^{-1} and to tumble twice a minute would need a habitat patch of several metres in diameter.

The model does, of course, give a very simplified version of the real world; in particular it is easy to mention a number of factors which would tend to increase the estimate of the critical patch size. Among such factors would be density-dependent growth of the population or turbulence which would tend to disperse patches. However, it is perhaps more surprising that isolated habitat patches can be much smaller in the real world than suggested by the above calculations: well defined patches of motile bacteria occur at a scale of 0.1 mm or less and protozoa may form communities at scales of a few millimetres (Fig. 35, see also Chapter 19). This reflects the significance of behaviour; that is, motility is not – and in contrast to the assumption of the model – invariant. Rather, microorganisms modify their motility as a function of environmental conditions; if these are favourable, motility is decreased and if they are unfavourable, motility is increased. Also, many such organisms display ‘phobic responses’: they tumble when moving from favourable to unfavourable conditions and so greatly increase their chance of returning to more favourable conditions again. Such primitive forms of behaviour and, of course, the much more complex behavioural patterns of higher animals, therefore allows the exploitation of smaller habitat patches than would otherwise be possible. One more radical way to utilise very small habitat patches is to become sessile and give up motility altogether; this is realised in many forms, but it is a poor strategy for transient habitat patches or patches which themselves migrate (e.g. chemical gradients).

The continued formation of new patches due to disturbance or stochastic extinctions represents an extremely important mechanism. Paine was among the first to study this for the invertebrate fauna of rocky shores along the west coast of the state of Washington. The rocks harbour a variety of sessile or motile invertebrates and among them the large, carnivorous

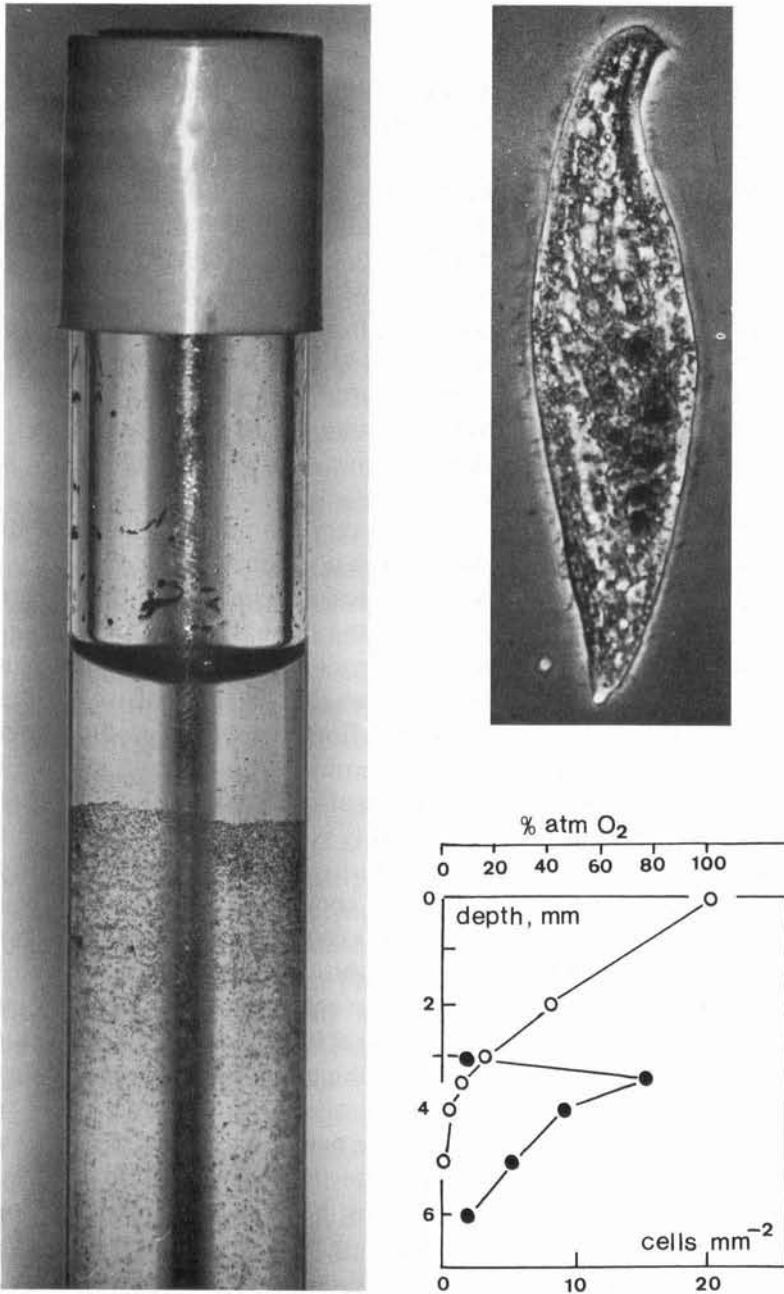


Fig. 35. Upper right: ciliated protozoan *Loxodes striatus*, which measures about 0.2 mm. Left: distribution of cells in a test tube with an oxygen gradient. This is also shown graphically (below, right; open circles: oxygen tension, closed circles: density of cells). Distribution pattern of the cells, and in particular the avoidance of oxygen tensions above about 10%, is based on chemosensory behaviour. After Fenchel & Finlay [94]

seastar, *Pisaster ochraceous*. When these were artificially removed from a stretch along the coast, the number of remaining species dropped and eventually the rocks were entirely dominated by mussels. Originally interpreted as an special effect of predation, the real explanation seems to be that the seastars remove everything from the cliffs while feeding, thus leaving a bare patch. Such patches are then colonised by a variety of planktonic larvae to establish a diverse community of invertebrates. Eventually, however, the mussels exclude all other forms through competition for space, but in the meantime the seastars have cleared new patches. It has also been shown that drifting logs which sometimes clear patches on the cliffs by scraping them free for the entire fauna has a similar effect on the diversity of the rocky shore [95].

This type of maintenance of species populations through the formation of patches has been termed 'fugitive' or 'extinction-migration' equilibria. A typical example is that of forests in which patches are cleared through natural fires, falling trees or lumbering. These will initially be invaded by a number of annuals or shrubs. Eventually, trees will exclude them from the patch through competition, but given a sufficient rate of patch formation and a sufficiently high rate of reproduction and dispersal of the 'fugitive species' they will persist regionally in the face of more efficient competitors. This again exemplifies the role of reproductive rate as a niche component in a heterogeneous environment.

Detailed analysis of grasslands have shown how this mechanism in conjunction with the effects of antagonistic competition (already discussed) maintains the variety of plant species. The dominating species maintain a matrix in the community largely based on the effects of allelopathic compounds. Empty patches are continuously created by grazing and hoof marks and these are initially colonised by small annual plants. In the absence of grazing the diversity of plants falls [96].

Formal models of fugitive equilibria and also intuitive reasoning makes it clear that the rate and extent of patch formation will influence the actual species composition in a particular area and lead to a mosaic structure of communities. Changing the rate of patch formation (which may be the result of changes in practices of forestry or other land use) may therefore create a whole universe of different biotic communities [97].

There are a variety of other ecological mechanisms which may create temporal and spatial heterogeneity. Some of these have mainly been studied theoretically and their importance in explaining patterns in nature has yet to be demonstrated. 'Diffusion-reaction' systems in which diffusion (or animal dispersion) combines with reactions (ecological interactions such as predation and competition) may create instabilities in the form of standing

or migrating waves. Such effects have been demonstrated in artificial ecological systems in the laboratory and the mechanisms are similar to those inferred for the explanation of chemical reactions with oscillatory behaviour [98].

Somewhat related to such phenomena are the migrating waves of epidemics, exemplified by plague as discussed in Chapter 3. It may be recalled that the host population must exceed a certain critical minimum density for an epidemic to occur. Once this density has been achieved, the epidemic can spread from a focal point like a migrating wave. The spread of plague over Europe after its first occurrence in the fourteenth century has thus been successfully modelled. Models of epidemics therefore exemplify both spatial and temporal heterogeneity [94].

An example which, perhaps, is more within the realm of ecology, but very related to the properties of epidemic diseases in man, is provided by the outbreaks of insects in forests. The spruce budworm has, or rather used to have (prior to the systematical spraying with insecticides) outbreaks in North American coniferous forests at intervals of 30 to 60 years. This system has been thoroughly studied and analysed [88]. Within any one forest the insects seem most of the time to be held at a relatively low population density by bird predation and this equilibrium is the only possible one in young or less dense forests (such as several years following a forest fire or a previous outbreak of these insects). In mature forests with a high branch density, however, there seem to be two possible equilibria for the spruce budworm population. The lower stable equilibrium is still due to the predator-prey interaction. However, if the population density (due to a local fluctuation or to the influx of individuals from another area) reaches a certain threshold size it may escape predation due to the (satiating) functional response of the predators whose reproductive rate does not allow the population to trace the increasing prey population. An outbreak is the result; it lasts a few seasons whereafter it crashes due to predation and especially to the destruction from the defoliation of the trees. A local outbreak also results in the dispersal of the insects into neighbouring areas and if these are covered by mature forests the outbreaks will spread in a wave away from the original focus. The system was modelled by a classical prey-predator model with a Holling type 2 functional response and with a diffusion term added to account for the spread of the insects. This model was surprisingly successful in generating patterns of outbreaks comparable to those observed.

16 The Structure of Biotic Communities

The term animal communities is really a very elastic one, since we can use it to describe on one hand the fauna of equatorial forest, and on the other hand the fauna of a mouse's caecum [99]

The structure of biotic communities seems for the time being to belong among the most popular topics in ecology [100]. Although the concept of biotic communities is far from new there is not a complete consensus concerning the exact definition. And this also applies to the term 'structure' in that different properties of organismic assemblages are studied as 'community structure'.

Most ecologists probably agree that communities are assemblages of organisms which are delimited in time and space so that e.g. a beech forest or a coral reef would constitute a biotic community. However, it is also implicit in most writings on community ecology that the component species populations interact through competition, predation and so on. Although this is rarely explicitly stated, the rationale for studying, for example, 'communities of seed-eating birds' or the 'microbial community of the rumen of a cow' is that most of the species populations confined within a certain physical space may not interact strongly or directly. By and large, most species seem to interact strongly with only few other species and mainly those with comparable body sizes. Groups of species which have mutually strong interactions of the types discussed in Chapter 13 are then believed to live in a matrix consisting of the physical, chemical and biological aspects of the environment. This environment, of course, influences the species populations, and some of its properties may be vital to the survival of individual species. From this also follows that the scale of time and space of communities depend on the group of organisms we study so that the above mentioned beech forest is really a mosaic of communities when smaller organisms are considered and the temporal scale of events may vary from a few days for microbial communities to centuries for those consisting of large species.

This is an important point to make, because by 'community structure' most ecologists think about the role of direct ecological interactions in shaping the species composition of biotic assemblages. The extent and intensity of such interactions in natural communities is central to community ecology (and source for some controversy). Failure to acknowledge the importance of scale and the choice of organisms in such studies may yield misleading results.

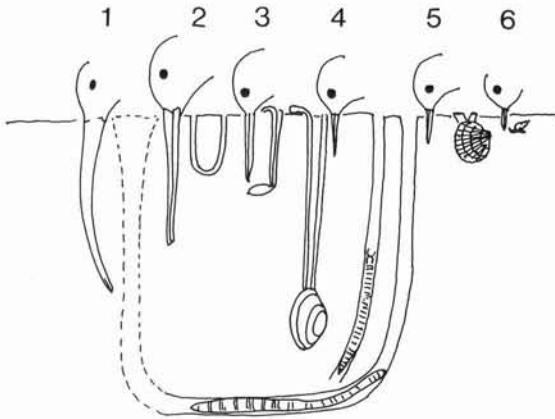


Fig. 36. 'Guild' of shore birds (1 = curlew, 2 = blacktailed godwit, 3 = redshank, 4 = knot, 5 = sanderling, 6 = ringed plover). Also shown are various burrowing invertebrates of shallow water sediments. The different beak dimensions of the different birds means that they at least in part exploit different food resources. After Green [99]

The concept of 'guilds' is useful in this context although it refers only to 'horizontal interactions' of communities, that is competition [101]. In medieval European towns, guilds were unions for different trades or crafts; among the functions of guilds was to make sure that their members did not suffer undue competition. In ecology, guild refers to a group of usually taxonomically related species which co-exist regionally and which have related if not totally overlapping resource niches or, if they exploit the same resources, have different habitats. Examples could be the 'guild' of birds of prey or of benthic, detritivore invertebrates (Fig. 36). It is often implied that the differences in resource utilisation among members of a guild have evolved through selective forces related to resource competition (Chapter 17) and hence illustrate the importance of exploitation competition in 'structuring biological communities'. This is what Connell has referred to as 'the ghost of competition past' [102], a topic to which I will return later. Under all circumstances, most analyses of community structure really refer to guilds or to fairly well defined groups of species which interact through prey-predator or mutualistic interactions with a restricted number of species not belonging to the guild.

The above considerations also explain why attempts to understand community structure through statistical patterns (regarding relative species abundance, indices of 'species diversity') of large samples from some area failed and why these heroic efforts, which were popular only a decade or two ago, have largely been given up. Distribution patterns are still useful or even indispensable for inferring ecological interactions. However, a meaningful way of choosing the group of organisms which are to be studied is necessary. To delimit such groups requires an *a priori* insight in the natural history of the creatures under study and this might seem a subjective way of

approaching the problem. On the other hand, the 'impartial' and 'Popperian' approach, most recently expressed by the requirements of 'null models' and of avoiding *a priori* choices of the species to be studied (e.g. guilds) when inferring ecological interactions from distribution patterns, may not be objective either, but can serve to obscure real patterns instead [103].

Leaving aside a variety of empirical descriptions of communities there has only been one approach which can be considered as a 'general theory of communities', *viz.* the 'theory of island biogeography' of MacArthur and Wilson [104]. Although inspired by the faunas of oceanic islands, the theory is really suitable for explaining species numbers of isolates in a wide sense: lakes, forests, individual trees, cow dung, or even the squares of an arbitrary grid imposed on a map. Its real novelty was to treat communities as the result of a dynamic equilibrium rather than the static picture which was once prevalent in the mind of many ecologists and naturalists. As such, the theory has had a large and deserved impact on community ecology during the last two decades [105].

The fundamental idea behind the theory is that the number of species populations established in an isolate represents the dynamic equilibrium between immigration of (not previously established) species and the extinction of previously established ones. Denote the rate of extinction by E , the rate of colonisation of not previously established species by I , the number of species which are established in the isolate by S and the total number of species which occur regionally by S^* . The simplest assumption is that the probability of species populations becoming extinct is constant and invariant with respect to the presence of other species. The rate of extinction in the isolate is then simply $E = aS$ and so increases linearly with S . The immigration rate (of not previously represented species) must take a maximum when S is zero and $I = 0$ if $S = S^*$, so $I = b(S^* - S)$. The equilibrium number of species of the isolate is then found when $I = E$, which is $S = S^*b/(a + b)$; see Figure 37.

Two mechanisms render it likely that the I and E curves will, in fact, not be linear, but rather have a concave shape. It is probable that some species have a higher ability for dispersal than others and the former are likely to arrive first so that the I function will tend to decrease at a higher rate at relatively low species numbers. If there is competition among the resident species of the isolate the average population size of each species decreases as a function of species numbers and so their probability of becoming extinct increases with increasing S making the E function concave (Fig. 37).

Two simple predictions emerge from this. One is that smaller isolates will have fewer species because a small isolate will have smaller average

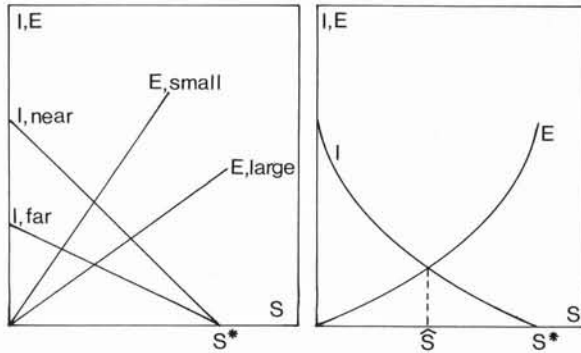


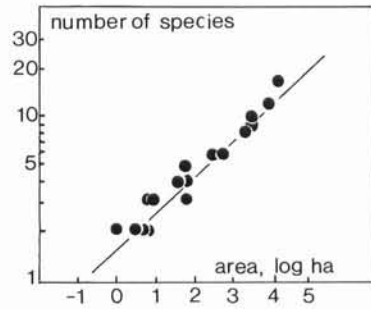
Fig. 37. Graphical representation of the basic idea underlying the theory of island biogeography. S = species numbers, and S^* = total species pool. E and I = the rate of immigration and extinction, respectively. Equilibrium species numbers \hat{S} is given by the point where E and I curves intersect. Simplest assumption of linear E and I curves (non-interactive case) is illustrated to the left; to the right the case assuming interspecific competition and a differential dispersal ability is shown. For further explanations see text. Original

population sizes and so an increased rate of extinction. Isolates with a migration barrier around them (for example, long distances to other isolates with a similar fauna and flora) also tend to equilibrate at lower species numbers because events of immigration will be rarer.

These and some other predictions, which can easily be derived from the model, have been established for many different types of isolates and for different taxonomic groups. The defaunation experiment of Simberloff and Wilson [105] is particularly elegant. They first surveyed and then killed the entire arthropod fauna of some small mangrove islands. They then followed the re-colonisation of the islands to show how they equilibrated at the previous species number (within 6 to 12 months), but the species compositions were not necessarily the same as before the defaunation. Diamond's study on the bird fauna of the Channel Islands off the Californian coast is also a classical contribution. It included a 50 year earlier survey of this fauna so it could be shown that during this time at least 17 and 62% of the bird species for the largest and the smallest islands, respectively, had been replaced by other species during that period; the total number of species, however, had remained fairly constant for each of the islands [105]. Some other examples are shown in Figures 38 and 39.

The theory of island biogeography is based on very simple and fundamental assumptions and a close agreement between its predictions and reality does not in itself yield much information about ecological interactions between species. The model can, however, be used in two ways to

Fig. 38. Number of species of freshwater snails in Danish oligotrophic lakes as a function of area. Redrawn from Lassen [105]



throw some light on this. One is to determine the functional form of the rate of extinction as a function of species numbers in that a 'concave upwards' shape of E plotted against S suggests a role of interspecific competition, albeit in a rather unspecified way. Unfortunately, such E and I functions have rarely been recorded; for larger organisms (such as birds, mammals and lizards, which have been the most popular groups studied in this respect) this would require very long-lasting surveys of faunas and floras of isolates. For communities of very small organisms for which not only size but also time is scaled down to fit the patience, longevity or resources of most ecologists, this can in principle be accomplished and an example is shown in Figure 39. This and similar results from other studies suggest that competitive interactions are at play, but the results do not – without further studies – suggest any details as to which species interact and by exactly which mechanisms.

The theory of island biogeography in its basic form predicts the species numbers of an isolate, but not anything about patterns in the species composition of the individual isolates; rather it is implied that this will be a

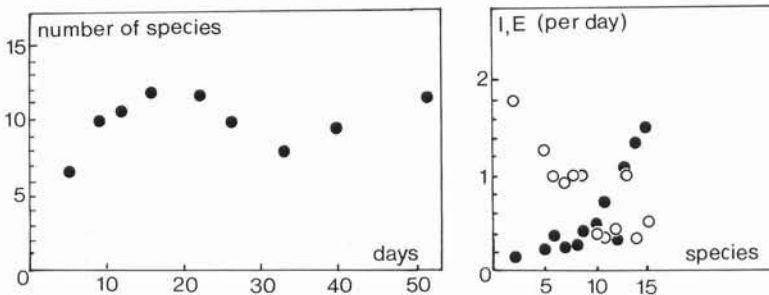


Fig. 39. Colonisation (left) and (right) the rates of immigration (open circles) and of extinction (filled circles) of species of ciliated protozoa in plastic cups with initially sterile sand placed in a small pond. Redrawn from Have [105]

random collection of species drawn from the total species pool. The detection of patterns which deviate from randomness then suggests the role of species interactions. There have been many attempts to detect such regularities and to interpret them in terms of interactions between particular species; bird faunas of Indo-Pacific islands and lizard faunas of islands in the Caribbean Sea and elsewhere have been especially popular. These studies have been successful in establishing such patterns and regularities. In particular, these patterns suggest that pairs or groups of species which do co-exist on islands tend to have displaced food niches and so exploitation competition does influence the composition of the faunas. Connor and Simberloff [103] have recently criticised much of this work on the grounds that the species included in the analysis have been pre-selected to include only those which show a disjunct geographical distribution and that instead all species within the studied taxa should be included. I feel that the intended objectivity of this approach does not really stand scrutiny. To pool the distribution patterns of a large number of ecologically unrelated species, e.g. of birds, will if anything obscure regularities which may actually exist due to competitive interactions within a rather restricted number of species with very similar niche relations [106].

Among the different types of population interactions, exploitation competition has had a special status in the discussion on community structure. The role of predation (at least for the survival of the predator) can hardly be refuted nor can the significance of mutualistic interactions or such biological interactions as insect and bird pollinators and flowering plants. These interactions are directly observable. Regarding exploitation competition there are two special problems. One is that the nature of exploitation competition is an indirect one, that is, it acts through the available resource spectrum rather than through the direct interference between individuals of the two species. In that sense it is, as discussed in Chapter 12, a 'soft' interaction. In deterministic models, co-existence is often allowed, given only small differences in the use of the available resources, but it will always lead to reduced population sizes of the involved species and hence an increased probability of extinction. Also important is the fact that in contrast to, e.g. predator-prey systems, competition leads to exclusion of species or to some sort of equilibrium whereafter there is no obvious effect. Competition in the field can therefore only be inferred from distribution patterns or from experimental manipulation; it cannot be observed directly in the same way as one may go into the field to watch a hawk catch small mammals.

On the other hand, it seems difficult for anyone who has tried gardening and so to combat weeds to question the fundamental role of competition.

Also, there is abundant (if often unintentional) experimental evidence from the introduction of exotic species. There are innumerable examples to show how, through competition, introduced species have excluded related, native species with a related ecology either from parts or from their entire previous range and that this exclusively affects one or a few species.

The Hawaiian islands have to an unusual degree been subject to the introduction of exotic species of passerine birds; from 1860 to 1983 altogether 50 species have been introduced on 125 occasions and during the same period there were 35 extinctions. The available data on these events allowed Moulton and Pimm to analyse co-existence and rate of extinction in the artificial bird communities as a function of morphological similarity (in particular beak dimensions which is a correlate of food choice). The data showed clear evidence for such a relationship whenever pairs of very similar species were compared and hence for the role of competition within feeding guilds. When the entire bird community was analysed together, such non-random patterns in the distribution of morphologies became obscured and not readily detectable [107].

A large body of data on 'ecological release' or 'ecological compression' also represents strong evidence for the role of exploitative interspecific competition regarding the distribution of different species with very similar ecologies. The two terms refer to the observation that species, where they co-occur regionally, are often restricted to non-overlapping habitats whereas where they are found isolated within a region they utilise the entire habitat range. Again, such observations suggest that strong competitive interactions are generally restricted to few, usually quite similar, species.

The picture of communities which emerges from contemporary ecology is one which is equally far from the two extremes which ecologists have argued about for most of the century (although some of the spirit of these feuds remain, in particular regarding the role of competition). To be a meaningful concept the definition of a community is first of all a question of scale; organisms of very different sizes live in different 'communities' even if they live within the same physical space and they mainly constitute a part of each others general environmental backgrounds. Within a given scale the composition of organisms is in part due to stochastic events as described by the theory of island biogeography and by mechanisms related to temporal and spatial patchiness as discussed in Chapter 15. It is also, in part, determined by strong ecological interactions. Among these, some (such as the necessity of the presence of certain prey species for a specialised predator) are trivial, but less obvious strong competitive interactions also play a role. For individual species populations, however, the number

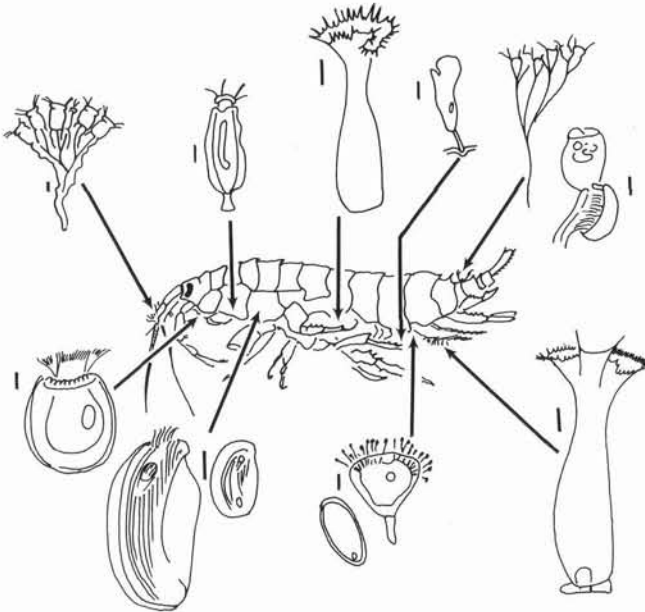


Fig. 40. Fauna of ciliates associated with the crustacean *Gammarus locusta* in inner Danish waters. The different species, whether sessile or motile, show a considerable degree of habitat selection on the surface of the host, but except for a ciliate predator of peritrich ciliates there are probably few if any direct interactions between the members of this specialised community. Scale bars = 10 μ m. After Fenchel [108]

of other species populations with which they interact strongly are probably few.

I will conclude the discussion on community structure with two examples of communities at two quite different scales. One is the community constituted by the ciliate fauna on the body surface of the crustacean *Gammarus locusta* [108], see also Figure 40. A large number of ciliate species specialised to this particular habitat exist. Most of them (the peritrich and the chonotrich ciliates) are filter feeders which take advantage of water currents generated by their host when filtering food particles from the water. Other ciliates are predators which feed on other ciliates associated with the crustacean and some feed on filamentous bacteria associated with the host cuticle. Finally, some forms obtain their nutrition directly from the host, but none of them seem to be pathogenic.

This micro-community seems highly 'structured'; its composition is fairly constant within gammarid populations although some of the species may be absent on individual gammarids. The different species, especially the sessile ones, have well-defined micro-habitats on the host surface. Some

occur only on the gills, others on the antennae, and so on. This last observation may well represent the 'ghost of competition past' [102]. Also, predation, of course, represents a strong and direct ecological interaction within this protozoan community. Otherwise, such direct interactions are not obvious within this specialised community, nor is the community likely to affect the larger surrounding aquatic community of which it is a part to any greater extent; rather it is a fairly isolated microcosm.

The other example is that of the fauna of the Baltic Sea. The present hydrographic conditions of this body of water resulted from postglacial changes in the sea level and from isostatic movements of the surrounding land masses and have existed for only about 5000 years. The Baltic is characterised by low and fairly constant salinities; the central part has a salinity of 6 to 7‰ (as opposed to an oceanic salinity of about 35‰). The fauna of the Baltic Sea is strongly impoverished relative to that of the surrounding inner Danish waters and the North Sea (Table 2) since few aquatic species in this part of the world tolerate brackish water. The fauna is mainly constituted by estuarine invertebrates which are tolerant to brackish water and which could invade the Baltic when it became a brackish water sea; it also harbours some species of marine bony fish as well as some freshwater organisms (mainly fish, pulmonate snails and insects). Most of the Baltic species populations have clearly diverged genetically from the ancestral populations outside the Baltic (see also Chapter 21) and show a number of phenotypic differences. If the Baltic Sea remains in its present state for perhaps a hundred thousand years, it is likely that a fauna of endemic brackish-water species will evolve and that the number of species will increase. This happened in the 'Sarmatian Sea', of which today the

Table 2. Species numbers of some taxa in the Baltic Sea and in the surrounding waters [109]

Taxon	North Sea Kattegat	Belt Sea	The Sound	Central Baltic
Foraminiferans	ca 80	47	?	0
Polychaetes	ca 250	ca 100	111	4
Cirripedes	10-12	5	10	1
Amphipods	147	55	76	9
Decapods	ca 50	12	32	2
Bivalves	92	32	58	4
Echinoderms	39	10	30	0
Bony fish	120	69	?	20

Caspian and the Black Seas and Lake Aral are remains. The origin of these brackish water bodies goes back to Tertiary times, and they have developed a rich endemic fauna [109].

Today the Baltic Sea may be considered as a large scale experiment in community ecology in which we can study the effect of removing a large number of species from a marine system. Certain effects are obvious. Thus, the population densities of the resident species are much higher than in other places where the same species occur; this is a general demonstration of the role of interspecific competition. More specific examples are also provided in terms of 'ecological release'. Many species have greatly expanded their habitat ranges in the absence of competitors. The small bivalve, *Macoma balthica*, for example, is in inner Danish waters and in the North Sea only found in very shallow water and in sandy sediments. In the Baltic Sea it occurs in all types of sediments and at all depths and the cause for this must be the absence of a number of related species which elsewhere occur at greater depths and in muddy sediments. The Baltic Sea therefore provides convincing evidence for the role of competition in structuring marine communities.

Yet, if we consider the overall properties of the marine communities of the Baltic Sea as compared with those in more saline waters, no particular features (in terms of population fluctuations, productivity or other such 'community properties') can be associated with the fact that species richness is drastically reduced. From an evolutionary point of view, the Baltic Sea is undersaturated with species and this has a historical explanation. From an ecological point of view, the Baltic Sea shows that even dramatic changes in species composition do not impair general properties and that biotic communities do not constitute a finely tuned machinery in which every little wheel is a vital and indispensable component.

17 Evolutionary Consequences of Species Interactions

Although the topic evolution does not strictly belong to ecology, it is intimately related to it; this is also reflected in most modern texts on ecology which integrate evolutionary problems with ecology. As discussed in Chapters 2 and 5 evolution adds an extra dimension to the explanation of ecological phenomena.

Ecological systems do not 'evolve' in a Darwinian sense; they change over time as a consequence of the evolution of the component species. Mendelian populations share pools of genetic material and the change in the frequency of genotypes due to mutation, genetic drift and natural selection

changes the gene composition of the population and therefore the appearance of individuals in the future. In asexual organisms the same can be said for each clone which also evolves over time. No such principle applies to ecological (*viz.* multiple species) systems which consequently change as a function of the properties of the individual species.

Evolutionary change in the individual species population is driven by changes in the abiotic and biotic environment, but it is constrained by the available genetical variance within the population and by physiological and physical constraints which may have been determined by past evolutionary events. Evolution is therefore opportunistic and the adaptations we observe in extant organisms are difficult to evaluate in any absolute sense. It is customary to be impressed by the complex and ingenious adaptations of organisms to various ecological conditions, but one could as well turn it around and wonder why better solutions have not appeared. An example is provided by the hereditary disease of man, sickle-cell anemia, which is especially common in large parts of Africa where a type of malaria caused by the protozoon *Plasmodium falciparum* occurs. Sickle-cell anemia causes a variety of symptoms and leads to premature death; it occurs in the homozygote carriers of a mutant gene specifying hemoglobin structure. The relatively high frequency of this apparently dysgenic gene is maintained through natural selection because the general health of the heterozygote carriers is relatively unaffected and at the same time they are resistant to malaria. This example clearly illustrates the opportunistic nature of evolution and the imperfection of adaptations.

A special pitfall in evolutionary ecology is what has been termed 'pre-adaptation'. This term must not be interpreted in a teleological way. Rather it means that a trait which has evolved in some context, quite fortuitously opens a new evolutionary potential or has ecological consequences in a quite different context. Thus, the ancestors of birds were 'pre-adapted' to flight in that these dinosaur forms had already become bipedal and so the anterior extremities were free to evolve for aerial gliding. When observing traits in extant organisms from an ecological view point the evolutionary origin of the traits may easily be misinterpreted. A few examples of this were already provided in the case of behavioural traits in Chapter 7.

A final problem in evolutionary ecology, on which I have already commented in the preceding chapters, is that in many theoretical models of population ecology, parameters are composite. Theoretical approaches in which different genotypes simply are assigned different values may yield quite misleading results or predictions [110].

In this chapter we will concentrate on the evolutionary consequences of species interactions. Such phenomena are also referred to as 'co-evolution'

since both components may evolve as a consequence of evolutionary changes in the other component. Co-evolution occurs as a consequence of all types of ecological interactions (predator-prey, parasite-host, exploitation competition, antagonistic competition and mutualistic interactions). To a large extent, these processes explain the diversity of life and they include some of the most fascinating observations of natural history [111].

The discussion in this chapter will in many ways parallel that of Chapters 12 and 13, only here we examine the evolutionary origin and consequences of the ecological interactions. We can distinguish between, on the one hand the evolutionary consequences of strong interactions, usually between two or a few species, and on the other hand the adaptations to the presence of a large number of other species each of which have only relatively weak interactions with the evolving species. The latter can be referred to as 'diffuse co-evolution'. Examples of diffuse co-evolution include such phenomena as general predator avoidance reactions (moving away quickly or hiding in response to sounds or to a moving object) or predators catching or probing any moving object of a suitable size. The adaptations in ruminant mammals for the exploitation of grasses and the adaptive traits of these plants (such as tolerance to grazing) may also qualify as diffuse co-evolution as may many traits of flowering plants and pollinating insects. There is, of course, not a sharp delimitation between diffuse co-evolution and the co-evolution of species pairs. Diffuse co-evolution has much in common with adaptations to the abiotic environment.

The co-evolution of predator-prey systems has appropriately been compared to the arms race between two comparable hostile nations. As one nation develops some new and more powerful sort of military hardware the other nation is forced to develop defensive countermeasures (and new kinds of offensive weapons) and so it continues, quite likely without any substantial change in the power balance between the two nations. This also applies for the arms race between predators and their prey species. Through natural selection antelopes have evolved acute sensory capabilities and the ability to run very fast as a response to the predatory pressure from large cats. Simultaneously the large cats have evolved special hunting strategies and impressive running speeds (like the cheetah) so tracing the evolution of their prey. Since the relative densities of antelopes and large cats on the African savannah is likely to have been rather constant over time the proportion of antelopes falling victim to predators is likely to have remained fairly constant.

Among predator-prey systems the co-evolution of vascular plants and herbivorous insects have attracted much attention. Different plants have

evolved a variety of adaptations which serve to reduce herbivory. These include mechanical devices such as thorns or hairs; among the more peculiar examples is that of the South American genus *Passiflora*. Several species develop structures that mimic the eggs of butterflies belonging to the genus *Helioconius* and these structures deter female butterflies from depositing their eggs on the plant. The production of toxic, secondary plant compounds, however, represents the most diverse type of anti-herbivory adaptation.

Most plants seem to produce such compounds and these display a great chemical diversity including phenols, tannins, alkaloids, cyanogenic compounds, steroids (which are analogues to insect hormones and so disturb the natural development of the insects) and many more. Many families of plants are characterised by particular chemical groups of compounds. In some cases the production of such compounds may not primarily have served for protection against herbivorous insects, but evolved as a protection against pathogens or simply be fortuitous by-products of metabolism. However, there is no doubt that most of these compounds do have an anti-herbivore effect and in some plants the production of secondary compounds increases in response to an attack by insects. Also, different populations of certain species of plants differ with respect to the amount of such compounds synthesised and this correlates with the local insect faunas. Regarding insects, their response has been the evolution of more or less specific metabolic pathways which de-toxify the secondary plant compounds.

There has been a particular interest in whether this 'arms race' between herbivorous insects and plants has led to host specificity rather than representing 'diffuse co-evolution'. There is indeed evidence that the mechanisms may lead to host specificity (at least at the family level) and that certain taxa of plants and insects have been coupled through their evolution. Most such evidence derives from butterflies. Members of the plant family, Umbellifera, contain furanocoumarins which are toxic to most insects. Larvae of swallowtail butterflies, however, are tolerant towards these compounds and papilionid butterflies seem to be evolutionarily linked to these plants. Cabbage butterflies not only tolerate a variety of secondary compounds produced as toxins or repellants (such as mustard oils) by crucifers, but these compounds even function as a clue for the female butterflies for egg deposition. In some cases the insects not only have acquired tolerance to such compounds, but use them themselves as protection against predators. Best known is the monarch butterfly, the larva of which feeds on milkweeds. These plants contain cardiac glycosides which are toxic to vertebrates; they are maintained in the adult butterfly and seem to offer protection against predation from birds [112].

The arms race of parasite-host systems differs qualitatively from that of predator-prey systems in that the parasite through killing its host destroys its own habitat and the more virulent it is, the shorter the time available for transferring into a new host individual (cf. the discussion on plague in Chapter 3). Consequently, while the host will over evolutionary time develop mechanisms to combat the parasite (such as development of immune systems) the parasite may evolve so as to decrease its virulence. There is ample evidence to that effect, not least in the evolution of diseases in man. An example is also provided in trypanosome diseases in African mammals. Trypanosomes are protozoa which live in the blood stream of vertebrates; they transfer from one host animal to another through blood-sucking arthropods, in particular dipteran insects. In man, two African species of *Trypanosoma* cause 'sleeping sickness'. Wild African mammals host various trypanosomes which do not seem to affect their hosts. However, when the same species of trypanosomes infect introduced European cattle this proves lethal. The interpretation of this is that the protozoa and their natural hosts have co-evolved over a long period of time resulting in decreased virulence for the host.

Detailed studies of trypanosome diseases (such as sleeping sickness) have yielded further insight into the mechanisms of co-evolution of host and parasite. In humans, sleeping sickness develops slowly (over a year or more) but untreated it eventually proves lethal. It has been shown that the immune system of an infected individual react by producing antibodies against cell-surface bound antigens on the protozoa. This leads to a rapid reduction in the number of trypanosomes. However, some individuals of the trypanosomes population are capable of changing their surface bound antigens and they start to increase in numbers. As a result, the host produces new antibodies and this cycle is repeated over and over again. It is not known exactly how many types of antigens that trypanosomes can produce, but it is very large and a substantial part of the trypanosome genome is dedicated to the production of antigens [113].

The number of mutualistic interactions described is vast and many of them have a profound impact on ecological systems. 'Syntrophic' interactions, that is, that the metabolic end product of one type of organism constitutes the resource of another type, are mainly to be considered as diffuse co-evolution (e.g. the evolution of aerobic organisms in response to the evolution of oxygenic photosynthesis, and many similar relations between a variety of microorganisms discussed in Chapter 19) although more intimate and species specific cases are very common as well. These include relations such as consortia consisting of a sulphate reducing bacterium on the surface of which a layer of photosynthetic sulphur bacteria are attached, en-

dosymbiotic photosynthetic organisms of many protozoa and aquatic invertebrates (Fig. 10), plant-fungal associations ('mycorrhiza'), nitrogen-fixing prokaryotes associated with plants and several others. Other types of mutualism are represented by the microbial degradation of structural plant compounds in the digestive system of herbivorous animals (which is found in practically all herbivorous mammals, in termites, in wood-boring beetles and in some marine invertebrates). More exotic are phenomena such as 'cleaning symbiosis' in which certain species of fish (mainly wrasses) or of shrimps remove food remains from the mouth of larger fish. The advantage for the host is supposed to be that ectoparasites are also removed by the cleaning fish. There cannot be any doubt about the fundamental evolutionary and ecological significance of mutualism; however, neither its documentation nor the theoretical understanding of how it evolves poses any particular difficulties, and although a fascinating subject it will not be discussed further here.

When addressing the question of the evolutionary consequence of competition, matters become more complicated; the problem is not quite simple from a theoretical view point and at the same time it may be difficult to document its role when discussing particular cases in nature. This situation quite parallels that of discussing competition in a purely ecological context. When discussing the evolutionary consequences of competition the fundamental difference between antagonistic competition and exploitation competition becomes more evident. We will first turn to the former type.

In some respects, antagonistic competition would seem to show some similarity with predator-prey systems regarding the evolutionary consequences, but there are also fundamental differences. Consider a pair of species engaged in exploitation competition. Any mechanism evolved in one species which somehow inhibits or kills the other one should favour the first one. However, in many cases it is not obvious how this can develop. Assume that the two species grow according to the Lotka-Volterra equations for competition:

$$dx/dt = rx[K - x - a'y]$$

and

$$dy_i/dt = ry[K - y - ax]$$

In this system we assume that species y consists of different genotypes which differ with respect to the magnitude of the interaction coefficient, a' . For example, genotype i may have a high value of a' since it produces some

toxin which inhibits individuals of species x . Obviously, an increase in a' will lead to an increase in the population size of y at the expense of x . However, as seen from the equations, all genotypes of y grow according to the same equation (which does not contain a') and so genotype i will not be favoured by selection. In other words, a gene which induces its carrier to inhibit a competitor will not increase individual fitness because it improves the fitness of all the genotypes simultaneously.

This argument would seem to exclude the evolution of interference competition. However, it only holds in a population of motile and homogeneously distributed individuals. Sessile organisms such as plants, corals or fungal hyphae on a piece of rotting wood all have to establish and defend themselves within a patch and in isolation from other individuals of the same species. Here such mechanisms will favour individual fitness and this is exactly the type of organisms in which interference competition has been well documented (see Chapter 13). However, there seem to be some exceptions to these generalisations. Certain plankton algae seem to produce antibiotic substances or toxins which are believed to inhibit or deter competitors or grazing plankton animals. Perhaps, this example does not contradict the above considerations in that these organisms may be asexual. The production of the toxins may be of significance during local blooms in which a large number of cells all belong to one clone and confined in a stable lens of water. In this case, the entire population may be considered as one individual, defending a patch.

A quite different type of co-evolution is that leading to a differential resource utilisation in species engaged in exploitation competition. As in an ecological context, the evolutionary response is an indirect one: natural selection acts so as to trace the change in the available resource spectrum due to the presence of another species. Consider again equations describing exploitation competition:

$$dx_i/dt = r_i x_i [K_i - x_i - a_{ij} x_j] / K_i$$

If it is assumed for species i that there are different genotypes having different values of a_{ij} , the one with the lowest value will increase in the population at the expense of the other genotypes. A decrease in the value of a_{ij} in this case means that species i will to a larger extent exploit resources not exploited by species j . It is therefore predicted that species involved in exploitation competition will over evolutionary time diverge with respect to their resource utilisation spectra.

This theory has been developed in considerable detail [114]. I will not give the formal derivation of this theory here, but only its major results and then turn to the evidence from nature.

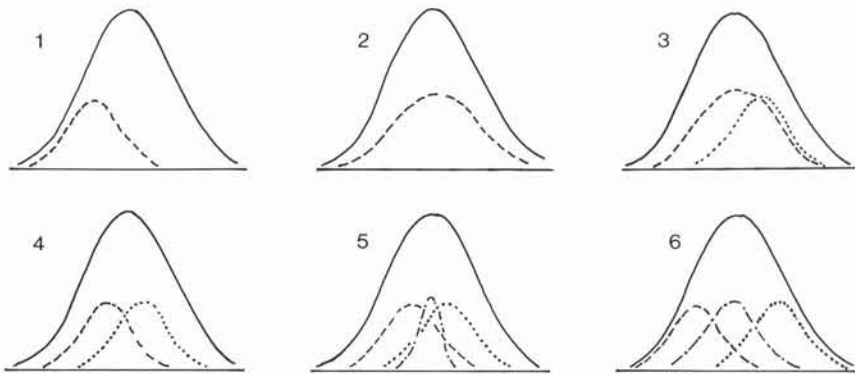


Fig. 41. Theory of the evolution of species establishing themselves on an island with a Gaussian food resource spectrum. Solid line = spectrum of resource qualities; other curves = niches of the consumer species. For further explanation see text.
Original

A simple way to summarise the results of the theory of the evolution of competing species is to consider an island with a given resource spectrum (Fig. 41) and then follow the evolutionary events as successive colonisations by different, ecologically related species occur. The first species to arrive is likely to adapt to the given resource spectrum by moving the mode of its resource utilisation function towards the mode of the available resource spectrum. A second species which arrives will experience a distorted resource spectrum as a result of the exploitation by the first species and it will evolve a niche position which is shifted relative to that of the first species. The first species will also respond to the exploitation pattern of the second species, so eventually their niche positions will be symmetric relative to the mode of the (un-exploited) resource spectrum. This pattern will be repeated as additional species arrive, although eventually competitive exclusion (or extinction due to demographic stochasticity in small populations) sets a limit to the number of co-existing species on our theoretical island. The model thus attempts to explain the patterns in resource utilisation found in co-existing feeding guilds (Chapter 12, Fig. 32 and 36) as a consequence of co-evolution of species which compete for similar resources.

The importance of the mechanisms outlined above for the diversity of organisms in nature remains controversial. An alternative explanation would be that species which have evolved in allopatry already had evolved differences in their use of resources and so were able to co-exist when later events led to sympatric occurrence. The basis of this controversy is, of course, the same as that of establishing the role of exploitation competition in ecological time: most evidence must be inferred from distribution pat-

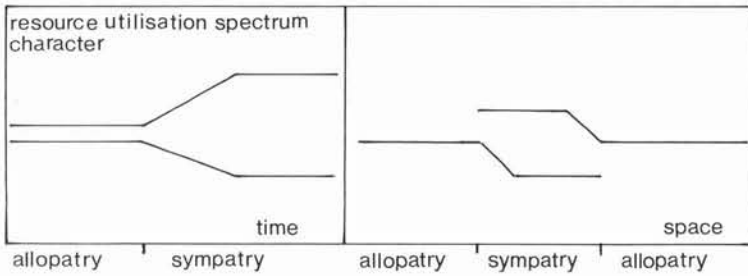


Fig. 42. Evolution of character displacement in time and its spatial distribution. Original

terns whereas direct observation of the events believed to be the underlying cause or experimentation is very difficult or sometimes impossible. My personal view is that co-evolution of competitors is, so far, the most convincing theory which can account for patterns of feeding guilds and for explaining the diversification of resource utilisation and that alternative explanations are insufficient or unlikely in most studied cases.

The basic idea behind the co-evolution of competitors is schematically shown in Figure 42. At some point in time two species co-occur in a region. Prior to their sympatry their feeding niches were identical, but they tend to diverge in sympatry. It is usually assumed that the time scale involved exceeds the life expectancy of biologists (although experiments such as shown in Figure 7 demonstrate that this is not necessarily the case). However, the events may also have a spatial dimension. Thus if two closely related forms occur in allopatry, but have a zone of overlap, the prediction is that their resource utilisation should diverge in the zone of sympatry.

This phenomenon is usually referred to as 'character displacement' [115]. The choice of this term is flavoured by the fact that in most cases the functional aspect of a niche displacement is inferred from morphological traits such as dimensions of the beak of birds or overall size. Furthermore, character displacement may really have two different causes: it may result from selection against hybridisation where two closely related species overlap ('reproductive character displacement') or it may be the result of exploitation competition. Here I will only be concerned with the latter type, but Chapter 21 shows that it may not always be easy to distinguish between them.

A substantial number of examples of character displacement exists; while most of these probably are correctly interpreted as such they are rarely supported by additional evidence so they may be open to other interpretations. In particular it is necessary to establish that the species actually

compete for resources, that the observed divergence of some character is related to food exploitation and that the change in character has a hereditary basis. I will here discuss two examples which at least in part fulfill these requirements.

The first of these is constituted by 'Darwin's finches'. These passerine birds occur on the Galapagos Islands. An ancestor of these forms which lived in continental South America must once have managed to establish itself on the remote islands. It is also possible that there were several successive colonisations. At any rate, in the absence of other related birds, speciation and ecological divergence took place and when Darwin visited the islands in 1835 he was struck by how these finches had filled a variety of ecological niches which elsewhere are occupied by other types of birds. Darwin's observations played a major role for his theory of evolution and his interpretation of the findings was close to the theory outlined above. Indeed, since Galapagos finches are not found elsewhere it is hard to escape the conclusion that their ecological and morphological divergence is a result of the co-evolution of competing species.

There would be no reason to assume that the evolutionary processes which must have led to present day patterns have stopped; that is, speciation in allopatry on individual islands, migration to islands where the ancestor lives and subsequent character displacement due to exploitation competition. When David Lack visited the islands about a century after Darwin he noted that some of the species diverge in beak dimensions in sympatry relative to where they occur in allopatry (Fig. 43). This has since been one of the standard examples of character displacement in texts on

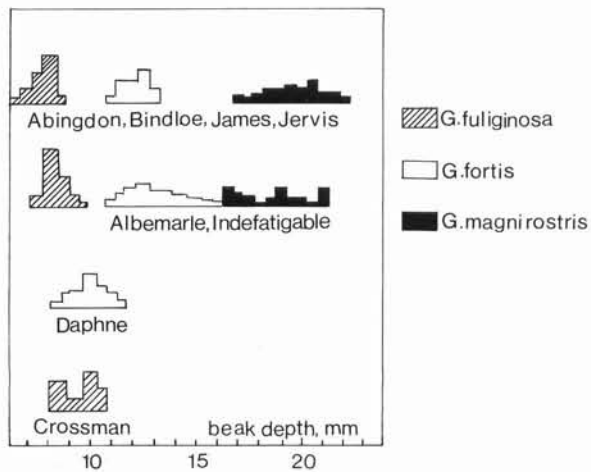


Fig. 43. Beak dimensions of three species of Darwin's finches on two islands where they all co-exist and on two islands with only one species. Redrawn from Lack [116]

ecology and evolution. Most recently Grant has studied the system again. It was convincingly demonstrated that interspecific exploitative competition for food is important for the involved species, that the beak dimensions do correlate with the type of food they can utilise and that beak dimensions are genetically determined. Deservingly, Darwin's finches represent the most thoroughly studied and best documented example of co-evolution of exploitation competition [116].

The other example I will bring derives from my own work on species belonging to the small prosobranch snail genus, *Hydrobia*. In Danish waters three species occur, *H. ulvae*, *H. neglecta* and *H. ventrosa*; here I will con-

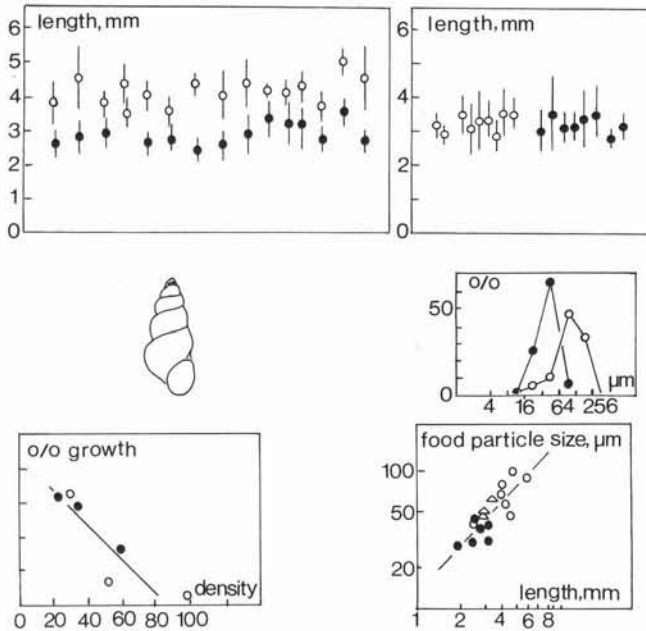


Fig. 44. Character displacement in the snail genus *Hydrobia* (open circles: *H. ulvae*, filled circles: *H. ventrosa*). Above: shell lengths on 15 localities with co-existence and on 17 localities where only one species occurs. Middle, right: food particle size spectra for the two species where they co-exist. Below, right: median food particle sizes as a function of shell length (triangles: the third species, *H. neglecta*). Below, left: competition experiment in containers with natural sediment (illuminated so as to secure growth of algae which serve as food). Open circle: growth of *H. ulvae* (% of weight in 26 days) as a function of its own density; closed circles: average growth of 20 *H. ulvae* as a function of the density of *H. ventrosa* of similar sizes. Growth of the species is inhibited equally as much by its own density as by the other species; hence (for equally sized snails) resource utilisation overlap is close to unity. After Fenchel & Kofod [117]

centrate on the former and the latter species. The snails occur in and on sediments of shallow water and mainly in protected places such as in lagoons, bays and estuaries. They mainly depend on diatoms for food, but they are rather unselective and so consume a large number of sediment particles along with the algal cells. They occur at great densities; several thousand individuals per square metre is not unusual. The species show some differential preference with respect to salinity, *Hydrobia ventrosa* occurs mainly in brackish water whereas *H. ulvae* occurs at higher salinities. At most places in the inner Danish waters the species occur in allopatry. However, in complex fjords and bays with fairly stable salinity gradients, stable co-existence of two of the species occurs over larger or smaller areas.

A collection of individuals from a large number of localities in the Limfjord in northern Jutland showed that the species diverge in size wherever they co-occur (Fig. 44), and although some environmental conditions (salinity, sediment type) differed somewhat between the sampling stations, none of these factors correlate with the size difference. This example of character displacement is interesting in that, in contrast to most other ones, it is reproducible. It is also interesting since a maximum time for the evolutionary events can be determined because the present opening of the Limfjord to the North Sea first came into being about 160 years ago. Prior to that, the Limfjord only opened to the east and contained dilute brackish water and it is unlikely that *Hydrobia ulvae* was established there.

Experimental work has since shown that the snails show interspecific competition in their natural habitat, that this competition is less intense between snails of different sizes, that there is a linear correlation between body size and the sizes of ingested particles and that different sized snails equilibrate with different size spectra of diatoms in the sediments (Fig. 44). The hereditary basis for size remains to be demonstrated [117].

18 The Evolution of Life Cycles

Organisms show a tremendous variation with respect to their life cycles and reproductive patterns. This holds even when we – as is largely done in this chapter – ignore absolute time scale. That is, we will not wonder about the fact that the generation time or the Malthusian parameter spans a factor of 10^7 or so when comparing a bacterium with a giant redwood. The reasons for, and the consequences of this were previously discussed. But even when we restrict ourselves to look at fairly related organisms of comparable sizes we find an astonishing variability. The oceanic sunfish genus *Mola* is said to produce about 10^8 eggs whereas sharks of comparable sizes produce only

a small litter of large offspring. Some herbaceous plants are annuals which die after producing seeds; perennial relatives may live for decades or centuries to flower every summer. Why is this so?

The theoretical treatment of the subject has often appeared rather confused and many conclusions and generalisations which do not really hold true have been arrived at. The reason, I believe, is that the subject has been approached from a wrong angle. Ecologists have tended to confuse the ecological consequences of reproductive patterns with the causal basis of their evolution. Thus, marine invertebrates with planktonic larvae are better at dispersal, and their adult population sizes tend to be more variable than what is found in forms with direct development. Attempts to explain the reproductive patterns from such correlates may be futile because they are a consequence of, rather than a cause for, the reproductive behaviour. Theoretical population geneticists, on the other hand, have uncritically assigned genetic variation into parameters of ecological models without analysing the significance of the particular parameters [118].

I will first consider the kind of questions we can ask. A multicellular organism appropriates a certain fraction, E , of its available energy for reproduction. This 'reproductive effort' can in practice be estimated as the total egg volume. So one question would be: how large should E be? Given an amount of energy for reproduction the organism can produce many small or few large eggs so that $B = E/S$, where B is the litter size and S is the size (volume) of the eggs and so the question is how to choose the optimal value of S . Furthermore, an organism may reproduce only once to die (semelparity, like an annual plant, or a 'big bang reproducer' as it has, somewhat vulgarly, been called in the literature) or it may have a long life span and reproduce many times (iteroparity, like a perennial plant).

Natural selection will tend to maximise individual fitness, that is to maximise the number of offspring which reach maturity. This fundamental principle together with the observation that the different options mentioned above represent opposing selective forces which must be balanced is the appropriate approach to the problem. For example, increasing fecundity (B) must lead to a decrease in egg size and this again to a decreased survival and so we must find the optimum value of B which maximises the number of eggs which make it to the adult stage. The principle of an evolutionary trade-off between fecundity and survival is exemplified in Figure 45. To this, as in all other considerations on evolutionary biology, must be added the caveat that there are constraints to evolution. For example, while a model may predict the evolution of smaller eggs a given organism may irreversibly have lost this option. In mammals the complex brood care is unlikely to allow genetic variance which could lead to a mass production of

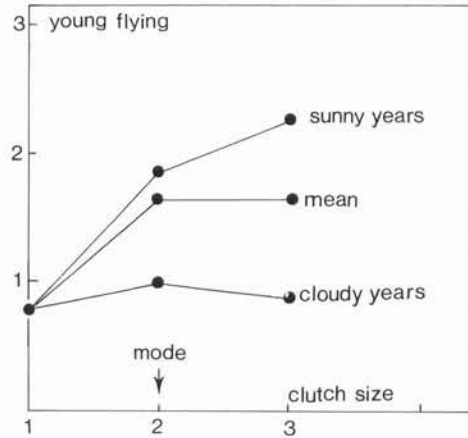


Fig. 45. Survival of young swifts as a function of clutch size: Maximum fitness is a compromise between numbers of eggs and survival probability which is higher in a small clutch due to the limited ability of the parents to find food. After Lack [118]

planktonic larvae and so it is pointless to ask why whales have not adopted the reproductive mode of the above mentioned sunfish. Undoubtedly, the physiological constraints and absence of hereditary variation greatly decrease the possibility of any mammal 'escaping' their characteristic reproductive mode. In the following I will exemplify some results of the approach outlined above.

Cole [119] seems to have pioneered this way of thinking about reproductive patterns. He asked why iteroparity exists at all. Consider an annual which produces $B(a)$ seeds (or eggs). If allowed to grow unlimited its population will increase by a factor of $B(a)$ per year, that is, its Malthusian parameter, $r = \ln[B(a)]$. Now suppose that it suddenly becomes immortal so that adult individuals continue to produce $B(a)$ seeds every following year. By what factor will the population then grow? The answer is $[B(a) + 1]$, where the second term simply represents the surviving adult; that is, $r = \ln[B(a) + 1]$ or, if a perennial and an annual have equal potential population growth, then $B(a) = B(p) + 1$. Thus the gain in fitness of an annual by becoming immortal simply equals that of producing one single additional seed. Obviously, if B is only moderately large this gain is symbolically small.

At the time of Cole's paper this result seemed paradoxical and it at least required an explanation of why iteroparity exists at all. Cole himself suggested that the result is different if the juvenile period exceeds the time interval between litters of the iteroparous adult. This was shown formally, but is easily understood intuitively: the surviving adult will contribute more to future population growth than any one of its own offspring since it can reproduce again before its offspring reaches maturity. This consideration

does perhaps explain that semelparous organisms are particularly common among those in which the juvenile period is less than a year and which at the same time have a seasonal reproductive period. The length of the juvenile period is mainly a size correlate and in these organisms the effective juvenile period (from egg to maturity) becomes the same as that of the intervals between litters for an iteroparous species. This is the fate of many insects or other small invertebrates and herbaceous plants which consequently are 'annuals'. In contrast, trees first become mature after many years, whereafter they can produce seeds every year and so they tend to be perennials.

There are other mechanisms which influence the relative advantage of being iteroparous. This becomes clear if we include considerations on mortality. Assume that juvenile survival (the probability of an egg or seed reaching sexual maturity) is C and that the probability of survival by an adult from one breeding season to the next is P . Now the annual population growth factor for the semelparous form is $CB(a)$ and for the iteroparous form it is $CB(p) + P$. Comparing these expressions it can be seen that for an annual to have a growth potential equal to the perennial form, $B(a) = B(b) + P/C$. Now the advantage of becoming iteroparous depends on the ratio between juvenile and adult survival. Since it is likely that P is larger than C (in some cases this is extremely so) the advantage of iteroparity may be considerable, making it intelligible, for example, that marine invertebrates with planktonic larvae (for which survival probability is exceedingly low) usually have a long adult life span.

There is another factor that may favour iteroparity, *viz.* that seasons vary with respect to how successful a litter may be. Thus blooms of planktonic algae may not occur at exactly the same time of the year so that larvae may miss them and consequently die of starvation and during some springs weather may be exceptionally dry so that seedlings die. A semelparous organism thus buys only one lottery ticket in a chancy game whereas the iteroparous species have several chances for reproducing successfully (that is, that some of its offspring actually make it to maturity). This mechanism has been termed 'bet hedging' and suggests that an organism in a temporally variable environment should sacrifice reproductive effort for longevity in order to increase the chance that it will at least once be successful in reproducing. Data which support this idea are exemplified in Table 3 which shows how variation in reproductive success from one year to the next correlates with longevity in some species of clupeoid fish [120].

A somewhat different type of bet hedging is found in annual plants (and in some insects), that is delayed germination (or hatching). In desert annuals (but the phenomenon does indeed occur in common garden weeds as

Table 3. Reproductive parameters of some clupeoid fish. Data from Murphy [120]

Species	Age at first maturity	Years of reproductive span	Variation in spawning success (highest/lowest)
Atlantic herring	5-6	18	25×
North Sea herring	3-5	10	9×
Pacific sardine	2-3	10	10×
Baltic herring	2-3	4	3×
Anchoveta	1	2	2×

well) not all seeds germinate the first year; a certain fraction waits until the second year and some germinate only after three years and so on. Cohen has modelled this phenomenon to arrive at predictions as to the fraction of seeds which should germinate each year and as a function of the frequency of favourably years [121].

I will now turn to the problem of many small versus few large eggs assuming a constant reproductive effort, E . I will not discuss the problem of an evolutionary stable value of E . This is not obviously coupled to the question of egg numbers (see also Fig. 43), but it can be shown that there is only one such stable value in contrast to egg sizes (for which two evolutionary stable values may exist). The number of eggs is assumed to be inversely proportional to their size, $B = E/S$. We denote juvenile survival C and the maximum we seek is that of the product BC . There must be a minimum size of the eggs below which survival is zero (an egg must at least contain a nucleus, a mitochondrion and some other parts to be viable at all). With increasing size we may assume that survival probability increases (Fig. 46) in that size in itself is likely to increase survival and because stored nutrients (yolk) makes it less vulnerable to variation in the availability of food. It also seems a robust assumption that C is a convex function of S , that is, that the increment in survival probability decreases with increasing size. With these simple assumptions it can easily be seen that the optimum egg size (for which the product CB takes a maximum value) is found as the point where a tangent line through the origin touches the $C(S)$ function.

The probability of survival thus influences the evolutionary stable egg size. Prolonging the juvenile period (for example because development takes place at a lower temperature or because the juveniles are exposed to a greater variability in food availability) will tend to decrease survival probability and so lower the $C(S)$ curve in Figure 46. The prediction is that if life becomes harsher for the juveniles, selection will favour fewer and larger

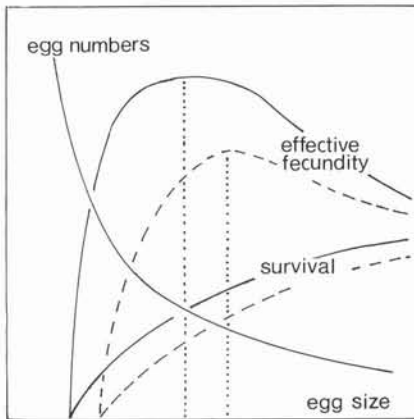


Fig. 46. Egg numbers (assumed to be inversely proportional to egg size) and survival as a function of egg size. Maximum effective fecundity (the number of offspring making it to the adult stage) is found as the maximum of the product of the two curves. If survival probability is decreased (dashed line) due to a 'harsher' or stochastic environment selection will favour an increase in egg size at the expense of egg numbers. After Kolding & Fenchel [122]

eggs, while conversely, if the juvenile period is shorter and survival higher, selection will favour a larger number of small eggs.

This is exemplified in Figure 47 showing egg numbers and sizes in five species of gammarid crustacea. Some of these breed in the summer and some in the winter and the latter have fewer, larger eggs than the former. Note that within each area, the reproductive efforts are nearly identical for all five species, but this differs for the two different areas studied. No explanation for this has been offered, but it shows that it is not coupled to the egg number versus egg size problem and that it would seem that some environmental factor in the two areas have the same effect on all these sibling species regarding the value of E [122].

I will finally discuss a somewhat more complicated version of the problem of many small versus few large eggs: the reproduction of marine invertebrates. There seems to be a number of relatively distinct types of reproduction in these forms. Some produce a large number of 'planktotropic' larvae that feed in the plankton and after reaching a certain size, metamorphose and settle on the bottom. Others have direct development; they produce fewer, but larger eggs which develop directly into a benthic juvenile without any metamorphosis; this latter type is sometimes associated with some sort of brood care. There are two variations on this dichotomous scheme. Some bivalves and echinoderms produce 'lecitotropic' larvae which are pelagic, but they are larger than planktotropic larvae and contain yolk so that they do not depend on finding their own food. In some prosobranch gastropods, 'nurse eggs' are found. The eggs are deposited in some sort of capsule, but only few of the eggs develop; the remaining serve as food for the developing snails which eventually emerge from the capsule with the metamorphosis size of relatives with planktotropic larvae.

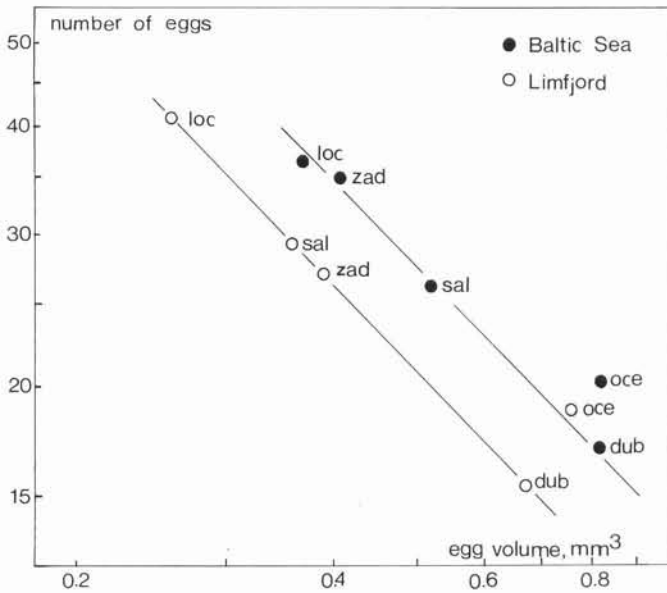


Fig. 47. Egg numbers versus egg sizes in five species of the crustacean genus *Gammarus*, in two areas. Except for *G. oceanicus*, all species within one area seem to produce nearly the same total volume of eggs, but for reasons unknown, this differs for populations in the Baltic Sea and in the Danish waters. Species breeding during the summer (*G. locusta*, *G. zaddachi*) produce many small eggs while species reproducing during the winter (*G. oceanicus*, *G. duebeni*) produce fewer, large eggs. *Gammarus salinus* reproduces during the winter in the Limfjord, but predominantly during summer in the Baltic Sea. Redrawn from Kolding & Fenchel [122]

A number of properties of these reproductive patterns require an explanation. First of all, it seems as if the extremes are always found; a species produces either planktotrophic larvae or it has direct development (or possibly lecithotrophic larvae in some taxa) whereas intermediate types do not seem to occur. If the size distribution of eggs of some fauna is plotted, a bimodal pattern is found (Fig. 48); if a wide range of taxonomic groups is included, this may be somewhat obscured, but it becomes very evident when the species within a single genus are compared. Figure 48 also shows that very closely related forms may have different modes of reproduction; in this case, however, metamorphosis size and the size of animals hatching without metamorphosis is about the same and in prosobranch snails, eggs with direct development have a volume which is 50 to 70 times larger when compared to forms with plankton larvae. Therefore, it seems as if there are two possible evolutionary stable situations: either many very small eggs or few large (metamorphosis size) eggs are produced. It is also suggested that

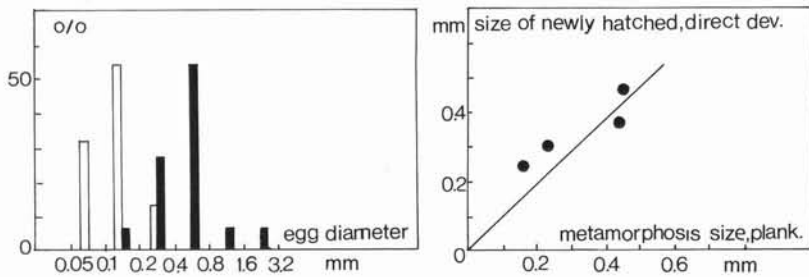


Fig. 48. Left: size distribution of eggs of all Danish, marine species of prosobranch snails with planktotrophic larvae (open bars) and with direct development (filled bars). Within any one genus of snails comprising both types of development the bimodal size distribution is even clearer: Species with direct development have a diameter which is about four times that of species with planktotrophic larvae. Metamorphosis size of the latter is identical to the newly hatched individuals of congeners with direct development (right). Graph shows the sizes of metamorphosed (planktotrophic development) and newly hatched larvae (direct development) for species of the genera: *Lacuna*, *Littorina*, *Rissoa* and *Hydrobia*. Redrawn from Christiansen & Fenchel [124]

the shift from one type to the other takes place frequently during evolution and that this shift is easier or more frequent than changing the metamorphosis size or the reproductive effort. There are also some characteristic distribution patterns for the different types. Among them, a clear correlation between the presence of planktotrophic larvae and latitude is evident; thus among arctic prosobranchs planktotrophic larvae are hardly found at all whereas about 70% of the species found around the Azorean islands produce planktotrophic larvae [123].

A theoretical analysis of this in principle proceeds as in Figure 46. However, in this case there is a complication of a two-step development and a fixed metamorphosis size. With the assumption of a sigmoid growth curve for the individual larvae and a size-dependent rate of mortality such an analysis shows that the type of development which will be favoured by evolution depends on the growth rate of the individual larva and on the mortality rate. If the former is high and the latter is low then a large number of small larvae is favoured and if the converse is true then metamorphosis size larvae are favoured. At some intermediate conditions either possibility represent an evolutionary stable situation; [124] offers a formal proof of this.

The model is satisfying in that it explains some of the patterns found. Thus the expectedly longer development time and presumably larger mortality due to unpredictability of food resources at higher latitudes will result in direct development whereas the converse is true at low latitudes. By

predicting two stable equilibria the model explains why only the two extremes are found and why the switching between them apparently is an evolutionarily simple and frequent event which may follow from slight changes in the environment or in the ecology of the species. The most important and general conclusion, however, is that the correlates of these two modes of reproduction (regarding fluctuations in adult population sizes and ability to disperse) now appear as fortuitous by-products of the evolutionary dynamics of a two-stage development rather than a causative agent for the development of the mode of reproduction.

IV Some Examples of Communities and Ecosystems

19 Microbial Communities in Chemical Gradients

This and the two following chapters examine three ecological systems in more detail. The systems exist in aquatic environments. I have contributed to their investigation over several years and during the course of research quite different questions have been asked and different methods used. This chapter mainly exemplifies problems of 'flows of energy and materials' (Chapter 11); Chapter 20 aspects of population interactions and environmental heterogeneity; and Chapter 21 aspects of evolutionary ecology.

Here we take a look at the microbial (that is, mainly prokaryote) communities which develop in association with anaerobic conditions. There is a multitude of reasons for studying such systems. They constitute a beautiful example of how physiological properties of the organisms in conjunction with physical and chemical properties of the environment lead to a characteristic spatial structure of the communities and of patterns of element cycling. Also, the ecological approach described here has led to the finding of novel types of metabolism in prokaryotes. Although these communities are not obvious to the casual observer their impact on the turnover of materials in the biosphere is substantial from a qualitative as well as a quantitative point of view. Under some circumstances the systems I describe become an environmental nuisance in that they create environments which may be lethal to higher life (and smelly as well) and eutrophication caused by human activity may locally lead to their expansion. They also have a romantic aspect because prokaryotes were the only existing organisms for about three quarters of the time that life has existed on earth. Free oxygen in the atmosphere originated with the appearance of blue-green bacteria; prior to that the atmosphere is believed to have had a very low oxygen tension. Many of the types (or at least physiological types) of organisms which we will discuss below must have dominated in Precambrian times. In some respects, at least, the ecological systems we discuss are 'living fossils' from an early stage in the evolution of life.

Anaerobic environments occur in different places. The digestive tracts of certain herbivorous animals constitute anoxic habitats with complex communities of prokaryotes (and sometimes also protozoa). The best studied and seemingly most complex systems are those found in the rumen of artiodactyl mammals and in the hind gut of termites, but such systems are also widely distributed among other groups of animals [125, 126]. They share many properties with those I describe below, but I will not refer to them further. Anaerobic systems also occur in stagnant water bodies and, nearly universally, in sediments (and water-logged soils). In some cases, notably in geothermal areas, the reducing power for the maintenance of these systems is due to non-biologically derived hydrogen sulphide or methane, but in by far the most cases, reduced carbon (dead organic matter) is the basic energy source of the systems. A special type of these systems is represented by 'stromatolites'. These are thick layers of various types of filamentous and other bacteria. While they have many characteristics in common with systems which develop in the surface layers of shallow water sediments, the characteristic thick laminated bacterial mats cannot develop due to the mechanical disturbance of animals and so only occur in places where animals cannot live: hypersaline waters and hot springs. Extant stromatolites have attracted special interest since they closely resemble fossil stromatolites which are 2 to 3×10^9 years old representing the earliest traces of ecological systems which were then probably omnipresent in shallow seas [127].

Here I mainly refer to ordinary shallow water marine sediments and also to some extent to stratified water columns. Anoxic conditions occur at some depth in many thermally stratified lakes, and in certain marine basins or fjords (the Black Sea, for example, is permanently anoxic beneath a depth of about 200 m); in aquatic sediments such conditions are always found. The systems I describe may develop around a sufficiently large particle of decomposing organic material; however, a vertical stratification is more typical. Oxygen and light is supplied from above whereas dead organic material tends to sink to the bottom of aquatic systems. The vertical extent of the systems varies considerably. In sediments the zonation patterns may be compressed to a scale of millimetres since the transport of dissolved material takes place by molecular diffusion and light penetrates only a few millimetres into a sediment. In the water column similar systems extend over many metres or tens of metres; transport of materials takes place in part through convection or turbulence, and light may penetrate to a considerable but restricted depth, whereas the dead organic matter which drives the whole thing sinks all the way to the bottom of the water body.

These ecological systems derive their properties from the fact that the supply of organic material exceeds the supply of oxygen needed for aerobic mineralisation. At some level oxygen therefore disappears. There are, however many processes by which bacteria can proceed with mineralisation under anaerobic conditions. More complex organic materials are first decomposed by fermenting bacteria. The end-products of their activity include low molecular fatty acids (in particular acetate, propionate and butyrate), hydrogen gas and some other reduced compounds, notably ammonia and sulphide. The organic compounds and hydrogen are then further mineralised or oxidised by what has been termed 'anaerobic respiration'. This refers to dissimilatory respiratory processes in which compounds other than oxygen serve as the terminal electron acceptor. There are several such processes, among them nitrate respiration (in which nitrate is used as an electron acceptor to produce mainly nitrogen gas, but also some other reduced nitrogen compounds). Quantitatively most important, however, is 'sulphate reduction' in which sulphate is reduced to sulphide (actually mainly the HS^- -ion at the prevailing pH). When sulphate is depleted, methanogenesis occurs. Here CO_2 is used for oxidising hydrogen into methane by 'methanogenic' bacteria; these bacteria can also produce methane from acetate; strictly speaking their dissimilatory metabolism is not a true respiratory process since cytochromes are not involved.

Due to the one-way supply of oxidants and the fact that the different dissimilatory processes have different energy yields they occur in a characteristic spatial order. All these processes are oxidation-reduction processes and their energetic yields depend on the capacities of the oxidants to accept electrons (Table 4). This shows in a schematic way the possible and realised

Table 4. Chemotrophic reactions of bacteria [126]

Oxidant (e^- acceptor)	Reductant (e^- donor)*							
	H_2	CHO	CH_4	HS^-	NH_4^+	N_2	NO_2^-	Fe^{2+}
H_2O	-	+	-	-	-	-	-	-
CHO	+	+	-	-	-	-	-	-
CO_2	+	+	-	-	-	-	-	-
SO_4^{2-}	+	+	+	-	-	-	-	-
NO_3^-	+	+	+	+	-	-	-	-
O_2	+	+	+	+	+	-	+	+

* CHO refers to a general organic compound

Table 5. Energetics of some dissimilatory reactions [126]

(1) Oxidation of hydrogen with different oxidants

$H_2 + 1/2 O_2 \rightarrow H_2O$	$\Delta G'_0 = -56.7 \text{ kcal}$
$H_2 + 2/5 NO_3^- + 2/5 H^+ \rightarrow 1/5 N_2 + 6/5 H_2O$	$\Delta G'_0 = -53.6 \text{ kcal}$
$H_2 + 1/4 SO_4^{2-} + 1/4 H^+ \rightarrow 1/4 HS^- + H_2O$	$\Delta G'_0 = -9.1 \text{ kcal}$
$H_2 + 1/4 CO_2 \rightarrow 1/4 CH_4 + 1/2 H_2O$	$\Delta G'_0 = -8.3 \text{ kcal}$

(2) Examples of chemolithotrophic reactions

$NH_4^+ + 3/2 O_2 \rightarrow NO_2^- + 2 H^+ + H_2O$	$\Delta G'_0 = -65.7 \text{ kcal}$
$HS^- + 2 O_2 \rightarrow SO_4^{2-} + H^+$	$\Delta G'_0 = -190.4 \text{ kcal}$

(3) Examples of phototrophic reactions

$6 CO_2 + 6 H_2O \rightarrow C_6H_{12}O_6 + 6 O_2$
$6 CO_2 + 12 H_2O \rightarrow C_6H_{12}O_6 + 12 S + 6 H_2O$

chemotrophic reactions in bacteria. The oxidants are arranged in the order of increasing capacity to accept electrons (from the top to the bottom) and the reductants are arranged in an decreasing order of capacity to donate electrons (from left to right). The processes with the highest energy yields are thus found in the lower left corner of the table. Table 5 shows the energetic yields of some of the processes (they are presented as standard free energy at pH 7 and do not exactly reflect physiological conditions, but their relative values are adequate for our discussion).

When competing for substrate, the physiological types of bacteria with the highest energy yield will win because they can grow faster at a given uptake of substrate. As long as oxygen is available, aerobic respiration will prevail. When oxygen is depleted, nitrate respiration will take over and below that zone, sulphate reduction dominates. Only when sulphate is depleted, will methanogenesis be important. The different electron acceptors will therefore be depleted one by one according to their capacity as oxidants so leading to a vertical zonation of chemical species and of metabolic processes ([126] and Fig. 49). The competition for, and relative role of, different types of organic substrates can be demonstrated in experiments as shown in Figure 50. Molybdate selectively inhibits sulphate reduction and when added to an anaerobic sediment the substrates of these bacteria immediately increase in concentration because they are no longer consumed, but still produced by fermenting bacteria. In general, the hydrolysis and fermentation of more complex organic materials (which cannot be used directly by, e.g. sulphate reducers) into low molecular compounds seem to limit the rate of mineralisation in sediments. Finally, we see that complete mineralisation can take place in anaerobic environments.

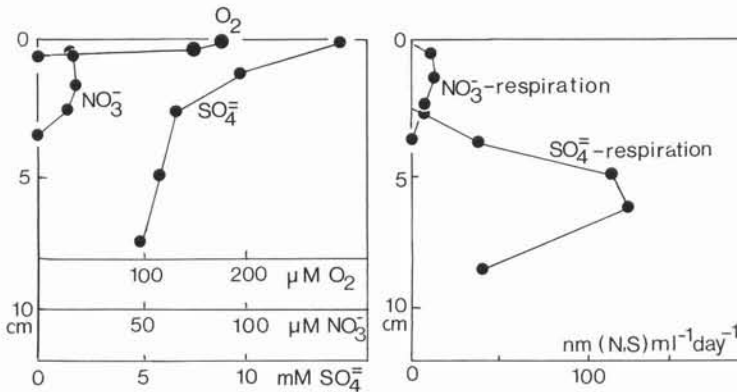
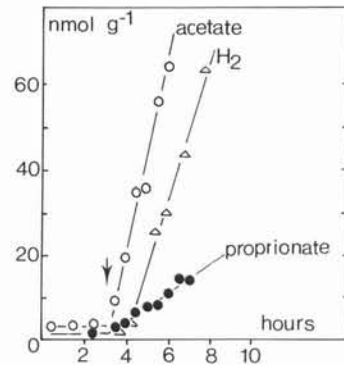


Fig. 49. Vertical distribution of oxygen, nitrate and sulphate (left) and of the rate of microbial nitrate and sulphate respiration in a Danish shallow water sediment. After Sørensen *et al.* [128]

Fig. 50. Concentration of hydrogen gas, acetate and propionate in an anaerobic sediment slurry following the addition of molybdate (arrow). This ion specifically inhibits bacterial sulphate reduction. After Sørensen *et al.* [129]



While the spatial zonation of organisms, chemical species and processes thus are determined by the energetics of the processes and by the competition for substrates, the quantitative importance of the processes is determined by the availability of the different electron acceptors. Nitrate usually occurs in only limited amounts in marine sediments and so nitrate reduction plays an accordingly small role. Due to its low solubility oxygen is quickly depleted in aquatic environments. In contrast, sulphate is plentiful in seawater, where it represents about 300 times more oxidation equivalents than does oxygen. Sulphate reduction is therefore a quantitatively dominating process in marine sediments and sulphate is only depleted at considerable depths where most readily decomposable organic substrate is already mineralised. Methanogenesis is therefore quantitatively less important. In

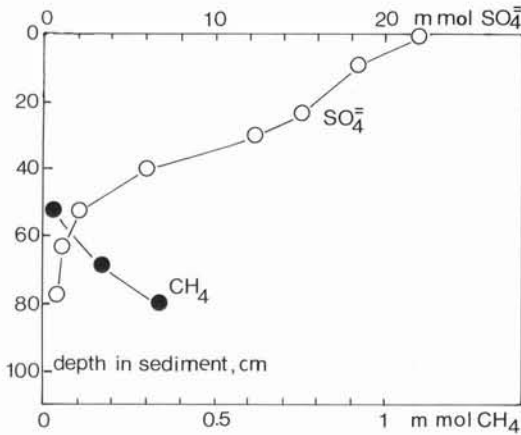


Fig. 51. Vertical distribution of sulphate and of methane in a sediment from Long Island Sound. Redrawn from Fenchel & Blackburn [126]

freshwater sediments, in particular in lakes with a low sulphate contents, methanogenesis plays a correspondingly larger role. In typical coastal seas, sulphate reduction accounts for around 50% of the entire mineralisation in the sediment [126].

The vertical gradient of electron acceptors leads to a net downwards flux of these compounds. Conversely, the endproducts of the anaerobic metabolic processes have a net upwards diffusion. Starting from below, methane diffuses upwards until it reaches the sulphate zone and here it is oxidised anaerobically by sulphate reducers (Fig. 51).

Sulphide is a bit more complex in that it reacts with iron to produce black iron sulphides; over a longer time period they are transformed into the somewhat more stable mineral, pyrite. Pyrite will under some conditions represent a sort of fossil fuel (although not a desirable component of e.g. lignite used for combustion). Most of the sulphide, however, does diffuse upwards until it comes into contact with oxygen. While this chemical mixture is not stable the potential energy of sulphide is utilised by 'chemolithotrophic' or 'white sulphur bacteria' which derive their energy from the oxidation of sulphide to sulphur and on to sulphate. They derive their name from the fact that some of them (notably the filamentous *Beggiatoa* species) store light-refracting granules of elemental sulphur in their cells. These bacteria are 'gradient organisms'; they have to live in the chemically unstable transition zone where hydrogen sulphide and oxygen co-exist. They are motile and capable of following vertical migrations of the zone. Where the anoxic zone reaches the sediment surface they form a white veil which covers the surface (Fig. 52 & 53). The 'nitrifying bacteria' are also chemolithotrophs; they make their living through the oxidation of ammonia to nitrite and further nitrite to nitrate, but in marine sediments

Fig. 52. Distribution of the chemolithotrophic sulphur bacterium *Beggiatoa* sp. in the transition zone between oxygen and sulphide. Redrawn from Nelson *et al.* [130]

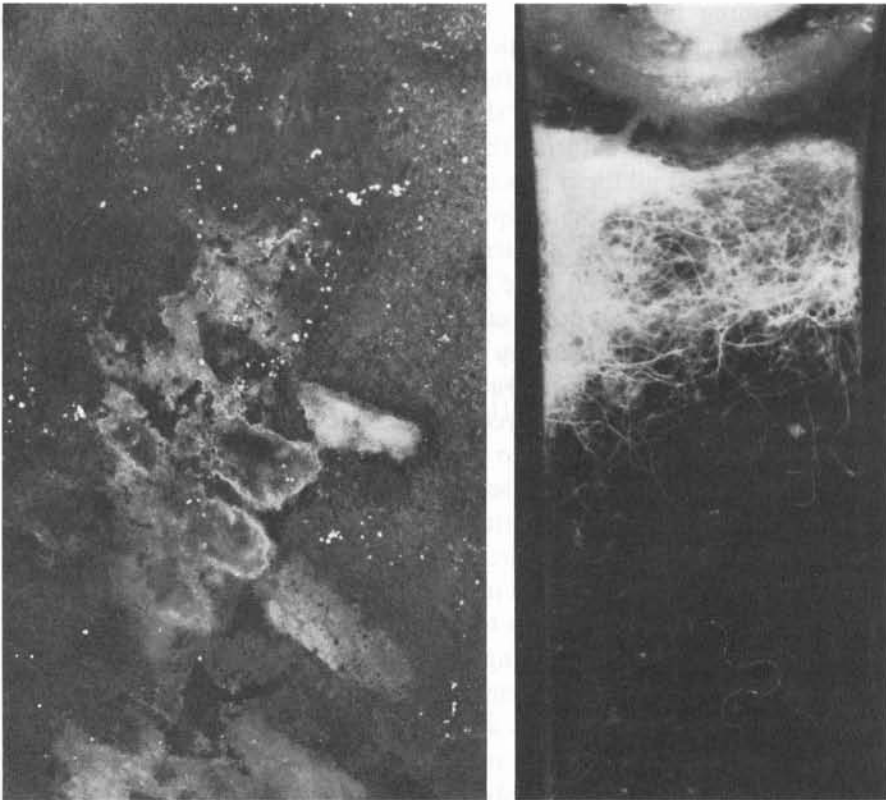
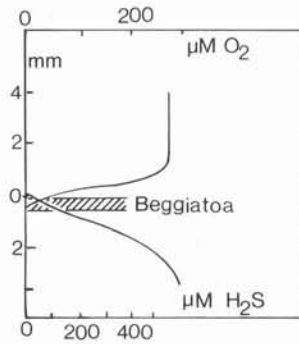


Fig. 53. Left: patches of white sulphur bacteria on the surface of a shallow water sediment (covering about 15×30 cm). Right: growth of the filamentous white sulphur bacterium in an (about 5 mm wide) glass tube. Oxygen diffuses downwards from the air-water interface seen above; beneath the 'bacterial plate' the water is completely anoxic, but contains sulphide, the oxidation of which is the basis for the energy metabolism of the bacteria. Original

their quantitative importance is more modest than that of the sulphur bacteria.

Wherever light penetrates to the anoxic zone another type of sulphide oxidation is carried out by photosynthetic sulphur bacteria of which two main groups exist; the green and the purple ones. Under anaerobic conditions they perform a photosynthetic process in which sulphide is used as a reductant rather than water (used in ordinary, oxygenic photosynthesis) thus producing sulphur or sulphate as a waste product. In shallow waters with large accumulations of organic matter they may occur in dense masses so that the sediment surface has a reddish-pink colour. Mostly they occur beneath a millimetre-thick layer dominated by blue-green bacteria and eukaryotic algae. Since they are inactive in the dark the anaerobic and sulphide containing layer migrates upwards during the night followed by white clouds of chemolithotrophic sulphur bacteria which again disappear after sunrise. The importance of the photosynthetic sulphur bacteria can also be seen from the fact that in shallow flats free hydrogen sulphide may escape to the atmosphere during the night [131]; Figure 54.

The net result of all these processes is the maintenance of mineral cycles exemplified by the microbial sulphur cycle in Figure 55. The main feature is that sulphur atoms act as carriers of oxidation equivalents from the oxidised and to the reduced zone (with a valency of + 6) and as carriers of reduction equivalents from the reduced zone and upwards (with a valency of - 2). The system is not entirely closed; as it grows it tends to accumulate sulphur from the overlying seawater and some of this may eventually become fossilised under certain circumstances. In shallow water, as we have already seen, it may contribute to the pool of atmospheric sulphur, but the exact extent of that on a global scale is not known. The above description also largely accounts for the patterns which develop in water columns in which the bottom layer is anoxic, only in this case the zonation is greatly expanded relative to what occurs in sediments.

My description of this system has mainly been in terms of compartment models in which 'boxes' containing some physiological process are the units which perform chemical transformations. This has been a natural approach since some of the first questions asked about the system have been on the rate of transformations (e.g. how much of the mineralisation of organic material is catalysed by sulphate reducers, how does it affect the return of nitrogen to the water column, etc.). It also fits methodology - chemical methods for studying gradients of substances and some fluxes of materials and the use of radioactive tracers or stable isotopes for the quantification of other fluxes, sometimes combined with specific inhibitors of certain metabolic processes.

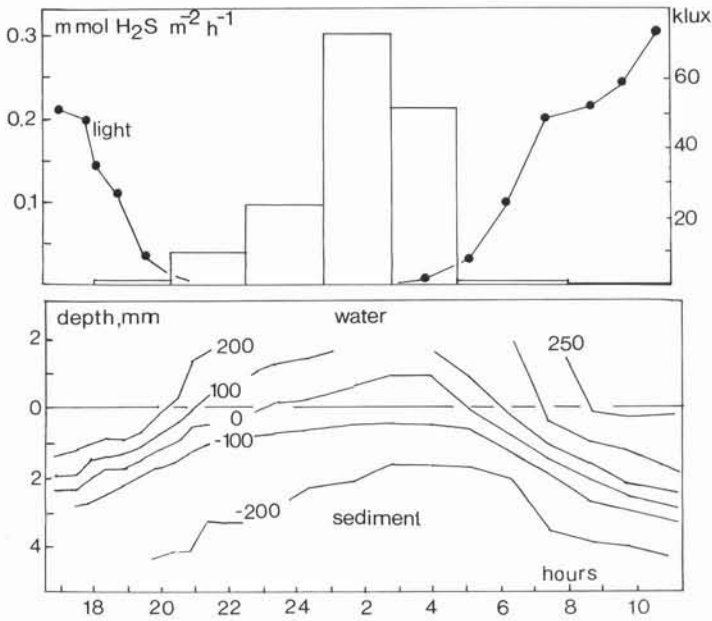


Fig. 54. Above: light intensity and release of hydrogen sulphide to the atmosphere from a shallow water marine sediment during the night. Below: the 'oxidation-reduction potential' of interstitial water during the same period; at redox potentials below ca +100 mV, anoxia prevails. In darkness, photosynthetic bacteria are inactive so that sulphide is not oxidised beneath the sediment surface during the night leading to vertical migrations of the chemical gradients. Redrawn from Hansen *et al.* [131]

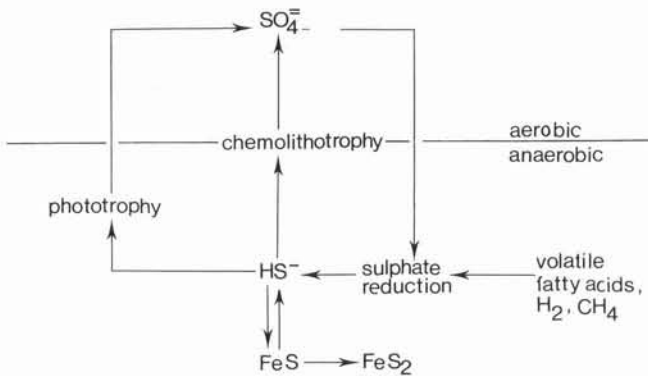


Fig. 55. The microbial sulphur cycle; for explanation see text. Original

I have simplified the above description somewhat in that some physiological types of bacteria have been omitted, and within the single functional groups mentioned there is quite some variation. The group of sulphate reducing bacteria, for example, include forms which utilise only lactate or hydrogen as substrates while others use acetate and some use elemental sulphur rather than sulphate for respiration. The photosynthetic bacteria include quite a variety in terms of photosynthetic pigments (and their absorption spectra), tolerance to sulphide, or their capability to use other reductants. In some cases (e.g. some photosynthetic bacteria) laboratory experimentation shows how different traits change competitive ability under certain conditions and altogether it is evident that the ecological system I have described is influenced not only by 'syntrophic interactions' (that is that the metabolic waste products of one physiological type constitutes a substrate for other types) but also by competition for common resources.

Nevertheless, in one sense we cannot use this system for answering questions on competition as they are often posed by (animal or plant) community ecologists: 'do the organisms defy the competitive exclusion principle?' As regards eukaryotic organisms the taxonomist describes species, often on the basis of some subtle morphological detail and perhaps supported by genetic analysis which can delimit Mendelian populations which then per definition are species. Ecologists then go into the field and ask whether two such co-existing organisms have sufficiently different niches in order to co-exist or whether we have to infer other mechanisms as an explanation.

This question is actually meaningless to a microbiologist in that 'species' of bacteria are defined by their niche properties (under what circumstances will it grow, which substrates can it utilise and by what metabolic pathways, and so on). The methods used to isolate and so name and study single types of bacteria are mainly based on the fact that they are particularly competitive under a certain set of environmental conditions. So while some microbial communities are, in a sense, the best understood communities and are certainly the ones most amenable to experimental analysis, they defy one of the classical problems of ecology.

Some eukaryotic organisms are also associated with these largely prokaryote communities, at least where they occur in the water column or in sandy sediments where small organisms can move within the interstia between individual sand grains; in muddy sediments eukaryotes seem largely to be excluded for mechanical reasons. We can distinguish between two main types of such eukaryote organisms. Some are genuine and obligatory anaerobes which only occur under strictly anoxic conditions. They are represented by a restricted number of types of protozoa (flagellates and ciliates

belonging to a few families) which have secondarily lost their mitochondria. Not too much is known about their metabolism, but it is fairly certain that they depend on fermentative pathways. The presence of 'hydrogenosomes' in their cytoplasm (a special organelle the function of which seems to be the excretion of hydrogen) suggests the presence of energetically more efficient types of fermentation than e.g. lactate fermentation known from ourselves. At any rate they are likely to produce substrates such as hydrogen and acetate for which the surrounding bacteria compete. This probably explains the ubiquitous association between anaerobic protozoans and ecto- as well as endosymbiotic bacteria. Some of these bacteria have been shown to be methanogens and by keeping the hydrogen tension low within the protozoans, they increase the energy yield of the host's metabolic processes.

A much richer protozoan fauna is found around the aerobic-anaerobic transition zone where its members take advantage of the high productivity of chemolithotrophic and photoautotrophic bacteria. This fauna may also include small metazoa which are tolerant to low oxygen tensions and together these organisms constitute a link in terms of food chains from the anaerobic world [132].

20 New Ways of Looking at Plankton

In the shallower parts of coastal seas much of the organic productivity is based on benthic photosynthetic organisms such as kelp, seagrasses and mangroves which either directly or via dead organic material (and its subsequent microbial degradation) sustain food chains. On a larger scale, however, these processes play a modest role because, by far, most of the organic productivity in the sea is based on the photosynthetic activity of minute suspended cells: the phytoplankton in the photic surface layers of the seas. This has been acknowledged for most of this century. The productivity of these cells can, in principle at least, be measured as oxygen production of a water sample in the light; in practice the rate of production is too low in many places for this method to work. Since the fifties, a method has been used in which radio-carbon labelled bicarbonate is added to samples and the radioactivity of the organic material produced during the incubation in the light can then be taken as a measure of production. Massive amounts of such data were collected from all seas during the following decades.

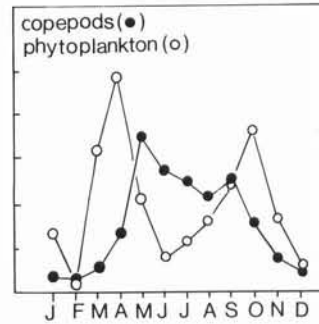
The rationale for this, of course, is to obtain insight into what controls the productivity of fish in various areas and this seemed reasonable in that the general structure of the food chains in the sea was believed to be well

understood. This classical paradigm of the planktonic ecosystem has appeared in virtually all ecology texts and popular accounts. It would typically be presented as a pyramid. The base of the pyramid, the primary producers, were believed mainly to include diatoms and dinoflagellates. Above them a compartment with copepods, which feed on these phytoplankters, was shown. The copepods were then eaten by herring, the herring by mackerel and finally a tuna fish and/or a human consumer figured at the top of the pyramid. The shape of the graph was supposed to reflect the fact that the flow of organic carbon decreases towards the top of the food chain because of respiratory and other losses; without giving it too much thought, it was probably also believed to reflect that the entire biomass in each compartment decreased towards the top, but as we have already seen (Chapter 10) this is not really the case. It was, of course, well known that the pelagial contains a lot of other kinds of organisms than diatoms, dinoflagellates, copepods, herring, mackerel and tuna. Any plankton sample contains a variety of other forms: planktonic larvae of benthic invertebrates, the carnivorous 'arrow worms', the 'gelatinous zooplankton' (salps and other pelagic tunicates, coelenterates, colonial radiolaria) and a lot of other things. Also the mere existence, at least, of some of the organisms I will discuss below was recognised.

Many other things were known about planktonic ecosystems. For example, it was recognised that the photosynthetic production is largely limited by the availability of nutrient salts. In warm seas with a stable thermal stratification of the upper water masses there are only small absolute amounts of available phosphorus and nitrogen; most of these elements are largely locked up in the organisms and so primary production depends on re-mineralisation by the consumer animals. Due to the sinking of dead plankters through the thermocline there is a continuous loss of nutrients in the photic zone. These parts of the seas are therefore like 'deserts'. In places with an upwelling of deep water (such as off the west coast of Peru) or in temperate waters where the thermal stratification breaks down during winter so that nutrient-rich deep water reaches the photic layers (like in the North Sea) productivity is much higher. In the latter case temporal successional patterns occur: a spring bloom of algae is followed by an increase in copepods which consume the bloom and this event may be repeated again later in the season until winter with low levels of light and low temperatures again sets limits to production (Fig. 56).

The concept of how planktonic systems may work in conjunction with a large body of observational data allowed for making models of the energy flow and productivity of planktonic systems and, altogether, it was believed that no other major ecosystem of the biosphere was understood so well

Fig. 56. Succession of phytoplankton and of copepods during the year in the northern part of the North Sea (arbitrary units). Redrawn from Steele [133]



[133]. On this background it is surprising that the last 10 to 15 years have radically changed this classical paradigm of the structure of pelagic ecosystems: that it accounts for perhaps only half of the actual flow of organic carbon and other materials and that organisms which were previously ignored or believed to be unimportant, play a substantial role in the sea.

The fundamental observation which led to a new view of plankton systems has been the recognition that organisms smaller than the 'traditional primary producers' are of substantial importance. First it was found that a large, and sometimes the largest, part of the primary production is due to 'nanoflagellates', a taxonomically diverse assemblage of 2 to 10 μm long eukaryote photosynthetic cells, and eventually the presence and significance of 1 to 2 μm long cyanobacteria was established. These organisms are largely lost when traditional collecting devices for the quantification of phytoplankton are used and their existence also questions the traditionally applied methods for the estimation of productivity as discussed below.

Even more surprising was the finding that heterotrophic bacteria are very important in seawater. The existence of bacteria in seawater had long been established. In order to quantify bacteria the traditional method has been to spread diluted water samples on nutrient agar plates and then count the bacterial colonies which appear after some days. This method, however, has proven to reveal only perhaps one percent and never more than ten percent of the bacteria actually present. This became apparent when methods for direct microscopical enumeration were developed. Extensive counts have shown that bacterial numbers in the surface layers of the sea typically are around one million cells per millilitre of water. This sounds like a lot, but, of course, bacteria are small so they represent only a volume fraction within the range of 10^{-7} to 10^{-6} . Actually that is a lot too: it represents a biomass which is comparable to that of the primary producers. It was for some time suggested that most of the bacteria were really dead cells which were just floating around. This would solve the dilemma of where the sub-

strates for all these bacteria came from. We know now that the bacterial population is turned over rapidly and that dead cells would become eaten within hours or days. Much effort was expended in order to measure the growth of bacteria in nature, a task which did not prove easy. One approach was to follow the rate of mineralisation of radioactively labelled substrates (e.g. glucose or amino acids). This method cannot give an absolute measure of bacterial activity (it is most likely that only a fraction of the bacteria will take up some given substrate and it also requires estimates of the natural concentration of the substrate and this is often a hard or impossible task for the chemist). Two other techniques have had more success. When bacteria grow they may take up thymidine for the synthesis of DNA, something that eukaryotes do not do. Adding radio-labelled thymidine to water samples and then quantifying its incorporation in bacteria has given estimates of bacterial growth rates. Another method has been based on the fact that the duration of the process of division in bacteria is invariant with the growth rate and so the fraction of cells undergoing division at any moment is a measure of the frequency by which cells initiate divisions (*viz.* the growth rate).

All these efforts have resulted in the following picture. Bacterial production rates are considerable: their generation time may be as short as about six hours and up to a day or two according to temperature and other conditions. This amounts to a productivity of 5 to 30 percent of the primary production (or rather of current estimates of primary production) and since the growth efficiency of bacteria is not likely to exceed about 50% this means that somehow as much as 60% of the primary production may be consumed by bacteria. This requires, of course, an explanation. So does the fact that bacterial densities are relatively constant over time within a given body of water and that the decrease in bacterial numbers when going from very productive to quite unproductive seas is fairly small and certainly less than a factor of ten so that a value of about 10^6 cells per millilitre remains a reasonable generalisation. This implies that the numbers are regulated somehow and the question is then by what mechanism [134].

Evidence seems to support the idea that the bulk of the substrates for bacteria come from the excretion of dissolved organic material from photosynthetic organisms. That such organisms do in fact tend to lose a substantial part of their photosynthate to the surrounding water has been known for some time. The role of these substrates is supported by the correlation between bacterial numbers and photosynthetic organisms in the water. It has also been shown that the bacterial life cycle may be coupled to photosynthetic activity on a diurnal basis. Thus bacterial cell volumes tend to increase during the day; during the evening the rate of cell divisions in-

crease and during night the numbers of bacteria tend to decline again [135].

Another question is what happens to the bacteria. While it would seem reasonable to assume that they are eaten, there were for a time no likely candidates for the predators. In accordance with our generalisations in Chapter 10, there is always some size relation between predators and prey. None (or nearly none) of the metazoan plankters seem capable of catching or retaining particles of bacterial sizes; copepods for instance retain only particles larger than about 5 μm . Although some species of ciliates do feed on bacteria these are rare in marine plankton; by far the majority of planktonic ciliates feed on flagellates or other smaller protozoa.

The likely candidates proved to be small, heterotrophic flagellates. These 3 to 10 μm large cells are ubiquitous in seawater; although previously ignored (except by taxonomically inclined protozoologists) they occur at typical densities of a thousand cells per millilitre. There is quite a diversity of these organisms, from a taxonomic as well as a functional point of view; some of this diversity is shown in Figure 57. Many of them are easy to grow in pure cultures in the laboratory. They may have generation times as short as three hours or as long as a day depending on the density of bacteria. Their activity in filtering the surrounding water for bacterial prey is impressive: they clear a volume of water which is around 10^5 times their own cell volume per hour. Such measurements allow for the calculation of their activity in the sea when their natural densities are known. It turns out that at least during the summer in coastal seas they filter the entire water column for bacteria within a day or so. Their activity as bacterial grazers can also be seen from experiments such as the one depicted in Figure 58. Removing larger plankters (like ciliates and anything bigger) from freshly collected samples of seawater leads to clear predator-prey oscillations. When flagellates are removed as well, the bacterial population increases to a certain level and then stops growing. The experiment shows, as do pure cultures, that the flagellates require a minimum concentration of bacteria of around a million per millilitre in order to grow and this, of course, is a satisfactory result in view of the natural density of bacteria.

Do such predator-prey cycles of bacteria and flagellates occur in nature as well? Daily counts of bacteria and various protozoan components of the plankton in fairly productive waters show rapid fluctuations, but often leave a confusing picture. This is perhaps not strange in that other interactions take place; for example the flagellates themselves are eaten by ciliates and other plankters. However, over some time periods, regular coupled oscillations take place (Fig. 59). Further analysis of such data (Fig. 60) shows that peaks of occurrence of flagellates and of bacteria occur at similar intervals and that the flagellate peaks lag behind those of the bacteria in

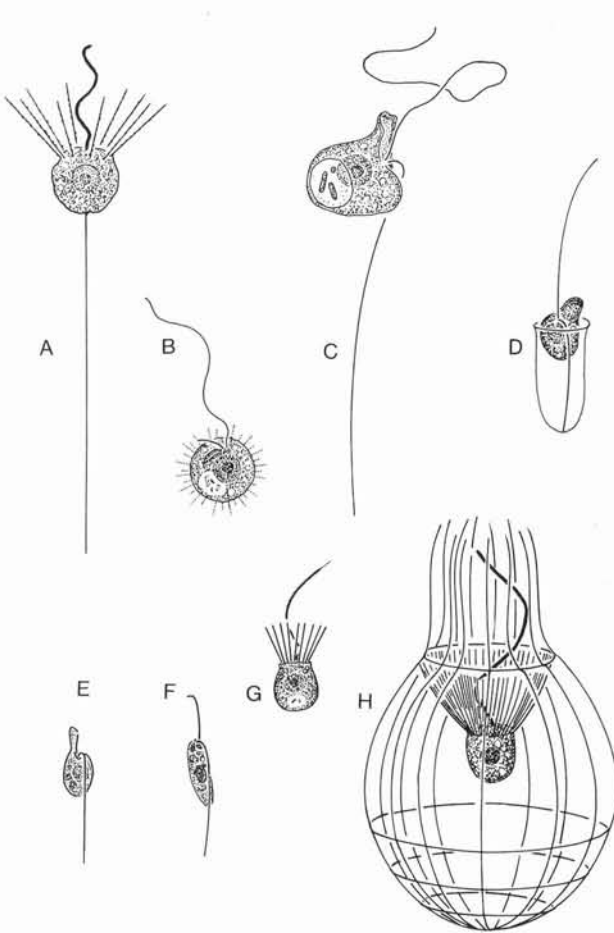


Fig. 57. Different types of planktonic, bacterivorous flagellates. A = *Pteridomonas*, B = *Paraphysomonas*, C = *Pseudobodo*, D = *Bicoeca*, E-F = kinetoplastid flagellates, G-H choanoflagellates. Scale bar: 10 μm . After Fenchel [136]

a regular fashion and this supports the idea that they are due to the prey-predator interaction.

Recalling the theoretical results of predator-prey models (Chapter 13 and Appendix 4) it is expected that an increase in the carrying capacity of the prey leads to increased predator populations and also that it destabilises the system leading to greater amplitudes. Comparing the ranges of recorded numbers of heterotrophic flagellates for different seas supports this latter expectation; while populations fluctuate widely in size in eutrophic and productive seas, they remain nearly constant in the oligotrophic Sargasso Sea [136].

The new view on planktonic food chains is shown schematically in Figure 61. The addition to the classical model has been referred to as the

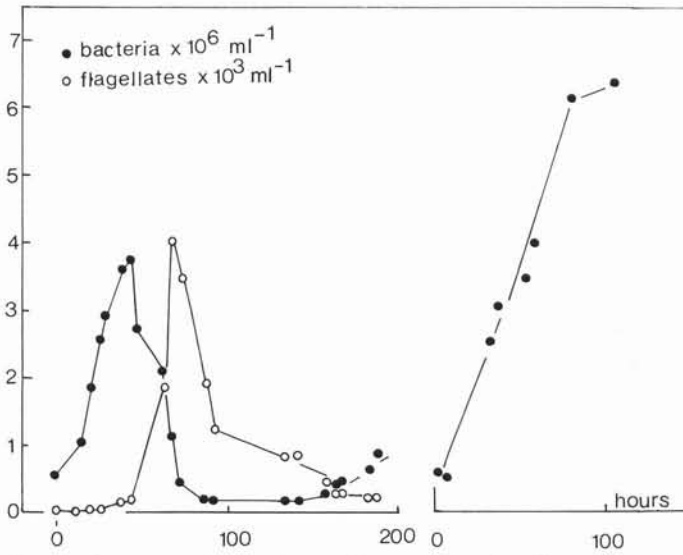


Fig. 58. Left: development of numbers of bacteria and of bacterivorous flagellates in a seawater sample filtered to remove larger plankters. Right: same water sample, but with the flagellates being removed as well. Redrawn from Fenchel [136]

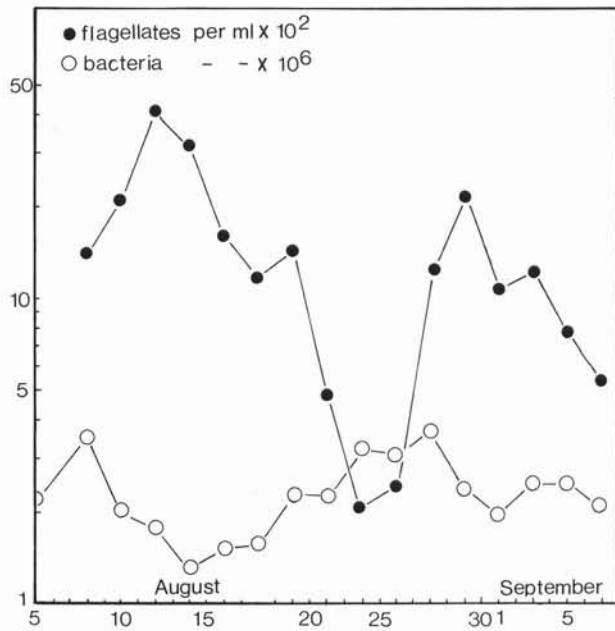


Fig. 59. Numbers of bacteria and bacterivorous flagellates in the surface waters of Limfjorden, Denmark, over one month. Redrawn from Fenchel [136]

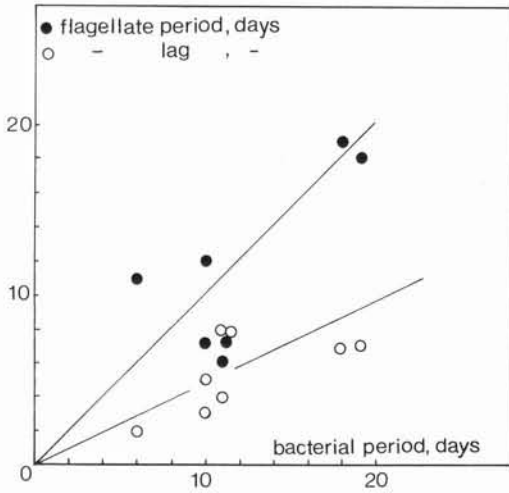


Fig. 60. Time intervals between peaks in bacterial numbers plotted against time intervals between peaks in flagellate numbers (filled circles) and time lag between a peak in bacterial numbers and the following peak in flagellate numbers (open circles) during a summer in surface waters of the Limfjord. Longer periods correspond to cooler periods. Redrawn from Fenchel [136]

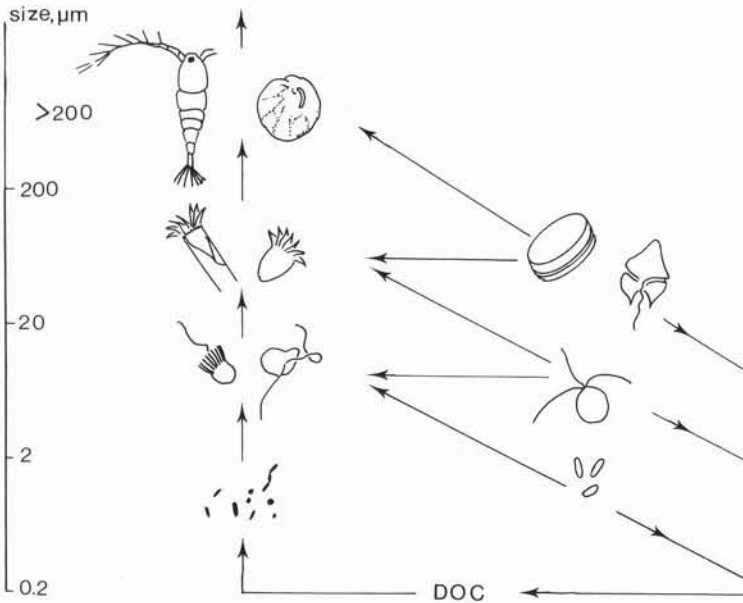


Fig. 61. Schematic presentation of the 'microbial loop'. Photoautotrophic organisms are depicted to the right; they serve as food for protozoa and animals and also excrete dissolved organic material (DOC) which is used as substrate by bacteria. For further explanation see text. After Fenchel [132]

'microbial loop'. In addition to the importance of discovering a new phenomenon there are two particularly important aspects to point out. One is the general energetics of the plankton system. The discovery of the microbial loop means that there are several more trophic levels in the planktonic food chains than hitherto believed. Since at each level we can at most assume a transfer efficiency of say 0.5, this means that at the top of a two-step food chain only 0.25 times the energy at the basis will be preserved, for a three-step food chain only 0.125, and so on. In short, there will be considerably less left over for the larger organisms (such as fish) in which we are interested. Indirect, but rather robust evidence that most of the potential chemical energy of the photosynthesis in the sea is actually lost at the lowest part of the food chains (the smallest organisms) come from measurements of the rate of nitrogen mineralisation of different size components of the plankton. As we have seen (Chapter 11), it is to be expected that in food chains of phagotrophs, nitrogen and carbon mineralisation are tightly coupled. A number of such studies on the ammonia production of different size fractions of the plankton have unambiguously shown that the bulk of nitrogen mineralisation (often more than 80%) is due to organisms of protozoan sizes (less than 50 to 100 μm) [137].

This again begs the question whether current estimates for primary production can account for the production of fish or other larger pelagic animals. The answer is no. Steele [133] who modelled the food chains of the North Sea on the basis of a classical view on the structure of plankton communities could hardly account for the secondary production; adding more trophic levels to the system would make this impossible. The consequence of all this, it seems, is that current estimates of primary production are much too low. Certain aspects of the microbial loop would seem to explain why this is. Typically, estimates of primary production are based on the incubation, for several hours, of a small sample of seawater with radio-labelled bicarbonate. After the incubation the sample is filtered and the radioactivity of the filtrate measured. The radioactive dissolved organic material passing the filter may, of course, also be monitored. This latter procedure compensates for the fact that many of the smallest (and previously ignored) photosynthetic organisms would be included even if they pass the filter or burst in contact with it. More important is the observation that the turnover of substances is much more rapid in the plankton than really allowed for by the long incubation times. During this period, the activities of the members of the microbial loop, that is, the tiny photosynthetic organisms, the bacteria and the bacterial predators are likely to have recycled much of the labelled organic carbon. The C-14 method in a sense

measures the net production rate, that is, it more or less accurately estimates what is left over for the 'traditional' plankton food chains.

The other important aspect of the microbial loop pertains to our general view of plankton communities. Its discovery is rather like looking at some known object with an improved microscope; its higher resolution reveals new and finer details. These are so far most obvious regarding the temporal scale. We have seen how materials are turned over much faster than was originally believed and that the scale of events is hours or days rather than weeks and months. Is there also a corresponding finer spatial heterogeneity in the plankton which we have so far overlooked?

Some considerations tend to suggest this. It would be easier to understand the rapid turnover of materials found if some sort of micro-patchiness occurred in the plankton. This is particularly so for very nutrient-poor oceanic water where dissolved phosphate for example is hardly detectable in the water. In analogy to the many especially large protozoa, such as radiolarians and foraminifera, which contain symbiotic algal cells and therefore represent a partly closed system for mineral cycling, it has been suggested that bacteria and heterotrophic protozoa cluster around algal cells by chemosensory mechanisms utilising the excreted organics and providing the algal cell with mineral nutrients. Theoretical considerations pose some difficulties and worse still, no-one has devised a way to observe such consortia if they exist. Another suggestion has been that the microorganisms in the plankton are mainly associated with suspended detrital particles of some sort, but with the same effect as above. There is some evidence that particles do harbour microbiota. However, with the current methods for quantifying planktonic microbes it seems as if most of them are freely suspended, but again, this may be because the treatment of the samples disrupt such patches [138].

21 The Evolution of Ecological Niches in Gammarids

Gammarus is a genus of amphipod crustaceans and the species belonging to it are widely distributed along shores on both sides of the North Atlantic (and some species occur in freshwater). In marine or brackish waters they are typically found among algae or stones in shallow water. A drawing of a *Gammarus locusta* is shown in Figure 62. The animals feed on decaying plant material as well as on other animals or carrion and they often occur at high densities. Like other amphipod crustaceans, sexually mature males attach to females forming a 'precopula'. Fertilisation takes place only during the moulting of the female, and so the male awaits this moment while hold-

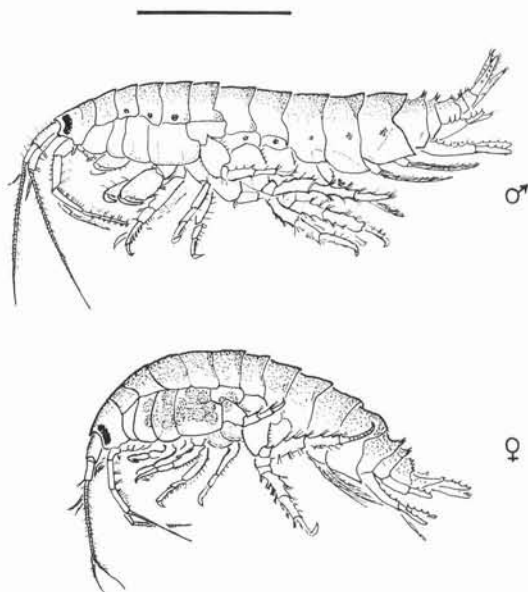


Fig. 62. Male and female (showing the eggs inside the brood pouch) of *Gammarus locusta*.
Scale bar: 5 mm. Original

ing on to its chosen mate. After fertilisation the eggs develop within a brood pouch of the female. Hatched juveniles are released from the pouch and they undergo a series of moults as they grow to become sexually mature. Gammarids have either one or two generations per year and consequently have an expected life span of either a half or a whole year (in cold areas some species live two years before they reproduce). During the reproductive period females produce from two and up to eight clutches depending on whether they are winter or summer breeders. Gammarids are easy to keep and grow in the laboratory over many generations.

Many species have been described, but they are difficult to distinguish and mainly differ in the number of setae on various extremities and in other such subtle characters. In the inner Danish waters and in the Baltic Sea five species are recognised and their evolutionary ecology is the subject of this chapter. Linnaeus originally thought they all belonged to one species, but during the last century the currently recognised species were discovered one by one as being distinct, and eventually Kinne established the species systematics as it is accepted today [139]. He also showed that these 'sibling species' differ with respect to their responses and tolerances to different temperatures and salinities. This species systematics has more recently been confirmed through isozyme electrophoresis which also shows that some of the species are very closely related and must have evolved re-

cently from a common ancestor, presumably during the Pleistocene period [139].

The five species are *Gammarus duebeni*, *G. zaddachi*, *G. salinus*, *G. locusta* and *G. oceanicus*. In most places their distribution seems to be governed by salinity; the first mentioned species occurs in very dilute brackish water, the last mentioned in undiluted seawater. However, there may be local variations in this pattern; *G. oceanicus*, for example, forms brackish water populations in some localities. About ten years ago Steen Kolding and I set out to investigate the habitat niches and the role of interspecific competition for explaining distribution patterns for this species complex in Limfjorden (a broad sound cutting through northern Jutland and which connects the North Sea with Kattegat). A survey of some hundred sampling stations showed that the species were indeed distributed according to salinity in the order mentioned above. When all the samples were pooled the pattern was one of broad overlap in distribution (Fig. 63) and this accords with studies on the tolerance to different salinities in the laboratory. Although the species clearly differed in this respect (for example, *G. locusta* and *G. oceanicus* populations from the Limfjord cannot survive indefinitely and cannot reproduce at salinities below 15 and 20‰, respectively, even if acclimatisation is attempted over several generations) they do have overlapping habitat niches and at salinities slightly above 20‰ all five species can complete their life cycle.

However, when the distribution of the species was studied in any one local salinity gradient a different picture emerged (Fig. 64). Boundaries between the species were usually very sharp and with very narrow zones of

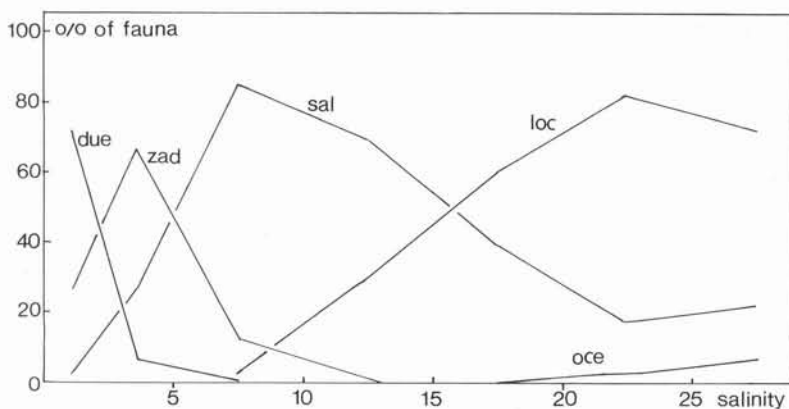
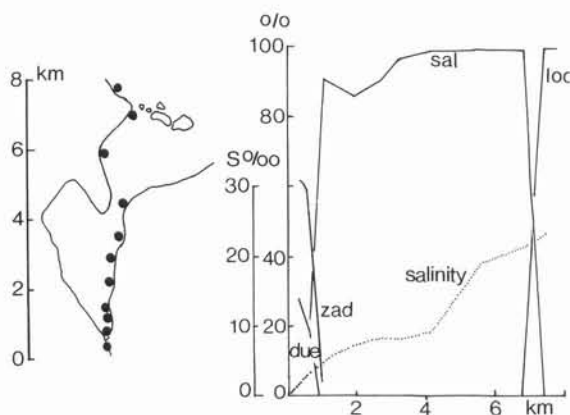


Fig. 63. Relative occurrence of the five *Gammarus* species in the Limfjord according to salinity when all samples are pooled. After Fenchel & Kolding [139]

Fig. 64. Zonation of four of the species in a small cove along the coast of Limfjorden and the salinity gradient (stippled line). The overlap between species is extremely narrow. After Fenchel & Kolding [139]



overlap, but the position of the boundaries for a given pair of species with respect to salinity varied among different localities. This distribution pattern required an explanation and this was not likely to be one involving exploitation competition. After all, this is a 'soft' type of competition (see Chapters 12 and 13) so even if the gammarids are not very motile, fairly broad zones of overlap could be expected. Interference competition (such as interspecific aggression) could explain the pattern, but no direct evidence for this could be found in laboratory populations.

There was one other clue to the solution of the problem. As mentioned, the gammarid species either reproduce in summer or in winter although they may do one or the other thing according to locality. In the Limfjord it turned out that neighbouring species in salinity gradients always have displaced breeding periods. Thus, *Gammarus duebeni* is a winter breeder, *G. zaddachi* a summer breeder, *G. salinus* a winter breeder, *G. locusta* a summer breeder and, finally, *G. oceanicus* a winter breeder (Fig. 65). Again, this is a trait which is subject to some variation in the individual species when populations from different geographical areas are compared; *G. salinus*, for example, has a winter as well as a summer generation in some areas, and breeds in the summer in the Baltic Sea.

This would suggest that there are selection forces acting against the simultaneous breeding of co-existing species. Interspecific precopula pairs had already been described by Kinne [139] and one possible explanation for the observed patterns would be the following. While experts on the taxonomy of crustaceans have had their difficulties in distinguishing gammarid species they seem eventually to have been more successful than the gammarids themselves. Assuming that interspecific crosses are sterile or that hybrids have a low fitness, then the formation of an interspecific pre-

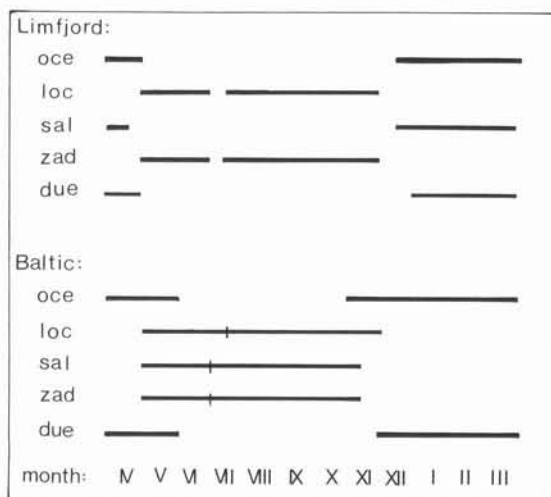


Fig. 65. Reproductive periods of the five *Gammarus* species in the Limfjord and the Baltic Sea. After Kolding [139]

copula must represent a considerable waste of time for both parts involved and a corresponding loss in Darwinian fitness. In an ecological context such a system could formally be described as interference competition with the most frequent species winning (because individuals belonging to the rarest species are most likely to mate with a member of the other species). In an evolutionary context it would result in strong selective forces which could explain the evolution of habitat selection and displaced breeding periods. This hypothesis implies that mechanisms which allow males to distinguish between females belonging to its own species and those belonging to related species did for some reason not evolve but instead the species evolved other traits pertaining to life cycle and habitat niches which indirectly lead to pre-mating isolation.

Systematic studies of the willingness of the species to form interspecific precopula pairs, which in some cases required artificial shifting of reproductive periods by treating the animals with special temperature regimes in the laboratory, illustrated this. Two experimental designs were used; in one, males of one species had the free choice between females belonging to its own and another species. In the other type of experiment, males of one species were combined with females belonging to another species. Two species (*G. oceanicus* and *G. duebeni*) never engaged in interspecific precopula formation. At the other extreme, *G. zaddachi* males do not discriminate between females of their own species and those belonging to *G. salinus* and in one out of four cases *G. zaddachi* males will mate with females of *G. locusta* when given a choice between that species and females belonging to its own species. In other combinations interspecific matings took place

only if there was no other choice. The interspecific precopulas seem always to lead to the fertilisation of the eggs. However, development usually stops after the eighth cleavage (256 cell stage). In one case hybrid juveniles (*G. locusta* × *G. salinus*) were released, but they died during their first moult.

There is thus evidence that the avoidance of interspecific precopula formation constitutes a strong selection pressure on co-existing gammarid species. Speciation must have taken place through repeated cladogenetic events. Since reproductive isolation is not yet complete among some species pairs, speciation must have taken place in allopatry. As the species came into secondary contact, postmating isolation mechanisms (that is reduced or no viability of hybrids) must already have been established, but premating isolation was not developed. Seemingly in the absence of genetic variance which allowed for an efficient discrimination between species, evolution led to habitat shifts and displaced life-cycles. Such a scenario is not improbable during the Pleistocene period when glaciations and changes in sea-levels must have led to local populations which later could come in contact again.

Circumstantial evidence for this explanation of the evolution of habitat niches as the result of selection against interspecific mating derives from the study of the same set of species in other areas. The conditions in the central Baltic Sea are in particular illuminating. Here there is a constant low salinity of 6 to 7‰, but all five species are found. *Gammarus duebeni* is confined to a marginal niche (rock pools) and is thus effectively isolated from the other four species which seem to co-exist. However, more detailed studies show that also in this area the breeding species populations are effectively isolated. This is in part brought about by displaced breeding periods as well as through distribution according to water depth and to somewhat complex annual migration patterns for some of the species. This supports the idea that the ecological niches of local gammarid populations resulted from selection for premating isolation and in general exemplifies the opportunistic nature of evolution. It can be speculated that this mechanism has fortuitously led to a higher regional number of gammarid species. Had premating mechanisms (direct discrimination between the species when choosing mates) already been established upon secondary contact there would not necessarily have been any other mechanism to evolve habitat selection and over time the number of regionally co-existing species would have been reduced due to exploitation competition.

The observations on the Baltic gammarid populations also suggest another speciation mechanism. It was already mentioned that two of the species (*Gammarus oceanicus* and *G. locusta*) from Danish waters require

high salinities and cannot complete their life cycles at salinities below 15 to 20‰. In the Baltic Sea the same species occur (there are subtle morphological differences, but isozyme patterns show only very slight differences between Danish and Baltic populations). However, the two species from the Baltic do not tolerate salinities exceeding about 10‰ and this remains unchanged even if the animals are grown through several generations in the laboratory and attempts are made to acclimatise them slowly to higher salinities. This evolutionary change of the Baltic populations must have taken place during the last 4000 years which is the approximate age of the present conditions in the Baltic Sea. In a certain sense, then, *Gammarus locusta* from the Baltic Sea and from Danish waters, respectively, represent two separate species because there is no way they can co-exist and so interbreed in the same locality. Should they somehow be brought together regionally (for example by transport of a gravid female attached to a bird's feet) they would still be confined to different local habitats and (provided no extinction takes place) eventually diverge as two entirely distinct species.

V Ecology and Society

22 Problems of Applied Ecology

Ecology is often viewed mainly as an applied science which covers a wide and diffuse variety of environmental issues and even one which is endowed with a certain set of general human and social values. Needless to say, I disagree with this. Ecology is a natural science along with e.g. physics, physiology and geology and its field of inquiry and its methodology must be delimited and defined. Like many other natural sciences, ecology can offer principles, methods and insight which are important in solving certain practical problems or in helping society to choose among alternative actions. Neither ecology (nor the nature it studies) holds any human values *per se*; that remains a problem for individual human beings and for society. Ecologists should not be prophets (although a few behave as if that is what they are) and – if they speak in public as professionals – they should limit themselves to subjects on which they have real expertise (although ‘false experts’ are not, unfortunately, uncommon among ecologists).

The concept of ‘applied research’ needs a few introductory comments as well. In my view, scientific research is an activity which is characterised by originality and carried out in order to describe nature and to obtain new insight and an understanding of connections between phenomena. This applies irrespective of whether the source of inspiration and motivation of the individual scientist is that of a practical problem or is simply the desire to understand nature. The history of science includes innumerable examples showing that the results of basic research proved to be of substantial (if often initially unpredictable) practical value and conversely that practical problems have been a source of inspiration for basic research. In the above sense, basic and applied sciences are not easy to separate or distinguish.

Conversely, studies which solely apply established methods, knowledge and insight in order to detect, quantify or solve a more or less concrete problem (*viz.* ‘monitoring’) should not qualify as scientific research. Such activity is necessary in many cases. However, it is unfortunate that this type

of activity is often mixed up with real research in the minds of many people (including politicians) and that the funding through agencies which emphasise quick results in conjunction with the increasing awareness of environmental problems has led to too many monitoring studies and a copious amount of trivial literature. I will return to this aspect later.

I feel that the preceding chapters have already to a large extent exemplified what ecology can offer with respect to applied aspects. Many of the problems I have discussed have been directly inspired by practical problems such as models of epidemics and some other population models. These in turn have served to contribute to general insight and to guide practice in epidemiology, fisheries biology, and conservation. Insight and knowledge of microbial element cycling is necessary in order to evaluate the impact of human activities on atmospheric chemistry or on the nutrient balances of soils and natural waters. The theory of 'island biogeography' not only guides conservation practice, but it also has a considerable didactic value in explaining non-trivial aspects which pertain to the preservation of animal and plant species. None of this could have been achieved only through the mindless monitoring of fish stocks, of phosphate contents of water or whatever.

Altogether I believe that ecological research has to a considerable extent been successful in yielding insight and methods which pertain to some of the fundamental problems of human societies that have a bearing on ecology: the preservation of animal and plant species in the face of human overpopulation and the overexploitation of land for farming or urbanisation, the rational exploitation of living resources (fish stocks and forests), the distribution and effects of pollutants on a global or a local scale and the combat against certain infectious diseases in tropical countries. Ecology (or other branches of science) has not completely solved any of these major problems, in part because there do not exist complete solutions and in part because they all include social, economical and cultural aspects.

The opposite point of view, that is, that ecology has not lived up to expectations as regards satisfactory models predicting environmental impact following various human activities or for managing fisheries or other living resources, is also frequently heard. This reflects the disappointment that in most cases it has not proved feasible to build models which yield exact quantitative predictions. I believe this expectation was naive from the beginning. The view that ecology would achieve such models was fairly widely held a few decades ago and it was based on the apparent success of the physical sciences in conjunction with the advent of computers which are capable of providing numerical solutions to whatever they are fed. First of all, even the physical sciences have not really achieved this goal when suf-

ficiently complex systems are to be described. I suppose simple mechanical physics can in principle explain all the consequences of a car crash in detail. Yet, this is hardly possible in practice and car manufacturers therefore crash real cars experimentally to see how they deform following an impact. Although climate and weather must depend on simple physical laws, meteorology and weather forecasting do not solely depend on theoretical predictions based on a set of initial parameter values, but also on empirical generalisations to obtain confident predictions. Even though weather forecasting has improved tremendously in recent years it is often still not possible to predict the passage of a front with a precision of say a hundred kilometres or so (at least in the part of the world where I live). Many other complex systems entirely based on elementary physical principles have not yet or only partly yielded to analytical treatment which allow for precise quantitative predictions. This applies to many problems of fluid mechanics and in some cases (for example, the optimal design of ship hulls) practical experience is necessary.

Ecology also shows some resemblance to economy in this respect. Both fields of inquiry study fairly complex systems. Both include schools of thought which adhere either to mathematical reasoning or to verbal descriptions and arguments. Both have yielded enlightening insight into the basic mechanisms of the systems they describe. But as every newspaper reader knows, when it comes to predicting the effect on the rate of inflation or the level of unemployment following some change in monetary or fiscal policy, economists tend to disagree and the predictive power of theoretical models of national economy is altogether rather unimpressive. Ecologists who feel frustrated because they cannot precisely predict all the effects following the addition of a certain amount of phosphate to a lake can take solace from the fact that economists maintain a high prestige in society (but also receive higher salaries than do most ecologists).

Ecological systems are in general very complex even though the behaviour of the individual components and their interactions may be relatively simple and well understood. In some cases it is possible to isolate parts of the systems conceptually in a way that permits analytically tractable models which yield surprisingly precise quantitative predictions. The plague model (Chapter 3) provides an example. In most cases this is not possible. Models of fish stocks, for example, are generally based on the conceptual isolation of the population of the particular fish species and the imposed fishing mortality. Such models have a general didactic value (see also below) but their value as predictive tools for e.g. imposing fishing restrictions is usually limited. The fish stocks interact with other species of fish through competition and predation and this already complicates matters consider-

ably. Furthermore there is a variation in recruitment success from year to year due to climatic stochasticity and this also limits the predictive value of general models. To this should be added the lesson from the 'chaotic behaviour' of a simple population model (Chapter 3): even a very slight variation in the initial population size in this type of models greatly changes the future behaviour of the modelled population. Therefore, in the real world even modest stochasticity in parameters or population sizes at some point in time may considerably affect the future behaviour of the system.

A similar point can be made regarding models for the flow of materials in ecosystems. These are usually compartment models (Chapters 3 and 19) which are of considerable value for understanding what is going on. However, the degree of simplification implied in these models – and in particular the fact that they implicitly assume a steady state situation and do not really model mechanisms which determine the future of the systems – has often been overlooked and so futile attempts to use these models beyond their actual predictive power have been made.

While the easy access to computers during the last decade has proven valuable in various ways in ecology, the naive expectation that computing power was the limiting factor for making precise quantitative predictions of systems at the complexity level of ecosystems has not been vindicated. Such 'ecosystem models' were generally based on already oversimplified conceptual models of the system in question and without too much regard for the details of the functional form of interactions. When simulated in the computer, the outcome would be one of two: either trivial predictions which could have been arrived at with common sense combined with a slide rule, or an example of advanced 'curve fitting' to observed data points that lacked the power to predict the behaviour of the system given an extrapolation of some parameter values beyond those already observed. As advice to local governments or administrative bodies concerning a given environmental problem, these models seem more to resemble the oracles of ancient Greece than scientific consultancy. Irrespective of whether one lives in an ivory tower or one is concerned with the pollution of a local lake, real progress in ecology first of all depends on an increase in qualitative insight, and computers cannot compensate for this.

I would like to return to the question on how economic, social and cultural aspects are components of applied problems which ecologists tend to consider as purely ecological ones. Some people (including ecologists) apparently believe in some kind of ecological ideology or ethics with a more or less universal application and often containing a certain measure of hypocrisy. Some of my colleagues and students are quite sceptical about nuclear energy. They do not seem to approve of the combustion of coal, lig-

nite or mineral oil either for environmental reasons. They may be somewhat disturbed by the high rate of consumption of energy and other goods in the western world in general. However, they rarely consider giving up their own car, hot bath or other energy consuming devices.

Generally it is often overlooked that while industrialisation has and still does pose a threat to the environment and to the natural flora and fauna it is at the same time the basis for a high standard of living and there is a general consensus in the western world that this is desirable. The ensuing affluence, on the other hand, is probably also a prerequisite for popular and political support for nature conservation in a wide sense and the willingness to pay the costs for maintaining e.g. a reasonable environmental quality of natural waters. While it is certainly necessary to control the activities of industry (and farming) regarding the impact on the environment through legislation, a general hostile attitude towards industry, which has been in vogue in western Europe for some time, may prove counter-productive from an environmental point of view. While it is true that the quantity and variety of industrial waste (and the excess use of fertilisers and pesticides in farming practice) has increased tremendously during the last part of this century, so has the general awareness about these problems and the unwillingness to accept a continued deterioration of the environment. It seems likely that this trend would reverse should the standard of living decline.

A major concern not only for ecologists and naturalists, but for a large part of the public as well is the conservation of nature and in particular the preservation of large mammals and birds in their natural environments. The entire Pleistocene and Holocene periods (that is, the last 1 or 2 million years) have been characterised by the extinction of many of the large types of mammals which evolved during the Tertiary period (Fig. 66). Some of these extinctions can be explained by the effects of the glaciations during

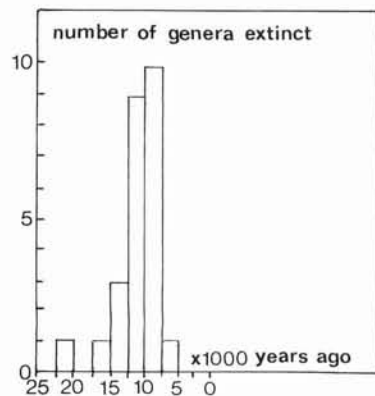


Fig. 66. Rate of extinction of North American mammals during the last glaciation. After MacArthur [140]

the period. The forming of the Panama isthmus towards the end of the Pliocene period also led to extinctions because the previously separated and different South American and North American mammal faunas came into contact, and this led to competitive exclusion (the South American forms being the main losers). The more recent incidences of extinctions, however, can to a large extent be ascribed to human activity. Today most attention is directed at the megafauna of tropical continents. Nearly everywhere the geographical distribution of these animals has been drastically reduced within historical time due to the spread of agriculture, overexploitation or even willful extermination. Many species are only found within a few scattered and relatively small areas (mainly national parks in Africa and South East Asia) and the absolute population sizes of some of these species are so small that in spite of all efforts some of them may become extinct in the near future. A more general threat to the natural ecosystems of the tropics is the drastic rate of clearing of rain forests in South East Asia and in South America in order to expand agriculture and for obtaining timber. This activity threatens a large range of animal and plant species with extinction and even the very existence of natural rainforests in many areas.

This development is psychologically deeply disturbing to most of us; in addition, the drastic reduction of rain forests may lead to soil erosion and reduction of soil fertility and it has been suggested that it will also affect the carbon dioxide balance of the atmosphere (enforcing the effect of the combustion of fossil fuels and possibly affecting world climate [141]). The great efforts to increase consciousness about this tragic development, to attempt to slow this process and to create protected national parks and forests and to accelerate the study of the threatened fauna and flora are among the finest recent achievements of ecologists and naturalists and fortunately some of these efforts seem to be fruitful.

There are other aspects to consider in this context. In Europe, natural (terrestrial) ecosystems had virtually all been replaced by agriculture already sometime during the Iron Age except for mountain regions and the northern parts of the Scandinavian peninsula. The naturally occurring species of large mammals and many large birds have also for a long time been heavily reduced with respect to population sizes and distribution ranges. At least the extinction of the aurochs and the near-extinction of the European bison is the result of human activity during recent centuries. In North America and in Australia smaller or larger areas of the original natural ecosystems remain, but by and large, Europeans have for centuries done the same that is happening in tropical countries today. This, and the fact that most of the tropical countries in which conservation of the natural fauna and flora and of natural ecosystems is so urgent also suffer from poor

economies and uncontrolled population growth, and often also from political and social unrest or chaos, requires a certain amount of tact when handled by western conservationists. It is conceivable that the fight against malaria and famine and the attempts to industrialise may have a higher priority in these countries than the preservation of some exotic bird species. It is also understandable that some of these countries in practice have difficulties in enforcing protection of individual species or of national parks. These points have recently been raised by colleagues [142]. In fact some of the third world countries (e.g. Costa Rica and Kenya) are making impressive efforts in supporting national parks and in raising the level of consciousness regarding the desirability of nature conservation.

An extreme example of 'ecologism' is provided by movements like 'Greenpeace' (although here professional biologists hardly have a strong representation). Greenpeace has especially concentrated on marine mammals. Most species of large whales have been heavily overexploited and conservation measures or, in some cases, total protection were absolutely necessary. Today no sane person would find it acceptable that these species should become extinct due to human exploitation. It is possible that the movement has contributed to the eventual introduction of such measures and to the drastic reduction of commercial whaling. However, the goal and argumentation of Greenpeace is not one of a rational exploitation of living resources, but one of sentimental appeal to affluent westerners. Their recent campaign against the use of seal furs in Europe has largely taken away the means of existence for some Eskimo communities in Greenland although the seal populations were in no way threatened and 'baby seals' never hunted. The seals are also used as food. The lack of compassion for the Eskimos by Greenpeace in this case is striking on the background of their sympathy with other beings. I do not wish to suggest that human beings are the only higher vertebrates that can feel pain or fear. However, and besides the fact that the change in the fur market has probably been regretted by minks and foxes, Greenpeace owes us an explanation of why it is more ethical to eat cows or poison rats than it is to eat seals and whales. Currently, Greenpeace seems to focus on the Faeroe Islands where pilot whales have been caught and eaten traditionally at least since the seventeenth century (when recordings of the number of whales caught began) and without any signs of a declining population size of the whales.

Fisheries biology provides examples of how ecological systems interact with social and economic ones. Fisheries (and other exploitation of natural populations) depend on the density dependent growth of the exploited population. When an additional mortality (fishing) is imposed on the population, it decreases in size, but due to the decreasing level of intraspecific

competition the population compensates by a higher population growth rate. Simple models of fisheries assume that the yield or catch exactly balances this additional population growth rate so that an equilibrium state is achieved. We will consider here a model based on the logistic equation (Chapter 12). More realistic models must take age structure and other factors into consideration, but for our purpose the simpler model will suffice [143].

The logistic model of density dependent population growth is given by $dx/dt = rx[1 - x/K]$, (see Chapter 12), where x is population size, r unlimited growth rate constant, and K 'carrying capacity' (population size at which the population will equilibrate under a given set of environmental conditions). For a given fish population we are likely to be ignorant about all the parameters of the equation. However, assume that the yearly catch (the 'equilibrium yield') is E and that we can measure a fishing effort, F . The fishing effort is measured as the number of boats \times days (with a defined size of boat and type of gear). Now E measures the productivity of the fish population of a given size and the ratio E/F is a measure of population size. Substituting in the logistic equation we have: $E = rE/F - rE^2/F^2C$, where we substitute C for K in order to scale the carrying capacity relative to our measure of population size. Re-arranging the equation we have:

$$E = FC - F^2 C/r$$

This shows that if the yield of the fishery, E , is plotted as a function of F we should expect a parabola (Figure 67) where $E = 0$ for $F = 0$ and for $F = r$ and E takes a maximum value for $F = r/2$. That is, if we slowly increase the fishing effort from a low level, then at first we may expect a nearly linear increase in our catch, but this increment decreases with increasing F and eventually becomes negative.

Now, a glance on the curve suggests that the best thing to do would be to apply a fishing effort so that E is maximised (the 'maximum sustainable yield', Point A in Fig. 67). This would provide us with the maximum number of fish we can obtain from the population without risking a decreased yield in the years to follow. However, if we include economic considerations this may not be so. Fishing costs money to cover salaries, oil and repairs. A simple assumption is that the costs are linearly proportional to F (Fig. 67). If the yield is measured in terms of its sales value, then there is a profit whenever the cost curve is beneath the yield-effort curve. Inspection of the figure shows that the value of F giving the highest profit turns out to be somewhat lower than that giving the highest yield. In the profit-driven

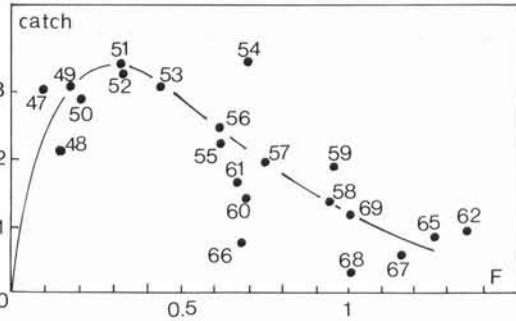
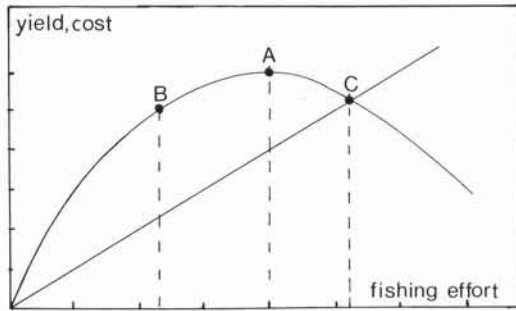


Fig. 67. Above: model of fishing yield versus fishing effort (for explanation see text). Below: catch of herring (in millions of adult individuals) plotted against fishing effort (arbitrary units) for the southern part of the North Sea in the period 1947–1969. Based on data from The Danish Institute for Fisheries and Marine Research

capitalist societies, then, we would expect the fishing effort to equilibrate at Point *B*. And this would be good because it would guarantee against overexploitation.

Unfortunately, this is not what really happens. As long as the fishery is profitable it will attract more fishermen and so the point of equilibrium will actually be at *C* and the profits of the fishery will be marginal. At this point, different things may happen. One is, to seek more efficient gear or fishing methods. Alternatively, society may feel sorry for the fishermen whose earnings have been decreasing and so they become economically subsidised in some way or the price of the fish may increase. In either case this is equivalent to the lowering of the cost curve and that means further increasing the fishing effort with consequently lower and lower yields. Eventually the fishery may crash and other fish stocks are exploited instead or the fishery may become regulated through national or international measures.

An example of this is shown in the lower part of Figure 67 in the case of North Sea herring which became heavily overexploited during the sixties. The example is in no way unique; already at the turn of the century fishes like plaice and haddock were overexploited in the North Sea (in the sense that a decrease in fishing effort would have given higher yields).

It has not been my intention with this example to discuss human irrationality in general, but only to point out that ecological principles alone do not suffice when applied aspects are to be understood. I will now turn to a last example in which ecologists themselves are sometimes partakers of a game.

Problems of pollution and in particular the pollution of natural waters seem to have a priority in the popular image of what an ecologist is concerned with. It is true that an impressive amount of resources and time has gone into the monitoring of polluted waters, and to become an expert on water pollution seems to be the fate of many biology students these days. It is also true that aquatic pollution is often a substantial problem at all scales from small lakes to the Baltic Sea where the load of chlorinated hydrocarbons seems to have a detrimental effect on seals, in particular. The question is rather whether 'research' and lengthy monitoring programs are really always necessary to the extent they are carried out or whether they to a certain extent are carried out due to the hard competition for research funds and whether they may even be counter-productive in terms of improving matters.

The following story is a caricature, but it is not a very exaggerated one; through the years I have experienced quite similar ones at several occasions. Assume that an industry leads cyanide into a river. Predictably the fish die off along some stretch of the river and this is noticed. The problem does not require research at all, but only a political decision on whether the industry must be forced to dispose of the cyanide in another way. The industry, however, claims that it cannot afford this and threatens to move to another part of the country or to close the plant altogether; it will under all circumstances fire the workers which will be a serious blow to the local economy. The obvious solution is to initiate a research program. Everyone is satisfied this way. The politicians avoid making an unpleasant decision and seem to be taking the issue seriously at the same time (and it is also relatively inexpensive), the industry is happy because the immediate threat has disappeared and gladly pays some of the expenses (even though it is aware that it may eventually be demonstrated that cyanide is toxic) and the scientists are happy because they receive some funds, work for their graduate students and they may even feel a little useful at the same time. This game can go on for a long time since it is quite likely that a first preliminary study strongly suggests further and more thorough studies, perhaps including laboratory studies on the survival of fish when exposed to cyanide. The whole thing will eventually be concluded with a useless report or some boring publications in order to further the careers of the participants.

I conclude this chapter, then, by pointing out that among applied sciences, at least some aspects of applied ecology are especially vulnerable to corruption. In most applied research with public support (e.g. medical research, meteorology or agricultural research) no social conflicts are implied; it is only a question of the quality and progress of the research. The same largely applies to industrial research (e.g. in the pharmaceutical or electronic industries). Applied ecologists are in many cases caught in between conflicting interests: farmers versus conservationists, industries versus green movements; and fisheries biologists may even be caught up in international conflicts on fishing rights and quotas.

VI Conclusions: Limits and Limitations of Ecology

Ecology is an attractive field to its students. It satisfies our childhood attraction to nature (and, I suppose, most of us in part owe our careers to an early passion for collecting butterflies or bird watching) and the possibility of visiting exotic places. At the same time ecology satisfies a perhaps more mature intellectual desire to analyse and understand nature. Many ecologists feel that their field is directly useful to society or even vital for the future of mankind and this, to a varying degree, also motivates many ecologists.

I think that ecology has proven itself in these respects and that this is documented in my book. However, this is not an original observation. I have therefore throughout the book stressed that ecology as it appears today needs some trimming and that this applies to ecology as a pure science as well as an applied field. It is perhaps natural that a rapidly growing discipline in conjunction with a growing awareness of environmental problems led to a certain degree of euphoria regarding the role and potential of ecology. While similar tendencies to consider some fashionable trend within social sciences as a panacea for intellectual life and society alike have occurred, anything quite similar has not taken place for other natural sciences.

In a pure scientific context it is imperative to acknowledge that the explanatory power of ecology is limited to explaining distribution patterns of organisms and how organisms affect their environment as functions of the properties of individual species. Beyond those limits, two complementary approaches, physiology and evolutionary biology, are necessary for a further understanding of organisms in nature. In my view – and this may sound strange when coming from an ecologist – biology curricula of universities and schools have during the last decades been unbalanced in favour of ecology and at the expense of a broader and more complete picture of biology. This intrusion of ecology into other biological disciplines is in many ways as narrow-minded as is the view held by some colleagues in molecular biology who believe that all biology started with the discovery of

DNA structure. Ecology is not a higher synthesis of all biology: it is a part (albeit an important one) of our contemporary understanding of life and its manifestations on equal footing with other biological disciplines.

Regarding applied aspects many ecologists have failed to understand that while ecology and ecological principles are necessary they alone are insufficient when dealing with the relationship between human societies and nature. To understand this relationship and certainly if it is to be changed it is necessary to include cultural, social and economic sides. Many of the 'ecological views' are well justified regarding the environment in industrial as well as in non-industrial countries, and the conservation of species and ecosystems. While I am not a doomsday prophet there are unfortunately reasons to be pessimistic in some respects. The largest threat (as regards the future of mankind as well as the future of what remains of natural environments) will in the long run prove to be human population growth. Under all circumstances, I am convinced that the potential of ecologists to influence future attitudes, and political decisions, will improve if they to a larger extent acquire insight into social and economic aspects and accept these as realities.

Notes to Chapters 1–22

1. Carson, R. (1962). *Silent Spring*. Houghton Mifflin, Boston; during the following two decades a flood of popular or semi-popular books on environmental issues appeared
2. Kingsland, S. E. (1985). *Modeling Nature*. University of Chicago Press, Chicago
McIntosh, R. P. (1985). *The Background of Ecology: Concept and Theory*. Cambridge University Press, Cambridge
3. See Egerton, F. N. (1968). Ancient sources for animal demography. *Isis* 59: 175–189
4. It has been claimed that Henry Thoreau used the term 'ecology' 8 years earlier, but this seems to be a misinterpretation of a handwritten word; see James, B. (1985). The origin of the word 'ecology'. *Bull. Brit. Ecol. Soc.* 16: 147
5. An interesting and detailed account on the earliest development of demography and population biology is found in Hutchinson, G. E. (1978). *An Introduction to Population Ecology*. Yale University Press, Yale
6. Examples of a recent interest among ecologists in infectious diseases are:
Anderson, R. M. (1982). *Population Dynamics of Infectious Diseases*. Chapman and Hall, London
Anderson, R. M., May, R. M. (1982). *Population Biology of Infectious Diseases*. Springer-Verlag, Berlin
Dobson, A. P., Hudson, P. J. (1986). Parasites, disease and the structure of ecological communities. *TREE* 1: 11–15
Kinne, O. (ed.) *Diseases of Marine Animals*, Vol. I (1980), II (1983), IV (1984–1985). Biologische Anstalt Helgoland, Hamburg
7. Scudo, F. M., Ziegler, J. R. (ed.) (1978). *The Golden Age of Theoretical Ecology: 1923–1940*. Springer-Verlag, Berlin
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9. For references to the older literature on communities see Christiansen, F. B., Fenchel, T. M. (1977). *Theories of Populations in Biological Communities*. Springer-verlag, Berlin
For a recent account on community ecology see Diamond, J., Case, T. J. (ed.) (1986). *Community Ecology*. Harper & Row Publishers, New York
10. Elton, C. (1927). *Animal Ecology*. Sidgwick and Jackson, London
11. The most influential papers were probably:
Lindeman, R. C. (1942). The trophic-dynamic aspect of ecology. *Ecology* 23:399–418
Riley, G. A. (1944). The carbon metabolism and photosynthetic efficiency of the earth as a whole. *Am. Sci.* 32:129–134
Hutchinson's own contributions to this sort of ecology and to biogeochemistry are reflected in *A Treatise in Limnology*, Vol. I–III. John Wiley & Sons, New York, 1967, and in Kuiper, G. (ed.) (1954). *The Solar System*, Vol. 2:371–433. The University of Chicago Press, Chicago
Many ideas on the effect of biological activity on the chemistry of the atmosphere were anticipated earlier, e.g. by the mathematician V. A. Kostizin (1935). *Evolution d'atmosphère: circulation organique, époques glaciaires*. Hermann, Paris
12. The most influential papers by G. E. Hutchinson within this area include:
'Concluding remarks', Cold Spring Harbor Sym. Quant. Biol. 22:415–427 (1957)
Homage of Santa Rosalia, or why are there so many kind of animals? *Am. Nat.* 93:145–159 (1959)
13. The most important work of F. G. Gause was:
The Struggle for Existence, Hafner Publishing, Company Inc. 1934 (reprinted 1964)
Later attempts to study species interactions in laboratory populations include among others:
Crombie, A. C. (1946). Further experiments on insect competition. *Proc. R. Soc. London* 133B:76–109
Huffaker, C. B. (1958). Experimental studies on predation: dispersion factors and predator-prey oscillations. *Hilgardia* 27:343–383
Park, T. (1962). Beetles, competition and populations. *Science* 138:1369–1375
14. H. Winogradsky studied glass columns with sediments and other material and with a mixed bacterial flora and could so study the biogeochemical processes carried out by different physiological types of bacteria. He distinguished between 'autochthonous' and 'zymogeneous' forms of soil bacteria; the former are adapted to low nutrient concentrations and the latter are specialised to exploit ephemeral patches with higher substrate concentrations. This anticipated ideas in 'traditional ecology' by many decades. Winogradsky summarised 50 years of research in microbial ecology in the book: *Microbiologie du Sol. Problèmes et Méthodes*. Masson et Cie, Paris (1945)

15. Odum, E. P. (1971). *Fundamentals of Ecology*, 3rd edn. W. B. Saunders Company, Philadelphia
For other references see Krebs, C. J. (1978). *Ecology. The Experimental Analysis of Distribution and Abundance*, 2nd edn. Harper & Row Publishers, New York
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Odum, E. P. (1977). The emergence of ecology as a new integrative discipline. *Science* 195:1289–1293
18. Odum, H. T. (1971). *Environment, Power and Society*. John Wiley & Sohns Inc., New York
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20. The poem 'biomodels' is reprinted from Burns, J. M. (1975). *Bio Graffiti. A Natural Selection*. The New York Times Book Co., New York
21. Tuchman, B. W. (1979). *A Distant Mirror. The Calamitous 14th Century*. MacMillan, London
Zinsser, H. (1934). *Rats, Lice and History*. The Atlantic Monthly Press Books, Boston (Reprinted 1963)
Data on the 1711 plague epidemic of Copenhagen derive from Johansen, H. Chr. (1979). *Et samfunds organisation i opbrud 1700–1870*. Gyldendal, København
Fig. 1. was originally published by a Copenhagen newspaper in 1712
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For ecological models with chaotic behaviour see also: May, R. M. (1985). Regulation of populations with non-overlapping generations by micro-parasites: a purely chaotic system. *Am. Nat.* 125:573–584; and Schaffer, W. M., Kot, M. (1985). Do strange attractors govern ecological systems? *BioScience* 35:342–350
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Andrewartha, H. G., Birch, L. C. (1954). *The Distribution and Abundance of Animals*. University of Chicago Press, Chicago
Davidson, J., Andrewartha, H. G. (1948). Annual trends in a natural population of *Thrips imagines* (Thysanoptera). *J. Anim. Ecol.* 17:200–222

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39. Margulis, L. (1981). *Symbiosis in Cell Evolution*. W. H. Freeman and Company, San Francisco
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- Wilson, E. O. (1975). *Sociobiology: The New Synthesis*. Belknap, Harvard
- Lapidus, R., Levandowsky, M. (1981). Mathematical models of behavioural responses to sensory stimuli by protozoa. In: Levandowsky, M., Hutner, S. H. (ed.) *Biochemistry and Physiology of Protozoa*, 2nd edn., Vol. 4. Academic Press, New York, p. 235–260
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 - Fenchel, T., Finlay, B. J. (1983). Respiration rates in heterotrophic, free-living protozoa. *Microb. Ecol.* 9:99–122
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 Holling, C. S. (1965). The functional response of predators to prey density and its role in mimicry and population regulation. *Mem. Entomol. Soc. Can.* 45:1–60 Figs. 19 and 22 are based on Fenchel, T. (1986). Protozoan filter feeding. *Prog. Protist.* 1:65–113
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66. Witkamp, M., Ausmus, B. S. (1976). Processes in decomposition and nutrient transfer in forest systems, p. 375–396. In: Anderson, J. M., MacFadyen, A. (Note 65)
67. The empirical composition of marine plankton algae is $[C_{106}H_{263}O_{110}N_{16}P_1 + \text{trace elements}]$; this is usually referred to as the 'Redfield ratio'. The idea on how the N:P ratio of seawater is adjusted to 16:1 is taken from Stumm, W., Morgan, J. J. (1970). *Aquatic Chemistry*. John Wiley & Sons, New York
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Hutchinson, G. E. (1978). *An Introduction to Population Ecology*. Yale University Press, New Haven
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Christiansen, F. B., Fenchel, T. M. (1977). *Theories of Populations in Biological Communities*. Springer-Verlag, Berlin

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Gee, J., Giller, P. (1987). *Organization of Communities Past and Present*. Blackwell, Oxford (Proceedings of a British Ecological Society Symposium in 1986)
Strong, Jr., D. R. et al. (ed.) (1984). *Ecological Communities: Conceptual Issues and the Evidence*. Princeton University Press, Princeton
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Connor, E. F., Simberloff, D. (1979). The assembly of species communities: chance or competition? *Ecology* 60:1132–1140
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Christiansen, F. B. (1987). Pleiotropy in dynamical parameters of models on the evolution of simple phenotypes. To appear in: Loeschcke, V. (ed.) *Genetic Constraints on Adaptive Evolution*. Springer-Verlag, Berlin
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Appendices 1 – 4

Appendix 1. The Biomass Distribution of Size Classes of a Steady State Planktonic Food Chain

Assume the weight specific growth and metabolic rates, respectively are given by the relations

$$r = a_r W^b \quad \text{and} \quad m = a_m W^b$$

The ratio: $a_r/[a_r + a_m]$ is the net growth efficiency.

Consider two trophic levels, i and $i + 1$ with total biomasses of B_i and B_{i+1} , respectively. The food consumption which covers power generation and growth of trophic level $i + 1$ must be

$$B_{i+1} W_{i+1}^b [a_r + a_m]$$

which must be covered by the production of level i which is

$$B_i W_i^b a_r e$$

Here e ($0 < e < 1$) compensates for the fact that the some of the production at level i may not be utilised by the predator because it is not digested or is otherwise lost.

Equating the two expressions yields:

$$B_i/B_{i+1} = (W_i/W_{i+1})^b [a_r e/(a_r + a_m)]$$

where the bracket represents the gross growth efficiency for which a reasonable estimate may be 0.2. If the body weight ratio for the individuals of the two trophic levels is assumed to be 1:1000 and $b = -1/4$, the equation predicts a ratio of the total biomass of the two levels of around unity.

Appendix 2. Uptake Kinetics for a Spherical Organism Utilising Dissolved Substrates

Assume a spherical organism with radius R taking up a substrate. Since the substrate is taken up at the surface of the cell there will be a concentration gradient

around it and so a net flux of the substrate towards the cell. The diffusion coefficient is D , the substrate concentration as a function of the distance from the center of the cell, r , is $S(r)$ and the bulk concentration (far away from the cell) is S' . Consider a spherical shell concentric with the cell and with a radius $> R$. The diffusion flux through a unit area is then:

$$J = D \, dS/dr$$

and since the flux through all such spherical shells must be the same, the total uptake of the cell must be

$$V = 4 \pi r^2 J = 4 \pi r^2 D \, dS/dr$$

Consider the case where the concentration at the cell surface, $S(R) = 0$. In this "diffusion-limited" case the uptake depends only on the diffusion of the substrate towards the cell, and not on the transport mechanism through the cell membrane which has a large excess capacity in this case.

We need an expression for dS/dr . In our case the solution must have the property that $S(R) = 0$ and $S(r)$ approaches S' as r approaches infinity. Furthermore, dS/dr must be of the form 'const $\times r^{-2}$ ' because V is invariant with r . The expression $S(r) = S'(1 - R/r)$, that is, $dS/dr = S'Rr^{-2}$, satisfies these requirements. Uptake rate at very low concentration of the substrate then becomes

$$V = 4 \pi RDS'$$

this expression (divided by S') corresponds to 'maximum clearance' in the case of a filter feeder, i.e. the volume of water cleared for substrate per unit time at low substrate concentrations, and it is a true measure of the competitive ability under such circumstances. Note that this is proportional to the radius of the cell. Since metabolic needs are nearly proportional to the square of length, this explains why it is mainly very small organisms which utilise dissolved substrates.

At higher substrate concentrations transport rate through the cell membrane becomes limiting. Define a 'transport coefficient', k , such that the maximum uptake achieved at very high substrate concentrations is given by:

$$V_m = k \, 4 \pi R^2,$$

with the dimension T^{-1} . Note that uptake now depends on the square of the length. By arguments totally identical to those used for deriving the 'Holling type II functional response' (Chapter 11), we find that the uptake of the cell as a function of S' is:

$$V = S'k \, 4 \pi R^2 / [S' + (k \, 4 \pi R^2) / (4 \pi RD)] = k \, 4 \pi R^2 S' / (S' + k R/D).$$

As S' approaches zero, V approaches $4 \pi RDS'$ and as S' approaches infinity, V approaches V_m . Note that also in this case the 'half-saturation constant' is an *ad hoc* parameter without any obvious biological or ecological interpretation except, perhaps, as the ratio between the limitation set by transport capacity of the cell membrane and that set by diffusion and also that it is linearly proportional to V_m .

Appendix 3. Analysis of Models of Competition

The Lotka-Volterra equations which describe competition can formally describe different types of competition as discussed in Chapters 12 and 13. However, the biological interpretation of the interaction parameters may differ in the different cases. The equations describing competition are

$$\begin{aligned} dx_1/dt &= r_1 x_1 [1 - x_1/K_1 - \beta_{12} x_2/K_1] \\ dx_2/dt &= r_2 x_2 [1 - x_2/K_2 - \beta_{21} x_1/K_2]. \end{aligned}$$

Here r = the Malthusian growth rate constants; K = the carrying capacity; β = interaction (or competition) coefficients; x = population sizes of the two competing species. The outcome of competition can be analysed graphically in the x_1, x_2 -plane (Fig. A1). The signs of the two derivatives depend on the sign of the brackets and the straight lines described by the linear equations depict the points for which the derivatives vanish. The outcome is then a result of the configuration of the isoclines. Co-existence is found if both $K_1/\beta_{12} > K_2$ and $K_2/\beta_{21} > K_1$, which can be taken as an expression that each of the species inhibit themselves more than they inhibit their competitor (intraspecific competition is more intense than interspecific competition). If one of the two inequalities are reversed one species will be excluded. If both inequalities are reversed, the outcome of the competition depends on the initial population sizes; this requires that the competition coefficients exceed unity and in biological terms this requires interference competition.

This treatment assumes linear isoclines; it is not obvious that this should be so and in fact for some experimental systems this is not the case. However, the qualitative predictions of the model remain unaffected.

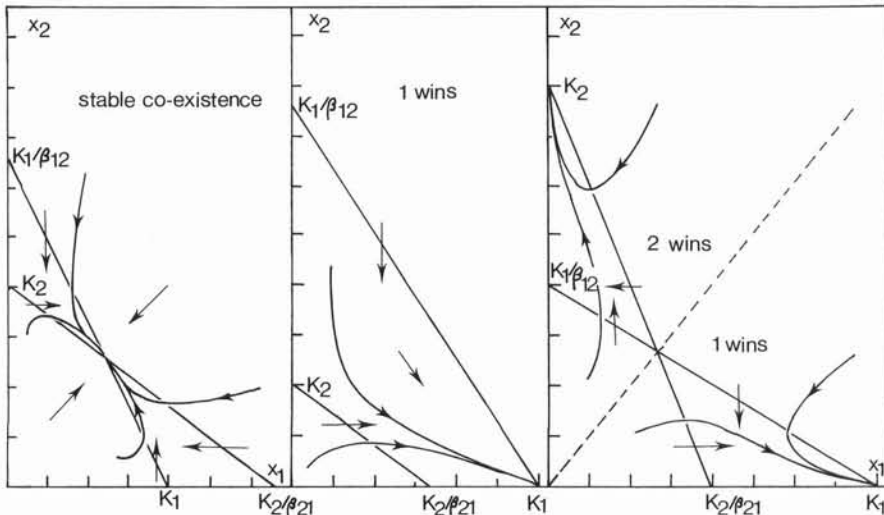


Fig. A1. The three possible outcomes for the Lotka-Volterra models describing two-species competition. Original

Appendix 4. Analysis of Predator–Prey Models

The simplest version of the Lotka-Volterra models of predator–prey relationships is:

$$dx/dt = x[r - ay]$$

and

$$dy/dt = y[bx - d]$$

Here x and y = the population sizes of the prey and the predator respectively; r = the growth rate of the prey species; d = death rate of the predator; a = proportionality constant for the (linear) functional response; b/a = growth efficiency of the predator. In the x, y plane, the lines $y = r/a$ and $x = d/b$ are the x and y zeroisoclines for which $dx/dt = 0$ and $dy/dt = 0$, respectively. For points in the plane below the x -isocline, x increases and above that line it decreases; similarly, to the right of the y -isocline y increases and to the left of this line it decreases. Inspecting Fig. A2 shows that this results in closed curves and the system owes its neutral stability to the vertical and horizontal orientation of the isoclines.

If density-dependent growth is assumed for the prey species:

$$dx/dt = x[r - ay - cx]$$

then the x -isocline has a negative slope and intersects with the x -axis at r/c , which is the carrying capacity of the prey species (its population size in the absence of predation). Figure A3 shows that this leads to dampened oscillation and a globally stable point of equilibrium.

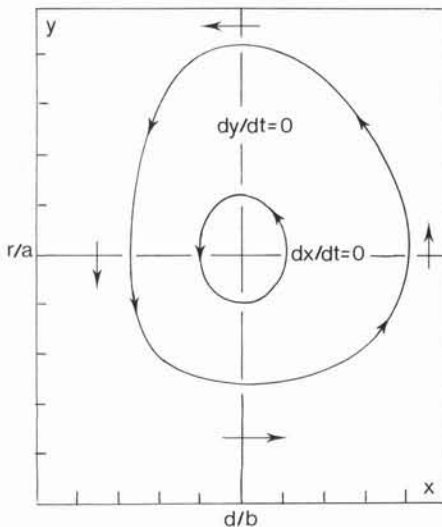


Fig. A2. Behaviour (neutral stability) of a prey-predator system according to a Lotka-Volterra model without density dependence of the prey species. Original

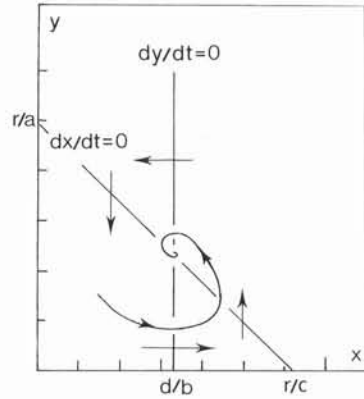


Fig. A3. Behaviour (global stability) of a predator-prey model with density dependent growth of the prey. Original

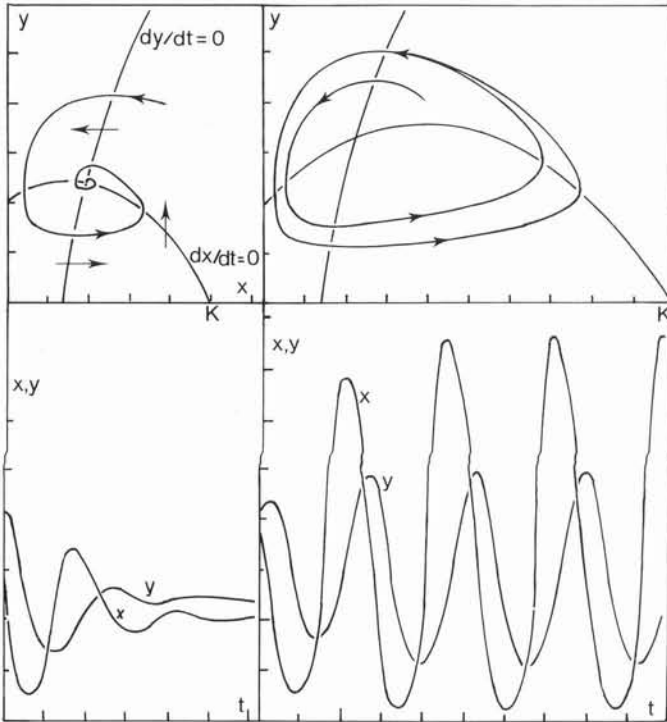


Fig. A4. Behaviour of a predator-prey system assuming a Holling type II functional response of the predator and density dependent (logistic) growth of predator as well as prey. Time-dependent behaviour is shown below. Parameter values of right and left examples are identical except for the carrying capacity (K) of the prey species. An increase in K leads to a de-stabilisation of the system (from a stable equilibrium point to a stable limit cycle). Original

Finally, Figure A4 shows a similar graphical analysis of a more realistic predator-prey system; it assumes logistic growth of the prey and a Holling type II functional response ('Monod kinetics') of the predator. This latter property results in the x -isocline having a "hump" which may lead to an oscillatory behaviour. The graphical presentation of this model as well as that of the Lotka-Volterra model with density-dependent growth of the prey shows that if the carrying capacity of the prey is increased relative to the position of the $dy/dt = 0$ isocline the oscillatory tendency of the system is enhanced as the $dx/dt = 0$ isocline has a more horizontal orientation or even a positive slope where the isoclines intersect.

About the Author and the Book

Professor Tom Fenchel won the ECOLOGY INSTITUTE PRIZE 1986 in Marine Ecology. Under the chairmanship of Professor John Gray (Oslo, Norway), the Jury of the Ecology Institute found Fenchel's contribution to ecological knowledge in a variety of research fields to be of the highest international class. Tom Fenchel was born in Copenhagen (Denmark) in 1940. He obtained his Dr. Phil. degree from the University of Copenhagen in 1969. From 1970 to 1987 he was Full Professor in Ecology and Zoology at the University of Aarhus; since March 1987 he has been Full Professor of Marine Biology at the University of Copenhagen, working mainly at the Marine Biological Station in Helsingør.



Tom Fenchel

The book is based on the author's long-standing experience and insight both as researcher and teacher. It focusses on important developments in ecological research and sets these in the context of science and society. The book addresses a wide readership concerned with ecology and environmental protection – ranging from students and interested laymen to researchers, teachers, administrators and politicians.

About the Ecology Institute (ECI)*

ECI is an international, not-for-profit organization of research ecologists. Director and staff – some 33 marine, terrestrial and limnetic ecologists of high reputation – strive to honor excellence in ecological research, to further exchange between marine, terrestrial and limnetic ecologists, and to bridge the gap between ecological science and its application for the benefit of nature and society.

In order to achieve these aims, one of ECI's activities is to annually select – in a rotating pattern – a marine, terrestrial, or limnetic ecologist distinguished by outstanding achievements who is able and willing to author a book addressing an audience beyond narrow professional borderlines. Published by ECI in the annual series 'Excellence in Ecology', the book is made available world-wide at cost price.

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