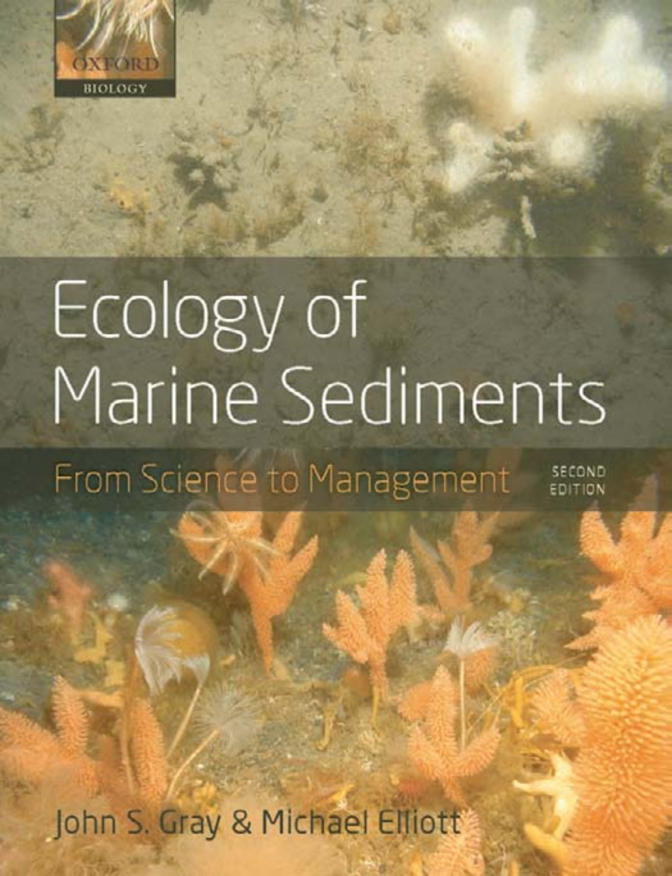

OXFORD
BIOLOGY

Ecology of Marine Sediments

From Science to Management

SECOND
EDITION

John S. Gray & Michael Elliott

Ecology of Marine Sediments

Ecology of Marine Sediments

From Science to Management

The late John S. Gray
University of Oslo, Norway

Michael Elliott
University of Hull, UK

Second edition

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Preface/acknowledgements

In 2004, during discussions with Ian Sherman at Oxford University Press (OUP) who was keen to expand the OUP marine science catalogue, we turned to the need for a book for higher level students and researchers on recent developments in the biology and management of the seabed. The field had continued to develop steadily, work at all levels of biological organisation from the cell to the ecosystem had appeared and the benthos had remained the mainstay of marine environmental assessments. In recent decades many new techniques had emerged, and an increasing field, laboratory and statistical capability had developed worldwide. The increasing numbers of users and uses of the sea together with concomitant threats to marine biodiversity made it vitally important that marine scientists and managers properly understood the structure and functioning of the seabed.

While I was keen to tackle such a book, I had the highest regard for John Gray's 1981 work: *The Ecology of Marine Sediments: an introduction to the structure and function of benthic communities* (Cambridge University Press). I had avidly read and reviewed it when it appeared, had long recommended it to students and found it an immensely valuable reference. I mentioned to OUP that they should first contact John to see whether he was planning on producing an updated version, possibly with a different publisher. John relished the idea but kindly asked me to contribute some of the chapters and so we started working on the present volume. John and I had known each other for a long time—since he was a lecturer at the Robin Hood's Bay Marine Laboratory of the University of Leeds and I was a PhD student at the University of Stirling in the 1970's. We had been involved together for many years on Editorial Boards of *Marine Pollution Bulletin* and *Marine Ecology Progress Series*, and we had met up at scientific meetings such as those of the Estuarine & Coastal Sciences Association (ECSA), the Baltic Marine Biologists (BMB) group and the European Marine Biology Symposia (EMBS). Notably, we had been the joint facilitators of a research marine nature conservation workshop—we were given the task of making the participants think outside of their cosy boxes, a task we both relished!

In juggling all our other commitments, we started the text in late 2005 but within a year John announced the devastating news of his illness. Despite this, he continued to work on the book and managed to produce the initial drafts of his chapters during the early part of 2007. Since then, whilst working through his chapters and adding my own, I gained a real insight into the discomfort that John had suffered while producing his chapters, as well as his bravery and determination in trying to complete the book. We managed some discussion on the concepts, content and format of the book but unfortunately our planned final get-together to work through the material was no longer possible because of his deteriorating condition.

The comments made by John in the Preface to the first edition (copied below) still generally hold true for benthic studies, although in the past 3 decades our knowledge of soft sediment subtidal areas has increased while interest in sedimentary shore studies may have declined. In addition, while John gave the first edition a European flavour, we have now taken a wider geographic view. In completing the book since John's death, I have tried to stay true to his ideas and way of thinking, carefully checking any aspects which were not as complete as John would have wished or where there was doubt. Despite this, there may still be errors and so

I would be grateful to readers for pointing out any remaining inconsistencies.

My thanks to my colleagues in the Institute of Estuarine & Coastal Studies at the University of Hull, especially Krysia Mazik, Jim Allen and Daryl Burdon, and to benthic workers throughout the world for discussions over the years. These are probably too numerous to mention but certainly include Erik Bonsdorff, Angel Borja, Dan Dauer, Jean-Claude Dauvin, Alasdair MacIntyre, Donald McLusky, Derek Moore, Tom Pearson, Victor Quintino, Hubert Rees, Ana Rodriques, Rutger Rosenberg, Heye Rumohr, Matt Service and Richard Warwick. My huge thanks to Ian Sherman, Helen Eaton and Carol Bestley at Oxford University Press for their help in producing this book.

Lastly, my special thanks to my wife Jan for her patience (and for drawing some of the figures!) and to John's wife, Anita, and their sons Martin and Anders for their forbearance in allowing him to spend some of his remaining moments working on this book.

Mike Elliott, University of Hull, September 2008

Preface to First Edition

It is a well-known fact that the sea covers three-quarters of the face of the earth. If a third dimension is added—the sea-bed, with its canyons and slopes—the sea comprises an even greater proportion of the surface of the earth. Most of the sea-bed consists of sediments and only a relatively small proportion is rocky or constructed of coral. Yet, the emphasis of ecological research has been firmly on the fauna and flora of hard substrata. In a way this is not surprising, since on a rocky intertidal shore one can see the fauna and flora and can count them directly and non-destructively; and most species are described. By contrast the fauna of sediments usually, lie buried must be sampled blind and destructively, and, at most, statistical estimates of abundance are obtained, typically with very wide confidence limits. Also, many taxonomic problems still remain, particularly with the small microscopic species constituting the microfauna and meiofauna.

In recent years great strides have been made in our understanding of rocky-shore ecology by the application of techniques and theory arising largely in terrestrial ecology. Indeed the field of research has progressed so far that now terrestrial ecologists are turning to the rocky-shore ecologists for new insights. In particular, predation theory, stemming from the works of Connell and Paine and their co-workers on the US west coast, can be singled out to illustrate this trend.

Sediment ecologists have made some important contributions to general ecological theory, such as the debate on the factors leading to high diversity in the tropics and deep sea that was stimulated by Howard Sanders. However, in the main, sediment ecologists have ignored theoretical aspects of ecology. This surprising and lamentable fact provoked Mills to claim that "Despite more than a century of intensive work on the collection and classification of shallow water benthic animals, much of benthic ecology seems a rather shabby and intellectually suspect branch of biological oceanography. Its methods are, for the most part, those of the nineteenth century; its results, too often, are of interest only to other students of the benthos; and its importance to other branches of biological oceanography has, in my opinion, been proportionately rather small, in spite of one origin of this discipline as a branch of fisheries research." Unfortunately, I have to agree with Mills!

This book is written to try to redress the balance by bringing to the attention of young research workers some approaches to sediment ecology possibly different from those traditionally used. It is not intended as a comprehensive review of the ecology of benthic communities, but more as an introduction to the subject. Where possible, attention is focused on new and promising research fields, such as the experimental manipulation of communities in which the importance of competition and predation in structuring the community has only recently been appreciated. These techniques stem directly from the rocky-shore work of Connell and Paine in America. In general, American workers already follow the approaches to be outlined; the book is aimed, therefore, at the European student, and as a consequence I have taken a European bias in the examples used.

John Gray, University of Oslo

Contents

A tribute to John Stuart Gray (1941–2007)*

The marine science community was greatly saddened to learn of the death of Professor John Gray PhD DSc on Sunday 21 October 2007 at the age of 66 following a battle with pancreatic cancer. John was an internationally renowned environmental scientist whose research was dedicated to moving benthic ecology and studies of marine pollution from observation to hypothesis testing and finally, in a natural progression, to practical, applied usage of monitoring techniques. John was also a dedicated educator, not only of undergraduate and postgraduate students in Norway and abroad but also of governments and the general public, and his intellectual contributions will undoubtedly continue to shape the future of marine benthic ecology, marine pollution studies and their various applications. Above all, John was a wonderful friend, colleague, mentor, and gentleman (in all senses of the word) and will be greatly missed.

Born in Bolsover, England in 1941, John undertook his BSc at the University of Wales (Bangor), followed by a PhD at the Marine Science Laboratories, again at Bangor. His initial research studies signalled the future for his long career examining the impacts of pollutants on marine benthos—his PhD thesis on the ecology of marine meiofauna won him the Zoological Society's T.H. Huxley Prize in 1965. After leaving Bangor, John moved to the University of Leeds' Wellcome Marine Laboratory at Robin Hood's Bay, Yorkshire. On joining an enthusiastic group of intertidal ecologists, led by Jack Lewis, he started to work on intertidal sediment ecology, including meiofauna which had not previously been studied. He also started working on applied problems such as the meiofauna of the polluted areas in the Tees estuary. John then decided to move to the University of Oslo, to take up a position as Professor and Head of the Department of Marine Biology and Zoology.

Further awards and honours marked John's distinguished career, including the Fridtjof Nansen Prize for Research from the Norwegian Academy of Arts and Science, a Charles Darwin Lectureship from the British Association for the Advancement of Science, and a Senior Queen's Fellowship from the Australian Government. The author of over 130 publications, John was also an ISI highly cited scientist and co-author of the influential John Martin Award-winning paper that introduced the concept of the 'microbial loop'. The first edition of the present book was published in 1981. John's most recent research focused on elucidating patterns of marine benthic diversity, marine pollution, and biomagnification, and he was involved in various interdisciplinary studies on recently discovered seabed 'pockmarks' in the Oslofjord and the North Sea and in applied benthic studies centred on Hong Kong's marine environment. Of course, as one could imagine from such a distinguished record, John was involved in many collaborations over the years, and he had the happy knack of including friends and colleagues from such widely separated parts of the world as South Africa, South-East Asia, North America, Europe, and Australasia in his research endeavours.

John was especially known for ensuring that the best science is used in tackling marine problems. For example, his determination for using feedback systems in marine monitoring was best

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* Based on an obituary published in *Marine Pollution Bulletin* 56;2008:1–4, with permission from Elsevier.

illustrated in his work chairing a committee monitoring the effects of the Sweden–Denmark bridge and tunnel crossing. He succeeded in having a system accepted whereby turbidity measurements could be used to control dredging and thus prevent potential problems for marine mussels, which in turn would affect eiderducks feeding on them. The feedback monitoring entailed expensive dredgers being told to stop working if they were causing high levels of suspended solids—such a scheme would not work in most countries and its acceptance required a strong voice, such as John's. Although this approach was based on a predictive capability, he was fully aware that the science was not perfect but that it was fit for purpose within a precautionary approach.

That perhaps summarizes John's attitude to environmental science—he was a scientific pragmatist, who always employed the best available knowledge, combined with his unique critical insights, to ensure the scientific integrity of any problem with which he was involved. For instance, Mike Elliott remembers sitting next to John at a symposium where he was typically questioning the meaning of aquatic monitoring and the use of data and then had to leave early. After he had left, the chairman commented in a rather derogatory way on John being an iconoclast, and Mike then had to explain the meaning of the term to a non-native English speaker. Mike suspects (quite rightly) that John would have been flattered to have been described as such—the term seemed to sum him up perfectly in that John would force us to question our views and defend our conclusions.

Similarly, in the early 1990s Mike was asked to facilitate a workshop with John in which the organizers wanted to make the participants think outside their comfort zone. The workshop was for marine nature conservation workers, and the organizers took the view that the participants would have to be deliberately provocative in order to challenge ways of assessing and managing marine areas. These instructions were followed, but John needed little encouragement as he had, for many years, been writing about and discussing the sloppy and poor thinking in these areas. John's ideas were widely appreciated by the scientific community, and his articles in learned journals were of course abundant, but he always wanted to touch a wider audience. For example, in the 1970s, he wrote in the popular science magazine *New Scientist* about the value (usually low) of marine baseline surveys. In this way, he has greatly influenced our present thinking on these aspects.

Professor Rudolf Wu, of City University of Hong Kong, has similar memories of John's critical expertise. Rudolf first came in contact with John in 1978 at a conference in Heligoland, and, although he was then too shy to introduce himself, he immediately recognized John as a role model: smart, articulate, logical, convincing, and eloquent. Through his friendship and scientific association with Rudolf, John later became closely associated with City University, where he and his wife Anita spent two six-month sabbaticals in 2001/02 and 2002/03. During this time at City University, John taught postgraduate courses on sampling and analysis in marine pollution and became actively involved in the Hong Kong research scene, inaugurating cooperative visits for students between Hong Kong and Norway, and laying the foundation for future research and consultancy which he would undertake in South-East Asia. It was John who suggested bringing Hong Kong students to the Biology Station of the University of Oslo during the summer, to let them experience a different culture and learning atmosphere. Since 2002, Paul Shin and other colleagues from City University have taken over 100 undergraduate students to Dræbak, where John enthusiastically provided them with an introduction to the marine ecology of the fjords. The students were excited by their visits and one of them, being interviewed by a local newspaper reporter, described it as 'a week in paradise'! In summer 2007, even though he had to undertake regular chemotherapy, John insisted on visiting the students at the Biology Station residence, showing his deep devotion to educating young marine scientists. Through John's efforts, one of his students, Annelise Fleddum, is now undertaking her PhD in Hong Kong with Paul Shin.

John's association with City University continued to grow, and he became a major overseas collaborator in a City University-led Area of Excellence initiative, entitled 'Marine Environmental Research and Innovative Technology' (MERIT), one of only

eight Areas of Excellence in Hong Kong, and the only one involved with environmental research. John's most recent work with his Hong Kong collaborators on the use of changes of benthic species in the field for early detection of pollution-induced effects on organisms has attracted much attention, and as Rudolf Wu notes, will undoubtedly have a significant impact on marine pollution research in the coming years.

Despite John's undoubted expertise, and his outstanding publication record, he often expressed his frustration about the way in which the science of nearshore and shallow marine areas was perceived. For example, his work and thinking ranked with the best but found little place in the pages of the journal *Nature*. He frequently complained, and was rightly aggrieved, that the journal often accepted papers on marine benthic concepts and processes for more 'sexy' areas such as the deep ocean but would not take papers on similar aspects of the shallow marine areas. John realised that funding for much of the marine work had to come from applied studies such as oilfield and aquaculture impact assessments rather than blue-skies academic funding, but he also knew that he could take information derived from the applied studies and use it in blue-skies thinking.

John was particularly prominent in his ideas on stress, disturbance, and pollution in marine systems, in bringing together cause and effect relationships, and in developing and using numerical methods for detecting trends. He was rigorous in defending experimental design, good science and science that was fit for purpose in determining change, hence his enthusiasm for 'After BACI-PS' (Before-After-Control-Impact–Paired-Series) designs. At the same time, he was rightly concerned about the way in which various statistical packages were used indiscriminately by benthic biologists, almost as a way of stopping thought and innovation—many researchers have had to rethink their approach after having a paper reviewed by John!

John maintained a long and fruitful association with *Marine Pollution Bulletin*. He was an editorial board member for many years and a regular contributor to the pages of the journal. Ever the provocateur, John sought no favours, and expressed the opinions he believed in. He was always provocative—in his regular scientific articles, and in his editorial commentaries, many of which invoked (sometimes irate) correspondence from other readers! But John was a 'relaxed' iconoclast—he would argue his point of view vigorously, but he would always concede right where it was due if he believed another scientist to be correct. Such is the making of a great scientist.

Some of his minor but important contributions to marine science have come from his careful refereeing work. By its nature, this work is anonymous, but careful corrections, prompts, and comments on the lines of 'Maybe the authors should think of… ' have steered many scientists to improve their own work, sometimes with important consequences. This is a valuable but unsung role, and many authors have benefited from it. Charles Sheppard can remember no authors disagreeing with John's always helpful and constructive criticism of their work.

For the last year of his life, instead of taking it easy, John was busy working on the current edition of this book and managed to produce most of the manuscript. Although there are new examples and methods of studying the topic, many of the basic ideas have not changed much since the original edition in 1981, but Mike Elliott had persuaded John that a new edition was needed. In the intervening years, John and his co-workers and students have added an immense amount to our knowledge of the benthic system. This in itself will be a fitting tribute to John's work and lifetime experience.

In April 2007, despite his deteriorating health, John visited the Institute of Oceanology at Qiandao and Xiamen University in China with

Rudolf Wu and colleagues from Hong Kong, and in June attended the 5th International Conference on Marine Pollution and Ecotoxicology at City University. During the conference, John gave his last, excellent keynote lecture and attended most of the conference programme. His critical abilities were, of course, to the fore. That's how we can best remember him—a scientist of outstanding calibre; an iconoclast, yes; but one whose work will continue to provide insight and have a significant impact on many benthic ecologists and marine pollution scientists around the world for years to come.

Bruce Richardson, Rudolf Wu, Paul Shin, Paul Lam, and Annelise Fleddum, *City University of Hong Kong*

Michael Elliott, *University of Hull*

Charles Sheppard, *University of Warwick*

Introduction

As the oceans cover 70% of the earth's surface, marine sediments constitute the second largest habitat on earth, after the ocean water column, and yet we still know more about the dark side of the moon than about the biota of this vast habitat. The primary aim of this book is to give an overview of the biota of marine sediments from an ecological perspective—we will talk of the *benthos,* literally the plants and animals at the bottom of the sea, but we will also use the term to include those organisms living on the intertidal sediments, the sands and muds of the shore. Given that most of that area is below the zone where light penetrates, the *photic zone*, the area is dominated by the animals and so we will concentrate on this component.

Many of the early studies of marine sediments were taxonomic, describing new species. One of the pioneers was Carl von Linnaeus (1707–1778), the great Swedish biologist who developed the Linnaean classification system for organisms that is still used today (but under threat from some molecular biologists who argue that the Linnaean system is outdated and propose a new system called *Phylocode*). Linnaeus described hundreds of marine species, many of which come from marine sediments. The British marine biologist Edward Forbes was a pioneer who invented the dredge to sample marine animals that lived below the tidemarks. Forbes showed that there were fewer species as the sampled depth increased and believed that the great pressures at depths meant that no animals would be found deeper than 600 m. This was disproved by Michael Sars who in 1869 used a dredge to sample the benthos at 600 m depth off the Lofoten islands in Norway. Sars found 335 species and in fact was the first to show that the deep sea (off the continental shelf) had high numbers of species. Following these pioneering studies, one of the earliest systematic studies of marine sediments was the HMS *Challenger* expedition of 1872–1876, the first global expedition. The reports of the expedition were extensive but were mostly descriptive, relating to taxonomy and general natural history.

Ecology as a scientific discipline developed in the late 1890s and the word was first used by Ernst Haeckel (1834–1919), in the German form *Öekologie*, to denote the comprehensive science of the relationships of the organism to the environment. Most of the important developments in ecological theory have been made in terrestrial ecology, and until the 1950s studies of marine biology were usually of a natural history type. One of the exceptions was the work of the Norwegian fisheries biologist Johan Hjort, who developed important insights into recruitment problems for fisheries. Hjort's research has led to topics that are relevant today, such as whether one can understand the biology of intertidal organisms by neglecting the planktonic larval phase used by many species. This has become known as *supply-side ecology*. Following this, marine ecologists have made a number of important contributions to general ecological theory. Among these is *competition theory*, the empirical basis of which came from Joe Connell's experimental studies of intertidal barnacles. The importance of predation in structuring assemblages was demonstrated by Connell and Robert Paine on rocky shore assemblages. Paine, Hessler, and Sanders, who worked on soft-sediment fauna in coastal and deep-sea areas, developed important insights into how marine biodiversity is organized and controlled.

Although an appreciation of the life in subtidal sediments requires either diving or specialized equipment, walking on an intertidal sandy beach makes most people aware that life exists within the sand, since there are often the telltale marks of holes, pits, and mounds caused by the activities of the inhabitants. As we will show later, unlike the hard, rocky seabed, the sedimentary system is three-dimensional even though often only the surface features are seen. If the beach has a gentle slope with fine sand and standing pools then the evidence of this activity can be highly dramatic, with a mass of changing contours caused by various organisms. Figure I.1 illustrates a typical intertidal beach in northern Europe where the principal agent causing the topographic variety is the lugworm *Arenicola marina*: the process causing such disturbance of the sediment is called *bioturbation*. Anglers can often be seen scanning the sand with keen eyes, looking for the two adjacent holes produced by the siphons of the razor shell *Ensis*, which they use for bait, or thriftily combing the beach for the shallow depressions made by the cockle *Cerastoderma edule*. These, then, are the common and easily observed marks of the beach inhabitants. A closer examination of almost any beach will show minute holes produced by a profusion of amphipod crustaceans and small polychaete worms, and often rings of sand that have been formed by an animal, usually a polychaete, lying with its head downwards and its tail sticking up, engulfing sediment and defecating at the surface. With snorkel and goggles the diver can see that the patterns continue below the tidemarks, and in fact persist right into the deep sea. We hope to illustrate here the processes which create the structures easily seen.

We can describe the variables and processes which create marine biological communities as a set of interlinked relationships (Fig. I.2). Physicochemical variables such as water movements and sediment type set up the conditions which constitute a fundamental niche and under which the benthic organisms colonize an area (the *environment–biology relationships*). Following this, biological interactions such as competition and predator–prey relationships modify the biological community structure and create the functioning (the *biology–biology relationships*).

Figure I.1 Bioturbation caused by the lugworm *Arenicola marina* L. on a European intertidal sandy beach.

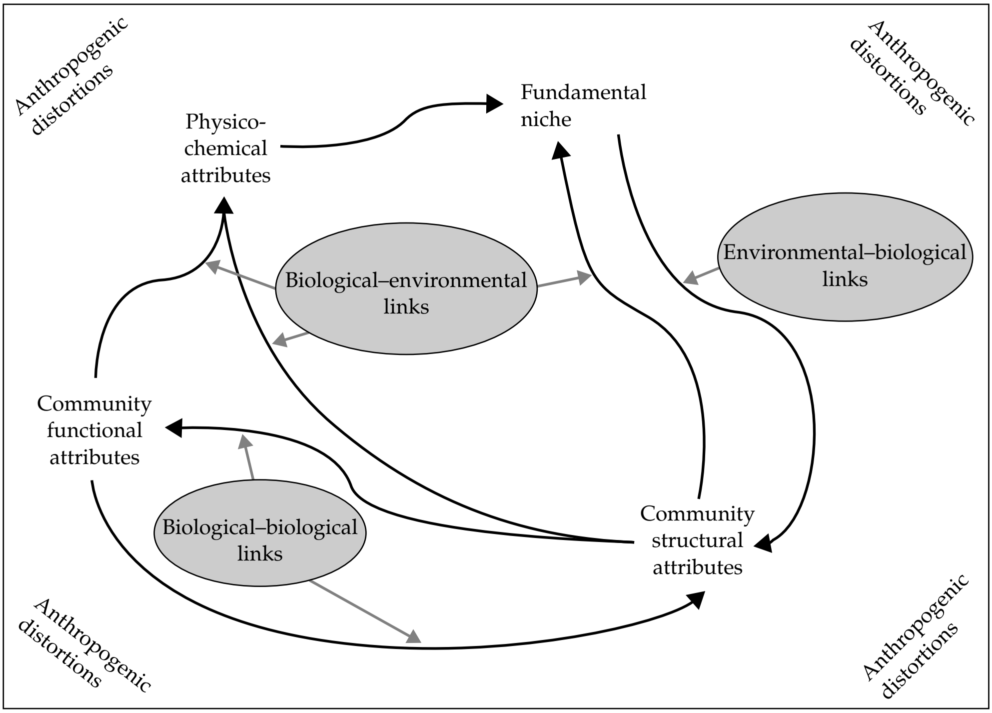


Figure I.2 Benthic community forcing factors – a conceptual model of the main relationships (from Elliott *et al.* 2006).

Then, the biological benthic community can modify the physical structure such as through sediment turnover and changes to sediment chemistry (the *biology–environment relationships*). Finally, human influences are superimposed on these processes.

Before we can discuss the benthic features in detail, we need to define the components of the system. We can separate the benthic organisms into the fauna and flora, and then according to their preference for hard or soft substrata, with the latter encompassing muds, sands, gravels, or even cobbles. Hard substrata include rock and hard, compacted glacial clay which can be colonized only by boring animals such as the bivalve piddocks (e.g. *Pholas*). Then we can separate the sedimentary organisms according to whether they are mobile, sedentary (i.e. moving within one place, not fixed), or sessile (fixed in one place, immobile) and their position in relation to the sediment. The latter separates organisms according to whether they are moving over the sediment (the mobile *hyperbenthic* animals), are on the sediment (the *epibenthos*—including the attached *epiflora* and *epifauna* and the mobile and sessile epifauna (some workers use the term *exofauna*)), or in the sediment (the *infauna* or, less commonly, the *endofauna*). In turn, each of these can be separated according to size—from the micro- to megafauna and the microflora (diatoms, euglenoids, yeasts, and also commonly including the bacteria) to the macroflora (the macroalgae and seagrasses). Finally, we can separate the organisms according to whether they occupy the *intertidal* zone, and can thus tolerate exposure, or are *sublittoral* (or subtidal) (Fig. I.3). Subtidally, the macro- and microflora and those animals feeding directly on these will be restricted to the photic zone, the *infralittoral*, whereas the fauna also penetrate deeper. The next zone in depth is the animal-dominated *circalittoral*; below that we come to the continental shelf and eventually to the abyssal plains and deep-sea vent areas.

The larger animals that leave the telltale patterns mentioned above are usually called the *macrofauna* and can be separated from the sand by sieving the

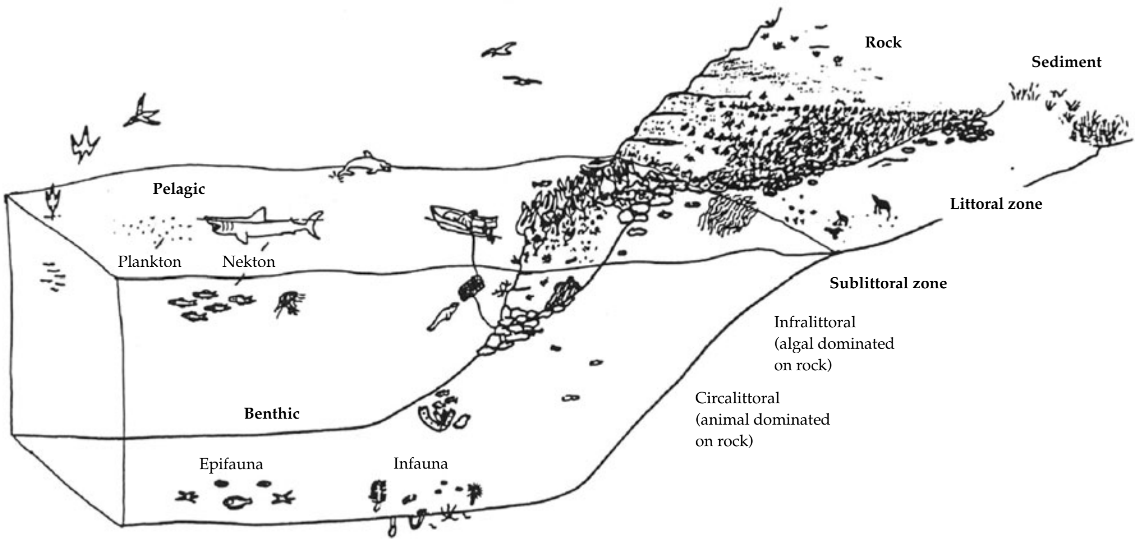


Figure I.3 The components of the nearshore system (drawing by Keith Hiscock 1996; taken from Hiscock 1996).

sediment through a fine screen (e.g. 0.5 mm) which retains the animals and coarser material. If the sand is first separated into different depth layers, the distribution of the animals can be mapped. From this the mode of life of the species can be reconstructed. The elegant Figures I.4a, b by Dörjes and Howard (1975) and Karsten Reise (1991) shows just how complex the distribution patterns can be and shows the three-dimensional nature of the benthic environment, the degree to which the organisms modify their habitat. Given that the figures are from the North Sea, South America, and South-East Asia, Fig. I.4b also shows that although the names of species change (as shown by the numbers on the diagrams), worldwide their roles in the sediment remain similar. The commonest animals are the polychaete worms, followed by the bivalve molluscs, amphipod and decapod crustaceans, burrowing holothuroid echinoderms, and an occasional burrowing anemone (Fig I.5). Each of these is affected by and in turn influences the structure of the sediment, creating an intimate link between the water column, surface, and sediment depth. In turn, the sedimentary fauna in general and the macrofauna in particular support the higher trophic levels, especially the mobile hyperbenthic crustaceans and the birds and fishes. The latter are often categorized as the *charismatic megafauna*, organisms which have a high resonance with the public. As both of us have spent many years examining the benthic fauna, especially the macrofauna, it has always been difficult realizing that for most people its importance is only as food for birds and fish!

The macrofauna is only a part of the fauna of sediments, and there are several classes of marine benthic organisms based on the size of the mesh used to retain them:

- microfauna (<63 μm)
- meiofauna (63–500 μm)
- macrofauna (500 μm–5 cm)
- megafauna (>5 cm)

or on a taxon basis:

- microfauna: ciliates, rotifers, sarcodines
- meiofauna: nematodes, oligochaetes, gastrotrichs
- macrofauna: polychaetes, amphipods, bivalves
- megafauna: echinoderms, decapods.

Living between the sand grains intertidally or subtidally, or on muddy beaches within the mud, is a whole variety of small animals that will pass through the meshes of the 0.5 mm screen. These small animals are called the *meiofauna*, to distinguish them from the even smaller protozoan and other microorganisms

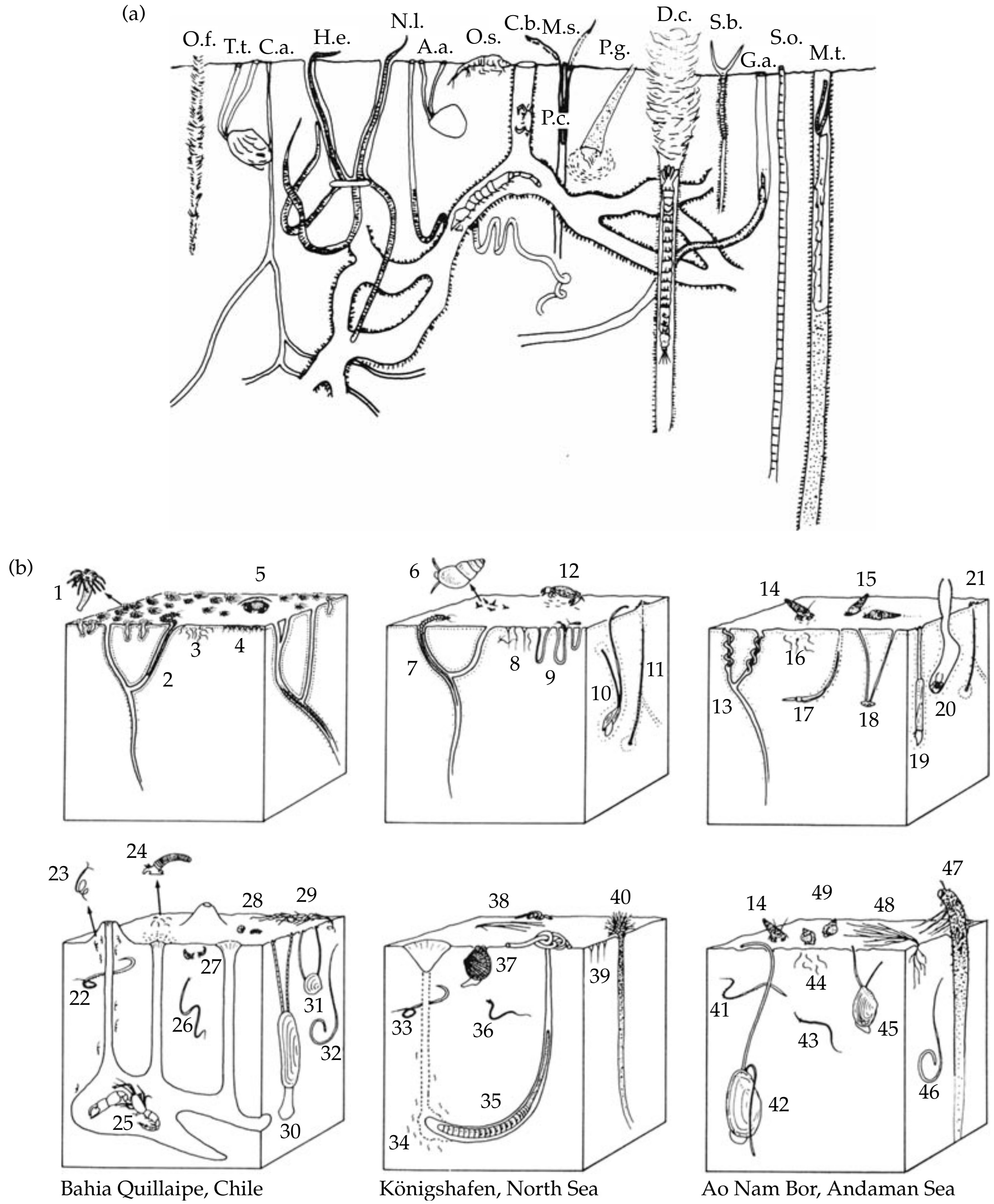


Figure I.4 (a) Location of most important benthic animals, burrow and tubes in a shallow-shelf environment in Georgia, USA. A.a., Abra aequalis; C.a., *Capitomastus* cf. *aciculatus*; C.b., *Calianassa biformis*; D.c., *Diopatra cuprea*; G.a., *Glycera americana*; H.e., *Hemipholis elongata*; M.s., *Magelona* sp.; M.t., *Mesochaetopterus taylori*; N.l., *Notomastus latericeus*; O.f., *Owenia fusiformis*; O.s., *Oxyurosthylis smithi*; P.c., *Pinnixa chaetopterana*; P.g., *Pectinaria gouldi*; S.b., *Spiophanes bombyx*; S.o., *Spiochaetopterus oculatus*; T.t., *Tellina* cf. *texana*. (After Dörjes & Howard, 1975.) (b) The three-dimensional nature of the benthos (from Reise 1991; the numbers refer to different species from the three geographic areas).

collectively called *microfauna* (Giere 1993, Coull 1999). Some of the meiofauna have been called *interstitial fauna,* since they live in interstices between sand grains. The prefix 'meio' comes from the Greek word *meios,* meaning intermediate, and thus the meiofauna is intermediate in size between the macrofauna and

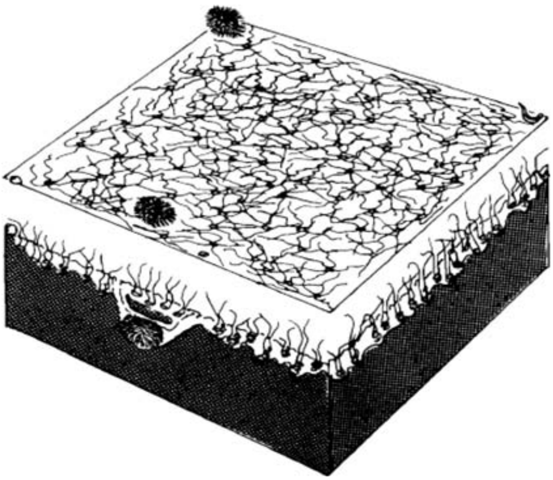


Figure I.5 Three-dimensional structure of benthos living in $0.1\ m^2$ sediment of Oslofjord, showing dominance of ophiuroid echinoderms (drawing by Dr T.H. Pearson).

microfauna. The exact definitions of macro-, meio-, and microfauna have been the subject of continuing controversy over many years and, as shown above, different workers use either size and/or phyla to separate the types. Some workers use a 1 mm screen to separate out the macrofauna, whereas others use a 0.5 mm screen and yet others will include nematodes only in the meiofauna, irrespective of their size, so that large nematodes retained on a sieve with the macrofauna will be grouped with the meiofauna. For example, in sewage-affected areas the very large nematode *Pontonema*, although retained with the macrofauna, will still be classed as meiofauna. Naturally the smaller screen collects more animals, but just how big an effect this can have often depends on the season of sampling, since in periods of high larval recruitment the finer screen will collect many more juveniles.

Nematode worms usually cannot be sampled with a 0.5 mm screen, nor can many of the harpacticoid crustaceans, so these two groups are included in the meiofauna (Giere 1993, Coull 1999). The lower limit of the meiofaunal size is set by use of a 0.062 mm screen (biologists follow geologists in using a decreasing geometric scale of screens: 1 mm, 0.5 mm, 0.25 mm, 0.125 mm, 0.062 mm, etc.). The meiofauna usually consists of nematodes, harpacticoid copepods, turbellarians, and a phylum unique to the meiofauna, the Gastrotricha. Since the meiofauna is often defined by size of screen used, the animals included in it may be juvenile members of the macrofauna which for a time are within the meiofaunal size range. Such animals are called *temporary meiofauna* and include in particular the larvae and newly settled stages of polychaetes and bivalves, although most phyla are represented. The permanent members of the meiofauna (nematodes, harpacticoids, etc.) are those that always remain within the meiofaunal size range. In fact, there are representatives of almost all marine invertebrate phyla in the permanent meiofauna: small sponges, ascidians, gastropod molluscs, and even a walking bryozoan, *Monobryozoon ambulans*, can be found. Giere (1993) summarized our knowledge of the biology of the meiofauna.

How abundant are the different size categories in a typical sandy beach? Comparative figures are hard to find since most workers concentrate on the macrofauna alone, some (an increasing number) are interested in the meiofauna, and only very few study the microfauna. Figure I.6 shows data from a typical intertidal beach where the smallest animals, the microfauna, dominate numerically, but the macrofauna dominates in terms of biomass.

The ratios of the different types found depend on the sediment type, with, for example, microfauna being very common in fine sand but scarcer in mud, where macrofauna and meiofauna dominate. As to the species found, a typical boreal (mid-northern latitudes) sand beach may contain 20–30 macrofaunal species and 200–300 meiofaunal species; no one has yet estimated the total number of microfaunal species. The taxonomic problems of working with the meiofauna and microfauna are large, and new species are still regularly being described in these groups. In many cases we may know more about intertidal beaches, not because the fauna is especially rich there, but because such beaches are better studied than subtidal areas, where boats and grabs or box-core samplers are needed to sample the sediments below diveable depths. Subtidally the number of species of macrofauna in a typical sample is much higher than in the corresponding sample size taken intertidally, and in an average sampling programme of say 8–10 grab samples, each about 0.1 m^2, there can be approximately 150 species. In contrast, few data are available on numbers of subtidal meiofaunal and microfaunal species.

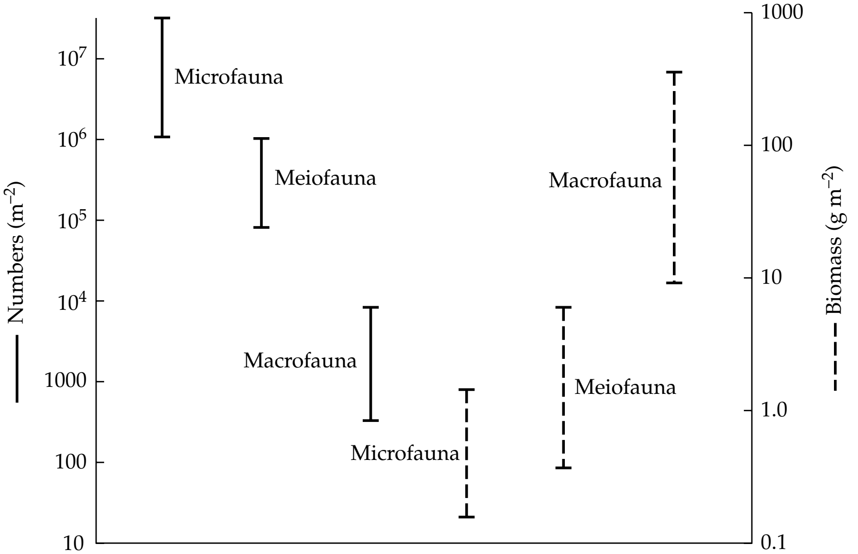


Figure I.6 Numbers and biomass of macro-, meio-, and microfauna from a typical sandy beach in Europe.

The habitat inhabited by and in turn modified by the benthos is the result of many interacting factors, of regimes which cover scales from the global to the local, and of the intimate linkages between the water column and its factors and the substratum and its factors. (Here we pedantically use the terms substratum rather than substrate, reserving the latter for materials required in chemical reactions!) Most central is the means by which the hydrographic patterns of currents, tides, and global forces such as Coriolis produce the sedimentary conditions. We can consider these factors as producing two fundamental niches—the water column and the substratum (Fig. I.7)—and so an understanding of these physical and chemical aspects is necessary in order to understand and explain benthic biological processes. Indeed, one cannot hope to understand the biological processes without first having a good grasp of the physicochemical ones.

This book is mostly about the substratum (bed sediment) fundamental niche, although of course we cannot separate processes there from those in the water column. Indeed, as most of the bed organisms rely on the water column for their food and larval dispersion, we require a good understanding of the processes there and the links with the benthos (the so-called *benthopelagic coupling*). The biological processes which occur in the organisms inhabiting the fundamental niches are the same as in any ecosystem (Fig. I.8). This includes the separation of the system into feeding (trophic) levels, the movement of materials between those levels, and the competition and partitioning of resources.

These then are the basics of the biota, especially the fauna, of marine sediments. The primary goal of this book is to illustrate these ecological principles as applied to the biota of marine soft sediments (muds, sands, and gravels). We do this by illustrating key concepts and especially how recent advances, in technology for example, have given us greater power to observe and understand the relationships between the biota and the physical environment in which it lives and the biological interactions that are so important in controlling the patterns and dynamics of marine species.

Following the discussion of the natural ecological features, we then discuss the effects of human activities on the marine benthos and the ways in which we can study those effects. While we refer readers to the many other books devoting much more attention to human impacts (e.g. McLusky and Elliott 2004, Clark 2001), we merely note here that human activities in the sea can be divided into

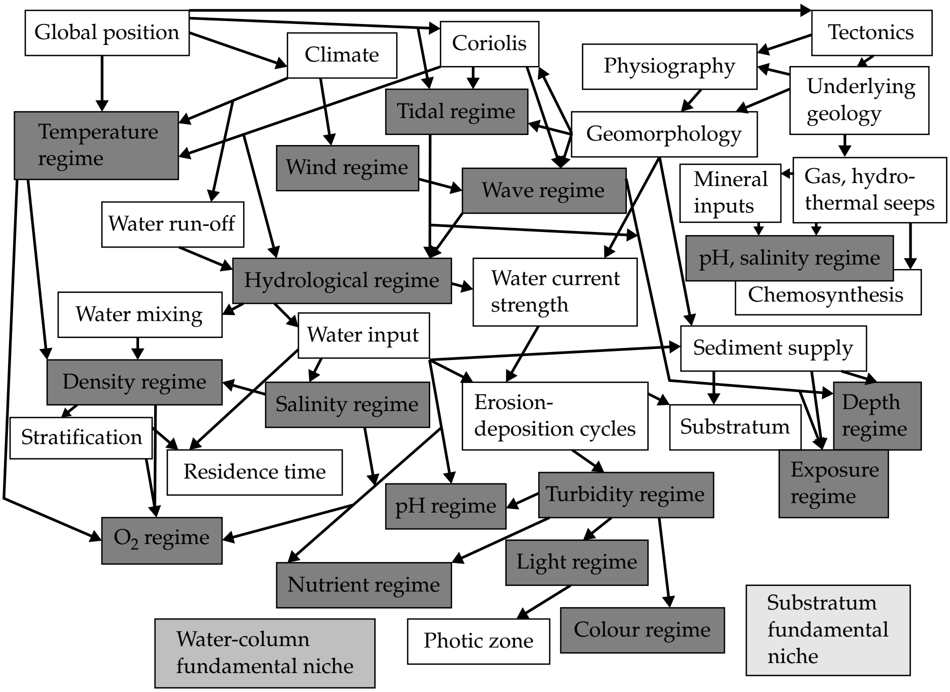


Figure I.7 The links between the physicochemical attributes resulting in the two main marine fundamental and overarching niches, for the water column and for the substratum (from Elliott *et al.* 2006, Borja and Elliott 2007).

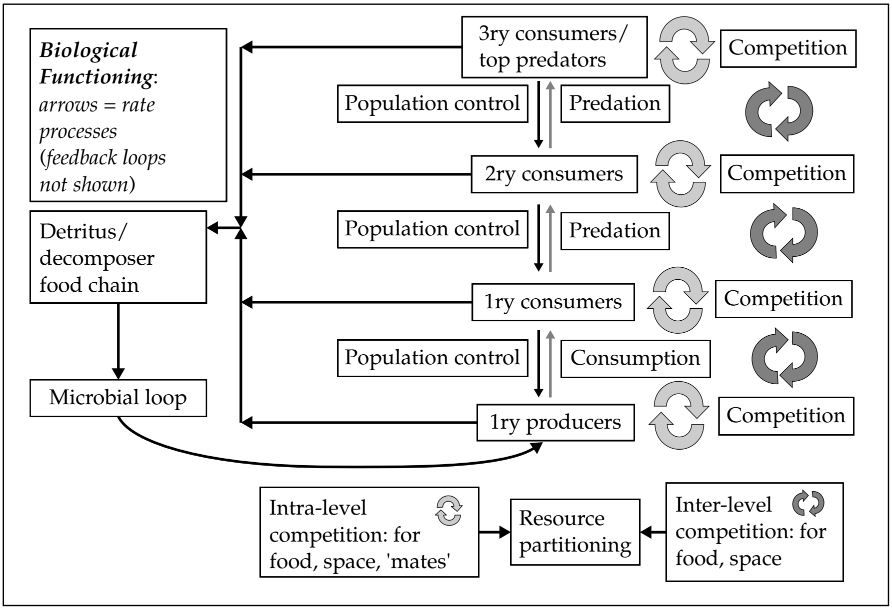


Figure I.8 Ecosystem functioning: the main ecological processes (from Elliott *et al.* 2006).

those *where material is added* and those *where it is removed*. Briefly, the materials added are:

- *physical:* small particles (sediments), large structures such as bridges and oilrigs
- *chemical:* pollutants/contaminants such as heavy metals, oils, radionuclides, etc. both in solution and as particles, organic matter. and nutrients
- *biological:* e.g pathogenic microorganisms from sewage, introduced species such as those from ballast water.

In contrast, the materials removed are:

- *water:* by abstraction for industry
- *space:* by land claim or occupying an area by structures
- *physical materials:* e.g. sand and gravel extraction for construction, fine sediment during dredging
- *chemicals:* e.g. salt in salt pans, desalination plants, mineral nodules
- *biological materials:* e.g. as fisheries, shellfisheries, curios by divers.

Because of the fundamental nature of the benthic system and its intimate links with the hydrographic system, described above, it is relatively easy to see that each of these stressors affects the sedimentary system and its associated fauna and flora. In this book, as an example, we use only two of the above categories to illustrate the effects on the benthos—firstly fishing and fisheries and secondly the introduction of organic and other chemicals as pollution—but we give the main considerations that can be used for other examples.

The literature on the marine benthos is now so large that it is not possible to do justice to it all, and so this book is very much our personal account. Despite this, hopefully we indicate the main processes and features and also the main and illustrative literature, current research, and suggestions for further research. In particular, we have mentioned reviews of the most important topics so that readers can take the subject further.

Chapter 1 covers the methods for studying the benthos and includes traditional methods as well as new technological discoveries such as multibeam sonar which enable us to map the seabed in a highly detailed manner. Cameras which allow mapping of the sediment structure vertically in sediments are described. Sampling strategies and designs (e.g. beyond BACI-PS (Before After Control Impact–Paired Series), gradient and transect design) and the instruments used to take samples of the benthos are described. New theoretical developments which take scale into account are covered so that appropriate numbers of samples are taken for the question being posed.

Chapter 2 deals with the key environmental factors that affect the fauna such as the physical properties of the sediment and the cycling of the major elements (carbon, nitrogen, phosphorus, sulfur) and materials into and out of the sediment. The basic biogeochemical processes and microbial systems in sediment are described and the importance of the sulfide system in particular is highlighted. Finally, the niche of a small sediment-living polychaete species is described as an illustration of the niche concept.

Chapter 3 shows how communities are described, together with species abundance models, with an emphasis on ranked abundance and distributional models such as the lognormal. We consider ideas regarding separation into groups of rare and common species, an idea developed in marine soft-sediment assemblages. Species size spectra are also covered. Finally, recent work using univariate and multivariate numerical modelling of community structure in intertidal and subtidal assemblages is described.

Chapter 4 treats the diversity of sediment assemblages from the standpoint of patterns of diversity. The importance of studying diversity at different scales has not been fully appreciated. Too often studies are done at small scales only, and at such scales it is ecological events that determine the diversity. Large-scale patterns such as the latitudinal, longitudinal, or coastal–deep sea gradients result from evolutionary events and can only be studied at large scales. The hypotheses for patterns of diversity are examined in detail and the importance of evolutionary history in interpreting such data is pointed out.

In Chapter 5 functional aspects of diversity are examined. We give details of how to calculate energy budgets for macro- and meiofauna using traditional and short-cut methods. Measures of the efficiency of systems using production:biomass ratios are covered, as are community metabolism measurements now done down to the floor of the deep sea using corers and remote-operated vehicles (ROVs).

Chapter 6 analyses spatial variations that occur in benthic systems. Key aspects of scale such as *grain* and *extent* are defined and then the spatial scales of processes that affect benthos are described. Many of the processes are biological and involve large small spatial extent (bioturbation) compared with large-scale physical processes that affect areas of many thousands square kilometres. Methods for analysing at different spatial extent and grain size are covered and examples given of biological responses. The effects of competition and predation are illustrated and many examples are given to illustrate the processes.

Chapter 7 covers scales of temporal variations in benthic assemblages. These range from seasonal and multiannual variations to decadal and longer periods in assemblages. Examples are given of such patterns, and in particular recent findings about the North Atlantic Oscillation which correlates well with changes in benthic (and terrestrial) systems. Finally, in order to give a theoretical framework, models of stability are considered in relation to the temporal changes recorded for benthic systems.

Chapter 8 examines the effects of trawling as a special form of disturbance that within the last 15 years has been recognized as increasingly damaging for benthic systems. The different types of gear used are illustrated and the effects of these gears on different sediment types described. Sandy sediments are less damaged by trawling, but muddy and gravelly bottoms are prone to severe damage of both structure and function. Recent analyses suggest that recovery periods are much greater than the trawling industry recognizes, and so recovery is unlikely without changed management.

In Chapter 9 data on the effects of pollution on benthic systems are presented. Firstly, effects of the widepread pollutant organic matter are discussed using examples to illustrate its effects on benthos. This is followed by coverage of the effects of the oil industry on benthic systems. These two examples illustrate how benthic systems are used in monitoring the 'health of the seas'. It is shown that in most marine organisms heavy metals (except in organic forms) are not generally a health problem, whereas organic chemicals often (but far from always) lead to biomagnification up food webs. Finally, strategies of how species adapt to pollution are presented and we consider the effects at various *levels of biological organization* from the cell to the ecosystem. In the latter, we also cover the recovery of systems.

In Chapter 10 the role of the benthos in the ecosystem is further considered. Determination of food web structure by use of stable isotopes is illustrated for George's Bank, USA and the Arctic. From this the food web is reconstructed and then models can be developed to quantify the trophic relationships. Network analysis is used to show the principles of an ecosystem model and the key properties of a network illustrated for Chesapeake Bay. Finally, the European Regional Seas Ecosystem Model (ERSEM) is used to show how a modern ecosystem model functions. ERSEM is particularly strong for the benthic component and the final simulation shown is for effects of predation by fish on benthic systems for different compartments of the benthic system.

Finally, Chapter 11 puts the use of the benthic information and data into a wider context and deals with the monitoring and management of marine sediments. This includes the role of the benthos in environmental impact assessments (EIAs) and in assessments of the quality of the seabed, recent ways of managing sedimentary systems, and the monitoring of the effects of human activities on the benthos. The analysis of these aspects relies on indicators of change and quality objectives, and these are illustrated by the way in which the benthos is incorporated into European, Australian, and North American marine quality assessments and management protocols and legislation. We discuss the role of numerical models and other numerical techniques in interpreting and predicting benthic change and the methods by which we can ensure quality in benthic data. Finally, the chapter gives some concluding remarks and lessons to be learned regarding the ecology and management of marine sediments.

CHAPTER 1

Sampling sediments

1.1 Sampling design

One of the truisms of sampling design is that the design depends on the objectives. Too often objectives are not defined properly, with the result that the data collected cannot be used to answer the questions posed. A good example is that of a monitoring programme that aims to detect changes in an assemblage of benthic organisms caused by eutrophication but where the magnitude of change was not specified in the objectives, with the result that the monitoring programme was so loosely designed that insufficient samples were taken. *A posteriori* analyses of the results may show that the monitoring would take 10 years to detect a 10% change in the faunal composition. You may think that this is an unrealistic and hypothetical example, but our experience shows that far too often results such as this are the norm.

We return to the types of monitoring in Chapter 11, but for now let us start with perhaps the simplest case: we wish to survey an area of coastal soft sediment simply to find out what is there (i.e. to map the habitats and prepare for a more detailed quantitative study of the benthic assemblages). Up to the last couple of decades, sampling subtidally below diveable depths was usually done blind. One had to resort to charts, perhaps prepared in the nineteenth century, which have depths and descriptions of sediments made from soundings done with hand-lines with candlewax in a hollowed-out part of the lead weight that touched sediment particles, enabling the sediment type to be crudely mapped. Since the 1980s huge technological advances have been made in mapping sediments. Two types of instrumentation have been developed: depth sounders of various types and remote-operated vehicles (ROVs). With sounders, accurate maps of the contours of the seabed can be produced and then indications of the hardness and roughness superimposed on the depth and good three-dimensional images produced with modern software. Sophisticated multibeam echosounders have been used to map the whole continental shelves of many countries. Now that the satellite-based differential global positioning system (DGPS) is generally available with an accuracy to a few metres, mapping of subtidal sediments has become much easier and more accurate. Once the data have been obtained from the multibeam surveys and the images have been processed, extremely detailed maps of bottom contours and structures are available. Figure 1.1 shows results of a recent multibeam mapping survey of the Inner Oslofjord, Norway.

The modern strategy is to map bottom contours and structures by multibeam surveys, then do ROV surveys to obtain habitat maps superimposed on the depth contours, and finally to sample the organisms by more conventional methods. ROVs are now used extensively, even down to great depths, and using laser-guided navigation aids and stored digital video images detailed maps of the sediment surfaces can be made; maps can even be made of the major faunal types present, from burrow formations and similar information. Figure 1.2 shows a ROV mounted with still and video cameras. If the multibeam surveys give the hardness and roughness of the bed then this information can be ground-truthed to indicate the nature of the bed. For example, the roughness signal will show a bare soft sediment, giving a signal different from soft sediment with a mussel bed on it, and the hardness signal will indicate a subtidal sandbank being different from a muddy bottom.

Once such a survey has been done, maps can be made of the area showing major habitat types and

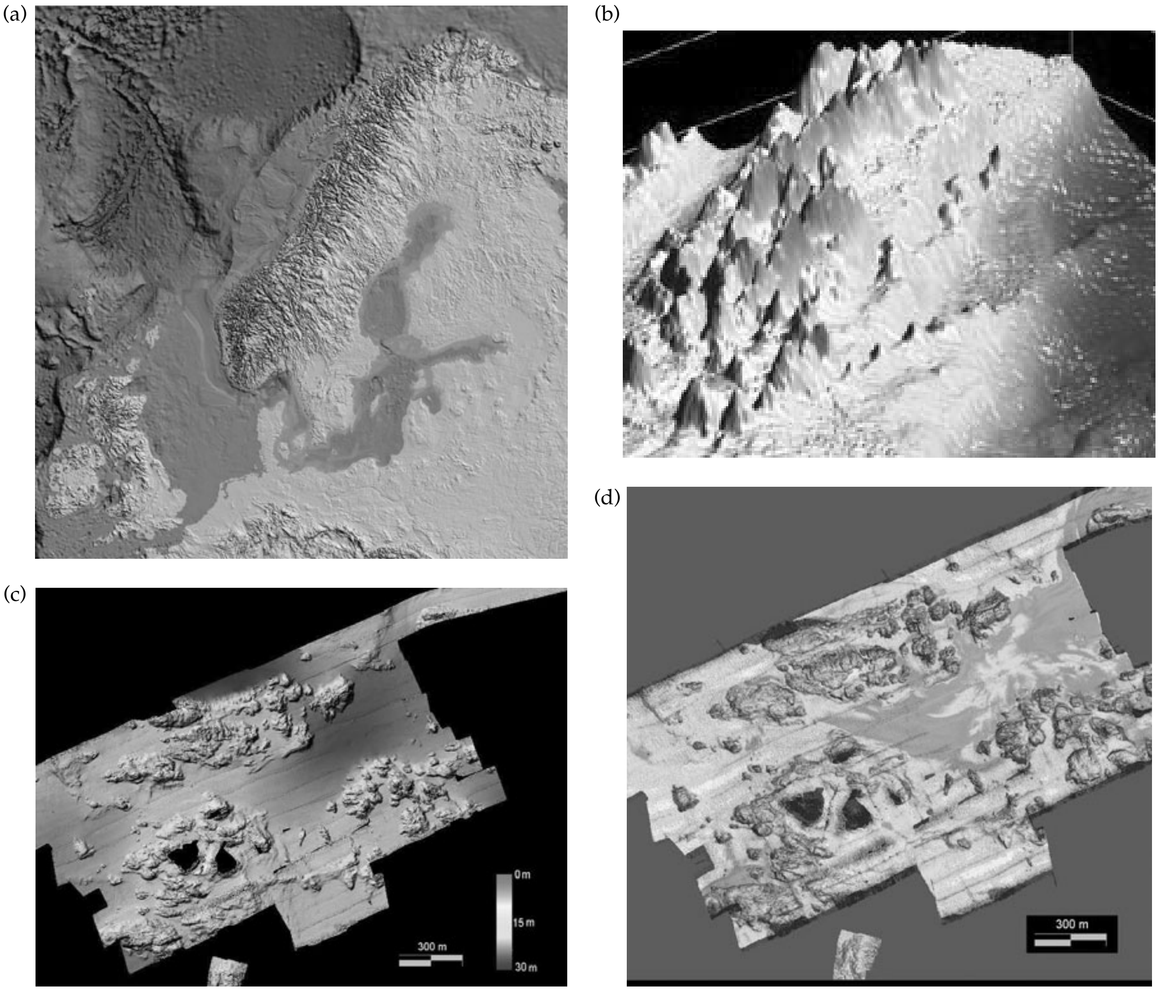


Figure 1.1 Multibeam survey image of bottom topography a) North Atlantic showing depth contours, b) bottom topography, c) small-scale topography d) colour processing to show sediment types (purple silt-clay). Images from Norwegian Geological Survey Terje Thorsnes.

depths. It is then possible to examine the structure of the sediment assemblages. Two recent ways of doing this are *acoustic methods*, which penetrate into the surface sediments and are able to classify the echo that bounces back to the receiver, and *sediment profile imaging cameras*. Sediment classification using echosounders has developed into a fairly reliable tool that can classify major sediment habitats, coarse to fine sand, and even signals provided by the main bioturbators (bioengineer animals that alter the properties of the sediment, such as burrowing bivalves). Systems that have been used are the RoxAnn and QTC-View sediment classification systems, as well as the new system developed by Simrad, Norway (for a good example of their use, see Magorrian *et al.* 1995).

There are several good studies which show the additional benefits of using several techniques in combination—for example, Michalapoulos *et al.* (1992) illustrate the combined use of underwater video and transect techniques. As an excellent example of the combined use of several techniques, Brown *et al.* (2004) mapped the spatial distribution of seabed biotopes (i.e. physical habitats and their associated benthic assemblages) near a shingle bank in the eastern English Channel. The survey was linked to an aggregate extraction area, producing sands and gravel for construction. As an

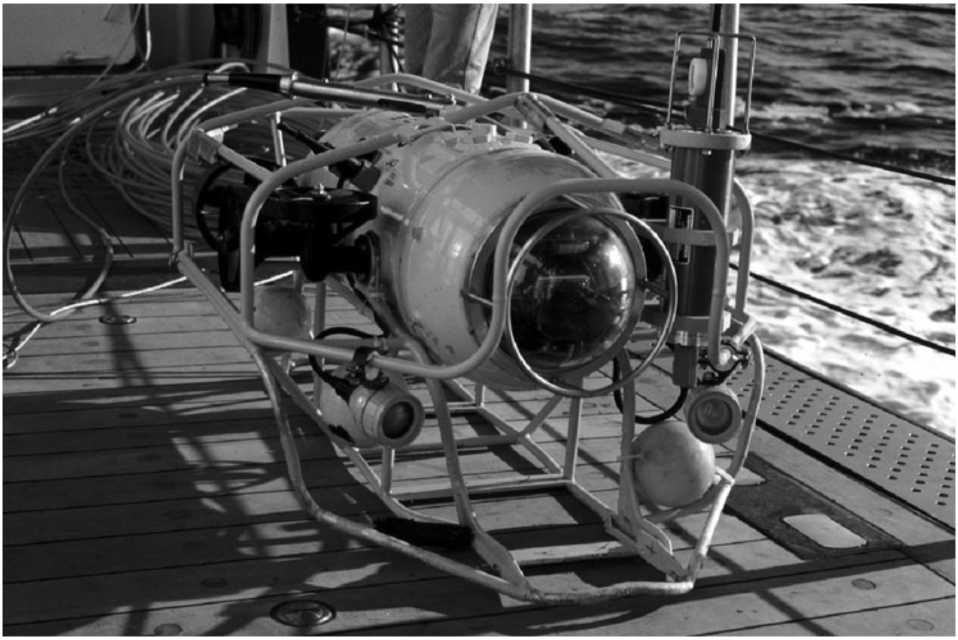


Figure 1.2 A remote-operated vehicle (ROV) (photo M. Elliott, with acknowledgement to Heye Rumohr). See Plate 1.

indication of the size of area which can be covered by the techniques, Brown *et al.* surveyed approximately 12 × 4 km using a high-resolution sidescan sonar system to produce a habitat mosaic covering the whole area. They then used the sidescan sonar data to divide the area into acoustically distinct regions and then ground-truthed the benthic communities and sediment types within each regions. The ground-truthing was done with a Hamon grab fitted with a video camera for the infauna and a heavy-duty 2 m beam trawl for the epibenthos. They also obtained further seabed information from still and video photography. The survey mapped both the substratum types and the presence of statistically distinct biological assemblages within each acoustic region, thus producing detailed scientific information which can be used for managing the aggregate extraction.

The sediment profiling imager (SPI) camera (Fig. 1.3), developed by Rhoads and Germano in the USA as REMOTS, has a wedge-shaped 'spade' with a vertical glass plate and prism inside linked to a digital camera. The sampler is lowered to the sea floor and penetrates the sediment. Pictures are obtained of the sediment type and, more importantly, the burrowing activities of the animals present, as well as visual information on sediment chemistry. Tubes of animals, methane gas bubbles, the depth of the deeper black (anoxic) zone, and the nature of the sediment are all given. Image analysis of the resulting photograph can then be used to quantify the sedimentary and biogenic features. The SPI camera can be deployed rapidly and surveys made over large areas to map the key habitats and organisms present prior to using more time-consuming and classical techniques. Recent additions are a hand-held SPI camera that can be operated by divers. For a description of how the SPI camera functions and the resulting image processing see Diaz (2005).

As indicated above, a map of the area to be sampled is prepared covering the main types of habitats and depths, since depth and substratum type are the major variables affecting the fauna of marine sediments. Once the area is mapped, the traditional approach is then to take samples following a *stratified random* approach. In this, the areas of each habitat are calculated and then a grid is superimposed over the whole with the grid size allowing at least one sampling site within each grid square. Then random numbers are chosen in order to allocate

(a)

(b)

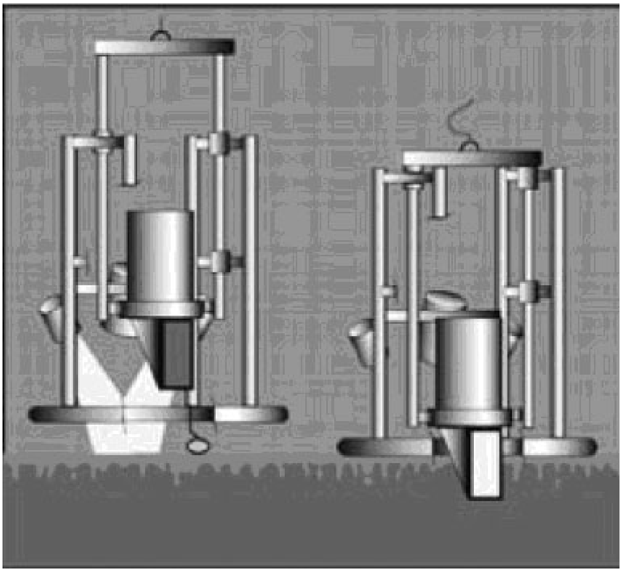


Figure 1.3 (a) A sediment profile imaging (SPI) camera (photo M. Elliott, with acknowledgement to Heye Rumohr). See Plate 2 (b) SPI camera (from H. Nilsson). The left image shows the SPI camera approaching the bed, the right image shows the prism pushed into the bed in order to take a photograph of the vertical surface.

the number of sites sampled within each habitat so that each receives the same sampling density. This is called *proportional allocation of sampling effort* (or *proportional sampling*). With such a plan it should be possible to map faunal patterns in an objective manner. In general, once the strata have been defined and chosen, then there are three ways of allocating sampling effort: simple random (the same sampling effort per stratum); proportionally random as described above whereby the number of samples relates to the area covered by the stratum, and optimal where more samples are placed in the more variable strata (see Figure 1.4; also see McCormick and Choat 1987 for further discussion).

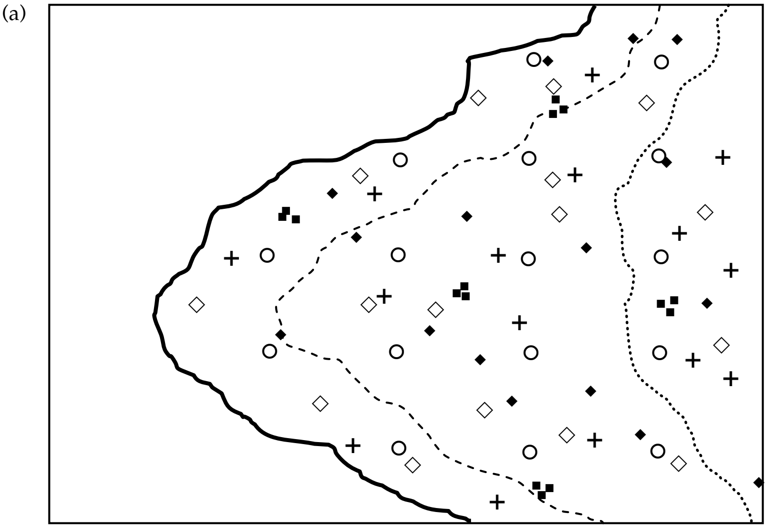


Figure 1.4 Illustrative but different benthic sampling designs each with similar sampling effort for the whole survey: ◆ random sampling; ○ systematic grid sampling; + stratified random sampling by depth showing equal effort per stratum sampling (solid line - coastline; dashed and dotted line are depth contours); ◇ stratified (by depth and hence area) random proportional sampling; ■ random replicate (clustered) sampling.

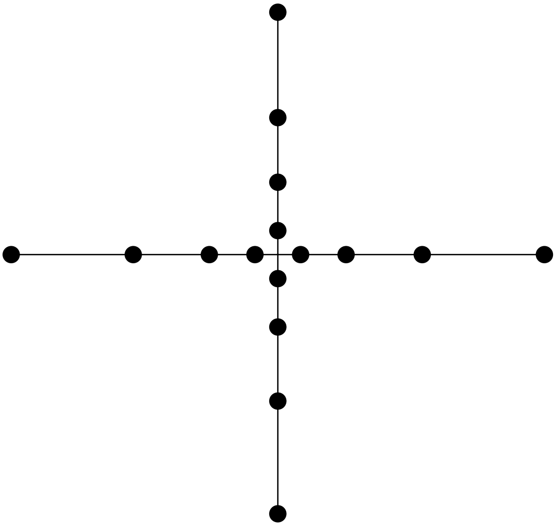


Figure 1.5 Gradient sampling design for a point-source pollutant. Sampling sites (dots) are at logarithmically increasing distances 500, 1000, 2000, 4000 m on each radius.

It is axiomatic that the sampling design depends on the questions being addressed by the survey and each type of design answers different questions. Figure 1.4 illustrates several different designs and shows that while a systematic grid makes no pre-judgements about the area and gives a uniform coverage, a stratified random design gives similar effort in each stratum (e.g. habitat or, in the case of Figure 1.4, depth). Random sampling may give an equal probability of visiting each type of area but proportional random sampling reflects better the benthos of the whole area by accounting for the disproportionate areas covered by different strata. Clustered, replicate sampling will give less spatial coverage but more statistical power to pick up subtle differences between areas; hence single samples per site will allow the characteristics of the whole area to be described but will not allow nested-model significance testing in space or time. Thus each strategy has its pros and cons in relation to detecting statistical differences within a site, between sites, between strata and between sampling occasions. Van der Meer (1997), Hansen et al (2006) and Rozas and Minello (1997) give a detailed description of sampling approaches for these designs. In addition, Alden et al (1997) reinforces the temporal dimension to sampling design.

Often we want to measure the effects of a pollutant on the marine environment. The sediment-living benthos is particularly suitable, and much used, for studying the effects of pollutants or other disturbances, as most organisms cannot move away so they must tolerate the pollution, adapt, or be killed (Chapter 9 covers these aspects in detail). Two types of sources can be envisaged: a point source and a more general widespread (diffuse) effect. For monitoring point sources it is usual to use a *gradient sampling design*. A good example would be the effect of an oil platform on the surrounding environment. A typical sampling design is the one shown in Fig. 1.5, which is used in the OSPAR Commission's guidelines (OSPAR 2004) for monitoring the effects of oil and gas platforms on the marine environment. Sampling stations are placed at logarithmically increasing intervals from the safety zone (within 250 m of the platform), doubling to 500 m, 1 km, 2 km, and 4 km (a distance where no effects are likely to be found). Four radii are used and often the alignment is not to due north but along the residual direction of current flow, hence increasing the likelihood of detecting a near-field effect influenced by the hydrographic regime. If the source is a sewage pipe discharging from a fixed point off the coast then you could use, say, three radii with smaller angles between the radii to give a sampling strategy approximately similar to the one illustrated in Fig. 1.5.

A key aspect of such sampling design is the necessity for a number of undisturbed control

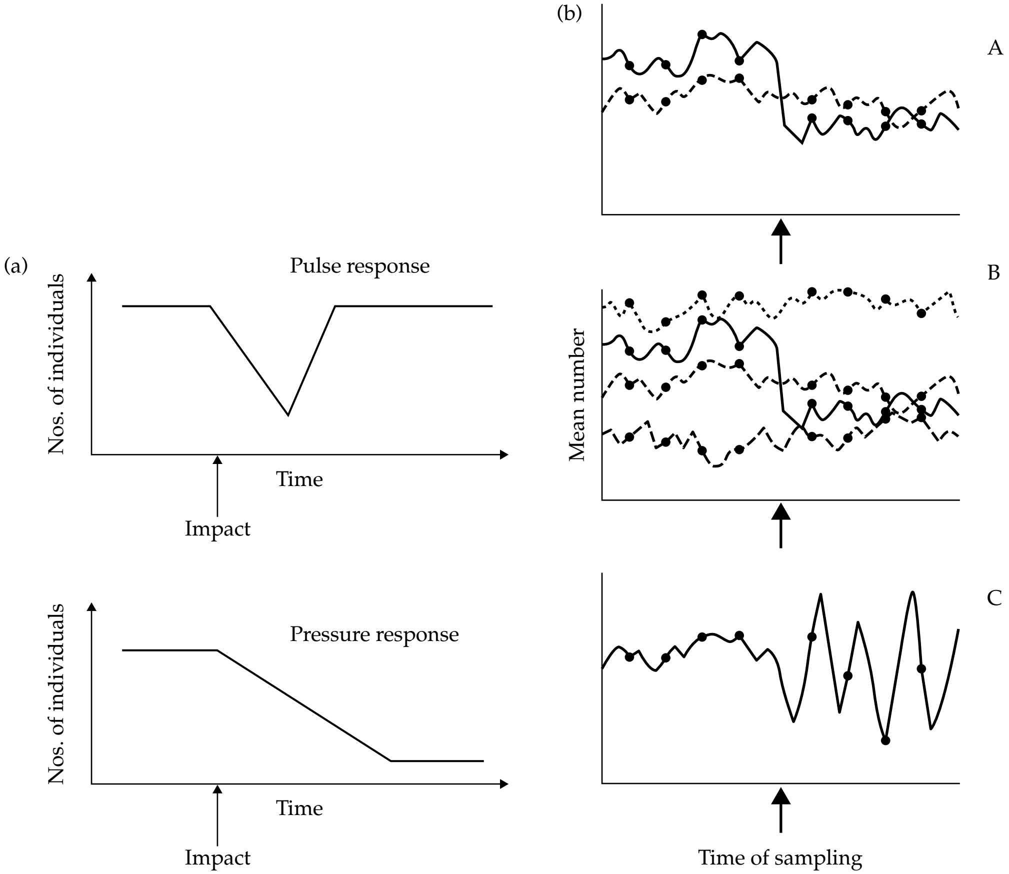


Figure 1.6 (a) Pulse and pressure responses to an impact, shown by the arrow. (b) A typical BACI design to measure responses (the impact is shown by the arrow). In A sampling is done at random temporal intervals before and after the manipulation (or impact of a pollutant) and in B at multiple control sites. C shows a third type of response that occurs frequently: the variance increases after the impact (modified from Underwood 1994).

sites. One is not sufficient; multiple control sites are essential, as in the design shown in Fig. 1.5 which always extends out beyond sites showing effects on each radius.

Another sampling design that has received much attention recently is the BACI-PS design (for the basis of this and further discussion see Schmidt and Osenberg 1996). In experimental studies, such designs are especially important since the aim is to distinguish effects due to the experimental manipulation from natural changes in the system studied. Responses to disturbances can be either a *short pulse response*, where the population (or other measured property) resumes its pre-disturbance level after a time, or a *pressure response* where there is a gradual decline over time (Fig. 1.6). In particular, there is a need for survey designs which adequately assess all the sources of error both within samples and between replicates and stations, hence there is an increasing move towards rigorous hypothesis testing using multiway analyses of variance. Underwood (1994, 1997) has developed such sampling designs further and provides details of the appropriate statistical analyses required to analyse such designs.

These, then, are some of the basic approaches to sampling design. Now we consider how to sample the fauna.

1.2 Sampling the fauna

Sampling intertidal beaches is relatively easy. The basic method is to remove sediment and then extract the animals by screening them from the sediment. Quantitative samples are taken by removing a given sediment area, usually 0.1 m^2 for macrofauna, and a 7 cm diameter coring tube is usually used for meiofauna (see Baker and Wolff 1987, Kramer *et al.* 1994 for methods). Within soft muddy sediments the fauna is usually so abundant that a small core will give an accurate estimate of the macrofauna, but in coarser sand and gravel sediments beach fauna may be so sparse that it requires either a large core or many more replicates, thus increasing the probability of detecting the rare occurrences.

When investigations of the subtidal sediment-living fauna first began, taxonomy was naturally the central interest and so large samples giving the widest possible variety of species were preferred. The cruise of HMS *Challenger* (December 1872–May 1876), perhaps the first wide-scale benthic sampling, searched for life in deep areas (down to 8185 m off the Philippines) and took almost 500 deep soundings at 362 stations; it was the first systematic use of dredges, corers, grabs, and trawls as well as giving information on currents, meteorology, and sediment distribution. The basic techniques used have changed little and the naturalist's triangular dredge was, and still is, one of the most effective tools for obtaining qualitative samples. In studies of the fauna of the deep sea, where obtaining one haul can take a whole day because of the long lowering and hauling time, a modified form of this dredge, the anchor-dredge, was widely used. An anchor-dredge has a base plate which controls the depth of penetration of the cutting edge; the bag is usually several metres long compared with the 1 m of the naturalist's dredge. Nowadays it is considered more important to obtain quantitative samples so the use of such 'primitive' methods is no longer usual.

Around the beginning of the last century attention turned to quantitative studies. Various grabs were produced (and many are still being produced) which sample a given area of sediment surface, usually 0.1 m^2. The size used was dictated not for biological reasons but by a compromise between obtaining sufficient sediment and unwieldiness of the grab. In fact there is no reason why the grab should cover 0.1 m^2 and for many purposes this size is probably not an appropriate sampling unit. One of the most widely used types is the *Van Veen grab*, some versions of which have long arms to increase its biting force (Fig. 1.7a, b and Plate 3). Other samplers such as the *Day grab* and the *Smith–McIntyre grab* are variations on the Van Veen but involve slightly different mechanisms for closing the jaws and also have a frame for stability of the seabed. All of these have top-opening doors in order to subsample or photograph the sediment (Eleftheriou and McIntyre 2005 give full details of these).

Although the Van Veen grab is still used in difficult sampling conditions (e.g. gravelly sediments or very compact sandy sediments), *box-corers* are now used more widely. The problems with traditional grabs of the Van Veen type are that the bite is often asymmetrical and that the depth of

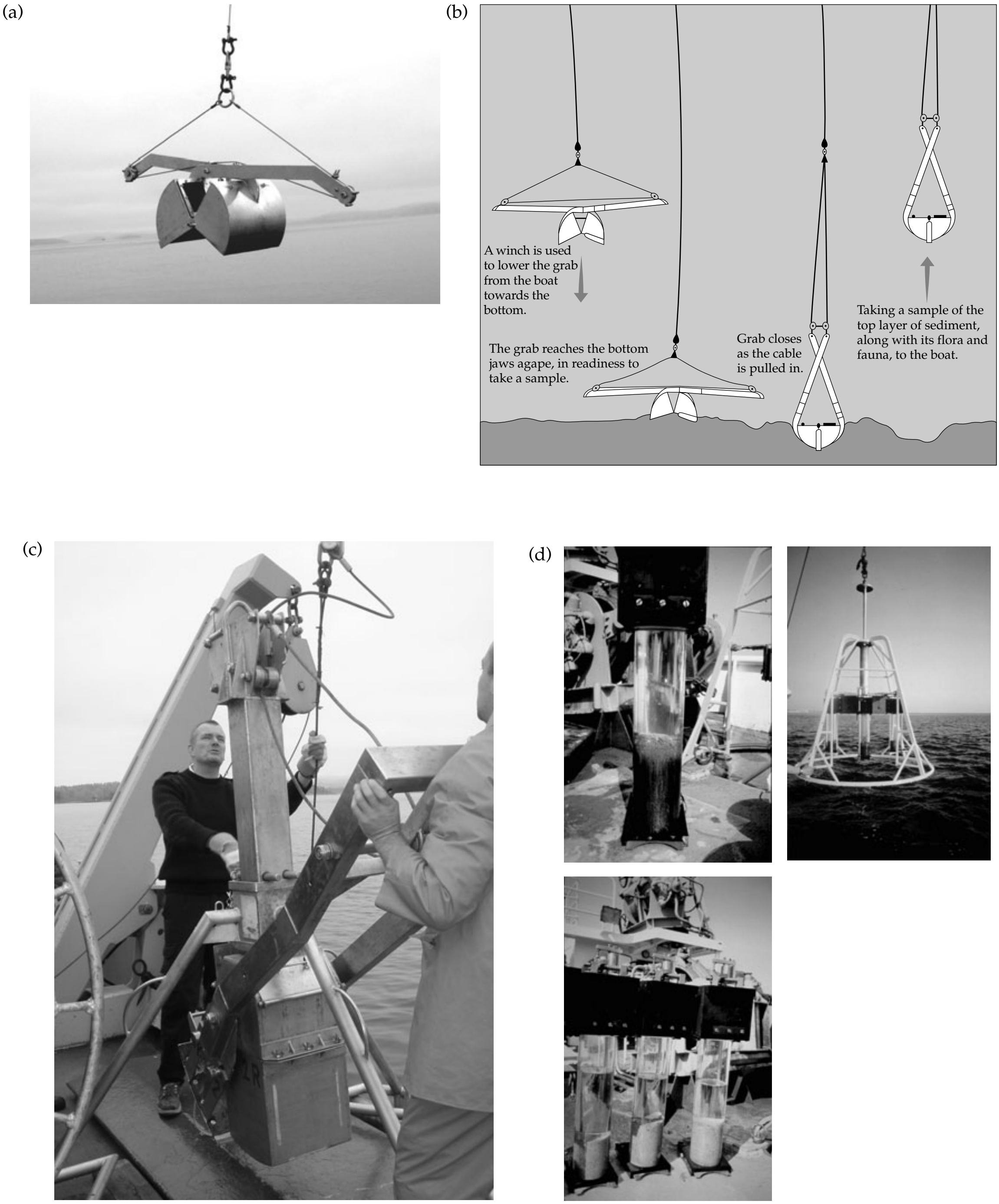


Figure 1.7 Modern sampling gear for subtidal benthos: (a) Van Veen grab; (b) operation of Van Veen grab; (c) box corer; (d) multicorer (in background) and multicore samples. (Photos a and c courtesy KC Denmark, Kenneth Christensen, Photos d courtesy of Victor Quintino, University of Aveiro, Portugal). See Plate 5.

penetration varies greatly with the sediment type. The box-corer takes a rectangular sample to a depth largely determined by the amount of weight attached to it. There is a swing arm which, when the corer is triggered, closes the sampler underneath and prevents the sample sliding out (Fig 1.7c and Plate 4). Box-corers are now widely used in both deep sea and shallow water for biological and geological studies. Most recently, a combined form of dredge and grab, the *Hamon grab,* takes a well-defined scoop volume and works well in gravel areas where the stones would otherwise prevent the jaws of a conventional grab from closing.

It was not until the 1950s that attention turned to the quantitative sampling of meiofauna and microfauna. The numbers of meiofauna and microfauna are usually two orders of magnitude greater than that of the macrofauna. Clearly then, special sampling techniques are needed for these faunal components. Grab samples covering 0.1 m^2 would be far too time-consuming to analyse, so smaller samples are taken, usually with a core. The size of the core depends on the fauna being sampled and its dispersion pattern; thus no general rules can be given except to say that the previously mentioned 7 cm diameter corer is an approximate universal size. Sampling the subtidal fauna can be done by taking samples with a multicorer, one type of which, the *Barnett multicorer* (Fig. 1.7d), has been used successfully in both shallow and deep-sea sampling. The sampler is lowered to the sediment, the cores are pushed slowly into the sediment by hydraulic means, and on hauling the ends of the core tubes are sealed. The samples are usually undisturbed, as can be seen by the surface floc visible through the transparent walls of the sampling cores. Such undisturbed cores can then be used to measure sediment parameters—physical, chemical, and biological—which change markedly with depth in the sediment. For example, changes in burrowing depth or redox potential will require an undisturbed sample. The multicorer's detachable core liners can then be brought into the laboratory on board or elsewhere and the sediment analysed. An alternative but much less recommendable sampling method is to take subsamples from a box-corer, but the sediment is often quite disturbed, and since the bulk of the meiofauna and microfauna lives in the uppermost few centimetres of the sediment, many can be lost if the surface material is washed away. It is better to take undisturbed cores by means of divers, if possible, but even then the problems can be severe; in fine muddy sediments (which are common) the diver has to be very careful not to stir up the surface layers.

The sample sizes given above are practical compromises between a range of competing demands for statistical precision, ease of manipulating often heavy gear on a rolling and pitching ship, and the time taken to sort large amounts of sediment. However, it should be remembered that no single sample size is appropriate for all quantitative ecological studies. Just because a grab is available that samples 0.1 m^2 does not mean that it is the correct sample size for the community or species under study. In general a large number of small samples are preferable to a small number of large samples, since for the same counting effort a greater spread of habitats can be covered and the number of degrees of freedom for statistical tests is increased, thereby reducing the error variance. However, if sample size becomes too small, edge effects of the sampler become important. So sample size is a compromise between all of these factors. Elliott (1993) gives a simple but nevertheless comprehensive account of general statistical problems of sampling and how to determine the appropriate sample size. In particular he discusses statistics denoting precision of the mean, thus giving a lead into power analysis (see below) which should be used to determine the number of replicates required based on the dispersion of the fauna being sampled.

Similarly, the number of samples to be taken in a given area to answer given objectives is often a compromise. The following example illustrates the sort of practical problems that occur. Ecologists are often interested in an estimate of how many species are in a given area (i.e. species richness) and thereafter how many samples are needed to sample the community adequately. Figure 1.8 shows a typical *species accumulation curve* obtained by pooling successive samples and determining the number of species in the pooled sample. The lower curve with 'steps' is obtained by plotting the cumulative number of species from the southernmost point

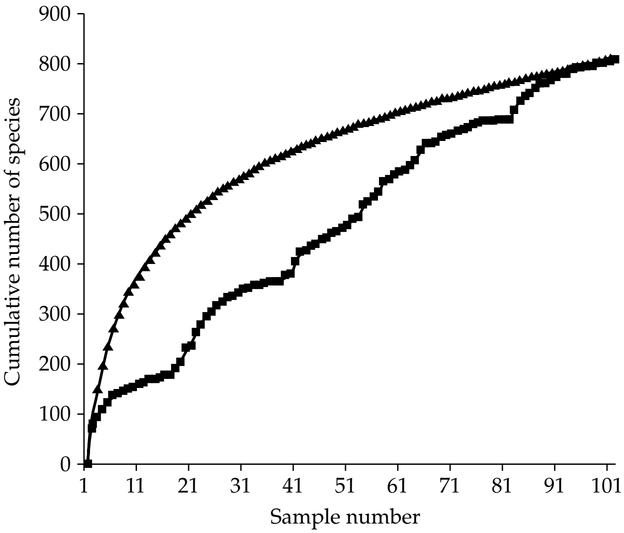


Figure 1.8 Species accumulation curve for the benthic fauna of the continental shelf of Norway derived using the analytical model of Ugland *et al.* (2003).

moving northwards. As a new region is sampled (there are five) there is a sudden influx of new species that are found initially before the curve levels off. The smooth curve is based on an analytical method developed in Oslo by Karl Ugland (Ugland *et al.* 2003; an Excel macro is available, see Gray 2005). Note there is a distinction between a species accumulation curve as shown here, where the newly discovered species are accumulated as the area sampled is increased, and a *species–area curve* which simply plots the number of species found in areas of different size. From the species–area curve it is impossible to tell whether the species are identical in two areas or completely different, as species identity is not recorded.

The number of samples taken is always a compromise between competing demands. First is the need to obtain a good description of the fauna. In the above example, to obtain approximately 90% of the species 30 m^2 of sediment needs to be sampled, giving 300 grabs of volume 0.1 m^2. Against this, one has to consider the cost of sorting and identifying all the species in the 300 samples.

A good example of a practical study of this kind is that of Ferraro *et al.* (1994) where the aim was to detect ecologically important impacts of pollutants on the benthic assemblages. They tested how the sampling design could be optimized taking into account the costs due to sampling, sorting, and identification of samples obtained using 14 sampling units (0.005–0.1 m^2 surface area) and two sieve mesh sizes (1.0 and 0.5 mm). An important point is that they used statistical power analyses. Readers should remember that there are two types of statistical errors: a *type I error* is rejecting a null hypothesis when it is true (false negative) and a *type II error* is accepting a null hypothesis when it is false (false positive). We guard against making a type I error by allowing 5% error due to chance (and as a result we set the statistical test α at a value of $p = 0.05$ for rejection of the null hypothesis). For type II errors, the criterion is usually set as $p = 0.20$ (or 80% certainty) since it has been found by practical experience that such a criterion gives a reasonable number of samples whereas a 90% criterion ($p = 0.10$) would mean taking an extremely large number of samples. Ferraro *et al.* (1994) used the well-known *t*-test of mean differences between samples as a measure of effect and estimated the minimum sample size ($n_{\min}$) needed to reliably reject the null hypothesis of no difference between a reference and a degraded station on 12 measures of community structure. The optimum sampling design for detecting impacts was determined as that with the lowest total cost $\times n_{\min}$ on most measures (where $n_{\min}$ is the calculated minimum number of samples). It was found that 5 replicate samples, 0.02 $m^2 \times 5$ cm deep, sieved on a 1.0 mm mesh screen, could reliably distinguish reference from impacted conditions on 10 measures of community structure. The cost of this sampling design was less than 25% of the cost of the standard sampling protocol (5 × 0.1 m^2 grab samples sieved on 1.0 mm mesh screens). Such pilot studies are essential since they set clear objectives and test the ability to detect change at a given level of statistical precision and power.

Although such statistical considerations are paramount, benthologists are usually constrained by the lack of funding and thus time to undertake fully statistically rigorous samples. It is then necessary to compromise between having sufficient replication at any site to allow statistical testing and having a wide enough coverage of sites to answer questions about the spatial patterns in the benthos. For example, both of us have used differing sampling patterns depending on the questions being addressed. In some cases, single samples per site have been used to good effect to describe wide-scale patterns (e.g. Elliott and Kingston 1987), whereas between 3 and 10 replicates per station have been used to enable statistical comparisons or to provide more material, e.g. for productivity studies (Elliott and Taylor 1989, Elliott and O'Reilly 1991). Similarly, when one of us (JSG) first came to the University of Oslo, the first study undertaken was to map the benthic fauna of the Oslofjord using the best methods available. We wanted to ensure that we obtained as many species as possible so we used a triangular dredge with a closed bag at one end. It dug deeply into the sediment and so we obtained good samples, but these were only semi-quantitative as we did not have an estimate of the exact surface area or depth sampled. Such methods are rarely used today and the tendency is now to use only quantitative methods (grabs or corers).

The sampling methods have to quantify, minimize, or explain all scales of variability in the benthos—within a station at a site, between stations within a site, between sites, between sampling occasions seasonally and annually, and between geographic areas. That inherent variability requires to be explained using sufficient replication although, as indicated above, the degree of replication depends on the spatial dispersion and frequency of the organisms being sampled. The variability of the primary (species richness, abundance, and biomass) and secondary or derived community parameters (diversity, evenness, abundance ratio, biomass ratio) can be described as the *% coefficient of variation* (the ratio of standard deviation to the mean) and of course varies greatly with the degree of heterogeneity of the area under study (for examples see Elliott and O'Reilly 1991, Edgar and Barrett 2002).

The problem with many of these techniques is that one may miss a large number of species. This came home to one of us (JSG) recently in taking a research group to the Pacific Ocean as part of a scientific expedition to census the marine diversity of the island of Santo, Vanuatu. The primary objective was to obtain all the species of molluscs and crustaceans that occurred there. All habitats were sampled, from the intertidal to several hundred metres depth, using every conceivable gear available. Particular attention was given to obtaining all the small species so typical of tropical areas. The group used mainly quantitative sampling using a box-corer, but the dredges on board the research vessel were used to supplement our samples. This type of exercise reinforces the message that to obtain all the species one must use a combination of gear. Grabs and cores alone are not sufficient if the aim is to estimate species richness—we hope that this lesson will be heeded in future studies aimed at assessing biodiversity!

Having mapped the areas to be studied and given consideration to the type of gear to be used and detailed sampling design, attention can be given to what properties of the sediment should be measured. As a guide for further studies, the excellent volume by Eleftheriou and McIntyre (2005) gives a full account of the methods of sampling the benthos. The volumes edited by Kramer *et al.* (1994) and Hiscock (1998a, b) also give the methods and approaches, but the latter has a particular emphasis on obtaining data and information for assessing the nature conservation importance of a marine area. We return to the topic of data analysis in Chapter 11.

CHAPTER 2

The sediment and related environmental factors

Our next major question is, how can we characterize the sediment as a habitat for biota? Marine sediments range from coarse gravels in areas subjected to much wave and current action, to muds typical of low-energy estuarine areas and to fine silts and clays in deep-sea sediments. The settling velocity of those particles and the ability of any particle to be re-suspended, moved, and redeposited depends on the prevailing hydrographic regime (e.g. see Open University 2002). The latter will in turn influence the transport of a species' dispersal stages, especially larvae which will then be allowed to settle following metamorphosis under the appropriate hydrographic conditions (defined as *hydrographic concentration*). Hence the presence of fine sediments will indicate the depositing/accreting areas which may also be suitable for passively settling organisms. Clearly the particle size is of major importance in characterizing sediments, although sediments can also be categorized by their origin (fluvial, biogenic, cosmogenic, etc.) and their material (quartz, carbonates, clays, etc.) (Open University 2002).

2.1 Grain size and related variables

On a typical sandy beach the coarsest particles lie at the top of the beach and grade down to the finest sediments at the waterline. The top of the beach is dry and there is much windblown sand, since coarse sands drain rapidly, whereas at the lower end of the beach the sediments are wet, with frequent standing pools. Coarse sediment is found at the top of the shore because as the waves break on the beach the heaviest particles sediment out first. Finer particles remain in suspension longer and are carried seaward on the wave backwash. Beaches change their slope over the seasons, being steeper in winter and shallower in summer. A greater degree of wave energy will produce steeper beaches, as particles are pushed up the beach and so may be stored there, whereas gentle waves produce shallow, sloping beaches. Waves hitting the shore obliquely will create sediment movement as longshore drift. Subtidally, waves are important in distributing and affecting sediments down to depths of 100 m, but the effect decreases exponentially with depth and so the dominant subtidal influences on sediment transport are currents. The type of deposit found depends on three main factors: *settling velocity*, which follows Stoke's law, the roughness of the sediment, and threshold velocity. Figure 2.1 shows the relationships between the important factors influencing the mobility of sediment particles. The *roughness* of the sediment is important as rough sediments are more easily picked up by currents flowing over the sediment than are smooth (round) particles. *Threshold velocity* is the force needed to pick up a particle when water flows over the sediment. The settled sediments may then be packed in a rhombohedral manner, with one particle nestling among others, or in cubic fashion whereby they sit on each other and thus require less energy to be moved (Open University 2002). If sediments are very fine or if they are of a mixed composition they pack more tightly, so that it is harder for water movement to pick up the particles, hence the reverse inflection in the curve. Curiously, particles 0.18 mm in diameter are the easiest to move. Particles coarser than this are difficult to pick up and transport because they are dense, whereas particles finer than 0.18 mm pack into a smooth bottom surface and are difficult to re-suspend. Thus a

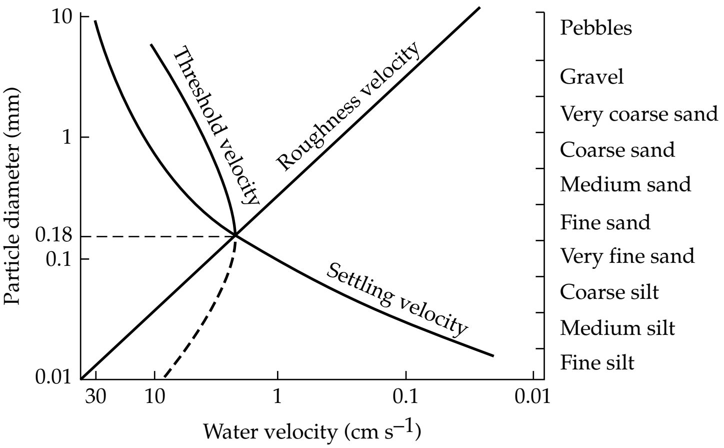


Figure 2.1 Key factors influencing mobility of sediment particles. Settling velocity follows Stokes' law. Roughness velocity is the velocity needed to transport particles of different sizes and threshold velocity is the flow needed to pick up particles from the seabed.

sediment composed largely of particles around 0.18 mm diameter can be expected to be the most stable of all, since where such sediments occur wave and current action must be minimal. With an increasing percentage of muds, the sediment becomes increasingly cohesive and thus requires an even greater force to re-suspend or erode the particles. The stability of the sediment is a major factor affecting the types of animals present in the sediment. Clearly then, *grain size*, measured as median particle diameter, is a key property. However, cohesiveness reaches a maximum in hard-packed glacial clays, to such an extent that we can regard these not as sediments but as a hard substratum colonized only by boring organisms.

In general, coarse intertidal sediments drain fast and retain little water or organic matter. They are therefore inhospitable habitats, or at least inhabited only by those species able to tolerate such mobile sediments, such as magelonid polychaetes and fast-burrowing venerid bivalves. At the other extreme, very fine sediments such as muds, which have grains tightly packed together, may preclude the presence of a meiofauna inhabiting the pore spaces between grains (interstitial fauna). They also have poor water circulation and often low oxygen tension, because there is only a small exchange of overlying oxygenated water, and any oxygen that diffuses into the sediments is rapidly used up by the aerobic bacteria and micro- and meiofauna. In addition, a greater amount of organic matter settles out in the same area as fine muds, again increasing the oxygen demand. Medium and fine sands usually have an abundant meiofauna and macrofauna, but because muds have more organic matter per unit area faunal densities are frequently highest here. As we discuss later, in muds and sandy muds the macrofauna create their own environment by burrowing into the sediment and thus increasing contact with the overlying waters.

2.1.1 Measuring grain size

The traditional method for analysing grain size is as follows. First, the silt–clay fraction is separated from the sand by use of a 0.062 mm screen, since different methods are used for the analysis of sands (coarser than 0.062 mm) and of silts and clays (finer than 0.062 mm). Sands are dried and sieved on a series of screens that usually follow a decreasing geometric scale, the *Wentworth scale*, which covers 32 mm, 16 mm, 8 mm, 4 mm, and so on down to 0.062 mm, which is then by convention transformed to the arithmetic phi (ϕ) scale. The latter is defined as the $-\log_2$ of the size in mm, hence 2 mm is -1ϕ, 1 mm is 0ϕ, 0.5 mm is $+1\phi$, etc. Table 2.1 shows the conversion.

In order to give sufficient points on plots of grain sizes, a half-phi scale is recommended. Sediment finer than 0.062 mm is analysed by various methods such as pipette analysis which is based on sedimentation rates in cylinders containing fresh water maintained at a constant temperature. The settlement rate is calculated on a decreasing scale of particle size and a pipette sample removed at various time intervals relating to the settlement velocities of the differing particles. The finer fraction may also be analysed by electronic counters or laser granulometry. The data obtained from both the sieve and finer analysis are in the form weight-per-size interval and although the distribution of particle sizes is continuous, discrete data are obtained.

Table 2.1 Description of sediments in mm and the phi scale used by geologists

Sediment description	Lower border (mm)	Lower border phi ϕ ($-\log_2$ mm)
Pebbles–boulders	>4.00	<–2
Granule	4.00	–2
Very coarse sand	2.00	–1
Coarse sand	1.00	0
Medium sand	0.50	1
Fine sand	0.25	2
Very fine sand	0.125	3
Silt	0.0625	4
Clay	<0.0039	>8–14

The simplest descriptive measure of a sediment is the *median particle diameter* (MPD). Sediment samples are, however, very rarely made up of a single homogeneous sediment type and mixtures of grain sizes are usual; a constant, uniform hydrographic regime with a uniform sediment supply may create a homogeneous sediment type, such as on some beaches. The degree of mixing of the different types can be represented by a *sorting coefficient*. Well-sorted sediments tending towards homogeneity are typical of area with high wave and current activity (high-energy areas), whereas poorly sorted sediments are heterogeneous and are typical of low wave and current activity (low-energy areas).

Figure 2.2 shows typical data for a sand sample, where the data are first expressed (a) as percentage dry weight of each fraction. Plotting as a cumulative percentage gives a sigmoid (S-shaped) curve

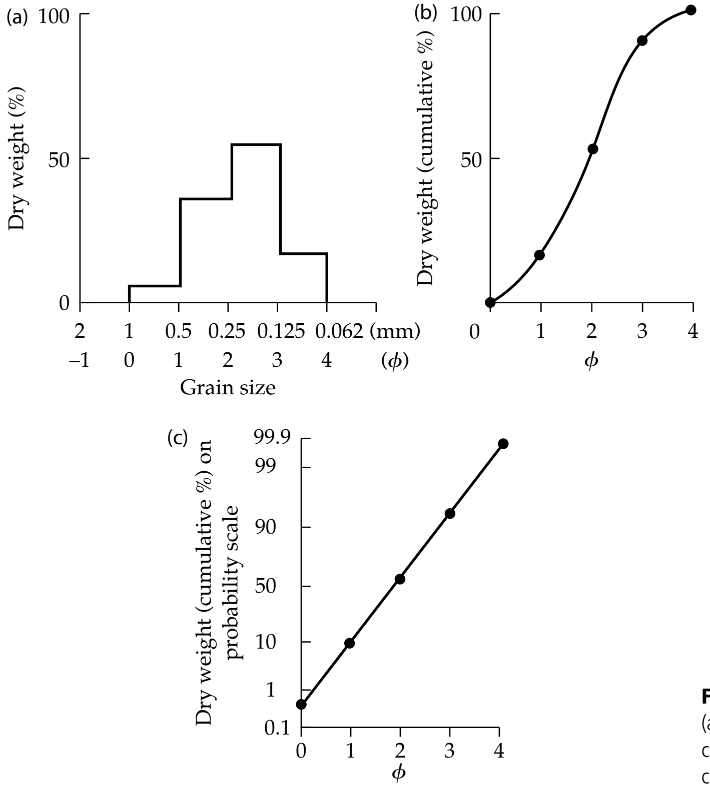


Figure 2.2 Determination of sediment properties: (a) grain size distribution of dry weight sediment; (b) cumulative dry weight sediment; (c) probit plot of cumulative dry weight sediment.

(b) and using a probability scale a straight line is obtained (c). From this the median particle diameter can be obtained as the 50% point and the ϕ percentile values for 84% and 16%, etc., can be read from the graph.

A measure of sorting, the *sorting coefficient* or *graphic standard deviation* (σ_g), is simply $(\phi_{84}-\phi_{16})/2$. A better index is the *inclusive graphic standard deviation* (IGSD, σ_1), given by the formula:

$$\frac{\phi_{84}-\phi_{16}}{4}+\frac{\phi_{95}-\phi_{5}}{6.6}.$$

The ϕ_{84} and ϕ_{16} values are one standard deviation (SD) from the mean, whereas the 95 and 5 percentiles cover 2 SD. This formula then covers over 90% of the distribution and is therefore preferred to the GSD. Table 2.2 shows the descriptions of sorting based on the IGSD. Although it is important to understand both the main descriptors of sediment and the nature of the measurements being made, today there are modern laser-based instruments for doing such analyses automatically, and these are widely used for routine analyses of many samples. Plots are obtained automatically giving summaries of the data, such as median particle diameter and sorting, although now these are calculated by the method of moments rather than by reading off cumulative percentage frequency curves. Grain size and sorting can vary over distances as small as a few centimetres, so in studying meiofaunal distribution patterns it is often necessary to record the fauna and grain size on the same sample. With macrofaunal studies a single sample of 50–100 g taken from the faunal grab is widely used for assessing grain size, again producing synoptic data.

Table 2.2 Sorting classes calculated from the inclusive graphic standard deviation (IGSD)

<0.35 ϕ	Very well sorted
0.35–0.50 ϕ	Well sorted
0.50–0.71 ϕ	Moderately well sorted
0.71–1.00 ϕ	Moderately sorted
1.00–2.00 ϕ	Poorly sorted
2.00–4.00 ϕ	Very poorly sorted
>4.00 ϕ	Extremely poorly sorted

2.2 Other important environmental variables

Grain size and sorting are probably the two most important characters that can be measured on sediment samples, but other biologically important physical properties include *porosity* (the size of the available pore space and thus the amount of water being retained in a waterlogged sediment) and *permeability* (the amount of water that can flow through the pores), which are particularly relevant for meiofaunal studies (Eleftheriou and McIntyre 2005 gives further details of the methods). Many of the sediment parameters are linked, and follow from the hydrodynamic regime—this influences the particle size and degree of fine particles and the sorting nature of the sediment (Fig. 2.3). In turn these affect the porosity and permeability which, with the compaction, influence the water movement through the sediment. These in turn influence the oxygen content and salinity and then the sediment chemistry (e.g. redox potential). The hydrodynamic nature and sediment type affect the organic nature of the sediment, which also influences the chemical nature (see Elliott *et al.* 1998 for further details). Figure 2.3 gives the relationships for a low-energy, muddy area but the opposite trends can be seen to occur in a high-energy, coarse (sandy) sediment area.

Light is a key factor that affects intertidal and shallow marine areas. Because of the nutrients in the overlying water column and in pore water, such sediments have an abundance of small plants, the *microphytobenthos* (benthic microalgae) which consists of unicellular eukaryotic algae and cyanobacteria that grow within the top few millimetres of illuminated sediments (e.g. see MacIntyre *et al.* 1996). These plants can often be seen as a brownish (e.g. diatoms) or greenish (e.g. euglenoids) tinge to the surface of intertidal sediments, and in shallow areas of the coast the biomass of benthic microalgae can exceed that of the phytoplankton in the overlying waters. In addition to the mat-forming species, there are many free-living species which move up to the light during daylight but may migrate deeper if the insolation is too strong. The organisms photosynthesize during light periods and the oxygen concentration in superficial sediments may be raised above that from simple

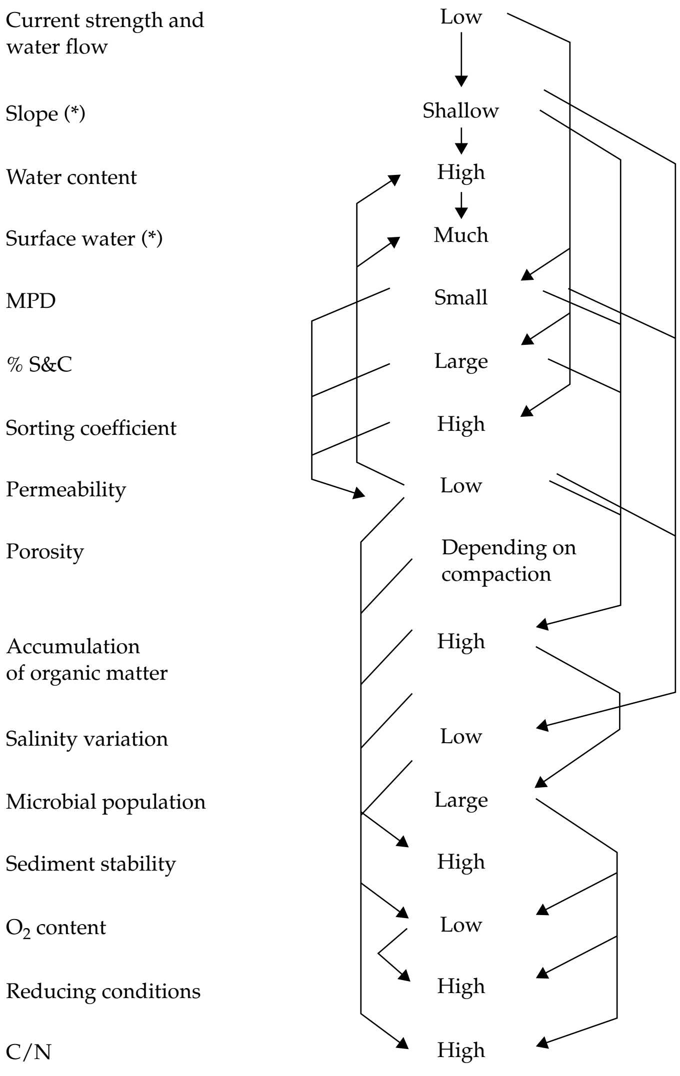


Figure 2.3 Relationships between the main sediment physicochemical parameters for a low-energy area (* denotes intertidal feature) (modified from Elliott 1979, Elliott *et al.* 1998).

diffusion processes. At night the plants respire and carbon dioxide is produced into the surface waters and atmosphere. Oxygen concentrations in sediments are measured using microelectrodes; huge technological advances have been made here in recent years, especially in the small size of modern electrodes. In Fig. 2.4 typical oxygen profiles for dark (night) and light (day) are shown, together with the main types of organisms and chemical processes that occur within the top few centimetres of an intertidal mudflat (here from a bay in Denmark) showing the microphytobenthic algal and bacterial communities. The depth of the green (photosynthetic) layer is determined by light penetration and contains cyanobacteria and photosynthetic eukaryotes (diatoms, dinoflagellates, cryptomonads, and euglenoids). Beneath this layer one often finds a dark blue-green layer of filamentous cyanobacteria (*Phormidium* and *Oscillatoria*) which bind the sand grains together. Beneath this there is a pink layer of the purple bacterium *Chromatium*, and *Thiocapsa* and chemolithic bacteria such as *Beggiatoa* which oxidize sulfides to elemental sulfur; the latter is deposited inside the cells of *Beggiatoa* and *Chromatium* but outside the cells of *Chlorobium*. Surface sediments are prone

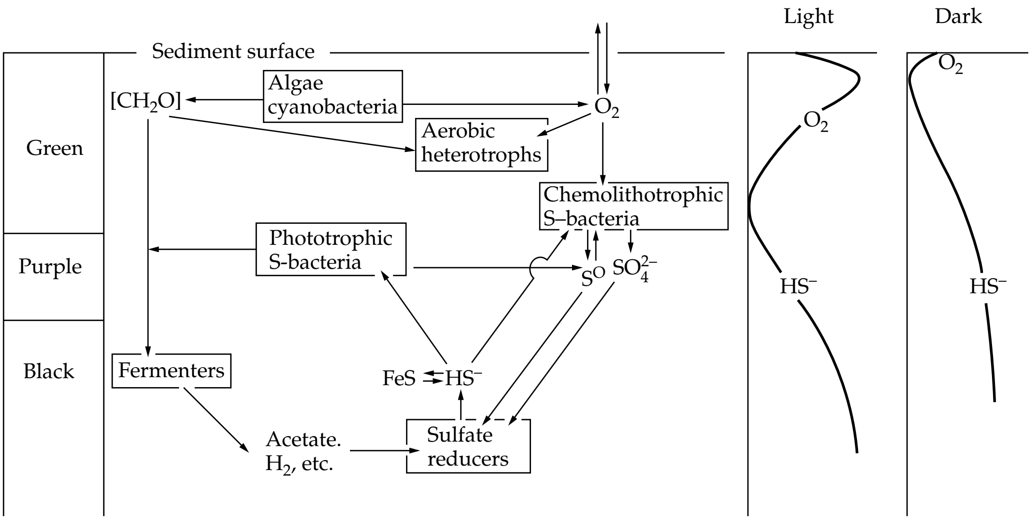


Figure 2.4 The quantitatively most important pathways of carbon cycling in a microbial mat. The microorganisms migrate according to the light available, as do the chemical processes that they control (from Fenchel and Finlay 1995).

to be disturbed by wave and current action and so the microphytobenthos may be spread evenly through the surface layers of sediment. The top few millimetres of the sediment thus constitute a zone of intense microbial and geochemical activity. In the bacterial assemblage below the purple layer the sediment is black and anaerobic; here the methanogenic fermenters and sulfate reducers dominate, and under certain conditions the rotten-egg smell of hydrogen sulfide can be detected as it is released to the air. Under extreme circumstances, methanogenic bacteria are in abundance and produce methane (CH_4).

In near-shore environments the organic content of the sediment typically increases with the fineness of the deposit, since particles of sedimenting organic matter behave in the same way as sediment particles (although, of course, their specific gravity is lower). There are two main sources of organic matter: that deriving from marine production and that from terrestrial material brought to the sea by rivers and streams. One of the commonest ways to distinguish between these two sources is to determine the ratios of isotopes of carbon, $^{13}C/^{12}C$. Other methods involve using high-performance liquid chromatography (HPLC) for analyses of the fatty acids and sterols contained in the material. Using compound-specific stable isotopes it has recently become possible to obtain a greater understanding of the flow of carbon through the microbial food web (see Boschker and Middelburg 2002).

Below the surface of the sediment, too deep to be affected by light, the sediment is brown in colour where oxygen occurs, and there is usually a thin grey layer before the deeper anaerobic black layer. In anaerobic sediments the major processes are sulfate reduction and methane production, and since there is a high concentration of sulfate in seawater, sulfate reduction dominates (90–99% of anaerobic mineralization). Sulfate reducers are also superior competitors to the methanogens and so can grow at lower sulfate concentrations than methanogens. The complete mineralization of 1 kg of organic matter yields 570 g of hydrogen sulfide (Fenchel and Finlay 1995). As the toxic gas diffuses upwards it is oxidized by the chemolithotrophic and phototrophic sulfur bacteria when light is present, so little enters the water column or atmosphere. Anoxic sediments have a complex biogeochemistry (as shown by Libes 1992), and it becomes important to understand the relationships between the physical, chemical, and biological sedimentary variables as these are all interlinked as shown in Fig. 2.5 (Elliott and Mazik, unpublished).

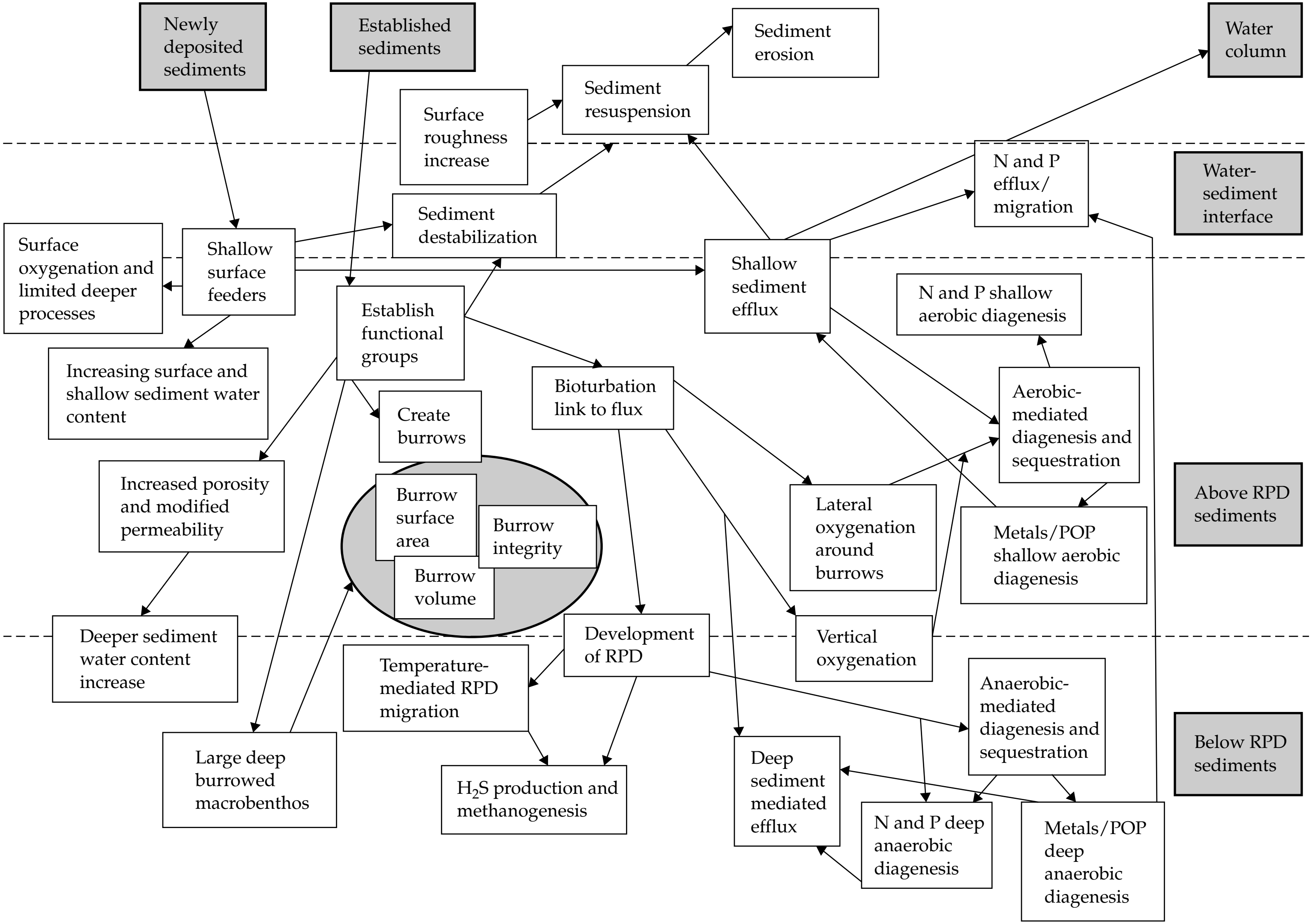


Figure 2.5 The relationships between the ecological, biogeochemical, and sedimentological features of sediment modified by bioturbation (from Elliott and Mazik, unpublished).

Figure 2.6 shows an image from an SPI camera where the black sulfide layer is clearly seen. The streaks of light-coloured sediment running down into the black are the result of smearing by the glass plate penetrating the sediment, as well as being formed by organisms bringing oxygen into deeper layers by creation of burrows or by tube-dwelling species pumping oxygen to deeper layers.

Molecular techniques may revolutionize our understanding of the types and amounts of bacteria occurring in marine sediments. The traditional methods were to culture living bacteria on agar plates, but it was widely accepted that at most 10% of the available bacteria could be grown. Specific staining techniques allow one to laboriously count the bacteria and by using thymidine incorporation into DNA it is possible to estimate the production rates of bacteria (Finlay *et al.* 1984). Now it is possible to section sediment into slices at different depths, isolate bacterial DNA, and then use 16S rDNA to identify the types of bacteria and archaea present (e.g. Fry *et al.* 2006). Wider use of these techniques is likely to bring great advances in our understanding of the processes controlled by bacteria and archaea and the relationships between them and the meio- and macrofauna.

Figure 2.6 SPI image of sediment from a subtidal area showing oxygenated (brown layer) and anaerobic (black layer) with stripes showing where burrowing organisms have altered the oxygenation of the deep layers (courtesy SAIC, Newport, RI). See Plate 6.

A number of species that live in sediments can utilize sulfide as a source of energy. Bivalves of the genus *Thyasira* are good burrowers and are able to take up free sulfide deep in the sediments since they contain chemoautotrophic sulfur-oxidizing bacteria in their gills (Dando *et al.* 2004). A remarkable adaptation was discovered in such sulfide-utilizing species by Giere and co-workers (see Giere and Langheld 1987), who found that a number of meiofaunal species lacked guts. In a study of the oligochaetes *Phallodrilus leukodermatus* and *P. planus* from Bermuda they found that the oligochaetes acquire food resources by having symbiotic bacteria in their bodies. The organisms become infected immediately at oviposition by two species of Gram-negative bacteria, from large 'stores' of bacteria found in a genital pad abutting the female pores. Older worms harbour mainly extracellular prokaryotes underneath their cuticle. The thick epidermis/cuticle complex is differentiated into regular zones and in the deeper layers bacteria are enclosed and digested intracellularly.

The sulfide system occurs in almost all marine sediments, thus being important in one of the largest environments (see review by Fenchel and Riedl 1970). Yet the significance of the sulfide system and the adaptations of the fauna to living in such a hostile environment were not fully appreciated until the deep-sea hot (hydrothermal) vent fauna was discovered. These vents are areas where hot water rich in sulfides and other minerals seeps from beneath the seabed in areas such as the mid-Atlantic ridge. The fauna of the hydrothermal vents also derives its primary energy source from oxidation of sulfides by the use of chemosynthetic bacteria. These organisms can be large: the tubeworm *Riftia*, belonging to the group of worms known as Sibloglinidae, which has chemosynthetic symbiotic

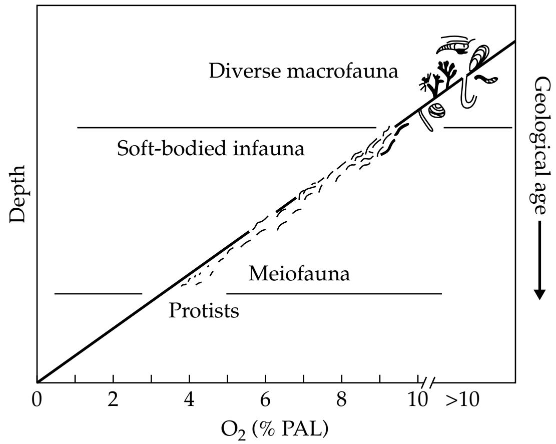


Figure 2.7 Oxygen concentrations and types of fauna that dominate suggesting the evolutionary origin (from Fenchel and Finlay 1995).

bacteria in its tissues, can be over 1.5 m long (see Gage and Tyler 1991 and Hsü and Thiede 1992 for a full coverage of the deep sea and its fauna).

Finally, it is useful to give an evolutionary perspective on sediment properties. Fenchel and Finlay (1995) point out an interesting parallel between the oxygen concentration of the earth's early atmosphere and the types of fauna present. The first metazoans were microscopic forms comparable with modern turbellarians, gastrotrichs, nematodes, and rotifers. As oxygen concentration increased, so the size of some groups increased (Fig. 2.7). Among the earliest metaozoa for which a fossil record exists are the famous Ediacarian fossils in Australia which include annelids and coelenterates as well as many other groups that are now extinct.

2.3 The fauna and environmental variables

2.3.1 The niche of a species

It is necessary to describe the nature of communities and ecosystems in terms of structure, i.e. their characteristics at one time, and function (by definition including rate processes). The most obvious way to unravel the factors influencing species in a community is to study a single species at a time. This is an *autecological* approach which was popular in the 1960s and 1970s, but more recently it has largely been replaced by studies of whole assemblages or system-level studies. However, autecology still has a place in modern approaches, combining the use both of fieldwork to analyse the distribution of the animals in relation to measurable environmental variables, and of laboratory experiments to determine the responses of the animals to these variables. Such information is important, as it is always a matter of concern that we know so little of the biology of most of the thousands of macro- and meiofaunal organisms. By tradition, the typical benthic ecological approach has been to concentrate on the responses of the organisms to physicochemical variables of the environment and usually to the tolerance responses of organisms to these variables. Yet preference experiments give a more accurate picture of the likely responses of organisms to environmental factors. As an illustration of this approach, the factors controlling the field distribution pattern of the meiofaunal polychaete, *Protodriloides symbioticus* (Giard) are used (Gray 1965, 1966a–d).

2.3.1.1 Defining the niche of a species

Protodriloides symbioticus is 2 mm long and lives in large numbers between sand grains on intertidal beaches of Europe. The population studied in Wales occurred in dense patches on an apparently uniform beach. The problem was to unravel the factors that gave rise to the pattern. In laboratory experiments *P. symbioticus* tolerated salinity extremes of 18–55 PSU for 12 hours and temperatures of −4 °C to +34 °C. Observations in the field over a 2 year period showed that natural variations in salinity and temperature were well within these limits. When given a temperature gradient of 5 to 25 °C, *P. symbioticus* always chose 15 °C. Thus in response to sand temperatures that were too warm or too cold, individuals would migrate to a preferred range. Yet counter-balancing this response are the worm's reactions to light and oxygen. From laboratory experiments it was found that *P. symbioticus* has a preferred illumination range which under natural conditions would keep the species at a depth of 4–5 mm below the sediment surface. In oxygen gradient experiments, however, the organisms always preferred the area of maximum saturation, which on the beach is at the surface. This oxygen response over-rides the temperature response. Thus a combination of these responses explains the vertical distribution of the individuals in the sediment. Figure 2.8 illustrates these responses diagrammatically for summer conditions. The same sorts of responses will be found with almost any species investigated, but of course most species will have different preferenda. The generality of such responses was appreciated many years ago in terrestrial ecology and has resulted in the theories of the *niche*.

The historical debate on the niche concept will not be discussed but interested readers are referred to the review of Vandermeer (1972). The most widely accepted view is that of Hutchinson who divided the niche into two parts. The first of these is the *fundamental niche*, which contains the full range of environmental conditions under which a species *can* exist (see Fig I.6, where the features that create the water column and sedimentary fundamental niches are indicated). No species in fact ever occurs over the full range of the fundamental niche but is restricted to a part of the area. This is called the *realized niche* and is defined as that area where the species *does* exist. The constriction of the fundamental niche is due in part to preferenda and tolerances for certain environmental conditions and in part to the effects of biological interactions such as competition and predation which prevent a species from occupying the whole of its fundamental niche. The actual number of dimensions that defines the niche for any species is the number of environmental variables that affects that species, and hence Hutchinson's idea has been called the *n-dimensional niche hypothesis*. The niche space can never be determined for a species since no one can ever be sure that all the appropriate dimensions have been measured. However, the hypothesis has proved extremely useful in the study of the factors affecting the distribution of species.

In the case of *P. symbioticus* the fundamental niche dimensions for temperature and salinity are −4 °C to +34 °C and 18–55 PSU respectively. But the organism's preferred temperature of 15 °C, together with the responses to light and oxygen, greatly reduce the fundamental niche space. The actual realized niche, however, is an even smaller part of the potential fundamental niche so far described.

In the field, the *P. symbioticus* population was localized in patches in narrow areas at mid-tide level. It seemed probable that variations in grain size could influence the organisms, if they could in fact choose between different sizes. Figure 2.9 illustrates the results of such a choice experiment. It shows that the fundamental niche of *P. symbioticus* has dimensions not only of salinity, temperature, light, and oxygen but also of grain size, since at the top of the beach particles coarser than the optimum 0.2–0.3 mm are present and at the lower end of the beach there are finer particles. Yet even within the favoured size range *P. symbioticus* occurred not in a uniform distribution but in patches.

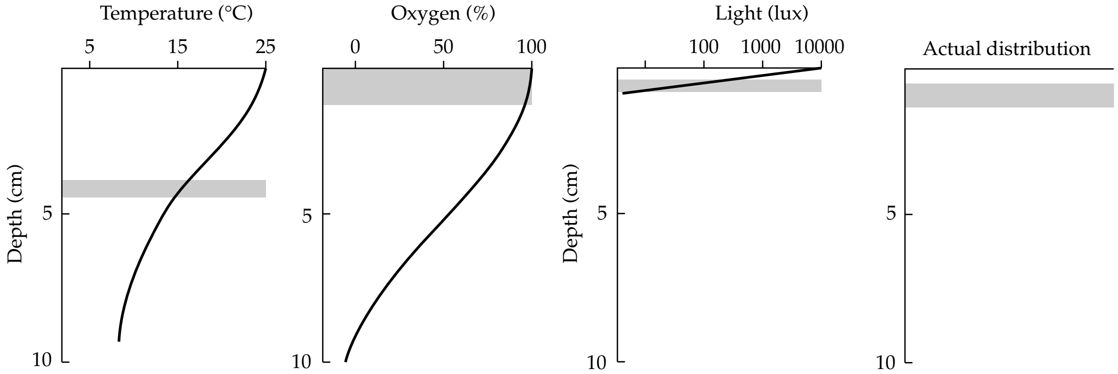


Figure 2.8 Responses of the meiofaunal polychaete *Protodriloides symbioticus* to environmental gradients occurring in sediment. Oxygen is the most important environmental variable (from Gray 1965, 1966 a–c). The shading represents the optimal conditions and actual distribution of the species.

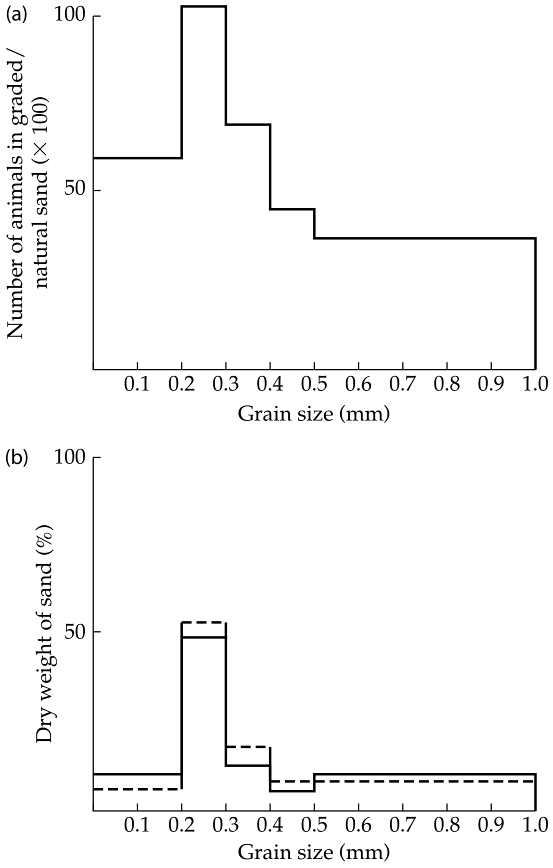


Figure 2.9 (a) Results of an experiment giving the meiofaunal polychaete *Protodriloides symbioticus* a choice of grain sizes in a multiple-choice experiment. (b) The distribution of the grain size in two samples from the field where *P. symbioticus* was abundant.

Sands from 10 localities which had contained varying abundances of *P. symbioticus* in the field were, after removing the individuals, used in a multiple-choice experiment. The results indicated that the order of preference corresponded to the abundances of the animals in the field samples. Certain sands therefore had an inherent attractive property. After a series of experiments, it was possible to show that this property was related to a favourable species of bacterium. *P. symbioticus* could distinguish between different species of bacteria and was localized in patches in response to the distribution of bacteria. Work on another meiofaunal species, done in collaboration with a bacteriologist, suggested that detection of the favoured species was by a tactile chemical response to the bacterial cell walls. *P. symbioticus* does not give off a chemical which attracts other individuals to a certain place. Subsequent to this work, it was found that *P. symbioticus* will not enter sands that have contained the gastrotrich *Turbanella hyalina*. The avoidance is a response to a chemical produced by *T. hyalina*, which thus restricts potential niche space for *P. symbioticus* by interference competition.

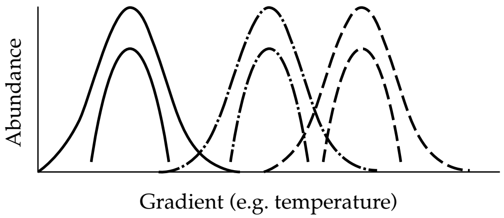


Figure 2.10 Fundamental (upper curve in the three sections) and realized niches (lower curves in the three sections) for three species along an environmental gradient (from McGill *et al.* 2007).

The above experiments have shown that the realized niche of *P. symbioticus* is only a very small part of the original fundamental niche described by tolerance responses and illustrate the importance of preference experiments and the experimental approach as tools in unravelling niche dimensions. Although the references to such research date from the 1960s, there has been a recent revival in interest in fundamental and realized niches by combining them with gradient analyses and functional attributes of species such as performance indicators and biological traits (e.g. Cheung *et al.* 2008).

Figure 2.10 shows fundamental and realized niches for three species along an environmental gradient. Each species has a specific preference along the gradient (e.g. temperature in the example, but for sediment this would more easily translate to grain size) and realized niches are narrower than fundamental niches due to niche overlap. McGill *et al.* (2007) call the two aspects illustrated in Fig. 2.10 *environmental gradients* and the *interaction milieu*. The gradient part is self-explanatory and has been discussed above; the interaction milieu covers the biotic interactions that constrain the fundamental niche to the realized niche. This was investigated in the 1960s by studies of pairwise interactions between species, but it is now recognized that most interactions between species are diffuse and hard to study. Thus McGill *et al.* suggest modelling a milieu or biotic background using traits that are important for a given interaction yet give an operational definition of the milieu. As an example they suggest that a histogram of heights of individual plants at a given site gives a first approximation of the competition for light milieu.

In this chapter we have examined the descriptive phase of sediment ecology dealing with the physical environment and what environmental variables are important and then how the distribution of fauna can be presented. This is, however, a rather 'static' approach and is merely descriptive. In the next chapter we discuss how assemblages of species can be described.

CHAPTER 3

Describing assemblages of sediment-living organisms

One of the most fruitful aspects of ecological research is the search for common patterns in the bewildering variability of nature. Given current concerns about global warming, climate change, and habitat degradation, the determination and protection of biodiversity has become paramount. There are essentially three ways of describing an assemblage of organisms, and each of these gives more information on the patterns and interrelationships. First, we have the classical *taxonomic* method of identifying all species in the assemblage, to the highest taxonomic separation possible (usually to species) and then counting the abundance and weighing the biomass of each taxon. Secondly, we can determine the *size and/or biomass spectra* of all organisms in the assemblage irrespective of their identities, on the basis that organisms of different sizes or body weights play a different role in the ecosystem. Thirdly, we can determine the role that each organism can play in the system, again irrespective of its name, and define these as *ecological groups or guilds*—hence separating those feeding in different ways or those building tubes from their free-living associates (e.g. see Elliott *et al.* 2007 for a discussion of the guild concept).

There are many methods of analysing assemblage data; for example Elliott (1994) identified over 25 groups of techniques for macrobenthic analysis (these are mentioned throughout this book and summarized in Chapter 11). Using these methods, when considering assemblages of marine organisms living in sediment, we can ask if there are any 'rules' that can be applied to patterns of abundance, size, and biomass distributions and how data on species distributions can be organized. Here, we first treat abundance, then size and biomass spectra, and finally how species assemblages can be assessed. Another way of describing assemblages is to examine the number of species and how abundance is distributed among species, although these are aspects of species diversity which will be addressed in the next chapter.

3.1 Abundance models

In any sample of a biological community, whether marine, terrestrial, or freshwater, the immediately observable pattern is that most species are rare, represented by one or a few individuals, and only a few species are very common, represented by many individuals. Research on this topic began in the 1930s when the Japanese biologist Motomura (1932) first described a model for assemblages which he called the *geometric series*. Then in the 1940s the great British statistician R.A. Fisher teamed up with two biologists, Corbet and Williams (Fisher *et al.* 1943) to analyse the patterns of the distribution of individuals among species in butterflies observed by Corbet in Malaysia. They produced a model of the frequency distribution called the *log-series*. Following this there was a flurry of interest in testing fits to the model and other models were derived, notably the *lognormal model* of Preston (1948). The original models were simply statistical descriptions of the frequency distributions and it was Robert MacArthur (1957) who first derived models that were based on ecological theory, giving rise to the *broken-stick model*.

Following these early papers there was sporadic interest in such models, notably in the 1970s when attempts were made to use departure from a lognormal distribution as an indicator of environmental disturbance in marine assemblages (Mirza and Gray 1981). Thereafter followed a lull until 2001 when a terrestrial ecologist, Steven Hubbell, developed a completely new model called the *zero sum multinomial* (ZSM) distribution to describe the abundance distribution of tree species in tropical rain forests (Hubbell 2001). Hubbell's work has revived interest in *species abundance distributions* (SADs) and there is much dispute as to whether the ZSM fits real data better than the older lognormal model. Magurran (2004) has summarised this research and gives details of how all these distributions can be fitted, providing a thorough description and analysis of all the models and their background which will not be repeated here. Instead we give a brief outline of methods that can be used.

There are two common ways of expressing such patterns: as a rank of abundance from the most to the least abundant species, or as a frequency distribution of the individuals per species plotted against the number of species.

3.1.1 Ranked abundance models

Rank abundance plots were first used by Whittaker in the 1960s (see Whittaker 1965 for a good account). In these plots a sequence of the species is plotted from the most to the least abundant, usually using a $\log_{10}$ base. Typical plots for some marine data are shown in Fig. 3.1, which illustrates two very simple models: the geometric series (Fig. 3.1a) and the broken stick (Fig. 3.1b). In relation to the biology of SADs the geometric series has been found to fit data from simple assemblages with few species, such as the flora of mountain tops or the benthos of a highly disturbed part of the Oslofjord, Norway. The broken-stick model, although fitting some real field data, proved to be unrealistic and was even abandoned by MacArthur. Rank abundance plots give an easily understood representation of the patterns and have been successfully used to follow changes in succession. More complex models such as the log series and the lognormal can be fitted to rank abundance data. It is possible to fit the exact models to the data, and Wilson (1991) gives methods.

3.1.2 Distributional models

The lognormal has been used as a universal model for SADs as it has been found to fit a wide variety of data (see Limpert *et al.* 2001 for a review). Preston (1948) derived the lognormal by dividing the abundances of individuals among species into what he called *octaves*. He argued that one would obtain a normal distribution of individuals among species if the individuals were grouped into doubling bins, e.g. 1, 2, 4, 8, 16,... The problem with this is that species that have exactly 1, 2, 4,... individuals fall on the bin boundary. He solved this problem by dividing the species between the bins. If 10

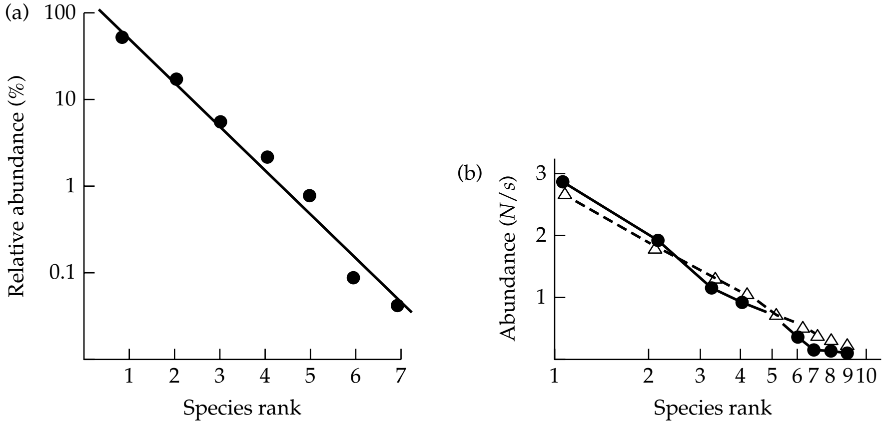


Figure 3.1 Rank abundance plots of marine data: (a) geometric series applied to benthos of the polluted inner part of Oslofjord; (b) broken-stick model of two transects of ophiuroids at Enewetok Island, Hawaii (data from King 1964).

species each have 1 individual, half (5 species) are assigned to the 0–1 bin and half (5 species) into the 1–2 bin, and so on. Preston argued that in fact the lognormal distribution for a sample was always truncated at the left-hand axis since it was most unlikely that all the species had been found; he called the left-hand axis the *veil line* as many species were hidden behind it. He also showed that as larger samples were taken more of the complete lognormal curve was revealed. Magurran (2004) gives a good example based on sampling fish in the Arabian Gulf.

Preston's (1948) method of binning the data to obtain a lognormal distribution was derived before the advent of computers and was aimed at turning discrete data into a continuous distribution. His method is now something of an anachronism as there are better ways to fit the lognormal distribution exactly. Of these the Poisson lognormal model is the best statistical approach, and software written in the widely used 'R' statistical protocol is available (Oksanen *et al.* 2006). Yet most ecologists like to see plots of the data to see how reasonably it approaches a normal distribution. Gray *et al.* (2005) reviewed binning methods for the lognormal and recommend a system based on doubling the number of individuals: 1, 2–3, 4–7, 8–15, and so on. Note that the boundaries between bins are not at exactly logarithmically increasing intervals, but the error is small.

This method of binning the data has been widely applied (Gray 1987 and Hubbell 2001 give examples). The truncation is clearly shown in both data sets and is clearer for the benthic data (Fig. 3.2a), which is a general occurrence with these data. We will come to why this is so later. In deriving the ZSM model Hubbell (2001) fitted the lognormal distribution to data on tropical trees in a 50 ha plot of forest in Barro Colorado Island, Panama. The data are remarkable in that each tree is identified to species and its location mapped. In all there are up to 900 species in the plot. Hubbell found that there was an overabundance of rare species compared with the lognormal distribution and so developed his ZSM model to account for the discrepancy (Fig. 3.2b). The ZSM is not simple to fit, but recent developments have greatly simplified this problem (Etienne and Olff 2004). Hubbell's model is built on sound biological principles and involves speciation, population dynamics, and extinction processes. It has attracted great interest in ecology, yet the model is not without its critics. One argument is that in fact the lognormal distribution fits real data just as well. Fitting models to SADs is, however, fraught with problems. As we mentioned earlier, for marine soft sediments we sample using grabs or corers which may be selective either for certain components (those living in the sediment, the infauna) or those with certain densities (i.e. rare species may not be taken

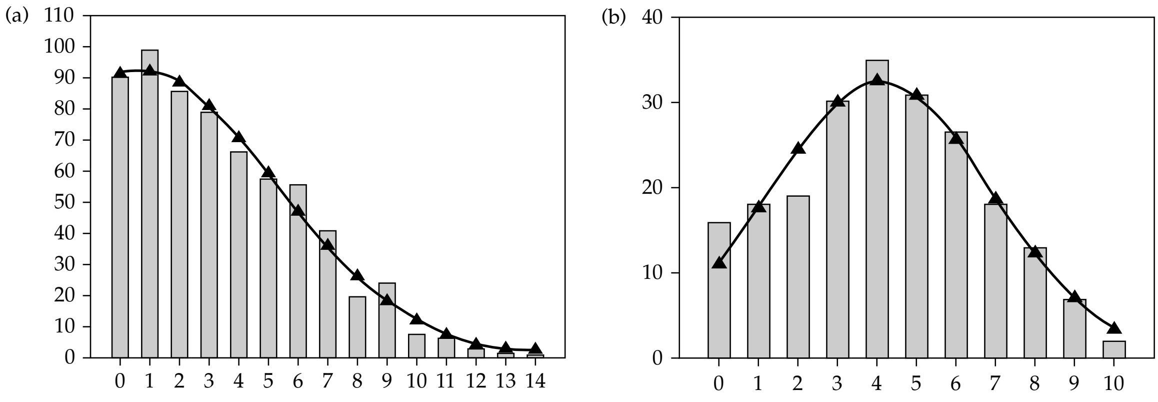


Figure 3.2 Lognormal plots of species abundance distribution for benthos of the Oseberg field (a) and for tropical trees of Barro Colorado island, Panama (b) (from Gray *et al.* 2005). The line is the fitted exact Poisson lognormal distribution. The cumulative number of species is plotted along the y-axis. On the x-axis the data are binned into $\log_2$ classes where 0=1,1=2–3, 2=4–7 individuals per species, etc.

by a small area) so that inevitably not all species are sampled or counted. It is therefore extremely likely that the area sampled may not be sufficiently large for the rare species to be estimated properly (even 50 ha may not be large enough to get representative data on species richness of tropical trees!). Hence an exact distribution is a theoretical abstraction and real data are measured with error. In statistics the process of fitting models to data is known as *goodness-of-fit testing*. There are many tests that could be used, and in one paper on testing the ZSM against the lognormal distribution, one of us (JSG) used eight different tests, all giving somewhat different results! There is, as yet, no simple answer of what is the best procedure, but since this is an active research field interested readers should follow the literature.

In order to explain the biology behind Hubbell's finding of an excess of rare species in real assemblages, Gray and co-workers developed a model suggesting there were groups of rare, moderately common, and common species in an undisturbed assemblage which gave the lognormal distribution. After disturbance the groups were 'pulled apart' and became easily discernible (Ugland and Gray 1982). This model was found to fit data on fish assemblages in the Severn estuary, UK, where Henderson and Magurran (2003) showed that the rare group of species were transient immigrants with different biological traits from the resident common species. Figure 3.3 shows Hubbell's original data and our suggested groups of rare and common species that give rise to the pattern. The rare group is quite small compared with the common group when measured over the whole 50 ha plot. Smaller samples, however, show a dominance of the rare group. With marine data the pattern is more stable, as shown in Fig. 3.3a for benthos of the Norwegian continental shelf. Here the rare group dominates at any scale sampled. We suggest that these patterns represent the rare group being comprised of immigrant species that are coming into the sampled area from outside. In terrestrial tropical forests, immigrants dominate at small scales. As larger areas are sampled the assemblage is dominated by better competitors and so there are proportionally fewer rare species. It is very important to remember that with the tropical tree data every individual tree has been counted, identified, and geo-referenced. With marine benthic assemblages, samples are taken by grab or box-core samples and cover only a small proportion of the total available area of sediment. The result is that even if larger and larger samples are taken, one still samples only a very small part of the total area. Thus the rare, immigrant group of species dominates at all scales. There are very many ecological systems that are similar to marine soft sediments in this respect. If you sample plankton or insects in a woodland you cannot sample the whole area, nor identify and count all species. In such systems we predict that the rare species group will dominate.

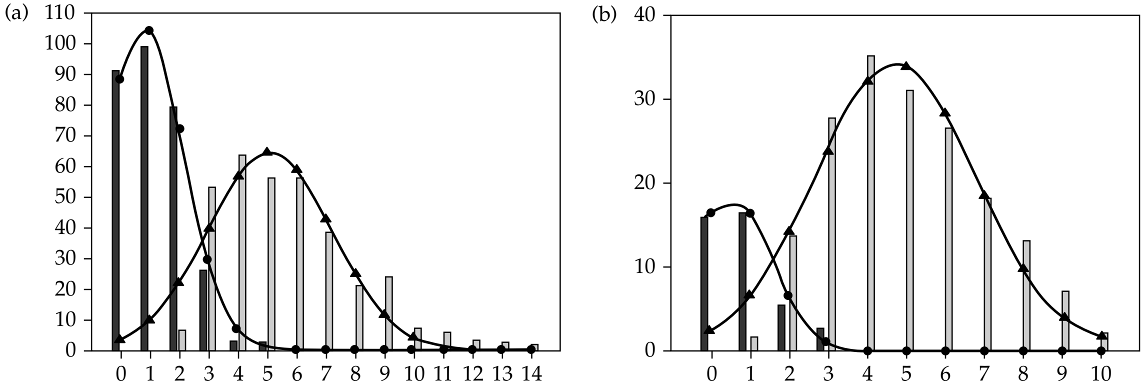


Figure 3.3 The two-group model of the lognormal distribution fitted to two data sets, Oseberg soft sediment benthos (a) and 50 ha plot of tropical trees at Barro Colorado island (b). (from Gray *et al.* 2005) The x- and y-axes are as in Fig 3.2.

Thus interpreting patterns of SADs needs careful consideration of the sampling regime.

It has been suggested that one particular data set, breeding birds in Britain, shows the ultimate SAD pattern since all species have been identified and counted, or at least numbers of the common species have been estimated sufficiently accurately. The SAD is what is called *log-left skewed*, having a long tail with few rare species and an abrupt right-hand end with the mode among the very common species. Yet there are very few data sets that show such patterns. The proponents of this as the ultimate SAD argue that very few assemblages have been fully censused and so have not been sufficiently detailed to reveal the true pattern. Yet the 50 ha plots of tropical trees contain up to 900 species and are exact counts, and they do not show the log-left skew that the bird data does. We may then question whether the British Isles are a natural ecological unit that can reveal a true ecological pattern. The data have also been adjusted to exclude introduced species, seabirds, and transients. For many ecological data sets we do not know enough about the species to make such adjustments, and so it is still too early to judge whether the data for tropical trees or British breeding birds approach the ultimate SAD. What we can conclude is that for open marine systems there will always be a dominance of rare species since we are sampling such a small part of the habitat. The rare species often make up 70% of the total number of species. Thus rareness is an intrinsic property of marine benthic assemblages and studies of biodiversity (see Chapter 4) are inevitably about the presence of rare species and their impact on the assemblages of which they are a part.

An interesting recent debate is that on microbial diversity. Finlay and Fenchel (1999) have studied protist diversity at a variety of sites globally and find identical species in localities as far apart as Denmark and Australia. As a consequence they argue that microbial diversity will in fact be rather low. The reason for this, they argue, is that protists are very old and have huge population abundances so that over geological time they have been able to colonize globally. Recent studies using microbial techniques, however, suggest that microbial diversity is very high. Craig Venter of human genome fame and co-workers (Venter *et al.* 2004) sampled seawater of the oligotrophic area off Bermuda and, using a 'shotgun' technique to estimate DNA fragments, suggested extremely high diversity with 1800 'genomic species'. Yet it still remains an open question as to whether these are real species, as only fragments of DNA have been found rather than the whole organisms that would be needed for a classical definition of a species.

Intensive studies of the sea water from the deep sea (Sogin *et al.* 2006) suggest findings of high genomic diversity similar to those of Venter *et al.* and although a few microbial species are very common, >75% of the species are in fact rare. Although this may seem contradictory to the results of Fenchel and Finlay (1999), relating the results to the lognormal distribution provides a possible solution. Even with benthic macrofaunal assemblages, most species (75%) are rare, occurring at frequencies of only 1 individual per sample whatever the sample size. Thus one can expect few abundant microbial species which may be ubiquitous, but the very many rare species will be more site-specific.

3.2 Species occurrences

Another way of plotting the distribution of species is to consider the frequency among sampling sites. In a study of the fauna of the Norwegian continental shelf, Ellingsen *et al.* (2005) studied five regions (Fig. 3.4). Within each region varying numbers of samples (comprising five replicate 0.5 m^2 grabs) were taken and then the frequency of species over sites was plotted.

Figure 3.5 shows that most species are rare, with 200 occurring only at one single site, 83 at only 2 sites, and no species occurring at all 101 sites studied. This pattern is a very general one and is found in nearly all assemblages examined, whether terrestrial or aquatic. In benthic soft-sediment systems it is a particularly notable feature of communities and so again we conclude that most species are rare. This may seem surprising; perhaps one would expect that if a larger sample were taken then fewer rare species would be found. This is not in fact the case: the same pattern occurs if larger samples are taken. The reasons for this are the ones touched on in the previous section (3.1.2) on distributional

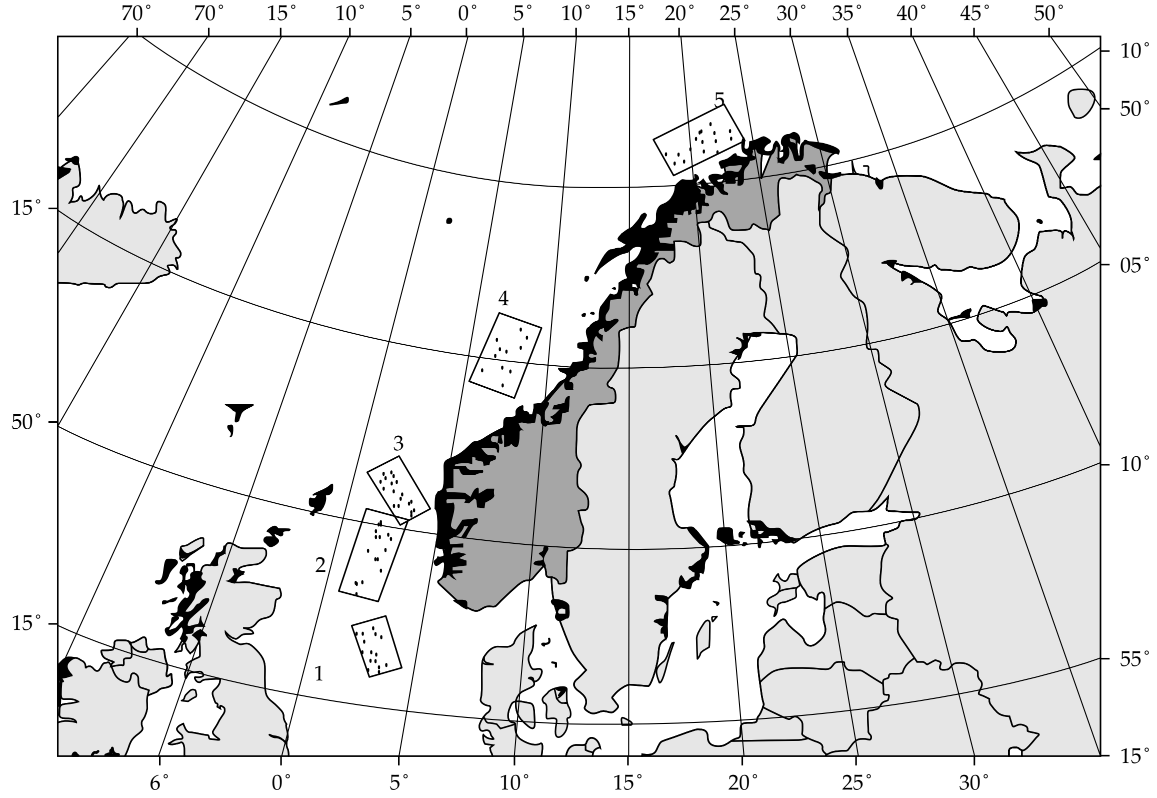


Figure 3.4 Sampling stations along the Norwegian continental shelf for soft sediment macrofauna (from Ellingsen *et al.* 2005).

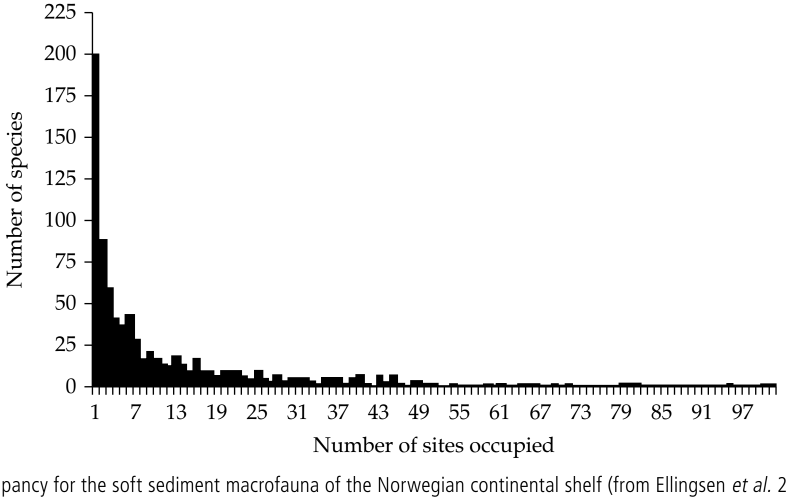


Figure 3.5 Site occupancy for the soft sediment macrofauna of the Norwegian continental shelf (from Ellingsen *et al.* 2005).

models. Marine systems are open, and thus immigrants can enter easily from outside the sampled area. With soft-sediment communities we never sample all the sediment with the result that the rare group of species is always the dominant one. Comparing the marine data in Fig. 3.5 with the terrestrial data, it is clear that there are fewer immigrants at the scale of the 50 ha plot sampled for trees in a tropical rain forest than in a marine soft-sediment system.

Rarity is a major feature of soft-sediment assemblages and if we are to understand patterns of diversity and how they are maintained we must devote more attention to it (see Gaston 1994 for a thorough discussion of this topic).

3.3 Size and biomass spectra

Sheldon *et al.* (1971) first studied the size spectra of pelagic assemblages and found a relatively simple pattern. They showed that if sizes were grouped into logarithmically increasing classes then biomass was similar at all size intervals. The method was then applied to benthos by Schwinghamer (1981, 1988). In this method the size of an organism has to be transposed to a uniform scale; by tradition the $\log_2$ scale has been used. Organisms within a size class are converted to equivalent spherical volumes using the formula

$$D = 2\sqrt[3]{3V/4\pi}$$

where D is the equivalent spherical diameter and V is organism volume. In his 1981 study Schwinghamer measured biomass of bacteria, microalgae, meiofauna, and most macrofauna to a depth of 10 cm. Thus 1 $\text{cm}^3\ \text{m}^{-2}$ is equivalent to a concentration of 10 $\text{cm}^3\ \text{m}^{-2}$ or 10 ppm.

Schwinghamer (1981) suggested that from these and other data the benthos showed a consistent pattern, with biomass maxima at the lower and upper extremes and another maximum, two to three orders of magnitude less than the others, at the centre (Fig. 3.6). The latter maximum is between 32 and 350 mm, which he suggested was associated with the meiofauna that live interstitially (between grains of sand).

There are still rather few studies that examine the full size spectrum. One is that of Warwick and Clarke (1984) who studied the fauna of a variety of benthic communities. They also used the $\log_2$ scale for the biomass spectra and their data show a slightly different pattern (shown in Fig. 3.7). For the benthos there was a consistent pattern among the sites studied. Fitted lognormal curves showed two peaks with a consistent trough. Warwick considered three explanations for this trough: (1) it could be a methodological artefact, which he dismissed; (2) it was due to environmental constraints on animals of around 45 µg, or (3) it was due to evolutionary processes. The environmental constraint argument, as developed by Schwinghamer (1981), is that the trough marks the boundary between species that

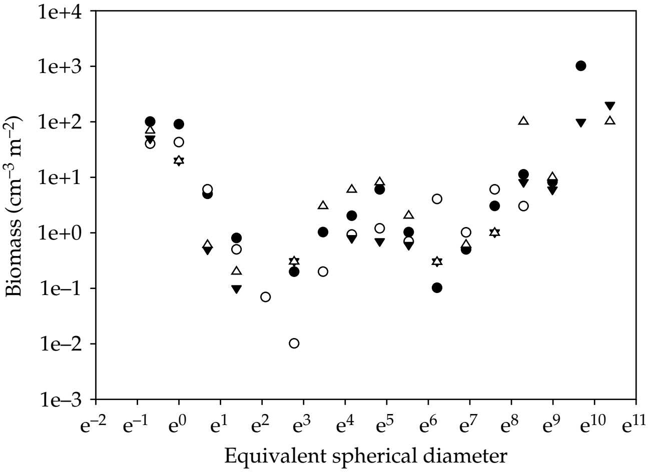


Figure 3.6 Sheldon size spectra for marine sediments showing three groups, microorganisms, meiofauna, and macrofauna (simplified from Schwinghamer 1981). Sampling stations: △ Petpeswick Inlet 30/12; ▼ = Petpeswick Inlet 26/1; ● Petpeswick Inlet 27/1; ○ Peck's Cove Station.

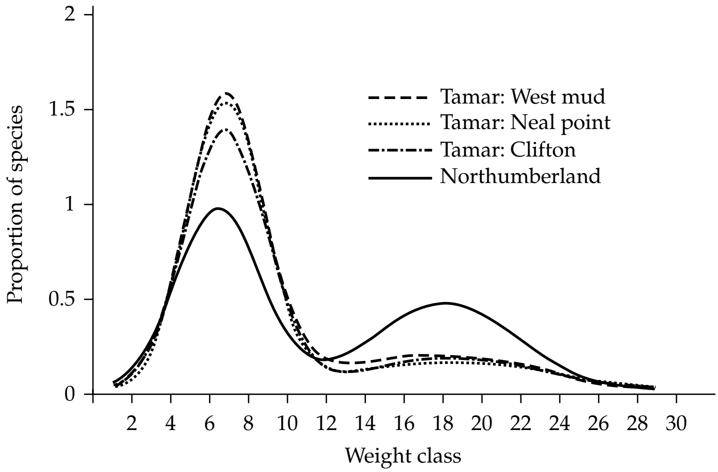


Figure 3.7 Size spectra of the fauna of intertidal mudflats, south-west England (from Warwick and Clarke 1984).

are interstitial fauna and those that are burrowers. Warwick and Clarke found that the same pattern occurred in muds and sands and thus dismissed this argument. Instead they favoured an evolutionary argument: that meiofauna and macrofauna had different natural history traits. Meiofauna, in general, had direct development, dispersed as adults, had generation times less than a year and were iteroparous. Macrofauna, in general, had mostly planktonic development, dispersed as larvae, had generation times more than a year and were semelparous.

Recent developments of the application of size spectra to benthic assemblages include comparing salinity gradients in the Baltic Sea (Duplisea 2000) and comparing life history traits of nematodes from intertidal sediments (Tita *et al.* 1999), where mean body width was found to emphasize the distinction between interstitial and burrowing species.

3.4 Describing faunal patterns

As mentioned throughout this book, we can divide the features relating to the sedimentary benthos into the primary factors, the physicochemical attributes that will cause habitat disruption, and secondary factors, the biological attributes that will reflect changes (see Elliott *et al.* 1998 for more details). The most appropriate physical features are:

- *area:* the expected size of the habitat, and in certain cases the *shape (physiography)* of the habitat
- *substratum:* the underlying nature of the bed material
- *depth and/or tidal elevation:* indicating either the coverage by water for subtidal mobile sandbank habitats or the extent to which intertidal sand and mudflats are exposed at low water; the depth also influences the light regime available to infralittoral plants
- *water chemical characteristics:* the underlying water chemistry, including salinity, temperature, and nutrient regime
- *hydrophysical regime:* the summation of tidal, wind-induced, and residual currents which influence the nature of the bed and the delivery of food and dispersive stages to an area
- *habitat mosaic:* an indication of the complexity of the environment created by the physical attributes and thus leading to biological complexity.

The *biological attributes* to be used include important features which describe community and structure and functioning. The most appropriate features are:

- *community structure:* the net result of taxa and individuals supported, the diversity of the area and, where necessary, the zonation created by the physical and biological features
- *biotopes:* the number and mixture of representative biological–environment entities and including where possible those listed by conservation managers, including the quality of biotopes and the maintenance of balance between them
- *species:* especially those that are rare, fragile, and/or considered important by conservationists; the dominant species in terms of functioning

and support of predators or as predators; the rare species could decline if their niche is removed, the area decreases, or the supplying population declines

- *community functioning:* as an indication of the overall health of the system and its support for important grazer and/or predator populations.

3.4.1 Intertidal beaches

As suggested above, intertidal beaches are influenced by three main factors: tides, waves, and sediment type (see Open University 2002). Where waves and tides are small and sediments are coarse, *reflective beaches* occur. These are characterized by waves breaking directly on the steep beach face and being reflected back to the sea. Such beaches have coarse sand where water drains rapidly. In *dissipative beaches* the beach is flat with a wide surf zone on which the waves dissipate their energy and there is little percolation of water into the sand. Such beaches occur where there are large tidal ranges, high wave energy, and fine sand; they often occur in higher latitudes.

The diagram in Fig. 3.8 shows a cross-section of a typical sandy beach showing the main zones. Moving landward, the *outer zone* has a relatively stable seabed, whereas the *transition zone* is subjected to strong wave energy and as a consequence the seabed is mobile. The *surf zone* has a highly mobile seabed and is a very inhospitable environment for fauna. In the *littoral zone* the water table is an important feature and is higher than sea level. The sand is damp but not fully saturated with water, but is flushed with each tide. The *supralittoral level* is characterized by dry sand and a deep water table and may be the start of sand dunes.

The steepness of a sandy beach is an important characteristic, which influences the ability of the fauna to survive. Steep beaches occur where wave action is strongest: beaches subjected to low wave action have shallow slopes and are more suitable for fauna. *Dean's parameter*, which measures the ability of wave energy to erode sand, is a dimensionless index (Ω) and is based on wave breaker height (m) divided by sand fall velocity (m s^{-1}) multiplied by the wave period (s^{-1}) (Rodil and Lastra 2004). Values of the index <2 characterize reflective beaches, whereas values >5 denote dissipative beaches (Defeo and McLachlan 2005). It is useful to have an index which measures such properties since the physical environment is hugely important in determining which faunal assemblages occur on a given beach.

3.4.2 Fauna on intertidal beaches

In general, steeply sloped beaches exposed to ocean swell are inhospitable places for beach fauna, although there are a number of species specifically adapted to live in such environments. Characteristic species are the beach crabs of the genus *Emerita* which can be seen scuttling back and forth as waves break, filtering the water for food. In similar environments bivalve molluscs of the genus *Donax* are common. Like *Emerita,*

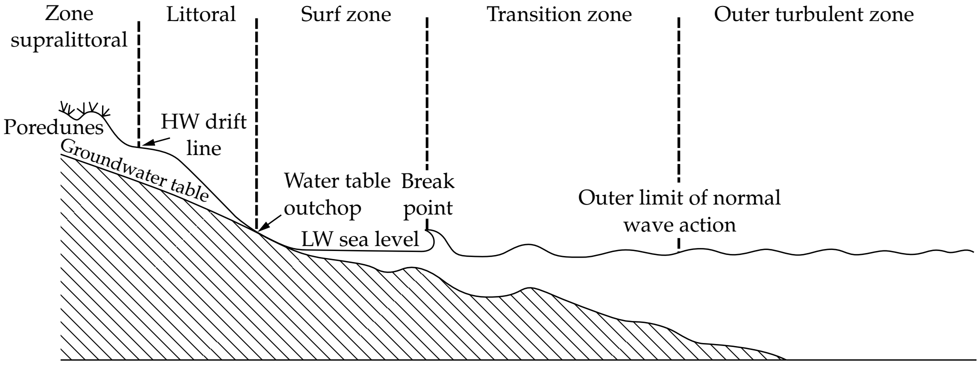


Figure 3.8 A typical sandy beach showing the main features.

Donax filters in the wave zone and with the swash they are seen in hundreds burrowing back into the sediment to avoid predatory birds. *Donax* is so well adapted to very mobile and well-washed sediments that it can easily colonize beaches affected by monsoon rainfall and erosion and rebury itself once washed out of the sand. (Brown and McLachlan 1990 give a very thorough account of the global extent of exposed sandy beaches and their fauna.)

Peter Schmidt (1969) made a very extensive study of the meiofauna of a sandy beach on the island of Sylt, Germany. He sampled by taking long cores into the sediment on the sandflat and the steeper slope at the top of the beach, which ends in the dry sand dunes. Then he subsampled the cores, extracted the meiofauna, identified them to species, and counted them. Figure 3.9 shows just two examples from his study. The polychaete *Ophelia rathkei* is restricted to the sandflat (Fig. 3.9a; data not shown) and extends up to where the water table is no longer at the surface but does not occur in the drier parts of the inner beach. In contrast, the polychaete *Protodrilus sp. 1* (Fig. 3.9b) occurs deep into the drier areas of the beach but avoids desiccation by occurring only at the water table, as do many other species.

In Fig. 3.10 the vertical distribution of the tardigrade *Batillipes mirus* is shown. This species (like many living in sandy beaches) avoids the surface layers of sediment, which are often much colder than the adjacent sea, by moving deeper into the sediment. In summer the species is found just below the sediment surface.

Figure 3.10 is a *kite diagram* (named from its shape) which is a classic and useful way of representing the distribution patterns of fauna along transects on sandy beaches. A recent example is that of Janssen and Mulder (2005). Figure 3.11 shows similar diagrams for data on the distribution of macrofauna down a sandy beach on the Dutch coast.

The depth at which species occur in the sediment and the distribution down intertidal beaches are clearly important aspects of the ecology of the species and in describing the patterns found. In the next section we will examine patterns of how species are organized into assemblages. One can of course map patterns of assemblages in intertidal areas also, but in general there are fewer assemblages in a given spatial area than in the subtidal zone and so the methods described below have been more generally applied to subtidal habitats.

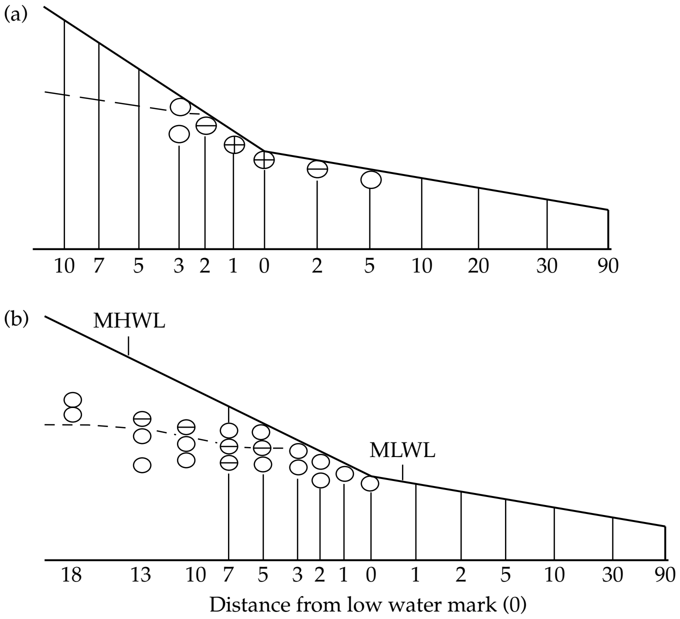


Figure 3.9 (a) Distribution of the polychaete *Opehlia rathkei* on an intertidal sandy beach at Sylt, Germany in June (from Schmidt 1969). (b) Distribution of the polychaete *Protodrilus sp.1* on an intertidal sandy beach at Sylt, Germany in June (from Schmidt 1969). The water table is shown as a broken line. MLWL, mean low water level; MHWL, mean high water level.

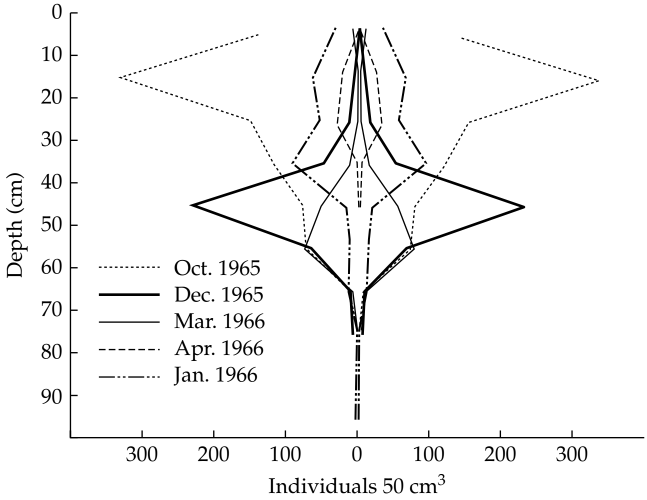


Figure 3.10 Seasonal variation in the vertical distribution of the tardigrade *Batillipes mirus* on an intertidal sandy beach at Sylt, Germany (from Schmidt 1969).

3.5 Describing assemblages

The basic data obtained from surveys of the benthos form a species–site matrix in which cells are populated either by an abundance or by binary data denoting presence or absence. As an intermediate between these extremes, it may be useful to denote quantities using the SACFOR scale: superabundant, abundant, common, frequent, occasional, or rare; a relative measure widely used by conservationists. In such a matrix, we are then usually interested in finding out whether groups of species occur together by dividing up the long lists of species and sites into more or less homogeneous groups of species, or at least species which all appear to coexist under similar environmental conditions. Here, you will note, we have used the term *assemblage* rather than *community* and although these terms are often used interchangeably, the term community is more often used. In addition, 'community' not only refers to mean groupings of species that co-occur in a similar habitat but also implies an interdependence between those species. In contrast, 'assemblage' is a more neutral term for a collection of co-occurring species that does not require links to a specific habitat and it does not imply interdependency (although of course that will occur between some or many species in an area); hence our preference for this term. We can then question whether there are assemblages of similar species occurring together over large areas of the seabed. Most experienced benthologists will recognize certain groups of species occurring under a given set of conditions; for example, there are what may be regarded as 'sandy species' or 'muddy species'. This approach was founded almost a century ago in classical work by the Danish biologist Johannes Petersen (1914, 1915, 1918, 1924), who produced a scheme that is still widely used today but is now based on modern statistical methods of analysis rather than subjective analyses.

3.5.1 Traditional methods: the Petersen–Thorson system

Working predominantly in the Kattegat around the Danish islands of Fyn and Zeeland, but also extending his work into the Skaggerak and the North Sea, Petersen sampled the shallow-water benthos quantitatively, recording species present and their numbers and weights (Fig. 3.12 shows his sampling stations). In all, he worked at 193 sites and listed 294 faunal records. Not all were recorded to the level of species (of which there were 260), but they were recorded as juveniles and adults separately. Petersen designated a series of assemblages by their so-called *characterizing species*. A characterizing species was one which was not seasonal and which, because of its numerical or biomass dominance, could be regarded as typical of a given assemblage. Constancy and dominance were, therefore, the two most important characters and Petersen's assemblages described the

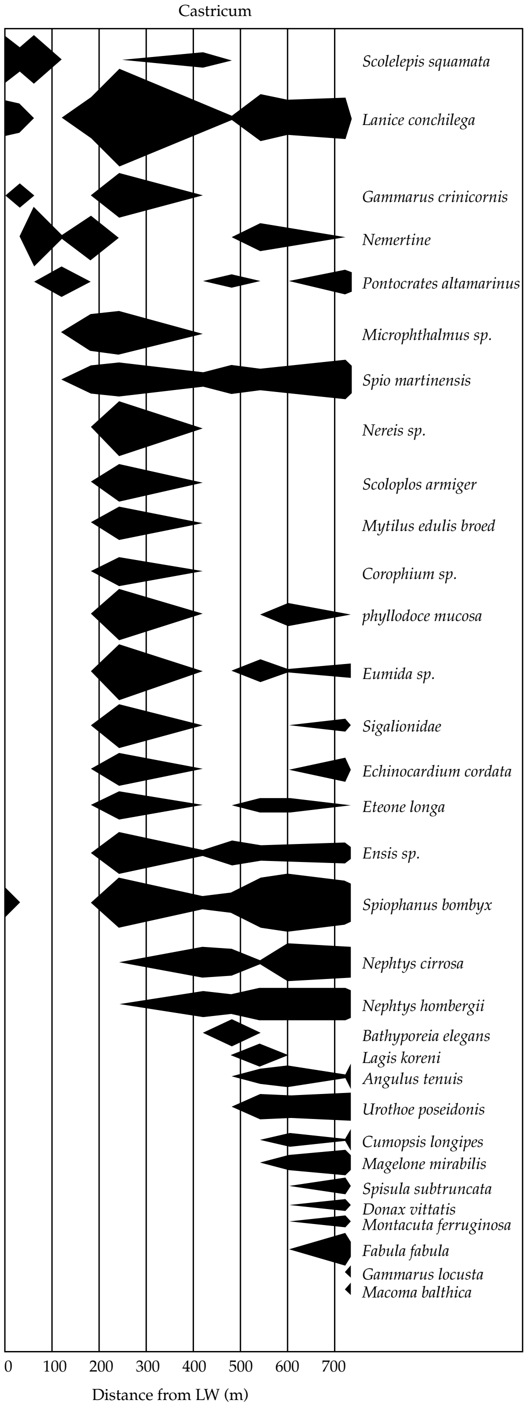


Figure 3.11 Zonation of fauna down an intertidal sandy beach in the Netherlands (from Janssen and Mulder 2005).

Figure 3.12 Peterson's sampling stations for soft sediment macrofauna in the Kattegat, from which he derived species assemblages.

dominant substratum types within the other major variable of depth. In all Petersen recognized seven major assemblages, characterized by the following species: (1) the bivalve *Macoma balthica*; (2) the burrowing echinoderm *Brissopsis*; (3) the burrowing echinoderm *Echinocardium*; (4) the bivalves *Asarte, Abra,* and *Macoma calcarea*; (5) the bivalve *Venus*; (6) the bivalve *Macoma calcarea,* and (7) the amphipod *Haploops*.

Many workers subsequently followed Petersen's scheme and found that similar assemblages could be recognized in many different parts of the world.

Thorson (1957), also Danish, extended Petersen's original ideas and defined the assemblages more precisely. In all, he recognized seven major types which often had the same or similar genera even though the precise species change with biogeographic regime:

1 *Macoma* assemblages. Typical of shallow waters and estuaries (brackish waters) between 10 and 60 m. Characterized by the bivalves *Macoma, Mya,* and *Cardium* (*Cerastoderma*) and the polychaete *Arenicola*. Occur on all types of bottoms, but where silty the deposit feeders *Macoma* and *Arenicola* dominate and where sandy the suspension feeding *Cardium* (now often *Cerastoderma*) dominates.

2 *Tellina* (now *Angulus* and other genera) assemblages. Shallow-water assemblages mainly inhabiting exposed beaches from intertidal to 10 m. Characterized by the bivalves *Tellina, Donax* and *Dosinia* and the echinoderm *Astropecten*. Typical of hard sand.

3 *Venus* (now *Chamelea* and other genera) assemblages. Found on sandy bottoms in open sea from 7 to 40 m. Characterized by the bivalves *Venus, Spisula, Tellina,* and *Thracia*, the prosobranch *Natica*, the echinoderms *Astropecten, Echinocardium,* and *Spatangus*, and the polychaete *Ophelia*.

4 *Abra* assemblages. Occur in sheltered or estuarine areas, often with reduced salinity, on mixed to muddy bottoms rich in organic matter, from 5 to 30 m. Characterized by the bivalves *Abra, Cultellus, Corbula,* and *Nucula*, the polychaetes *Pectinaria* and *Nephtys*, and the echinoderm *Echinocardium*. This community grades into the *Venus* community if the amount of sand increases and into the *Amphiura* community if the amount of silt increases.

5 *Amphiura* assemblages. Soft-bottom assemblages occurring from 15 to 100 m depth. Characterized by *Amphiura, Turritella, Thyasira, Nucula, Nephtys, Terebellides, Limbriconereis, Dentalium,* and one of *Echinocardium, Brissopsis,* or *Schizaster*. With a sandy substratuma *Echinocardium* and *Turritella* dominate, while more mud will lead to an increase in *Brissopsis, Thyasira* and sedentary polychaetes such as *Maldane*.

6 *Maldane–Ophiura sarsi* assemblage. Found in soft fine muds in shallow estuaries and down to 100–300 m in the open sea. Characterized by the polychaetes *Maldane* and *Terebellides*, the echinoderm *Ophiura sarsi*, the bivalves *Nucula, Abra,* and *Thyasira*, the gastropod *Philine*, the polychaetes *Aricia, Melinna, Praxilella, Clymenella, Glycera,* and *Pectinairia*, the amphipod *Ampelisca,* and the echinoderms *Brissopsis* and *Echinocardium*.

7 Amphipod assemblages. Estuarine or brackish-water assemblages usually on soft bottoms. Characterized by various amphipods each typical of its own community: e.g. *Pontoporeia* in the Baltic, *Haploops tubicola* in some areas of Denmark, *Ampelisca* in Japan and Massachusetts.

Thorson studied assemblages in many parts of the world and was struck by the fact that while the same genera often occurred on the same types of bottom in different areas, the species were different in going from the Arctic–boreal regions to, say, the Pacific coast of North America. He called these *parallel assemblages*. For example, the *Macoma* assemblages could be split up into four parallel assemblages: the *M. calcarea, M. balthica, M. nasuta–M. secta*, and *M. incongrua* assemblages. The first two are found in the North Atlantic, occurring in east Greenland and most of Europe respectively, whereas the *M. nasuta–M. secta* community is typical of the north-east Pacific in the San Juan archipelago of Washington State, USA. The *M. incongrua* community is the typical north-west Pacific community of Japan. Similar parallel assemblages were recognized by Thorson for the *Tellina* and *Venus* assemblages. Given that similar morphological species with similar environmental preferences were found in similar environmental conditions, the benthologists started to consider the assemblages as functional groups, hence returning to the community concept.

In the late 1950s more research was concentrated on the benthic fauna of warmer waters and many reports indicated that the Petersen–Thorson assemblages could not be identified in tropical and subtropical areas. This was because there were many more species in warmer waters and so dominance patterns similar to those in colder waters were not to be expected. Then in the 1960s an increasing number of reports appeared where assemblages could not be adequately defined even in the colder waters. Questions were raised about the validity of the Petersen–Thorson community concept; perhaps these communities did not occur at all but were merely an artefact imposed by workers whereby broad groupings were superimposed on parts of a continuum.

3.5.2 Rigid assemblages or continua?

The use of multivariate methods of ordination and classification analyses for ecological interpretation started in terrestrial botany during the 1950s, but it was not until the 1970s that they were used in marine ecology. Similarly, the debate on whether there are rigid assemblages or simply that species distributions overlap in an irregular manner had been raging in terrestrial plant ecology about two decades earlier than in the marine system! The botanists had been divided into two camps. First, there were those who believed that it was possible to classify groups of species into assemblages and that there were sharp boundaries between adjacent assemblages corresponding to discontinuities in the habitat. This view corresponds roughly to the Petersen–Thorson ideas on classifying benthic assemblages. Other botanists believed that rather than occurring in discrete groups with sharp boundaries, plant species occurred along gradients of environmental factors, with each species having an optimum somewhere along the gradient. The species overlapped in distribution and there were no discrete boundaries; one 'community', therefore, graded into another. Figure 3.13 diagrammatically illustrates the two ideas. Which of the two is most appropriate for benthic assemblages?

Each species has a tolerance to each environmental variable (e.g. salinity, temperature, sediment type, oxygen level) and as we move through an area, each of those variables will change, albeit slightly, thus causing the new mixture of species present to change in line with their preferences. There now seems to be little doubt that most recent data favour the idea that species are distributed in the form of continua although where there are abrupt changes of environment, such as a rock platform giving way to a sandbank, then there of course will be a large change in community. A good example of the continuum hypothesis is provided by the study of Hughes and Thomas (1971) from an intertidal beach in Canada. Figure 3.14 shows their data, which indicate that species are distributed in approximately normal distributions along the gradient of distance (probably reflecting sediment grain size). The gradient could just as easily be salinity, in which case there would be another pattern of species. If the *y*-axis is plotted on a logarithmic scale, the distributions are even more typically normal. Thus species seem to be distributed in log-normal curves of abundance along environmental gradients, i.e. they do not form discrete assemblages. From such data stems a modern definition of community (by Mills, 1969) which has met widespread acceptance: "community means a group of organisms occurring in a particular environment, presumably interacting with each other and with the environment, and separable by means of ecological survey from other groups". It is important to note, however, that Hughes and Thomas are only plotting the common group of species. You simply cannot plot distributions for species of which only a few individuals occur. From data such as Fig. 3.2, where the rare group of species comprises 70% of the total number of species, it is clear that we really do not know how these species are in fact distributed along an environmental gradient.

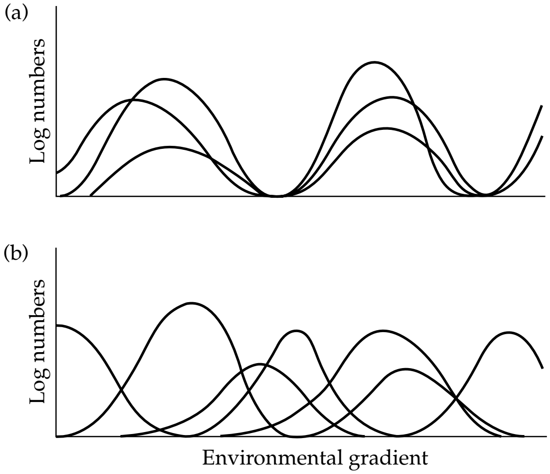


Figure 3.13 The two models of species assemblages: (a) sharp boundaries between assemblages that are separated into clear groups; (b) the modern concept, with species occurring lognormally distributed along one or more environmental gradients with no clear boundaries or groups.

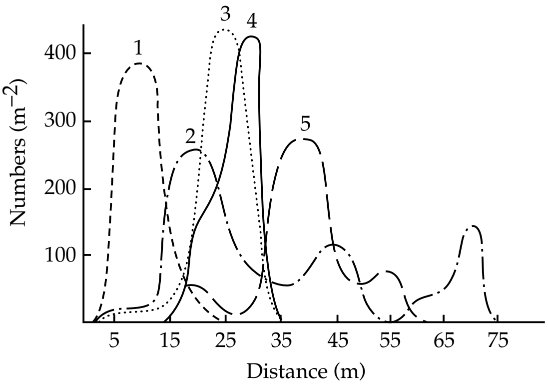


Figure 3.14 Distributions of species (numbered) along an estuary in Canada showing lognormal distributions along the distance gradient (from Hughes and Thomas 1971).

Both Petersen and Thorson selected the species that they intuitively thought were the most appropriate to indicate a certain community, the numerically or biomass dominating species, and their choice was often highly subjective. A computer, on the other hand, will only sort data on specific criteria given in advance and specified by the program. Computer-based sorting techniques are often called objective, but in fact much of the objectivity disappears on close examination of the methods used since, for example, species are subjectively eliminated before the data are submitted for analysis and there are often many choices of methods to be used. Juveniles, colonial species, or species identified to higher taxonomic levels such as order may all be eliminated before analysis. It is therefore preferable to decide on a set of common methods and stick to these, rather than simply trying a variety of methods and then choosing results which happen to fit the hypothesis being tested.

The analysis of site–species–abundance matrices is regarded as multivariate numerical analysis as each site and species is a variable; this type of analysis interrogates data whereby samples (sites) can be ordered according to their attributes (species). Although we usually wish to group sites together according to their similarity in their fauna (this is called *Q-mode analysis*), we may also wish to rotate the matrix and group together species according to where they occur at the sites (*R-mode analysis*)—the latter would thus indicate which species occur together and may therefore be regarded as an assemblage. The outputs of such analyses are then given as either cluster (classification) dendrograms or ordination plots. The latter are often the result of techniques such as detrended correspondence analysis (used as DECORANA), principle components analysis (PCA), or non-metric multidimensional scaling (MDS) whereby similarities between sites or species are shown in a two-dimensional space after summarizing the variability in the many dimensions given by the variables. The description of these techniques is outwith the scope of this book, and the reader is referred to books on ecological methods such as Zuur *et al.* (2007) for further details (see also the data analysis summary in Chapter 11).

One of the most widely used techniques for deriving groupings of sites is *classification analysis*. Figure 3.15 illustrates diagrammatically the stages in the analysis. First the raw data table of n samples and s species containing abundance data is transformed to the form $\log_{10}(x + 1)$ where zeros occur in the data set (log transformations are also used to reduce the overall weighting of a few large-abundance species in the data). From these transformed data, a *similarity matrix* is derived, i.e. the similarity of each site as compared to each other site, by calculating a *similarity coefficient*. Although there are many such coefficients, even correlation coefficients and Euclidean distance, the most common, which is widely used in benthic data analyses, is the *Bray–Curtis index:*

$$D = \sum_{i=1}^{s} \left| \frac{x_{1j} - x_{2j}}{(x_{1j} + x_{2j}} \right|,$$

where x_{1j}, x_{2j} are the abundances of species j in sites 1 and 2, and s is the number of species. (In studies in which only presence–absence data have been obtained, the *Jaccard coefficient* is used. This determines the ratio of common/non-common species in a pair of samples.) From this matrix, a dendrogram is prepared showing the relationships between groups of samples whereby the highest index value is chosen and shows the link between the most similar sites, then the next highest is chosen and so on, eventually building up the dendrogram. There are several methods of dendrogram construction, but

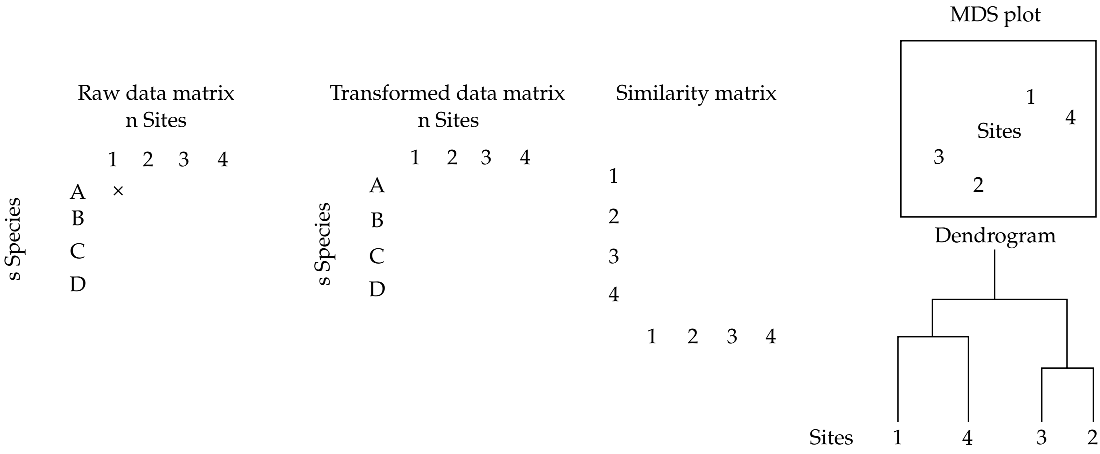


Figure 3.15 Multivariate statistical analyses: the procedures for deriving clusters and a dendrogram. First the species–site matrix is transformed to reduce the dominance of common species. From the transformed matrix similarities (or dissimilarities) between all combinations of stations are calculated. The dendrogram is constructed by linking the most similar stations then fusing these and recalculating the similarity matrix and fusing the next most similar and so on (from Clarke and Warwick 2001).

the group-average sorting strategy is widely used. The books by Zuur *et al.* (2007) and Henderson (2003), and the slightly older one by Krebs (1998), give an extensive description of the available techniques, their rationale, and methods of calculation. Although the benthic literature is now overburdened by papers giving multivariate analyses, here a classification analysis of 68 sampling stations from F.B. Mirza's study of the benthic macrofauna of the Oslofjord is used as an example (Mizra and Gray 1981). A total of 146 species was found, but the analyses were done on only 69 species since rare species comprising <5% of the species were excluded. Four major groups of stations (A–D) were found. Group A includes all those stations that contain large numbers of *Capitella capitata, Polydora ciliata,* and *Heteromastus filiformis*, opportunistic species which are common in highly organically enriched sediments. Other groupings of stations (B, C, and D) show fauna characteristic of only slight pollution (see Chapter 8 for a fuller discussion of these aspects). Thus the classification analysis has divided the stations into groups containing similar species, presumably with similar environmental preferences. Plotting the groups onto a map of the fjord (Fig. 3.16) indicates patterns of similar stations. These show that the most polluted area (that containing group A species) occurs in the innermost part of the Oslofjord, to which the bulk of the sewage from the city of Oslo was discharged.

Multivariate statistical analyses are now routinely used to analyse patterns in benthic assemblages, thanks to the development of easy-to-use statistical software. The most widely used, and perhaps now the 'industry standard', is PRIMER-E, developed at the Plymouth Marine Laboratory in the UK (Clark and Warwick 1994, 2001, Clark and Gorley 2006, PRIMER-E 2006). This software has excellent, easy-to-use approaches and guides the user through the steps needed to understand the procedures and make sound analyses.

The multivariate analysis software produces results that generate patterns of species groupings and distributions which can then be related to environmental (or contaminant) loadings, so that relationships can be inferred. However, it has to be remembered that the results obtained are correlations and these do not necessarily mean cause and effect. Indeed, it is often the case that patterns from multivariate analyses are regarded as generating hypothesis rather than testing them, although recent PRIMER routines such as ANOSIM and PERMANOVA are suitable for hypothesis testing (e.g. Anderson *et al.* 2005). Thus in essence, the patterns produced will then lead to further

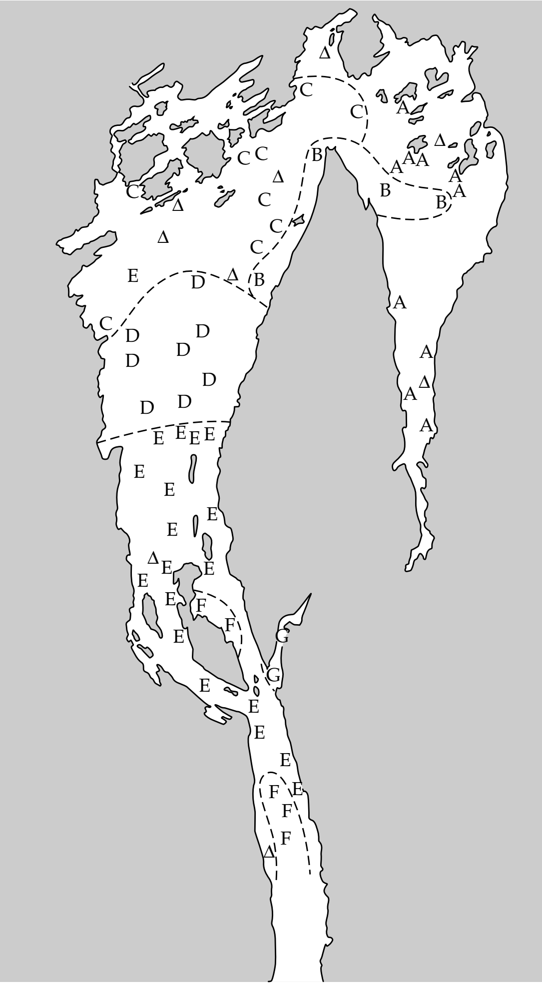


Figure 3.16 Results of a multivariate statistical analysis of the benthos of the Oslofjord (from Mirza and Gray 1981). The map shows groups of stations with similar faunal composition and a clear gradient from the inner to the outer part of the fjord.

investigation. As editors of marine journals we receive many papers that collect samples, analyse them with multivariate statistics, and then assume that the results are of immediate interest. Our response as editors is often 'So what! The results have generated hypotheses that need to be tested further—community structure is about more than the ordination and cluster patterns!'

Two other aspects need to be considered. In the early discussions of the community concept in benthic ecology much debate centred on whether assemblages should be described on the basis of the substratum that they occupied, i.e. the *biotope* (see Olenin and Ducrotoy 2006 for a discussion of the history and use of the biotope concept). There is often a close relationship between the type of sediment and the species composition, since many metamorphosing larvae (and adults) are able to discriminate between sediment particle sizes, or at least settling stages are deposited where hydrographic conditions allow (termed *hydrographic concentration*). However, grain size is only one of many niche variables, and from niche theory one cannot expect to classify assemblages solely on the basis of that one variable.

Another debate centred on whether assemblages were, as Petersen believed, merely statistical entities, i.e. descriptions of species which occurred together, or whether they were groups of species that responded together, i.e. had clear biological interactions with each other (and thus were communities *sensu stricto*). Such biological interactions implied that a group of species had similar ecological requirements and hence acted as a cohesive unit, and this was termed a *biocoenosis*. Describing biocoenoses was common in countries bordering the Mediterranean, notably France and Spain, but held little sway in northern Europe. So, in conclusion, today we have come back to Petersen's idea of assemblages being merely helpful descriptive units and not implying any rigidity in the patterns found.

In this chapter we have mainly considered species and descriptions of which individual species occur in assemblages. Little mention has been made of what the species do, nor of what characteristics the species that occur at a given site have in common. Recently, there has been a strong trend to take more account of the traits that species exhibit rather than concentrating simply on nomenclature, hence the *functional guilds* approach (Pearson 2001, Cheung *et al.* 2008). Examples of functional traits are metabolic rates, body size, age at sexual maturity, size of eggs, and feeding types. Ideally such traits should vary more between than within species and preferably be measured on continuous scales (McGill *et al.* 2007). Thus analysis of traits, as an alternative to species, perhaps offers more ecological generality and predictability. Furthermore, and perhaps most importantly, it gives us the chance to analyse the functional (i.e. rate process) attributes rather than just the structural ones. Some of the ideas have been used in marine benthic ecology for several decades, for example the work of Tom Pearson in Scotland (Pearson *et al.* 1982, Pearson 2001) and Fauchald and Jumars (1979) in the USA. These authors identified feeding traits in the benthic species, especially polychaetes, and their relationship with sediment preferences (see also Cheung *et al.* 2008).

McGill *et al.* (2007) propose a research programme for rebuilding community ecology. In this they seek to combine studies of environmental gradients (fundamental and realized niches) and the interaction milieu (competition predation and other biotic interactions), and they see the need to develop a performance currency. They suggest that a common currency is needed to compare traits across species and along gradients so that one can study how trait variation affects performance. Examples are energy intake and expenditure (discussed in Chapter 5), and numbers of gametes produced as a measure of reproductive strategy. McGill *et al.* favour energy allocation and expenditure since these are closely connected to environmental gradients and the interaction milieu. As an example they use photosynthetic rate in plants in relation to specific leaf area and nitrogen content (Fig. 3.17). There is clearly a tight relationship which shows the generality of the processes involved.

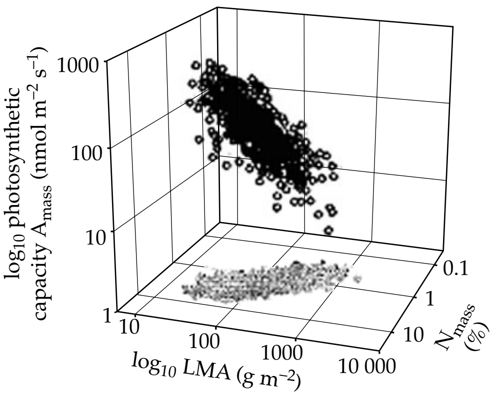


Figure 3.17 Photosynthetic rate (a performance currency) related to specific leaf area (SLA) and nitrogen content (from McGill *et al.* 2007).

The research programme described by McGill *et al.* (2007) is new and thus has not been applied fully to marine sediments. Initial studies on biological traits analyses have begun, and a broadening of these to encompass other aspects is needed if we are to make generalizations and predictions. These will be covered in later chapters.

CHAPTER 4

Diversity

In the previous chapter we covered ways of describing samples of benthos, but specifically did not include diversity. We can talk of primary community variables, such as abundance (*A*), species richness (*S*) and biomass (*B*), and derived variables from these such as true diversity indices, evenness indices, and ratios indicating the relationship between species richness and abundance (*A/S*, the *abundance ratio* or the average abundance per species) and between biomass and abundance (*B/A*, the *biomass ratio* or the mean biomass per individual). Diversity is not just simply about the number of species found in a sample or area, but also uses data on the abundances of individuals among the species and the way those abundances are distributed among the species within the assemblage. There are many ways of describing diversity. Here we give a summary of the most important ones and reference sources of recent literature on the subject (see also the data analysis summary in Chapter 11).

In the following section we consider simple indices (univariate) as measures of diversity; multivariate methods of analysing patterns will be covered in Chapter 7 on the effects of disturbance.

4.1 Measuring diversity

The simplest way to measure diversity is the number of species found in a sample, called the *species richness* (*S* or *SR*). Yet diversity is not just about numbers of species; it is also concerned with the distribution of numbers of individuals per species. For example, if one assemblage has 50 individuals of each of 2 species A and B whereas another assemblage has 99 individuals of species A and 1 individual of species B, then both have the same species richness but the first assemblage is the more diverse. Thus a measure of diversity (an index) must take into account not only the number of species, but also the number of individuals per species. To distinguish this from species richness, the combination of individuals per species and number of species is called *heterogeneity diversity*. In fact there are a large number of diversity indices, and we do not propose to consider them all here (Magurran 2004 gives an excellent and detailed account and others are mentioned in the summary in Chapter 11). Instead, we describe the most commonly applied indices to the fauna of marine sediments, namely the Shannon–Wiener information statistic and plotting methods such as species accumulation curves and rarefaction curves. However, readers should be aware that common methods may be used widely just because they are used widely and not necessarily because they are the most appropriate!

4.1.1 The Shannon–Wiener information statistic

The Shannon–Wiener information statistic relates cybernetic and information theory to ecology. The organization of an assemblage can be represented by the number of species and the number of individuals per species. The cybernetic analogy comes in by equating the organization to an information channel running from the present state into the future, with the width of the channel being a measure of the organization (Margalef 1968). More explicitly, the formula for calculating diversity is:

$$H' = -\sum_{i=1}^{s} p_i \log_2 p_i$$

where $p_i = n_i/N$ (n_i being the number of individuals of the *i*th species and *N* the total number of individuals) and s is the total number of species. Given its basis in information theory, it has been suggested that H' is less relevant to areas with low numbers of species and high abundances, hence its doubtful use in naturally low-diversity brackish and estuarine areas; in stressed low-diversity areas it should be treated with caution. Similarly, workers determining seasonal trends should be aware of the influence of high recruitment of one or two species for a short period.

The use of H' may seem a little complicated, and it is hard for a benthic biologist to envisage what the index is actually measuring. So let us take a simple example. If there are eight species A–H, each with say 2 individuals, what the index measures is how many binary decisions ($\log_2$) are necessary to decide whether a new individual belongs to these eight species or not. Figure 4.1 shows the process. First one has to make a distinction between groups ABCD and EFGH, i.e. one binary decision is made. If we first take the ABCD route, then we have to distinguish between AB and CD (binary decision 2), and finally between A and B (binary decision 3). So in this case, using logarithms to the base 2, there are three binary decisions and the Shannon–Wiener index H' is 3.0. Of course there are never exactly the same number of individuals among species so the index will always be fractional, e.g. 4.45 in a species-rich assemblage or 1.67 in a species-poor assemblage.

Although the above example uses $\log_2$, as was used by Shannon and Weaver (1949, from an original idea by the Austrian Wiener, hence the name), it is more usual to use other bases for the logarithms: $\log_e$ is often used, as is $\log_{10}$. In general, as the number of species increases so does the diversity index. But the diversity index will also increase as the proportion of individuals per species becomes more constant. Table 4.1 illustrates some simple hypothetical examples, here using $\log_e$ as the base, as is common in many software packages. These calculations were done with Species Diversity and Richness III from the program CAP (Community Analysis Package, Pisces Conservation Ltd; see also Henderson 2003).

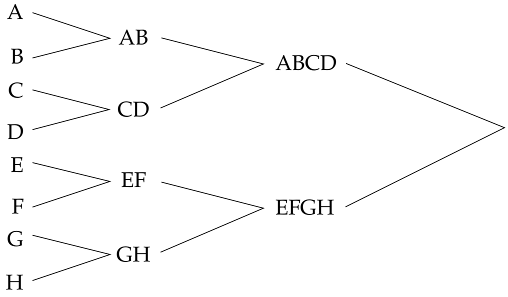


Figure 4.1 Example illustrating the biology behind the Shannon–Wiener diversity index using $\log_2$ as base. See text for an explanation.

Another widely used index is that of Simpson (1949),

$$D = \Sigma p_i^2$$

where p_i is the proportion of individuals in the ith species. This measures the probability that any two individuals drawn at random from an infinitely large assemblage belong to the same species. For a finite community the form of the index is:

$$\sum (n_i(n_i - 1)/N(N - 1))$$

Table 4.1 Shannon–Wiener diversity index (using $\log_e$) and Pielou's index of evenness J.

Species	Individuals	Diversity index
A	100	
B	10	
C	1	
D	1	
Diversity A–D		
Shannon–Wiener index ($\log_e$)		0.40
Pielou's J		0.29
E	45	
F	23	
G	3	
H	2	
I	1	
J	1	
Diversity A–J		
Shannon–Wiener index ($\log_e$)		1.32
Pielou's J		0.57

where n_i is the number of individuals in the ith species; and N is the total number of individuals.

As D increases, diversity decreases so the more usual way to express Simpson's index is as a reciprocal. Whittaker (1972) first suggested using the reciprocal of Simpson's index (which Gray (2000) called HD_2) as a diversity index:

$$HD_2 = 1/(p_1^2 + p_2^2 + p_n^2)$$

where p_1 is the proportional abundance of the first species compared to the total number of individuals in the n samples. Whittaker (1972) argued that the Simpson index is primarily a measure of dominance, taking special account of the three most dominant species, whereas the Shannon–Wiener index is more strongly affected by species in the middle of the species rank sequence. Thus these two indices measure different aspects of species diversity.

The idea of species diversity encompasses two aspects, species richness and species evenness. The latter aspect, evenness, can be derived by dividing the observed diversity value by the maximum possible value which would be obtained if each individual belonged to a different species. Evenness (J) is:

$$J = H'/H'_{\max}$$

where H' is the Shannon-Wiener diversity and $H'_{\max} = \log_e s$, where S is the number of species. Unfortunately the value of the diversity index is often reported merely as H' and the evenness component is not given. One is then not sure whether the value of any observed change in diversity is due to an increased number of species or a more even distribution of individuals per species. Furthermore, J is the inverse of dominance so a simple way of calculating dominance is $1-J$.

For typical benthic communities, if we plot diversity, H', against $\log_e s$ and against evenness, J, we can establish whether the diversity index is more responsive to an increase in the number of species or to an increasing evenness in the distribution of individuals among species. H' is usually poorly correlated with number of species and better correlated with J. Thus the addition of rare species to the assemblage has little effect on diversity, whereas changing dominance has a larger effect. Such findings are typical for most subtidal macro- and meiobenthic assemblages, but not all communities show such trends. Bird communities show a higher correlation of H' with $\log_n s$, indicating that addition of rare species is relatively more important than a change in dominance pattern. This may be explained by the fact that bird species are largely territorial and that as a consequence dominance patterns remain fairly constant.

Examples of the use of some of the above methods are shown in Fig. 4.2 below, but first it is important to understand how scale affects the interpretation of diversity data.

4.1.2 The Berger–Parker dominance index

A very simple way of calculating dominance is that devised by Berger and Parker (1970). This is defined as the percentage of the total fauna represented by the single most abundant species:

$$d = N_{\max}/N$$

where $N_{\max}$ is the number of individuals of the most abundant species. Dominance is a useful index that should be reported together with other measures of diversity.

4.1.3 Species accumulation, species area, and rarefaction curves

4.1.3.1 Species accumulation and species area

A species accumulation curve (sometimes erroneously referred to as a species–area curve) was shown in Chapter 1 (Fig. 1.8). This plots the number

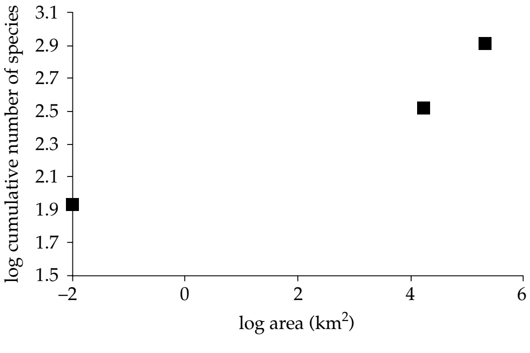


Figure 4.2 Species–area relationship for the fauna of the Norwegian continental shelf (from Gray *et al.* 2005).

of new species found as the new samples are added. If samples are added sequentially, say over a gradient such as latitude, then the curves are often not smooth; no new species may be found on adding 2–3 new samples. If one moves to a new area the accumulation rate of new species nearly always shows a jump and then flattens out. This is clearly shown in Fig. 1.8. Traditionally, a randomization process was used to obtain a smooth species accumulation curve, but recently a more sophisticated analytical model has been developed (Ugland *et al.* 2003) and it was shown that such curves are always semi-logarithmic. (A modification of the Ugland method is used in the EstimateS software; Colwell 2001.) In species accumulation curves, the identity of species is clearly important as one is adding the new species found as more samples are taken. There is a fundamental difference between these and typical species–area curves, where one simply plots the number of species found in areas of different size. A large sample may include all the species found in a smaller sample, or all the species in the smaller sample may be different to those in the large sample. Species–area curves are used to ask more fundamental ecological questions than simply illustrating how many species are found as sample size increases.

The species–area relationship is

$$S = cA^z$$

where S is the number of species, c is a constant measuring the number of species per unit area, A is area, and z is a constant measuring the slope of the line relating S to A. There are two commonly used versions of this relationship. The first is the power (or log–log) curve of Arrhenius (1921), where

$$\ln(S) = z\ln(A) + c$$

An example is shown in Fig. 4.2 for the soft-sediment benthos of the Norwegian continental shelf. A straight line on the log–log scale seems to be the rule, usually with little variance about the line for species–area relationships (that is, how many species occur in areas of different size).

The alternative form is the exponential (or semi-log) curve of Gleason (1922), where

$$S = z\ln(A) + c$$

An example of this was shown in Fig. 1.8, where the semilogarithmic shape is found for species accumulation curves (that is, how many new species are found as different sizes of a habitat sample are taken).

For the Norwegian data three different scales were sampled: the sample itself, a large area, and the whole continental shelf (approximating a biogeographical province). In terrestrial ecology much effort has been spent on determining such relationships to compare islands with parts of the mainland and to compare different habitats and ecological regions such as tropical and temperate areas (Rosenzweig 1995). Few such relationships have been established for the marine environment. An important question that remains to be answered is whether tropical or deep-sea areas show steeper slopes than those on the continental shelf of Norway.

4.1.3.2 Rarefaction

Another method of presenting diversity data, which has been widely applied to marine benthic data, is the *rarefaction method* of Sanders (1968). The method may be most useful in comparing areas where there are differing levels of sampling effort. Sanders wanted to compare samples he had taken with an anchor dredge, which unfortunately does not take quantitative samples. He found that some of his samples contained relatively few individuals and some had many, which influenced the estimates of species richness. He therefore calculated curves of the number of species that would be found in samples containing fewer individuals than in the total sample. By repeatedly recalculating for a smaller and smaller number of individuals a curve was produced (going backwards to the origin)! In this graphical method of expressing diversity, steep curves show high diversity and shallow ones low diversity. Rarefaction curves were then used where data was only available on the number of individuals per species. Where the area sampled has been determined, species accumulation curves are more appropriate. (Gotelli and Colwell 2001 have reviewed such methods and should be consulted for more details of where and when to use different methods.)

Hurlbert (1971) suggested that the method as described by Sanders overestimates the real number of species and made a correction. Easy-to-use software has been developed and Colwell's EstimateS program (Colwell 2001) can be recommended. Note that in this package it is the Coleman curve that should be plotted, and it is almost exactly the same as Hurlbert's rarefaction curve. Although the rarefaction method is widely used, there are some problems of which the user must be aware. The assumption is that the distribution of individuals among species that is found in the whole sample occurs at all samples of smaller size (i.e. with fewer individuals). Yet this assumption is probably invalid. As an example, take a sample with 50 individuals of species A and 1 individual of species B. Clearly dominance is high. Then assume that sample 2 has 1 individual of species A and 50 individuals of species 2, giving the same dominance as in sample 1. Combine the two samples and species A has 51 individuals and species B 51 individuals, so dominance decreases. In fact dominance always decreases as sample size increases. Therefore, the assumption that similar dominance patterns occur at smaller sample sizes than those sampled is unfounded, yet it is widely assumed to be the case. To illustrate this, Fig. 4.3 shows a scenario for rarefaction with maximum evenness and with minimum evenness. At a smaller sample size than the complete sample the predicted number of species can in fact be anywhere between the two curves for a given number of individuals, depending on the actual dominance pattern that occurs in real samples at that sample size. For example, for 200 individuals the estimated species richness lies between 5 and 40 species depending on the real dominance patterns at this sample size.

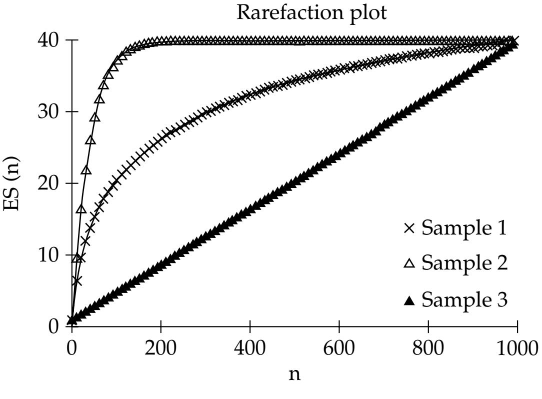


Figure 4.3 Comparison of rarefaction curves. Sample 1 (x) from data in Sanders (1968); sample 2(Δ), all 40 species have equal numbers of individuals; sample 3(▲), 1 species with 961 individuals and 39 species each with 1 individual (from Gray 2000, after Fager 1972).

Having discussed the methods for measuring diversity, it is important to understand the scales over which diversity can and should be measured. (The use of diversity indices to measure the effects of pollution on communities is discussed in Chapters 9 and 11.)

4.2 Scale and biodiversity

It has often not been appreciated that one must study at appropriate scales, and this is one factor that bedevils studies of patterns of diversity. Too many studies have taken a few grabs in the Arctic and a few in a temperate and/or tropical area and then compared species richness. There may or may not be differences at these small scales, and it is not possible to generalize diversity patterns from small-scale studies alone since diversity varies with scale. So we should ask, what is an appropriate scale over which to measure diversity?

Whittaker (1960) suggested that the most basic level of species richness was the number of species in a sample, which he called alpha diversity. Later (Whittaker 1972), he suggested that diversity could be measured at four different scales: *point diversity* (a single sample), *alpha diversity* (samples within a habitat), *gamma diversity* (the diversity of a larger unit such as an island or landscape), and finally *epsilon* or *regional diversity* (the total diversity of a group of areas of gamma diversity). (*Beta diversity* is discussed below on p 57; *delta diversity* is used by plant landscape ecologists to refer to the change in flora from one landscape or area to another (Kruger and Taylor 1979) and is not considered further here. There was much controversy over these definitions (see Gray 2000 for a fuller discussion). In an attempt to produce a logical scale, the review by Gray (2000) proposed the scales shown in Table 4.2.

If one records the number of species in a grab as the point sample, then the total number of species in five grabs within a small area gives the sample

Table 4.2 Proposed unifying terminology for scales of diversity, where *SR* is species richness

	Definition
Scale of species richness	
Point species richness: SR_P	Species richness of a single sampling unit
Sample species richness: SR_S	Species richness of a number of sampling units from a site of defined area
Large area species richness: SR_L	Species richness of a large area which includes a variety of habitats and assemblages
Biogeographical province species richness: SR_B	Species richness of a biogeographical province
Type of species richness	
Habitat species richness: SR_H	Species richness of a defined habitat
Assemblage species richness: SR_A	Species richness of a defined assemblage of species

species richness (or heterogeneity diversity if a diversity index is calculated). *Sample richness* SR_s is equivalent to Whittaker's alpha diversity. If we compare SR_s in two or more small areas we may or may not find differences simply because SR_s varies over small scales (actually called *extent* in a more strict scientific sense). You may find high values of SR_s in a small area of the continental shelf in a tropical area or low values in a tropical estuary. Studies at the sample level are not at the appropriate scale to analyse trends in species richness with latitude or any other gradient; despite this, many such studies are reported in the literature! SR_s is controlled mainly by factors such as the availability of niches, on which are superimposed competition and predation (or other disturbances covered in Chapter 6). These factors are acting on ecological scales. Changes in species richness with latitude and depth are related more to evolutionary events than to ecological ones and thus need to be studied over quite different (larger) spatial scales. Good examples of such large-scale studies are those of Grassle and Maciolek (1992) in the deep sea, or Ellingsen *et al.* (2005) along the continental shelf of Norway, where species were accumulated over many hundreds of kilometres. In the terrestrial literature, a biogeographical province is defined as an area in which all the species have arisen by natural speciation processes. Although there have been attempts to define such provinces in the sea, and we do refer to biogeographical realms such as the Arctic, Boreal, or Lusitanian, the sea is an open system and there are no clear boundaries as there are on land, so in general we have not made studies at the province level. Thus it should be remembered that the SR_B scale (see Table 4.2) is not equivalent to a biogeographical province on land.

Figure 4.4 shows diversity measures for benthic fauna from the continental shelf of Norway (Ellingsen *et al.* 2003). The figure shows that species richness alone shows greater variability in the patterns compared with Shannon–Wiener and dominance indices. This is a rather general finding, and the Shannon–Wiener index has very low discriminatory power.

4.3 Turnover (beta) diversity

Whittaker's pioneering research (1960) compared the species richness across altitudinal gradients in terrestrial forests in North America. All his studies were concerned with line transects along one or more environmental gradients. Thus, his definitions and methods for measuring species richness relate to line transects and gradients. If the transect is sufficiently long, it will traverse different habitats and thus will become a between-habitat study. Whittaker (1975) defined beta (between-habitat) diversity as: 'the degree of change in species composition of communities along a gradient'. Whittaker stated that beta diversity 'should be measured as the extent of change in, or degree of difference in composition among, the samples of a set'. Magurran (2004) uses the term *turnover diversity* rather than beta diversity since this better describes the ecological process of species replacement along a gradient. Turnover diversity relates to the species composition and the extent

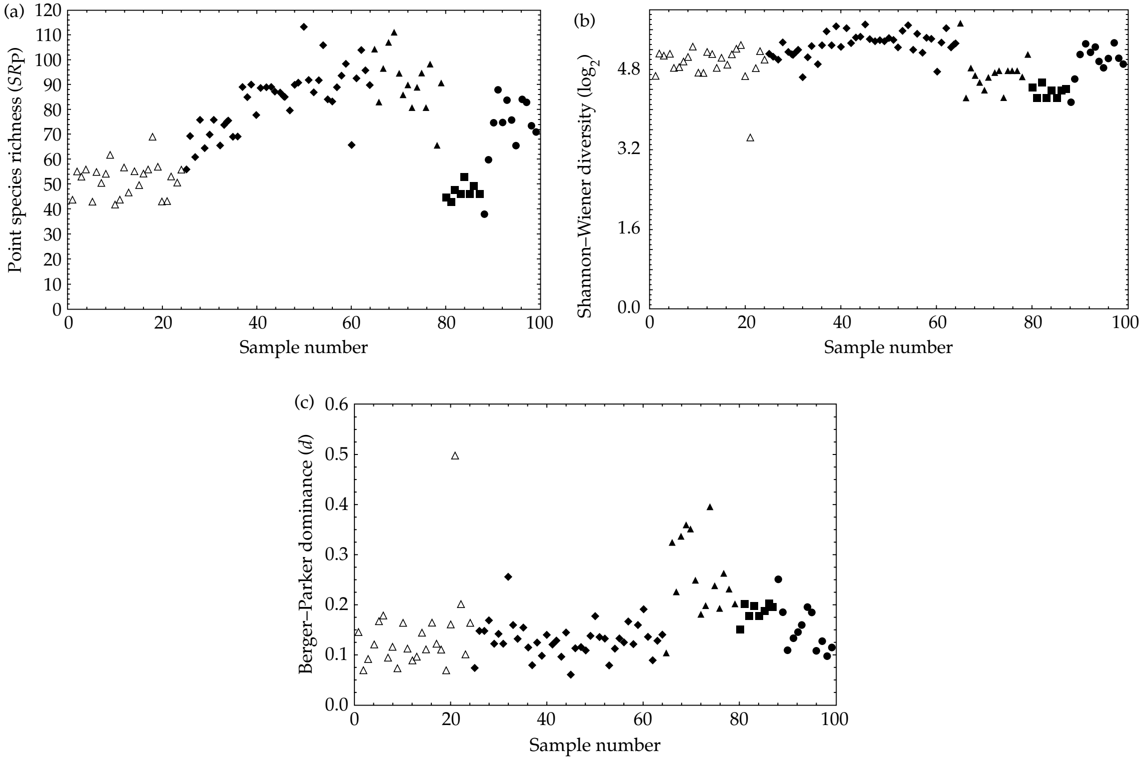


Figure 4.4 Species richness along the Norwegian continental shelf from south to north. The different symbols refer to different regions along the continental shelf. (a) Point species richness for each sample; (b) Shannon-Wiener index for the same data; (c) Berger–Parker dominance index for same data.

of change in, or degree of difference in composition among the samples along a gradient.

The simplest measure of turnover diversity is that of Whittaker (1960):

$$b = \gamma/\alpha$$

where γ is the number of species resulting from sampling a large area and α is the number of species in a single sample. For a single sample $b = 1$ (Whittaker 1975) and for two samples that have no species in common, $b = 2$. For three samples sharing no species, or a larger set of samples with the same total number and mean number of species as those three, $b = 3$, implying that the extent of difference in composition among the samples of the larger set is equivalent to that in three samples with no species in common. Where there is more than one measurement of sample richness it is preferable to use the mean value, and this version of Whittaker's index is widely used:

$$\beta = (S/\bar{\alpha}) - 1$$

An alternative is simply to add the number of new species encountered as new samples are included and subtract the number of species lost. This has been formulated by Wilson and Shmida (1984) as:

$$B_t = \frac{[g(H) + l(H)]}{2\bar{\alpha}}$$

where $g(H)$ is the number of species gained and $l(H)$ the number of species lost, standardized by the average sample richness, and $[\bar{\alpha}]$ is the average number of species found within the samples. Koleff *et al.* (2003) have reviewed all the turnover diversity indices (24 in all) and should be consulted

Table 4.3 Turnover diversity for benthos of five areas of the Norwegian continental shelf measured at two scales β_S and β_L using Whittaker's beta diversity index as modified by Gray (2000).

Area	$\beta_S = SR_S/(SR_P)$	$\beta_L = SR_L/(SR_S)$
Heidrun	3.12	3.80
Snorre	3.94	1.88
Gullfaks	3.19	2.12
Ekofisk	2.77	4.30
Tommeliten	2.23	3.80

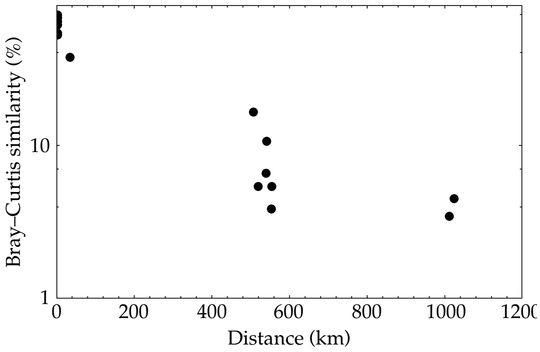


Figure 4.5 Bray–Curtis similarity between the fauna of different areas along the Norwegian continental shelf (from Ellingsen *et al.* 2005).

for a detailed coverage of the merits of the different indices.

Turnover diversity is in many ways more interesting than simple diversity indices such as the Shannon–Wiener, since it considers the biology behind changes in scale. The simplest indices compare the number of species in the regional pool with that in the local one. A high index means that they are very different. An example from the Norwegian continental shelf is shown in Table 4.3. By considering the numbers of species that are found at each of two scales, an idea of possible factors that control local richness can be obtained. Overall values of around 3 for the Whittaker index are quite common in the ecological literature. Yet the surprising aspect is that there is considerable variation at larger scales. The Ekofisk area of the North Sea is flat (72 m ± 2 m depth) and comprised of fine sand with a low number of species. The Snorre field is much more heterogeneous in both depth and sediment type and so this area has a far larger component of the regional pool than does Ekofisk. As discussed in Chapter 3, soft-sediment assemblages are characterized by large numbers of species that occur at only a few sites. Thus immigration from the regional species pool to the local is a major factor affecting the structure of the assemblages.

Another way of expressing turnover is to use measures of similarity based on multivariate statistical analyses (Chapter 3). Using the same data as in Table 4.3, analyses were done to compare the similarity between samples within and between the areas (Fig. 4.5). Not surprisingly, similarity changes with distance and sites that are 1000 km apart share around 5% of species. The interesting aspects of turnover diversity are concerned not just with calculating an index but with going back and examining species lists to discover which species are changing along a gradient and then trying to understand the biology of how the species are changing and the life history characteristics that are associated with such changes. It is worrying that authors are often so eager to report the statistical patterns in their data that they often forget to go back and interrogate the information with regard to the biological and ecological features!

Anderson *et al.* (2006) have developed a new measure of turnover diversity based on multivariate statistics. However, it has not yet been applied to many data sets and so its utility remains to be studied.

4.4 Patterns of diversity in benthic assemblages

In assessing aquatic biodiversity, we have long taken the view that there appear to be a few accepted main principles: that diversity decreases with increasing latitude and with increasing depth, that it increases with increasing habitat complexity (and thus with a greater number of niches), that it increases with the size of a habitat and with the productivity of that habitat (as long as that productivity is not artificially increased through eutrophication), and decreases in what may be regarded as stressed areas such as estuaries. Hence, putting these together, complex shallow tropical areas such as coral reefs will (and do) have a high diversity, and temperate estuaries will (and do) have a low diversity. Furthermore, it is well known that on land there is a gradient of species richness with the tropics having more species than the boreal regions and the boreal more species than the polar regions. It was therefore natural to assume that this latitudinal gradient would also be found in the marine environment. Initial studies in the 1960s indeed found evidence that this was the case; there were found to be fewer species of bivalve molluscs in temperate areas than in the tropics, and fewer still in the Arctic. Yet remarkably few studies had been done in the southern hemisphere, so whether there was the same gradient there remained unknown. On land there is also a well-known gradient with altitude; the species richness of trees, for example, decreases the higher up one samples. What about the species richness of marine soft sediments in the deep sea where depths down to over 11 000 m occur?

One of Britain's most illustrious nineteenth-century naturalists, Edward Forbes, predicted in 1843 that no animal life would be found below a depth of 550 m since there was no light and the pressure was too great. Forbes had overlooked the work of Sir John Ross and his nephew Sir James Clark Ross, who as early as 1817 had obtained many living animals from depths of 1800 m in Baffin Bay, Canada. In 1869, the Sars (1872) (father Michael and son, Georg Ossian), trawled up a variety of marine life from depths greater than 550 m off the Norwegian Lofoten Islands. Forbes's views, however, were influential, and there was still no general acceptance that life existed at great depths. Thus, when the Royal Society set the aims for the *Challenger* expedition, one of the problems to be tackled was the distribution of organic life at all depths of the ocean and on the seabed. This expedition, which lasted from 1872 to 1876, was the first truly scientific oceanographic expedition; it obtained in all 133 dredge samples from the deep sea, which showed conclusively that life does exist at great depths. The number of animals obtained was relatively small, but most were new to science. For almost the next 100 years the pattern was repeated, with expeditions finding many new species of deep-sea animals, but each species being represented by relatively few individuals. Initially this pattern was thought to be an artefact resulting from the fact that the trawls and dredges were not closed, for it seemed likely that many animals were winnowed out on the way up from the great depths. In the 1950s and 1960s better gear became available and it became clear that the earlier expeditions had certainly lost material and that the density of animals was higher than they had found; however, more importantly, far more species were found than were anticipated. The pioneering work of Sanders (1968), Hessler (1974), and Hessler and Sanders (1967) showed clearly that the deep sea held large numbers of species. The question that arises, therefore, is whether there are differences between species richness in tropical, temperate, and polar regions and between the coasts and the deep sea.

4.4.1 The coast–deep sea continuum

Sanders (1968), in his paper describing the rarefaction method for comparing diversity, stimulated a debate that caught the imagination of many workers and resulted in a whole new direction in marine ecological research. Working at the Woods Hole Oceanographic Institution in the USA, Sanders had been studying the benthos of the deep sea for many years. He had amassed data from a wide variety of depths and geographical regions and was struck by two things. First, the deep sea had a high number of species, although the number of individuals per square metre was low. Since the total number of individuals is low and the number of species high, diversity is high however one measures it. Secondly, just as on land, the tropics had a higher diversity than boreal regions. A possible explanation is that natural selection has had a longer time to act in the tropics than it has in the ice-age-prone polar and boreal regions. The processes leading to high tropical diversity are, however, still under dispute. Another theory is that competition there is intense, which means that niches are smaller and so there are more species per unit area. A third theory is that there are more predators in the tropics, which keeps the abundance of prey species low, prevents competition, and thereby allows more species to coexist. The competition and predation theories appear to be mutually exclusive and, as will be shown later, this is at the root of the deep-sea diversity debate.

Sanders' rarefaction curves (Fig. 4.6) indicate that the diversity of the deep sea is higher than that of shallower areas, that tropical areas have a higher richness than boreal areas, and that the Pacific coast of the USA has a higher richness than the Atlantic coast. He explained this high–low diversity pattern by the *stability–time hypothesis*. He postulated that at one environmental extreme, the high intertidal, the fauna is subjected to environmental factors that fluctuate in an unpredictable manner, and as many species are not able to tolerate these unpredictable fluctuations the species complement is low. At one time species A may be dominant, but competitive exclusion does not occur because before this can happen the environment changes, giving a competitive advantage to species B. Sanders suggests that this results in species in intertidal areas having broad, overlapping niches. However, competition and predation effects also operate, and these lead to large fluctuations in population sizes and low diversity. This part of Sanders's argument has been misunderstood and wrongly quoted. Sanders regards species as adapting to the environment and not to each other, hence he calls this the physically controlled habitat. However, he does *not* say, as he has sometimes been quoted, that there are no biological interactions here. In fact, biological interactions of competition and predation may be very severe. The important point is that niche specializations do not occur since the environment is constantly fluctuating.

This point has also been made recently at the other end of the depth spectrum. Estuaries are also highly variable and so the environment is constantly fluctuating, particularly with respect to salinity, temperature, and dissolved oxygen. Its benthos is adapted to those conditions but, by default, other species with narrower environmental tolerances cannot exist there (Elliott and Quintino 2007). There are still biological interactions but within a low diverse system and so these are more likely to be intraspecific rather than interspecific. Finally, estuaries are geologically ephemeral (in many cases existing only since the last ice age), again resulting in little inherent speciation but more dependent on colonization, occasionally from fresh water but usually from the sea.

By contrast, the deep sea is an extremely constant environment, with no light and almost no changes in temperature, salinity, or oxygen from month to month and year to year. Furthermore, it has remained constant for a very long time (probably hundreds of thousands of years) compared to the glaciated boreal and polar regions. This constant environment over evolutionary timescales has enabled species to adapt to each other rather than

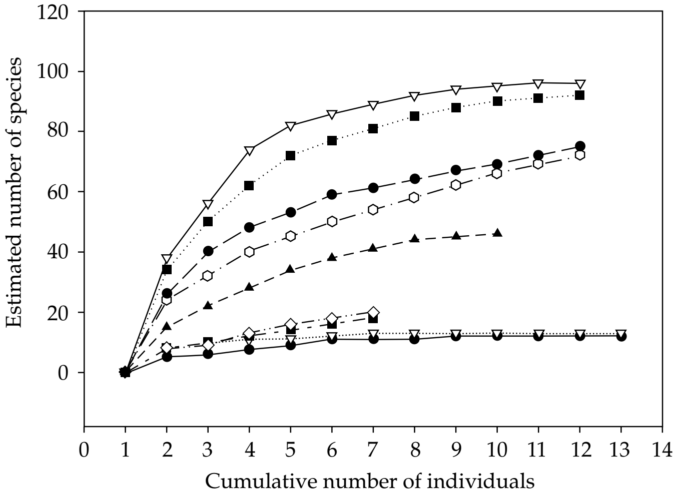


Figure 4.6 Sanders's stability–time hypothesis was developed in analysing anchor-dredge samples of the benthos of soft sediments of shallow and deep sea areas. Here rarefaction curves are shown. ▽, ■ tropical shallow; ●, ○ deep sea; ▲ boreal Pacific; ◇ boreal Atlantic; lowest curves, ●, ▽ tropical estuary.

needing to adapt to the rigours of the environment, as is the case in the intertidal area. The deep-sea species at one time competed for the most important limiting resource: food. Since the amount of available food reaching the deep-sea bottom from the surface is small, densities of animals per square metre are low. Over evolutionary time the species have become what Sanders called *biologically accommodated* to each other and now have narrow, non-overlapping niches. The main point of Sanders's argument, then, is that competition is the causal mechanism that, over evolutionary time, has led to high deep-sea diversity. The problem is that this must remain a hypothesis since it cannot really be tested.

Following the publication of Sanders's stimulating paper, Dayton and Hessler (1972), from the Scripps Institute of Oceanography at the University of California, suggested that rather than competition being the causal mechanism of high deep-sea diversity, predation was the key. They argued that there was no evidence that deep-sea species were more specialized than their shallow-water counterparts, as would be necessary in a competitive situation. Dayton and Hessler lowered bait (dead fish) and arranged a camera with flash so that any species coming to the bait could be photographed over various time periods. Surprisingly, they found that high abundances of fish, amphipods, isopods, and ophiuroids were attracted to the bait within a few hours, in an area where food was supposedly very scarce. Dayton and Hessler termed these organisms 'croppers' rather than predators since they surmised that their effect on the benthic sediment of living organisms may not be a direct predator–prey response but rather the result of unselective feeding or even chance destruction by the cropper without the benthic organisms being ingested. It is these croppers, they suggested, that account for the high deep-sea diversity, by holding benthic population densities below the level where competitive exclusion can occur. (This is an analogous argument to that of predators being responsible for high tropical diversity.) The input of food in this way, as a sudden and localized deposition of a carcass, say, can be regarded as 'an ephemeral oasis of organic matter' in an otherwise poor area which then attracts scavengers and thus gives an inverted food pyramid (Gage and Tyler 1991). Since food is argued to be the limiting resource that is competed for in the deep sea, all the deep-sea species with non-overlapping niches must have specialized in utilizing the food in different ways in order to avoid competing with each other. Dayton and Hessler also reviewed all the available data on feeding specializations in deep-sea infaunal species and suggested that rather than their being specialized, most were generalists eating anything that was available, which is in keeping with the predictions of the cropping and ephemeral-oasis argument.

In the best scientific tradition, back came Sanders with a counter-argument, with Grassle as co-author (Grassle and Sanders 1973). They showed by the size-frequency distributions of known deep-sea species that there was a high proportion of older individuals. If cropping was indeed general in the deep sea, one would expect that there would be a superabundance of young stages, since in terrestrial habitats prey species adapt to high predation pressure by producing more young, thus ensuring that a sufficient number of individuals survives to reproduce. But size-frequency analyses of the deep-sea species that have been studied show that there are relatively few individuals in the smallest classes. Furthermore, Grassle and Sanders argued that feeding specializations need not be to different food items (such as mechanisms for dealing with different sized particles) but could be biochemical in nature, such as those specializations in digestive enzymes that are known to allow up to four species of polychaete to coexist on apparently the same food source. Deep-sea species may well show such specializations, but no one has as yet tested this suggestion.

Jumars (1975), one of Hessler's former students, took the obvious next step: he measured another possible source of niche specialization, spatial pattern, that would result if there was competition for space between deep-sea species. The argument here is that species may show more intense patchiness in the deep sea than in shallow areas, since deep-sea species are supposedly more specialized. He took large box-corer samples of deep-sea sediments and divided the samples into many small subsamples. He found that most species were, in fact, randomly distributed and there was no direct evidence that patchiness was more intense in deep-sea species. The problem is that since the food supply to the deep sea is so low and therefore densities are low, much greater areas must be sampled in the deep sea than in shallow areas in order to determine distribution patterns. Hence it is very difficult to make direct comparisons and one cannot expect to find the same patterns in the deep sea and shallow areas.

Houston (1979) was able to reconcile these apparently opposing views. He was concerned with diversity patterns in general and not specifically deep-sea diversity and he noticed a number of anomalies in the arguments as to why diversity was high in some areas and lower in others. For example, none of the current theories on diversity could explain the low-diversity communities which occur in highly predictable environments (coastal redwoods, freshwater marshes) or the high-diversity communities in unpredictable environments (Sonoran desert, some marine communities). Houston's argument was that there is a population level at which a species begins to compete with other species. This he calls *competitive equilibrium*, and it varies from species pair to species pair. If there are many species in an assemblage, all with low growth rates, then competitive equilibrium will not be reached for a long time and diversity remains high over the time period in question. If one species grows fast, however, it can rapidly reach competitive equilibrium and begin to exclude the other species, and so diversity decreases. So one important variable determining diversity values is the relative growth rate of species within a community.

If the species which potentially can outcompete the other species in the above case is removed, either by predators or by an environmental factor, then diversity can still be kept high since competitive exclusion does not occur. Therefore, the frequency of population reduction is another important variable affecting diversity. Figure 4.7 illustrates these ideas. Where growth rates of competitors are low, diversity is low at low frequencies of disturbance, provided that the time between successive disturbances is long enough for species to approach competitive equilibrium. Moving up the growth rate axis, diversity is maximized when the frequency of disturbance just prevents competitive equilibrium being reached. If growth rates of all competitors are high, then diversity will be low because at low frequencies of population reduction there is a rapid approach to competitive equilibrium. Along the other axis, at a low frequency of disturbance, diversity rises rapidly with a small increase in growth rate. But if frequency of disturbance rises when there are low growth rates, diversity becomes low since some species are eliminated. With high frequencies of disturbance and high growth, a higher diversity will be achieved because populations are able to recover from the disturbance—thus Houston's argument is very convincing.

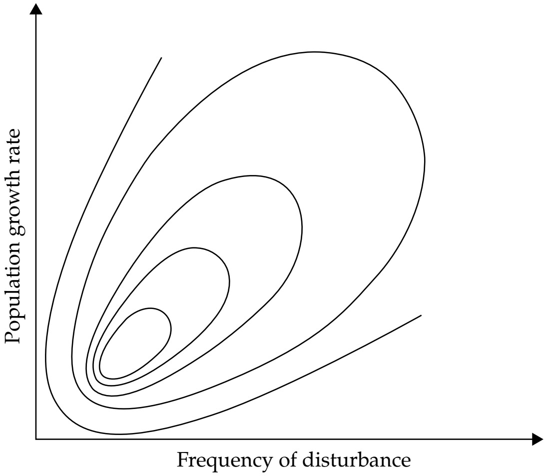


Figure 4.7 Houston's model of diversity; the optimal conditions for development of diversity are where the frequency of disturbance is low and population growth rates are low, as is found in the deep sea; the contours indicate a decrease from those optimal conditions.

In support of Houston's arguments, the deep-sea benthos is characterized by *K*-selected species (see p. 118) in which good competitors have long turnover rates and long lifespans and where growth rates in the deep sea are probably exceedingly slow (Turekian 1975, Hsü and Thiede 1992). Living specimens of the bivalve *Tindaria callistiformis*, which measures only 8.4 mm, were obtained from 3800 m depth and dated using radium (^{228}Ra) dating. *Tindaria* does not reproduce until it is around 50–60 years old and it can survive for over 100 years. If such properties are general, then growth rates are low. However, the important point as regards

Houston's argument is *relative* growth rates and the rate at which populations approach competitive equilibrium. On this we have no information. It also seems probable that the frequency of disturbance is lower in the deep sea than in coastal areas. The chance of a falling carcass, as used by Dayton and Hessler in their baited camera, is probably low over the whole area of the deep sea and so disturbance from croppers reducing population densities must be of low frequency. From these two considerations, then, it might be expected that the deep sea lies near the optimum region of Fig. 4.7 where diversity is maximum. There is, however, a potential source of disturbance in the deep sea which has not been studied, and that is deposit feeders reworking the sediment and thus affecting potentially competing species by interference competition (see Chapter 7).

In shallow areas the frequency of disturbance is high, both from environmental factors and from predation, and so diversity is lower there. Similarly, the more rapid growth rates associated with increased food resources also tend to lead to a more rapid approach to competitive equilibrium. As in the deep sea, though, reworking as a disturbing agent could counteract the growth rate effect. The balance between the two factors is crucial to our understanding of diversity patterns. It is interesting to note that in a highly predictable environment with no environmental disturbance Houston's model predicts lowest diversity, whereas the stability–time hypothesis predicts maximal diversity.

Despite the above generalizations, however, it should be noted that diversity does not increase linearly with depth. There appears to be a depth zone between 1500 and 2500 m where diversity is highest. This has been shown for a variety of organisms, not only the benthos but in fish assemblages and in foraminiferan assemblages. The deepest parts of the deep sea go down to over 10 000 m, but below 2500 m diversity gradually decreases and is lowest in the deepest deep sea. The very deepest parts are in trenches and it could be argued that here occasional turbidity currents rolling down the slopes give a more unstable environment than in the flat plains, thus leading to lower diversity. But the average depths of the deep sea are around 5000–6000 m and here diversity values are lower than on the slopes. The reason for the low density of organisms on the deep-sea floor is clearly the small amount of food available, either as settling organic matter or produced *in situ*—indeed, most of the organic matter entering the system is from 'marine snow' resulting from the surface photic zone or the coastal margins or, to a lesser extent, emanating from ephemeral vent areas supporting chemosynthetic production. The settling organic material is broken down on its passage downwards and relatively little nutrient remains by the time the particles reach the seabed. Similarly, since there is no light there is no primary photosynthetic production on the deep seabed, and bacterial production must be limited since the organic substrate is limited except at the vent areas.

The reasoning above was the state of the art until the 1990s, when the ideas about the high diversity of the deep sea were questioned. Grassle and Maciolek (1992) showed extremely high diversity in soft-sediment assemblages sampled off the coast of New Jersey (USA eastern seaboard). Along a 1200 km transect at depths between 1500 m and 2100 m they recorded 900 species from just 12 km^2 of sediment area sampled. Sanders had previously only worked with polychaetes and bivalves, which he claimed represented the whole fauna. The number of species he found was only 100 even in the tropical areas, compared with Grassle and Maciolek's 900. Grassle and Maciolek went a huge step further in predicting how many species could be found in the deep sea and came up with a figure of 10 million! This was based on the rate of capture of species and the area of the deep sea. It was soon pointed out that you cannot extrapolate beyond the scale in which you have sampled and since there are only 1.4 million species described for planet earth, 10 million deep-sea species seems highly unlikely.

One of us (JSG) used data available for the coastal areas of Norway to show that the number of species was not very different from the deep sea (Gray 2000; Fig. 4.8). Just over 600 species were found in the samples from the deep sea. The continental shelf of Norway had species accumulation rates that were similar to those of the deep sea and similar numbers of species. Note the rapid increases in number of species as samples are taken from new

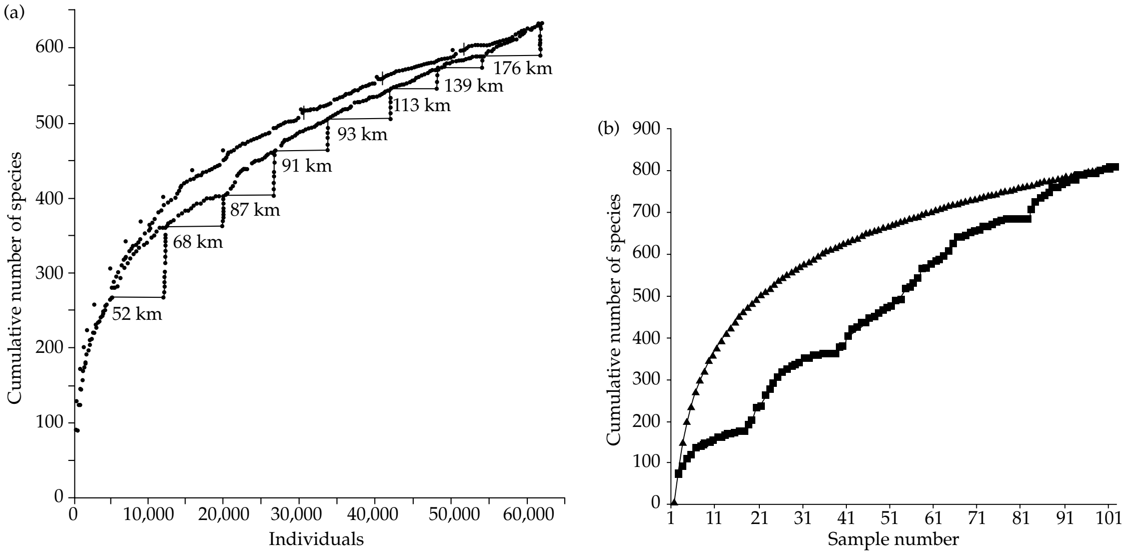


Figure 4.8 Plots of species accumulation curves: (a) Deep sea (Grassle and Maciolek 1992); top curve, rarefaction curve; lower curve, samples combined over time within stations and then a geographical accumulation north-west to south-east; middle curve, samples accumulated according to station within each time interval. (b) Coastal areas of Norway, species accumulation curve (▲) using analytical model and geographical accumulation curve (■) from south to north.

areas, both in the deep sea and in coastal areas. However, the deep-sea data covered just 10 m^2 whereas the Norwegian data covered 50 m^2. In the Bass Strait, Australia, richness was even higher than the deep sea with 800 species occurring in just 10 m^2 of sediment; hence we can conclude that some coastal areas have richness comparable to that of the deep sea.

The deep-sea researchers argue that in the deep sea the curves do not approach asymptotes and if one compares shallow and deep seas then the deep-sea curves are steeper. This may be true in general but is not so for the Bass Strait sample. Gray (2005) agreed that the deep sea had higher numbers of species for a given area, called *species density*, compared with coastal areas. His review argued, however, that it was by no means clear that overall the deep sea had higher richness and what one needed to compare was richness over different spatial scales, which has not yet been done. It is quite likely that species accumulation curves for a comparable large area of the deep sea are higher than for coastal areas, but such data are not yet available. Too often data are compared for point or sample richness rather than the large areas that need to be studied if valid comparisons are to be made to test evolutionary rather than ecological hypotheses. Another point that needs to be made is that deep-sea researchers often argue that one can only compare the species richness of very fine deep-sea sediments with very fine coastal sediments, thus confining the comparison to one small part of coastal sediments. We should then question why it is not reasonable simply to ask whether species richness is greater in coastal sediments than in the deep sea. Since coastal areas have many more habitats (are more heterogeneous) and more patchy habitats than the rather uniform deep-sea soft sediments, overall species richness (and probably diversity) must intuitively be higher in coastal areas than in the deep sea.

4.5 Latitudinal and longitudinal gradients of diversity

As indicated earlier, one of the most widespread patterns of diversity known is on land, where there is a cline of increasing diversity as one goes from the poles to the tropics. When studies were first done in the 1950s it appeared that a similar gradient occurred in the sea. Yet recent data suggests that the patterns in the sea are far more complicated and the explanation more complex than a simple cline suggests. Most of the data, not surprisingly, is from the northern hemisphere. On the eastern and western seaboards of the USA, gastropod molluscs show an increase in richness from the Arctic towards the equator, but there is maximal richness in the subtropics rather than in the tropics. Similar trends have been suggested for Europe, but here the influence of the North Atlantic drift is strong and in the Barents Sea at 70°N there is high species richness in the soft-sediment benthos. The Mediterranean Sea has relatively high richness and the Baltic Sea low richness. However, the Baltic Sea is only 8000 years old—it was a freshwater lake before that—so species are still invading and the sea has not yet had time to reach an ecological equilibrium.

We have little data on soft-sediment species richness from the coasts of South America or Africa. We know that Australia has very high richness and Antarctica is not species poor and, for some taxa (such as sponges and amphipod crustaceans), richness is remarkably high. Teleost fishes and bivalves have lower richness in the Antarctic and it has been suggested this is because species have not yet had time to reach the area and to equilibrate with the existing species.

Figure 4.9 shows two centres of patterns of species richness in living bivalve molluscs: in Indonesia and in the Caribbean (Crame 2000a). The highest richness for corals is in the Indonesian archipelago, and coral richness (like bivalve richness) decreases in all directions from this area. This is similar to the pattern on land, and it suggests that the Indonesian archipelago is a 'cradle' for the evolution of diversity (Crame 2000a, 2000b). However, others argue that the pattern is in fact the result of extinctions rather than speciation and what we have left is a 'museum' of past extinction rates. Again this debate is unresolved. The bivalve data in Fig. 4.9 also show a centre of high richness

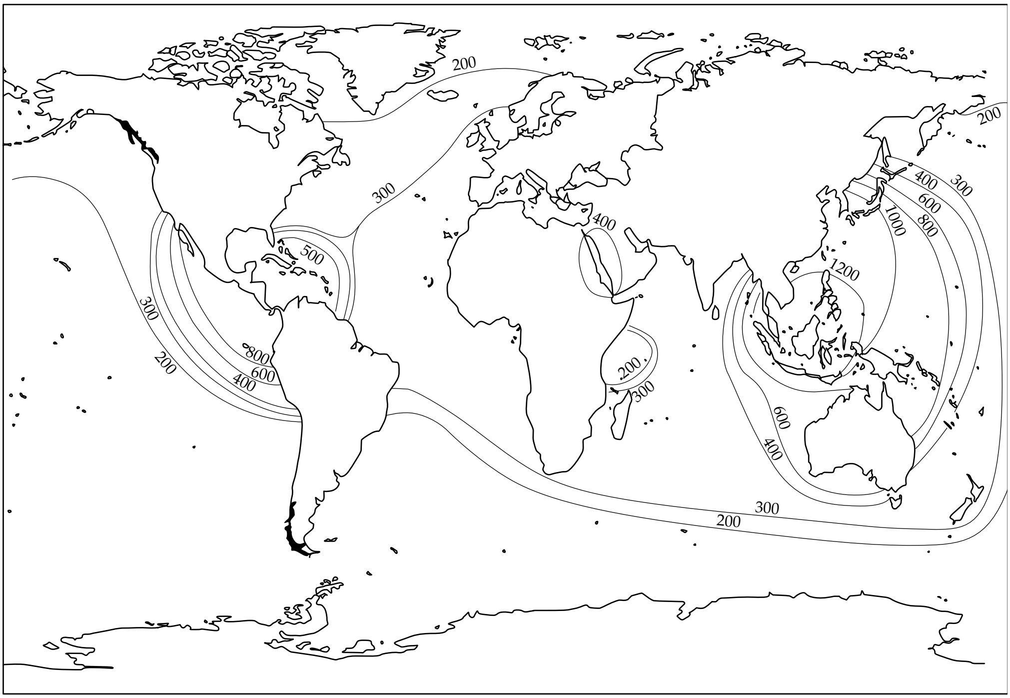


Figure 4.9 Diversity patterns of bivalve molluscs (from Crame 2000a).

in the Caribbean which does not occur in corals—the Caribbean has low coral richness (60 species compared with Indonesia's 600 species). To our knowledge there are no theories as to why there is a 'hot spot' of high richness for molluscs in the Caribbean. Thus we can conclude that we need far more studies of soft-sediment diversity in the tropics and in the southern hemisphere before we are able to draw firm conclusions about the general patterns of marine biodiversity.

4.6 The link between species richness and system function

One of the key questions that is a worldwide focus for research today is the link between diversity, structure, and function of communities and in particular how important are the species and their diversity in the functioning of the sediment system. A second question is whether this link exists in any, several, or all marine habitats from estuaries to the deep sea (Elliott *et al.* 2006). This is referred to as the *biodiversity–ecosystem functioning debate* (Loreau *et al.* 2002) in which it is often assumed that a higher biodiversity produces better functioning. The extensive review of this topic by Hooper *et al.* (2005) indicates that we need to consider the links between biodiversity and ecosystem functioning but, together with Loreau *et al.* (2002), indicates that the marine system has been relatively overlooked in gathering evidence compared to terrestrial and microbial systems. As we have seen, many marine soft sediments are species rich, but are all the species needed for the efficient functioning of the system? We have shown (in Chapter 3) that most species are rare in typical undisturbed assemblages. In sandy sediments off the Norwegian coast approximately 70% of the species occur as single individuals, whatever the size of sample. We suggested that this was possibly an artefact because we sample only a very small proportion of the whole available sediment. Assuming this figure is a general one, it seems reasonable to presume that only a few species are really important in providing the functions and these will be the dominant species in relation to biomass and numerical abundance. Another way of expressing this is that most species are redundant and provide little to functional processes. However, others argue that all species are important and most if not all are needed for the efficient functioning of a system.

There are a number of hypotheses relating to structure–function relationships (Fig. 4.10):

- The *all species are equal* hypothesis: it is assumed that loss of any species has some impact on the functioning of the system and loss of functioning is proportional to the number of species lost.

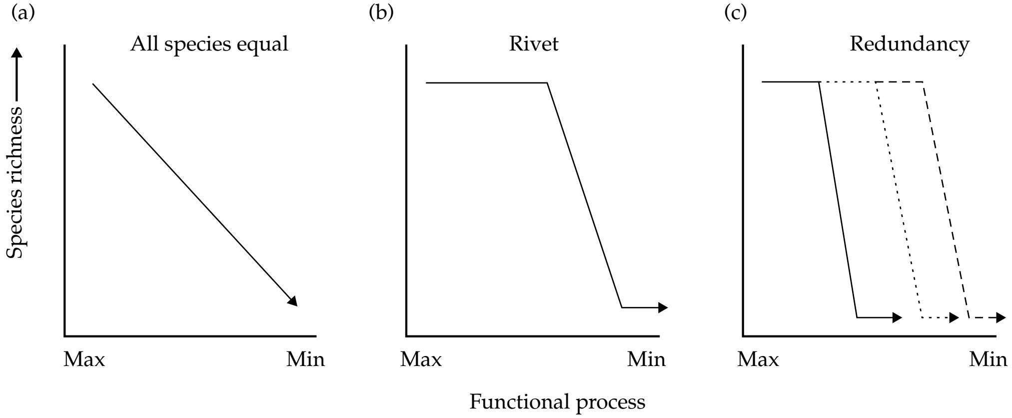


Figure 4.10 Hypotheses of the relationship between species richness and function in communities: (a) all species equal; (b) rivet hypothesis; (c) redundancy hypothesis. For explanation see the text (vertical axis represents number of species).

- The *rivet hypothesis*: species are envisaged as the rivets holding together the wing of a plane. As rivets (species) are removed, nothing happens until a critical rivet (species) is removed, the wing falls off and the plane crashes (functional processes change abruptly).
- The *redundancy hypothesis*: most species in the assemblage have few interactions with other species and the loss of a species has little overall impact on the functioning of the system until a point when a critical species is lost, which leads to collapse of the system with functional properties greatly affected. The point where this occurs will depend on the specific assemblage and species composition and other environmental factors. Figure 4.10 illustrates three places where the loss of an important species occurs.

In terrestrial and microbial ecology, where the theories are most well advanced and even tested, there has been a heated debate over this issue (e.g. Loreau *et al.* 2002). Proponents of the redundancy hypothesis argue that only a few species actually matter functionally in an assemblage since most species are redundant and play little or no role in functional processes. Experiments with plants done in mesocosms (large experimental facilities where fairly natural assemblages could be manipulated) and in the field in the USA showed that the loss of only a few species changed overall primary production, a functional process. This resulted in a counter-argument that the reason for the change in overall productivity was because by chance a species of legume was included and since these fix atmospheric nitrogen it was not surprising that productivity increased. This effect was called the *sampling effect*. This suggests that the identity of the species involved is important; it is clearly not simply how many species are removed, but which species are removed (or are present) that counts. Following these findings, large-scale experiments were done all over Europe on plant systems in an attempt to resolve the controversy. A large meeting was called and the outcome was a book *Biodiversity and Ecosystem Functioning* (edited by Loreau *et al.* 2002) which summarizes the issues. However, although Loreau *et al.* (2002) devote a large amount of attention to terrestrial and microbial systems and even some to fresh waters, the marine system is notable by its absence, thus even suggesting that perhaps the biodiversity–functioning link is less well developed in more open systems. The summary points out that although significant effects of species richness on primary production and nutrient retention in grasslands have been found, it is not clear that these results can be generalized to other systems. In particular many issues are not studied, and of these a very major one is the below-ground processes affecting nutrient retention and plant productivity. Here microorganisms hold the key to understanding the processes, and as important research has begun in this using marine systems, this topic will be covered in Chapters 7 and 10 on system function.

There is an increasing number of macrobenthic studies attempting to determine whether reductions in diversity can affect essential ecosystem processes, especially productivity. Bolam *et al.* (2002), for example, studied the relationships between macroinvertebrate species richness and biomass and ecosystem functions in a soft-bottom, intertidal system. In a field experiment using cages with different mesh sizes (195, 300, and 3000 μm), they created low, medium, and high values for species richness and biomass treatments through differential colonization of defaunated sediments. All treatments contained species within the same five main functional groups of macroinvertebrate, but species identity varied both within and between treatments and a total of 27 macroinvertebrate species were sampled across all treatments; 37% of these occurred in the low, 52% in the medium, and 74% in the high-diversity treatments. In measuring many sediment variables at the end of the 6 week experiment they found that changes in biomass and species richness had significant effects on oxygen consumption and that these relationships were caused in particular by the presence of the largest species in the study, the catworm *Nephtys hombergii*. They concluded that there was no relationship between ecosystem functions, diversity, and biomass but that the diversity–biomass–ecosystem function relationships in the soft-sediment benthos may depend more on functional groups than on species richness.

Another area in which the biodiversity–ecosystem functioning debate needs to be further explored is where the marine system contains some areas which have naturally low diversity, for example brackish and estuarine systems and environmentally stressed areas. In areas of naturally low diversity, because of natural stressors and a high inherent variability, there are only a few, highly tolerant species although these may occur in high abundances (Elliott and Quintino 2007). Despite this, the areas still function well and indeed support high levels of wading bird and fish predators. This yet again indicates the need to explore these debates in marine and coastal systems.

CHAPTER 5

Functional diversity of benthic assemblages

Now that we have discussed how assemblages of marine soft sediments are structured, we need to consider functional aspects. There are a few main interrelationships that need to be discussed here—inter- and intraspecific competition, feeding and predator–prey interactions, the production of biomass, and the production and delivery of recruiting stages. Other functional aspects, such as the effects of pathogens and parasites and the benefits of association (mutualism, parasitism, symbiosis, etc.) are of less importance in the present discussion. By function we mean the rate processes (i.e. those involving time) that either affect (extrinsic processes) or are inside (intrinsic processes and responses) the organisms that live in sediments. Hence these include primary and secondary production and processes that are mitigated by the organisms that live in sediments, such as nutrient and contaminant fluxes into and out of the sediment. We begin with the historical development of the field since such aspects are often overlooked in these days of electronic searches for references.

5.1 Ecological functioning

Functional studies of ecosystems really began with Lindeman's classic paper (1942) on trophic dynamics. Rather than regarding food merely as particulate matter, Lindeman expressed it in terms of the energy it contained, thereby enabling comparisons to be made between different systems. For example, 1 g of the bivalve *Ensis* is not equivalent in food value to 1 g of the planktonic copepod *Calanus*, so the two animals cannot be compared in terms of weight, but they can be compared in terms of the energy units that each gram dry weight contains. The energy unit originally used was the calorie, but this has now been superseded by the joule (J), 1 calorie being equivalent to 4.2 joules. *Ensis* contains 14 654 J g^{-1} dry wt and *Calanus* 30 982 J g^{-1} dry wt.

The basic trophic system is well understood and can be summarized as we showed earlier in Fig. I.8 which gives the links between various trophic levels and the role of competition, organic matter transport, and resource partitioning. In systems fuelled by photosynthesis (so excluding the chemosynthetic deep-sea vent systems), the primary source of energy for any community is sunlight, which is fixed and stored in plant material, which thus constitutes the first *trophic level* in the ecosystem. When herbivores feed on plants the energy stored in the plant protoplasm is transferred to the animal's protoplasm (i.e. to the next trophic level). But, according to the second law of thermodynamics, the efficiency of the transfer can never be 100%; much energy is 'lost', for example by respiration. When carnivores consume herbivores, a similar loss of energy results. Energy therefore flows constantly through the system, the rates of flow for the seabed being measured as J m^{-2} d^{-1}.

Lindeman measured the ecological efficiency between two trophic levels of an ecosystem as

$$I_t / I_{t-1} \times 100$$

where I is energy intake and t is trophic level. In his study area, Cedar Bog Lake in Minnesota, USA, Lindeman found an average ecological efficiency over all trophic levels of 10% (range 5.5–22.3%). Since his work, the value 10% has been widely accepted, although in marine planktonic systems, at least, efficiencies appear to average around 22–25%.

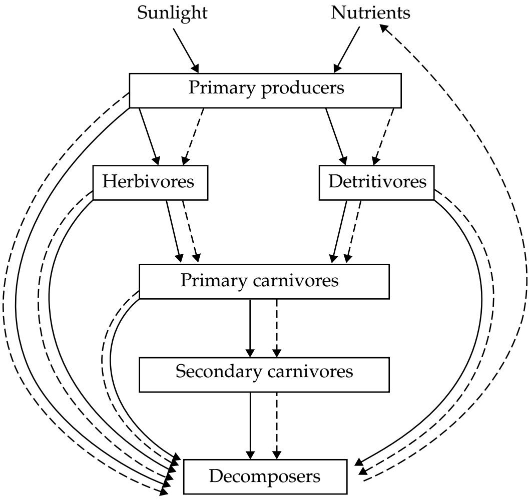


Figure 5.1 Flow of energy and elements in an ecosystem.

Figure 5.1 illustrates diagrammatically the idealized trophic structure of a typical ecosystem. Much material passes directly to the decomposer cycle to be ultimately recycled as nutrients. Of course, no system is closed as shown here, and material is exported and imported by migrating species and transported by physical forces such as the hydrographic regime. Many species also feed at more than one trophic level, or occur at differing trophic levels depending on age and stage (the so-called *ontogenetic shift*), greatly increasing the complexity of the system.

The calculation of the ecological efficiency of a complete ecosystem is an inordinately complex and time-consuming task, and one that has rarely been tackled. As a first approach to functional studies, many workers have concentrated on comparing how much organic material is produced by different species in the course of a year. This is a much more realistic goal than calculating ecological efficiencies of all the species, and indeed is the approach that has been adopted, over a long period, in studies of benthic communities.

5.2 Secondary production in benthic macrofauna

The organic material produced within a community by plants is called *primary production*, since green plants produce their organic matter directly from sunlight via photosynthesis. Animals have to obtain their energy by ingesting other animals or plants, and hence production by animals is called *secondary production* (e.g. Elliott and Taylor 1989). Production may be defined as the increase in biomass (organic matter) by organisms whether that organic matter is accumulated as growth (i.e. somatic production) or as reproduction which may, in the case of many benthic organisms, be liberated as eggs, sperm, and larvae. This was a priority area of research from the 1960s to the 1980s, culminating in the International Biological Programme (e.g. Crisp 1984 in Holme and McIntyre 1984), but it has now largely gone out of fashion, even though it is fundamental for determining the material available to support higher predators and therefore determining the carrying capacity of the system. Somatic production is based on the *method of Allen curves*, in which, for any given year class or cohort, a decrease in abundance over the lifespan is more than matched by the increase in average weight of a member of the cohort. The integration of the area under this abundance–mean weight curve thus gives the cohort production. Although few such studies are done today, the methods are important to understand and so we make no apology for giving a detailed coverage of the topic.

The earliest data on production of benthic species are those of the Danish biologist Boysen-Jensen (1919). In an 8-year study of the fauna of a bay in the Limfjord he estimated population numbers in April each year and from these and data of weights he calculated production. For example, in *Corbula gibba*, a bivalve which reproduces annually, he found in April 1912 a recruitment of 162 individuals to the population under study. These had a total weight of 3.9 g. By April 1913 there were only 90 of these individuals left, with a total weight of 3.4 g. His estimate of consumption (today called elimination, E) by the plaice *Pleuronectes platessa* was

$$N_1 - N_2 \times 0.5\,(\bar{w}_1 + \bar{w}_2),$$

where N_1 is the original number of individuals, N_2 the final number, and $\bar{w}_1$ and $\bar{w}_2$ the respective average weights. In this case:

$$E = 162 - 90 \times 0.5\,(3.9/162 + 3.4/90)$$
$$= 2.23\ \text{g}.$$

He also calculated the production (P) during the year, by adding the stock (the biomass of the population at a given point in time) at the year-end (B_1) to elimination and subtracting the standing stock at the beginning of the year (B_0):

$$P = 2.23 + 3.4 - 3.9 = 1.7\,\text{g}.$$

Today this method of calculating production is still used. It can be written formally as

$$P = (B_1 - B_0) + E. \tag{5.1}$$

Boysen-Jensen realized that *Corbula*, which has infrequent recruitment, was a special case and that normally recruitment (in g) must be added to equation 5.1 to give a proper estimate of production. Recruits will, of course, be included in the change in standing stock biomass at the year-end.

The problem with Boysen-Jensen's method, of which he was aware, is that it assumes that all elimination occurs at the end of 6 months (0.5 × 1 year) and on the mean weight of animals. Boysen-Jensen regarded the likely errors resulting from this to be small, whereas, in fact, they can be very large. Predation, if it occurs at a constant rate, will lead to a constantly diminishing population, and the mean mortality (and hence biomass) will be reached well before 6 months.

The obvious refinement is to take samples more frequently; Crisp (1984) points outs that the shorter the sampling interval, the better will be the final production estimates. Howard Sanders (1956) produced a curve of log weight of individuals against time (growth) and log numbers against time (survivorship). The population was assumed to be composed entirely of recruits that had settled just prior to the first sampling, so that the initial standing stock biomass (B_0) was assumed to be zero. Figure 5.2 shows the results obtained for the polychaete *Nephtys incisa*. Instead of annual measurements, observations were made at 3 month intervals, but the curves were derived using Boysen-Jensen's method. Elimination and growth could be calculated over each time interval and figures for annual production obtained.

Sanders reports for the first time the production/biomass ($P/\bar{B}$) ratio, where $\bar{B}$ is the average annual standing stock biomass, which is now a widely used measure of ecological efficiency. In the above example $P/\bar{B}$ is 9.34/4.32 = 2.16. Boysen-Jensen gives the equation for production (what he calls growth) as:

$$P = E + B_1 \div \bar{B}$$

This equation was faithfully reproduced by Sanders in his paper (p. 391) and he went on to compare annual production in different species by means of this ratio. Unfortunately, the '÷' sign in Scandinavian languages means minus and not divided by. It seems possible, therefore, that the widely used $P/\bar{B}$ ratio arose fortuitously from a misunderstanding!

Although there are few examples of detailed estimates of production of species in recent literature, it is important that students understand the principles of how production is calculated. An example is Kirkegaard's (1978) study of the polychaete *Nephtys hombergi* in the Isefjord, Denmark. Table 5.1 shows the detailed calculations. The

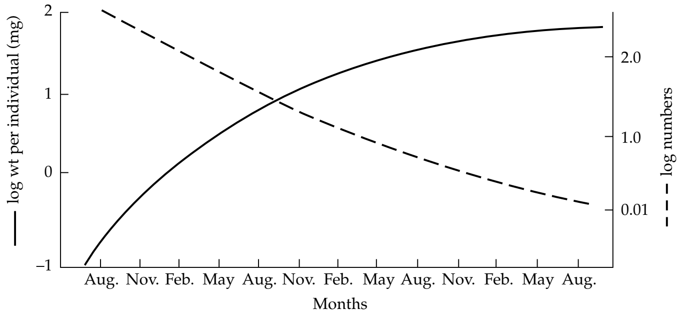


Figure 5.2 Survival (dotted line) and growth (solid line) of a population of the polychaete *Nephtys incisa* (from Sanders 1956).

Table 5.1 Production calculations for the polychaete *Nepthys hombergi* from Isefjord, Denmark, 1970–1 (from Kirkegaard 1978).

Age (months)	Mean density (m^{-2})	Mean weight (mg)	Biomass (mg m^{-2})	Growth increment (mg m^{-2})	Elimination loss (mg m^{-2})	Production (mg m^{-2} $months^{-1}$)	Annual net production (mg m^{-2})	Annual mean biomass (mg m^{-2})	$P/\bar{B}$
0 (1 Aug)	47	–	–	–	–	–			
1	42	20	840	840	50	890			
2	38	40	1520	760	40	800			
3	34	48	1632	272	16	288			
4	31	50	1550	62	3	65			
5	28	51	1428	28	2	30			
6	25	52	1300	25	2	27			
7	22	53	1166	22	2	24			
8	20	54	1080	20	1	21			
9	18	55	990	18	1	19			
10	16	60	960	80	5	85			
11	15	80	1200	300	10	310			
12	14	120	1480	560	20	580	3139	1262	
13	13	160	2080	520	20	540			
14	10	185	1850	250	38	288			
15	8	200	1600	120	15	135			
16	6	208	1248	48	8	56			
17	5	209	1045	5	1	6			
18	3	210	630	3	1	4			
19	3	212	636	6	0	6			
20	2	214	428	4	1	5			
21	2	216	432	4	0	4			
22	1	220	220	4	2	6			
23	1	245	245	25	0	25			
24	1	280	280	35	0	35	891	1110	
25	1	320	320	40	0	40			
26	1	340	340	20	0	20			
27	1	355	355	15	0	15			
28	1	360	360	5	0	5	80	344	
Total							4329	2497	1.73

shorter the time period over which the changes are measured then the more accurate the estimates, so in this case the mean density and biomass are estimated each month and the mean weight can be derived from these figures by division of biomass by numbers of individuals. Production is usually calculated directly rather than as the sum of growth and elimination, as Kirkegaard has done, but Kirkegaard's method of presenting production is easier to understand and therefore is used here. Traditionally, production is calculated either by:

$$P_{(t_1-t_2)} = \sum_{t=t_1}^{t=t_2} \Delta N \Delta \bar{w} \qquad (5.2)$$

or

$$P = N_1\bar{w}_1 + \sum_{t=1}^{t=2} \Delta\bar{w}\Delta N, \qquad (5.3)$$

where N is the number of survivors at time t, $\bar{w}$ is the average weight of an individual over the time interval $t_1 - t_2$, and ΔN and $\Delta\bar{w}$ are the changes in numbers and weight respectively over the same time interval. Equation 5.2 calculates production increments and equation 5.3 elimination increments—again, essentially this is the method of Allen curves (Crisp 1984; see also Bagenal 1978) in which the production is estimated from each cohort and for each time period and then summed to give the production over the whole lifespan of the cohort and the whole set of cohorts which constitute a population. Both of the above methods will give the same result over similar time periods. In the case of Kirkegaard's data, using either equation 5.2 or equation 5.3 gives the same figure for production *over the life cycle of the species*, namely 4329 mg m^{-2} (although one has to assume that the last individual is eliminated at a weight of 880 mg to balance the equation!).

Production estimates are fairly easy to obtain provided that recruitment occurs at one point in time or that age classes are easily separable—again see the very clear description and tables for calculation given by Crisp (1984). As an example, in assessing the production of several benthic infaunal species, Elliott and Taylor (1989) showed that for many species the low densities and continuous or lengthy periods of settlement made it difficult to identify cohorts and thus calculate production. However, the echiurid *Echiurus echiurus* has a single, well-defined spawning and settlement each year and an easily followed cohort which then persists only until the spawning the following year. Consequently, production was easily calculated.

In other species, if recruitment occurs continuously at the same rate as mortality, then using the methods outlined above there would be no change in numbers, mean weight, or standing stock biomass, and, hence, no production. But if the age classes can be separated then production can still be calculated. In the case of the polychaete *Nephtys*, Kirkegaard was able to use the chitinous jaws to age the specimens, since they bear discernible growth disturbance rings. Figure 5.3 shows fairly typical size–frequency data for two species of bivalve, *Mya arenaria* and *Macoma balthica*. Here the age classes were separated by growth rings and by using probability paper. Such methods were then combined to give the production for dominant species in a

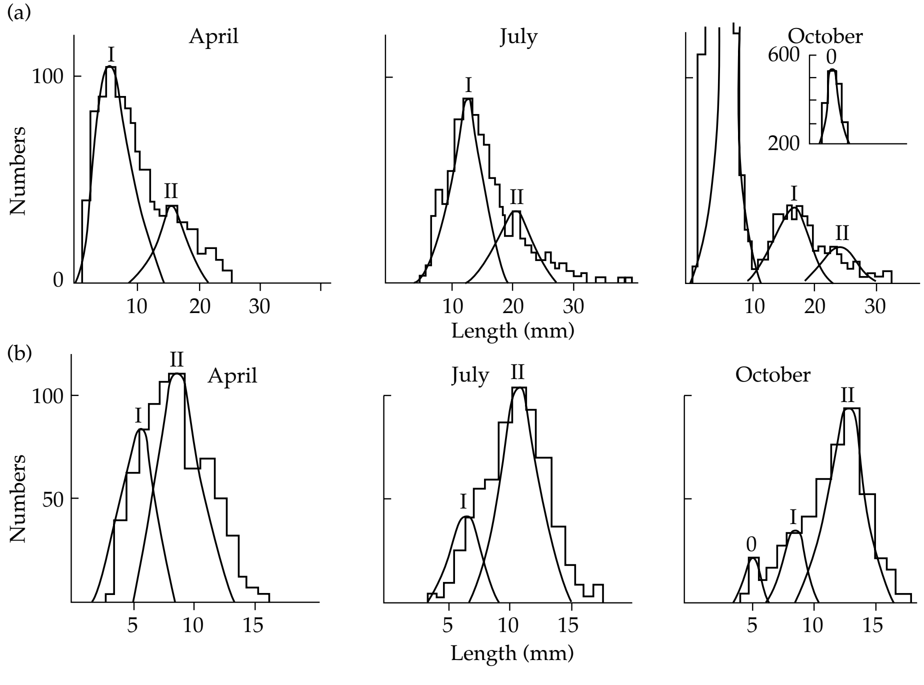


Figure 5.3 Size–frequency histograms for the bivalves (a) *Mya arenaria*, (b) *Macoma balthica* from eastern Canada. Normal curves for each age class (I and II) were obtained from probability plots and interpretation of growth rings (after Burke and Mann 1974).

Table 5.2 Rapid method for calculation of $P/\bar{B}$ ratio

	Mean G m^{-2}	Production kJ	Mean g m^{-2}	Biomass kJ	$P/\bar{B}$ y^{-1} g m^{-2}	$P/\bar{B}$ y^{-1} kJ
Polychaeta	32.3	120.8	43.0	160.4	0.75	0.75
Crustacea	1.9	4.2	4.2	6.9	0.45	0.61
Mollusca	9.0	12.7	26.1	36.9	0.35	0.34
Echinodermata	2.9	7.3	8.6	22.8	0.37	0.32
Total	89	185	307	441	0.29	0.42

community, thus giving community production (e.g. see Elliott and Taylor 1989). Such laborious methods were widely used a generation ago, but today simple computer programs are available to do the tedious size–frequency calculations (e.g ELEFAN (ELEctronic Frequency ANalysis), as part of FiSAT (FAO-ICLARM Fish Stock Assessment Tools)), and spreadsheet analysis makes the calculations straightforward.

Production can be calculated from the curves in Fig. 5.3 and is shown in Table 5.2.

Kirkegaard calculated his $P/\bar{B}$ratio over the whole lifespan of the species whereas Sanders did not, and thus Sanders underestimated the true ratio.

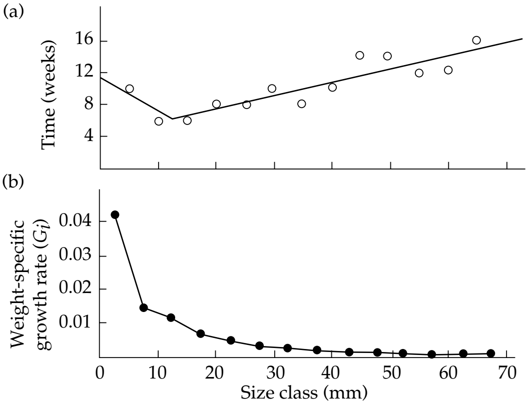


Figure 5.4 Growth of *Nereis diversicolor:* (a) Time taken for different size classes to grow to the next size class, (b) Relationship between weight-specific growth rate (*Gi*) and size.

Production estimates are most difficult when age classes are not easy to separate. In this case one needs to know the density, mean weight, and specific growth rate of each size class. A good example of the calculation of production in such a case relates to the data on the polychaete *Nereis diversicolor* (Heip and Herman 1979). Here the growth rate was calculated by measuring the time taken for an individual to grow from one size class to the next. This can be done by plotting the data for two consecutive time intervals (here fortnightly intervals) and sliding the *x*-axis of one along the *x*-axis of the other until the patterns have the maximal fit. Heip and Herman, however, used a statistical technique involving the calculation of cross-correlation functions; their paper should be consulted for more details. (Also note that the earlier seminal work by Crisp 1984 has now been updated by Van der Meer *et al.* 2005, although the latter does not give the same depth of calculations of production.) Figure 5.4(a) shows the data, which indicate that the smallest worms grew from one class to the next slowly at first and then more rapidly, but that once over 12 mm the growth rate decreased linearly. Such a sigmoid growth curve is common for many organisms. Figure 5.4(b) shows weight-specific growth rate determined from (a). From these data, production was estimated at 398 g wet wt m^{-2} y^{-1} or 61.3 g dry wt m^{-2} y^{-1}. The average biomass was 158 g wet wt m^{-2}; the $P/\bar{B}$ratio was 2.51.

Growth increment is calculated as the number of animals at time *t*, multiplied by the increase in mean weight over the time period t_0 to *t:*

$$N_1(\bar{w}_1 - \bar{w}_0)$$

where N is the number of individuals and $\bar{w}$ is the mean weight, e.g.

$$42(20 - 0) = 840$$
$$38(40 - 20) = 760$$
$$34(48 - 40) = 272$$

Elimination loss is calculated as the difference in mean density between one time period and the next multiplied by the average mean weight over the time period:

$$(N_1 - N_0) \times 0.5(\bar{w}_1 - \bar{w}_0)$$

e.g.

$$47 - 42 \times 0.5(20 - 0) = 50$$
$$42 - 38 \times 0.5(40 - 20) = 40$$
$$38 - 34 \times 0.5(48 - 40) = 16$$

$$G_i = \frac{\ln w_{i,2} - \ln w_{i,1}}{t_2 - t_1}$$

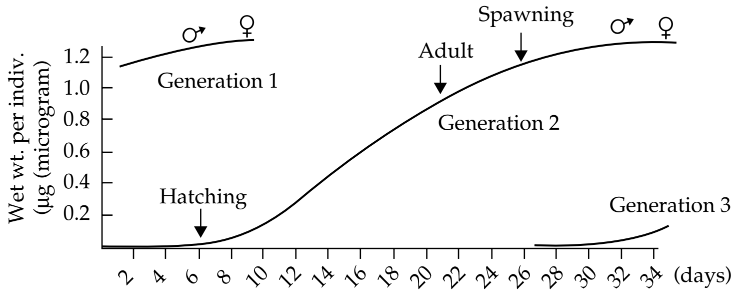
where $w_{i,1}$ and $w_{i,2}$ are weights of an individual in size class i, t_1 and t_2 are the time intervals, and G_i is the instantaneous weight-specific growth rate (after Heip and Herman 1979).

5.3 Production estimates in meiofauna

There are within the meiofauna a fairly large number of species where reproduction occurs continuously and asynchronously and where cohorts (distinct size classes) cannot be separated. Hence it is extremely difficult to calculate production for such species using the traditional Allen curve methods, and one often has to resort to indirect methods. For example, an earlier study by one of us (JSG) of field samples of the meiobenthos off Northumberland showed it was impossible to ascertain either the number of nematode generations per year or the number of eggs laid. Nematodes were therefore brought into the laboratory in order to obtain estimates of generation times.

It has been found, however, that in contrast to macrofauna, which usually have one generation per year, generation times of meiofauna vary widely. The nematode *Enoplus communis* and the ostracod *Cyprideis torosa* have only one generation per year but some species may only reproduce once every 2 or 3 years. Even species with short life cycles may have long resting periods between cycles. For example, several species of ostracods have resting eggs, and egg hatching in one nematode took 150 days, although the life cycle was thereafter completed in a few weeks. In the copepod *Asellopsis intermedia* egg masses produced in August hatch the following May. In an exhaustive summary of life cycle data, Gerlach (1972) concludes that *on average* meiofauna have three generations per year, but clearly large variations from species to species occur.

The life cycle of *Chromadorita tenuis* (Fig. 5.5) as obtained from laboratory studies can be used as an



				Numbers				
	2	1			4	3	2	Adult
20	18	13	8	5				Eggs and juveniles
	2	6	6	3	1	1	1	Dead animals
				Biomass (μg)				
2.9	3.0	2.6	3.2	4.0	4.0	3.3	2.4	Standing stock
	0.1	1.8	2.8	2.0	0.9	1.0	1.2	Elimination

Figure 5.5 Calculation of turnover rate in the nematode *Chromadorita tenuis* (after Gerlach 1972).

illustration of the difficulty of meiofaunal production studies. Two adults produce 20 fertilized eggs which, assuming they hatch after 5–6 days, reach the adult stage on day 21. We have no reliable estimate of elimination, but assuming this is around 10% per day during juvenile life, we can obtain an average standing stock biomass ($\bar{B}$) of 3.2 μg wet weight, with elimination of 20 animals totalling 9.8 μg during the life cycle. Thus, the life cycle turnover rate ($E/\bar{B}$) is $9.8/3.2 = 3$. Assuming that there are three generations per year, the annual $P/\bar{B}$ ratio is 9. However, the relation between P and $\bar{B}$ over time depends on the shape of the growth and elimination curves, and methods such as those used here must be treated with great caution.

Heip (1976) produced an ingenious alternative solution to the problem of estimating $P/\bar{B}$ ratios for species that reproduce continuously. Using a combination of field estimates of population density and laboratory studies of population growth rates, he calculates numbers eliminated from the population. The details of his method are too complex to reproduce here, but in essence he calculates the $P/\bar{B}$ ratio from numbers of individuals, since the mean weight appears in both numerator and denominator and can therefore be cancelled out. In a population of the brackish-water copepod *Tachidius discipes* he found 4175 individuals eliminated per 100 cm^2 and a mean standing stock biomass of 278 individuals per 100 cm^2; this gives a $P/\bar{B}$ ratio of $4175/278 = 15.0$, which is very similar to that obtained by more complex methods based on calculations of successive elimination increments. This method looks to be highly promising for estimating production in other meiofaunal species, but very few species have as yet been studied. The figure of 15 obtained for *Tachidius* is similar to that for planktonic copepods that have many generations per year; $P/\bar{B}$ ratios will be appreciably lower in species such as *Enoplus* and *Cyprideis* that have only one generation a year.

From these limited and scanty data it is difficult to draw many meaningful conclusions on meiofaunal production figures, although the results agree with the elevated $P/\bar{B}$ for small, short-lived organisms and so may be used to give approximations of meiofaunal production. Despite this, the figures are likely to be as varied as those for macrofauna or maybe even more so.

5.4 Energy budgets for single species

The components of an energy budget for a single species have been standardized by the International Biological Programme (again see Crisp 1984). The total budget is:

$$\begin{aligned} C &= P + R + G + U + F \\ Ab &= C - F = P + R + G + U \\ A &= P + R + G \end{aligned}$$

where C denotes consumption, R respiration, Ab absorption, G gonad output, A assimilation, U urinary excretion, P production, and F faeces.

The measurement of production has been discussed above in some detail and so here we give an example of a fully determined budget and discuss some general aspects.

One of the most complete studies of the energetics of a benthic species is that by Roger Hughes (1970), who worked under Denis Crisp on the bivalve *Scrobicularia plana* from a mudflat in North Wales. Production was determined by the standard techniques of measuring growth and eliminated biomass. The most difficult and time-consuming part of the energy budget to determine is respiration (R). What one is really interested in is the animal's metabolic heat loss, but since it is impractical to measure this directly, oxygen consumption is usually studied. This is then converted into heat output using the oxycalorific coefficient of 14.15 J mg^{-1} O_2 or 20.22 J ml^{-1} O_2 at NTP. Since *Scrobicularia* is not thought to respire anaerobically, oxygen consumption was measured using a continuous-flow respirometer. This is basically a sealed vessel with a constant flow of water through it into which the animal is put. The difference in oxygen content between the inflow and outflow is multiplied by the current speed to give the rate of oxygen consumption. The vessels were maintained within the range of temperatures found in the field. Typically there is a wide scatter in the values obtained, as shown in Fig. 5.6. For each of the temperatures used a regression equation was calculated, and using field data on temperatures the metabolic heat

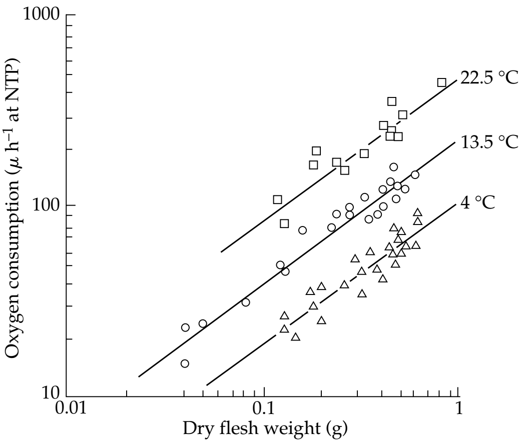


Figure 5.6 Oxygen consumption of the bivalve *Scrobicularia plana* in a continuous-flow respirometer (after Hughes 1970).

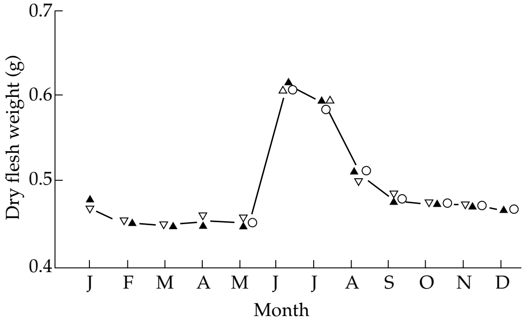


Figure 5.7 Seasonal variation in dry flesh weight of *S. plana* with a shell length of 40 mm. ○ 1996; ∇ 1967; ▲ computed from regression lines with a fixed slope of 3.0 (after Hughes 1970).

loss could be estimated by means of the oxycalorific coefficient.

Determining the amount of energy that goes into gamete production was difficult because it was not possible to induce the animals to spawn in the laboratory (otherwise it would have been easy to collect the spawn and measure its energy content directly). The method adopted was to determine the decrease in dry flesh weight that occurred after spawning and multiply that by the energy content per gram (Fig. 5.7). Urinary wastes could not be estimated, and in the marine environment this component of the energy budget is frequently neglected. Faecal pellets were collected from animals of various sizes and over the annual temperature range. From these data the amount of energy lost in the faeces for each month for the total population could be calculated, although the energy content of faecal pellets did not vary much during the year.

Hughes studied two populations, one high up the shore and one lower down; the two separate energy budgets and the average combined budget were (in kJ m^{-2}):

Lower sample:

$$\begin{aligned}C &= P + R + G + U + F\\ &= 519 + 1993 + 268 + \text{n.d.} + 1624\\ &= 4404\end{aligned}$$

Upper sample:

$$\begin{aligned}C &= 73 + 228 + 17.6 + \text{n.d.} + 198\\ &= 516.6\end{aligned}$$

Average:

$$\begin{aligned}C &= 296 + 1110 + 143 + \text{n.d.} + 911\\ &= 2460\end{aligned}$$

As a check on the budget it was then possible to calculate consumption also by determining the energy content of the sediment that *Scrobicularia* ingested, making a correction for pseudofaeces produced, and then subtracting the energy lost as faeces. The figures in this case were (in kJ m^{-2}): lower sample, 3562 kJ m^{-2}; upper sample, 436 kJ m^{-2}; average, 1999 kJ m^{-2}. The difference between these and the first set of figures were 20%, 16%, and 19% respectively.

A surprisingly large proportion of the energy budget goes to gamete production (31% of the production in the upper sample and 52% in the lower). The energy lost in respiration is an average of 45% of the consumed energy but the relative sizes of the various components are usually compared in terms of efficiencies. Since there are no data on urinary waste, assimilation is defined as $A = C - F$, e.g. $4404 - 1624 = 2512$ kJ m^{-2} for the lower sample.

5.5 Elemental budgets

The budgets in the previous section were calculated in terms of the total energy flow, measured as kJ m^{-2} y^{-1}. It is equally possible to calculate a budget for a chemical element. The difference between the two is that while energy is used only once and therefore appears as a flow going in one direction through the system (except for that energy that is lost as heat produced in respiration), elements can be recycled. This difference was illustrated in Fig. 5.1.

Most of the organic matter in ecosystems is usually found as detritus. This detritus is then broken down by microorganisms and the elements can then be recycled (the *microbial loop*). Carbon has been widely used in element budgets but there are advantages in using nitrogen. Nitrogen values can be used to measure excreted waste and furthermore nitrogen is often the nutrient that limits primary production in the sea. By calculation of a nitrogen budget for a given species or for the whole ecosystem, more information on factors directly relevant to the functioning of the system are obtained.

Specific elements are assimilated by animals with a greater efficiency than is organic matter as a whole, so element budgets will give different efficiencies compared with energy budgets. To obtain the best picture of the trophic relations of a species both energy and element budgets should be compiled, so that in addition to knowing the total energy flow the carbon budget could be used to estimate respiration (as carbon dioxide produced) and the nitrogen budget to estimate growth (as protein anabolism) and excretion. However, this has not been done for any species and would be inordinately time-consuming.

5.6 Production: biomass ratios

Calculating the $P/\bar{B}$ ratios allows populations of different biomass to be compared on a common basis and also gives a short cut to deriving an estimate of production when only a biomass value is known (Elliott and Taylor 1989). Table 5.3 illustrates published data on $P/\bar{B}$ ratios for a variety of macrobenthic species. In a number of cases $P/\bar{B}$ ratios have been calculated for the same species at different localities. In some of these the values are in good agreement (e.g. *Nephtys hombergi*, 1.9 and 1.7), whereas others show a wide discrepancy (e.g. *Macoma balthica*, 2.1 and 0.8). Elliott (1979) calculated the $P/\bar{B}$ ratios for five intertidal mollusc species and showed the large variability over an intertidal area. Some of the differences related to better feeding conditions in optimal parts of the mudflat, whereas others were due to inherent difficulties of calculating such $P/\bar{B}$ ratios in areas where there are small populations. Indeed, both that study and Elliott and Taylor (1989) indicated that the most accurate ratios are calculated in the best (optimal) areas for a species as the population size is greater, the cohort separation is clearer from better size-frequency histograms, and the errors in the calculations are less—for example in detecting individuals in a cohort in one sampling occasion and not those before and after, due to patchiness in the cohorts. This is a particular problem in older cohorts which

Table 5.3 Mean (±SE) annual production (log10) and $P/\bar{B}$ ratio for main taxonomic groups, functional guilds, and substratum type (Algae: including sediment with high organic enrichment; Hard: mainly bedrock, but also including wood structures and boulders; Muddy and Sandy: dominant fraction)

	Mean production ($\log_{10}$; kJ m^{-2} y^{-1})	**Mean $P/\bar{B}$ (y^{-1})**
Taxonomic group		
Mollusca	1.94 ± 0.08 (n = 227)	1.77 ± 0.14 (n = 230)
Annelida	1.42 ± 0.09 (n = 123)	3.37 ± 0.38 (n = 120)
Arthropoda	1.30 ± 0.08 (n = 140)	4.85 ± 0.31 (n = 140)
Echinodermata	1.34 ± 0.23 (n = 27)	0.34 ± 0.06 (n = 28)
Functional guild		
Deposit feeders (DF)	1.47 ± 0.09 (n = 175)	2.54 ± 0.15 (n = 175)
Filter feeders (FF)	1.96 ± 0.11 (n = 134)	1.82 ± 0.20 (n = 136)
Grazers (GR)	1.64 ± 0.08 (n = 81)	2.81 ± 0.43 (n = 82)
Omnivores (OM)	1.25 ± 0.11 (n = 96)	4.94 ± 0.54 (n = 95)
Predator (PR)	1.37 ± 0.13 (n = 45)	3.41 ± 0.49 (n = 42)
Substratum type		
Algae	1.10 ± 0.15 (n = 65)	4.18 ± 0.48 (n = 62)
Hard	2.21 ± 0.16 (n = 69)	1.09 ± 0.18 (n = 70)
Muddy	1.46 ± 0.07 (n = 219)	3.25 ± 0.21 (n = 216)
Sandy	1.67 ± 0.08 (n = 184)	2.90 ± 0.30 (n = 188)

of course have fewer and more patchy members which may not be easily sampled. Hence it is likely that ratios are overestimated for many species. It is quite possible therefore that methodological differences account for many of the differences indicated above, since the lower figures may, for example, have underestimated the growth of the smallest juveniles. Conversely, a population including a higher proportion of small, newly recruited and thus faster growing stages will have a higher ratio than one composed predominantly of older stages.

One of the attractions of calculating $P/\bar{B}$ ratios is the hope that a common pattern may emerge so that production can be calculated merely from estimates of biomass, itself much easier to measure; and indeed, because of this, we recommend that biomass measurement should be part of all macrobenthic studies. However, there are many factors that influence $P/\bar{B}$ ratios. Low temperatures, slow growth rates, a dominance by older cohorts, a reduction of newly recruited stages, and varying predation rates all lower the ratio. In addition, natural and unnatural stress such as in lower salinity areas like the Baltic may reduce the ratio. Most importantly, both growth-rate changes and predation alter the ratio by causing changes in the age distribution of species, and it is population growth rate and size structure that are the major factors influencing $P/\bar{B}$ ratios. Robertson (1979) plotted most of the data in Table 5.3 against lifespan in years (Fig. 5.8). The equation representing the data is

$$\log_{10} P/\bar{B} = 0.660(\pm 0.089) - 0.726(\pm 0.147)\log_{10} L$$

where L is lifespan in years. All groups (bivalves, gastropods, polychaetes, crustaceans, and echinoderms) fitted the above equation and gave a significant correlation ($r = -0.835$) and there was no significant difference between each group plotted separately. Thus, a significant and important trend has emerged: that there is a general relationship between annual $P/\bar{B}$ values and lifespan for all marine macrobenthos. Robertson suggests that the equation could be used to predict production from biomass, provided that the sampling gear is not age-selective and that age can be determined. As yet there are insufficient data on meiofauna to be able to see whether the same equation applies or whether a different equation will be appropriate.

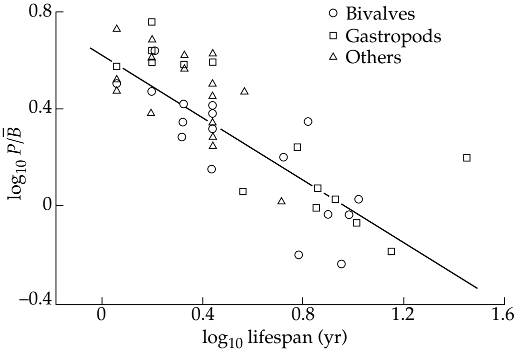


Figure 5.8 Annual $P/\bar{B}$ ratio against lifespan for marine macrobenthos (after Robertson 1979).

$P/\bar{B}$ ratios are often all that is studied in relation to the energy requirements of a given species. However, much of the energy actually utilized by an organism goes not to increase its biomass, but to respiration, and a significant proportion can go into gamete production. The calculation of a detailed energy budget for benthic species has been done rather seldom, but in order to predict the production capacity of various areas of the seabed one must know the *total* energy requirements of the species, not merely the energy utilized in growth or eliminated.

5.6.1 Alternative methods of calculating production/biomass ratios

One of the most comprehensive modern descriptions of methods to calculate production is the Virtual Handbook developed by Thomas Brey (2006) (see also papers such as Cartes *et al.* 2002). This gives an excellent coverage of all the available methods and an easy-to-use guide to the calculations, with a series of Excel macros.

As shown above, calculating production is a tedious process. Brey (1999a, b) found an empirical relation to estimate $P/\bar{B}$ from maximum age, maximum body mass, and water temperature. Brey (2006) explains the use of empirical models:

> If we know the relation between production or $P/\bar{B}$ ratio and other characteristic but easy to measure parameters in many natural populations, we can construct a model based on these empirical data and use this empirical model to predict P or $P/\bar{B}$ in other populations.

The empirical, linear multiple regression model he developed is:

$$\log(P/B) = 1.672 + 0.993\log(1/A_{\max}) - 0.035\log(M_{\max}) - 300.447[1/(T + 273)]$$

where $A_{\max}$ is the maximum observed age (years), $M_{\max}$ is the maximum observed body mass (kJ), and T is the average water temperature (°C).

The fit to data was remarkably good, with $R^2 = 0.880$ for 907 data sets. The data sets used were from a variety of studies from different areas of the world and contained marine and freshwater data.

Brey (1999a, b) also showed that when growth rate does not follow a *von Bertalanffy growth curve* or is unknown, the mortality rate (M) and $P/\bar{B}$ are linearly related in unexploited benthic invertebrate populations. (The von Bertalanffy growth curve is a sigmoid growth curve typical of many organisms whereby an initial low growth lag phase is followed by a logarithmic phase and then finally a slow growth phase as the asymptotic size (maximum theoretical size) is reached (see Bagenal 1978).) From this he derived the following empirical model which can be used to estimate the natural mortality rate (M) if $P/\bar{B}$ is known:

$$M = 0.082 + 0.925\,P/\bar{B}$$

The relationship gave $r^2 = 0.961$ for $n = 103$.

A recent example using Brey's method is that of Nilsen *et al.* (2006) who studied the fauna of Sørfjord in Arctic Norway. Rather than calculating production for individual species they calculated production and biomass for a series of groupings of fauna. Here they grouped all polychaetes together but separated molluscs and echinoderms into the dominant and/or large biomass species and lumped all the smaller species. To calculate $P/\bar{B}$ ratios for the groups of species they used Brey's equation:

$$\begin{aligned}\log P/\bar{B} = {} & 8.256 - 2.226\log M \\ & - 2432.055(1/T + 273) + 0.239(1/D) \\ & + 0.241D_{\text{subt}} + 0.203D_{\text{inf}} + 0.242D_{\text{moti}} \\ & - 0.287D_{\text{moll}} - 0.203D_{\text{poly}} - 0.128D_{\text{crust}} \\ & - 0.457D_{\text{echi}} - 0.116D_{\text{lake}} \\ & + 562.218\log M(1/T)\end{aligned}$$

where M is average body mass (kJ), T is temperature (°C), and D is depth (m). Dummy variables were set to 0 (no) or 1 (yes) for the categories of species:subtidal species (D_{subt}), infauna (D_{inf}), motile epifauna (D_{moti}), molluscs (D_{moll}), (5) polychaetes (D_{poly}), (6) crustaceans (D_{crust}), (7) echinoderms (D_{echi}), and lake (D_{lake}).

In order to derive production, they simply multiplied $P/\bar{B}$ by wet weight biomass or kJ for the respective group at each station. This gave the results shown in Table 5.2.

This is certainly a much simpler way to calculate production and biomass. However, as with any models, especially empirical ones, they are only as good as the data used in their derivation and one should observe the words of caution that Tom Brey so rightly states in his Virtual Handbook:

> Do not believe in predictions of population P or P/B made by empirical models! These models are accurate only 'on average', hence prediction error for a single population P or P/B is easily somewhere between −60% to +150%. Prediction error reduces rapidly when estimates of several populations are pooled, e.g. into production of all filter feeding species or production of all species in the community.

Cusson and Bourget (2005) reviewed the available global data on production and biomass of benthic species. In all 207 taxa were included in the analyses. Of these 36% were bivalves, 20% polychaetes, 15% amphipods, 7% gastropods, and 5% echinoderms. Table 5.3 shows the summary data. Molluscs had the highest production and arthropods the highest $P/\bar{B}$ ratios, followed by polychaetes, molluscs, and echinoderms. However, deposit feeders tended to have higher $P/\bar{B}$ than filter feeding molluscs. Another interesting finding for soft sediments was that predators on sandy substrata had higher $P/\bar{B}$ than other feeding guilds, yet arthropods had lower ratios than other feeding guilds in muddy sediments. Perhaps surprisingly, depth did not show strong relationships to $P/\bar{B}$ even though the maximum depth covered was 930 m.

The most significant variables affecting community production and $P/\bar{B}$ were biological traits. Mean biomass explained 75% of the variance in a linear regression model of production and there was an almost linear relationship between biomass and production. Lifespan was also important in explaining 17% of the variance in the model and there was a negative linear relationship for amphipods, echinoderms, and polychaetes. Both production and $P/\bar{B}$ ratios were negatively affected by biomass and lifespan. As indicated earlier, $P/\bar{B}$ ratios are high in assemblages dominated by young cohorts since young individuals invest more energy in growth and have a higher turnover than older individuals, which use more energy for respiration than for growth.

In a further development, Cartes *et al.* (2002), also using data from the literature (91 estimates for 49 different species), compared the $P/\bar{B}$ ratios of hyperbenthic (i.e. those mobile species moving above the bed) marine crustaceans with the benthic (infauna+ epifauna) crustacean species. The hyperbenthic ratios were statistically significantly greater than both the benthic crustacean and also of other (non-crustacean) benthic invertebrates. A similar multiple linear regressions approach to that described above showed the $P/\bar{B}$ to depend significantly on mean annual temperature (T) and mean individual weight (W) ($R^2 = 0.367$) and a further 15% of variance was explained by adding the variable swimming capacity. Hence they concluded that the higher $P/\bar{B}$ of the mobile hyperbenthic crustaceans compared to the benthic compartment appeared to be related to the crustaceans' most notable feature, their mobility. They also concluded that studies which do not include the hyperbenthos are in danger of missing a notable part of total benthic production. This reinforces the fact that calculations of energy flow and trophic transfer have to include as many components as possible, not only all the life stages of a population but also all the various species in the community.

Finally, in relation to latitude, Cusson and Bourget (2005) found that $P/\bar{B}$ ratios were higher in the northern hemisphere than in the southern and were highest in mid-latitudes, with low values above 60°S and 60°N and between 40°S–20°N. These aspects need much more research in order to be explained and to help us further determine benthic functioning.

5.7 Community metabolism

Another trend that developed in the 1970s was that of measuring integrative processes in sediments. It was realized that it would be extremely difficult to model food webs containing all the individual species in an ecosystem, hence integrated measures were developed of the performance of the whole benthic assemblage. For example, rather than measuring the oxygen uptake of single species isolated in the laboratory, the oxygen uptake of whole sediments (which include all the micro-organisms and the micro-, meio- and macrofauna) was measured.

Rather than obtaining an energy budget for every single member of a given food web, the alternative is to take a holistic approach and measure the metabolism of the community as a whole. If the community in question is strictly aerobic, then there is no great methodological problem, as metabolism can be measured in terms of oxygen uptake.

5.7.1 Oxygen uptake

Teal and Kanwisher (1961) suggested that the rate of oxygen uptake by the sediment surface could be an integrated measure of both aerobic and anaerobic metabolism. Measurements were made by placing black bell-jars over the sediment and monitoring the oxygen uptake directly by means of an electrode system. Using such methods Pamatmat and Banse (1969) studied the seabed in Puget Sound, USA. They found that there was no relation between oxygen consumption and mean grain size or silt–clay fraction, nor was there a relationship with organic content or organic nitrogen, nor with ash-free dry weight of the macrofauna. Temperature was a significant factor, with higher temperatures giving higher oxygen consumption. The lack of correlation between oxygen consumption and organic matter seems to be a common phenomenon. Much of the organic matter in sediments is therefore presumed not to be easily oxidized, and there is certainly little chance of it being oxidized once it is buried. It is more likely that oxygen uptake is linked to seasonal changes in the rates of deposition of organic matter, such as organic matter sedimenting from the plankton.

To estimate the relative importance of bacterial and faunal oxygen uptake, these can be measured under a bell-jar before and after the injection of antibiotics into the jar. The antibiotics are presumed to inhibit the bacteria without affecting other organisms, and thus the difference in oxygen consumption before and after the antibiotic injection gives an estimate of bacterial respiration. In practice inhibition is seldom more than 90%, and in some cases oxygen consumption can increase as a result of one species of bacterium not being killed and so being able to increase in abundance because of the lack of competition. After bacterial respiration has been measured, the chemical oxygen demand can be estimated by injecting formalin to kill the fauna.

For a mudflat in Washington, USA, Pamatmat (1968) estimated not only the partitioning of community respiration between microfauna and bacteria/microfauna plus meiofauna but also the contribution of the benthic microphytobenthos (benthic microalgae and microflora). He used dark and light bottles to estimate gross production of the microflora and then estimated the oxygen consumed. The partitioning of the oxygen demand showed that bacterial respiration was much higher than that of the macrofauna; seldom, in fact, does macrofaunal respiration contribute more than 20% of the community respiration and bacteria usually account for 50–80% of the total. The role of the meiofauna and microfauna is certainly not constant and it is likely that, in general, they consume as much oxygen as do the macrofauna. In sediments, however, there are many species that are facultative anaerobes and most of the bacteria concerned with the sulfur cycle are obligative anaerobes. In anaerobic respiration the terminal electron acceptor used may be hydrogen sulfide (H_2S), methane (CH_4), ammonium (NH_4^+), ferrous iron (Fe^{2+}), nitrate (NO_3^-), etc. (Libes 1992). Thus, in most sediments the data obtained from oxygen uptake studies may be underestimates of community metabolism, since the anaerobic pathways are neglected.

Modern approaches use cores rather than bell-jars, but the methods are similar to those of the pioneers. Today we have highly sophisticated instrumentation that can be placed on the seabed at almost any depth to measure oxygen consumption and flux rates of various elements into and out of the sediment.

Using data on stable isotopes of carbon and a variety of techniques including pigment analyses and fat and sterol components, Cook *et al.* (2004a, 2004b) showed that the coastal sediments were dominated by inputs of terrigenous matter. Yet this is usually highly degraded by the time it reaches the marine environment, such that it is refractory with a high C:N often up to 15–20 and does not undergo remineralization. The C:N value is an indication of the relative importance of the refractory/labile nature of the residual carbon remaining from detritus (the C component), and the microbial heterotrophic populations (the N component) able to degrade it. An analysis of the marine organic carbon (Fig. 5.9) showed a clear seasonal trend, with the largest pool of marine matter in sediments in winter and the highest input of marine organic matter in spring. This algal-derived material is, however, labile and has a much lower C:N of around 7–9. (In oceanic waters the atomic ratio required for efficient primary production is C:N:P = 106:16:1, known as the *Redfield ratio* after its originator; see also various chapters in Steele *et al.* 2001.)

Nitrogen is usually the limiting nutrient for phytoplankton growth and so it is important to obtain knowledge of the fluxes of various nitrogen compounds from sediments to the water column. This is done by taking core samples which are then incubated in the light and dark and the fluxes are measured in the overlying water. The data in

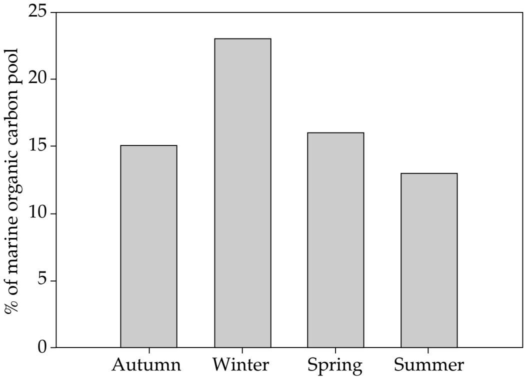


Figure 5.9 Origin of organic matter in intertidal sediments in Tasmania (from Cook *et al.* 2004b).

Fig 5.10 are from a seasonal study of fluxes at intertidal sites in a Tasmanian estuary.

Often *dissolved organic nitrogen* (DON) is not measured but here the data show that effluxes from the sediment were highest in late spring when the microphytobenthos respiration is highest. The *dissolved inorganic nitrogen* (DIN) fluxes of nitrite (NO_2^-), NO_3^-, and NH_4^+ show that DIN was either taken up or released at a lower rate in light conditions than in the dark. Both NO_2^- and NO_3^- were taken up by the sediments from the water column, whereas NH_4^+ was taken up by the sediments in the light but had an efflux in the dark in late spring and summer. These fluxes can be explained by the microphytobenthos taking up the nutrients, even for NH_4^+ in the dark. *Oscillatoria* sp. was the dominant species and is highly motile, moving several centimetres vertically according to the light regime.

New technological developments such as benthic landers have enabled us to increase our understanding of flux rates of nutrients, carbon, and oxygen in sediments from shallow depths to the deep sea. These high-tech instruments are deployed from research vessels on to the seabed and send data through a cable to shipboard computers. Figure 5.11 shows the construction of one of these developed at the University of Gothenburg, Sweden.

The lander contains an incubation chamber so that oxygen and carbon dioxide fluxes can be measured to assess community metabolism. Other electrodes measure a variety of nitrogenous and phosphorus fluxes. From such landers, data can be obtained that parallel those shown in Fig. 5.10, but allow comparisons between upwelling areas, oligotrophic and eutrophic areas, or tropical and polar regions.

As an example of these processes we can take the North Sea. It is shallow, and so wave and current action carries much of the sedimented organic material to deposition areas, the largest of which is the deep Skagerrak basin (700 m deep) (Ducrotoy *et al.* 2000). Hall *et al.* (1996) studied the NO_3^- flux rates on the seabed of the Skagerrak and found that low C:N ratios were associated with high NO_3^-

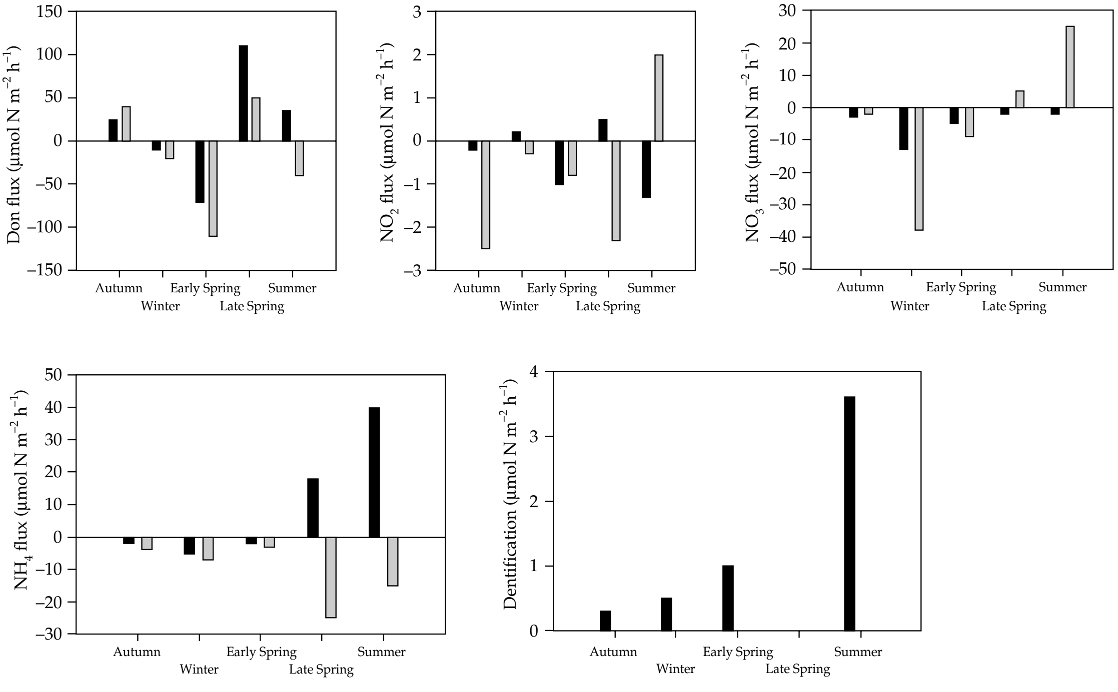


Figure 5.10 Fluxes of nitrogen compounds in intertidal sediments at a site in Tasmania (from Cook *et al.* 2004c).

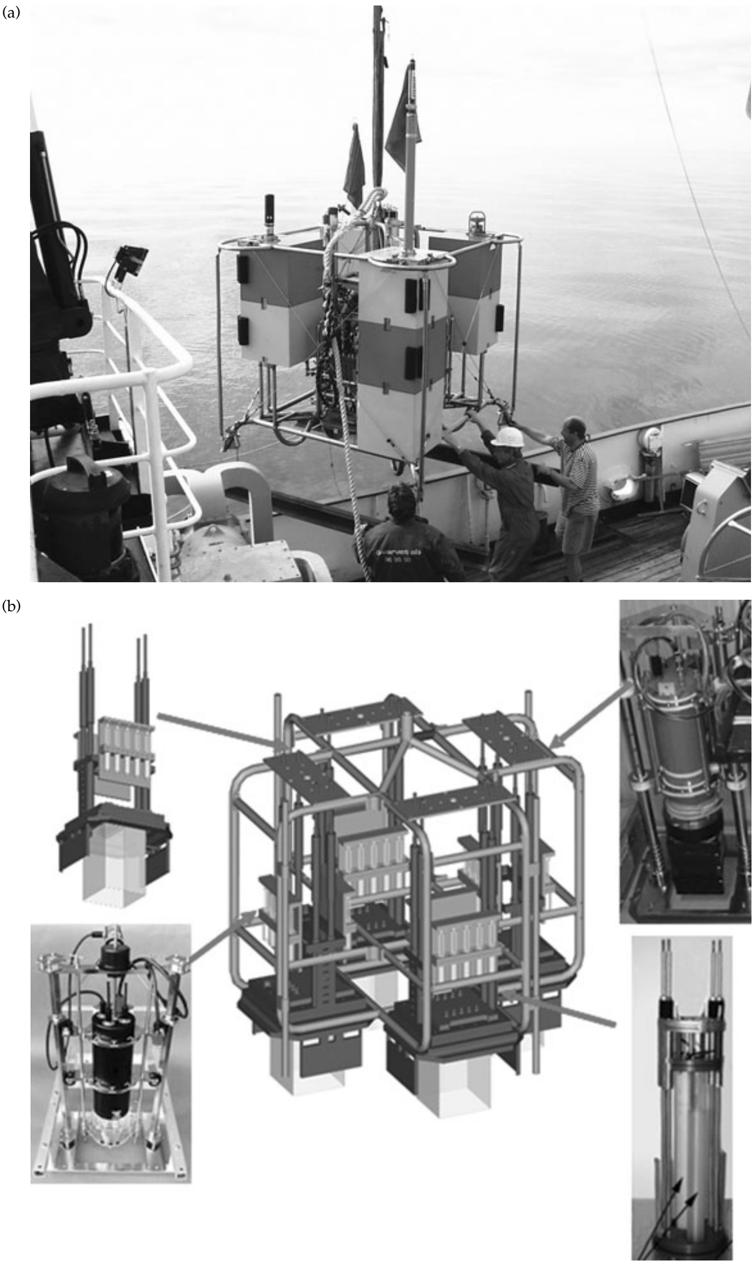


Figure 5.11 (a) Benthic lander for measuring flux rates on the seabed from shallow waters to the deep sea; (b) inner frame (courtesy of Professor Per Hall, University of Gothenburg, Sweden). See Plate 7.

effluxes from the sediment, whereas high C:N ratios were associated with high NO_3^- fluxes into the sediment. Thus the fastest regeneration rates of nitrogen occurred in nitrogen-rich sediments (low C:N ratio) and where the labile carbon is greater than the refractory carbon. It is likely that the bacteria responsible for these flux rates are simply respiring carbon dioxide to be able to utilize the limiting nutrient for their growth nitrogen. Studies like these are highly important if we are to obtain an understanding of the way ecosystems work. Most of the North Sea contains relatively coarse sediments, a result of wave and tidal action, and so regeneration of nutrients essential for phytoplankton growth occurs in limited areas where organic matter is deposited, such as the Skagerrak.

5.7.2 Factors controlling community metabolism

The previous section suggested that total oxygen uptake was found not to be correlated with the total organic content of the sediment but rather with the oxidizable fraction. This is because much organic matter becomes buried within the sediment and often there are large pools of undegraded organic matter. Within the buried sediment, anaerobic metabolism produces sulfides, which give the sediment a black colour often accompanied by a smell of hydrogen sulfide (see Libes 1992). In areas where eutrophication is a problem, such as the inner part of the Oslofjord, the superabundance of organic matter settling out in the water column uses all the available oxygen and leads to anaerobic conditions where black, abiotic sediment occurs at the surface. Such sediments are usually devoid of macrobenthic life.

Normally, however the sediment has a brown surface layer where aerobic conditions hold and the anaerobic layer is found beneath this, the exact depth depending on grain size, water flow, etc. (see Chapter 2). The extent of this brown layer has been claimed to be limited by the rate of oxygen diffusion into the sediment, in which case the rate of diffusion, and thus of course the temperature, will affect the rate of oxidation of settling organic matter. It is likely, however, that the reworking activities characteristic of most deposit feeders, during which sediment is brought up to the surface from depth, often play a more significant role than does diffusion (Rhoads 1974, Mazik *et al.* 2008). In general, however, more quantitative information is required on this subject and so we consider it to be a highly promising research area.

Tube builders can also play an important role in the degradation of organic matter. This is because most tube builders respire aerobically and actively pump the oxygen they need into the sediment, often forming brown oxidized areas down the sides of their tubes within the black layers (Mazik *et al.* 2008). Again, few quantitative data are available although recent techniques such as computer-aided microtopography are now allowing us to quantify bioturbation rates and the surface areas and volumes created by burrow formation (Rosenberg *et al.* 2007, Mazik *et al.*, 2008). Hence it can be seen that the correlation that has been found between the oxygen uptake of the sediment and temperature is a complex one, related not only to the changes in diffusion rates that occur with temperature but also to the increased biological activity of reworking and pumping that raised temperatures produce.

Oxygen consumption by benthic communities seems to be proportional to the supply of sedimenting material from the photic zone. Pamatmat's studies in Puget Sound (1968) show that there is a clear relationship between benthic respiration and chemical oxidation and phytoplankton production. This is confirmed by Davies' (1975) findings that benthic respiration increased with the amount of sedimenting organic carbon. This relationship has been formalized by Hargrave (1978) as:

$$C_o = 55\left(\frac{C_s}{Z_m}\right)^{0.39}$$

where C_o is the benthic oxygen consumption (L O_2 m^{-2} y^{-1}), Z_m is the mixed layer depth (depth of thermocline (in m) during stratification), and C_s is the annual primary production (g C m^{-2} y^{-1}). Hargrave analysed some 13 different data sets to arrive at the above equation. It is of note that deep-sea sediments consume oxygen at rates one or two orders of magnitude lower than those of the coastal waters described by Hargrave's equation. Also, it is generally believed that the organic matter arriving at deep-sea sediments from the plankton has been completely mineralized during its journey through the water column, and thus no clear relationship of the type above would be expected.

At high levels of primary production, proportionately less oxygen is used at the sediment surface, since much material becomes buried and anaerobic metabolism takes over. The fact that all of the sedimenting carbon was utilized in the sea loch that Davies (1975) studied probably indicates that the material, in this case sedimenting phytoplankton, was readily oxidizable. In areas where much terrigenous material occurs it has been found that as little as 23% of the available organic matter is oxidized. Thus the source of the sedimenting material plays a large role in determining how much is metabolized aerobically. On the other hand, the amount of sedimenting organic matter may not always be sufficient to meet the oxygen uptake requirements of the sediment. In such areas it is likely that organic matter produced by benthic algae *in situ* makes up the deficit. This was the case in Pamatmat's data for the intertidal mudflat in Washington. In salt marshes community oxygen consumption may account for only one-half of the organic matter produced in the marsh sediments. Thus, the metabolic activity in the sediment is closely linked to the amount of sedimenting organic matter, especially that from the plankton. The interrelations of the benthos with the water column are explored in Chapter 10, which deals with models of ecosystems.

It is important to consider these community respiration and flux concepts together with analyses of community structure and functioning. For example, Emmerson *et al.* (2001) did a series of experiments testing structural–functional relationships in marine soft-sediment systems. They used artificially constructed assemblages comprising different numbers of species (from 2 to 4) in Scotland, Sweden, and Australia. The measure of function was NH_4^+ flux from the sediment which, although the result of microorganism activity, is strongly influenced by the macrofauna. Burrowing organisms disturb the sediment, increase the amount of reactive surface (i.e. the sediment surface extends into the sediment through burrowing surfaces, as shown by Mazik *et al.*, 2008) and may increase or decrease NH_4^+ flux. In these experiments only the most dominant species were selected and then assembled in aquaria in different combinations with sediment.

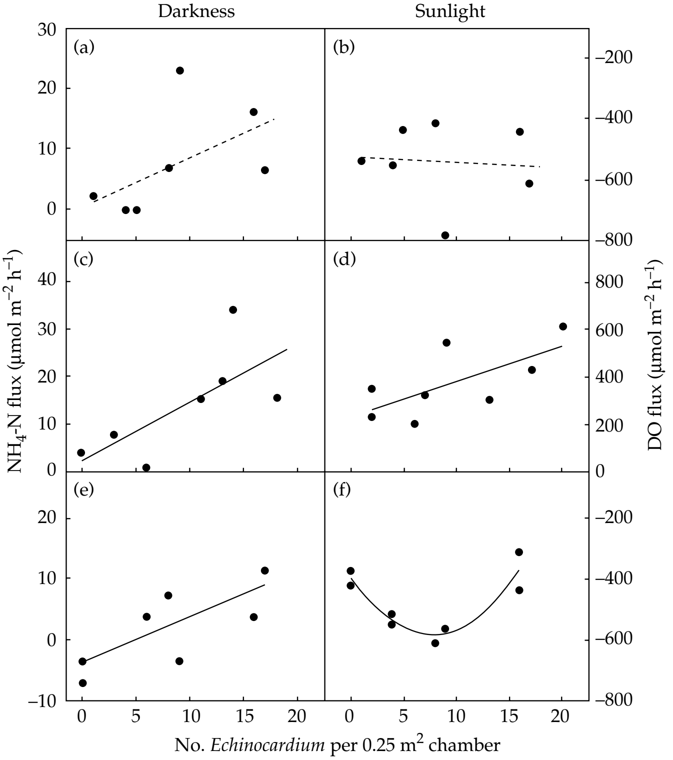


Figure 5.12 Changes in fluxes of ammonium and oxygen in a New Zealand subtidal area caused by changes in densities of the burrowing echinoderm *Echinocardium*. a and b, c and d, and e and f are from experiments done in January 2003, May 2003, and January 2004 respectively. Positive values indicate efflux and negative values uptake by the sediment. Solid lines significant regressions and broken lines non-significant regressions.

The results showed that the NH_4^+ efflux from the sediment varied in proportion to the biomass of the experimental animals and that responses varied with the identity of the species concerned, called an *idiosyncratic response*. In other words sometimes two species enhance efflux, but other combinations led to reductions of efflux compared to the species tested alone. Such findings are common also in terrestrial systems, and it is unlikely that we can make generalizations about the redundancy or rivet hypotheses. The conclusion from such experiments is that the identity of the species is important and understanding the biology of the individual species and what they do functionally is the key to understanding the relationship between structure and function in sediment systems.

Lohrer *et al.* (2004a) similarly conducted elegant experiments manipulating the densities of the burrowing sea urchin *Echinocardium* at a subtidal (6 m depth) site in New Zealand (Fig. 5.12). Where natural densities were 11 ± 4 individuals m^{-2}, they measured flux rates of NH_4^+ and oxygen to and from the sediment in darkness and light. In darkness NH_4^+ effluxed from the sediment at rates proportional to the echinoid density. In sunlight the microphytobenthos on the sediment surface photsynthesized and oxygen was produced. The results indicate varying responses to echinoid density, but in general efflux occurred. The reason for the more complex reactions is that *Echinocardium* consumes benthic primary producers and the benthic microphytes used NH_4^+ during the day. Changes in weather and hydrographic conditions such as cloudiness and water turbidity had clear effects on oxygen fluxes and so there were no consistent patterns but rather complex interactions and feedbacks.

Studies such as these link together the structure of the system with the functions that the organisms perform. It is clear that many more such studies are needed before we can make any generalizations about the functional roles of species in systems. We are just at the beginning of this exciting research phase.

CHAPTER 6

Spatial variations in sediment systems

In this chapter the primary emphasis is on spatial scales of disturbances, and we will follow on from our earlier discussions on the mechanisms of competition and predation and the controversy over their importance in controlling species richness. Huston (1994) realized that the effects of competition, predation, and general physical disturbance were similar in that individuals were removed from the assemblage. We now show that there is a need to link these aspects with the tolerances of individual species, for example to determine in which of these cases the organisms are absent because the conditions now fall outside the optimal tolerance ranges. Thus we discuss disturbance as a general phenomenon which includes the effects of any processes that lead to a reduction in numbers of individuals and/or biomass. Disturbance includes physical disturbance as well as biological processes such as the effects of competition and predation on assemblages. The spatial scales covered range from micrometres to many hundreds of kilometres for the effects of bottom trawling, which is now considered to be one of the most serious and damaging threats to sediment habitats and assemblages. Disturbance effects caused by trawling and by pollution are considered in the following chapters. First, it is necessary to consider scale since many new insights have developed in the past few years of research.

6.1 The importance of scale

In the past couple of decades a new branch of ecology, *landscape ecology,* has developed, devoted to considering patterns over large areas, and a terminology of spatial scales has been defined. *Grain* is the first level of spatial resolution; it relates to the individual data unit and can be described as fine-grained to coarse-grained. *Extent* refers to the overall size of the study area. A map of 100 km^2 and one of 100 000 km^2 differ in extent by a factor of 1000. Grain and extent are illustrated in Fig. 6.1. A third component is *lag,* which is the between-sample distance.

Figure 6.2 summarizes temporal and spatial scales of disturbances (modified from Zajac *et al.* 1998). The figure shows the main types of disturbances affecting soft-sediment systems, and separates them into natural and anthropogenic effects (see also Chapter 11, which indicates some of the management responses to these effects). The temporal scales are from seconds and minutes to many thousands of years for glacial cycles.

As indicated in earlier chapters, modifications to the sedimentary habitat come both from physical processes, such as the hydrophysical regime, and from the actions of the organisms themselves. We can separate the latter into different types of biological modification of the substratum (see reviews by Rhoads 1974 and Snelgrove and Butman 1994 indicating the main animal–sediment links and Elliott *et al.* 1998, Widdows *et al.*, 1998a, b, 2000 for further details of biomodification and the use of flumes for studying those links).

The types of biomodification are:

- *Biodeposition*: as the result of feeding by suspension feeders and the production of pseudofaeces leading to increased sedimentation from the water column to the bed, resulting in the build-up of beds (e.g. the mussel beds of *Mytilus*, *Modiolus*), sedimentation in crevices (e.g. dead barnacles), and the creation of additional niches.

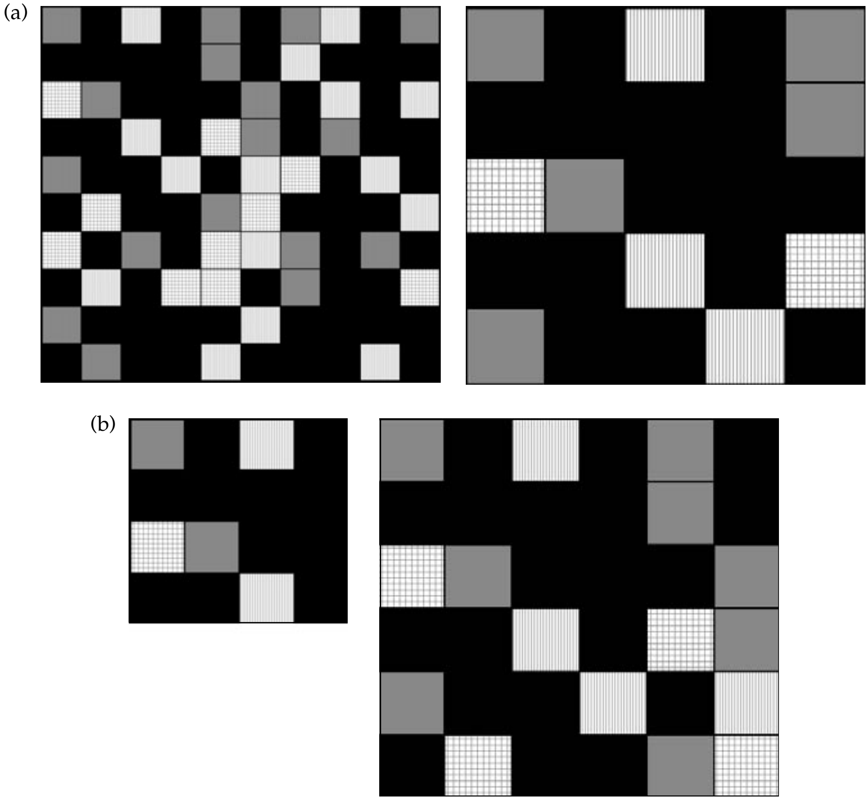


Figure 6.1 Schematic figure illustrating (a) increasing grain size, fine-grained on the left and coarse-grained on the right and (b) increasing extent in a landscape data set (from Turner *et al.* 1989). The different shadings signify patches of different species composition.

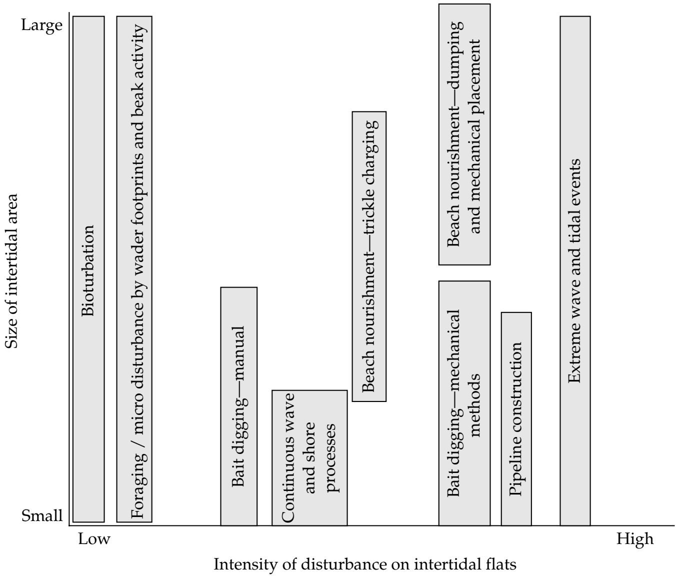


Figure 6.2 A conceptual model of spatial and temporal changes to intertidal sediments (from Elliott *et al.* 1998).

- *Bioturbation:* the result of egestion, disturbance, and turnover of the bed, the increase in the 'surface' layer (being carried into the sediment), irrigation and increased oxygenation at depth, and the creation of habitats suitable for further colonization (e.g. the Norwegian lobster *Nephrops* creating a habitat for the red band fish *Cepola rubescens*).
- *Biomodification/bioerosion:* in which the boring of hard substrata by boring polychaetes and bivalves (e.g. *Polydora*, *Petricola*) can lead to increased erosion and also increased niches.
- *Biostabilization:* whereby different types of organism stabilize the sediments, for example by infauna (such as the effect of spionid polychaete tubes which disturb the laminar flow across the bed), by macroflora (such as the effect of the eelgrass *Zostera* stems and rhizomes which again affect bed turbulence but also bind sediments), and by microorganisms (such as the effect of the microphytobenthos producing mucopolysaccharides which stick the grains together) (see also Black and Paterson 1997).

At the smallest extent, interactions within and between microflora and microfauna occur at the micrometre scale (Fig. 6.3). Disturbance at the 1 cm^2 extent is often by individuals, for example a fish such as flounder taking bites of sediment while feeding, which results in effects on the infauna and creation of small pits. Alternatively, individual organisms living in the sediment bioturbate and affect the immediate areas surrounding the tube or burrow where they live (Mazik and Elliott 2000). Recovery rates from those types of disturbances are usually rapid. For example, Rhoads and Boyer (1982) found that the organic film coating sand grains could be restored in just 10 min. Tidal currents will also eradicate most of these small-extent disturbances within the normal tidal cycle.

At an extent of 1 cm^2–1 m^2, other processes act as natural disturbers of sediment. Bioturbation was briefly described in the Introduction, and Fig. I.4 shows a cross-section of a typical sandflat with the key bioturbating species illustrated. Bioturbation also occurs over larger extents covered by the intermediate scale and of course is dependent on the size of population of the key bioengineers. The key bioturbation processes are by individuals feeding at the surface and defecating deeper into the sediment, or alternatively by head-down feeders, which defecate at the surface, as does the common European burrowing polychaete *Arenicola marina* (or sipunculid worms on the east coast of the USA). Such disturbance is of an intermediate extent but may lead to significant changes in the local RPD (Redox Potential Discontinuity) layer (see Chapter 2). Reise (1981) has shown that some species of meiofauna live in specific areas of worm tubes and are thus dependent on the disturbance by the bioturbator for their existence.

The bioturbation effects of a variety of species (the polychaetes *Heteromastus filiformis* and *Arenicola marina* and the bivalve *Macoma balthica*) have been studied in the Waddensee (Cadee 1995) where it was estimated that collectively they reworked a sediment layer of *c.*35 cm annually. Jim Atkinson, at the Millport Laboratory in Scotland, has used epoxy resin casting to show that some burrowing decapod

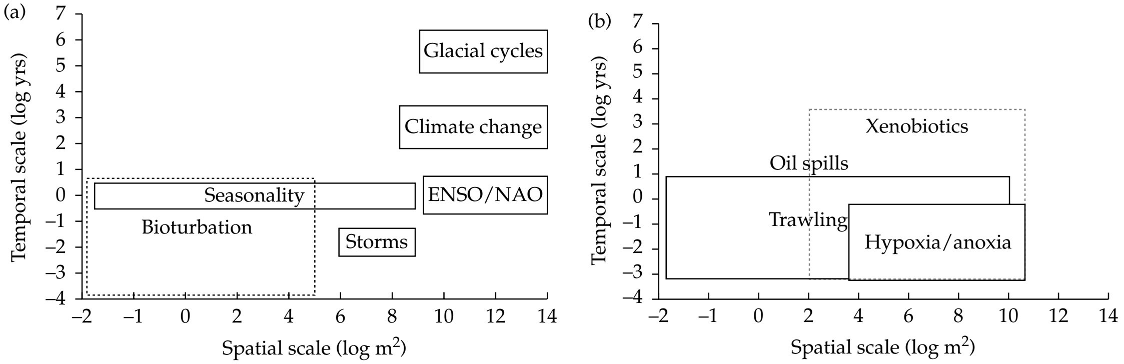


Figure 6.3 Temporal and spatial scales of (a) natural and (b) anthropogenic disturbances affecting soft bottom systems (modified from Zajac *et al.* 1998).

species make burrows and tunnel networks that go down to 0.5 m or more in the sediment and stretch over similar areas laterally. Similarly, Mazik and Elliott (2000) created similar casts but at a smaller scale for polychaetes, and more recently computer-aided microtomography (CAT) scanning has been used by Rosenberg *et al.* (2007) and Mazik *et al.* (2008) for macrofauna. The latter authors also observed meiofaunal burrows and then used novel software to interrogate the scans to give the surface area and volume of the burrow structures. Figure 6.4 shows such burrow structures similar to those created by Atkinson and Fig. 6.5 shows the very visual outputs from computer-aided microtomography (from Mazik *et al.* 2008). The latter study has now taken the field further by first increasing the resolution in order to measure not only macrofaunal burrows (the polychaete *Nereis diversicolor* and an *in situ* bivalve *Macoma balthica* are shown) but also the structure produced by meiofaunal nematodes. In addition, their use of detailed software as used in medical scanning systems has allowed the burrow surface area and volume to be accurately measured. The plate shows a core scanned to high resolution and then reconstituted.

At a larger scale, Fig. 6.6 shows disturbance caused by rays on an intertidal sandflat in New Zealand. Hall's 1994 review shows there are many species that cause similar effects, such as shorebirds, crabs, walruses, and grey whales, although with different sizes of disturbance, rays being intermediate (see also Daborn *et al.* 1993).

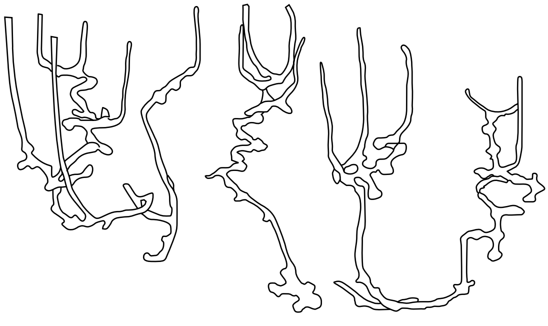


Figure 6.4 Schematic drawing of extent of burrows of ghost shrimp found by injecting epoxy resin into holes and then excavating. Scale:top to bottom of picture 50 cm.

At a larger extent (m^2 to km^2) storms have been shown to remove patches of sand and mud at depths between 6 and 12 m off the coast of Wales, UK (Rees *et al.* 1977). As a result of the storm actions, mass strandings of macrofauna occurred on beaches.

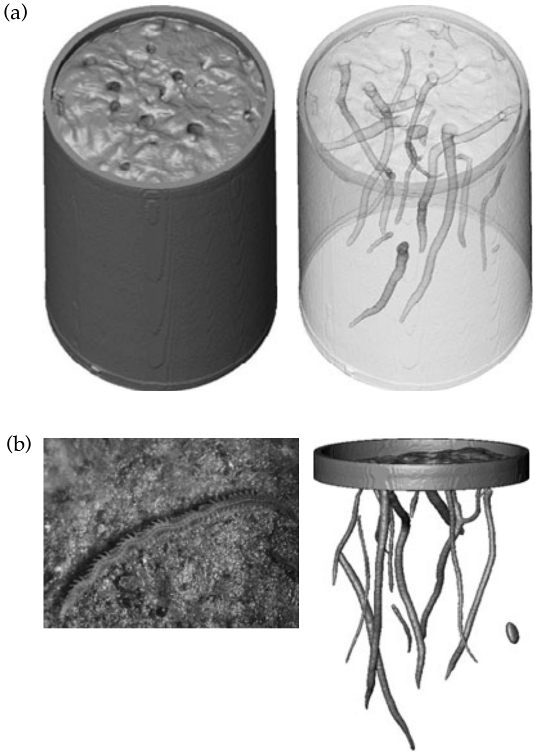


Figure 6.5 Bioturbation created by the ragworm *Nereis (Hediste) diversicolor* and the bivalve *Macoma balthica* shown using microtomography (expanded from Mazik *et al.* 2008). (a) CAT scans of reconstituted core and burrow structure;
(b) photograph of *Nereis (Hediste) diversicolor* and 3-D image of surface and burrows; note the deeper bivalve shell. See Plate 8.

Figure 6.6 Pits formed by feeding rays on an intertidal sandflat in New Zealand (courtesy Simon Thrush, NIWA, New Zealand). See Plate 9.

Such disturbance can be on a large scale as there is evidence that storms can affect the benthos down to water depths of *c*.100 m. Similar effects are found where icebergs ground and scour the sediment. Figure 6.7 shows areas in Antarctica where individual icebergs have had effects over tens of square metres. When combined, the effects are over much larger areas covering tens of square kilometres.

Studies have been made of the recovery rates from iceberg scouring and show that in such areas there is a patchwork of areas with different successional stages of the local benthos, dependent on the time since the last passage of an iceberg over the area.

Most benthic ecologists now believe that one of the most severe disturbances of sediment assemblages globally is that caused by bottom trawling. Heavy gear is pulled over the seabed to disturb fish, which are caught in the trawl, but in the process sediment is disturbed and the heavier the gear the greater the disturbance. In the North Sea it has been calculated that the whole of the seabed is trawled over twice per year, some areas are trawled 3-4 times per year, and many areas have been trawled 10-16 times in recent years. The effect is dramatic: Watling and Norse (1998) likened it to clear-cutting of tropical forests. This topic has received much attention in recent years and since there is a considerable amount of new data the subject is discussed separately in Chapter 8.

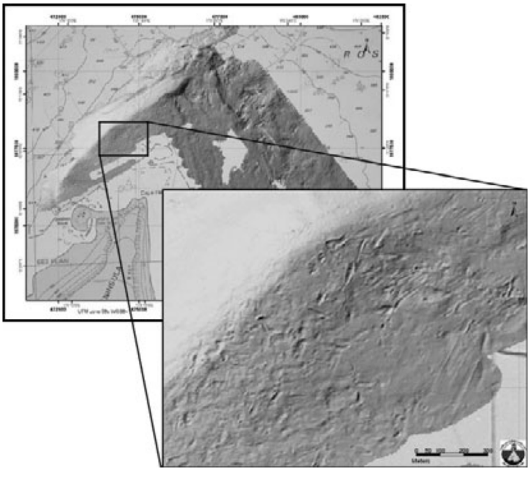


Figure 6.7 Iceberg scour (courtesy NIWA Hamilton, New Zealand). See Plate 10.

The large physical processes that affect the earth also have major effects on benthic systems, and so the North Atlantic Oscillation (NAO) and the El Niño–Southern Oscillation (ENSO) are covered in the next chapter. Climate change is being extensively studied and polar systems are especially vulnerable since temperature changes are predicted (and have already been measured) as showing the greatest increases there. As yet we do not have data showing or predicting large-scale effects on benthos, but much research is being conducted on this topic.

Finally, glacial cycles have played a major role in shaping modern assemblages and benthic systems. Only 15 000 years ago most parts of northern Europe and North America were covered by ice caps. The North Sea did not exist: the area was dry land until around 8000 years ago. Surprisingly, the first land areas available for colonization after the ice age were in the north of Norway and colonization came from the east, Russia. We do not know if the benthic systems moved deeper and then recolonized or whether shelf systems were wiped out and were recolonized later. The Baltic Sea was a freshwater lake until 7000 years ago, so it is not surprising that species are still colonizing from adjacent sea areas. Invasive species are thus a major topic of research in the Baltic Sea.

6.2 Measuring scale effects on sediment systems

There have been many benthic studies measuring scale effects, from the centimetre scale to hundreds of kilometres (e.g. Solan *et al.* 2003). Some of the large-scale studies relate to distributions within biogeographic realms, for example in the north-east Atlantic where there is a gradation from the Arctic progressing southwards to the Boreal and then to the Lusitanian realm. The benthic assemblages can be based both on temperature regimes and thermal stability of the water column; for example, Glemarec (1973) separated the benthic assemblages into *étages* depending on depth and temperature variation. For the North Sea he identified:

- *infralittoral étage:* depth <40 m, temperature variation >1 °C

- *coastal étage:* depth 40–100 m, temperature below 12 °C and variation <5°C
- *open sea étage:* >100 m depth, temperature <10 °C and little variation.

This separation of the communities contrasted with that of Dyer *et al.* (1983) based on depth and that of Basford *et al.* (1990) based on substratum for the same geographical area. It is of note that each of these produced similar patterns, most notably a separation of the North Sea along the Flamborough–Helgoland line that separates benthos in the deeper, summer-stratified northern part from that in the shallow, summer-non-stratified southern part (also see Ducrotoy *et al.* 2000).

A good example showing the effects of disturbance at different scales is that of Hewitt *et al.* (2002) who studied the influence of a large habitat-creating bivalve, the pinnid *Atrina zelandica. A. zelandica* is a large (up to 50 cm) suspension feeder which protrudes many centimetres above the sediment surface. By its physical presence and its feeding and defecation processes it alters the local hydrodynamic regime and sediment chemistry, which affects other species. Hewitt *et al.* (2002) used an interesting spatial design to determine the scale of influence. They took transects through dense patches of *A. zelandica,* where patch size was up to 100 m^2. Cores were taken for macrofauna analysis along the transects through high-density and low-density patches and from sediment where *A. zelandica* was absent. Then samples were taken to reflect different grain sizes (as defined in section 6.1). These were: (1) video quadrats from each core taken, (2) three contiguous quadrats centred around the core, (3) five contiguous quadrats centred around the core, (4) seven contiguous quadrats centred around the core, and (5) nine contiguous quadrats centred around the core. The total density of *A. zelandica* was averaged over the quadrats (Fig. 6.8).

The patches of *Atrina* were located by video transects, and transects were made along the principal axis of tidal flow as well as at right angles to this. Cores (10 cm diameter) were then taken to a depth of 10 cm along each transect and the fauna extracted, counted, and identified. The results (Table 6.1) show that the effects of *Atrina* are not simply localized to the immediate area around the shells but extend to grain of 0.4 × 4.5 m. In fact overall (i.e. at all sites) there is a consistent increase in the effectiveness of the spatial arrangement of *Atrina* in explaining the benthic community with increasing grain size. Although only low amounts of variance were explained (which is typical for analyses of soft-sediment fauna) in fact measurements made at the smallest grain size (0.4 × 0.5 m) were least effective in explaining benthic macrofaunal community composition.

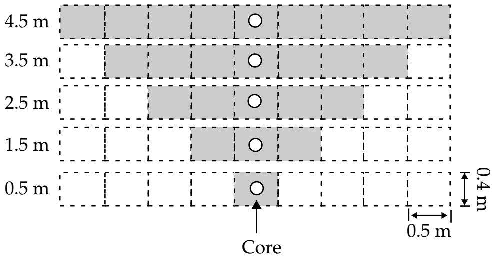


Fig 6.8 Sampling design for assessment of effects at different grain sizes of the suspension-feeding bivalve *Atrina zelandica* on macrofauna of sediments (from Hewitt *et al.* 2002).

Table 6.1 Relationships between macrofauna and *A. zelandica* at different grain. Data are explained variance % from a multivariate statistical analysis (canonical coordinates analysis) (see Hewitt *et al.* 2002 for details)

Grain (m)	All sites	Inside harbour sites	Outside harbour sites
0.4 × 0.5	5.0	5.5	12.1
0.4 × 1.5	9.2	6.1	19.8
0.4 × 2.5	9.5	6.7	21.3
0.4 × 3.5	10.1	6.9	19.5
0.4 × 4.5	10.6	6.9	21.4

The important message from this study is that benthic macrofauna were related to the spatial distribution of *Atrina* and the pattern was strongest at scales greater than 2 m. This means that far too often experimental manipulative studies are done at too small a grain size, the alpha size , and not at larger grain sizes (also see Chapter 2).

Thrush and Hewitt's research group have made highly influential studies on the importance of measuring effects at different grain size (Hewitt *et al.*

1996, Thrush 1997, Thrush *et al.* 2000, 2003, 2006). In a large experimental study of the effects of one of the commonest forms of disturbance, deposition of sediment, they studied recovery over a period of 212 days. Three sites in a large estuary were used and varying amounts of terrestrial sediment were deposited on the natural sediment, with five treated plots of 3 m diameter and five similar-sized controls within each site. Results of multivariate analyses of the deep burrowing (2–15 cm depth) fauna are shown in Fig. 6.9. The Outer Harbour sites show clear separation between experimental and control assemblages in the trajectories of development.

The other sites show a more variable response, and so making interpretations from the wealth of data given the high site-to-site variability is difficult. Thrush *et al.* (2003) solved this problem by using what is becoming a common technique—applying a meta-analysis that simply compares trends. This showed clearly that using number of taxa, number of individuals, and Bray–Curtis similarity indices, the effect of adding terrestrial material was to slow recovery rate and the larger the area that was covered the slower was the rate of recovery. Extending this research, other members of the team have shown that as little as 3 mm thickness of sediment on top of natural sediment leads to significant changes in the benthic fauna (Lohrer *et al.* 2004b).

An interesting study of an intermediate-scale effect was made in a pan-European study of the influence of man-made structures on the fauna of soft sediments (Martin *et al.* 2005). The sampling design was similar at a variety of sites (Fig. 6.10).

The study examined the effects of the structures on the sediment itself using variables characterizing the sediment (grain size, organic carbon content, macrofauna of soft sediments, chlorophyll *a*, and depth) and the fauna where species were determined; the data were then analysed using univariate and multivariate statistical methods. As is often the case, the univariate methods did not show clear effects whereas the multivariate methods did. Figure 6.11 shows the results of an ordination (MDS) analysis. There were clear differences between the landward and seaward sides of the constructions, with the landward side showing high variability between replicate samples. Near the constructions fine sediments were less abundant than at the control sites and, as is usual with disturbances, the opportunist polychaete *Capitella capitata* increased enormously in abundance on the landward side of the construction compared with the controls (Fig. 6.12). This dominance of

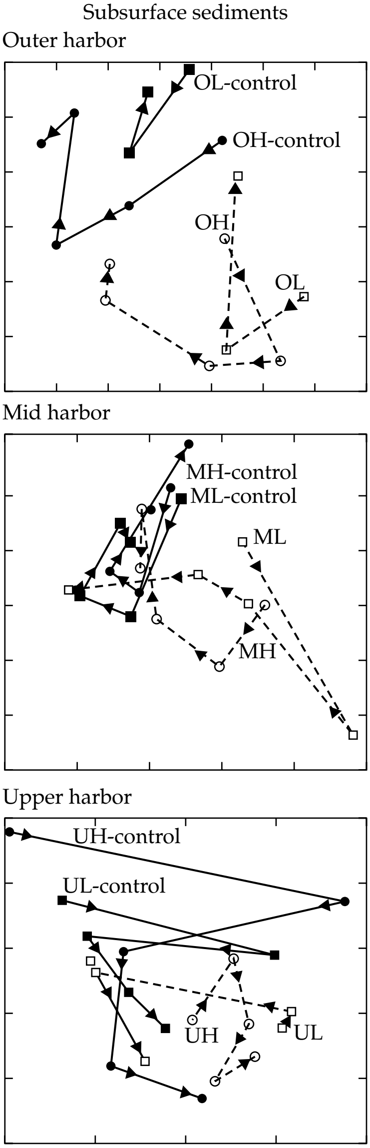


Figure 6.9 Non-metric multidimensional scaling analyses of changes in macrofauna of intertidal sediments following addition of sediment to 3 m experimental patches (Thrush *et al.* 2003). The lines represent trajectories of development at each experimental site (high (H) and low (L) tide areas of the Upper (U), Mid (M) and Outer (O) Harbour areas).

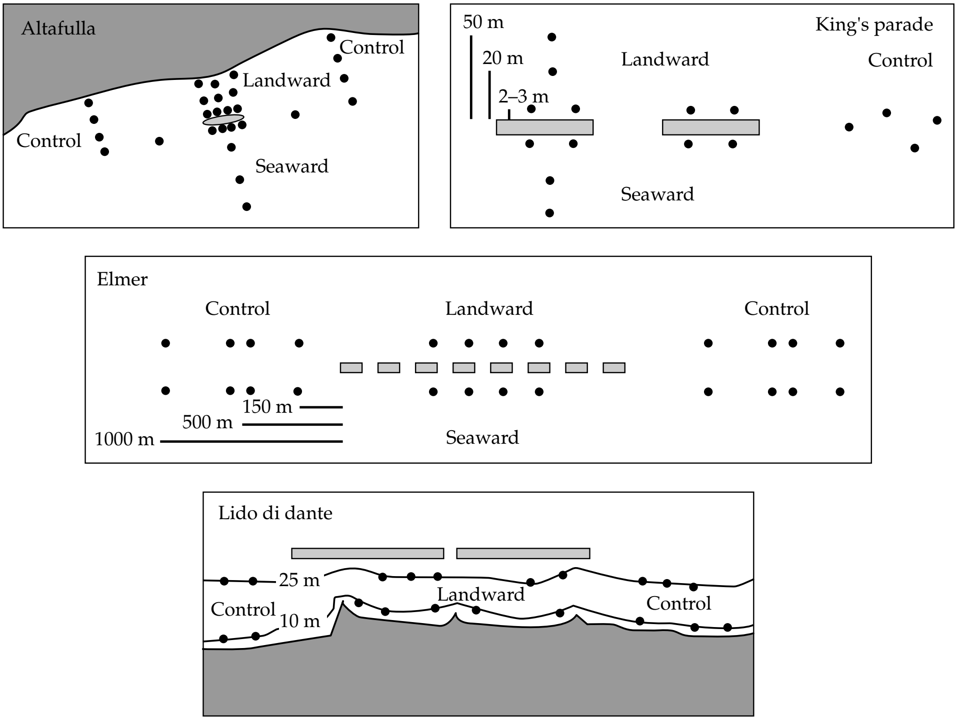


Figure 6.10 Sampling strategies to study effects of coastal defence structures on benthic assemblages (from Martin *et al.* 2005). Altafulla, Spain; King's Parade, UK; Elmer, UK; Lido di Dante, Italy.

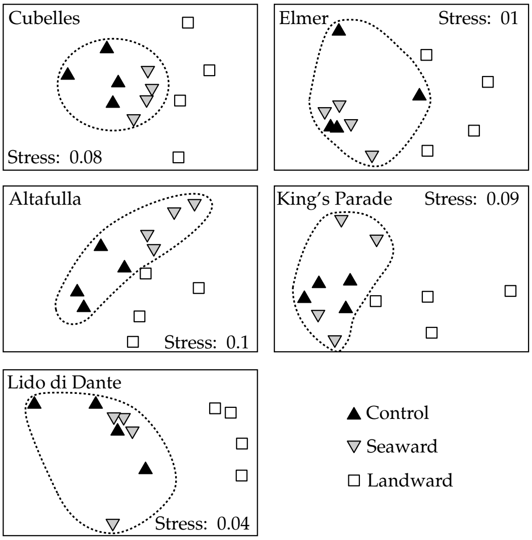


Figure 6.11 Non-metric multidimensional scaling analyses of responses of benthic macrofauna to sea defence structures at sites across Europe (from Martin et al. 2005). Sites as in Fig 6.10 with the addition of Cubelles, Spain.

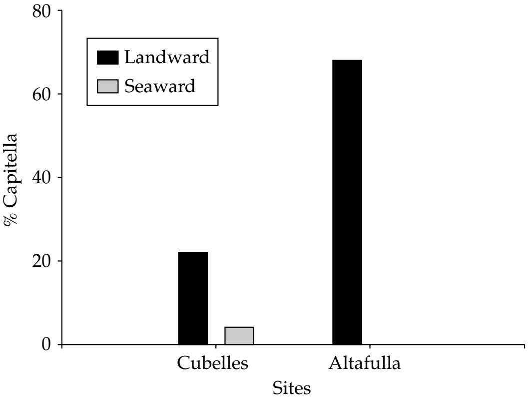


Figure 6.12 Response of *Capitella capitata* to the presence of defence structures (from Martin *et al.* 2005). There were no *C. capitata* in the control sites at Altafulla.

opportunists at disturbed sites will be discussed further in Chapter 9 in relation to adaptation strategies to pollution/disturbances.

6.3 Biological interactions causing disturbances

Some forms of biologically induced disturbance are relatively easy to observe. Predation caused by flocks of birds feeding over an intertidal mudflat or sandflat can be observed by their consumption of bivalves and polychaete worms. Other effects have a less obvious cause but often have highly significant effects, such as the large pits excavated by predating rays feeding on bivalve mussels at high tide (Fig. 6.6). Competition has been alluded to in previous chapters where dominance patterns change seasonally. In the 1960s and 1970s it was generally believed that competition was the main factor controlling the structure of assemblages, and elegant experiments were done particularly in the rocky intertidal zone. Connell (1961a,b) showed clearly how competitive interactions could explain the distribution patterns of barnacles, and yet the distribution pattern of some species was also partly controlled by predation by gastropod snails. Paine's (1966) experiments on predatory starfish controlling the structure of intertidal assemblages on rocky shores gave rise to a whole new field of study. So why today do we believe that competition and predation are less important than they were thought to be in the 1970s?

6.3.1 Competition

Direct competition occurs where individuals of the same or two different species are competing for a resource which is in limiting supply—this is referred to respectively as *intraspecific* or *interspecific competition*. As with most habitats, within the benthic realm the main resources required by invertebrate organisms are space and food. It is widely recognized that whereas space is limiting for suspension-feeding benthos, such as the number of mussels or barnacles able to occupy a given area, it is food supply that is limiting for deposit and detritus feeders (Levinton 1979). Wildish (1977) elegantly summarized the biological interactions defining benthic communities as food supply, the supply of colonizing larvae, and intra- and interspecific competition and interactions.

Indirect competition occurs where some individuals prevent others from utilizing a resource (*interference competition*) but if the organisms can adjust their use of the resource to avoid competition then we regard this as *resource partitioning*. For example, the early elegant work of Fenchel (1975) showed that two deposit-feeding estuarine intertidal organisms, the gastropod *Hydrobia ulvae* and the amphipod *Corophium volutator*, were able to coexist with minimal interspecific competition by taking different sizes of particle. Intraspecific competition leads to effects such as lowered growth rates at high densities (i.e. a density-dependent effect) whereas interspecific competition may be more ecologically interesting. Interspecific competition occurs where two different species compete; over time the better competitor will outcompete the other. This will lead either to the population of one species disappearing locally, a process known as *extirpation*, or to individuals of the population of one of the species changing so that they no longer compete for a limited resource and so become a separate species. (The term extinction should be reserved for the process where a species no longer exists anywhere.)

Competition is widely regarded as a cornerstone of ecological theory, yet attempts to demonstrate its importance in soft-sediment assemblages have been problematic. Classical theory postulates that when individuals compete for a limiting resource, competition will be shown by a decrease in, for example, population abundance or growth rate of individuals of the less competitive species. As discussed above, space is known to be an extremely important resource for which species compete. Many sediment-living species produce an abundance of eggs and larvae that live for a period in the plankton and then settle to the sediment after metamorphosing when time and conditions (i.e. hydrographic concentration) are suitable. This was demonstrated by Levin (1981, 1984) who showed that the population of the spionid polychaete *Pseudopolydora pauchibranchiata* is maintained at a constant density by direct competitive interaction between individuals. Despite this, *P. pauchibranchiata*, in building its tubes, also prevents other infauna from colonizing due to interspecific competitive interactions.

Some of the first experiments done with sediment-living species used bivalve molluscs, where growth rates are relatively easy to measure using growth cessation rings indicating annual, daily, or even tidally induced growth bands (Richardson *et al.* 1980, Lønne and Gray 1988). By experimentally manipulating densities (e.g. augmenting natural densities), it has been shown that growth rates were reduced and thus both intra- and interspecific competition is a major factor affecting sediment-living species (Peterson 1982). In these experiments Peterson showed that due to intraspecific competition, growth rates of *Protothaca staminea* and *Chione undatella* were reduced by respectively 49% and 38% when densities were increased from 0.5–1× to 3–4× natural densities. Yet it can be argued that this does not demonstrate that such competition is important in the field, since results were obtained only by raising densities to 3–4× the natural levels.

For competition to occur, there must be a limiting resource. It is quite possible for two species within the same genus to exist in the same habitat because the resource is not in fact limiting, or alternatively the two species utilize different resources (see Fenchel 1995). Often it is not known what resource the individuals or species might in fact be competing for, since specializations between species may be very subtle, even to utilizing different components of ingested organic material. In his review of competition and predation effects in marine soft sediments, Wilson (1991) points out that it is very difficult to increase food material for deposit feeders in a consistent manner and hence there are few experiments manipulating food resources.

In classical studies of the benthos of Long Island Sound, New York, USA, Sanders (1956) found that over a 2 year period only two species constituted more than 10% of the total number of individuals (except for one month when the cephalocarid *Hutchinsoniella* reached 12%), although there were a total of 98 species in the community (Fig. 6.13). There is an oscillatory pattern within each year; when *Nucula* is dominant *Nephtys* is not, and vice versa. This pattern of oscillating dominance is quite common. In the Forth estuary, on the east coast of Scotland, some of the intertidal areas oscillate between being dominated by the polychaete *Nephtys hombergi* and *Nereis (Hediste) diversicolor*, apparently depending on the prevailing salinity and thus reflecting the respective species tolerance to lowered salinity (D.S. McLusky, Stirling, personal communication). Competition is inferred from both of these cases and it may be the result of the prevailing environmental conditions favouring one species over the other and thus the former having a competitive advantage. However, without experimental proof this remains only a hypothesis.

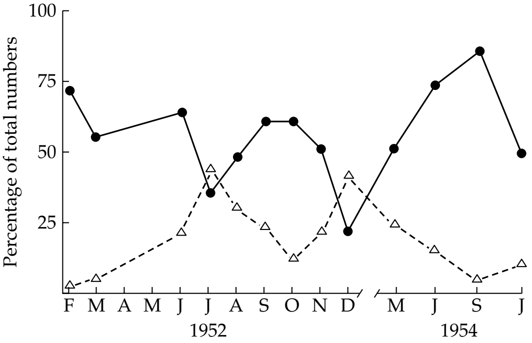


Figure 6.13 Seasonal changes in dominance in the benthos of Long Island Sound, New York (from Sanders 1956). Solid line, bivalve *Nucula;* dotted line, polychaete *Nephthys.*

One of the most interesting examples of such cyclical oscillation patterns is from a study in Barnstaple Harbor, Maine, USA by Mills (1969). He found the pattern shown in Fig. 6.14. In the winter the sediment was dominated by the mud snail *Nassarius obsoletus*, which occurred in large numbers and fed on the detritus in the sediment. In spring a few individuals of the tube-building amphipod *Ampelisca abdita* became established and since *Ampelisca* (like all amphipods) is a brooder, a rapid build-up of the population occurred. The tubes of *Ampelisca* hindered the feeding of *Nassarius* and so the latter population declined, outcompeted for space by *Ampelisca*. The tubes increased the spatial heterogeneity of the habitat and other species were able to coexist with *Ampelisca*, subsequently increasing species richness. In the autumn, storms began to dislodge the *Ampelisca* tubes, which were rolled up like a carpet, and a rapid decline in the

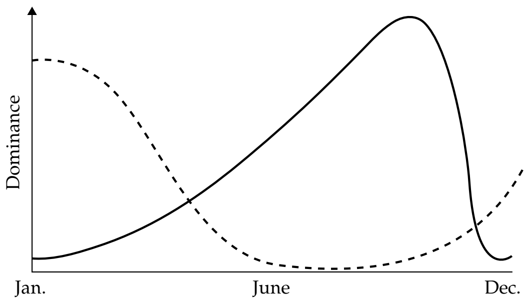


Figure 6.14 Seasonal changes in benthos of Barnstaple Harbor, Maine. Dotted line, gastropod *Nassarius;* solid line, tube-building amphipod *Ampelisca.* (data from Mills 1969).

Table 6.2 Changes in dominance in the fauna of an intertidal mudflat in Washington State, USA caused by excluding the larvae of tube-building polychaetes by the use of cages for a 4-month period.

Experimental conditions	**Percentage abundance**	
	Tube-dweller *Platynereis bicaniculata*	**Burrower *Armandia brevis***
No cage	51.2	7.6
Cage	8.5	33.4

population resulted. The sediment was then available for recolonization by *Nassarius*, and so the cyclical pattern continued. Given the large influence that sediment-dwellers have over their environment and their ability to modify their local sediment, this pattern of one species making the habitat unsuitable for another species is a rather interesting property of sediment-living species and is of course rare on rocky shores (see also the review by Gray 1974 for other examples). One point that should be borne in mind is that Sanders' (1956) study described here was concerned largely with a single station, whereas Mills' data concerns a much larger area, in this case many hundreds of square metres.

One of the simplest and yet most effective ways of demonstrating that competition can be responsible for changes such as those shown above is by manipulating the natural populations. Pioneering research in this area was done by Sally Woodin (1974). She excluded the settlement of a tube-building polychaete by means of a cage placed over the sediment on an intertidal mudflat and was able to show that this resulted in a dramatic increase in the abundance of a burrowing polychaete (Table 6.2).

Within a period of only 4 months, she was able to demonstrate the importance of competition for space, which would have taken decades by traditional methods of recording and then interpreting. By adding crabs to cages she was able to show that predators could equally alter the dominance pattern. Perhaps the most significant aspect of Woodin's research was that of *adult–larval interaction*, which has spawned a whole new branch of research. Woodin suggested that discrete, densely populated patches of infaunal invertebrates are maintained by the prevention of recruitment of larvae of other species. That is, species that are intense bioturbators will disturb the sediment and lead to prevention of larvae surviving; suspension feeders will filter out the larvae of burrowers thus preventing their accumulation in the sediment, and tube builders will occupy space and defecate and thus prevent larvae establishing on the sediment surface. Yet, although it is generally found to be true, field studies do not always support this adult–larval interaction hypothesis (Wilson 1991).

As Thrush (1997) points out, larvae can travel over very large distances and there are scale-dependent relationships between hydrodynamics and larval recruitment. For example, the maintenance of a population of a species with planktonic larvae on one part of the seabed will rely on there being another population of the same species somewhere else in the hydrographic realm, i.e. linked by currents. Thus the larvae from one population can seed the other as long as there are suitable currents to deliver the larvae to the area. The classical studies of Joe Webb (e.g. Webb and Hill 1958) on the populations and larval transport of amphioxus *Branchiostoma* showed that the larval distribution was related to hydrographic features (as shown by sediment characteristics) but that an intimate knowledge of current patterns was needed in relation to the relative positions of the adults and settlement areas. Because of this, it is important for studies of adult–larval interactions to be done over different grain sizes (see Fig. 6.1) to elucidate the range of factors influencing recruitment processes.

An evolutionary outcome of competition is that species become specialized to utilize different resources so that they no longer compete for a limiting resource. This is referred to as *resource partitioning,* in which the partitioning may be on a spatial or temporal basis and where the species adopt a strategy for taking a resource in a different area or at a different time. Most speciation events are thought to occur over very long periods of time (usually millions of years), yet changes to avoid competition can occur over ecological timescales. Fenchel (1975) studied three species of intertidal gastropod and showed what is known as *character displacement,* where some part of the organism changes so that different parts of the limiting resource are utilized. In the Limfjord in north Jutland, three species of the genus *Hydrobia* are very common, and their distribution in the field suggests that salinity is an important niche dimension. The results of preference experiments in the laboratory and those from field investigations are summarized in Table 6.3.

Clearly, there is considerable overlap in the salinity ranges where these species are found in the field, and their distribution pattern cannot be exclusively related to salinity preferences. *H. neglecta* should, in terms of salinity preferences, be the commonest species, since most of the habitats investigated had the preferred salinity for this species. *H. ulvae* occurred predominantly in the deeper, more saline areas, but its distribution extended right into the fjords, where it excluded *H. neglecta*. Fenchel (1975) suggested that *H. ulvae* is a superior competitor to *H. neglecta*. Yet, as the salinity is reduced, *H. ventrosa* becomes a superior competitor to *H. ulvae. H. neglecta*, therefore, is confined to areas with low population densities of the other two species. The changeover point from one species dominating to another species dominating depends on the intensity of the competition between the species, the relative competitive abilities at different salinities, and the rates of dispersal, as well as the differing salinity tolerance of these species.

In his studies, Fenchel (1975) concentrated on competition between *H. ventrosa* and *H. ulvae*. Niche theory states that no two species can coexist on the same limiting resource; one or other must win control of the resource, while the loser either becomes absent at that location or, over evolutionary time, develops specializations so that the two species no longer compete. The populations of *Hydrobia* occurring in the Limfjord have very high population densities and are almost certainly food-limited. Studies of their feeding habits indicate that all three species are indiscriminate feeders, ingesting sediment and utilizing microorganisms. They all appear to subsist on the same food items, yet the size range of particles ingested is dependent on shell length and so if two species have different shell lengths, they can coexist because they are not utilizing the same food resource. When *H. ventrosa* and *H. ulvae* live allopatrically they have almost

Table 6.3 Salinity preferences in laboratory experiments, and field salinities from localities in Limfjord, Denmark, for three species of *Hydrobia* (from Fenchel 1975).

	H. ventrosa	*H. neglecta*	*H.ulvae*
Laboratory preference (PSU)	20	25	30
Field range (PSU)	6–20	10–24	10–33

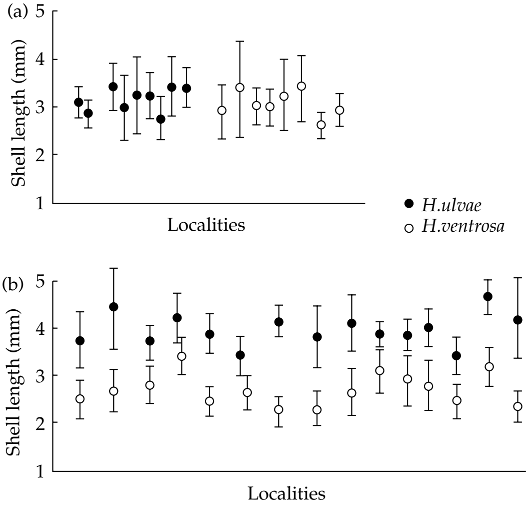


Figure 6.15 Character displacement in hydrobiid snails: when allopatric, species have similar sizes (a) but when sympatric, sizes are displaced (b) (from Fenchel 1975).

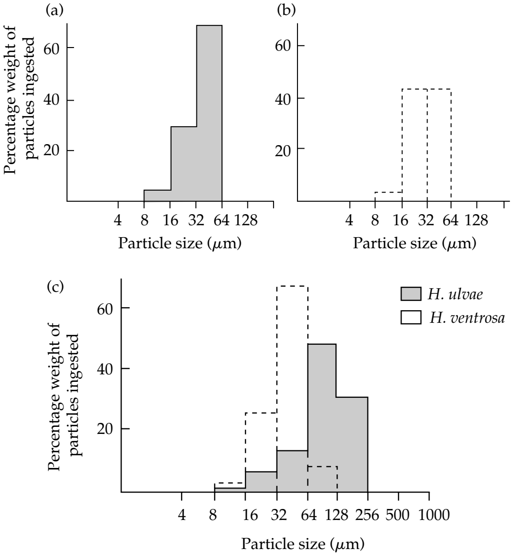


Figure 6.16 Character displacement in hydrobiid snails. Sediment grain sizes utilized by species when allopatric (a and b) and sympatric (c), showing size separation when sympatric.

identical size ranges (Fig. 6.15a), but it is remarkable that when they occur sympatrically their size ranges differ (Fig. 6.15b). This type of mechanism whereby two species avoid competing for a limiting resource is called *character displacement.* Curiously enough, Hutchinson (1967) had predicted that if food was the limiting resource the important dimensions of the mouth-parts of two related species should differ by 1.3 units to avoid competition. Fenchel's data show that on the appropriate $\log_2$ scale, Hutchinson's prediction is supported (Fig. 6.16). Although these studies are now somewhat dated, they elegantly indicate the need for further research applying simple ecological theory to marine benthic species in order to further our understanding of the biology of the species.

That such changes can occur over relatively short time intervals has recently been shown by Grant and Grant (2002), where studies on finches in the Galapagos shows that beak sizes changed over periods of around 10 years.

6.3.2 Predation

In the 1970s the first experiments were done to discover the effects of predation on benthic assemblages. The importance of predators in structuring benthic assemblages was estimated simply by using cages to exclude or confine predators. By comparing caged and unmanipulated areas the effects of predation can be determined, although great care must be taken to avoid cage artefacts (e.g. see Bolam *et al.* 2002). A cage will alter water flow and other properties of the sediment, making it difficult to derive clear conclusions from such experiments. Ingenious solutions involve removing sides and tops of different cages as part controls, and some experiments have even been done by tethering crabs to stakes to see how they influence the infauna where they predate.

There are three basic types of predators of benthos: *epibenthic predators, infaunal predators,* and *sublethal browsers.* Epibenthic predators are often highly mobile and include birds, fishes, mammals, starfishes, and crustaceans. Such predators will feed preferentially on high densities of prey populations, and prey location is a key aspect of the behaviour of such species. Epibenthic predators disturb the sediment to varying degrees. Whereas birds' feeding depths are determined to some extent by the shape and size of their bills, some of the fishes such as rays and flounders dig pits in the sediment and disturb larger areas. However, aggregated feeding, by flocks of birds for example, can have effects over many hundred of square metres (reviewed by Goss-Custard 1985, Hall *et al.* 1990).

The most commonly studied infaunal predators are predatory worms such as nereids and nephtyds, although other large predators such as nemerteans may be locally important (Ambrose 1991). Yet if birds take predatory polychaetes as their preferred food then a cascade effect can result. By manipulating densities of the infaunal predatory polychaete *Glycera dibranchiata* in mudflats in Maine, USA, Commito (1982) was able to show in an elegant experiment that the survival of other polychaetes, notably *Nereis virens,* was severely affected (Fig. 6.17). Yet if *N. virens* is present in large numbers it reduces the abundance of the amphipod *Corophium volutator.* Thus a cascade of predator–prey relationships may be the rule for most soft-sediment assemblages.

Later, Commito and Shrader (1985) were able to show that, contrary to expectations, if

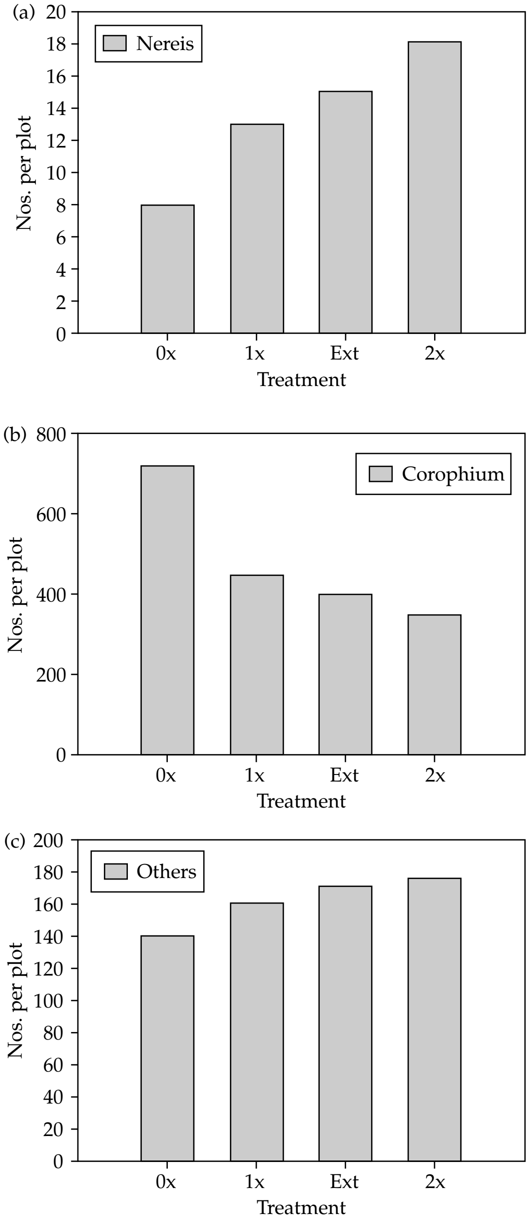


Figure 6.17 Numbers (mean ± s.e.) in 0.049 m^2 experimental plots of (a) *Nereis virens* adults, (b) *Corophium volutator*, and (c) other infaunal species (from Commito 1982).

*C. volutato*r was absent the presence of *N. virens* led to an increase in abundance of prey species. The explanation for this was that *N. virens* most likely preyed upon a key intermediate predator, the polychaete *Glycera dibranchiata*, which when reduced in numbers allowed its prey to increase in abundance. It is likely that such complex predator–prey interactions are usual in many soft-sediment systems. However, few have been studied in detail and there is a need for many more such experiments, particularly in little-studied areas such as the subtropics, tropics, and southern hemisphere, before we are able to make generalizations about the importance of predation.

Reise (1977) showed in experiments on the fauna of the Wadden Sea in Germany that small predators such as shore crabs (*Carcinus maenas*) have a much larger effect than do larger predators such as birds and fish. Likewise, Woodin (1981) used metal stakes to exclude the king crab *Limulus* from intertidal mudflats and showed again that there was much stronger predation pressure on macrofauna from portunid crabs than from the king crab.

In reviewing the caging experiments done in the 1970 and 1980s, Peterson (1979) and Wilson (1991) found that competitive release, where a predator feeding on one prey species allows another species to increase in abundance, did not occur. They concluded that competition almost never led to competitive exclusion in soft sediments. In reviewing 66 caging experiments, Olafsson *et al.* (1994) found that in <2 m deep unvegetated habitats, strong effects of predators were recorded in 44% of the experiments whereas in deeper areas the strong effects were only found in 22% of experiments and were rarest in vegetated sediments (15% of experiments). Thus epibenthic predators have a strong influence in unvegetated but not in vegetated habitats. Yet perhaps the main finding was that many experiments did not find any effects! The reason for this may be that there was no resource competition, the generalist nature of many predators, the presence of multiple trophic levels, or the mobility of predator and prey (Thrush 1999). Thrush here suggests another intriguing idea, that we are using inappropriate or incomplete study techniques. Specifically, he argues that one must consider the biological attributes of a particular predator's role in structuring the community as well as the rate of prey consumption, the behaviour morphology and mobility of the predator, and the sediment disturbance accompanying feeding. It is of note that these functional responses have previously been largely neglected.

A good example of a more complete study is that of Seitz *et al.* (2001) who studied the feeding of an epibenthic predator, the blue crab *Callinectes sapidus,* on two bivalve species *Mya arenaria* and *Macoma balthica.* From monitoring over 15 years they had determined that *Mya* was more common in sand than in mud and *Macoma* was widely distributed and at higher densities than *Mya* in both sand and mud. They combined detailed field studies of population dynamics of the species with field and laboratory experiments on functional responses of the predators to prey species that used different forms of protection from predation (Fig. 6.18).

Finally, in considering the spatial scales over which experiments have been done, Thrush (1999) states that there has been a lack of proper consideration of grain (plot size). One should not assume that the results of experiments done at one size are representative of what is happening at different scales. As indicated above, the change in spatial grain of experiments shows variations in the strength of predator effects related to predator behaviour and mobility and spatial patterns of prey. Thrush summarized this as follows: 'we need to know more about the natural history of predators and prey, particularly in relation to different scales of heterogeneity within the sediment'.

We need to remember, however, that it is easy to do manipulative experiments in the intertidal but far more difficult to do them in the subtidal, and yet it is the subtidal that is the dominant habitat. Again, much more research is needed on such systems and especially at different spatial scales, as will be covered below.

6.4 The settlement process

Throughout this account, we have emphasized the links between the nature of the benthos, the influence of the sedimentary and hydrophysical regimes, and the role of currents influencing deposition and accretion. In essence, fine particles—whether inert, organic, or biological—will be treated in the same way and will be deposited where the prevailing current strength permits. This causes us to question how larvae find areas to settle and what effect do such processes have on the patterns of species abundances found in marine sediments. Evidence suggests that settlement of larvae from the water column to the sediment is far from being a random process (Woodin 1991). First, there is a series of behavioural responses which vary as the larvae age, i.e. according to the age in relation to the time of larval metamorphosis. Larvae become photonegative and swim away from light and down to the sediment. Whether the settlement process is simply passive sedimentation as by inert particles or is an active process has been the topic of much debate and research. There seems to be little doubt that hydrographic factors play a significant role in influencing the overall abundance of larvae in a given area. Woodin (1991) looked at the types of cues required by the larvae, and the review by Rodriguez *et al.* (1993) separated the main factors influencing benthic larval settlement into biological (e.g. larval behaviour), physical (e.g. water flow velocity, contour and surface chemistry, light intensity), and chemical aspects. They separated the latter into natural inducers (those associated with conspecific individuals, microbial films, and prey species) and artificial inducers, such as neurotransmitters (e.g. catecholamines) and their precursors (e.g. choline), and ions such as potassium. The authors then give an extensive set of suggestions for further research which points out the need to combine the physical, possibly passive, influences with the active biological and chemical cues.

Using both models and observations, Young *et al.* (1998) showed that in the Wash (a large open bay on the east coast of England), wind force and direction could give up to 40-fold differences in the number of larvae of the edible cockle *Cerastoderma edulis* (a commercially fished species) that settled successfully. Yet the settlement processes and post-settlement mortality were also major factors influencing successful recruitment. Thus one of the main factors influencing which sediments larvae are able to contact is the hydrography of a given locality. It has been shown that current patterns and tidal regime are extremely important in determining where larvae accumulate. This research demands a strong interdisciplinary approach, with use of a variety of physical oceanographic instruments

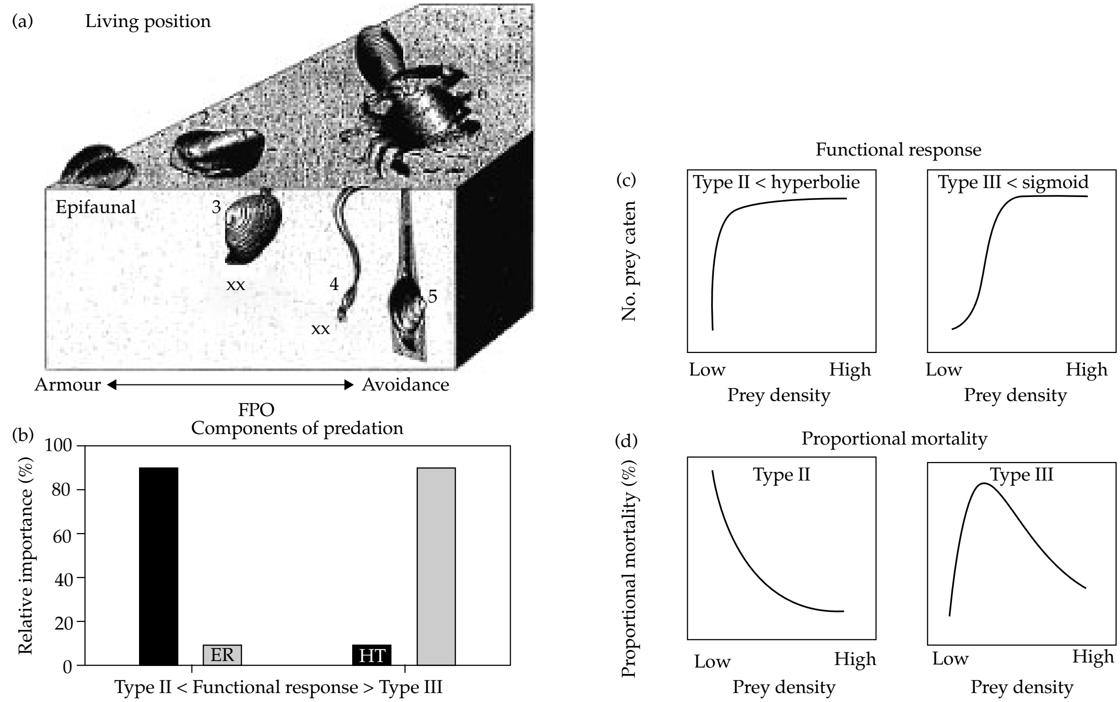


Figure 6.18 Seitz *et al.*'s (2001) conceptual model of the associations between antipredator defences (i.e. armour and avoidance), living position (i.e. epifaunal or infaunal, both shallow and deep-burrowing) of bivalve molluscs, the relative importance of the basic components of predation (i.e. handling time and encounter rate), the functional response, and proportional mortality. Panels on the left side of all graphs correspond to armoured prey, whereas panels on the right side refer to prey utilizing avoidance as a defence tactic. (a) Living position of prey ranging from those with armour, such as (1) the epifaunal mussel *Mytilus* and (2) oyster *Crassostrea,* to (3) the infaunal shallow burrowing hard clam *Mercenaria* and (4) deep-burrowing clams *Macoma balthica* and (5) *Mya areanaria* which are preyed upon by (6) the blue crab, *Callinectes sapidus.* (b) Components of predation (i.e. handling time (HT) and encounter rate (ER); and their relative importance along a range of antipredator tactics from armour to avoidance. Handling time is relatively more important in prey employing armour (e.g. morphological size refuge) as an antipredator tactic, whereas factors affecting encounter rate (e.g. habitat structure, low densities) become more important for prey using avoidance as an antipredator tactic. (c) The functional response changes form from inversely density dependent (type II) in prey utilizing armour to density dependent (type III) in prey using avoidance or burrowing. Note that the number of prey eaten at low prey densities is higher in the type II response than in the type III response. (d) Proportional mortality of prey ranging from inversely density dependent to density dependent. Note the low-density refuge from predation with the type III (density dependent) extreme characterizing species using avoidance, burrowing or habitat refuges from predation. The model predicts that predators foraging on bivalves living in or near the sediment surface will exhibit a type II functional response, but those foraging on deep-burrowing prey with a low encounter rate will exhibit a type III functional response.

such as current meters and sediment traps together with records of how many larvae settle and where. Roegner (2000) used hydrodynamic modelling to investigate the retention of molluscan larvae in estuarine systems; the study showed that the larvae can concentrate in certain reaches and in areas of a certain sediment type which supports large numbers of adults. As with much modelling of benthic systems, the explanation of final patterns using physical processes does not fully explain the resulting biological features and so biological information and understanding are needed. These studies show that the selection process is far from random and that organisms use both hydrography and their sense organs to select the site for settlement.

There is strong evidence that when larvae have developed to the stage at which they are ready to settle, a series of cues operate to trigger metamorphosis and settlement. Although these features have been most studied with regard to hard-substratum sessile epibenthos such as barnacle cyprid larvae, some studies relate to soft-sediment benthos. Bivalve larvae at this stage (known as pediveligers) are able to regulate their depth in the water column and thus are best able to locate the right sediment type for settlement. Experiments done *in situ* using divers and plankton pumps showed clearly that some species preferred muddy sediments and others sandy sediments (Snelgrove *et al.* 1999). Thus the spatial patterns described earlier of assemblages that vary from substratum to substratum may in part be due to larval choices. Despite this, it is extremely difficult to test these ideas using field experiments and so laboratory experiments have been done on testing for various settlement-inducing cues. Gray (1966a, b) carried out a series of experiments on a species of polychaete and a gastrotrich of meiofaunal size and showed that the individuals first discriminated between sediment particle size and then, within a given size, individuals aggregated in response to certain species of bacteria.

Other cues that are likely to be used, but not yet extensively tested in the marine environment, are symbiotic species and predators seeking out their hosts and prey by means of chemical cues (Rodrigues *et al.* 1993). It is likely that many species are able to select quite specific parts of the sedimentary habitat in which to settle, so that patterns of species assemblages are determined by larval settlement. There are many cases of juveniles settling in an area adjacent to or surrounding that occupied by the adults, allowing us to question whether this is an active or passive process. For example, in the case of intertidal populations of the lugworm *Arenicola marina*, it is still not fully known whether this is the result of an active process by the larvae settling outside the adult area (to avoid cannibalism or smothering by adult feeding), or alternatively the result of mortality of the settling stages inside the area. Some of these aspects have been investigated using laboratory experiments but these have been criticized on the grounds that static water tests are not realistic (see the review of Snelgrove and Butman 1994). Field experiments are now being used to investigate settlement patterns; for example, Huxham and Richards (2003) studied the substratum selection abilities of two common intertidal benthic bivalves, *Cerastoderma edule* and *Macoma balthica*. Their experiments suggested that these species had poor sediment selection abilities, and that the resultant patterns after settlement were due to the post-settlement movement (relocation) after an apparently random settlement by the spat in the accreting areas. Although hydrodynamic processes are clearly important factors, it may be that the bulk of larval settlement actually occurs at slack tide, when there is in fact static water (see also Bouma *et al.* 2001), but this hypothesis of hydrographic concentration still has not been fully tested.

6.5 Causes of change in dominance patterns

In section 6.2 it was shown that changes in the dominant species are often due to biological interactions where one species alters the habitat and makes it unsuitable for another. Such competitive interactions may also lead to spatial patterns. A good example is from the continental shelf of North America where large areas are dominated by a large ecosystem engineer, the holothurian *Molpadia oolitica*: in Cape Cod Bay, for example, it occurs over 440 km^2 at densities of around 6 m^{-2}. *Molpadia* feeds by ingesting sediment, and thus eliminates most infaunal species; the only common co-occurring species are the tube-building polychaetes and a caprellid amphipod, which attaches to the polychaete tubes by means of its gripping legs. Both the polychaete and amphipod can exist only on the faecal mounds produced by *Molpadia*, since these are relatively stable and are not reingested. Thus *Molpadia* controls its own environment and persists at fairly constant densities from year to year because it structures its own community. Such species can in fact be called ‘key’ species, by analogy with the terminology used for rocky-shore habitats (where, for example, the echinoderms such as *Asterias* in Europe and *Pisaster* on the west coast of North America control the community structure by ingesting the potentially dominant competitor for space, the bivalve *Mytilus* (*edulis* or *californianus*, respectively).

Thus the patterns described above—oscillating dominance and persistence through time—are in all probability mediated by biological interactions. In the former case it seems that changes in competitive interactions, geared to the short life cycle of the organisms concerned, together with seasonal effects such as autumn storms, produce the patterns at frequencies of less than a year. In the latter case the dominant role of the territoriality of *Calocaris* or the sediment-reworking of *Molpadia* produces rather constant numbers of the individual species concerned, by means of competition for space. This pattern may persist over many years even though other species within the same community may not show the same patterns. The changes that occur in time and space can be put into a more theoretical framework, that of global and neighbourhood stability.

6.6 Generalizing effects of disturbance

An important synthesis of the processes following disturbance has been made by Zajac *et al.* (1998), summarized in Fig. 6.19. They use a model for the recovery processes (succession) after disturbance based on work by Rhoads (1974) and Pearson and Rosenberg (1978)—these have led to the Pearson–Rosenberg (or alternatively the Rhoads–Germano) models or paradigms. Initial phases of colonization are by opportunist species (the so-called *r-selected strategists*) that are shallow burrowers and do not bioturbate to any great depth in the sediment. In this early phase of colonization which, following McCall (1977), they call stage 1, the species that colonize are small polychaete worms such as capitellids and spionids which reproduce many times a year, have high recruitment, turnover, and death rates and short life cycles, are small, sedentary deposit feeders and often have brood protection (within their tubes) as both of these polychaete families have—all of these are the characteristics of *r*-strategists. Over time these species are replaced by species which disturb the sediment and which are better competitors such as bivalves and echinoderms—the *K-selected strategists* (see Chapter 7 for a further discussion of *r*- and *K*-selected strategists). These species are usually large and motile with few reproductions per year, are slow developers with a low death rate, and are long-lived with planktotrophic larvae.

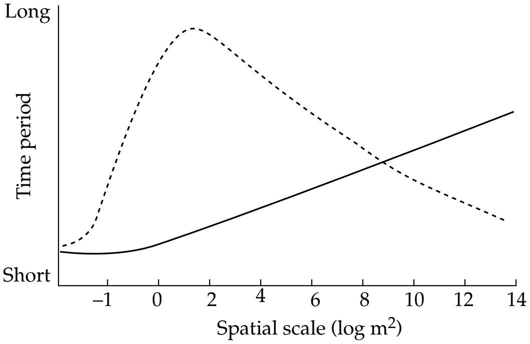


Figure 6.19 Changes in balance between opportunist (broken line) and competitive (non-opportunist) species (solid line) over different spatial extent (from Zajac *et al.* 1998).

Zajac *et al.* (1998) proposed that activities of individuals would influence processes at a small scale, whereas at larger spatial extents population demography and species life history were the key attributes determining succession. Thus again the spatial scale studied is highly important in interpreting the successional and recovery process. As an example, Olive and Morgan (1984) studied populations of species of the polychaete *Nepthys* in widely separated beaches around Britain and found that they had similar age structures, which suggests that similar factors were controlling population dynamics over large areas. They also found that recruitment failures were general and not localized.

In general, species dominant in soft-sediment assemblages show three basic forms of reproduction: *monotelic*, where species reproduce once and die; *polytelic*, with one major reproduction per year; and *semi-continuous breeders,* which reproduce when they reach maturity (Olive and Clark 1978). Larval development may be planktonic or benthonic, but within these categories there are broad variations; some species brood eggs to a late stage of development and then release them to the plankton. The presence of chemical cues inducing spawning is becoming an important area of research especially in species mixtures, for example the work of Watson *et al.* (2003) who experimented with extracts of gonad, body fluid, and the water where gametes had been released. In particular they looked for the presence of spawning-inducing activity (SIA) on both sexes of the polychaetes *Nereis succinea* and *Platynereis dumerilii*. They found that gonadal and body fluid extracts from the echinoderms *Asterias rubens* and *Echinus esculentus*, the polychaete *Arenicola marina*, and the herring *Clupea harengus*, and body fluid and spawning water of the polychaete *Nereis virens* all exhibit SIA on male *N. succinea*. They also found that herring male gonad extract also had SIA on male *P. dumerilii*. By testing phytoplankton monoculture extracts they were able to determine whether the presence of certain species had an effect on spawning of several of the benthic species as a potential mechanism for ensuring that the resulting larvae would occur at a time of abundant food. The cryptomonad *Rhodomonas baltica* induced SIA on male *P. dumerilii*, and the diatom *Phaeodactylum tricornatum* induced some activity in the mussel *Mytilus edulis*. Finally, in attempting to explain the nature of the chemical signal, they found that the active fraction of *Rhodomonas* is chromatographically similar to uric acid which is the natural sperm-release pheromone produced by females of *P. dumerilii*. This type of research shows the importance of chemical signals but also the need to consider the system as a whole with a large mixture of species and their signals.

The release may also occur under the best hydrographic conditions for dispersal, e.g. spring tides or equinoctial tides; see for example the short but interesting review by Ernest Naylor (1999). This factor has particularly been included in studies on the swarming behaviour of nereid polychaetes. For example, Hardege *et al.* (1990) experimentally studied the interaction of tidal state and temperature in spawning of *Nereis succinea*. They found that the metamorphosis to the heteronereid stages, as well as swarming at a minimum temperature of 12 °C, was induced by rising temperatures around the time of the new moon. However, although they found evidence of lunar periodicity under natural temperatures, abnormal and abrupt temperature increases disrupted that periodicity.

It is therefore obvious that there are several major factors, both chemical and physical, controlling spawning, dispersal, and settlement, but the usual result is that species with planktonic larvae have an ability to spread over much larger areas than species with benthic larvae. From these characteristics of species Zajac *et al.* (1998) proposed a model of the relative importance of the different factors in controlling successional dynamics (Fig. 6.20). Biotic interactions become less important at larger spatial extent, where life history traits and environmental conditions become more significant.

Combining the two models into one for the successional process as a whole, Zajac *et al.* (1998)

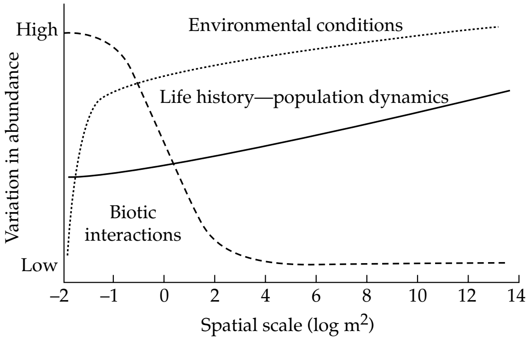


Figure 6.20 The change in relative importance of factors influencing succession over different spatial extent (from Zajac *et al.* 1998).

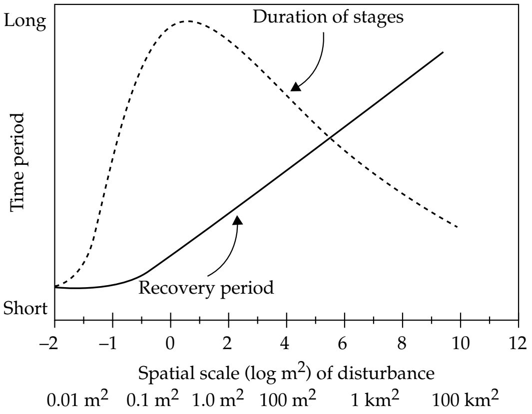


Figure 6.21 The temporal and spatial process of recovery from disturbance in marine sediment assemblages (from Zajac *et al.* 1998).

suggested that the initial successional process (the pioneering species, stage 1 of McCall 1977) covers a small spatial extent and is of short temporal duration. Once larval dispersal and recruitment becomes the dominant process then the successional process covers a larger spatial extent and takes place over longer time periods (Fig. 6.21). This is an important refinement of the traditional models of succession in that it takes account of the fact that succession occurs over a variety of spatial scales.

In this chapter we have stressed the importance of the proper consideration of spatial scales when studying recovery from disturbance. This is a dynamic and active research area where we expect much progress in the near future.

CHAPTER 7

Temporal variations in benthic assemblages

Most (but by no means all) benthic species have larval stages which use the water column for dispersal. As indicated in the previous chapter, a key process affecting recruitment to sediment systems is the need to disperse larvae in order to colonize new areas, even to the extent of releasing larvae at spring tides when the tidal excursion will be greatest, thus effecting an even greater dispersal. Seasonal release of larvae is the norm: most species develop gametes in spring and spawn in late spring or early summer (see Rasmussen 1973 for an excellent data set of the times of planktonic larval occurrence and settlement by many important north-west European boreal benthic species). Some species, however, avoid the high competition for food at this time and release gametes in autumn and winter. Thus larvae of benthic organisms are a key and often dominating component of the spring–summer plankton and play important roles as food for planktonic species such as fish larvae.

Conversely, a number of planktonic species have resting stages in sediments. The most important of these are undoubtedly the diatoms and many flagellates, and also certain calanoid copepods such as *Acartia*, which are of course key components of the phytoplankton and zooplankton respectively. Diatom cysts are often found, and there is increased interest in the survival and hatching processes of dinoflagellate cysts that lead to harmful algal blooms. Similarly, the seasonal occurrence of many zooplankton species results from hatching of resting stages in the sediment (see Smetacek (1995), Boero *et al.* (1996), Pati *et al.* (1999) and Boero and Bonsdorff (2008) for reviews). The implication of many important planktonic species having benthic resting phases is that by predating cysts, benthic species may be able to control abundances of planktonic species. In this context the meiofauna are important predators (Pati *et al.* 1999).

It is now important to consider the scales of temporal variation in benthic assemblages. First, seasonal changes occur in benthic assemblages of soft sediments even in the depths of the deep sea (e.g. Hsü and Thiede 1992). In spring, as light levels and temperature increase, a plankton bloom occurs. Although most of the bloom is eaten by grazing zooplankton, varying proportions are not grazed and sink to the seabed along with sedimenting faeces from zooplankton and partially consumed plant cells. This p*articulate organic matter* (POM) provides the main food source for the benthos (the so-called 'marine snow') and the amounts of POM settling vary greatly with latitude. In tropical regions where waters are oligotrophic with low nutrient levels there is strong direct coupling between phytoplankton production and zooplankton production, so that most of the material is eaten and little falls to the sea floor. Since the seasonal change in nutrient or light input is small, the seasonal signal for the benthos is not well developed and strong seasonal changes in the benthos are not expected. In temperate areas the coupling between the phytoplankton and zooplankton blooms is delayed so that much plant material sinks directly to the seabed. In polar regions the coupling is even less tight and large amounts of the spring phytoplankton bloom sink directly to the seabed, providing a rich source of food material that is used directly by benthic species. Microalgal (microphytobenthos) production of organic matter at the sediment surface is also important and in tropical areas with clear, non-turbid water this production can occur at large depths (>50 m). This view of the production cycle is the classical one, with a tight coupling between phytoplankton production and its grazing by zooplankton, which in turn are eaten by fish and other consumers.

Recent research, however, has shown that much of the organic material in the water column is in the form of *dissolved organic matter* (DOM), which is utilized by a microbial food web. Where the water column is stable and unmixed most of the production is by bacteria, which are consumed by microflagellates, and these in turn are consumed by ciliates and other organisms. The result is that much material simply loops around this system, which has been called the *microbial loop*. The discovery of this system (Azam *et al.* 1983) led to a revolution in our understanding of nutrient and organic matter cycling and remineralization in the water column. More recently (Zhukova and Kharlamenko 1999) the role and production of different biochemical components in the microbial loop has been investigated. While the microbial loop converts DOM into bacterial biomass, thus made available for higher consumers, the bacteria are deficient in certain components such as polyunsaturated fatty acids (PUFA) which are a requirement of those higher levels. Zhukova and Kharlamenko (1999) found that the flagellates and ciliates are able to produce PUFA, thus making up for the bacterial deficiency. It is expected, but not yet fully quantified, that the microbial loop plays a significant role in sediment systems, although Danovaro (2000) found that the sediment meiofauna and microbial components play a major role in driving the microbial loop following artificially high inputs of organic matter through oil spills. However, under natural conditions, and from our knowledge of the dynamics of the small heterotrophic species, it is unlikely that they play such a dominant role as they do in the stratified water column. Our knowledge of these links and the importance of the microbial loop in relation to sediment faunal functioning is improving: Coull (1999) also indicates the role of these processes and the meiofauna in the functioning of the marine system, and Echeverría and Paiva (2006) found that bacterial remineralization supported the benthos at times of poor primary productivity (in Antarctic systems).

7.1 Seasonal patterns

Seasonal cycles in the sea influence species from the shallow areas down to the depths of the deep sea. Annual variations in temperature, light, and primary production can be expected to have a great influence on species occurring in shallow areas, and indeed it seems that the shallower the benthic community the greater the fluctuations it exhibits.

Figure 7.1a shows data from 50–80 m depth in a community from sand–silt off the coast of Northumberland, north-east England (Buchanan *et al.* 1978). The pattern is of a clear annual cycle, with an increase in numbers and biomass in the summer and autumn followed by a large winter mortality. The overall mean density and biomass remained approximately constant over the 4 year period. Many similar examples of such repeatable annual cycles could be shown. The main reason for the large annual changes in the total community is that the spring bloom in temperate areas is rapidly turned into gametes and large larval recruitment occurs in summer. Typically, many species recruit annually, with a large overproduction of larvae which results in a massive mortality produced by competitive interactions or predation together with natural environmental influences. This, then, is probably the commonest pattern that occurs in benthic communities with fairly repeatable annual cycles.

It used to be assumed that such seasonal cycles did not persist into the deep seabed, given the buffering capacity of the large distances that organic matter produced at the surface would have to sink. That is to say, it would take so long for the surface primary-produced material to reach the bottom, coupled with assimilation and use during sinking, that any surface cycles would not be seen at the deep seabed. Consequently it was assumed that deep-sea populations, having a more constant food supply (and temperature regime), would not show such strong seasonal cycles. However, recent evidence has shown that there are clear signals of annual cycles in the deep sea also. Figure 7.1b

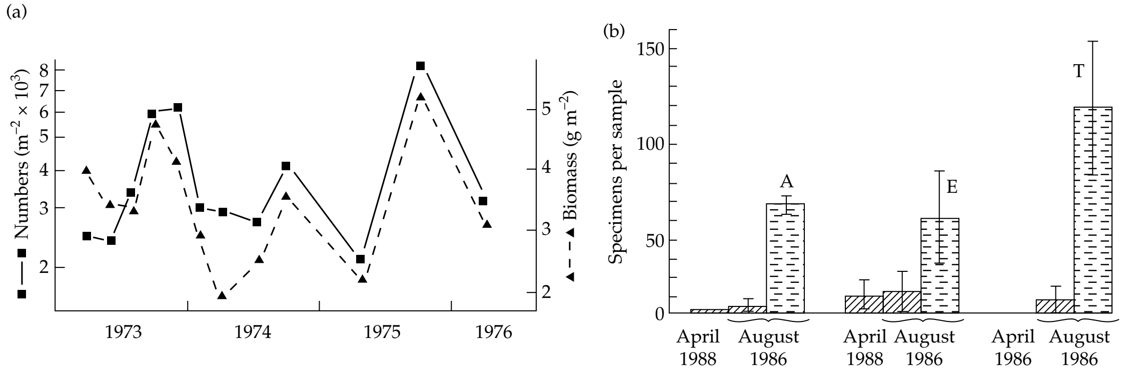


Figure 7.1 (a) Fauna off Northumberland, UK showing seasonal patterns (from Buchanan *et al.* 1978). (b) Deep-sea foraminfera of the Porcupine Sea Bight (from Gooday and Turley 1990). The abbreviations identify the species involved in the figure: A = Alabaminella weddellensis (Earland 1936), E = Epistominella exigua (Brady 1884), T = Tinogullmia riemanni (Gooday 1990).

shows data from the Porcupine Seabight (off the south-west coast of Ireland) at depths of 4500 m for three species of Foraminfera (Gooday and Turley 1990). The settling phytodetrital material has been rapidly utilized by the organisms and population densities change accordingly, being higher in August than in May. Not all species, however, show annual recruitment patterns; some recruit much more sporadically and this can produce patterns that vary over many years. Many of the annual changes are mediated by biological responses—one species being replaced by another as the dominant. We discuss this elsewhere in relation to competition.

A good example of a population that does not show large variations in numbers over time is that of the burrowing decapod crustacean *Calocaris macandrae*. Off the Northumberland coast, Buchanan *et al.* (1978) found that over a 10 year period this had a population density of 13.7 m^{-2} with a coefficient of variation of only 5% (the coefficient of variation is defined as SD/$\bar{x}$ × 100%). In contrast, for many benthic species the coefficient of variation can typically be over 100% (i.e. a degree of variability exceeding average values). *Calocaris* is territorial, so presumably if one animal dies it is rapidly replaced and the territorial spacing maintained to give the same density per square metre. Similar effects could therefore be expected in other territorial species. Within the community associated with *Calocaris*, however, the other species showed marked fluctuations.

One of the consequences of seasonal recruitment patterns is that if samples are taken in summer there are large numbers of juveniles that are extremely difficult to identify to species. Most of these will die as a consequence of competition for space or limited food resources, and by autumn fewer individuals are found. Thus in setting up a benthic monitoring programme it is often advisable to avoid sampling in early summer, when many of the species cannot be identified and when daily mortalities are high. For example, for monitoring the effects of the oil industry on the benthos of the Norwegian continental shelf, sampling is done in May–June before the peak of seasonal recruitment occurs.

In high latitudes, where the seasons are even more marked, we would intuitively expect greater seasonal cycles in the benthos. Echeverría and Paiva (2006) studied such patterns in community structure at two stations (12 and 25 m depth) in Admiralty Bay, King George Island, Antarctica, and compared Antarctic summers and winters. They found that although there was a notable seasonal cycle in the sediment organic matter, with the minima in the middle of the winter as expected, the benthic communities showed little variation in density and composition. There were no temporal differences at the 25 m depth station and the variability at 12 m could only be explained by iceberg impact and wind-induced hydrodynamic changes (related to wind direction, intensity, and fetch). They concluded that the poor winter primary productivity did not affect the macrobenthic abundance and that the winter nutrient availability for the macrobenthos was dependent on the bacterial remineralization of sediment organic matter.

The smoothing of the seasonal planktonic production cycles, and thus the input of organic matter to the bed fauna, has also been suggested for other organically rich areas such as estuaries (McLusky and Elliott 2004). The estuarine macrobenthic fauna is highly dependent on the constant input of detritus, especially from the fringing saltmarshes, seagrasses, and reed beds, such that seasonal cycles are the result of temperature changes and reproductive cycles rather than primarily produced organic matter.

7.2 Long-term patterns

Our knowledge of long-term patterns in the benthos comes from a few detailed studies, although we do not have time series of the same intensity or value as the Continuous Plankton Recorder (www.sahfos.ac.uk/CPR_Survey.htm) for the planktonic system. Unfortunately, funding systems for research do not support long-term monitoring in all countries and so we often have to rely on investigating proxies or surrogates from which we can infer the patterns. For example, one of the advantages of studying population dynamics in bivalve molluscs is that a single sample can, if the species is long-lived, give a picture of the recruitment and growth rates of the species for some years in the past. This is because many species in boreal and Arctic waters show growth checks by which annual cycles can be determined and the individuals aged.

Figure 7.2 shows population figures based on studies of annual growth rings of the bivalve *Tellina* (now *Angulus*) *tenuis*, taken from exposed beaches in Scotland. Recruitment was low in 1957, 1961, and 1964, and further data showed that there was no recruitment between 1964 and 1968. In this species, therefore, one can expect that population density will fluctuate quite widely depending on whether or not recruitment occurs. The species appears to be typical of many bivalves in that a very good recruitment period is followed by several years of poor recruitment (Dame 1996). There is a suggestion that recruitment varies with water temperature, but this has not been confirmed and still requires further long-term data sets and their analysis.

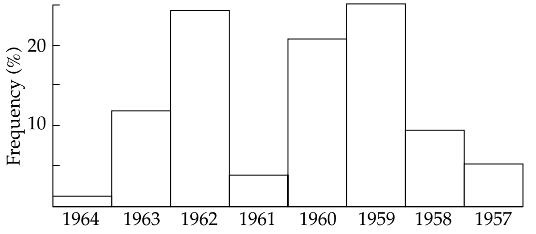


Figure 7.2 Recruitment variations in the bivalve *Tellina* (now *Angulus*) *tenuis* on a Scottish beach (from McIntyre 1970).

The existence of long-term data sets for the benthos is often due more to the persistence of individuals who start monitoring for their own interest rather than detailed planned and funded programmes. For example, see the excellent work of Jan Beukema and colleagues at the Netherlands Institute for Sea Research on Texel who have been monitoring Wadden Sea benthic bivalve populations for several decades (e.g Beukema 1988) and have thus been able to investigate the effects of environmental and biotic forcing factors in population dynamics. Beukema *et al.* (1998) investigated the effects of winter temperatures on settlement of the bivalve *Macoma balthica* and found that summer recruitment is more successful after a cold winter than after a mild winter. Using field survey and experiments, they concluded that this relationship could be the result of two types of process related to winter temperature. The first is that the number of eggs spawned in April (both per female and per m^2) was higher after cold winters than after mild winters. They showed that this was due to a higher body condition in late winter/early spring after cold winters than after mild winters, resulting from lower rates of weight loss at low than at high winter temperatures (in itself the result of food availability). Secondly, however, they found that the more important process was the result of the densities of juvenile shrimps *Crangon crangon* on the tidal flats being significantly lower in springs after cold winters than after mild winters. The shrimps are important predators of recently settled postlarval *Macoma*, and this biological interaction caused the number of recruits to be higher at low shrimp densities than at high shrimp densities in late spring. This work shows the importance of understanding both the biotic and environmental variable changes and their interactions.

In another long-term study, of the benthic community off the coast of Northumberland, the long-term changes were clearly associated with changes in water temperature (Buchanan and Warwick 1974). Between the winters of 1969–70 and 1970–1 the average winter water temperature increased by over 1 °C. As a consequence, from this point on some species declined in numbers while others increased (Fig. 7.3); the net total number remained almost the same. Structural changes occurred, but biomass, numbers, and production remained constant. Taking all species together or all stations together, there were no significant annual or long-term linear trends. The dominant cycles shown by most species are, however, annual and the timing of these can vary from year to year.

Another long-term study, but on a single population, is that done by Segerstråle (1978) in the Gulf of Bothnia (Baltic Sea) on the relict amphipod *Pontoporeia affinis*. Figure 7.4 shows the population cycle, which has a periodicity of around 6–7 years. It is likely that such long-term trends will be shown to occur in many species. In the plankton of the English Channel and the North Sea, cycles of 20–30 years are known and seem to be related to long-term changes in the weather patterns, particularly the wind directions associated with changes in pressure fronts. Such patterns are likely to occur in the benthic systems but, as mentioned earlier, there is a paucity of long-term monitoring to show them.

The Baltic data on *Pontoporeia* have been recorded since the 1920s and show a pattern of oscillating dominance with the bivalve *Macoma balthica*: when *Pontoporeia* dominates, *Macoma* is scarce and when *Macoma* dominates, *Pontoporeia* is scarce. The period of dominance of each species is around 6–7 years and the change in dominance pattern is mediated by competition for space. *Pontoporeia* adults outcompete the larvae of *Macoma* by destroying them in their feeding activities (rather than by predation) and *Macoma* can only recruit when *Pontoporeia* densities are low. So here is an oscillating pattern which occurs over a long timescale, not within a year or annually, as shown in earlier examples.

When it was first documented that there were long-term cycles in benthic assemblages that lasted over periods of decades and perhaps centuries, the data was simply correlated to physical processes without there being any clear causal mechanisms. Gray and Christie (1983) analysed a variety of long-term data sets and found that a 6–8 year cycle was common among benthic data sets. At that time this was thought to be related to an atmospheric circulation system called the Namias circulation. Recently, much progress has been made in understanding the physical links between atmospheric and ocean processes. Two major atmosphere–ocean links have been described: the North Atlantic Oscillation (NAO) and the El Niño–Southern Oscillation (ENSO) in the southern hemisphere (Stenseth *et al.* 2002). These atmospheric systems are now known to control many biological events not only in the ocean but also, because of their influence on rainfall and land run-off and other features, in the

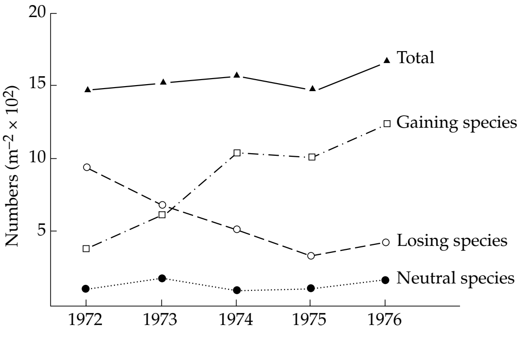


Figure 7.3 Long-term changes in a benthic assemblage off the coast of Northumberland, UK (from Buchanan and Warwick 1974).

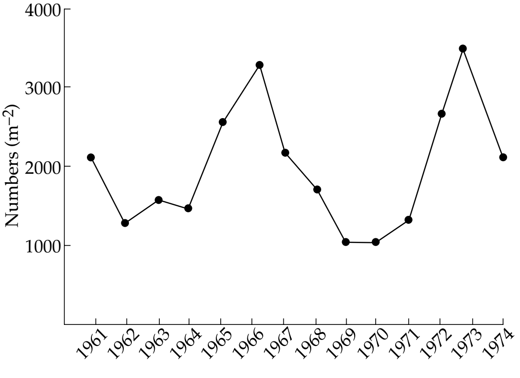


Figure 7.4 Long-term variations in the population of the amphipod *Pontoporeia affinis* in the Baltic Sea (from Segerstråle 1978).

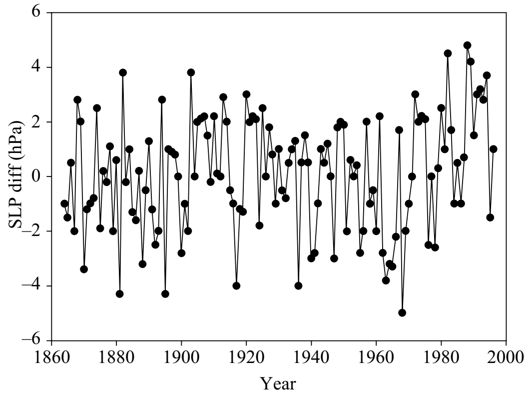


Figure 7.5 NAO calculated as sea level pressure (SLP) difference between Iceland and Lisbon, Portugal (from Visbeck *et al.* 2001).

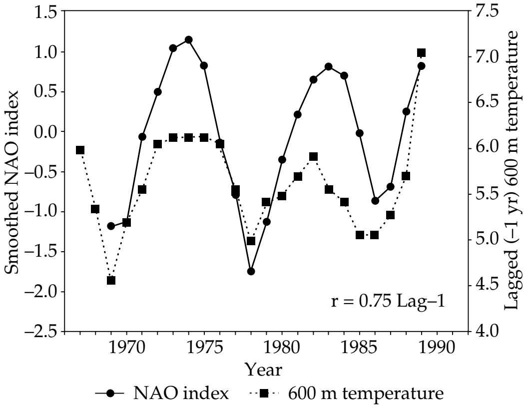


Figure 7.6 Correlation between the smoothed NAO index and temperature at 600 m depth in the Skagerrak (lag −1 yr) (from Tunberg and Nelson 1998).

estuaries and coastal areas (Warwick *et al.* 2002). The NAO is measured as a pressure difference in the atmosphere between Iceland and Portugal (Hurrell 1995) (Fig. 7.5). This influences the atmospheric pressure systems and thus affects the passages of the high and low pressure systems, with their accompanying winds, and thereby alters current systems. With a positive NAO index there is low pressure over the polar regions and high pressure at mid-latitudes, resulting in stronger trade winds and warm wet weather in Europe. In negative NAO periods the polar regions have a less cold atmosphere with weaker trade winds and cold dry weather in Europe.

The ENSO is the equivalent dominating system in the southern hemisphere. In El Niño years the equatorial surface waters of the Pacific warm considerably from the International Date Line to the coast of South America. This is due to exchanges of air between the eastern and western hemispheres centred in tropical and subtropical latitudes. In El Niño years the whole Pacific is changed; the normal upwelling system off Peru where cold, nutrient-rich water reaches the surface slows down, and as a result plankton production and anchovy numbers decline greatly.

Although few examples of benthic changes have been linked to NAO or ENSO phenomena, Tunberg and Nelson (1998) show clearly that the benthos in the Skaggerak changes in periods linked to the NAO and similar changes have been recorded in foraminiferans. Figure 7.6 shows the correlation between bottom-water temperature changes and the NAO and Fig. 7.7 shows the abundances in benthos in relation to the NAO. There is an exceedingly good correlation between the NAO and bottom-water temperature, and a spectral analysis of all the NAO data shows a periodicity of 7–9 years. The benthic faunal data showed peaks in abundance in 1976–7 and 1983–6, also giving an oscillatory component of 7–9 years. Tunberg and Nelson (1998) showed that there was a strong negative correlation between NAO and the flows of streams entering the Skagerrak. There is also a negative correlation between stream flow and bottom-water oxygen concentrations. During periods of low NAO values, winter precipitation is higher than average and flows of nutrients to coastal waters are increased. Thus primary production is enhanced and sinking organic matter leads to a reduction in oxygen concentration and direct influences on the benthos, albeit with different time lags at different depths.

In a similar study, using a long-term (1973–96) benthic series created by monitoring the effects of industrial discharges in the Tees estuary and Tees Bay, north-east England, Warwick *et al.* (2002) found a serial pattern of community change over

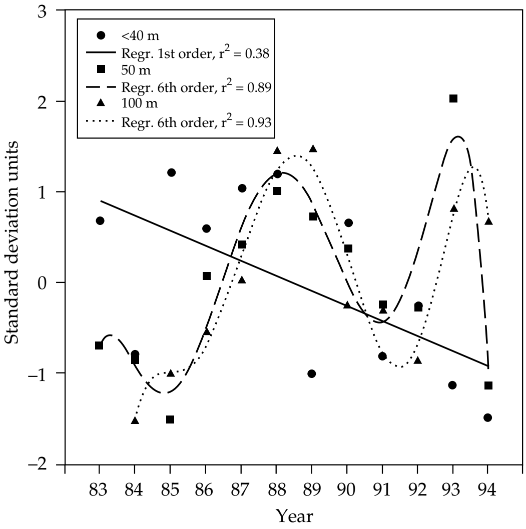


Figure 7.7 Least squares polynomial regressions of benthos abundances in Skagerrak showing cyclical changes related to the NAO (from Tunberg and Nelson 1998).

years for all areas, but with a major regime shift in community composition between 1986 and 1988. They found that interannual variability in community composition was significantly greater after 1987 than before 1987 in all areas and that this variability was greater close to the estuary mouth than further away, even though the direction of community change and the timing of the discontinuity were the same in all areas. Although species richness did not show a clear pattern of change over the sampling period, there was a large increase in Shannon diversity *(H′)* after 1987, due to an increase in evenness caused by the reduction of a few previously dominant species, especially the small spionid polychaete *Spiophanes bombyx*. Using other measures of taxonomic distinctness and change they showed that there were other abrupt detrimental changes which coincided with the well-documented regime shift in several components of the North Sea ecosystem during the same period (see the work of Chris Reid and the Continuous Plankton Recorder team at the Sir Alistair Hardy Foundation for Ocean Science in Plymouth, UK: e.g. Beaugrand *et al.* 2002). Warwick and colleagues concluded that overall patterns of biodiversity and community composition in Tees Bay were affected temporally by regional changes in the North Sea ecosystem, including the effects of the NAO, and spatially by the effects of the estuarine outflow (as shown by salinity fluctuations). However, to complicate things even further, they also found a major change in community composition in 1994 coinciding with the construction of a barrage in the estuary as well as the effects of pollution reduction. This work emphasizes above all the interconnected nature of the climatic, hydrographic, sedimentological, and benthic community aspects (as well as the effects of human activities—we return to this in Chapter 11). Further details and examples are given in Stenseth *et al.*'s (2002) excellent review of the state of knowledge of the way in which several terrestrial and marine systems are connected to these large-scale climatic phenomena.

Clearly, measuring the effects of such phenomena is hugely important for a variety of reasons. We need to know the scales of natural change so that we can then manage systems within the framework of understanding the natural variation. It is, for example, important to know that declines (or even increases) in abundance (and changes in species composition) can occur over periods of 3–4 years for natural reasons, so that monitoring to find effects of pollutants over time must run for decades. We refer to the detection of such anthropogenic change against a background of natural variation as the *signal/noise ratio*—hence the importance of determining and then quantifying inherent, normal variability in any aspects of the benthos before we can hope to detect the effects of pollution and other human-mediated effects. We return to this discussion in later chapters.

These aspects reinforce the importance of measuring real changes in the environmental variables and their influence on biological processes, and with an increasing awareness of global change, especially in climate, we need to use whatever techniques and species are suitable. For example, with present-day techniques it is often possible to determine daily growth rates over many past years. One of the most extreme cases of using a shell to determine long-term changes is that of the bivalve *Arctica* (now *Cyprina*) *islandica* (the quahog) which lives to an age of 150 years. Figure 7.8 shows data on growth patterns from the Fladen Ground, North Sea, and

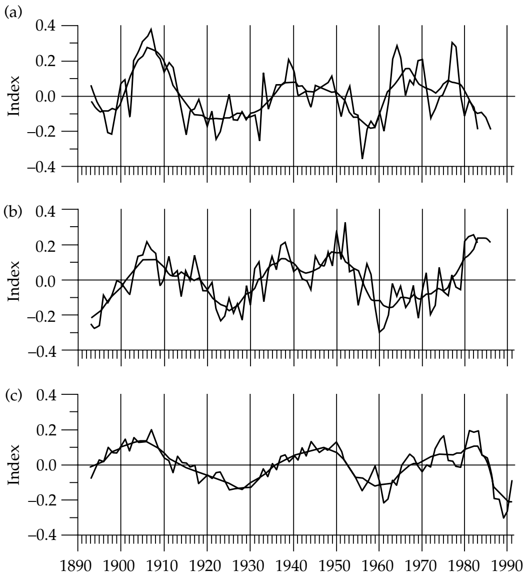


Figure 7.8 Standardized growth variation in old shells of the bivalve *Arctica islandica* showing long-term growth cycles (from Witbaard *et al.* 1997). Data are from different areas and sampling occasions on the Fladen Ground, central northern North Sea: (a) south 1983, (b) north 1983, (c) north 1991.

autocorrelation analysis of these data shows a period of 33 years. Witbaard *et al.* (1997) related these changes to hydrography, showing strong correlation with the inflow of Atlantic water to the North Sea.

It has also been shown that the shell's oxygen isotope ($\delta^{18}O$) signal is in phase with its growth banding, confirming the annual periodicity of this species' growth bands, and is in oxygen isotopic equilibrium with the ambient seawater. Shell growth shuts down at a temperature of *c*.6 °C, which translates into a *c*.8-month (May–December) period of shell growth at the site studied; hence shell growth reflects changes in the ambient bottom temperature with a precision of ±1.2 °C (Marchitto *et al.* 2000).

7.3 The stability of benthic communities

Three general patterns for populations emerge from the foregoing. There are some species in which populations maintain constant numbers through time (e.g. *Calocaris*), that is they are *persistent*. Another common pattern found in benthic species is that of repeatable *cycles*, either annual or long term with periods from 6–7 years to as much as 33 years or longer (Gray and Christie 1983); and finally there are responses to long-term physical processes (ENSO/NAO) which are not cyclical (or at least not on cycles that we yet can understand). These patterns can be regarded as being stable since the changes through time are, within certain limits, predictable—of course, this is with the proviso that we need monitoring that covers the relevant length and encompasses the cycles. The limits vary with the vagaries of recruitment and may be quite narrow in regularly recruiting species but very wide in species such as tellinid bivalves. Therefore the latter populations are possibly more unstable, but this really depends on the repeatability of the 'cycles', although insufficient information is available on this. In fact, so little data is available on long-term cycles and variations in recruitment that the patterns described above may in time prove not to be typical at all. Understanding recruitment variability and the factors causing that variability is one of the central problems in understanding long-term fluctuations in benthic communities.

The other aspect considered above was the variability of species within communities over time. We suggested that the oscillating dominance patterns shown by a number of species combinations, e.g. *Nucula/Nephtys, Nereis/Nephtys, Macoma/Crangon, Ampelisca/Nassarius,* and *Pontopereia/Macoma,* can be changed by environmental factors (*Ampelisca* to *Nassarius* and *Nereis* to *Nephtys*), competition for space (*Nassarius* to *Ampelisca*), or predation (removal or absence, through a poor year class, of the potential competitive dominant by crabs or shrimps). Physicists have given the name *neighbourhood stability* to stability of this kind, where the system is resistant to small changes but a larger disturbance moves it to another *basin of attraction* (here, another species dominating). In Fig. 7.9a the community is envisaged as a ball in a basin of attraction, here with species A dominating. The community is resistant to small changes and A continues to dominate. If the environment changes enough, though, the ball may be forced into another basin of attraction where species B dominates, and a predator might shift the dominance pattern to C or back to A. Although the diagram is shown in two dimensions, the system

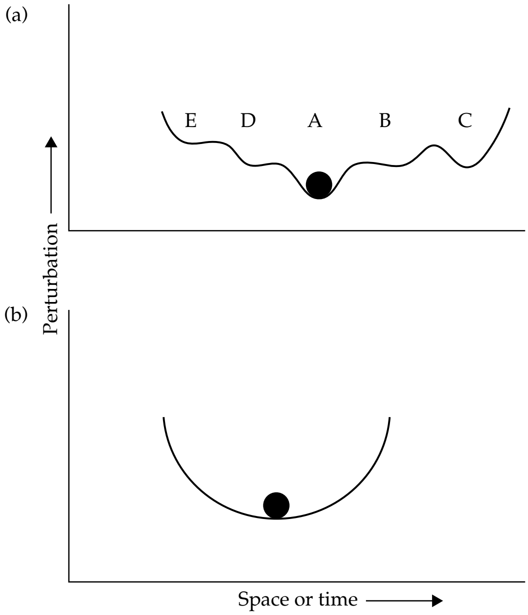


Figure 7.9 Neighbourhood (a) and global stability (b). In neighbourhood stability the system is resistant to small perturbations, but large changes lead to different species dominating the assemblage (A–E). In global stability the system returns to the same species dominating from small or large perturbations.

may of course be multidimensional, and a species may be highly resistant to, say, a salinity change but easily affected by competition; thus the basin of attraction would be shallow in the competitive axis and deep in the salinity axis. This model therefore seems to represent quite adequately many cases of local temporal changes in benthic communities: at one point in time species A dominates, but is replaced by species B which may then go back to A or on to C, depending on which factors are operating.

In plankton ecology the same trends have been found, with local temporal patches of dominance occurring, and in this field the wonderful term *contemporaneous disequilibrium* has been applied. This implies that there are local-scale patches which have fluctuating dominance patterns over time. Thus, the neighbourhood stability model applies not only to temporal scales but also to spatial scales. At one point in space species A dominates, while a few metres away species B is dominant, and so on. In benthic ecology we have often see that adjacent grab samples differ more than do two samples further away from each other, and this reflects contemporaneous disequilibrium occurring over small spatial scales. Many benthic publications try to interpret and explain a large amount of inherent and local heterogeneity but within systems which may overall be fairly homogeneous. The patchiness of benthic species is to be expected if we accept neighbourhood stability as a realistic model for some benthic communities (Gray 1977).

Physicists have described an alternative to neighbourhood stability, and that is *global stability*. In global stability the system always returns to the same equilibrium point no matter how large the disturbance (Fig. 7.9b). In ecological terms this means that the community always returns to the same equilibrium point with the same species dominating. The difference between neighbourhood and global stability is, therefore, a question of the scale of the disturbance and so we should question whether global stability is a realistic model for ecological systems. The data in the previous section is not appropriate for testing this model. The ecological analogy here is whether a system will return to the same dominance patterns if it is grossly disturbed by a storm or a transient pollution incident such as an oil spill.

In terrestrial systems the sequence of colonization has been well studied, and it has been found that one species follows another in a set successional sequence. This sequence was thought by one group of workers to lead to a *climax community*. Under a given set of environmental conditions one species was thought to prepare the way for another, until finally the succession culminated in the climax where one or occasionally two species dominated. The succession could take many years but was directional and entirely predictable in outcome; if an oak forest was destroyed by a forest fire, then over many decades an oak forest would reappear. However, other workers believed that the end-point of the succession was any one of a group of four or five species, and that the sequence leading to these species varied from place to place and time to time. The outcome was not as predictable as was the climax and was termed the *polyclimax*.

The colonization sequence in benthic communities has been studied only rarely. The pattern seems to be that if one ignores the initial microbial aspects, then the first macroscopic species to colonize the sediment are the *r*-selected opportunist species. Such species obtain their name from the logistic equation for population growth:

$$\frac{dN}{dt} = rN\left(\frac{K-N}{K}\right)$$

where r is the intrinsic rate of natural increase, N is population size, K is the asymptotic density or carrying capacity of the environment, and t is time.

MacArthur and Wilson (1967) suggested that there were basically two extreme types of life cycles. When the population N is very small compared with K, then r is the main determinant of population size and so species with attributes ensuring a high value of r will be selected for—hence *r-selected species.* As colonization proceeds, competitive ability becomes increasingly important as K is approached, and so species at later successional stages—so-called *K-selected species*—have competitive ability as their main attribute.

Wherever such colonization sequences have been followed in benthic communities the initial colonizers always seem to be the same, namely the small polychaetes: first *Capitella capitata* (family Capitellidae) and then members of the family Spionidae, often of the genera *Polydora* or *Malacoceros*. Even within this, *Polydora* seems to colonize where sediment instability is the cause of change but, for example, *Malacoceros* may be in the succession where the change is due to pollution, especially from organic matter. Figure 7.10 shows a typical colonization sequence, here the recovery after an oil spill had eliminated the benthic fauna.

After a relatively short period of time these *r*-selected species are replaced, according to the theory of *r* and *K* selection, by supposedly better competitors. Whether the replacement sequence is in fact a competitive replacement has not been adequately tested, and it may well be that the sequence merely reflects the cycle of larval availability and mortality. *Capitella* is able to produce larvae all the year round and can reproduce by both planktonic and benthic phases. Thus, should any space become available (through the fauna either being killed off or moving away), then *Capitella* can occupy it. Then, using its other *r*-selected attributes of rapid reproduction and completion of its life cycle within 3 weeks, it builds up a large population in a short time. Densities of up to 200 000 m^{-2} have been recorded. *Polydora* has many of the same characteristics as *Capitella* (a flexible life history strategy, short life cycle, etc.), but is not quite the opportunist that *Capitella* is and therefore comes later in the colonization sequence. But it is not known why the large *Capitella* population declines. As mentioned above, the classical argument would be that *Capitella* is outcompeted, but no one has shown this. It may just be that the population becomes senile and dies down, leaving space for later colonists that have a more limited breeding cycle with larvae available only over relatively short periods.

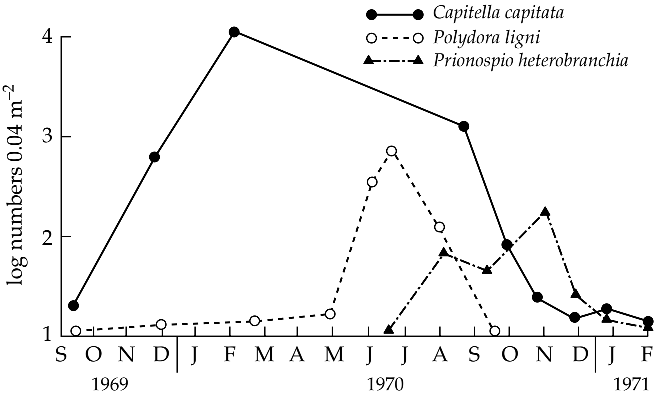


Figure 7.10 Colonization sequence of species following an oil spill in Massachusetts, USA (from Sanders *et al.* 1980).

The initial stages of the successional sequence always seem to follow this pattern, with the same species dominating; indeed, these species (or near relatives) are cosmopolitan. From here on, though, the sequence varies from time to time and especially from place to place, and no fixed rules apply. Thus, benthic communities follow a successional sequence that parallels the polyclimax idea in terrestrial systems. Indeed, the polyclimax with an unpredictable end-point seems to be a general ecological rule. We will return to discussing *r*- and *K*-strategists later in relation to unnatural disturbance through pollution.

In some cases, the community appears to be held by the precise nature of environmental conditions in a state prior to a climax. For example, if the environmental conditions were constantly changing then the community would not progress to stability. Allen (2000), in analysing and predicting community change along the constantly eroding Holderness coastline (eastern England), found that the cirratulid *Chaetozone setosa*, a small polychaete, colonized the areas where the sediment was being constantly influenced by cliff-eroded material settling and then being moved on by prevailing currents. However, the community did not progress to a final community incorporating large-biomass benthic species. Allen (2000) suggested that this natural state seemed to mirror that of areas affected by dredging and disposal of dredged material.

The conclusion from these examples, then, is that the early stages of succession in benthic communities are predictable and the same species dominate almost universally, but that later in the sequence the pattern is more varied. This is illustrated in Fig. 7.11 in relation to the neighbourhood and global stability models shown in Fig. 7.9.

These models suggest that the whole 'valley' is globally stable and the species and their relative abundances are predictable. However, while early stages (the steep slopes of the valley) follow a set pattern, the floor of the valley is bumpy and neighbourhood stability is the rule here, which means one cannot predict the abundance patterns of species at any given point in space or time. This may seem confusing, so let us take a simple analogy from rocky intertidal shores. Given the particular exposure and aspect of the shore an ecologist will be able to predict fairly accurately the abundance patterns and distribution patterns to be expected over the shore as a whole, i.e. the globally stable valley. But the ecologist will not be able to predict which species will occur in a given square metre of shore because on the small scale spatial and temporal variations exhibit neighbourhood stability (the bumps on the valley floor), and the ecologist cannot know the historical events that have happened at any given point. Thus a natural (e.g. storm) or unnatural (e.g. oil spill) event occurring at one time of the year will allow initial colonization by whichever species are breeding at that time of the year and then those initial colonizers will dictate the nature of the community. As an example of this, the barnacle *Semibalanus balanoides* in North Sea areas has a very short and well-defined settlement period, usually over a couple of weeks in May, and so any period of disturbance which ends just before that could result in a barnacle-dominated area. Events at a different time of the year will allow other initial colonizers. Eventually, perhaps after several years, that initial pulse will be smoothed out and the community will regain a composition irrespective of the initial colonizers.

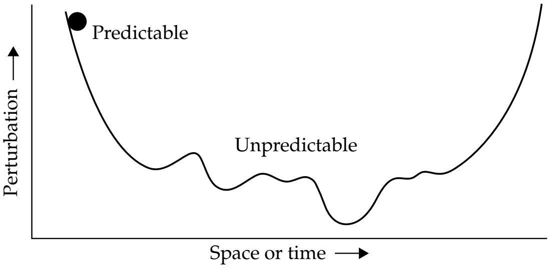


Figure 7.11 Model of recolonization sequence in relation to global and neighbourhood stability. Initial colonization sequences are predictable, whereas later stages are unpredictable.

Finally, we have to consider how global stability relates to populations. Taking an example already used, we know that if the density of *Calocaris* is reduced from the equilibrium level of 14 m^{-2} to 10–11 m^{-2}, then the density will return to the 14 m^{-2} level since the coefficient of variation (defined as the standard deviation in relation to the mean) is so low over long time periods. Thus, *Calocaris* responds to small disturbances by returning to equilibrium; that is, it shows neighbourhood stability. We do not know what will happen if we reduce the density to 1–2 m^{-2}—whether the population will die out or return to 14 m^{-2}. In the former case it would not be globally stable and in the latter it would.

The two concepts of neighbourhood and global stability, therefore, are not mutually exclusive—one or both may apply. Thus the physical concepts are difficult to use in dynamic ecological systems. The acceptance or rebuttal of either model depends on the extent of the disturbance and the scale of the effects.

One of the main ecological debates in the 1970s centred on the relationship between diversity and stability. The great English ecologist Charles Elton (1966), in his *girder concept*, first suggested that the more diverse a community was, the more stable it was. Elton likened a food web to a building with girders. If one or two of the basal girders are removed from a complex food web then the structure will remain almost undisturbed, but if the same is done to a simple food web the structure will collapse. This may also be the same in comparing species—those with wide tolerances and feeding preferences will be more stable and able to withstand change than more specialized ones (compare humans and the giant panda!). Simple systems are, therefore, unstable and subject to the vagaries and variability of the natural system. However, much effort has been concentrated on mathematical models of simple and complex food webs. These studies have shown that there is not necessarily a link between high diversity and high stability (see May 1975 for a review of such aspects). Often the reverse may be true, and simple systems can be more stable than complex ones. Although this debate has been going on for some time, the implications for benthic ecology seem to be largely unknown.

The debate regarding simple vs complex ecosystems, the effects of variability in environmental parameters, and biodiversity–ecosystem functioning has recently been taken further in relation to estuaries and especially the estuarine benthos. Elliott and Quintino (2007) suggest that assemblages in ecosystems that are inherently variable with regard to environmental parameters, such as estuaries which undergo salinity and substratum changes on very short (hourly) timescales, are more able to withstand stress and disturbance than are more environmentally stable systems. Because of the high environmental variability, the estuarine assemblage is dominated by small annelids, both polychaetes and oligochaetes, which all have the same reproductive and colonizing characteristics of *r*-strategists, forming a poorly diverse assemblage albeit of tolerant species with very high abundances. However, despite its poorly diverse assemblage, the estuary has a high degree of functioning and a high carrying capacity, especially of higher consumers such as juvenile fishes and overwintering birds. It is also a stable ecosystem, in terms of its overall assemblage structure in terms of abundance and species richness.

In summary, then, marine benthic communities typically show a polyclimax and neighbourhood stability with a number of alternate dominant species when measured over a small spatial scale or over time. When measured over large spatial scales global stability may be the rule, but since most investigations are over relatively small spatial scales neighbourhood stability is probably the more appropriate model. Populations of territorial species and constant competitive dominants show persistence stability, whereas most marine species typically show cyclical oscillations and bounce-back stability, and the estuarine benthos shows stability within a poorly diverse system. No clear relationship between diversity and stability is to be expected, but this has not been studied in a comparative way in benthic communities.

Finally, there is a much larger temporal scale that is relevant for understanding modern patterns of species richness gradients, and that is glacial cycles. At the height of the last ice age, 15 000 years ago, the areas that are now the North Sea and the Baltic Sea were covered by ice. As the ice retreated, 9500 years ago the southern part of North Sea was dry land (stretching roughly from Flamborough Head in Yorkshire to the northernmost tip of Jutland in Denmark). The Baltic Sea at this time was a true sea with an opening to the northern part of the North Sea. Between 9000 and 7000 years ago, however, the entrance to the Baltic was blocked and because of the river discharges from catchment areas the Baltic became a freshwater lake. Only about 7000 years ago did salt water incursion start again. Along the Norwegian coast, the first areas to be ice free (11 000 years ago) were in the far north, so colonization of land plants (and presumably marine coastal flora and fauna) came from the east and Russia. An open water channel appeared first in the middle of Norway and only later did southern areas become ice-free (Andersen and Borns, 1994). It is not surprising that the Baltic Sea is species poor, as species are still colonizing from adjacent areas.

In North America the ice cap had less of an influence on the marine biota than in Europe, and as early as 11 500 years ago the whole of the eastern and western seaboards of the USA and Canada were ice-free.

Such large-scale disturbances are clearly highly important in interpreting many of the distributional features of today's flora and fauna in coastal areas. With the advent of concerns about global warming and climate change, we are again looking for evidence of natural and anthropogenic changes in species distributions. This makes the presence of good background and long-term benthic data and the understanding of community forcing variables even more important.

CHAPTER 8

Human impacts on soft-sediment systems—trawling and fisheries

Given the discussion above regarding natural changes in the marine benthos, we should now consider the human-mediated (anthropogenic) changes and the response of benthic systems to human impacts. From the 1960s to the 1980s the general opinion seemed to be that pollution (considered in the next chapter) was the most important marine problem, but we now realize that habitat change and habitat loss are of greater concern: see, for example, the Quality Status Report 2000 (OSPAR 2000). One of the greatest effects on the integrity of the seabed and hence its biota is now known to be caused by bed trawling. This has now generated an enormous literature, and the reader is directed to Daans and Eleftheriou (2000) and Hollingworth (2000) for more details. We can take this information and summarize the overall ecosystem effects of fisheries in detailed flow diagrams (referred to as 'horrendograms'!) to show the interlinked and complex nature of the impact—the effects trawling are included here, but see also those in McLusky and Elliott (2004) (e.g. Fig. 8.1).

8.1 Ecological effects of trawling

Historically, the effects of trawling on benthos caused concern as early as 1376 when a petition was made to the English parliament by fishermen concerned over the damage done to the seabed and fisheries by bottom trawling (De Groot 1984). This was despite the gear used by sailing vessels in those days being relatively light and towed at slow speeds and in shallow water only. When steam trawlers were developed in the early 1900s, everything changed. The weight and size of trawls increased and use of tickler chains (mounted on the bottom rope to disturb bottom-living fish upwards and into the trawl net) were of great concern, although studies done in the 1970s to allay the fears of fishermen did not find long-term effects on macrobenthos (Jones 1992). At the end of World War II the otter trawl was developed and its use became widespread. This and the beam trawl (see Fig. 8.4) were (and still are) the types of gear most widely used to fish the seabed. A further gear that is widely used and can be severely damaging is the scallop dredge, a rectangular metal box to which a metal-mesh bag is fixed. As an example of the change in technology, Jones (1992) reports that whereas the average weight of a beam trawl in the 1960s was 3.5 t, by 1980 the average weight was over 10 t. Yet it was the tickler chains that were thought to be most damaging aspects of the gear. The French Institut Scientifique et Techniques des Pêches Maritimes made studies around Corsica and demonstrated the damaging effects on the benthos, which resulted in a ban in the use of such gear in the Mediterranean. A similar ban was sought on the French Atlantic coast, mainly fished by Dutch beam trawlers, but fisheries laboratories bordering these areas were not convinced that large negative effects occurred and so no ban was imposed (De Groot 1984). Even the influential Intergovernmental Council for the Exploration of the Sea (ICES) was not convinced of the negative effects of trawling in the late 1980s, and it was only in 1990 that a working group was established to evaluate the effects of fishing on the marine ecosystem, including effects on marine mammals, birds, and benthos (Jones 1992).

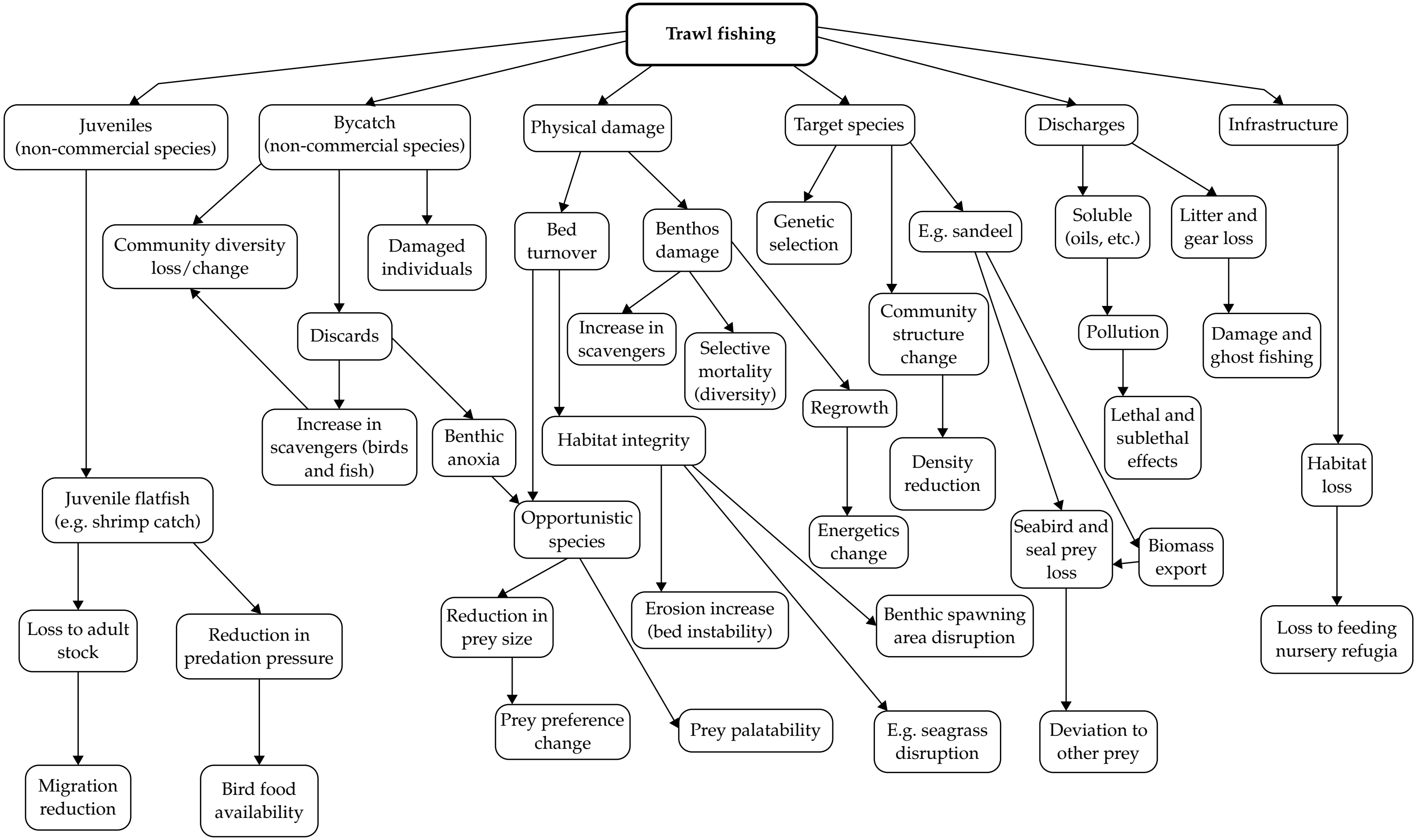


Figure 8.1 A conceptual model ('horrendogram') of the ecosystem effects of trawl fishing (from McLusky and Elliott 2004, based on case studies in Blaber *et al.* 2000) .

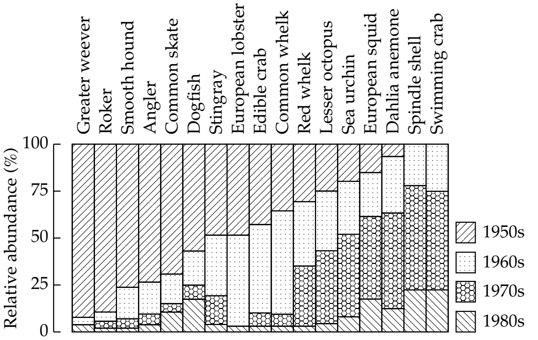


Figure 8.2 Long-term trends in the relative abundance of demersal fish and megabenthos, SE North Sea, 1947–1981 (from Philippart 1998).

As indicated in the flow diagram in Fig. 8.1, the influence of this technology on the bed community is most notable. The overall influence of this large increase in bed fisheries on the demersal fish and the benthic fish and megafauna was demonstrated by Philippart (1998) (Fig. 8.2). In particular, the study shows the progression towards a benthic system dominated by scavengers which are benefitting from damage to the surface-dwelling and shallow-burrowing macrobenthos.

There are many other technological developments in the fishing industry that have made it more efficient in catching fish. Global positioning systems (GPS) that allow accuracy of ±5 m in a vessel's position, coupled with pingers mounted on the gear, now allow trawlers to operate in areas and to target precise stocks that would not have been possible 10 years ago. Fishing right up to oil pipelines and around wrecks would have risked damaging gear and so was avoided in the past, but today almost any soft-bottom area is open to trawling. The heavy tickler chains and bobbins (large, round, metal objects attached to the bottom lines of the trawl which roll over the seabed and crush rocks) are widely used. Rock-hopping trawls have been developed that do not snag and so allow fishing on rough bottoms. Fishermen themselves use a variety of methods to ensure good catches. For example, when one of us (JSG) worked on the coast of north-east England, the skipper of the research vessel mentioned two Dutch beam trawlers that had over a period of a year made a 'seaway' in a rocky area by removing large stones which were transported to the Netherlands and used to make a port. When finished, the seaway traversed a rocky area where trawling was othewise impossible. Two boats worked this area continuously; while one boat was *en route* to or from port the other was working the seaway. Fish moved from the rocky areas to the seaway and were caught, and so this fishery was very profitable in the short term. However, no environmental impact assessment (EIA) was done, nor were there any scientific studies of the cost-benefit of such a scheme!

In the 1960s and 1970s fishing was confined to the continental shelves, but recently there has been a trend to fish in deeper waters and in more difficult areas such as around seamounts. With technological developments today it is possible to fish these and other areas at many hundreds of metres depth. The problem is that many of the fish species exploited at depth are extremely slow-growing, so that the sustainability of the stocks is rarely studied before they are over-exploited. Good examples are the orange roughy *Hoplostethus atlanticus* and the Patagonian tooth fish *Dissostichus eleginoides* which have been severely overfished in a short period of time (e.g. Clark 2001).

Seamounts are underwater volcanoes that do not breach the ocean surface. There are many hundreds in the North Atlantic and many thousands in the Pacific, and they have an often unique and very species-rich fauna. Trawling fleets have discovered that they have unexploited fish resources, and already many seamounts have been severely disturbed in the frenzy to get at the fish catches. Figure 8.3 shows the effects of trawling on a seamount at ~1000 m depth south of Tasmania. Although this refers to epifauna rather than soft sediment, it is an important example of how the fishing industry is responding to decreasing global fish catches by exploiting key areas of high biodiversity in non-sustainable ways.

Perhaps one of the most notable and contentious marine conservation issues since the early 1990s has been the protection of the cold-water deep coral *Lophelia pertusa* along the north-west European shelf and especially at the Darwin Mounds and Norwegian shelf areas (Fosså *et al.* 1999). The species was known to be unique and to represent a

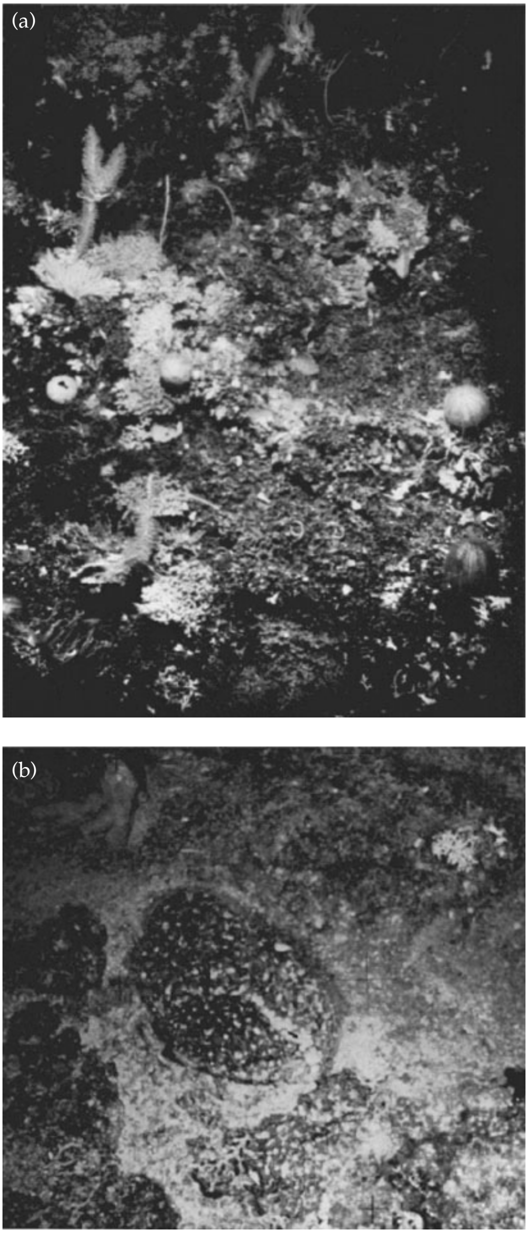


Figure 8.3 Photographs of the benthos of a sea mount at ~1000 m south of Tasmania: (a) Unfished area showing scleractinian coral substratum with gorgonians, ophiuroids, urchins, and sponges. (b) Heavily fished area showing a coralline community with bare rock and the broken base of a large bamboo coral at upper left (from Koslow *et al.* 2000).

special and fragile habitat. The threat to these areas from bottom fisheries led to the re-evaluation of species protection legislation in Europe, such as the European Habitats Directive, and the eventual implementation of the Directive out to 200 nautical miles (370 km), thus leading the way for the protection of all continental waters. However, as a cautionary postscript to this, Gass and Roberts (2006) found that *Lophelia* grows well in anthropogenic and disturbed habitats.

Trawling effort is usually estimated by the number of vessels at sea at any one time, taking into account the size of the vessel and the size of trawl used to fish a given area. This has led many authors, such as Rijnsdorp *et al.* (1998), to suggest that most of the North Sea is trawled over at least once and in some areas, such as the southern beam trawling areas, up to six times a year. The overall trawling effort is therefore huge; few laymen have any idea that it is so great. However, fishermen are very conservative and prefer to fish in areas where they have traditionally had good catches. (In the 1960s and 1970s when a successful skipper retired, his charts were often sold for large sums of money.) Thus many areas are not fished intensively whereas others are, e.g. by beam trawling off the Dutch coast (Rijnsdorp *et al.* 1998). Today in most countries vessels over 6 m have to report via a vessel monitoring system using GPS systems onboard that tell the fisheries authorities where they are at all times. From such data we have in the past few years obtained a much better overall picture of fishing effort—where it is heaviest and where lightest. Such data are invaluable in determining the effect on the benthos and also in the good management of fisheries.

From this brief historical overview it is clear that the realization that trawling is one of the most widespread and most damaging disturbances of coastal and now deep-water areas of seabed is very recent (see Jennings and Kaiser 1998 for a detailed review). To exemplify the newness of the science, Collie *et al.* (2000) in reviewing effects of fishing impacts on shelf sea benthos cite 57 papers, all published since 1980, and Thrush and Dayton (2002) in their review of the effects of trawling on benthos cite 37 reports, all of which were written after 1990.

8.2 Common types of trawls and dredges

The basic types of trawls used today are otter trawls, beam trawls, pair trawls, scallop dredges, hydraulic dredges, and shrimp trawls (Fig. 8.4). Beam trawls are used on sandy bottoms to catch flatfishes and are especially well-used in the southern North Sea. Otter trawls are widely used on continental shelves, as are pair trawls . Shrimp trawls are used primarily on muddy bottoms and have smaller meshes and dimensions than the otter trawls used for catching bottom-living fish species.

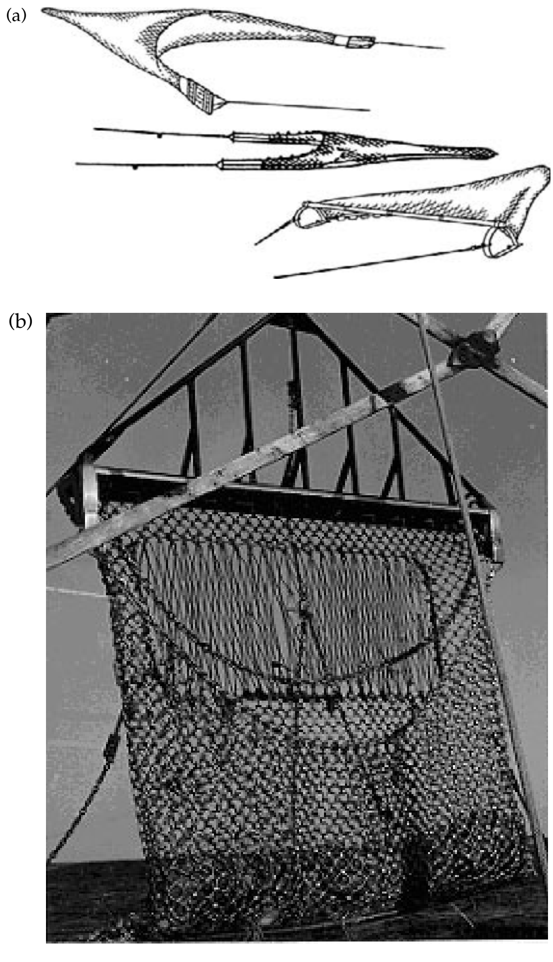


Figure 8.4 Various types of bottom trawl. (a) Top: Otter trawl showing otter boards to keep net open, with a bottom line and a headline. Middle: Pair trawl where the net is kept open by use of two vessels. Bottom: Beam trawl with a heavy beam to keep the trawl sides apart (from FAO fishing gear fact sheet). (b) Scallop dredge made of metal chain link.

Assuming a bottom trawl has a net opening of 100 m and trawls for 6 h at an average speed of 3 knots (1.5 m s^{-1}), this disturbs a minimum area of 3.25 km^2. From these figures it is easy to see that huge areas of the seabed can be damaged by trawling fleets in a short period. Given the frequency of trawling mentioned above for intensively fished areas such as the North Sea and the Irish Sea, if the seabed is to recover from fisheries it must do so in less than a year. As will be shown, this is highly unlikely, so the seabed is progressively more and more disturbed over time.

Dredges in general are designed to dig into the sediment and plough through it, and so not surprisingly they cause far more damage than do trawls. Hydraulic dredges use jets of water injected in front of the dredge to dig up deep-living bivalves such as razor clams (*Ensis* spp.) which are then caught in a net bag. Again, such dredges cause great disturbance to the sediment.

8.3 Effects of gear on different sediment types

Trawling gear is designed to do specific tasks. Scallops live on coarse bottoms and so the gear used to catch them must be robust enough to take account of the rough and sharp seabed. Beam trawling, on the other hand, is almost universally confined to sandy sediments and skims the seabed rather than digging into it as do dredges, although the tickler chains on beam trawls re-suspend the sediment surface layers and damage the epifauna and shallow infauna. Hall (1999) showed that different types of gear, and especially dredges, can penetrate up to 25 cm into the sediment. Collie *et al.* (2000) report large differences in the number of studies done on each gear and each sediment type. Of the 57 studies they cite, 22 were on effects of otter trawling, 14 on intertidal dredging, 13 on scallop dredging, 8 on beam trawling, 3 on intertidal raking, and 1 on hydraulic dredging. There was also a regional bias, with 43% of studies done in northern Europe and 28% in North America followed by Australia and New Zealand (9 and 7% respectively).

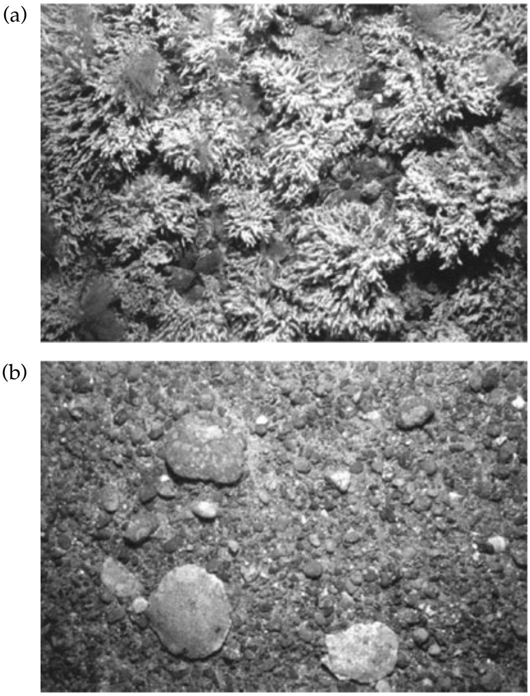


Figure 8.5 Effects of trawling on George's Bank (from Sheppard 2006). A rich natural seabed with large numbers of epibenthic species (a), which is reduced to coarse gravel with few living species (b). (Photos from Page Valentine and Dann Blackwood, US Geological Survey, taken from Sheppard 2006). See Plate 11.

Table 8.1 Initial impacts on total number of individuals and total number of species. Values are mean percentage changes (from Collie *et al.* 2000)

	Total number of individuals	Total number of species
Gear		
Intertidal dredging	−56	−39
Scallp dredging	−51	−30
Otter trawling	−51	1
Beam trawling	3	−23
Habitat		
Biogenic	−59	N/A
Mud	−57	−36
Gravel	−58	−34
Sand	−21	−15

Figure 8.5 shows results of a study of effects of trawling on George's Bank off the eastern seaboard of the USA. Dramatic effects such as these have been described and documented for many areas, but there is a need to quantify such changes. Collie *et al.* (2000) found that of 33 studies where data were available the numbers of individuals and species were most severely reduced by intertidal dredging and least damaged by beam trawling (Table 8.1).

Most otter and beam trawling is done in sandy habitats and here there is little evidence of impact on numbers of individuals. Although the data suggest severe reductions in both numbers of individuals and species, Collie *et al.* (2000) showed that there were no statistically significant effects. This is due to the large variance in the data and the fact that many different types of study were combined. However, this means that the probability of detecting significant effects using such an experimental design is probably very low. This is clearly shown by the fact that one cannot detect a significant difference between a 56% reduction and a 3% increase in abundance of individuals. It is surprising that no indication of the power to detect a change was shown, but it must have been less than 50%, i.e. an extremely poor experimental design. Thus one should not assume that there are no negative effects on numbers of individuals and species since one would be committing a large type II statistical error if one assumed that there were no significant differences! (See later in this chapter for a fuller discussion of type II statistical errors in a fisheries assessment context.) The problem illustrated in Table 8.1 can be partly overcome by using the statistical technique of meta-analysis which simply looks at the direction and magnitude of change in a standardized manner. Kaiser *et al.* (2006) analysed 101 different fishing impact studies and dealt clearly with the lack of power of more traditional methods of analysis. Again analysing fishing gear against sediment type, Kaiser *et al.* (2006) found that the greatest impact was caused by scallop dredging on biogenic habitats (Fig. 8.6).

Although this study is more comprehensive than that of Collie *et al.* (2000) it nevertheless includes the same data. Again most studies were done in Europe, followed by North America. There was a 72% reduction in the response variable (abundance or total number of species) caused by intertidal dredging compared to no effect of otter trawling

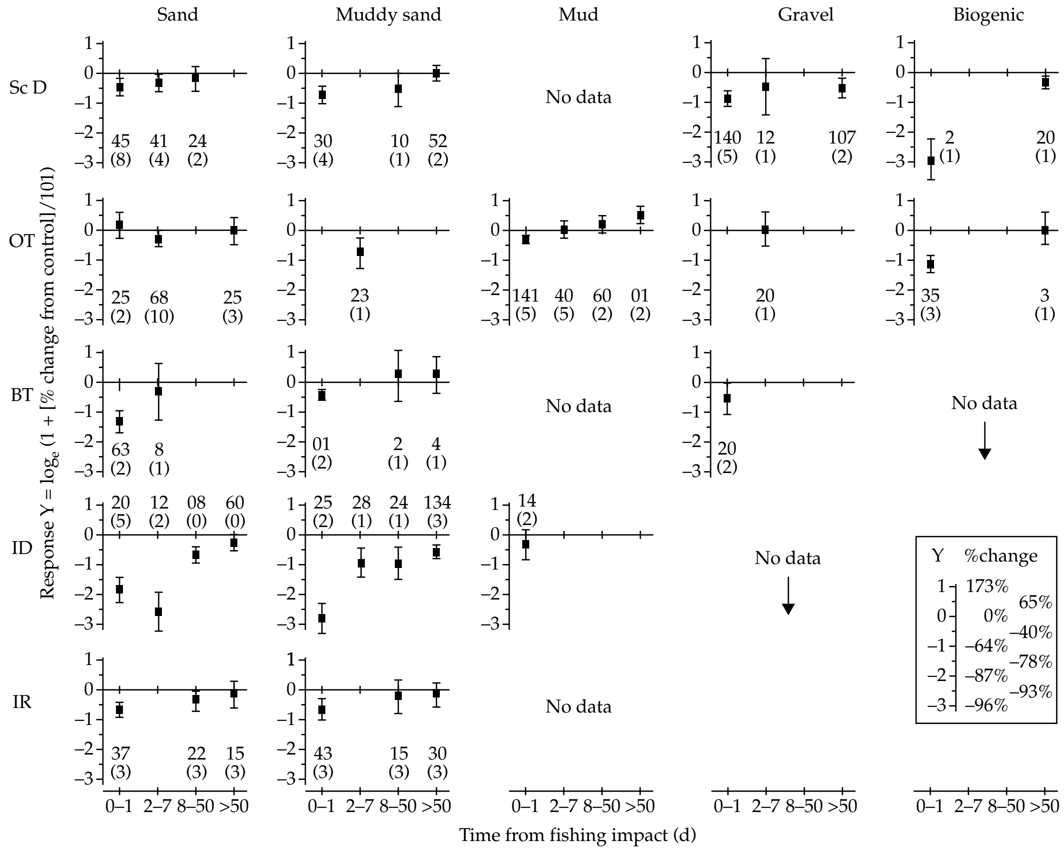


Figure 8.6 Response of benthic taxa to disturbance by various types of fishing gear in different sediment types from a meta-analysis (from Kaiser *et al.* 2006). *Y* is the log-transformed percentage change in abundance of each taxon in relation to control conditions. ($Y = -4.6$, complete removal; −2.2, 90% reduction; −0.7, 50% reduction; −0.22, 20% reduction; 0, no change; +0.22, 25% increase; +0.7, 100% increase). The response is shown for four time categories (0–1, 2–7, 8–50, and >50 days); note that the final time bin varies between days 50 and 1460 after a disturbance event. Data are means ±SE (from the pooled SD for each plot); hence, there is no significant difference from a zero response (no impact of trawling) if the error bar intersects the *x*-axis. For certain combinations of fishing gear and habitat there were insufficient or no data. Numbers at the bottom or top of each graph: numbers of data points for that time interval and (parentheses) number of different studies contributing data points. ScD, scallop dredging; OT, otter trawling; BT, beam trawling; ID, intertidal dredging; IR, intertidal raking.

on mud. Over time the data show that although there is a strong initial response (58% reduction in variable between 0–7 days), after >8 days the reduction was only 16%. Thus recovery is rapid on some sediment types. Although otter trawling had no significant initial effects on sand habitats, there was a delayed response which showed effects in the second time-interval. All the other fishing gears recorded significant early-stage impacts for mud and sand habitats. Scallop dredging had the most significant effects of all gears on biogenic habitats.

Kaiser *et al.*'s (2006) study also measured recovery rates, as shown in Fig. 8.7. The results show that only with intertidal dredging in muddy sand was recovery not achieved after 50 days. Yet the impacts of trawling are of course more subtle, and some species are more adversely affected than others. Kaiser *et al.* (2006) found that whereas annelids in sand habitats disturbed by intertidal dredging recovered in 98 days, in muddy sand habitats full recovery was estimated to be achieved only after 1210 days. In muddy sand recovery rates for annelids, crustaceans, and molluscs combined was estimated at 870 days. (However, it must be remembered that the study period lasted only 540 days.)

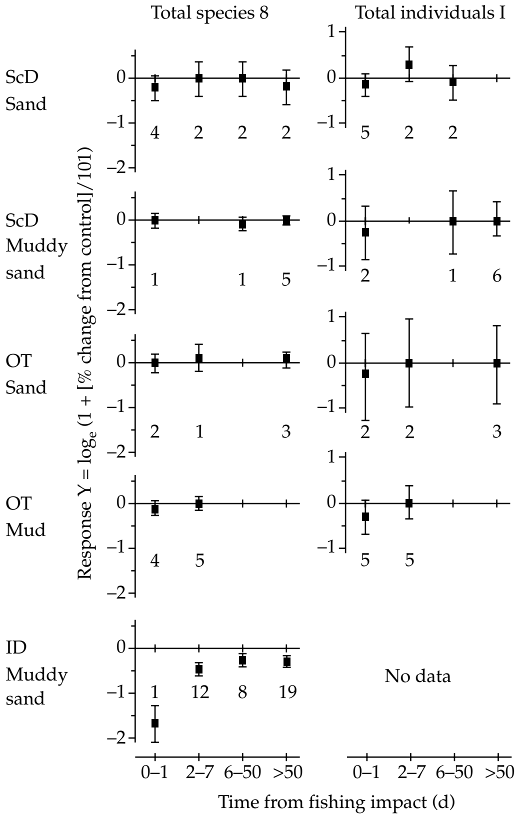


Figure 8.7 Response of the total number of species (S) and total number of individuals (I) to different types of fishing disturbance (abbreviations as in Fig. 8.6) in different habitat categories after an initial disturbance event, recorded at four time intervals (from Kaiser *et al.* 2006). Intersection of 95% CIs with the zero-response line indicates no impact of trawling. Numbers at bottom of plots are numbers of points on which means are based.

One of the problems of analysing a wide variety of data sets as done above is that they are not uniform and lend themselves poorly to combinatorial treatment for traditional statistical analyses such as analyses of variance. The fishing industry is of course keen to show that the effects of trawling are not as damaging as some scientists claim. The UN Food and Agricultural Organization (FAO) commissioned a paper with the aim of giving an objective appraisal of the effects of trawling on soft-sediment benthos (Løkkeborg 2005). The problem was that in analysing the data, Løkkeborg made the (not uncommon) error that if you cannot show statistical differences between control and disturbed sites, then you conclude that there are no effects. In statistical terms this is committing a type II statistical error. A type II error is accepting that there is no effect when there is one (false negative), and this is a far more serious environmental error than committing a type I error, assuming an effect when there is none (false positive). The report has been thoroughly analysed (Gray *et al.* 2006) and its main conclusions can be rejected: trawling has had large-scale negative effects on benthic assemblages globally. Perhaps the most surprising aspect of the FAO promoting a paper purporting to show that bottom trawling was not damaging to benthic communities is that FAO has generated its own Code of Conduct for Responsible Fishing (FAO 1995). The code emphasizes that where there is doubt, one should take a precautionary approach. That is, one should give more weight to type II statistical errors and only accept that there are no effects where the data have sufficient statistical power to make such judgements.

Following on from Kaiser *et al.*'s meta-analysis (2006), Allen and Clarke (2007) have used the ERSEM model of benthic–pelagic coupling to examine effects of trawling on system functioning. (ERSEM is described more fully in Chapter 10.) ERSEM is particularly strong in the way the benthic system is treated and it is possible to simulate effects of trawling on flux rates of nutrients. The simulation used the removal of the oxic layer of sediment, mortality to deposit and suspension feeders and meiofauna, and changes in abundance of aerobic bacteria as variables affected by trawling. Mortality rates were similar to those found by Kaiser *et al.* (2006). The simulations were also able to assess the times necessary for recovery from such disturbance events. Biogeochemical effects were greatest where trawling frequency and bed type caused high levels of filter-feeder mortality. Oxygen consumption by the benthic system increased dramatically, and phosphorus absorption and nitrification of ammonia increased significantly, whereas silicate cycling was reduced. On complete cessation of benthic trawling, recovery rates were estimated to be within 5 years except in extreme cases where the deposit- or filter-feeding function is removed. However, complete cessation of trawling is almost certainly not a scenario that is likely to be achieved and one must assume that if the seabed is re-trawled in <5 years then serious reduction in the functional properties of the seabed will result.

8.4 General effects of trawling on benthic systems

It is often argued that following the *intermediate disturbance hypothesis* (IDH) (Connell 1977), disturbance of the seabed leads to increased species richness. This argument is widely used in fisheries circles to argue that trawling is 'good for the environment' since limited disturbance will lead to higher numbers of species of benthos and a richer fishery as a result. Thrush and Dayton (2002) dismiss this myth. According to the IDH, maximal species richness occurs where there is some disturbance of the environment since in an undisturbed environment one or a few species will outcompete all others for a limited resource and thus species richness will not be maximal. Where the competitive dominant species are reduced in abundance by disturbance then species richness will be higher. It has been difficult to show that in soft sediment, competition (for food or space as limiting resources) is a major factor influencing community structure (see Chapter 4), a feature especially true over broad spatial scales. As has been shown, sediment systems are often structured by multitrophic level systems and disturbance has no effect on the persistence of competitors. Thus it is quite inappropriate to use the IDH in the context of trawling.

Thush and Dayton's review shows clearly that in addition to species loss, diversity is reduced and abundances and biomass are also reduced. Such effects were found on muddy, sandy, and gravel habitats, although in a number of studies of sandy substrata there were less clear negative effects. Sand, and especially well-sorted sand, is a less rich habitat for benthic assemblages than muds and gravels and this may be related to life-history characteristics of the species that occur. Such species are adapted to a harsh physical environment by being more motile and having relatively shorter life cycles than their counterparts in the other sediment types. For example, magelonid polychaetes such as *Magelona mirabilis* are well adapted and have a body form suitable for burrowing through mobile and easily disturbed sands.

One of the most significant aspects of disturbance caused by trawling is that the species that are removed (or whose populations are most greatly impacted) by trawling are habitat-structuring species, and/or large, long-lived, and often rare species. Even if organisms are not killed outright, they are damaged or exposed such that scavengers enter the areas in large numbers (Jennings and Kaiser 1998). The removal of certain components, leaving disturbance-tolerant species, leads to the sediment community becoming homogeneous. Animals such as anemones, soft corals, bryozoans, and sponges are particularly affected by trawling. Sponges in polar seas often form huge colonies, metres high, which make spectacular three-dimensional habitats. In 2006 a ROV survey of a once-rich sponge area, Tromsøflaket in the Arctic Sea, showed that trawling had destroyed nearly all the sponge colonies.

The large macrobenthic organisms living either on the surface or just underneath it are most at risk of damage from trawling. Fragile brittlestars easily lose their legs and although they may recover, this will be at the expense of growth and reproduction. Shell damage due to trawling to the large bivalve *Cyprina islandica* (the quahog) has both allowed an estimate of the overall impacts of trawling and indicated long-term patterns in the benthos (Witbaard and Klein 1994). It has also shown that the amount of damage to the shells of these large bivalves is directly proportional to the amount of fishing as indicated by the engine power prevailing in an area (Fig. 8.8). Given the slow growth and long life of this species, it is suggested that the recovery time from any damage to the population due to trawling will be long.

In a modelling study of effects of homogenization compared to simple loss of area of an intertidal habitat (estuarine areas in New Zealand), Thrush *et al.* (2006) showed that homogenization had far greater effects on species richness than did loss of area *per se*. Thus habitat homogenization caused by trawling is undoubtedly one of the major threats to coastal and deep-sea biodiversity.

It was shown in Chapter 3 that describing assemblages using biological traits rather than species abundances may offer new insights into changes that occur across environmental gradients. Bremner *et al.* (2006) sampled the megafauna

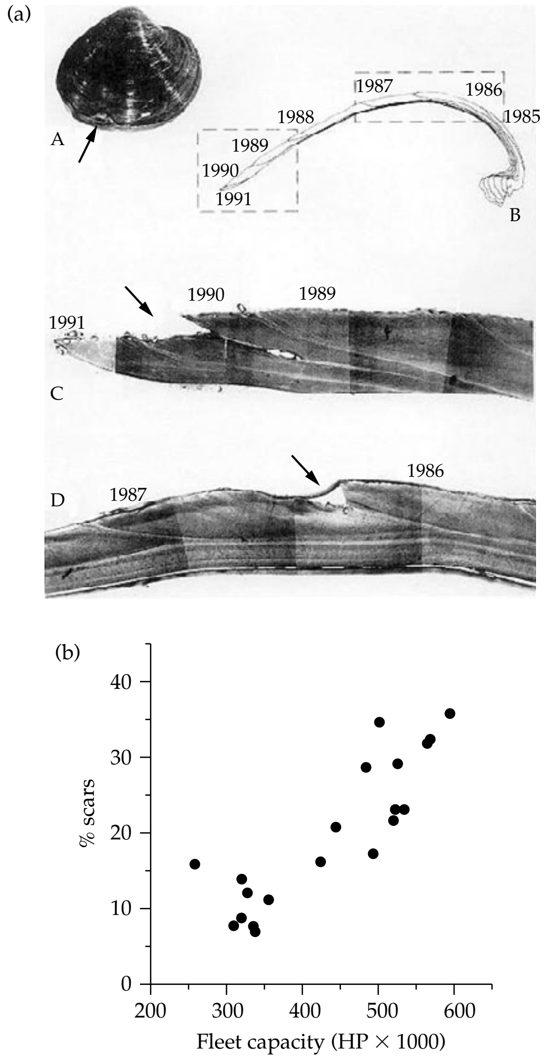


Figure 8.8 Detection of trawl damage: (a) *Arctica (Cyprina) islandica:* incidence of trawl damage as shell scars indicating repair (A, D) and recent damage (C). (b) Correlation between average scar incidence and Dutch beam trawl fleet size (as engine power) (from Witbaard and Klein 1994 and Klein and Whitbaard 1995).

of soft sediments using trawls in the North Sea and English Channel. In all they measured 14 biological traits (individual/colony size, relative weight, adult longevity, reproductive mode, relative adult mobility, degree of attachment, adult movement, body flexibility, body form, feeding habit, sexual differentiation, sociability, migration, and living habit). Each was scored on a 3–4 unit scale and a verbal description was also used. In all, 99 stations were sampled and they used three different multivariate methods to analyse the data. Although two of the methods, Fuzzy Coding Analysis (FCA) and CoInertia (CoI) analyses, had greater power to detect impacts of anthropogenic disturbance, the nmMDS (non-metric multidimensional scaling) ordination plot was the easiest to interpret.

Figure 8.9 shows that the FCA and CoI figures are similar and there is a non-random distribution of traits over samples. The traits whose variability between stations were most affected by trawling were mobility, degree of attachment, and body form. The nmMDS showed a similar pattern but with less discrimination over axis 1. Bremner *et al.* (2006) tested the sensitivity of methods by reducing the numbers of traits used and reanalysing the data. The two dominating traits were body flexibility and individual/colony size, whereas sociability had no effect on the results. Thus, these analyses show that it is possible to generate patterns of sites having similar biological traits and that these traits can be clearly related to the functioning of the species at these sites.

Studies have now shown the longevity of trawling effects and thus reinforced the recoverability of areas as long as trawling is not repeated. For example, Currie and Parry (1996) shows that although the effects are large scale and immediate, in sedimentary mobile areas subject to scallop dredging recovery occurs within a year (Table 8.2). Hall-Spencer and Moore (2000) also showed the long-term effects of fishing on another habitat type, maerl beds, and the long-term implications for the biotope. However, unlike extensive studies on rocky shores which have investigated the recovery potential and cycles of recovery depending on recruitment periods, this information is poorly known for soft-sediment areas.

From the above it is clear that the change in focus that occurred in the 1990s to the negative effects of trawling on the benthic environment has led to a general appreciation of the problems. What is needed is a focus by fisheries management on how the problems can best be resolved so that a sustainable industry is developed. Part of the solution is to designate *marine protected areas* (MPAs) where fishing is controlled or completely excluded. Yet the design and placement of such MPAs is a highly complex science and there is

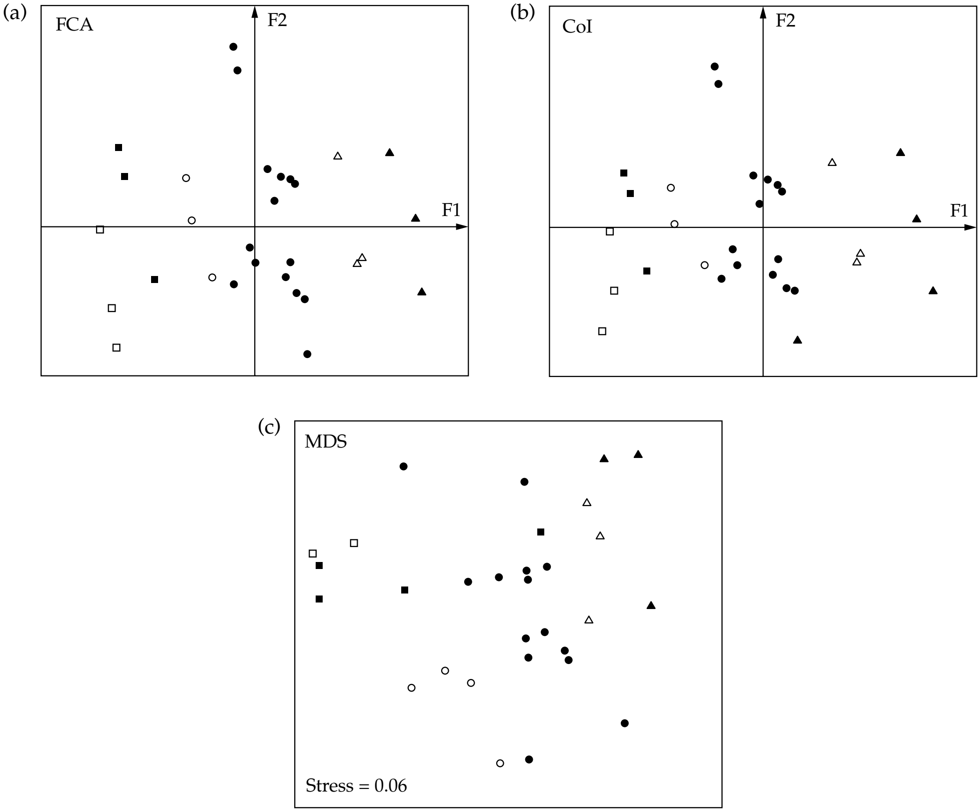


Figure 8.9 Ordination plots of biological trait composition of faunal assemblages, based on (a) fuzzy coding analysis (FCA), (b) Coefficient of inertia analysis (CoI) and (c) Multidimensional scaling analysis (MDS) of simulated biological traits data. Symbols represent manipulations of low mobility fauna biomass: □ complete removal, ■ extreme decrease, ○ subtle decrease, △ subtle increase, ▲ extreme increase, ● baseline samples.

Table 8.2 Experimental time series of changes between scallop-dredged areas and control site (adapted from Currie and Parry 1996)

Time	Features
Before dredging	Bedforms dominated by low mounds as depressions caused by Callianasids; 1.2 features m^{-2}; adjacent pits and depressions often trapped detached macrophytes
+ 8 days	Seafloor mostly very flat, mounds and depressions filled by 'grader like' action of dredge Dredge tracks still evident.
+ 1 month	Seafloor still flat Dredge tracks still distinguishable
+ 6 months	Mounds and depressions present over most of area and similar to pre-dredge condition Dredge tracks no longer visible Detached macrophytes present Some flattened areas present.
+ 11 months	No distinguishable differences between dredge and control sites.

no simple one solution that fits all cases; indeed the debate is increasing in Europe with the 2008 agreement of the Marine Strategy Directive and the political will to take an ecosystem approach to the management of the seabed out to 200 nautical miles (370 km). This will include the need for MPA and marine spatial planning (see Chapter 11). The interested reader is referred to the large and growing literature being developed on this topic (e.g. Jameson *et al.* 2002).

CHAPTER 9

Human impacts on soft-sediment systems—pollution

A widely accepted definition of marine pollution is

> "the introduction by man, directly or indirectly, of substances or energy into the marine environment (including estuaries) resulting in such deleterious effects as harm to living resources, hazards to human health, hindrance to marine activities including fishing, impairment of the quality for use of seawater, and reduction of amenities". (Wells *et al.* 2002).

This differs from contamination since it results in biological damage, whether to the natural or human system, whereas contamination can be regarded merely as the introduction of substances by human activities (McLusky and Elliott 2004). Furthermore, pollution and pollutants can refer to biological and physical materials as well as chemicals (Gray 1992, Elliott 2003). In the case of the benthos, there is an extensive literature indicating that every type of pollutant has an effect on the benthos and so it is not surprising that the benthos is the mainstay of any monitoring and investigative programme.

Pollution can affect organisms living in sediments by physical variables associated with the pollution source, such as increased sedimentation of particles, which leads to smothering of the fauna. In such cases the effect can in fact be regarded as a disturbing factor if the effects lead to mortality of individuals (Gray 1992). Alternatively, pollution can affect the fauna by toxicity where increased concentrations of contaminants lead to biochemical and physiological effects and ensuing mortality if certain thresholds for adaptation are exceeded. Here, however, we first treat the effects of the most widespread form of pollution affecting the marine environment—increased organic matter in sediments.

9.1 Effects of increased organic matter on numbers and biomass

Excess organic matter enters the marine environment principally as sewage, although it can also include waste from paper pulp mills or changed river run-off, for example. Excess organic matter causes physical effects such as smothering and also leads to reduced oxygen concentrations in the water column or pore-water in sediments. Sewage discharged into confined bodies of water frequently leads to the well-known symptoms termed *eutrophication*, resulting, in the most extreme cases, in a total lack of oxygen and the presence of hydrogen sulfide in the sediment, with a corresponding absence of fauna (e.g. de Jonge and Elliott 2001). As one moves away from the source of pollution there is typically a sudden and rapid increase in biomass and abundance of the fauna and number of species. Plots of abundance and biomass provide a simple way of illustrating complex effects on biological systems. Figure 9.1 shows data from Kiel Bay where a sewage outfall (discharging 50 000 m^3 d^{-1}) produces an effect on the benthic fauna to 1 km from the discharge point; beyond this limit populations are normal (Pearson and Rosenberg 1978). The restriction of effects to such a relatively small area is probably due to tidal currents, which not only wash away some organic matter but also renew the oxygen supply. Strong tidal currents occur in many areas of Europe, with the result that effects of outfalls are often confined to areas within a few hundred metres of the source. By contrast, in extremely sheltered areas with little water exchange, such as the Olsofjord, effects of eutrophication stretch over many kilometres.

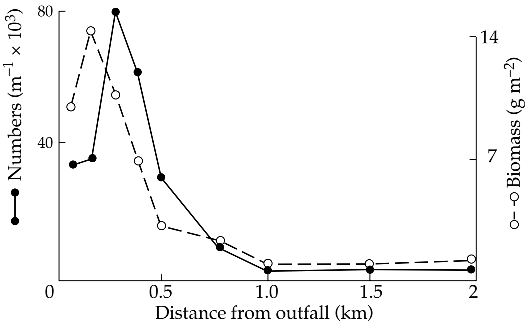


Figure 9.1 Effects of a sewage outfall on the abundance and biomass of the benthic macrofauna in Kiel Bay, Germany (from Pearson and Rosenberg 1978).

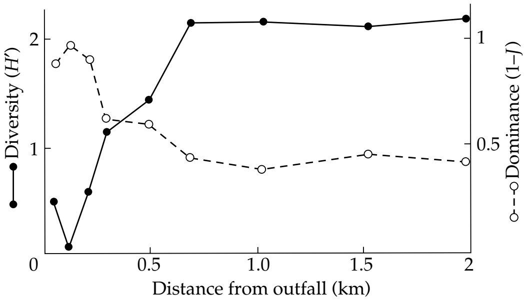


Figure 9.2 Changes in diversity (*H′*) and dominance (1–*J*) of macrobenthos along a gradient from a sewage outfall in Kiel Bay, Germany (from Pearson and Rosenberg 1978).

Pearson and Rosenberg (1978) suggest that the preferred method for illustrating such gradients in a simple way is to use *species–abdundance–biomass* (SAB) plots. In general, species numbers change before abundance and biomass do.

Referring to Fig. 9.1, one might argue that if more sensitive techniques were used then effects might be found much further away from the outfall. Diversity indices have been seized upon as a sort of panacea in this context. Following the engineering practice of producing simple indices for complex phenomena, administrators and legislators concerned with pollution problems have jumped at the idea of an index which integrates all the species on the interminable lists and tables of numbers that the biologists produce. The naively held view is that this is a simple measure of biological well-being; if the index is high there is no pollution and all is well, if the index falls then one should be concerned. Is this view really tenable in practice?

9.2 Effects of organic enrichment on diversity

In Chapter 4 we pointed out that there were two aspects of diversity to be considered: species diversity (H') and the evenness component (J). Evenness is the inverse of dominance, and so here we shall use $(1 - J)$ and term this dominance.

Figure 9.2 shows diversity (H') and dominance $(1 - J)$ of benthic fauna in response to the same sewage discharge shown in Fig. 9.1. Diversity is extremely low near the outfall, but rises rapidly so that at a distance of 700 m it is back to its 'normal' level. Dominance is the mirror image of diversity. Thus, H' is merely reflecting changes in the dominance pattern. A diversity index in this case is no more sensitive than the total abundance or biomass pattern in detecting the effects of pollution and takes longer to determine.

The problem of high levels of organic matter—whether from sewage, paper and pulp-mill waste, or weathered oil—and its resulting anoxia or hypoxia has been extensively studied with respect to the benthos. This problem occurs worldwide, sometime in large areas such as the Baltic Sea and has given us our best understanding of the way the system responds (Diaz 2001). One of the most detailed studies done on the impact of pollutants on a benthic community is that of Tom Pearson (1975) at the Scottish Marine Biological Association's laboratory. Studying a sea loch, Pearson followed the changes in the benthos over a 10 year period, for 4 years before discharge of waste began from a pulp mill and for a further 6 years after. Figure 9.3 shows the changes in diversity and dominance he found. From 1963 there was a gradual decline in diversity. When pollution began in 1966, diversity continued the steady decline of pre-pollution years. The question is, at what stage can we say there is a clear effect of pollution? Certainly by 1969 diversity was very low and pollution was having an effect, but we can question whether 1968 was or was not part of the pre-pollution trend of falling diversity. The interpretation is highly subjective and can be argued both ways. Again, dominance is the mirror

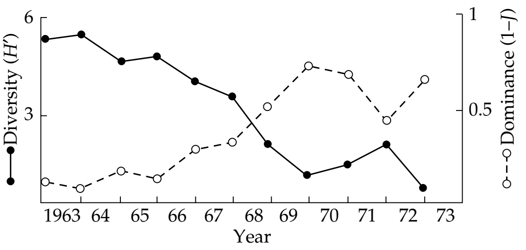


Figure 9.3 Changes in diversity (*H′*) and dominance (1–*J*) of macrobenthos following abatement of waste discharge from a paper pulp mill in Scotland in 1966 (from Pearson 1975).

image of diversity; when diversity is high dominance is low, and at minimal diversity dominance approaches the maximum of 1, when only one species would be present.

Interpreting the changes in values of diversity is, therefore, rather difficult. This is not really surprising if we think back to the factors that influence diversity. Diversity is affected by changes in competition between species, by variations in predation pressures, by variations in structural heterogeneity of the habitat, and by alterations in environmental predictability; it also alters over evolutionary time. Unless all of these factors remain constant from one sampling period to the next, we cannot conclude that any observed change in diversity is caused by pollution. Certainly diversity is lowered by severe pollution stress compared with control areas or years, but a diversity index does not appear to be a sensitive tool for measuring pollution effects.

Another example of the lack of sensitivity of diversity indices is from a study done in a polluted Norwegian fjord, Frierfjord (Gray *et al.* 1988). Frierfjord receives effluent from a large chemical complex, so the effects reflect not only changed organic enrichment but also chemical contamination. Here replicate samples were taken so confidence intervals (CI) were calculated. (Remember that with 95% CI it is possible to compare data visually. If the CI overlap there will be no significant difference using a Student's *t* test, whereas if they do not overlap they will be significntly different.) Figure 9.4 shows that the unpolluted site A is different from all the others and E and G are different from C, whereas there are no differences between the other sites . Again, little discrimination is shown using a diversity index (and it does not matter which index is used!). Thus, for a change in diversity to be statistically significant it would have to be equivalent to losing half the species (given initially the distribution of individuals among species and number of species of a typical benthic community). No index is needed to show that half the species are missing, and the changes are so obvious that the index tells you very little!

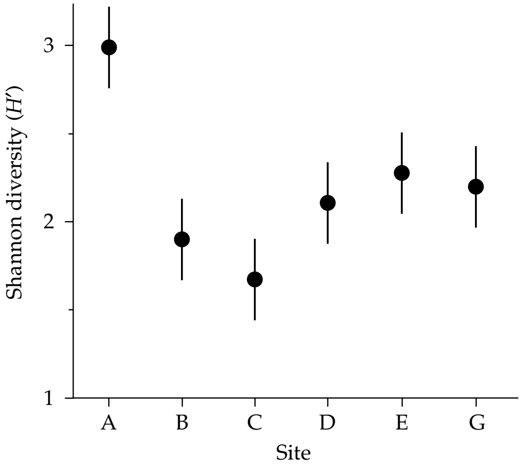
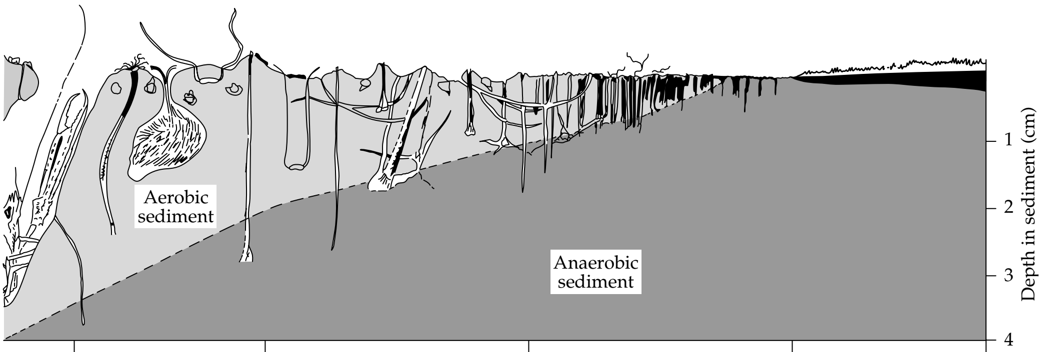


Figure 9.4 Means and 95% confidence intervals for diversity (*H′*) of macrobenthos at sites in the polluted Frierfjord, Norway (data from Gray *et al.* 1988). See text for details.

Pearson and Rosenberg (1978) reviewed the effects of organic enrichment on benthic fauna. This review is now a classical paper in marine biology and is one of the most cited papers in the field. They summarized the effects of organic enrichment in a schematic figure (Fig. 9.5). The related paper by Rhoads and Germano (1986) gives a very similar synthesis and final model of the response of the benthos to organic enrichment, consequently we now often refer to it as the Pearson–Rosenberg model (or paradigm) or, less commonly, the Rhoads–Germano model.

Figure 9.5 shows that as enrichment of the organic content of the sediment increases, at first the deep-burrowing species such as decapods and echinoderms and the sensitive surface dwellers, the bivalve *Nucula* and the ophiuroid *Amphiura*, are replaced by a variety of transitory species. The *redox discontinuity layer* (RPD), shown as a broken line, moves closer to the surface. With increased organic matter



Zone:	Normal	Transitory		Polluted	Grossly polluted
Typical macrofauna dominants:	*Nucula* *Amphiura* *Terebellides* *Rhodine* *Echinocardium* *Nephrops*	*Labidoplax* *Corbula* *Goniada* *Thyasira* *Pholoe*	*Chaetozone* *Anaitides* *Pectinaria* *Myriochele* *Ophiodromus*	*Capitella* *Scolelepis*	No macrofauna: surface covered by fibre 'blanket'

Figure 9.5 A schematic view of the effects of increasing organic enrichment on the fauna of soft sediments in northern Europe (from Pearson and Rosenberg 1978). The gradient increases from left to right.

loading, only opportunist species such as the polychaete *Capitella* and in the case of the Gyda oilfield the polychaete *Chaetozone* are dominant. Finally, the redox layer touches the surface which becomes black and anoxic and only a few specialized sulfide-loving species such as nematodes survive. In severe cases, the sediment surface is then covered by a layer of the sulfur-oxidizing (sulfate-reducing) bacterium *Beggiatoa* (Mußmann *et al.* 2003). This successional model has been verified on numerous occasions; the species composition varies from location to location but the guilds of species found are similar. This then is a general model for the effects of eutrophication on benthic systems.

Research since 1978 has concentrated on trying to relate the changes above to inputs. Can we quantify the amounts of organic matter that are associated with the different successional stages? Gray (1993), Jørgensen and Richardson (1996), Cloern (2001), and de Jonge and Elliott (2001) have summarized the main features and effects of marine eutrophication and recent research. Whereas some studies take the view that eutrophication refers to organic enrichment, these studies make it clear that it is the collection of a set of adverse symptoms. The latter include fish kills through dissolved oxygen reduction, toxic and nuisance microalgal blooms ('red tides'), macroalgal mats, and, of greatest relevance here, macrobenthic community changes (de Jonge and Elliott 2001).

9.3 Effects of discharges from the oil industry

In Chapter 4 we described multivariate statistical analyses and showed that they could be applied to generate and then test hypotheses about organization of assemblages along environmental gradients. It has been firmly established since the 1980s that such methods are the most sensitive way to show effects of disturbance on natural assemblages. One of the first analyses done on the effects of oil on benthic assemblages using multivariate analyses was at the Ekofisk field (Gray *et al.* 1990) , and a comprehensive analysis of many fields has been done by Olsgard and Gray (1995).

The beyond-BACI-PS sampling designs and gradient analyses were introduced in Chapter 2. In order to illustrate how multivariate methods can be used to describe effects we used data on the effects of oil exploration and production in the Gyda oilfield on the Norwegian continental shelf. Pollution from oilfields in the early days of the oil industry in the North Sea and along the Norwegian continental shelf was from discharges of drilling cuttings into the sea near the boring well or production platform.

The drilling cuttings contain oil, which is of course organic matter. Cuttings also contain other chemicals, and thus effects cannot be attributed to organic matter pollution alone. The monitoring programme used a classical design with sampling at logarithmically increasing distances from the production platform (the discharge source), at 250 m, 500 m, 1000 m, 2000 m, and 4000 m on four radii spaced at 90° intervals with the main axis along the residual current direction (see Fig. 1.5).

The results of analysing diversity show some effects but little discrimination between samples. Thus again diversity indices are very crude indices of the effects of pollution. Using multivariate statistics, we can obtain the results shown in Fig. 9.6. The two statistical methods used, classification and ordination (MDS), are numerically different and should be used in a complementary way to determine robust patterns. However, we often see papers where classification and ordination analyses have been used to support each other but where the two techniques have been based on the same algorithm such as the Bray–Curtis similarity measure; the authors then state (erroneously) that as the same patterns are produced then the patterns must be robust—they should remember that the patterns have to be the same, given the method of calculation!

Although the classification determines groups, it does not give any spatial representation of these groups. Imagine the plot as a mobile hanging from

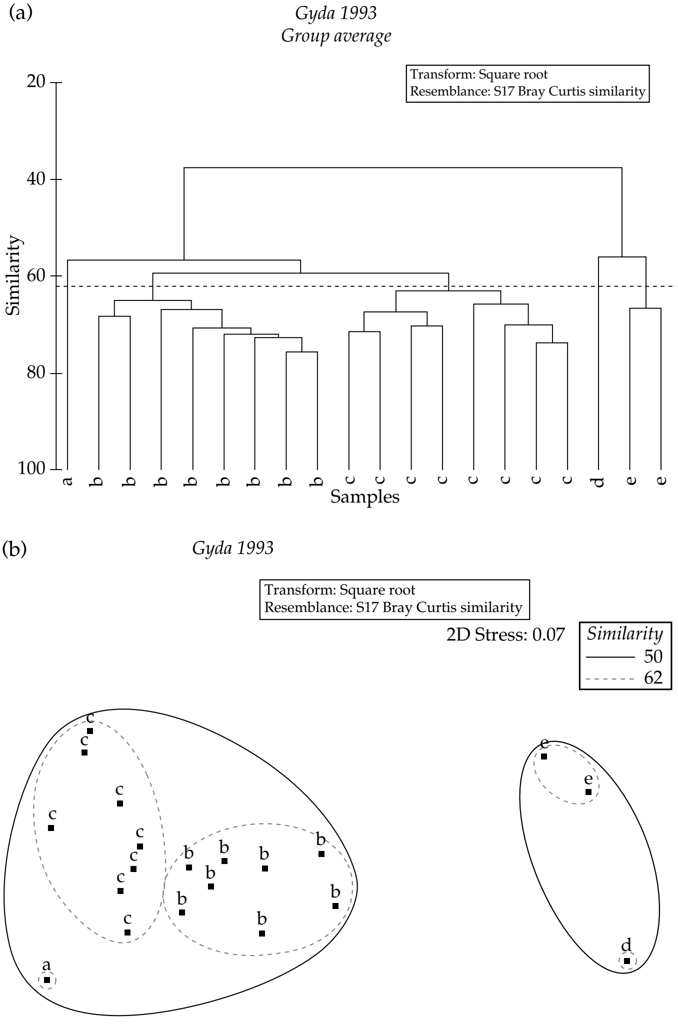


Figure 9.6 Multivariate analyses of the effects of oil discharges from Gyda platforms on benthic macrofauna, based on double root transformed data and Bray–Curtis dissimilarity index: (a) classification analysis; (b) non-metric multidimensional scaling analysis (MDS). The PRIMER software, version 6.0, was used.

the ceiling where the groups can spin around on the top branches. The ordination MDS gives spatial arrangement and the groupings on the MDS are those from the classification drawn on the MDS plot. The gradient goes from A to D or D to A. (Note that ordination techniques such as MDS give relative positions for each site, whereas other ordination techniques such as DECORANA give set positions based on eigenvalues in which the axis scores can then be used in correlations with environmental variables to determine relationships; see Gauch 1982.)

In order to see how the patterns in the multivariate analyses relate to oil pollution, two indicators used are the barium content and total hydrocarbon content (THC) (Fig. 9.7). Here the concentrations are superimposed on the MDS plot of stations that have similar faunal assemblages, and show a clear contamination gradient. Barium is not considered toxic, and barium sulfate is used during the drilling process to control pressure. It is likely that their effect on benthic assemblages is to smother the fauna.

An often posed question is, can we separate the contaminated sites using a diversity index such as Shannon-Wiener? Figure 9.8 shows the result using bubble plots. There is only a slight difference between the contaminated and uncontaminated stations and so in this case the Shannon–Wiener index is insensitive.

One of the interesting aspects of using multivariate methods is that one can examine the likely biology behind the effects observed. In Fig. 9.9 are plotted the abundances of two species: a species that is sensitive to oil—the ophiuroid *Amphiura filiformis*—and an insensitive opportunist polychaete *Chaetozone setosa.* The abundance patterns of these species provide clear illustration of the biology that underlies the multivariate analyses. The adaptive

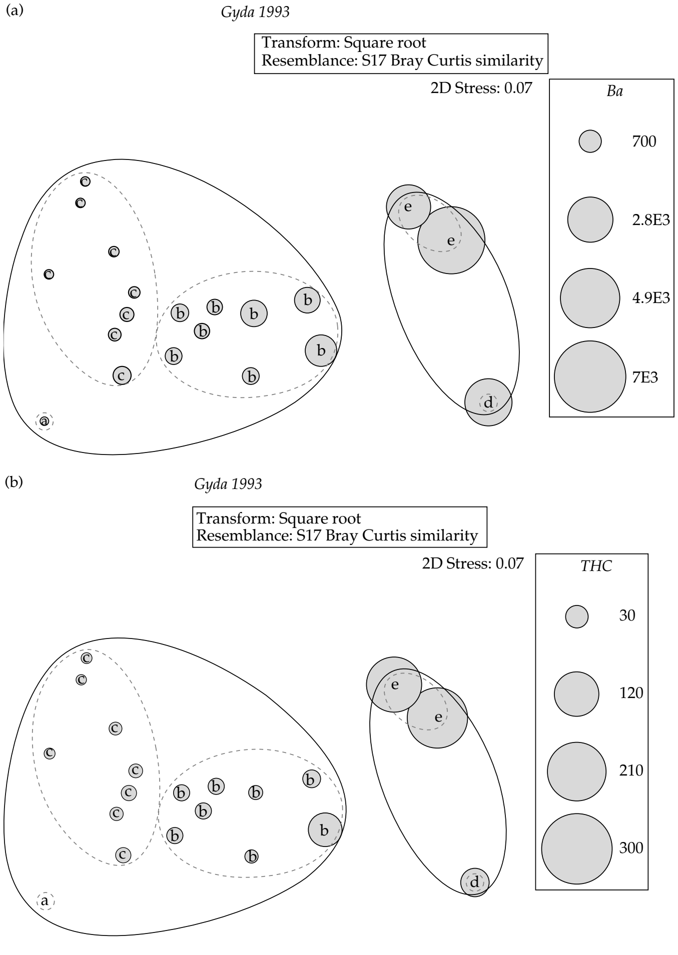


Figure 9.7 Bubble plots of concentrations of (a) barium and (b) total hydrocarbons on the MDS plot of station groupings based on faunal composition.

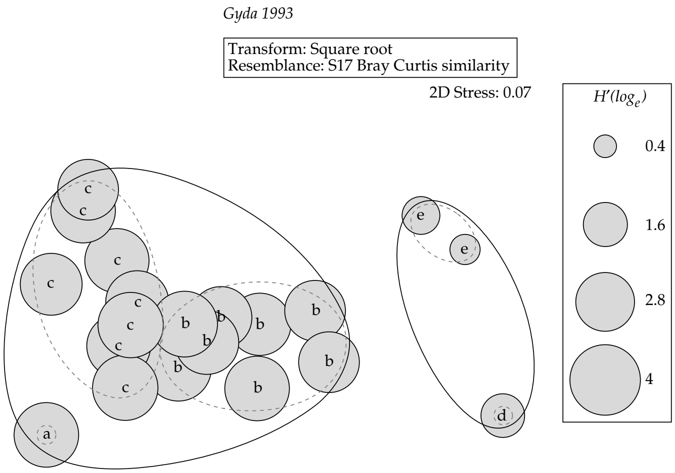


Figure 9.8 Plots of diversity (FT) of macrobenthos at the Gyda oilfield using base $\log_e$.

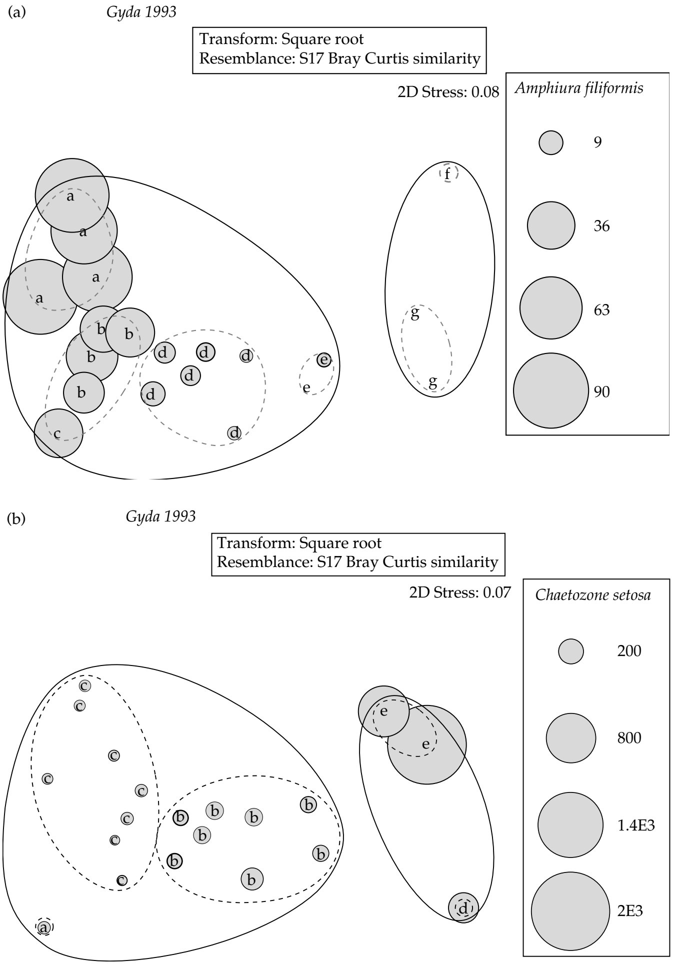


Figure 9.9 Bubble plots of the abundances of (a) *Amphiura filiformis* and (b) *Chaetozone setosa* on the stations of the MDS analysis shown in Fig. 9.8.

strategies shown by species will be discussed later in this chapter.

Multivariate methods are widely used to assess effects on benthic assemblages of soft sediments. The reason why such methods are successful is that benthic assemblages contain many species (typically over 300). Clearly there are many that will respond to small influences and change in abundance. It is the changes in abundance of many species that are analysed using the multivariate methods. Recent techniques such as CANOCO are valuable in allowing simultaneous ordinations of the sites, the species and the main environmental vectors in a data set, thus giving a tri-plot (see Jongman *et al.* 1995). Furthermore, assessing the effects of pollution in coastal systems using benthic fauna and multivariate statistical methods is now part of international legislation, such as the OSPAR Commission (OSPAR 2004) and many national programmes (e.g. USEPA 2006).

Oil spills usually get large headlines in newspapers and on television, and the word catastrophe is often used. This is not surprising, as the sight of oil-covered seabirds and mammals such as sea-otters is a very visual image of the distressing effects of oil spills. Yet scientists have studied many oil spills in different parts of the world, and we have a very good understanding of their effects (see Clark 2001, McLusky and Elliott 2004). With the exception of the Gulf War oil spill, where 150 000 t of oil leaked from bombed wells in Kuwait, oil never covers the whole coastline. It comes ashore in patches, so that there are always unaffected areas that can provide sources of animals and plants to recruit to affected areas once the concentration of oil has been reduced by natural degradation processes. From major studies such as those of the *Torrey Canyon* oil spill (119 000 t in March 1967, Smith 1970) and the *Exxon Valdez* (37 000 t in March 1989, Petersen *et al.* 2003) it can be concluded that exposed shores recover in 3–5 years and protected bays in 10–15 years; indeed in the case of the *Exxon Valdez*, Michel Glemarec at the University of Brest suggested that the effects of oil on the intertidal benthos lasted about the same length of time as the effects of a harsh winter. Even seabird populations seem to recover rapidly from spills. For example, the *Sea Empress* spill in Milford Haven killed about 10 000 birds but 3 years later populations were back to normal (Countryside Commission for Wales 2006). From the above it is clear that if oil penetrates sediment in areas sheltered from wave action, the effects can last for over 10 years and, most notably, because of increasing long-term monitoring at spillage sites, contamination can be detected several decades after an oil spill (e.g. Reddy *et al.* 2002).

Some of the best studies of long-term effects of oil spills relate to perhaps the largest one so far: the *Amoco Cadiz*, which went aground in Brittany in April 1978, spilling 223 000 t of oil. Majeed (1987) took the methods described above relating to assemblage succession following other types of organic enrichment and showed a similar succession due to the different sensitivity/tolerance of macrobenthic species to oil, leading to the following categories of species:

- GI: species very sensitive to organic alteration, abundant in normal conditions
- GII: species always present in low densities with little temporal variation, mainly carnivores
- GIII: species tolerant of organic enrichment, may come and go in response to perturbation (often appear in higher than normal densities
- GIV: second-order opportunists, mainly small polychaetes
- GV: first-order opportunists, high densities in most polluted zones.

This clearly indicates that, as far as the benthos is concerned, after the weathering of the oil and initial physical and chemical degradation whereby the more toxic fractions are lost shortly after spillage, oil pollution is merely another form of organic enrichment.

These studies were accompanied by the excellent and extensive time series of Jean-Claude Dauvin (1998) who studied the bivalve *Abra alba* community in the fine sand in the protected Bay of Morlaix following the oil spill. He found that the dominant amphipod *Ampelisca* took over 10 years to recover to pre-spill levels. During the recovery period the biomass produced was less that the pre-spill level and thus effects probably occurred on higher trophic levels such as fish which prey on the benthic community (Dauvin 1998).

9.4 Effects of heavy metals and xenobiotic chemicals on benthic fauna

In the 1960s, heavy metals were widely regarded as the most serious pollutants affecting the marine environment, although this may have been the result of a greater perceived understanding of these and the development of widely available atomic absorption spectrophotometers (and the fact that we were not yet aware of persistent synthetic organic micropollutants). Monitoring programmes that measured concentrations of heavy metals in fish and shellfish were developed alongside international initiatives such as the OSPAR Commission which aimed to control pollutants respectively from vessels and land-based sources (entering the north-east Atlantic area). One of the best was a programme called the Global Mussel Watch. Concentrations of metals in seawater are difficult to monitor because they are low, even in contaminated areas, and vary greatly both spatially and temporally. Hence it was agreed to use mussels (such as the ubiquitous blue mussel *Mytilis edulis*) which concentrates metals and thus will provide a value of metal contamination which has been integrated over time (e.g. see Cantillo 1998). The programme became a global network with a wide variety of different bivalves being used in different regions, since *M. edulis* does not, of course, occur everywhere even though it occurs widely in northern and southern temperate areas—coincidentally, the areas receiving large amounts of pollutants!

In attempting to determine the fate and effects of chemicals entering the marine environment, we need a large amount of information. It is first necessary to understand the behaviour of the chemical in the environment: i.e. is it in solution, adsorbed onto mineral particles, absorbed into organic material, or does it precipitate out of solution? Once the contaminant is in particulate form, via any of these routes, it can then can be transported and deposited in the same way as any other particle. A knowledge of the physical (hydrographical and sedimentological) environment is then needed to understand the fate of those particles and the possibility of accreting areas to act as pollutant sinks. Once the pollutant has been deposited on to the sediment, it becomes assimilated into the sedimentary system. Its behaviour in the sediment relies on the physical and chemical aspects of the sediment—for example, a metal in an anaerobic, reduced sediment may be immobile after being precipitated out of solution if the metal sulfide produced is insoluble under those conditions. This behaviour of materials in sediments, i.e. after deposition, is known as *diagenesis*. That pollutant will then stay in the sediment unless either the sediment's physicochemical conditions change (e.g. by erosion, aeration, or bioturbation by organisms) or it is absorbed by deposit-feeding organisms.

Secondly, we need to know the behaviour and ecology of the organisms potentially at risk from the pollutant. Will they absorb the pollutant in ionic form across gill or body surfaces, take up particles by suspension feeding or by feeding on deposited particles and organic matter in or on the sediment, or will they be exposed to the pollutant through predation of their prey? Thirdly, we need to know the behaviour of the pollutant inside the organisms. Will it be free ionically in the cells and thus likely to interfere with biochemical processes, will it be stored and thus out of harm's way (for example in the jaws of nereid polychaetes), will it be chemically detoxified by binding (for example by metallothionein or heavy metal binding protein induction), or will it be excreted? Consequently, when metals (or any other contaminants) are taken up by fauna there are a number of processes that occur that must be distinguished. These are:

- *Bioconcentration*: the simplest process—the uptake of a chemical by an organism directly from the abiotic environment resulting in a higher concentration within the organism; for example, the degree of assimilation from the surrounding water through the body wall and/or gills.
- *Bioaccumulation*: the uptake of a chemical by an organism from the abiotic and/or biotic (food) environment; higher concentrations may result in the body (usually measured either in the whole body, or in the muscles/liver) and sediment-living species can take up contaminants from both the water and through their food (ingested sediment and organic matter); the concentration in the organism may or may not be higher than the source.
- *Biomagnification*: the transfer along the food chain of a chemical resulting in elevated concentrations

with increasing trophic level; note that biomagnification requires a predator–prey relationship to achieve high concentrations at higher trophic levels.

The fact that bioconcentration and bioaccumulation occur in blue mussels makes them well suited as monitoring organisms. Results of the Mussel Watch programme showed that in certain areas of Europe and the USA, near estuaries that were discharging large quantities of metals, concentrations of these metals were high in mussels and posed health risks for humans (e.g. Cantillo 1998). Despite the large effort studying contamination in mussels, few studies have attempted to determine uptake across many components of the ecosystem in general and the benthos–sedimentary system in particular. Elliott and Griffiths (1986) studied mercury contamination from an industrial plant in many components of the ecosystem of the Forth estuary, Scotland, and attempted to quantify the standing mass of mercury within these components. They found spatial differences in mercury levels in most components (sediments, plankton, infauna, epifauna, macroalgae, and fish) although the standing mass of mercury in the biota was 1% of that in the non-biotic components (sediments, suspended material, and soluble phase). As an indication of their role as a sink for pollutants, sediments alone were found to contain 97% of the standing mass. The study concluded that the critical pathways in this system are: (1) that of the sediment–infauna–estuarine demersal fish and wading birds; and (2) that for suspended material–mussels–oystercatchers. Therefore, the top consumers in each of these pathways were most at risk from increased contamination.

As a result of the concern regarding persistent pollutants in north-west Europe, ministers of the North Sea countries decided to reduce discharges of metals by 50%. This was achieved, and further monitoring suggests that metals are no longer a serious problem in coastal areas of Europe (for further information see OSPAR 2000). In regions where there are less stringent environmental laws and metals are still discharged, such as in many parts of Asia, metal contamination is still a problem.

As indicated above, the behaviour and ecological preferences of the organisms are a major determinant of their ability to accumulate pollutants. Figure 9.10 shows data from a review of bioaccumulation of heavy metals by aquatic macroinvertebrates of different feeding guilds by Goodyear and McNeill (1999). The data for copper are shown as an illustration, as copper is accumulated from both water and particulate sources. Thus sediment-living species are expected to have higher concentrations of metals than the ambient water or sediment and can be used as monitors of the environment. Yet the concentrations of metals can be regulated, and most species are able to excrete metals or detoxify them so that there are no adverse effects on the organism.

In the data shown in Fig. 9.10 there was no difference between the intercept values for the various guilds, and thus the authors conclude that there was no evidence for biomagnification. This is in fact a common finding and maybe one that will surprise readers. Metals in general do not show biomagnification

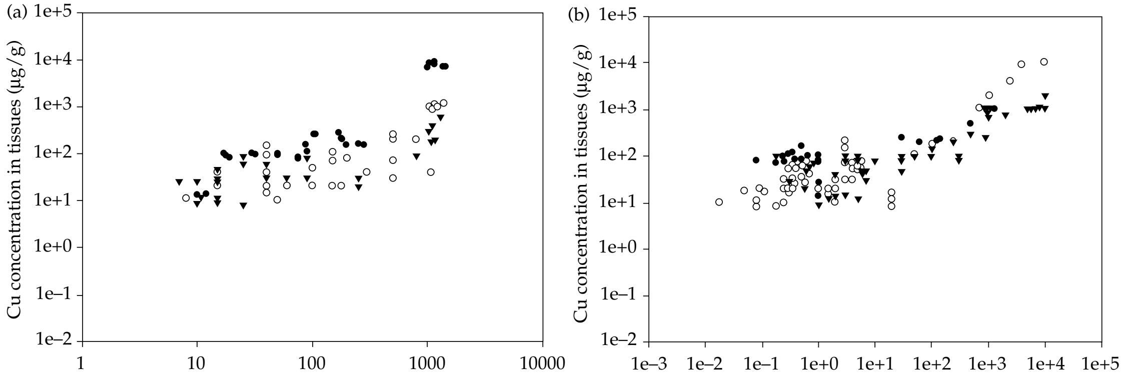


Figure 9.10 Accumulation of copper in a variety of aquatic feeding guilds from particulate matter (a) and water (b) (from Goodyear and McNeill 1999). ○ collector grazer, ● scraper grazer, ▼ predator.

up marine food chains. The exceptions are organic forms of metals such as methyl mercury and organotin compounds, and it should be remembered that organic metals have a higher degree of bioavailability than inorganic forms, i.e. organisms can assimilate them more easily than inorganic forms. Organic tin (such as tributyl tin, TBT) was found to cause disruptions in the reproductive system of the dog-whelk *Nucella lapillus*, which inhabits intertidal rocky shores in Europe (Bryan *et al.* 1986). TBT was applied to ship hulls to prevent biofouling and led to large-scale declines in *N. lapillus* populations around Britain and to damaging effects on oysters and the oyster fishery in France. Whelks inhabiting sediment were also shown to suffer from effects of TBT (Ten Hallers-Tjabbes *et al.* 1994) and many other molluscs were also affected (Evans *et al.* 1995). Fortunately, a worldwide ban has been imposed on the use of TBT, initially on boats up to 25 m in length and more recently on larger vessels; the ban on all vessels entered into force in September 2008 and so the problem will largely disappear with time.

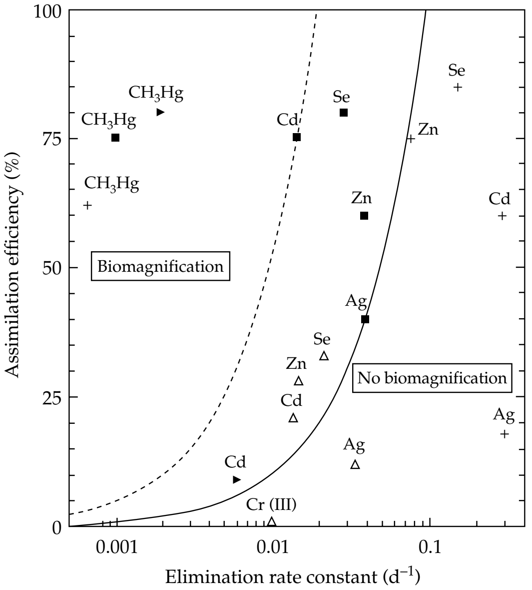


Figure 9.11 Prediction of biomagnification of metals in marine organisms based on accumulation and elimination data (from Reinfelder *et al.* 1998). + zooplankton, △ marine mussels, ■ other bivalves, ▲ fish; lines represent steady-state trophic transfer potentials for fish (---) and invertebrates (—).

Predictions of biomagnification by marine organisms have been made by Reinfelder *et al.* (1998) and their data illustrate the point that only methyl mercury (and presumably TBT) is liable to biomagnify (Fig. 9.11).

Synthetic chemicals, such as DDT and polychlorinated biphenyls (PCBs), pose different problems for organisms since they are not natural products, i.e. they are true xenobiotics; they are not normally excreted and, as they are lipid soluble, they accumulate to higher levels in organisms rich in fat. Nowadays it is relatively easy to predict which chemicals will biomagnify by using the octanol/water partition coefficient and the assessing the quantitative structural–activity relationships (QSAR) (Gray and Brewers 1996, Widdows *et al.* 2002). This has been shown to be a reliable way of predicting the biological concentration factor (LeBlanc 1995).

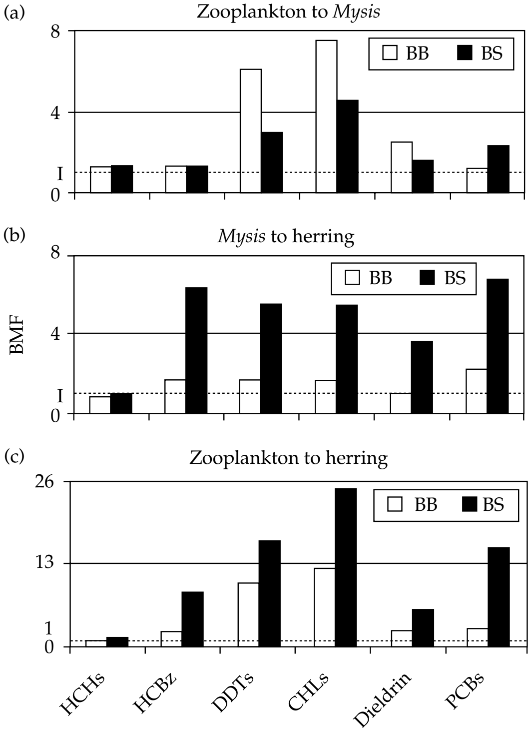


Figure 9.12 Biomagnification in Baltic Sea system of POPs (from Strandberg *et al.* 1998). Bothnian Bay (BB) is innermost in the Gulf of Bothnia and Bothnian Sea (BS) further out towards the open Baltic. HCHs, hexachlorocyclohexanes; HCBs, hydrochlorobenzene; CHLs, chlordane; PCBs, polychlorinated biphenyls. BMF, Biomagnification factor, a value >1 indicates biomagnification.

The data in Fig. 9.12 show concentrations of a variety of organochlorine compounds in the fauna of the semi-enclosed Bothnian Bay and the more open Bothnian Sea in the Baltic Sea (Strandberg *et al.* 1998). Hexachlorocyclohexanes (HCH) do not show evidence of biomagnification, whereas hexachlorbenzenes (HCBs), DDT, chlordanes (CHLs), dieldrin, and PCBs all show higher values in the predator than in the prey. Surprisingly, the more open Bothnian Sea has higher values than the Bothnian Bay, which suggests that sources come from the open Baltic Sea rather than from land-based sources within the bay. However, we should exercise caution in the interpretation of these studies of biomagnification as often there is no standardization of the tissues that are analysed. Whole organisms are analysed at the bottom of food webs whereas separate tissues are analysed at the top and, not surprisingly, higher values are found in the liver than in the skin. In the above study, the data were from the analysis of whole organisms in zooplankton and mysids, but no information is given on what part of the fish was analysed. It is not altogether clear whether biomagnification does in fact occur in marine systems.

Persistent organic pollutants (POPs) are of great concern because they are not degraded and may lead to endocrine effects such as changed sex ratios; their lipophilic nature makes them easily accumulated through fatty tissues in higher predators or even oil droplets within zooplanktons. They are easily dispersed globally and accumulate in polar regions due to the three-celled atmospheric circulation system, which has been dubbed the *'grasshopper effect'*. We are constantly finding environmental effects of new synthetic chemicals. A recent example is flame retardants, which are now known to be significant endocrine disrupters. Again, bans have been imposed in western countries but yet not in Asia.

9.5 Adaptive strategies to pollution/disturbance

This may seem a strange title, but in fact there is good evidence from the patterns of species changes along pollution and disturbance gradients that different species do in fact show similar characteristics at the various stages along these gradients. Although there is, as discussed earlier, a role for summarizing community biological features according to the primary and derived community parameters (such as species richness, abundance, biomass, diversity, evenness, etc.), multivariate analyses are extremely good at determining stations that differ and listing the species that differ between the stations; hence such analyses have generated a series of questions or hypotheses that need to be tested further. It is the biology behind the patterns revealed by the multivariate analyses that is important. Why is it that species A can survive in a highly disturbed/polluted area whereas species B disappears? Why, for example, does the polychaete *Capitella capitata* occur in the most organically enriched areas? The standard answer is that *Capitella* is the most tolerant species—more tolerant of lower oxygen tension and higher hydrogen sulfide than any other species—and that such conditions are to be found in the most polluted areas. In fact, *Capitella* is not particularly tolerant of low oxygen tension, and in comparative studies three other polychaetes typical of polluted areas were found to be more tolerant. Yet it is *Capitella* that is consistently found in the most polluted areas, and so an explanation other than tolerance must be found.

Gray (1979) has suggested that pollution effects can be loosely separated into two categories: disturbance and stress. By disturbance is meant an effect whereby individuals are physically destroyed or removed from an area. Chemical stress, on the other hand, results in the productivity of an individual being reduced. The adaptive strategies shown by organisms to these two factors are illustrated in Table 9.1.

Organisms adapt to high chemical stress by increasing their tolerance. Under high disturbance the best adaptive strategy is to have a high *r* value by having a rapid reproductive rate and turnover time, reaching maturity rapidly, and being relatively short-lived. This confers benefits especially

Table 9.1 Adaptive strategies to disturbance/pollution (based on Grime 1979 and Gray 1989)

	Low stress	High stress
Low disturbance	Competitive (K)	Tolerant (T)
High disturbance	Reproductive (r)	Non viable

in areas where less-tolerant species have been removed (or have moved away) as the result of a stressor. Under normal conditions without pollution stress, *r*-selected species are gradually outcompeted and replaced by *K*-selected species, which reproduce more slowly, are slow to reach maturity, and are long-lived. There is no adaptive strategy to a combination of high stress and high disturbance, and under such conditions no animals can exist.

Sewage pollution is primarily fine particulate matter falling on to the sediment. The particles are rich in organic matter and bacterial activity is consequently high. The biological responses are well known, so if the prevailing hydrography and sedimentology are also known we can generate a predictive numerical model linking the physicochemical and biological effects (e.g. see the DEPOMOD model of Cromey *et al.* 2002). If the sewage loading is high, many species are simply smothered by the falling particles and cannot survive. *Capitella* survives because it is a classical *r*-selected species: it can reproduce both by planktonic larvae and by benthic larvae, has a short life cycle, and reaches maturity from the egg in about 3 weeks. It can, therefore, continuously repopulate sediments subjected to pollution from organic matter. *Capitella* does not use tolerance as an adaptive strategy but adapts to continuous disturbance by continuous reproduction.

An oil pollution incident occurred at West Falmouth, Massachusetts, USA, in 1969. In the recovery sequence *Capitella* was the first species to recolonize and rapidly built up a large population, reaching densities of over 200 000 m^{-2} (Sanders *et al.* 1980). Then, just as rapidly, the population declined and was replaced by another polychaete, *Polydora ligni*. What had happened here? The oil killed the natural fauna and in the disturbed environment *Capitella* had the ideal life-history strategy to recolonize, by means of the ever-present planktonic larvae. Once the population was established, it could be built up rapidly by reverting to benthic larval production. Yet, according to the theory of *r*-and *K*-selection, *Capitella* is not a good competitor and is therefore removed by *Polydora*. However, it must be added that there is no direct evidence that *Polydora* does in fact outcompete *Capitella*. It may well be that the *Capitella* population becomes senile and *Polydora* occupies the newly available space. The competitive exclusion theory is, however, more satisfying and it should be a simple matter to verify. Interestingly, *Polydora* also shows many attributes of an *r*-selected species, but it is clearly not quite so opportunistic as *Capitella*. *Polydora* usually reproduces by means of a planktonic larva, but can also brood within its tube—again, a life-history strategy ideally adapted to disturbance. *Capitella* has been found in high numbers following a tropical storm, a red tide, sediment excavation, etc., and indeed is to be expected wherever the sediment is newly disturbed.

In contrast to species adapted to disturbance, stress-tolerant species are slow-growing and of low competitive ability. Arctic and desert plants are typical examples of tolerant communities, but others also exist (Grime 1979). If the environment becomes less stressful, then these *T* species will be outcompeted by *K* strategists, which are also slow-growing but are better competitors.

Capitella has been suggested as a universal indicator of organic pollution, i.e. where it is abundant there is likely to be organic pollution (Pearson and Rosenberg 1978). Yet as can be seen from the above examples, *Capitella* is abundant only in disturbed areas, such as those affected by a storm or an oil spill. Furthermore, the large *Capitella* populations that build up following these disturbances are transient; as colonization proceeds *Capitella* is outcompeted and returns to its normal low population densities. It may indicate organic enrichment if it continuously occurs in large numbers, but even then this is only a possibility. We can conclude that *Capitella* represents an end-point in the effects of organic pollution, as shown in Fig. 9.5, and as such this gives us important information regarding the success of a species in coping with pollution. However, we also need species that indicate the first stages of decline of an ecosystem. In this respect, it is of value to further consider the transitory species, or those isolated from break-points in the log-normal distribution, and try to find out whether or not they adapt to pollution in the same way that *Capitella* and *Polydora* appear to do.

The examples of pollution-tolerant species that we have used have inevitably biased the data towards pollution in terms of disturbance, since this is the principal effect on communities both of oil spills and of organic pollution. Chemical pollution can lead to quite different species-abundance patterns from those produced by disturbance, if the effect of the chemical is merely to reduce the productivity of the competitive dominant *K*-selected species without killing it; for while the *K*-selected species physically occupy space, the *r*-selected species will not be able to establish themselves. But if a chemical kills a species then a disturbance effect will occur, and we can expect, the *r*-selected species to become established. Thus it is rather difficult to predict the effects of chemical pollution, and we take the view that it will be extremely difficult to fit the effects of chemicals into general patterns. Some species will be affected by one chemical and not another, and only when species are killed will the *r*-selected species have a chance to establish themselves. Furthermore there is the difficulty that in most field situations there is not just a single stressor, e.g. metals, oils, and organic matter may all be discharged together. As yet, we know little about the biochemical and physiological responses of different benthic species to chemicals, even though studies were started over 20 years ago, e.g. Blackstock *et al.* (1986) attempted to determine the metabolic responses by marine polychaetes exposed to sewage discharges and organic pollutants. Thus, since each effluent varies in chemical composition and concentration, all manner of species combinations can be expected.

Figure 9.13 illustrates the three adaptive strategies species may show to pollution. At the lower left are those species that, according to the hypotheses suggested, are expected to occur in the most polluted environments. Although we believe that these hypotheses will be found to be correct, much more evidence is needed in order to test them adequately. In particular, the life-history strategies and tolerance capacities of the potentially sensitive species need to be studied. Recent work investigating the strategies used by benthic invertebrates in tolerating trace metals has indicated that there are such strategies for essential metals, and as such the organisms regulate the metals, whereas there are no similar strategies for non-essential metals such as cadmium (Blackmore 2001). In addition, although we have come a long way in identifying biochemical responses to stress (e.g. see the extensive review by Moore *et al.* 2004), much of the information we have is from fish, mobile crustaceans, or sessile epifauna such as marine mussels. We still do not have extensive information for the dominant members of the benthos—the polychaetes, amphipods, and infaunal bivalves.

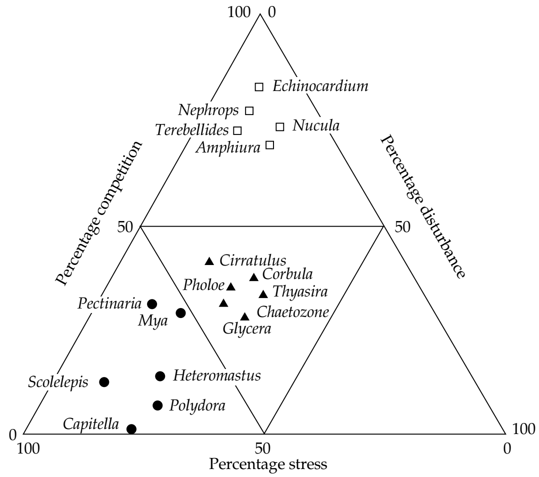


Figure 9.13 Adaptive strategies to organic enrichment of sediment-living fauna from north-west Europe, based on the three strategies shown in Table 9.1.

Another interesting point regarding adaptive strategies to pollution is the important finding of Grassle and Grassle (1974) of the Wood's Hole Oceanographic Institute. Working on the *Capitella capitata* population that followed the Massachusetts oil spill they found that, on the basis of enzyme polymorphisms, rather than being one species there were in fact six sibling species. Using classical cross-breeding techniques they showed that crosses between the species were infertile and that they were indeed true species; but they were hard to separate using conventional morphological characters. The different species varied in type of larval development, length of larval life, and season of maximal abundance. In fact, the successional sequence that followed the oil spill should probably include a succession of the different species of *Capitella*. In a highly opportunistic species such as *Capitella* selective forces probably lead to a continual evolution and extinction of species. Interestingly, *Polydora*, which also lives in highly polluted areas and is highly opportunistic, is also taxonomically difficult. In the Oslofjord *P. ciliata* shows an interesting temporal adaptation: populations in the most polluted innermost part of the fjord produce larvae for 12 months of the year, populations 10 km down the fjord, where it is less polluted, produce larvae for 6 months of the year, and those in the relatively unpolluted area near the inner sill produce larvae for only 3 months of the year.

Two other species typical of polluted areas are, like *Capitella* and *Polydora*, cosmopolitan: the polychaete *Heteromastus filiformis* and the oligochaete *Tubificoides* (formerly *Peloscolex) benedei* (or *benedeni*). The genetics of these organisms has not been studied, but we believe that if they are studied in depth they too will be found to have the same life history and genetic adaptations as *Capitella* and *Polydora*. It is encouraging that there is increasing research in the genetic aspects of marine invertebrates and especially their adaptations to marine pollution. Dixon and Wilson (2000) show a bioassay identifying chromosomal aberrations in the benthic sessile polychaete *Pomatoceros lamarcki*, a typical *K*-strategist, and suggest that new genetic methods will allow us to study survival and mutation under extreme conditions such as the high temperatures and concentrations of metals found in deep-sea vent areas.

Taking all of the responses to stress and disturbance, we can identify both the conceptual basis and the assumptions inherent in macrobenthic impact studies (Table 9.2). There seems to be a well-defined set of characteristics which, as indicated above, occur under polluted conditions as well as being caused by other stressors. This conceptual model includes the relative proportions of *r*- and *K*-selected strategists, the climax or otherwise nature of the community, and the average size and weight of individuals as

Table 9.2 Conceptual basis and assumptions inherent in macrobenthic impact studies. Source: modified and expanded from Warwick (1986) and McManus and Pauly (1990), and taken from Elliott and Quintino (2007).

Natural state

A natural macrobenthic assemblage either tends towards or is in an equilibrium state

Under non-impacted conditions, there are well-defined correlation and relationships (which therefore may be modelled) between faunal and environmental (abiotic) variables

In approaching the normal equilibrium state, the biomass becomes dominated by a few species characterized by low abundance but large individual size and weight

Numerical dominance is of species with moderately small individuals; this produces among the species a more even distribution of abundance than biomass

The species are predominantly *K*-selected strategists

Moderate pollution or stress

The larger (biomass) dominants are eliminated, thus producing a greater similarity in evenness in terms of abundance and biomass

Diversity may increase temporarily through the influx of transition species

Severe pollution or disturbance

Communities become numerically dominated by a few species with very small individuals

Those small individuals are often of opportunist, pollution-tolerant species which have *r*-selected strategies

Any large species that remain will contribute proportionally more to the total biomass relative to their abundance than will the numerical dominants

Thus the biomass may be more evenly distributed among species than is abundance

However, species with large individuals may be so rare as to be not taken with normal sampling

The change in assemblage structure with increasing disturbance is predictable, follows the conceptual models, and is amenable to modelling and significance testing

Recovery

Opportunists are inherently poor competitors and may thus be outcompeted by transition species and *K*-strategists if conditions improve.

McManus and Pauly (1990) also consider that under normal conditions:

The biomass dominants will approach a state of equilibrium with available resources

The smaller species are out of equilibrium with available resources

The abundances of the smaller species are subject to more stochastically controlled variation than the larger species well as their ecological preferences and abundance per species. Consequently, because of the good fundamental understanding of these responses, we can then develop methods, indicators, and indices for detecting stress and the management of the benthos (as discussed in Chapter 11). In summarizing these responses, McManus and Pauly (1990) indicate the features of normal, degraded, and recovering assemblages. Furthermore, we can then link the biological response to the fate and effects of the pollution and create numerical models such as DEPOMOD for organic enrichment (see Cromey *et al.* 2002).

We have seen from the above discussion that in relation to organic pollution, at least, the adaptive strategies adopted by species do not appear to be based on tolerance. Yet the classical way of trying to predict what effect chemicals are likely to have in the marine environment is to do laboratory toxicity tests. In such tests, organisms are placed in various concentrations and, over a given period, usually a standard 96 hours (although there appears to be no greater rationale for this time except that the test can be accomplished in the working week!), the concentration is recorded which produces either 50% mortality (LC_{50}, lethal concentration) or 50% of a defined effect, possibly a behavioural response (EC_{50}, effective concentration). Similarly, the data can be interpreted to give the lethal or effective time to affect 50% at a given concentration (LT_{50}, ET_{50}). Nowadays these calculations are made using probit regression analysis, which has the added advantage of estimating the confidence limits on the toxicity parameters (LC_{50}, EC_{50}, etc.) such that the statistical significance of differences between treatments can be assessed (see Rand 2008 for an extensive review of aquatic toxicology). By linking these concentrations or times to the prevailing hydrographic conditions, it is possible to determine whether benthic organisms in the area receiving polluting discharges will be exposed to lethal or effective levels after the effluent has been diluted and dispersed with distance from the outfall pipe. Water environment managers may then use a discharge limit of say 1/10, 1/100, or 1/1000 of the toxicity value as the environmental standard, thus giving a safe limit.

Although such testing is used as an industry and regulatory standard, and as such is used in defining effluent discharge licences, it has its failings in that the testing of individual substances under laboratory conditions on single species does not indicate the antagonistic or synergistic effects of multiple chemicals nor the effects on species complexes. Furthermore, the use of lethal testing is no longer regarded as a sensitive method and it is recognized that sublethal bioassays, such as burrowing bioassays, are more likely to give a precautionary approach (see below). Hence, taking all these aspects together, it will be seen that the toxicity test does not in fact allow us to predict the ecological consequences of pollution, since the species adapt to increased stress by altering their life-history strategies rather than increasing their tolerance. Despite this, toxicity tests still have a role in that they are used to derive sediment quality standards. A recent development, however, is the move towards *whole effluent testing* or *direct toxicity assessment* (DTA), as used extensively by the US Environment Protection Agency, in which the testing is done using the whole effluent from a wastewater discharge (Wharfe 2004). In this way, the interactions between chemicals are assessed and, using a knowledge of dispersion in the receiving environment, can be extrapolated to indicate the overall concentration to which the ambient biota are exposed.

Even with correlations between contamination and biological effects (the definition of pollution), there is still the need to determine cause and effect. Borgmann (2000) emphasized that despite the large amount of published information on toxicity and contamination, especially by metals, there are relatively few data showing the biological impact of this contamination. He also noted that biological impacts such as changes to the communities and the demonstration of toxicity in environmental samples often occur at metal-contaminated sites, but this does not prove that metals are actually responsible for these effects. Borgmann (2000), like many others, concluded that correlation is not proof of cause and effect and metal-induced biological effects cannot usually be inferred from measured environmental concentrations because metal bioavailability can vary dramatically from site to site. He found that there were differences in metal bioavailability leading to differences in metal bioaccumulation, which in turn led to differences in metal-induced effects. Thus it is accepted that bioaccumulation levels are better indicators of potential biological impact than concentrations in the environment, given the manner in which organisms integrate ambient concentrations depending on both the bioavailability of the contaminant and the means of uptake by the organism. Finally, Borgmann (2000) concluded that while measuring the body concentration of metals is a powerful tool for predicting metal effects, especially for non-essential and non-regulated metals, which are likely to be the toxic metals (e.g. mercury, cadmium, arsenic), the approach is more limited when applied to essential metals such as copper and zinc. Consequently there is a need for alternative methods which provide useful information on metal bioavailability, especially for copper and zinc, such as the measurement of metals in the overlying water during sediment toxicity tests, or sediment spiking with additional metal.

Of greatest value in explaining the benthic community indications of stress are marine sediment toxicity bioassays in which organisms are exposed to either natural, polluted, or artificially-spiked samples. These assays provide a realistic indication of how organisms respond to poor-quality sediments either by death or, more usefully and possibly as an early warning of harm, by a change in behaviour. There are now many such bioassays, for example the bivalve-burrowing bioassays in which the speed and success of burrowing by bivalves such as *Macoma balthica* and *Ruditapes philippinarum* is the measure of toxicity (e.g. Shin *et al.* 2002), and faecal cast production by lugworms *Arenicola marina* as the end-point (Thain *et al.* 1997, Allen *et al.* 2007). Bioassays using benthic infaunal amphipods are becoming standard testing procedures and have been used across large geographical areas (e.g. see the recent work by Allen *et al.* 2007, and also Long *et al.* 2001, described below).

As a recent excellent example of the use of such bioassays, and giving lessons for sediment toxicity testing, Castro *et al.* (2006) give a very detailed sediment toxicity survey using acute and full life cycle (chronic) tests with an indigenous soft-sediment infaunal species, the amphipod *Corophium multisetosum*. In the acute test, adult specimens were exposed to sediments from 144 sites in the Ria de Aveiro, northern Portugal, for 10 days. In the full life cycle test, 5–7 day old specimens, obtained in laboratory cultures, were exposed during 21 days to sediments from 56 sites. Three end-points were used for the testing: survival (for the acute and the chronic test), fecundity (number of gravid females per replicate at the end of the exposure), and growth (weight increase) for the chronic test. The acute tests showed that in general adult survival was high and very few stressed areas were identified. However, in contrast, the chronic end-points, in particular growth and fecundity, when corrected for the number of survivors, were the end-points that showed the greatest degree of harm. These chronic end-point results could not be related to the baseline sediment variables analysed (grain-size, total organic content, and redox potential), suggesting that these do not play a part in the biological responses and that the results were due to levels of sediment-bound contaminants. Castro *et al.* (2006) comment that a tiered sediment bioassessment approach including an initial comprehensive ecotoxicological screening phase should not rely solely on acute responses, even though these are obtained from simpler and more rapid laboratory testing procedures.

9.6 Sediment quality standards

Marine environmental managers have long used water quality standards as a means of protecting the environment and also setting pollution discharge permits (e.g. see McLusky and Elliott 2004 for further discussion). The monitoring of the water can then be linked to determining whether standards are met (we will return to this in Chapter 11). Similarly, sediment quality standards are levels of contaminants in sediments where the standard is set so that the fauna and flora living in such sediments will not be adversely affected. Traditionally such standards are derived by using toxicity tests where typical species are tested and safe levels assessed from laboratory tests in much the same way as described above. However, as indicated above, whereas water-borne contaminants can be tested as individual compounds or even mixtures, e.g. testing the level of a particular metal or its effect under different temperature and salinity conditions (e.g. see McLusky *et al.* 1986), it is more difficult to determine the toxicity of chemicals within sediments and so water managers usually rely on water testing. Hence sediment standards have been poorly developed and are not yet widely accepted, nor do they have any legal backing, unlike water quality standards that have been incorporated into European Directives (see McLusky and Elliott 2004). Worldwide, there are some examples of sediment quality guidelines for the protection of aquatic life, such as those produced for the Canadian Council of Ministers of the Environment (CCME 2001), but it is generally acknowledged that these should be used in supporting decisions rather than as legally defendable levels.

There are many problems with such sediment standards. Often the organisms used in the tests are not typical sediment-living species and usually the species are simply those that can be kept in the laboratory, the marine equivalents of laboratory rats. Furthermore, even if sediment-dwelling species are used, it is easier to test them in water as the endpoint is easier to detect. The tolerances of species to various chemicals are tested singly, and at best it is assumed that mixtures of chemicals act additively. As indicated above with regard to DTA, methods are needed that can assess whether the effects are in fact additive or whether the interactions between contaminants may be synergistic or antagonistic. The result is that the standards are not consistent from country to country and there is little evidence as to whether they do in fact protect the fauna. Although most developed nations have large monitoring programmes for coastal sediments where chemical and biological data are obtained, such data are rarely used to devise standards—merely to test conformance to the standards. Because of this, one of us (JSG) developed a method to derive sediment quality standards based on field data.

The monitoring programme used was that for assessing the effects of the Norwegian oil and gas industry on the environment, as chemical and biological data are available for the whole continental shelf of Norway. The chemical data are on metals and oil-related chemicals such as total hydrocarbon content and polycyclic hydrocarbons (PAHs) as measured from surface sediment samples. The biological data are species analyses at sites where chemical data were obtained and these are analysed by multivariate statistical methods (as illustrated with the Gyda data described on p. 136 *et seq*). In these analyses, it was first necessary to determine which of the 2500 species found were sensitive and responded to changes in concentrations of metals and hydrocarbons, especially as not all species respond negatively. Figure 9.14 shows responses of two species, a sensitive species, the amphipod *Harpinia antennaria* which decreases in abundance with small increases in concentration of a contaminant (in this case barium), and an opportunist, the polychaete *Chaetozone setosa*, which increases in abundance with moderate increases in contaminant levels. The first criterion used was a 50% reduction in abundance from the average abundance found at background concentrations of the studied metal or hydrocarbon. It should be noted that there is no reason to expect any particular abundance of an organism at any given concentration from background levels upwards. Abundances vary naturally

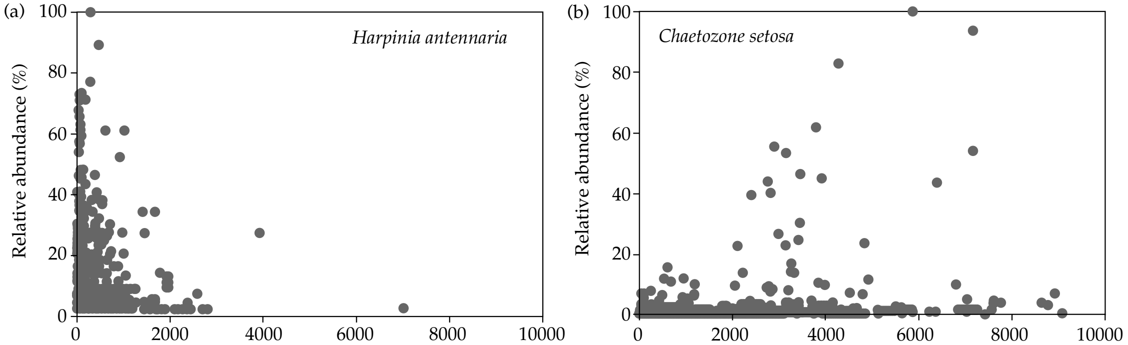


Figure 9.14 Changes in abundance of (a) a sensitive species *(Harpinia antennaria)* and (b) an opportunist species *(Chaetozone setosa)* to increased concentrations of barium.

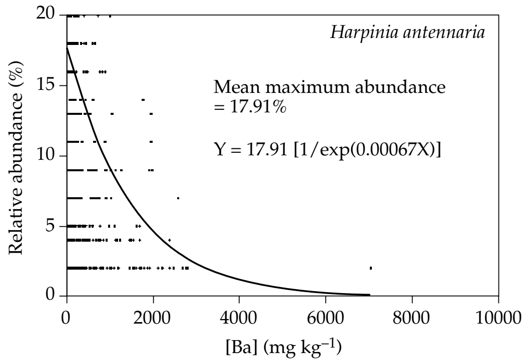


Figure 9.15 Change in abundance *of Harpinia* with increased concentrations of barium on the Norwegian continental shelf.

from low to high numbers at background levels, but for example the high abundances do not occur at increased concentrations of barium for *Harpinia*.

Barium sulfate is used to hold the pressure when boring after oil and gas and is not considered toxic. The effects shown may rather indicate a physical smothering effect at increased concentrations. In the analysis, an effect was defined as a 50% reduction from the abundance at mean background concentrations; this is the effective concentration affecting 50% (EC_{50}). Figure 9.15 shows the data for *Harpinia*. A regression line is fitted and the 50% reduction point calculated. Figure 9.15 shows that the mean relative abundance was 17.91, so a 50% reduction is to 8.95 at 1800 ppm Ba. Such calculations were repeated for all the 191 species defined as sensitive. Then all the data for each species are combined into a *species-sensitivity distribution* (SSD), but since the data used are field data this is called an f-SSD. The surprising fact is that the data show the typical sigmoid log dose–response curve with the sensitive species occurring at low concentrations and tolerant species at high concentrations. Figure 9.16 illustrates such a response for cadmium.

The curves are calculated using bootstrapping methods, a robust statistical technique to generate confidence intervals (see Leung *et al.* 2005 for further details). The plot in Fig. 9.16 is for cadmium, given that there are other metals and oil hydrocarbons present. Curves for different metals differ in shape and so it is clear that the method is capturing effects of different but interacting chemicals. In order to derive a sediment quality standard, the accepted approach attempts to protect 95% of the species in a given assemblage, so we use the 5% value from the SSD curve as the standard. For cadmium this gives a value of 0.46 ppm dry weight of sediment, which is 1/10 of the value used by the US Environmental Protection Agency. We believe that the lower concentration results from the fact that the species we use are highly sensitive; in addition, the criterion used as an effect is reduction in abundance, not mortality as in traditional methods.

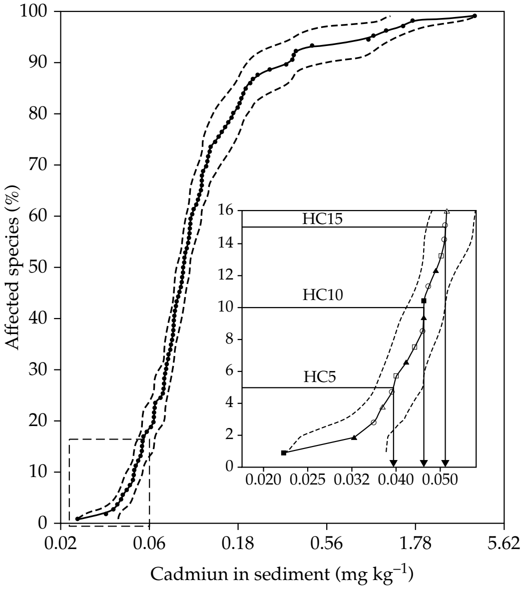


Figure 9.16 Field-based species sensitivity distribution (f-SSD) for cadmium for fauna along the Norwegian continental shelf. HC5 is the concentration where 5% of the species are affected, HC10 10%, and HC50 50%.

The above method for defining sediment quality standards has now been taken further to produce sediment quality guidelines as explained in detail by Bjørgesæter and Gray (2008). This shows that many more tests are needed using a variety of data from different regions before the method can be accepted for general application. Data from Hong Kong also gives preliminary results which show similar SQS values (Leung *et al.* 2005). Approaches such as this, which combine routine monitoring data with new insights, can lead to new and better knowledge of how we can protect the environment.

9.7 Integrative benthic assessments

As shown above, we have long realized that no single aspect of benthic assessments provides a complete view of the status of an area, nor does any single aspect allow us to explain the changes observed. However, we have also long realized that we have many tools at our disposal in order to detect change. These tools range from the genetic and molecular, through behavioural assays, assessments of pathology and health of organisms, to physiology, and population and community ecology. The effects of pollution can therefore be observed at all levels of biological organization from the cell and individual organisms, through populations and communities up to the whole ecosystem (see Lawrence and Hemingway 2003 and McLusky and Elliott 2004 for further discussion and examples). Of greatest relevance here, readers are directed to the results of international workshops integrating these aspects given by Bayne *et al.* (1988a, 1988b) and Stebbing *et al.* (1992). As a starting point, readers are strongly recommended to consult the initial excellent volume edited by McIntyre and Pearce (1980). These volumes reinforce our contention that for a long time we have had the tools at our disposal to understand the effects of marine pollution. We aim here to show how the benthic and sedimentary system fits in with this framework.

As shown throughout this book, we now have conceptual models and data for the benthos which describe assemblage changes in areas subject to natural and anthropogenic factors. At the same time, we have data for levels of contaminants which may or may not cause the changes in the benthos, and we have laboratory and field approaches indicating toxic responses, whether at the lethal or sublethal level. In many cases, we have this information for large geographic areas as part of regional, national, or international monitoring programmes. Since the 1980s these aspects have been combined in integrative studies, giving the idea of a *sediment quality triad*, and there are now many papers on this topic; see Chapman *et al.* (1997), Long *et al.* (2001), and Silva *et al.* (2004) for the rationale and examples.

The sediment quality triad links (1) sediment contamination analysis, as the potential cause of any observed change; (2) sediment toxicity as shown by bioassay, as an example of the effects at the individual level of biological organization; and (3) macrobenthic community analysis, the effect at the community level of biological organization which is likely to integrate effects throughout the system and which has a major influence on the higher predators. Thus the triad aims to give both cause and effect but the effect is both at an early warning stage (the individual bioassay) and at the final community stage. If the individual bioassay relates to a sublethal effect, such as a behavioural change, rather than a lethal effect then it acts even more as an early warning signal.

One of the most comprehensive integrative studies was carried out by Long *et al.* (2001) who took data from acute sediment toxicity tests and examined these with benthic community structure data from almost 1500 marine samples. The data, taken from the coasts of the USA, were used to relate changes in acute toxicity to those in benthic infaunal abundance and diversity of infauna resources. Although, as expected, the data showed a large degree of variability in relating the laboratory toxicity and benthic measures, in 92% of the samples classified as toxic at least one measure of benthic diversity or abundance was less than 50% of the average reference value. Furthermore, in two-thirds of the samples, at least one benthic metric was less than 10% of the average reference conditions. In common with other studies which have shown benthic amphipods to be more sensitive than polychaetes or bivalves (e.g. Mclusky *et al.* 1986), Long *et al.* (2001) failed to find amphipods in 39% of samples that were classified as toxic, whereas they were absent from only 28% of the non-toxic samples. This conclusion was reinforced in many areas where the abundance of infaunal crustaceans, especially the amphipods, decreased in tandem with the laboratory toxicity, as shown by amphipod survival. This extensive analysis has thus produced empirical data linking ecological and toxicological patterns and in particular explaining a reduced benthic community, as abundance and diversity, through laboratory tests.

As a further good example of the use of the sediment quality triad, Silva *et al.* (2004) used the approach to study sediment disturbance patterns in the coastal area off the Tagus estuary, Portugal.

The study showed the utility of the method in cases of complex stressors, as in this study the potential sources of disturbance included residual, chronic contamination of the fine sediments originating from the estuary, a local point-source input from a long-sea sewage outfall, and occasional high run-off episodes following torrential rain, i.e. diffuse pollution. The study combined environmental chemistry (organic contaminants), macrofaunal benthic community, and laboratory sediment toxicity assays on sediment samples from 20 sites. The samples were collected before the outfall commenced operation and 4 years after commissioning, in order to investigate the relative importance and influence of these different sources of environmental damage. Interestingly, the point-source pollution, from the sewage discharge was shown to have a lesser effect on overall sediment and biological health. The residual sediment contamination created by the estuary appeared to be the main cause of reduced sediment quality, as disturbance in all three components of the sediment quality triad was found only in a site located near the estuary.

More recently, the degree of contamination and uptake of pollutants in marine organisms has been linked to indications of biochemical and physiological health in benthic organisms, albeit sessile epifaunal species. Throughout a large regional area, the Irish Sea, Widdows *et al.* (2002) used the *scope for growth* (SFG) technique in mussels, which aims to summarize the instantaneous energy budget of the organisms exposed to different levels of environmental stress. They linked this bioassay to the quantitative structural–activity relationships (QSAR) approach (see p. 143), to indicate the ease with which pollutants are accumulated. These measures of the ability of a chemical to be absorbed by tissues were then combined to give a *quantitative toxicological interpretation* (QTI) of contaminant concentrations in the tissues. Widdows *et al.* found that ambient contaminant levels, especially of toxic metals such as arsenic, were sufficient to reduce the SFG especially in combination with phosphate levels resulting from sewage discharges. While SFG thus gives a screening bioassay tool, there is still the need to show how such changes eventually feed through to affect and influence population and community functioning.

The molecular and biochemical responses by marine organisms to stress and pollution have increasingly attracted attention; for example, see PRIMO (2006). In order to illustrate this field, however, it is of value to look at the integration of these techniques with community studies. For example, Blackstock *et al.* (1986) used coordinated environmental, ecological, and biochemical studies to assess the impact of sewage disposal along a spatial gradient in a fjordic system near Bergen, Norway. In certain areas the benthic community, as shown by the species richness and distribution of individuals among species, was considerably affected by the sewage. Consequently, and by building on previous similar work and on the basis of its distribution along spatial gradients of organic enrichment, its role as a pollution-sensitive species, and its suitability for biochemical analysis, the authors used the polychaete *Glycera alba* as the test species. They found that maximal activities of phosphofructokinase, a regulatory glycolytic enzyme, and alanopine dehydrogenase, a pyruvate oxidoreductase, were very low in polluted areas. Activities of several other enzymes associated with carbohydrate catabolism were also lower at the test site compared to the reference group and they concluded that the ecological and biochemical measures both correlated with the changes in environmental conditions along the gradient of sewage effects. By linking the studies with other work, including experimental studies on the effects of pollutants and hypoxia on the energy-yielding metabolism of polychaetes, they were able to suggest why certain benthic organisms can tolerate, or otherwise, organically polluted conditions. For example, they suggested that the enzyme changes in *G. alba* may be a sensitive component of an integrated metabolic response, which may involve a decrease in glycolytic energy production for the fuelling of muscular activity. This type of study attempts to link a benthic community change, including the presence or absence of certain taxa, with a biochemical and physiological cause which in turn was mediated by environmental conditions. This study is already two decades old and yet we still need more studies of this type if we are to link cause and effect in benthic change.

As we showed earlier, benthic science has advanced through new techniques in surveying and sampling. However, we can also benefit from new laboratory analytical approaches and techniques. As a new development, and one which has the potential to link population and community with molecular approaches, the field of *metabolomics* has now entered the marine field (Viant 2007). Metabolomics comprises all analytical approaches aiming to study the complete set of low-molecular-weight molecules in biofluids, cells, or tissue samples associated with its metabolism. This set of metabolites is known as the *metabolome* and represents the end-point of biological processes and genetic expression. It characterizes the metabolic phenotype of the organism and its metabolic status or response to a stimulus. In recent years, as we have indicated above, the science has been moving towards research with an emphasis on the whole organism and thence to the population and community response by looking at more specific effects. These global studies involve mainly genomics, proteomics, transcriptomics, and metabolomics. In many instances, a systems biology approach is used where several of these fields are measured in parallel creating large data sets that can be analysed using bioinformatics (Dr M Alvarez, IECS, University of Hull, personal communication).

In the present benthic context, there are some current uses of metabolomics such as:

- *biomarker development:* metabolite levels that change as a result of disease, environmental changes, etc.
- *assessment of physiological changes* due to stress: biological stress, oxidative stress, heat stress, environmental stress
- *study of pathways:* metabolic, regulatory, toxicological
- *organism status:* embryogenesis, energetic, reproductive status.

Applications of metabolomics have therefore expanded from being a complementary technique to genomics, proteomics, and transcriptomics to describe gene function and expression under different conditions. A variety of analytical techniques have been applied to metabolomic analyses, such as high-performance liquid chromatography (HPLC), Fourier transformed infrared (FTIR) spectroscopy, mass spectrometry (MS) including liquid or gas chromatography combined MS (LC-MS, GC-MS), direct injection MS (DIMS), and nuclear magnetic resonance (NMR). However, MS and NMR are the analytical techniques used in the majority of metabolomics studies. These, coupled with the increasing computing ability and availability of multivariate packages, mean that we can now further use molecular techniques to understand the causes and consequences of pollutant responses in the marine benthos (Viant 2007).

This section has indicated the value of integrative techniques, and it is valuable to show how these are being combined in international coordinated monitoring to give an holistic view of the health of the regional seas. For example, the signatories of the OSPAR Convention have agreed a monitoring and assessment programme for the north-west European seas (e.g. Stagg 1998). Previously, their assessment relied heavily on measures of contamination by chemicals in water, sediments, and key organisms (flatfish, mussels, etc.) but in the past decade they have adopted a programme aimed at linking these to biological effects. Those effects cover such diverse aspects as fish pathology, macrobenthic community analysis, a sediment-based toxicity bioassay using oyster embryos, and the EROD (ethoxyresorufin-O-deethylase) technique which assesses the ability of organisms to detoxify persistent organic compounds via the cytochrome *P450* biochemical pathways. Hence, again this framework links cause to effects at various levels of biological organization from the cellular to the community. Most notably, and of most relevance to our discussion here, is the central position of the benthic community assessment. It is of note that although there continues to be debate regarding the meaning of the biochemical techniques, their practical nature, and their ability to be translated to overall measures of ecosystem health, benthic community analysis remains the cornerstone of quality assessment.

9.8 Recovery of the benthic community after stress

Much of this chapter and the previous one has discussed the impacts on the benthos due to human activities, especially the way in which its structure and functioning have been adversely affected. Current marine environmental management is now encouraging us to create or even recreate marine habitats to compensate for this (e.g. Elliott and Cutts 2004, Livingston 2006). In doing this, our main aim is to either increase or reinstate the *carrying capacity* of the marine areas. That carrying capacity may be for the benthos itself (e.g. the amount of benthic organisms), the predators on the benthos (e.g. the amount of food provided), or the goods and services provided by the sedimentary system (e.g. the ability of the sediment to sequester pollutants or carry out denitrification) (Macleod and Cooper 2005, Elliott *et al.* 2007). We can assess these changes by determining what degree of stressor is required to change a community but then what the path of recovery is following the removal of the stressor; see for example Costanza and Mageau (1999), who consider the change in organization, vigour, and ascendency in these systems. In some cases, after an area has been degraded but the activity has stopped, for example after an oil spill, there are few possible actions to increase recovery other than to do nothing and let the area recover naturally (Hawkins *et al.* 2002). For example, Schratzberger *et al.* (2003) showed the speed and sequence of benthic recovery by both the macrofauna and the meiofauna following oil-spill remediation. In other cases, active management of the habitat may be used to increase recovery, for example by manipulating sediment types and quality (Elliott *et al.* 2007).

An example of benthic recovery once an activity has ceased is given by Boyd *et al.* (2003) following recovery after extraction of aggregate (sand and gravel) for construction. The recovery at an extraction site used for 25 years was studied after 4 years since cessation. The aggregate extraction reduced the abundance and species richness of the site compared to a reference, and also produced a statistically significantly different community structure. In addition, there were substratum changes in that the sediment in the area subjected to the highest dredging intensity contained more sand than other sampled sediments. Univariate and multivariate analyses indicated a strong relationship between macrofaunal community structure and dredging intensity, and also that the last year of dredging was the main influence on the benthos. However, the fauna remained degraded some 4 years after the dredging stopped. Boyd *et al.* (2003) concluded that their results show that despite it being widely believed that the benthos has relatively rapid recovery rates, such as 2–3 years for European coastal gravelly areas, this may not be true and needs to be further tested. The same group (Cooper *et al.* 2007), at a different site, studied an aggregate extraction site for 8 years following cessation of dredging and concluded that the benthos took up to 7 years to recover from low-level dredging and more than this for high-level dredging.

In cases where the habitat that is recovering and the stressor which caused the benthic effect may both be at a small scale, the benthos can recolonize fairly quickly by migration from adjacent areas. This was shown by McLusky *et al.* (1983) with the intertidal benthos recovering from bait-digging (essentially the smothering of the fauna). On a larger scale, we now have recent research results to show the patterns and processes of recovery, for example where the benthic fauna and sediments are modified, such as by re-nourishment of the sediment. Sediment nourishment may be used in certain areas in order to compensate intertidal areas for erosion or sea-level rise; new sediment is added and so the fauna have to re-establish. Mitchell (2008) has shown experimentally that the benthic fauna will recover from such sediment input by several processes—migration from underneath the new sediment, migration from adjacent areas, and through larger-scale dispersal processes. The speed and sequence of recovery depended partly on the time of the sediment input in relation to the periods of recruitment; for example, nourishment just before the main recruitment period led to a more rapid re-establishment of the community than that done once settlement has occurred. However, it also depended on the amount of sediment being added over the bed—some mudflat invertebrates such as the bivalve *Macoma balthica* were able to withstand a 25 cm loading of sediment height as long as the material was added slowly, whereas a rapid input of material killed the fauna.

We are now obtaining sufficient evidence for the recovery of benthic areas following stress, for the resistance to change and the resilience to stressors (e.g. Elliott *et al.* 2007 and references therein). Tett *et al.* (2007) produced an earlier conceptual model regarding the nature of and recovery from 'undesirable disturbance' to marine ecosystems

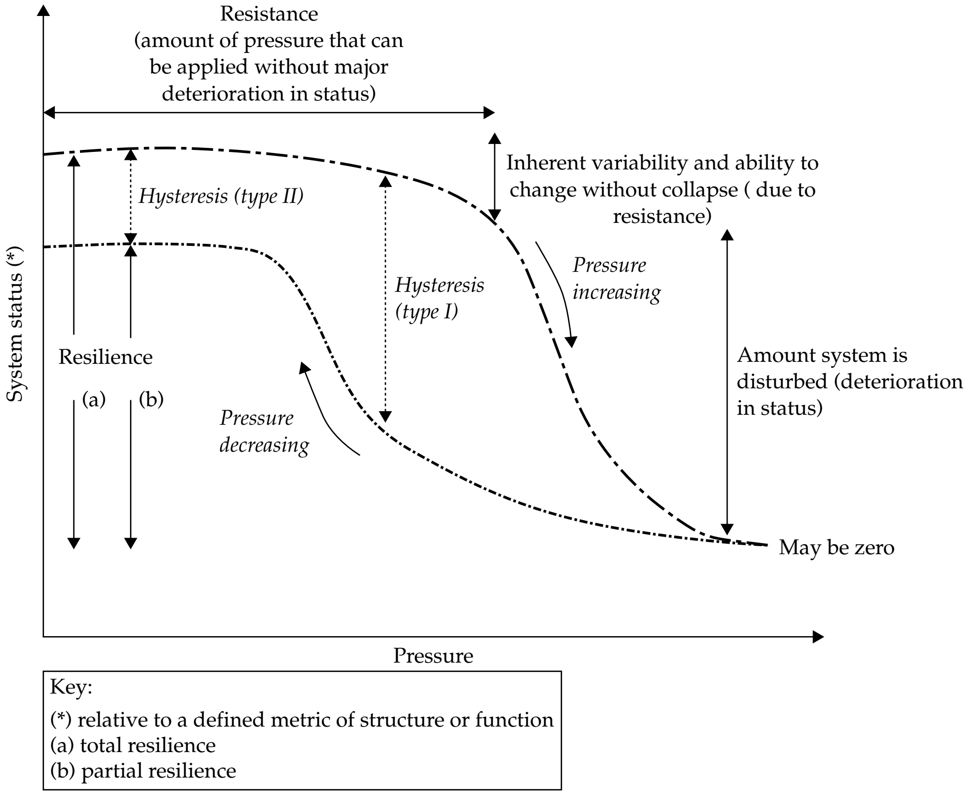


Figure 9.17 A conceptual model of changes to the state of a system with increasing pressure showing resistance and resilience (from Elliott *et al.* 2007, modified from Tett *et al.* 2007).

as the result of eutrophication. By revising this model, together with information from the models of benthic change described earlier (e.g. McManus and Pauly 1990, see Table 9.2), Elliott *et al.* (2007) have produced a model which indicates the possible way benthic communities will be degraded by a human disturbance and then recover (Fig. 9.17). The ability of a benthic community to withstand or absorb the effect of a stressor before it changes can be termed *resistance* whereas its ability to return to a previous state after the stressor has been removed can be regarded as *resilience.* The difference in the sequence of community recovery from the sequence shown during degradation can be termed *hysteresis* although, as shown by the two types of hysteresis in the model, we are now getting evidence that the community may or may not return to an original state.

This chapter has shown that we already have a good knowledge of the way in which benthic communities degrade with stress, but we need better information to test and modify our models of recovery, especially following human activities. These ideas and models now need testing for open marine areas as well as coastal areas, and in particular we emphasize that in order to take this research further we will need a combination of field survey and experimental approaches.

CHAPTER 10

The soft-sediment benthos in the ecosystem

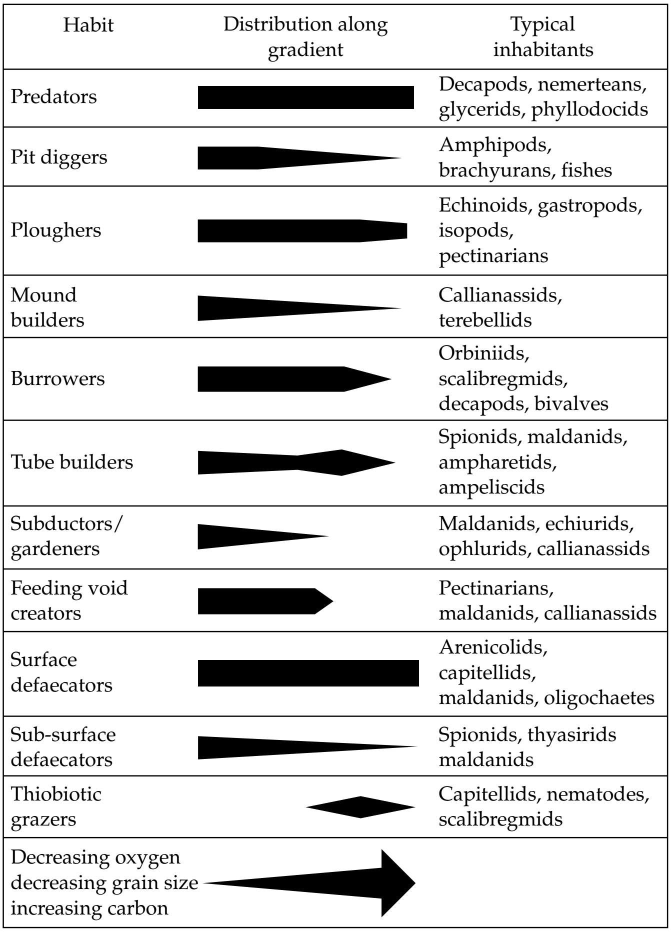
The benthos does not, of course, live in isolation from other parts of the ecosystem. Here we consider the roles that the benthos plays in the system and how the complex interactions that are found can be modelled using ecosystem models. First, we examine methods that allow us to establish food webs based not only on examining each species in the field and in laboratory feeding studies, but also using stable isotopes of carbon and nitrogen to ascertain the likely feeding mode of a species.

10.1 Food webs, and feeding and functional groups

It is relatively easy to determine the mode of feeding of some benthic organisms (see for example the excellent review of Fauchald and Jumars 1979, although this is now slightly dated and requires revision). Polychaetes have characteristic feeding structures, so one can determine from their morphology whether they are filter feeders, deposit feeders, or predators. Bivalves show similar morphological characteristics and it is easy to determine whether they are deposit or filter feeders. Some polychaetes have large jaws, e.g. the nereids, and one might assume that they are predators. Yet when *Nereis vexillosa* was studied in detail (Woodin 1977), it was found that it attached pieces of algae to its tube, which grew and were used for food, so-called 'gardening'. Nereids also are able to filter feed by creating a mucous bag and pumping water through their burrows, which filters the water; the mucous bag is then consumed. More recently, studies have shown varied and possibly opportunistic feeding by different benthic species; for example Christensen *et al.* (2000) showed how the suspension- and deposit-feeding abilities of nereids influenced sediment nutrient fluxes. These studies show that it is perhaps not so straightforward as once thought to interpret feeding mode simply from morphological features.

The definition of functional groups and feeding guilds is increasingly used to help explain and interpret ecological functioning (e.g. Elliott *et al.* 2007 discuss the rationale behind functional groups). The eminent and immensely experienced benthic biologist Tom Pearson (2001) shows in detail that while the concept of functional groups gives us a greater understanding of the benthos, the idea is criticized by some as we do not have sufficient information about feeding types and modes of life of many benthic species. Perhaps this is because this type of science, including morphology and feeding analyses, is looked down upon as 'natural history' and unfortunately is no longer fashionable (or publishable)! However, the information is needed if we are to further our understanding of benthic processes. Pearson (2001) shows that our knowledge is good enough to partition the benthic infauna into functional groups which in turn are then used to explain changes, for example along gradients of organic enrichment (Fig. 10.1).

Increasingly, studies are listing the problems or inadequacies of relying only on taxonomic information (species identities) when comparing areas and so are looking at other, more functional attributes. For example, Mouillot *et al.* (2006) advocate the use of body size, abundance amongst functional groups, functional diversity, and productivity descriptors in order to describe the community. The concept of feeding guilds in the benthos has been taken further to be included in measures and indices



Habit	Distribution along gradient	Typical inhabitants
Predators		Decapods, nemerteans, glycerids, phyllodocids
Pit diggers		Amphipods, brachyurans, fishes
Ploughers		Echinoids, gastropods, isopods, pectinarians
Mound builders		Callianassids, terebellids
Burrowers		Orbiniids, scalibregmids, decapods, bivalves
Tube builders		Spionids, maldanids, ampharetids, ampeliscids
Subductors/ gardeners		Maldanids, echiurids, ophlurids, callianassids
Feeding void creators		Pectinarians, maldanids, callianassids
Surface defaecators		Arenicolids, capitellids, maldanids, oligochaetes
Sub-surface defaecators		Spionids, thyasirids maldanids
Thiobiotic grazers		Capitellids, nematodes, scalibregmids
Decreasing oxygen decreasing grain size increasing carbon		

Figure 10.1 The distribution of functional groups along an organic enrichment gradient based on bioturbatory activity; the width of the bars denotes relative abundance (from Pearson 2001).

of environmental quality. For example, using an extensive benthic time series from Chesapeake Bay, Weisberg *et al.* (1997) developed a multimetric *benthic index of biotic integrity* (B-IBI) which was based on 17 candidate measures. These included primary and derived community indices (species richness, abundance, diversity, etc.) as well as percentage abundance of different functional groups. By accommodating differences in salinity and substratum, comparing test and reference areas, and using a rank-scoring system for the deviation by different metrics to reference conditions, Weisberg *et al.* (1997) were able accurately to separate stressed benthic areas from reference conditions. This type of study again shows the value of an understanding of the functioning of the benthic system as well as the structure—we return to discussing the use of these multimetrics and other indices in Chapter 11.

In order to determine intake pathways and preferred modes of feeding, stable isotope analysis is increasingly used and in particular the stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) have been used to infer the position of species in food webs. The distribution of the isotopes is closely related to dietary compositions and enrichment occurs in animals compared with their food. The enrichment is estimated to be *c.*1‰ per trophic level for carbon and 3–4‰ for nitrogen, and a good example is Fry's study of the food web structure of George's Bank (Fry 1988). Figure 10.2 shows the results of the $\delta^{15}N$ analyses. The results show clearly that bivalves and brittle stars and some amphipods are filter feeders whereas polychaetes range from filter feeders to predators. Most fish were omnivores, but some were clearly predators. A recent study has applied similar techniques to analysing the benthos of an

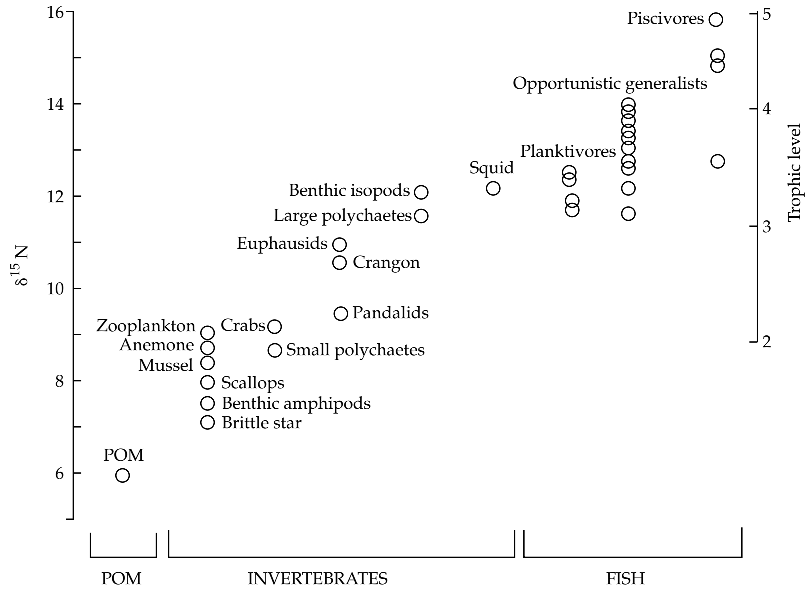


Figure 10.2 Trophic level estimation for George's Bank, USA using $\delta^{15}N$. The lowest trophic level is that of herbivores (from Fry 1988). (ZPL - zooplankton)

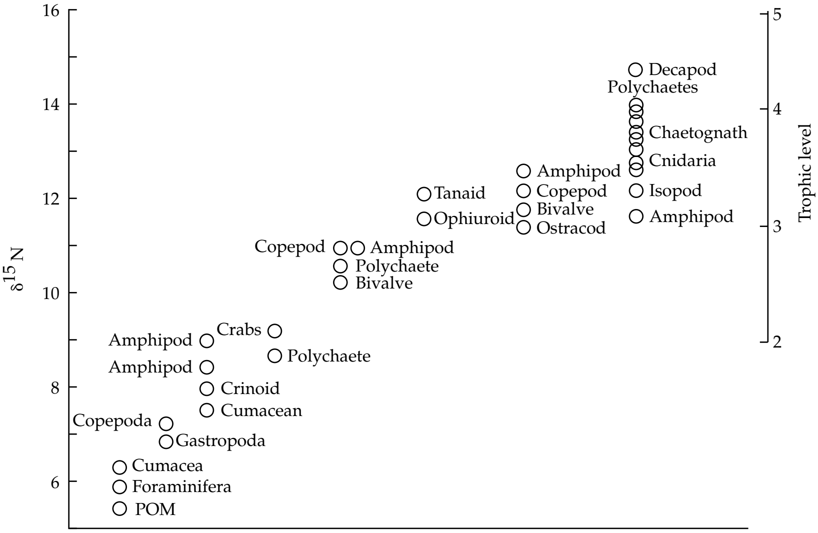


Figure 10.3 Trophic level estimation for Georges Bank biota using $\delta^{15}N$. Points are mean $\delta^{15}N$ values of groups or species (Table 1). Trophic level 1 represented by phytoplankton was not extensively sampled, and so trophic level estimations begin with well-sampled herbivores and detritivores (TL 2). A 3.6% increase in ^{15}N equals an increase of one trophic level (Table 2). (ZPL–zooplankton).

area between 800 m and 2000 m in the Arctic basin off northern Canada (Iken *et al.* 2005). Figure 10.3 shows the results of this analysis.

The data show similar patterns to the George's Bank results, although one curious aspect was that cumaceans fed at the lowest trophic level on phytoplankton-derived material. At such depths it was not thought likely that there would be organisms that relied on sedimenting phytoplankton, but the data clearly indicate that this is indeed a key resource for benthic species at these depths. Similar results have been reported for the many areas of the deep sea and in fact a number of species rely directly on sedimented phytoplankton even at depths down to 2000–3000 m. Figures 10.2 and 10.3 show that for the benthos there are few filter feeders, many are omnivores, and some are predators.

Once this knowledge is available then food webs can be constructed; for example Grebmeier and Dunton (2000) have constructed such a web for the Chukchi Sea off Alaska (Fig. 10.4). The benthos is particularly well developed as it utilizes the large primary production (300 g C m^{-2} y^{-1}) in the area, and as in all polar regions most of this sediments directly to the seabed fuelling the benthic system. It is also of note here that bivalve molluscs are the staple diet of the walrus, indicating that in such systems not only fish but also a marine mammal is sustained by benthic productivity.

The structure of a food web is rarely used to make a model of an ecosystem. One can, of course, model predator–prey relationships or population dynamics of a few species, but modelling all the interactions shown in Fig. 10.4 is not possible. In addition, Fig. 10.4 is a very simplified model and does not include, for example meiofaunal species living in the sediment. The solution is to try to encompass the functioning of the system, i.e. what the species together do.

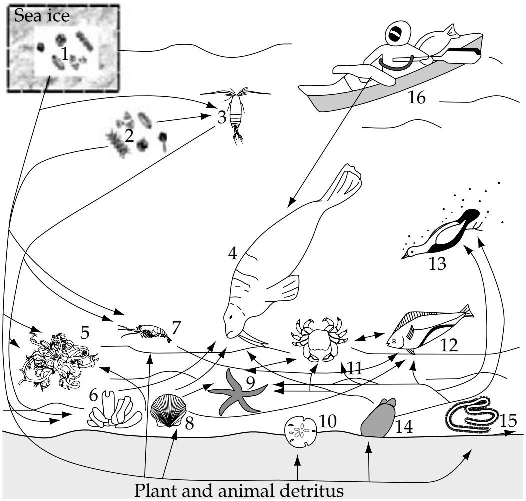


Figure 10.4 Reconstruction of the Chukchi Sea food web (from Grebmeier and Dunton 2000). Organisms are: 1, ice algae; 2, phytoplankton; 3, copepods; 4, walrus; 5, basket stars; 6, ascidians; 7, shrimps; 8, filter-feeding bivalves; 9, sea stars; 10, sand dollars; 11, crabs; 12, bottom-feeding fishes; 13, diving seabirds; 14, deposit feeding bivalves; 15, polychaetes; 16, native subsistence hunters.

10.2 Ecosystem models

When ecosystem models were first developed the common ‘currencies’ used were carbon or energy (calories or joules). Primary production is measured in amounts of carbon produced per square metre of ocean surface per year. (The reason for using an area rather than a volume is that one of the rate-limiting processes is the amount of light available and this is measured per unit area.) Thus it was an obvious step to measure how much carbon was consumed by zooplankton, how much went to the benthos, how much was buried in sediment, and how much was recycled back to the water column. When the amounts had been determined this gave the first ecosystem models. Yet what was needed for an understanding of the ecosystem was the amount of carbon or energy flowing through the system, hence the suggestion that energy would be a better common unit. In the 1970s much work was done on measuring the calorific content of benthic (and other organisms), especially as part of the International Biological Programme. This led to energy budgets, which could integrate the single-species budgets (described in Chapter 5) and transform them into system budgets. Special symbols were developed to describe and distinguish between producers, storage compartments, and sinks which allowed comparison across systems (terrestrial, freshwater, and marine) and across system boundaries. The symbols devised for energy transfers are now used in a class of models called *network analysis*, which is discussed briefly in the following section.

10.3 Network analysis: cycling index and average path length

Network analysis stems from work done on economic systems, where the amounts of raw materials and industrial services required to produce consumer goods were quantified. The result was a diagram showing the flow from raw materials to the consumer goods and back to the raw materials, a so-called *flow diagram* based on an *input–output* *analysis*. In ecology this has led to the term *ecological network analysis* (ENA), where linear functions describe the flow into and out of an ecological compartment, such as the benthos or plankton or subdivisions thereof (e.g. Ulanowicz 2004). It allows links between simulation modelling of ecosystem dynamics by summarizing the connections in trophic (food web) dynamics. It further allows the performance of the whole system to be quantified and investigated and so has the potential for looking at bottlenecks in performance, such as suboptimal functioning as the result of human activities and pollution. Network analysis proper is more than just an input–output analysis but includes analyses of cycles, through-flows, storage, and information (Patten 1985). As with any development of conceptual models and flow diagrams, for our purposes network analysis provides tools to convert the arrows shown between the species in the food web in Fig. 10.4 into flows of energy, materials, or elements. The compartments in network analysis may be species (as in Fig. 10.4) but more usually will be functional groups such as detritivores, carnivores, or even particulate organic matter. The flows are rates per unit of time, which is usually a year, and so the technique has the potential to integrate over time. One of the strengths of network analysis is that it allows comparisons between different systems using a uniform terminology and uniform symbols; for example, see Fig 10.5 for Chesapeake Bay, USA (Baird *et al.* 1991).

Within ecological network analysis, the *cycling index* assesses the proportion of the flow in the system that is recycled compared with the total flow, a very useful component when comparing systems. For example, coral reefs have a high cycling index for phosphorus but a smaller one for nitrogen since there is much nitrogen fixation on reefs (Wulff *et al.* 1989). There is also a large difference in cycling indices between currencies—energy is hardly recycled and its index is small, whereas carbon is exported from the system as carbon dioxide and thus a large cycling index results.

The *average path length* measures the average number of steps a unit of flow (flux) must take from its entry into the system until its exit from the system. For some systems such as upwelling regions, planktonic food webs are short, with primary producers (large diatoms) simply being grazed by large zooplankton and fish. In contrast, in Chesapeake Bay (Fig. 10.5) the food web links are much longer and the average path length is also much longer.

Figures 10.5 and 10.6 show the results of ecological network analyses for Chesapeake Bay and the Baltic Sea respectively. The carbon stocks of biomass (living and non-living components) are shown in the hexagonal boxes. The pools of particulate organic carbon (POC) and dissolved organic carbon (DOC) and the producers (pelagic and benthic) have different symbols. For the benthos there are some flows entering the sediment shown as sinks (symbolized in the diagram by the electrical earth symbol, e.g. 78 for benthic producers and 56 for meiofauna). The flow from fish is, in fisheries terms, the yield, i.e. that which is harvested, and the flow rates are those for respiration, production, and consumption. As with many uses of ENA in the literature, not all aspects can be measured in each area and so many of the data and the transfer coefficients were obtained from the literature. This point has led us to question the value of using ENA for making comparisons between areas when indeed many of the aspects are obtained as literature values from common studies. (Benthic workers may find useful the collation of data by Rumohr *et al.* 1987 giving conversion factors for energetics studies.)

Despite the drawbacks, these two models show us that the *net primary production* (NPP) is 950 mg C m^{-2} d^{-1}in Chesapeake Bay and 452 mg C m^{-2} d^{-1} in the Baltic, although in terms of NPP efficiency the figure for the Baltic is 87% and Chesapeake Bay 42%. Thus there is lower utilization of primary production, but much of the material goes to the detritivores. The average number of path lengths is similar (Baltic 3.27, Chesapeake Bay 3.61), yet the recycling of material occurs over shorter lengths in Chesapeake Bay than in the Baltic. In addition, the Baltic Sea is more efficient in transferring material to higher trophic levels than Chesapeake Bay. It must be remembered that the fundamental difference between the two systems is, however, in the numbers of species. The Baltic is a young sea (7000 years old) and of low salinity,

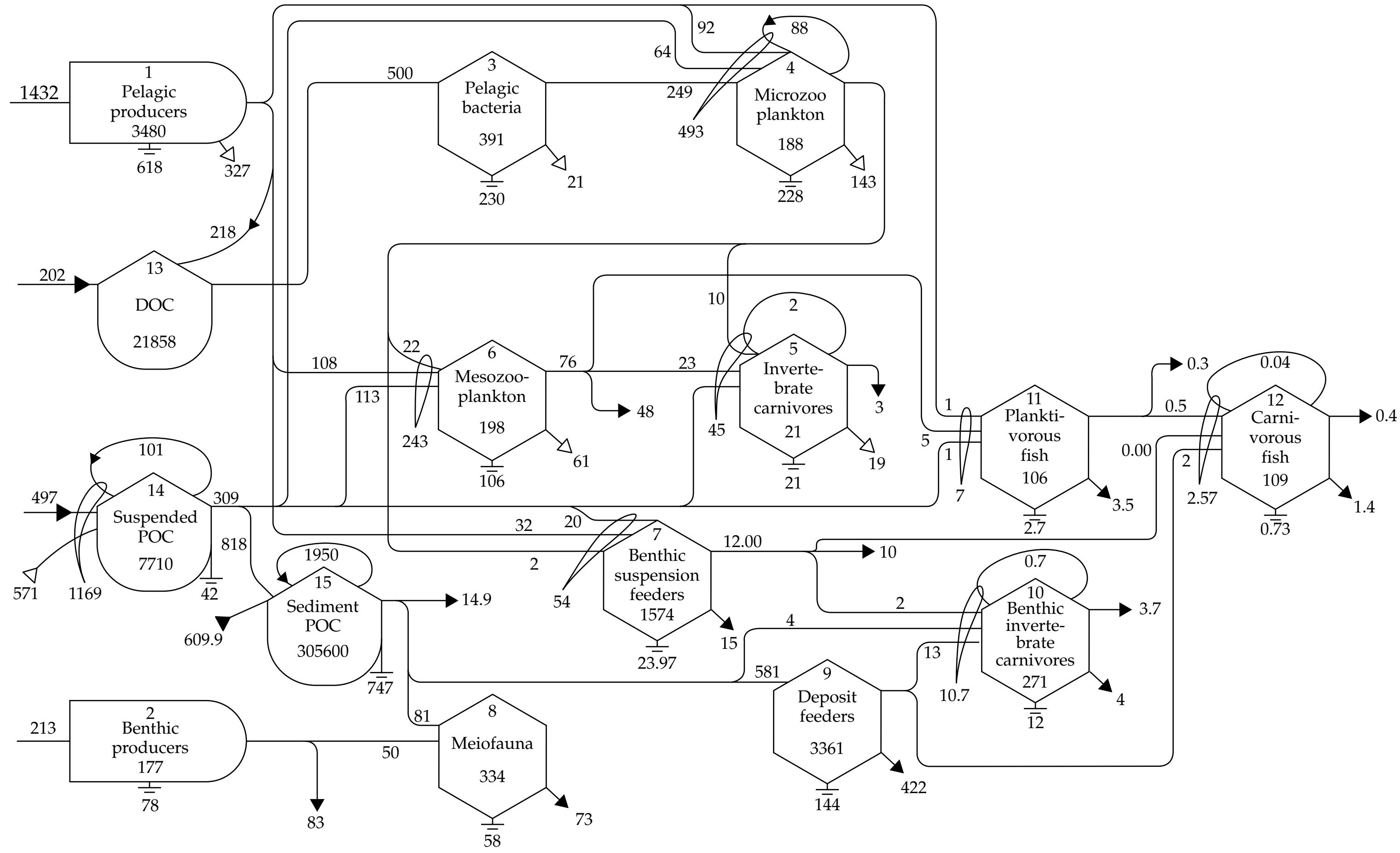


Figure 10.5 Energy flow network of the Chesapeake Bay (mg C m^{-2} for biomass and mg C m^{-2} d^{-1} for flows) (from Baird *et al.* 1991).

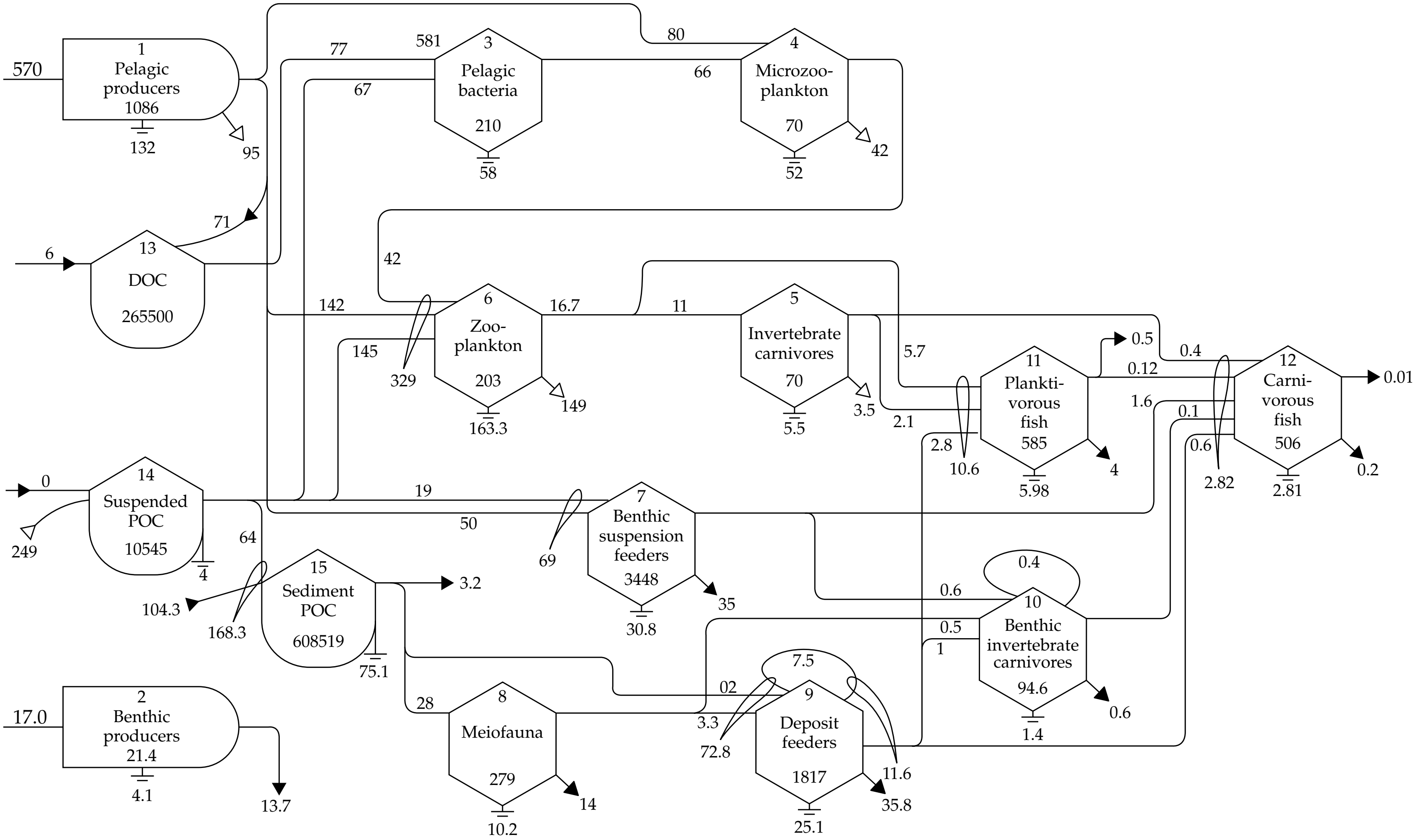


Figure 10.6 Energy flow network of the Baltic Sea (units as in Fig 10.5) (from Baird *et al.* 1991).

and hence species numbers are much lower than in Chesapeake Bay. Despite this, both the primary production and fish production levels are similar: the output of fish from 1 unit of phytoplankton for Chesapeake Bay is 0.35 for pelagic fish and 0.08 for carnivorous fish; for the Baltic it is 1.74 and 0.63 respectively. This raises the question of whether most species are redundant; that is, do we need all the species in the system to maintain system functioning? This issue was discussed in Chapter 5.

Once the basic structure and the flows for the system are known (as in Figs 10.5 and 10.6), equations are formulated to describe the rates linking the compartments. A good, relatively simple example is found in Field *et al.*'s. (1989) network analysis of a simulated upwelling event. For example, production is represented by two functions $\mathrm{d}PC_j/\mathrm{d}t$ and $\mathrm{d}PN_j/\mathrm{d}t$ for carbon and nitrogen respectively. For these terms:

$$\begin{aligned}\frac{\mathrm{d}PC_j}{\mathrm{d}t} = {} & \text{carbon fixation} \\ & -\text{photosynthetically produced dissolved organic carbon} \\ & -\text{respiration} - \text{grazing} - \text{sinking.}\end{aligned}$$

$$\frac{\mathrm{d}PN_j}{\mathrm{d}t} = \text{nitrogen uptake} - \text{grazing} - \text{sinking}$$

With the equations formulated the model can be run to test a variety of hypotheses about how carbon and nitrogen cycle through the system. The results can then be verified against real field data to ensure that the model is giving reliable results. Today, ENA is widely used (e.g. see Baird and Ulanowicz 1993) and has even been suggested as having a role in defining marine monitoring and aiding marine management (de Jonge *et al.* 2006).

10.4 The European Regional Seas Ecosystem Model (ERSEM)

Those taught oceanography in the mid-1960s would have started with physics, then moved to chemistry and finally to biology. There was a clear view that the physics drove the chemistry and the chemistry drove the biology. In the 1970s and 1980s this way of thinking was changed and it was realized that the most significant linkages were direct couplings between physical processes and biology. Large-scale processes such as upwelling were known, but the importance of stratification and mixing in controlling development of primary production was little studied. Benthic studies in the 1970s and 1980s started quantifying the influence of the physical processes on the benthos and then, as discussed earlier, we moved on to quantifying the role of the benthos in modifying the physical state such as sediment structure. For example, see the classical paper by Warwick and Uncles (1980) who studied the importance of shear stress acting on the seabed in controlling sediment structure and thereby the faunal assemblages that occurred in the Bristol Channel, UK. It rapidly became apparent that we cannot hope to understand and then eventually model the benthos unless we have a good knowledge of the importance of physical forcing variables; only then would we be able to include both physical and biological aspects in ecosystem models. A good example of a recent model for ecosystems that includes physical forcing processes is the European Regional Seas Ecosystem Model (ERSEM) (Baretta *et al.* 1995), which was developed during a collaborative project between many institutions and funded by the European Union's Marine Science and Technology (MAST) programme (Fig. 10.7).

This is a generic model and was coupled to a qualitatively correct physical model designed to simulate the spatial pattern of ecological fluxes throughout the seasonal cycle and across eutrophic to oligotrophic gradients. In ERSEM the benthic system was one of the main focuses, hence its usefulness here. The model decouples carbon and nutrient dynamics and this leads to better simulations of how nutrient limitation acts on cells. The model also includes not only 'classical' production and grazing dynamics but also the microbial loop (se p. 110). In the simple classical food web, nutrients and light lead to production of diatoms which are then eaten by large copepods which in turn are eaten by fish. The microbial loop (Azam *et al.* 1983) postulates that in the water column much of the primary production is by small flagellates which are consumed not by copepods, but by heterotrophic flagellates, which in turn are consumed by small copepods.

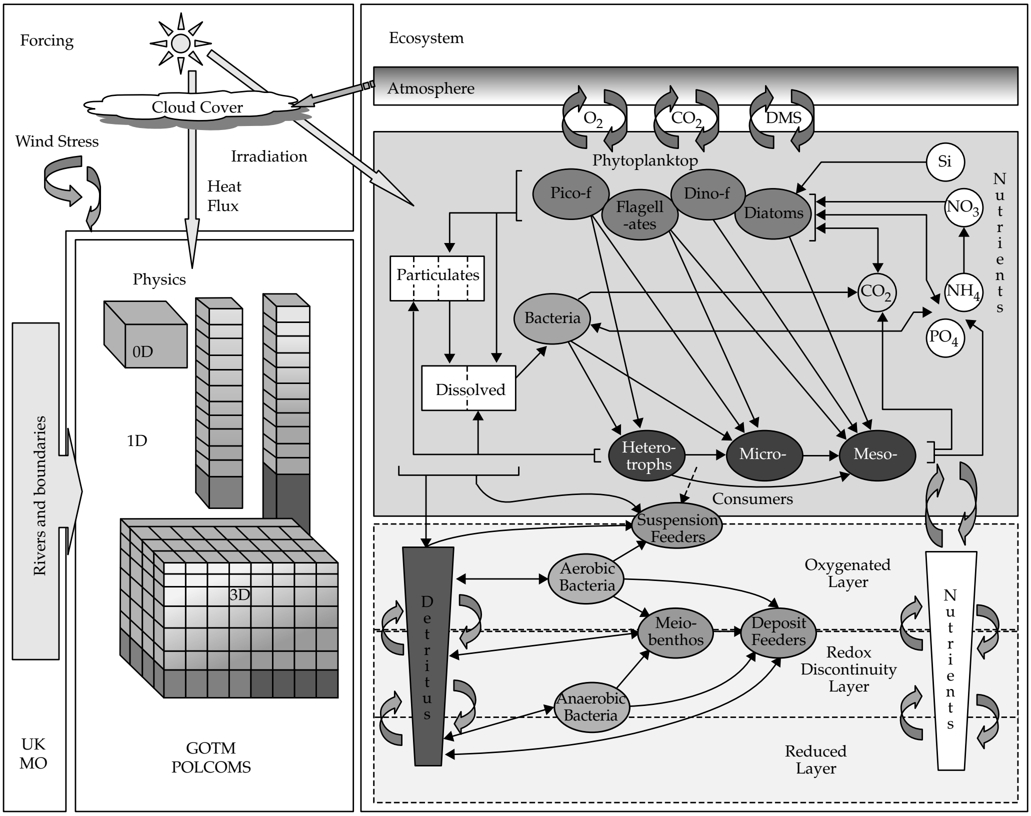


Figure 10.7 The ERSEM model (from http://web.pml.ac.uk/ecomodels/ersem.htm). See text for details. POLCOMS – Proudman Ocenaographic Laboratory Community Model; GOTM – General Ocean Turbulence Model (see http://www.gotm.net/); UK MO – UK Meteorological Office – data sources and component models. See Plate 12.

Much material however, is utilized directly by bacteria and mineralized and cycled back into the system, hence the microbial loop. The loop is dominant under stratified conditions, whereas the classical system occurs under mixed conditions.

The main processes that the benthic model takes into account are:

- deposition of particulate organic matters from the pelagic system
- cycling of carbon and macronutrients through the benthic food web
- aerobic and anaerobic mineralization in the form of dissolved nutrients in the pore-waters and subsequent molecular exchanges with the nutrient pools in the water column.

The benthic component of the ERSEM model (Fig. 10.8) has a physical descriptive part which covers the surface oxygenated layers of sediment, the denitrification layer, and the anoxic layer. In the oxic layer, aerobic mineralization processes occur and the nitrification of ammonium (NH_4^+) is modelled. In the denitrification and anoxic layers, anaerobic mineralization of organic matter is modelled and these are the main process controlling the distribution of dissolved nutrients, oxidized iron and sulfates. The benthic part of the model is not constructed using species, instead there are five different functional groups belonging to the benthos: suspension (filter) feeders, deposit feeders, meiobenthos, infaunal predators, and epibenthic predators (megabenthos) (Fig. 10.9). The suspension feeders feed directly from the pelagic layer, whereas all other groups utilize food that is deposited on sediments. Deposit feeders feed on benthic detritus and benthic organisms, often very

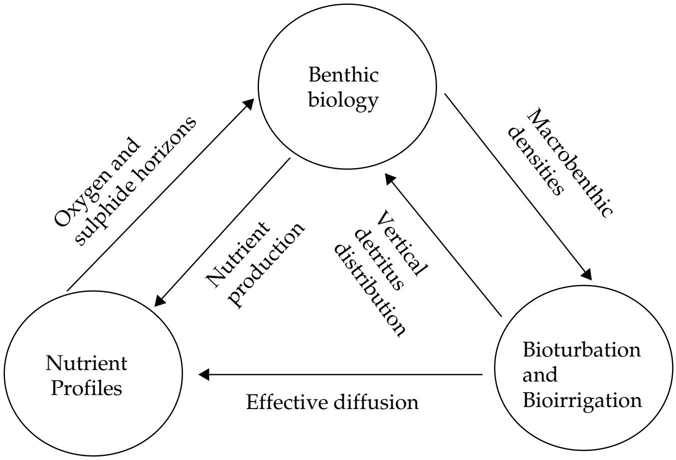


Figure 10.8 Information flow in the benthic compartment of the ERSEM model (from Ebenhöh *et al.* 1995).

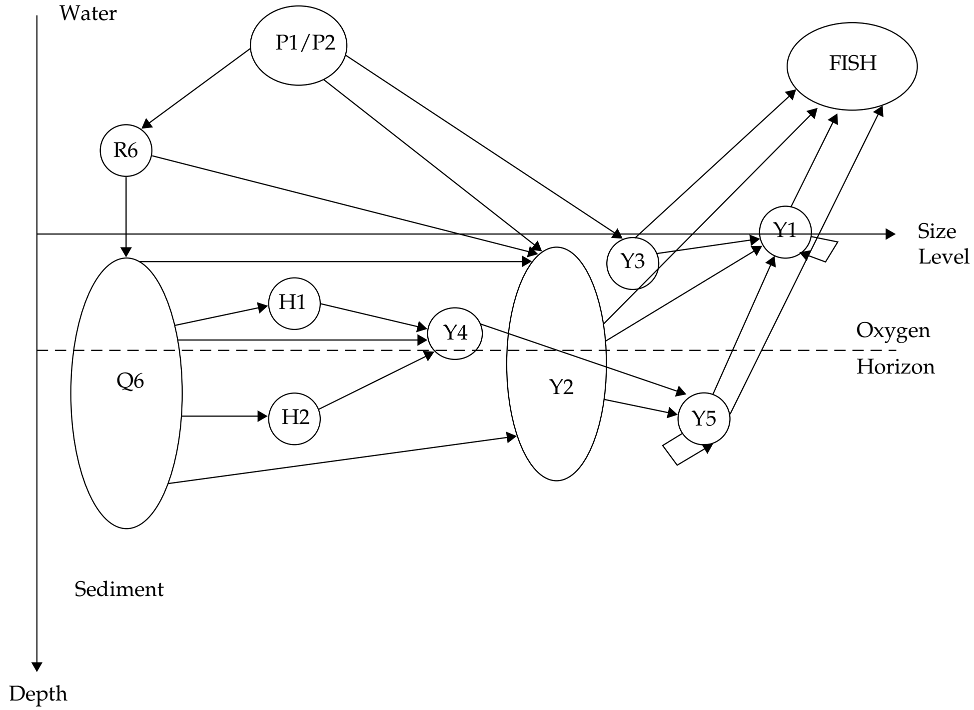


Figure 10.9 Benthic food web in ERSEM (from Ebenhöh *et al.* 1995). The horizontal axis represents a compromise between size and trophic position. H1, aerobic benthic bacteria; H2, anaerobic benthic bacteria; Yl, epibenthic predators; Y2, deposit feeders; Y3, suspension feeders; Y4, meiobenthos; Y5, infaunal predators; R6, Q6, particulate detritus; P1, diatoms; P2, autotrophic flagellates.

much smaller than themselves. Infaunal predators use different measures of prey capture to deposit feeders and often eat prey of a similar size to themselves. Epifaunal predators are often large and mobile, acting on the sediment surface by taking bites out of the sediment or making large feeding-pits as rays do. The feeding behaviour of benthic species includes the bioengineers which have a large impact on bioirrigation and bioturbation processes in the sediment; the infaunal predators move through the sediment in search of prey and thus are often active re-workers of sediment.

Pelagic particulate organic matter (POM) is the key input of biomass to the sediment. POM is characterized by its content of carbon, nitrogen, and phosphorus, but silicate is also important in the benthic nutrient model. In addition to sedimenting POM, diatoms are also important in spring and summer. In ERSEM there are two different groups of microbial decomposers: the aerobic and anaerobic bacteria. The sedimented organic material is decomposed and processed by bacteria, meiobenthos, and deposit feeders. Much material is not easily degradable (i.e. it is refractory) and the degradability in the model is related to the nutrient content so that carbon penetrates deeper than do nitrogen and phosphorus. Secondary producers are modelled using the usual functions performed by the benthic compartments: consumption minus respiration, excretion, growth, production of gametes, mortality rates, and losses to predation.

From this brief coverage, it can be seen that the ERSEM model is very comprehensive and is currently the best available for modelling and testing hypotheses about how the benthos functions in marine systems. As yet resuspension processes are not included, but it is to be hoped that these key aspects will be included in future versions of the model. Baretta *et al.* (1995) and Ebenhöh *et al.* (1995) describe the benthic section of the model in detail and give the equations and parametrization used. The latter was a particularly difficult process and is based on expert opinions. For calibration of the model the only data available were standing stock biomass of the macrofaunal functional groups in each of 10 regions of the North Sea. Figure 10.10 shows an example of a model run with and without fish predation and for suspension and deposit feeders. Here the predation was a simple increase in mortality and the fish did not react dynamically to the available food. Fish predation has little effect on suspension feeders but has more effect on deposit feeders in some areas.

This example shows the utility of such models, especially as a wide variety of scenarios can be simulated to study the behaviour of the benthic system. In particular, important aspects such as nutrient cycling can be simulated (Ruardji and van Raaphorst 1995). Baretta *et al.* (1995) and Ebenhöh *et al.* (1995) give a thorough review of various aspects of the model and should be consulted for details. Although this is one of the most sophisticated available models for the benthic system, it has not yet been adequately validated against real data. This is partly because there are often simply no data available that cover all the aspects included in the model. The strength of the modelling approach is that it forces one to consider what are the main processes that need to be quantified and especially the processes that need to be measured. It also allows the main questions 'so what?' and 'what if?' to be addressed. We regard scenario testing using this

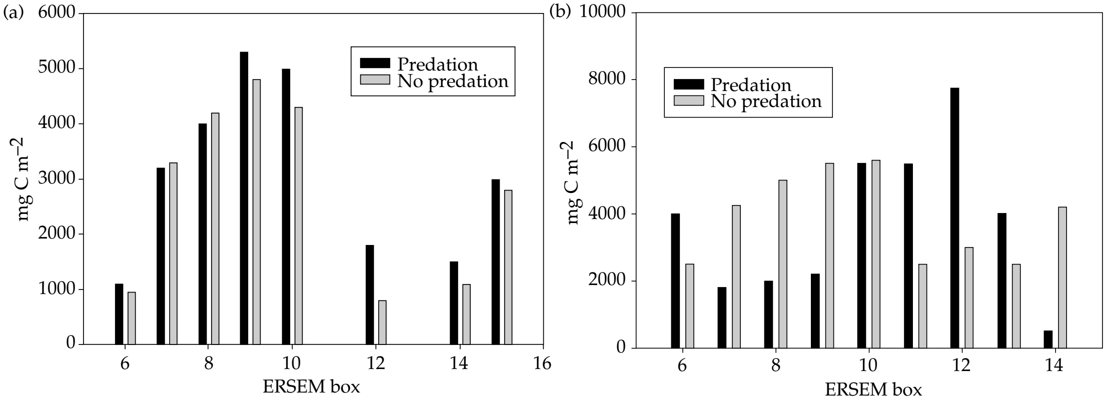


Figure 10.10 Effects of epibenthic fish predation on deposit and suspension feeders in different areas (boxes) of the North Sea simulated by the ERSEM benthic compartment model: (a) suspension feeders, (b) deposit feeders (from Ebenhöh *et al.* 1995).

model as much-needed research, especially where the model can be used as the basis for deciding what data to collect and where. Once such data are available then we will be able to make simulations and test hypotheses of important events such as effects of nutrient enrichment and eutrophication, effects of habitat homogenization on nutrient processing, and—last but not least—the effects of climate change on benthic processes.

As a second approach, there has long been the need for a different model that deals with bioturbation and the extinction of marine species, areas where we have surprisingly few data. The reason for this, as discussed in earlier chapters, is that we simply do not know how many species occur in the oceans, even in well-studied areas such as coastal areas of the North Atlantic. Thus, it is difficult to know what we might be losing by our human-induced disturbance and pollution of coastal and deep-sea areas. As an example of this, Mazik and Elliott (2000) used field surveys and experiments to determine the effects of pollution from a petrochemical plant on removing species and thus changing the amount of bioturbation present in an adjacent mudflat. In particular, they wanted to know about the changes to the amount of energy which could be absorbed by intertidal sediments with and without a surface roughened by bioturbation. The study indicated an increase in bioturbation with increasing distance from the source of pollution, not only because of differences in abundance, animal size, and depth of activity but also because of the difference in species composition between the communities. As a means of interpreting the responses, the species present were broadly classified in terms of their feeding strategy and sediment modification potential. The authors were then able to quantify the potential impact, in terms of effect on sediment transport, of selectively removing the different guilds (by pollution).

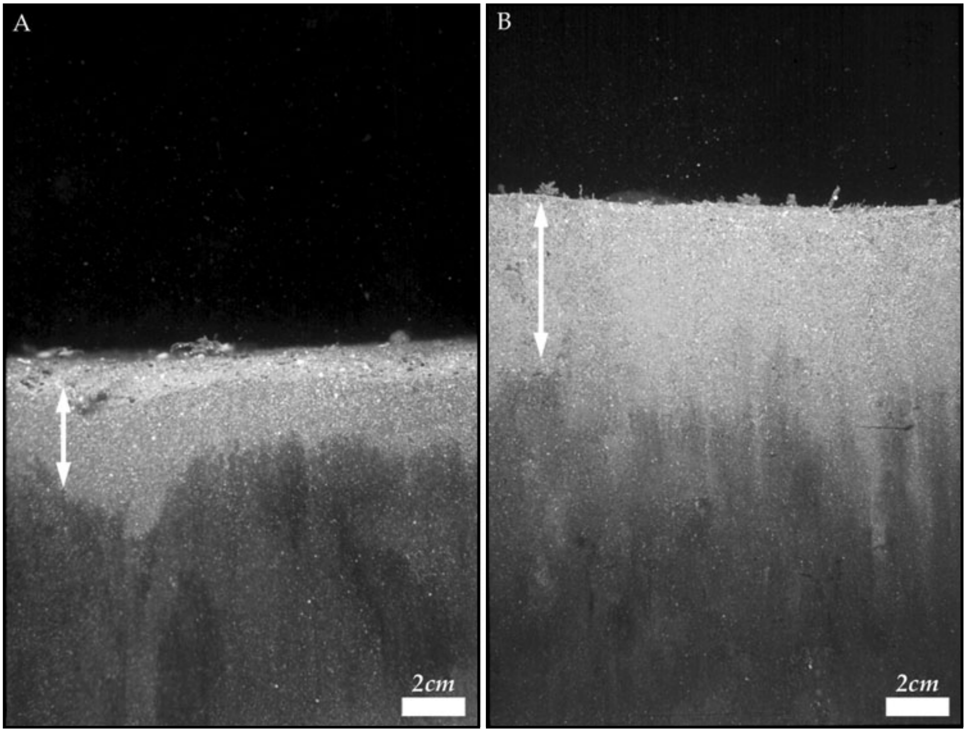


Figure 10.11 The biogenic mixing depth (BMD, white arrows) of sediments (A, site 1; B, site 2) in Inner Galway Bay, Ireland. BMD was related to the bioturbation potential of a community (BPc), an index that accounts for each species' population size and life-history traits (body size, mobility, mode of bioturbation) to estimate the capacity of a community to mix sediments (from Solan *et al.* 2004). See Plate 13.

Solan *et al.* (2004), in a pioneering paper, also examined the possible effects of losing species that played key roles in sediment systems. The roles were assessed by the impact of bioturbation performed by individual species. From a long-term study of the benthos of Galway Bay, Ireland, data were available on 139 benthic invertebrates. The authors then calculated an *index of bioturbation potential* (Fig. 10.11) that took account of each species' body size, abundance, mobility, and mode of sediment mixing. They had data from monthly samples over 1 year of the benthic community and derived the bioturbation potential of the community. They then simulated how the bioturbation potential would change as species became extinct either randomly or ordered by the sensitivity of species to environmental stress, body size, or population size. (It is important to note that this is really extirpation rather than extinction since the simulation is only of disappearance from a local community.)

Two types of simulation were made: the first was with no interaction between species so that surviving species did not change in population size. The results (Fig 10.12) show that a loss of species diversity led to a decline in the mean *biogenic mixing depth* (BMD). In Fig. 10.12 the random extinction led to a bifurcation within the results due to the presence (or absence) of a single species: the dominant burrowing brittlestar *Amphiura filiformis.* Thus changes in the BMD largely depend on whether or not *A. filiformis* is among the survivors.

The second type of simulation allowed interactions where species abundances were limited by competition with other members of their functional guild. In this model, substitutions of abundances maintained total community density. *A. filiformis* is of average sensitivity to stress, so the results show (Fig. 10.12f) that the pattern is similar to that for random extinction (Fig. 10.12e). In relation to body size, large species tend to be lost before smaller species, leading to a faster decline in the mean BMD compared with random extinction (Fig 10.12a, c). Extinction risk was high for rare species (of low abundance), and rare species were 6000 times more likely to be lost than the most common species. Yet extinction of rare species had little impact on BMD (Fig 10.12d, h) until *A. filiformis* was lost.

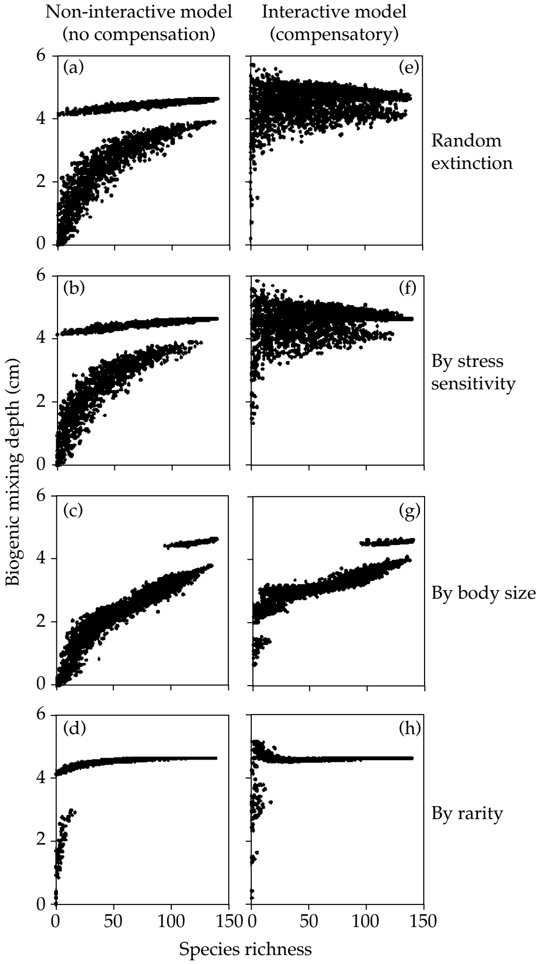


Figure 10.12 Predicted changes in the BMD following benthic invertebrate extinctions. The boxes show the results of 20 simulations per level of species richness, with different models of species extinction. Simulations a–d are for a non-interactive model of community assembly assuming no numerical compensation by surviving species. Simulations e–h are for an interactive model that assumes full numerical compensation following extinction of competitors.

In ecology it is generally believed, based on terrestrial and microbial systems, that when species that are strongly interacting go extinct, increases in the population size of species released from competition will compensate for loss of ecological function (Loreau *et al.* 2002). The key conclusions from Solan *et al.*'s (2004) study are that this is true only when extinction is not correlated with species functional traits (the random loss and stress sensitivity simulations). When the risk of extinction of a species was correlated with its body size or abundance, compensatory responses did not alter the consequences of species loss; small species have little impact on bioturbation and do not compensate for functions performed by larger species. Similarly, the loss of rare species, even with full compensation, had no effect on BMD since rare species had little impact on BMD. It can be concluded that the order in which species are lost is important, especially when species that play large roles in a functional property, such as bioturbation, are lost. In this case, the consequences can be a reduction in the depth of bioturbated sediments and in extreme cases an increase in anoxia. Solan *et al.* (2004) conclude that

> "if we are to predict the ecological impacts of extinction and if we hope to protect coastal environments from human activities that disrupt the ecological functions species perform, we will need to better understand why species are at risk and how this risk covaries with their functional traits."

This conclusion has been reinforced throughout this book, especially as it illustrates future research directions in the face of the increasing pressures on coastal sediment ecosystems globally.

CHAPTER 11

The benthos in the management of marine sediments

Throughout the previous chapters, we have focused on our understanding of the benthic system, its processes, structure, and functioning but, hopefully, we have also shown some of the changes to the system as the result of human activities. It is now relevant to look at the way in which management relies on and uses benthic data and information, the way in which benthic information and data are put into a wider context, and the way we manage marine sediments. Although examples in this chapter are mainly taken from European initiatives, the same examples exist in other regions. In all countries, there are many agencies and bodies involved directly or directly in the science and management of marine sediments—some carry out marine benthic studies and/or the monitoring, some require others to carry out the monitoring, and others use the benthic research and monitoring information (Table 11.1).

11.1 The use and analysis of benthic data

Throughout this book we have indicated many of the numerical techniques at our disposal for analysing benthic data, for linking them to the environmental variables, and for using them in understanding the functioning of the marine system, not least in relation to human activities. Indeed, Elliott (1996) suggested that there were approximately 26 groups of techniques for analysing the benthos and Gray (2000) describes recent methods and the progress made recently in analysing benthic data—by now we have added even more techniques. We have indicated here how some of the techniques have been adapted from other fields of ecology, such as terrestrial systems and even, in some cases, from other fields altogether; for example the main diversity index used, Shannon–Wiener *H'*, was obtained from information and systems analysis.

Figure 11.1 indicates how many of those methods link together in order to obtain a large amount of information from the benthos—it is axiomatic that no single technique gives a large amount of information and many of them rely on several techniques being used together. Figure 11.1 indicates how we start with community structural and primary variables (abundance, biomass, etc.) and move on from these into univariate and derived community variables as well as graphical techniques for community structure. From there we move into the analysis of functional attributes and also to multivariate techniques; in particular it is important to point out that we need a combination of statistical hypthesis-testing techniques, such as ANOVA, ANCOVA, etc., and hypothesis-generating techniques such as ordination and classification analyses. Similarly, in order to communicate and interpret the data we need a combination of graphical and tabular techniques.

All of the techniques have their uses, and all of them also have their limitations. Hence while a diversity index merely gives a single figure summarizing the diversity, other techniques such as ordination and cluster analysis are needed to further illustrate the relationship between the species and samples. Similarly, some of the indices and methods have an acknowledged relationship with a defined stressor such as organic enrichment (e.g. SAB curves, the Pearson–Rosenberg paradigm) whereas many others have an unspecified relationship with any single stressor.

Table 11.1 Types of bodies undertaking benthic monitoring and management

Body	Role/activities
Environmental protection agencies	Flood and erosion risk, water quality, monitoring for ecological status, habitat creation, compliance with licences, etc., monitoring for diffuse pollution, eutrophication
Nature conservation bodies	Habitat and species status, monitoring of designated areas and species (e.g. marine protected areas, special areas of conservation), monitoring of habitat loss and gain, appropriate assessments, etc.
Regional and national fisheries bodies	Stock size, impacts of fishing on seabed and water column, monitoring of no-trawl zones and shellfish stocks, compliance, catches, etc.
Governmental agencies	Food quality, national marine monitoring plans, OSPAR, data collation/reporting, SEA (Strategic Environmental Assessment), etc.
Industry and developers	Licence compliance, operational aspects, etc., impact prediction (EIA), operational aspects for dredging, aggregate extraction, waste disposal, oil and gas exploration and extraction
NGO/green groups	Public awareness, non-statutory/volunteer recording (especially 'charismatic megafauna', e.g. birds and marine mammals)
Water supply and purification companies	Trade effluent and sewage treatment plants licence compliance, quality (drinking-water), monitoring of receiving waters, etc.
Municipalities/public authorities	Environmental performance, change and quality (erosion, beach quality, air, etc.)
International bodies	Data collation, reporting (quality status reports, biological assessments, pollution action plans, etc.)
Researchers, educationalists	Investigative monitoring, pure and applied research, learning and teaching, etc.

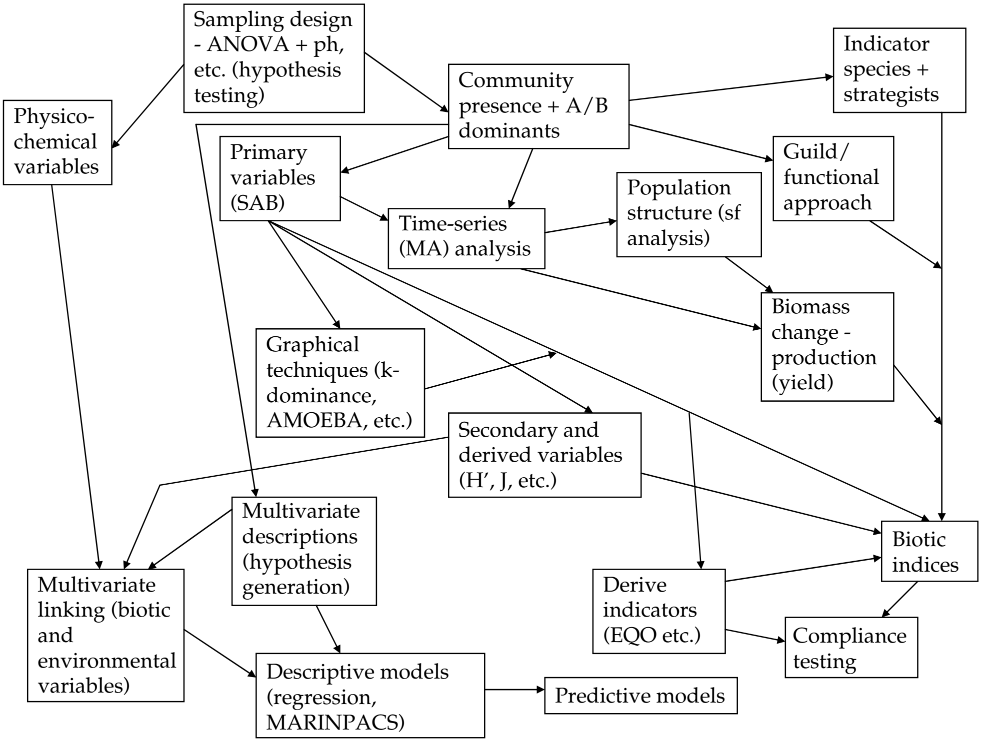


Figure 11.1 An indication of the sequence of using numerical methods to derive information from benthic surveys.

In order to indicate the breadth of techniques and give some of the key and useful references available, Table 11.2 lists the methods in use. This table also leads the reader towards the literature, indicating the concepts on which we base our analysis. Furthermore, as shown by the dates of the references used, it also indicates something of the history of benthic data analysis. The reader is advised to start with earlier literature which gives the main ideas behind a topic before moving to more recent references.

The references in Table 11.2 represent only a very small subset of the literature available and we are sure that experienced benthologists will also have

Table 11.2 Concepts and techniques for analysing benthic data

Concepts and techniques	Illustrative references
General texts giving an overview of the methods and concepts	Southwood and Henderson 2000; Rees *et al.* 1990; Henderson 2003; Bayne *et al.* 1988; Gauch 1982; Warwick and Clarke 1991, 2001; Diaz *et al.* 2004; Eleftheriou and McIntyre 2005; Jørgensen *et al.* 2005; Borja and Dauer (2008); Green (1982)
Ecological statistics and numerical methods—general texts (* with accompanying software)	Ludwig and Reynolds 1988*; Jongman *et al.* 1995 (CANOCO); Legendre and Legendre 1998; Krebs 1998*; Clarke and Warwick 1994/2001; Clarke and Gorley 2006 * (PRIMER); Kovach 1999* (MVSP); Henderson 2003* (CAP); Zuur *et al.* 2007* (BRODGAR R-package)
Sampling design, ability to detect effects cost-effectively, replication required, precision of means derived	Green 1979, 1982; Downing 1979, 1989; Skalski and McKenzie 1983; Elliott 1993; Stewart-Oaten and Murdoch 1986; Caswell and Weinberg 1986; Clarke and Green 1988; Riddle 1989; Rees *et al.* 1991; Ferraro *et al.*, 1994; Eberhardt and Thomas 1991; Nicholson and Fryer 1991; Fairweather 1991; Zuur *et al.* 2007
Use of multiway ANOVA for inter- and intra-site and inter- and intra-time analysis, BACI-PS design, multivariate ANOVA, PERMANOVA	Schmidt and Osenberg 1996; Underwood 1994, 1997; Underwood and Chapman 2005; Anderson *et al.* 2005
Time series analysis, moving-average data treatment, spatial heterogeneity, spatial/temporal trends	Rees *et al.* 1991; Warwick *et al.* 2002; Rodrigues *et al.* 2007
Concept of indicator species; opportunist transition and climax community species	Gray *et al.* 1988; Majeed 1987
Determination of numerical or biomass dominants (10 highest ranked species, species composing the first 50% of cumulative abundance or 90% of cumulative biomass), species–area curves	Berger and Parker 1970; Ugland *et al.* 2003; Gotelli and Colwell 2001; Hiddink and Kaiser 2005
r-strategists and *T*-strategists vs *K*-strategists.	Majeed 1987; McManus and Pauly 1990; Rees *et al.* 1990
SAB trends (primary community parameters, species (or family) richness, abundance biomass—Pearson–Rosenberg model).	Pearson and Rosenberg 1978; Rhoads and Germano 1986.
Secondary or derived parameters—Diversity H′, J′, 1−J′, E; turnover diversity indices	Southwood and Henderson 2000; Henderson 2003; Hurlbert 1971; Heip and Engels 1974; Pielou 1966, 1975, 1984; Ludwig and Reynolds 1988; Wu 1982; Gray 2000; Koleff *et al.* 2003; Marques *et al.* 2005
Secondary or derived parameters—ratios B/A, A/S (biomass and abundance ratios).	Pearson and Rosenberg 1978;
Taxonomic ratios—polychaete:amphipod, nematode:copepod	Raffaelli and Mason 1981; Raffaelli 1987; Marques *et al.* 2005; Dauvin and Ruellet 2007
ABC (abundance biomass comparison) characteristics	Warwick and Clarke 1991, 1994; Meire and Dereu 1990; Clarke and Warwick 2001; Warwick 1986; Beukema 1988; Dauer *et al.* 1993
S(N-B) and DAP index (resultant difference (and difference in area, %) in abundance and biomass profiles)	McManus and Pauly 1990.
SEP (Shannon–Wiener evenness proportion, as development of ABC and comparison of H′ (or E) derived on both abundance and biomass)	McManus and Pauly 1990.

Table 11.2 *Continued*

Concepts and techniques	Illustrative references
Taxonomic distinctness; taxonomic resolution	Salas *et al.* 2006a, 2006b; Leonard *et al.* 2005; Clarke and Warwick 2001; Olsgard *et al.* 1998; Warwick 1988.
Biomass and size spectra	Schwinghamer 1988; Tita *et al.* 1999; Duplisea 2000; Harris *et al.* 2006; Mouillot *et al.* 2006.
Rarefraction, log-normal and *k*-dominance patterns (graphical representation of community characteristics)	Southwood and Henderson 2000; Henderson 2003; Gray and Mizra 1979; Platt and Lambshead 1985; Clarke 1990; Rosenberg *et al.* 2004; Ugland and Gray 1982; Limpert *et al.* 2001; Gotelli and Colwell 2001; Gray *et al.* 2006.
Abundance models (zero sum multinomial (ZSM), species abundance distributions (SAD), rank abundance plots)	Wilson 1991; Hubbell 2001; Magurran 2004.
AMOEBA-type changes (abundance of dominants from one period to another).	Ten Brink *et al.* 1991.
Change of feeding or ecotrophic guilds (e.g. Word infaunal trophic index, UKITI); functional diversity, life history traits	Word 1979, 1990; Codling and Ashley 1992; Bremner *et al.* 2003, 2004 ; Cheung *et al.* 2008
Energetics indices—exergy index, specific exergy	Marques *et al.* 2005; Pranovi *et al.* 2007
Energetics indices—ecological network analysis	Field *et al.* 1989; Wulff *et al.* 1989; Ulanowicz 2004; Patricio *et al.* 2006
Biotic index (indication of dominants with respect to tolerant forms); (e.g. benthic response index, M-AMBI, Benthic IQI, B-IBI, BENTIX)	Smith *et al.* 2001; Weisberg *et al.* 1997; Simboura and Zenetos 2002; Rosenberg *et al.* 2004; Marques *et al.* 2005; Quintino *et al.* 2006; Muxika *et al.* 2007; Simboura and Reizopoulou 2008
Integrated biotic indices—BQI and BPI (biological quality index, benthic pollution index, reduction through community change) and link with PLI (pollution load index); environmental integrative indicators; coefficient of pollution, community disturbance index	Jeffrey *et al.* 1985; Maurer *et al.* 1991; Wilson 2003; Rosenberg *et al.* 2004; Aubry and Elliott 2006; Flater *et al.* 2007
Benthos and environmental variables interaction (predictive models, e.g. multiple regression, RIVPACS/MARINPACS type; overlay techniques; correlation techniques from multivariate analysis)	Wright *et al.* 1989; Elliott and O'Reilly 1991; Clarke and Ainsworth 1993; Allen 2000; Allen and Elliott 2004 ; Brinkman *et al.* 2002; Ysebaert *et al.* 2002; Edgar and Barrett 2002; Harris *et al.* 2006; Zuur *et al.* 2007.
Role of Q and R multivariate statistical analyses (respectively for sample affinities based on faunal attributes, and faunal (species) affinities based on sample (station, distribution) attributes)	Gauch 1982; Ludwig and Reynolds 1988; Field *et al.* 1982; Kenkel and Orloci 1986; Ter Braak 1986; Jongman *et al.* 1995; Henderson 2003; Zuur *et al.* 2007
Ecosystem models incorporating benthos	Baretta *et al.* 1995; Radford and Ruardij 1987; Baretta and Ruardij 1988;
Benthic environmental quality standards/objectives derivation, relevance of mixing zone, Treatment/control pairing and significance of changes; biological significance vs statistical significance	Efron and Tibshirani 1986; Dickson *et al.* 1987; Rees *et al.* 1990; Jackson *et al.* 1990; Rees and Pearson 1992; Elliott 1996; Brown and Shillabeer 1997; Lanters *et al.* 1999; Rees *et al.* 2006
Degree of compliance with any standards set and the required action following non-compliance	Cotter and Rees 1993; Hiscock *et al.* 2003; Rees *et al.* 2006

preferred techniques. Despite this, some of the general references mentioned in the first two rows of the table should give readers a good grounding in the subject. We have also indicated which references are accompanied by readily available software, some of which is free (e.g. CAP (PISCES software), Krebs 1998); other programs are provided during training courses, e.g. PRIMER (Clarke and Gorley 2006) or BRODGAR (Zuur *et al*. 2007).

11.2. The DPSIR approach—indicators and objectives

Many of the numerical methods mentioned above were derived as the result of applied studies where, for example, benthologists were asked to indicate comprehensively the change to community structure as the result of human activities. Recently, most notably, national and international legislation and agreements have been the impetus for creating new ways of analysing and presenting benthic data, not least including the widespread derivation of indicators. As shown throughout this book, we often use the benthos to determine the quality and health of the marine ecosystem. In order to have successful management of the seabed, we need to indicate what we, as society, require of it—using management-speak, we need a *vision* and *objectives* for it. As an example, the UK Department for Environment, Food and Rural Affairs (Defra) has its vision for the UK shelf to achieve 'clean, healthy, safe, productive and biologically diverse seas' (Rogers and Greenaway 2005). Following this, work is under way to provide a more explicit set of objectives which can then be used as the end-point of successful management. Rogers *et al.* (2007) thus give the objective for the seabed habitat (fauna, flora, and physical structure) as to 'protect a sufficient proportion of every habitat from pressures of human activity to maintain their natural distribution, extent and structural/functional integrity'. Such objectives have been with us for a while and can easily be derived as a standard on which any monitoring can be based (e.g. see Elliott 1996; Table 11.3). More recently, *ecological quality objectives* (EcoQO) have been embraced by regional bodies such as the OSPAR Commission (1992) under its Article V to protect the marine environment of the north-east Atlantic. It should now be obvious to the reader how the benthos becomes an integral part of marine management.

Following the statement of a vision and objectives, and our analysis of the system, we then need to summarize the status of the benthos and communicate this to marine users and policy-makers. In order to represent the relations between the environment and the human system, indicators can be structured following the *driver–pressure–state change–impact–response* (DPSIR) framework adopted by the European Environment Agency and others (EEA 1999, Elliott 2002 ; Fig. 11.2). Social and economic developments (as *driving forces*, e.g. industries, demands for food and other resources from the sea) create *pressures* on the environment (e.g. by producing effluent discharges or removing seabed). Consequently, the *state* of the environment (e.g. the benthic or water column system) is changed and undergoes *impacts* which affect society (e.g. degraded habitats, human health problems, or barriers to fish migration affecting our food resources). The latter then require to be addressed by human *responses* (e.g. legal control and administrative arrangements) that feed back to the driving forces, the state, or the impacts, through adaptation or curative action (EEA 1999, Elliott 2002, McLusky and Elliott 2004).

The *response* boxes on Fig. 11.2 refer to the 12 principles of the ecosystem approach as given by the UN Convention on Biological Diversity (UNEP undated), the PEST analysis (where environmental management relies on the prevailing *political, economic, social,* and *technological* forces), and the achievement of the *7 tenets*. The latter require that our responses to change should be *environmentally sustainable, economically viable, technologically feasible, socially desirable or tolerable, administratively achievable, legally permissible, and politically expedient* (Elliott *et al.* 2006). In essence this means that if we want to manage the benthos and sediments, do we have the technologies and laws, the statutory bodies, and

Table 11.3 Benthic-related environmental quality objectives and null hypotheses

The benthic populations and sediments are of a quality sufficient to support the fish (and when necessary) bird populations
The biological functioning of an area has not been/will not be changed unacceptably by waste disposal or other anthropogenic changes
The levels of persistent toxic and tainting substances in the biota are insignificant and do not affect their biology, their predation-risk, or the health of their predators including humans
The structure of the intertidal/subtidal benthic community and populations are consistent with the hydrophysical regime
The diversity, abundance, biomass and population structure of the intertidal and subtidal rock community are as expected given the physical features of the area
The concentrations and body burdens of toxic and tainting substances either agreed or defined in conventions and legislation are not exceeded in the relevant biological component

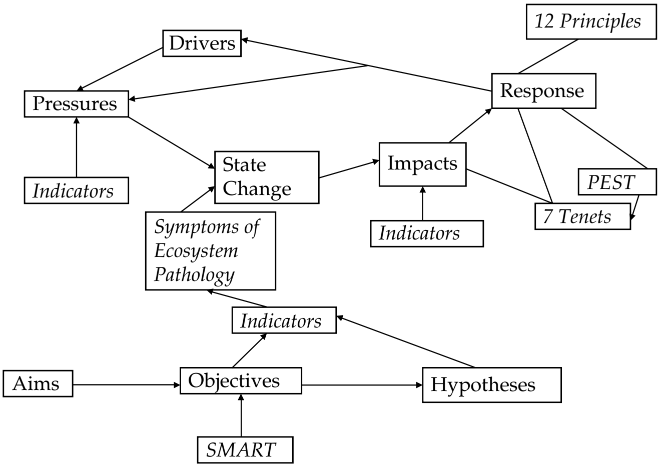


Figure 11.2 The framework linking the DPSIR approach to the use of indicators and objectives (from Elliott *et al.* 2006) all abbreviations in text except SMART - this refers to objectives which should be 'specific, measureable, achievable, realistic and time-bounded'.

money to do so within what society, politicians, and the environment demand? Hence the DPSIR framework and the ecosystem approach inherently combine both the natural and social sciences and, most importantly, require marine scientists wishing to engage in these debates to think as widely as possible.

The pressures, state change, and impact parts of the DPSIR framework rely heavily on *indicators.* These are quantitative measures that quantify the amount of activity in the marine system causing a change (e.g. how many tonnes of seabed material are dredged in an area), the amount of change in the natural system (e.g. did the dredging result in the removal of important benthic species), or the effects of this on human uses of the system, whether for food production (fisheries) or general health (e.g. has a fishery declined as the result of the dredging).

In recent years there has been a huge increase in the development of marine indicators, especially those giving the levels of contamination and the health of the system (e.g. Kabuta and Laane 2003). The development of marine benthic indicators has followed this trend. The papers by Marques *et al.* (2005) and Borja and Dauer (2008) and the extensive recent review by Rees *et al.* (2006) summarize the current state of thinking regarding indicators and give the background to their derivation and use. As the conclusions given by Rees *et al.* (2006) have a very wide significance and are relevant to benthic indicator use worldwide, they are presented in modified form in Table 11.4. Figure 11.3 summarizes the way in which indicators are used within an applied science and management framework. In particular, it demonstrates that indicators are needed to show when management actions require to be taken.

However, for a more coherent approach to the management of the marine environment, including a better and regular reporting, some governments (e.g. Defra 2002) , take the view that there needs to be an agreed set of indicators. For example, the UK marine regulatory authorities are developing marine indicators for issues such as eutrophication or marine litter and the workshop held in 2002 (CEFAS 2003) identified potential indicators for near-shore seabed disturbance. These were subsequently grouped by Aubry and Elliott (2006) into three *environmental integrative indicators* (EIIs): EII1, Coastline Morphological Change; EII2, Resource Use Change; and EII3, Environmental Quality and its Perception. Of relevance here is the fact that many of the component indicators relate to the health of the benthos, as individuals, populations, or communities, and the modifications to the hydromorphological regime (including the sediments) of an area. In this, the scheme builds on the earlier use of ecological health in coastal classification schemes used by the pollution control agencies in the UK (see McLusky and Elliott 2004 for details).

Indicators of ecosystem response have to fulfil several criteria in order to be valuable in management. They are required to give a high *signal/noise ratio* in that they indicate a change in the system

Table 11.4 Conclusions regarding benthic indicator use (modified from Rees *et al.* 2006)

The formulation and use of indicators must be founded on good science and, at the same time, should be understandable by and readily communicable to non-specialists
The science must by hypothesis driven and with well defined aims and objectives where the latter are the actions required to attain the aims; if these are maintained then the statistical approaches will easily follow
A good conceptual understanding and knowledge of the likely nature of human impacts is a prerequisite for effective regulatory applications
Indicators are central to the design of monitoring schemes and approaches and should serve as the trigger for management actions
The scientific and management needs are likely to be satisfied by the use of complementary measures
The statistical requirements of compliance-testing (against licences) will influence not only the choice of measures but also survey design and sampling practices, which typically will vary between sites and activities
In evolving cross-disciplinary strategies for indicator applications, more attention should be given to dependencies of scale, i.e., the search for universal indicators must vie with operational effectiveness in meeting practical management needs
It is likely that top-down response indicators, such as for the top predators, will have a greater resonance with the user groups than do bottom-up indicators (showing the physico-chemical processes creating the system)
There is a need for a more dispassionate approach to evaluating indicator efficacy against scientific and management criteria
Caution should be exercised in initial indicator applications, and some allowance made for adaptation in the light of practical experience
Indicator schemes should be responsive to new knowledge and, attendant on this, changing perceptions of the environmental significance of human impacts at sea
More attention should be paid to existing operational experience in evolving regulatory frameworks for achieving aspirational goals

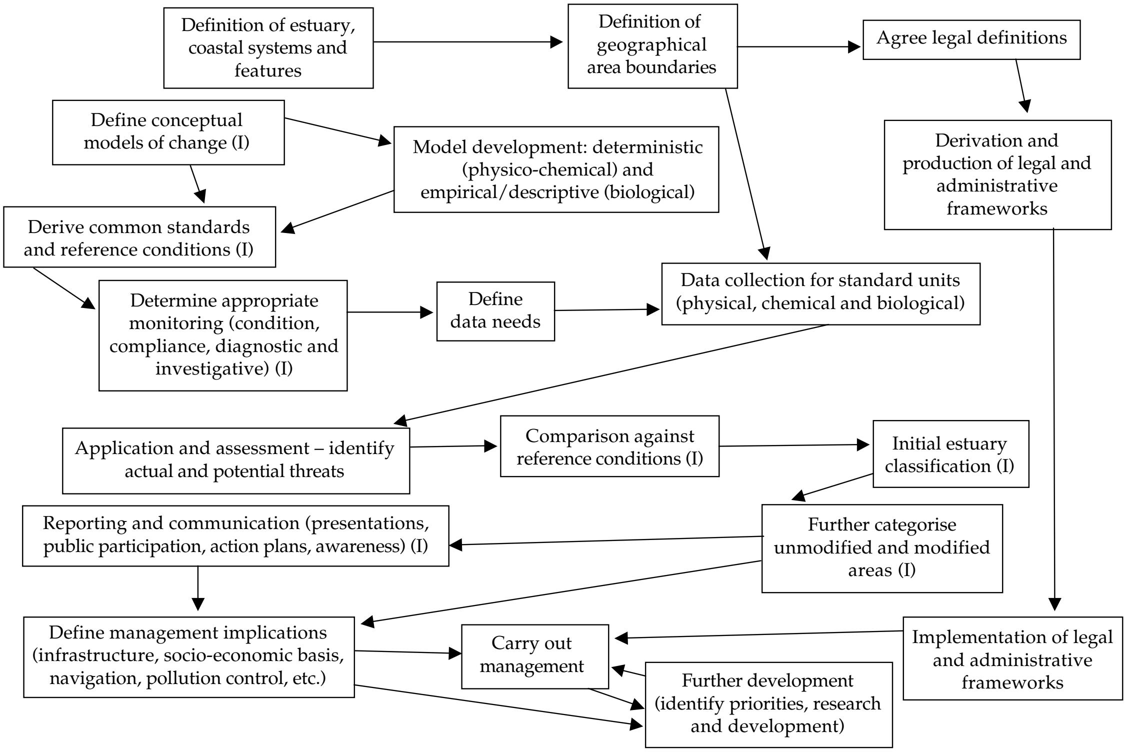


Figure 11.3 A generic framework for indicator use (I denotes the need for indicators) (modified from Elliott and McLusky 2002, Whitfield and Elliott 2002).

due to human actions against a background of natural environmental variability. Hence there is the need, in the case of the benthos, to determine the sources of natural variability in the community parameters before anthropogenic change can be detected—as discussed earlier, that inherent variability can be termed *noise* in relation to the anthropogenic change (the *signal*). Secondly, if the monitoring is to be useful in marine management then there needs to be a rapid and reliable/specific response. Once a change is detected then management actions are required to prevent further deterioration, i.e. at the outset we decide that if a given amount of change is detected then we know in advance what our action will be. For example, if we detect a change in the benthos from a normal community to one dominated by opportunistic polychaetes then we should have decided to remedy the cause of the change. Because of this, we need to be sure that the change detected, for example the change along the Pearson–Rosenberg continuum, can be reliably assumed to reflect organic enrichment. Thirdly, monitoring should be easy and economical: if methods are either too complex or too costly they will not be adopted. Lastly, the monitoring should be relevant to the end-point and should feed back either into management action or into regulation. Within all of this, we take the view that the methods should have a general applicability and be backed up by good science.

Benthic indicators have to be of several types (e.g. Marques *et al.* 2005, Rees *et al.* 2006, Borja and Dauer 2008). They should indicate both the structure and functioning of the system and so cover the community parameters such as species richness, biomass, and diversity as well as the growth rates, size-frequency analysis, and reproduction. They should include the spatial and temporal aspects in giving changes across parts of the seabed, between different sea areas, and at different times to measure deterioration (or improvement). In order to link the species to their environment, the indicators should be both taxonomic (relating to species) as well as non-taxonomic (relating to physicochemical variables). Finally, and again to reflect the whole system, they should relate to the bottom-up causes and the top-down responses. As an example of the latter, we should have indicators of the sediment structure and its oxygen regime, which will ensure a healthy benthos that will in turn support fish and bird predators.

The importance of these indicators of change and quality objectives is illustrated by the way in which the benthos is incorporated into marine quality assessments and management protocols and legislation in Europe, Australia, and North America. For example, see the NOAA eutrophication review (Bricker *et al.* 1999), the Australian and New Zealand environmental quality guidelines, the European Water Framework Directive, and the OSPAR Commission strategies for protecting marine systems (e.g. see Ministry for the Environment (NZ) 2001; Ward *et al.* 1998, Heinz Centre 2002, European Commission 2006).

Finally, with regard to indicators and objectives, we should consider the unit of habitat to be protected. The *Ecosystem Approach* requires that the natural features and the human (socio-economic) system are integrated and should be managed accordingly. The unit may be a length of coastline or an estuary, but we are now moving towards the management of sea areas, for example areas out to 200 nautical miles (370 km) from a country's coastline or semi-enclosed seas such as the North Sea, Baltic, or Mediterranean. Hence, we need objectives, indicators, and management units relating to the seabed areas that we use and may impact, whether these are geopolitical, hydrographical, geographical, or ecological units.

As an example, conservation management revolves around the definition of habitats and species which require to be protected. In turn this requires schemes for defining the unit of the ecosystem to be managed—hence we have habitats, biotopes, physiotopes, biomes, etc. (Olenin and Ducrotoy 2006). In the UK, as an example, Connor *et al.* (2004) describes the marine benthic biotopes, many of which were defined following a large-scale multivariate analysis of the faunal community type and the environmental characteristics using TWINSPAN (Two-Way Indicator Species Analysis) (Dr Jim Allen, IECS, University of Hull, personal communication). Such biotopes are linked to the European EUNIS (2005) system (Fig. 11.4) in which the maps produced communicate the habitat mosaic to environmental managers. Diaz *et al.*

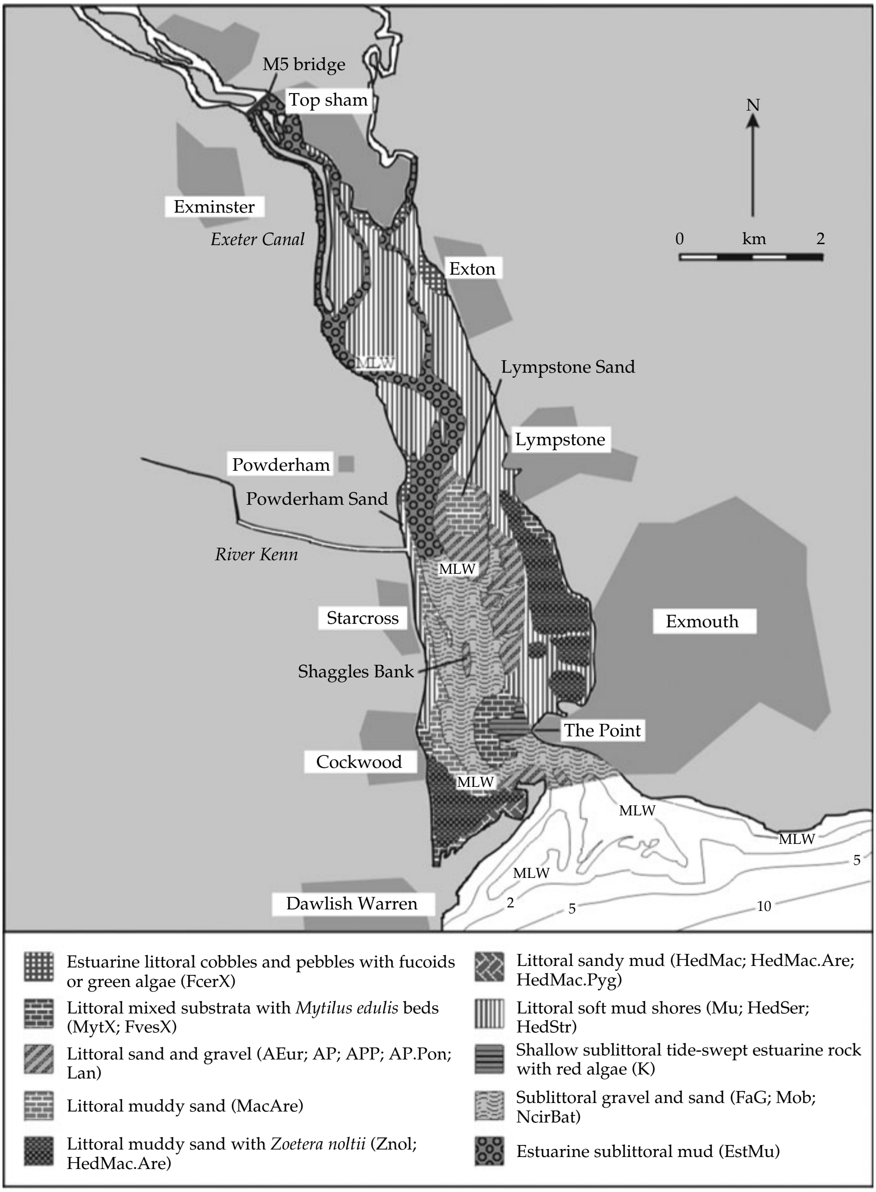


Figure 11.4 Biotopes and sediment mosaic in the Exe estuary, south-west England, according to the EUNIS scheme (provided by Roger Proudfoot, Environment Agency, Peterborough UK).

(2004) indicate the need for, and recent advances in, benthic mapping techniques, and discuss cost-effective ways of obtaining information needed by managers but also of linking the physical and biological aspects. Hence, these frameworks require a good knowledge of the benthic system and, at the very least, the dominant organisms in each habitat type. More recently, these conservation descriptions have been incorporated into the definition of marine landscapes and then towards marine zonation and marine spatial planning (e.g. Boyes *et al.* 2007).

11.3 Benthic monitoring

Marine environmental managers, in common with those who manage other systems, will take the view that unless you can measure something then you cannot manage it. Repeated or systematic measurement can be regarded here as monitoring and as we have used the concept of monitoring throughout this book, we should discuss monitoring as an integral part of management. However, like many others, we have used the term widely and loosely and so we should now define and explain the various types of marine monitoring (Table 11.5). This shows that we monitor for various reasons: to provide background information, to inform environmental management systems, and to provide the data to judge compliance with indicators and the triggering of management actions by passing thresholds. Hence the use of monitoring in reporting changes in quality, compliance with standards, and the meeting of objectives is paramount. However, although not discussed further here, this also includes the use of benthic monitoring in industrial production—for example, a dredging company will have to monitor the seabed to determine where and when to dredge a channel.

- *Surveillance monitoring* is aimed to supplement/validate impact assessments (see below), to inform future monitoring, and to assess long-term natural and anthropogenic change. It may be of a sufficient intensity to characterize whole basins, such as the benthic monitoring carried out as part of the OSPAR quality assessment for the north-east Atlantic area (OSPAR 2000). Surveillance monitoring will need to be at the appropriate spatial and temporal scales—the micro, meso, macro, or mega scale depending on the questions being addressed and the data to be collated. However, we also refer to *de facto* monitoring at the meta-analysis scale in which data from various studies are collated.
- *Operational monitoring* is in many ways more precise than surveillance monitoring and is related to a particular human activity or problem. It is carried out to establish the status of a sea area at risk and to assess changes in that status resulting from programmes of measures, e.g. remedial actions to reduce the effects of pollution. It therefore needs to be sufficient to allow the determination of the magnitude and impact of point source and diffuse pollution and hydromorphological pressures, such as the presence of a structure (bridge, gas rig, etc.). The monitoring is required to assess the scale and magnitude of any change where these can be separated into the spatial extent (the area of change) and the duration (the temporal extent). Of course those paying for the monitoring (usually industry or developers under the 'polluter pays principle') will need to be aware of the costs and benefits of these scales of sampling and monitoring. There is a long history of lessons learned from other monitoring protocols (e.g. dredging, eutrophication, biotope mapping). As indicated in Chapter 1, the monitoring can be as defined for both individual threats (e.g. using the BACI-PS approach; see p. 9) as well as that required for a wider, holistic approach.

As operational monitoring will often be demanded of an operator, developer, or discharger by a regulatory body, such as an environmental protection agency, then it will be scrutinized much more than the 'look-see' approach of surveillance monitoring. It is therefore valuable to use a *decision tree approach* to identify the monitoring required and justify that monitoring. McLusky and Elliott (2004) give an example of such a decision support system whereby the monitoring decision is the result of a set of precise questions being posed. There will need to be a rigorous adoption of sampling strategies to determine both the biological and statistical significance of change but also, as discussed in Chapter 1, it must be realized that fully quantitative approaches may be prohibitively expensive. As described above, there will need to be uni- and multivariate numerical techniques in the interpretation of data and perhaps power analysis to determine sampling intensity once the level of required and/or anticipated change has been defined.

As an example of operational monitoring we can look at the monitoring required for what is perhaps one of the largest modifiers of marine sediments—dredging and disposal of dredged material (e.g. see Newell *et al.* 1998 and McLusky and Elliott 2004 for a review of the effects of dredging). Dredging is of two main types—*capital* where the dredging is moving

Table 11.5 Types of monitoring

Type	Nature/reasons	Benthic example
Surveillance monitoring	A 'look-see' approach (i.e. what is there?), it may be started without determining the end points and relies on *post hoc* detection (*a posteriori* detection of trends with action then determined)	A wide-scale survey of an area, the primary and secondary community characteristics (species, diversity, abundance, etc.)
Condition monitoring	Nature conservation bodies (surveillance) to determine the present status of an area; it could be linked to biological valuation	If a nature conservation area has been designated for its benthic community or for the presence of a rare benthic species then its condition needs to be monitored
Operational monitoring	Carried out by industry (e.g. dredging scheme) and may be linked to the aims for management	To determine whether an area is silting and needs further dredging for deepening to allow vessel movements
Compliance monitoring	To determine if an area or an industry complies with a set of conditions laid down by a licence; the licence could be for effluent discharge, disposal at sea, etc. As part of the 'polluter pays principle', the industry will be required to fund the monitoring.	An industry, e.g. a sewage or chemical works will be given a licence/permit (e.g. from an Environment Protection Agency) to discharge which may contain a condition to monitor the bed community to ensure no harm is caused by the activity. A dredging company will be given a disposal licence which includes a monitoring requirement
Check monitoring	Related to licensing of activities or discharges, for a regulatory body to ensure that a developer is performing monitoring to best standards	The regulating authority may carry out or arrange to be carried out a set of benthic and sediment samples to check the quality of analyses performed by the industry under condition monitoring
Self-monitoring	Being carried out by the developer/industry under the 'polluter pays principle' but often subcontracted to independent and quality-assured/controlled laboratory	Monitoring of the seabed and receiving area carried out by the industry or dredging company
Toxicity testing	Testing either in the field or laboratory; may be to predict an effect or derive a licence setting, carried out by industry through 'polluter pays principle'; can be linked either to operational monitoring to determine compliance with required standards or analysis required to set the licence conditions; DTA (direct toxicity assessment) may be used for prioritisation and to account for synergism/antagonism	Use of benthic species in sediment bioassays or in water column assays; using lethal or sublethal (e.g. behavioural) endpoints
Investigative monitoring	Applied research (cause and effect), once any deviation from perceived or required quality is detected then aim to look for explanations	To carry out field or laboratory studies on the benthic community, the biochemistry or physiology of the benthic species to attempt to explain reasons for change (cause and effect); possibly using the sediment quality triad
Diagnostic monitoring	Determining effects but link to cause	As above
Feedback monitoring	Real time analysis, linked to predetermined action; e.g. monitoring during an activity on the condition that the activity is controlled/prevented/stopped if a deleterious change is observed (it relies on acceptance that any early-warning signal will be related to an ultimate affect	Monitoring of the bed and water column during dredging whereby of suspended sediment levels exceed a threshold likely to harm the benthos then the dredging ceases until conditions return to normal

the seabed for the first time, as when a pipeline is constructed, and *maintenance* where the repeated removal of recently settled sediment is needed in order to keep a channel clear and of sufficient depth (e.g. see CEFAS 2003). A dredging company will usually need permission both to remove the sediment in one area and, if it is to be disposed of at sea, to dump the sediment elsewhere. Increasingly, if the sediment to be moved is too highly polluted to be dumped back into the sea then it may be put in a secure storage area on land or a bunded area (see McLusky and Elliott 2004). For example, the Port of Rotterdam has to dredge approximately 20 million m^3 of sediment annually, of which about 10% is so contaminated that it cannot be disposed of at sea. Since 1992 the contaminated material has been stored safely in the Slufter/Papasbiek bunded storage areas, while at the same time measures are taken to reduce the polluted nature of material being deposited in the port, such as a pollution reduction programme upstream in the Rhine (see Vellinga and Eisma 2005). Where possible, the clean dredged material is used beneficially such as for building materials or deposited on intertidal areas as beach nourishment to counter erosion or sea-level rise (Weinstein and Weishar 2002).

In being required to monitor the benthos and seabed as part of their operations, usually as a condition of a dredging licence, dredging companies require guidance and transparency in decision-making, especially as most do not employ benthic biologists and so have to rely on outside consultants. The monitoring will have to focus on the physical and chemical aspects of the sediment being dredged and the physical, chemical, and biological characteristics of both the area being dredged and the receiving (disposal) areas. As an example of this, the UK set up the Dredging and Dredged-Material Disposal Monitoring Task Team to provide a structured framework for the procedure to determine monitoring requirements for the disposal of dredged material at sea (CEFAS 2003). Figure 11.5 shows the flowchart which is accompanied by structured tables to indicate the need for and type of monitoring. In essence, the type of monitoring and likely effects will be the result of several factors—the dredging equipment used, the source, type, and amount of the material, and the near- and far-field characteristics of the dredging and disposal areas. For example, a larger operation where environmental damage is more likely needs to be monitored more thoroughly than if an operator is merely moving clean, recently settled material (for this reason, dredging companies prefer us to talk of 'the relocation of dredged material' rather than 'the dumping of dredged spoil'!). Of course, in addition to monitoring the dredging and disposal areas for their environmental consequences, the dredging companies will have to monitor the bathymetry and sediment characteristics to know when they have dredged sufficiently and when the disposal site is reaching capacity.

The third main type of monitoring, *investigative (diagnostic) monitoring*, will be required in cases where the surveillance, condition, or compliance monitoring indicates that there is a problem. This may be where there is reduced benthic quality or the conditions of a licence have been broken. It may also be required to detect the magnitude or impact of accidental pollution (see also Hardman-Mountford *et al.* 2005). For example, during dredging for aggregate extraction, it may be observed that species further away from the dredging site are being affected adversely but the underlying knowledge of the prevailing hydrographic conditions or the biology of the species involved may not initially be sufficient to determine cause and effect (and therefore management). Additional techniques, perhaps including field and laboratory toxicological assays, will then be required to determine cause and effect.

11.4 The role of the benthos in *a priori* assessments

Environmental managers, pressure groups, and indeed industry require (or are required by law) to determine whether there will be an effect on the benthos of a human activity being given permission to go ahead. These *a priori* assessments (i.e. done before the activity is given permission to go ahead) take several forms but almost all attempt to answer the question 'what if... [an activity goes ahead]?'. In order to answer this question, it is necessary to determine rigorously whether there will be a change from a reference or baseline benthic condition. That reference state may be the present situation at the place under study (i.e. without the potential stressor) or it may be a comparable area. This is the essence of an *environmental impact assessment* (EIA) which, in most countries, has to be performed before permission is given for an activity to go ahead. Within the European Union, the EIA

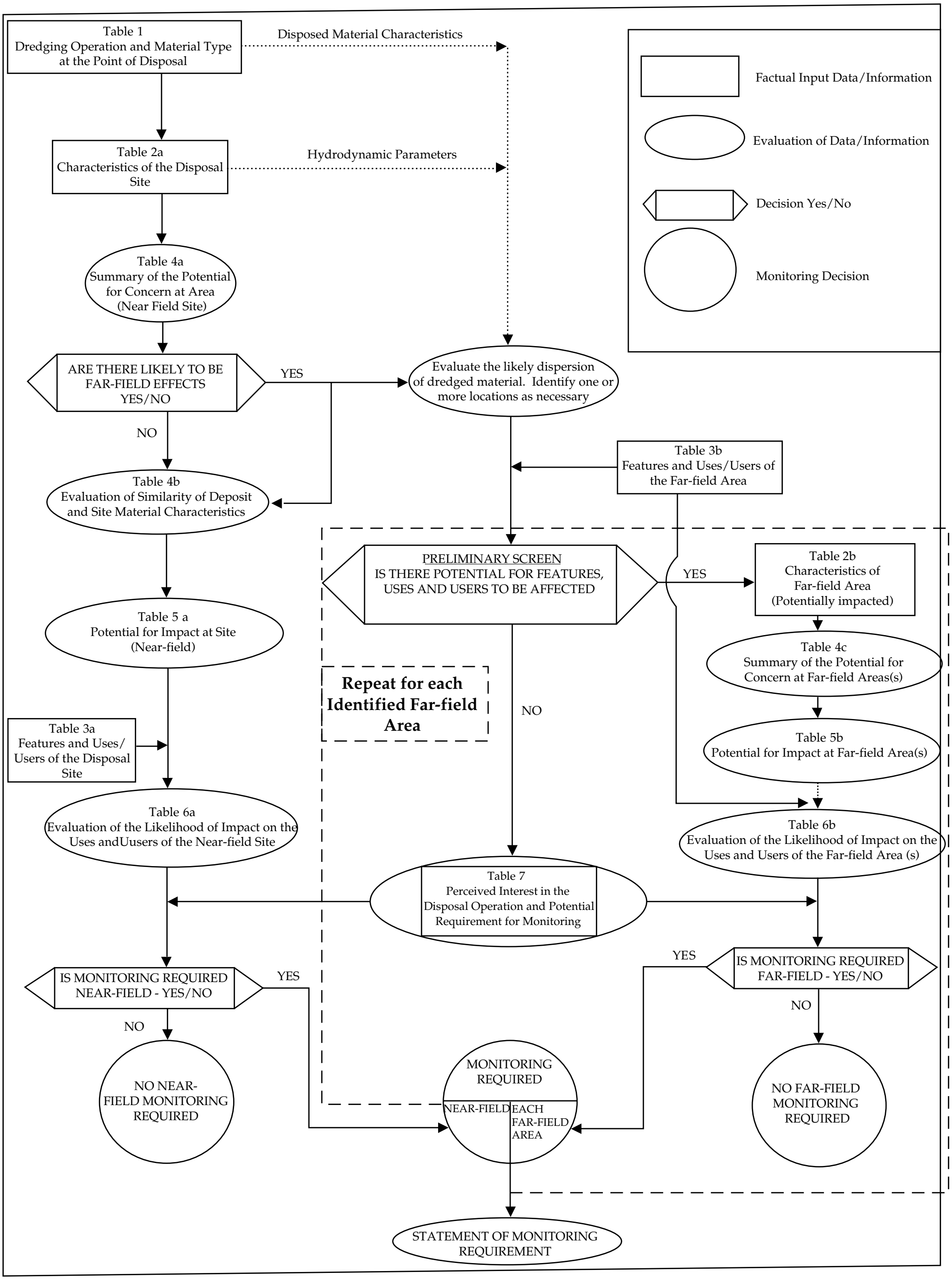


Figure 11.5 Transparency in decision-making: the procedure to determine monitoring requirements for the disposal of dredged material at sea (from CEFAS 2003).

Directive (European Commission 1985) makes this assessment mandatory for very large and potentially environmentally damaging projects such as new ports, large petrochemical works, and power plants, but smaller projects require an EIA at the discretion of the member state. In most developed countries, an EIA is required in order for planning permission to be given. For example, if a new bridge is to be built then, given its likely impact on the hydrodynamics of an area, a benthic and sedimentological survey will be required. After an EIA is carried out, an e*nvironmental statement* (ES) is produced (e.g. see Glasson *et al.* 2005). In essence an EIA is very simple—what is the effect of this activity, being carried out in this way, at this time and place, with this degree of mitigation and/or compensation and being communicated and consulted in a wide way. Despite this, a fashion seems to have developed for first making these more complex than is necessary, and then not checking afterwards to see if any predictions were correct.

To give an example, one of the biggest marine construction works in Europe in recent years was the construction of the Great Belt Link between Sweden and Denmark, a 13 km four-lane motorway and two-lane rail link. The bridge construction needed excavation of bottom sediments and construction of artificial islands. These activities were expected to lead to increased sediment turbidity, thus affecting the mussel beds (and in turn their predators the eider ducks), and nutrients would be released into the water column. From baseline surveys and hydrographical models, the spatial extent and duration of the effects were predicted. A major concern was that of the possible effects of the nutrients released from the sediments. As a result of eutrophication, the Great Belt is subject to low oxygen concentrations in late summer and early autumn each year. Increased nutrient supply could enhance plankton blooms and produce even lower oxygen concentrations and consequent adverse effects on marine life. The EIA for the development predicted likely effects which were then related to quantifiable limits for change; the latter was then the basis of the monitoring. Expert scrutiny of the predicted effects and limits of change led to a statistically robust feedback monitoring scheme, including power analysis (Gray 1999). As an example, oxygen and suspended solids were monitored in the Great Belt part of the Kattegat (Fig. 11.6). Gray (1999) gives further details, but in essence the monitoring, for both near- and far-field effects, was agreed such that any decrease in oxygen concentrations below 4 mg l^{-1}, or increase in suspended sediments due to the dredging, led to the cessation of the dredging until conditions improved. This was a major breakthrough in getting a dredging company to cease its activities (at very great expense). Although it was relevant in this case, not all monitoring can be done in a feedback mode, as time-lags in effects mean that they cannot affect the operation directly.

Many countries are now revising their EIA guidelines as they are often seen to be too cumbersome (see Gray 1999). Recent developments in EIAs are required to give environmental authorities a much better way of controlling potentially environmental damaging activities. The process needs detailed and careful science to: (1) make quantitative and realistic predictions of effects, (2) suggest criteria for testing such predictions, and (3) design a proper and adequate monitoring programme. Statutory agencies need to involve all parties in the decision-making process, not only the company concerned and its experts, and to insist on a scientifically based investigation and monitoring programme.

Within Europe, as well as the EIA Directive, the Habitats and Species Directive (European Commission 1992) requires that any plan or project likely to affect the conservation objectives for a designated site or species has to be subject to an *appropriate assessment*. Hence an area may be designated for its subtidal sandbanks or intertidal sand- and mudflats and so the features of these sedimentary environments need to be protected against the effects of a plan or project (see Elliott *et al.* 1998). In this case, the appropriate assessment has to be a rigorous analysis of the physical (hydromorphology, sedimentology) and biological features and processes. The decision to undertake an appropriate assessment is fairly simple when an activity is within or immediately adjacent to a designated marine conservation area, termed a *special area of*

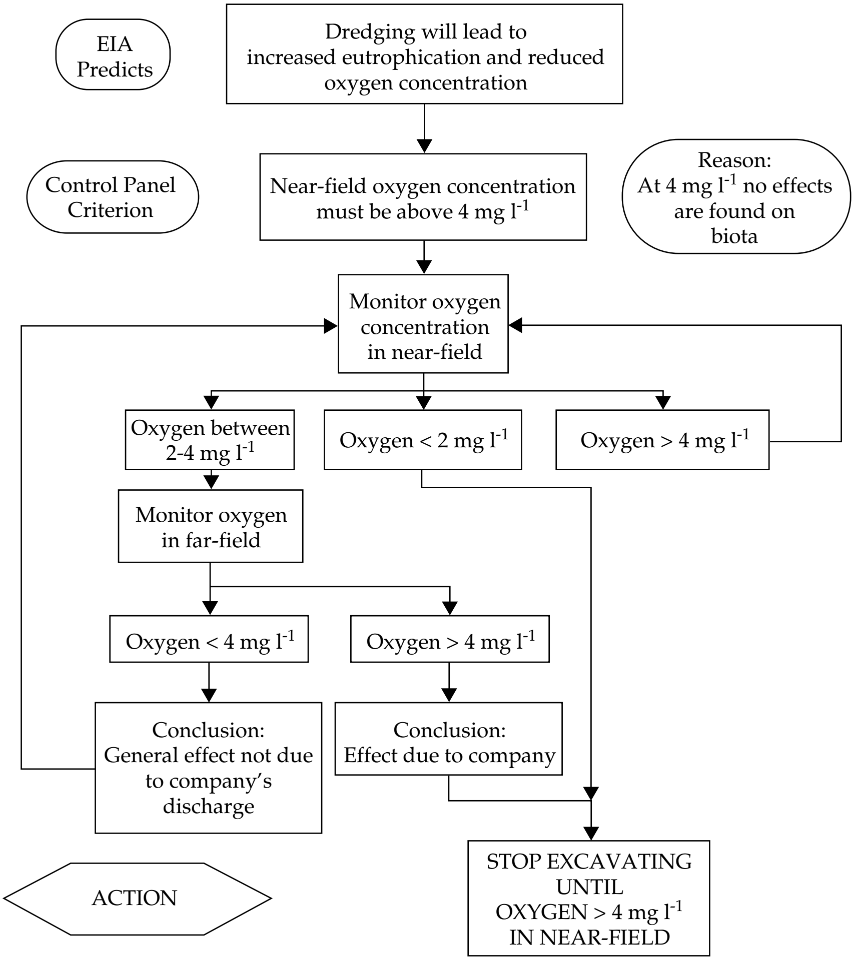


Figure 11.6 An example of a feedback loop for a monitoring programme: oxygen concentration in the Great Belt, Denmark (from Gray 1999).

conservation (SAC) under the EU Habitats Directive (Apitz *et al.* 2006). However, it is more difficult when the SAC is not close to the planned project but, because of the dynamic nature of the marine environment, is still potentially affected. An example is the planned 1000 ha expansion of the Port of Rotterdam, called Maasvlakte 2. Figure 11.7 illustrates the extent of the development on the local and adjacent benthos and the effects, given the loss of seabed, the sand extraction for construction, and the resulting distortion to the coastal hydrography. However, the recent debate has been on the effects of the development on the conservation features, especially the benthos and its predators, not only on the Rotterdam area at one end of the Dutch coast but also those in the Wadden Sea, a major conservation area at the other end of the country. Hence the science is required to understand the links and transport processes influencing the physical and biological nature of the whole Dutch coast. Given the uncertainty in this understanding, it is impossible to state categorically that the development will not have an impact on the Dutch coastal zone including the Wadden Sea. Hence the Dutch government will have to make a choice—either to adopt the precautionary approach, which would take the view that it is not possible to say that the development will not have an effect (and so not permit the port

Figure 11.7 An artist's impression of Maasvlakte 2 development, Rotterdam (from www.maasvlakte2.com). See Plate 14.

extension), or to defend the development as being in the national (and European) interest.

11.5 The role of benthos in quality assessments

As we have mentioned in passing several times in this book, benthic information is used extensively in assessing marine quality. Other European Directives also involve the detailed use of benthic information—for example those requiring strategic environmental assessments, cumulative impact assessments, and integrated pollution prevention and control (which relates to industrial processes and requires toxicological assessments), and, most recently, the Marine Strategy Directive (MSD) (European Commission 2006) (see Apitz *et al.* 2006). Readers from outside Europe will see the similarities between these initiatives and other legislation, especially the Clean Water Act in the USA and the Canadian Environmental Protection Act (e.g. see McLusky and Elliott 2004 for more discussion).

As an indication of the way in which benthic monitoring is being used in these initiatives, it is valuable to discuss the EU Water Framework Directive (WFD) (European Commission 2000) and, given the likely links and framework, the MSD. The WFD establishes a framework for the protection of groundwater, inland surface waters, estuarine (= transitional) waters and coastal waters. As highlighted by Borja (2006), it has several objectives—to prevent water ecosystem deterioration, to protect and to enhance the status of water resources—but the most important aspect is to achieve a *good ecological status* (GES) for all waters by 2015. In essence, the WFD requires a water body to be compared against a reference condition and then its ecological status designated. If the water body does not meet good or high ecological status, i.e. it is in moderate, poor, or bad ecological status, then remedial measures have to be taken (e.g. pollution has to be removed).

It is not necessary here to present all the aspects of this major piece of environmental legislation but merely to concentrate on the aspects relating to the benthos. In the WFD ecological status is defined in relation to the health of five biological elements in coastal and transitional waters, of which three are benthic (the benthic macrofauna, macroalgae, and angiosperms such as seagrasses and saltmarshes)—the others are phytoplankton and fishes (the latter are assessed only in transitional waters). The WFD centres on the influence of hydromorphology in affecting the biota, although the chemical status of the water body is also assessed. The reference condition relates to what is expected for an area and is defined in one of four ways: by choosing a similar but unimpacted areas (i.e. a physical control similar to the test area but without human influences), by hindcasting (i.e. assessing what the area was like at some previous time), by deriving predictive models (i.e. predicting the benthic community of an area based on the physical characteristics—see below) and, lastly, by using expert judgement (again, see below).

The ecological quality is based upon the status of the biological, hydromorphological, and physicochemical quality elements. Consequently many methodologies have been proposed recently to assess the benthic ecological status of marine water bodies within the WFD (for details, for example see Borja *et al.* 2004 , Borja 2006, Quintino *et al.* 2006, Devlin *et al.* 2007, Simboura and Reizopoulou 2008). Of relevance here is the development, for the benthos within the WFD, of multimetric approaches to defining good ecological status. In particular this has produced benthic indices such as the AMBI (Muxika *et al.* 2007), BENTIX (Simboura and Reizopoulou 2008), and the biological quality index (Rosenberg *et al.* 2004) which in turn encompass many of the univariate and biotic community indices described earlier in this book.

Given that many studies in different countries are deriving indices of benthic quality, it is necessary to ensure that they are all producing equivalent results and conclusions. Hence this has led to intercalibration exercises and other comparison exercises whereby the same data sets have been used with different indices. For example, Quintino *et al.* (2006) analysed data from the Portuguese coasts to produce the univariate indices used for the WFD: abundance (*A*); species richness (*SR*); biomass (*B*); Margalef index (*d*); Pielou evenness index (J'); Shannon–Wiener ($\log_e H'$); Simpson's index $(1-\lambda')'$; the applied marine biological index (AMBI; Borja *et al.* 2004) and its reciprocal (1/AMBI); ecological quality ratio (EQR), calculated according to the UK MBITT Multimetric Approach (Borja *et al.* 2004); Biological Quality Ratio (BQI, Rosenberg *et al.*, 2004); abundance ratio (*A/S*); biomass ratio (*B/A*, Pearson and Rosenberg 1978). They found that some of the indices under-represented the ecological status and others over-represented it. They cautioned that this was not merely of academic interest, as misclassifying a area of good status as being of moderate status could result in expensive and unnecessary remedial work. Secondly, it was particularly notable that many of the indices needed refining to cope with the naturally low-diversity areas in estuaries and other brackish areas. This in turn has produced discussions about the *estuarine quality paradox* (Elliott and Quintino 2007) which emphasize the similarities between normal estuarine benthic fauna and flora and those subjected to anthropogenic stress. This type of anomaly is leading to refinements of many of the indices used for defining ecological status.

While the WFD will set the background for the applied science and management of European estuarine and coastal waters for the next decade, the MSD will take these ideas out to the 200 nautical mile (370 km) limit, or the midline between countries across a sea area (European Commission 2006). It will require countries to adopt marine spatial planning and marine protected areas and to define the concept of good environmental status (Borja 2006, Mee *et al.* 2008). Although the detailed implementation of the Directive is still being worked out, it is expected that good environmental status will be defined in terms of the physical, chemical, and biological state of the seas and thus will require extensive monitoring of the seabed.

As can be seen from this discussion, the development of benthic indicators is developing extensively and, in some countries, appears to moving towards a recipe-book approach for carrying out monitoring and for defining status. It is a matter of concern that there is the danger of creating a system which uses 'expert judgement' only as a last resort, after carrying out very detailed surveys. We take the view that we should train benthologists so that assessments can be made more cost-effectively, and that more effort should be directed towards the understanding of the science than merely running data through detailed statistical packages. We welcome the move in recent papers (e.g. Weisberg *et al.* 2008) towards evaluating the role of expert judgement in using indicators.

11.6 Predictive models and marine benthic management

As indicated above, there is an increasing need, especially by environmental managers, for models which can predict the nature of the benthic community in relation to environmental variables. In this way, the models can then be used to indicate whether the benthos in a given area differs from what is expected and also to indicate the results of management measures for the seabed. Several examples of current benthic predictive models are given below. First, Elliott and O'Reilly (1991) used the data for the communities and associated substrata at over 150 subtidal sites in the Forth estuary and Firth of Forth, eastern Scotland, during the period 1979–89 to create multiple stepwise linear regression equations for primary and derived community parameters (species richness, abundance, biomass, diversity, evenness) as the dependent variables. The models used the common environmental variables of depth, salinity, and substratum type as the independent variables. The computed equations explained up to 60% of the inherent variability in the dependent (biological) variables and it was not surprising that the best models were for species richness and diversity, which rely on the nature of the physical environment in producing available niches—the main indicator of the way an area supports different species. The parameters under much greater biological control, such as abundance and biomass, produced poorer models, as expected. Brinkman *et al.* (2002) also used a multiple regression model linked to a geographic information system (GIS) to derive a capability of predicting mussel beds in relation to environmental characteristics. More recently, Edgar and Barrett (2002) also used a multiple regression approach to predicting benthic community size but as well as including environmental variables, they started including biological variables likely to influence the benthic fauna, such as macrophyte biomass. Ysebaert *et al.* (2002) then used logistic regressions to create ecological response surfaces for 10 estuarine macrobenthic species. The regressions predicted the probability of occurrence of macrobenthic species in the Scheldt estuary (Belgium/Netherlands) as a response to the predictor variables salinity, depth, current velocity, and sediment characteristics. Although single logistic regressions provided good descriptions of the occurrence along a single environmental variable, the response surfaces obtained by multiple logistic regressions provided estimates of the probability of species occurrence across the spatial extent of the Schelde estuary with a relatively high degree of success. Ysebaert *et al.* (2002) concluded that this gave a good macrobenthic predictive capability in cases where patterns of distribution were strongly and directly coupled to physicochemical processes, as is the case at the estuarine macro- and meso-scale. Furthermore, they stated that the predictive models would be valuable in evaluating the results of estuarine management options.

Finally, as a potential management tool, Allen (2000) and Allen and Elliott (2004) developed the predictive model MARINPACS which was based on the same methodology used to produce the widely used freshwater invertebrate predictive model RIVPACS (Wright *et al.* 1989). Both MARINPACS and RIVPACS took detailed data sets linking the benthic community (species presence) with the main environmental variables and then used multivariate methods such as TWINSPAN (Gauch 1982) and canonical correspondence analysis to determine which environmental variables predict the community members. The MARINPACS model was developed using the UK National Marine Monitoring Plan benthic data set. The method makes it possible to predict what assemblage, and with what probability, is likely to occur under given conditions. Hence the models are then used to determine if an area differs from expectation. RIVPACS has been widely used in freshwater management, but MARINPACS still requires to be tested widely.

We take the view that research into methods which increase our predictive ability for the benthos are very much needed and will play an important role in the management of the seabed.

11.7 Benthic analytical quality control and quality assurance (AQC/QA) and data reliability

As indicated above, the management of marine areas relies heavily on the use of benthic biological and sedimentological information. There is an increasing trend to combine data sets produced by different laboratories and for different purposes, for example the Quality Status Reports for the North-East Atlantic (OSPAR 2000). In this case, it is increasingly important to ensure the quality and comparability of the methods used and the data produced (Ellis and Cross 1981, Ellis 1988, Elliott 1993). This, in laboratory analysis terms, is referred to as *analytical quality control and quality assurance* (AQC/QA) and it is always surprising that AQC/QA have always been regarded as of greater importance in analytical chemistry than in marine biology (Gardner *et al.* 2002)—indeed, since the 1970s in statutory agency laboratories it has been common for 40% of chemical analytical time to be spent on AQC/QA. In Europe, however, since the early 1990s there have been several QA schemes including QUASIMEME for chemicals and BEQUALM for biological effects and bioassays (Hylland 2006). Individual benthic studies include AQC/QA in order to provide greater confidence in the results produced (e.g. Silva *et al.* 2004), but national and international schemes are needed. It is now acknowledged that our methods for studying the benthos have to be standardized and quality controlled; accordingly many countries have adopted standard methods (e.g. see Davies *et al.* 2001 for the UK; SCCWRP 1998 for California; Rumohr 1999 in Germany for the ICES area, and the production of an ISO standard for benthos by NIVA in Norway). To this end, benthic workshops have also been organized by regulatory bodies in order to determine the comparability of methods (e.g. Proudfoot *et al.* 1997). *Intercomparison exercises* are organized to check on techniques and *intercalibration exercises* are organized to check on data production.

There are a few long-standing examples of AQC/QA in benthic work, for example the Southern California Coastal Water Research Project (SCCWRP 1998). In the UK, the National Marine Biological AQC scheme (UKNMBAQC) was started in the early 1990s because of the need to standardize methods and combine data under the UK National Marine Monitoring Plan (e.g. Gardner *et al.* 2002). The UKNMBAQC scheme aims to ensure comparable benthic methods and a high standard of sample preparation, sorting, and identification (Cooper and Rees 2002). It sets standards for the extraction and identification of benthic organisms, on the basis that laboratories performing poorly will have their data treated with caution.

Stribling *et al.* (2003) take this discussion further by differentiating taxonomic analyses for different types of investigations—research and what they call 'production taxonomic investigations'. In these, but especially in the latter, they emphasize the importance of evaluating and producing high-quality data and state that a knowledge of AQC/QA is essential before drawing and communicating conclusions from surveys. Benthologists should take the same view as analytical chemists and remember that their results are included in licence conditions, for example for dredging or pollution discharge, and that they could therefore be required to defend their data in a court of law.

It is now acknowledged that there are several elements of good practice to ensure that the benthic data produced are reliable and comparable (Table 11.6). AQC/QA are becoming increasingly important, not least because student training and competence in benthic taxonomy appear to be decreasing worldwide. Indeed, in many universities benthic taxonomy is relegated to a few days on a field course. As university educators, we have often remarked that while present undergraduate marine biologists are given training in DNA sequencing, the time they spend on identifying marine organisms is decreasing (it is no longer a sexy topic and seems to be seen as merely natural history!).

With regard to data reliability, we should always remember that a measurement is never exact, although it can be precise and accurate within certain limits, and also that measurements are made for a reason. Because of this, we should reinforce the difference between precision and accuracy in recording during marine benthic analyses. *Precision* means that the same measurement or class is achieved on each occasion an observation

Table 11.6 AQC/QA: components suggested for benthic taxonomic quality assurance and control

Adoption of standardized laboratory methods, i.e. laboratories to agree a set of well-documented methods, to join in accreditation schemes (e.g. ISO14001) if available
Use of inter-laboratory comparison exercises, i.e. samples to be exchanged between laboratories such as a ring-test of specimens circulated for checking and the cross-checking of whole samples (the sorting of the samples; the extraction, counting, identification and biomass determination of the specimens)
Use of an accepted species checklist and taxonomic literature, i.e. ensuring that all laboratories have an agreed species list (e.g. Picton and Howson 2000) with agreed taxonomic nomenclature and also that all laboratories have access to up-to-date taxonomic literature
Attendance at taxonomic workshops, as a means of increasing the skill base
Maintenance of a voucher specimen collection and comprehensive sample-storage procedure; again aiming for good laboratory practice
Use of expert checking of difficult specimens, i.e. acknowledging that certain benthic taxa need to be identified by experts

is made; for example, the weight of a specimen on a particular balance or the same identification of a taxon by one taxonomist. In contrast, *accuracy* means that the correct measurement or class is obtained on every occasion that an observation is made, for example the weight of a standard calibration material or the correct identification of a taxon by any competent taxonomist. Hence measurements can be precise without being accurate, for example a badly maintained balance could weigh precisely but not accurately.

In recent years the idea of *taxonomic sufficiency* has occasionally been debated, i.e. what level of taxonomic identification in benthic work is required to answer the questions being posed. Of course the detection of large populations of opportunistic polychaetes probably does not require high-level taxonomic separation (to species)—family- or order-level identification will provide sufficient information. The debate goes back to Richard Warwick's (1988) suggestion that for some questions, higher-level identifications will suffice, i.e. why go to species level when family level will provide the same amount of information. In some countries, this suggestion was seized upon by environmental managers who saw it as a way of reducing the time and thus the costs of benthic analyses. Dauvin *et al.* (2003) and Diaz *et al.* (2004) have recently returned to the discussion, with the former advocating a lower level of taxonomic separation (e.g. to order or family) as being sufficient for benthic impact assessments. However, we agree with Maurer (2000) who, while acknowledging that often the main benthic patterns can be seen with a lowered taxonomic separation, in this time of concern regarding biodiversity, threats to rare and fragile species, and introductions of alien and invasive species, higher taxonomic resolution is required. In considering this, the steering committee of the UK National Marine Biological AQC Committee, including one of us (ME), quantified the cost and time savings but concluded that the latter occur only when benthologists are trained to a high level—in essence, identifying organisms to family and order is only quicker if you are trained to identify them to species. We are concerned that a widespread use of low-level taxonomy would rapidly lead to an overall loss of competence.

Concluding remarks

As shown throughout this book, we now have a good background of knowledge about the marine benthos and its habitat and we are using that knowledge both to understand the science of marine sediments and to improve their management. Following the terms that we used in the introduction, we have a good conceptual and quantitative knowledge of the way in which the environmental characteristics influence the biota (what we called the *environment–biology relationships*) and a relatively good conceptual and semi-quantitative knowledge of the biological interactions (the *biology–biology relationships*). However, our knowledge of the way in which the benthic biota modify and structure the sediments (the *biology–environment relationships*) still needs to increase both conceptually and quantitatively. We have some good models of disturbance (such as the Pearson–Rosenberg paradigm) and excellent quantitative analysis techniques which have increased our knowledge of temporal and spatial variability. We have, for many geographical areas, a relatively good spatial coverage although there is still variability due to the methods used, but we can build on many national and international projects.

We have started to define the objectives for managing the seabed and we have a plethora of indices and indicators, although we still cannot fully quantify the behaviour of those indicators.

Despite all this, and our frequent uncertainty about what the results are showing, the environmental managers and legislators and statutory bodies still demand that we use quantitative indicators even for naturally highly variable systems. We have laws and directives (statutory instruments) which merely say 'test an area to see if it differs from a clean reference' without a full appreciation that natural variability can mask a human-induced change. We have spent a large amount of effort quantifying the spatial and temporal variability in benthic systems and, building on this, we have shown a willingness, despite our reservations, to interpret management initiatives and create some tentative standards as treatment/reference comparisons. Nevertheless, industry and regulators are requiring us to do more.

As indicated many times throughout the book, we have shown that we are aware of the limits and constraints to benthic monitoring and data quality but we emphasize that monitoring has to have a sound, hypothesis-based approach. However, because of the potentially high costs of doing seabed monitoring, and if benthologists are to be taken seriously, then the surveys also have to be cost-effective and proportionate to the problem being assessed. The surveys have to be at the appropriate taxonomic level and with the adequate confidence and precision in classification, they have to build on and link with the physicochemical understanding. Furthermore, the frequency of monitoring of the biological elements has to be biologically relevant. However, all of this, if carried out properly, will be expensive. As expected, we make a plea for the availability of adequate resources (skills, finances, and time) for benthic research, including monitoring. We also give a warning to those requiring benthic information in decision-making: *you get what you pay for!* Again, we have often been subjected to discussions where marine developers and industry want benthic information but do not appreciate that obtaining it is both time-consuming and costly. In fact, we have occasionally got the impression that non-benthologists think that the specimens retrieved have a barcode for identification and that as the laboratory work involves labour rather than an expensive piece of equipment then it must be cheap!

In our careers we have often heard the cry that we do not have sufficient data to make decisions. We take the view that, in this less than perfect world, managers will have to make decisions based on the best available data and information. Furthermore, as we have cautioned throughout this book, we have created systems in which data are gathered for the wrong reason, that they are of an insufficient spatial and temporal resolution to be of use, and that their quality is insufficient to answer questions, especially for inter- and intra spatial and temporal comparisons.

Our numerical treatment of the benthic data is vast and the methods available are increasing annually. There are still many occasions, however, where applied users of the benthic data must find their eyes glazing over at the sight of yet another ordination plot purporting to show community benthic structure—perhaps we should continually stress the need for more information rather than more data. Furthermore, within our approaches, we seem to be very good at deriving new methods although perhaps we are not so good at pointing out methods that have outlived their usefulness. But there are exciting developments—we are now developing realistic predictive models from multivariate approaches and will therefore soon be in the same position as our freshwater colleagues in being able to predict the type of marine benthic community based on the physicochemical characteristics.

Throughout this book we have described the type of data and information resulting from benthic studies but we have also come across many examples where the data are not used fully. We therefore point out that benthologists should beware of data collation for its own sake but also ensure that the data can be used for wider analysis (meta-analysis). Sometimes, however, there appears to be data overload but information paucity, meaning that data have not been translated to information. Similarly, we have seen many examples concentrating on structural aspects in the benthic system when in fact the studies could and should be taken further into benthic functioning to increase our understanding. It is often the functional aspects that are of greater importance to increasing our understanding of the processes and responses in the system. Given the intimate relationship between the benthic biology and physical chemistry, studies should cover these aspects synoptically.

From the examples presented here, we have shown that there should be a logical framework in the applied collection and use of benthic data:

surveillance → monitoring → targeted/automated
or best available evidence → modelling
→ feedback into management

within which are embedded a good conceptual understanding and hypothesis generation and testing. Of course, some of the aspects are still being developed but this is the direction for future research. As yet, our ecological predictive models are good at the conceptual level and they allow us to develop and test ecological theory and to do scenario-testing but, if ever they were plotted, we would assume large confidence limits in the outputs. We thus continually need to give a health warning on the use of the data and information. Because of this, we continually question whether the ecological models will be adequate for management but, despite that, we are convinced of the need for their further development.

Our methods for use in studying the benthos are sufficiently developed, and 'how' to do the measurements is easy once the 'why' and 'what' are agreed. However, often the 'why' (the objectives) is not sufficiently well thought out and so, consequently, the data analysis and interpretation become muddled. In addition to this, as researchers who have spent a large amount of time using marine techniques to help solve environmental problems, we often see a dichotomy between the pure scientists and the applied scientists/environmental managers in that the former wish to carry out studies merely for gathering knowledge (the 'nice-to-know' approach) whereas the latter require science, including monitoring, to be 'fit-for-purpose' and on a 'need-to-know' basis. Indeed, in this time of reduced research funding, our benthic research still has to fit the criteria of creating knowledge, aiding wealth creation, and enhancing the quality of life. As we hope to have shown here, benthic research certainly does fulfil these criteria.

Benthic information will continue to be a mainstay of marine environmental management and impact assessment. Of course, we can further develop recipe-book monitoring where every detail is given, where statistical rigour is paramount, where decision support systems are available, and where data analysis results in indicator values that lead to management actions. However, we reiterate that such an approach could require a prohibitively expensive survey and so it may sometimes be better to base management on a 'best available, expert knowledge' approach.

We also hope to have shown that benthic research will continue to be the breeding and testing ground for ecological theory. Given concerns about global change, introductions of alien and invasive species, pollution, and the loss of biodiversity, benthic research has to devote more attention to the biodiversity–ecosystem functioning debate. Benthic research has an important role within integrated marine science and management where that integration covers several levels of biological organization, from the cell to ecosystem and society and where we take the ecosystem approach in merging the natural sciences and the social sciences. It links the understanding of biodiversity and ecological goods and services to the provision of economic goods and services and thus forces us to ask what society wants from the seabed and how this can be assured without damage to ecological functioning. Benthic research and monitoring will continue to provide much-needed information on problems from the local to global scale and the short to long term.

Finally, we point out that marine environmental science and management requires a strong and rigorous benthic component and that the latter requires a suitable education and training. We further emphasize that an understanding of the benthic biological system is only possible if we have an understanding of the physicochemical system, and so the education and training of benthologists has to be broad and integrated. However, benthic science requires such an approach and induces such a way of thinking that it should not only be included in all marine biology education but also embedded in all environmental education. There are aspects of marine benthic training that are fundamental to all biological knowledge—for example, studying the benthos as part of a marine biological field course is the only way biologists will see most of the invertebrate phyla. Hence we make a plea for maintaining training in marine invertebrate taxonomy, now so often mimimized in university biology courses, as otherwise we will have a generation of marine biologists skilled in molecular techniques but unable to recognize a polychaete!

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