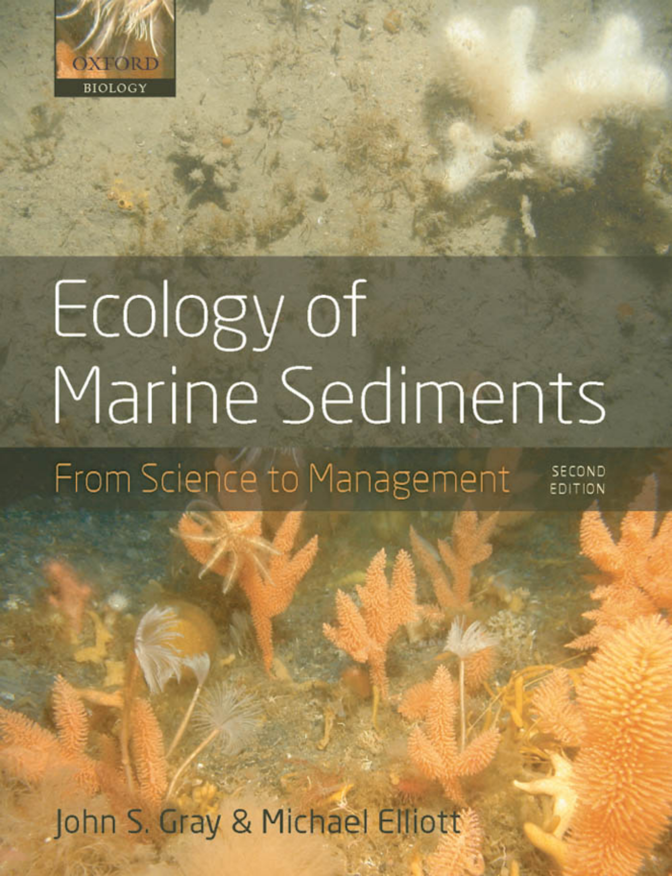

OXFORD BIOLOGY

Ecology of Marine Sediments

From Science to Management

SECOND EDITION

John S. Gray & Michael Elliott

Ecology of Marine Sediments

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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

* 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*

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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.

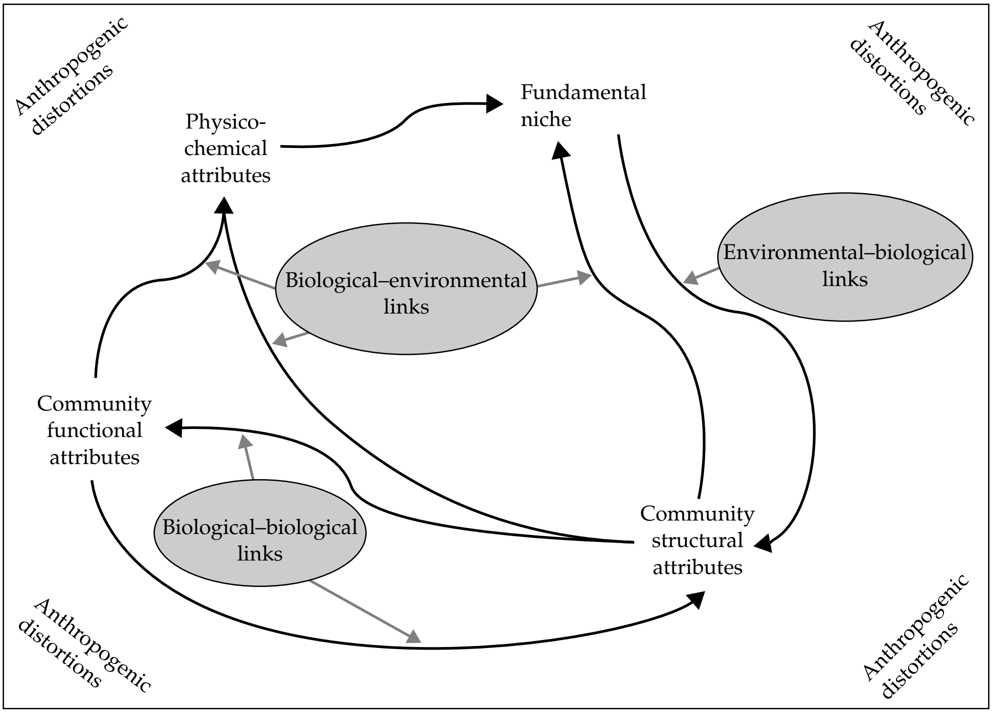

Figure I.2 Benthic community forcing factors – a conceptual model of the main relationships (from Elliott *et al.* 2006).

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

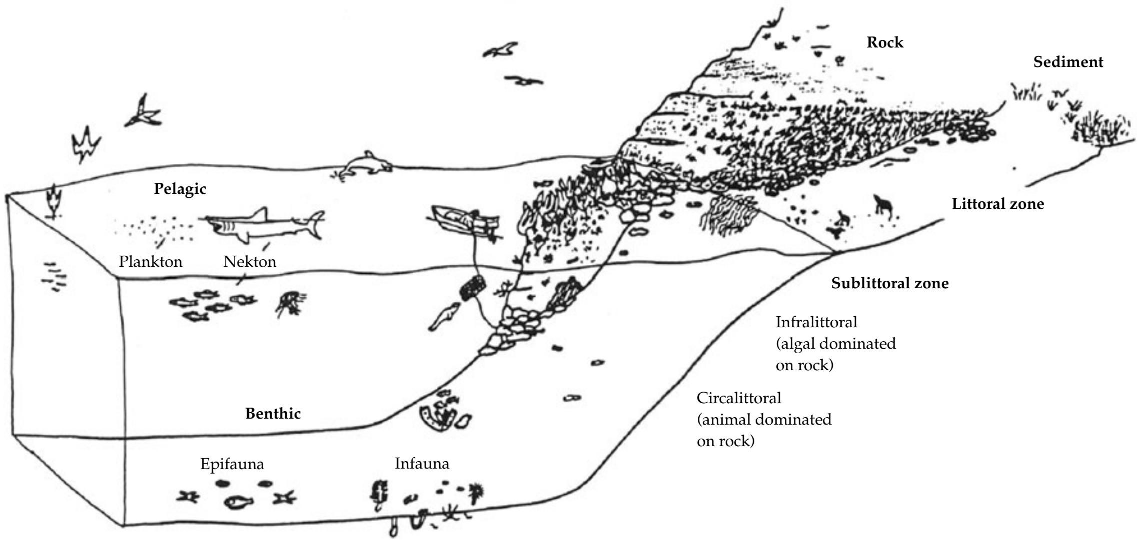

Figure I.3 The components of the nearshore system (drawing by Keith Hiscock 1996; taken from Hiscock 1996).

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

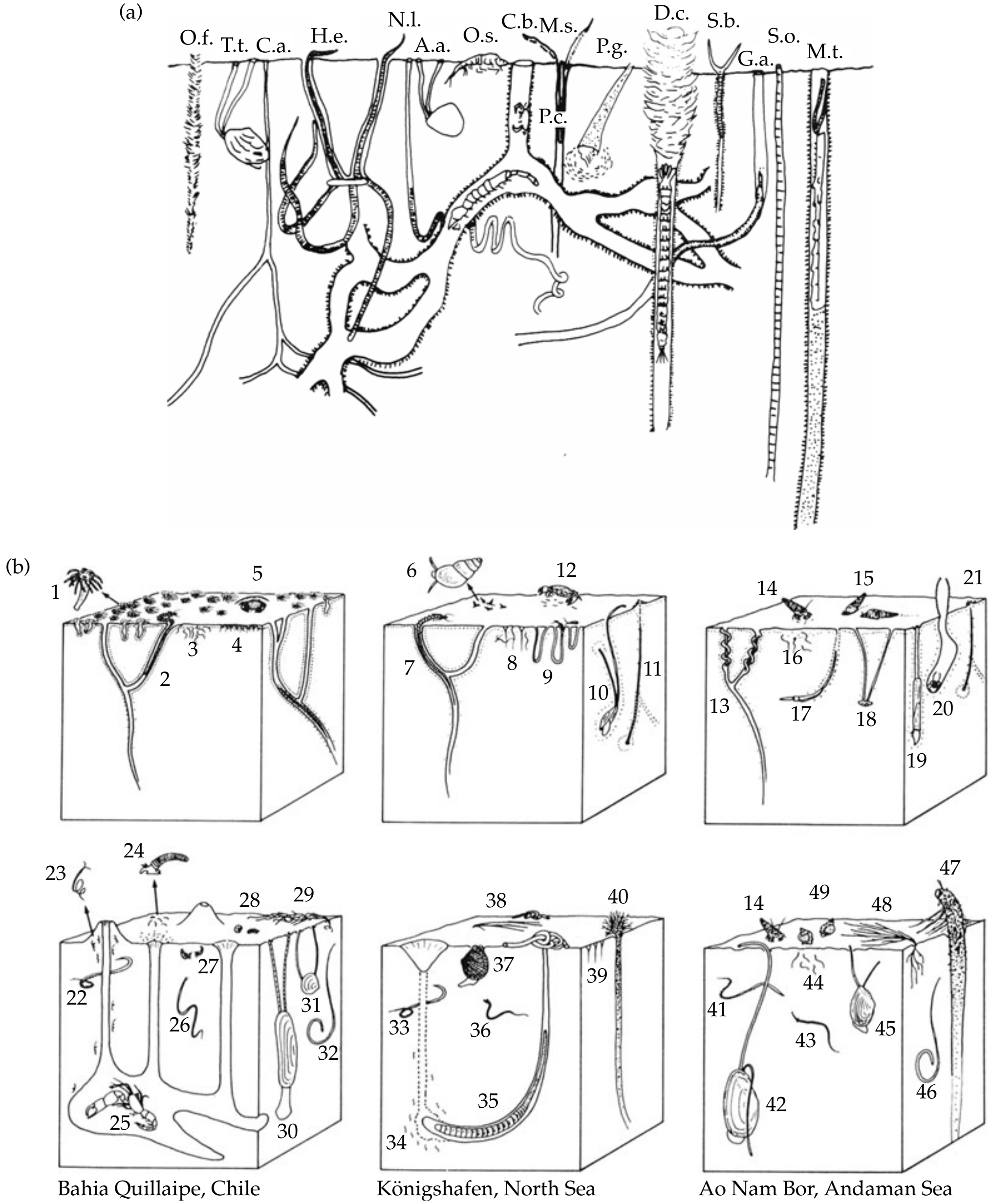

Figure I.4 (a) Location of most important benthic animals, burrow and tubes in a shallow-shelf environment in Georgia, USA. A.a., Abra aequalis; C.a., *Capitomastus* cf. *aciculatus*; C.b., *Calianassa biformis*; D.c., *Diopatra cuprea*; G.a., *Glycera americana*; H.e., *Hemipholis elongata*; M.s., *Magelona* 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