ECOSYSTEMS OF THE WORLD

28

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Edited by

P.A. Tyler

School of Ocean and Earth Science,
Southampton Oceanography Centre,
European Way,
Southampton SO14 3ZH,
United Kingdom

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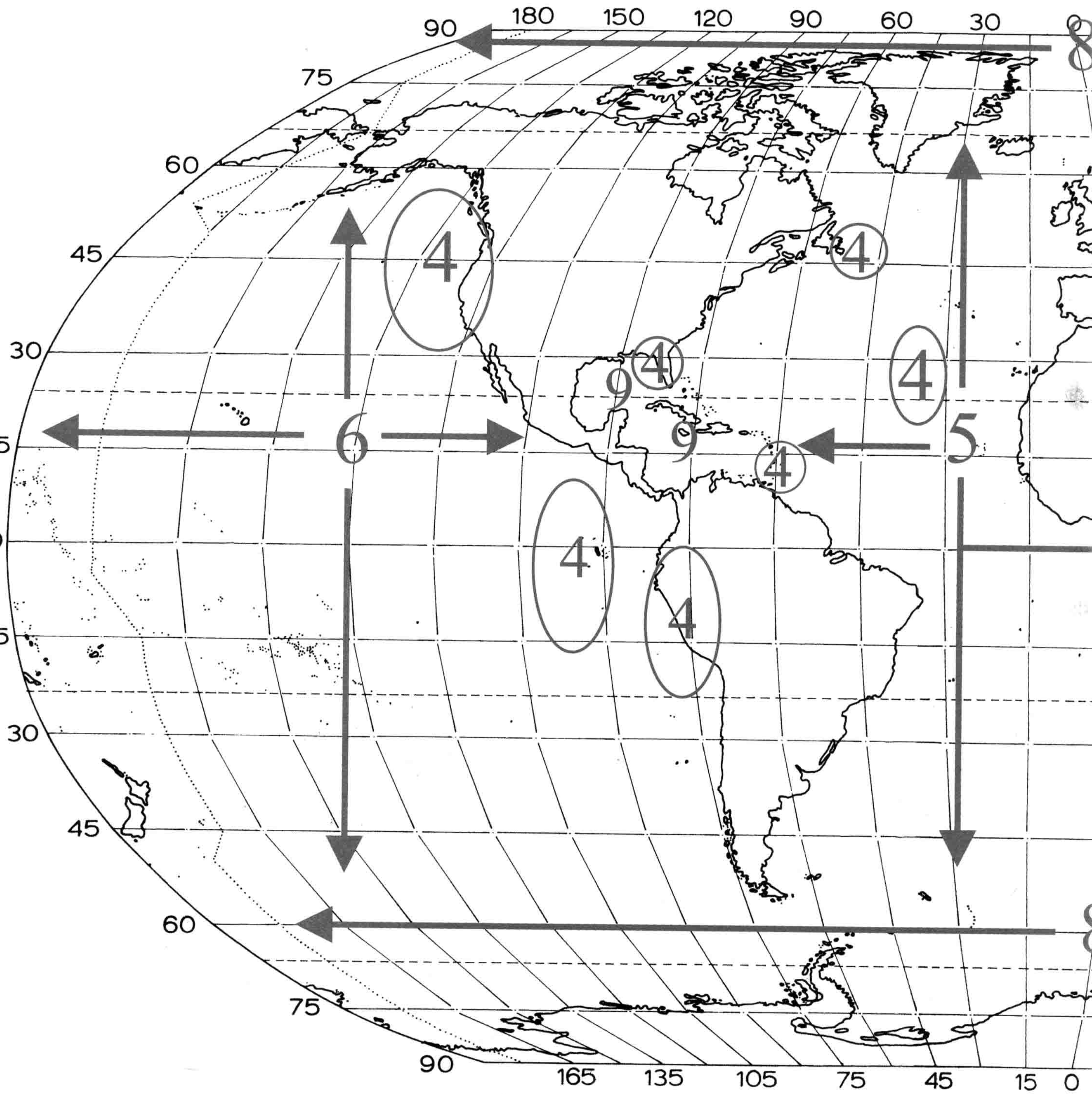

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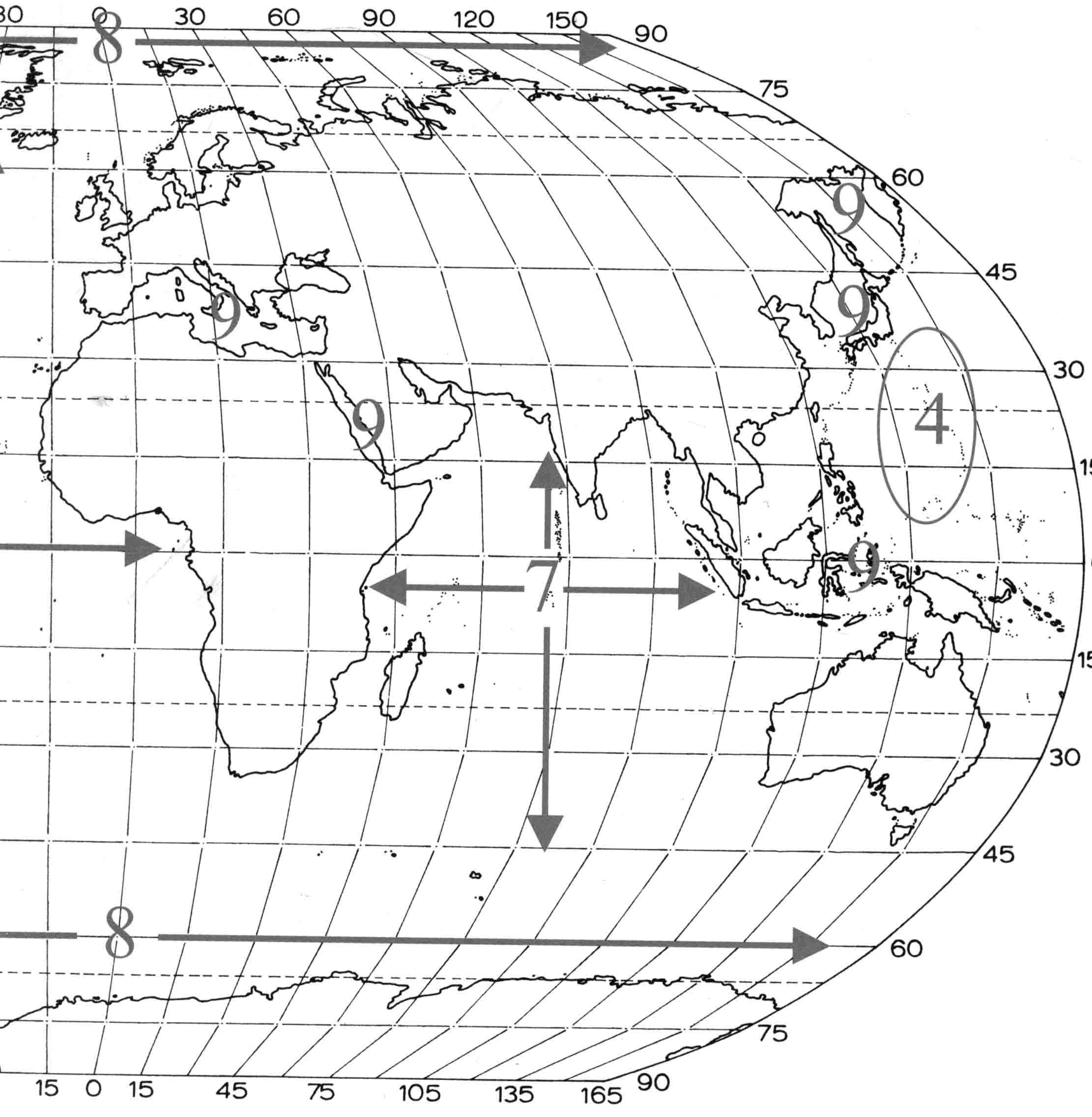

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Editor in Chief:

David W. Goodall

Centre for Ecosystem Studies, Edith Cowan University, Joondalup, W.A. (Australia)

PREFACE

The deep ocean floor covers over 50% of the surface of the earth. It is often said that we know more about the surface of the moon than we do about the deep ocean floor and the water column above it. While this is not strictly true, we do know remarkably little, as a proportion of the total, of the deep ocean environment. Paradigms are continually changing, and we know now that the deep sea is an ecosystem of high species diversity, that it may have seasons as seen in temperate land ecosystems, and that in certain areas turbulence can be a great as anything seen in coastal shallow waters. Last, but by no means least, the originally perceived idea that the deep sea was an oligotrophic environment in which all environmental processes were gentle and physiological processes slow is no longer valid. We know now that the deep sea is essentially a heterotrophic system fuelled by organic carbon from surface waters, with the notable exception of hydrothermal vents and cold seeps where substantial ecosystems are fuelled by chemosynthetic processes. The continuing theme of this volume is how this energy input affects the deep-sea ecosystem.

All science has its eras of exploration, observation and experimentation. Exploration in deep-sea biology is often considered to have come to a finale with the *Galathea* cruise of 1950 to 1952. Subsequent discoveries of hydrothermal vents and cold seeps show that the deep-sea age of exploration is still with us and will continue. The 1960s saw the first change in our perception of the deep-sea with the introduction of more sophisticated sampling gear. This has been used from then and still continues to be used for much observation work. The introduction of submersibles, and, more recently, remote operated vehicles and landers, has allowed us to conduct manipulative experimentation on the deep sea bed and in the water column.

This volume is a review of where our knowledge stands at this point. All the chapters are written by authorities on their respective subjects, all of whom are still practicing deep-sea biologists. The volume is divided into sections covering the environment of the deep sea, specific deep-water seas and oceans, and lastly a review of the processes that occur there. All the chapters have been peer-reviewed by other experts in deep-sea biology, to all of whom I extend my thanks for their care and advice.

I wish to say a special thank you to all the authors. As I have said above, all are active research scientists, often working for extended periods at sea. I know their scientific lives are full, and I am delighted they were willing to write chapters and put up with my impatient prodding. I would also like to thank the series editor David Goodall for his advice, enthusiasm, patience and his unremitting courtesy when I failed to answer his requests! Lastly, I would like to express my sincere thanks to Lida de Maaijer Hoek of Isys Prepress Services for her patience, good humour and exceptional care in the desk editing of this volume.

Paul A. Tyler
Editor

LIST OF CONTRIBUTORS

M.V. ANGEL
Southampton Oceanography Centre
University of Southampton
Southampton SO14 3ZH
United Kingdom

A. CLARKE
Biological Sciences Division
British Antarctic Survey
High Cross
Madingley Road
Cambridge CB3 0ET
United Kingdom

A.W.J. DEMOPOULOS
Department of Oceanography
University of Hawaii at Manoa
1000 Pope Road
Honolulu, HI 96822
USA

R.J. ETTER
Department of Biology
University of Massachusetts
100 Morrissey Boulevard
Boston, MA 02125
USA

J.D. GAGE
Scottish Association for Marine Science
PO Box 3
Oban Argyll PA37 1QA
United Kingdom

A.J. GOODAY
DEEPSEAS Benthic Biology Group
George Deacon Division for Ocean Processes
Southampton Oceanography Centre
European Way
Southampton SO14 3ZH
United Kingdom

S.K. JUNIPER
GEOTOP
Université de Québec á Montréal
Montreal, Quebec H2X 3Y7
Canada

L.A. LEVIN
Integrative Oceanography Division
Scripps Institution of Oceanography
La Jolla, CA 92093-0218
USA

M.A. REX
Department of Biology
University of Massachusetts
100 Morrissey Boulevard
Boston, MA 02125
USA

M. SIBUET
DERO/EP
IFREMER Centre de Brest
29280 Plouzane
France

C.R. SMITH
Department of Oceanography
University of Hawaii at Manoa
1000 Pope Road
Honolulu, HI 96822
USA

C.T. STUART
Department of Biology
University of Massachusetts
100 Morrissey Boulevard
Boston, MA 02125
USA

H. THIEL
Poppenbuettler Markt 8A
Hamburg, 22399
Germany

D. THISTLE
Department of Oceanography
Florida State University
Tallahassee, FL 32306-4320
USA

V. TUNNICLIFFE
Department of Biology
University of Victoria
Victoria, BC V8W 2Y2
Canada

P.A. TYLER
School of Ocean and Earth Science
and DEEPSEAS Benthic Biology Group
Southampton Oceanography Centre
University of Southampton
Southampton SO14 3ZH
United Kingdom

C.M. YOUNG
Oregon Institute of Marine Biology
University of Oregon,
PO Box 5389
Charleston, OR 97420
USA

To my wife Amanda for her love and support over the years, and her patience with the amount of time I spent at sea!

CONTENTS

Chapter 1

INTRODUCTION

Paul A. TYLER

The largest single ecosystem on earth is the deep sea. The sea surface occupies ~70% of the surface of the earth, and 50% of the surface of the earth is covered by more than 3000 m of ocean, with a mean depth of ~3800 m. It is the very remoteness of the deep sea and the difficulties encountered in its exploration that have resulted in it being one of the least understood environments on earth. At the present time there is detailed information about specific areas of the deep sea, but these are mere pinpricks in the vastness of this environment. The understanding of the deep-sea ecosystem is entwined with some of the most exciting aspects of scientific exploration and with the development of technologies for sampling and penetrating this environment. This volume is a status report, at the beginning of the 21st century, on current knowledge of the deep sea, on how perceptions of it have changed and where the exciting scientific discoveries will be made in the future.

CHANGING PARADIGMS

Explorers and commercial interests have used the sea as a means of transport for millennia. However, they always looked to the horizon, and it was only in the latter part of the 19th century that scientists went to sea with the specific aim of looking downwards into the impenetrable depths.

One of the first was Forbes (1844), who sampled down to a depth of 600 m in the Aegean. Today one would consider this choice of sampling station as unfortunate, since this region of the Mediterranean deep sea is faunistically very poor, and the lack of animals in Forbes's samples led to the 'azoic theory' that little or no life existed below 600 m. The establishment of such a paradigm was in direct opposition to observations of the ophiuroid *Astrophyton* being brought up on a sounding line from a depth of 1800 m in Baffin Bay (Tyler, 1980), and the pioneering work of Michael and G.O. Sars in Norwegian fjords (Sars, 1864, 1868).

Establishing the presence of a fauna in the deep sea presented irresistible challenges to a small group of scientists led by Charles Wyville Thomson. Wyville-Thomson used HMS *Porcupine* to sample the ocean to the northwest of Scotland and to the west of Ireland in the late 1860s, and found a fauna at depths exceeding 4000 m (Thomson, 1873). This series of cruises established the first ecological observation in the deep sea by showing that there was a marked temperature difference associated with faunal change as one moved across what is now called the Scotland–Faroes–Iceland Ridge from the warm deep North Atlantic to the cold deep Norwegian Sea (see Chapter 6). The results of the *Porcupine* sampling programme led directly to the HMS *Challenger* expedition of 1872 to 1876. This expedition traversed the oceans of the globe and demonstrated a widespread and varied fauna in the deep sea, as well as taking numerous physical and chemical measurements. The results of this cruise, now considered the forerunner of modern oceanography, were published in a series of detailed volumes edited by, and at the expense of, John Murray. A readable account of the *Challenger* expedition has been published by Linklater (1972).

The *Challenger* expedition led directly to the 'heroic' age of deep-sea exploration, with expeditions sampling many areas of the world's oceans (Menzies et al., 1973; Mills, 1983). The heroic age culminated in the Danish *Galathea* expedition of 1950 to 1952, which demonstrated that life could be found in the deepest of all the oceans, in the ocean trenches. One of the main outcomes of this age of exploration was the publication of descriptions of the fauna collected on these voyages.

Taking stock of deep-sea ecology at this point in time would have led to the establishment of the following paradigms:

- The deep sea was species-poor.
- It was a tranquil quiescent environment.
- There was a slow rain of material from surface to the deep (although see Moseley, 1880).
- No primary production occurred within the deep sea.

The 1960s heralded a new approach to deep-sea ecology, driven by technology. Quantification became the name of the game, and to get accurate data it was necessary to replace the coarse-meshed qualitative sampling gear of the heroic age with more refined quantitative gear. This was initially achieved by Howard Sanders and Robert Hessler from the Woods Hole Oceanographic Institution, who used an anchor dredge (later an anchor box dredge: Gage and Tyler, 1991) to sample a series of stations down to a depth of 5000 m between Gay Head, Massachusetts and Bermuda. The fine mesh of the anchor dredge collected a wide variety of species, many new to science, which had been missed by the coarse dredges of the heroic age. Thus the concept of high biodiversity in the deep sea was established, although the absolute diversity is still very much subject to debate (see Chapter 10); but it is now believed that the deep oceans are as diverse as tropical rain forests.

Although known to be diverse, it was assumed that the deep-sea system was heterotrophic, relying on the slow sinking of material from surface waters to provide an energy source for the inhabitants. The 1970s and 1980s provided evidence that this environment was more dynamic than originally thought. The first example was the discovery of hydrothermal vents along the Galapagos Ridge in 1977 (see Chapter 4). For the first time there was evidence that primary production could take place within the deep sea, and an ecosystem independent of sunlight had been discovered. This discovery led to one of the most active programmes in deep-sea biology, and the discovery of hydrothermal vents continues to this day. There can be few people interested in the natural environment who have not seen photos or videos of these spectacular environments. Subsequently, a second type of primary-production environment was observed in the form of cold seeps (see Chapter 4). Both hydrothermal vents and cold seeps are driven by the availability of reduced chemicals such as hydrogen sulphide and methane, the main difference being the temperature of emission.

In terms of energy availability a parallel, but no less important, revolution was occurring in understanding the input of material from surface primary production. The concept of the slow rain of surface primary production to the seabed was challenged by technological advances, particularly in the use of sediment traps to collect the sinking material. Such sediment traps, together with other techniques (see Chapters 2 and 11) showed that, particularly at temperate latitudes, surface production sank rapidly to the seabed – on average, at a rate of $\sim 100\,\mathrm{m\,d^{-1}}$. As a result, the signal of seasonal surface production was transmitted to the seabed, and it is now known that a number of organisms on the deep-sea bed respond seasonally to this input. This theme is explored in many chapters in this volume.

This seasonal perturbation is mild in comparison to the last major shift in paradigms. Over certain areas of the seabed, especially under areas of high surface-eddy kinetic energy, benthic storms are created by the input of energy to the seabed. These storms are analogous to the blizzards of Antarctica. They create strong currents transporting sediment, which is then deposited in drifts on the seabed, smothering the local fauna (see Chapter 2).

Lastly, technology has allowed humans to penetrate this 'remote' environment. SCUBA diving is limited to the top 30 m of the water column; but the development of submersibles has allowed scientists to dive to the deep-sea bed and conduct manipulative experiments as though they were working at the laboratory bench. Current knowledge of hydrothermal vents and cold seeps would be insignificant if it were not for the submersible. Submersibles are still used today; but the Remote Operated Vehicle (ROV) allows similar access from the comfort of the surface tender without the potential dangers of manned submersibles.

Today one may summarize the paradigms for the deep-sea environment as:

- High species diversity.
- Periods of benthic storms perturbing an apparently gentle environment.
- Seasonal input of surface-derived energy for heterotrophic organisms.
- Primary production at vents and cold seeps.

The change in understanding of the deep sea has been a function of an increase in the ability of scientists to gain knowledge from this environment. Despite recent recognition of the above paradigms, all of them are natural phenomena. As yet the deep sea is exploited only to a very limited extent, but this may change in the future. Disposal of waste has become prominent on the political agenda, particularly as land-based disposal areas become saturated. The deep sea has already been used for the disposal of low-level radioactive waste, pharmaceuticals and dredge spoil (see Chapter 13). Possibly more insidious is the use of the deep sea in relation to climate change. There is evidence of 'natural' decadal-scale changes in the fauna of the northeast Atlantic, possibly related to climate change. The deep sea has also been suggested as a repository for the excess carbon dioxide causing the so-called 'greenhouse effect'. The vastness of the deep ocean aids its very stability, but in localized areas this is already being challenged. The public outcry over the 'Brent Spar' (see Chapter 13) demonstrates that public awareness of this environment is increasing rapidly. Finally, with the decline of continental-shelf fisheries, fishing fleets are moving into deeper and deeper water, and there is evidence that at least one deep-sea fish, the orange roughy (*Hoplostethus atlanticus*), is already overexploited.

THE DEEP SEA TODAY

What is the deep-sea? Ask virtually any deep-sea biologist and you get a slightly different answer. For most, it is the region below 200 m, representing the transition from the continental shelves to the continental slope. This is the boundary that has been selected for this volume (see Chapter 2). Definitions based on light penetration, depth of the mixed surface layer, or temperature may be just as valid (see Gage and Tyler, 1991).

The approach to this volume has been to examine the deep sea from a number of facets, and differs from the approach of most previous volumes in this series. The linking theme between all the chapters is the availability of energy for organisms in the water column and at the deep-sea floor. Chapters 2, 3 and 4 examine environmental aspects of the deep sea – specifically the deep-sea floor, the water column and reducing environments. Chapters 5, 6, 7, 8, and 9 examine the ecology of the major oceans and those seas peripheral to the main ocean that have waters of oceanic depth. Chapters 10, 11 and 12 examine some of the specific processes that occur within the deep-sea ecosystem; and Chapter 13 explores the anthropogenic impact that has taken place or that may occur in the future.

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I would like to take this opportunity to thank all the authors who have contributed to this volume. I may be editor but it has been a collective enterprise by a series of world-class scientists whose passion is for the marine environment and the deep sea in particular. I would also like to thank David Goodall for his forbearance throughout its production.

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Chapter 2

THE DEEP-SEA FLOOR: AN OVERVIEW

David THISTLE

INTRODUCTION

This chapter provides a general introduction to the ecosystem of the deep-sea floor, beginning with a description of the physical environment of the deep sea. A section on how information is obtained about the deep-sea-floor ecosystem follows, because knowledge of this ecosystem is greatly influenced by the effectiveness of the available technology. Introductions to the fauna of the deep sea where the substratum is sediment (soft bottoms) and where it is not (hard bottoms) follow. The chapter concludes with a section on the pace of life in the deep sea.

The geographic extent of the deep-sea-floor ecosystem

The deep sea is usually defined as beginning at the shelf break (Fig. 2.1), because this physiographic feature coincides with the transition from the basically shallow-water fauna of the shelf to the deep-sea fauna (Sanders et al., 1965; Hessler, 1974; Merrett, 1989). The shelf break is at about 200 m depth in many parts of the ocean, so the deep sea is said to begin at 200 m.

The deep-sea floor is therefore a vast habitat, covering more than 65% of the Earth's surface (Sverdrup et al., 1942). Much of it is covered by sediment, but in some regions (e.g., mid-ocean ridges, seamounts) bare rock is exposed. In the overview of environmental conditions that follows, the information applies to both hard and soft bottoms unless differences are noted. The ecosystems of hydrothermal vents and cold seeps are special cases and are described in Chapter 4.

Environmental setting

The deep-sea floor is an extreme environment; pressure is high, temperature is low, and food input is small. It has been characterized as a physically stable environment (Sanders, 1968). Below I review the major environmental variables and indicate circumstances under which these environmental variables constitute a biological challenge. I also show that the image of the deep-sea floor as monotonous and stable

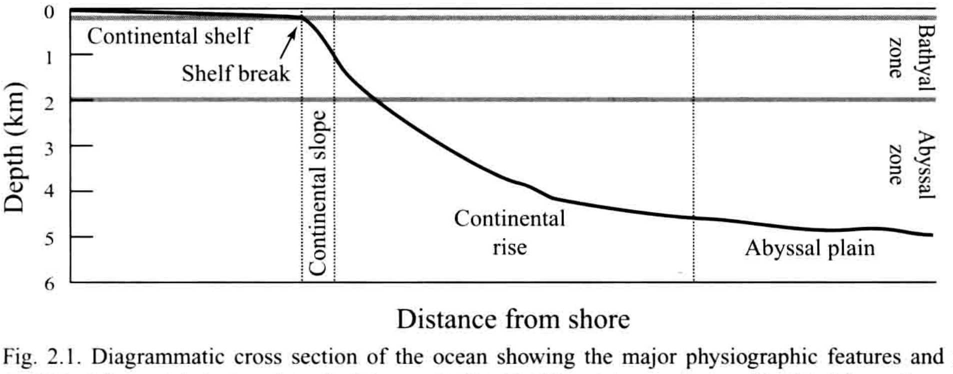

Fig. 2.1. Diagrammatic cross section of the ocean showing the major physiographic features and major depth zones. The sublittoral zone (0–200 m) is not labeled, and the hadal zone (6000–10 000+ m) is not shown. Modified from Gage and Tyler (1991). Copyright: Cambridge University Press 1991. Reprinted with the permission of Cambridge University Press.