AN INTRODUCTION TO MARINE ECOLOGY

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Preface

Several books have been written in which the words 'marine ecology' form part of the title and many more have been devoted to 'marine biology'. Why yet another? Once, when we knew very little of the lives and interactions of marine organisms, it was possible to outline the biology of the seas within one pair of covers; but it was possible only because of the extent of our ignorance. Who, during the same period, would have contemplated writing (or reading!) a book entitled 'terrestrial biology'? We now know much more of the biology of the sea, including its ecology, yet many introductory accounts still adopt the early descriptive approach concentrating on what organisms live where, how they are zoned in space, how they are adapted to their environment, etc. All worthy subjects, no doubt, but only a small part of 'ecology'. As university teachers faced with the task of providing undergraduates with their first taste of marine ecology, we have felt unable whole heartedly to commend any existing book as introductory or background reading to our courses. Available texts either suffered from the drawbacks mentioned above or were too specialized. Hence we set out to produce the sort of text which contained the information which we wished our students to know. To some extent the selection of topics and information is therefore a personal one, but we felt that there must be others besides ourselves faced with the same difficulties and who would find useful an introductory book concentrating on the trophic, competitive and environmental interactions of marine organisms and on the effects of these on the productivity, dynamics and structure of the marine system. Fortunately for us, Blackwell Scientific Publications agreed.

The book is therefore intended for students with some knowledge of ecology in general but about to venture for the first time into the *Mare Incognitum*. Each chapter covers a distinct process or subsystem of the ocean, and to that extent is complete within itself. Within this format, however, each possible subject-area is not covered in equal depth in each chapter: some processes operating throughout the sea are mainly described in relation to a single habitat type. Our knowledge of the effects of competition and predation on marine communities, for example, have largely been derived from work on rocky shores, and the following text cannot but reflect this.

It follows from the paragraphs above that we feel that the approach and synthesis presented here are different from those obtainable elsewhere—not least in our attempt to break away from 'classical marine biology'—and so we would like to hope that the book will also appeal to a wider audience as an introduction to

this rapidly growing subject.

Both authors accept responsibility for all the material in the book: each amended the labours of the other. Nevertheless, RSKB was mainly responsible for Chapters 1, 2, 3, 4, 7, 8, 11 and 12 and RNH for Chapters 5, 6, 9 and 10. Several people gave generously of their time and knowledge to save us from sins of omission and commission: in no way are they responsible for any errors which remain. Robert Campbell of Blackwell Scientific Publications was involved in the preparation of the book from the moment of its inception; we are sincerely grateful for his copious help, constructive criticism and advice. The authors are also delighted to record their appreciation of the labours of Jan Parr who drew the vignettes for many of the figures and who drew the illustrations of whole organisms for this book. The index was prepared by Hilary Barnes and Jean Hardy.

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1 The Nature and Global Distribution of Marine Organisms, Habitats and Productivity

1.1 Introduction

At the most gross level of analysis, the solid surface of the globe is formed by two different types of crustal materials: thin, dense oceanic crust and thick, light continental crust. Both float on the denser, upper layers of the mantle—the oceanic crust as a thin skin and the continental crust as a large lump—and both move in response to convection currents in that mantle. The oceanic crust is geologically young and is created continually along the mid-oceanic ridges; it then moves away from the ridges and is eventually resorbed into the mantle beneath the oceanic trenches. The continental crust, in contrast, is much older and it floats above, but is moved by, this sea floor spreading.

The existence of these two forms of crust is reflected in the earth's surface relief. Most of the ocean bed is a level expanse of sediment (with slopes of less than 1 in 1100) lying 3–4000 m below sea-level. From this plain, the huge continental blocks rise steeply, with an average upward slope of some 1 in 14 but in some areas with an average slope of more than 1 in 3, up to a depth of between 20 and 500 m (with an average of 130 m) below sea-level. At this point, representing the angle between the side and top of the continental mass, the gradient usually changes dramatically, falling to about 1 in 600. The average height of the top surface of the continent is less than 1000 m above this point.

Thus, ignoring the water for a moment, we have a scenario of a level ocean bed from which arise sheer-sided, topped or gently domed blocks averaging just over 5300 m in height. Also arising from our level plain would be volcanoes and the mid-oceanic ridges. Of course this is a considerable over-simplification, not least because the movement of sediment from the continents to the oceans tends to blur the starkness of the relief. Major rivers, when they discharge into the sea, do not lose their integrity but flow in submarine canyons scoured out by sediment-laden water. The 'river water' is no longer fresh but a dense suspension of sediment in sea-water and this descends the sides of the continental mass, the sediments being discharged into the angle between that mass and the oceanic bed. Great fans of sediment may extend out up to 600 km from the continental base, resting at an average slope of about 1 in 60 and forming ramps leading from the ocean floor to the continental sides.

This surface topography spans a height of almost 20 km (from the highest point on any continental block to the lowest point in an oceanic trench) but nevertheless this is an insignificant fraction of the earth's radius (0.3%). If, arbitrarily, we set the base of

the rising continental blocks at a depth of 2000 m, then they would occupy 41% of the earth's surface. This is not to say that the land occupies that proportion of the surface, however, since as we have seen the sides and parts of the rims of the continents are below sea-level. Today, some 73% of the continental surface area projects above the waves and so the sea in total accounts for 70% of the earth's. 510×10^6 km^2 surface—59% being that covering the ocean floor plus 11% over the submerged continental margins. The surface area of the continental masses appears more or less constant and so, therefore, is that of the ocean floor. However, the area of continental margin beneath the sea is, because of its shallow slope, subject to marked variation dependent on sea-level. A 100 m decrease in sea-level (such as might occur during the next glacial phase) would decrease the 11% of today to around 7%, whilst a 100 m rise in sea-level (which might result from the melting of all the earth's ice) would increase it to nearly 20%. Changes of this magnitude have occurred in the past and have greatly affected the abundance and diversity of the shallow marine fauna.

The sea therefore covers the largest portion of the earth's surface and it is even more important a habitat in terms of the total volume of the earth regularly inhabited by living organisms. On land the inhabited zone usually extends only a few tens of metres above the ground and a metre or so below it; the oceans are inhabited from their surface right down to their greatest depths (in excess of 11 000 m): the sea therefore provides 99% of the living space on our planet. Although the largest, it is also the least known and least knowable portion, particularly with regard to its biology.

Sir Alister Hardy likened our attempts to investigate the ocean to a person in a hot-air balloon slowly drifting over a land hidden from view by dense fog. Every so often, the balloonist would let down a bucket on the end of a large rope, let it drag along the ground for a while, and then, after pulling it up, examine the contents. What sort of an impression and understanding of terrestrial biology would an observer gain using such a technique? We have perhaps progressed beyond this limitation—but not very far. Maintenance of a research ship at sea is also very much more expensive than operating a hot-air balloon. We know most about life in shallow, coastal waters and about the relatively slow-moving and small to medium-sized organisms; we know least of life in the depths and of the smallest and largest, fastest-moving species. The reason for the depth limitation is self-evident. Note also, however, that fish population densities at depth are low (see

p. 293)—1 × 1000 m³ for example—and this imposes severe sampling problems. That relating to size of organism is not immediately obvious and is often overlooked. Most ecological information is still obtained from the sea by use of nets or by washing samples through a sieve. Neither nets nor sieves can be used to retain the smallest or most delicate organisms; they either pass through or are fragmented beyond recognition or study. Small water or sediment samples have to be taken *in situ* with consequent problems of sampling accuracy and adequacy, and with respect to bacteria, problems of changes in the relative proportion of the individuals and species originally caught after culture. Neither can nets capture large, fast-swimming species: they simply avoid the net. Our knowledge of the largest squids, for example, is entirely derived from the occasional specimen cast up on a beach (and examined by a biologist before scavengers and decay render it useless) and from the hard-parts (beaks) recovered from the whales which feed on them. Yet *Architeuthis* the giant squid may attain a total length of 17 m (and over 30 m has been claimed). Some whales (e.g. *Mesoplodon* and *Stenella* spp.) are also known only from a few specimens or fragments stranded on the shore, never having been seen alive. There is no scientific or probablistic reasons why Heuvelmans' (1968) thesis that several huge and as yet unknown fish and mammals occur in the oceans should not eventually be found to be correct.

There are therefore many areas of complete and almost complete ignorance, and there are several areas of controversy and doubt; but there is much that we do know and even more of which we are fairly certain. The following pages set out to introduce the reader to this body of knowledge and to present what currently appear to be the outlines of the ecology of the seas.

1.2 The nature of the ocean

We have already considered the basic shape of the crustal container housing the world's ocean and we must now put rather more flesh on these bones and describe those aspects of oceanic structure and those properties of sea-water that have a particular bearing on marine ecology. The study of marine science in general—oceanography—is of course a large field embracing physics, chemistry, geology and several other disciplines besides biology; here we must be very selective and many only marginally-relevant topics cannot be covered. The reader is referred to Wright (1977–1978) for additional information.

As we will see several times later, marine organisms appear

particularly to respond to and reflect three all-important environmental gradients: the latitudinal gradient in magnitude and seasonality of solar radiation from the poles to the equator (which will be deferred for detailed consideration to pp. 36–41); the depth gradient from the sea surface to the abyssal sea bed; and the coastal to open water gradient which often coincides with that in respect of depth. In fact all three are interlinked and are often superimposed.

The most straightforward of the three is the depth gradient. Although a host of terms have been coined for specific sections of the 0–11 000 m gradient, the most important distinction is between the uppermost few metres of the water column which can be illuminated by sunlight and the remaining 97.5% which cannot. Light is exploited for different purposes by different organisms, and different intensities will limit different processes. Therefore 'illuminated' must be qualified by reference to the process concerned. The light intensity at the sea surface also varies in regular diurnal and seasonal patterns and in relation to cloud cover, and hence any illuminated zone will vary with the light intensity and with the translucency of the water. Much of the incident light is scattered at the surface and of that which does penetrate this barrier, most is very quickly absorbed so that light intensity decreases logarithmically with depth. In the Sargasso Sea, for example, where the water is particularly translucent and light penetration is greatest, only a maximum of 1% of the red light penetrating the surface remains by the 55 m depth, only 1% of the yellow-green and violet light by 95 m, and only 1% of the blue by 150 m.

In order to photosynthesize, plants require light (particularly of the shorter wave lengths) and one can calculate the depth down to which the light is sufficient to permit their growth. In the most translucent, oceanic water and under conditions of full sunlight, the limiting depth for photosynthetic production is of the order of 250 m; in clear, coastal waters this reduces to about 50 m; and in highly turbid waters it is to be measured only in centimetres. Clearly, therefore, all primary fixation of organic compounds by photosynthetic organisms must be a phenomenon confined to the surface waters. The depth zone in which this is possible, the 'photic' (or 'euphotic') zone, averages some 30 m deep in coastal waters and some 150 m in the open ocean; the remainder of the depth gradient (and at night the whole ocean) is 'aphotic'. Below about 1250 m, there is insufficient sunlight for any biological process and hence, except for light produced by the organisms themselves, the ocean is thereafter lightless.

Light is one form of energy arriving from the sun; the second of great ecological consequence is heat. It is no accident that the element of a domestic kettle is situated at the bottom of the water mass enclosed within this heating appliance. As the water in contact with the element is warmed so it becomes less dense and rises, thereby allowing more, cooler water to replace it and be heated in turn. The heating process operates on convection currents which would not form if the element was positioned near the surface of the water mass. But, discounting geothermal sources, this is precisely the situation with respect to the source of heat and the oceans. The surface waters of the sea receive heat from the sun; therefore they become less dense and float at the surface: therefore they receive yet more heat: and so on. The end result is a body of hot, less dense water floating on top of a much larger mass of cold, dense water; the interface between the two, or more strictly the zone of rapid change in water temperature (Fig. 1.1), is termed the 'thermocline'. As with the photic zone, the position and magnitude of the thermocline are variable, but as water has a high specific heat it can absorb much heat with relatively little change in temperature and it will retain its heat for a long time in the presence of a temperature gradient. Diurnal changes in temperature are confined to the uppermost few metres and even there are rarely more than 0.3°C in the open ocean or more than 3°C in coastal areas.

The thermocline is therefore a feature of the upper 1000 m, below which the temperature of the ocean falls from a maximum of 5°C down to between 0.5 and 2.0°C. In contrast, at the surface, temperature may vary from −2°C to more than 28°C

Fig. 1.1 Characteristic temperature profiles at different latitudes in the open ocean. (The presence of cold, low-salinity water near the surface in polar latitudes disturbs the otherwise vertical profile there.) (After Wright 1977–78.)
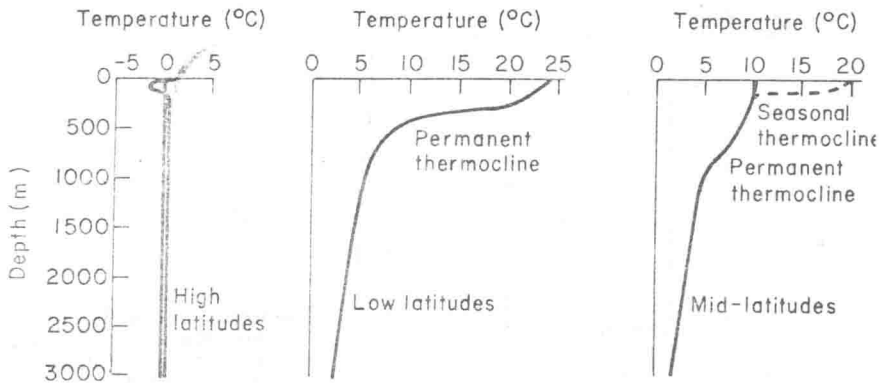
dependent on latitude (in contrast to fresh water, the density of sea-water decreases uniformly with a decrease in temperature down to near $-2°C$). Thermoclines are permanent features of the oceanic depth gradient in all but the highest latitudes, their magnitude depending on the temperature differential between surface and bottom waters. In regions experiencing an alternation of hot and cold seasons, a marked, though shallow and temporary, seasonal thermocline is superimposed on the relatively weak, permanent thermocline during the hot season (Fig. 1.1). The importance of this surface water/bottom water density difference is that it produces a barrier to mixing of these two water masses. Those dissolved substances taken out of the water in the photic zone and incorporated into living tissue which sink through the thermocline (as a result of gravitational forces) cannot be replaced by local mixing. Waters above a thermocline may therefore become depleted in these essential dissolved nutrients whilst the bottom waters hold large, untappable stocks (Fig. 1.2).

The third and final feature associated only with the surface
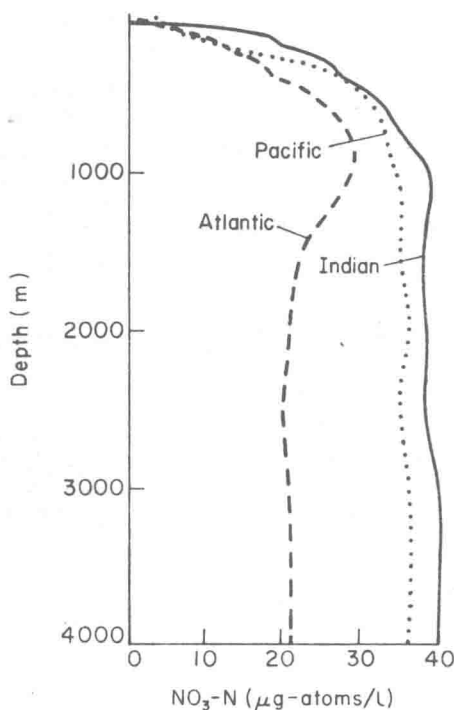

Fig. 1.2 The vertical distribution of nitrate in tropical and subtropical regions of the Atlantic, Indian and Pacific Oceans. (After Sverdrup *et al.* 1942.)

layers of the sea which must be mentioned here is wind-induced mixing. Winds blowing over the surface of the ocean impart some of their energy to the water, causing waves to form and inducing turbulent mixing of the surface layers down to maximum depths in the order of 200 m. This potential zone of mixing is therefore within the same depth range as the potential photic zone and the temporary seasonal thermocline of temperate latitudes; the precise relationships between these three depths at any one time are of great importance with respect to the potentiality of photosynthetic production. If, for example, mixing extends well below the photic zone, photosynthetic organisms may spend much more time below their threshold light intensity than above it and be unable to achieve sufficient production to balance their own energetic requirements (see pp. 45–9). Moreover, if mixing does not extend down to the thermocline, then photosynthetic production may also be reduced to low levels because of exhaustion of the nutrient supplies (Fig. 1.2).

The second major gradient is that stretching outwards from the coast into the open ocean, and it also involves variation in nutrients, depth and mixing. Several important subdivisions of the marine habitat can be made on this basis:

1.   The immediately coastal or 'littoral' region from the upper limit of sea-water cover down to some 30 m depth.

2.   The areas of submerged continental margins—the so-called 'neritic' water and the underlying 'continental shelf'.

3.   The rapidly descending sides of the continental masses—the 'continental slope' with the more gently sloping 'continental rise' at the base of the slope.

4.   The oceanic floor, usually termed the 'abyssal plain'.

5.   The mid-oceanic ridges—vast mountain chains rising from the abyssal plain to within 2000 m or so of the surface (and occasionally breaking surface in the form of mid-oceanic islands).

6.   The 'hadal regions' of the deep-ocean trenches—chasms in the abyssal plain descending from 6000 m to, in several cases, below 10 000 m.

The waters cradled within the continental slopes and the deep ocean floor are differentiated from the coastal neritic waters by being termed 'oceanic' (see Fig. 1.3). For present purposes, the three basic sections of the coastal to open water gradient are: (a) the littoral; (b) the neritic/continental shelf; and (c) the oceanic/abyssal (the latter including the continental slopes and rises, the mid-oceanic ridges and the deep trenches).

The essential feature leading to the separation of the littoral zone as a distinct part of the marine ecosystem is the extreme
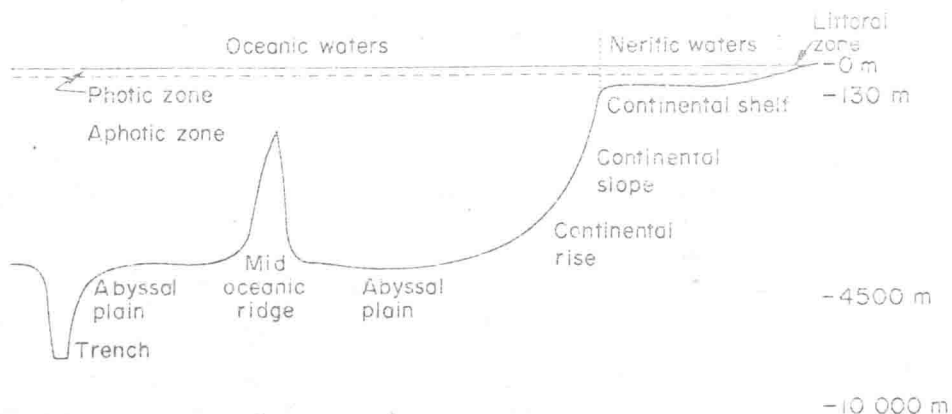
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Fig. 1.3 'Section of the ocean showing the major habitat subdivisions.

shallowness of the water. Light may penetrate to the sea bed and, indeed, in areas with tidal water fluctuations part of the bottom may become exposed temporarily to the air and receive solar radiation directly, diurnally or semi-diurnally. Plants associated with the sea bed can survive there and add their contribution to the total marine production. As we shall see later, the plants occupying this littoral fringe of insignificant area on a world basis may contribute quite markedly to this total. The transitional position of the littoral zone between land and sea has many other repercussions on the ecology of its characteristic organisms. Marine species, for example, may diminish interspecific competition by colonizing high intertidal levels; and the upper parts of marine shores may support luxuriant stands of semi-aquatic vegetation of basically terrestrial ancestry. Such salt-marshes, mangrove-swamps and, at slightly lower levels, sea-grass meadows (Chapter 4) also contribute significantly to essentially marine food webs.

Light more rarely penetrates to the bed of the somewhat deeper shelf seas (from 30 m to an average 130 m depth), and bottom-living, photosynthetic organisms are here much less significant. Nevertheless, shelf seas differ in many respects from open oceanic waters. Since wind action can keep surface waters mixed down to depths of some 200 m, shelf seas are well mixed and the impoverishment which can result from the loss through gravity of nutrients incorporated into tissue in the surface waters, is much less marked than in deeper systems. Coastal waters also receive the discharge of ground waters and rivers draining one hundred million square kilometres of land, and river water on average contains twice as much nutrient per unit volume as sea-water (organic and inorganic materials dissolving in the water which percolates through rocks and the soil before being discharged by river and groundwater flow). For both these reasons (and in some areas also as a result of the upwelling considered on pp. 11–12), shelf seas are particularly productive.

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Many bottom-living, coastal animals have evolved larval stages which swim for a time in the water, in part perhaps to exploit the productive, nutrient-enriched waters (pp. 239–49). Hence neritic waters may also be characterized by the abundance of these larvae. Once again therefore, although shelf seas only comprise some 3% of the ocean's area, they contribute much more than their proportional share to its total productivity. They are also locally very important and extend out from the coast for distances of up to 1500 km: such seas as the North and Baltic, Yellow and East China, Chukchi and Bering, Hudson Bay, much of the South China, Java, Arafura and Timor and even the Arctic Ocean are shelf seas.

Most of the world's ocean is the open sea cradled between the continental masses (Table 1.1). From what has been said above it

Table 1.1 Percentages of the world ocean comprised by various habitat types and depth intervals.
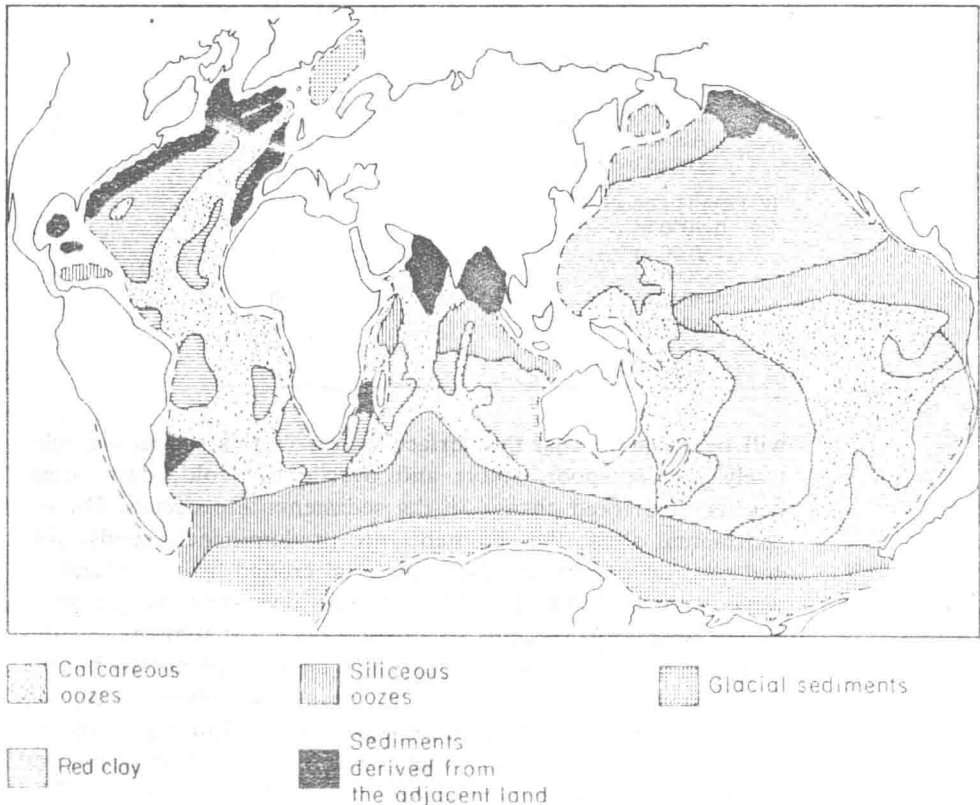
A. Habitat types	
Littoral zone	negligible
Continental shelf	3
Oceanic area	97
Continental slopes	12
Continental rises	5
Mid-oceanic ridges, mountains, etc.	36
Abyssal plain	42
Ocean trenches	2
B. Depth intervals	
0–1000 m	12
1–2000 m	4
2–3000 m	7
3–4000 m	20
4–5000 m	33
5–6000 m	23
> 6000 m	2

will be apparent that the surface waters of this region are relatively nutrient-poor, stable and overlie the cold, dark ocean depths. A marked change in the sediments also occurs. On the continental shelf, the sediments are predominantly sands, silts and clays of terrestrial origin (material eroded from the land by wave action, discharged by rivers or deposited by glaciers), locally with high percentages of the pulverized remains of molluscs, corals, etc., and with exposed bedrock in areas of rapid water movement. Over much of the abyssal plain, calcareous oozes formed from the skeletal remains of minute protists suspended in the water mass (e.g. coccolithophores' and foraminiferans) dominate down to depths of 4500 m. The

solubility of the carbonate ion ($CO_3^=$) varies with temperature and pressure, and below about 5000 m calcium carbonate goes into solution; hence below this depth there are no calcareous oozes. Other minute protists of the water column possess siliceous hard-parts (e.g. diatoms and radiolarians) and oozes formed largely of their remains are locally common in high latitudes, especially around Antarctica, and are also an important deep-sea sediment in low latitudes between depths of 4000 and 6000 m. In the deepest areas of the ocean (below 6000 m) the dominant sediment is a fine, inert red clay (Fig. 1.4). The open ocean as a whole is very poorly known; only of the surface photic zone do we have a reasonable biological understanding.

Thus far we have neglected the properties of the water itself and to these we now turn. The water forming the world ocean is, of course, salty. In fact it approximates a 3.5%—or 35‰—solution (by weight) in which the dominant anion is chloride (19‰ by weight, comprising 86.8% of the total anions) and the dominant cation is sodium (10.5‰ by weight and 83.6% of the total cations). The concentration of salts in sea-water is remarkably constant; below 1000 m depth it varies only between 34.5‰ and 35.2‰, although clearly surface waters will be diluted

Fig. 1.4 Distribution of ocean-floor sediments. (After Wright 1977–78.)

Calcareous oozes

Red clay

Siliceous oozes

Sediments derived from the adjacent land

Glacial sediments

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in areas of freshwater discharge and concentrated in regions with a marked excess of evaporation over precipitation—to over 36‰ in the tropical open oceans and to even higher values in semi-enclosed areas such as the Red Sea.

With the exception of the nutrient salts required by photo-synthetic organisms, however, the chemical composition of sea-water and variation in this composition appear to play a very small role in marine ecology. Indeed, it has been argued (Barnes & Mann 1980) that the basic form taken by the ecology of aquatic systems is almost completely unrelated to the nature of the aquatic medium and is essentially similar in fresh, brackish and marine waters. Nevertheless, the abundance of such nutrients as nitrate and phosphate is often of very great significance. Both are only minor constituents of sea-water, nitrate averaging $0.5 \, p/10^6$ and phosphate an order of magnitude less; both may reach potentially limiting concentrations in surface waters. Their distribution, abundance and flux, and the consequences for marine productivity, will reoccur frequently in the following pages.

Although, nutrients excepted, details of the composition of sea-water are of little ecological import (but of great interest in marine physiology), the movement of the water is critical and underlies many ecological processes and distributions, being particularly important in the circulation of nutrients and oxygen. Discounting tidally induced mixing which generally is of significance only in very shallow waters, the two main categories of large-scale water movement are density-driven currents and the various processes responsible for upwelling (and its converse, downwelling).

Upwelling, as its name suggests, is the movement of water from relatively deep in the ocean into the photic zone, i.e. movements parallel to the depth gradient and perpendicular to the surface. Its importance is that it is one of the few mechanisms by which the nutrient stocks of the aphotic regions can be introduced into the surface waters. Three processes may induce upwelling. First, deep currents when they meet such an obstacle as a mid-ocean ridge will be deflected upwards and may gush forth into surface waters. Secondly, when two contiguous water masses are moved apart, as for example when water immediately to the north of the equator moves northwards under the influence of Coriolis force and similarly water to the south of the equator is moved southwards, a 'hole' is left between them and water up-wells to fill it. The depth from which water upwells is then dependent on the quantities of surface water moved laterally and on their current velocity. This is upwelling due to areas of