An Introduction to
Marine Ecology

THIRD EDITION

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With contributions from
John Field, Dan Baird & Michel Kaiser

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Exposed rocky shore, Tsitsikama, South Africa.
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The first two editions of this book were aimed at students with some knowledge of ecology who were about to venture into the *mare incognitum* for the first time. The marine environment and its inhabitants are exciting and stimulating subjects for amateur naturalists, students and professionals, and continue to inspire each of the contributors to this book. The previous texts provided the reader with a broad introduction to distinct processes or subsystems of the ocean. Since then, the information base has continued to increase exponentially; much more is now known about ecological processes in the oceans than ever before. As in any branch of science, however, progress is spread unevenly among subdisciplines which is reflected in the content of the chapters. All have been revised in the light of new information, but in some areas growth has been so prodigious that we felt compelled to enlist specialist expertise. John Field deals with fisheries, an issue that has started wars and continues to cause political strife within and between nations. Dan Baird takes a more detailed look at ecosystems, the understanding of which are essential if we are to predict the effects of major changes such as global warming in our environment. Finally, Michel Kaiser has focused on the issues surrounding human interference and conservation that have become so prominent in recent years with the concept of biodiversity and its importance to mankind. As before, editorial co-operation among co-authors has ensured consistency and co-ordination. The result is a new book, inheriting parental character while offering the freshness of a new generation.
1 The nature and global distribution of marine organisms, habitats and productivity

1.1 Introduction

*Homo sapiens* is a terrestrial species and perhaps not surprisingly it tends to regard ecology as being mostly about the other terrestrial organisms with which it comes into daily contact. Ours is a planet largely covered by water, however; terrestrial habitats comprise less than one third of its surface; and of that liquid water, 99.7% is in the ocean. Some 99% of the planet’s inhabited space is that ocean. To a first approximation, therefore, the ecology of the Earth is the ecology of its seas.

The ocean basins are not just ‘drowned land’: the sea floor and the land-masses are made of 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 large lumps—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 3000–4000 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 continents 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, flattish-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 oversimplification, 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, for, 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 $510 \times 10^6 \text{km}^2$ 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%, whereas 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 all but 1% 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—1 per 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, although the use of scuba techniques and minisubmersible craft has increased dramatically. 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 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 probabilistic reason 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. Indeed, the discovery in 1976 of the previously unknown megamouth shark (5 m long and 750 kg weight) is a case in point. Completely new types of animals are still being discovered: since 1980, two new phyla (the Loricifera and Cyclophora) and two new classes in well-known phyla (the Remipedia in the Crustacea, and the concentricycloid echinoderms) have been described.

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 Bearman (1989) 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 below); 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 55 m depth, only 1% of the yellow–green and violet light by 95 m, and only 1% of the blue by 150 m.

To photosynthesize, algae require light (particularly of the shorter wavelengths) 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 dependent on latitude (in contrast to fresh water, the density
of sea-water increases uniformly with a decrease in temperature down to near \(-2^\circ\text{C}\). 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 whereas the bottom waters hold large, untappable stocks (Fig. 1.2). (It should be noted that it is thought that before mid-Miocene time deep-ocean water was some 10°C warmer than at present. This would have had considerable repercussions on nutrient availability.)

The third and final feature associated only with the surface 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 of 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,
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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 Sections 2.2.1 and 2.2.2). 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 immediate 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 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 and algae associated with the sea bed can survive there and add their contribution to the total marine production. As we shall see later, the photosynthetic organisms 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...