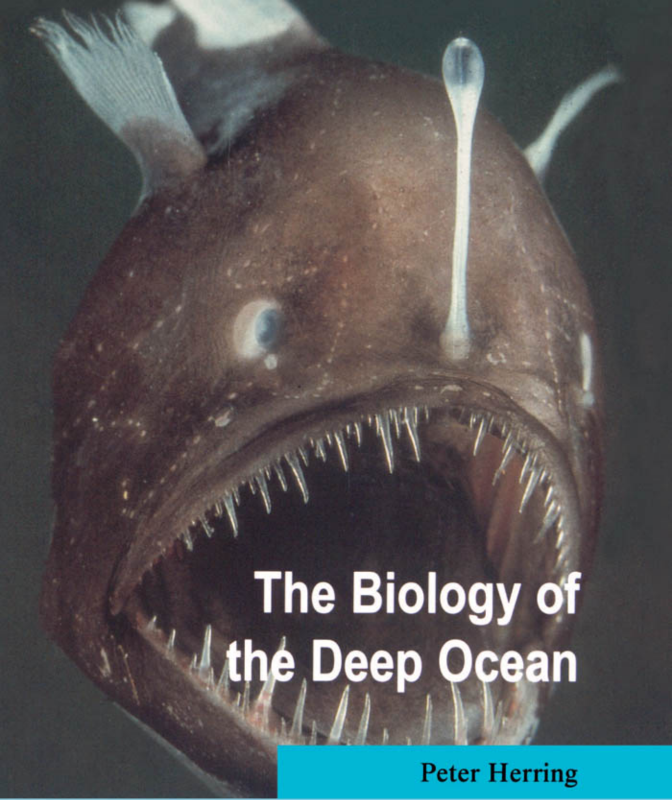
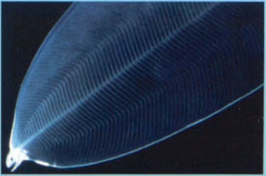


The Biology of the Deep Ocean

Peter Herring



Biology of Habitats

The Biology of the Deep Ocean

Biology of Habitats
Series editors: M.J. Crawley, C. Little, T.R.E. Southwood, and S. Ulfstrand

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Preface

I find the inhabitants of the deep ocean to be a constant source of surprise and delight. Every time we think we understand the ecosystem and the organisms they manage to produce a new rabbit out of the oceanic hat, so that we are required to readjust our previous perspective (picoplankton, iron limitation, hydrothermal vent communities, microscale vortex perception, red bioluminescence, phytodetritus, Archaebacteria, gelatinous zooplankton, to name a few of the rabbits). I find that audiences at every level are equally enthused about the novelty and potential of deep ocean biology and it is my hope that this book will help to inform those who already have some information but are looking for more. It is driven by personal enthusiasm and therefore inevitably somewhat unequal in its emphasis on particular topics. Its organization is based on an annual series of lectures given to Cambridge third year students. Another author would probably have had a different view of the same landscape. Although I have limited the number of references in the text (because this was never intended to be an exhaustive survey) I hope the interested reader will be able to pursue a particular topic through the ones I have cited. This has meant that some colleagues will recognize their contributions but without direct accreditation. To them I apologize. For those who may be unfamiliar with some of the organisms present in the deep ocean I have added a eucaryote bestiary in the form of the Appendix, emphasizing the attributes and deep ocean contributions of particular taxa.

Oceanography and its associated technology has dismantled the barriers between the classical disciplines of science. The biology, geology, physics and chemistry of the deep ocean are inseparably entwined on all scales from the global to the individual, a commonality which is reflected in the present emphasis on biogeochemistry. The organisms and events in the depths of the ocean cannot be divorced from the processes and conditions nearer the surface, and I make no clear distinction between deep ocean biology and biological oceanography. Organisms interact with each other and with their environment, in the ocean as on the land. The different scales and details of the interactions require different techniques for their elucidation. The skills of, for example, the ecosystem modeller, the fluid dynamicist, the visual physiologist and the molecular biologist are all essential to interpret the interactions that drive the deep ocean system.

My own interest in, and knowledge of, the deep ocean is a consequence of the stimulus and enthusiasm of the many colleagues who have fed and nurtured my initial curiosity. I have been fortunate in the scientific comradeship and collaboration which has made seagoing the most rewarding aspect of my working life and in the opportunities for new observations and understanding that research cruises in all the worlds oceans have provided. The periodic accessibility of live (or at least fresh!) deep-sea animals has been the spur to much of my work and it has been a particular delight to see and experience the new opportunities that have become available through the use of ROVs and manned submersibles. After studying the midwater fauna for many years using nets not greatly different from those employed by the *Challenger* expedition my first experience of exploring the animals' own environment in the Johnson Sealink was truly inspirational. May all deep ocean biologists be similarly inspired by exposure to the realities of the habitat and its communities.

Many friends and colleagues have been involved in this book, not only through their science but also through their kindness in commenting on some or all of it in earlier drafts. Their comments were invariably helpful and agreeably robust, and have greatly improved the final text. I owe a particular debt in this respect to Tom Anderson, Martin Angel, Richard Barnes, David Billett, John Blaxter, Quentin Bone, Geoff Boxshall, Sir Eric Denton, Ron Douglas, Gwyn Griffiths, Patrick Holligan, Ian Joint, Michael Land, Justin Marshall, Nigel Merrett, Julian Partridge, Philip Rainbow, Paul Tyler, and Edith Widder. If I have not always followed their advice to the letter I hope they will forgive me.

Above all others I must acknowledge the help and continual encouragement and coercion of my series editor Colin Little, who carefully read all the first drafts of chapters as they emerged erratically into the light and cheerfully accepted all my excuses for dilatoriness. My thanks are due, too, to Cathy Kennedy and Ian Sherman at Oxford University Press for their patience and for the occasional prodding that has finally brought this project to fruition.

Mike Conquer, Kate Davis, and Roger Hollies helped greatly in the preparation of figures. Brian Bett, David Billett, Geoff Boxshall, Harry Bryden, Martin Collins, Daniel Desbruyeres, John Gould, Steve Haddock, Francois Lallier, Richard Lampitt, Justin Marshall, Monty Priede, Paul Tyler, and Craig Young kindly provided a number of them.

Everyone involved in deep-sea biology owes a great debt to the work and writings of the late N.B. 'Freddy' Marshall. I have not only enjoyed his writing but also had the pleasure of his friendship on land and company at sea. After his death it was a great privilege to be able to read an unpublished biographical essay which he was preparing. I am most grateful to Mrs Olga Marshall and Freddy's obituarists for making it available to me. I have not specifically cited it in this book but I know that I have been influenced by it.

There are so many exciting discoveries in deep ocean biology that the problems for an author are how to keep up and what to leave out. The pace of research is accelerating and has caught the public imagination, greatly aided by some excellent scientific journalism and by the stunning images of the deep sea and its inhabitants now available both from television broadcasts and from a wide range of websites. The old attitude of 'out of sight, out of mind' has been swept away on this tide of new information. The biology of the deep ocean concerns us all and I hope that this book will offer each reader some new fact or insight to spark their interest and to heighten their awareness of its significance — and its magic.

Contents

1 The deep-sea dimension

The scale of the task

Look out across the ocean on a calm day, from the shore or from the deck of a ship. The vista is daunting in its scale yet innocuous in its features. But beneath this tranquil skin lies a teeming horde of organisms, from the tiniest viruses to the mightiest whales, all of which are continually influenced by the physical features of the seawater within which they move—and by which they are moved. Evolution occurs apace: 'Even the most peaceful place is full of strife, with any weakness of its inhabitants at once exploited' (Jones 1999). This is the open-ocean ecosystem; it encompasses the whole ocean and excludes only the coastal seas where water depths are less than 200 m. We struggle to describe and to interpret the complexity of its interactions and relationships, yet we must succeed: the immense but ill-understood effects of the ocean upon our climate and upon our future will in turn determine the evolution of our planet.

The whole open ocean and its populations comprise a single ecosystem; a perturbation in any one region may, in time, affect locations far removed from the original site. Nevertheless, the scale of this ecosystem is so daunting that, in order to describe, analyse, and ultimately predict the interrelations within it, a pragmatic approach has to be taken, which recognizes particular subsets of the whole system. Each of these can then be examined separately. Useful subsets include recognizable assemblages of organisms (i.e. species), which are associated with particular combinations of the physical and chemical features of the environment. The seas cover 71% of the Earth's surface: 65% is open ocean. The immense horizontal extent of this area suggests that biogeographic divisions might comprise one such group of subsets, separating, for example, the high-latitude faunas (Arctic and Antarctic) from the low-latitude Equatorial ones. These distinctions are certainly real, and useful, as we shall see later (Chapter 2).

The vertical extent of the open oceans, however, suggests another, unique, group of ecological subsets, based on depth of occurrence. The oceans have a maximum vertical extent of almost 11 km. 88% of the oceans are deeper than 1 km and 76% have depths of between 3 and 6 km. The *average* depth of the oceans is some 3.8 km. This huge third dimension immediately sets the oceans apart from the primarily two-dimensional terrestrial ecosystem. There is no terrestrial equivalent to the colossal volume of the pelagic oceans, inhabited by countless organisms most of which pass their entire lives suspended in its midst. If we assume that the *average* depth of the continental life zone is 0.05 km (the height of a very tall tree) then 99.5% of the volume occupied by life on Earth is contained in the oceans.

The vertical dimension

The unique vertical dimension has led to the conceptual division of the oceanic environment into three main realms or zones, namely the epipelagic (from the surface to 200 m), the mesopelagic (from 200 to 1000 m) and the bathypelagic (from 1000 to 6000 m) (Fig. 1.1). The boundaries between these realms correlate approximately with different ecological levels of light intensity in clear oceanic water. The epipelagic realm marks the limits of the photic zone, where daylight is adequate for photosynthesis. In the mesopelagic realm light from the surface (though very dim) may still be visible in the clearest of oceanic water. The bathypelagic realm is beyond the reach of daylight. The 6000 m lower limit of the bathypelagic realm includes the vast extent of the abyssal plains but excludes the deep trenches, which constitute the hadal realm and extend from 6000 m to the greatest depths. Their contribution to the open-ocean ecosystem is relatively small because they make up less than 2% of the seafloor area.

For descriptive purposes I shall apply the term 'deep-sea' loosely, and use it for all habitats below the epipelagic zone. The biological populations of these watery realms are divided conveniently into the plankton (plants or animals which drift in midwater, or are unable to swim against a current) and the nekton (larger midwater animals, such as fish, squid, and shrimp, which can swim quite strongly). Beneath them all live the benthos (animals which dwell on or in the seafloor). But first we must be aware of how the oceanic ecosystem differs from the one with which we are most familiar.

Differences between marine and terrestrial ecosystems

We are components of the terrestrial ecosystem and so we are inclined to assume its structure is the norm and can be used to interpret the oceans. We have already seen that the scale of the oceanic ecosystem makes this a dangerously self-centred assumption. The oceans are different.

The first need is to adjust our mindset from an aerial to an aquatic one. The physics of water determines much of the uniqueness of the oceanic ecosystem (Denny 1990) and it is important that we recognize the consequences. The difference in density is perhaps the most striking feature. At sea level water has a density 830 times that of air; its density varies by only about 0.8% over the physiological range of temperatures and is equally insensitive to pressure (increasing by only 0.5% for every kilometre of depth).

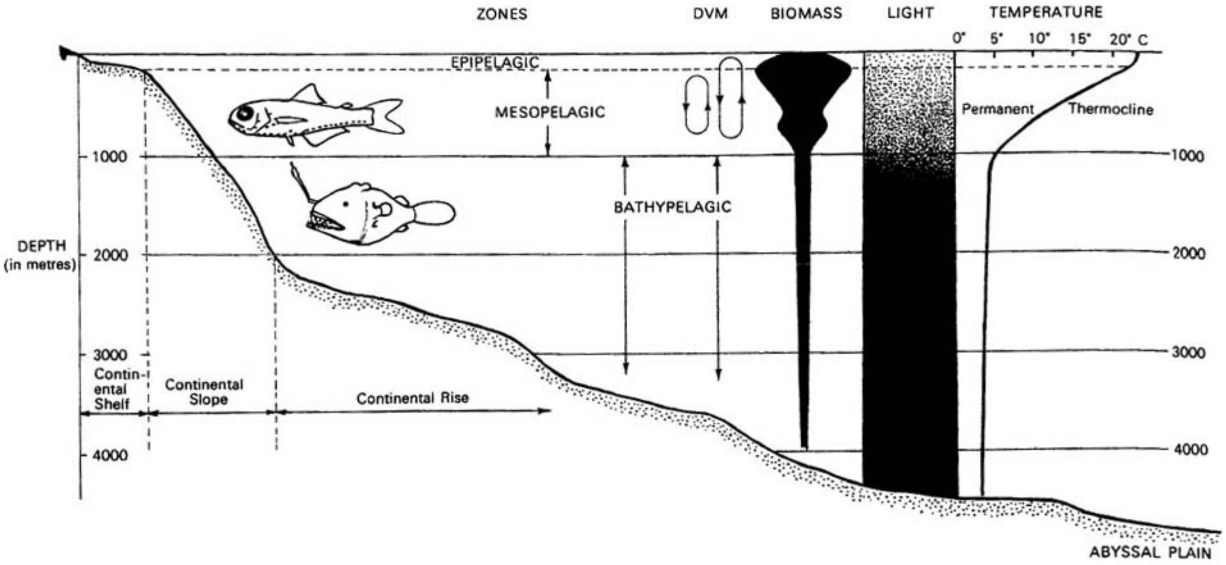


Fig. 1.1 Some descriptive features of the oceanic environment. Meso- and bathypelagic inhabitants are represented by a lanternfish and an anglerfish, respectively. Also indicated are the extent of diel vertical migration (DVM; Chapter 4), the relative biomass of zooplankton, the light regime, and the temperature profile of a warm ocean. (Illustration by N.B. Marshall and Lesley Marshall reprinted by permission of the publisher from Marshall 1971. Copyright © by the President and Fellows of Harvard College.)

The high, relatively invariant density combines with the circulatory motion to provide the ocean waters with momentum. Momentum, combined with the carrying capacity of water (whether for salt, heat, or carbon dioxide), gives the environment its defining characteristics and sets the basic rules for successful survival within it. In contrast, the density of air is strongly dependent on both temperature and pressure; at one atmosphere the density of air decreases by 13% over the range 0–40°C and the density (and pressure) at 5850 m is half that at sea level.

The weight of an organism depends on the difference in density between it and the surrounding fluid; most biological materials have densities of 1050–1200 kg m^{-3} in air and therefore effective densities of 25–175 kg m^{-3} in seawater of density 1025 kg m^{-3}. Their weights in air are thus between 50 and 7 times that in seawater. Gravity places major constraints on terrestrial life, requiring structural investment that is quite unnecessary in the sea (cf. a tree and a kelp frond). The gravitational costs of locomotion on land are potentially higher because both walking and crawling involve expenditure of energy against gravity, a cost that does not exist for a neutrally buoyant animal in the sea. Flying is even more costly. However, for a marine organism the energy gained on the swings of neutral buoyancy may be lost on the roundabouts of drag. The density of the medium directly affects the pressure drag, the force exerted on a stationary body by a moving fluid; an object of a given size will experience a pressure drag in seawater 830 times that in air. Dynamic lift is similarly affected, so a fin in seawater provides 830 times the lift it would in air. Life for an aerial organism is a largely concerned with the struggle against gravity; staying aloft is generally a bigger problem than wind speed. For an oceanic animal the situation is reversed; neutral buoyancy can be achieved in a variety of ways (Chapter 5) but swimming is energetically costly and for all but the largest species the currents and motions of the ocean are well-nigh irresistible.

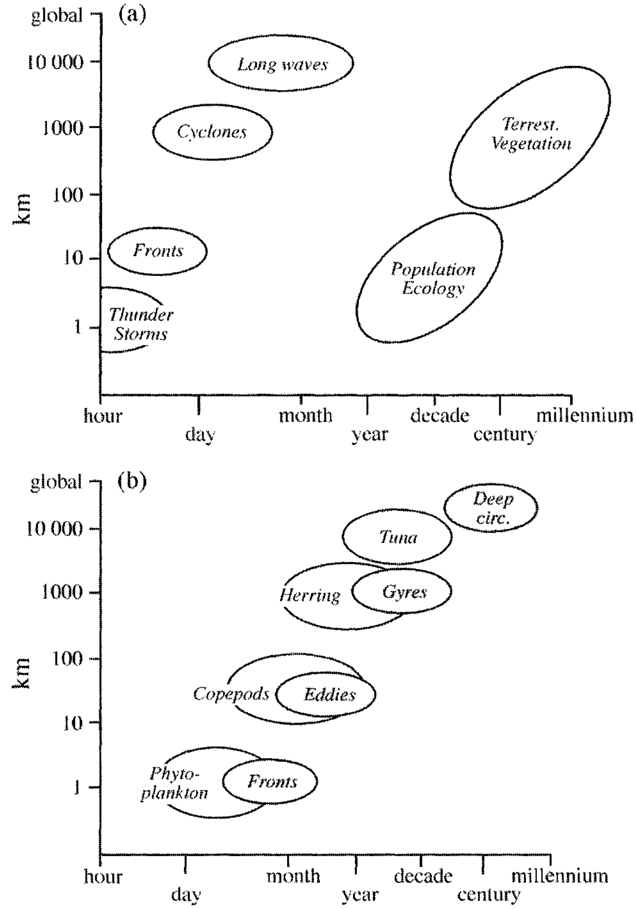
Seawater has a viscosity at 20°C some 60 times that of air, and the effects of temperature on viscosity are reversed in the two media. Over the range 0–30°C the viscosity of air increases by 9% whereas that of water decreases by 45%. The frictional (viscous) drag experienced by a deep-sea fish (or one in cold polar waters) is considerably greater than that facing a similar fish in warm surface water. A bird, on the other hand, would find flying harder work in the tropics. A planktonic organism trying to remain in near-surface waters against gravity faces a harder time in the tropics than in the polar regions. Many species of tropical plankton have an increase in the number or size of surface projections that help to offset the effects of the reduced viscosity of the water by increasing the drag and reducing the rate of sinking.

Seawater affects the passage of both sound waves and electromagnetic waves much more than air. The bulk modulus of a medium is the reciprocal of its compressibility and it determines the speed of sound. Sound travels 4.3 times faster in water than in air (1500 and 350 m s^{-1} respectively). The wavelength at a given frequency is directly proportional to speed so the wavelength in water will also be 4.3 times that in air. Higher acoustic frequencies will therefore be needed in water than in air for the echolocation of objects of similar sizes. The attenuation of sound in water is much lower than that in air so the range over which echolocation or sound communication can be used is substantially greater (Chapter 6). The attenuation of light, on the other hand, is much higher in water than in air. On a clear night the lights on aircraft, ships, and beacons are visible over tens of kilometres; in the ocean the brightest of underwater lights are invisible at a range of little over 100 m. This has the overwhelming effect of consigning the whole deep-ocean environment to total darkness, and has stimulated the evolution of the bewildering arrays of living lights outlined in Chapter 9.

The ocean's density has the most direct and immediate effect on the activities of its inhabitants. Its heat capacity, on the other hand, combined with the density, is probably the greatest modulator of the ecosystem as a whole. Water has a heat capacity almost 4000 times that of air. The surface temperature of the sea changes only very slowly in response to changes in air temperature; the deep sea is at such a great range from these surface effects, and its heat capacity is so large, that any deep temperature changes are largely imperceptible except on geological time-scales. Temperature changes on land fluctuate (with other weather) on a much shorter time-scale of days or even hours and only at the seasonal level do they begin to interact with the generation times of organisms. The shorter-term fluctuations are effectively decoupled from the ecology. In terrestrial ecosystems 'weather' can therefore be regarded as high-frequency noise and 'climate' change is the level at which physical and ecological coupling occurs, on time-scales of centuries or greater (Steele 1991, 1995). Yet the physical processes in the ocean and the atmosphere have the same basic fluid dynamics; it is the differences in their time and space scales that set the marine and terrestrial ecosystems apart. A cyclonic atmospheric system of about 1000 km in diameter lasts for about a week; the equivalent oceanic eddy has a diameter of about 200 km and persists for months or years.

In the oceans the coupling of the physical processes with the ecology is much closer; the organisms are much more closely linked to the oceanic 'weather' of fronts, eddies, and gyres, and the 'climate' of deep circulation patterns (Fig. 1.2). The primary producers of the ocean (phytoplankton) are very small and respond to brief local mixing and turbulence. Herbivores are larger than the phytoplankton, and invertebrates and vertebrates are on an increasing scale of size and lifetime. There are few vertebrate (or other) large herbivores. On land the primary producers are the largest and the longest-lived organisms (perhaps 90% of plant biomass occurs in trees) and are largely independent of local weather. Vertebrate herbivores are common (and include the largest species), yet they and invertebrates are frequently smaller than the plants they eat. The dominance of large primary producers on land is shown by a comparison of the mean body mass at maturity of organisms in the two environments: the mean mass of land organisms is 10^7–10^8 times that of oceanic ones. Large body size (for plants and animals) could be considered a terrestrial adaptation to combat short-term environmental variability (Cohen 1994).

Fig. 1.2 Logarithmic space- and time-scales for (a) atmospheric processes and terrestrial populations and (b) ocean circulation processes and biological size groups in pelagic ecosystems. The figures demonstrate the temporal separation between atmospheric and ecological processes on land and the close correlation in the ocean. (Adapted from Steele 1991.)



There are 3–5 orders of magnitude more biomass per unit volume or per unit area on land than in the sea. Much of the biomass on land is structural material supporting plants (e.g. wood); animal biomass is only around 0.01% of the total. In the sea it is 10%, 1000 times greater. The net primary productivity of the land is about 56 × 10^{12} kg C per year (56 Gt; Table 2.1). That of the oceans is similar but when the two are compared per unit volume the land value is almost 200 times higher than that of the oceans, emphasizing the nutritionally dilute nature of much of the oceanic environment. Far fewer species have been described from the oceans, perhaps in part a result of the absence of large primary producers, each of which on land supports a whole community of species. Benthic marine communities appear to be more diverse than pelagic ones, probably because the spatial patchiness of this environment lasts much longer than its equivalent in midwater (Chapter 11). Analysis of a number of different food webs has shown that despite the fewer marine species, the trophic interactions in the sea appear to be more complex than on land, and pelagic webs have the longest food-chain lengths (Cohen 1994) though the reasons are not yet clear. Another unexpected result of the analysis is that in marine food webs the average relative biomass of animal predators, and of animal prey, is larger than in terrestrial food webs. Again no satisfactory explanation has yet been proposed.

Measurements and methods

What do we know about the physics, chemistry and biology of the deep oceans, and how do we measure the different features? What measurements matter? Our knowledge of the oceanic ecosystem is entirely dependent upon our skills of observation, sampling, and measurement. Our interpretations of the dynamics of the system will be profoundly biased by the limitations of our data set. 'Classical' interpretations and assumptions have been regularly overturned by improvements in sampling techniques; in the early nineteenth century, for example, the oceans were considered bare of plant life and the deep sea devoid of animal life. *We* believe that today's paradigms are more robust—but this is no guarantee that they will fare any better under the scrutiny of future generations.

The study of the physicochemical patterns, boundaries, and characteristics of the aquatic features of the Earth (the hydrosphere) constitutes the science of hydrography (cf. geography). The coastal seas and open oceans dominate the hydrosphere; indeed, to an alien visitor, this would be a world composed largely of water. Oceanographers measure features of the water column ranging from those (such as pressure) that are universally consistent, predictable, and unaffected by the biology, to those (such as nutrients and oxygen) that are patchy and greatly modified by the organisms. Another way of looking at the water is to consider its components (e.g. salts, heat, etc.) and reflect on how they affect its other parameters (e.g. density, light attenuation).

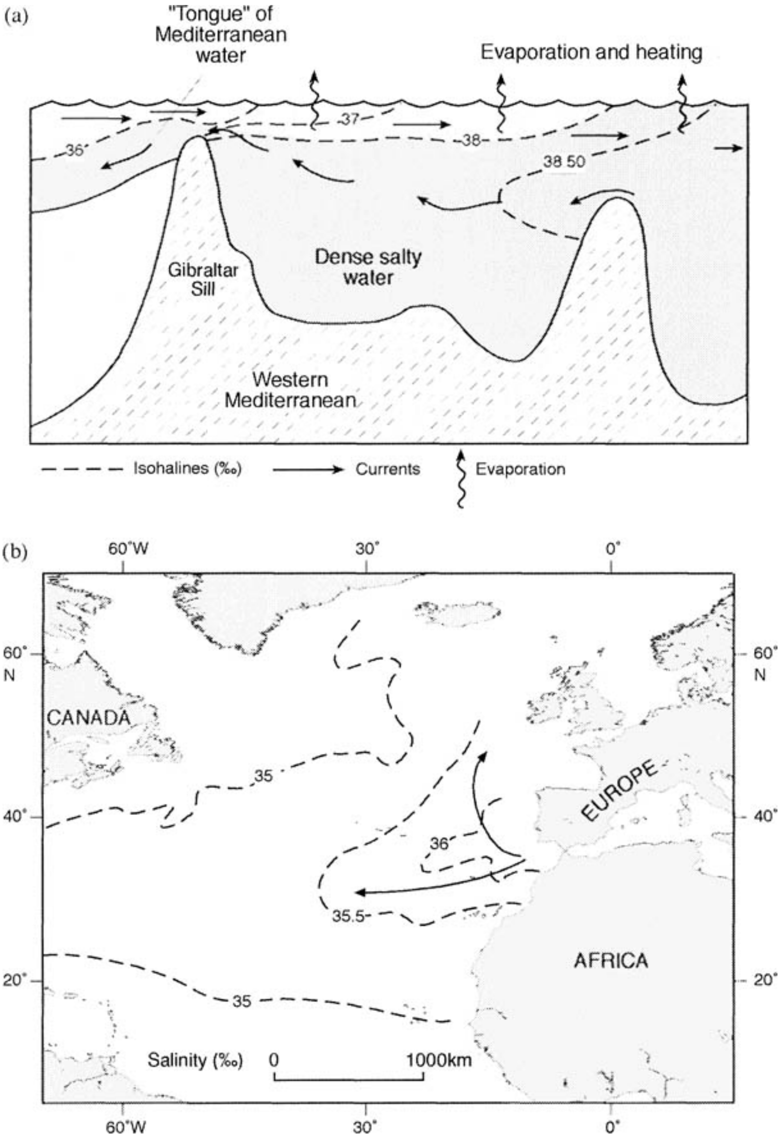
Pressure is a continuous variable in that it is largely unaffected by other factors and is linearly correlated with depth throughout the entire water column. Its measurement is relatively simple and it is often used as a surrogate for depth because pressure increases by approximately 10^2 kPa (~1 bar or 1 atmosphere) for every 10 m of water depth. No other parameter has this continuously linear relation with depth throughout the water column. Density is the nearest equivalent, for gravity determines that this will increase with depth, though the resulting gradients will not be the same in different parts of the ocean. The density of seawater is affected by pressure—but not very greatly. Seawater at 5°C has a density at the surface of 1028 kg m^{-3}; this increases at 4000 m to only 1049 kg m^{-3}. The old tales of ships and their contents sinking until they reached a layer so dense that they would hang there suspended for eternity were only myths. It *is* possible to design instruments that will sink to a particular density horizon, and whose drift (described as Lagrangian) then indicates the current at that depth, but skill and great precision are required to do so. The local density gradients are by no means inviolate; they are likely to be disturbed by any neighbouring water movement.

Light intensity is one of the very few features that vary continuously with depth; the relationship is exponential, not linear, and the absolute level is greatly affected by the concentration and size of light-scattering particles in the water, as well as by the day/night cycle. Different colours (wavelengths) are differently affected by both scattering and absorption within the water itself (Chapter 8). Daylight is an ecological factor only in the epi- and mesopelagic realms; indeed in turbid waters its influence may be restricted to little more than the top 10 m.

The two physical parameters that together have the most profound effects on the oceans are the temperature and salinity of the water. Both have a direct effect on water density and their combined effects determine much of the ocean structure, through the consequences of this link. Salinity is a measure of the total salt content, not just that of sodium chloride, although these are the ions that occur at highest concentrations (Table 5.1). Salinity is most conveniently measured as electrical conductivity. At a given temperature, the higher the salinity the greater is the density of water. Similarly, at a given salinity, the lower the temperature the higher is the density of water. A particular mass of water will have a characteristic combination of temperature (T) and salinity (S), which in turn will determine its density and hence its position in the layers of decreasing densities stacked one above the other which make up the entire water column. The characteristic T/S profile provides a recognizable signature for water of a particular origin, allowing its fate and movements in the ocean to be followed over long periods of time. Thus high-salinity warm water from the Mediterranean Sea spills over the sill into the Atlantic Ocean at the Straits of Gibraltar and, despite its higher temperature, is denser (by virtue of its salinity) than the surface Atlantic Ocean water. It therefore sinks until it reaches an equilibrium density and fans out at that depth (600–1000 m) for several thousand kilometres into the Atlantic, being readily recognizable as far north as the British Isles and west to the Azores as a thick anomalous layer of deep water which is warmer and saltier than the layers both above and below it (Fig. 1.3). As the Mediterranean Water flows round the obstruction of the southwest corner of the Iberian peninsula (Cape St Vincent), it throws off numerous eddies (known as Meddies) which are examples of similar processes occurring throughout the oceans (Chapter 4). Meddies are up to 100 km in diameter and their effects extend down to 2000 m. They travel westwards, last up to 5 years, and some even reach the Caribbean, although most collide fatally with seamounts along their way (Richardson *et al.* 2000).

On a larger scale, density differences combined with the effects of the Earth's rotation drive the great ocean currents and circulation patterns. Cold surface water from the Norwegian Sea, for example, sinks into the deep Atlantic and flows round into the Indian and Pacific Oceans, finally returning to its surface

Fig. 1.3 (a) Warm salty Mediterranean water, produced by surface evaporation and heating, flows into the Atlantic over the Gibraltar sill and is replaced by a less saline surface flow. (b) The outflow can be followed in its deep spread across the Atlantic by the salinity contours (isohalines) at a depth of 1000 m. (After Pinet 1996, from Wüst 1961 copyright © by the American Geophysical Union.)

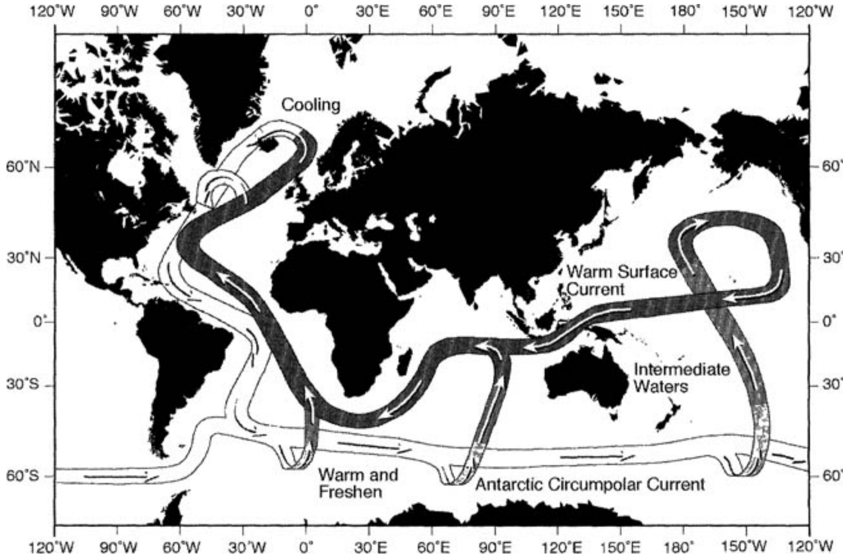


origin after a millennium of travel (Fig. 1.4) (Gordon 1986). This circulatory system is sometimes known as the Global Conveyor. The range of temperatures and salinities encountered in the oceans is not large. Temperatures range from some 35°C to –2°C and salinities from 34 to 38‰ (parts per thousand). There is therefore a relative constancy of temperature and salinity on a coarse scale. Most organisms, as they move through the water, will experience only gradual changes in these and in most other physical parameters. Sharper boundaries (known as clines) may occur under specific conditions where limited mixing allows the formation of steeper chemical or physical gradients (e.g. of density at the pycnocline, of temperature at the thermocline, or of oxygen at the oxycline). The only real physical boundaries occur at the sea surface and the seafloor. Density differences between adjacent layers of water greatly affect the degree of mixing. The greater the density difference between contiguous layers, the greater is the energy input (e.g. as wind at the surface) that is required to mix them, and hence the greater is their stability.

The effects of organisms

Temperature and salinity are almost entirely unaffected by the activities of organisms in the water. This is certainly not the case for many other components of seawater, particularly nutrients, oxygen, and carbon dioxide. Dissolved nutrients (particularly nitrate, phosphate, and silicate) are taken up by phytoplankton and incorporated during photosynthesis into new tissue where they are locked in and made unavailable to other organisms (apart from predators). Only

Fig. 1.4 The Global Thermohaline Conveyor Belt drives the ocean circulatory system. Surface water cools and sinks in the Norwegian Sea, flowing south and ultimately rising again from the southern hemisphere where it freshens and warms during its centuries-long circulation round the world's oceans. (Courtesy W. J. Gould.)



during the processes of excretion, or death and decay, are these nutrients released back into the seawater (in the process known as remineralization). Usually this occurs as corpses (or faecal pellets) sink into deeper water as part of the export flux from the euphotic zone. Deep water therefore contains higher levels of these dissolved nutrients. They may, however, disappear almost entirely from surface layers (above the thermocline) when active photosynthesis is taking place and they are locked into the phytoplankton, unless they are continuously replenished from deeper water by mixing processes.

Oxygen is described as a 'conservative' element, for it enters the oceans only from the atmosphere by direct solution in the surface waters or from its production and release by phytoplankton during photosynthesis—a process which also takes place only in the surface layers. All oxygen in the deep sea thus derives from the surface, usually carried down in the cold, dense currents produced by the extreme cooling of Arctic and Antarctic surface waters. In these cold waters oxygen (and other gases) is also more soluble than elsewhere. Nevertheless, all organisms in the sea, at all depths, need oxygen for respiration and they gradually use up what has been brought down from the surface. The residual oxygen concentrations in the water mark the difference between the original levels and the uptake, and give an indication of the level of biological activity (both of microbes and of larger organisms) in particular regions of the ocean.

Carbon dioxide, too, enters the sea by solution from the atmosphere (as bicarbonate), but organisms at all depths also produce it during the process of aerobic respiration. A major 'sink' for carbon dioxide is its incorporation (as carbonate) into the calcareous skeletons and shells of both plants and animals. When the organisms die the calcium carbonate often ends up as vast seafloor deposits (e.g. foraminiferal ooze, pteropod ooze, coccolithophore plates, coral sand, bones, and shells), which geological processes may eventually convert into chalk or limestone. The budget of carbon dioxide in the oceans is a complex one and its uptake from, and discharge into, the atmosphere is affected by the acidity, or pH. The process has a high scientific profile, because the oceans may have the potential for limiting the damage done by the artificially increased levels of carbon dioxide in our industrial atmosphere. If much of the excess can be absorbed by the oceans and locked into new tissue by increased near-surface photosynthesis (and this material is then exported from the surface into the sediments to form insoluble deposits on the seafloor), then the increases in atmospheric carbon dioxide and the anticipated climate changes (global warming) may not be so severe.

The oceans contain all the naturally occurring elements (as well as, increasingly, many man-made isotopes, compounds, and materials). Many of the so-called 'trace' elements (those present in very low concentrations) may also be important requirements for one or more species and limit their distributions or numbers. Copper, iron, strontium, vanadium, sulphur, and boron, for example, are all necessary for some organisms. Particular organic compounds may also be essential. Organisms compete both for the critical inorganic elements and for organic compounds such as vitamins when the levels of these substances become limiting.

Remote sensing

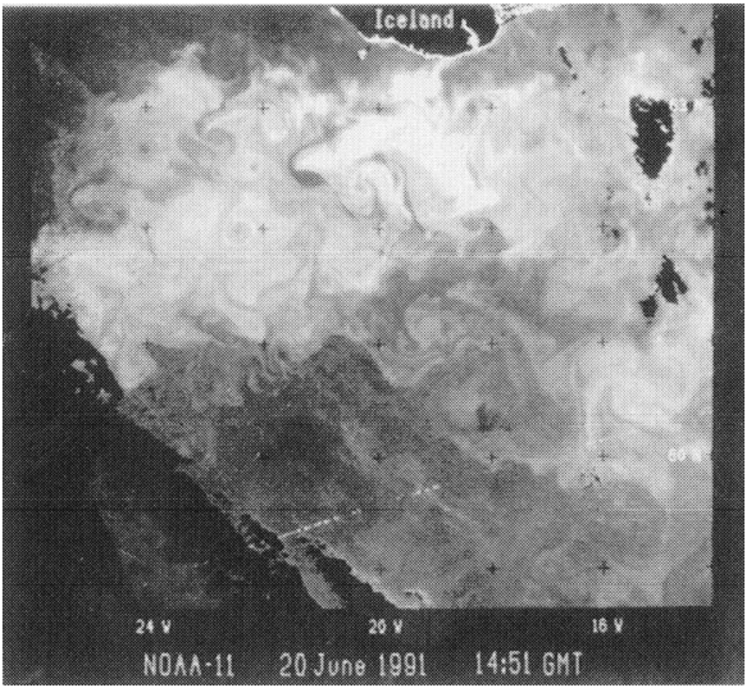
Our ability to determine the concentrations of the elements and of compounds that are apparently necessary for different species has improved greatly in recent years. The laborious methods of wet chemistry necessary for the quantitative analyses of trace elements, and the ultra-clean conditions required to avoid contamination and spurious data, are being combined and automated. One of the major advances has been the development of remote sensors capable of continuous readings of temperature, conductivity, pressure, light, oxygen, nutrients, fluorescence, and many other parameters. By incorporating such sensors into a towed vehicle, continuous profiles of these features can now be obtained in real time over large areas of the oceans, opening the way for large-scale mapping and the determination of global budgets. The advent of the various sensors criss-crossing the oceans mounted on ships, on towed vehicles, on tethered but mobile remotely operated vehicles (ROVs), on free-ranging autonomous underwater vehicles (AUVs), on fish, birds, or mammals (McCafferty *et al.* 1999), and coordinated into networks of sub-sea observatories (Oceanus 2000), gives great hope for larger-scale analyses of the oceans' properties and populations. The data from sensors on towed or autonomous vehicles are now supplemented by the information from similar systems mounted on anchored or drifting buoys, providing long-term monitoring at particular locations and in particular water masses, respectively.

Remote sensing of primarily physicochemical parameters has extended to satellites, some of which are now dedicated to marine observations. Their data have demonstrated the ubiquity of eddies and whorls (Richards and Gould 1996) at all scales from the 'mesoscale' (100s of km diameter, Fig. 1.5) to the Kolmogorov scale (mm or less, Chapter 6), each scale having different impacts on the organisms. Biological conclusions can be drawn from some of these data, particularly those involving the distribution of surface reflectance characteristics at different wavelengths. Such spectral data can then be converted to phytoplankton concentrations and correlated with sea-surface temperatures. The huge areas covered by satellite observations provide a comprehensive inventory of ocean surface characteristics (Fig. 2.1). These characteristics are convertible, with varying degrees of difficulty and accuracy, into global carbon budgets and their associated seasonal and geographical fluctuations. It has been less easy to develop biological sensors capable of quantitatively converting the three-dimensional populations in the oceans to electronic signals, but considerable progress is now being made in the use of automated optical methods of particle (and plankton) counting, pump sampling, flow cytometry, holography, and, particularly, acoustic measurements of animal populations (Foote 2000; Foote and Stanton 2000).

Acoustic methods

Acoustic techniques have been perfected by the fishing industry for their particular target species but are now being aimed at a much wider range of animal

Fig. 1.5 The ubiquitous complexity of eddies and whorls in the surface ocean are made visible in this 1991 satellite image by the high surface reflectance caused by a bloom of the coccolithophore *Emiliana huxleyi* between Iceland (top) and the Faeroe Islands (upper right). (Photo: P. Holligan.)



sizes (i.e. smaller species, and all kinds of animals, from jellies to krill) (Holliday *et al.* 1990). There are still problems because the reflected acoustic signal is not necessarily related to the size of the organism but to both its 'acoustic impedance' and its orientation in the beam of sound. Nevertheless, the techniques allow remote observations of populations in the sea on the same time and space scales as the physical measurements (Foote and Stanton 2000). It is the only practicable means of assessing, for example, the Southern Ocean biomass of krill, the pivotal species for so much of the open-ocean ecosystem in that particular region. The krill are now subject to substantial commercial fishing effort and accurate quantitative assessment of their populations is essential for effective management of both that fishery and others (such as those for icefish and squid) which may ultimately depend on the krill stocks.

In general, an animal will only reflect sound of wavelengths shorter than itself. Sound travels at some 1500 m s^{-1} in seawater, so a sound of frequency 150 kHz has a wavelength of 10 mm. Lower frequencies will reflect a signal off larger animals (e.g. commercial fishes) but for measurements of zooplankton populations, frequencies higher than 100 kHz are essential. High frequencies are, unfortunately, much more rapidly attenuated by seawater than low frequencies, so their effective range is much less. Acoustic methods have to balance the power output required for a particular frequency against the minimum range required to reach the species of interest.

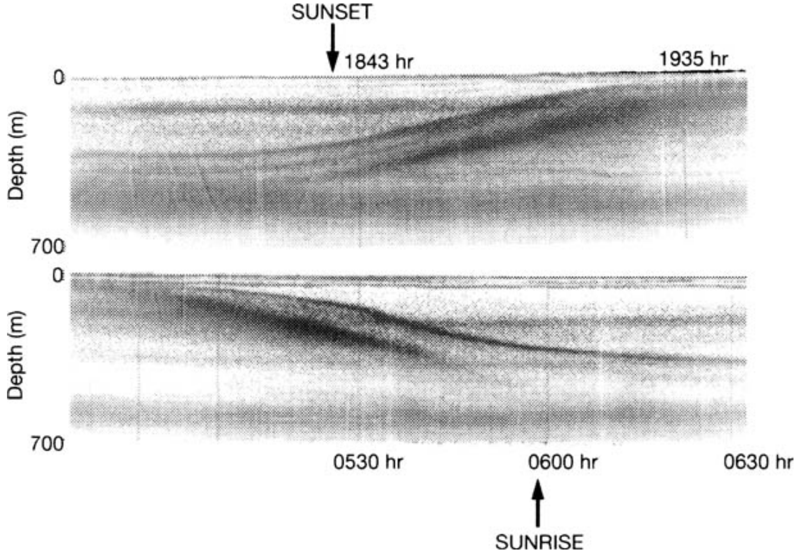
Midwater organisms of small size (<10 mm) and living at depths of a few hundred metres cannot easily be detected by high-frequency pulses from surface ships. The solution is to mount the acoustic system on a towed vehicle and send it to the depth of the animals, where the signal range of the system will not be so limiting. Zooplankton populations are rarely dominated by a single species, so the reflected acoustic signal needs to be interpreted in the context of a range of species and sizes, each with its own acoustic characteristics. This can be done by using a range of frequencies simultaneously (Pieper *et al.* 1990), but the methods need 'ground truthing' to identify the species likely to be contributing to the signal at any given locality. Net hauls are still the most effective way of achieving this, though simultaneous optical and acoustic imaging of zooplankton is also practicable (Benfield *et al.* 1998; Jaffe *et al.* 1998). Trials of an acoustic source mounted on a net have recently shown good correlations between the two sampling methods, but the slow speed of a net precludes this being used during large-scale surveys (Greene *et al.* 1998).

Certainly acoustic methods are now capable both of discriminating between taxa of similar size and of identifying the main contributors to the observed backscatter. They are also the only effective present means of determining the three-dimensional structure of zooplankton patches.

The strength of a reflected acoustic pulse is a function of the acoustic impedance of the animal relative to seawater and the area presented to the beam. Acoustic impedance is the product of the density of the tissue and the speed of sound. A gelatinous animal has similar impedance to seawater and gives a relatively poor signal. Very high reflective signals are given by gas-filled spaces; small animals with gas bladders (e.g. some siphonophores and many fish) give much stronger signals than larger ones without them.

The early recognition of the importance of the use of acoustics in biological oceanography resulted from the use of relatively low-frequency echosounders (10–40 kHz) for continuous measurements of the water depth and for studies of the surface features of the seafloor. Unexpected layers of sound scattering were encountered in midwater, at depths of several hundred metres. Even more unexpected at that time was the fact that these layers appeared to move nearer the surface at dusk and descend again at dawn, often separating into several discrete layers (Fig. 1.6). We now know that these 'deep scattering layers' (DSLs) are populations of animals undertaking a regular migration to and from the surface (Chapter 4). Strong sound scatterers do not have to be very abundant to give a strong DSL, so initial attempts to identify the scatterers by fishing in and out of the DSLs were not very conclusive. Better depth control of modern net samplers, combined with direct observations from submersibles, have shown that DSLs may be caused in different regions and seasons by animals such as fish, shrimp, and siphonophores.

Fig. 1.6 Echosounder records made at a frequency of 36 kHz in the northeast Atlantic show multiple layers of backscattering. Some of the layers move up from about 400 m just before sunset (above), reaching the surface waters about an hour later. In the morning (below) they move down again just before sunrise. These layers are probably produced by mesopelagic fish or shrimp undertaking a typical diel vertical migration (Chapter 4).



Biological sampling

All estimates of biological populations, distributions, and productivity in the open-ocean ecosystem depend on the validity of the sampling techniques (Angel 1977). The organisms range in size from viruses to whales. We can neither harpoon a virus nor filter a whale; no one sampling method can be effective across the whole size spectrum and different techniques are used to sample different size ranges within it (Table 1.1) (Clarke 1977; Omori and Ikeda 1992; Harris *et al.* 2000). In addition, the techniques for sampling the pelagic populations in the open ocean and the benthic ones on the seafloor are very different, although the questions that the samples are intended to answer are often similar. Benthic sampling methods are summarized in Chapter 3.

Small organisms

At the smallest size ranges of interest are organisms such as viruses and bacteria (<1 μm). These can be collected in seawater samples that are then concentrated by centrifugation or by suction filtration through filters with very fine pores. Bacteria and viruses can then be stained, identified, and counted directly on the

Table 1.1 Size ranges of different categories of plankton

Pico	Nano	Micro	Meso	Macro	Mega
0.2–2.0 μm	2.0–20 μm	20–200 μm	0.2–20 mm	2–20 cm	20–200 cm

Plankton is functionally divisible into zooplankton (the animal heterotrophs) and phytoplankton (the photosynthesizing autotrophs). Some species have intermediate styles of nutrition. Bacterioplankton is a term sometimes used for pelagic heterotrophic bacteria; they are usually included in picoplankton.

Nekton comprises the larger animals (e.g. crustaceans, squid, fish, etc.) that can swim against a current.

filters, using electron microscope techniques. This is a very laborious procedure and every manipulation of the sample reduces the accuracy of the result. The procedure has been greatly improved by the use of bacteria-specific fluorescent stains, which allow the organisms to be counted (much more rapidly) under a light microscope. Some differentiation between different groups of bacteria can be achieved with these methods, but for complete identification it is usually necessary to culture the organisms. This is a very inefficient process, because only a very small proportion (<5%) of the bacteria recognizable in seawater can be grown in culture.

A recent approach has been to extract bacterial ribonucleic acid (RNA) from seawater samples and then to examine the genetic diversity in this material, rather than looking directly at the organisms. This method shows that there is a great range of genetic diversity in the bacterioplankton, very much more than that present in known species of marine bacteria (Giovannoni and Cary 1993). The corollary is that there are many more species of bacteria out there than are at present recognized. The same variety is to be found among the smaller eukaryotes (Lopez-Garcia *et al.* 2001; Moon-van der Staay *et al.* 2001).

Most early studies of marine bacteria assumed that they were free-living in seawater. It is clear from more recent work that many (probably a majority) are in practice associated with one or other type of particle, ranging from marine snow to the surfaces and gut flora of larger animals. This greatly compounds the problem of achieving accurate values of abundance. The small pore size of the filters limits the collection of samples by filtration to relatively small volumes of water; organisms may also adhere to the walls of containers during collection and preparation. In addition, the mechanical processes of filtration easily disrupt the more delicate species of microorganisms, rendering them unrecognizable.

The problems of sampling at the smallest size range of organisms are gradually being overcome. Developments in flow cytometry allow the characterization and counting of particular kinds of microorganism on a continuous basis. The effort is being fuelled by the increasing evidence of their importance in the energy budgets of the oceans (Chapter 2). Some abundant animals (e.g. larvaceans) rely on microorganisms for their main energy source. Their success at capturing this size range of particles is much envied by many marine microbiologists.

Medium-sized organisms

Organisms larger than about 20 μm are routinely sampled with nets. Different methods are preferred for the more delicate species at the lower end of the size spectrum (e.g. flagellates and ciliates); in order to quantify these organisms water samples are centrifuged or carefully filtered and microscope preparations of live or stained organisms in the concentrated sample are subjected to image analysis. Nets are used for a size range extending over almost 5 orders of magnitude (from 20 μm phytoplankton cells to 2 m tuna) and provide a means of concentrating the organisms from the seawater in which they live (Omori and Ikeda 1992; Sameoto *et al.* 2000). The net is towed (or pursed) through the water and it is assumed that the water flows smoothly and freely through the meshes and that everything larger than the mesh size is retained.

The design of a net is critical to its effective use: the area of the holes in the mesh must be sufficient for all the water entering the mouth (at the intended towing speed) to flow smoothly out through the mesh of the net. Any reduction in the filtration area below the required minimum will cause water to back up in the net and will result in a pressure wave in front of the mouth, keeping many organisms out. For each net there is therefore a compromise between mouth area, length, mesh size (= area of filtration), and tow speed. The compromise is determined primarily by the size range of the organisms that the net is designed to sample (Omori and Ikeda 1992).

In the three-dimensional environment of the oceans it is essential to determine the depth at which particular organisms live. The depth range over which a net fishes is therefore a very important piece of information. The simplest means of achieving this is to lower a net with a weight on the end to a known depth (which can be determined approximately by the length of line paid out) and then to haul it back vertically to the surface. All the organisms in it will have been living between its maximum depth and the surface, and their concentrations in the filtered column of water can be calculated. By increasing the depth of successive hauls, and subtracting from the deep ones those animals already caught in the shallower ones, a crude picture of the depth of occurrence of different species can be built up. For many years this was the only method available.

Vertically hauled nets have a disadvantage in that the bridles attaching the towing line to the net mouth, and the line itself, plough through the water immediately in front of the net, and produce a pressure wave ahead of it, frightening away many animals that are active swimmers. One solution to this problem has been to mount nets in rigid frames (usually in pairs) on either side of the towing line, rather like a pair of Bongo drums (not surprisingly these are known as Bongo nets), so that there is nothing directly in front of the mouth. Another solution is to use a free-rise net; this has no attached line and has buoyancy spheres round the mouth but is weighted with ballast so that it sinks slowly when put in the water. At a particular depth the ballast is released (either by an acoustic signal from the ship, or a timing device) and the net then rises slowly to the surface under its own buoyancy, fishing all the way. Such nets can potentially be made very large (>10 m diameter) if assembled in the water, but have proved difficult to deploy.

There are obvious disadvantages in only being able to fish a net from a fixed depth back to the surface; a much better indication of where animals live can only be achieved by opening and closing the nets at known depths. For vertical nets this was (and often still is) done by sliding a heavy weight (or 'messenger') down the wire to activate a closing mechanism which throttles the net at a specific depth or (for smaller nets) closes the mouth by means of a spring-loaded butterfly valve. The resulting sample has a well-defined vertical depth range. The volume of water filtered by a vertical net is determined by the vertical range over which it fishes. It is therefore not possible for a vertical net to filter a large volume of water over a limited depth range (unless of course it were to have an unmanageably vast mouth area). Nets towed obliquely or (better) horizontally get over this difficulty. One ingenious system used in the past hung several nets at different points (i.e. depths) along a trawl wire and closed them with a messenger system that throttled each net as the messenger hit, at the same time releasing another messenger to continue down the wire and activate the next net. The system used conical nets and still had the problem of bridles (and the main trawl wire) in front of the mouth, but Bongo nets can be used in a similar way.

Modern net systems use remote signals to trigger events such as opening and closing (Clarke 1977). These signals may be either acoustic pulses or, if the nets are towed on an electrically conducting or fibre optic cable, electrical or optical signals sent directly down the cable. A single net tow at a given depth requires that the net be first lowered to the correct depth, then opened, fished, and closed again, and finally recovered by hauling back to the surface. Much time can be saved, particularly in deep-water sampling, if several nets can be fished in sequence after lowering and before hauling back to the surface. Multiple net systems have therefore been developed, with up to 20 separate nets, fished one after the other (Sameoto *et al.* 2000).

In the MOCNESS gear (Multiple Opening and Closing Net Environmental Sampling System) the nets are mounted in a fixed frame and opened in sequence by the release of spring- or elastic-loaded arms. These multiple nets can be any one of a variety of sizes and meshes, depending on the target organisms, and can carry a variety of environmental sensors, including the bioacoustic systems noted above (Wiebe *et al.* 1985). Another multiple system is based on the Tucker trawl. The original trawl was a single net with a rectangular mouth, designed to fish at an angle of 45°. The Rectangular Midwater Trawl system developed from it has an 8 m^2 net with 4.5 mm mesh and mounted above it is a 1 m^2 net with 0.33 mm mesh. This system is designed to catch a wider (and overlapping) size range of organisms than either net would do by itself. Because the nets open and close simultaneously the catches are directly comparable. A modification of the system has three such pairs of nets, which are fished in sequence, saving the lowering and recovery time. These nets may be operated either acoustically or by direct electrical signals down the wire.

Multiple nets can be used to examine either the horizontal distributions of organisms (several nets are fished one after another at the same depth) or their vertical stratification (the nets are fished in contiguous vertical strata). Smaller-scale distributions can be examined with the Longhurst–Hardy Plankton Recorder (LHPR), a modification of the Continuous Plankton Recorder that was designed for routine towing by merchant ships. In this system the catch reaches the tail of the net, where it is strained through a section of a gauze mesh wound on a reel. At predetermined intervals the reel winds on, advancing the filtering region. The previous, used, section with its captured plankton is sandwiched with another roll of gauze and the two are wound onto a storage drum, with the plankton trapped between them. The resulting long strip of plankton sandwich comprises a series of, say, 5-minute samples which, once analysed, can be 'read' rather like a series of film frames.

The LHPR acts like a single net with very many sequential opening and closing codends (the bucket in which the catch collects). Multiple codend buckets have been designed for use on larger trawls, but all such tail-closing devices have the problem that plankton may not wash rapidly down the net and some will 'hang up' on the mesh on the way. This means that animals caught in the net in one time period may take different times to reach the codend, blurring the spatial distinction between adjacent samples. This can only be overcome by having the opening and closing taking place at the mouth of the net rather than at the codend. This is now the method of choice for larger nets.

Hang-ups are only one problem to be faced in the accurate quantitative use of net samples. Another is that of mesh clogging. If spiny or gelatinous animals are caught they may well stick to the mesh of the net, blocking some of the filtration area, so that the area is finally reduced below the minimum value for smooth filtration. The water backs up as a forward pressure wave, which greatly reduces the sampling efficiency (rather like trying to catch a fish in an aquarium with a jar already full of water). Even without a pressure wave ahead of it, a net will be clearly visible in well-lit water and will further signal its presence to the animals in front by its noise, turbulence, and, in the dark, even by the luminescence it may cause. Many animals are undoubtedly able to avoid such nets. The responses of fish to bottom trawls, for example, have been well-documented: several species swim for long periods of time just ahead of the net, finally falling back into it only when they become exhausted. When the catches of a particular species are consistently lower by day than they are by night the cause is probably visual avoidance, but it can easily be confused with the effects of diel vertical migration (Chapter 4). The more active a species, the more likely it is to be able to avoid a net, and larger individuals will find it easier to do so than small ones. This may well result in an apparent bias towards smaller specimens in a sampled population. In contrast, some active animals that would normally avoid a net (e.g. squid) may go into it specifically to feed on those specimens already there. The presence in the catch of fish with squid beak bite-marks, despite the absence of squid, gives away what has happened. Sometimes the perpetrator is slow in escaping after its meal and is also caught.

Attempts to reduce the problem of avoidance have focused either on such attributes as net colour and visibility or on designing faster nets. The larger nets are usually towed at speeds less than 2 m s^{-1} and one way of increasing the practicable towing speed is to have a much smaller mouth area opening into a much larger filtration chamber behind it. High-speed (4–5 m s^{-1}) plankton samplers, for example, used in fisheries surveys for fish larvae, have a large net enclosed in a rigid torpedo-like frame with a small circular mouth opening in the centre of the nose cone, i.e. a very high ratio of mesh area to mouth area. The fast flow through the mouth is rapidly decelerated by the conical expansion of the space behind it so that flow through the mesh is relatively slow and the catch remains undamaged.

One programme attempting to sample those mesopelagic animals that are *not* caught by smaller research trawls used a very large commercial fishing trawl (an Engels trawl) fished on twin wires in the South Atlantic. This net caught both more and larger specimens of the known mesopelagic fauna but not a different fauna. It could not be closed, and its huge area meant that the increased drag prevented it from being used at bathypelagic depths because there was not enough wire on the winches! The experiment was not continued. Comparisons between the benthopelagic fish populations of one area sampled with different gears, based on catches made by the same Engels trawl and two other (smaller) bottom trawls, showed marked differences in the sizes and abundances of particular species when calculated from the different nets (Haedrich and Merrett 1997).

Biologists generally prefer to make consistent use of a single gear and to regard their data from different depths, areas, or seasons as relative comparisons rather than absolute truths. If samples are to be taken from abyssal depths (either in mid-water or on the bottom) even small trawls present difficulties. For a small semi-balloon otter trawl towed on a single wire at 2–3 knots (1–1.5 m s^{-1}) it may be necessary to pay out some 15 000 m of wire to reach the abyssal plain (at 5000 m), by which time the trawl will be some 13 km behind the ship. With this much wire out the drag on the wire will be much greater than that of the net on the end of it! Larger nets, like the Engels trawl, are therefore impracticable for deep deployment, as noted above. The one certainty is that all population estimates, by whatever gear, and of whatever species, will be underestimates.

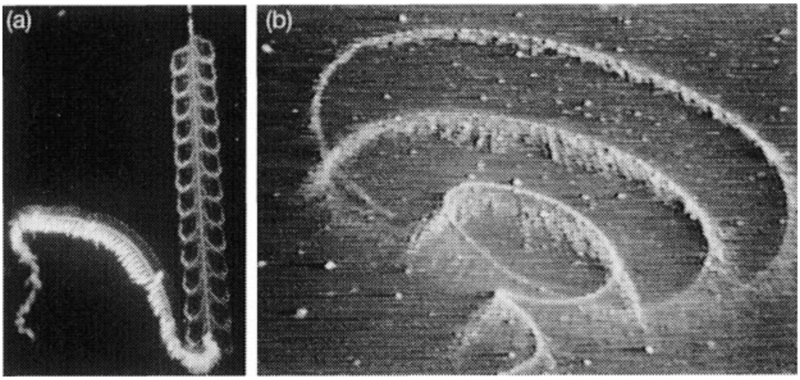
Optical techniques are now becoming routinely available to survey the plankton in real time from platforms travelling at up to 5 m s^{-1} (Foote 2000). In the optical particle counter (OPC) the organisms flow through a narrow slit, interrupting a light beam as they pass. Their number and equivalent spherical diameter are then continuously recorded. Particle sizes of up to a few millimetres can be monitored, but active and larger organisms will not be counted. Laser-scanning systems are being developed to increase the effective aperture size and to monitor larger effective 'slices' of the water, thereby including a larger size range of organisms. Imaging systems, including holographic ones, allow identification of plankton types at fine spatial resolution and are demonstrating how both phytoplankton and zooplankton are often aggregated in very thin layers of water stratified by virtue of their density differences and just centimetres to a few metres thick. The value of these kinds of techniques is that they are effectively remote and non-intrusive and the organism's behaviour can be monitored without necessarily altering it.

These methods are getting to grips with the huge sampling problem of determining the three-dimensional distribution of species in the ocean so that the separation between individuals can be more accurately assessed than nets presently allow. One oceanographer suggested that the ideal system would be an endothermic nuclear device that would instantly freeze a cubic kilometre of water; it could then be towed to a laboratory for gradual thawing and the spatial coordinates of all of its inhabitants determined! An interesting recent approach has been to push a mesh slowly through the water on the front of a submersible and record the luminous flashes of plankton species as they are encountered. This establishes the spatial arrangement of those species with distinctive flashes that occur within the passage volume of the mesh (Widder and Johnsen 2000). It is, of course, limited to particular luminous species—and assumes that they all flash on contact with the mesh and make no attempt to avoid it.

Nets present a particular problem when sampling delicate organisms (e.g. many gelatinous species). Animals such as siphonophores and ctenophores are very easily damaged or destroyed by the mechanical abrasion of the net and may either break into fragments small enough to go through the mesh or simply disintegrate into an unrecognizable jelly. Working with net-caught specimens is akin to trying to reconstruct a snowball after it has hit a wall. Recognition of the importance of such animals in the economy of the oceans has had to wait for better methods of observation and sampling, particularly open ocean (or 'blue water') scientific Scuba diving and the use of manned submersibles and ROVs with video cameras (Fig. 1.7). Siphonophores and medusae are known to consume large numbers of fish larvae, with daily consumptions of up to 60 and 90%, respectively, of the available larvae. Their predatory importance emphasizes the void in our ecological knowledge which results from our inability to determine their populations accurately. The luminescence technique noted above is applicable to some of these animals.

Net catches seriously underestimate the numbers of the more delicate species and are rightly criticized for potentially capturing only the slow, the stupid, the greedy, and the indestructible. Nevertheless, they are still the best general tools available for sampling most oceanic organisms. If they are to be used for accurate quantitative work then it is very important that the flow through the net is known; most nets now incorporate a flow meter in the system. Knowledge of the distance travelled by the towing vessel is not enough for calculation of the volume filtered, even with today's Global Positioning System (GPS) precision, because the currents at the depth of the net may be quite different in both direction and speed to those experienced at the surface. Almost any sensor can potentially be added to a net to transmit information back to the operator. It is perfectly practicable to fish not just at a specific depth but, with the appropriate

Fig. 1.7 Siphonophores, such as (a) *Bargmannia elongata*, are very delicate and impossible to capture intact with a net. This specimen was captured by a manned submersible, the Johnson Sealink, which also (b) videorecorded the extraordinary fishing posture of this specimen (3–4 m long) of an undescribed siphonophore. The ecological importance of these animals would never have been appreciated without the sampling and observations achieved by using submersibles and remotely operated vehicles (ROVs). (Images: S. Haddock and Harbor Branch Oceanographic Institution.)



sensors, along a temperature interface, at a defined light intensity, or within the particle plume of a deep-sea hydrothermal vent. Acoustic and direct telemetering of real-time information not only about environmental variables but also about features of net performance, such as mouth height and width, depth, aspect, height off the bottom, flow, etc., have been pioneered by both the commercial fishing industry and biological oceanographers. The first set of users are seeking to maximize the effectiveness of the net in catching the target species, the second are also trying to improve our quantitative understanding of the three-dimensional distribution of open-ocean animals in time and space.

One feature of using nets as quantitative samplers, to estimate the abundances of the organisms they catch on the basis of a random distribution, is that the nets sample such a small fraction of the environment that any animal of which we have but a single specimen should in reality be very numerous. Thus if just *one* specimen of an animal is taken during the course of, say, 100 trawls using a net with a mouth area of 8 m^2, each towed for 2 h at 1 m s^{-1}, we would regard it as very rare. Yet its abundance would be 1 per 5.8×10^6 m^3, that is individuals would be about 200 m apart if evenly spaced. Were it to be globally (and randomly) distributed at all depths we should expect there to be about 2.5×10^{11} individuals worldwide. Of course the animal would not be distributed like that, but whatever pattern we assumed would still imply a lot of individuals (if it has any avoidance ability it will be even more abundant). Anything we catch frequently should be massively abundant. Scaling up like this has huge pitfalls (see Chapter 11) but does emphasize what a pitifully small fraction of the oceanic environment we have actually sampled and how wary we should be in our interpretations of those samples. We must appreciate that 'rare' in oceanic terms simply means 'rarely caught'.