Chapter 1

The physical template

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Introduction

The physical environment determines the most fundamental constraints acting upon life. Life is only possible over a small part of the potential range of physical variables such as temperature that may occur on Earth and all species have evolved adaptations optimized for particular conditions. However, the physical conditions on Earth which all life, including man, are constrained by are not purely the result of physical processes. Life on our planet, and particularly life in the oceans, modifies the physical environment and makes the planet more suitable for life. The physical template we observe is to some extent the product of organisms over millions of years. Since life began in the oceans about 3.5 billion years ago, factors such as salinity, temperature, oxygen and nutrient levels have been shaping the evolution of the myriad of marine organisms alive today and they have in turn been changing these and other variables. Before we examine in detail these organisms and their interactions, it is appropriate to consider the major physical processes acting within the oceans that form the template upon which every ecological community is built.

Marine regions

The sea covers 70% of the surface of the earth and offers greater than 98% of the total space available to life. The Earth from space (Figure 1.1) is clearly a water world; observers approaching from a distance would likely assume all dominant life is marine, simply from the color of the distant planet. Indeed, the preponderance of terrestrial species is a geologically recent phenomenon. Further most of the habitat is in deep water; only about 3% of the world's waters lie over the continental shelf, which have an average depth of around 200 m. The average depth of the oceans is 3200 m and the maximum depth of about 11,200 m is at the bottom of the Challenger Deep in the Marianas Trench near Guam in the western Pacific.

As shown in Figure 1.2, working from the land towards increasing depth, a number of major habitat divisions are recognized. The zone that is influenced by the sea but not always covered in water is the intertidal, or littoral. Next, the sublittoral extends from the extreme low water level down to about 40 m, which is around the safe limit for recreational scuba diving on compressed air. From the edge of the continental shelf the depth increases down the continental slope then slopes more gently down the continental rise to reach the abyssal zone. The continental shelf is the submerged gently sloping border of the land, the width of which varies from 100 m to 1300 km. The continental slope marks the edge of the continents and the region where the seabed slopes at an average angle of 4 degrees to a depth of about 2000 m. The foot of the slope marks the beginning of the abyssal plain.

Marine Ecology: Concepts and Applications, 1st edition. By M. Speight and P. Henderson. Published 2010 by Blackwell Publishing Ltd.

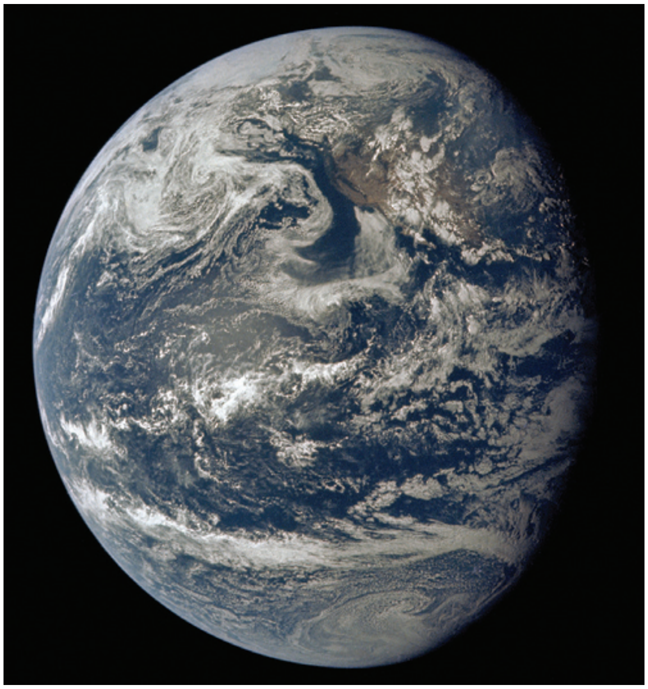

Figure 1.1

Earth from space. Planet Earth taken by Apollo 11, July 16, 1969. (Photograph courtesy of NASA.)

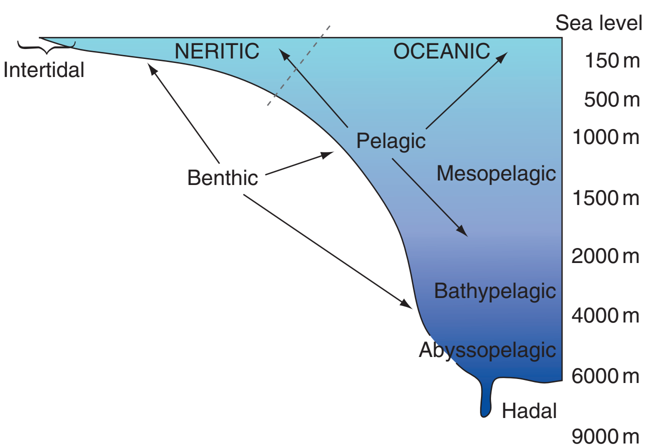

Figure 1.2

Diagram showing location of major marine habitats in relation to depth.

Aquatic habitats are classified by depth and locality within the water body. The term benthic is used to describe living on or within the seabed at any depth. In comparison, the neritic zone extends from the low-tide level to a depth of 200 m, and is thus at or near coastlines in contrast to the oceanic zone which occurs away from land. Pelagic is used to describe the open water habitats, which may lie close to shore and they can also be described as neritic. Pelagic habitats are divided into four depth zones, epipelagic (0–200 m), mesopelagic (200–1000 m), bathypelagic (1000–4000 m), and abyssopelagic (below 4000 m). The term hadal is used for the deepest parts of the oceans below 6000 m in depth.

The ocean floor is not featureless and the boundaries of the tectonic plates (Figure 1.3) are marked by towering underwater mountain ranges. Figure 1.3 shows the Mid-Atlantic Ridge running down the centre of the Atlantic Ocean, roughly parallel to the shores of Africa and Europe to the east, and the Americas to the west. Similarly, in the Pacific Ocean, approximately 3000 km off the South American coast, there is the East Pacific Rise. This oceanic ridge towers about 2 km from the ocean floor, and stretches from the Gulf of California to the southernmost tip of South America. Submarine ridges owe their formation to the movement of the continental (tectonic) plates. As these plates slowly move away from each other, they leave gaps in the Earth's crust. This allows molten rock from beneath the Earth's crust to move up into the gap, forming a new ocean floor. As the molten rock seeping through these gaps is under pressure, it spews upward, forming a ridge. These ridges cause oceans and seas to be divided into basins. It is in these gaps that hydrothermal vents occur (Figure 1.4), where seawater is superheated by the volcanic activity and discharged in black or white "smokers." This water is rich in dissolved sulfur, iron, and other minerals, and such sites may have supported the first appearance of life on earth.

Mid-ocean ridges are regions of high volcanic activity and are estimated to produce 75% of the total annual output of molten volcanic rock, magma, on earth. It has been estimated that there are more than one million submarine volcanoes and perhaps as many as 75,000 of these volcanoes rise over 1 km above the ocean floor. Some break the surface to form isolated volcanic islands. The Galapagos archipelago in the Pacific Ocean off the coast of South America is a well-known example of a volcanic island group. Ocean trenches are also linked to the boundaries of tectonic plates and are formed as two plates collide and one moves under the other.

Salinity and mineral content

Ocean water has an average salinity of 34.72 parts per thousand (ppt) (or 3.472%) of sodium chloride (NaCl), normally approximated to 35 ppt. This reduces in coastal waters, for example, inshore British or East Coast American Atlantic waters have a salinity around 33–34 ppt. Mixtures of salt and freshwater are termed brackish when the salinity ranges between 8 and 33 ppt and fresh below 8 ppt. In seas where surface evaporation is not balanced by freshwater inputs, salinity can be higher than the average. The Mediterranean Sea has a surface salinity of about 38–39 ppt. Surface water salinity varies across the globe and is, on average, lowest towards the North Pole, probably associated with melting icecaps, and highest in more tropical latitudes where surface evaporation is greatest (though not necessarily exactly at the Equator due to ocean circulation patterns). Salinity also varies somewhat with depth and lower salinity water is less dense

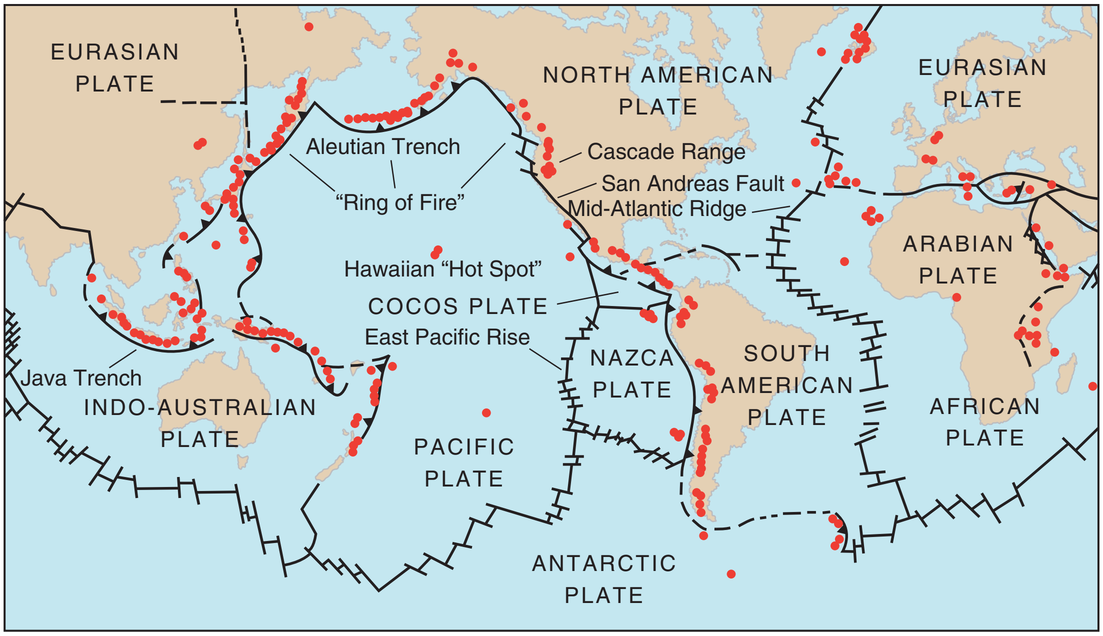

Figure 1.3

The boundaries of the tectonic plates showing the areas of greatest geological activity. (Reproduced with permission of Cascades Volcano Observatory, US Geological Survey.)

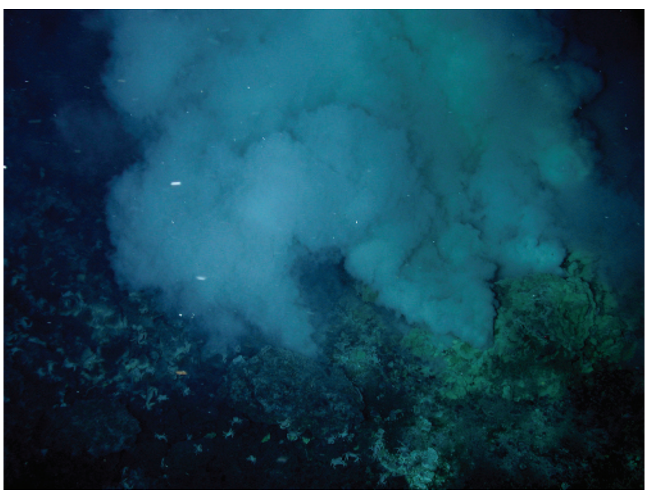

Figure 1.4

Hydrothermal venting from sulphur mounds. (Photo courtesy of Submarine Ring of Fire 2006 Exploration, NOAA Vents Program.)

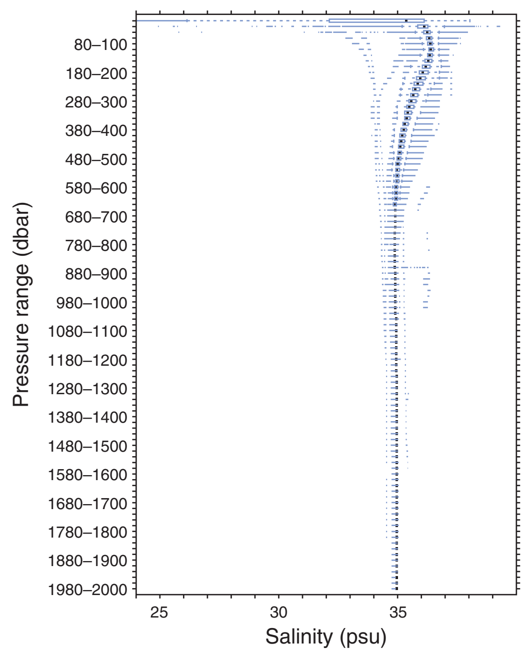

Figure 1.5

Box and whisker plots of salinity within 20 dbar pressure intervals. Data collected from the Gult of Mexico. (From Thacker 2007; reproduced with permission of Elsevier.)

and will lie over higher salinity water of the same temperature. But as can be seen from Figure 1.5, as depth increases, in this case measured by water pressure measured in dbar or decibars (2000 dbar = 200 bar = 197 atmospheres = 2040 m H_2O), salinity in the open sea (in this example in the Gulf of Mexico) stays fairly constant at just under 35 ppt (Thacker 2007).

As we shall see later in this chapter, temperature and depth are linked, so that deeper water tends to be colder than surface water at least in temperate and tropical seas, though close to deep-sea hydrothermal vents where volcanic activity just beneath the seabed produces superheated seawater from cracks in the Earth's crust, the temperatures can become extremely high. As temperatures reach upwards of 350°C, salinities may drop to less than 10 ppt (1‰ Figure 1.6, Fontaine et al 2007). Maximum salinities of water leaving vents such as black smokers are limited as a result of phase separation, where seawater which enters a vent system becomes separated into a low-salinity vapour phase, which rapidly rises and pours out through the vent chimneys, and a highly saline brine phase, which stays pooled within the vent system and is only released slowly.

The mineral content of seawater is not a simple solution of sodium chloride, but is dominated by 11 chemicals which in order of concentration are chloride, sodium, sulphate, magnesium, calcium, potassium, bicarbonate, bromide, strontium, boron, and fluoride. In addition, there is a large number of trace elements that are listed in Table 1.1. Many of these trace components have important biological functions. For example, calcium is of course a vital building block for exoskeletons, potassium an important fertilizer for marine primary productions, whilst boron is a trace element used for cellular processes by plants such as seagrass. We shall revisit some of these actions in later chapters.

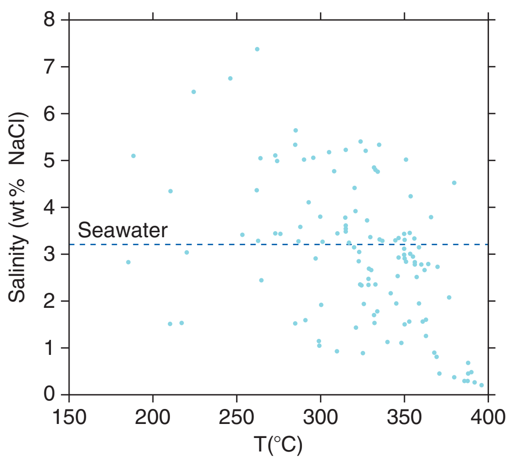

Figure 1.6

The salinity and temperature relationship for high temperature vents. (From Fontaine et al 2007; reproduced with permission of Elsevier.)

Table 1.1 Detailed composition of seawater at 35 ppt salinity in order of abundance (based on values given by Turekian (1968) *Oceans*, published by Prentice-Hall)

	ELEMENT	ATOMIC WEIGHT	CONCENTRATION PPM OR MG L^{-1}
1	Oxygen H_2O	15.9994	883000.0000000
2	Hydrogen H_2O	1.00797	110000.0000000
3	Chlorine NaCl	35.453	19400.0000000
4	Sodium NaCl	22.9898	10800.0000000
5	Magnesium Mg	24.312	1290.0000000
6	Sulfur S	32.064	904.0000000
7	Calcium Ca	10.08	411.0000000
8	Potassium K	39.102	392.0000000
9	Bromine Br	79.909	67.3000000
10	Carbon C	12.011	28.0000000
11	Nitrogen ion	14.007	15.5000000
12	Fluorine F	18.998	13.0000000
13	Strontium Sr	87.62	8.1000000
14	Boron B	10.811	4.4500000
15	Silicon Si	28.086	2.9000000
16	Argon Ar	39.948	0.4500000
17	Lithium Li	6.939	0.1700000
18	Rubidium Rb	85.47	0.1200000
19	Phosphorus P	30.974	0.0880000
20	Iodine I	166.904	0.0640000
21	Barium Ba	137.34	0.0210000
22	Molybdenum Mo	0.09594	0.0100000
23	Nickel Ni	58.71	0.0066000
24	Zinc Zn	65.37	0.0050000
25	Ferrum (Iron) Fe	55.847	0.0034000
26	Uranium U	238.03	0.0033000
27	Arsenic As	74.922	0.0026000
28	Vanadium V	50.942	0.0019000
29	Aluminium Al	26.982	0.0010000
30	Titanium Ti	47.9	0.0010000
31	Copper Cu	63.54	0.0009000
32	Selenium Se	78.96	0.0009000
33	Stannum (tin) Sn	118.69	0.0008100
34	Manganese Mn	54.938	0.0004000
35	Cobalt Co	58.933	0.0003900
36	Antimony Sb	121.75	0.0003300
37	Cesium Cs	132.905	0.0003000
38	Argentum (silver) Ag	107.87	0.0002800
39	Krypton Kr	83.8	0.0002100
40	Chromium Cr	51.996	0.0002000
41	Mercury Hg	200.59	0.0001500

Table 1.1 (*Cont'd*)

	ELEMENT	ATOMIC WEIGHT	CONCENTRATION PPM OR MG L^{-1}
42	Neon Ne	20.183	0.0001200
43	Cadmium Cd	112.4	0.0001100
44	Germanium Ge	72.59	0.0000600
45	Xenon Xe	131.3	0.0000470
46	Gallium Ga	69.72	0.0000300
47	Lead Pb	207.19	0.0000300
48	Zirconium Zr	91.22	0.0000260
49	Bismuth Bi	208.98	0.0000200
50	Niobium Nb	92.906	0.0000150
51	Yttrium Y	88.905	0.0000130
52	Aurum (gold) Au	196.967	0.0000110
53	Rhenium Re	186.2	0.0000084
54	Helium He	4.0026	0.0000072
55	Lanthanum La	138.91	0.0000029
56	Neodymium Nd	144.24	0.0000028
57	Europium Eu	151.96	0.0000013
58	Cerium Ce	140.12	0.0000012
59	Dysprosium Dy	162.5	0.0000009
60	Erbium Er	167.26	0.0000009
61	Ytterbium Yb	173.04	0.0000008
62	Gadolinium Gd	157.25	0.0000007
63	Ruthenium Ru	101.07	0.0000007
64	Praesodymium Pr	140.907	0.0000006
65	Beryllium Be	9.0133	0.0000006
66	Samarium Sm	150.35	0.0000005
67	Thorium Th	232.04	0.0000004
68	Holmium Ho	164.93	0.0000002
69	Thulium Tm	168.934	0.0000002
70	Lutetium Lu	174.97	0.0000002
71	Terbium Tb	158.924	0.0000001

Defining and measuring salinity

Salinity is expressed as either parts per thousand (ppt) or on a practical salinity scale (PSS) often termed practical salinity units (psu). For most purposes and waters there is little numerical difference between ppt and psu measurements. Originally salinity was defined to be the total amount of dissolved material in grams in one kilogram of seawater. This is not useful in practice because the dissolved material is impossible to measure. Because salinity is directly proportional to the amount of chlorine in seawater, and chlorine can be measured accurately by a simple chemical analysis, salinity, S, was redefined using chlorinity, Cl, as

$$S = 1.80655 \text{ chlorinity}$$

where chlorinity is defined as the mass of silver required to precipitate completely the halogens in 0.3285234 kg of the seawater sample.

Oceanographers now use conductivity meters to measure salinity, where the passage of an electrical current through water is related to the amount of salts dissolved within it. The equation relating conductivity to salinity is termed the practical salinity scale (PSS). With careful calibration, an accuracy of 0.002 PSS and a precision of 0.001 PSS can be achieved. Biologists working in coastal and estuarine waters are more likely to use refractometers which measure the salt content by the change in direction of light as it passes across a film of water placed on the instrument. The accuracy at best is 0.1 ppt.

Estuaries and sediments

Within estuaries there are salinity gradients ranging from 0 in the river to 35 ppt at the seaward limit. In the water column, salinity varies with the tide, wind and river flow creating a rapidly and constantly varying habitat for organisms that maintain a fixed position on the seabed. Because saline water has a higher density than freshwater there is a tendency for marine waters to flow in along the bottom and freshwater to flow out on the surface. The intrusion of higher salinity waters along the bed of an estuary is often termed the salt wedge. These flows and changes in salinity also cause the flocculation of clay and the deposition of sediments. Flocculation occurs when very small clay particles combine into groups to form larger crumbs or flocs which sink to the bottom, removing significant amounts of metal ions from the water column. As shown in Figure 1.7, the dramatic changes in water salinity observed in estuarine water do not occur within the bottom sediments. Within a few centimeters below the sediment surface, salinity concentrations remain fairly constant no matter what is happening in the water above. This relative stability within the sediments is important for bottom-living organisms that are unable to tolerate changes in salinity.

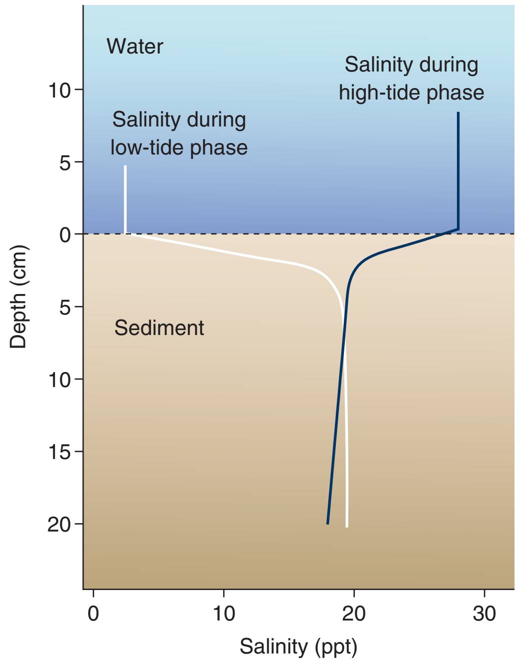

Figure 1.7

Variation in the salinity within the water column and within the bottom sediments of an estuary.

Figure 1.8

The shore or green crab, *Carcinus maenas*. (Photograph courtesy of Paul Naylor.)

Figure 1.9

European eel, *Anguilla anguilla*, a catadromous species of fish that during its lifecycle moves from freshwater to the sea and back to freshwater. (Photograph courtesy of Richard Seaby, Pisces Conservation Ltd.)

Salinity tolerance

Organisms are classified by their ability to withstand variation in salinity. Obligate freshwater organisms do not live in waters that exceed 8 ppt and obligate fully marine organisms, which will not tolerate salinities below about 30 ppt, are termed stenohaline. Echinoderms such as starfish and sea urchins are stenohaline, predominantly due to their unique water vascular systems which will only function if their internal body fluids are isosmotic (having an equal osmotic pressure) with the surrounding seawater. Both freshwater and stenohaline marine species cannot survive in the variable salinities of estuaries. Animals able to withstand wide salinity variation are termed euryhaline, and include many of the familiar Crustacea such as shore crabs (Figure 1.8) which can be found in all estuaries, salt marshes, and rock pools, and fish such as salmon, flounder, shad, and eel. Many fish and lamprey, including river lamprey, salmon and shad, undertake most of their growth in the sea and only return to freshwater as adults to breed. These species are termed anadromous. Species such as eels (*Anguilla* spp.) (Figure 1.9) start their life at sea and may enter freshwater to grow, only returning to the sea to spawn. These species are termed catadromous. These fish are discussed in more detail in Chapter 8. In addition to reproductive movements between marine and freshwaters, there are also many species of marine fish that use estuaries as nursery grounds (Elliot et al 2007) as they offer rich feeding and sheltered habitat such as salt marsh.

Salinity variation lies at the core of estuarine biology, acting as a physiological barrier for species lacking the physiological ability to adapt. Euryhaline animals use several different strategies to adapt to salinity change. Among the vertebrates, blood osmotic concentrations are regulated within a narrow range by hormonal controls of ion fluxes and the accumulation of organic chemicals (amino acids and their derivatives) called osmolytes, which adjust the water content of cells and maintain their volume under varying environmental salinity levels (Pequex et al 1988). Invertebrates show several adaptive strategies, but they can be roughly classified as conformers, regulators, or a mixture of the two. The common shore crab *Carcinus maenas* (Figure 1.8) demonstrates both invertebrate approaches. At salinities above 25 ppt, the blood osmotic concentration tracks that of the ambient water, it is a conformer. At salinities below 25 ppt, it uses physiological mechanisms to regulate blood salt levels. This regulation can be maintained down to salinities of 8 ppt; it cannot survive in freshwater.

Man also discharges hypersaline water into estuaries and the ocean. The effects of these artificial elevations are discussed on page 190.

Depth, pressure, and topography

It is notable that more than 60% of the earth surface is more than 2 km below sea level, and physical conditions at this depth differ greatly from those on the surface. The pressure at the surface of the sea is approximately 1 atmosphere (depending on weather conditions), and increases by roughly 1 atm for every 10 m increase in depth. 1 atmosphere (atm) = 14.69 pounds per square inch (psi), or 1.03 kilograms per square centimeter (kgf/cm^2), or 0.1 megapascals (MPa). At 1000 m depth, the pressure is just over 100 atm, 1472.6 psi, 103.5 kgf/cm^2, or 10.2 MPa. These pressure conditions have resulted in the evolution of organisms specially adapted to living in deep water. Interestingly, it has been suggested that all life on earth may have originated in the stable, calm, protective depths of the deep ocean, maybe 3.8 billion years ago (Daniel et al 2006). The external pressure (and temperature) affects membrane and enzyme systems (Carney 2005) resulting in a vertical zonation of species, adapted to different (but relatively constant) pressures (Blankenship et al 2006). An example of this type of zonation is shown by bacteria (Figure 1.10, Daniel et al 2006 after Margesin & Nogi 2004). Organisms specially adapted to life in very deep water at very high pressures are termed piezophilic, and organisms such as these bacteria are specialized to grow optimally at particular depths and pressures. Similar species are partitioning the depth resource resulting in the avoidance of interspecific competition (see Chapter 6).

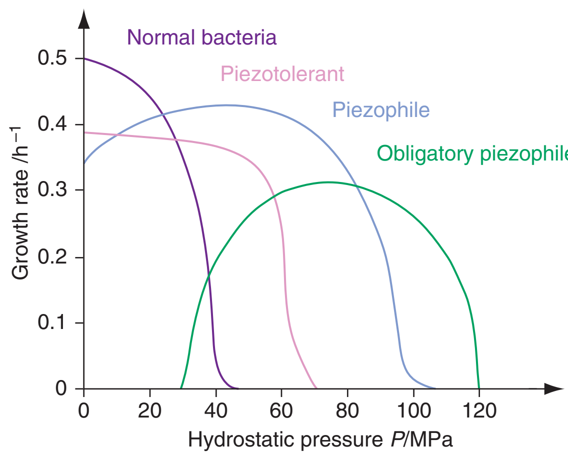

Figure 1.10

Definitions of the relationships between growth rate of microorganisms and pressure. Atmospheric pressure (surface) = 0.1 MPa; 120 MPa = 1200 atmospheres or 12,000 m. (After Margesin & Nogi 2004; reproduced with permission of Chemical Society Reviews.)

Light and irradiance

Only a small fraction of the sunlight incident on the sea surface is reflected, the greater proportion entering the water. The rate at which sunlight is attenuated determines the depth that is lit and heated by the sun. Attenuation is due to absorption by pigments and scattering by dissolved molecules and suspended particles. The rate of attenuation depends on the wavelength of the light. Blue light is absorbed the least and red light is absorbed most strongly. Thus, as divers move down through clear ocean water they perceive an environment that becomes increasingly blue; bright colors, especially the reds and yellows, quickly fade to grey. The change in the light spectrum with depth is shown in Figure 1.11 and the

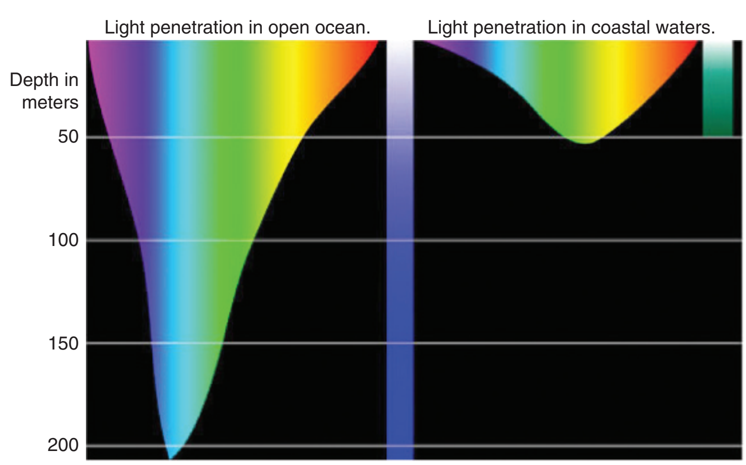

Figure 1.11

Light penetration with depth in open ocean and coastal waters. (Courtesy of Kyle Carothers, Ocean Explorer, NOAA.)

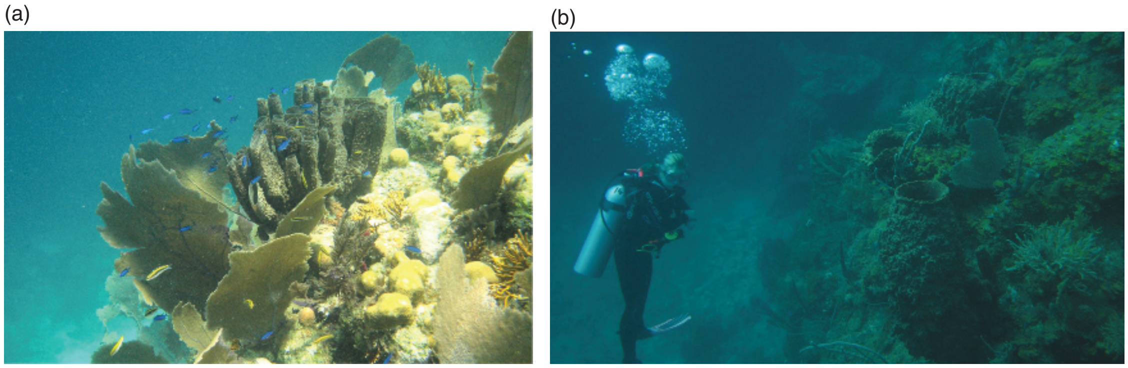

Figure 1.12
(a) Bay Islands (Honduras) coral reef at 2 m depth. (b) Bay Islands (Honduras) coral reef at 20 m depth. (Photographs Martin Speight.)

photographs in Figure 1.12 show sections of the same coral reef on the island of Utila in the Caribbean off the mainland of Honduras taken using natural light only with the same camera on the same dive. Note that the vast majority of wonderful photos of marine life showing striking colors are taken with powerful flash guns (strobes). These colors are normally invisible to the local fauna and visitors alike. The physical mechanisms for differential light absorption are complex. Put simply, pure water is itself very slightly blue because water molecules absorb light at the red end of the visible spectrum (Braun & Smirnov 1993), In fact, if the absorption coefficient is constant, the light intensity decreases exponentially with depth:

$$l_x = l1\ \exp^{(-cx)}$$

where l is the original radiance or irradiance of light, and l_x is the radiance at depth x and c is the absorption coefficient.

In addition, coastal waters are typically more turbid (less clear) than offshore ocean waters. They contain pigments from land (sometimes called gelbstoffe which just means yellow stuff) and suspended sediments from rivers and the action of waves on the seabed in shallow water. Very little light penetrates more than a few meters into these waters. In some particularly turbid estuaries where high tidal currents result in levels of suspended solids as high as $1\,g\,l^{-1}$ or more, light may penetrate less than 1 m. Crucially of course, light fuels the primary production of shallow seas via photosynthesis, so that if it is unable to penetrate far into the water, primary productivity will be highly constrained. Further, photosynthetic organisms such as macroalgae (seaweeds), microalgae (phytoplankton), and symbiotic algae such as zooxanthellae in coral polyps and other cnidarian tissues also respire, so that if their energy capture by photosynthesis is less than that used by respiration, there is a net loss of production. The depth at which respiration losses equal photosynthetic gains is called the compensation depth, where light penetration is just sufficient for production to match that lost by respiration (see Chapter 3). Above this depth, light can influence the distribution of organisms, and/or their abilities to survive and grow, as shown in the example of corallimorph, *Rhodactis rhodostoma* (Cnidaria: Anthozoa) from Red Sea coral reefs (Kuguru et al 2007). As mentioned above, almost all corals, and many other marine organisms, contain intracellular symbionts, dinoflagellates called zooxanthellae in the genus *Symbiodinium*, which photosynthesize using nutrient chemicals from their host. The abundance of zooxanthellae within polyps, and the quantity of chlorophyll *a* pigment they hold, increases significantly with depth. Both these changes are responses to reduced light levels with depth. Because of this response animals like *Rhodactis* are able to exist successfully over a range of depths and varying light levels. It seems that different strains of zooxanthellae with different responses to irradiance levels occur in polyp tissues at different depths. In contrast to the limitations caused by low light levels, too much light (high irradiance) can have severe affects on marine organisms. Coral bleaching is one of the most serious global threats to shallow marine tropical ecosystems and, in part at least, seems to be a function of intense light levels, especially from the ultraviolet end of the spectrum. In very high light levels, the zooxanthellae either lose their chlorophyll, and/or die. Either way, the photosynthetic ability of the symbionts declines catastrophically, to the detriment of the host animal. This condition may not be irreversible. In the case of *Rhodactis* at least, removing the stressing effects of light (and temperature) enables the zooxanthellae to regain their photosynthetic ability.

Temperature

Figure 1.13 shows the variation in seawater surface temperature (SST) with latitude from less than 0°C (<32°F) close to the poles to over 30°C (86°F) in the tropics. This latitudinal gradient is linked to variation in the light energy received per unit area. However, surface temperatures are not perfectly correlated to the received energy because of

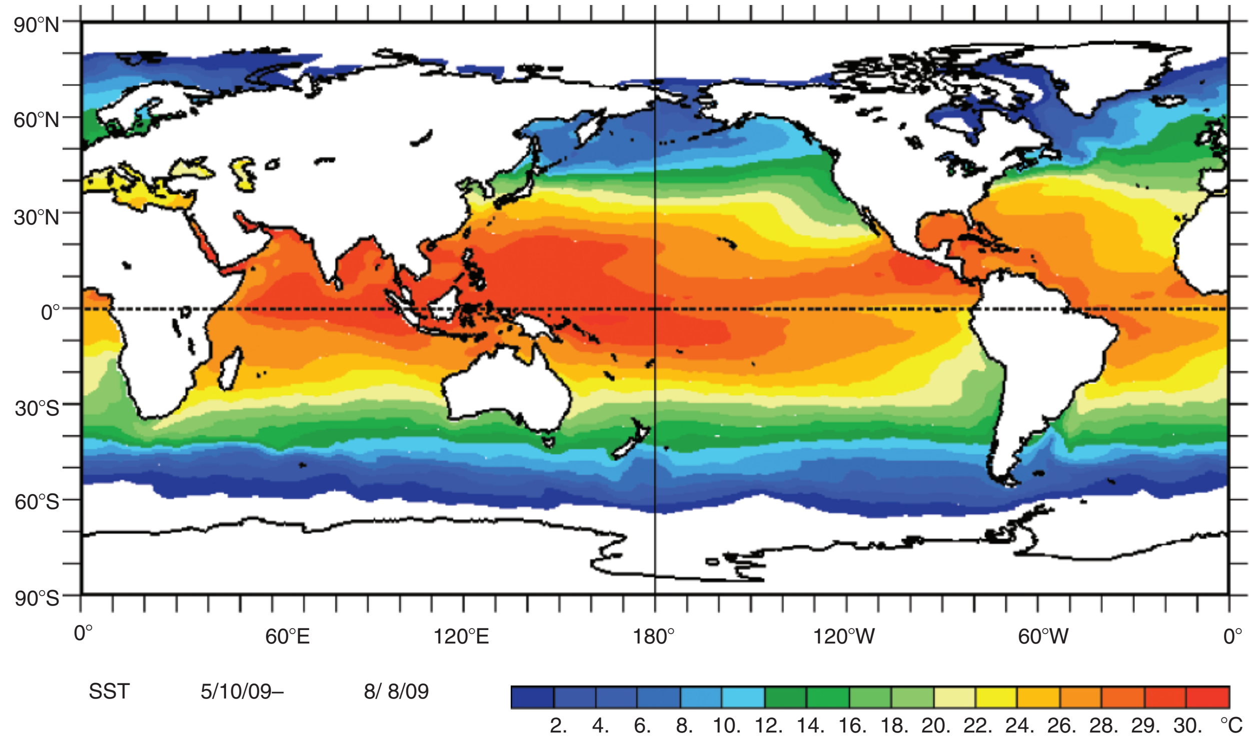

Figure 1.13

Global variations in sea surface temperatures (SST). (Courtesy of NOAA – www.cdc.noaa.gov/map/images/sst/sst.gif)

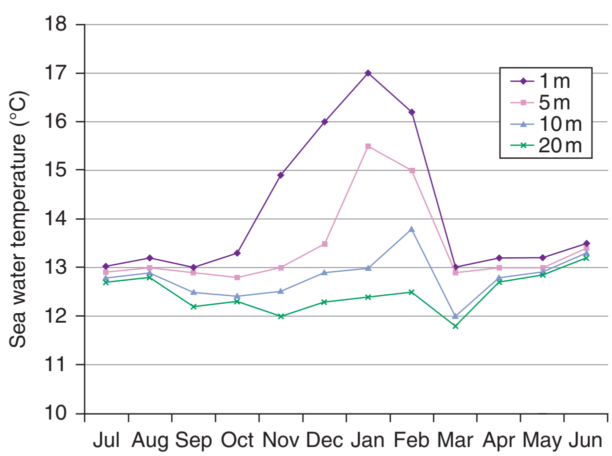

Figure 1.14

Annual variation in sea temperature according to depth at Las Cruces in central Chile. (From Narváez et al 2004; reproduced with permission of Elsevier.)

ocean currents. Notice, for example, the incursions into the otherwise warm areas along the west coasts of South America and Africa, caused by cold currents from the Antarctic (Humboldt and Benguela currents respectively).

Deep ocean waters are fairly constant in temperature, ranging from about 0°C to 4°C (32°F to 39°F), though high pressures at depth cause slight adiabatic warming because of compression. However, deep-sea hydrothermal vents are a notable local exception as we mentioned earlier in this chapter: water from these can raise local temperatures to well over 100°C (212°F), and may exceed 400°C at the point of emergence. In the shallow temperate zones there are considerable seasonal temperature variations. Some of the most extreme occur on the North American East Coast. In the River Hudson Estuary near New York, for example, surface temperature can vary from below 0 to 30°C. As shown in Figure 1.14 coastal waters do not show the same degree of variation and this variation declines with depth (Narváez et al 2004). In this example from the southern hemisphere, notice that the coldest seawater can be experienced not in mid-winter, but in spring, due to the time lag in the cooling and heating of the huge mass of water. In general, most marine organisms living in deep water experience relatively small variations in temperature, when compared to terrestrial life, they are not well adapted to extremes of temperature. The only exceptions are organisms specially adapted to changing conditions such as those of littoral habitats. An example of an animal with a particularly narrow and limited temperature adaptation is the mussel *Bathymodiolus childressi* (Mollusca-Bivalvia: Mytilidae) (Figure 1.15), which occurs around cold seeps in 750 m of water in the Gulf of Mexico (Berger & Young 2006). Cold seeps were only discovered in the 1980s, and are places where water from the underlying bedrock flows out, rather like an underwater spring. This water is rich in methane and sulfides which provide the chemosymbiotic bacteria in the mussel tissues with fuel for primary production (see Chapter 3). Unlike the very hot hydrothermal vents, cold seeps are at the same temperature as the surrounding water, perhaps 2 or 3°C. Under these stable conditions, *Bathymodiolus* is unable to survive in water warmer than 20°C for very long.

Water temperature at the sea surface can vary considerably, and studies of sea surface temperature (SST) are an important research topic. SST can now be measured using high-resolution satellites such as those deployed by NOAA (National Oceanic & Atmospheric Administration), and NASA (National Aeronautics & Space Administration), both in the USA (Mesias et al 2007). Clearly, any increase in temperature will have some influence on the metabolic rate of most marine organisms, since the vast proportion of species living in the sea are poikilothermic ("cold blooded"), and as we shall see in detail in Chapter 3, oceanic primary productivity is closely linked to water temperature, though not necessarily in a simple linear manner. The SST can influence the whole structure of marine communities, as shown for example in intertidal habitats in California (Blanchette et al 2006). The percentage cover of filter feeders such as barnacles, *Chthalamus* and *Balanus* spp. (Crustacea: Cirripedia), and mussels, *Mytilus* spp., (Mollusca-Bivalvia: Mytilidae) increases linearly as mean SST increases, linked to the increasing numbers of juveniles settling (so-called recruitment rate) with increasing SST. However, the cover of primary producers such as seaweeds decreases with increasing SST, probably linked to increased numbers and activity of herbivores (see Chapter 4).

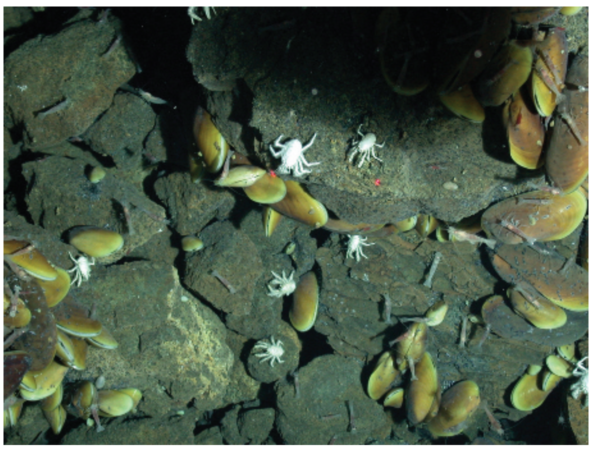

Figure 1.15

Deep sea mussel community with squat lobsters and shrimps. (Photo courtesy of Submarine Ring of Fire 2006 Exploration, NOAA Vents Program.)

SSTs that exceed normal variations, or are atypical at various temporal scales, may indicate changes which can have serious, even catastrophic, consequences for marine ecosystems and indeed global climate patterns. One illustration of these SST anomalies is shown in Figure 1.16 (Behrenfeld et al 2006). The diagram shows positive (pink) and negative (blue) anomalies by comparing SSTs from 1999 to 2004. Changes in SSTs to warmer conditions can be seen parts of the Arctic, Atlantic, Indian and especially Pacific oceans, as well as the Caribbean. One of the most threatening physical factors in marine ecology today is that of elevated SSTs on coral survival. Figure 1.17 illustrates a clear relationship between SST anomalies and coral bleaching in the Caribbean (McWilliams et al 2005). It seems that as little as a 1°C increase in SST during the hottest months of the year can cause bleaching, when the symbiotic zooxanthellae either lose their chlorophyll or die. The optimum temperature for most hard (scleractinian) corals is between 25 and 29°C, and even increases in water temperature to 30 or 31°C can cause serious losses of zooxanthellae

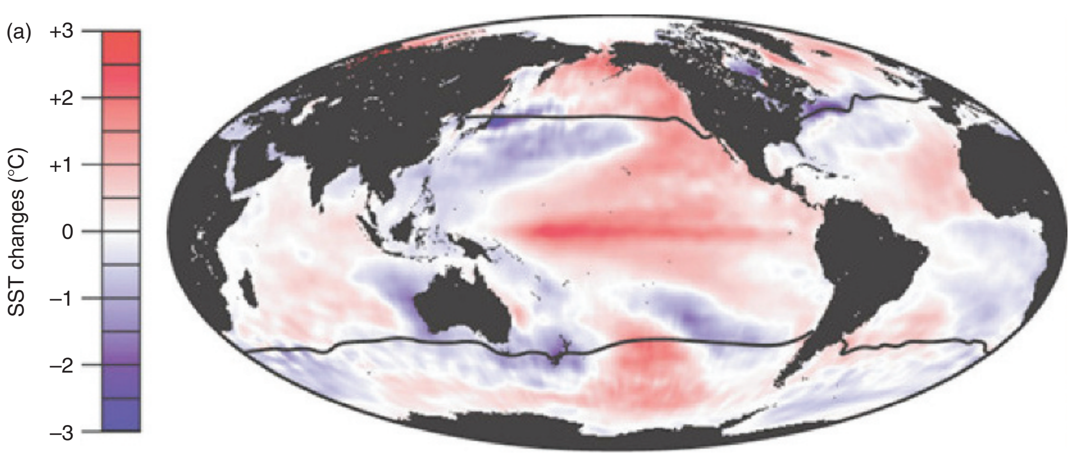

Figure 1.16

Global changes in annual average sea surface temperatures (SSTs) for the period 1999 to 2004. (From Behrenfeld et al 2006b; reproduced with permission of *Nature*.)

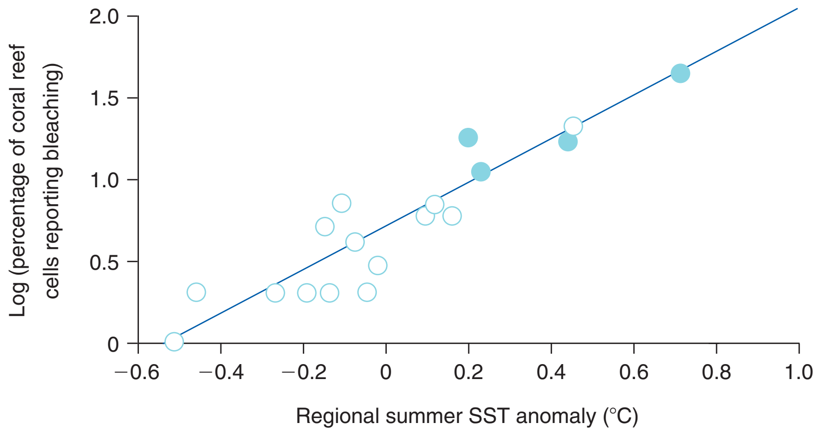

Figure 1.17

The relationship between the regional SST anomalies and the percentage of coral bleaching. (From McWilliams et al 2005; reproduced with permission of *Ecology* – ESA.) Each data point represents 1 year. Solid circles represent years described in the literature as mass-bleaching events; open circles represent other years.

(Sammarco et al 2006). If the symbionts are unable to recolonize, or the warm conditions persist for too long, corals may die on a massive scale. It may be that variations in temperature are more destructive than steady but stable increases. The above authors looked at SSTs using discriminant function analysis (DFA) to group their data on coral bleaching events on reefs around Puerto Rico. Three groups were identified: cool water with no bleaching; warm water also with no bleaching; and warm water with bleaching. The coefficient of variation (CV) of the data measures variability (degree of fluctuation), and the likelihood of bleaching in warm water was found to increase at lower temperatures as the temperature CV increased. Without doubt, climate change and global warming (see later in this chapter) are exerting pressures on some of our most precious marine ecosystems. As we suggested above, all may not be lost; some coral species seem able to thermally acclimatize to increasing water temperatures, and their symbionts, the zooxanthellae, are able to exchange temperature-tolerant genotypes. Berkelmans & van Oppen (2006) suggest that "though such mechanisms might not enable corals to survive all of the SST increases predicted for the next 100 years, it may buy them time."

Man also discharges heated water into estuaries and the ocean. The effects of these artificial temperatures are discussed in Chapter 9 (see p. 184).

Oxygen

In the open ocean the oxygen content at the surface is relatively high (about 6 ml l^{-1}) and is replenished from the air. Deeper in the water the oxygen content begins to decrease with depth until at about 1000 m (3082 feet) the value reaches a minimum. The reason for the decrease is the consumption by bacteria of the rain of organic debris (marine snow) falling through the water. The exact amount of oxygen at the minimum varies with location in the ocean. The oxygen concentration profile for the Eastern tropical Pacific Ocean, which is noted for the severity of the oxygen minimum, is shown in Figure 1.18. This minimum is known to reduce the abundance and diversity of life in the mid-water region (Wishner et al 1990). The deep water in the ocean starts out at the surface in polar regions and when it sinks it carries dissolved oxygen from the surface (see p. 16 for information on currents).

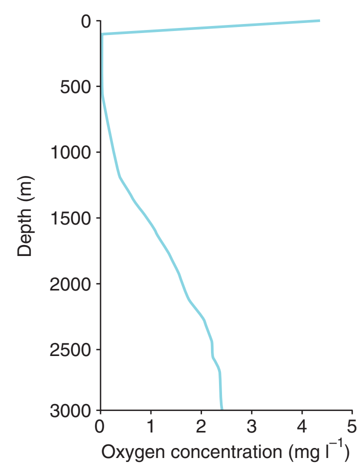

Figure 1.18

The variation in oxygen concentration with depth in the eastern tropical Pacific Ocean at 13°23′N, 102°27′W. (Modified from Wishner et al 1990.)

In inshore, shallow waters oxygen concentration can vary greatly both spatially and temporally. It is not uncommon for bottom waters in some parts of estuaries to be almost anoxic because of oxygen consumption by bacteria and other micro-organisms. In estuarine and shallow coastal waters the oxygen concentration is one of the key physical variables determining the abundance and diversity of life. While hypoxic and anoxic waters occur naturally, there are clear indications that oxygen deprivation is increasing and that this is linked to the activities of man. Diaz (2001) in a review of hypoxia concluded "that many ecosystems that are now severely stressed by hypoxia may be near or at a threshold of change or collapse (loss of fisheries, loss of biodiversity, alteration of food webs)." He also noted that several large systems for which we have reliable nineteenth century oxygen concentration data (including the Kattegat, between Denmark and Sweden) and did not then suffer from hypoxia, now experience severe seasonal hypoxia. Reports of a decline in ocean oxygen levels are generally becoming more frequent, and oxygen concentration decline is likely to be an important area of concern for the foreseeable future.

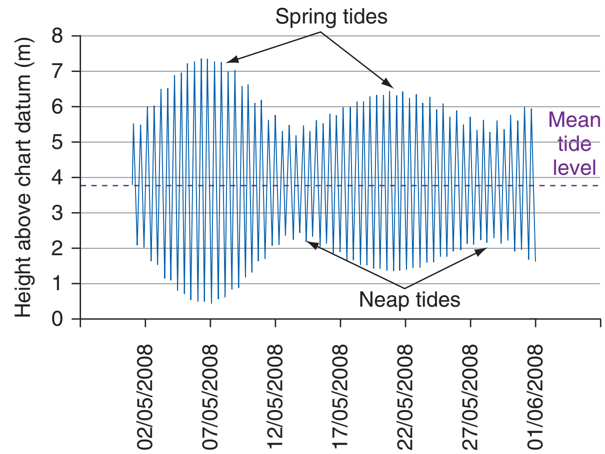

Figure 1.19

Typical series of tidal cycles over a month from Milford Haven in Southwest Wales. Chart datum (*y*-axis) is mainly used on nautical charts and is the lowest possible astronomical tide which may never actually be achieved over many years. (Data from 'Tide Plotter', Belfield Software.)

Tides

Tides are the periodic rise and fall of the sea. They are one of the most important physical features for life in coastal waters, creating the productive but challenging conditions within the littoral zone and the currents used by animals and plants for dispersal (see Chapter 7). The most important tidal waves are caused by the gravitational interaction between the Earth and the Moon (lunar waves), with other components such as the interaction between the Earth and the Sun (solar waves) being significant but of lower magnitude. The gravitational attraction of the Moon causes the oceans (simply a very large volume of incompressible fluid) to bulge out in the direction of the Moon. Another bulge occurs on the opposite side, since the Earth is also being pulled toward the Moon (and away from the water on the far side). As the Earth is rotating, there are about two high tides per day, but the Moon actually takes about 24 hours and 50 minutes to return to the same position in the sky from one day to the next. Thus in general, each high tide is 12 hours and 25 minutes later than the one before it.

Spring tides are especially strong tides that occur when the Earth, Sun, and Moon are aligned and the gravitational pull of the Moon and the Sun are working together. This alignment occurs at the full and new moons, so that there are two spring tides every month. Note that the term "spring" has nothing to do with the seasons. In contrast, the smallest tidal ranges over the lunar cycle, called neap tides, occur when the sun and moon are pulling in opposite directions. Not all springs and neaps are of equal extent however, since the Moon comes closer to the Earth at certain times of the year. When the Moon is closest to the Earth, it is said to be at apogee, and when it is furthest away, it is at perigee. If the Moon at apogee is directly in line with the Sun, then an extra pull on the oceans occurs and so produces extreme spring tides. The highest and lowest tides of a year take place a day or two after the nearest new or full moon to the spring (now a season) and autumn equinoxes in March and September. To summarize, Figure 1.19 shows typical tidal cycles in South Wales over a month, indicating that the tides go in and out twice a day, that springs and neaps occur twice a month, and that the extent of a spring tide also varies over a few weeks. Most importantly, notice that whatever the peaks and troughs, or high tide and low tide extents, the average of a tidal cycle (between high and low tide on a particular cycle at a particular place, is always the same. We shall return to the ecological significance of mean tide level (MTL) below.

Tides differ in periodicity and the rate of rise and fall between localities because the tidal wave is reflected from the continental edges creating interference patterns and can be funneled within inlets creating exceptionally large tidal ranges. The tidal range varies dramatically between localities (Figure 1.20, Kowalik 2004). The M_2 tides are depicted in Figure 1.20; these are the principal lunar component of total tidal cycles with an absolute periodicity of 12.42 hours. The Figure shows that the highest and lowest M_2 tides can be experienced on the Atlantic coast of Western Europe and North Africa, on the Indian Ocean coasts of East Africa, and on the Pacific coasts of Alaska, British Columbia and Washington State, Columbia, and Ecuador. The largest tidal ranges of more than 15 m occur in the Bay of Fundy, Canada, in estuaries in Northern France, islands in the western English Channel (Figure 1.21) and in the Bristol Channel, UK. These huge tides are created by the flow of tidal waves into funnel-like water bodies. The exceptional long narrow funnel of the Bay of Fundy results at Burntcoat Head in a tidal range of 16.1 m, the greatest on the planet. In contrast, Eureka, on Ellesmere Island, Canada

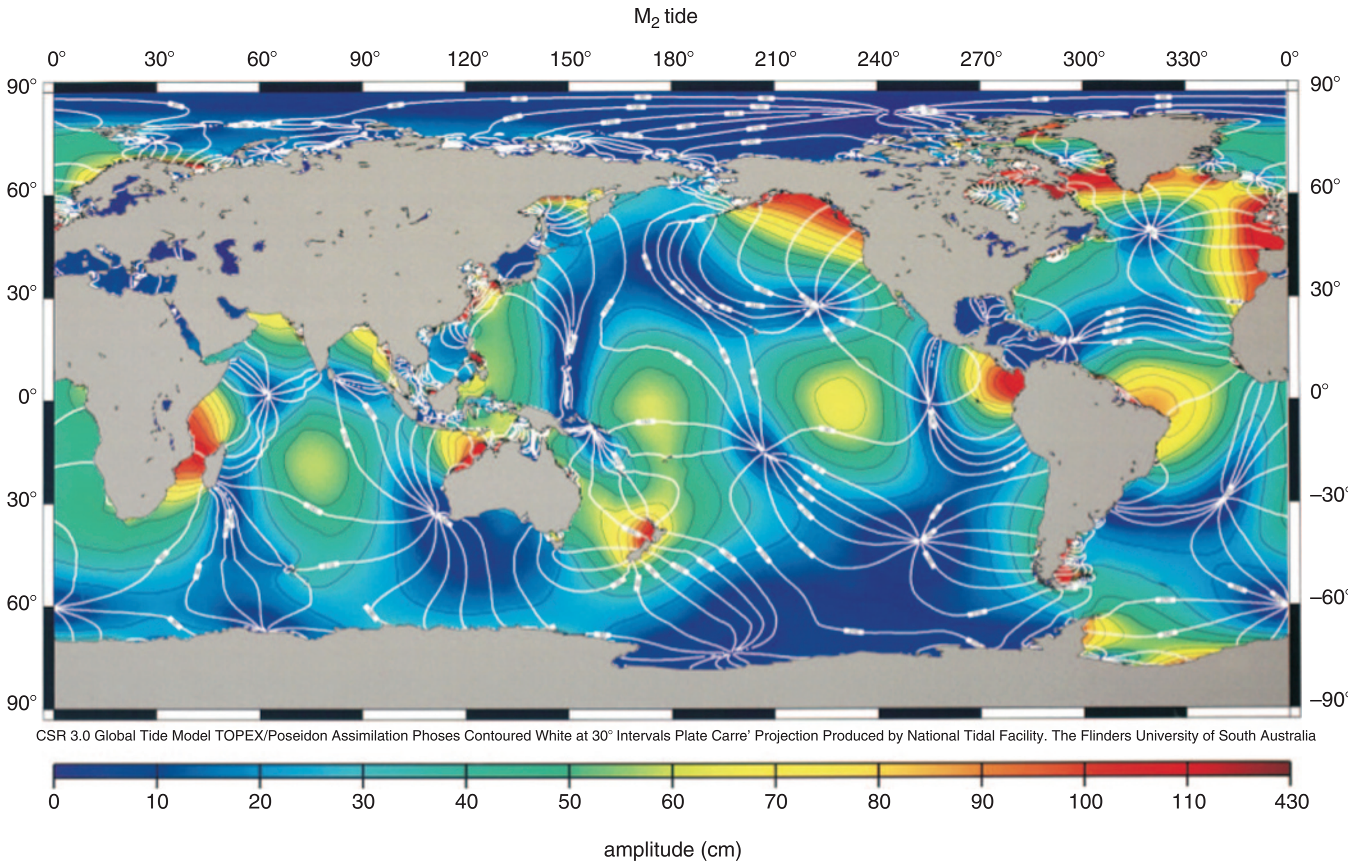

Figure 1.20

The geographical variation in tidal height. This figure shows the M_2 tidal component which is the dominant tidal component caused by the movement of the Moon. (From Kowalik 2004; reproduced with permission of Institute of Oceanology PAS.)

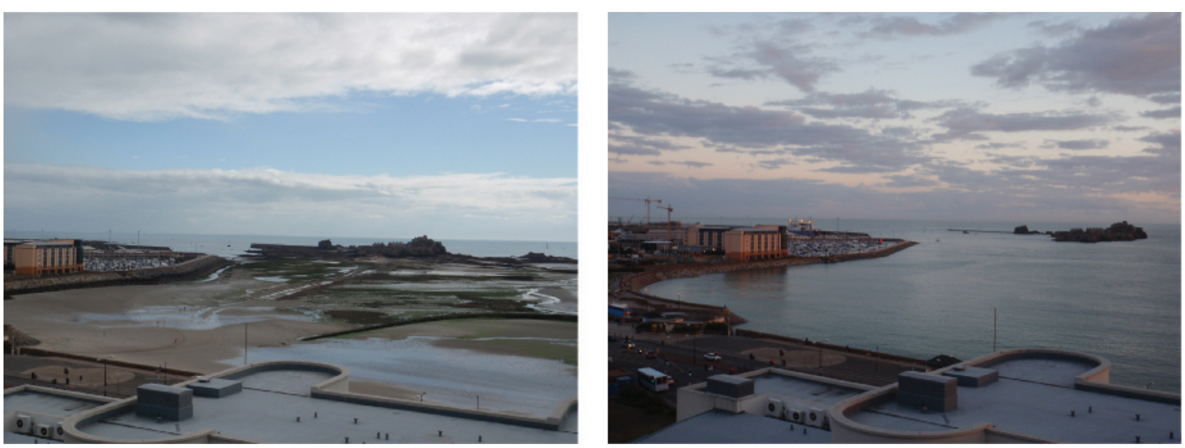

Figure 1.21

Low and high tides in Jersey. (Photographs courtesy of Jonathan Shrives.)

probably has the smallest tidal range of only 0.1 m. In the mouths of some rivers, the incoming tide meets the out flowing current and builds up forming tidal bores. These are fast-moving currents that travel as a wave front or wall of water. They can produce spectacular waves that in the River Severn, England and the Amazon estuary, Brazil, can be used by surfers.

Mean tide level (MTL) has particular significance for organisms living between the tides. Any organism living on a rock, in a pool or in sediment at this point will spend

50% of its time away from the direct influence of the sea. Above MTL, life for marine organisms becomes more and more difficult, requiring complex physiological, morphological and/or behavioral adaptations to cope with living in a terrestrial environment for increasing periods of time. Of course it is perfectly possible and indeed normal on all but the most sheltered shores for the sea's influence to extend much further than the height of an extreme high tide by virtue of splash driven by winds and waves. We discuss the phenomenon of exposure in this context in the next section. Note finally that although tides are usually thought of as operating at the sea's surface, they can also occur in the deep ocean as internal tides (Garrett & Kunze 2007). Internal tides are produced by the interaction of deep currents with the varying seabed topography, and can cause the vertical displacement of water by tens or even hundreds of meters, enabling mixing of water masses. Mixing in a fluid such as seawater increases dramatically over a region of structurally complex seabed as compared with a homogeneous, smooth topography, and this turbulence can extend for many meters above the seabed. These tides are not much influenced by astronomical bodies, but mainly by pressure and topography, hence their name of barotropic tides. It is not hard to imagine the great potential for sediment suspension, and the nutrient and propagule mixing in the deep-sea derived from internal tide generation.

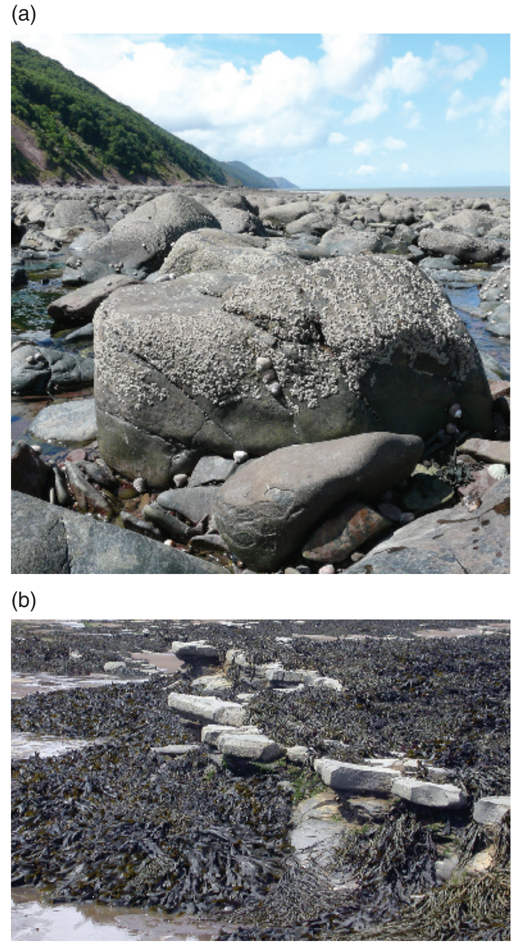

Figure 1.22

Rocky shore communities under two exposure extremes. Both habitats are in close proximity on the North Somerset coast, England. High exposure shows domination of species that attach tightly such as barnacles, low exposure shows luxuriant macroalgal growth and few barnacles. (a) Very exposed to wave action. (b) Very sheltered from wave action. (Photographs courtesy of Richard Seaby, Pisces Conservation Ltd.)

Waves

Wind causes surface waves. The wind transfers energy to the water, through friction between the air molecules and the water molecules. Waves of water do not move horizontally, they only move up and down. The wave height is the distance between the wave crest and trough. This can vary dramatically from negligible to extreme, with a maximum of probably in excess of 30 m, although such monster waves have rarely been measured. In 1998, a buoy moored 500 km southeast of Cape Breton recorded a maximum wave height of 27 m when the eye of Hurricane Danielle passed nearby. In September 2004 Scientists at the Stennis Space Centre measured a record ocean wave of 27.7 m in height when the eye of Hurricane Ivan passed over moorings deployed in the Gulf of Mexico. The highest average wind speeds occur in the Southern Ocean where wave heights frequently exceed 6 m. The distance between wave crests is termed the wavelength and the maximum depth at which the wave motion is experienced is half the wavelength. It follows therefore that the deeper the water for a wave of a given length, the less affected organisms and habitats will be. For example, with a wavelength (distance between one wave and the next following it) of say 30 m, a diver or any other object would hardly feel the movement or swell at all. As all SCUBA divers know, it is the ascent to the choppy or even violent surface that can be the worst part of a dive.

The degree of exposure of the coast to wave action determines the nature of the substrate and the community of plants and animals. There is a clear change in the temperate rocky shore community that can be related to wave action. W.J. Ballantine invented a system of exposure rating in the UK in 1961 which depends on the distribution and occurrences of common sessile or sedentary intertidal organisms. In a very sheltered region (exposure scale 7 or 8), large, luxuriant species such as brown seaweeds (fucoids or wracks) dominate, whereas on exposed shores (exposure scale 1 or 2), where large weeds would be washed away, encrusting species are most common such as barnacles and a few small, tightly attached macroalgae (Figure 1.22a,b). This concept of exposure in relation to shallow-water community structures also has parallels in the tropics.

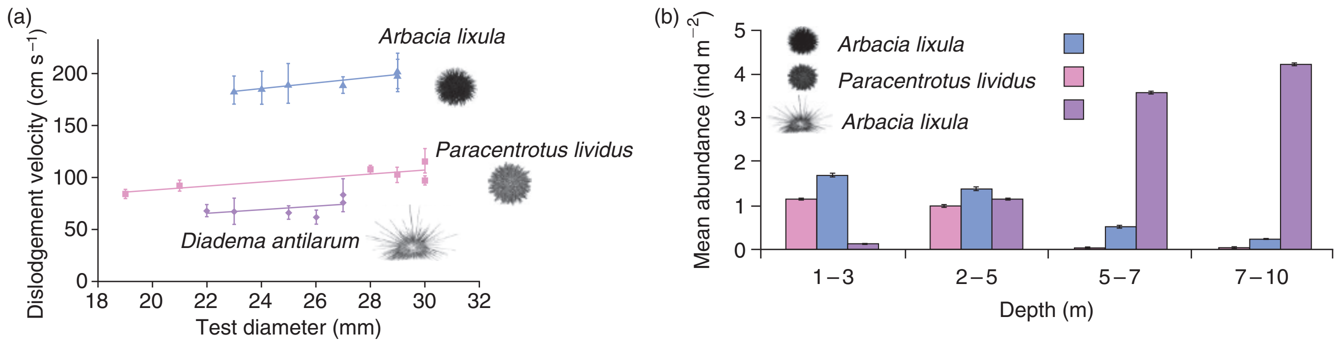

Figure 1.23

(a) Mean "velocities of dislodgement" for each individual of three sea urchin species calculated from hydrodynamic experiments. Error bars represent ±s.e. of means. (b) Mean abundances of each sea urchin species at each depth stratum across the study area. Error bars represent ±s.e. of means; $n = 140$ for each species. ((a,b) From Tuya et al 2007; reproduced with permission of Elsevier.)

For example coral reef structure is influenced by wave action caused by storms (Hubbard and Dennis 1989). For example, Caribbean reef type is determined by the wave energy and three types of habitat can be defined:

- TYPE I: algal ridges with reef crests dominated by coralline algae rather than coral. The exposure to frequent storm damage breaks corals and provides coral substrate for algae. High wave energy reduces fish grazing which would otherwise inhibit algal growth.
- TYPE II: branching elkhorn coral, *Acropora palmata*, dominates. There is high wave energy, but less frequent storms.
- TYPE III: only scattered coral cover with open "pavements" and a relatively low diversity community. Frequent storms disrupt the reef-crest, but low wave energy conditions between storms permits grazing, reducing the deposition of thick algal crusts, but also discouraging coral recruitment.

On an even more general scale, whole regions of coral reefs can be recognized (see also Chapter 2). Caribbean reefs, for example, have many more soft corals than those in Indonesia or Australia, since the ones in the Caribbean have evolved over thousands of years with annual storms and even fairly regular hurricanes (especially in recent years), which soft corals are better able to withstand than hard species.

The distribution of individual species can be determined by wave action and exposure. Experiments by Tuya et al (2007) with three species of sea urchin showed that whilst the abundance of *Diadema antillarum* increased with depth (Figure 1.23a,b), two other species, *Arbacia lixula* and *Paracentrotus lividus*, showed a reverse zonation. These distributions were directly related to the dislodgement water velocity for each; *Diadema* with the biggest body and largest spines being most easily dislodged by waves and tides and hence occurred only at deeper, quieter, depths.

Ocean currents

Ocean circulation includes both horizontal and vertical flows that are important for the movement of heat over the planet. Vertical flows are the movement of water up or down the water column, which may take place over many hundreds if not thousands of meters of depth. Ocean circulation, both horizontal and vertical, is induced by the wind acting on the sea surface, and by buoyancy changes caused by the alterations in salinity and especially density. Warm air at the Equator rises leaving a less dense, low pressure region into which air flows from both the north and the southern hemispheres producing the trade winds well known to ocean explorers. At about 30 degrees north and south, this warm air cools and sinks again, some returning to the Equator, but the rest heading towards the poles as westerly winds in both north and south hemispheres. Finally, cold air at the poles sinks and flows away from the poles to meet the westerlies. All these winds cause a frictional drag on seawater at the surface, and move it with them; typically, a surface current is around 2 or 3% of the speed of the wind which blows over it. Buoyancy differentials between surface and deeper waters are capable of inducing overturning currents (they are termed overturning because they bring bottom water to the surface and visa versa) that reach from the surface to the seabed. Cooling and evaporation both make surface seawater denser and therefore reduce buoyancy, so that surface water tends to sink at the poles. In contrast, solar heating and rain reduce surface density and therefore increase buoyancy. The rotation of the Earth rotates current flow to the right of the wind direction in the northern hemisphere, and to the left of the wind direction in the south, via Coriolis forces. Coriolis was a French scientist who described the ways in which winds flow from high to low pressure areas, and he discovered that because of the planet's rotational spin, this air flow does not occur in a straight line but is bent relative to an observer on Earth. Note that Coriolis forces are zero at the Equator.

As currents on the surface are shifted by these forces, so frictional coupling with slower, deeper water layers drags subsurface currents along with the surface ones, but since Coriolis forces also act on these deeper currents, the latter are deflected further around in a spiral fashion which moves further left or right depending on hemispheres. This produces a phenomenon known as Ekman transport, named after the Swedish physicist, which adds to Coriolis forces moving currents further right or left relative to wind direction. The lowest layers of seawater may be rotated up to 90 degrees compared with those at the surface.

The major horizontal currents

The sum of wind, buoyancy, Coriolis effects and other forces produce the major ocean surface currents, which are listed in Table 1.2 and shown in Figure 1.24. These currents circulate in paths called gyres, which rotate in a clockwise direction in the northern hemisphere and a counter-clockwise direction in the southern hemisphere. One of the most well known gyres is the Gulf Stream that flows across the Atlantic Ocean from the southern states of the USA to Western Europe including the UK. The most important consequence of this is that this part of Europe has the warmest climates of anywhere on the globe at this latitude. Without the Gulf Stream the UK would be a very much colder place in winter. This surface current moves at an average of 3 or even 4 km h^{-1} in a narrow band perhaps only 50–75 km wide, and it is quoted as transporting more than 30 million cubic meters of water per second (Lund et al 2006), with the transportation potential of heat and solids of almost unimaginable quantities.

Horizontal currents also occur in the deep-sea. Indeed, the Earth's climate is regulated to a great extent by the movement of large, deep-water masses such as the Antarctic Bottom Water (AABW) and the North Atlantic Deep Water (NADW). These currents are termed global "motors" for the exchange of large masses of water (Schlüter & Uenzelmann-Neben 2007).

Table 1.2 The major ocean surface currents

NAME	LOCALITY	TEMPERATURE
Agulhas Current	Indian	Warm
Alaska Current	North Pacific	Warm
Benguela Current	South Atlantic	Warm/Cool
Brazil Current	South Atlantic	Warm
California Current	North Pacific	Cool
Canaries Current	North Atlantic	Cool
East Australian Current	South Pacific	Warm
Equatorial Current	Pacific	Warm
Gulf Stream	North Altantic	Warm
Humboldt (Peru) Current	South Pacific	Cool
Kuroshio (Japan) Current	North Pacific	Warm
Labrador Current	North Atlantic	Cool
North Atlantic Drift	North Atlantic	Warm
North Pacific Drift	North Pacific	Warm
Oyashio (Kamchatka) Current	North Pacific	Cool
West Australian Current	Indian	Cool
West Wind Drift	South Pacific	Cool

Vertical currents and the global conveyer belt

Vertical motions in the ocean are driven by small differences in water density due to differences in salinity and/or differences in temperature. These water movements are termed thermohaline circulation. Increased salt content increases the density of water, and above 4°C the density of water decreases with increasing temperature. However, below 4°C the density of pure water starts to decline with decreasing temperature and this property is very important in Arctic and Antarctic waters. It is easy to remember this important feature of cold water, as icebergs float. The fact that ice is less dense than water is very important for the biology of temperate regions, if the reverse were true, lakes and seas would freeze from the bottom upwards and it would be impossible for fish and other organisms to survive in waters in the far north or south as some water bodies would freeze completely.

As was discussed earlier in this chapter, the oceans do not have a uniform salinity. As water flows towards the poles from the Equator, it passes the subtropical high-pressure zones where there is little rain but high levels of sunshine producing high rates of evaporation. Evaporation increases the salt content of the surface water raising the density. The influence of evaporation is particularly apparent in the Mediterranean Sea that receives relatively low inputs from rivers but has a large evaporative loss due to high levels of solar radiation. As a result, dense water is created in the basin that flows out of the Straits of Gibraltar close to the seabed. This is replaced by an inflow of less salty Atlantic Ocean water at the surface.

In contrast to the Mediterranean there are also regions where reduced surface salinities are generated. In regions where rainfall is high, such as the Intertropical Convergence

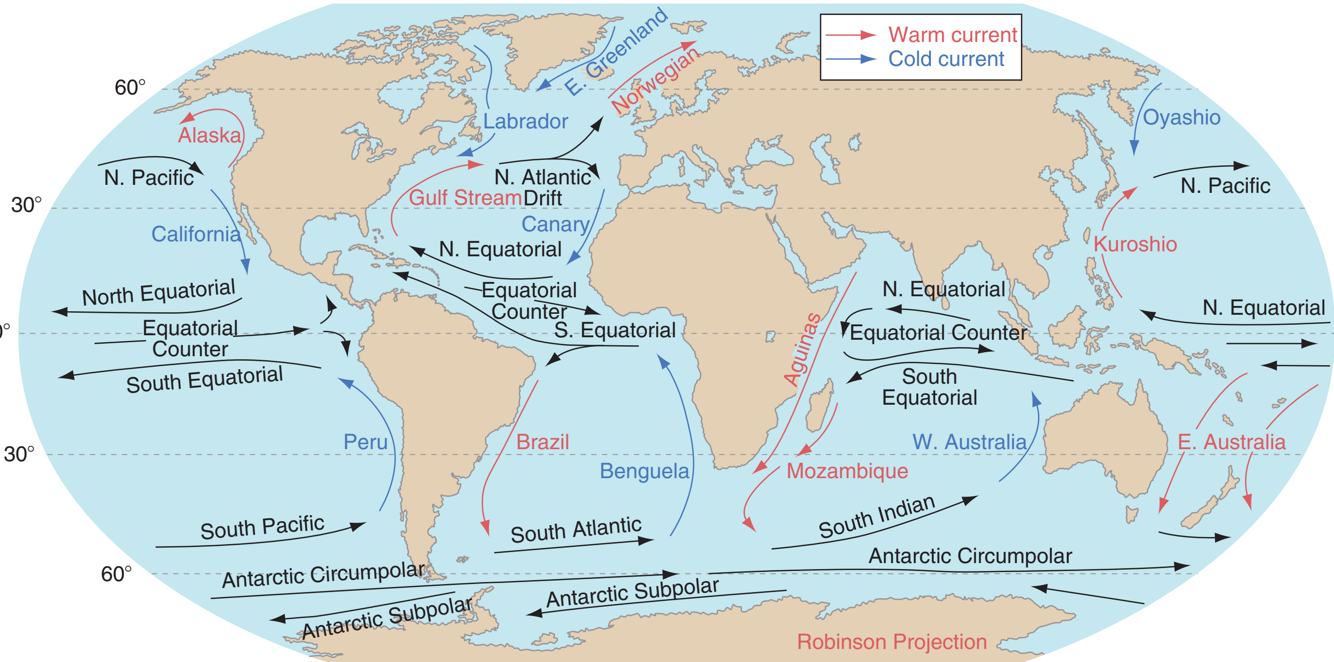

Figure 1.24

The major ocean currents. Surface currents are shown in red and bottom currents in blue. (From http://www.geni.org/globalenergy/library/renewable-energy-resources/oceanbig.shtml; reproduced with permission of Michael Pidwirny.)

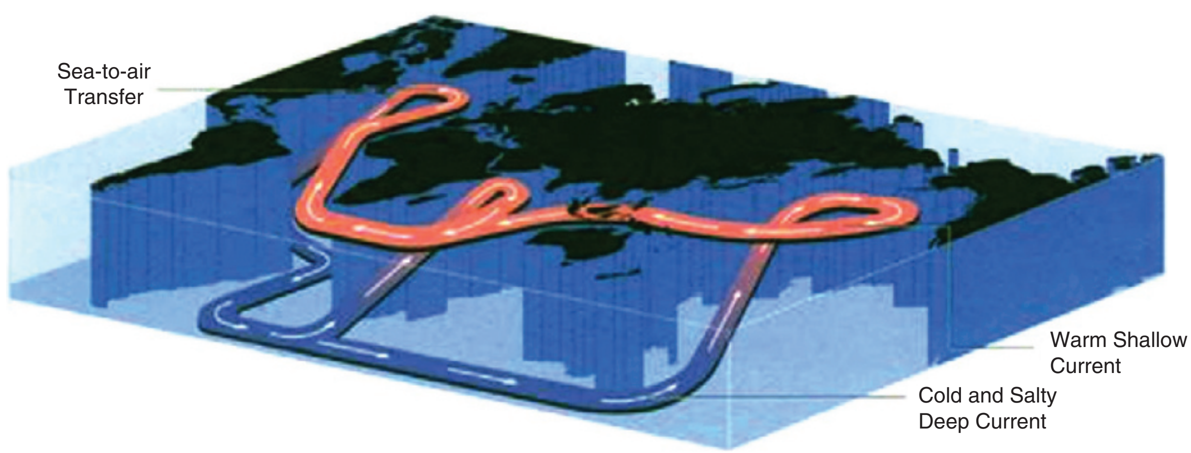

Figure 1.25

A diagram of the global conveyer belt – the circulation pattern which moves water heat and organisms around the globe. (From Haupt & Seidov 2007 after Brasseur et al 1999; reproduced with permission of Elsevier.)

Zone in the central Pacific Ocean, low salinity water floats on top of the more saline ocean water. Similarly melting ice in polar regions reduces the density of surface waters both because of the lack of salt and the reduction of the surface temperature below 4°C. It is currents caused by density differences that link the surface and abyssal ecosystems. These various interactions result in three-dimensional ocean circulations. In the North Atlantic, for example, water flowing north at the surface passes through the subtropical high-pressure zone where density increases. As it continues north the surface water cools, causing a further increase in density. Finally, to the north of Iceland, the density increases sufficiently as freshwater freezes out to cause the water to sink to the ocean bed and then flows south close to the seabed. This North Atlantic current is one part of a global pattern of ocean circulation, called the conveyer belt (Figure 1.25), which circulates throughout the entire expanse and depth of the world's ocean system. Arbitrarily starting in the Arctic, cold, dense, surface water sinks and flows south along the Atlantic Ocean bottom. The area of greatest downwelling is off Greenland. This dense water flowing south combines with sinking Antarctic water and flows around Africa into the Indian Ocean and onwards to Australia into the Pacific. In the Pacific basin it warms and wells up toward the surface. From there, surface currents move in the opposite direction towards the Atlantic and the cycle starts again. One of the crucial factors which keeps the conveyer belt moving is the slight salinity differential between the Pacific and Atlantic Oceans (Haupt & Seidov 2007). It may take 1000 years or more to complete one global cycle, but there is no doubt that the global conveyer is a vital basis for the world's food chains. It transports nutrients and respiratory gases as well as warmth from areas rich in these essentials for life to those where one or more are in short supply. Indeed, there have been fears that climate change might weaken the conveyer belt by warming Arctic waters or altering salinity differentials, and if this were to occur the impacts on life on our planet could be enormous.

We have already mentioned upwelling in a rather different context, but this phenomenon also has crucial consequences for marine primary productivity, especially near to coasts on Continental Shelf systems. Winds blowing parallel to a shoreline influence surface currents via Ekman transport (see above), whilst other winds blowing from the land out to sea drag surface waters with them. Either way, seawater under these influences tends to flow away from land, causing deep water to upwell to replace it. This deep water brings vital nutrients accumulated at the bottom of the sea to the surface. Even without wind effects, deep currents will bring nutrient-rich bottom water up into the shelf regions because of seafloor topographies. Therefore for a number of reasons near-shore productivity is enhanced (Phillips 2005). The same strong winds which in these regions produce upwelling also tend to disperse or "export" nutrients once they have reached the surface layers, but sufficient nutrient retention seems to occur to fuel subsequent algal blooms (Roughan et al 2006). Once phytoplanktonic primary productivity is enhanced in this way, a cascade of effects occurs further up marine food chains. Planktonic marine larvae of many species near to shore may be transported in upwelling currents, and indeed may be exchanged with offshore water in high speed currents (Shanks & Brink 2005). Upwelling-driven production influences even the largest animals in the sea, so that the migrations of blue whales, *Balaenoptera musculus*, for example, may be affected by seasonal patterns in this productivity (Croll et al 2005). Not only does upwelling significantly affect the abundance of primary producers and their consumers, it can also dictate the structure of communities. Herrera & Escribano (2006) studied the species composition of phytoplankton (mainly diatoms and dinoflagellates) off the coast of Chile, and found clearly distinctive communities using principle components analysis (PCA) between upwelling and nonupwelling conditions.

Local currents

While the great ocean currents influence all life on Earth, there are local currents which extend a mere few meters or, indeed, a few centimeters, that are also of great ecological importance, just on a much smaller scale. Tidal currents, which range in speed from zero to above 5 knots (260 cm s^{-1}), are the most important local currents and together with wind and wave action mold the physical features of littoral and sublittoral habitats. Of course, many marine organisms are adapted to tidal currents and can use them to advantage. For example, as is shown in Figures 1.26a,b and 1.27, the lugworm, *Arenicola marina*,

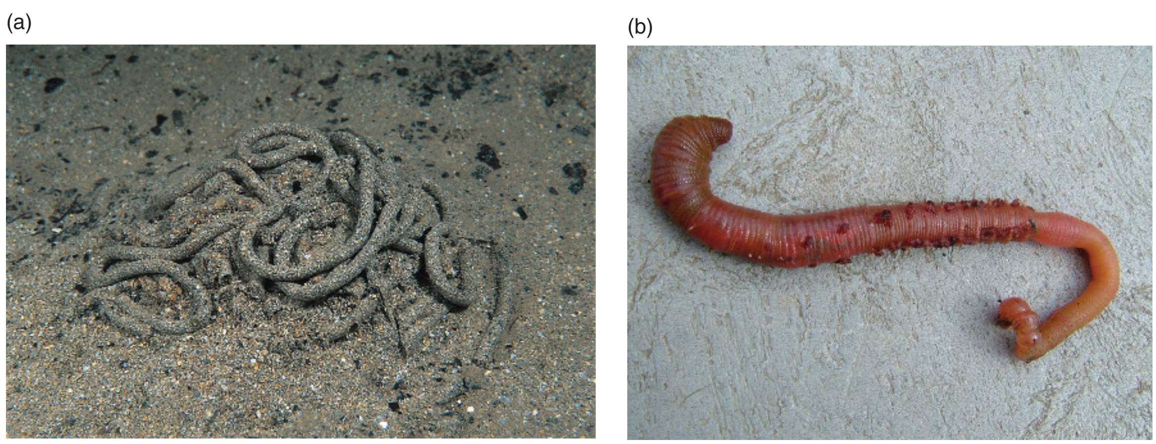

Figure 1.26

(a) Lugworm (*Arenicola marina*) casts at low tide on a sand/mud beach (Photograph courtesy of Paul Naylor.) (b) Lug worm. (Photograph courtesy David Fenwick, www.aphotomarine.com)

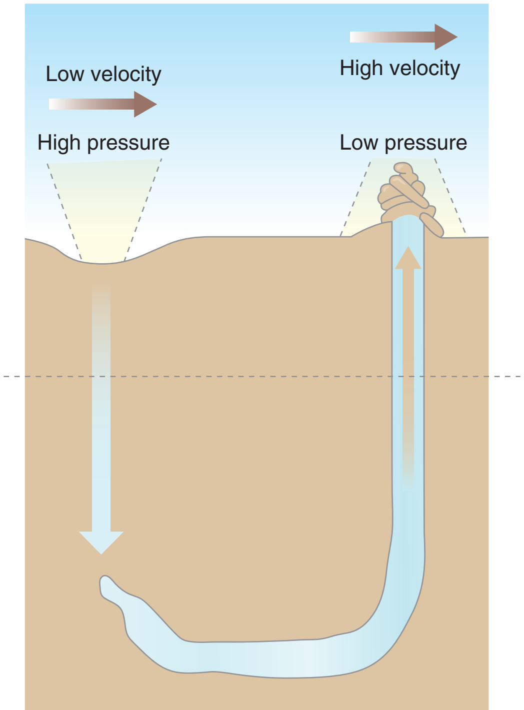

Figure 1.27

The U-shaped tube of the lugworm, *Arenicola*, showing the effects of water movement on the pressure at the two entrances to the burrow. The pressure differential results in a flow through the burrow.

lives in a U-shaped tube in sand or mud. The waste opening of the tunnel is raised above the seabed by only a centimeter or so, but the other opening is flush with the sand surface. When the tide is flowing this tiny, but physically (and ecologically) significant, height differential creates a pressure difference by the Bernoulli effect, which in turn causes water to flow into the lower opening and so helps to supply the worm with fresh seawater and hence food and respiratory gases (Figure 1.27).

Current speeds vary with distance from the seabed and there is a region termed the benthic boundary layer close to the seabed in which currents are appreciably reduced in speed. The benthic boundary layer can itself be subdivided. In the zone up to about 2 mm from the seabed frictional forces greatly reduce current speeds. From about 2 mm to 1 m from the bed there is the logarithmic layer in which the speed increases linearly with the logarithm of the distance from the bed. Between about 1 and 9 m above the bed marks the top of the benthic boundary layer. Above this zone the current flows at a constant speed. This reduction in current velocity close to the seabed influences the distribution of filter feeders. Active feeders (animals that create their own feeding currents such as bivalves, sponges, and sea squirts) are most abundant in the lower current speed benthic zone and passive filter feeders (animals that cannot generate their own currents such as cnidarians) higher in the water column where currents are faster. For example, Figure 1.28 shows the vertical distribution of four species of sessile filter feeders on the hydroid *Nemertesia* (Figure 1.29). The active filter feeders, *Electra* and *Scruparia*, are both more abundant closer to the seabed than the passive filter feeders, *Plumularia* and *Clytia*, where though the current velocity is slow relative to higher above the seabed, these two species can still feed because they can create their own water currents (Hughes 1978). This of course demands some expenditure of energy, so the passive species may be able to outcompete the active ones as long as there is sufficient current to supply them with food, hence their location higher up the living substrate.

Suspended sediments

Sediment, which is denser than water, is lifted and held in the water column by water movement. When the seabed is composed of soft sediments such as mud or fine sand, the quantity of suspended particulate material (SPM – frequently expressed as turbidity) increases with the current speed. This is because faster flows lead to greater turbulence and higher rates of vertical mixing and re-suspension. As currents slow down, particles suspended within them will drop out, the largest first. Simple fluid dynamics has fundamental consequences for marine habitat creation. Imagine an island around which tides and currents are flowing. The velocity of the currents at particular locations will be determined by the topography, so that water speeds up as it flows around a headland and slows down in a sheltered bay. Faster currents mean that small particles stay in suspension and only the large ones such as rocks or boulders are left in position. In slow current regions, even very small particles such as sand and mud drop out of suspension. This process therefore creates and maintains physical habitats in the sea, which in turn dictates the types and ecologies of organisms able to live in these places. Slow currents mean soft sediments containing burrowers and detritus feeders; fast currents support encrusting species that filter feed, and so on (Figure 1.30a,b). Note also that this basic system can work over a range of spatial scales, so our island in the diagram may be miles across or alternatively, a few meters or even centimeters. The same old rules apply.

Estuaries with high tidal currents can be exceptionally turbid. For example, the Bristol Channel, UK, has a maximum tidal range of about 15 m and tidal currents and tidal current speeds generally exceeding 1.5 m s^{-1} at springs and 0.75 m s^{-1} at neaps, so that a suspended particle can move up to 25 km over a flood or ebb tide. These high currents over a muddy bed result in suspended sediment loads as high as 4 g l^{-1}. It is not only tidal currents that generate

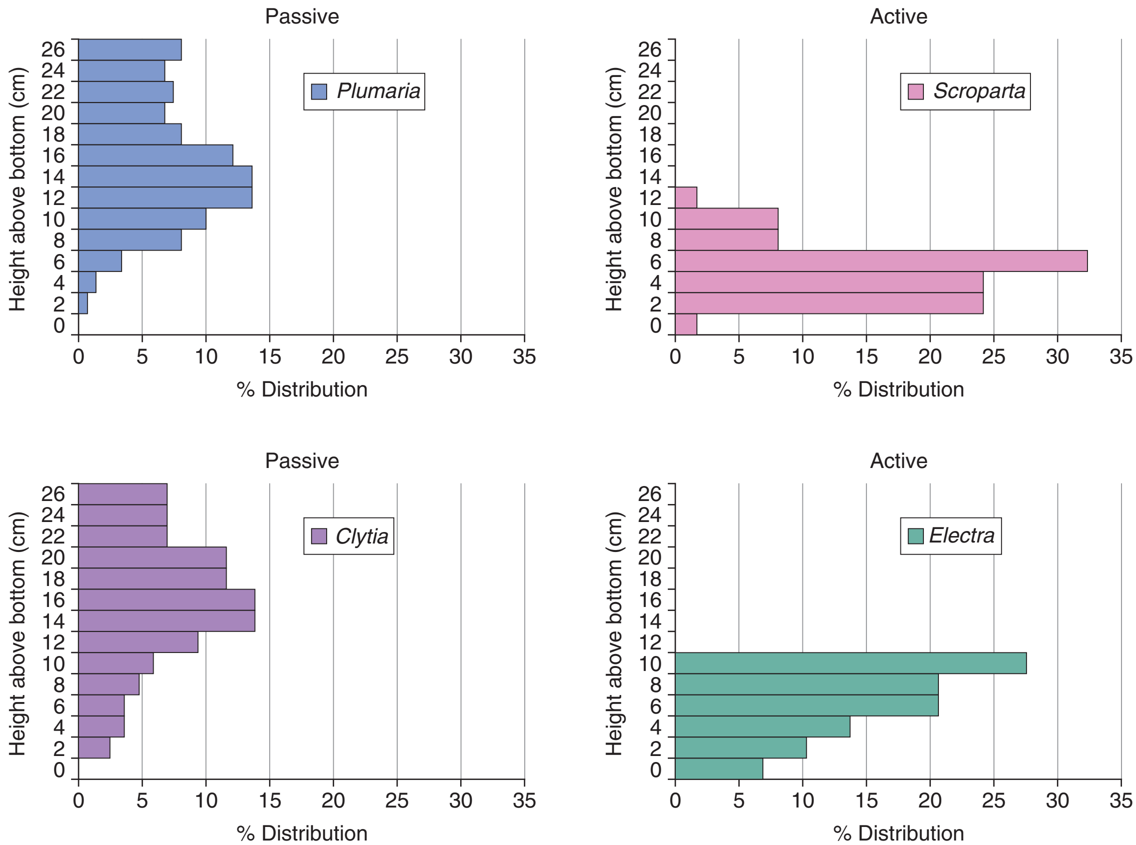

Figure 1.28

The differential vertical distribution of active and passive filter feeders growing on the hydroid *Nemertesia*. (From Hughes 1978.)

suspended sediment loadings, these are also influenced by wind and wave action, and suspended sediment loads can vary greatly both seasonally and also from day to day. Figure 1.31 shows the variations in both suspended particulate matter, SPM (in mg l^{-1}), and the size of suspended particles off the coast of Belgium over 24 hours, according to current velocity and variations in depth due to tidal fluctuations (Fettweis et al 2006). Several relationships can be identified. High SPM is clearly linked to high current velocities, though there seems to be a lag in the system such that peak SPM occurs an hour or more after peak velocity is reached. Water depth appears less significant.

As we have already suggested, the amount of suspended solids in the water column has a considerable influence on the community of plants and animals living in an area. The higher the turbidity the lower the light penetration and light levels can be reduced to such a low level that sublittoral plants do not occur. This is the case in parts of the Bristol Channel in the UK. High tidal currents can also produce regular sand and mud storms as the bottom sediment is taken into suspension by the flow and then resettles at slack water. This can result in a greatly impoverished benthic infauna (organisms that live within the sediments) because of the smothering and a lack of oxygen. In many localities the effects are not so extreme, but suspended sediment loads can still have a great effect on the species present. Even the deep-sea experiences remarkable fluctuations in suspended loads.

The ecological effects of elevated suspended sediment depend primarily on two factors: the size range of the sediment particles, and the food content of the suspended sediment. The percentage organic content of SPM tends to decrease as the suspended solids loading increases (Yukihira et al 1999). This change has a considerable effect on filter feeders. If the food content decreases, animals have to expend more energy to collect their food, or alternatively, live their lives more slowly. Even closely related species may vary in their suspended sediment tolerance. For example, black lip, *Pinctada margaritifera*, and silver lip, *Pinctada maxima*, pearl oysters occupy quite different habitats. *P. margaritifera* is typically found in coral reef waters which are oligotrophic and of low turbidity. In contrast, *P. maxima* inhabits mud, sands, gravels and seagrass beds and is most abundant in water with relatively

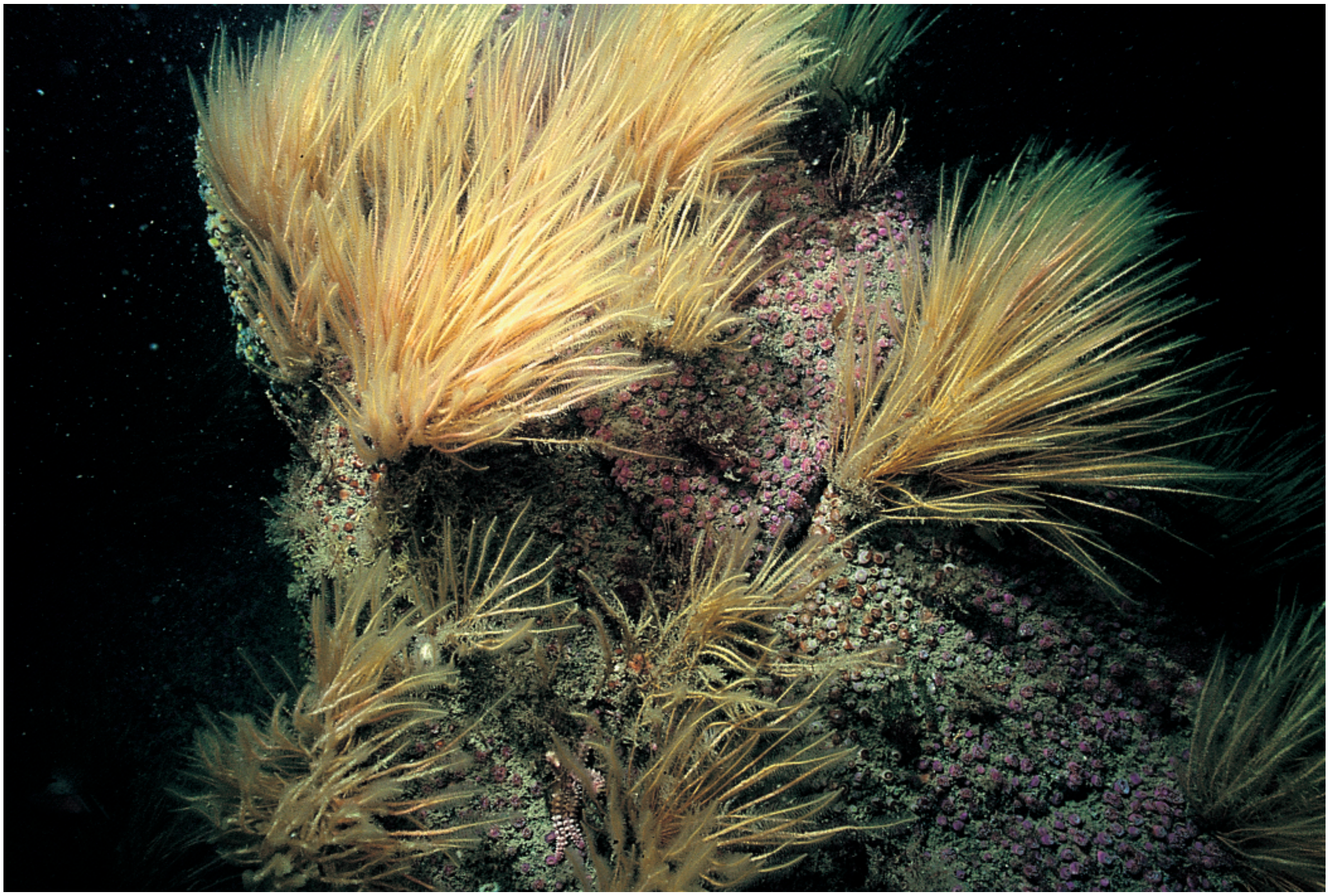

Figure 1.29
The hydroid *Nemertesia antennina*. (Photograph courtesy of Paul Naylor.)

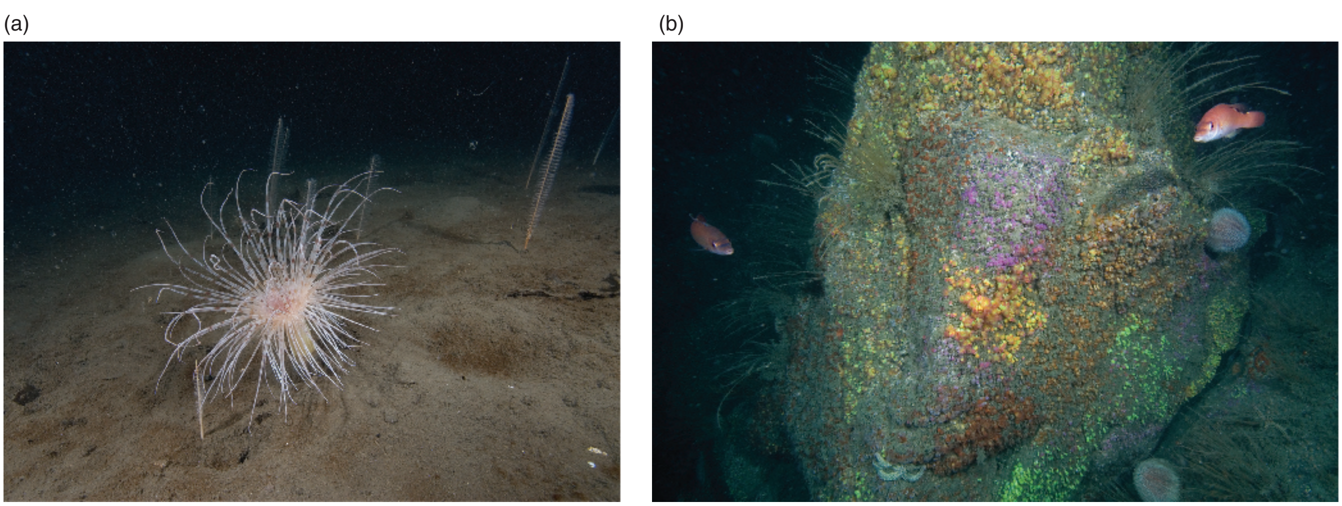

Figure 1.30
(a) Low current velocity community, with fireworks anemone and sea pens, Duich, W Scotland. (b) High current velocity community, with jewel anemones and cuckoo wrasse, Manacles, SW England. (Photographs courtesy of Paul Naylor.)

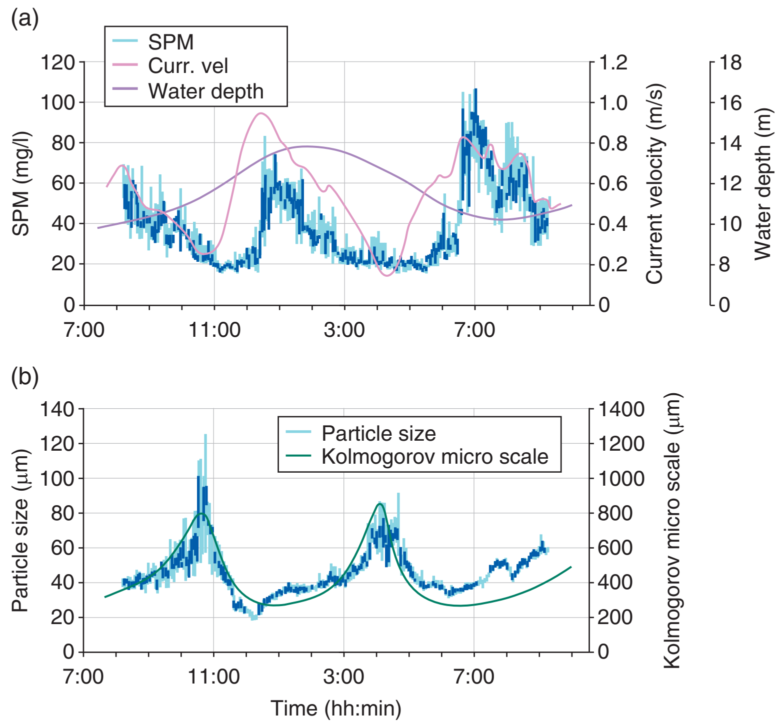

Figure 1.31

Zeebrugge site survey 2003/22. Through tide measurements from September 8, 2003, 8.00p.m. until September 9, 2003, 9.00a.m. (a) SPM concentration, water depth and vertical averaged current velocity. (b) Averaged particle size and Kolmogorov microscale of turbulence. Measurements have been taken at about 3 m from the bottom. (From Fettweis et al 2006; reproduced with permission of Elsevier.)

high sediment and nutrient loadings. Studies on the filtering capacity of these two oysters has shown that the species from clear water (*P. margaritifera*) is able to retain much smaller particles and to absorb energy from the smallest of them, as compared with the turbid water species (*P. maxima*) which is unable to retain small particles and gains maximum energy from medium size particles. This is an example of resource partitioning to avoid interspecific competition between similar species, which we discuss in more detail in Chapter 6.

Some organisms do well in conditions of high SPM and elevated turbidity, such as copepods (Islam et al 2005). However, environmental concerns have been expressed about increased suspended sediment concentrations resulting from all sorts of human impacts, such as paddlers on reefs, boat traffic, and dredging and disposal plumes. One of the worst-case scenarios of this type involves the logging of tropical forests resulting in increased erosion that dumps huge quantities of soil on fringing coral reefs (see Chapter 9). These unnatural events harm fish eggs, reduce growth and survival of larval and early juvenile fish, stunt the growth and reduce survival of bivalves and corals. Deposited sediments may simply smother sessile and sedentary animals and plants, or the suspended material may reduce feeding efficiency and impair the function of gills and other respiratory surfaces.

The activities of man also cause elevated suspended solids levels. The effects of these are discussed in Chapter 9.

Climate change

Physical conditions in the sea may be thought of as fairly stable and predictable, especially when compared with many terrestrial locations, but the rather obvious effects of climate fluctuations for example on land are also reflected in the sea. Climate change is the best known cause of physical change. There are many actual or potential consequences of climate change, global warming and so on for marine ecosystems, and a thoughtful review of this chapter may indicate what might happen if temperatures rise or storms increase in frequency and intensity. Two of the most important aspects of climate change are increases in sea level, and changes to the infamous El Niño.

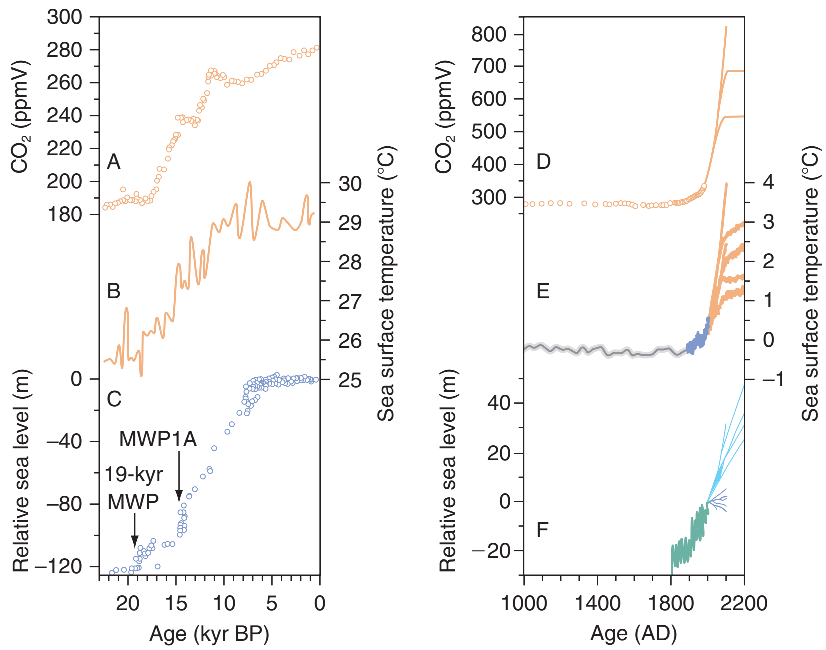

Figure 1.32

Time series of key variables encompassing the last interval of significant global warming (last deglaciation) (left) compared with the same variables projected for various scenarios of future global warming (right). (A) Atmospheric CO_2 from Antarctic ice cores. (B) Sea surface temperatures in the western equatorial Pacific based on Mg/Ca measured in planktonic forminifera. (C) Relative sea level as derived from several sites far removed from the influence of former ice sheet loading. MWP = meltwater pulse. (D) Atmospheric CO_2 over the past millenium (circles) and projections for future increases (solid lines). Records of atmospheric CO_2 are from Law Dorne, Antarctica and direct measurements since 1958 are from Mauna Loa, Hawaii. Also shown are three emission scenarios of atmospheric CO_2 over the course of the 21st century and subsequent stabilization over the course of the 22nd century. (E) Temperature reconstruction for the Northern Hemisphere from 1000 to 2000 AD (grey time series), global temperature based on historic measurements, 1880 to 2004 (blue time series), and projected warming based on simulations with two global coupled three-dimensional climate models with the use of three emission scenarios (orange time series). (F) Relative sea-level rise during the 19th and 20th centuries from the tide gauge record at Brest, France (green time series), projections for contributions from combined Greenland and Antarctic ice sheets (dark blue time series), and projections from sea-level rise from thermal expansion based on climate simulations shown in (E) (light blue time series). (From Alley et al 2005; reproduced with permission of *Science* – AAAS.)

In Figure 1.32 we can look back in history as much as 20,000 years, and notice that on a large time scale, increases in atmospheric CO_2 concentration, sea surface temperature and sea level all follow the same pattern. 20,000 years ago, the atmosphere contained much less CO_2, and the sea was appreciably colder and 120 m or more lower than now (Alley et al 2007). The graphs also suggest that little has changed in the last 5000 years. However, on a time scale of a mere 1000 years, we notice that the last 200 years have seen an almost exponential increase in CO_2 levels, SSTs, and a steep but linear increase in sea levels. By the year 2200, sea levels are predicted to be around 0.5 m above present levels, which roughly equates to an annual sea level increase of 2 or 4 mm, but these types of predictions are notoriously unreliable. What we can say is that the rate of change in global sea level is related to temperature anomalies (Figure 1.33) (Holgate et al 2007), and it seems that apart from a slight dip in the 1950s and 1960s, annual mean global temperature has risen steadily, and is now about 0.5°C warmer than it was 100 years ago. This anomaly is reflected in a roughly three-fold increase in the rate of sea level change.

Though rising seas levels will have serious consequences for low-lying coastal areas on land, it would seem likely that the majority of marine species will be little affected. However, temperature changes can have a much greater impact on marine systems, and the phenomenon of El Niño is a prime example. Essentially, sea surface temperatures are significantly enhanced in El Niño years, so that a band of unusually warm water extends virtually all the way across the Pacific Ocean from west to east. Figure 1.34 provides more details of the mechanism, where weakened trade winds allow warm water to move eastwards. These effects can have general impacts on the planet's weather. One of the most serious effects can occur over large parts of Southeast Asia which become dry during an El Niño; rain forests do not do well in dry conditions. The most rapid climate change of this type is predicted to take place

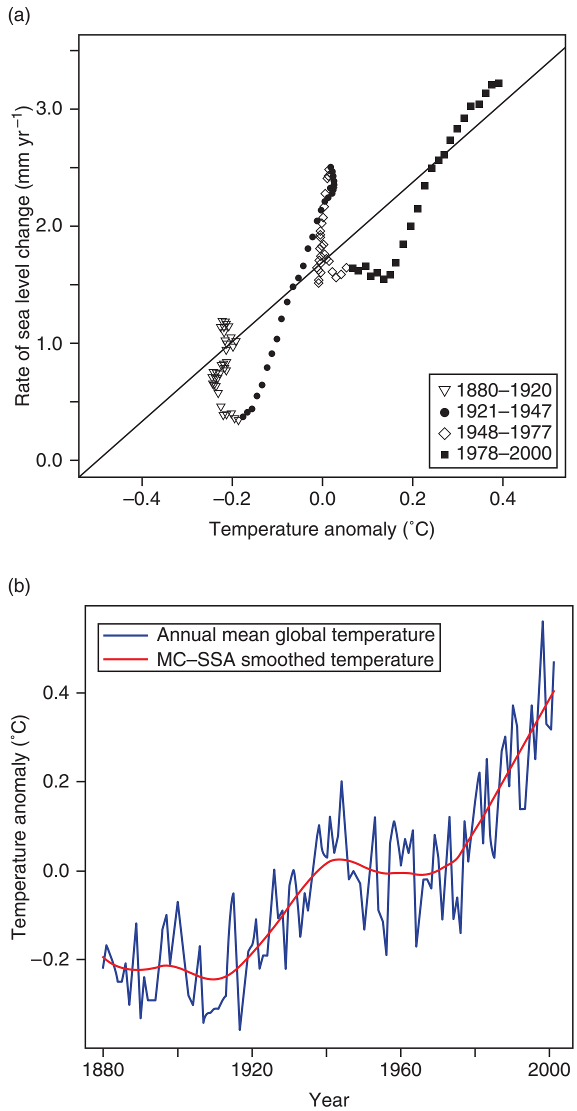

Figure 1.33

(a) The relationships of the rate of global mean sea-level rise to global mean sea-level surface temperature with the data divided into four epochs, each showing a different relationship between the variables. (b) The global mean surface temperature record, annual data and data smoothed using the MC-SSA method. The four epochs described in (a) relate to the four sections of the temperature record that can be clearly seen. (From Holgate et al 2007; reproduced with permission of *Science* – AAAS.)

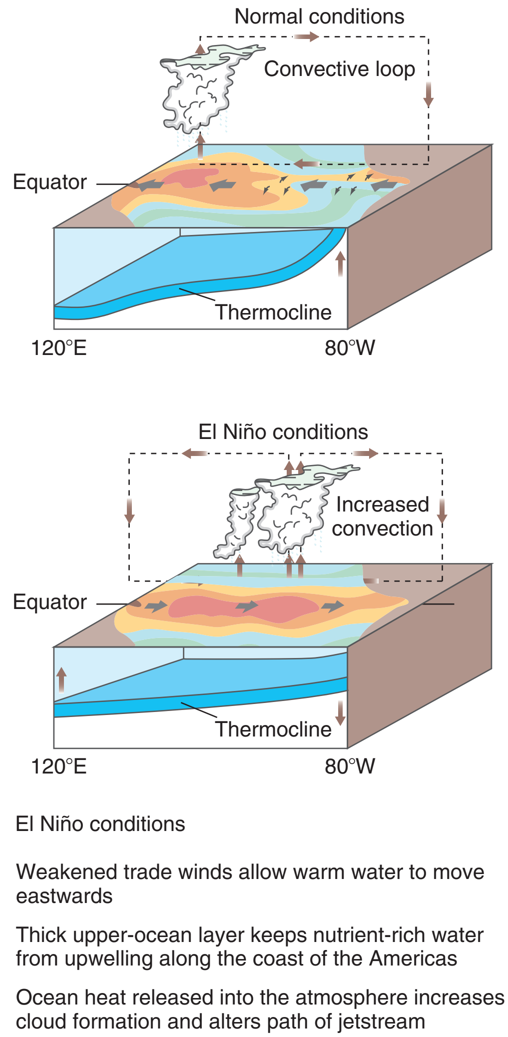

Figure 1.34

Marine and atmospheric conditions in the mid-Pacific under normal and El Niño conditions. (Courtesy of NOAA/PMEL/TAO Project Office, Dr. Michael J. McPhaden, Director.)

in the Southern Ocean (Trathan et al 2007), which comprises much of the Antarctic and Polar seas. El Niño effects here have been called "El Niño–Southern Oscillations" by virtue of their variations, known as ENSO for short, and they have been blamed for a series of catastrophes such as the reduction in krill populations in the south Atlantic with all the associated food chain effects on marine megafauna such as whales.

In the sea, one of El Niño's biggest influences is on primary productivity (see also Chapter 3). Rising convection currents occur in mid-ocean, resulting in significantly altered wind patterns, jet streams and cloud formation, but most importantly, nutrient-rich water is prevented from upwelling in various parts of the world with huge impacts on marine productivity. One of these areas occurs along the west coast of the Americas, and a lot of research work has centred on Peru and Chile where fisheries for anchovy and sardine are some of the biggest in the world (see also Chapter 8). In Peru, El Niño events were recorded in 1972/73, 1982/83, and 1997/98 (Niquen & Bouchon 2004). Figure 1.35 summarizes the major changes in environmental conditions on pelagic communities over the various ENSO periods, and as can be seen the results are complex. Commercially, the most significant effects of El Niño are on fishing stocks, and two species show opposite

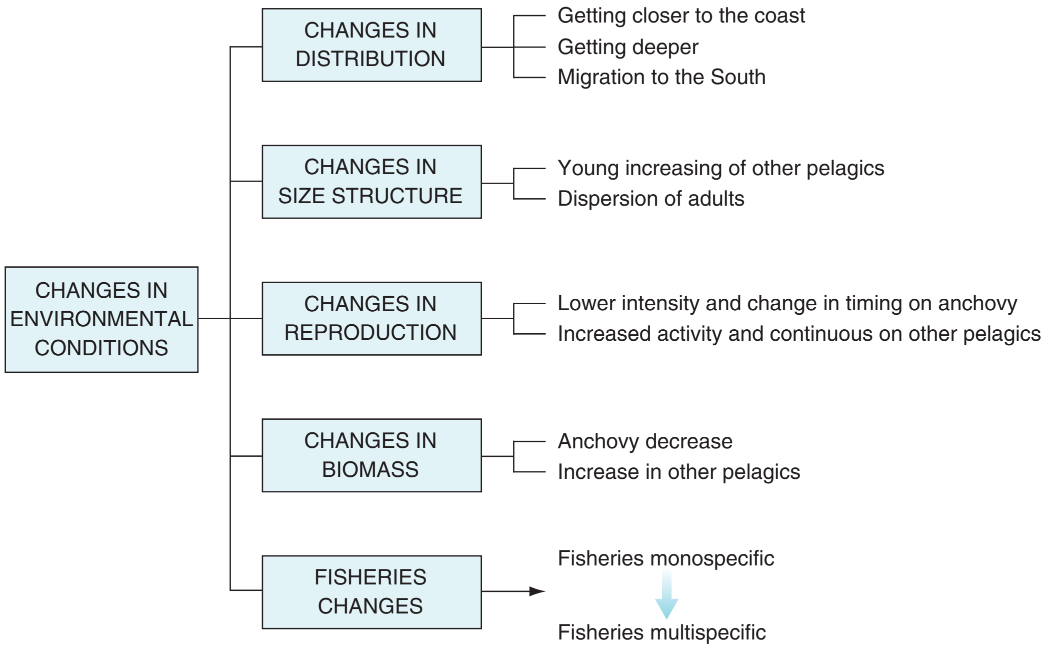

Figure 1.35

Effects of El Niño events from the 1970s to 1990s on pelagic resources in Peruvian waters. (From Niquen & Bouchon 2004; reproduced with permission of Elsevier.)

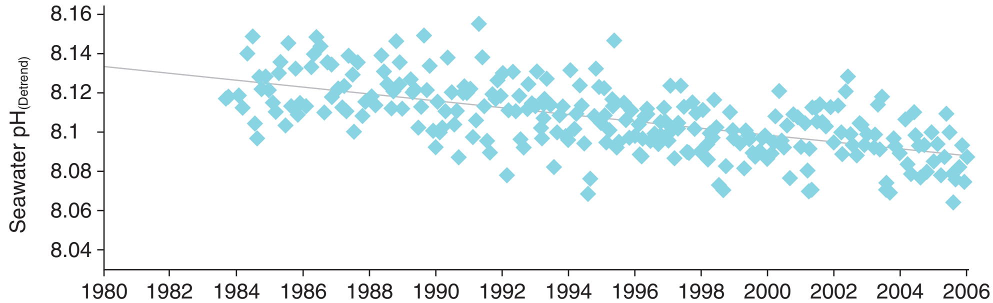

Figure 1.36

Trends in oceanic surface water pH in the northeast Atlantic near Bermuda. (From Bates & Peters 2007.)

reactions. Anchovy suffered huge declines in stocks in all three decades, whereas sardine stayed fairly constant in the 1970s and 1990s but showed large increases in the 1980s. In neighboring Chile, Escribano et al (2004) reported the total anchovy catch remained stable in 1997 at a maximum of around 1 million tons. In 1998, however, the anchovy catch declined to 400,000 tons, before recovering to 1.2 million tons in 1999. These sorts of fluctuations can have serious impacts on the socioeconomics of a region.

Finally, one of the most potentially serious physical changes for the future of our oceans involves acidity. As CO_2 levels in the atmosphere rise, the pH of seawater is likely to fall (become more acidic as the hydrogen ion concentration increases). Acid rains and direct absorption of CO_2 by surface seawater may add to the problem, though its extent and consequent ecological effects are still uncertain. For example, Bates & Peters (2007) studied the changes in pH of surface seawater near Bermuda, and were able to detect a slight decrease over 25 years (Figure 1.36). The authors concluded that surface seawater pH in this part of the Atlantic Ocean decreased by 0.0017 (±0.0001) pH units per year. In this study, there was no obvious impact on coral growth, but since coral skeletons are made of a form of calcium carbonate called aragonite, then the ability of hard corals to lay down skeletons will be reduced if seawater becomes too acidic. On a small scale, however, Jokiel et al (2008) were able to detect a reduction in calcification of skeletal material in the hard coral *Montipora capitata* held in 1 × 1 × 0.5 m fibreglass tanks treated with diluted hydrochloric acid at a concentration designed to simulate the increase in seawater acidity expected during the twenty first century. Overall, this experiment found a 20% reduction in calcification rate, but there appeared to be no effect of increased acidity on gamete production in the coral. It remains to be seen whether or not declining pH in our global seas will indeed add significantly to the already large list of troubles ahead for our coral reefs (see also Chapter 9).

Conclusions

Clearly there are numerous physical factors and conditions that influence life in the sea. Depth, temperature, salinity, turbidity, velocity, pressure and so on, all combine to produce a myriad of physical and chemical habitats which provide a huge number of combinations and permutations. The oceans are not at all the bland, homogeneous expanse that we might think, and with this in mind, it should be no surprise that the diversity of life in the sea is as rich and varied as the physical conditions in which it lives. Biodiversity is the subject of Chapter 2.