Martin Speight and Peter Henderson

Marine Ecology

Concepts and Applications

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MARINE ECOLOGY
CONCEPTS AND APPLICATIONS

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MARINE ECOLOGY

To our families:
Angela, Cate, Claire, James, Nick, Richard, Rowena and Toby

PREFACE

The book *Silent World* was written by Jacques Cousteau, and published by Hamish Hamilton in 1953. In it, Cousteau describes his first encounter with the undersea world using goggles which enabled him to see underwater. He says: "One Sunday morning in 1936 … I waded into the Mediterranean and looked into it through Fernez goggles. I was a regular Navy gunner, a good swimmer interested only in perfecting my crawl style. The sea was merely a salty obstacle that burned my eyes. I was astounded by what I saw in the shallow shingle …, rocks covered with green, brown and silver forests of algae, and fishes unknown to me, swimming in crystal clear water. Standing up to breathe I saw a trolley-bus, people, electric street-lights. I put my eyes under again and civilization vanished with one last bow. I was in a jungle never seen by those who floated on the opaque roof."

Marine ecology has always been fascinating, mysterious, and indeed for many centuries, downright dangerous. Sea monsters such as giant squid and krakens lived in the deep and dragged ships to their doom. Sirens lured unprepared sailors onto rocks, whilst mermaids lured the same sailors into other activities. The bottom of the sea was as far removed from almost everyone as the surface of the moon, and catching fish was a mysterious, hunter-gatherer sort of activity with random and often unpredictable outcomes.

Whilst terrestrial ecologists could walk out into their habitats and ecosystems with a pencil and paper, butterfly net and hand lens, their marine counterparts had to resort to buckets, grabs and cores dangled from boats or piers, somewhat akin to sampling a woodland with a grapnel suspended from a hot-air balloon. The deeper the sea, the bigger the problem, so that anywhere beyond the reach of a depth sounding line or a fishing net was pretty much completely unknown. As Sydney Hickson said in his *Fauna of the Deep Sea* published in 1893, "The bottom of the deep sea was until quite recently (first half of nineteenth century) … terrae incognitae. It was regarded by most persons, when it entered into their minds to consider it at all, as one of those regions about which we do not know anything, never shall know anything, and do not want to know anything" (our parentheses). Ambitious expeditions were nonetheless mounted to explore the sea using the available technology, the most famous of which was the Challenger Expedition that lasted for 4 years beginning in 1872. *HMS Challenger* covered over 120,000 km, surveying, trawling and dredging, and eventually discovering over 4000 new species. Fifty or so years later, another famous and influential marine biological expedition set sail, this time to explore the cold seas of the southern oceans. On board the *Discovery* was the marine scientist Alistair Hardy, later to become Sir Alistair Hardy. Hardy became Linacre Professor of Zoology in Oxford in 1946, and two of his longstanding achievements were firstly the invention of the continuous plankton recorder, and later the publication of the classic two-part book, *The Open Sea*.

Back at the individual level, free diving – holding the breath and reaching far below the surface to collect food or sponges, or attack the enemies' fleets – has been going on since ancient times. Throughout history, we have invented machines to enable us to descend deeper into sea and stay there for longer than a single breath-hold. These new systems enabled us to see a little more of the marine realm first hand, albeit from the bottom of a primitive diving chamber or bell. Aristotle apparently described a diving bell, but it wasn't until the fourteenth and fifteenth centuries that Europeans began to use such apparatus in attempts to raise the valuable bits of shipwrecks, such as cannon and treasure. In 1535, the Italian inventor and explorer, Guglielmo de Lorena, was attributed with the invention of the first proper diving bell, though Leonard da Vinci had produced designs for such a device some years earlier. Leather seals and manual pumps increased the sophistication of diving bells, and by the 1930s, William Beebe was able to descend to nearly 1000 m off Bermuda in his bathysphere. The remaining problem was that such machines had to be lowered by cranes from the surface, and venturing any deeper was very difficult. What followed was the bathyscaphe, a somewhat similar machine, but this time the pressure-proof sphere containing the divers was attached to a large flotation device, allowing the machine to move independently of the surface. The culmination of this development came in 1960, when *Trieste*, a bathyscaphe piloted by Jacques Piccard and Don Walsh, reached the bottom of the Challenger Deep in the Marinas Trench, a depth of 10,916 m. Today, there are many deep submersible vehicles (DSVs), such as *Alvin* owned by the Woods Hole Oceanographic Institute and *Mir* run by the Russian Academy of Sciences, but none can go anywhere near as deep as *Trieste*.

As alternatives to diving bells, at least for shallow waters, the use of individual diving suits became routine in the 1830s when Augustus Siebe formed the company Siebe Gorman to produce the traditional copper-helmeted diving dress. All but a very few of the designs thus far depended on an air supply from the surface, pumped down to the diver under pressure. What was needed by the budding science of marine biology and ecology was a self-contained underwater breathing apparatus (SCUBA) to free the diver from a surface supply.

Various attempts were made to produce a safe and effective SCUBA device, and the first half of the twentieth century saw a series of inventions, such as the oxygen closed circuit systems used by navy frogmen in the Second World War. Though effective enough at depths above 10 m or so, the pure oxygen became toxic at deeper depths and higher pressures, seriously limiting any recreational or scientific applications for the apparatus. The real breakthrough came in 1943, when Jacques-Yves Cousteau and Emile Gagnan invented a demand valve (regulator) that supplied the diver using it with air from steel cylinders on his or her back at the same pressure as that of the surrounding water; the "aqualung" was born.

New institutions for the study of marine biology and ecology were already established. In the USA, Scripps Institute of Oceanography in southern California has its origins in 1903, whilst Woods Hole Oceanographic Institute in Massachusetts was incorporated early in 1930. In the UK, the Marine Biological Association was founded as far back as 1884, and it opened its Citadel Hill Laboratory in Plymouth in 1888. The Monaco Aquarium on the Mediterranean coast was founded in 1910, and in Australia, the Commonwealth Scientific and Industrial Research Organization (CSIRO) set up its Fisheries Investigation Section, later to become the CSIRO Division of Fisheries in 1937. So, marine research around the world was active well before the invention of the aqualung.

Undoubtedly, the aqualung opened the floodgates for the exploration of shallow seas, down to 50 m or so, and we would suggest that detailed marine ecology only really began in the early 1950s as post-war scientists and recreational divers started to explore and study coral reefs and kelp beds alike. Of course the aqualung also enabled much easier exploitation of marine organisms from sponges to scallops, fish to lobsters. SCUBA diving with a speargun was hardly sporting, but very rewarding to some. So, marine ecology in shallow waters at least has burgeoned over the decades since then. For example, a trawl through ISI Web of Knowledge using the search terms "marine and ecology" yielded an average of 5000 or so publications in the 1990s, over 6000 in 2002, over 7000 in 2003, nearly 10,000 in 2004, and more than 11,000 per year in 2005, 2006, and 2007. Human-derived impacts are becoming more far-reaching and serious as the years go by, and climate change such as temperate and sea level rises, is now feared to be having severe and irrevocable effects on shallow marine ecosystems.

In the deep sea, all was thought to be quiet, calm, and possibly boring, until 1977 when scientists from Woods Hole Oceanographic Institute used the DSV *Alvin* to explore areas of underwater volcanic activity near the Galapagos Islands in the eastern Pacific. The enormous diversity of life on newly discovered hydrothermal vents amazed and delighted the scientific world and amateurs alike, and the far-reaching and fundamental research, even down to the origins of life on earth itself, have continued apace. The sheer excitement of vent communities, as well as cold seeps, whale-falls, and so on, is hard to describe.

Critics will no doubt ask the questions "why should Speight and Henderson write such a book?". and "What do they know about marine ecology?". First and foremost, we believe strongly that a textbook for students should be written by teachers, tutors, and lecturers. Research papers are excellent for reporting exciting and challenging new findings at the cutting edge of their fields, but someone has to convert such scholarly works into summaries and syntheses suitable for communication with undergraduates and other students. Secondly, we feel that people who write these textbooks should be good communicators, familiar and practiced with converting sometimes cryptic information into palatable, understandable and indeed enjoyable accounts which will captivate as well as inform.

Martin Speight has been teaching marine biology, ecology, and conservation to university students at undergraduate and postgraduate level for over a quarter of a century. Peter Henderson has done large amounts of university teaching in the field for many years, and also has made his livelihood by examining marine ecological problems and communicating his findings successfully to complete nonexperts. It has never been our intention to steal other people's work, and we have taken great pains throughout the lengthy writing of this book to consult as widely as possible and to seek all approvals and permissions to report the findings of experts in their specific fields. In short, we believe, some will say immodestly, that we are both good teachers and good communicators, and hence well qualified to deliver such a book.

We have strived to base the book on modern primary literature, predominantly post 2000. Some classic work dating back to times before this has of course been required on occasion, but we hope that the book will represent the "state of the art" as perceived at the time of writing this preface. Clearly, research never stays still and we hope to be able to provide new editions as the years go by which will reflect the new findings as they are published. Another problem with this approach, especially when the applied aspects of marine ecology are considered, is that information such as management plans, conservation strategies, and regional or local tactics are not officially published, but merely stay as "grey literature," usually web-based and difficult to verify or attribute. Although we have tried very hard to check such information, and report it as accurately as possible, we apologize to source and reader if we have made mistakes or provided misinformation. Any corrections to this type of error will be gratefully received, and put right in the next edition of the book.

Chapter 1 presents aspects of oceanography and other physical and chemical aspects of the sea which impinge on living things. Chapter 2 discusses the levels of diversity (more realistically, species richness) of marine communities and the various factors which influence them. The remaining chapter structure of the book follows a functional approach as much as possible, rather than describing different types of marine ecosystems separately. Thus, Chapters 3, 4, 5, 6, and 7 discuss various levels of functionality, primary production, herbivory and detritivory, predation and parasitism, competition, succession, and dispersal as major topics in marine ecology. Examples to illustrate concepts have been taken from all parts of the sea as appropriate, from the shallowest intertidal to the abyssal depths. Chapter 8 looks at global fisheries and the problems of sustainable resource use in the sea, and the final two chapters, 9 and 10, consider all aspects of anthropogenic impacts on marine ecosytems, from pollution to tourism, and finally the complex issues of marine conservation and management.

Martin Speight, Oxford
Peter Henderson, Pennington
December 2009

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Chapter 1

The physical template

CHAPTER CONTENTS

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.

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Figure 1.1

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

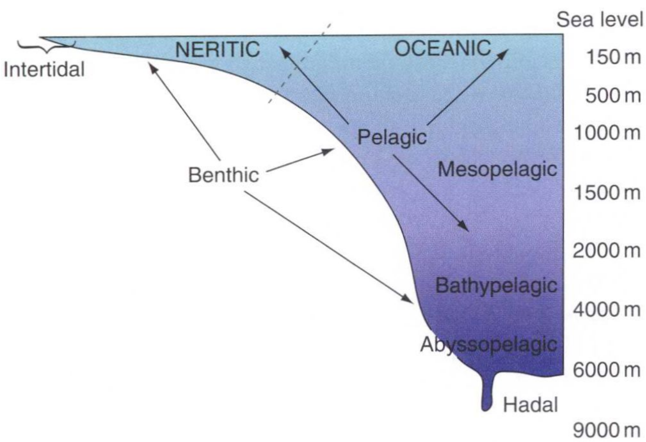

Figure 1.2

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

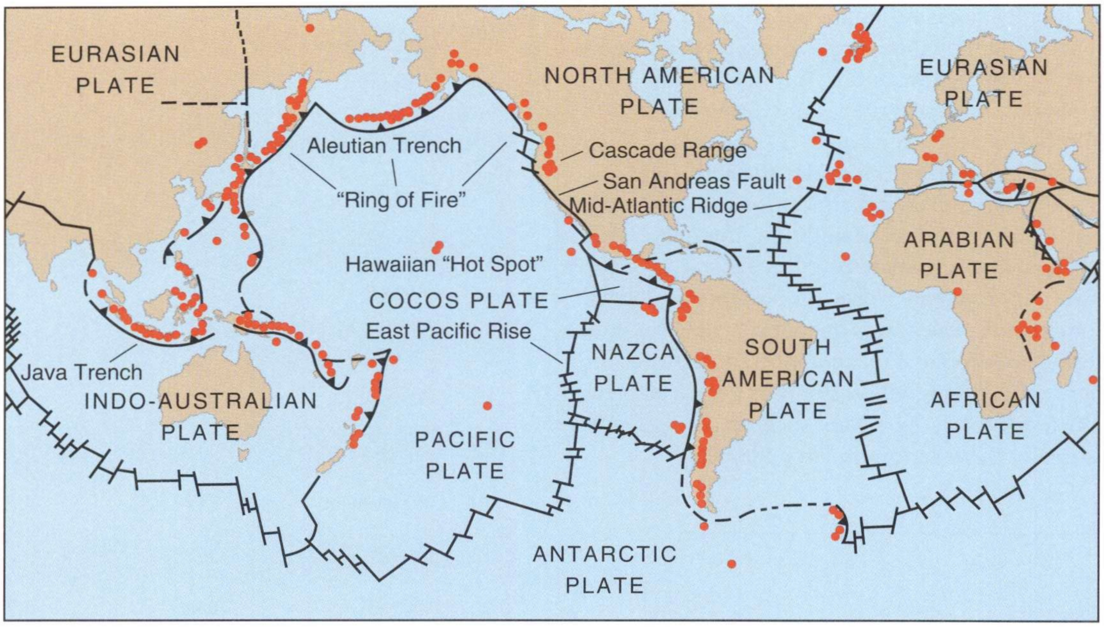

Figure 1.3

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.)

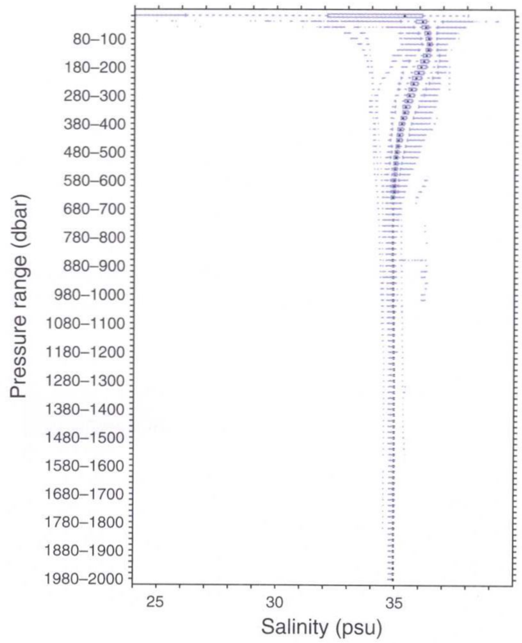

Figure 1.5

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.

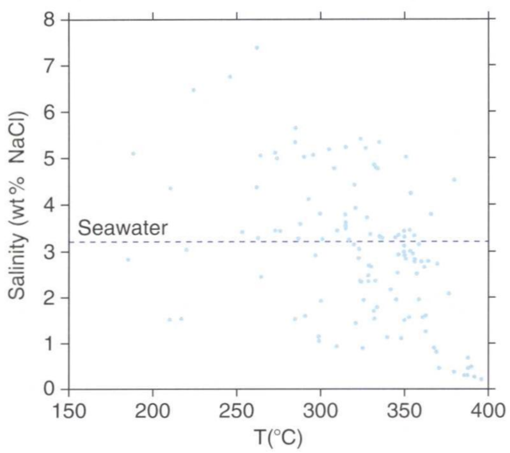

Figure 1.6

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.

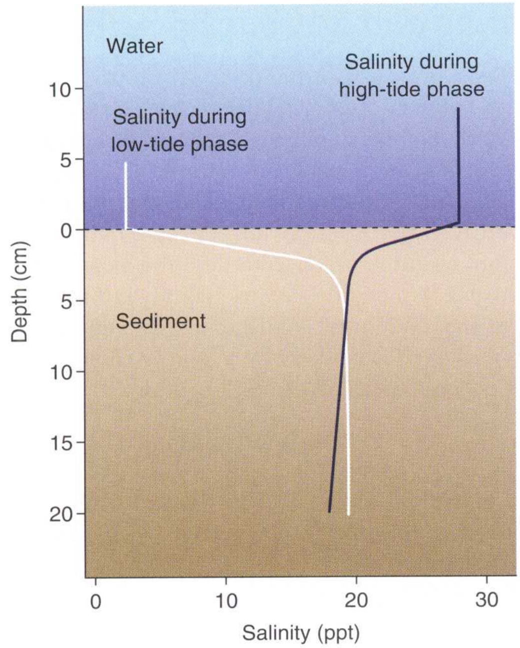

Figure 1.7

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

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.

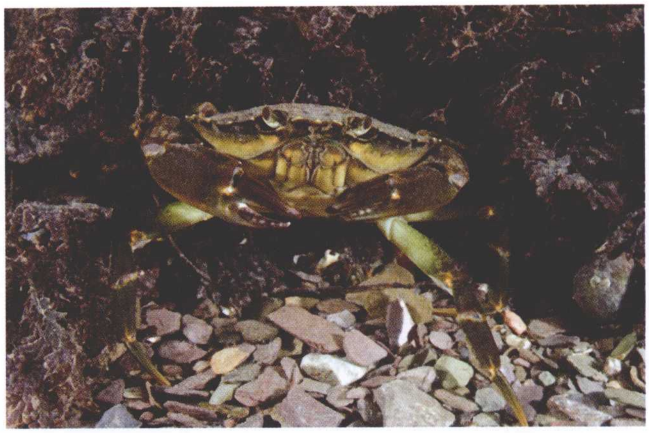

Figure 1.8

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.)

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).

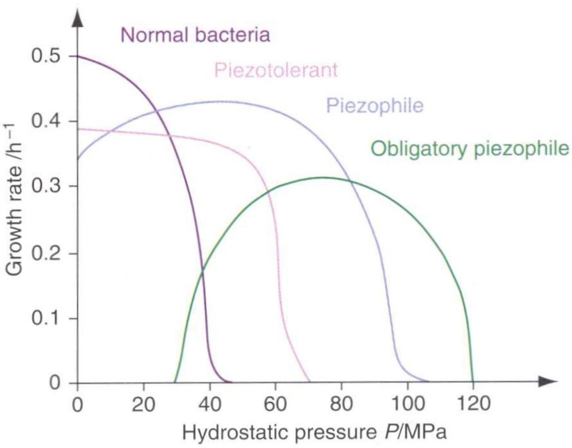

Figure 1.10

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

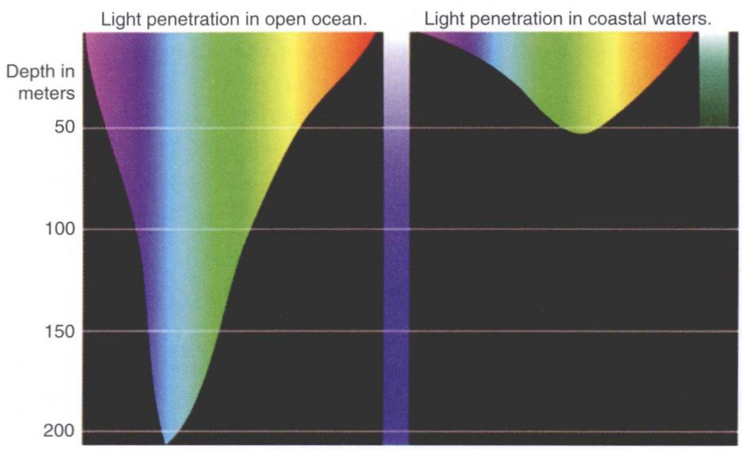

Figure 1.11

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