Chapter 1

Ocean ecology: some fundamental aspects

Biological oceanography could also be termed ocean ecology. The term encompasses the ecology of oceans just a short distance from the shore – perhaps from the lowest low-tide level onward, right out to the centers of the great oceanic gyres. Often, estuarine habitats are included in the study of the oceans. Oceanographers deal with questions like: what sorts of organisms inhabit different sectors and depths, and why? How is organic matter produced, by what types of "plants" (although we rarely say that word, as we will explain), and what controls their growth? Which animals constitute the herbivores and which the carnivores; and how do the carnivores locate their prey? How do the changing seasons affect the biota? What relationships prevail between organisms – from microbes to whales – and the chemical and physical character of seawater? How can worms and isopods make a living in mud beneath 4000 m of water in near-total darkness? What can we expect to harvest from the sea, and how can exploitation of fisheries or seafloor mines be achieved without damaging the resource or the habitat? How will ocean biota be affected by global climate change? Sometimes the key issues and answers to our questions come from marine biology, sometimes mostly from chemistry or physics. Fundamentally, biological oceanography straddles many disciplines, a fact which makes it a joy for the oceanographer.

Seawater

The root word in "ecology" is *oikos* (οικοσ), which is Greek for "house" or "habitat". It is the study of life in relation to its habitats, and obviously the key habitat in oceans is water – salt water. So, let us begin by considering water in some detail. The molecular structure of water, dihydrogen oxide, involves moderately strong covalent bonds between each of two hydrogen atoms sharing their single electrons with an oxygen atom. The water molecule is not linear; rather the hydrogen protons repel the overall electron shell to the far side of the oxygen atom and assume an angle of 105° from each other. Thus, the overall molecule is polar, being electropositive on the hydrogen side, and negative near the oxygen atom. This polarity creates a weaker bonding potential among the water molecules, especially in the liquid and solid phases. These *hydrogen bonds*, H-side to O-side, create a chaining effect, amounting in the liquid phase to arrays of "flickering clusters", and, in ice, to a weakly ordered crystal. As liquid water cools, the hydrogen bonds are less frequently disrupted by thermal motion, and the spatial array of more tightly bonded clusters progressively occupies less space. This means that water reaches its maximum density at 3.98°C (Caldwell 1978). However, the molecular ordering within ice is such that more space is filled by fewer molecules, so that the volume of ice is actually ~10% greater than the liquid phase at the density maximum, with the result that ice floats on water. Appropriately, much has been made of this unusual way in which water differs from comparable liquids. Lakes, for example, must cool entirely to ~4°C, becoming vertically homogeneous, before surface freezing can begin. Ocean salt water has a rather different equation of state (density being a function of temperature, salinity, and pressure), such that the temperature at which the maximum density occurs decreases with both salinity and pressure (see the data in Caldwell 1978), and overturning is not a necessary preliminary to freezing.

Biological Oceanography, Second Edition. Charles B. Miller, Patricia A. Wheeler.

In addition, because of the hydrogen bonding, water has a very large *specific heat capacity* ("specific" means relative to the mass). The amount of heat required to warm a gram of water by 1°C (the specific heat) is defined as 1 calorie. The calorie is now considered to be an "archaic" unit equal to ~4.180 joules g^{-1} °K^{-1}, varying somewhat with temperature and pressure (Why should anything be left as easy to remember?) which is a very large amount of energy when compared with the requirement for, say, ethanol with weaker hydrogen bonding at 0.58 calories g^{-1} °C^{-1}. This means that oceans are very slow to warm and very slow to cool, enabling currents headed poleward from the tropics to carry massive amounts of heat to high latitudes. In addition, very large amounts of heat must be added to water to force evaporation (2257 kJ kg^{-1} = 540 calories g^{-1}), and removed to allow ice formation (334 kJ kg^{-1} = 80 calories g^{-1}). For reasons that we will leave to the physical chemists, the temperature of liquid water remains fixed during freezing, at 0°C for pure water, and a few degrees lower for salt water (hence the salting of icy highways). Once frozen, ice can become even colder. Water also has a fixed boiling point at a given pressure, where the molecules escape explosively to the gaseous phase. This is 100°C at 1 atmosphere pressure. The effect of pressure on the phase transition is important in deep-sea hydrothermal vents, such that the boiling point of water at a depth of 2000 m is over 330°C. Thus, magma-heated water can emerge from the seafloor without exploding into steam. Water does evaporate into overlying air at sub-boiling temperatures, and this evaporation is more rapid when the temperature difference between the air and the water is greater. Thus, oceans, lakes, puddles, wet sand, and plant transpiration all pump water vapor into the atmosphere, leading to cloud formation, enhanced reflection of sunlight back to space, and rainfall that varies geographically, seasonally, and year to year. As is becoming obvious here, every aspect of the chemistry and physics of water is ecologically important.

The electrostatic polarity of water molecules also means that they will take on a preferential orientation adjacent to ionically bound molecules, to salts. For sodium chloride, for example, the oxygen atoms will tug on the sodium ion, and the hydrogen atoms will pull on the chloride. This tugging will be sufficient to dissociate the ionic bonds of many salts, and the water molecules will then encase the freed ions. Thus, dissolved salts will accumulate as the water flows over the land and rises through magma-heated rocks. These salts will then be transported into the sea. The sea is at the bottom of the hill, so to speak – an enormous evaporation basin in which the salts accumulate. Over sufficient time, a balance will emerge between the delivery rate and the processes that convey the salts into sedimentary structures (coastal salt-beds, manganese nodules, hydrothermal vent towers, etc.), such that the proportions of the different ions are relatively constant. Thus, the overall "salinity" is established by the remarkably constant proportions of the major dissolved ions (see Table 1.1).

All of those are termed *conservative* ions, and their proportions vary only slightly – a fact recognized by Forchhammer in 1864, but confirmed by the careful analytical work of William Dittmar (1884) with samples collected from the world's oceans on the Challenger Expedition (1873–1876). Calcium content does vary somewhat with depth, due to dissolution, under high pressure, of shells made from $CaCO_3$, and the bicarbonate content varies according to the amount of carbon dioxide in solution (the CO_2 content of the oceans is rising because seawater is absorbing the carbon dioxide generated by the burning of fossil fuels). Because of the near-constant proportions of major salts, the total salinity can be quite closely estimated by determining any one of the dissolved ions, e.g. chloride can be measured using a silver nitrate titration, or by measuring the overall electrical conductivity of the water. In modern practice, salinity of a sample is expressed as a ratio of its conductivity to that of a "standard" seawater, and is taken to have no units (the units in the ratio cancel), and is expressed on a "practical salinity scale". Salinity is often expressed simply as, say, $S = 35$, a number related to the grams of salt per kilogram of seawater, but no longer stated as such (parts per thousand). $S = 35$ is

Table 1.1 The proportions of the major dissolved ions in seawater. Total salts = 35.17 g kg^{-1} seawater.

CATIONS	IN SEAWATER (g kg^{-1})	ANIONS	IN SEAWATER (g kg^{-1})
Na^+	10.78	Cl^-	19.35
Mg^{2+}	1.28	SO_4^{2-}	2.71
Ca^{2+}	0.41	HCO_3^-	0.126
K^+	0.40	Br^-	0.067
Sr^{2+}	0.008	$B(OH)_4^{3-}$	0.026
		F^-	0.001

close to the overall average of ocean salinity. The upper range of *S* is ~40 in parts of the Red Sea. Unlike those conservative ions, others, like nitrate (NO_3^-), that are taken up by photosynthesizing algae and by bacteria, can vary *non-conservatively*. Nitrate varies from almost immeasurable amounts in the surface layers of oligotrophic central gyres to 45 μM (micromolar) in the deep North Pacific. These μM quantities are not large enough to make the measurement of chloride or conductivity unreliable as an index of the overall mass of dissolved salts, *S*, although nitrate does make a measureable addition to seawater density in very deep waters in the Pacific.

Cell membranes mostly only pass salt ions through specific, energy-using, protein channels, but water passes through more freely, passing from the side with the lower solute (salt and everything else) concentration to the side with the higher solute concentration. This *osmotic* flow is actually down the gradient of water concentration. Cells and tissue fluids of much marine life, including algae and most invertebrates, are *isosmotic* with seawater. That is, solute and water concentrations are the same inside and outside their cells. Cells of freshwater plants and animals, on the other hand, must contain some salts and dissolved organic matter, so they have water pushing in through any porous cell surface. To avoid over-inflation, rupture, and death, they must steadily pump water back out. Protists have specialized organelles which do that, and metazoans have kidneys at several levels of complexity to perform this function for the body as a whole.

Fish evolved in fresh water. The impermeability of their skin and scales limits water influx to the gill membranes, which must be exposed to the water for oxygen exchange, and that lessened influx is pumped out by their efficient kidneys. When some fish colonized the estuaries and oceans (probably stepwise in that order), the problem was reversed, with water moving out through the gills. Several solutions evolved. Sharks and rays came to tolerate large tissue concentrations of urea, giving their tissues osmotic equivalence with the sea. Bony fishes developed a system of swallowing water and then excreting the salts both via the kidneys and from desalination glands on the gills. Fish that come and go between fresh water and salt water, including salmon, shad, eels, and others, must shift between these modes, in some cases (e.g. steelhead trout) back and forth many times. Many seabirds, although not impacted by the osmotic differential with seawater, must drink to replace water lost at their lungs; they eliminate the salt with glands in their nostrils. Marine mammals do not have much cell membrane exposed to water, and by and large they avoid drinking. They are very efficient at retaining water from their prey and water produced by their metabolic reactions. Their specialized kidneys manage the balance of tissue electrolytes (salts). Estuarine animals and plants living in brackish water have a variety of means for tolerating both the intermediate and highly variable osmolarity. Studies of osmoregulation support a minor research industry favored by university faculty members spending the summer at marine stations.

The covalent bonds of hydrogen to oxygen in water are labile enough that the oxygen side of one molecule occasionally pulls one of the hydrogen atoms off another, producing hydronium (H_3O^+) and hydroxyl ions (OH^-). In suitably pure water (actually rather difficult to obtain), the abundance of each is 10^{-7} molar. In solutions of acid, the acid protons form more H_3O^+, increasing its molarity to 10^{-6} or much less, and neutralizing an equivalent amount of the OH^-, reducing its molarity to 10^{-8}. In solutions of bases, the opposite happens. The balance in any given acid or base solution is given by the negative logarithm of the hydronium molarity, or pH value, which then is 7 at neutrality, 1.0 for 1 M acid and 14.0 for 1 M hydroxide. Seawater is buffered at pH values ranging in surface waters from 7.9 to 8.4 (the near-surface ocean average is ~8.1) by a combination of its carbonate and borate components, with the carbonate contributing about 95% of the buffering effect. The chemistry of the system is complex, primarily because it involves the multiple dissociations of the carbonic acid (H_2CO_3) that forms when carbon dioxide (CO_2) dissolves in water. A very large part of the total carbonate load is as bicarbonate (HCO_3^-), which can both dissociate further – acting as an acid, or take up a proton – i.e acting as a base, hence the strong buffering action. The entire system is under stress from increasing dissolution of carbon dioxide from fossil-fuel burning and other human activities, a topic to be considered later. However, the most important concern arises from the fact that the dissociation of more carbonic acid both reduces the stability of shells and coral skeletons and increases their formation costs. Organisms have some capability for internal pH management, but, as acidity increases, the energetic costs of regulation increase. The acid–base relations of seawater have been extensively and carefully studied, and therefore we will leave their description to the ocean chemists. A point to keep in mind is that the pH scale, so commonly used, is logarithmic to base 10. Thus, a change from pH 8.1 down to7.8, which may come about, would represent a factor of two increase in hydronium-ion molarity – a very large shift indeed.

Pelagic autotrophs are small

In sharp contrast to the land, large complex plants are usually absent. Sargassum weed (*Sargassum* spp.) suspended from gas bladders in the subtropical gyre of the North Atlantic is a special and localized exception. However, it provides a model that it is a little surprising not to find everywhere; examples exist of large, floating plants, but they just are not typical. Instead, almost all of the photosynthetic organisms in the water itself, that is in *pelagic* habitats, as opposed to attached to the bottom, are small, unicellular algae known as *phytoplankton*. The word "plankton" comes from Greek (πλαγκτος) and implies a necessity to drift with the currents. Clytemnestra, in Aeschylus's *Agamemnon*, used it in denying that her thoughts were wandering (*planktos*). A classical scholar suggested the word to Victor Hensen, a founder of planktology, to describe relatively passive swimmers. Phytoplankton range in cell diameter from about 1 μm to about 70 μm, with a few representatives up to 1 mm. It is important to form a mental sense of this size range. Typical bacteria are 1 μm diameter; red blood-cells are 7 μm; an object of 50 μm is just visible to the naked eye if contrast is high. Most algal cells in the sea are at the lower end of this range. Definitions for the "size jargon" of biological oceanography are in found in Box 1.1.

Why are pelagic autotrophs so small? Biological oceanographic dogma, which will not be contradicted here, says they are small in order to provide a large surface area relative to their biomass in order to absorb nutrients like nitrate, phosphate, and iron from extremely dilute solution. Soil water in land habitats provides somewhat higher levels of nutrients (Table 1.2). The modest difference is augmented in the soil-water case, however, by rapid resupply from the closely adjacent mineral phase; nutrients do not become so thoroughly depleted in soil water. Thus, rootlets and root hairs over a small fraction of a plant's surface can supply nutrients for growth and maintenance of very large structures. In the sea, the rate of supply is limited by diffusion from dilute solution to the absorbing cell surface, so surface area must be maximized relative to cell volume. This is achieved by being small. For example, diatoms are an abundant group among the phytoplankton. Many of them are cylindrical, and if we fix the length/diameter ratio at 1, then the surface-area to volume ratio varies as 6/length, increasing strongly as size gets smaller. The surface area of a 30 μm diatom of this shape is 4241 μm^2, while that of a 15 μm one is a quarter of that, 1060 μm^2. However, the smaller one has twice the *surface area per unit volume*. Surface-to-volume (*S/V*) ratios of spheres vary similarly as 6/diameter. The effect of size on *S/V* is stronger for more elongate shapes (you can prove that to yourself by doing the calculations).

Box 1.1 Plankton sizes

Several sets of prefixes have been proposed to distinguish size classes of plankton. We seem to have settled on those proposed by Sieburth *et al*. (1978).

CHARACTERISTIC LENGTH	TERM (EXAMPLES)
<0.2 μm	Femtoplankton (viruses)
0.2–2 μm	Picoplankton (bacteria, very small eukaryotes)
2–20 μm	Nanoplankton (diatoms, dinoflagellates, protozoa)
20–200 μm	Microplankton (diatoms, dinoflagellates, protozoa, copepod nauplii, etc.)
0.2–20 mm	Mesoplankton (mostly zooplankton)
2–20 cm	Macroplankton

It is not surface *per se* that matters, since phytoplankton cells only cover a small fraction of their surface with transport enzymes to move nutrients from outside to inside. The importance of small size is to provide a large *relative* surface toward which diffusion can move nutrients; it is the rate of diffusion that is limiting at low concentrations. At the size scale of phytoplankton, the boundary layers (see below) next to cell surfaces in contact with the water are large relative to the cells, inhibiting fluid exchange next to the boundary. Turbulent shear is mostly at larger scales than the size of cells. Specifically, there is shearing mostly at dimensions larger than the Kolmogorov length scale, typically multiple centimeters at ocean rates of turbulent energy dissipation. Below such dimensions, viscosity dominates, and the impact of turbulence is small (Lazier & Mann 1989). Thus, effectively, the water next to a cell exchanges only slowly, and, although sinking and turbulence can increase nutrient availability at a distance from a cell,

Table 1.2 Relatively low values of major nutrient concentration in surface waters compared to natural (as opposed to fertilized) soil-water values. Units are micromoles liter^{-1} (μM).

UPPER-OCEAN CONCENTRATIONS IN WINTER	NO$_3^-$	PO$_4^{3-}$
North Atlantic subarctic	6	0.3
North Pacific subarctic	16–20	1.1
Natural soil water	5–100*	5–30**

*Soil and agricultural chemists use strange units like kg NO$_3^-$ hectare^{-1} to 20 cm soil depth. They rarely attempt to extract soil water *per se*, which is difficult because soil is relatively dry and much of the water is associated with organic matter.

**Also hard to characterize. This range came from a soil-science text, but do not put much faith in it (units were 0.05 to 3.0 ppm, a usual unit in that field). Most published data are measured in μg PO$_4^{3-}$ (g soil)$^{-1}$.

supply is effectively limited to molecular diffusion. The diffusive flux of a dissolved solute, such as nitrate, toward an absorbing surface of area A is given by Fick's Law, which Fick derived (Cussler 1984) by analogy to Fourier's Law for heat conduction:

$$\text{flux (amount arriving/time)} = -AD\ \delta C/\delta x,$$

where D is the substance-specific diffusion coefficient and $\delta C/\delta x$ is the gradient of concentration (amount/volume) away (hence the minus sign) from the surface. As stated, diffusion is slow enough that only a small fraction of the cell surface needs to be occupied by transport enzymes to acquire the specific molecules that the cell must absorb. Estimates by Berg and Purcell (1977), based on rates of diffusion and handling time per molecule, can be interpreted to imply that only a few percent of the cell surface needs to be devoted to transport enzymes for any required solute. More would not be useful, due to limitation of diffusive supply to the surface. In a sense, this is life-enabling, since *many* different solutes require a membrane transporter or at least a passage channel. Experimental data (Fig. 1.1) from Sunda and Huntsman (1997) show that, at growth-limiting concentrations of ferric iron, phytoplankton cells of all sizes have equal (the diffusion-limited maximum) rates of iron uptake per unit area. Because the iron requirement is general, and only met by the Fe^{3+} ion, sufficient areal density of transporters evolves in most (all?) species, such that uptake is, in fact, diffusion-limited, not transporter-limited. Smaller cells with less mass relative to surface area, however, receive enough iron to sustain growth when large cells are iron-limited. In addition, small, oceanic phytoplankton have evolved to require less iron per unit mass by substantial rearrangements of both photosynthetic and oxidative metabolism.

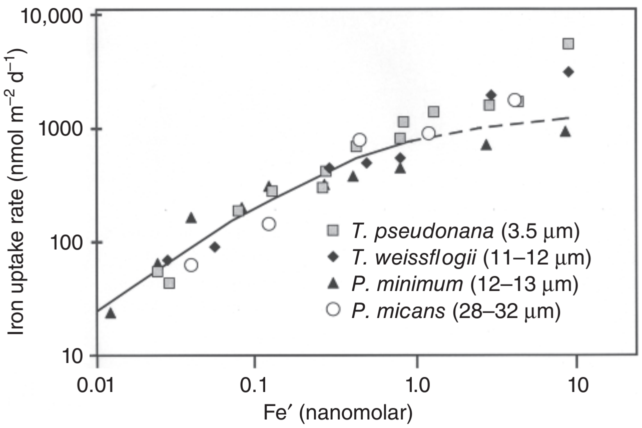

Fig. 1.1 Cellular uptake rate (per m^2 of cell surface area) of ferric iron from a culture medium (on a logarithmic scale) by phytoplankton cells of different mean diameters as listed, two species of *Thalassiosira* (diatoms) and two of *Prorocentrum* (dinoflagellates). Uptake was determined with radioactive iron as a tracer. Fe′ is a total of dissolved Fe(3+) species. Above [Fe(3+)] ≈ 0.75 nM at 20°C, ferric hydroxide precipitates, dashed curve, maintaining Fe′ at ≈0.75 nM. In the experiments, Fe′ was set by means of an iron chelating agent (After Sunda & Huntsman 1997).

Because phytoplankton are small, they are also individually ephemeral compared to terrestrial plants or to algae attached along the shore. Grazing terrestrial animals typically take a bite from a plant, which then heals; pelagic grazers typically ingest the entire phytoplankton cell, so it is gone. Therefore, maintenance of a population of cells, a *phytoplankton stock*, depends upon their rapid reproduction. And reproduction can be rapid. Many (not all) phytoplankton can double in number one or more times per day. Thus, if grazers are few and growth conditions (light, nutrients, temperature) are good, then stocks can grow exponentially. Doubling once per day, they can increase 1000-fold in 10 days. Rapidly growing diatoms can increase twice that fast. This potentially rapid increase is the basis for phytoplankton population outbursts or "blooms", and also for harmful algal blooms. However, blooms generally do not develop at the rate that phytoplankton cells divide. There is always substantial grazing, and stock increase is generally limited to modest daily percentages. Blooms most commonly occur (where they occur) in the spring, and spring phytoplankton blooms have been and remain a central interest in biological oceanography. We will consider them in some detail (see Chapter 11), including explanations for those wide oceanic stretches where they generally do not occur.

Water is heavy and, for small particles, sticky

Water, fresh or salt, has mass, and the principal unit of mass, the gram (g) was chosen to approximate unity for a convenient volume of water, the cubic centimeter (cm^3). Thus, the density of water at 1 atmosphere pressure and 0°C is $1.0\,g\,cm^{-3}$. Redefinitions of units of measure have caused tiny deviations that for most purposes can be ignored. Like all substances, water expands and contracts with temperature changes, expands both above and below 4°C. Seawater, because of the changed intermolecular attractions due to the electrostatic forces from its constituent ions, does not have a similar temperature of minimum density. It contracts down to its freezing point, which is well below 0°C because of so-called colligative effects. Thus, the density of warm seawater is less than that of cold, over the global ocean temperature range from ~–2°C in the Antarctic to ~40°C. Moreover the density varies with the salinity. Finally, water is not incompressible (contrary to a commonly taught myth); at deep ocean pressures it contracts substantially.

Oceanographers use Greek symbols for different aspects of density, particularly σ_t for a measure of seawater's density if it is brought to the surface without heat exchange or salinity change, just decompression: $\sigma_t = 1000(\rho - 1)$, in which ρ is the actual density, usually a number like 1.02437 for which $\sigma_t = 24.37$. Thus, σ_t (sigma-t) is just shorthand for the modest but critically important variations of density due to salinity and temperature (not depth). A further refinement is often used, σ_θ (sigma-theta), accounting for adiabatic cooling from expansion (expanded, it will have the "potential temperature").

For rough calculations, the changes of density with temperature, T, and salinity, S, are:

$$\Delta\sigma_t \approx 0.20°\mathrm{C}$$

(less useful than the approximate S effect because quite non-linear with T)

$$\Delta\sigma_t \approx 0.77 \text{ unit } S^{-1}$$

Actual density (ρ not σ_t) changes with depth (almost consistently symbolized as z), about

$$\Delta\rho = 0.0000044\,\mathrm{g\,cm^{-3}}/\text{atmosphere pressure,}$$

and (again, for approximations) P increases 1 atmosphere for each 10 m of depth. Thus, at the bottom in the Marianas Trench, the density is ~1.069 g cm^{-3} (1069 kg m^{-3}). Just being in a stack adds to the stability of the ocean water column. It turns out that compression also affects the shape of organic molecules in deep-sea organisms, including bacteria, deep-diving seals, and whales. Enzymatic modulation of organic reaction rates depends upon very weak forces among atoms at the active sites of enzymes: hydrogen bonds and van der Waals' forces. Small distortions of an enzyme's shape can change the effectiveness of the bonding or bond release. Such effects become important at depth differentials around 1000 m (100 atmospheres). Thus, biochemistry and sometimes viability are affected by transfers of deep-sea fish, squid, shrimp, etc. to shipboard for experimentation. The biochemical reactions of deep-sea benthic bacteria must be studied in pressure chambers. On the whole, decompression does not tear enzymes apart, and they function again when placed back under pressure.

For precise calculation of density from conductivity (C, a measure of S), temperature (T) and pressure (D, because depth is proportional to pressure, hence "CTD") data, it is necessary to use empirical polynomial functions with extraordinary numbers of terms. For a current version, see Feistel's (2005) equation with 101 constants (many relating to sound speed, enthalpy, and other values of occasional interest) approximated to 15 decimal places.

Much of the significance of all this T–S–z detail is that the ocean is a vertical stack in which density increases downward, and the stacking is remarkably stable. Moreover, the stacking has major ecological consequences. Organization of the stack is created partly by sinking of cold, salty water near the poles: in the North Atlantic where the salty inflow of the Gulf Stream is refrigerated by frigid Arctic air, then sinks, whereas, in the Antarctic, exclusion of salt from forming sea ice into the water below adds to the density of extremely cold surface layers that also sink. These deep waters spread through the world ocean, making the deep waters cold everywhere. At the same time, the surface is heated by sunlight from above, decreasing the surface density, increasing the stability. Over the full range of depth, typically 4 km and in places 8 km or more, the compression of the water by pressure enhances the stability of the stacking. In order to open volume at depth for the sinking cold, salty water, the ocean everywhere is slowly being vertically mixed. This is most active in the upper layers driven by wind, tides, and internal waves, but must proceed at all depths. The deep limb of the circuit is (in large part) from the Norwegian and Irminger Seas to the vicinity of Drake Passage, then east across the South Atlantic and Indian Oceans and finally filling the deep Pacific. That full passage takes several thousand years. It is termed the "thermohaline circulation". Balancing the budget of sinking volume with that of upward mixing is not a simple set of measurements and is not yet accomplished. So-called internal tides provide only about half the necessary mixing energy. There has been recent interest in the possibility that stirring derived from the swimming motion of larger animals, from krill schools to whales, might provide nearly as much energy (Dewar *et al*. 2006; Visser 2007; Katija & Dabiri 2009).

Stable vertical stacking of the ocean "water column" (an essential bit of oceanographic jargon) is most significant ecologically because of the limits it sets on upward mixing of inorganic nutrients like nitrate, phosphate, and trace metals into the lighted surface layers where photosynthesis can support phytoplankton growth. The stability of stacking, the depths of the prominent pycnoclines (levels of strongest density change and, thus, most stable stratification), and the forces available to drive upward flow (upwelling) and vertical mixing, vary strongly over the world ocean, affecting the photosynthetic production potential of distinctive regions. This is a theme we shall return to repeatedly, a fundamental aspect of biological oceanography. Here, we give just one example of the density stacking and its variation with season. In discussing the variation of ocean biomes, we will consider the ecological consequences of different stacking patterns and mixing regimes. In the Atlantic north of the Gulf Stream, winter winds often mix the upper water column to below 300 m, making the profiles (Fig. 1.2; see also Fig. 11.23) of T, S, nutrients, and oxygen vertical to that depth. That is, those habitat conditions are homogeneous up and down. There is residual stratification below that depth, stratification that

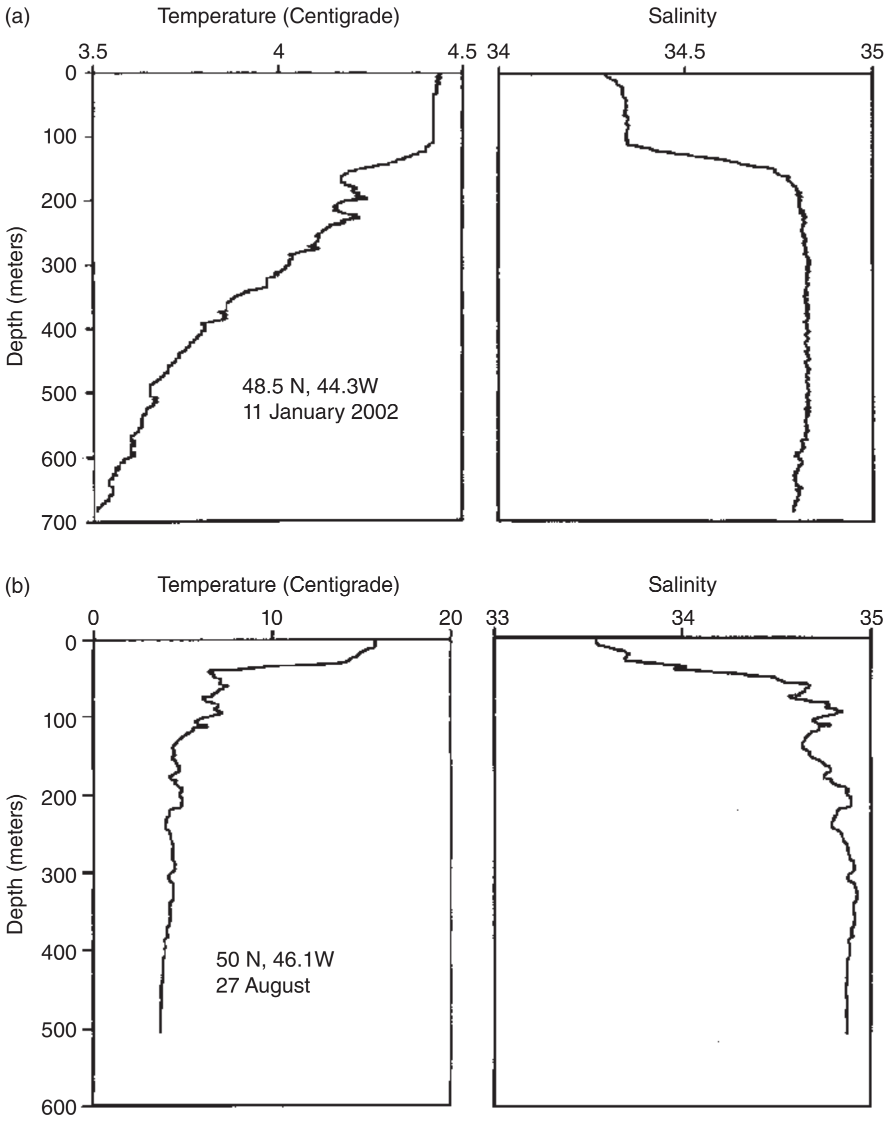

Fig. 1.2 (a) Winter and (b) summer profiles of temperature (*T*) and salinity (*S*) in the subarctic Atlantic Ocean south of Greenland. Note the differences between winter and summer scales. Summer is much more stratified than winter for both density-determining variables. Later mixing in winter from continued surface cooling and storms can homogenize the water column much deeper, to >300 m (see also Fig. 11.6). (Data from NOAA's World Ocean Database, WOD09: http://www.nodc.noaa.gov/OC5/WOD09/pr_wod09.html.)

the mixing does not overcome. Note that during mixing there is net temperature gain in the deeper reaches, net cooling above. Winds and mixing slow in the spring, and at some point solar heating warms and stabilizes an upper layer. This is set up and broken down several times by the spring alternation of calms and storms. By mid-summer there is strong stratification, primarily maintained by the elevated surface temperature above a gradient at variable depths around 35–45 m termed a seasonal thermocline. Blooms tend to occur after stratification is established at some level shallow enough to keep phytoplankton in the sunlit upper zone most of the time.

Atmospheric gases also dissolve in seawater

Nitrogen, oxygen, argon, and carbon dioxide all dissolve in seawater, and all of them obey Henry's Law: the equilibrium solubility is proportional to the partial pressure (in suitable units such as atmospheres) in the air above the water surface. The proportionality constant changes inversely with temperature, and for oxygen is approximately two-fold greater at −1°C than at 40°C. That is, saturation concentration *decreases* not quite linearly with rising temperature from 360 μmol kg^{-1} at −1°C down to

165 μmol kg^{-1} at 40°C. Salinity reduces the saturation concentration; for example, at 0°C and salinity = 34, saturation is 351 μmol kg^{-1} vs. 457 μmol kg^{-1} in fresh water (the salt effect is slightly less strong at higher temperature). Units used in quantifying oxygen concentration most often now are μmol kg^{-1} seawater; in an era not very long back they were ml $O_{2,\ \mathrm{STP}}$ liter^{-1}, referring to the gas volume at "standard temperature and pressure" of 0°C and 1 atmosphere. Both units (and also mass units, parts/million, partial pressures, . . .) appear in useful literature. Oxygen concentration can be measured with good precision and to low values by the Winkler titration, a series of redox reactions that are relatively simple to carry through to a sharp endpoint. It can also be measured with Clark electrodes and recently with optodes, in which luminescence from molecules embedded in an oxygen-permeable plastic is variably quenched depending upon adjacent oxygen concentration, and is measured by a light meter. Optodes have fairly long response times (many seconds), depending upon the permeability of the plastic, but the non-linear calibrations are stable over long periods and can cover the seawater concentration range.

If oxygen-depleted water is brought into the surface mixing layer and churns against the interface with the atmosphere, its oxygen content will rise toward saturation. However, the equilibration occurs relatively slowly, mostly because the mixing layer can be thick, but also because the oxygen itself has no particularly great "drive" around reaching saturation. The subjects of gas exchange coefficients and "piston velocities" are left to texts on chemical oceanography (e.g. Pilson 1998). Despite the slow oxygen-exchange rate, most deep water is "formed" at high latitudes where the water is very cold. Thus, the initial charge of oxygen for much of the subsurface ocean is close to the coldest possible saturation level.

Once oxygen is in solution, consumption by respiration of everything from bacteria to tiger sharks begins. Not all life depends upon oxygen (there are anaerobic microbes), but larger organisms with high activity levels and high metabolic rates depend upon oxidative respiration, a function primarily carried out in eukaryotic organisms by mitochondria – cell organelles specialized for this function. Down in the stratified layers well below vertical mixing from the surface, oxygen used is only replaced by the horizontal flow of water that left the surface some distance, often a very great distance, away. Thus, as organic matter sinks into these layers and is eaten and respired, the oxygen levels decrease. Additional decrease comes from animals that move between feeding near the surface and resting or hiding at depth, where those fish, squid, and plankton continue to use oxygen. Depletion generates oxygen-minimum zones in intermediate levels of the water column, particularly in the Arabian Sea and Pacific and most reduced from saturation in the Pacific toward the north (Plate 1.1).

There are also some nearly or completely anoxic layers beneath upwelling areas, particularly parts of the Peru Current and the Arabian Gulf. In the latter sites, dissolved oxygen as O_2 can be completely exhausted. Microbes in the anoxic layers continue to respire, at least to a point, using the oxygen atoms in nitrate and sulfate ions. The later activity releases sulfide, S^-, which is toxic to other life-forms and readily detected by odor in water collections. The limits of toleration for hypoxia among aerobic animals are variable among animal groups, species, and individuals. Mortality rates rise in bivalve mollusks and brittle stars at $[O_2] \sim 1$ ml liter^{-1} (45 μmol kg^{-1}) with sharply greater mortality (often after emergence from the sediment) at <0.5 ml liter^{-1} (Diaz & Rosenberg 1995). Similarly low oxygen levels cause death or emigration in many other groups. Some pelagic animals that feed near the sea surface can migrate into very hypoxic, even anoxic, zones in order to rest and hide. An example is the Humboldt squid (or jumbo squid, *Dosidicus gigas*) of the eastern tropical Pacific and, lately, the California Current. It is equipped with very finely divided filaments in a very large gill for uptake of dilute oxygen. *Dosidicus* also has extreme capability for prolonged survival by anoxic metabolism, generating an "oxygen debt" that suitably adapted physiology (and the high exchange capability of the gills) relieves very quickly on return to the surface. In addition, the squids and midwater fishes that do spend time in such layers move very, very slowly. Movies of predator-attack and prey-escape events look like animal tai-chi exercises.

In recent decades, hypoxic and anoxic zones have appeared in many coastal areas, particularly offshore of major rivers like the Mississippi, Rhine, and Chang Jiang. This has been attributed to eutrophication near shore by agricultural nutrients washing into the coastal zone, greatly increasing algal production and subsequent oxygen-consuming decay above the seabed. Such coastal anoxia kills fish and benthos. Kills of continental shelf fauna by hypoxia have also been observed in recent times in areas where no obvious anthropogenic eutrophication has occurred. Off coastal Oregon, USA, recurring hypoxic episodes during the 2000s, some involving die-offs of fish and benthos, have been attributed to greater onshore transport of oxygen-depleted water from oceanic oxygen-minimum zones. Because more organic matter has been oxidized in such waters, they also contain more nutrients, which may have enhanced production of organic matter that then increases oxygen demand and depletion. In the Oregon case, a change in cycling between upwelling and relaxation events may have reduced the flushing of bottom layers with oxygenated water. Ocean ecology can be complex, and explanations of events can be both fuzzy and uncertain. Processes occurring on just one stretch of coast, or in just one fjord, may be more important there than the interactions that typically determine conditions and ecological relationships.

The types and importance of fluid drag

The mass density of seawater (any water) has other ecological effects, particularly the requirement for force to accelerate it aside during swimming. This force requirement produces what is known as *inertial drag*. It is the dominant resistance to sinking through water by large, dense objects and to swimming forward by larger, faster animals. There is another source of drag, which is the requirement for force to rearrange the intermolecular connections among water molecules in order to move through them. That is called *viscous drag*. The relative importance of inertial and viscous drag is expressed as a ratio, the Reynolds number, Re, which has the product of factors proportional to inertial drag in the numerator and the water viscosity in the denominator. Inertial drag is proportional to the linear size (l) of the moving body, often best chosen as the longest dimension perpendicular to the path, to the velocity (v) relative to the water, and to the water density (ρ): $lv\rho$. The viscosity (as discussed here, the *dynamic viscosity*) is the molecular resistance to shearing forces, symbolized μ (or often η), with SI units of Pascal·s (Pa·s) = Newton·s m^{-2}. Work with the units here. After some conversions, it will become apparent that those of the Reynold's number numerator (m, m s^{-1} and kg m^{-3}) and denominator cancel. Re is a dimensionless number.

Experimental work (also some theory) shows that at high Re, >~100, viscosity can be neglected in drag calculations, at least for processes like swimming, because inertial effects are so dominant. At Re less than ~1, inertial effects are small and viscous effects dominate. Algal cells, other protists, and many smaller metazoans like clam larvae or copepod nauplii, live in an apparently very viscous world, because both their l and v values are small. This has important effects on the mechanics of swimming and of approaching nearby food particles. The viscosity of water (and seawater, the effect of salt is small) varies not quite linearly with temperature, from ~0.65 mPa·s (milliPascal·s) at 40°C to ~1.8 mPa·s at 0°C. This difference approximately triples the work that ciliated or flagellated protists must do to move at 0°C compared to 40°C.

So, how does swimming work? When drag is principally inertial, so is the force exertion of an animal against water. A fin or tail sweeps through the water at an angle to the intended trajectory, and pushes a mass of water backward. There is an equal reaction on the mass of the fish or seal moving it forward. There are often elegant details. For example, a tuna that can swim at ~20 m s^{-1} has an ideal fusiform shape, minimizing the distance that water must be accelerated to the side and then back to the center line behind as it passes through the water. It has scales along its tail peduncle that lie flat during initial acceleration, and then extend out to initiate turbulence at intermediate speeds. That is useful because drag actually drops substantially at the transition from smooth laminar flow along the skin surface to turbulent churning. To avoid drag from laterally extended pectoral and dorsal fins, tunas can pull them flat against the body into precisely fitted grooves.

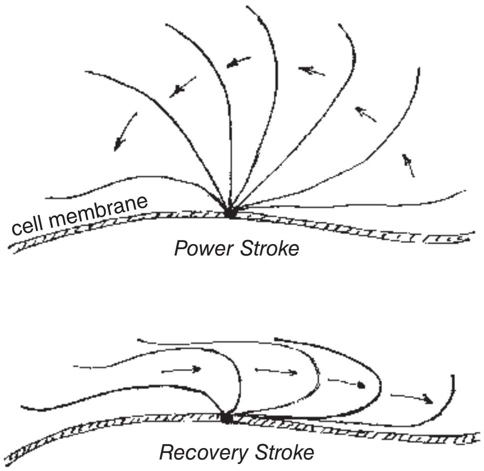

Fig. 1.3 Successive positions in the power and recovery strokes of a cilium.

Swimming by ciliated and flagellated cells is substantially different (Purcell 1977). Mass moved behind by a flagellum stroke is so small that the forward reaction is ineffective. But motion is achieved from the differential in the amount of intermolecular attractions that must be spatially rearranged between sliding a tube (a flagellum, say) lengthwise versus sideways through water. For reasons that may or may not be intuitively obvious (depending upon your brain wiring), the difference is ~1.7-fold. So, a cilium can be pushed backward perpendicular to the direction of motion, and then pulled back forward with most of the motion parallel to the trajectory (Fig. 1.3).

In the return stroke, the cilium's flexibility completes the motion as a rolling curl along the length. The viscous drag differential shoves the cell ahead. An alternate mode of exploiting the difference between along-shaft and across-shaft drag is use of flagellae wound into spirals. When rotated relative to the cell, often by molecular-scale rotary "motors", the vector component of the motion that is perpendicular to the axis of the spiral is sufficient to drive the cell steadily forward. There are many features of swimming (or filter feeding for that matter) in the viscous mode that are unexpected based on our experiences of swimming. When dominant, viscous drag is sufficiently powerful that there are no eddies shed aft or to the side. There is no inertial "carry" comparable to the long forward drift you experience after a swimming stroke. Rather, when force is not being exerted, there is remarkably close to zero continued forward motion; the stop is effectively instantaneous.

These two modes of swimming appear to be similar in some respects. Both ciliary motion and propulsion by lateral fins involve pushing back with a high drag element, then sliding it back forward by feathering or switching angles. The sources of the effective drag force, however, are substantially different. Some plankton, most particularly copepods, exploit the interface between drag dominated by inertia and drag dominated by viscosity. Because they are of intermediate size, with $l = 0.1$ to 1.0 cm, they can accelerate to sufficient v to enter the realm of inertial swimming (raising the Re), using paddle-like feet and tail-fan sweeps to accelerate to achieve extremely fast relative speeds (hundreds of body lengths s^{-1}). However, when power strokes are stopped, drag rapidly drops into the viscous range, with the advantage that at rest the sinking rate is very slow despite a moderate excess of density over the surrounding water. Little work is required to maintain a vertical location.

That brings us to sinking rates. A cannonball that missed its target (most of them did) would accelerate downward until inertial drag equaled the gravitational force attracting it, and then it proceeded to the bottom at that substantial terminal velocity (>100 $\mathrm{m\,min}^{-1}$). The effective mass would, of course, be reduced by buoyancy from the water, the differential density determining the "effective" mass. Thus, a sufficiently hollow, perhaps aluminum, cannonball might move up not down after splashing in. The size of the cannonball makes only a miniscule difference. Sinking of a tiny fecal pellet from a zooplankter, partly filled with dense opal from diatom shells, will be affected primarily by viscous drag, and for a spherical fecal pellet the sinking velocity, V_S, is given by Stokes's Law:

$$V_s = \frac{2}{9}\frac{(\rho_p - \rho_f)}{\mu} g R^2,$$

in which g is gravitational acceleration, ρ_p and ρ_f are the densities respectively of the pellet and the fluid, R is the pellet radius, and μ is the dynamic viscosity. A modest difference from this depends upon the shape of the pellet, but use of an equivalent diameter of a sphere of the same volume will give a decent approximation. Care with units is required (!), but left to your attention. Notice that the larger the particle, the faster it sinks, with V_S varying with the square of the linear dimensions. If ρ_p is less than ρ_f, then the particle will rise. Consider the impact, mentioned above, of temperature on μ: a particle of ρ_p will sink about three times faster at 40°C than at 0°C, despite the effect of T on ρ_f. Stokes's Law is a simplified (viscous drag only) version of the Navier–Stokes's equation, the version of Newton's acceleration law $F = ma$, to which hydrodynamicists have given lifetimes of thought and a googol (10^{100}) of computer calculations.

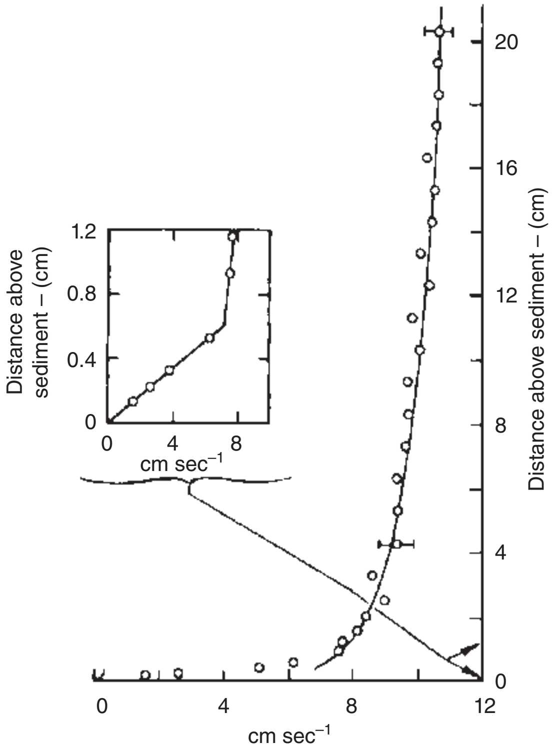

Fig. 1.4 A vertical profile of average velocity upward from a sandy-silt seabed at 199 m through the viscous boundary layer, in which velocity increases linearly with distance above bottom (inset), and then on upward (larger graph) through the "buffer layer". In the latter the velocity approaches that at a distance, ~10.5 $\mathrm{cm\,s}^{-1}$ here, within about 20 cm. Measurements were with a heated-thermistor velocity probe by Caldwell and Chriss (1979). Very mild turbulence (±0.5 $\mathrm{cm\,s}^{-1}$ at 20 cm, much less in the viscous layer; see Chriss & Caldwell 1984) has been averaged out.

Drag effects take on special characteristics at boundaries between water and solid surfaces, even soft ones like jellyfish skin or algal cell membranes. The fluid alongside, except in shear regimes strong enough to induce cavitation, remains stuck to the surface, so that exactly at the surface there is no relative motion. This is the "no-slip" condition. Velocity relative to the solid surface, the scales of a fish, say, increases away from the surface, reaching the full background relative velocity asymptotically at a considerable distance out. The zone of outward acceleration (Fig. 1.4) is called the fluid "boundary layer". As the figure shows, very close to a surface, up to about 1 cm but varying with the distant velocity, the local velocity increases linearly outward because viscous effects are dominant, and in this range viscosity damps turbulence in the flow. Away 0.5 to 1 cm, velocity increases more rapidly as inertial effects become more important, reaching an asymptote several dm out, or, in the case of the seabed, several dm up. Velocity in this range plots linearly vs. a logarithmic scale of distance from the surface. With distance from a surface, the potential for turbulence in the flow increases.

Boundary layers have many ecological effects that are well reviewed by Mann and Lazier (2006). They require that a swimming animal, particularly a small one, effectively must push along a mass somewhat larger than itself. It adds further dominance to the role of molecular diffusion for final transport of molecules to gills and cell surfaces. It means that small hairs side-by-side in a palisade, such as cilia on a ctenophore or setae on a euphausiid's (krill) leg, will have intersecting boundary layers and effectively form a solid paddle. Similarly, animals filter-feeding with setal or mucus meshes must generate substantial pressure to force water through their webs by narrowing the boundary layer of each strand. Boundary layers are less extensive at greater relative velocity. Because of boundary layers, drag tending to tip over benthic animals extending up into passing currents or to pull them out of the sediment is much reduced. As already stated, they mean that the supply of nutrients to algal cells depends upon molecular diffusivity, that is on the background concentrations, the potential cell-surface uptake rates and the solute-specific diffusivity constants. This list of boundary-layer effects is far from exhaustive.

For an extensive discussion of hydrodynamic effects on biological processes, refer to Steven Vogel's (1996) book *Life in Moving Fluids*.

Effects from having sun above, water below

Ocean water is held against the Earth by gravity, filling basins and with surfaces almost parallel to the so-called geoid, parallel apart from mild, long-range slopes created by the dynamics of flow on the curved and rotating form of the planet and, of course, except for surface waves. These sheets of water, thin relative to the Earth's diameter, are thus illuminated from above by sunlight and on some nights by moonlight. Light that is not reflected back into the atmosphere (and in part back into space) is progressively absorbed by the water and by both dissolved and particulate substances. Absorption increases with depth (z), following Beer's Law: $dE/dz = -kE$, for which the solution is $E_z = E_0e^{-kz}$. That is, irradiance, E, declines exponentially with depth. The constant, k, an extinction rate for the overall spectrum of sunlight, has a value of $0.067\,\text{m}^{-1}$ for just seawater, and actual values in oligotrophic subtropical gyres are remarkably close to that when chlorophyll concentrations are on the order of $0.05\,\mu\text{g liter}^{-1}$ or less. More pigment-containing phytoplankton or more suspended sediment increase k, shoaling the levels reached by specific levels of irradiance. However, k also varies with the wavelengths of light. The wavelength of maximum transmission in pure water and in clear oceanic waters is around 435 nm (blue). Other wavelengths are more rapidly stripped out, eventually leaving only blue, with the only color vision distinguishing shades of blue below about 100 m, and systems of photosynthetic and visual pigments must absorb near 435 nm. They do, mostly shifted toward the green at 465 nm (the extinction rate is almost constant from 410 to 475 nm). In neritic regions the inclusion of larger amounts of colored, dissolved organic substances (yellow transmitting, termed Gelbstoff or gilvin) and of phytoplankton (green transmitting) causes a shift in the wavelength of maximum transmissivity toward the green. Absorbance rapidly increases for longer wavelengths.

Actually all absorption of light by water has a minimum with respect to wavelength, a "window of clarity" (Yentsch 1980), right at the peak range of wavelengths of solar irradiance (Fig. 1.5) the wavelengths of visible and photosynthetically active light. This match of window and available light is one of the remarkable coincidences that make life on Earth possible. The coincidence of the solar spectrum to the window of water clarity allowed selective tuning of the light-absorbing pigments energizing photosynthesis by phytoplankton to the blue-dominated spectrum of light available at even moderate depths. The only light reaching depths below 100 m or so peaks very narrowly in the blue, so visual pigments of deep-sea fish and invertebrates (shrimp, squid) are adapted for generation of visual nerve impulses by absorption of those specific wavelengths.

The ocean layer that is sufficiently illuminated to support positive net photosynthesis, meaning more organic-matter generation than phytoplankton will respire themselves, is often considered to extend down to about the level receiving 1% of mid-day irradiance, and is termed the *euphotic zone*. It is not fully dark below that depth, and in clear tropical waters net photosynthesis may extend somewhat deeper, reaching to 120 m or so. In waters of a natural ecosystem, much additional absorbance comes from dispersed cells containing pigments, shoaling the euphotic zone depth. The effect of pigments is roughly proportional to chlorophyll concentration; chlorophyll will add about 0.02 (m^{-1}) to the absorbance coefficient in the blue (otherwise the absorbance minimum) for each $1\,\mu\text{g liter}^{-1}$. An extended treatment on the effects of pigments on the absorbance spectrum can be found in Morel (1991).

Most bioluminescence also has a narrow spectrum in the vicinity of 465 nm. In the deep sea, that makes possible matching by photophores on the undersides of fish, squid, and shrimp of downwelling irradiance to obliterate silhouettes that might be spotted by animals looking upward from below. In other applications, such as signaling between individuals, it would allow transmission of "messages" to the maximum possible distance. More will be said about the interaction of light with photosynthetic pigments as a function of depth when we discuss primary production. More will be said about deep vision and bioluminescence when we discuss mesopelagic habitats. The limits of water clarity (Fig. 1.5) are also important, both eliminating almost

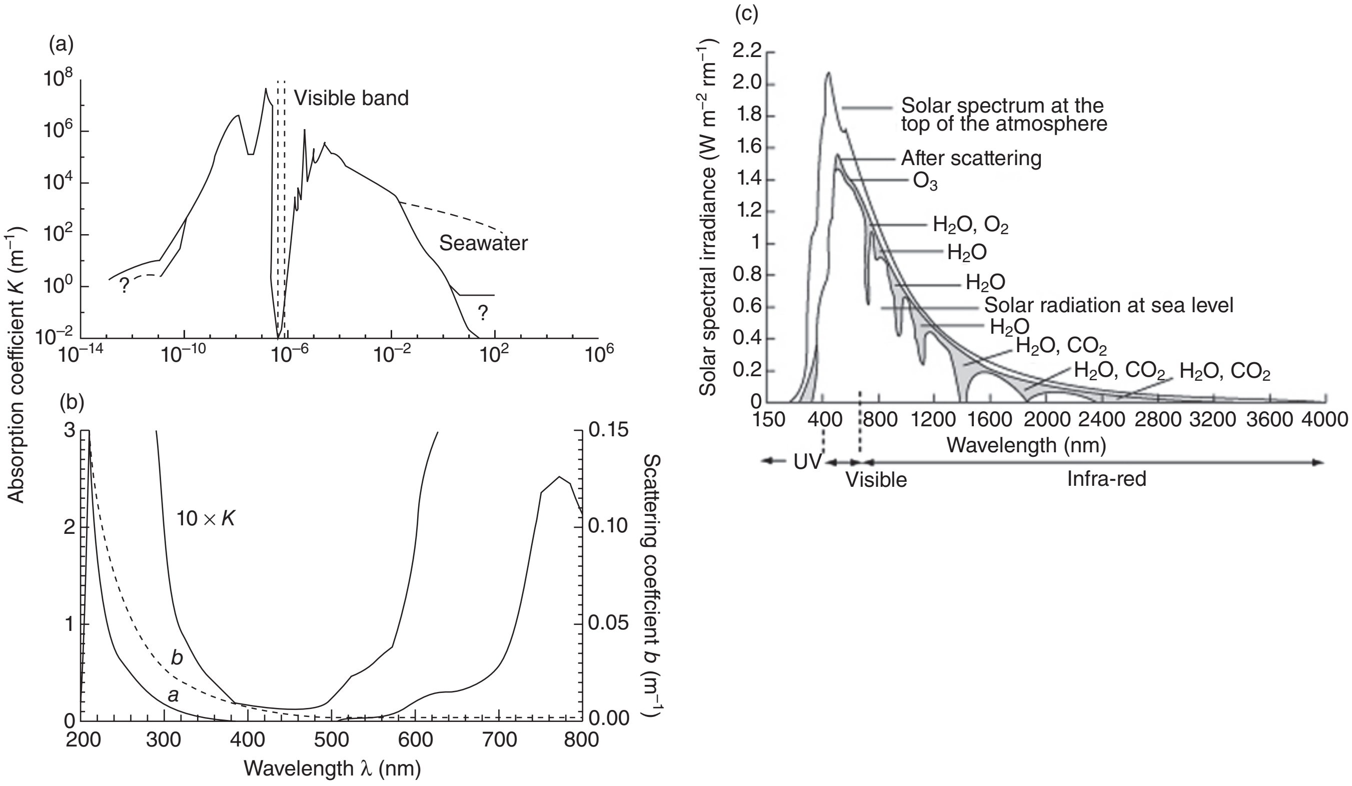

Fig. 1.5 (a) Light absorbance coefficients, *k*, of pure water (solid line) and seawater (dotted line) as a function of wavelength, showing a window of clarity around the visible band. (Data compiled from various sources.) (b) Detail of absorption (*k*) and scattering (*b*) spectra of seawater in the visible band plus near UV and near IR (data of Smith & Baker 1981). (c) Spectrum of radiative solar energy arriving at the surfaces of the atmosphere and ocean, with the differences labeled according to the principal absorbing gases in the atmosphere accounting for the difference. (Repeatedly published without attribution. Reproduced here from Falkowski & Raven 2007.)

all of the UV irradiance capable of damaging organic molecules (like DNA, for example) in the first few meters and reducing escape of warmth back to the atmosphere at infrared wavelengths.

Of course, the sun does not shine down from exactly the zenith on more than a very small part of the Earth at any time and there, in the tropics, only at local noon. The rest of the time, sunlight passes through the atmosphere to the surface at substantial angles that vary seasonally and through the day. Moreover, the familiar seasonal cycles of daylength, that are accompanied by changes in height of the sun above the horizon, change the depth of light penetration, duration of illumination for vision, the irradiance available in the day for photosynthesis, and the amount of surface layer heating. The lower the sun angle, the greater the area over which its light is spread, reducing the arriving photons per unit area. Many units are used in irradiance measurement. Those most commonly seen in oceanographic literature are watts m^{-2} (a measure of power, that is irradiance) moles of photons arriving at a one square meter surface per second (with energy or power depending upon wavelength). "Photosynthetically active radiation" (PAR), which will be discussed together with photosynthesis, is often determined in μmol photons s^{-1} m^{-2}. The equivalent unit μeinsteins s^{-1} m^{-2} is also in common use.

A key impact of this vertical arrangement, the sun heating the ocean from above, is the installation of relative buoyancy at the sea surface, adding stability to the stratification of the water column. Stable stratification limits vertical mixing by winds and tidal energy, and reduces the upward transfer of dissolved nutrients. Daily and seasonal variation in stratification and vertical exchange are key aspects of ecological processes in the sea.

Taking the individual or event-by-event viewpoint

A good deal of interest is expended in biological oceanography on bulk rates and quantities: the amount of photosynthesis occurring under a square meter of ocean surface, the biomass of zooplankton (mg m^{-3} or g m^{-2}) and its seasonal variations, the rate of downward "rain" of particulate organic matter into the deep sea, and more; the list is extensive. However, from the viewpoint of one predacious arrow worm (chaetognath), what matters are the potential for and rates of encounters with prey organisms (in their case mostly copepods) or with other chaetognaths of the same species that are also ready for mating. From the viewpoint (although it doesn't "look" *per se*) of a nitrogen-limited algal cell, the key to its growth potential is the likelihood that an ammonium or nitrate molecule will come adjacent to its cell membrane, that a ferric ion will diffuse near enough to bring it on board to act as a cofactor for nitrate reductase (to convert nitrate to ammonium). When the encounters needed for life processes are not occurring fast enough, there will be no photosynthesis, no food, no growth, no reproduction, no something, and ecosystem function will wind down. Looked at in this way, what matters are the event rates, and those depend in the first order upon the product of the concentrations of the two entities that must meet for an ecological interaction. Consider, for example, mating encounters by zooplankters. Copepods are the dominant small crustaceans in the sea, and they are dioecious (male and female functions in separate individuals). So, the probability of a mating encounter in an interval can be written

$$P_{\mathrm{m}} = \beta\ [\text{males}][\text{females}],$$

in which brackets indicate volume concentrations and β is termed an "encounter kernel". That terminology has been developed extensively, and with many examples, in a book by Thomas Kiørboe (2008). While he deals with plankton, as his title implies, the viewpoint can apply anywhere in marine (or any) ecology, including in the benthos.

A great deal of complexity can enter into establishing the value of β, by which we mean both establishing it in reality, for the organisms in the field, and in estimation of it by ecologists. We can think about, observe, and experiment upon the component factors affecting β, but in most cases we will not be able to measure every significant aspect of the encounter situation, especially not in the ocean where we inevitably remain rather clumsy observers. We are not even very good at measuring the effective concentrations. Of course, organisms from bacteria to whales are very good at raising their own concentrations at spots with high concentrations of the molecules, prey, or mates they need to encounter. Some of them are also very good at dispersing away from high concentrations of their predators, or only visiting those sites when the predators are somehow disabled, perhaps for example too dark for them to see. Suitable concentrating and avoidance behaviors are among the most obvious products of natural selection. Despite the difficulties, studying what matters to individual organisms in obtaining the encounters they require generates some of our best insights. As Kiørboe has shown, trying to find explicit functions to quantify β can be a fruitful mode of research. Among many variables, the relative motions of the encountering individuals (from molecules to whales) are often the most critical components of β. Signaling can also be important, as in the case of copepod mating when the female lays out tracks of attractant pheromones to alert males to a mating opportunity. Thus, in many cases β involves increasing apparent individual size, effectively a modification of volume concentration. The range of possibilities exploited in nature is wide. Sometimes attempts to apply this viewpoint will be explicit in the following chapters; just as often it will be an implicit alternative you can apply in thinking about what matters to life in the oceans.

General terminology for habitat partitions in the ocean

Habitats within the water column are termed *pelagic*, and seafloor habitats are termed *benthic*. Organisms living in pelagic zones are *plankton* (defined above) and *nekton* (from ηεκτος), large animals that swim well enough to move independently from displacements by horizontal currents. Successive pelagic layers downward are termed the *epipelagic*, *mesopelagic*, *bathypelagic* and *hadopelagic* zones. Respectively, they extend to about 200 m, to 1000 or 1200 m, to perhaps 4500 m and to the bottoms of the deepest trenches. The mesopelagic has enough light for useful vision, which strongly conditions life within it. Below that solar photons are uselessly rare and for some reason even bioluminescence is mostly removed from the adaptive repertoires of bathypelagic animals. Layers below the upper epipelagic, which is the euphotic zone, all depend upon downward transfer of food as sinking particles and vertically migrating animals.

Organisms living on the bottom are termed *benthos*. Benthic (the adjective) and benthos apparently are versions of the Greek "bathos" (βαθος), meaning depth. Benthic habitats share characteristics with both pelagic and terrestrial ones. They are (more-or-less) solid substrates, like the land, but they are continuously submerged in seawater. Thus, the basic physiological problems are the same as those for pelagic ocean life, but the two-dimensional aspect (at least relatively thin vertically) of a land habitat operates as well. Benthic habitats also grade downward in a series: *intertidal*, *subtidal* (shallow bottoms near shore), *bathyal* (continental slope depths), *abyssal* and *hadal* (trenches).

The solid Earth has two principal surfaces, the continental shields above sea level, and mostly at the level of steppe or lowland rainforest (~300 m elevation), and the abyssal

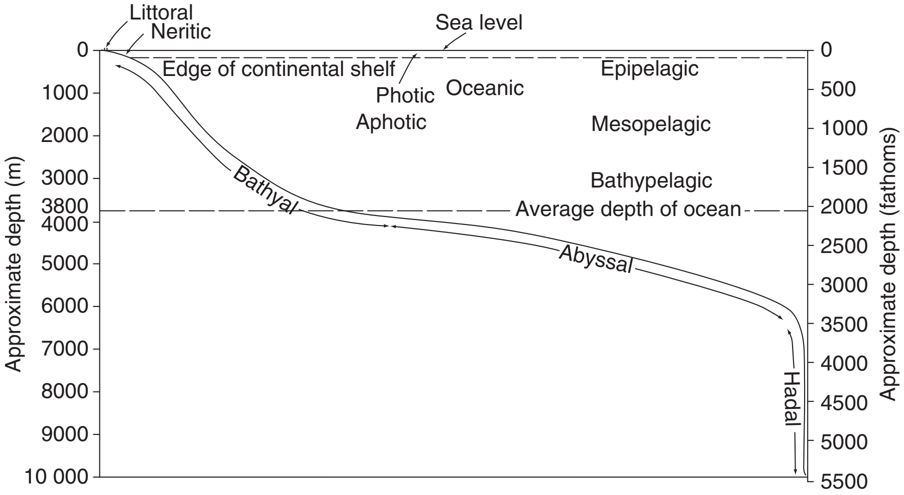

Fig. 1.6 Hypsographic curve for the world's oceans. Length along the abscissa is proportional to the area occupied by a given depth in the world's oceans. For example, depths in the abyssal category occupy about 60% of the seafloor (After Hedgpeth 1957).

plains at depths of about 4500 m. This deep-sea zone occupies about 60% of world ocean area (Fig. 1.6).

There are some rocky deep-sea sites, particularly at spreading centers, but most of the ocean is underlain by sediment-covered bottom 2000 to 5500 m below the surface productive layer. The extent to which both pelagic and benthic habitats have been studied with respect to the organisms living in them and their ecology declines rapidly as depth increases. While deep habitats are difficult to access and sample, they have been studied and much is known about them.

A few mathematical reminders

I The exponential function

This is, of course, basic mathematics, but, to refresh the concepts, we provide these notes. The exponential function appears repeatedly in biological oceanographic discourse. It appears repeatedly throughout science. It appears in analytical chemistry as Beer's Law, discussed above – the relationship between light absorption by a not quite fully transparent medium of transmission and the length of the absorbing column of medium. It appears in population dynamics, nuclear decay theory, everywhere.

Any function of the form $y = a^x$ can be termed exponential. We use the values of 10^x where x is an integer to give the place values in our usual number system:

X	10^x	2^x
0	1	1
1	10	2
2	100	4
3	1,000	8
4	10,000	16
5	100,000	32

However, when the term "exponential function" is invoked, the meaning frequently is the sequence of values for $y = e^x$, where "e" is the irrational number 2.71828. . . . This particular exponential function has the special property that the slope of the function (the change in y divided by the change in x, or dy/dx) at $x = 0$ is 1, *and* that the [slope of e^x] = $de^x/dx = e^x$ at all x. This function turns out to be (yes, lots of mathematics is hidden in that phrase) the exact relationship for any compound-interest problem when bank interest is compounded continually. The important thing isn't the compounding interval, but the interest rate (however much banks may try to convince you otherwise). Let's try an example. Let the interest rate, r, be 8% per year. If interest is compounded once per year, then the principal at T years $P_T = P_o(1 + r)^T$. If it is compounded n times per year, then it is $P_T = P_o(1 + r/n)^{nT}$. If it is compounded continuously, then the principal at T is $P_T = P_o e^{rT}$.

Let P_o be \$1000 (or yen, or rubles, or euros):

	Values after *T* years of compounding interest *N* times per year				
T	***N*=1**	**2**	**3**	**4**	**∞**
0	1,000	1,000	1,000	1,000	1,000
1	1,080	1,082	1,082	1,082.4	1,083.3
2	1,166	1,170	1,171	1,171.7	1,173.5
3	1,260	1,265	1,267	1,268.2	1,271.2
4	1,360	1,369	1,371	1,372.8	1,377.1

Even continuous compounding doesn't get you much. In fact, a change from 8% to 8.3%, i.e. a small change in the annual rate, is all it takes to cover all the possible effect of more frequent compounding. This continuous compounding is an excellent model for many processes such as the decline in concentration of phytoplankton when animals are filtering parts of the water and returning the water to the suspending volume.

Let us expand slightly on the mathematics for downward light extinction; the results are so important that immediate review is in order. The continuous-interest formula (or exponential function) turns out to be the solution (or integral) for an equation for the slope at any point of the curve of light intensity vs. depth. Such equations are differential equations, and their solutions when they have simple ones are always functions, such as the exponential. The absolute amount of change in the light between two depths depends upon: (i) the amount of light there is to be absorbed, E (principal); (ii) the fractional rate at which it is absorbed per meter, k (in this case a rate for negative interest); and (iii) the thickness of the absorbing layer, z ("time" at interest). We write:

$$\mathrm{d}E/\mathrm{d}z = -kE.$$

Differential equations of this sort are called "first order" (they involve first derivatives), "separable" differential equations (using this as an example, they can be rearranged to have dE and all functions of E on one side and dz and all functions of z on the other). They are "solved" by rearranging, then integrating:

$$ {}^{\mathrm{d}E}\!\!/_{\mathrm{d}z} = -kE \Rightarrow {}^{\mathrm{d}E}\!\!/_{E} = -k\mathrm{d}z \Rightarrow \int_{\text{surface}}^{z} \frac{\mathrm{d}E}{E} = -k\int_{0}^{z} \mathrm{d}z $$

The integral of dE/E is natural log E, ln E. The integral of dz is z. Thus, the integrals become:

$$ \int_{\text{surface}}^{z} \frac{\mathrm{d}E}{E} = -k\int_{0}^{z} \mathrm{d}z \Rightarrow \ln E\Big|_{0}^{z} = -kz\Big|_{0}^{z} $$

And, finally, taking differences and antilogarithms, the "solution" is $E_z = E_0 e^{-kz}$, in which E_z is the intensity remaining at depth z relative to the just-below-surface intensity of E_0.

Populations above a reasonably small size grow exponentially, statistically exactly so if reproduction isn't synchronized in some way. When it is, then the exponential pattern appears for counts at equal intervals measured in reproductive cycles. If we use N for population numbers, then we get $N_t = N_o e^{rt}$, and we talk of "r" as the rate of population increase (or decrease if its sign is negative). Both birth (b) and death (d) can occur as exponential functions, so we can write: $r = (b - d)$. If N(t) and b are known, then you can solve for d, or conversely.

Examples of the exponential function will continue to appear in this book. Please practice with it, using a calculator. Get a very clear understanding of its characteristics.

Problem 1: It is desired to get an idea of the growth rate of some phytoplankton cells. A few are inoculated into a jar of sterilized seawater enriched with various fertilizer compounds (nitrate, phosphate, etc.). At the end of two days there were 200 cells per ml. At the end of four days there were 800. What is the exponential rate of growth? What is the doubling time? What is the formula relating doubling time to the exponential rate of growth?

Problem 2: A "simple" extension of the exponential function is the logistic equation, often used to characterize the increase of a population up to the limiting carrying capacity of its habitat. The logistic represents that by reducing the natural rate of increase, r, according to the fraction of the carrying capacity remaining:

Unlimited exponential increase	Logistic model
$\mathrm{d}N/\mathrm{d}t = rN$	$\mathrm{d}N/\mathrm{d}t = r(1 - N/K)N$,

where K is the carrying capacity, and N/K is the fraction of the "resource space" used. Find the solution to this equation. Serious mathematics students will determine the integral. Hint: it's a straightforward, first-order, separable differential equation. Review integration by parts. Others should not be embarrassed to use an integral table.

II Limiting factors

The notion of limiting factors is often traced to a German agricultural chemist named Baron Justus von Liebig (1803–1873). He was one of the early organic chemists, and he worked on the elemental content of plants in order to design effective fertilizers (Moulton 1942). One of his famous experiments was growing a plant in a pot using a known weight of soil. By later separating the plant and soil, he was able to show that the plant was made up of something other than constituents of the soil – invoking a conservation law of a sort. He was able to show that the plant was derived from water and air. His own statement of the concept of a limiting factor is now termed "Liebig's Law of the Minimum":

> ". . . growth of a plant is dependent upon the amount of the food stuff which is presented to it in minimum quantity."

We would add the qualifying phrase, "in proportion to its need for it". Note the singularity of this limiting factor; plural, interacting factors are not mentioned. The importance of interaction among potential limiting factors remains an issue of debate in ecology.

There are many examples of limiting factors as they affect living things. The characterizing signature of an analysis of a limiting factor is a hyperbolic function. Classic examples are the rates at which fish grow on different levels of feeding. In general, food eaten and growth both follow such hyperbolic patterns as food becomes more readily available. Thus, food availability is said to be a factor limiting growth. At the asymptote, other factors, including the intrinsic capacity for growth, become limiting. Hyperbolic relationships play a large part in marine ecology, and we use several functional forms to represent them in our models. Popular ones include:

1 Two linear segments meeting above the point of maximum curvature;
2 the Michaelis–Menten curve (Fig. 1.7) from enzyme kinetics (also known as the Monod function); and
3 the Ivlev equation.

In some instances there is little to choose among these representations, since the scatter of the data is usually great. The choice is made on the basis of convenience to the application. We will develop the list above so you have a reference. Two linear segments can usually be fitted by eye. These will represent the two basic parameters of the relation: the asymptotic growth rate and the slope of the initial response to increase of the limiting factor.

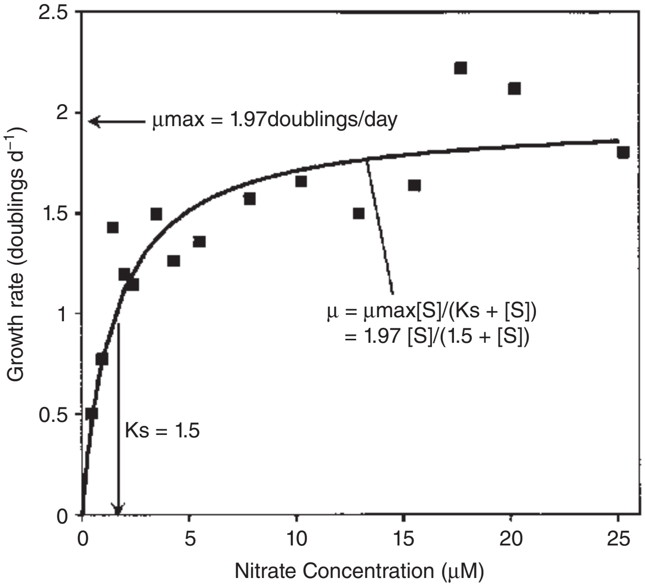

Fig. 1.7 Growth rate of the diatom *Asterionella japonica* as a function of available nitrate (squares), fitted by the hyperbolic Michaelis–Menten relationship. (Data and curve parameters from Eppley & Thomas 1969.)

The Michaelis–Menten equation is borrowed from biochemistry. Enzymes are often characterized in terms of their reaction kinetics. The data are measures of reaction velocity at various substrate concentrations. Reaction rate takes the form shown in Fig. 1.7.

Suppose there are a number of active sites on an enzyme to which a substrate can bind, and let the concentration of those sites be $[E]$. Binding is the slowest (limiting) step in conversion of substrate to product. The reaction is $E + S \leftrightarrow ES \rightarrow$ Product. The dissociation constant for the enzyme–substrate complex, ES, is $\mathrm{k_s} = ([E] - [ES])[S]/[ES]$. Solving for $[ES]$:

$$[ES] = [E][S]/(\mathrm{k_s} + [S])$$

Since ES will be transformed to product at a rate proportional to $[ES]$, we have

$$V = \text{Reaction Rate} = c[ES] = \mathrm{c}[E][S]/(k_s + [S]),$$

where c is a proportionality constant. The maximal rate, $V_{\max}$, will be attained when $[ES] = [E]$, that is when $V_{\max} = \mathrm{c}[E]$. Substituting, we have the Michaelis–Menten relation:

$$V = V_{\max}[S]/(k_s + [S])$$

The graph of V vs. $[S]$ is hyperbolic with asymptote $V_{\max}$. When $V/V_{\max} = 0.5$, then $[S] = k_s$. Therefore, k_s is called the "half-saturation constant". It can readily be determined, and it is often used as a simple measure of enzyme substrate affinity. It can be used to characterize the slope of the initial portion of an ecological relationship of hyperbolic form. Note that k_s is a "backwards" variable: high k_s values denote *low* affinity, or slow approach to saturation.

The Ivlev (1945) approach is to suppose that with a great plethora of food, animals will eat some amount R_{max}, the maximum ration, and no more. At lesser food abundance, they will eat fractionally less. The maximum ration is approached asymptotically. The resulting equation is:

$$\text{Ration} = R_{\max}(1 - e^{-\lambda\rho}),$$

where food density is ρ and λ is a constant, the Ivlev constant. To derive this, differentiate with respect to ρ, and then establish an argument for assumptions leading to the resulting differential equation. It is just as useful to simply examine the approach of Ration to R_{max} as ρ increases (the limit of $e^{-\Lambda\rho} \rightarrow 0$ as $\rho \rightarrow \infty$).

Other functions for hyperbolic relationships are in use, and some will appear later in the text, for example the hyperbolic tangent function recommended by Jassby and Platt (1976) to characterize the increase of photosynthetic rate toward an asymptote with increasing available irradiance. When hyperbolic ecological or physiological data are strongly variable, it may not matter which deterministic function is used to represent the central tendency of responses to some forcing variable. The best choice may depend upon mathematical convenience, say in a numerical model, not on precision of fit.

Threshold effects are frequent in ecological relationships. It is sometimes found, for example, that animals won't feed at all unless there is more than some minimum of available food. This minimum is a threshold. Threshold effects are readily added to either the Michaelis–Menten (here restated in terms of food) or Ivlev equations:

$$R = R_{\max}(\rho - \rho_t)/(D + \rho - \rho_t), \text{ and}$$
$$R = R_{\max}(1 - \exp[-\lambda(\rho - \rho_t)]\}.$$

In both, ρ_t is a threshold food abundance for feeding. Both of these equations must be applied only where $R \geq 0$; that is, where $\rho \geq \rho_t$ use the equation, otherwise $R = 0$. Failure to follow this restriction (as in computer code for ecosystem models) will induce "negative" ingestion, nutrient uptake, . . . , all of which have unrealistic stabilizing effects on modeled ecological interactions.

Limiting factors are usually thought of as material or energetic requirements that an organism must draw from the habitat. However, the response to varying levels of limiting factor availability may be modified by other factors like temperature, salinity, ultraviolet radiation, frequency of large rocks in the path and endlessly on. For animals, growth rate (for copepods as an example, see Vidal 1980) varies not only with resources and conditions, but with life stage and growth already completed (body size). Growth rate does vary with food availability in the expected hyperbolic fashion, but, at least for small ectotherms, the height of the asymptote drops with increasing temperature. At higher temperatures they have greater metabolic costs, leaving less nutriment to support growth. In sum, control of most processes depends upon many variables in the habitat.

Deterministic functions (and models) vs. real data

Recall that "functions" defined mathematically assign *one* value of an output variable for each set of input variables supplied to it. They are very rigid things, said to be *deterministic*. There are also "relations" that assign a set or range of values for given inputs, but those are much harder to use, and they have not become popular in biological oceanographic representations. Consider Figs. 1.8a and 1.8b from Richardson and Verheye (1998) and from Hurtt and Armstrong (1999). The first shows measures of copepod egg production at different temperatures and chlorophyll concentrations (a measure of available food). The variations are more prominent than the trends, with just hints that there are relationships. Richardson and Verheye did not fit a function to the data at various temperatures, although the greatest production rates mostly were in the middle of the observed range. Some workers would have added a distribution function. They did fit an Ivlev curve to the chlorophyll data, a single value of the response variable (egg output) for each value of the phytoplankton abundance measure. Its predictive value is small.

The second shows the output of a modestly elaborate pelagic ecosystem model intended to represent the seasonal cycling of phytoplankton stocks. That is really just a function which issues one value of the quantity of phytoplankton for each set of system variables provided to it, including previous stock abundance. We will examine several such models in some detail. Hurtt and Armstrong were satisfied with this result, which does pass through the central tendency of the actual data from the model. Sometimes the best we can do in biological oceanography is to find rough approximations.

A note on biological terminology

Biological vocabulary has been undergoing a transformation, some of it driven by results from molecular genetics that have revised the understanding of phylogenetic relationships and, thus, taxonomy. Higher taxonomic categories within all subsets of the eukaryotes have recently been subject to recurring revision, as data revealing their phylogenetic relationships continue to accumulate. Stable systematics remain well ahead in the future. Mostly we will

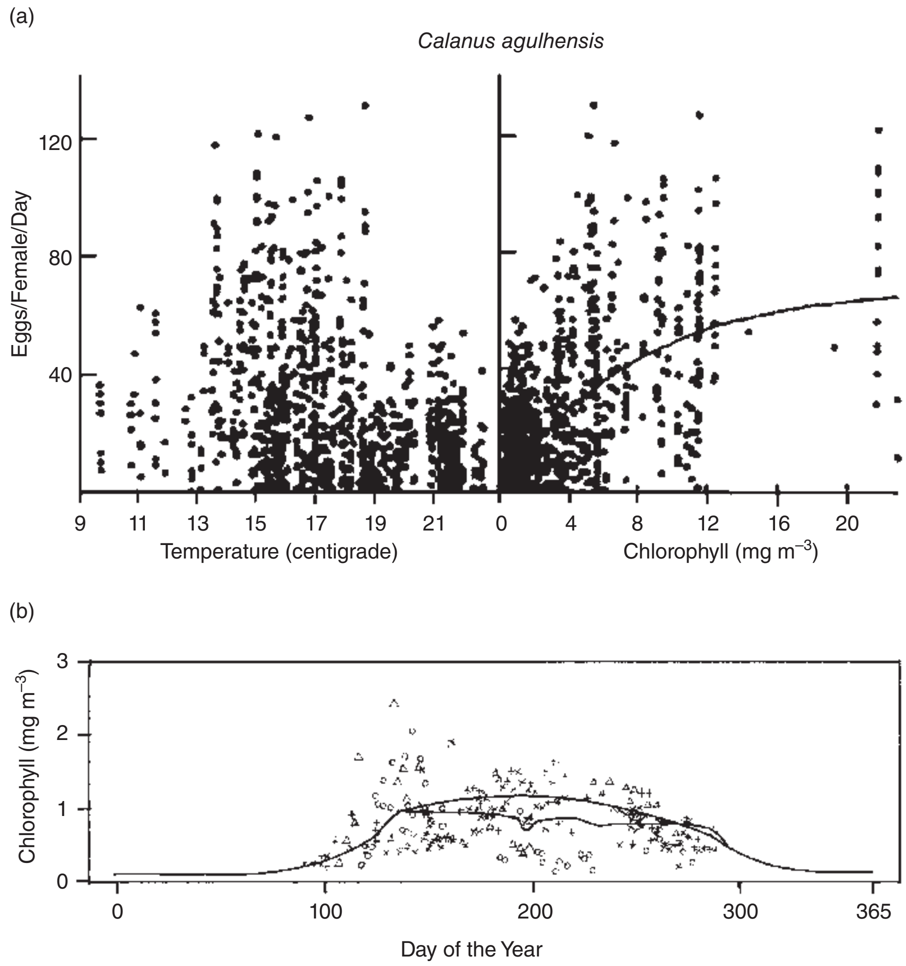

Fig. 1.8 Two examples of deterministic relationships fitted to marine ecological data affected by strong variation; the data were scattered by stochastic factors not considered by the deterministic models that are simplifying "best fits". (a) Egg production of *Calanus agulhensis* at different temperatures and chlorophyll concentrations in the Benguela coastal upwelling region. (After Richardson & Verheye 1998.) (b) Results from a pelagic ecosystem model similar to those described in Chapter 4. The two lines compare the chlorophyll concentration outputs from model versions generated by two modestly different fitting routines to actual chlorophyll concentration measures in several years (different symbols) at 59°N, 19°W in the Norwegian Sea compared with field time-series data (points) (After Hurtt & Armstrong 1999).

use quite classical category names that should remain recognizable, for example the usual names of zoological phyla. The vocabulary transformation has cast clouds of uncertainty around terms such as bacteria, protozoa, plant, and animal. We will only refer to multicellular, rooted, autotrophic organisms, not including large algae, as "plants". In common parlance, animals are heterotrophs, eating plants, fungi, and other animals. For protists making their living in that manner, we will sometimes use the word *protozoa*, meaning "simple animals", also "protozoan". We are aware that those are not considered taxonomic terms, but they are more direct than, say, "microheterotroph". Some protists function as both auto- and heterotrophs, that is as "mixotrophs". We will use that term when discussing their specific biology, but as they participate in community photosynthesis or heterotrophy, they may be lumped with phytoplankton or protozoa. We intend to use "bacteria" only for eubacteria and "archaea" for that group quite recently recognized as profoundly distinct.

Conclusion

There are more fundamental aspects of seawater chemistry and physics, of the layout and motion of the oceans on the Earth, of "eco-math" that has roles in biological oceanography, but the introduction here should be sufficient preparation for studying the more interesting topics just ahead. The authors are excited to be getting on with it. Enjoy the ride.