

in which there is a continuum from an adverse or lethal level (e.g. freezing or very acid conditions), through favorable levels of the condition to a further adverse or lethal level (heat damage or very alkaline conditions). There are, though, many environmental conditions for which Figure 2.1b is a more appropriate response curve: for instance, most toxins, radioactive emissions and chemical pollutants, where a low-level intensity or concentration of the condition has no detectable effect, but an increase begins to cause damage and a further increase may be lethal. There is also a different form of response to conditions that are toxic at high levels but essential for growth at low levels (Figure 2.1c). This is the case for sodium chloride – an essential resource for animals but lethal at high concentrations – and for the many elements that are essential micronutrients in the growth of plants and animals (e.g. copper, zinc and manganese), but that can become lethal at the higher concentrations sometimes caused by industrial pollution.

In this chapter, we consider responses to temperature in much more detail than other conditions, because it is the single most important condition that affects the lives of organisms, and many of the generalizations that we make have widespread relevance. We move on to consider a range of other conditions, before returning, full circle, to temperature because of the effects of other conditions, notably pollutants, on global warming. We begin, though, by explaining the framework within which each of these conditions should be understood here: the ecological niche.

2.2 Ecological niches

The term *ecological niche* is frequently misunderstood and misused. It is often used loosely to describe the sort of place in which an organism lives, as in the sentence: ‘Woodlands are the niche of woodpeckers’. Strictly, however, where an organism lives is its *habitat*. A niche is not a place but an idea: a summary of the organism’s tolerances and requirements. The habitat of a gut micro-organism would be an animal’s alimentary canal; the habitat of an aphid might be a garden; and the habitat of a fish could be a whole lake. Each habitat, however, provides many different niches: many other organisms also live in the gut, the garden or the lake – and with quite different lifestyles. The word *niche* began to gain its present scientific meaning when Elton wrote in 1933 that the niche of an organism is its mode of life ‘in the sense that we speak of trades or jobs or professions in a human community’. The niche of an organism started to be used to describe how, rather than just where, an organism lives.

The modern concept of the niche was proposed by Hutchinson in 1957 to address the ways in which tolerances and requirements interact to define the conditions (this chapter) and resources (Chapter 3) needed by an individual or a species in order

to practice its way of life. Temperature, for instance, limits the growth and reproduction of all organisms, but different organisms tolerate different ranges of temperature. This range is one *dimension* of an organism’s ecological niche. Figure 2.2a shows how species of plants vary in this dimension of their niche: how they vary in the range of temperatures at which they can survive. But there are many such dimensions of a species’ niche – its tolerance of various other conditions (relative humidity, pH, wind speed, water flow and so on) and its need for various resources. Clearly the real niche of a species must be *multidimensional*.

It is easy to visualize the early stages of building such a multidimensional niche. Figure 2.2b illustrates the way in which two niche dimensions (temperature and salinity) together define a two-dimensional area that is part of the niche of a sand shrimp. Three dimensions, such as temperature, pH and the availability of a particular food, may define a three-dimensional niche volume (Figure 2.2c). In fact, we consider a niche to be an *n-dimensional hypervolume*, where *n* is the number of dimensions that make up the niche. It is hard to imagine (and impossible to draw) this more realistic picture. None the less, the simplified three-dimensional version captures the idea of the ecological niche of a species. It is defined by the boundaries that limit where it can live, grow and reproduce, and it is very clearly a concept rather than a place. The concept has become a cornerstone of ecological thought.

Provided that a location is characterized by conditions within acceptable limits for a given species, and provided also that it contains all the necessary resources, then the species can, potentially, occur and persist there. Whether or not it does so depends on two further factors. First, it must be able to reach the location, and this depends in turn on its powers of colonization and the remoteness of the site. Second, its occurrence may be precluded by the action of individuals of other species that compete with it or prey on it.

Usually, a species has a larger ecological niche in the absence of competitors and predators than it has in their presence. In other words, there are certain combinations of conditions and resources that can allow a species to maintain a viable population, but only if it is not being adversely affected by enemies. This led Hutchinson to distinguish between the *fundamental* and the *realized* niche. The former describes the overall potentialities of a species; the latter describes the more limited spectrum of conditions and resources that allow it to persist, even in the presence of competitors and predators. Fundamental and realized niches will receive more attention in Chapter 8, when we look at interspecific competition.

The remainder of this chapter looks at some of the most important condition dimensions of species’ niches, starting with temperature; the following chapter examines resources, which add further dimensions of their own.

the *n*-dimensional hypervolume

fundamental and realized niches

niche dimensions

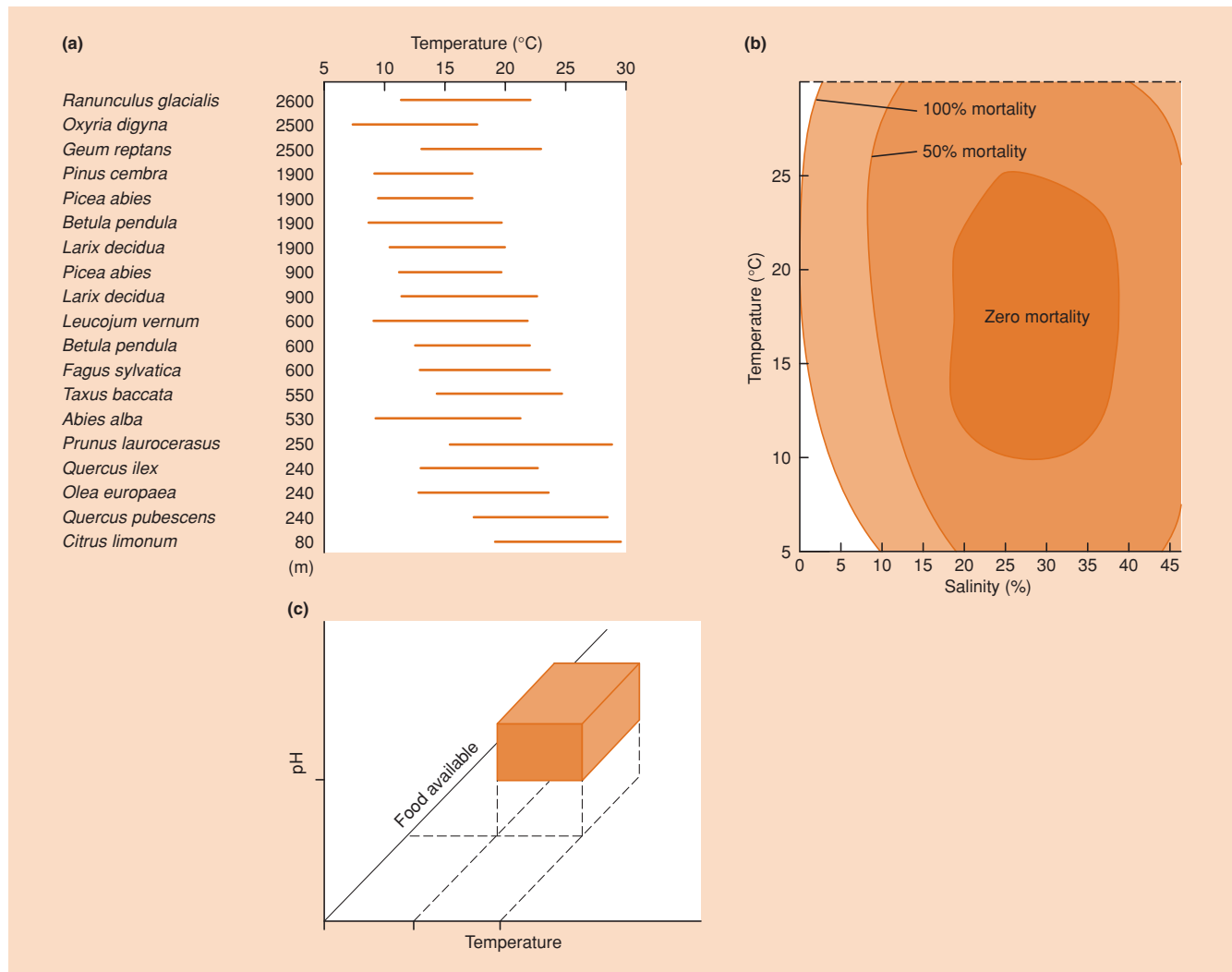


Figure 2.2 (a) A niche in one dimension. The range of temperatures at which a variety of plant species from the European Alps can achieve net photosynthesis of low intensities of radiation (70 W m^{-2}). (After Pisek *et al.*, 1973.) (b) A niche in two dimensions for the sand shrimp (*Crangon septemspinosa*) showing the fate of egg-bearing females in aerated water at a range of temperatures and salinities. (After Haefner, 1970.) (c) A diagrammatic niche in three dimensions for an aquatic organism showing a volume defined by the temperature, pH and availability of food.

2.3 Responses of individuals to temperature

2.3.1 What do we mean by 'extreme'?

It seems natural to describe certain environmental conditions as 'extreme', 'harsh', 'benign' or 'stressful'. It may seem obvious when conditions are 'extreme': the midday heat of a desert, the cold of an Antarctic winter, the salinity of the Great Salt Lake. But this only means that these conditions are extreme *for us*, given our particular physiological characteristics and tolerances.

To a cactus there is nothing extreme about the desert conditions in which cacti have evolved; nor are the icy fastnesses of Antarctica an extreme environment for penguins (Wharton, 2002). It is too easy and dangerous for the ecologist to assume that all other organisms sense the environment in the way we do. Rather, the ecologist should try to gain a worm's-eye or plant's-eye view of the environment: to see the world as others see it. Emotive words like harsh and benign, even relativities such as hot and cold, should be used by ecologists only with care.

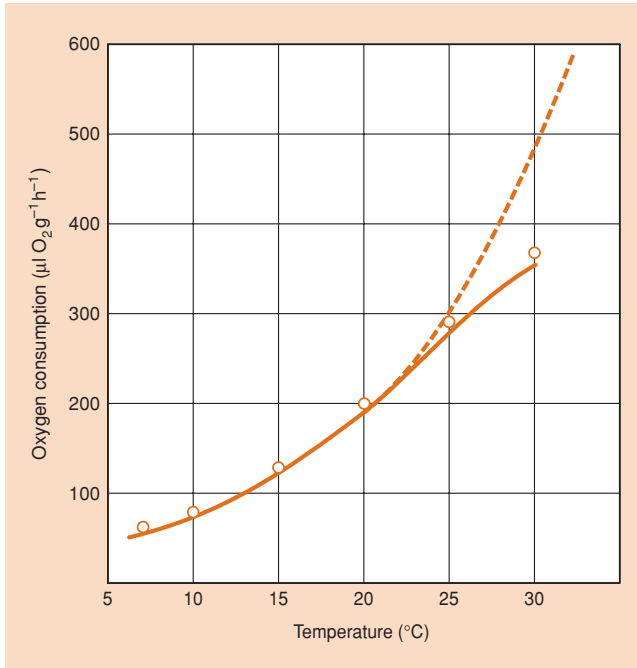


Figure 2.3 The rate of oxygen consumption of the Colorado beetle (*Leptinotarsa decemlineata*), which doubles for every 10°C rise in temperature up to 20°C, but increases less fast at higher temperatures. (After Marzusch, 1952.)

2.3.2 Metabolism, growth, development and size

exponential effects of temperature on metabolic reactions

Individuals respond to temperature essentially in the manner shown in Figure 2.1a: impaired function and ultimately death at the upper and lower extremes (discussed in Sections 2.3.4 and 2.3.6), with a functional range between the extremes, within which there is an optimum. This is accounted for, in part, simply by changes in metabolic effectiveness. For each 10°C rise in temperature, for example, the rate of biological enzymatic processes often roughly doubles, and thus appears as an exponential curve on a plot of rate against temperature (Figure 2.3). The increase is brought about because high temperature increases the speed of molecular movement and speeds up chemical reactions. The factor by which a reaction changes over a 10°C range is referred to as a Q_{10} : a rough doubling means that $Q_{10} \approx 2$.

effectively linear effects on rates of growth and development

For an ecologist, however, effects on individual chemical reactions are likely to be less important than effects on rates of growth (increases in mass), on rates of development (progression through lifecycle stages) and on final body size, since, as we shall discuss much more fully in Chapter 4, these tend

to drive the core ecological activities of survival, reproduction and movement. And when we plot rates of growth and development of whole organisms against temperature, there is quite commonly an extended range over which there are, at most, only slight deviations from linearity (Figure 2.4).

day-degree concept

When the relationship between growth or development is effectively linear, the temperatures experienced by an organism can be summarized in a single very useful value, the number of ‘day-degrees’. For instance, Figure 2.4c shows that at 15°C (5.1°C above a development threshold of 9.9°C) the predatory mite, *Amblyseius californicus*, took 24.22 days to develop (i.e. the proportion of its total development achieved each day was 0.041 (= 1/24.22)), but it took only 8.18 days to develop at 25°C (15.1°C above the same threshold). At both temperatures, therefore, development required 123.5 day-degrees (or, more properly, ‘day-degrees above threshold’), i.e. $24.22 \times 5.1 = 123.5$, and $8.18 \times 15.1 = 123.5$. This is also the requirement for development in the mite at other temperatures within the nonlethal range. Such organisms cannot be said to require a certain length of time for development. What they require is a combination of time and temperature, often referred to as ‘physiological time’.

temperature–size rule

Together, the rates of growth and development determine the final size of an organism. For instance, for a given rate of growth, a faster rate of development will lead to smaller final size. Hence, if the responses of growth and development to variations in temperature are not the same, temperature will also affect final size. In fact, development usually increases more rapidly with temperature than does growth, such that, for a very wide range of organisms, final size tends to decrease with rearing temperature: the ‘temperature–size rule’ (see Atkinson *et al.*, 2003). An example for single-celled protists (72 data sets from marine, brackish and freshwater habitats) is shown in Figure 2.5: for each 1°C increase in temperature, final cell volume decreased by roughly 2.5%.

These effects of temperature on growth, development and size may be of practical rather than simply scientific importance. Increasingly, ecologists are called upon to predict. We may wish to know what the consequences would be, say, of a 2°C rise in temperature resulting from global warming (see Section 2.9.2). Or we may wish to understand the role of temperature in seasonal, interannual and geographic variations in the productivity of, for example, marine ecosystems (Blackford *et al.*, 2004). We cannot afford to assume exponential relationships with temperature if they are really linear, nor to ignore the effects of changes in organism size on their role in ecological communities.

Motivated, perhaps, by this need to be able to extrapolate from the known to the unknown, and also simply by a wish to discover fundamental organizing principles governing the world

‘universal temperature dependence’?

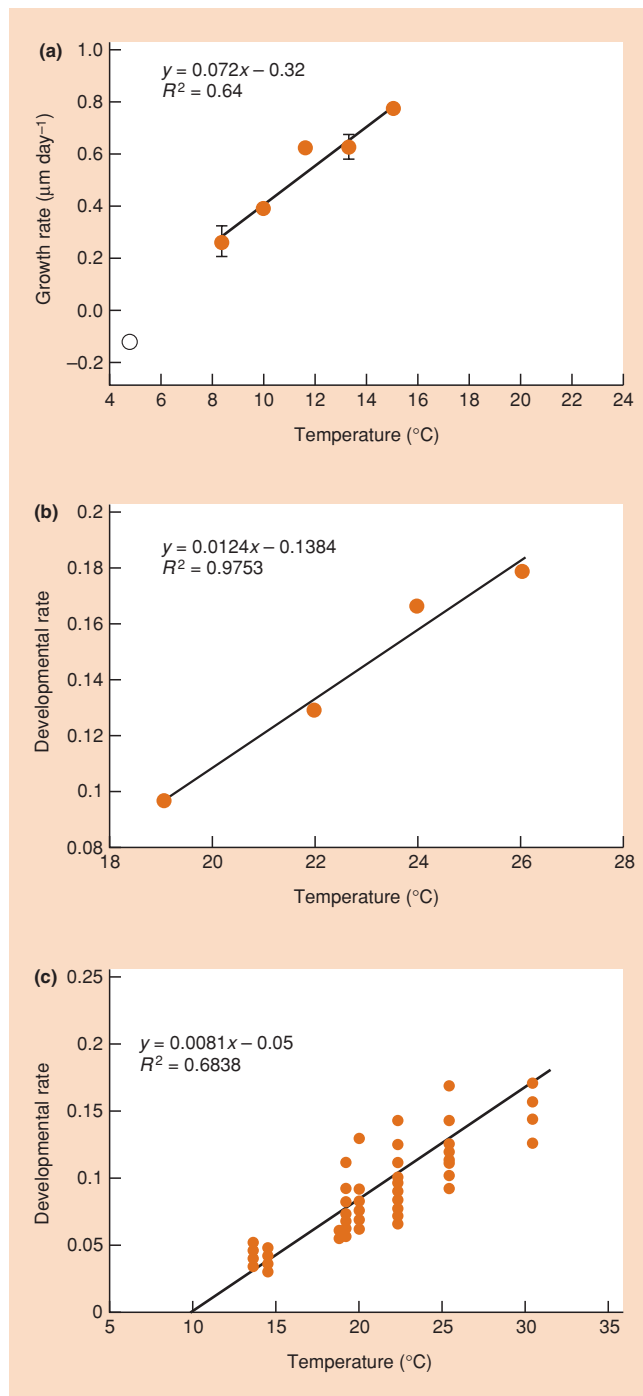


Figure 2.4 Effectively linear relationships between rates of growth and development and temperature. (a) Growth of the protist *Strombidinopsis multiauris*. (After Montagnes *et al.*, 2003.) (b) Egg development in the beetle *Oulema duftschmidi*. (After Severini *et al.*, 2003.) (c) Egg to adult development in the mite *Amblyseius californicus*. (After Hart *et al.*, 2002.) The vertical scales in (b) and (c) represent the proportion of total development achieved in 1 day at the temperature concerned.

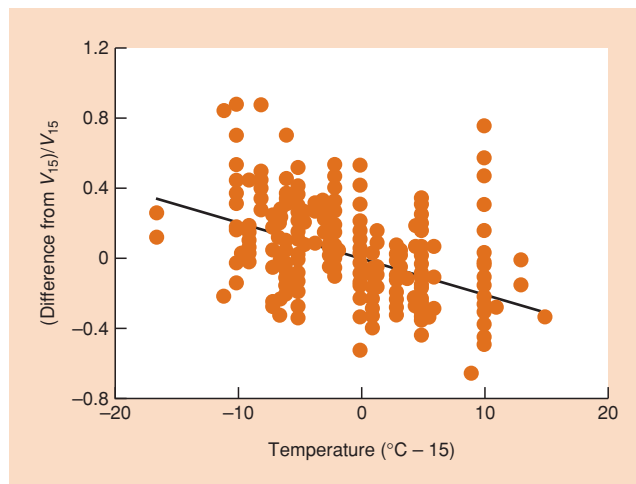


Figure 2.5 The temperature–size rule (final size decreases with increasing temperature) illustrated in protists (65 data sets combined). The horizontal scale measures temperature as a deviation from 15°C . The vertical scale measures standardized size: the difference between the cell volume observed and the cell volume at 15°C , divided by cell volume at 15°C . The slope of the mean regression line, which must pass through the point (0,0), was -0.025 (SE, 0.004); the cell volume decreased by 2.5% for every 1°C rise in rearing temperature. (After Atkinson *et al.*, 2003.)

around us, there have been attempts to uncover universal rules of temperature dependence, for metabolism itself and for development rates, linking all organisms by scaling such dependences with aspects of body size (Gillooly *et al.*, 2001, 2002). Others have suggested that such generalizations may be oversimplified, stressing for example that characteristics of whole organisms, like growth and development rates, are determined not only by the temperature dependence of individual chemical reactions, but also by those of the availability of resources, their rate of diffusion from the environment to metabolizing tissues, and so on (Rombough, 2003; Clarke, 2004). It may be that there is room for coexistence between broad-sweep generalizations at the grand scale and the more complex relationships at the level of individual species that these generalizations subsume.

2.3.3 Ectotherms and endotherms

Many organisms have a body temperature that differs little, if at all, from their environment. A parasitic worm in the gut of a mammal, a fungal mycelium in the soil and a sponge in the sea acquire the temperature of the medium in which they live. Terrestrial organisms, exposed to the sun and the air, are different because they may acquire heat directly by absorbing solar radiation or be cooled by the latent heat of evaporation of water (typical

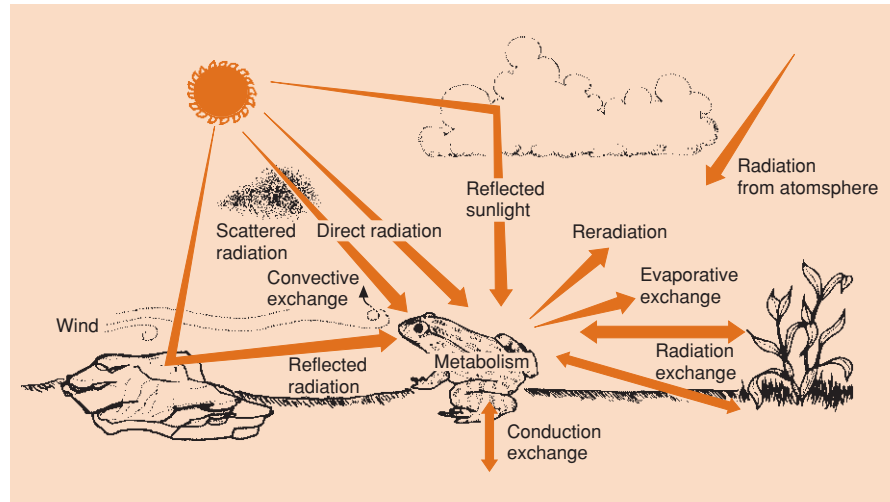


Figure 2.6 Schematic diagram of the avenues of heat exchange between an ectotherm and a variety of physical aspects of its environment. (After Tracy, 1976; from Hainsworth, 1981.)

pathways of heat exchange are shown in Figure 2.6). Various fixed properties may ensure that body temperatures are higher (or lower) than the ambient temperatures. For example, the reflective, shiny or silvery leaves of many desert plants reflect radiation that might otherwise heat the leaves. Organisms that can move have further control over their body temperature because they can seek out warmer or cooler environments, as when a lizard chooses to warm itself by basking on a hot sunlit rock or escapes from the heat by finding shade.

Amongst insects there are examples of body temperatures raised by controlled muscular work, as when bumblebees raise their body temperature by shivering their flight muscles. Social insects such as bees and termites may combine to control the temperature of their colonies and regulate them with remarkable thermostatic precision. Even some plants (e.g. *Philodendron*) use metabolic heat to maintain a relatively constant temperature in their flowers; and, of course, birds and mammals use metabolic heat almost all of the time to maintain an almost perfectly constant body temperature.

An important distinction, therefore, is between *endotherms* that regulate their temperature by the production of heat within their own bodies, and *ectotherms* that rely on external sources of heat. But this distinction is not entirely clear cut. As we have noted, apart from birds and mammals, there are also other taxa that use heat generated in their own bodies to regulate body temperature, but only for limited periods; and there are some birds and mammals that relax or suspend their endothermic abilities at the most extreme temperatures. In particular, many endothermic animals escape from some of the costs of endothermy by hibernating during the coldest seasons:

at these times they behave almost like ectotherms.

Birds and mammals usually maintain a constant body temperature between

35 and 40°C, and they therefore tend to lose heat in most environments; but this loss is moderated by insulation in the form of fur, feathers and fat, and by controlling blood flow near the skin surface. When it is necessary to increase the rate of heat loss, this too can be achieved by the control of surface blood flow and by a number of other mechanisms shared with ectotherms like panting and the simple choice of an appropriate habitat. Together, all these mechanisms and properties give endotherms a powerful (but not perfect) capability for regulating their body temperature, and the benefit they obtain from this is a constancy of near-optimal performance. But the price they pay is a large expenditure of energy (Figure 2.7), and thus a correspondingly large requirement for food to provide that energy. Over a certain temperature range (the thermoneutral zone) an endotherm consumes energy at a basal rate. But at environmental temperatures further and further above or below that zone, the endotherm consumes more and more energy in maintaining a constant body temperature. Even in the thermoneutral zone, though, an endotherm typically consumes energy many times more rapidly than an ectotherm of comparable size.

The responses of endotherms and ectotherms to changing temperatures, then, are not so different as they may at first appear to be. Both are at risk of being killed by even short exposures to very low temperatures and by more prolonged exposure to moderately low temperatures. Both have an optimal environmental temperature and upper and lower lethal limits. There are also costs to both when they live at temperatures that are not optimal. For the ectotherm these may be slower growth and reproduction, slow movement, failure to escape predators and a sluggish rate of search for food. But for the endotherm, the maintenance of body temperature costs energy that might have been used to catch more prey, produce and nurture more offspring or escape more predators. There are also costs of insulation (e.g. blubber in whales, fur in mammals) and even costs of changing the insulation between

endotherms:
temperature regulation
– but at a cost

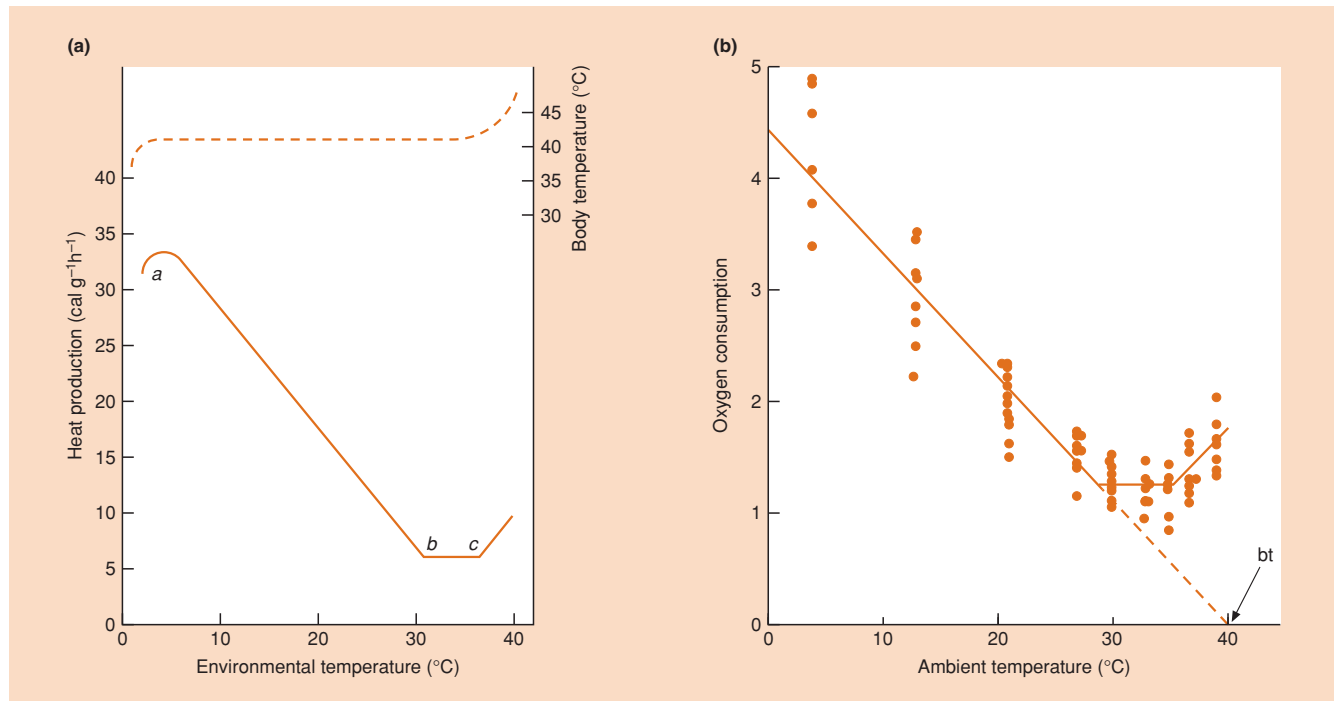


Figure 2.7 (a) Thermostatic heat production by an endotherm is constant in the thermoneutral zone, i.e. between *b*, the lower critical temperature, and *c*, the upper critical temperature. Heat production rises, but body temperature remains constant, as environmental temperature declines below *b*, until heat production reaches a maximum possible rate at a low environmental temperature. Below *a*, heat production and body temperature both fall. Above *c*, metabolic rate, heat production and body temperature all rise. Hence, body temperature is constant at environmental temperatures between *a* and *c*. (After Hainsworth, 1981.) (b) The effect of environmental temperature on the metabolic rate (rate of oxygen consumption) of the eastern chipmunk (*Tamias striatus*). *bt*, body temperature. Note that at temperatures between 0 and 30°C oxygen consumption decreases approximately linearly as the temperature increases. Above 30°C a further increase in temperature has little effect until near the animal's body temperature when oxygen consumption increases again. (After Neumann, 1967; Nedergaard & Cannon, 1990.)

seasons. Temperatures only a few degrees higher than the metabolic optimum are liable to be lethal to endotherms as well as ectotherms (see Section 2.3.6).

ectotherms and
endotherms coexist:
both strategies 'work'

It is tempting to think of ectotherms as 'primitive' and endotherms as having gained 'advanced' control over their environment, but it is difficult to justify this view. Most environments on earth are inhabited by mixed communities of endothermic and ectothermic animals. This includes some of the hottest – e.g. desert rodents and lizards – and some of the coldest – penguins and whales together with fish and krill at the edge of the Antarctic ice sheet. Rather, the contrast, crudely, is between the high cost–high benefit strategy of endotherms and the low cost–low benefit strategy of ectotherms. But their coexistence tells us that both strategies, in their own ways, can 'work'.

2.3.4 Life at low temperatures

The greater part of our planet is below 5°C: 'cold is the fiercest and most widespread enemy of life on earth' (Franks *et al.*, 1990). More than 70% of the planet is covered with seawater: mostly deep ocean with a remarkably constant temperature of about 2°C. If we include the polar ice caps, more than 80% of earth's biosphere is permanently cold.

By definition, all temperatures below the optimum are harmful, but there is usually a wide range of such temperatures that cause no physical damage and over which any effects are fully reversible. There are, however, two quite distinct types of damage at low temperatures that can be lethal, either to tissues or to whole organisms: chilling and freezing. Many organisms are damaged by exposure to temperatures that are low but above freezing point – so-called

chilling injury

'chilling injury'. The fruits of the banana blacken and rot after exposure to chilling temperatures and many tropical rainforest species are sensitive to chilling. The nature of the injury is obscure, although it seems to be associated with the breakdown of membrane permeability and the leakage of specific ions such as calcium (Minorsky, 1985).

Temperatures below 0°C can have lethal physical and chemical consequences even though ice may not be formed. Water may 'supercool' to temperatures at least as low as -40°C, remaining in an unstable liquid form in which its physical properties change in ways that are bound to be biologically significant: its viscosity increases, its diffusion rate decreases and its degree of ionization of water decreases. In fact, ice seldom forms in an organism until the temperature has fallen several degrees below 0°C. Body fluids remain in a supercooled state until ice forms suddenly around particles that act as nuclei. The concentration of solutes in the remaining liquid phase rises as a consequence. It is very rare for ice to form within cells and it is then inevitably lethal, but the freezing of extracellular water is one of the factors that prevents ice forming within the cells themselves (Wharton, 2002), since water is withdrawn from the cell, and solutes in the cytoplasm (and vacuoles) become more concentrated. The effects of freezing are therefore mainly osmoregulatory: the water balance of the cells is upset and cell membranes are destabilized. The effects are essentially similar to those of drought and salinity.

freeze-avoidance and freeze-tolerance

Organisms have at least two different metabolic strategies that allow survival through the low temperatures of winter. A 'freeze-avoiding' strategy uses low-molecular-weight polyhydric alcohols (polyols, such as glycerol) that depress both the freezing and the supercooling point and also 'thermal hysteresis' proteins that prevent ice nuclei from forming (Figure 2.8a, b). A contrasting 'freeze-tolerant' strategy, which also involves the formation of polyols, encourages the formation of extracellular ice, but protects the cell membranes from damage when water is withdrawn from the cells (Storey, 1990). The tolerances of organisms to low temperatures are not fixed but are preconditioned by the experience of temperatures in their recent past. This process is called *acclimation* when it occurs in the laboratory and *acclimatization* when it occurs naturally. Acclimatization may start as the weather becomes colder in the fall, stimulating the conversion of almost the entire glycogen reserve of animals into polyols (Figure 2.8c), but this can be an energetically costly affair: about 16% of the carbohydrate reserve may be consumed in the conversion of the glycogen reserves to polyols.

acclimation and acclimatization

The exposure of an individual for several days to a relatively low temperature can shift its whole temperature response downwards along the temperature scale. Similarly, exposure to a high temperature can shift the temperature response upwards. Antarctic springtails (tiny

arthropods), for instance, when taken from 'summer' temperatures in the field (around 5°C in the Antarctic) and subjected to a range of acclimation temperatures, responded to temperatures in the range +2°C to -2°C (indicative of winter) by showing a marked drop in the temperature at which they froze (Figure 2.9); but at lower acclimation temperatures still (-5°C, -7°C), they showed no such drop because the temperatures were themselves too low for the physiological processes required to make the acclimation response.

Acclimatization aside, individuals commonly vary in their temperature response depending on the stage of development they have reached. Probably the most extreme form of this is when an organism has a dormant stage in its life cycle. Dormant stages are typically dehydrated, metabolically slow and tolerant of extremes of temperature.

2.3.5 Genetic variation and the evolution of cold tolerance

Even within species there are often differences in temperature response between populations from different locations, and these differences have frequently been found to be the result of genetic differences rather than being attributable solely to acclimatization. Powerful evidence that cold tolerance varies between geographic races of a species comes from a study of the cactus, *Opuntia fragilis*. Cacti are generally species of hot dry habitats, but *O. fragilis* extends as far north as 56°N and at one site the lowest extreme minimum temperature recorded was -49.4°C. Twenty populations were sampled from diverse localities in northern USA and Canada, and were tested for freezing tolerance and ability to acclimate to cold. Individuals from the most freeze-tolerant population (from Manitoba) tolerated -49°C in laboratory tests and acclimated by 19.9°C, whereas plants from a population in the more equable climate of Hornby Island, British Columbia, tolerated only -19°C and acclimated by only 12.1°C (Loik & Nobel, 1993).

There are also striking cases where the geographic range of a crop species has been extended into colder regions by plant breeders. Programs of deliberate selection applied to corn (*Zea mays*) have expanded the area of the USA over which the crop can be profitably grown. From the 1920s to the 1940s, the production of corn in Iowa and Illinois increased by around 24%, whereas in the colder state of Wisconsin it increased by 54%.

If deliberate selection can change the tolerance and distribution of a domesticated plant we should expect natural selection to have done the same thing in nature. To test this, the plant *Umbilicus rupestris*, which lives in mild maritime areas of Great Britain, was deliberately grown outside its normal range (Woodward, 1990). A population of plants and seeds was taken from a donor population in the mild-wintered habitat of Cardiff in the west and introduced in a cooler environment at an altitude of

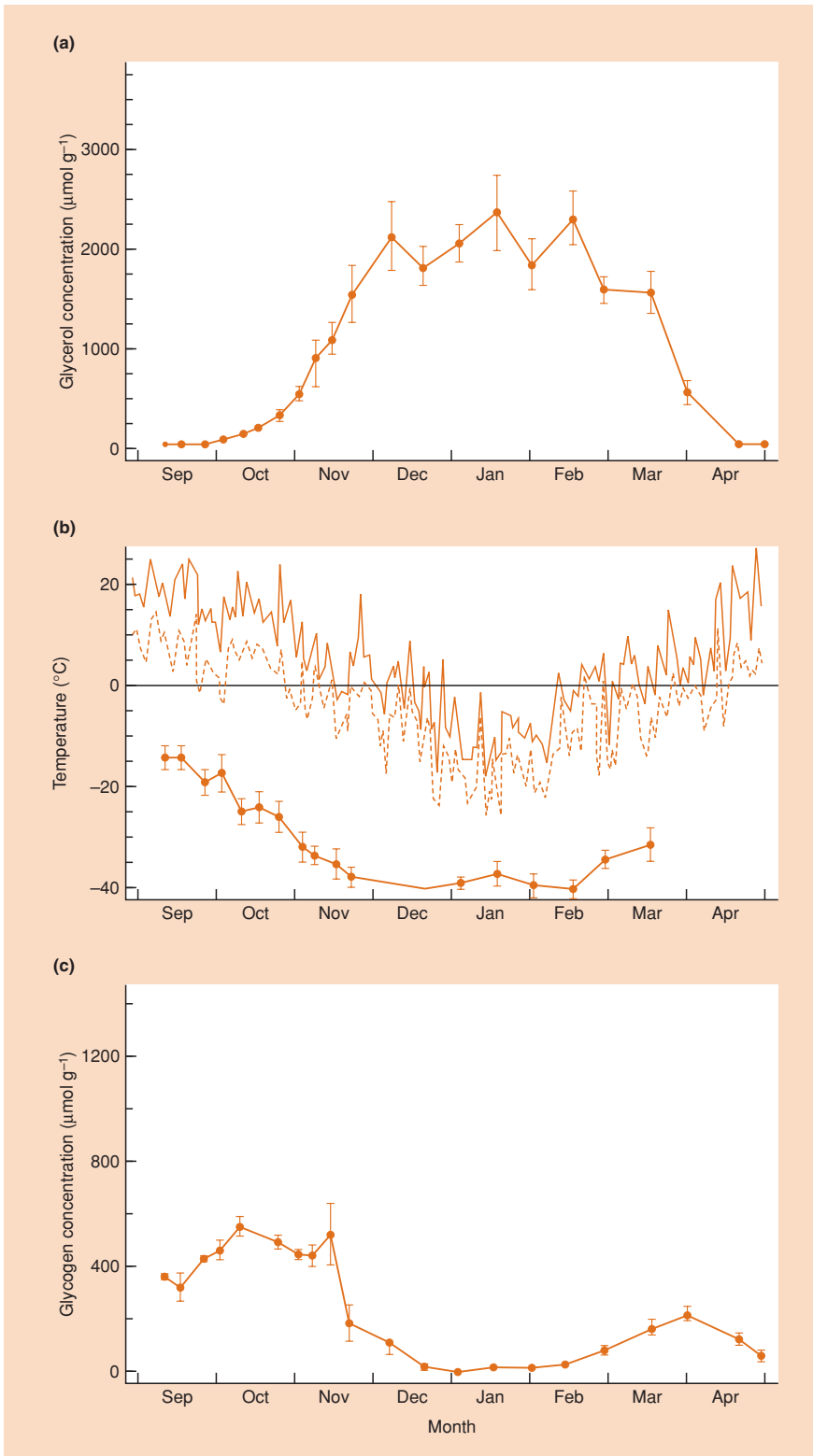
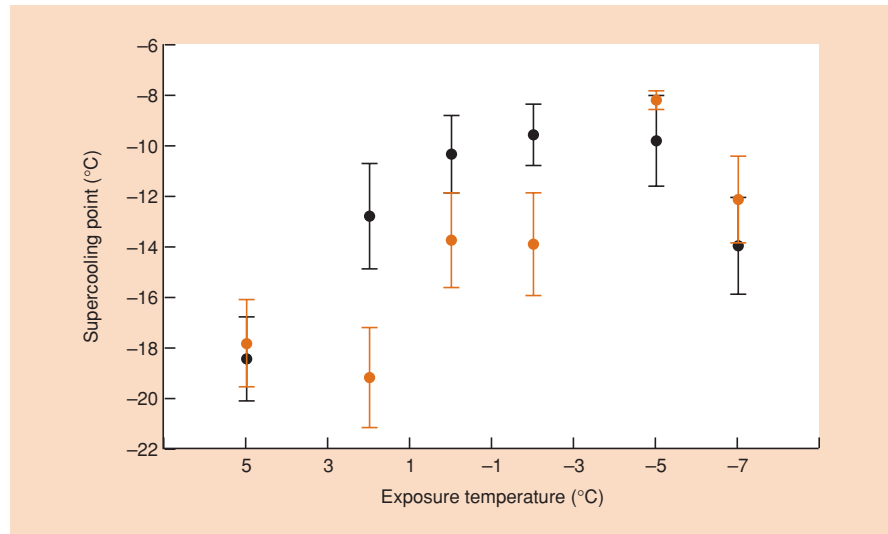


Figure 2.8 (a) Changes in the glycerol concentration per gram wet mass of the freeze-avoiding larvae of the goldenrod gall moth, *Epiblema scudderiana*. (b) The daily temperature maxima and minima (above) and whole larvae supercooling points (below) over the same period. (c) Changes in glycogen concentration over the same period. (After Rickards *et al.*, 1987.)

Figure 2.9 Acclimation to low temperatures. Samples of the Antarctic springtail *Cryptopygus antarcticus* were taken from field sites in the summer (c. 5°C) on a number of days and their supercooling point (at which they froze) was determined either immediately (●) or after a period of acclimation (●) at the temperatures shown. The supercooling points of the controls themselves varied because of temperature variations from day to day, but acclimation at temperatures in the range +2 to -2°C (indicative of winter) led to a drop in the supercooling point, whereas no such drop was observed at higher temperatures (indicative of summer) or lower temperatures (too low for a physiological acclimation response). Bars are standard errors. (After Worland & Convey, 2001.)



157 m in Sussex in the south. After 8 years, the temperature response of seeds from the donor and the introduced populations had diverged quite strikingly (Figure 2.10a), and subfreezing temperatures that kill in Cardiff (-12°C) were then tolerated

by 50% of the Sussex population (Figure 2.10b). This suggests that past climatic changes, for example ice ages, will have changed the temperature tolerance of species as well as forcing their migration.

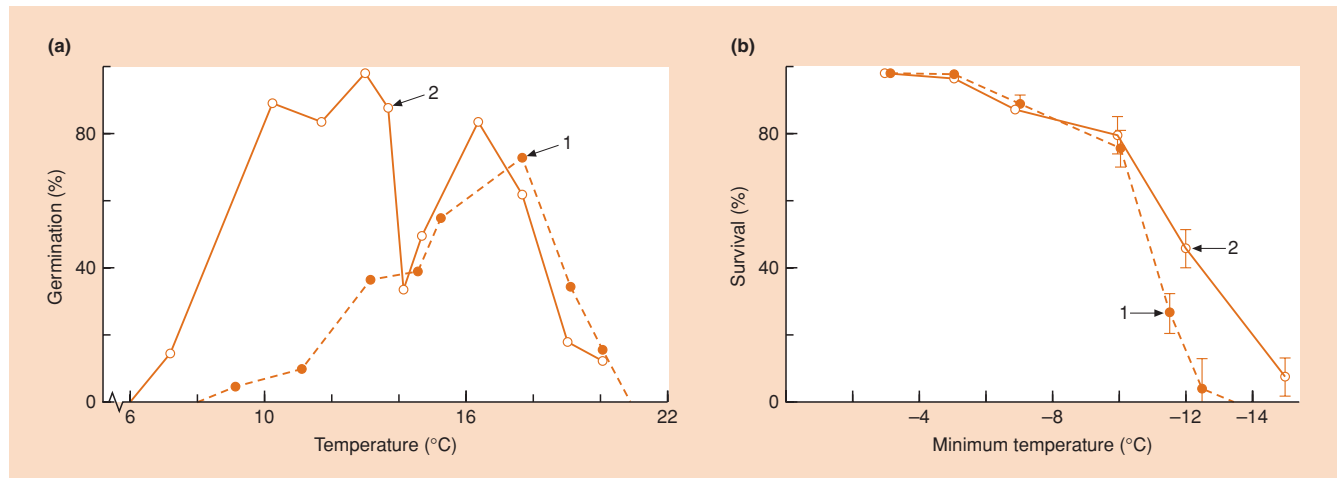


Figure 2.10 Changes in the behavior of populations of the plant *Umbilicus rupestris*, established for a period of 8 years in a cool environment in Sussex from a donor population in a mild-wintered area in South Wales (Cardiff, UK). (a) Temperature responses of seed germination: (1) responses of samples from the donor population (Cardiff) in 1978, and (2) responses from the Sussex population in 1987. (b) The low-temperature survival of the donor population at Cardiff, 1978 (1) and of the established population in Sussex, 1987 (2). (After Woodward, 1990.)

2.3.6 Life at high temperatures

Perhaps the most important thing about dangerously high temperatures is that, for a given organism, they usually lie only a few degrees above the metabolic optimum. This is largely an unavoidable consequence of the physicochemical properties of most enzymes (Wharton, 2002). High temperatures may be dangerous because they lead to the inactivation or even the denaturation of enzymes, but they may also have damaging indirect effects by leading to dehydration. All terrestrial organisms need to conserve water, and at high temperatures the rate of water loss by evaporation can be lethal, but they are caught between the devil and the deep blue sea because evaporation is an important means of reducing body temperature. If surfaces are protected from evaporation (e.g. by closing stomata in plants or spiracles in insects) the organisms may be killed by too high a body temperature, but if their surfaces are not protected they may die of desiccation.

high temperature and water loss

Death Valley, California, in the summer, is probably the hottest place on earth in which higher plants make active growth. Air temperatures during the daytime may approach 50°C and soil surface temperatures may be very much higher. The perennial plant, desert honeysweet (*Tidestromia oblongifolia*), grows vigorously in such an environment despite the fact that its leaves are killed if they reach the same temperature as the air. Very rapid transpiration keeps the temperature of the leaves at 40–45°C, and in this range they are capable of extremely rapid photosynthesis (Berry & Björkman, 1980).

Most of the plant species that live in very hot environments suffer severe shortage of water and are therefore unable to use the latent heat of evaporation of water to keep leaf temperatures down. This is especially the case in desert succulents in which water loss is minimized by a low surface to volume ratio and a low frequency of stomata. In such plants the risk of overheating may be reduced by spines (which shade the surface of a cactus) or hairs or waxes (which reflect a high proportion of the incident radiation). Nevertheless, such species experience and tolerate temperatures in their tissues of more than 60°C when the air temperature is above 40°C (Smith *et al.*, 1984).

fire

Fires are responsible for the highest temperatures that organisms face on earth and, before the fire-raising activities of humans, were caused mainly by lightning strikes. The recurrent risk of fire has shaped the species composition of arid and semiarid woodlands in many parts of the world. All plants are damaged by burning but it is the remarkable powers of regrowth from protected meristems on shoots and seeds that allow a specialized subset of species to recover from damage and form characteristic fire floras (see, for example, Hodgkinson, 1992).

Decomposing organic matter in heaps of farmyard manure, compost heaps and damp hay may reach very high temperatures. Stacks of damp hay are heated to temperatures of 50–60°C by

the metabolism of fungi such as *Aspergillus fumigatus*, carried further to approximately 65°C by other thermophilic fungi such as *Mucor pusillus* and then a little further by bacteria and actinomycetes. Biological activity stops well short of 100°C but autocombustible products are formed that cause further heating, drive off water and may even result in fire. Another hot environment is that of natural hot springs and in these the microbe *Thermus aquaticus* grows at temperatures of 67°C and tolerates temperatures up to 79°C. This organism has also been isolated from domestic hot water systems. Many (perhaps all) of the extremely thermophilic species are prokaryotes. In environments with very high temperatures the communities contain few species. In general, animals and plants are the most sensitive to heat followed by fungi, and in turn by bacteria, actinomycetes and archaeobacteria. This is essentially the same order as is found in response to many other extreme conditions, such as low temperature, salinity, metal toxicity and desiccation.

thermal vents and other hot environments

An ecologically very remarkable hot environment was first described only towards the end of the last century. In 1979, a deep oceanic site was discovered in the eastern Pacific at which fluids at high temperatures ('smokers') were vented from the sea floor forming thin-walled 'chimneys' of mineral materials. Since that time many more vent sites have been discovered at mid-ocean crests in both the Atlantic and Pacific Oceans. They lie 2000–4000 m below sea level at pressures of 200–400 bars (20–40 MPa). The boiling point of water is raised to 370°C at 200 bars and to 404°C at 400 bars. The superheated fluid emerges from the chimneys at temperatures as high as 350°C, and as it cools to the temperature of seawater at about 2°C it provides a continuum of environments at intermediate temperatures.

Environments at such extreme pressures and temperatures are obviously extraordinarily difficult to study *in situ* and in most respects impossible to maintain in the laboratory. Some thermophilic bacteria collected from vents have been cultured successfully at 100°C at only slightly above normal barometric pressures (Jannasch & Mottl, 1985), but there is much circumstantial evidence that some microbial activity occurs at much higher temperatures and may form the energy resource for the warm water communities outside the vents. For example, particulate DNA has been found in samples taken from within the 'smokers' at concentrations that point to intact bacteria being present at temperatures very much higher than those conventionally thought to place limits on life (Baross & Deming, 1995).

There is a rich eukaryotic fauna in the local neighborhood of vents that is quite atypical of the deep oceans in general. At one vent in Middle Valley, Northeast Pacific, surveyed photographically and by video, at least 55 taxa were documented of which 15 were new or probably new species (Juniper *et al.*, 1992). There can be few environments in which so complex and specialized a community depends on so localized a special condition. The

closest known vents with similar conditions are 2500 km distant. Such communities add a further list to the planet's record of species richness. They present tantalizing problems in evolution and daunting problems for the technology needed to observe, record and study them.

2.3.7 Temperature as a stimulus

We have seen that temperature as a condition affects the rate at which organisms develop. It may also act as a stimulus, determining whether or not the organism starts its development at all. For instance, for many species of temperate, arctic and alpine herbs, a period of chilling or freezing (or even of alternating high and low temperatures) is necessary before germination will occur. A cold experience (physiological evidence that winter has passed) is required before the plant can start on its cycle of growth and development. Temperature may also interact with other stimuli (e.g. photoperiod) to break dormancy and so time the onset of growth. The seeds of the birch (*Betula pubescens*) require a photoperiodic stimulus (i.e. experience of a particular regime of day length) before they will germinate, but if the seed has been chilled it starts growth without a light stimulus.

2.4 Correlations between temperature and the distribution of plants and animals

2.4.1 Spatial and temporal variations in temperature

Variations in temperature on and within the surface of the earth have a variety of causes: latitudinal, altitudinal, continental, seasonal, diurnal and microclimatic effects and, in soil and water, the effects of depth.

Latitudinal and seasonal variations cannot really be separated. The angle at which the earth is tilted relative to the sun changes with the seasons, and this drives some of the main temperature differentials on the earth's surface. Superimposed on these broad geographic trends are the influences of altitude and 'continentality'. There is a drop of 1°C for every 100 m increase in altitude in dry air, and a drop of 0.6°C in moist air. This is the result of the 'adiabatic' expansion of air as atmospheric pressure falls with increasing altitude. The effects of continentality are largely attributable to different rates of heating and cooling of the land and the sea. The land surface reflects less heat than the water, so the surface warms more quickly, but it also loses heat more quickly. The sea therefore has a moderating, 'maritime' effect on the temperatures of coastal regions and especially islands; both daily and seasonal variations in temperature are far less marked than at more inland, continental locations at the same latitude. Moreover, there are comparable effects within land masses: dry, bare areas like deserts suffer greater daily and seasonal extremes of temperature

than do wetter areas like forests. Thus, global maps of temperature zones hide a great deal of local variation.

It is much less widely appreciated that on a smaller scale still there can be a great deal of microclimatic variation.

microclimatic
variation

For example, the sinking of dense, cold air into the bottom of a valley at night can make it as much as 30°C colder than the side of the valley only 100 m higher; the winter sun, shining on a cold day, can heat the south-facing side of a tree (and the habitable cracks and crevices within it) to as high as 30°C; and the air temperature in a patch of vegetation can vary by 10°C over a vertical distance of 2.6 m from the soil surface to the top of the canopy (Geiger, 1955). Hence, we need not confine our attention to global or geographic patterns when seeking evidence for the influence of temperature on the distribution and abundance of organisms.

Long-term temporal variations in temperature, such as those associated with the ice ages, were discussed in the previous chapter. Between these, however, and the very obvious daily and seasonal changes that we are all aware of, a number of medium-term patterns have become increasingly apparent. Notable amongst these are the El Niño-Southern Oscillation (ENSO) and the North Atlantic Oscillation (NAO) (Figure 2.11) (see Stenseth *et al.*, 2003). The ENSO originates in the tropical Pacific Ocean off the coast of South America and is an alternation (Figure 2.11a) between a warm (El Niño) and a cold (La Niña) state of the water there, though it affects temperature, and the climate generally, in terrestrial and marine environments throughout the whole Pacific basin (Figure 2.11b; for color, see Plate 2.1, between pp. 000 and 000) and beyond. The NAO refers to a north-south alternation in atmospheric mass between the subtropical Atlantic and the Arctic (Figure 2.11c) and again affects climate in general rather than just temperature (Figure 2.11d; for color, see Plate 2.2, between pp. 000 and 000). Positive index values (Figure 2.11c) are associated, for example, with relatively warm conditions in North America and Europe and relatively cool conditions in North Africa and the Middle East. An example of the effect of NAO variation on species abundance, that of cod, *Gadus morhua*, in the Barents Sea, is shown in Figure 2.12.

ENSO and NAO

2.4.2 Typical temperatures and distributions

There are very many examples of plant and animal distributions that are

isotherms

strikingly correlated with some aspect of environmental temperature even at gross taxonomic and systematic levels (Figure 2.13). At a finer scale, the distributions of many species closely match maps of some aspect of temperature. For example, the northern limit of the distribution of wild madder plants (*Rubia peregrina*) is closely correlated with the position of the January 4.5°C

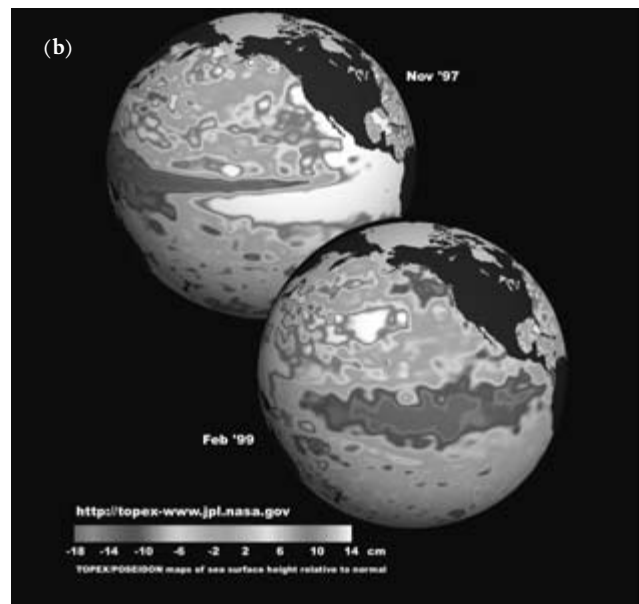
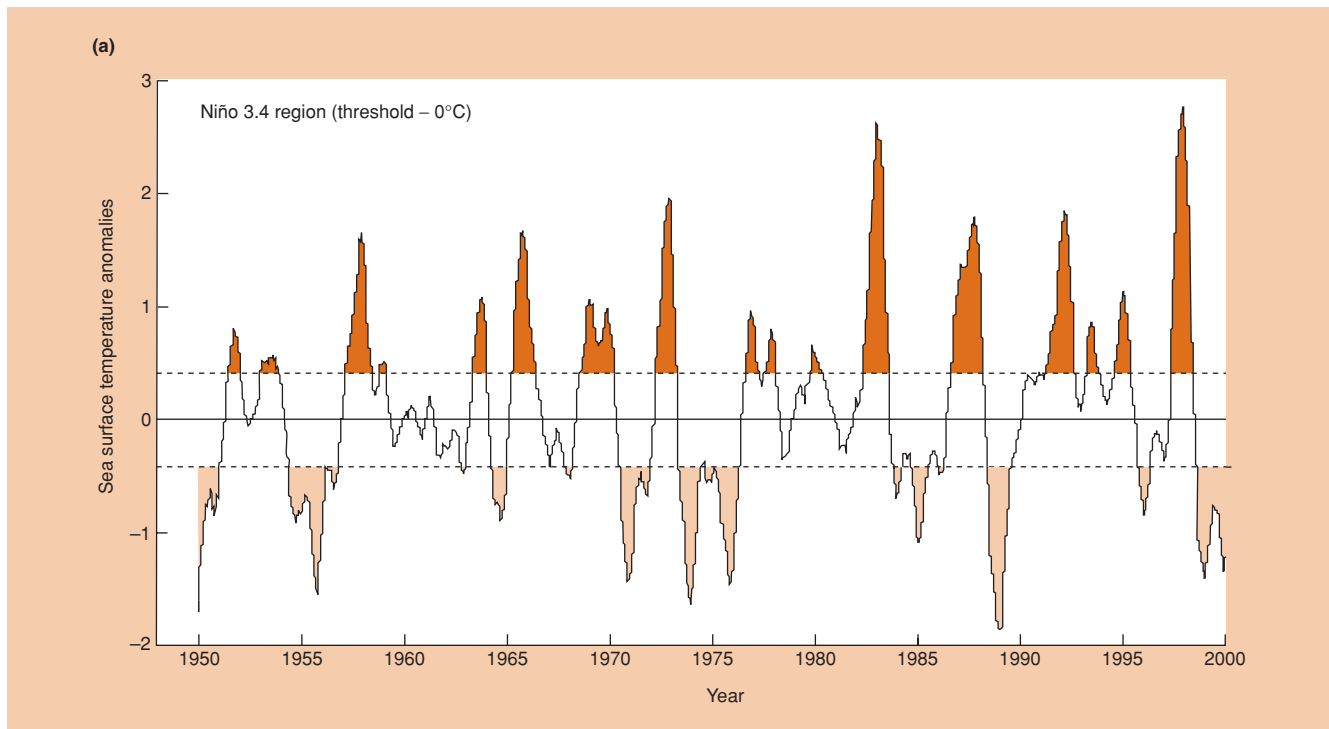


Figure 2.11 (a) The El Niño–Southern Oscillation (ENSO) from 1950 to 2000 as measured by sea surface temperature anomalies (differences from the mean) in the equatorial mid-Pacific. The El Niño events ($> 0.4^{\circ}\text{C}$ above the mean), and the La Niña events ($> 0.4^{\circ}\text{C}$ below the mean) are shown in dark color, and the La Niña events ($> 0.4^{\circ}\text{C}$ below the mean) are shown in pale color. (Image from http://www.cgd.ucar.edu/cas/catalog/clinind/Nino_3_3.4_indices.html.) (b) Maps of examples of El Niño (November 1997) and La Niña (February 1999) events in terms of sea height above average levels. Warmer seas are higher; for example, a sea height 15–20 cm below average equates to a temperature anomaly of approximately $2\text{--}3^{\circ}\text{C}$. (Image from <http://topex-www.jpl.nasa.gov/science/images/el-nino-la-nina.jpg>.) (For color, see Plate 2.1, between pp. 000 and 000.)

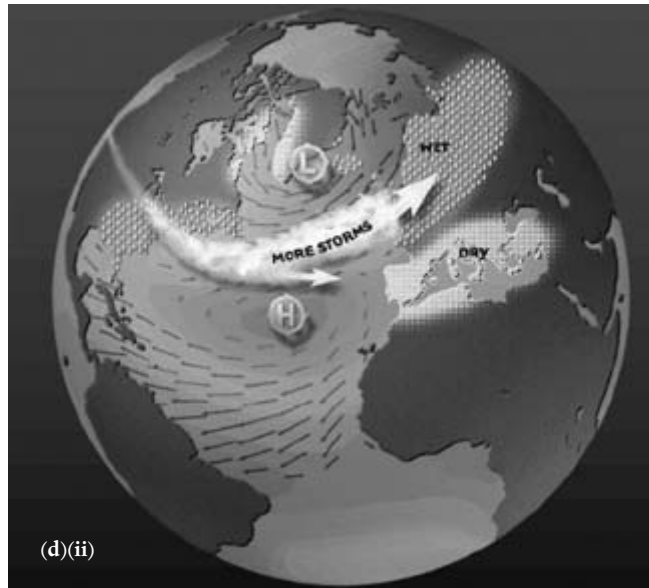
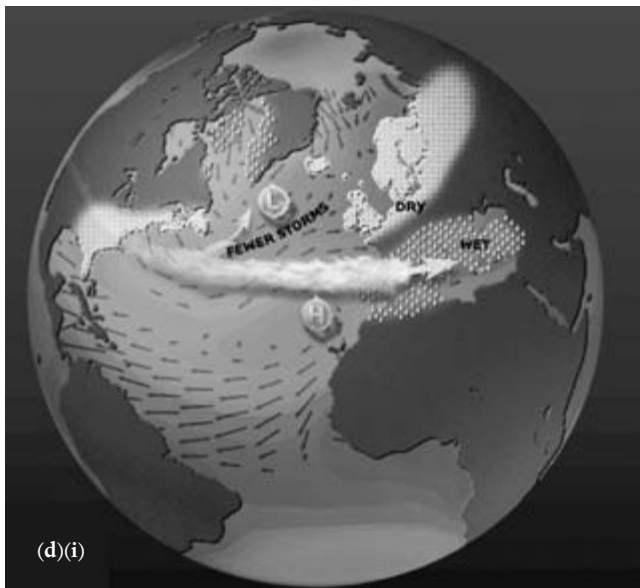
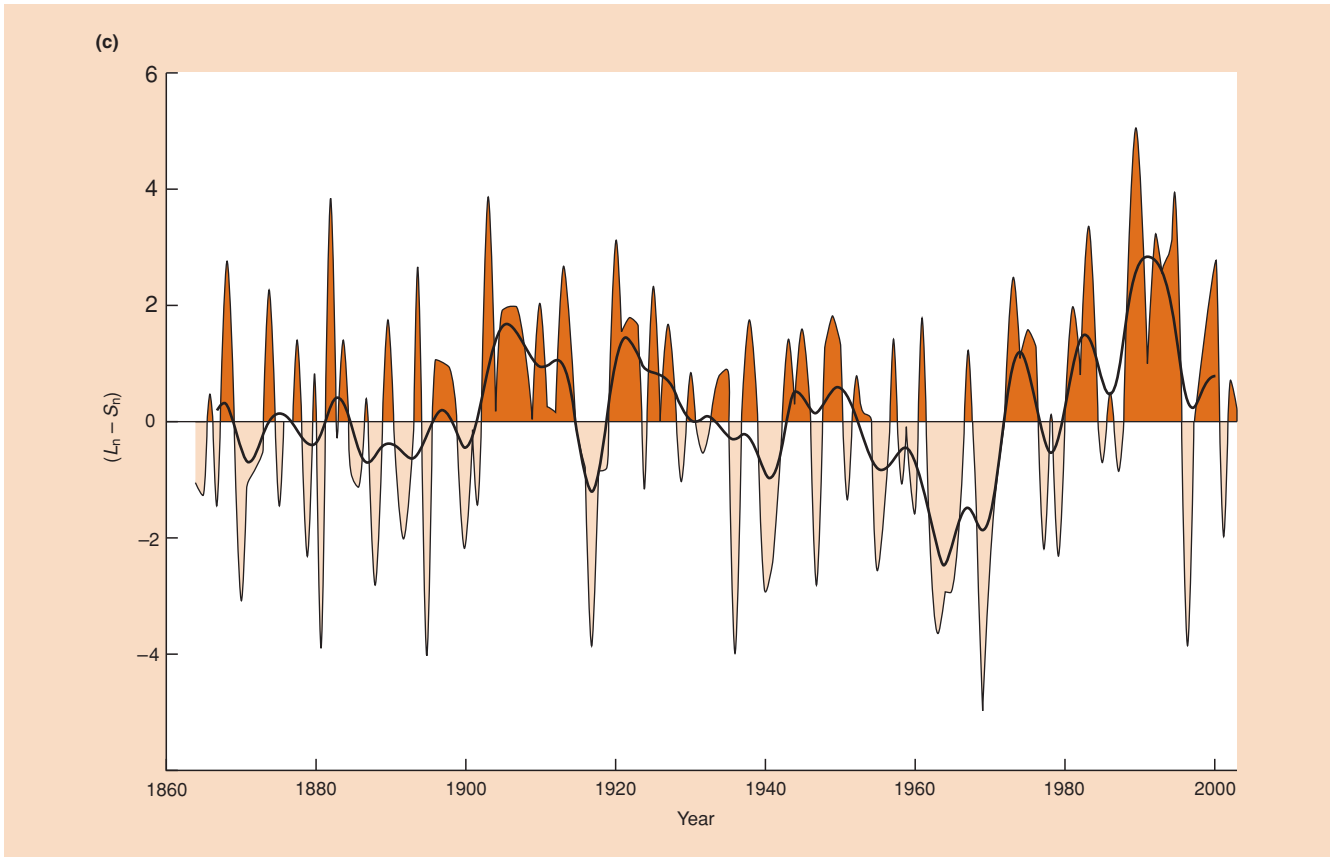


Figure 2.11 (continued) (c) The North Atlantic Oscillation (NAO) from 1864 to 2003 as measured by the normalized sea-level pressure difference ($L_n - S_n$) between Lisbon, Portugal and Reykjavik, Iceland. (Image from <http://www.cgd.ucar.edu/~jhurrell/nao.stat.winter.html#winter>.) (d) Typical winter conditions when the NAO index is positive or negative. Conditions that are more than usually warm, cold, dry or wet are indicated. (Image from <http://www.ldeo.columbia.edu/NAO/>.) (For color, see Plate 2.2, between pp. 000 and 000.)

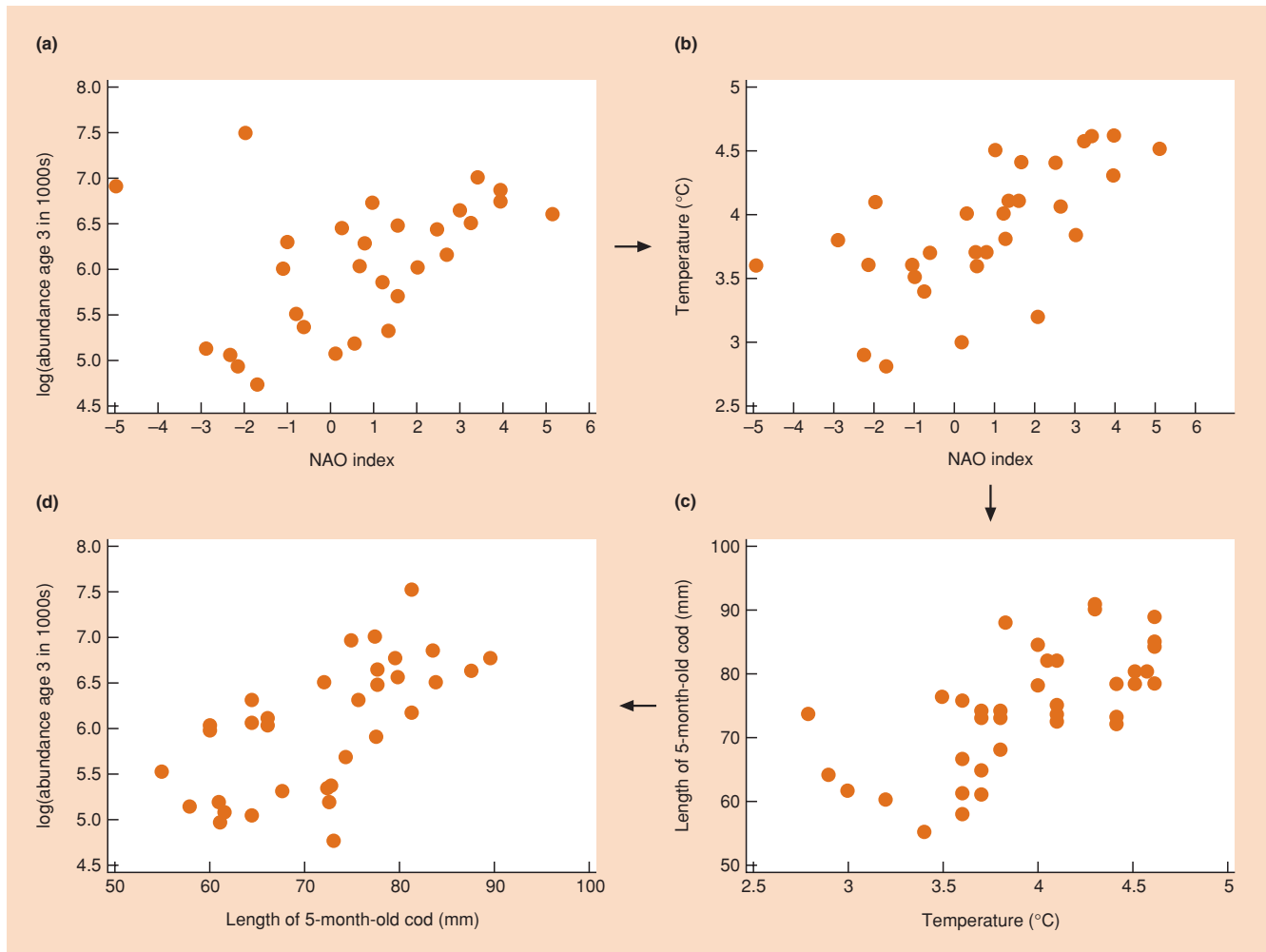


Figure 2.12 (a) The abundance of 3-year-old cod, *Gadus morhua*, in the Barents Sea is positively correlated with the value of the North Atlantic Oscillation (NAO) index for that year. The mechanism underlying this correlation is suggested in (b–d). (b) Annual mean temperature increases with the NAO index. (c) The length of 5-month-old cod increases with annual mean temperature. (d) The abundance of cod at age 3 increases with their length at 5 months. (After Ottersen *et al.*, 2001.)

isotherm (Figure 2.14a; an isotherm is a line on a map joining places that experience the same temperature – in this case a January mean of 4.5°C). However, we need to be very careful how we interpret such relationships: they can be extremely valuable in predicting where we might and might not find a particular species; they may suggest that some feature related to temperature is important in the life of the organisms; but they do not prove that temperature *causes* the limits to a species' distribution. The literature relevant to this and many other correlations between temperature and distribution patterns is reviewed by Hengeveld (1990), who also describes a more subtle graphical procedure. The minimum temperature of the coldest month and the maximum temperature of the hottest month are estimated for many places within and

outside the range of a species. Each location is then plotted on a graph of maximum against minimum temperature, and a line is drawn that optimally discriminates between the presence and absence records (Figure 2.14b). This line is then used to define the geographic margin of the species distributions (Figure 2.14c). This may have powerful predictive value, but it still tells us nothing about the underlying forces that cause the distribution patterns.

One reason why we need to be cautious about reading too much into correlations of species distributions with maps of temperature is that the temperatures measured for constructing isotherms for a map are only rarely those that the organisms experience. In nature an organism may choose to lie in the sun or hide

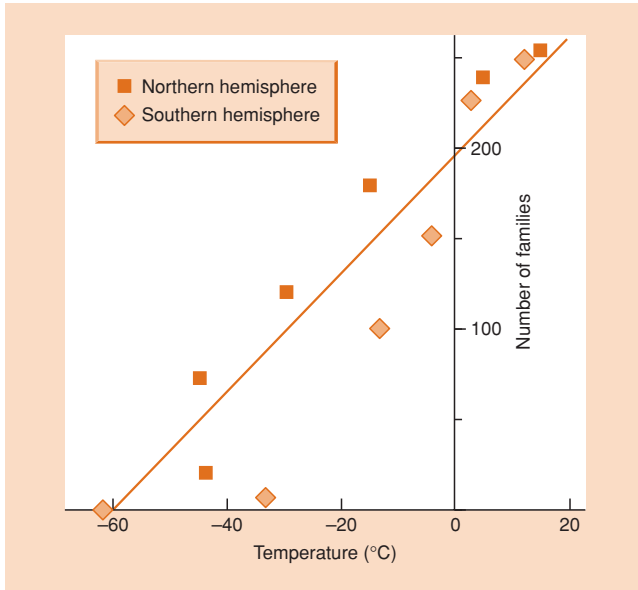


Figure 2.13 The relationship between absolute minimum temperature and the number of families of flowering plants in the northern and southern hemispheres. (After Woodward, 1987, who also discusses the limitations to this sort of analysis and how the history of continental isolation may account for the odd difference between northern and southern hemispheres.)

in the shade and, even in a single day, may experience a baking midday sun and a freezing night. Moreover, temperature varies from place to place on a far finer scale than will usually concern a geographer, but it is the conditions in these ‘microclimates’ that

will be crucial in determining what is habitable for a particular species. For example, the prostrate shrub *Dryas octopetala* is restricted to altitudes exceeding 650 m in North Wales, UK, where it is close to its southern limit. But to the north, in Sutherland in Scotland, where it is generally colder, it is found right down to sea level.

2.4.3 Distributions and extreme conditions

For many species, distributions are accounted for not so much by average temperatures as by occasional extremes, especially occasional lethal temperatures that preclude its existence. For instance, injury by frost is probably the single most important factor limiting plant distribution. To take one example: the saguaro cactus (*Carnegiea gigantea*) is liable to be killed when temperatures remain below freezing for 36 h, but if there is a daily thaw it is under no threat. In Arizona, the northern and eastern edges of the cactus’ distribution correspond to a line joining places where on occasional days it fails to thaw. Thus, the saguaro is absent where there are occasionally lethal conditions – an individual need only be killed once.

Similarly, there is scarcely any crop that is grown on a large commercial scale in the climatic conditions of its wild ancestors, and it is well known that crop failures are often caused by extreme events, especially frosts and drought. For instance, the climatic limit to the geographic range for the production of coffee (*Coffea arabica* and *C. robusta*) is defined by the 13°C isotherm for the coldest month of the year. Much of the world’s crop is produced in the highland microclimates of the São Paulo and Paraná districts of

you only die once

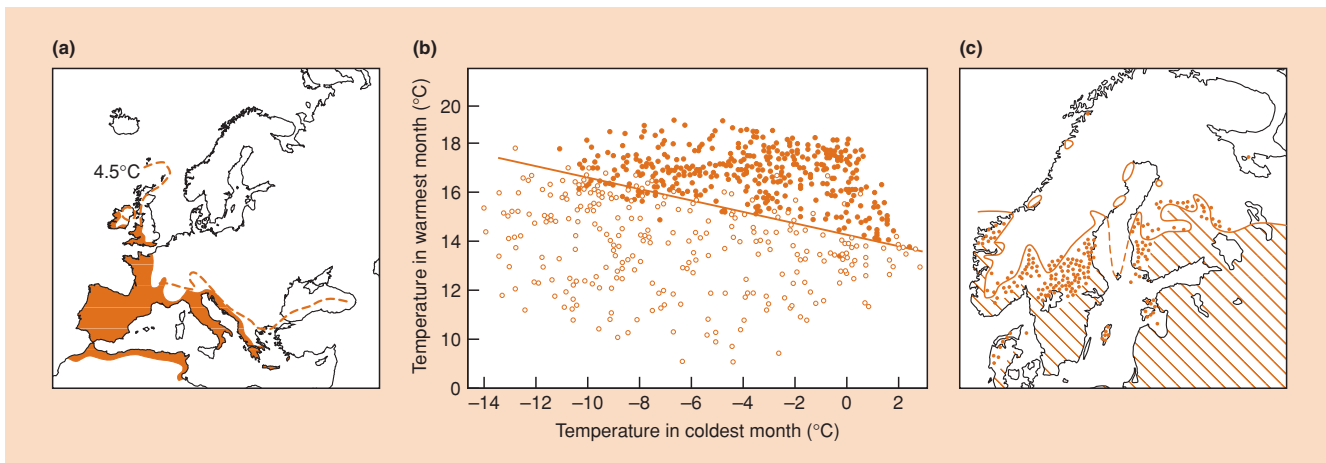


Figure 2.14 (a) The northern limit of the distribution of the wild madder (*Rubia peregrina*) is closely correlated with the position of the January 4.5°C isotherm. (After Cox *et al.*, 1976.) (b) A plot of places within the range of *Tilia cordata* (●), and outside its range (○) in the graphic space defined by the minimum temperature of the coldest month and the maximum temperature of the warmest month. (c) Margin of the geographic range of *T. cordata* in northern Europe defined by the straight line in (b). ((b, c) after Hintikka, 1963; from Hengeveld, 1990.)

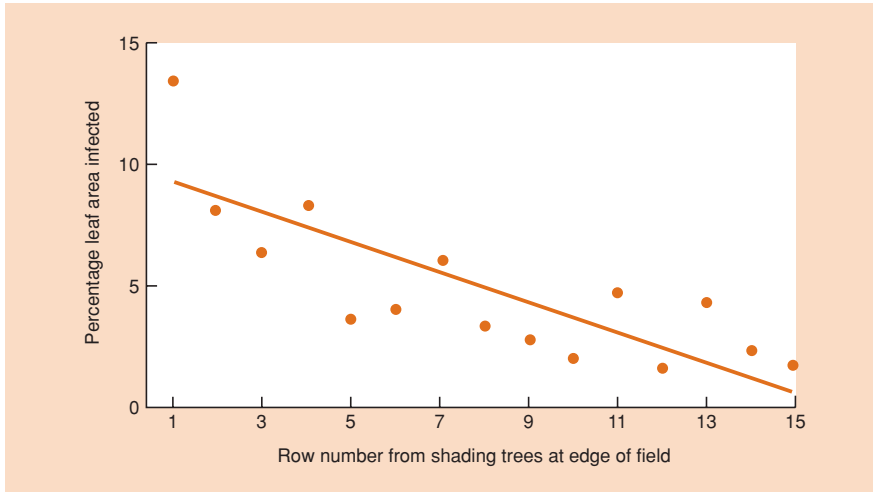


Figure 2.15 The incidence of southern corn leaf blight (*Helminthosporium maydis*) on corn growing in rows at various distances from trees that shaded them. Wind-borne fungal diseases were responsible for most of this mortality (Harper, 1955). (From Lukens & Mullany, 1972.)

Brazil. Here, the average minimum temperature is 20°C, but occasionally cold winds and just a few hours of temperature close to freezing are sufficient to kill or severely damage the trees (and play havoc with world coffee prices).

2.4.4 Distributions and the interaction of temperature with other factors

Although organisms respond to each condition in their environment, the effects of conditions may be determined largely by the responses of other community members. Temperature does not act on just one species: it also acts on its competitors, prey, parasites and so on. This, as we saw in Section 2.2, was the difference between a fundamental niche (where an organism *could* live) and a realized niche (where it *actually* lived). For example, an organism will suffer if its food is another species that cannot tolerate an environmental condition. This is illustrated by the distribution of the rush moth (*Coleophora alticolella*) in England. The moth lays its eggs on the flowers of the rush *Juncus squarrosus* and the caterpillars feed on the developing seeds. Above 600 m, the moths and caterpillars are little affected by the low temperatures, but the rush, although it grows, fails to ripen its seeds. This, in turn, limits the distribution of the moth, because caterpillars that hatch in the colder elevations will starve as a result of insufficient food (Randall, 1982).

The effects of conditions on disease may also be important. Conditions may favor the spread of infection (winds carrying fungal spores), or favor the growth of the parasite, or weaken the defenses of the host. For example, during an epidemic of southern corn leaf blight (*Helminthosporium maydis*) in a corn field in Connecticut, the plants closest to the trees that were shaded for the longest periods were the most heavily diseased (Figure 2.15).

Competition between species can also be profoundly influenced by environmental conditions, especially temperature. Two stream salmonid fishes, *Salvelinus malma* and *S. leucomaenis*, coexist at intermediate altitudes (and therefore intermediate temperatures) on Hokkaido Island, Japan, whereas only the former lives at higher altitudes (lower temperatures) and only the latter at lower altitudes (see also Section 8.2.1). A reversal, by a change in temperature, of the outcome of competition between the species appears to play a key role in this. For example, in experimental streams supporting the two species maintained at 6°C over a 191-day period (a typical high altitude temperature), the survival of *S. malma* was far superior to that of *S. leucomaenis*; whereas at 12°C (typical low altitude), both species survived less well, but the outcome was so far reversed that by around 90 days all of the *S. malma* had died (Figure 2.16). Both species are quite capable, alone, of living at either temperature.

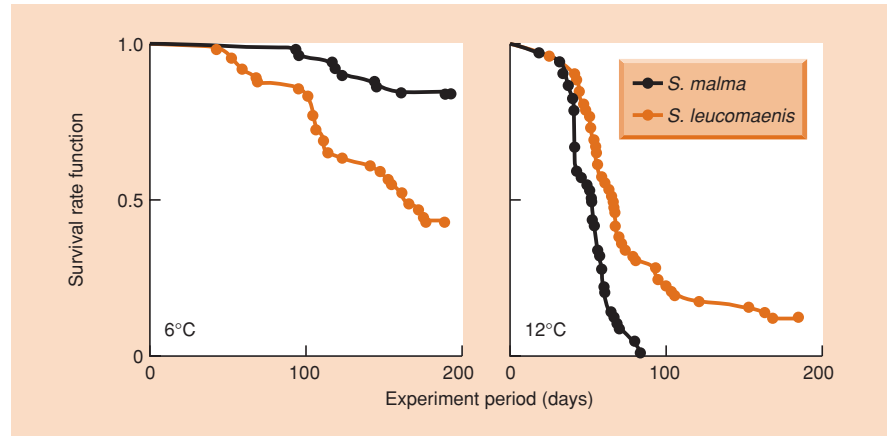
Many of the interactions between temperature and other physical conditions are so strong that it is not sensible to consider them separately. The relative humidity of the atmosphere, for example, is an important condition in the life of terrestrial organisms because it plays a major part in determining the rate at which they lose water. In practice, it is rarely possible to make a clean distinction between the effects of relative humidity and of temperature. This is simply because a rise in temperature leads to an increased rate of evaporation. A relative humidity that is acceptable to an organism at a low temperature may therefore be unacceptable at a higher temperature. Microclimatic variations in relative humidity can be even more marked than those involving temperature. For instance, it is not unusual for the relative humidity to be almost 100% at ground level amongst dense vegetation and within the soil, whilst the air immediately above, perhaps 40 cm away, has a relative humidity

competition

temperature and humidity

disease

Figure 2.16 Changing temperature reverses the outcome of competition. At low temperature (6°C) on the left, the salmonid fish *Salvelinus malma* outsurvives cohabiting *S. leucomaenis*, whereas at 12°C, on the right, *S. leucomaenis* drives *S. malma* to extinction. Both species are quite capable, alone, of living at either temperature. (After Taniguchi & Nakano, 2000.)



of only 50%. The organisms most obviously affected by humidity in their distribution are those 'terrestrial' animals that are actually, in terms of the way they control their water balance, 'aquatic'. Amphibians, terrestrial isopods, nematodes, earthworms and molluscs are all, at least in their active stages, confined to microenvironments where the relative humidity is at or very close to 100%. The major group of animals to escape such confinement are the terrestrial arthropods, especially insects. Even here though, the evaporative loss of water often confines their activities to habitats (e.g. woodlands) or times of day (e.g. dusk) when relative humidity is relatively high.

2.5 pH of soil and water

The pH of soil in terrestrial environments or of water in aquatic ones is a condition that can exert a powerful influence on the distribution and abundance of organisms. The protoplasm of the root cells of most vascular plants is damaged as a direct result of toxic concentrations of H^+ or OH^- ions in soils below pH 3 or above pH 9, respectively. Further, indirect effects occur because soil pH influences the availability of nutrients and/or the concentration of toxins (Figure 2.17).

Increased acidity (low pH) may act in three ways: (i) directly, by upsetting osmoregulation, enzyme activity or gaseous exchange across respiratory surfaces; (ii) indirectly, by increasing the concentration of toxic heavy metals, particularly aluminum (Al^{3+}) but also manganese (Mn^{2+}) and iron (Fe^{3+}), which are essential plant nutrients at higher pHs; and (iii) indirectly, by reducing the quality and range of food sources available to animals (e.g. fungal growth is reduced at low pH in streams (Hildrew *et al.*, 1984) and the aquatic flora is often absent or less diverse). Tolerance limits for pH vary amongst plant species, but only a minority are able to grow and reproduce at a pH below about 4.5.

In alkaline soils, iron (Fe^{3+}) and phosphate (PO_4^{3-}), and certain trace elements such as manganese (Mn^{2+}), are fixed in relatively

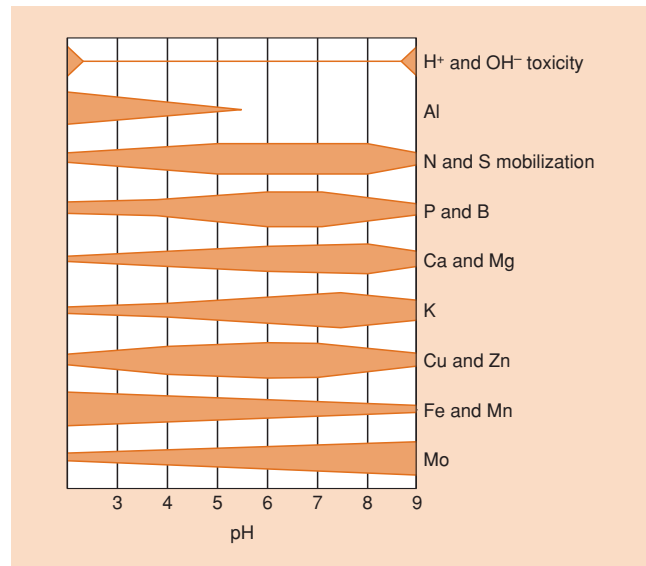


Figure 2.17 The toxicity of H^+ and OH^- to plants, and the availability to them of minerals (indicated by the widths of the bands) is influenced by soil pH. (After Larcher, 1980.)

insoluble compounds, and plants may then suffer because there is too little rather than too much of them. For example, calcifuge plants (those characteristic of acid soils) commonly show symptoms of iron deficiency when they are transplanted to more alkaline soils. In general, however, soils and waters with a pH above 7 tend to be hospitable to many more species than those that are more acid. Chalk and limestone grasslands carry a much richer flora (and associated fauna) than acid grasslands and the situation is similar for animals inhabiting streams, ponds and lakes.

Some prokaryotes, especially the Archaeobacteria, can tolerate and even grow best in environments with a pH far outside the range tolerated by eukaryotes. Such environments are rare, but occur in volcanic lakes and geothermal springs where they are

dominated by sulfur-oxidizing bacteria whose pH optima lie between 2 and 4 and which cannot grow at neutrality (Stolp, 1988). *Thiobacillus ferrooxidans* occurs in the waste from industrial metal-leaching processes and tolerates pH 1; *T. thiooxidans* cannot only tolerate but can grow at pH 0. Towards the other end of the pH range are the alkaline environments of soda lakes with pH values of 9–11, which are inhabited by cyanobacteria such as *Anabaenopsis arnoldii* and *Spirulina platensis*; *Plectonema nostocorum* can grow at pH 13.

2.6 Salinity

For terrestrial plants, the concentration of salts in the soil water offers osmotic resistance to water uptake. The most extreme saline conditions occur in arid zones where the predominant movement of soil water is towards the surface and crystalline salt accumulates. This occurs especially when crops have been grown in arid regions under irrigation; salt pans then develop and the land is lost to agriculture. The main effect of salinity is to create the same kind of osmoregulatory problems as drought and freezing and the problems are countered in much the same ways. For example, many of the higher plants that live in saline environments (halophytes) accumulate electrolytes in their vacuoles, but maintain a low concentration in the cytoplasm and organelles (Robinson *et al.*, 1983). Such plants maintain high osmotic pressures and so remain turgid, and are protected from the damaging action of the accumulated electrolytes by polyols and membrane protectants.

Freshwater environments present a set of specialized environmental conditions because water tends to move into organisms

from the environment and this needs to be resisted. In marine habitats, the majority of organisms are isotonic to their environment so that there is no net flow of water, but there are many that are hypotonic so that water flows out from the organism to the environment, putting them in a similar position to terrestrial organisms. Thus, for many aquatic organisms the regulation of body fluid concentration is a vital and sometimes an energetically expensive process. The salinity of an aquatic environment can have an important influence on distribution and abundance, especially in places like estuaries where there is a particularly sharp gradient between truly marine and freshwater habitats.

The freshwater shrimps *Palaemonetes pugio* and *P. vulgaris*, for example, co-occur in estuaries on the eastern coast of the USA at a wide range of salinities, but the former seems to be more tolerant of lower salinities than the latter, occupying some habitats from which the latter is absent. Figure 2.18 shows the mechanism likely to be underlying this (Rowe, 2002). Over the low salinity range (though not at the effectively lethal lowest salinity) metabolic expenditure was significantly lower in *P. pugio*. *P. vulgaris* requires far more energy simply to maintain itself, putting it at a severe disadvantage in competition with *P. pugio* even when it is able to sustain such expenditure.

2.6.1 Conditions at the boundary between the sea and land

Salinity has important effects on the distribution of organisms in intertidal areas but it does so through interactions with other conditions – notably exposure to the air and the nature of the substrate.

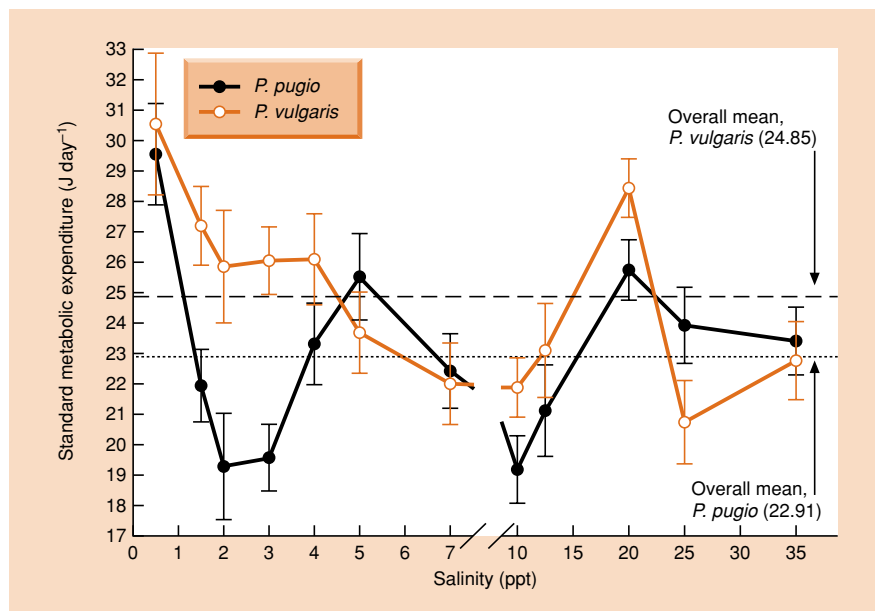


Figure 2.18 Standard metabolic expenditure (estimated through minimum oxygen consumption) in two species of shrimp, *Palaemonetes pugio* and *P. vulgaris*, at a range of salinities. There was significant mortality of both species over the experimental period at 0.5 ppt (parts per thousand), especially in *P. vulgaris* (75% compared with 25%). (After Rowe, 2002.)

Algae of all types have found suitable habitats permanently immersed in the sea, but permanently submerged higher plants are almost completely absent. This is a striking contrast with submerged freshwater habitats where a variety of flowering plants have a conspicuous role. The main reason seems to be that higher plants require a substrate in which their roots can find anchorage. Large marine algae, which are continuously submerged except at extremely low tides, largely take their place in marine communities. These do not have roots but attach themselves to rocks by specialized 'holdfasts'. They are excluded from regions where the substrates are soft and holdfasts cannot 'hold fast'. It is in such regions that the few truly marine flowering plants, for example sea grasses such as *Zostera* and *Posidonia*, form submerged communities that support complex animal communities.

Most species of higher plants that root in seawater have leaves and shoots that are exposed to the atmosphere for a large part of the tidal cycle, such as mangroves, species of the grass genus *Spartina* and extreme halophytes such as species of *Salicornia* that have aerial shoots but whose roots are exposed to the full salinity of seawater. Where there is a stable substrate in which plants can root, communities of flowering plants may extend right through the intertidal zone

in a continuum extending from those continuously immersed in full-strength seawater (like the sea grasses) through to totally non-saline conditions. Salt marshes, in particular, encompass a range of salt concentrations running from full-strength seawater down to totally nonsaline conditions.

Higher plants are absent from intertidal rocky sea shores except where pockets of soft substrate may have formed in crevices. Instead, such habitats are dominated by the algae, which give way to lichens at and above the high tide level where the exposure to desiccation is highest. The plants and animals that live on rocky sea shores are influenced by environmental conditions in a very profound and often particularly obvious way by the extent to which they tolerate exposure to the aerial environment and the forces of waves and storms. This expresses itself in the *zonation* of the organisms, with different species at different heights up the shore (Figure 2.19).

The extent of the intertidal zone depends on the height of tides and the slope of the shore. Away from the shore, the tidal rise and fall are rarely greater than 1 m, but closer to shore, the shape of the land mass can funnel the ebb and flow of the water to produce extraordinary spring tidal ranges of, for example, nearly 20 m in the Bay of Fundy (between Nova Scotia and New Brunswick, Canada). In contrast, the shores of the Mediterranean Sea

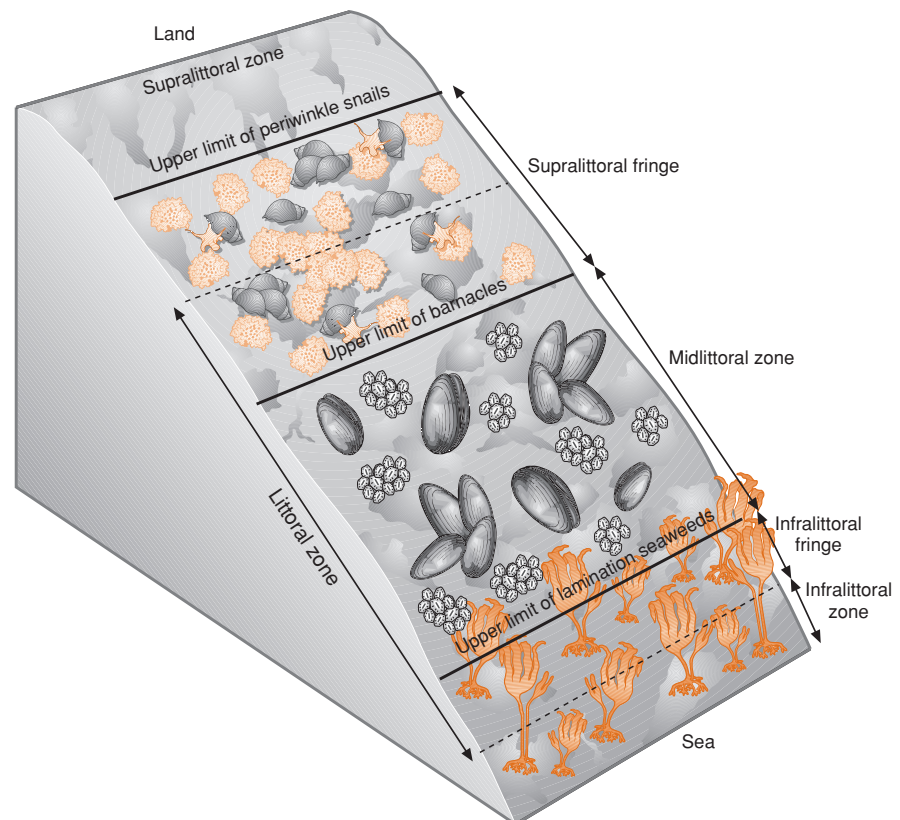


Figure 2.19 A general zonation scheme for the seashore determined by relative lengths of exposure to the air and to the action of waves. (After Raffaelli & Hawkins, 1996.)

experience scarcely any tidal range. On steep shores and rocky cliffs the intertidal zone is very short and zonation is compressed.

To talk of 'zonation as a result of exposure', however, is to oversimplify the matter greatly (Raffaelli & Hawkins, 1996). In the first place, 'exposure' can mean a variety, or a combination of, many different things: desiccation, extremes of temperature, changes in salinity, excessive illumination and the sheer physical forces of pounding waves and storms (to which we turn in Section 2.7). Furthermore, 'exposure' only really explains the *upper* limits of these essentially marine species, and yet zonation depends on them having lower limits too. For some species there can be *too little exposure* in the lower zones. For instance, green algae would be starved of blue and especially red light if they were submerged for long periods too low down the shore. For many other species though, a lower limit to distribution is set by competition and predation (see, for example, the discussion in Paine, 1994). The seaweed *Fucus spiralis* will readily extend lower down the shore than usual in Great Britain whenever other competing midshore furoid seaweeds are scarce.

2.7 Physical forces of winds, waves and currents

In nature there are many forces of the environment that have their effect by virtue of the force of physical movement – wind and water are prime examples.

In streams and rivers, both plants and animals face the continual hazard of being washed away. The average velocity of flow generally increases in a downstream direction, but the greatest danger of members of the benthic (bottom-dwelling) community being washed away is in upstream regions, because the water here is turbulent and shallow. The only plants to be found in the most extreme flows are literally 'low profile' species like encrusting and filamentous algae, mosses and liverworts. Where the flow is slightly less extreme there are plants like the water crowfoot (*Ranunculus fluitans*), which is streamlined, offering little resistance to flow and which anchors itself around an immovable object by means of a dense development of adventitious roots. Plants such as the free-floating duckweed (*Lemna* spp.) are usually only found where there is negligible flow.

The conditions of exposure on sea shores place severe limits on the life forms and habits of species that can tolerate repeated pounding and the suction of wave action. Seaweeds anchored on rocks survive the repeated pull and push of wave action by a combination of powerful attachment by holdfasts and extreme flexibility of their thallus structure. Animals in the same environment either move with the mass of water or, like the algae, rely on subtle mechanisms of firm adhesion such as the powerful organic glues of barnacles and the muscular feet of limpets. A comparable diversity of morphological specializations is to be found amongst the invertebrates that tolerate the hazards of turbulent, freshwater streams.

2.7.1 Hazards, disasters and catastrophes: the ecology of extreme events

The wind and the tides are normal daily 'hazards' in the life of many organisms. The structure and behavior of these organisms bear some witness to the frequency and intensity of such hazards in the evolutionary history of their species. Thus, most trees withstand the force of most storms without falling over or losing their living branches. Most limpets, barnacles and kelps hold fast to the rocks through the normal day to day forces of the waves and tides. We can also recognize a scale of more severely damaging forces (we might call them 'disasters') that occur occasionally, but with sufficient frequency to have contributed repeatedly to the forces of natural selection. When such a force recurs it will meet a population that still has a genetic memory of the selection that acted on its ancestors – and may therefore suffer less than they did. In the woodlands and shrub communities of arid zones, fire has this quality, and tolerance of fire damage is a clearly evolved response (see Section 2.3.6).

When disasters strike natural communities it is only rarely that they have been carefully studied before the event. One exception is cyclone 'Hugo' which struck the Caribbean island of Guadeloupe in 1994. Detailed accounts of the dense humid forests of the island had been published only recently before (Ducrey & Labbé, 1985, 1986). The cyclone devastated the forests with mean maximum wind velocities of 270 km h⁻¹ and gusts of 320 km h⁻¹. Up to 300 mm of rain fell in 40 h. The early stages of regeneration after the cyclone (Labbé, 1994) typify the responses of long-established communities on both land or sea to massive forces of destruction. Even in 'undisturbed' communities there is a continual creation of gaps as individuals (e.g. trees in a forest, kelps on a sea shore) die and the space they occupied is recolonized (see Section 16.7). After massive devastation by cyclones or other widespread disasters, recolonization follows much the same course. Species that normally colonize only natural gaps in the vegetation come to dominate a continuous community.

In contrast to conditions that we have called 'hazards' and 'disasters' there are natural occurrences that are enormously damaging, yet occur so rarely that they may have no lasting selective effect on the evolution of the species. We might call such events 'catastrophes', for example the volcanic eruption of Mt St Helens or of the island of Krakatau. The next time that Krakatau erupts there are unlikely to be any genes persisting that were selected for volcano tolerance!

2.8 Environmental pollution

A number of environmental conditions that are, regrettably, becoming increasingly important are due to the accumulation of toxic by-products of human activities. Sulfur dioxide emitted from power stations, and metals like copper, zinc and lead, dumped