1 Introduction: extreme life

In 1989, I was lucky enough to visit the Antarctic for the first time, as part of the New Zealand Antarctic Research Programme. I was looking for nematodes, a group of worm-like invertebrate animals that live associated with the algae and moss that grow in the meltwater from snow and glaciers, and around the edges of lakes and small ponds. I visited various sites around the McMurdo Sound area of Antarctica, including the Dry Valleys which form the largest area of ice-free land on the continent. Parts of the Dry Valleys are called 'oases', because they support some visible signs of life. If you were expecting palm trees, however, you would be disappointed. Small patches of moss are as good as it gets in this part of Antarctica. The organisms that live here face some of the most extreme conditions experienced on Earth.

We all have ideas as to what might be normal and extreme environmental conditions. We might like our normal environment to be lying on the back lawn in the dappled sunlight with a gin and tonic. The heat of the desert (without the gin and tonic!) or the cold and wind of the Antarctic or Arctic might, in contrast, seem somewhat extreme. For other organisms (and even other humans), however, these places are home. In this book, I aim to explore the adaptations that have enabled organisms (including plants, animals and microbes) to live in situations that we might consider extreme and to try to develop a framework for thinking about organisms and extreme environments.

WHAT IS EXTREME?

Many organisms experience environmental conditions that seem to us to be relatively 'normal', but some are able to survive or even thrive in conditions which we might regard as 'extreme'. This judgment is based on our own experience of our environment. The great majority of organisms live permanently in the sea. We would find more than a brief immersion beneath the waters of the sea an extreme stress, unless we had special equipment, but what we would find extreme is normal for marine organisms. There is clearly a problem with defining extreme conditions by our own experience. Can we develop less subjective criteria for determining what might be normal and what might be extreme for an organism?

Measuring the responses of organisms to changes in environmental conditions might provide the tools we need. Let us use the effect of temperature as an example. The responses of organisms to temperature are complex. The simplest response to temperature is that there is an optimum, at which activity, growth rates and metabolism are greatest, and a range of temperatures that an organism will survive (Figure 1.1). As the temperature increases or decreases from the optimum, the metabolism of the organism decreases. If the temperature becomes more extreme, the organism may display heat or cold stupor, in which movement becomes disorganised and normal processes are disrupted. Close to the limit of the tolerable range of temperatures, the organism will display heat or cold coma and cease activity altogether. Once the temperature limits are exceeded, it will die. Establishing the temperatures at which these changes in activity occur for an organism may allow us to determine what is 'normal' and 'extreme' with respect to temperature for that organism. Defining these transition temperatures may, however, not be easy because the organism may respond to changing temperature by initiating biological responses that extend the survivable limits. In the case of low temperatures, the temperature at which metabolism ceases may not represent the point at which the organism dies.

There are important differences between the lethal effects of high and low temperatures. The damage caused by high temperature is destructive as proteins become denatured and other irreversible changes occur. The effect of low temperature may be rather different. As the temperature falls, metabolism slows (and if the temperature is low enough, it ceases) as the kinetic energy imparted to chemical reac-

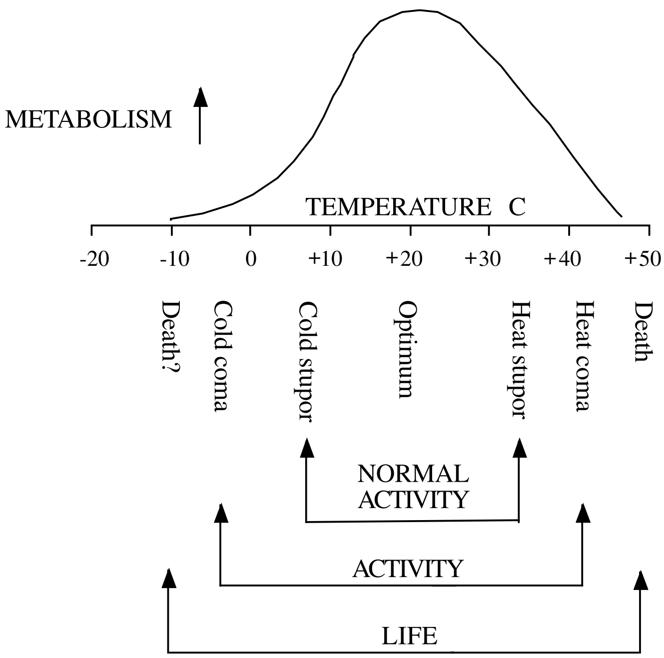

FIGURE 1.1 The responses to temperature in a hypothetical organism. At low temperatures, metabolism is undetectable. As the temperature increases, the rate of metabolism increases due to the increased kinetic energy supplied to reactions. Beyond the optimum temperature, however, metabolism slows and eventually ceases due to the damaging and lethal effects of high temperature. Changes in activity are associated with these changes in temperature. As the temperature increases or decreases from the optimum, the organism may become disorientated and normal processes disrupted (heat or cold stupor) and then cease altogether (heat or cold coma). Death may then result. These transitions define the ranges over which normal activity and life can occur.

tions decreases. This effect is potentially reversible. Death may result, however, from events such as irreversible changes in membrane function, although freezing, or the risk of freezing, is likely to be the major hazard. Freezing involves a change in the state of water within the organism from a liquid to a solid. This can be a sudden and violent event, and initiates a number of changes that may result in death, unless the organism has mechanisms which enable it to survive the stresses involved. The lethal effects of heat are unlikely to be due to a change of state in body water since, for most organisms, their upper lethal temperature is many degrees lower than the temperature at which water boils.

THE LIFE BOX

Just as there are ranges for survival and activity with respect to temperature, the same is true for other environmental variables (such as salinity, conditions of acidity or alkalinity, oxygen concentration etc.). We could measure conditions (temperature, pH, salinity etc.) in the environment adjacent to an organism. If we did this lots of times over the lifespan of the organism, we could determine the range of conditions it has experienced. Some organisms move around, experiencing changes in environmental conditions, and conditions themselves change with time. Plotting these measurements in multidimensional space would thus define the overall range of conditions that the organism has experienced (its 'life box'; Figure 1.2). I have experienced −26 °C in the Antarctic and +45 °C in the Australian desert and so my life box would extend between these two values for the parameter of temperature. If we did the measurements for all organisms of the same species, we could define the life box for that species, and thus the sort of habitats in which that species could live. If we did the measurements for all organisms of all species, we could define the life box for life in general. If conditions change such that an organism finds itself outside the life box for its species, it will die. If conditions are such that they are outside the life box for life in general, there will be no life. Ecologists call an organism's life box its 'ecological niche'. This is determined by both the physical characteristics of its environment (temperature, pH, water availability etc.) and its interactions with other organisms (predation, competition, disease, the food source it exploits etc.). I have used the term 'life box' to focus attention on the range of physical conditions that organisms can tolerate and because it might help us to identify what is extreme for organisms.

To decide what might be an extreme organism, it might be useful to think in terms of the life box for the majority of organisms or for the

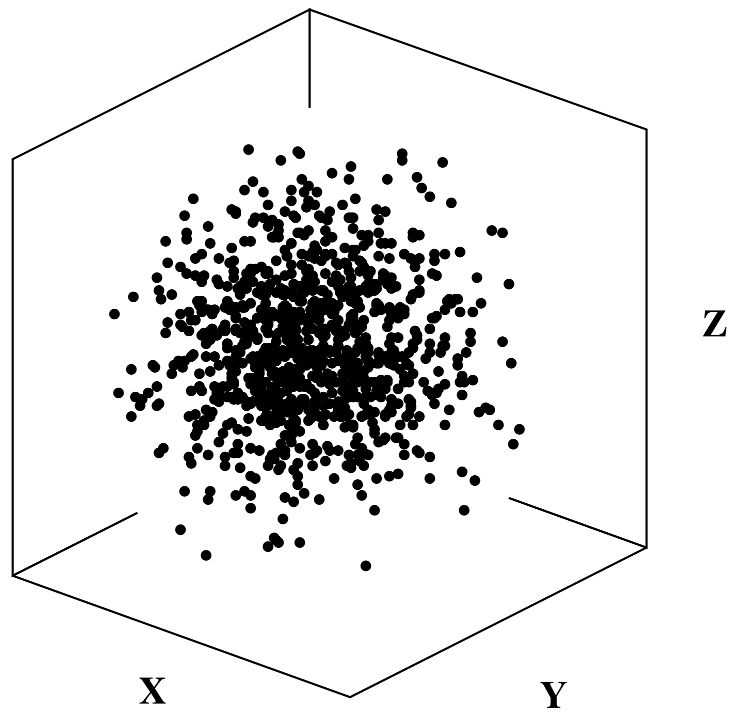

FIGURE 1.2 The life box of a hypothetical organism with respect to three environmental variables (x, y, z; e.g. temperature, pH, oxygen availability). Each point represents the conditions experienced and survived by the organism at a particular place and moment in time. The conditions experienced and survived at all places and times defines the life box for the organism or species of organism. If the conditions go beyond its life box, the organism dies.

majority of species of organism. An extreme organism would, therefore, be one that tolerates conditions beyond those tolerated by most organisms. The range of conditions for such an organism will be different from that for the majority of organisms, and it will have a life box which occupies a different theoretical space from that of most organisms (Figure 1.3). Such organisms have been called extremophiles (they love conditions which are far removed from the ordinary or average). The best-known examples are thermophilic bacteria that live associated with hot springs and deep-sea hydrothermal vents, where the temperatures they experience are much higher than those experienced

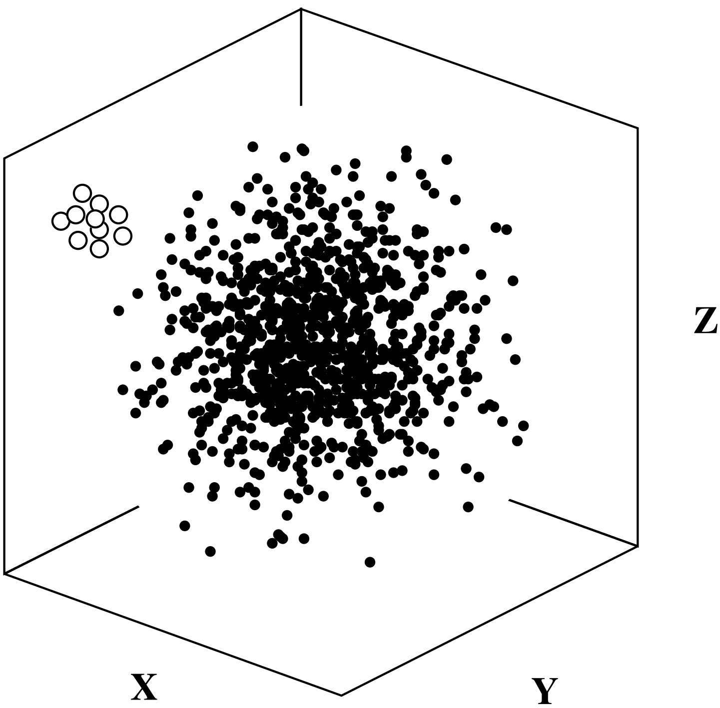

FIGURE 1.3 The life box of an extremophile (○) compared with that of the majority of organisms. For the extremophile, the range of conditions that it will survive is different from that survived by the majority of organisms. Its life box thus occupies a different theoretical space.

by most organisms. There are extremophiles that colonise other types of extreme environments – such as very saline habitats (halophiles), acidic or alkaline conditions (acidophiles, alkaliphiles), low temperatures (psychrophiles) and high pressures (piezophiles).

There is, however, another group of organisms that can be considered to be extreme. In terms of the conditions in which they can maintain activity, their life box is the same as, or considerably overlaps, the life box of the majority of organisms. However, when conditions change to the point where the organism can no longer sustain metabolic activity, rather than dying, they cease metabolism and enter into an ametabolic dormant state. When conditions return to normal, they

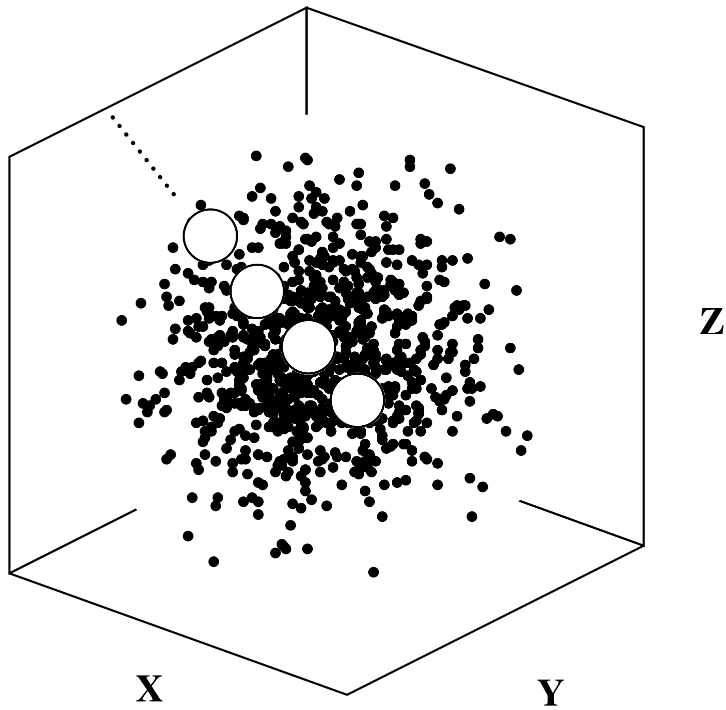

FIGURE 1.4 The life box of a cryptobiote, only here the symbols represent conditions under which the organism can metabolise rather than survive. Its life box is thus the same as, or considerably overlaps, the life box for the majority of organisms (see Figures 1.2 and 1.3). When conditions change to beyond those in which the cryptobiotic organism can metabolise (····○····), metabolism ceases, but the cryptobiote can resume metabolism once conditions become favourable again.

resume activity. In other words, if we think of life in terms of metabolism, they have the capacity to step outside their life box and to become active again once conditions become favourable (Figure 1.4). This phenomenon has been called cryptobiosis (hidden life), anabiosis (renewed life) or latent life. Latent life is perhaps the most appropriate term, since, in the latent state, the capacity for life is present but is not apparent. Cryptobiosis is, however, the most commonly used term. Some cryptobiotic organisms can enter this state at any stage in their life cycle. Others have special survival and dispersal stages, which act as lifeboats that carry organisms to new habitats, or which enable them to survive periods unsuitable for growth. This ability enables them to survive in space and time until conditions are favourable. These lifeboats include spores, eggs, cysts, seeds and resistant larval stages.

Cryptobiotic organisms can survive a variety of environmental stresses. Some can survive the complete loss of their body water. This phenomenon has been called 'anhydrobiosis' (life without water). Other types of cryptobiosis include cryobiosis (extreme cold), thermobiosis (heat), osmobiosis (osmotic stress, such as high salt concentrations) and anoxybiosis (lack of oxygen). A number of organisms enter a period of dormancy in which their activity levels are lowered in response to these types of environmental stresses. The lowering of metabolic rate may be to as little as 80 per cent of normal resting levels, but more typically to a point in the range of 5–40 per cent of resting levels. Cryptobiosis is distinguished from dormancy by resulting in a depression of metabolic rate to less than 1 per cent of resting levels or even ceasing altogether.

WHO WANTS TO LIVE FOREVER?

How long can organisms survive in a state of cryptobiosis? For nematodes, the record is 39 years. Rotifers (another group of microscopic invertebrate animals) have been revived from dried herbarium specimens that were 120 years old. Plant seeds can lie dormant for many years. The ancient English herbs weld and mullein grew from soil from a Carthusian priory that was closed during the dissolution of the monasteries by Henry VIII between 1536 and 1540. These 400-year-old seeds, the plants of which had not been seen in England since medieval times, grew after the soil containing them was brought to the surface after an archaeological dig. The oldest seed ever germinated is a 1300-year-old lotus seed from China.

Microorganisms hold the most remarkable records for longevity. Bacteria have grown from spores from a 118-year-old can of meat (canned veal taken on Parry's Arctic expedition, 1820–1830). Beer has been brewed from yeast isolated from a bottle of porter ale which was taken from the wreck of a sailing barge that lay off the coast of the English port of Littlehampton for 166 years. Somewhat more controversial are reports of bacteria that may be millions of years old. Bacteria have been isolated from rocks, salt deposits and permafrost (permanently frozen soil). Many have doubted these reports since it is difficult to prove that samples have not been contaminated with bacteria of more recent origin. The most convincing claims concern those from specimens that are naturally protected against contamination. Bacterial spores (from the genus *Bacillus*) were isolated from a bee preserved in amber estimated to be 20–40 million years old. The material was protected against contamination by the amber, the surface of which was carefully sterilised before the sample was taken. Bacteria (also a *Bacillus*) have been isolated from liquid inclusions enclosed within salt crystals and estimated to be 250 million years old. Like those isolated from amber, the material was protected from contamination by the salt crystal and extreme care was taken to prevent contamination during sampling. If the evidence for these sorts of claims holds up, there is no reason not to believe that bacterial spores can be immortal.

EXTREME LANGUAGE

I have mentioned a number of terms that describe organisms which grow in or survive extreme environmental conditions. Perhaps I'd better explain these terms a bit more before we go any further. There is an imposing terminology that has been developed by scientists working on different types of organisms and different types of environmental stress. Organisms that grow best under extreme conditions (the conditions for their optimal growth is much higher or lower than the average for most organisms) are referred to as being extremophilic. The ending '-philic' means 'loving' (from the Greek 'philia', meaning affection or fondness). Organisms that can survive extreme conditions but whose optimal growth conditions lie within the more normal range are referred to as being 'tolerant'. The extreme conditions result in a reduction in metabolism and a period of dormancy which the organism can survive. Where metabolism ceases altogether, organisms are called cryptobiotic. This means 'hidden life' and is derived from the Greek words for hidden ('kryptos', hide or conceal) and life ('biosis').

Terms which describe the responses to different environmental stress are derived by adding these endings to roots for the particular stress. The roots are: thermo- (heat, from the Greek 'therme'), cryo- or psychro- (cold, from 'kryos' for icy cold and 'psychros' for cold or frigid); anhydro- or xero- (desiccation, from 'anhydros' for waterless and 'xeros' for dry); piezo- or baro- (pressure, from 'piezo' for press and 'baros' for weight); halo- or osmo- (osmotic stress, from 'halos' for salt and 'osmos' for pushing); and acido- or alkali- (low and high pH). A lack of oxygen is referred to as anaerobic (without air) or anoxic (without oxygen). These terms are summarised in Table 1.1.

EXTENDING THE LIFE BOX

Extremophiles thrive in extreme environments, while cryptobiotes can survive extreme conditions until more moderate conditions return. There are, however, other responses to extreme conditions. Organisms may avoid the extreme conditions by migrating to more favourable ones. Snow geese avoid the cold of the Arctic winter by migrating south to more moderate conditions. Desert insects avoid desiccation and heat during the day by burrowing into the sand. Some organisms can modify their external or internal environment to make conditions more normal and less extreme. In the case of temperature, this type of response is mainly found in birds and mammals.

Most organisms are ectotherms – they are at the same temperature as that of their environment. Birds and mammals, however, are endotherms. They can generate their own heat and maintain a higher temperature within their bodies than that in their surrounding environment. This is achieved firstly by burning fuel (food) to generate heat through metabolism and secondly by mechanisms to reduce the loss of heat to the environment, such as through insulation (fur,