

Prospects for survival in the Southern Ocean: vulnerability of benthic species to temperature change

L.S. PECK

*British Antarctic Survey, NERC, High Cross, Madingley Rd, Cambridge CB3 0ET, UK
lspe@bas.ac.uk*

Abstract: Organisms have a limited number of responses that enhance survival in changing environments. They can: 1. Cope within existing physiological flexibility; 2. Adapt to changing conditions; or 3. Migrate to sites that allow survival. Species inhabiting coastal seabed sites around Antarctica have poorer physiological capacities to deal with change than species elsewhere. They die when temperatures are raised by only 5–10°C above the annual average, and many species lose the ability to perform essential functions, e.g. swimming in scallops or burying in infaunal bivalve molluscs when temperatures are raised only 2–3°C. The ability to adapt, or evolve new characters to changing conditions depends, at least in part, on generation time. Antarctic benthic species grow slowly and develop at rates often x5–x10 slower than similar temperate species. They also live to great age, and exhibit deferred maturity. Longer generation times reduce the opportunities to produce novel mutations, and result in poorer capacities to adapt to change. Intrinsic capacities to colonize new sites and migrate away from deteriorating conditions depend on adult abilities to locomote over large distances, or for reproductive stages to drift for extended periods. The slow development of Antarctic benthic species means their larvae do spend extended periods in the water column. However, whereas most continents have coastlines extending over a wide range of latitude, Antarctica is almost circular in outline, is isolated from other oceans by the circumpolar current, and its coastline covers few degrees of latitude. Thus in a warming environment there are fewer places to migrate to. On all three major criteria Antarctic benthic species appear less capable than species elsewhere of responding to change in ways that can enhance survival.

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Introduction

One of the main current topics in biology concerns how environments are changing, and how these changes are affecting, or going to affect life on Earth. There is an overwhelming body of evidence showing the Earth has warmed over the last 100 years and global air temperatures are now around 0.75°C warmer than they were in the early years of the 20th century (Jones *et al.* 1999, IPCC 2001a). There is also now wide acceptance that warming will continue, that other environmental characters are also changing and will change further (MacCracken *et al.* 2003). It is clear that human activity is probably playing the major part in this change through the burning of fossil fuels and the consequent atmospheric increase in greenhouse gasses such as carbon dioxide (IPCC 2001a).

Consequent with the environmental change is concern over what the impacts will be on life and how it might respond. There is great concern for the future of agricultural systems and also for major ecosystems, and the effects that their disruption may have for human societies. There is particular concern for the effects of degradation of soil and water resources on global productivity (IPCC 2001b). For coastal zones and marine ecosystems global predictions are that sea level will rise, sea ice cover will decrease and there

will be changes in salinity, alkalinity, wave climate and ocean circulation.

One of the main areas where we lack knowledge is the potential for faunas to respond to this change, and this is especially so for polar marine groups. In this review I will evaluate the various mechanisms available to organisms to respond to change, and how species living on the seabed in coastal regions of Antarctica compare to species from elsewhere in their ability to cope with change.

Environmental variation and organism responses to change

In general terms we can envisage that under normal conditions organisms have a certain amount of capacity to use to sustain their biological requirements and that as the environment varies more or less of that capacity is used to cope with the demands (Fig. 1a). Any remaining capacity above that required proximately can be viewed as spare capacity, or scope, and this can be used for other functions. If the environment changes and the costs are raised then the amount of spare capacity remaining is reduced. As long as the environmental load is maintained within the overall biological capacity long-term survival is not compromised

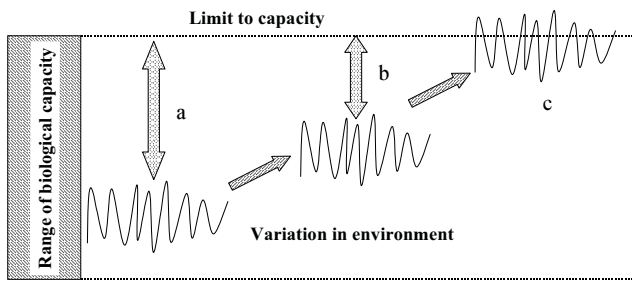


Fig. 1. Schematic representation of the physiological cost to an organism presented by varying environmental conditions. **a.** Physiological costs to exist in the conditions are well within the organism's capabilities, and significant spare capacity exists. **b.** The environment has changed and costs have generally increased, decreasing the remaining spare capacity. **c.** The environment has changed to a point beyond the organism's capacity range, and survival is compromised. Short-term environmental variations (fluctuations/oscillations in signals at either a, b or c) indicate variations on daily, monthly or seasonal levels, and cause variations in costs that organisms experience outside of any global or regional scale change.

(Fig. 1b). However, if environmental requirements are moved beyond the bounds of the biological capacity then survival becomes time limited (Fig. 1c).

Some scientists are concerned with the possibility that climate will change in a non-linear fashion, and that variability in the earth system will increase. A few recent models have even tested this possibility and indicated that climate variability is increasing and may increase further in the coming decades (Schär *et al.* 2004). Increased variability changes the stresses on organisms and would, at least initially, be expected to take them outside their biological capacity range for shorter periods than would a consistent change in conditions (Fig. 2). In these circumstances conditions and costs to the organism go outside the range of biological capacity for relatively short

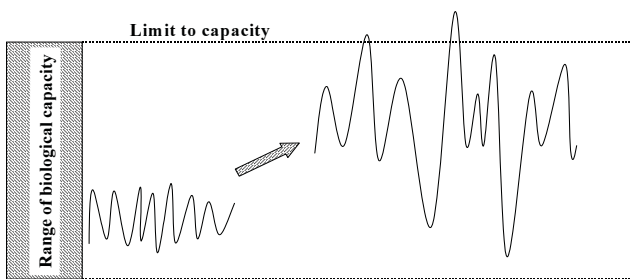


Fig. 2. Schematic representation of the change in physiological cost to an organism when the environment changes such that variation in conditions and costs are increased. In this example conditions do not change to maintain the range of short-term environmental fluctuation as seen in Fig. 1, but the change produces a marked increase in short-term environmental fluctuation.

and infrequent periods. Survival here depends on the organisms' ability to sustain biological processes in markedly sub-optimal conditions. An analogous situation to this is where animals perform activity and can maintain aerobic conditions in their tissues until the levels of activity are increased to a point beyond that of the oxygen delivery system. This is seen in human sprinters, where activity levels are high and anaerobic metabolism is recruited, but can only be sustained for short periods. Over longer timescales it may mean that in some seasons conditions preclude animals from breeding, but longer-term survival is possible because reproduction is possible in other years. A similar situation to this is seen in metapopulations of animals where within the core range all aspects of the biology of a given species are possible. Populations exist outside the core range, but these are maintained by colonisation from populations within the core (Hanski 1998, 1999). Thus as conditions deteriorate further from the core of the distribution organisms in the metapopulation have decreasing biological capacity to perform all of their functions until there is insufficient scope to maintain populations. At this point populations are maintained from individuals in the core range.

A second way that organisms can cope with a changing environment is to adapt to the new conditions and alter the range of biological capacity. This response to a changing environment means that either the range of capacities is expanded or moved to a different position (Fig. 3). This is effected either within individuals by adaptation or from generation to generation via mutation and evolutionary processes. These different responses work at very different timescales.

The third main response that organisms can have to changing environments is to migrate to areas where conditions are favourable. Abilities to migrate depend on many factors, including numbers of propagules produced, distances to, and size of, colonisable areas and time spent

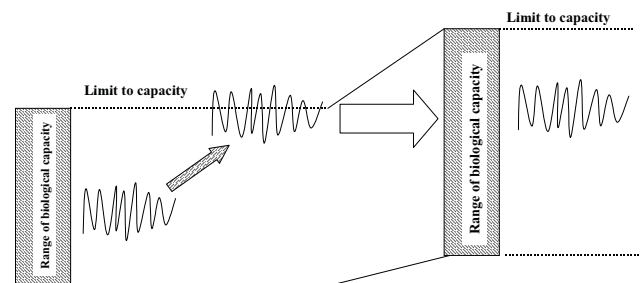


Fig. 3. Schematic representation of adaptational responses to changing environmental costs. Initially costs are within the organism's biological capacity. The environment then changes and moves outside of the capacity range. Through adaptational or evolutionary mechanisms the biological capacity of the organism is changed to encompass the new environmental range.

dispersing by propagules. For species living and dispersing in the sea via larvae the strength and direction of oceanic currents can also have a major effect. In a changing environment the rate of change and stability of habitats becomes important as well, because the time required for the establishment of new communities, and the suitability of new environments are all affected by rate of change.

The remainder of this review will evaluate Southern Ocean benthic environments, the characteristics of Antarctic marine benthic species, and their potential to respond to change.

Southern Ocean benthic environments

The Southern Ocean has an area of 35×10^6 km², of which 7×10^6 km² are permanently ice covered and 14×10^6 km² are seasonally covered in ice (Clarke & Johnston 2003). The 28×10^6 km² of seasonally or permanently open water account for around 7.7% of the world's oceans by area. The length of coastline in the Southern Ocean is 39 200 km, 86.3% of which is either ice front or permanently ice covered (Clarke & Johnston 2003). These areas are therefore unavailable for colonization by benthic species. The remaining 5370 km of rocky coast accounts for around 1% of global coastlines, although this measure varies somewhat with the scale of measurement. Continental shelf area is difficult to assess for Antarctica, because the 35 quadrillion tonnes of ice in the ice sheet pushes the continent into the Earth, depressing the continental shelf by up to 1 km. If the break between continental shelf and slope is used as the criterion the Antarctic continental shelf extends to over 1 km depth and covers an area of about 3×10^6 km², or 11% of the world's continental shelf area (Clarke & Johnston 2003). However, continental shelves around the world rarely extend beyond 200 m depth (Walsh 1988), and continental shelves are not considered to extend beyond 400 m depth. Also, 1000 m depth is sometimes considered deep-ocean. Certainly depths of 500–1000 m are biologically very different from shallower sites. If Antarctica's shelf is taken to extend to 400 m depth its area is around 1.3×10^6 km², or just under 5% of the earth's continental shelf. These two definitions of continental shelf differ in that one is based on the change in slope of seabed morphology and occurs at 1000 m depth, while the other, at 400 m depth is based on biological criteria.

The interface between the Southern Ocean and its adjacent oceans, called the Polar Frontal Zone (PFZ) is marked by a sharp temperature discontinuity between water masses. Southern Ocean surface currents also circulate in a clockwise direction around the continent. These two factors have formed a barrier to colonization from outside since Antarctica and South America separated around 35 m.y.a. (Livermore *et al.* 2004). This forms a distinct barrier to colonisation currently, but may not have been a complete barrier over the whole of the last 35 million years, as shown

by relatedness studies of bivalve molluscs inside and outside the PFZ (Page & Linse 2002).

Temperatures in the Southern Ocean are both low and stable. At the most variable sites, such as Signy Island in the South Orkney Islands temperatures range from -1.8°C in winter to between $+0.5^\circ\text{C}$ and $+1.0^\circ\text{C}$ in summer (Clarke 1988), whereas at the most stable sites, such as McMurdo Sound temperatures rarely, if ever, range above -0.5°C and the total annual variation in sea temperature is less than 1.5°C (Hunt *et al.* 2003). Other environmental characters vary markedly. Light regimes vary from 24 h darkness in winter to 24 h light in summer and almost the entire Antarctic coastal zone and continental shelf is seasonally covered in ice. This drives an extreme seasonality of primary production, which feeds into the whole of the benthic ecosystem, making it one of the most seasonal environments on Earth (Clarke 1988, Clarke & Leakey 1996). This is especially so for herbivorous suspension feeders, who see their food supply vary by over three orders of magnitude from winter to summer. This seasonality also becomes more intense with latitude, with summers becoming progressively shorter towards the pole.

Antarctic benthic environments are also characterized by physical disturbance. This disturbance varies with depth, exposure and proximity to ice fronts or calving glaciers. In shallow sites, less than 20 m depth, some areas are impacted at least once per year and 60% of seabed in some bays is disturbed by icebergs (Brown *et al.* 2004). In shallow sites recovery varies with the dispersal and colonization mechanisms of the organisms involved. Recovery can be fast for mobile species such as the isopod *Serolis polita* Pfeffer, small species that can be advected back to the impact site, such as the small bivalve *Mysella charcoti* Lamy can return due to strong currents or storm induced water movements, but recovery can take several years for species such as the large infaunal bivalve *Laternula elliptica* (King & Broderip) that return via new larval recruitment (Peck *et al.* 1999). In deeper sites recovery from disturbance is evaluated in terms of community structure and the species composition present (Teixidó *et al.* 2004). Because recovery from disturbance takes many years in Antarctic seas, and disturbance varies in intensity with several factors, but is also a stochastic event, the result is a very patchy environment, with shallow sites often permanently in stages of recovery (Brown *et al.* 2004, Teixidó *et al.* 2004).

When the strong variation in disturbance with both depth and site is combined with the latitudinal gradients in light regime, ice cover and seasonality of phytoplankton productivity, a markedly heterogeneous environment is produced. This marked heterogeneity produces a very wide range of habitat for species to exploit.

Characteristics of Southern Ocean benthos

There is currently a strong debate worldwide on how biodiversity should be measured (e.g. Gray 2000), and there are many formal definitions of what biodiversity is (Clarke & Johnston 2003). There are three main ways of measuring biodiversity. The first is purely to count the species present. Species can be viewed as the fundamental unit of diversity (Claridge *et al.* 1997), but there are some drawbacks with this approach. Clearly a community comprised predominantly of species of fungus living in a soil has a different type of diversity from a soil community made up of algae, fungi and invertebrates, even though the same number of species may be present. This is called taxonomic distinctness, and several interesting diversity indices have been developed recently that include taxonomic distinctness (Webb 2000, Warwick & Clarke 2001). Of the two, species counts are the easiest and most rapid way of making biodiversity evaluations, and they are especially useful when large geographic areas are being compared. The third commonly used method to measure diversity is to measure molecular diversity. This is a new and challenging way of measuring diversity. It is used to evaluate the functional diversity of communities, and it also allows cryptic species

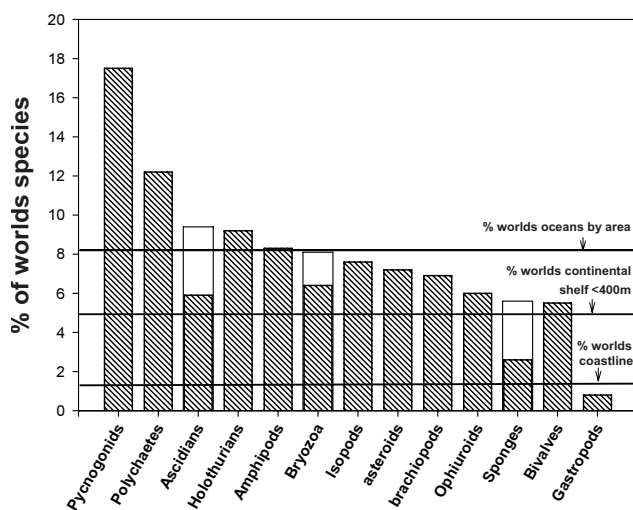


Fig. 4. Proportions of world species located in the Southern Ocean for the major benthic taxa. Data are from Clarke & Johnston (2003), with the exception of that for brachiopods (new data) and for isopods, where many recent species have been described and the current number of identified species is over 670 (A. Brandt, personal communication 2004) compared with the 257 quoted in Clarke & Johnston (2003). Taxa with open and closed bars indicate groups with minimum and maximum possible values in Clarke & Johnston (2003). Southern Ocean proportion of world oceans by area, continental shelf and coastline are also shown. The continental shelf measure is taken as seabed area shallower than 400 m depth (see text). Proportion of world's coastline is taken as rocky coast not covered by ice shelf or ice front.

that look alike to be differentiated. Currently molecular diversity methods are only used extensively for microbial studies, but their use for macro-organisms is rising rapidly.

Recent investigations have shown that the species diversity of animals living on the seabed (benthic species) in the Southern Ocean is higher than expected. Between 4000 and 4500 species living on the seabed have been described from Antarctica. In a detailed review of biodiversity in Antarctic marine benthos Clarke & Johnston (2003) showed that while some groups, notably the reptant decapods and gastropod molluscs, are markedly under represented or absent, other groups are more diverse and have more species in Antarctic waters than the average for the rest of the world (Fig. 4). The most striking of these are the sea spiders (*Pycnogonida*), where 17.5% of the world's species are in the Southern Ocean, and polychaete worms, where the figure is 12.2%. This compares with the Southern Ocean accounting for around 8.5% of world's oceans by area, just under 5% by continental shelf area, and under 2% by rocky coastline length. Many other benthic groups have between 5% and 10% of the world's total of species described so far in the Southern Ocean, including ascidians, holothurians, bryozoa, amphipods, isopods, brachiopods and sponges. On the basis of seabed area these groups are all more highly represented than the average for the planet. In an evaluation across all taxa Gutt *et al.* (2004) concluded that Antarctic benthos exhibit species richness that falls within the ranges for tropical, or temperate regions. Thus biodiversity on the Antarctic seabed is higher than expected, which is in marked contrast with the Arctic, where diversity is much lower (Piepenburg *et al.* 1997).

The Antarctic marine benthic fauna is characterized by slow physiological rates and extended life histories (Peck 2002). Growth rates, with one or two exceptions are generally x2 to x5 or more slower than related or

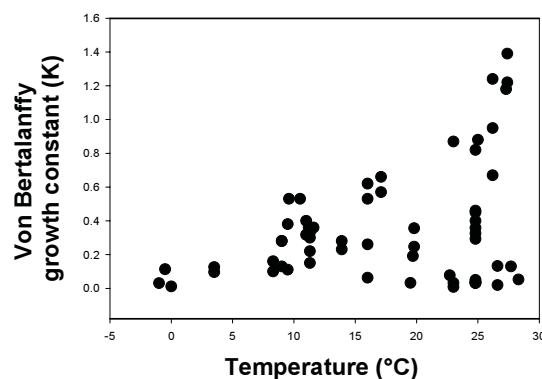


Fig. 5. Growth constant values (k) from the von Bertalanffy growth equation for echinoids from different latitudes. Temperature data used were either taken directly from published growth papers or calculated from the LEVITUS94 Ocean Climatology data set (<http://ingrid.Ideo.columbia.edu>). Figure from Brockington 2001.

ecologically similar species from lower latitudes (Everson 1977, Arntz *et al.* 1994, Peck *et al.* 2000). The quoted exceptions are two sponges (Dayton *et al.* 1974), three ascidians (Rauschert 1991) and a bryozoan (Barnes 1995). The growth rates for these species are quoted as comparable with temperate species, and hence demonstrating compensation for polar conditions. However, these are the fastest growth rates reported from the Southern Ocean, and they are much slower than the fastest rates for comparable species from lower latitudes. If the overall range of growth observed in Antarctic waters is compared with temperate and tropical species then growth is significantly slower at the higher latitudes. This was shown clearly in a study of growth in echinoderms by Brockington (2001), who compared values for the growth constant *K* from the von Bertalanffy growth equation for tropical temperate and polar echinoids (Fig. 5). Here the highest *k* values for polar species are higher than the lowest values for temperate and tropical species, but it is clear that the whole range of growth rates decreases with latitude.

The corollary of slow growth is extended life spans and deferred sexual maturity, leading to slowed overall life histories. Data on life spans and life histories are more limited. However, the brachiopod *Liothyrella uva* Broderip lives to over 50 years (Peck & Brey 1996), and does not reproduce until it is at least 20 years old; the bivalve *Yoldia eightsi* Courthouy lives to well over 40 years (Nolan & Clarke 1993) and does not begin reproducing until it is at least 12 years old (Peck *et al.* 2000). These values are greatly extended over most temperate brachiopods and bivalves, although some northern bivalves with Arctic and cool temperate distributions such as *Arctica islandica* Linn.

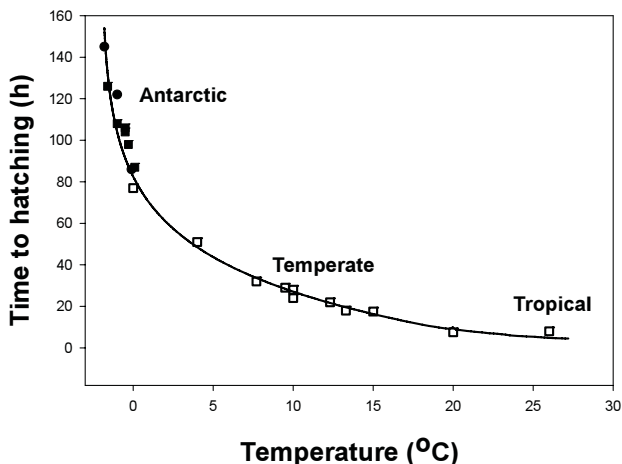


Fig. 6. Duration of embryonic development for echinoids from different latitudes. Data shown are the time taken from fertilisation of eggs to hatching of embryos from tropical, temperate and polar species. All experiments were conducted at naturally occurring temperatures for that species. Figure modified from Bosch *et al.* (1987) (open symbols) and Stanwell-Smith & Peck (1998) (closed symbols).

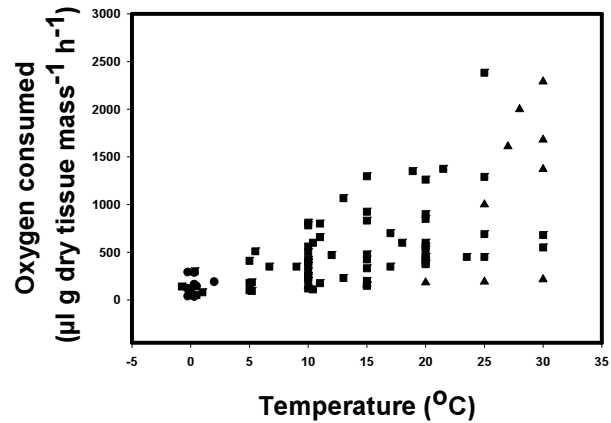


Fig. 7. Oxygen consumption values for bivalve molluscs from different latitudes. Data presented are resting, routine or standard rates for species held within the range of their normal habitat temperatures. Where data were available for winter and summer rates for species inhabiting a wide temperature range two values are included. ▲ indicates tropical species, ■ indicates temperate species, ● indicates polar species. For each 10°C rise in temperature the average, maximum and mean rates of oxygen consumption all rise by factors of x2 to x3. From Peck & Conway (2000).

also live to great age.

Development rates of Antarctic marine benthos are also markedly slowed compared to species from lower latitudes, and so far no exceptions have been identified. The best data published so far are for echinoderms (Bosch *et al.* 1987, Stanwell-Smith & Peck 1998) show that development in Antarctic echinoids is slowed around x5 compared with temperate species (Fig. 6). Strong data showing markedly slowed development have been compiled for other groups including amphipods (Klages 1993), isopods (Wägele 1987), nemertean (Peck 1993), brachiopods (Peck & Robinson 1994), and for a range of bivalve molluscs (Powell 2001). Similar slowing is evident in both free spawning species and those that exhibit protected larval development (e.g. Hain 1991). In these studies development rates in Antarctic benthic invertebrates were between x2 and x20 slower than temperate species. In a detailed analysis of factors controlling development rate of marine invertebrate larvae across latitude, Hoegh-Guldberg & Pearse (1995) concluded that temperature is the dominant factor, as opposed to seasonality of resource supply.

Like growth and development, metabolic rates of species inhabiting the seabed around Antarctica are slow. In a similar way to the growth comparison, the fastest Antarctic metabolic rates are higher than the lowest from temperate and tropical zones, but analyses of the whole range of metabolism show a consistent decrease in metabolic rate with latitude (Fig. 7). Good data for this exist for fish (Clarke & Johnston 1999) and bivalve molluscs (Peck & Conway 2000). Early claims of elevated metabolic rates in

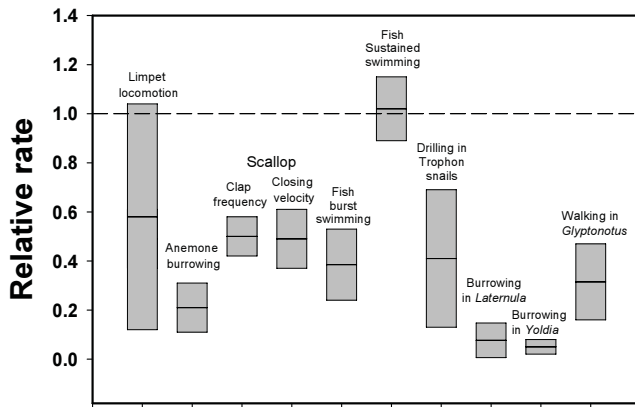


Fig. 8. Rates of accomplishing various activities for a range of Antarctic marine invertebrates and fish compared with related or ecologically similar temperate species. The hatched line indicates representative rates for temperate species and is set at a value of 1. Boxes show the range of values, with the midline indicating the mean. Figure modified from Peck *et al.* (2004a), including data on walking in the isopod *Glyptonotus* from Young (2004).

Antarctic ectotherms, and mainly in studies of fish have been generally discounted (Holeton 1974). The consensus now is that metabolic rates of Antarctic marine ectotherms are low compared to other latitudes. Over the whole latitudinal range oxygen consumption in bivalve molluscs increases by x2 to x3 for every 10°C rise in temperature (Peck & Conway 2000). Thus, metabolic rates in Antarctic benthic species are x8 to x27 lower than species living at 20°C. These low metabolic rates reflect the slower pace of life. They also bring a large advantage in that much less energy is required to survive periods of low food availability in winter, and this may be the driving force producing the low observed metabolism. Because less energy is needed to survive winter large fat stores are absent in the benthos, in contrast with pelagic species, and many Antarctic marine benthic species utilize proteins during periods of starvation (Clarke & Peck 1991). Over the last 10 years this strategy has been shown to be widespread in the Southern Ocean, with bivalve molluscs (Ahn *et al.* 2003, Brockington & Peck 2001), gastropod molluscs (Fraser *et al.* 2002), echinoderms (Brockington 2001) and brachiopods (Peck *et al.* 1986) all using protein as the major reserve for winter.

As might be expected from a fauna that is characterized by low metabolic rates, activity is also markedly slowed. Comparisons here have only recently been made, but with one exception they show activities are carried out at rates that are generally x2 to x10 slower than the same activities in comparable temperate species (Fig. 8). Thus walking in limpets, burrowing in anemones and molluscs, swimming in scallops, burst swimming in fish, and drilling in predatory snails are all markedly slower in Antarctic than temperate species. The only exception is for sustained swimming in

fish, where Antarctic species perform at the same rate as temperate species and the activity is perfectly compensated for temperature. The reason for this is that the red muscles in Antarctic fish have evolved to contain nearly twice as many mitochondria (nearly twice the mitochondrial volume density) of temperate species (Johnston *et al.* 1998). Mitochondria in polar species work more slowly than those in temperate or tropical species (Johnston *et al.* 1998). Thus activities should be slower in Antarctic species, because the amount of energy produced by mitochondria, if all else is equal should be less. A specific adaptation is needed in Antarctic fish to overcome this restriction in energy availability from mitochondria, and in fish red muscle the increase in numbers of mitochondria offsets this decrease in capacity, allowing sustained swimming to proceed at similar rates to lower latitude fish.

Temperature limits

The fact that cold-blooded Antarctic marine species can only live within restricted temperature ranges, that they are stenothermal, is now well documented. Overall most Antarctic ectotherms can only live in temperature windows of 6°C to 12°C width (Peck & Conway 2000). The lower limit is set by the freezing point of seawater at -1.8°C and most species die in experiments at temperatures between 4°C and 10°C. Several species of fish die in experiments when temperatures are raised to 4°C (Somero & DeVries 1967, Somero *et al.* 1998). In the invertebrates the bivalve *Limopsis marionensis* Smith (Pörtner *et al.* 1999a) and the brachiopod *Liothyrella uva* (Peck 1989) are similarly sensitive, whereas other species including the large bivalve *Laternula elliptica* (Pörtner *et al.* 1999b, Peck *et al.* 2002), the limpet *Nacella concinna* (Stebbing) (Peck 1989), the eelpout *Pachycara brachycephalum* (Pappenheim) (van Dijk *et al.* 1999) can survive in experiments to temperatures near, or in some cases slightly above 10°C. Some studies have shown higher temperature capacities e.g. 12°C for the amphipod *Paramoera walkeri* (Stebbing) (Rakusa-Suszczewski & Klekowski 1973). These investigations, however, only held animals at elevated temperatures for very short periods, and duration of exposure markedly affects survival. Wells (1978) showed that the amphipod *Orchomonella plebs* could survive over 24 h with no mortality at 8°C, but at 12.5°C 100% mortality occurred in less than 5 h. The temperature windows of 6°–12°C for survival compare with ranges of in excess of 20°C for many temperate species (Peck & Conway 2000). Acclimation to a new temperature regime is an indication of the flexibility to cope on timescales of months to a few years. There have been few studies investigating the effects of acclimation to higher temperatures in Antarctic marine species. However, data from the few studies to date vary markedly. Bailey (2001) was able to acclimate Antarctic scallops, *Adamussium colbecki* (Smith) to temperatures up to +2.0°C,

but attempts to acclimate specimens to +4°C resulted in loss of condition and 50% mortality in less than 20 days. Acclimation to +2°C also failed to change the swimming characteristics of the scallops. The most stenothermal Antarctic marine species, such as the brachiopod *Liothyrella uva* and the bivalve *Limopsis marionensis* also die at temperatures below or near 4°C in experiments (Peck 1989, Portner *et al.* 1999a). In contrast to this Lowe (2005) found that acclimating Antarctic notothenioid fish to temperatures between 0°C and 4°C allowed them to survive at higher temperatures, possibly up to 6°C or 8°C.

In recent years a significant effort has been put into identifying the underlying physiological mechanisms for the restricted ability of this fauna to survive temperature change. Oxygen supply failure has been recognized as possibly the major factor limiting thermal tolerance in marine ectotherms worldwide (Pörtner 2001, Frederick &

Pörtner 2002, Pörtner *et al.* 2004). Oxygen limitation of thermal tolerance was discovered in Antarctic species by the identification of a transfer to anaerobic metabolism in mitochondria and tissues at temperatures close to those for survival in both invertebrates (Pörtner *et al.* 1999b) and fish (Hardewig *et al.* 1999). The critical temperatures for transfer to anaerobic metabolism in tissues was correlated with a dramatic decrease in oxygen content of the blood in the Antarctic bivalve mollusc *Laternula elliptica* (Peck *et al.* 2002). A mismatch between increased metabolic requirement and oxygen supply mechanisms with elevated temperature therefore appears to be the proximate cause for the stenothermal nature of the Antarctic benthos. Animals can survive for periods above the critical temperatures by transfer to anaerobic metabolism. However, the duration of survival above the critical temperatures depends on the individual's ability to cope with progressively more anaerobic tissues, and this is a strictly time limited condition.

The transfer to anaerobiosis at upper critical temperatures is caused by two factors. Firstly, in cold-blooded species resting metabolic rate varies with temperature, and any increase in temperature is accompanied by a rise in metabolic rate and metabolic costs. Secondly, the ability to provide oxygen to the tissues is regulated by processes at respiratory surfaces and circulatory systems that have a maximum rate at which oxygen can be supplied. Thus as temperature rises the ability for ectotherms to raise their rate of oxygen supply to meet requirements above maintenance demands is progressively restricted. A prediction from this model is that animals would progressively have less ability to perform other biological activities as the critical temperatures are approached. This has recently been

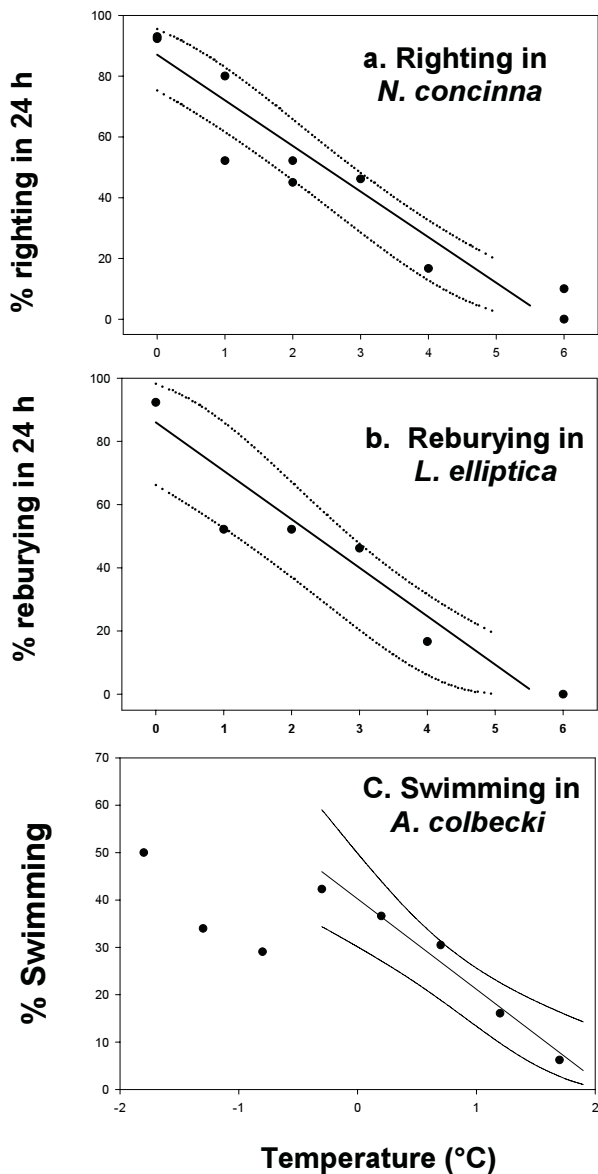


Fig. 9. (opposite) **a.** righting responses in the Antarctic limpet *Nacella concinna* with temperature. Data shown are the proportion of limpets righting in 24 h. For each point $n = 20\text{--}31$. All regressions were made following square root and arcsin transforms of % data ($\arcsin(\sqrt{\% \text{righting}}) = 1.20 - 0.180T^{\circ}\text{C}$; $r^2 = 0.90$, $F = 77.9$, $P < 0.001$, 9 df). **b.** reburying in the bivalve mollusc *L. elliptica* with temperature. Data show the proportion of animals reburying in 24 h ($n = 18\text{--}26$). Regression line: $\arcsin(\sqrt{\% \text{burying}}) = 0.95 - 0.173T^{\circ}\text{C}$ ($r^2 = 0.85$, $F = 22.4$, $P = 0.009$, 5 df). **c.** The proportion of Antarctic scallops, *Adamussium colbecki*, swimming in response to freshwater stimulation. Each point is the proportion swimming at that temperature ($n = 57\text{--}175$). A regression was fitted to data for temperatures above -0.3°C , where a clear temperature effect was apparent. This regression was fitted to square root and arcsin transformed percentage values. Regression Line: $\arcsin(\sqrt{\% \text{swimming}}) = 0.682 - 0.230T^{\circ}\text{C}$ ($r^2 = 0.93$, $F = 51.5$, $P = 0.006$, 4df). In all figures dotted lines indicate 95% confidence intervals for regressions. For all plots lines and confidence intervals shown were plotted following sine and square back transforms. Figure from Peck *et al.* (2004b).

demonstrated in Antarctic species for burrowing in *Laternula elliptica* and righting in the limpet *Nacella concinna* (Peck *et al.* 2004b), where over 95% of animals were capable of performing activity at 0°C, only 50% were capable at 2.5°C and none could bury or right at 5°C (Fig. 9), and both have been demonstrated to have upper lethal temperatures between 5°C and 10°C. The situation is even more severe for the Antarctic scallop *Adamussium colbecki*, where the ability to swim is completely lost at 2°C (Fig. 9). A significant loss of behavioural capability at 2.5°C would indicate survival problems at least at the population level, because capacities to perform other functions including feeding, digestion and reproduction will also be affected by this loss of capacity.

Current and predicted change

Air temperatures over most of Antarctica have not changed significantly in recent years. However, in the Antarctic Peninsula and sub-Antarctic regions there has been rapid change. Mean annual air temperatures on the peninsula have risen by as much as 3°C in 50 years, and winter minimum temperatures have risen by over 5°C in the same period (King *et al.* 2003). This has had a dramatic effect on the ecology of both terrestrial (Convey 2003) and freshwater (Quayle *et al.* 2002, 2003) systems on the peninsula. There is, however, much less data on trends in sea temperature, mainly because of the lack of long-term data. Published studies indicate very little change in sea temperature in recent years, although Gille (2002) showed that Antarctic mid-water warmed by 0.17°C between the 1950s and the 1980s.

Global sea temperature is predicted to rise by around 2°C in the next 100 years (Mitchell *et al.* 1998, IPCC 2001a). Predictions for the Southern Ocean are more difficult than elsewhere, because of uncertainties concerning the responses of sea ice to environmental warming. Conclusions vary, but several studies show little or no change in sea ice extent around Antarctica in the last 25 years (Fichefet *et al.* 2003), whereas some indicate significant reductions in extent (Curran *et al.* 2003). The IPCC predict a reduction in Antarctic sea-ice extent of around 25% in the next 100 years (IPCC 1998). Models currently predict marked warming of seawater at the surface by 2099 around Antarctica by up to 4°C, but little or no change in sea temperature at depths of 5 m and below. However, these predictions must be viewed with care, as no existing models show the near 3°C increase seen in air temperatures on the Antarctic Peninsula over the last 50 years.

Prospects for Antarctic benthos

Animals living anywhere have three possible responses to a changing environment. These are:

1. To cope with the change using internal physiological flexibility and capacities.
2. To evolve adaptations to the new conditions
3. To migrate to areas consistent with survival.

Compared to species from lower latitudes Antarctic benthic species are characterized by markedly slowed physiological rates and poor capacities to change their physiological state in response to change. Thus, their ability to cope with change using intrinsic physiological flexibility is poor compared to temperate and tropical species. This is shown most clearly by the work on the effects of temperature on activity rates in molluscs, where abilities to burrow in bivalves, right in limpets and swim in scallops is compromised at temperatures between 2°C and 3°C (Peck *et al.* 2004b).

Abilities to evolve new adaptations to changing environments depend on many factors. The main amongst these are the magnitude and rate of change, and the rate at which new characters can be produced via modifications of the genetic code. It is not possible to predict when, or to what degree Antarctic nearshore environments will change. However, a warming world will bring with it changes in current regimes in the world's oceans, and this is likely to bring rapid fluctuations in local conditions where adjacent water masses fluctuate in velocity and size. Rates of evolution of new characters depend on variation between, and the turnover rate of, individuals in populations. These are reflected in the level of underlying genetic variation between individuals, numbers of offspring for selection to act on and how often genetic material is mixed through reproduction. Many characteristics of reproduction in Antarctic marine species are important here. Eggs of marine species tend to be larger at higher latitudes, as has been shown for a wide variety of groups including decapod and amphipod crustaceans, molluscs, echinoderms, polychaetes and fish (Thorson 1936, 1950, Clarke *et al.* 1985, 1991, North & White 1987, Clarke 1993, Gambi *et al.* 2001). There is also a tendency to the production of fewer eggs per spawning. These factors would tend to reduce the number of opportunities for selective pressure to bring about adaptive evolutionary changes. In some groups, such as gastropod and bivalve molluscs there also appears to be more protected development in Antarctic groups than elsewhere, although this is not the case for many other taxa, including echinoderms (Clarke 1992, Pearse 1994). However, there is little or no information on the effective genome sizes of populations of Antarctic marine species, or of factors such as genetic drift or effects of gene flow across populations of Antarctic brooding and broadcast spawning species. Thus cogent analyses of these effects on capacity to evolve are restricted.

In the key parameters of how often offspring are produced and how long development takes for maturity to be reached

Antarctic benthos perform poorly. They live to great age and show deferred maturity, and although lifetime reproductive effort may be similar to species from lower latitudes, annual reproductive output is markedly less in the Southern Ocean (Clarke 1987).

Recently Gilooly *et al.* (2005) have put forward evidence indicating rates of DNA evolution may be slower at low temperatures and in larger bodied species. Their data suggest that when these two factors are allowed for rates of nucleotide substitution in a wide range of organisms are similar, and hence the molecular clock runs at the same rate when size and temperature are removed from the analysis. If this proves correct then Antarctic marine species would evolve more slowly than similar taxa from lower latitudes because they live at lower temperatures. In a detailed global study of size characteristics in amphipod crustaceans Chapelle & Peck (1996, 2004) showed that body sizes are significantly larger at lower temperatures than from warmer latitudes. Antarctic species would, therefore, be expected to have lower intrinsic rates of mutation than species from elsewhere, if Gilooly *et al.* (2005) are correct.

The third possible response, migration, depends primarily on the dispersal capabilities of the species concerned, and the availability of new habitable sites. Because Antarctic benthic organisms develop very slowly, species with dispersing larval phases have the capability to colonize over extended distances. Thus, Antarctic echinoderms (Pearse *et al.* 1991), nemertean (Peck 1993) and brachiopods (Peck *et al.* 2001) all have larvae that spend several months in the water column. Some Antarctic species with intracapsular development have also been shown to colonize long distances, because their eggs and embryos are buoyant (Bosch & Pearse 1988). However, colonization of new habitable areas depends critically on the availability of such new sites. Most continents have coastlines that cover many degrees of latitude. The coasts of South America and Africa stretch from the tropics to cool temperate or sub-Antarctic latitudes, North America and Asia range from tropical to polar latitudes, and Australia covers tropical to cool temperate zones. Many species living on their coasts, therefore, have considerable potential to migrate away from warming conditions to more habitable sites. Major problems for migrating species on these coasts come in the form of natural barriers such as the Amazon River delta. The freshwater lens from the Amazon can extend 120 km offshore (Gibbs & Konwar 1986), and it produces a 1600 km long downdrift mud shoreline. This is a very large barrier to migration of rocky shore species. However, Antarctic benthic species face a potentially much greater problem in migrating away from deteriorating environments. The outline of much of Antarctica is approximately circular, and most of its coastline lies between 65°S and 70°S. This is a major barrier for the migration of marine species, as the sites available at different and more habitable latitudes are severely

restricted. In essence for Antarctic nearshore marine species the habitable temperature window would not have moved towards the poles, but disappeared completely.

In all three potential responses to changing environments Antarctic marine benthic species are at a disadvantage to faunas from elsewhere. They would appear to be more at risk in terms of long-term survival from changing conditions than faunas from other continents.

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References

- AHN, I.Y., SURH, J., PARK, Y.G., KWON, H., CHOI, K.S., KANG, S.H., CHOI, H.J., KIM, K.W. & CHUNG, H. 2003. Growth and seasonal energetics of the Antarctic bivalve *Laternula elliptica* from King George Island, Antarctica. *Marine Ecology Progress Series*, **257**, 99–110.
- ARNTZ, W.E., BREY, T. & GALLARDO, V.A. 1994. Antarctic zoobenthos. *Oceanography and Marine Biology Annual Review*, **32**, 241–304.
- BAILEY, D.M. 2001. *The thermal dependence of swimming and muscle physiology in temperate and Antarctic scallops*. PhD thesis, University of St. Andrews, St. Andrews, 138 pp. [Unpublished].
- BARNES, D.K.A. 1995. Seasonal and annual growth in erect species of Antarctic bryozoans. *Journal of Experimental Marine Biology and Ecology*, **188**, 181–198.
- BOSCH, I. & PEARSE, J.S. 1988. Seasonal pelagic development and juvenile recruitment of the bivalve *Laternula elliptica*. *American Zoologist*, **28**, 89A.
- BOSCH, I., BEAUCHAMP, K.A., STEELE, M.E. & PEARSE, J.S. 1987. Development, metamorphosis and seasonal abundance of embryos and larvae of the Antarctic sea urchin *Sterechinus neumayeri*. *Biological Bulletin*, **173**, 126–135.
- BROCKINGTON, S. 2001. *The seasonal ecology and physiology of Sterechinus neumayeri (Echinodermata: Echinoidea) at Adelaide Island, Antarctica*. PhD thesis, Open University, Milton Keynes, UK, and British Antarctic Survey, Cambridge, UK, 209 pp. [Unpublished].
- BROCKINGTON, S. & PECK, L.S. 2001. Seasonality of respiration and ammonia excretion in the Antarctic echinoid *Sterechinus neumayeri*. *Marine Ecology Progress Series*, **259**, 159–168.
- BROWN, K.M., FRASER, K.P., BARNES, D.K.A. & PECK, L.S. 2004. Links between the structure of Antarctic shallow-water community and ice-scour frequency. *Oecologia*, **141**, 121–129.
- CHAPELLE, G. & PECK, L.S. 1999. Polar gigantism dictated by oxygen availability. *Nature*, **399**, 114–115.
- CHAPELLE, G. & PECK, L. 2004. Amphipod crustacean size spectra: new insights in the relationship between size and oxygen. *Oikos*, **106**, 167–175.
- CLARIDGE, M.F., DAWAH, H.A. & WILSON, M.R. 1997. *Species: the units of biodiversity*. London: Chapman & Hall, 439 pp.

- CLARKE, A. 1987. Temperature, latitude and reproductive effort. *Marine Ecology Progress Series*, **38**, 89–99.
- CLARKE, A. 1988. Seasonality in the Antarctic marine environment. *Comparative Biochemistry and Physiology*, **90B**, 461–473.
- CLARKE, A. 1992. Reproduction in the cold: Thorson revisited. *Invertebrate Reproduction and Development*, **22**, 175–184.
- CLARKE, A. 1993. Reproductive trade-offs in caridean shrimps. *Functional Ecology*, **7**, 411–419.
- CLARKE, A. & JOHNSTON, N.M. 1999. Scaling of metabolic rate and temperature in teleost fish. *Journal of Animal Ecology*, **68**, 893–905.
- CLARKE, A. & JOHNSTON, N.M. 2003. Antarctic marine benthic diversity. *Oceanography and Marine Biology an Annual Review*, **41**, 47–114.
- CLARKE, A. & LEAKEY, R.J.G. 1996. The seasonal cycle of phytoplankton, macronutrients and the microbial community in a nearshore Antarctic marine ecosystem. *Limnology and Oceanography*, **41**, 1281–1294.
- CLARKE, A. & PECK, L.S. 1991. The physiology of polar marine zooplankton. *Polar Research*, **10**, 355–369.
- CLARKE, A., HOPKINS, C.C.E. & NILSSEN, E.M. 1991. Egg size and reproductive output in the deep-water prawn *Pandalus borealis* Krøyer, 1838. *Functional Ecology*, **5**, 724–730.
- CLARKE, A., SKADSHEIM, A. & HOMES, L.J. 1985. Lipid biochemistry and reproductive biology in two species of Gammaridae (Crustacea: Amphipoda). *Marine Biology*, **88**, 247–263.
- CONVEY, P. 2003. Maritime Antarctic climate change: signals from terrestrial biology. *Antarctic Research Series*, **79**, 145–158.
- CURRAN, M.A.J., VAN OMMEN, T.D., MORGAN, V.I., PHILLIPS, K.L. & PALMER, A.S. 2003. Ice core evidence for Antarctic sea ice decline since the 1950s. *Science*, **302**, 1203–1206.
- DAYTON, P.K., NEWMAN, W.A., PAINE, R.T. & DAYTON, L.B. 1974. Ecological accommodation in the benthic community at McMurdo Sound, Antarctica. *Ecological Monographs*, **44**, 105–128.
- EVERSON, I. 1977. Antarctic marine secondary production and the phenomenon of cold adaptation. *Philosophical Transactions of the Royal Society of London*, **B279**, 55–66.
- FICHEFET, T., TARTINVILLE, B. & GOOSSE, H. 2003. Antarctic sea ice variability during 1958–1999: a simulation with a global ice-ocean model. *Journal of Geophysical Research-Oceans*, **108**, 3102.
- FRASER, K.P.P., CLARKE, A. & PECK, L.S. 2002. Feast and famine in Antarctica: seasonal physiology in the limpet, *Nacella concinna* (Strebel, 1908). *Marine Ecology Progress Series*, **242**, 169–177.
- FREDERICH, M. & PÖRTNER, H.O. 2002. Oxygen limitation of thermal tolerance defined by cardiac and ventilatory performance in spider crab, *Maja squinado*. *American Journal of Regulatory and Integrative Comparative Physiology*, **279**, R1531–R1538.
- GAMBI, M.C., PATTI, F.P., MICALETTO, G. & GIANGRANDE, A. 2001. Diversity of reproductive features in some Antarctic polynoid and sabellid polychaetes, with a description of *Demonax polarsterni* sp. n. (Polychaeta, Sabellidae). *Polar Biology*, **24**, 883–891.
- GIBBS, R.J. & KONWAR, L. 1986. Coagulation and settling of Amazon river suspended sediment. *Continental Shelf Research*, **6**, 127–149.
- GILLE, S.T. 2002. Warming of the Southern Ocean since the 1950s. *Science*, **295**, 1275–1277.
- GILLOOLY, J.F., ALLEN, A.P., WEST, G.B. & BROWN, J.H. 2005. The rate of DNA evolution: effects of body size and temperature on the molecular clock. *Proceedings of the National Academy of Science*, **102**, 140–145.
- GRAY, J.S. 2000. The measurement of marine species diversity, with an application to the benthic fauna of the Norwegian continental shelf. *Journal of Experimental Marine Biology and Ecology*, **250**, 23–49.
- GUTT, J., SIRENKO, B.I., SMIRNOV, I.S. & ARNTZ, W.E. 2004. How many macrobenthic species might inhabit the Antarctic shelf? *Antarctic Science*, **16**, 11–16.
- HAIN, S. 1991. Life maintenance of benthic mollusks from the Eastern Weddell Sea, Antarctica. *Proceedings 10th International Malacology Congress (Tübingen 1989)*, 339–341.
- HANSKI, I. 1998. Metapopulation dynamics. *Nature*, **396**, 41–49.
- HANSKI, I. 1999. *Metapopulation ecology*. Oxford: Oxford University Press, 328 pp.
- HARDEWIG, I., PECK, L.S. & PÖRTNER, H.O. 1999. Thermal sensitivity of mitochondrial function in the Antarctic Nototheniid *Lepidonotothen nudifrons*. *Comparative Biochemistry and Physiology*, **A124**, 179–189.
- HOEGH-GULDBERG, O. & PEARSE, J.S. 1995. Temperature, food availability and the development of marine invertebrate larvae. *American Zoologist*, **35**, 415–425.
- HOLETON, G.F. 1974. Metabolic cold adaptation of polar fish: fact or artefact? *Physiological Zoology*, **47**, 137–152.
- HUNT, B.M., HOEFLING, K. & CHENG, C.H.C. 2003. Annual warming episodes in seawater temperatures in McMurdo Sound in relation to endogenous ice in nototheniid fish. *Antarctic Science*, **15**, 333–338.
- IPCC. 1998. *The Regional Impacts of Climate Change: An Assessment of Vulnerability*. Cambridge: Cambridge University Press.
- IPCC. 2001a. *Climate Change 2001: the scientific basis*. In HOUGHTON, J.T., DING, Y., GRIGGS, D.J., NOGUER, M., VAN DER LINDEN, P.J., DAI, X., MASKELL, K. & JOHNSON, C.A., eds. *Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge: Cambridge University Press.
- IPCC. 2001b. *Climate Change 2001: impacts, adaptation and vulnerability*. In MCCARTHY, J.J., ANZIANI, O.F., LEARY, N.A., DOKKEN, D.J. & WHITE, K.S., eds. *Contribution of Working Group II to the Third Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge: Cambridge University Press.
- JOHNSTON, I.A., CALVO, J., GUDERLEY, H., FERNANDEZ, D. & PALMER, L. 1998. Latitudinal variation in the abundance and oxidative capacities of muscle mitochondria in perciform fishes. *Journal of Experimental Biology*, **201**, 1–12.
- JONES, P.D., NEW, M., PARKER, D.E., MARTIN, S. & RIGOR, I.G. 1999. Surface air temperature and its changes over the past 150 years. *Review of Geophysics*, **37**, 173–199.
- KING, J.C., TURNER, J., MARSHALL, G.J., CONNOLLEY, W.M. & LACHLAN-COPE, T.A. 2003. Antarctic Peninsula climate variability and its causes as revealed by instrumental records. *Antarctic Research Series*, **79**, 17–30.
- KLAGES, M. 1993. Distribution, reproduction and population dynamics of the Antarctic gammaridean amphipod *Eusirus perdentatus* Chevreux, 1912 (Crustacea). *Antarctic Science*, **5**, 349–359.
- LIVERMORE, R., EAGLES, G., MORRIS, P. & MALDONADO, A. 2004. Shackleton Fracture Zone: no barrier to early circumpolar ocean circulation. *Geology*, **32**, 797–800.
- LOWE, C.J. 2005. *The effect of acute and chronic elevation of temperature on aspects of the physiology of Antarctic nototheniid fishes*. PhD thesis, University of Canterbury, New Zealand, 308 pp. [Unpublished].
- MACCRACKEN, M.C., BARRON, E.J., EASTERLING, D.R., FELZER, B.S. & KARL, T.R. 2003. Climate change scenarios for the US National Assessment. *Bulletin of the American Meteorological Society*, **84**, 1711–1741.
- MITCHELL, J.F.B., JOHNS, T.C. & SENIOR, C.A. 1998. Transient response to increasing greenhouse gases using models with and without flux adjustment. *Hadley Centre Technical Note*, No. 2, 1–26.
- NOLAN, C.P. & CLARKE, A. 1993. Growth in the bivalve *Yoldia eightsi* at Signy Island, Antarctica, determined from internal shell increments and calcium-45 incorporation. *Marine Biology*, **117**, 243–250.
- NORTH, A.W. & WHITE, M.G. 1987. Reproductive strategies of Antarctic fish. In KULLANDER, S.O. & FERNHOLM, B., eds. *Proceedings, V Congress of European Ichthyologists, Stockholm 1985*. Stockholm: Swedish Museum of Natural History, 381–390.
- PAGE, T.J. & LINSE, K. 2002. More evidence of speciation and dispersal across the Antarctic Polar Front through molecular systematics of Southern Ocean *Limatula* (Bivalvia: Limidae). *Polar Biology*, **25**, 818–826.

- PEARSE, J.S. 1994. Cold water echinoderms break "Thorson's Rule". In YOUNG, C.M. & ECKELBARGER, K.J., eds. *Reproduction, larval ecology and recruitment of the deep-sea benthos*. New York: Columbia University Press, 26–43.
- PEARSE, J.S., MCCLINTOCK, J.B. & BOSCH, I. 1991. Reproduction of Antarctic benthic marine invertebrates: tempos, modes and timing. *American Zoologist*, **31**, 65–80.
- PECK, L.S. 1989. Temperature and basal metabolism in two Antarctic marine herbivores. *Journal of Experimental Marine Biology and Ecology*, **127**, 1–12.
- PECK, L.S. 1993. Larval development in the Antarctic nemertean *Parborlasia corrugatus* (Heteronemertea, Lineidae). *Marine Biology*, **116**, 301–310.
- PECK, L.S. 2002. Ecophysiology of Antarctic marine ectotherms: limits to life. *Polar Biology*, **25**, 31–40.
- PECK, L.S. & CONWAY, L.Z. 2000. The myth of metabolic cold adaptation: oxygen consumption in stenothermal Antarctic bivalves. In HARPER, E.M., TAYLOR, J.D. & CRAME, J.A., eds. *The Evolutionary Biology of the Bivalvia*. Geological Society, London, Special Publications, No. 177, 441–45.
- PECK, L.S. & BREY, T. 1996. Radiocarbon bomb signals verify biennial growth bands in the shells of 50 year old brachiopods from Antarctica. *Nature*, **380**, 206–207.
- PECK, L.S. & ROBINSON, K. 1994. Pelagic larval development in the brooding Antarctic brachiopod *Liothyrella uva*. *Marine Biology*, **120**, 279–286.
- PECK, L.S., ANSELL, A.D., WEBB, K., HEPBURN, L. & BURROWS, M. 2004a. Burrowing in Antarctic bivalve molluscs. *Polar Biology*, **27**, 357–367.
- PECK, L.S., BROCKINGTON, S., VANHOVE, S. & BEGHYN, M. 1999. Community recovery following catastrophic iceberg impacts in Antarctica. *Marine Ecology Progress Series*, **186**, 1–8.
- PECK, L.S., COLMAN, J.G. & MURRAY, A.W.A. 2000. Growth and tissue mass cycles in the infaunal bivalve *Yoldia eightsi* at Signy Island, Antarctica. *Polar Biology*, **23**, 420–428.
- PECK, L.S., MEIDLINGER, K. & TYLER, P.A. 2001. Developmental and settlement characteristics of the Antarctic brachiopod *Liothyrella uva* (Broderip 1833). In BRUNTON, C.H.C., COCKS, L.R. & LONG, S.L., eds. *Brachiopods Past and Present. Proceedings 4th International Congress on Brachiopods*, London, July 1999, 80–90.
- PECK, L.S., MORRIS, D.J., CLARKE, A. & HOLMES, L.J. 1986. Oxygen consumption and nitrogen excretion in the Antarctic brachiopod *Liothyrella uva* (Jackson, 1912) under simulated winter conditions. *Journal of Experimental Marine Biology and Ecology*, **104**, 203–213.
- PECK, L.S., PÖRTNER, H.O. & HARDEWIG, I. 2002. Metabolic demand, oxygen supply and critical temperatures in the Antarctic bivalve *Laternula elliptica*. *Physiological and Biochemical Zoology*, **75**, 123–133.
- PECK, L.S., WEBB, K.E. & BAILEY, D. 2004b. Extreme sensitivity of biological function to temperature in Antarctic marine species. *Functional Ecology*, **18**, 625–630.
- PIEPENBURG, D., VOSS, J. & GUTT, J. 1997. Assemblages of sea stars (Echinodermata: Asteroidea) and brittle stars (Echinodermata: Ophiuroidea) in the Weddell Sea (Antarctica) and off North East Greenland (Arctic): a comparison of diversity and abundance. *Polar Biology*, **17**, 305–322.
- PÖRTNER, H.O. 2001. Climate change and temperature dependent biogeography: oxygen limitation of thermal tolerance in animals. *Naturwissenschaften*, **88**, 137–146.
- PÖRTNER, H., HARDEWIG, I. & PECK, L.S. 1999b. Mitochondrial function and critical temperature in the Antarctic bivalve *Laternula elliptica*. *Comparative Biochemistry and Physiology A*, **124**, 179–189.
- PÖRTNER, H., PECK, L.S., ZIELINSKI, S. & CONWAY, L. 1999a. Temperature and metabolism in the highly stenothermal bivalve mollusc *Limopsis marionensis* from the Weddell Sea, Antarctica. *Polar Biology*, **22**, 17–30.
- PÖRTNER, H.O., MARK, F.C. & BOCK, C. 2004. Oxygen limited thermal tolerance in fish? Answers obtained by nuclear magnetic resonance techniques. *Respiratory Physiology and Neurobiology*, **141**, 243–260.
- POWELL, D. 2001. *The reproductive ecology of Antarctic free-spawning molluscs*. PhD thesis, University of Southampton, 142 pp. [Unpublished]
- QUAYLE, W.C., PECK, L.S., PEAT, H.J., ELLIS-EVANS, J.C. & HARRIGAN, P.R. 2002. Extreme responses to climate change in Antarctic lakes. *Science*, **295**, 645.
- QUAYLE, W.C., CONVEY, P., PECK, L.S., ELLIS-EVANS, J.C., BUTLER, H.G. & PEAT, H.J. 2003. Ecological responses of maritime Antarctic lakes to regional climate change. *Antarctic Research Series*, **79**, 335–347.
- RAKUSA-SUSZCZEWSKI, S. & KLEKOWSKI, R.Z. 1973. Biology and respiration of the Antarctic amphipoda (*Paramoera walkeri* Stebbing) in the summer. *Polski Archiwumhydrobiologii*, **20**, 475–488.
- RAUSCHERT, M. 1991. Ergebnisse der faunistischen Arbeiten im Benthall von King George Island (Südshetlandinseln, Antarktis). *Berichte für Polarforschung*, **76**, 1–75.
- SCHÄR, C., VIDALE, P.L., LÜTHI, D., FREI, C., HÄBERLI, C., LININGER, M.A. & APPENZELLER, C. 2004. The role of increasing temperature variability in European summer heatwaves. *Nature*, **427**, 332–336.
- SOMERO, G.N. & DeVRIES, A.L. 1967. Temperature tolerance of some Antarctic fishes. *Science*, **156**, 257–258.
- SOMERO, G.N., FIELDS, P.A., HOFMANN, G.E., WEINSTEIN, R.B. & KAWALL, H. 1998. Cold adaptation and stenothermy in Antarctic nototheniid fishes: what has been gained and what has been lost? In DI PRISCO, G., PISANO, E., CLARKE, A., eds. *Fishes of Antarctica: a biological overview*. Milan: Springer, 97–109.
- STANWELL-SMITH, D.P. & PECK, L.S. 1998. Temperature and embryonic development in relation to spawning and field occurrence of larvae of three Antarctic echinoderms. *Biological Bulletin Woods Hole*, **194**, 44–52.
- TEIXIDÓ, N., GARRABOU, J., GUTT, J. & ARNTZ, W.E. 2004. Recovery in Antarctic benthos after iceberg disturbance: trends in benthic composition, abundance and growth forms. *Marine Ecology Progress Series*, **278**, 1–16.
- THORSON, G. 1936. The larval development, growth and metabolism of Arctic marine invertebrates, compared with those of other seas. *Meddelelser om Grønland*, **100**, 1–155.
- THORSON, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biological Reviews*, **25**, 1–45.
- VAN DIJK, P.L.M., TESCH, C., HARDEWIG, I. & PÖRTNER, H. 1999. Physiological disturbances at critically high temperatures. A comparison between stenothermal Antarctic, and eurythermal temperate eelpouts (Zoarcidae). *Journal of Experimental Biology*, **202**, 3611–3621.
- WÄGELE, J.W. 1987. On the reproductive biology of *Caratoserolis trilobitoides* (Crustacea: Isopoda) - latitudinal variation of fecundity and embryonic development. *Polar Biology*, **7**, 11–24.
- WALSH, J.J. 1988. *On the nature of continental shelves*. San Diego, CA: Academic Press, 520 pp.
- WARWICK, R.M. & CLARKE, K.R. 2001. Practical measures of marine biodiversity based on relatedness of species. *Oceanography and Marine Biology Annual Review*, **39**, 207–231.
- WEBB, C.O. 2000. Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. *American Naturalist*, **156**, 145–155.
- WELLS, R.M. 1978. The lethal temperatures of Antarctic marine invertebrates. *New Zealand Antarctic Record*, **1**, 9–13.
- YOUNG, J.S. 2004. *Effects of temperature on elements of the motor control of behaviour in eurythermal and stenothermal crustaceans*. PhD thesis, University of Cambridge, Cambridge, 177 pp. [Unpublished].