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ANTARCTIC MARINE BIODIVERSITY: ADAPTATIONS, ENVIRONMENTS AND RESPONSES TO CHANGE

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Abstract

Animals living in the Southern Ocean have evolved in a singular environment. It shares many of its attributes with the high Arctic, namely low, stable temperatures, the pervading effect of ice in its many forms and extreme seasonality of light and phytobiont productivity. Antarctica is, however, the most isolated continent on Earth and is the only one that lacks a continental shelf connection with another continent. This isolation, along with the many millions of years that these conditions have existed, has produced a fauna that is both diverse, with around 17,000 marine invertebrate species living there, and has the highest proportions of endemic species of any continent. The reasons for this are discussed. The isolation, history and unusual environmental conditions have resulted in the fauna producing a range and scale of adaptations to low temperature and seasonality that are unique. The best known such adaptations include channichthyid icefish that lack haemoglobin and transport oxygen around their bodies only in solution, or the absence, in some species, of what was only 20 years ago termed the universal heat shock response. Other adaptations include large size in some groups, a tendency to produce larger eggs than species at lower latitudes and very long gametogenic cycles, with egg development (vitellogenesis) taking 18–24 months in some species. The rates at which some cellular and physiological processes are conducted appear adapted to, or at least partially compensated for, low temperature such as microtubule assembly in cells, whereas other processes such as locomotion and metabolic rate are not compensated, and whole-animal growth, embryonic development, and limb regeneration in echinoderms proceed at rates even slower than would be predicted by the normal rules governing the effect of temperature on biological processes. This review describes the current state of knowledge on the biodiversity of the Southern Ocean fauna and on the majority of known ecophysiological adaptations of cold-blooded marine species to Antarctic conditions. It further evaluates the impacts these adaptations have on capacities to resist, or respond to change in the environment, where resistance to raised temperatures seems poor, whereas exposure to acidified conditions to end-century levels has comparatively little impact.

Introduction

Antarctica and the Southern Ocean have many unique characteristics. Several are well known, including having the lowest temperatures and the greatest mass of ice on Earth. Others are less well known but have marked consequences for the organisms living there. These include isolation, where the combination of the separation of Antarctica's continental shelf from that of adjacent continental

shelves is unique amongst the continents, and the circulation of the circumpolar current with the polar frontal zone produces a singular degree of biological isolation at the continental level. All of these factors have, over long evolutionary time, produced a range of attributes and adaptations in the Southern Ocean fauna that are either extreme because they are at one end of the relevant biological continuum, or only exist in Antarctica.

One of the earliest overviews of Antarctic marine biodiversity was given by Dell (1972). Since then there have been several good reviews on various aspects of Antarctic marine life, including Clarke (1983), who gave a seminal critique of adaptations to polar marine environments and followed this with more specific reviews of cold adaptation in 1991 and temperature and energetics in 1998. Arntz et al. (1994) reviewed Southern Ocean life from a biodiversity and life-history perspective, and Arntz et al. (1997) reviewed biodiversity with emphasis on community structure, biomass and spatial heterogenenity. Peck (2005a,b) concentrated on physiological performance, Peck et al. (2006b) evaluated the effects of environmental variability and predictability on organismal biology, Pörtner et al. (2007, 2012) evaluated thermal limits and temperature adaptation, and Clark and Peck (2009a) reviewed heat shock proteins and the stress response in Antarctic marine species. Adaptations in fish, including the recent discovery of neuroglobins (Cheng et al. 2009a) have been reviewed by Cheng and Detrich (2007), Patarnello et al. (2011) and Giordano et al. (2012b). Biodiversity patterns were evaluated by Convey et al. (2012) and physical gradients and their effects on biodiversity patterns by Convey et al. (2014). In recent years, a combination of increased access and scientific effort with, in some areas, dramatic improvements in technology have provided significant enhancements of understanding. This has been especially so in the 'omics technologies' where high-throughput next generation sequencing is enabling access to the fine-scale cellular and molecular functioning of Antarctic species (Huth & Place 2016a,b, Clark et al. 2017). Significant improvements in understanding have also come from technological breakthroughs in remote sensing and the ability to manipulate very large amounts of data. Many of these factors were highlighted in a recent Horizon Scan conducted by the Scientific Committee for Antarctic Research (SCAR) (Kennicutt et al. 2014, 2015).

Further to the above is the rapidly increasing need and impetus for research in the polar regions because they have become recognised as the fastest changing regions due to climate change impacts, and they contain faunas that are possibly the least capable of resisting change globally (e.g. Peck 2005a,b, Barnes & Peck 2008, Turner et al. 2009, 2013, Peck et al. 2014). Research here is of further importance because the coldest regions will be the first to disappear as the Earth warms.

This review aims to provide a comprehensive view of the current understanding of biodiversity patterns of benthic life in the Southern Ocean, including addressing questions about why diversity is higher than would be expected even a few decades ago, and also how the history of the continent has moulded the biodiversity. It also aims to describe and explain the wide range of life-history characteristics and physiological, cellular and molecular adaptations so far discovered in the fauna. These range from attributes that have been known for 50 years or more such as the presence of antifreeze in fish and the very slow growth rates exhibited by nearly all species, to attributes only recently identified including the lack of a heat shock response in many marine species and the discovery of new families of globin molecules, several of which remain to have their functions fully described. Finally, it aims to evaluate both the research that has been done on abilities to respond to altered environments and the impacts of the adaptations to extreme environments on capacities to respond. This is done predominantly in respect to temperature where most marine benthos appear limited in capacities to respond to temperature, and ocean acidification where conflicting results have been published, but many species appear little impacted by end-century conditions. The review focusses on benthic cold-blooded species, primarily animals because, although history will never accept difficulties as an excuse, to include a review of research on the microbes, plants, mammals and pelagic species that live in the Southern Ocean would have taken this work beyond the scope of a review of this type.

The physical environment

The Southern Ocean encircles the Antarctic continent (Figure 1). It ranges from the coastline to the polar frontal zone (PFZ), an area that fluctuates over time but represents a total area of around 22×10^6 km^2, around 6.1% of the world's oceans (www.NOAA.gov). The PFZ is the area where Southern Ocean waters abut those of the Pacific, Atlantic and Indian Oceans, and there is a sharp 3–5.5°C drop in temperature over a distance of 30–50 km when moving south into the Southern Ocean (www.eoearth.org). Ice is one of the dominant environmental factors in the region, both from the effects of scour from icebergs and from sea ice. At the winter maximum, sea ice extends over an area of around 20×10^6 km^2, and this is reduced by $10–15 \times 10^6$ km^2 at the summer minimum (Comiso 2010). Antarctica has 45,317 km of coastline, but over 80% of this is covered by ice shelves and glaciers in summer (Figure 1, Table 1). The world's total coastline length is 1.634×10^6 km (Burke et al. 2001). Antarctica thus accounts for 2.7% of the world's coastline but only 0.33% of the world's ice-free coastline in summer, and much less than this in winter. Significant portions of the ice-free coastline are in the South Orkney, South Shetland and Kerguelen Islands. However, in winter all the continental coastline is covered in ice. In terms of seabed, the area of continental

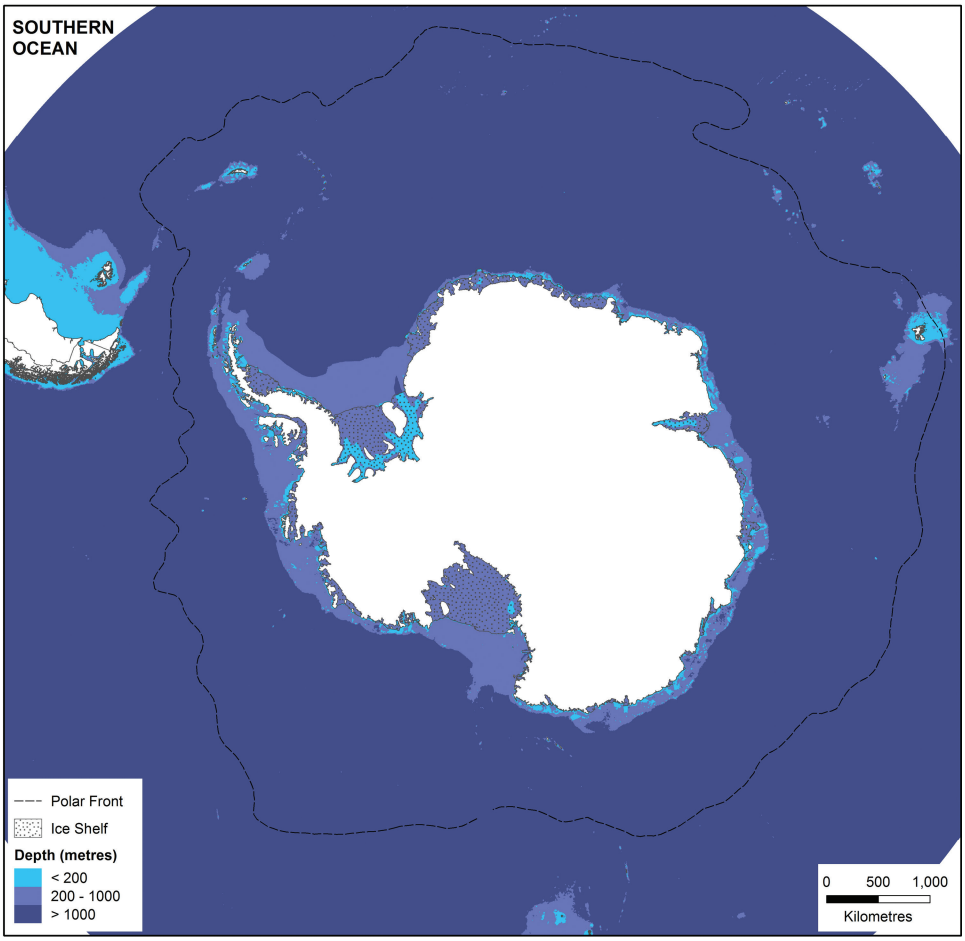

Figure 1 Map of the Southern Ocean (area south of the polar frontal zone) showing ice-covered and ice-free areas shallower than 200 m, 200–1000 m depth and deeper than 1000 m. (Image provided by P. Fretwell, British Antarctic Survey.)

Table 1 The areas in each of the categories shown in Figure 1 and the coastline length, both under, and free of glacier and ice shelf cover

Zone	Description	Area (km^2)	Length (km)
Southern Ocean	Total area (km^2)	36,415,505	
Southern Ocean	Not covered by ice	34,995,119	
Continental Shelf	Total area	4,623,202	
Continental Shelf	Not covered by ice	3,202,816	
Continental Shelf	Shallower than 200 m	593,547	
Continental Shelf	Shallower than 200 m (ice free)	390,071	
Antarctica coastline	Total length		45,317
Antarctica coastline	Ice-free length		5468

Sources: General Bathymetric Chart of the Oceans (GEBCO) and the SCAR Antarctic Digital Database (ADD) using a South Pole Azimuthal Equal Area projection for all areas quoted, and https://www.bas.ac.uk/science/science-and-society/education/antarctic-factsheet-geographical-statistics/

shelf available for biological colonisation, free from permanent ice, is around 4.62×10^6 km^2, but only 3.20×10^6 km^2 of this is not covered by ice shelves. This is approximately 7.3–10.6% of the world's continental shelf area (www.NOAA.gov, Barnes & Peck 2008). The continent and its shelf are depressed by the mass of ice on the land and previous ice scour at depth during glacial maxima (Huybrechts 2002), and the continental shelf break occurs at 800–1000 m depth as opposed to approximately 200 m depth elsewhere. Areas shallower than 200 m cover only 593,547 km^2, which is 2.1% of the world's ocean area shallower than 200 m.

The main physical factors affecting living organisms in polar marine environments are salinity, temperature, ice in its many forms, seabed topography and depth. Many physical factors change markedly with depth, especially between 0 and 100 m, but also to greater depths of 1000 m and beyond. These factors have large impacts upon the habitats in which marine organisms live. Phytoplankton productivity predominantly occurs in the top 100 m of the water column and mostly in the top 30–50 m (Clarke et al. 2008). Energy supply to primary consumers in habitats less than 50 m is usually dominated by phytoplankton. At progressively deeper depths, sedimenting biomass is modified during its passage through the water column, often aggregating, but significant fractions are consumed by pelagic species or broken down by microbial activity during the descent, and the material reaching the seabed is less available to suspension-feeders and more to deposit grazers (Kiørboe 2001). Light penetration is variable, depending on many factors including turbidity, phytoplankton productivity and, in polar regions, sea ice cover. Thus, a deeper continental shelf provides a markedly different environment for life in Antarctica than continental shelves elsewhere.

Ice has several major effects on habitats in the Southern Ocean. In open water, sea ice formation in winter reduces wind-induced mixing, causing stratification of the water column. It also markedly reduces light penetration to the water column beneath. The break-up of sea ice in summer allows mixing, bringing nutrients to photosynthetic depths, and increases light levels. However, the relationship between ice cover and water column productivity is complicated. Reductions in ice cover in a given system can increase or decrease productivity. If permanent ice cover is removed, increased light penetration can result in higher productivity (e.g. Arrigo et al. 2008, Montes-Hugo et al. 2009), and this can lead to increased productivity and biomass that is significant on a global scale (Peck et al. 2010a). Ice cover early in the growth season can increase stratification, which can reduce productivity (Vernet et al. 2008, Montes-Hugo et al. 2009, Venables et al. 2013, Meredith & Brandon 2017). However, more recent studies on the Antarctic Peninsula have shown that overall reductions in sea ice cover combined with low levels of water column stratification are associated with years of low phytoplankton biomass (Rozema et al. 2017). Salinity variation, from melting or freezing sea ice or

from glacial melt, can also affect phytoplankton blooms (Moline et al. 2008). In nearshore Antarctic systems, removal of winter sea ice cover in spring can result in very intense blooms, probably because of the relatively high availability of key nutrients such as nitrate, phosphate and silicate, but also including iron from glacial meltwater run-off (e.g. Gerringa et al. 2012, Venables et al. 2013).

Sea ice itself has positive aspects for some biota, as productivity on or just within the basal surface of ice (epontic) can result in large standing biomass on the undersides of the ice that many species exploit, including juvenile krill in winter (Marschall 1988, Nicol 2006, Wiedenmann et al. 2009). A reduction in sea ice on the Antarctic Peninsula has been identified as related to reductions in krill numbers (Atkinson et al. 2004). High levels of productivity are also associated with the sea ice edge (Smith & Nelson 1985). There are specific epontic communities living in close association with sea ice (McMinn et al. 2010, Thomas & Diekmann 2010). These communities can include fish predators such as *Trematomus bernacchii, Pleuragramma antarctica* and *T. hansoni* (DeVries & Wohlschlag 1969).

On the seabed, ice disturbance is a major structuring ecological factor in both shallow and deep habitats down to 550 m (Barnes & Conlan 2007). Iceberg impacts have been shown to remove over 99.5% of all macrofauna and over 90% of meiofauna (Peck et al. 1999). Numbers of iceberg impacts on a regularly monitored grid at Rothera Point on the Antarctic Peninsula were shown to have increased between 2002 and 2010 by around 4-fold, and this increased the annual mortality of a common bryozoan, *Fenestrulina rugula*, from 89.5% to over 93% (Barnes & Souster 2011). Downstream impacts might be expected because *Fenestrulina rugula* is a pioneer species, often one of the first to settle and colonise newly cleared seabed following events such as iceberg impacts, and it plays a strong role in dictating later community composition (Barnes et al. 2014a).

Temperatures of water masses vary regionally and with depth. In the Ross Sea, possibly the coldest inhabited large water mass on Earth, winter temperatures are close to the freezing point of seawater (−1.86°C) in the water column. Temperatures can be even lower than this where salinity is raised during freezing events either associated with sea ice or ice growing on the seabed close to land. In summer, temperatures in shallow water only rise to around −1.5°C (Orsi & Wiederwohl 2009). At depths below around 500 m in the Ross Sea, water temperatures are higher, up to around +1.5°C, as this is the depth that circumpolar deep water (CDW) intrudes to in this region. Circumpolar deep water is a large relatively warm saline water mass that occupies mid-water depths of the Antarctic circumpolar current. It is characteristically 2–4°C warmer than surface waters and is split into upper circumpolar deep water (UCDW) and lower circumpolar deep water (LCDW) by oceanographers.

Other regions of the Antarctic have warmer surface regimes. Along the Antarctic Peninsula and South Shetland and South Orkney Islands, near-surface winter temperatures are similar to those in the Ross Sea, but in the summer significantly positive values are achieved. At Rothera Station on Adelaide Island, summer peak temperatures are often around +1.5°C (Clarke et al. 2007, 2008), as they are further north along the Antarctic Peninsula, for example, at Palmer Station on Anvers Island where temperatures can reach 2°C (Schram et al. 2015a), and on into the South Shetland Islands (Martinson et al. 2008) and South Orkney Islands (Clarke & Leakey 1996). Along the Antarctic Peninsula, UCDW penetrates onto the continental shelf to depths shallower than 300 m in most years (Martinson et al. 2008, Martinson & McKee 2012), and this can have strong influences on sea ice, coastal glaciers, ice shelves and marine productivity (Ducklow et al. 2013).

Salinity varies over both small and large spatial scales in the Southern Ocean. This variation comes from two main sources, the formation and melt of sea ice and run-off and melt from land-based glaciers and coastal ice shelves. The lowering of salinity associated with coastal run-off declines with distance from shore, but a reduced salinity signal is still detectable in surface waters hundreds of kilometres out across the continental shelf and beyond (Meredith et al. 2013). In nearshore environments, and over small spatial scales and shallow depths, salinities can be close to freshwater, which is an important factor for species inhabiting intertidal and intertidal fringe localities near melting glaciers. Very high salinities are produced locally when sea ice forms, which

can result in brine channels in the ice and ice plumes under sea ice when cold brine sinks (Thomas & Diekmann 2010). Species inhabiting shallow water, especially those close to shore, experience very wide salinity fluctuations over both short periods when inundated with glacier run-off and seasonally when the environment freezes in winter.

The Antarctic marine environment is physically heterogeneous and patchy, both spatially and temporally, and this significantly impacts biodiversity patterns. This heterogeneity is evident not only on the seabed but also in the water column and associated ice cover. In the water column, patchiness exists over a range of scales due to variation in nutrient dynamics, length of the summer period of high light availability (which varies with latitude and factors such as ice cover), salinity changes and run-off from glaciers. Sea ice habitats are patchy over small spatial scales because of vertical gradients and strong salinity variation over small spatial scales (e.g. Petrich & Eiken 2010). They are patchy over larger scales because of interactions with differing levels of light input with latitude, because of the effects of land causing bottlenecks, and because of currents, heat transfer and wind that can cause open water polynyas all year round in the midst of otherwise continuous sea ice. Benthic and demersal organisms have even been shown to exist under ice shelves, sometimes many kilometres from the nearest open water (Littlepage & Pearse 1962, Lipps et al. 1979, Hain & Melles 1994, Domack et al. 2005). This includes a unique fauna that lives attached to the ice on the undersides of ice shelves. A recently described member of this fauna is an anemone, *Edwardsiella andrillae* that was discovered on the underside of the Ross Ice Shelf (Daly et al. 2013). Populations living under ice shelves must depend on particulate organic material advected from open water by currents or zooplankton moved under the ice by water currents during their daily vertical migrations. Many of the populations living under ice shelves must recruit by larval transport from distant locations.

Seabed patchiness in shallow water is primarily caused by variations in ice impacts (Barnes & Conlan 2012). Average annual wind speeds are highest globally in the latitudes between 50°S and 70°S, reaching values around 10 m s^{-1}, and average oceanic wave heights are also the largest in these latitudes at around 4 m (Barnes & Conlan 2007). These factors combine with the presence of ice in its many forms to make the shallow Southern Ocean seabed massively disturbed and only the most human-impacted seabeds due to trawling approach these levels of disturbance (Barnes & Conlan 2012). At depths of around 10–15 m, a site in North Cove, Rothera Point on Adelaide Island, Antarctic Peninsula was monitored for iceberg impacts, and over 90% of the site was impacted within one year, with several areas in the study experiencing multiple impacts. In another nearby bay, however, only around 40% of the area monitored was impacted per year (Brown et al. 2004). Shallower exposed sites are impacted more often. Other forms of ice also have strong effects on shallow benthos, with anchor ice growing from cold seabed extending down to 30 m depth at the highest latitudes. An ice foot often forms in the shallowest 2–3 m depth that can be several metres thick and persists for much of the year in some sites (Barnes & Conlan 2007).

In areas protected from scour, dense and diverse biological communities often develop. The interplay between levels of exposure to scour, wave action, protection and topography has led to the understanding that seabed communities in sites shallower than 100 m depth are usually held in various stages of early development because of the disturbance (Dayton et al. 1974), and this has been described as a dynamic mosaic (Barnes & Conlan 2012).

Biodiversity

Historical patterns

The biodiversity patterns seen in the Southern Ocean today are the product of both the prevailing environmental conditions and the history of the environment. Historically Antarctica was part of the Gondwana supercontinent bordered by the land masses to become South America and Australia, and 500 million years ago (mya), Gondwana was in the northern hemisphere (Crame 1994). It progressively

moved across the globe and south until by 100 mya it was over the South Pole, still connected to South America and Australia, but its climate was warmer because of the transfer of heat from lower latitudes via large ocean currents (Crame 1994). The origins of some of the present fauna stem from this period and the subsequent break up of Gondwana. This is especially so for an element of the fauna that appeared through vicariance in the Weddellian Province (Clarke & Crame 1989, 2010). The notothenioid fishes may be one of the best examples of this and are one of the few examples of a marine species flock (Eastman & McCune 2000). They are currently the dominant group of Antarctic fishes. Their early diversification was along the Gondwana coast. There are now three non-Antarctic notothenioid groups (Eleginopsidae, Bovichtidae and Pseudaphritidae) living in South America, southern Australia and on Tasmania's coasts, and their distributions result from vicariance that occurred during the Gondwanan fragmentation 100–35 mya (Near 2004). Other groups with good evidence of origins during the Gondwanan break-up include the buccinid snails (Beu 2009).

Antarctica finally separated from South America, its last remaining Gondwanan neighbour, around 34 mya, when the Drake Passage opened. This initiated deep-water flow in the Antarctic circumpolar current, and, on land, large-scale glaciations began (Maldonado et al. 2003, 2014, Livermore et al. 2004). The link between the two continents became progressively weaker from around 40 mya, or even earlier (Livermore et al. 2005), but full separation did not occur for at least another 5 million years. After the separation, biodiversity patterns were mainly set by evolution *in situ* but with some movement of species to and from the deep sea and also by the same process along the Scotia Arc (e.g. Lipps & Hickman 1982). Clarke & Johnston (2003) argued that the relative representation of many of the major taxa may result from accidents of history rather than the nature of the Antarctic marine environment, with climatic change and glaciation causing extinction in some groups, which provided opportunities for others to expand.

Since the opening of the Drake Passage, temperatures in the Southern Ocean have generally cooled. There has been a steady decline in Southern Ocean temperature over the last 15 million years. Forty mya, sea temperatures around Antarctica were around 10–12°C warmer than at present (Zachos et al. 2008). There was a sharp fall in sea temperature around the separation of the continents approximately 35 mya of ~3–4°C, followed by a rise back to preseparation temperatures during the early Miocene period (23–17 mya). From 15 to 17 mya, Southern Ocean temperatures declined gradually by around 10–12°C until current values were reached within the last 1 million years (Zachos et al. 2008). There were further small periods of warming in the late Miocene and early Pliocene (4.8–3.6 mya). These were, however, overlaid on the gradual cooling. Since Antarctica's isolation and cooling to current temperatures, there have been cooling and warming cycles in the environment caused by three main factors, the Milankovitch cycles: variations in the elliptical orbit of the Earth around the sun (eccentricity, 400,000- and 100,000-year cycles); changes in the tilt of the Earth's axis (obliquity, 41,000-year cycles); and wobbles in the rotational axis (precession, 23,000-year cycles) (Zachos et al. 2001). These have combined to give the glacial cycles observed and have been described from ice core records.

The cooling of the Southern Ocean has been accompanied by changes in sea ice, which have had profound effects on not only the present biodiversity but also how it was shaped during glacial cycles and interglacial periods. The extension of ice across the continental shelf reduced the area available for colonisation, made shallow sites unavailable and fragmented previously continuous ranges. This effect was increased by lowered sea level as the ice sheets increased in volume. The regular progression and retreat of ice restricted distributions to the outer sections of the continental shelf and to small areas on the continental shelf (refuges), only to return during interglacial periods. This process was identified as one that likely produced new species by isolation during periods of large ice extent, followed by range expansions in interglacials. Regular sequences of this around Antarctica during glacial cycles was called the 'biodiversity pump' by Clarke & Crame (2010).

In the early part of the first decade of the twenty-first century, data showing ice scour marks extending over the whole of the continental shelf suggested that ice sheets covered all available

seabed, effectively reducing areas for biodiversity colonisation to zero (e.g. O'Cofaigh et al. 2002, Thatje et al. 2005). The idea of complete exclusion of life from the Antarctic continent was first challenged on land where continuous mountain and coastal refugia were identified as having been present throughout all previous glacial cycles from genetic analyses of living terrestrial groups (Stevens et al. 2006, Convey & Stevens 2007). This was followed by studies progressively showing marine life returned to the continental shelf and shallow sea from refugia on the continental shelf and possibly in shallow areas around Antarctica that persisted throughout previous glacial cycles (Graham et al. 2008, Thatje et al. 2008, Barnes & Kuklinski 2010). The fact that groups of organisms exist in the Southern Ocean which have persisted in isolation from other regions of the world since the Mesozoic confirms that sufficiently large refugia must have occurred during all previous glacial maxima. The important current questions lie around identifying where these refugia existed.

Current biodiversity

The extreme conditions and the long history of extremes in the Southern Ocean have produced a current fauna that is unique, with poor representation in some groups and with notable absences of representatives in many groups of fish, including scombrids and salmonids and some decapod crustaceans, including brachyuran crabs. Key papers developing many of the current ideas on the patterns and characteristics of current Antarctic marine diversity possibly began with Dearborn (1965), who worked in McMurdo Sound and was one of the first to assess benthic diversity. Hedgepeth (1971), Dell (1972) and White (1984) produced some of the first analyses of biodiversity patterns and the identification of provinces or regions. These were developed and clarified by Dayton (1990). Many of the more recent ideas on biodiversity patterns were erected by Arntz et al. (1994), Clarke (1996), Clarke & Crame (1992) and Clarke & Johnston (2003). More recently, the rapid development in genomic technologies has allowed an explosion in diversity research in Antarctica, but most of the patterns identified by the earlier researchers still remain as overarching paradigms. Overall diversity (in terms of species richness) is much higher than the non-specialist would expect from a polar ocean, with over 8000 species of marine invertebrate described to date (De Broyer et al. 2014) and an estimated at least 17,000 species living on the continental shelves (Gutt et al. 2004). Low levels of sampling and poor sampling in some areas (Clarke & Johnston 2003), combined with molecular taxonomic techniques identifying increasing numbers of cryptic species, means that such numbers, or more, are feasible, although there are examples where insufficient account has been taken of morphological variation when setting up taxonomic keys (e.g. Peck et al. 2018). However, such cases are rare. The fish fauna on the continental shelf is dominated by one group, the notothenioids that account for over 70% of the species present and over 90% of the biomass. They form a species flock that is similar in biodiversity terms to the cichlid fishes of the great lakes in Africa (Eastman & McCune 2000). In deeper water, another group, the snail fish (Liparidae), forms a large part of the fauna. Decapod crustaceans have representatives among the stone crabs (superfamily Lithodidae), but there is only a handful of species of caridean shrimps and no lobsters or true crabs (infraorder Brachyura), even though they are the most speciose crustacean group with over 6500 species worldwide. Other groups with poor representation include gastropod molluscs and balanomorph barnacles. The absence of some of these groups, such as the balanomorph barnacles, may be because elsewhere they predominantly inhabit shallow or intertidal sites, and the lack of suitable coastline may preclude their colonisation. There are also geographic areas or features where understanding, or even evaluations, of Antarctic marine biodiversity are poor. These include parts of the Bellingshausen and Amundsen Seas and also hydrothermal vents and seeps, which have only recently begun to be evaluated, but several of which have been located, for example along the Scotia Arc, including the Kemp Caldera (Rogers et al. 2012).

For some groups, on the other hand, a significant proportion of the world's total species is found in Antarctica. The sea spiders are especially well represented at around 21% of the world's total, but over

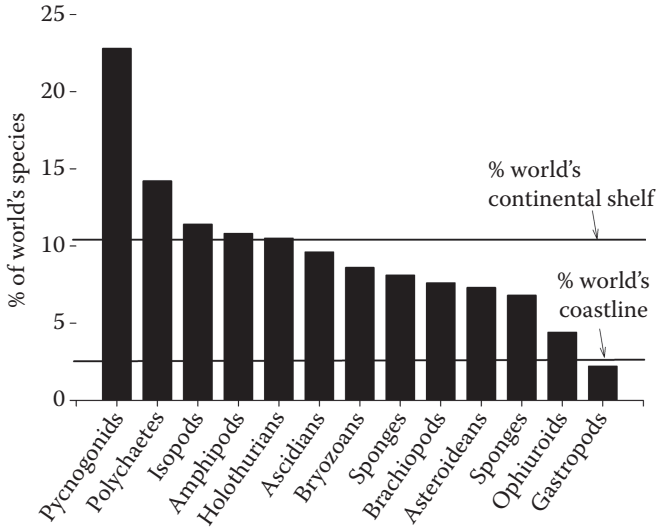

Figure 2 Proportion of total number of global species present in the Southern Ocean for several major animal groups. Data primarily from Clarke and Johnston (2003), updated using data by Linse et al. (2006), Barnes and Griffiths (2008), Munilla and Soler Membrives (2009), O'Loughlin et al. (2011), Emig (2017), Barnes (pers. comm.) (for bryozoans), and the World Register of Marine Species. Horizontal lines: proportions of global coastline and shelf area for the Southern Ocean. (Updated from Barnes, D.K.A. & Peck, L.S. 2008. *Climate Research* **37**, 149–163.)

13% of global polychaete species and over 10% of bryozoans, isopods and amphipods are also Southern Ocean species (Figure 2). These species all occur in an area of ocean that accounts for 7.3–10.6% of the world's continental shelf, 2.1% of marine seabed shallower than 200 m and 0.33% of global ice-free coastline. Thus, several taxa are represented at higher levels than would be expected on average for the areas of seabed or coastline available for colonisation and at higher levels than global averages. Several other groups, including brachiopods, echinoids, asteroids, holothuroids and bivalve molluscs, are all represented at levels near to 10% of global averages. The idea that the Antarctic benthic marine fauna is poorly represented is true for some of the most studied groups globally, such as molluscs and sponges, but it is not the case for several of the major taxa inhabiting the world's oceans.

A major issue when making biodiversity comparisons is making like-with-like analyses. The distributions of depths in the Southern Ocean are different from most others, with around two-thirds of them being deep sea beyond 3000 m, and the continental shelf being depressed by the mass of the ice sheet and previous scouring during glacial maxima to an average depth of around 450 m (Clarke & Crame 2010). The edge of the continental shelf is often taken as the 1000-m contour (e.g. Convey et al. 2012). However, depth makes a difference to the environment, especially in shallower depths as light, water movement, variations in food quality and salinity all change more on average in shallower depths. The issues then are making comparisons at set depth ranges, for instance, making comparisons at the usual continental shelf depths of 200–300 m, or to compare faunas on continental shelves that differ markedly in depth, and possibly average distance from the coastline and the enhanced nutrient inputs from that source. None of these are fully appropriate comparisons and should be made with caution and appropriate caveats. In many lower latitude regions, numbers of species living in the first 5–10 m below the intertidal can be very high. Numbers of scleractinian corals alone have been reported to be over 200 in some tropical intertidal habitats, and the associated faunas make this an exceptionally diverse, very shallow system (e.g. Richards et al. 2015). Further to this, both tropical and temperate intertidal and shallow wetlands can be highly diverse, which is

especially so for mangroves (e.g. Dangan-Galon et al. 2016). Shallow-water diversity is particularly high in tropical coral reefs, formed by coral species with zooxanthellae, which predominantly exist in the top 100 m, and even within this are mainly within the top 50 m (Briggs 1996, Spalding et al. 2001). These are depths that experience high levels of ice disturbance in Antarctica. Future studies should attempt to account for these differences and limit comparisons to similar but restricted depth ranges. Investigations should also include assessments of the relative areas available for colonisation to those sampled, to identify where the biggest biodiversity differences occur between Antarctica and other regions. Further issues with factors such as depth are the lack of information for Antarctica and often for the polar regions in general. Thus, for sediments, some authors have suggested that diversity decreases with increasing latitude (e.g. Snelgrove et al. 2016), but Arctic sediment diversity has been demonstrated to be as high or higher than that in the Canadian Pacific and Atlantic (Archambault et al. 2010), and very recent research at a site on the Antarctic Peninsula has found higher levels of sediment species richness and animal abundance than at most lower latitude sites (Vause pers. comm.). Data are limited, but there may not be a latitudinal trend in diversity in soft sediment environments similar to that seen on hard substrata or on land.

The intertidal and sea ice

Two areas in Antarctica where understanding of biodiversity levels has advanced markedly in recent decades are for the intertidal and epontic sea ice communities. For many years, the intertidal of the Southern Ocean was thought to be only very sparsely colonised and for macro and meiofauna to be largely absent (e.g. Fogg 1998). In open intertidal areas, ice scour removes all obvious organisms with the possible exception of the mobile limpet *Nacella concinna* (Zacher et al. 2007). In areas protected from ice scour, however, such as in cobble boulder fields, a recognisable community can develop. Waller et al. (2006a) and Waller (2013) showed that over 40 species of marine invertebrate are present, 17 of which were sessile and attached, and some of those were at least four years old, demonstrating continuous multiyear survival. Zonation was also identified for the first time in the Antarctic intertidal, as communities changed with depth within a boulder field (Waller 2013).

Sea ice is far from uniform, and it provides a variety of habitats that supports a surprising level of biodiversity. It is colonised by a wide range of organisms that includes viruses, bacteria, meiofauna, invertebrates and fish that higher predators including birds and mammals can exploit (Thomas & Diekmann 2010). Only around a dozen species are categorised as truly ice-inhabiting and sympagic from both polar regions, but these species have to survive temperatures down to −10°C and salinities varying from close to freshwater to up to three or four times more concentrated than seawater (Schnack-Schiel 2008). A much larger fauna has been identified as associated with sea ice as a habitat. This consists mainly of nematodes and rotifers in the Arctic, although copepods and turbellarians dominate in Antarctica. The distribution of organisms in the sea ice varies with the age of the ice and whether it is annual or multiyear ice. Most species occur in the lower layers of the sea ice, which are often flushed with seawater and physically closest to the subsea ice environment. This is where harpacticoid copepods are found, and even here they avoid narrow channels in the ice (Krembs et al. 2000). Some groups penetrate into the higher levels, and amongst these, some rotifers and turbellarians have been shown to pass through channels less than two-thirds of their body diameters by stretching and flexing their bodies (Schnack-Schiel 2008).

The isolation of the Antarctic marine environment, combined with environmental heterogeneity and historical environmental cycles that produced the biodiversity pump (Clarke & Crame 2010), has resulted in many new species evolving *in situ*. The result is that several Southern Ocean groups exhibit very high levels of endemism, often around 50%, including ascidians (Primo & Vasquez 2007), anemones (Rodriguez et al. 2007), bryozoans, bivalve molluscs and pycnogonids (Griffiths et al. 2009). Some other taxa exhibit even higher levels of endemism, including gastropod molluscs (around 75%, Griffiths et al. 2009), gammaridean amphipods (around 80%, De Broyer et al. 2007),

and octopods (around 80%, Collins & Rodhouse 2006). It should be noted, however, that all of these figures have changed in recent years because of the significant efforts put into identifying new species through large-scale initiatives such as the Census of Antarctic Marine Life (CAML, www.caml.aq) and SCAR MarBIN (www.scarmarbin.be).

The overall outcome is a diverse and cold-adapted Southern Ocean fauna which has a range of general, and some unique, adaptations and life-history characteristics. These attributes have been shaped not only by physical factors such as isolation, cold, ice and seasonality, but also by biological factors such as predation.

Predation

From the earliest ecological studies of predation in Antarctic marine environments, it has been recognised that the types of predation, especially on the seabed, and numbers of specific types of predators are lower than elsewhere. However, there are trends that run contrary to this, and one is the high level of spongivory in Antarctic asteroids, where several species of starfish are primarily spongivorous (McClintock 1994, McClintock et al. 2005). Dayton (1990) and Arntz et al. (1994) highlighted differences with the Arctic in the absence or markedly reduced numbers of many bottom-feeding fish groups (e.g. sharks, rays, gadoid cods and flatfishes). The notothenioids are predominantly a demersal group, but there are no species so far identified in Antarctica that, for instance, regularly eat brittle star arms or the tips of infaunal bivalve mollusc siphons as do some lower latitude and Arctic flatfishes. There is also nothing analogous to the Arctic benthic feeding whales and walruses.

It can be argued that predation must be important for many species in Antarctica because chemical defences, or noxious, or repellent substances have been identified as present in the tissues of a wide range of species in the Southern Ocean. These include the brachiopod *Liothyrella uva* (McClintock et al. 1993, Mahon et al. 2003); the nudibranchs *Bathydoris hodgsoni* (Avila et al. 2000) and *Doris kerguelenensis* (Iken et al. 2002); the sponge *Latrunculia apicalis* (Furrow et al. 2003) and several other sponges (Peters et al. 2009); the ascidians *Distaplia cylindrica* (McClintock et al. 2004), *Cnemidocarpa verrucosa* (McClintock et al. 1991) and a range of other ascidians (Koplovitz et al. 2009); three soft corals (Slattery & McClintock 1995); and eggs, embryos and larvae of a range of invertebrate species (McClintock & Baker 1997). In a multispecies study, Núñez-Pons & Avila (2014) found that 17 of 31 Antarctic marine species contained lipophilic fractions that repelled the starfish *Odontaster validus.* Repellent substances have also been isolated from a range of Antarctic macroalgae (Amsler et al. 2005, Aumack et al. 2010, Bucolo et al. 2011). Large populations of herbivorous and omnivorous amphipods have been found associated with Antarctic macroalgae, which may explain the high incidence of macroalgal chemical defences (Amsler et al. 2014). It should be noted here that chemical defences are not the only factors that bear on likelihood of attack and success by predators, as the return compared to the effort needed to gain access has been identified as important (e.g. Peck 1993a, 2001a,b), and large size can provide a refuge from predation in prey species (Harper et al. 2009).

It is well recognised in the literature that predation pressure is a major structuring factor in the composition of biological communities, both in the present and over evolutionary time (Vermeij 1987). Several studies have described latitudinal gradients in predation pressure, although global-scale data are sparse (e.g. MacArthur 1972, Bertness et al. 1981), and few have produced data from the tropics to the poles. Recently Harper and Peck (2016) analysed frequencies of damage and repair in the shells of rhynchonelliform brachiopods to demonstrate a decrease in durophagous predation pressure across latitudes and with depth in the oceans. In the Southern Ocean, the main hypothesis is that the lack of durophagous-crushing predators over evolutionary time has resulted in a fauna that is archaic compared to lower latitude and Arctic marine benthic faunas, with similarities to Palaeozoic marine faunas (Aronson & Blake 2001, Arntz et al. 2005, Aronson et al. 2007). The top invertebrate predators are generally slow-moving asteroids and nemerteans and sessile anemones. Seabed protected from ice scour is often dominated by dense populations of epifaunal

suspension- or deposit-feeders characterised by ophiuroids, crinoids, bryozoans, brachiopods, urchins and polychaetes that can extend over hundreds of square kilometres in deep water (Clarke et al. 2004a, Gili et al. 2006, Aronson et al. 2007, Convey et al. 2012). It should be noted that the fauna is often described as ancient, and the species composition is often thought to be reminiscent of past assemblages (e.g. Aronson et al. 2007). Some species, however, have evolved *in situ*, and there are recent colonisers, and in this sense, some are highly derived (Clarke & Crame 1989, Aronson et al. 1997). In this debate, however, it should be noted that the measured predation pressure is from durophagous predation. Levels of predation from engulfing predators such as nemerteans and anemones and from grazing predators such as urchins and limpets may be very intense, especially on early life stages, but these predation pressures have generally not been evaluated in the Southern Ocean benthos. Predation pressure is one of the main factors shaping the characteristics of the life histories of species living in a given environment. Other factors impacting life histories include competition and physical constraints, some of which can be clearer in extreme environments such as the Southern Ocean than elsewhere.

Life histories

The study of life histories is based around the concept that the phenotype is the product of a range of demographic traits including growth rate, overall size, age and size at maturity, number and size of offspring, reproductive investment and longevity. The interaction of these characteristics is key to setting the fitness of the individual in any particular environment (Stearns 1992). Life-history analyses of Antarctic marine species are rare, even though many of the relevant characteristics have been gathered for several decades (e.g. Arntz et al. 1994), and general physiological adaptations have been investigated for several groups (see reviews by Clarke 1983, 1998, Peck 2002a, Peck et al. 2006b, Pörtner et al. 2007, 2012).

Many life-history characteristics in studies of Antarctic benthic species in the early decades of marine biological research were identified as being K-selected attributes (Clarke 1979). These were detailed by Arntz et al. (1994) and included slow growth rates; seasonal growth; prolonged gametogenesis; seasonal reproduction; slow embryonic development; large, yolky eggs; low fecundity; delayed maturation; high incidences of brooding and protected development; extended longevity; large adult size; and low mortality.

Research in all of these areas has progressed markedly in the last 20 years, and understanding of the underlying mechanisms has advanced, but many of the attributes of polar marine ectotherms are still described as largely conforming to expectations of a K-selected fauna (e.g. Węslawski & Legezynska 2002). The next sections will deal with most of these characteristics in detail and show where understanding has improved to give greater insight into the adaptations of animals and limitations posed by living in a cold, highly seasonal polar ocean.

Growth

From the earliest studies of growth in Antarctic ectotherms, a pattern of slow growth has emerged for invertebrates and fish (Pearse 1965, Bregazzi 1972, Rakusa-Suszczewski 1972, Dayton et al. 1974, Everson 1977). These were followed by further studies showing generally slow or very slow growth across a wide range of benthic taxa, including fish (Eastman 1993), gastropods (Seager 1978, Picken 1979, 1980, Wägele 1988) and bivalve molluscs (Brey & Hain 1992, Nolan & Clarke 1993, Peck & Bullough 1993, Heilmayer et al. 2005, Higgs et al. 2009), decapods shrimps (Clarke & Lakhani 1979, Gorny et al. 1993), isopods (Luxmoore 1985), brachiopods (Brey et al. 1995b, Peck & Brey 1996, Peck et al. 1997b, Peck 2008), echinoids (Brey et al. 1995b), bryozoans (Barnes 1995, Brey et al. 1998, Bowden et al. 2006, Barnes et al. 2006b), octocorals (Peck & Brockington 2013) and polychaetes (Desbruyeres 1977). Some studies have reported relatively rapid growth in some ascidians

(Rauschert 1991, Kowalke et al. 2001) and bryozoans (Barnes 1995). Rapid growth was also reported for sponges by Dayton et al. (1974) and more recently for the giant sponge *Anoxycalyx joubini*, where a near 50-year study showed around 22 years of little growth and no recruitment followed by episodic recruitment and rapid growth at some time between 1989 and 2004 (Dayton et al. 2016). However, the rapid growth rates reported in these studies were still at least five times slower than the fastest growth rates reported for temperate species of the same groups. It should be noted here that most of the growth rates reported previously are for annual growth, and growth can be restricted to relatively small parts of the year. To identify correctly temperature effects on growth, comparisons should assess relative maximum rates of growth in species from different habitats. Data on maximum growth rates are rare globally but very rare in Antarctica. However, one way to address this issue may be to compare daily growth rings in skeletons of marine invertebrates living, or held, in different temperatures.

The question arises as to how to make reasonable comparisons of growth between Antarctic and lower latitude marine species. Comparisons using limited numbers or comparing the fastest rates in Antarctica with average or slow rates elsewhere are clearly flawed. Recently Peck (2016) collated data for von Bertalanffy or Richards growth functions for 37 species of echinoid sea urchins across latitudes from the tropics to the poles. These data showed a consistent decline in growth rate with latitude, even though the fastest Antarctic rates were faster than the slowest at temperate latitudes (Figure 3A). The most appropriate analysis of the effects of temperature on a biological rate is through an Arrhenius plot (Clarke 2017). This plots the logarithm of the rate against the inverse of temperature on the Kelvin scale as 1000/T, and such plots are usually straight lines for biological functions, and the slope can be used to calculate the Arrhenius activation energy (E_a) for the reaction or process plotted (Hochachka & Somero 2002, Clarke 2017). When the K growth coefficients for echinoids in Figure 3A are replotted as an Arrhenius plot, a consistent relationship is obtained for temperate and tropical species living between 5°C and 30°C (Figure 3B). The K values for growth rates for the four Antarctic species investigated are all below the extension of the line for temperate and tropical species, and the difference between the Antarctic values and those predicted from this line is significant ($t = -2.83$, 4 d.f., $P = 0.047$). This shows that the growth rates for Antarctic urchins are slowed beyond the normal effects of temperature on biological systems. Peck (2016) termed this the cold marine physiological transition (CMPT).

An alternative mechanism for evaluating the effect of temperature on biological functions is by using the Q_{10} value of van't Hoff (Hochachka & Somero 2002, Clarke 2017). This metric expresses a change in a biological rate and converts it to that for a 10°C alteration in temperature using the equation:

$$Q_{10} = \left(\frac{R_2}{R_1}\right)^{10/(t_2 - t_1)}$$

where R_2 and R_1 are biological process rates at temperatures t_2 and t_1 respectively (Schmidt-Nielsen 1997). Most biological systems commonly follow Arrhenius relationships and there is a 2-fold to 3-fold increase for every 10°C temperature rise (a Q_{10} of 2–3), and a range of 1–4 covers all normal effects of temperature on enzyme mediated biological processes (Hochachka and Somero 2002). This 'rule' has been a cornerstone of temperature biology for around 100 years and is still quoted widely from research on molecular biology through biochemistry to physiology and ecology, and in all major texts (Hochachka & Somero 2002, Schmidt-Nielsen 1997, Clarke 2017) and reviews (e.g. Clarke 2004) on the thermal biology of biological systems.

Some studies of growth in Antarctic marine species have reported very large increases in growth for a small temperature rise in experiments. For example, in the scallop *Adamussium colbecki*, an increase from 0°C to 3°C produced a rise in growth with a Q_{10} of 71 (Heilmayer et al. 2005), and a 1°C rise in temperature gave a Q_{10} of 1000 for *in situ* growth in some Antarctic bryozoans

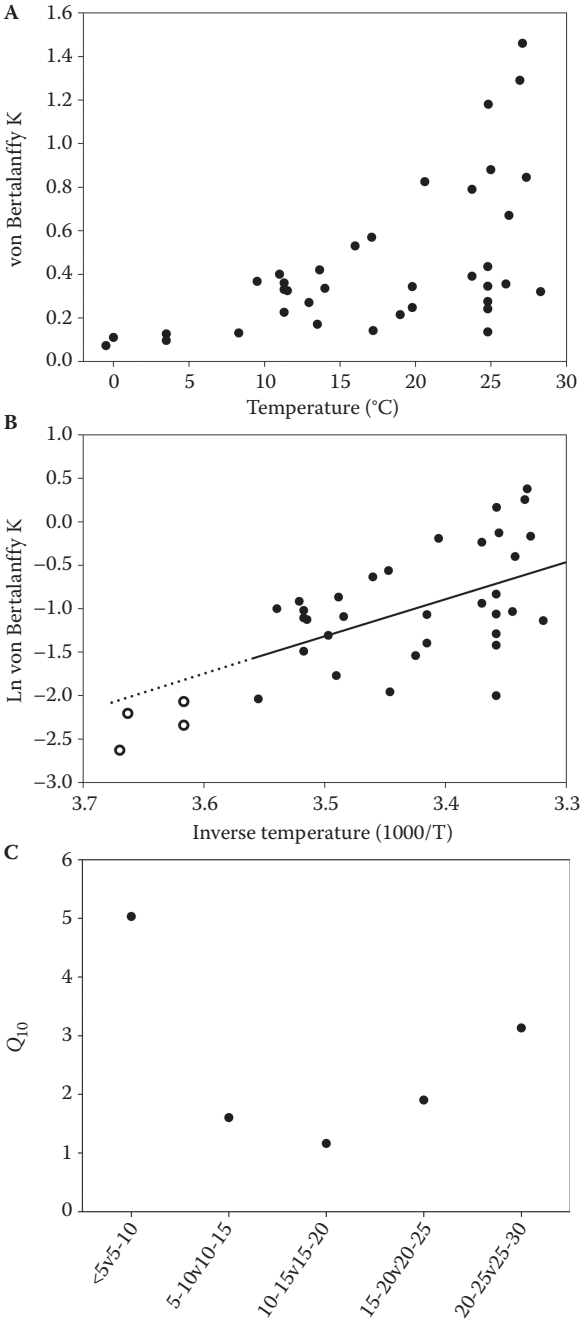

Figure 3 (A) Richards or von Bertalanffy K coefficients for echinoids from tropical to polar latitudes plotted against habitat temperature. (B) Arrhenius plot of K for echinoid growth rate. Solid line is the relationship for temperate and tropical species (Ln K = 13.72 – 4.297 1000/T; $r^2 = 0.27$, F = 25.1, 66 d.f., $P < 0.001$); dotted line is an extension of this relationship to polar temperatures. Open symbols are used to denote Antarctic species and emphasise they are below the Arrhenius line for growth in temperate and tropical echinoids. (C) Q_{10} coefficients for comparisons of mean K coefficient values for each 5°C block compared to its neighbour. (Modified from Peck, L.S. 2016. *Trends in Ecology and Evolution* **31**, 13–26.) Data for figures (A) and (B) are for 39 species with a minimum of 30 individuals per species.

and spirorbid worms (Ashton et al. 2017a,b). An analysis of Q_{10} values comparing mean echinoid von Bertalanffy K coefficients for 5°C blocks in Figure 3A, across the full temperature range and each block compared with adjacent neighbours, shows values are in the expected 1–4 range for temperatures between 5°C and 30°C (Figure 3C). The value for the comparison between species living below 5°C and in the 5–10°C range was, however, 5.2, suggesting that some factor other than the normal impact of temperature on enzyme mediated systems is having an effect. Combining these data with analyses of embryonic development rate and the duration of the postprandial rise in metabolism (the specific dynamic action [SDA] of feeding) showing similar slowing outside the normal effects of temperature led Peck (2016) to suggest that the likely cause is due to problems associated with protein synthesis and folding.

Growth and seasonality versus temperature

Two of the main reasons put forward to explain the observed slow annual growth in polar marine ectotherms are the extreme seasonality of the environment and the low temperature (Dehnel 1955, Dunbar 1968, 1970, Dayton et al. 1974, Clarke 1980, 1983, 1988, 1991, Clarke & Peck 1991). Most marine ectotherms grow when they feed (e.g. Peck et al. 1996), and this has been identified as part of the SDA for many years (Peck 1998, Secor 2009), and growth has also been demonstrated to be highly seasonal in several species (Bregazzi 1972, Seager 1978, Picken 1979, Richardson 1979, Sagar 1980, Clarke 1988, Berkman 1990, Urban & Mercuri 1998, Fraser et al. 2002, Ahn et al. 2003, Bowden et al. 2006). The relatively fast growth reported for some species (although still markedly slower than fast-growing species at lower latitudes) has been used in support of the idea that seasonality is the reason for slow growth because it shows that at least in some taxa the biochemical and physiological machinery to allow fast growth exists. It has also been argued that there should exist a capacity for fast growth at low temperatures because metabolic rates, and therefore metabolic costs, are greatly reduced at low temperature (Clarke 1983, Peck 2016). Metabolic costs are the measure of the instantaneous requirement for energy and are essentially a loss to the animal. They often include a large cost for homeostasis. Growth, reproduction and metabolism usually form the largest three fractions of an animal's energy budget (Kleiber 1961, Bayne 1976, Peck et al. 1987b), although in marine snails, mucus can be a large fraction, from between 5% and 10% of ingested energy (Paine 1965) to values between 25% and 30% (Peck et al. 1987b), and even up to 70% (Horn 1986). The reduction in metabolic losses at low temperature should allow more energy for growth, increasing growth efficiency as the proportion of energy consumed devoted to growth, and also potentially overall growth rate (Clarke 1983, 1987a, 1991, 1998). As seen earlier in this section, however, growth rates are generally low in Antarctic marine species and often slower than would be expected from the normal effects of temperature on biological processes (Peck 2016), which suggests other factors than energy availability are affecting growth.

Not all growth is seasonal in Antarctic marine species, even in some suspension-feeding species dependent on the short phytoplankton bloom. Barnes (1995) found that growth was consistent through the year in some bryozoans but was highly seasonal in others, and the differences were attributed to differences in the size range of phytoplankton consumed. Peck et al. (2000) found that shell growth in juveniles of the sediment dwelling bivalve mollusc *Yoldia* (now *Aequiyoldia*) *eightsii*, continued at the same rate in winter as summer, whereas tissue mass increased in summer but decreased in winter. In a more extreme case, in a mark-recapture tagging field experiment, winter shell growth was 12 times faster than summer increments in the brachiopod *Liothyrella uva* (Peck et al. 1997b). Like the bivalve *Aequiyoldia eightsii*, the brachiopod *Liothyrella uva* had a tissue mass cycle in phase with summer phytoplankton productivity. The conclusion drawn in both cases was that either tissue and shell growth are decoupled, or all growth is decoupled from the period of summer productivity, and growth is fuelled from stored reserves. These studies also emphasised that measuring growth only as change in mass or in length can lead to misleading conclusions as to the seasonality of the various growth processes.

The currently accepted major reason for slow annual growth in Antarctic marine species is that it is due to the effects of low temperature. Low temperature has been widely proposed as the cause of slow overall growth in polar latitudes from some of the earliest studies (Dunbar 1970, Kinne 1970, Arnaud 1974, 1977, Arntz et al. 1994). The alternative argument that adaptation to polar temperatures should allow fast growth, and that seasonality and resource limitation are the proximate causes of slow growth has also been a dominant idea since the 1970s (Dunbar 1970, Clarke 1980, 1983, 1988, 1991, White 1984). Seasonality clearly does restrict the biology of some species, but the argument that low temperature is the major factor has gained more traction in the last two decades. This change has come mainly from two directions, the demonstration that the slowing of development is most likely a temperature-related phenomenon (e.g. Hoegh-Guldberg & Pearse 1995, and this review), and also the finding that the synthesis of fully functional proteins is much more difficult at temperatures around and below 0°C than in warmer habitats (Fraser et al. 2007, Peck 2016). This difficulty at low temperature results in a larger proportion of the proteins being made on ribosomes being recycled immediately, and a smaller proportion of the protein made being deposited or retained for growth. This adds a large extra unseen cost to growth and reduces the efficiency of growth markedly in terms of the manufacture of structural protein and the increase in body size.

Protein synthesis, retention and folding

All organisms grow. Growth of cells is mainly via, and ultimately dependent on, the synthesis of proteins both for structural and functional purposes and the retention of those proteins post synthesis. The total protein content of an organism is known as its protein pool, and this pool is dynamic with newly synthesised proteins adding to the pool, and degradation removing them. Changes in the total protein content of an organism is called protein growth. The combination of synthesis, degradation and growth is called protein metabolism (Fraser & Rogers 2007). Studies of protein metabolism and its components at low temperature have only been conducted for the last 20 years.

Most research on the effects of temperature on proteins in the last 30 years has focussed on enzyme activities and questions such as are the function rates of enzymes adapted to low temperature or are concentrations of enzymes changed to compensate for reduced temperature (Hochachka & Somero 2002). Some cellular processes such as microtubule assembly (Detrich et al. 2000), and a few enzyme function rates (Fields et al. 2001, Kawall et al. 2002), have been demonstrated to be cold-compensated and to proceed at rates similar to warmer water orthologues. The enzyme function rate is measured as the rate that a substrate is converted to product per unit time per active site in an enzyme catalysed reaction and is called k_{cat}. From the very few studies conducted, it seems the overall outcome of adaptation to different temperatures has resulted in higher k_{cat} values in polar species than those from lower latitudes and, hence, more active enzymes (Fields & Somero 1998), although it seems that concentrations of enzymes are not modified to a great extent (Hochachka & Somero 2002). It should be noted here that comparisons of the effect of temperature on cellular or physiological process rates require clear interpretation of what is being measured. In many studies, process rates are measured at the studied organism's ambient temperature (and in ectotherms body temperature is predominantly very close to ambient). In these cases, polar investigations are conducted at lower temperatures than studies on temperate or tropical species. In such comparisons, the rate in the polar species is lower than that of the warmer analogues, and this is predominantly true for measures of cellular processes, for example, k_{cat} through to whole-animal physiologies. In the case of cellular processes, the requirement for complete or perfect temperature compensation of function would be to increase the amounts of enzymes in the cell to considerably higher levels. This seems unlikely from two aspects: energetic costs and physical space available. A considerable increase in the levels of thousands of proteins within a cell might not be possible due to limitations in cell size (but this would be a driver towards the observed larger cell size at lower temperatures – see later section 'Egg size, fecundity, reproductive effort and life histories'). However, even if this

were possible, it seems unlikely that this level of protein metabolism could be maintained at low temperatures, especially because there is evidence that proteins are less stable at low temperature than in warmer regions (Fields et al. 2015, Peck 2016).

For the majority of comparisons, for example, whole-animal respiration rate, differences between warm-water and polar taxa are in line with predicted differences from Arrhenius relationships. However, where studies are conducted at overlapping temperatures, warmed colder-water species usually have faster rates than cooled species from warmer environments. This indicates that either there is some compensation for the lower temperature but that compensation is incomplete, or that the slope of the relationship between the biological function rate and temperature is different for a single species or population than for between species and population comparisons.

Protein synthesis rate

The main cellular energetic costs during normal function are protein synthesis, RNA/DNA synthesis, proton leak, Na^+/K^+-ATPase and $Ca2^+$-ATPase. Protein synthesis is a major component of cellular costs accounting for between 11% and 42% of the cellular budget in temperate species (Hawkins et al. 1989, Houlihan et al. 1995, Podrabsky & Hand 2000). The requirements for functioning proteins remain high in Antarctic marine species at low temperature, even though metabolic rates have been demonstrated to be low (Fraser et al. 2002). Studies of whole-animal protein synthesis in Antarctic marine ectotherms started in the 1990s with measures of the fraction of whole-animal protein content that is synthesised each day (k_s). Values were reported for the isopod *Glyptonotus antarcticus* of 0.24% day^{-1}in fed individuals at 0°C (Whiteley et al. 1996), and k_s ranged from 0.16% day^{-1} and 0.38% day^{-1} in starved and fed animals, respectively, also at 0°C (Robertson et al. 2001). In the holothurian *Heterocucumis steineni*, k_s values ranged from 0.23% day^{-1} in winter to 0.35% day^{-1} for body wall in summer. In the limpet *Nacella concinna*, whole-animal winter values were reported at 0.29% day^{-1} and 0.35% day^{-1}, whereas in summer, these were 0.40% day^{-1} and 0.56% day^{-1} (Fraser et al. 2002), but higher values (0.56% day^{-1} to 0.84% day^{-1}) were recorded for the same species in a later study (Fraser et al. 2007). The interannual differences in the studies on *N. concinna* were attributed to different food availability in different years (Fraser et al. 2007). These data indicate a reduction in protein synthesis of between 25% and 50% in winter over summer in Antarctic species. The cause for the reduction is probably a mixture of lower temperature and seasonal resource reduction in winter.

The few studies of protein synthesis in Antarctic species have all produced values much lower than those for warmer-water species (Fraser & Rogers 2007), with k_s averaging around 0.48% ($\pm$0.05 s.e.) day^{-1}, compared to 3.7% ($\pm$0.72 s.e.) day^{-1} for temperate marine species. Fractional rates of protein synthesis are thus around eight times lower than those for temperate species, and there is evidence that $k_s$declines markedly at temperatures below 5°C, which parallels the trend for growth.

Very few studies have investigated the effect of temperature on protein synthesis rates in Antarctic species, but Fraser et al. (2007) found that both fractional and absolute protein synthesis rates were fastest at approximately 1°C in *N. concinna*, declining both above and below this temperature. They argued that predicted warming in Antarctic waters could result in reduced, rather than increased, rates of protein synthesis and, in turn, possibly growth if changes happened faster than the animals' abilities to adapt (Fraser et al. 2007). The logical conclusion to be drawn from these data is that some factor associated with protein synthesis is very sensitive to temperatures near 0°C. Peck (2016) has suggested this is likely protein folding as folding is sensitive to viscosity, and seawater viscosity changes markedly more at low polar temperatures than at temperate or tropical latitudes. Protein stability decreases and unfolding increases at low temperature, which appears to be due to changes in the free energy relationships between nonpolar groups and water. This results in the penetration of water molecules into the edges of the protein, which weakens the hydrophobic bonding strength and makes the protein core less stable (Lopez et al. 2008, Dias et al. 2010).

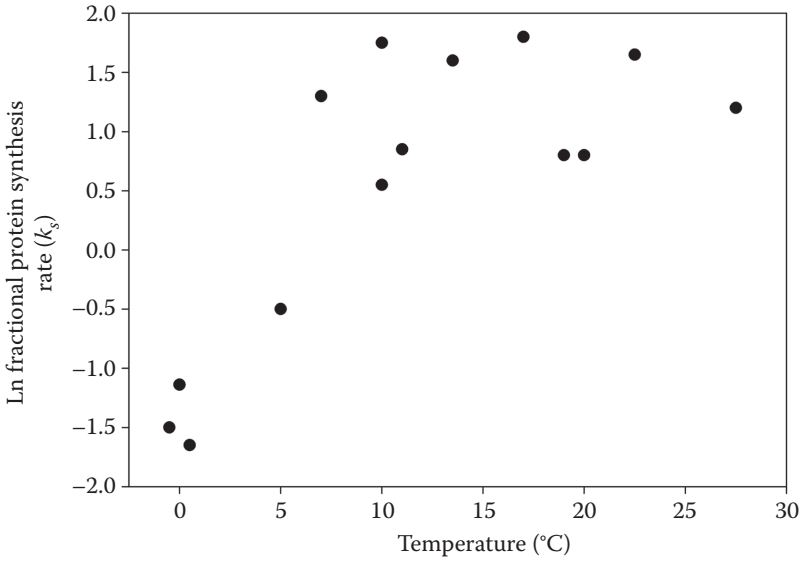

Figure 4 Mass standardised whole-animal fractional protein synthesis (k_s) rates plotted for ectotherms (fish, molluscs and crustaceans) at natural habitat temperatures for polar to tropical species. Note k_s values are Ln transformed. (Figure modified from Fraser, K.P.P. & Rogers, A.D. 2007. *Advances in Marine Biology* **52**, 267–362.)

Making good comparisons of protein synthesis rates between species living at different temperatures requires the same measures to be made and also comparable techniques used. Fraser & Rogers (2007) compiled data for a range of ectotherms across latitudes and a temperature range of more than 25°C for whole-animal rates of protein synthesis. Temperate and tropical animals living at temperatures between 5°C and 30°C had k_s values in the range 1.65%–6.3%, whereas the one species studied living at 5°C, the isopod *Saduria entomon*, had a k_s of 0.6% (Robertson et al. 2001), and the two Antarctic species where data were available had values of 0.24% day^{-1} (*Glyptonotus antarcticus*, Whiteley et al. 1996) and 0.40% (*Nacella concinna*, Fraser & Rogers 2007). These data all fitted a consistent pattern when the k_s values were logarithmically transformed, showing similar values for species living at temperate and tropical temperatures, but a marked decline occurs as temperatures fall below 5°C (Figure 4). Antarctic whole-animal fractional protein synthesis rates are thus around an order of magnitude lower than temperate and tropical species.

Much higher rates of protein synthesis have been reported in larvae, with values similar to those for temperate species in the Antarctic starfish *Acodontaster hodgsoni, Glabraster* (previously *Porania*) *antarctica* and *Odontaster meridionalis* (Ginsburg & Manahan 2009), and the echinoid *Sterechinus neumayeri* (Marsh et al. 2001). The high rates were associated with very high efficiencies of production (Pace & Manahan 2006, 2007). These were later correlated with high rates of biosynthesis of protein at the ribosome in embryos of *S. neumayeri* (Pace & Manahan 2010). There is some uncertainty over the efficiencies of protein synthesis reported for Antarctic urchin embryos, as Fraser and Rogers (2007) noted that the efficiencies quoted were beyond the theoretical thermodynamic limits, in terms of the number of adenosine triphosphate (ATP) equivalents needed per peptide bond during protein synthesis (usually four).

Protein synthesis retention efficiency

Protein synthesis is only the first part of the process leading to the production of well-conformed functional proteins. The second aspect is how well made the proteins are, and this is measured

as the protein synthesis retention efficiency (PSRE). When protein synthesis results in a poorly conformed or non-functional protein, a mechanism is entrained to identify these proteins and break them down for recycling of the amino acids. The identification of badly formed protein that is then degraded is usually achieved via tagging with ubiquitin. PSRE is a measure of the proportion of synthesised proteins that are well formed (the percent retained as opposed to recycled) and functional (Hochachka & Somero 2002). It is usually calculated as:

$$PSRE = \frac{k_g}{k_s} \times 100(\%)$$

where k_g is the change in total body protein content (protein growth, % day^{-1}), and k_s is fractional protein synthesis (% day^{-1}). Protein synthesis retention efficiency has only been measured in one Antarctic species to date, the limpet *Nacella concinna*, where values of 15.7% in winter and 20.9% in summer were reported (Fraser et al. 2007). If the various studies on tissues and not whole animals are included, then Antarctic species exhibit low PSRE values, and there is a general decline in PSRE at lower temperatures that follows an Arrhenius relationship (Fraser et al. 2007, Figure 5). If *N. concinna* is representative of Antarctic ectotherms in general, then PSRE is two to six times lower in polar marine species than those living in temperate and tropical latitudes (Figure 5).

There is further strong support for low PSRE levels in Antarctic marine species from measures of ubiquitination, where very high levels have been reported in fish (Todgham et al. 2007), and high levels of expression of genes associated with ubiquitination have been reported in fish tissues (Shin et al. 2012). Low PSRE in Antarctic species has important consequences because it suggests that growth in polar ectotherms is less efficient than in lower latitude species because of the greater losses. This probably results from biochemical constraints on protein synthesis. This result contrasts with a few studies that have reported higher growth efficiencies at lower temperatures (e.g. for scallops, Heilmayer et al. 2004), but reduced efficiency at low temperature appears the more common outcome. Why a higher proportion of body proteins are degraded at low temperatures is currently unclear, although there is good evidence that the proportion of an animal's proteome that is denatured

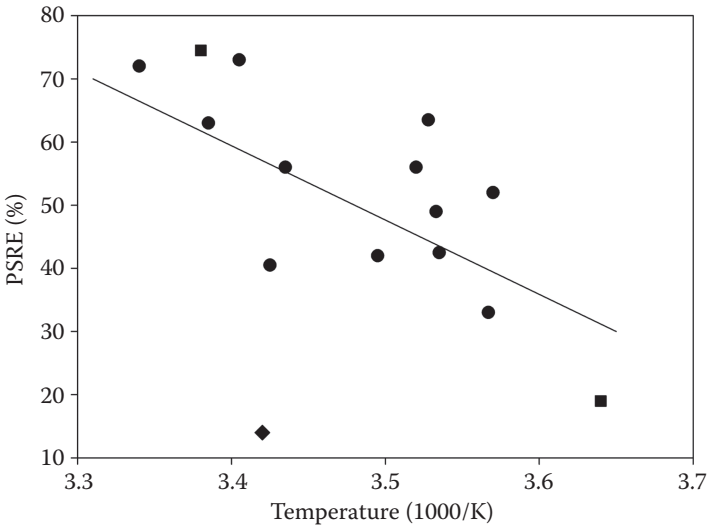

Figure 5 Mass standardised protein synthesis retention efficiency (PSRE) plotted against habitat temperature for a range of tropical to polar ectotherms. Data fit an Arrhenius relationship ($PSRE = 450–115$ T, $r^2 = 0.29$, 14 d.f., $P < 0.05$). Circles denote data for fish species, squares for molluscs and the diamond for a crustacean. (Redrawn from Fraser, K.P.P. et al. 2007. *Journal of Experimental Biology* **210**, 2691–2699.)

is higher in species living at cold polar water temperatures than elsewhere (Buckley et al. 2004, Place et al. 2004, Hofmann et al. 2005, Place & Hofmann 2005, Peck 2016).

Earlier it was shown that larvae of Antarctic marine invertebrates exhibit high rates of protein synthesis. These high rates of synthesis appear to be accompanied by low or very low rates of protein retention or deposition. Thus, Ginsburg and Manahan (2009) measured protein retention in larvae of the starfish *Odontaster meridionalis* and the urchin *Sterechinus neumayeri*, and found values of 5.1% and 3.8%, respectively. These compared with protein retention of ≥28% for larvae of the temperate starfish *Patiria* (previously *Asterina*) *miniata* (Pace & Manahan 2007) and 21% for the temperate urchin *Lytechinus pictus* (Pace & Manahan 2006). Fast growth is often seen as one of the most important attributes of embryonic and larval stages of marine invertebrates, to minimise exposure to predators in what is seen as the most vulnerable part of the life cycle (Pechenik 1991, Pechenik & Levine 2007). It thus seems likely that the poor rate of protein deposition reported for Antarctic marine larvae constrains their growth rates, and one adaptation to minimise this problem is to increase, as far as possible, rates of protein synthesis. The compensation is, however, clearly incomplete because larval development rates in Antarctic marine ectotherms are much slower than for temperate species and slowed beyond the normal effects of temperature on biological systems (see section on 'Embryonic and larval development').

Costs of protein synthesis

Studies reporting the cost of synthesising proteins in temperate and tropical species vary somewhat, but most values are in the range 5–15 mmol O_2 g^{-1}, when energetic cost is expressed as a metabolic oxygen requirement (Fraser & Rogers 2007). Reports of the costs of protein synthesis in Antarctic ectotherms vary very widely, from values of 0.92 mmol O_2 g^{-1} protein in the urchin *Sterechinus neumayeri* (Marsh et al. 2001), which is below the theoretical minimum thermodynamic costs for synthesising protein, to 4.0 mmol O_2 g^{-1} protein for the starfish *Odontaster validus*, to 7 mmol O_2 g^{-1} protein for the scallop *Adamussium colbecki* (Storch et al. 2003), and up to 147 mmol O_2 g^{-1} protein for the isopod *Glyptonotus antarcticus* (Whiteley et al. 1996). The value for *Adamussium colbecki* was measured in a comparative study with the temperate scallop *Aequipecten opercularis*, which had a cost of 9 mmol O_2 g^{-1} protein. The Antarctic and temperate scallops thus had very similar protein synthesis costs when measured at the same time using the same techniques in the same laboratory. It is not clear why the various studies measuring costs of protein synthesis in Antarctic marine species have produced such massively variable data covering two orders of magnitude. It is also not clear why the cost *per se* should vary markedly between tropical, polar and temperate species because the effect of temperature should be measured on a Kelvin scale, and hence differences should be around 10% when comparing species living in Antarctica at −2°C with tropical species at 25°C. From a pure physics standpoint, the rate that a biochemical reaction changes with temperature over the normal physiological range (273–313 K) is governed by the change in mean molecular speed as this dictates the energy of collisions between molecules (Clarke 2017). The Q_{10} for mean molecular speed over this range is 1.07. That most biological systems have Q_{10} values between one and four shows that temperature generally has a much larger effect than would be dictated by changes in molecular speed and that other, possibly many other factors affect changes in the rate of biological functions with temperature. Further studies of the rates, efficiencies and cost of protein synthesis are needed on a wide range of Antarctic marine species before several of the above issues can be resolved.

RNA to protein ratios

The signal to make proteins from deoxyribonucleic acid (DNA) in the nucleus is ribonucleic acid (RNA). The amount of RNA produced is a measure of the strength of the signal. In studies of protein metabolism, the ratio of the amount of RNA to the protein content of the organism is an indication

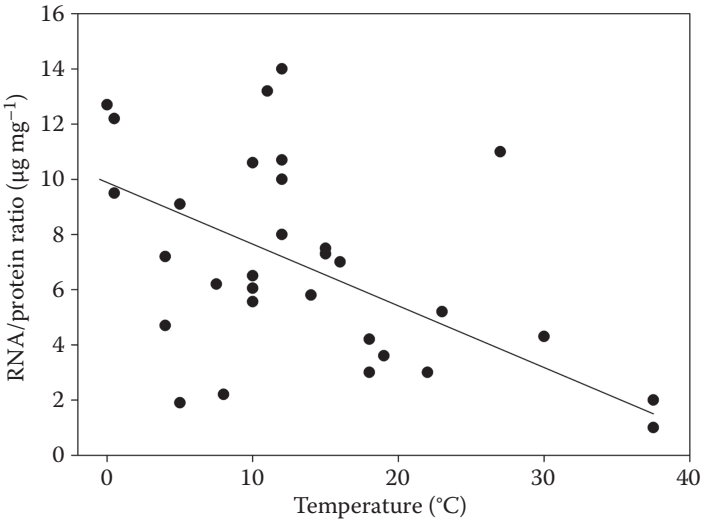

Figure 6 Whole-animal RNA-to-protein ratios mass standardised to a body mass of 129 g plotted against temperature. Masses were standardised using a scaling coefficient of 0.24. The ratio declines with temperature following the relationship shown (RNA: protein = 9.34–0.175 temperature, $r^2 = 0.22$, 30 d.f., $F = 8.18$, $P = 0.008$). (Figure modified from Fraser, K.P.P. et al. 2002. *Marine Ecology Progress Series* **242**, 169–177, adding data from, and quoted in Rastrick, S.P.S. & Whiteley, N.M. 2013. *PLoS ONE* **8**, e60050.) Where data are available for a species at more than one temperature, values shown are means for RNA-to-protein ratio and temperature.

of the difficulty involved in making proteins. The lower the signal to final protein product, the more efficient the processes between, and the less error involved, and the larger the signal to product ratio, the more difficulty and the greater the error. In the few studies of RNA-to-protein ratios in Antarctic species, there were clear seasonal variations in both RNA concentrations and RNA-to-protein ratios. These followed similar patterns to the variation in k_s. Seasonal changes have been documented in RNA concentrations and RNA-to-DNA ratios in tissues of temperate species (Bulow et al. 1981, Robbins et al. 1990, Kent et al. 1992, Melzner et al. 2005). Food intake and quality affect RNA concentrations in tissues, which also has an impact on k_s (Fraser et al. 2007).

RNA-to-protein ratios for Antarctic marine species are high when compared with marine ectotherms from temperate and tropical latitudes. When ratios are plotted against habitat temperature, a decline from polar to tropical species is evident, where on average values decline by 2.3 for each 10°C rise in temperature (Figure 6). An increase in RNA signal at low temperature is one way that thermal compensation of protein synthesis could be achieved. As seen previously, however, rates of protein synthesis are lower in Antarctic species and any compensation is thus not complete, and problems making fully conformed functional proteins only partially overcome. A further reason why this compensation may be only partial is that RNA activity appears to decline at lower temperatures (Fraser et al. 2002), compounding problems at the ribosome and during the folding phases of protein synthesis.

Gamete development and gametogenic cycles

Gametogenic cycles have been described for a range of Antarctic marine invertebrates. These include: in the molluscs, the small brooding bivalve *Kidderia subquadratum* (Shabica 1974), the infaunal clam *Laternula elliptica* and limpet *Nacella concinna* (Powell 2001); and in the echinoderms, the starfish *Odontaster validus* (Pearse 1965, Chiantore et al. 2002, Grange et al. 2007), the urchin *Sterechinus neumayeri* (Brockington 2001a, Chiantore et al. 2002, Brockington et al. 2007)

and the brittle star *Ophionotus victoriae* (Grange et al. 2004, Grange 2005). Other taxa studied include the actinarian anemone *Epiactis georgiana* (Rodriguez et al. 2013). These species all take 18–24 months from the initiation of gametogenesis to spawning (e.g. Figure 7) except *Kidderia subquadratum*, which takes 15–19 months. These were the first species identified to take longer than 12 months for gametogenesis, where most temperate and tropical species complete the process within six months. Studies of Antarctic fish have also identified extended periods of gametogenesis, with predominantly two-year periods required to complete oogenesis (Everson 1970a, Sil'yanova 1982, Everson 1984, Kock & Kellerman 1991, Parker & Grimes 2010, Hanchet et al. 2015). Similar extended periods required to complete gametogenesis have also been reported for high Arctic species living permanently at temperatures around or below 0°C (Falk-Petersen & Lønning 1983, Pearse & Cameron 1991, Junquera et al. 2003).

A small number of Antarctic species complete gametogenesis faster than 18–24 months; specifically, the nemertean worm *Parborlasia corrugatus* requires 15 months from initiation of oocyte development to spawning (Grange et al. 2011a), and the scallop *Adamussium colbecki* needs only 12 months (Chiantore et al. 2002, Tyler et al. 2003). Both of these, however, like the molluscs and echinoderms, take significantly longer for gametogenesis than related or ecologically similar temperate species, although Tyler et al. (2003) concluded gametogenesis in *A. colbecki* is 'more scallop than Antarctic' and Lau et al. (2018) concluded that reproduction in the Antarctic nuculanid bivalve *Aequiyoldia eightsii* fitted neither the expected Antarctic patterns nor the characteristic nuculanid pattern. Overall, the general slowing in Antarctic marine invertebrates compared to temperate species is around five times (Peck 2016).

An unusual gametogenic cycle is demonstrated by the rhynchonelliform brachiopod *Liothyrella uva*. In this species, histological analyses of the gonad over a two-year period failed to reveal the double cohorts of developing eggs as seen in nearly all other Antarctic species investigated (Meidlinger et al. 1998). There was considerable interannual variation in reproductive output and also in numbers of the smallest size class of oocytes. There was, however, no seasonal signal present, and the conclusion drawn was that the absence of seasonal trends for all oocyte size classes showed that oocyte maturation in the population was continuous but asynchronous (Meidlinger et al. 1998). *Liothyrella uva* is a brooding species, but broods were very variable, as seen in other rhynchonelliforms (Hoverd 1985, Chuang 1994). Different females sampled at the same time held broods at markedly different developmental stages, and some females even contained broods with several developmental stages at the same time (Meidlinger et al. 1998). Single females of this species have also been noted to release larvae of markedly different developmental stages from swimming gastrulas to fully competent 3-lobed larvae (Peck et al. 2001). The marked variability exhibited by *L. uva* in its gonad and embryonic/larval development suggests there is extreme plasticity in the reproductive cycle of this species.

It might be expected that with markedly extended gametogenesis Antarctic marine ectotherms would not reproduce annually. Every species investigated to date does, however, spawn on an annual basis. This is achieved in most cases by having two cohorts of eggs developing simultaneously in the female gonad, one to be spawned in the current season and a second to be spawned in the following year (Figure 7). This double egg cohort in female gonads was first identified in the starfish *Odontaster validus* at McMurdo Sound by Pearse (1965) but has since been recognised as the most common gametogenic developmental cycle exhibited by Antarctic marine species (Pearse & Cameron 1991, Pearse et al. 1991, Gutt et al. 1992, Chiantore et al. 2002, Grange et al. 2004, 2007, 2011a, Servetto & Sahade 2016). Although, as noted previously, a few species do not follow this pattern, including the scallop *Adamussium colbecki* (Tyler et al. 2003), the nuculanid *Aequiyoldia eightsii* (Lau et al. 2018), and the brachiopod *Liothyrella uva* (Meidlinger et al. 1998).

Most multiyear studies of reproduction in Antarctic marine ectotherms have reported large, or very large levels of interannual variation. In the brittle star *Ophionotus victoriae*, reproductive effort was assessed as the proportional decrease in gonad size on spawning over a four-year period between 1997 and 2000 on Adelaide Island, Antarctic Peninsula. Decreases were: 12.5% (1997), 90% (1998),

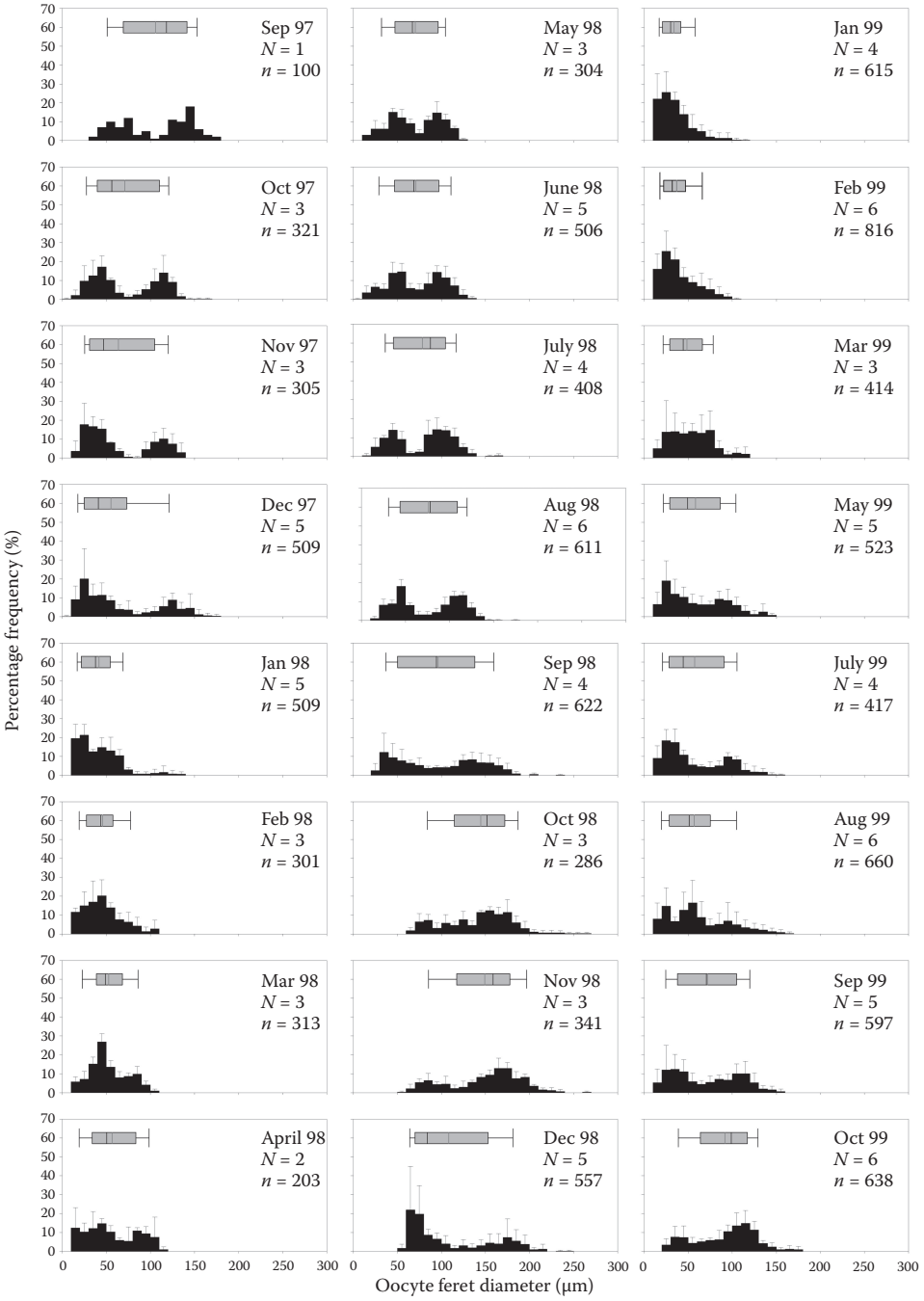

Figure 7 Oocyte diameters for eggs of the brittle star *Ophionotus victoriae* sampled from Rothera Point, Adelaide Island, Antarctic Peninsula. Data shown are for monthly samples collected between September 1997 and October 1999. Measures are feret diameters (±SD), measured on a compound microscope. N = number of females assessed each month, n = number of oocytes measured. Box plot margins indicate the 25th and 75th percentiles for oocyte size, whiskers on boxes indicate 10th and 90th percentiles. Note in most months there are two peaks in the distribution denoting cohorts of eggs, and oogenesis requires 18–24 months to complete. (Figure adapted from Grange, L.J. et al. 2004. *Marine Ecology Progress Series* **278**, 141–155.)

96% (1999) and 88% (2000), indicating nearly an 8-fold change in reproductive effort between smallest and largest years (Grange et al. 2004). In the starfish *Odontaster validus*, interannual variation in proportion of gonad spawned between 1997 and 2000 at the same site as the *Ophionotus victoriae* study showed less variation than the brittle star, but values still ranged from 34% to 62% for females and 52% to 78% for males (Grange et al. 2007). The smaller interannual variation in *Odontaster validus* was attributed to the highly catholic (broad) diet of the starfish.

Very few studies have examined variation in reproductive characters between populations of the same species in Antarctica. In such an investigation of the sea urchin *Sterechinus neumayeri*, gonad mass varied markedly between three sites, less than 10 km apart (Brockington et al. 2007). At one site, gonad dry mass, expressed as the value for a standard 30 mm diameter urchin, varied between 0.06 g dry mass and 0.17 g dry mass between April 1997 and October 1998 and then increased to 0.33 g dry mass by January 1999, and there was no evidence of spawning, as a decrease in gonad mass, over the whole period. At a second site, gonad mass ranged from 0.62 to 0.74 g dry mass between March and November 1997. It then declined to 0.16 g dry mass over the next two months, a loss of 77% on spawning, and values gradually increased to 0.45 g dry mass by January 1999. At the third site, gonad mass ranged between 0.15 and 0.4 g dry mass in the first half of the study and between 0.34 and 0.57 g dry mass in the second year of the investigation, again with no evidence of spawning. The site with the largest gonad mass thus had values around six to seven times higher than the lowest, and two sites showed little evidence of spawning, while the third, which was between the other two and less than 5 km from each, exhibited a very large spawning event over the same period (Brockington et al. 2007). There can thus be very large variations in gonad status and reproductive effort over both small spatial and temporal scales. The main explanation of this is variation in food supply through environmental factors such as seasonality, ice cover affecting productivity and advection, and also through resource limitation due to biotic factors such as competition (Clarke 1987b, 1988, 1991, Clarke & Peck 1991, Brockington et al. 2007, Grange et al. 2011a).

Embryonic and larval development

Development in marine invertebrates and fishes is affected by a wide range of factors (Pechenik 1986, 1999). Development in Antarctic species, especially echinoderms, has been reviewed by Pearse (1994), Hoegh-Guldberg and Pearse (1995), Pearse et al. (1991) and Peck (2002a). Temperature is generally accepted as the major factor controlling differences in the rate of development between species and across latitudes (Hoegh-Guldberg & Pearse 1995). One of the key pieces of evidence in this argument is that feeding (planktotrophic) and non-feeding (lecithotrophic) larval development rates are equally slowed at low temperature compared to temperate and tropical species, and resource limitation should impact planktotrophy more than lecithotrophy. Furthermore, development rates in brooding species appear to be slowed as much, if not more than for broadcast reproducing species (e.g. Peck et al. 2006b, Peck 2016), which again would not be predicted as an outcome of seasonal resource limitation effects on embryonic and larval development rate.

From the first investigation of embryonic and larval development in Antarctic marine ectotherms in the 1960s (Pearse 1969), it has been clear that the times required to reach a given developmental stage are greatly extended in comparison with temperate and tropical species. Since then, investigations of development in broadcast spawning species, including the starfish *Odontaster validus* (Pearse 1969, 1994, Stanwell-Smith & Peck 1998), the sea urchin *Sterechinus neumayeri* (Bosch et al. 1987, Pearse et al. 1991, Shilling & Manahan 1994, Stanwell-Smith & Peck 1998), the bivalve molluscs *Laternula elliptica* and *Adamussium colbecki* (Peck et al. 2007b), the limpet *Nacella concinna* (Peck et al. 2016a), the ascidian *Cnemidocarpa verrucosa* (Strathmann et al. 2006), and the nemertean *Parborlasia corrugatus* (Peck 1993b), have all exhibited development rates slowed by around or more than an order of magnitude compared to lower latitude species. Investigations of brooding species, including the isopods *Ceratoserolis trilobitoides* (Wägele 1987), *Aega antarctica*

(Wägele 1990) and *Glyptonotus antarcticus* (White 1970), the amphipod *Eusirus perdentatus* (Klages 1993), the caridean shrimps *Chorismus antarcticus* (Clarke 1985), *Notocrangon antarcticus* and *Nematocarcinus lanceopes* (Arntz et al. 1992, Gorny et al. 1992, 1993), the actinarian anemone *Epiactis georgiana* (Rodriguez et al. 2013), the gastropods *Trophonella* (previously *Trophon*) *scotiana, Neobuccinum eatoni, Doris* (previously *Austrodoris*) *kerguelenensis, Antarctophiline alata, Nuttallochiton mirandus* (Hain 1991), *Torellia mirabilis* and *Marseniopsis mollis* (Peck et al. 2006b), and the bivalve *Lissarca notorcadensis* (Brey & Hain 1992) have all demonstrated that brooding periods are markedly extended in Antarctica compared to lower latitudes.

In most cases, the comparisons of development rates between Antarctic and lower latitude species involve a limited number of species, and evaluations of changes of rate either with temperature or between regions do not contain enough data for useful comparisons to be made. In a few cases, however, sufficient data do exist to allow such analyses. The first comprehensive analysis across latitudes was done for echinoids by Bosch et al. (1987), and this showed a marked slowing in development rate at temperatures around 0°C and below, compared to values at 5°C and above. Similar results were published for echinoids by Stanwell-Smith and Peck (1998) and for bivalve molluscs by Peck et al. (2007b). One of the best examples of this pattern is in brooding period for marine gastropods, where sufficient numbers of published evaluations for tropical, temperate and polar species exist to allow a good analysis of changes in rate across latitudes (Peck 2016, Peck et al. 2006b, Figure 8A). Brooding period ranges from a few days to one to two weeks for tropical species and up to 15 weeks for temperate species living at 15–20°C. At temperatures around 0°C and below brooding period ranges from 17 to 102 weeks. When the values for brooding period are replotted as an Arrhenius plot, a clear linear relationship between temperature and Ln development rate is apparent for temperate and tropical species (Figure 8B). Values for Antarctic brooding gastropods are, however, all below an extrapolation of the relationship for temperate and tropical species when

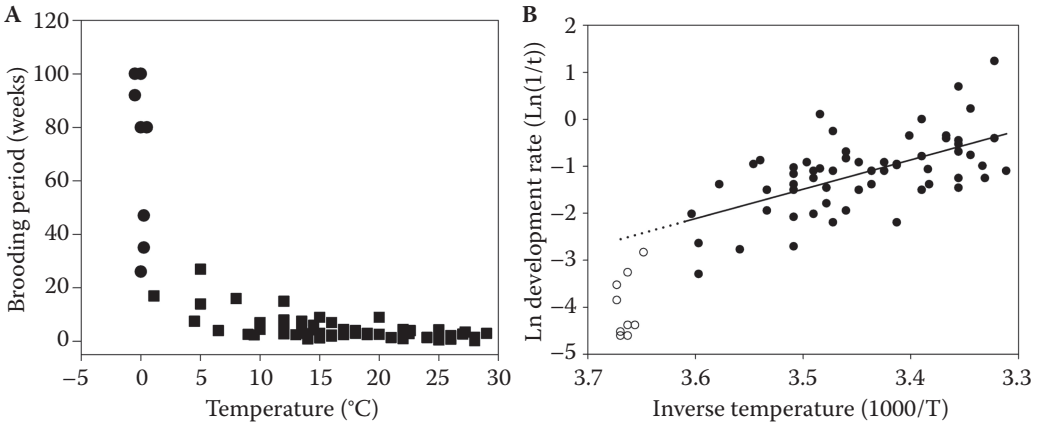

Figure 8 Brooding period and development rates of brooding marine gastropod snails at ambient temperatures for tropical to polar species. (A) Time from brood initiation to release (1/development rate). Circles denote Antarctic species whereas squares denote Arctic, temperate and tropical species. In most cases, release is of crawling juveniles, but for two Antarctic species, *Torellia mirabilis* and *Marseniopsis mollis* release is of veliger larvae, and development time to juvenile is approximately double that of brooding, *per se* (Peck et al. 2006a). Data for 68 gastropod species, nine of which live at temperatures around 0°C, and are the full development period to juvenile. (B) Arrhenius plot of Ln developmental rate to juvenile stage for brooding gastropod molluscs. Open circles denote species living at temperatures below 3°C and closed circles show data for species living above 3°C. Fitted line is for temperate and tropical species (brooding rate (1/weeks) = 20.37 – 6.25 1000/T; $r^2 = 0.36$, $F = 32.4$, 58 d.f., $P < 0.001$). (Figure from Peck, L.S. 2016. *Trends in Ecology and Evolution* **31**, 13–26.)

it is extended to lower temperatures (Figure 8B), and the difference is highly significant ($t = -6.73$, 8 d.f., $P < 0.0001$). Peck (2016) further showed that the Q_{10} for the slowing of development in Antarctic brooding gastropods is over 12. This means that development rates in Antarctic species are slowed more than the normally expected effect of temperature where Q_{10} values are in the range one to four (Clarke 2004) and beyond the Arrhenius relationship for warmer species. Peck (2016) argued that, as for growth, this showed a factor other than the normal impact of temperature on biological systems is having an effect in Antarctica, and that problems with synthesising proteins, especially protein folding, is the likely cause.

Ecological implications of slow development rates

The very slow development rates of Antarctic marine ectotherms have significant consequences for life-history traits, and these differ markedly between species with broadcast and brooding modes of reproduction. The earliest life-history stages, embryos and larvae, usually have much higher rates of mortality than later stages due to factors such as predation, advection to areas unsuitable for settlement, and starvation (Thorson 1950, Morgan 1995, Pechenik 1999, Marshall & Morgan 2011). Marshall et al. (2012) also showed that planktonic larvae are more common in regions where food levels and temperature are high. Recent work has, however, demonstrated that larval mortality is significantly lower in Antarctica than previously expected, and life-history and population dynamics models need to be modified in this respect (White et al. 2014). This suggests that mortality in the later settlement, metamorphosis and very early juvenile stages may be higher than previously thought, and that projections and possibly conservation measures should focus on models that include evaluations across life-history stages, as advocated by Marshall et al. (2012).

Periods that larvae spend in the water column increase as development rate decreases and the time spent at the various development stages increases. This factor has been recognised as potentially important for Antarctic broadcast spawning species for several decades (e.g. Pearse & Bosch 1986, Bosch et al. 1987, Stanwell-Smith & Peck 1998, Peck & Prothero-Thomas 2002, Peck et al. 2007b, Ginsburg & Manahan 2009). Indeed, the time required for embryos of the starfish *Odontaster validus* to hatch is around nine days at −1.8°C (Stanwell-Smith & Peck, 1998), and for larvae to develop to settlement, around 180 days are likely needed (Pearse & Bosch 1986). Antarctic coastal current speeds range from 2.5 to 25 cm sec^{-1} (Fahrbach et al. 1992), and average speeds are in the range 5–10 cm sec^{-1} (Le & Shi 1997). At a conservative 5 cm sec^{-1} and a pelagic period of 170 days, a larva could travel 734 km, and at 10 cm sec^{-1}, over 1400 km would be possible.

However, dispersal in Antarctic broadcast spawning species may be less than previously expected in some taxa because of larval behaviours in relation to water currents. There are few data on larval behaviours in Antarctic marine species beyond those often reported during culture studies, such as swimming towards the surface or towards the bottom of culture vessels. In wild populations, behaviours resulting in larvae spending much of their developmental period in benthic habitats or avoiding moving water have been reported for several temperate marine benthic species (Cowen & Sponaugle 2009, Pringle et al. 2014). Such behaviours often result in settlement that is more local to parent populations than realised previously. Although such mechanisms are yet to be documented for Antarctic species, it is highly likely that some will fit this pattern.

Protected development reduces mortality during development. It also reduces dispersal during the development phase to zero. It has been recognised for over three decades that Antarctica has significantly higher levels of protected development than species living at lower latitudes in many taxa (Picken 1979, 1980, White 1984, Arntz et al. 1994). Marshall et al. (2012), in a meta-analysis, showed that around 80% of Antarctic marine species have a planktonic development, most of which exhibit protected development systems. Different taxa, however, exhibit markedly different levels of protected development, with molluscs and echinoderms showing strong decreases in the prevalence of planktonic larvae with latitude in Antarctica, but annelids do not (Marshall et al.

2012). Interestingly, their study also demonstrated that trends in reductions of planktonic forms with latitude are much stronger in the southern than in the northern hemisphere.

It has been suggested that protected development at high latitude may be an evolutionary response to the increased mortality at the larval stage that is a consequence of the greatly slowed development rates at temperatures around and below 0°C, possibly to avoid larvae being carried away from suitable habitat during development. These data have been used regularly in the past as evidence to support Thorson's rule, that there is a strong trend towards non-pelagic development and to brood protection in polar seas because of the problems associated with extended larval periods and very short, highly seasonal periods of phytoplankton productivity (Thorson 1950). Thorson's rule was mainly based on observations comparing Arctic sampling expeditions with data from temperate sites, especially Denmark (Thorson 1936, 1946). Although it was first called Thorson's rule by Mileikovsky (1971), Thorson was more circumspect on the universality of the paradigm than later authors. In Antarctica, there were several studies aimed at testing this rule in the 1980s and 1990s. Clarke (1992) showed a trend of markedly reduced pelagic development in gastropod molluscs at high latitude. Bosch and Pearse (1990) and Pearse (1994) showed that in echinoderms the proportion of species that exhibit protected development is very similar in Antarctica and California. They found that Thorson's rule did not apply to echinoderms in the proportions of brooding species, but that there was a shift in proportions of planktotrophy (feeding larvae) versus lecithotrophy (non-feeding larvae that depend on stored reserves), with higher levels of lecithotrophy in Antarctica. This trend to non-feeding larval development is often confused with Thorson's rule, which concerns the prevalence of pelagic versus protected development in marine faunas in different regions. Several studies showed that proportions of different larval types are similar in South America and Antarctica in echinoderms and molluscs (Pearse et al. 1991, Hain & Arnaud 1992, Gallardo & Penchaszadch 2001). Later studies showed that numbers of pelagic larval taxa in Signy Island, South Orkneys (Stanwell-Smith et al. 1999) and at Rothera Point, Adelaide Island, Antarctic Peninsula (Bowden et al. 2009) were similar to those from temperate latitudes, and similar to those reported by Thorson (1946) for Denmark, but an order of magnitude higher than values for the Arctic. Fetzer and Arntz (2008) and Sewell (2005) also noted high numbers of planktotrophic larvae at high latitudes.

Studies of larval development and physiology have also demonstrated there is no low temperature barrier to completing development (e.g. Bosch et al. 1987, Peck et al. 2006b, Pace & Manahan 2007). Thus, on three counts, data appear contrary to Thorson's rule, and the conclusions drawn by Pearse (1994) and Pearse and Lockhart (2004) that the rule does not apply are generally accepted. More recent investigations conducting meta-analyses of developmental mode from tropical to polar sites and using very large datasets have confirmed that there is no trend away from pelagic larval phases in the development of marine invertebrates, but there is an increase in proportions of non-feeding pelagic larvae with latitude (Marshall et al. 2012, Marshall & Burgess 2015).

Indeed, many of the most common and abundant species living in shallow Antarctic marine habitats are broadcast reproducers, for example, the limpet *Nacella concinna*, the sea urchin *Sterechinus neumayeri*, the starfish *Odontaster validus*, the bivalve *Aequiyoldia eightsii* and the brittle star *Ophionotus victoriae*. A similar situation, where the most common species living in shallow habitats are predominantly broadcast spawners, while proportions are lower in rarer taxa and deeper habitats was noted for the Arctic over 60 years ago (Thorson 1950). It may be that in shallow environments, where physical disturbance from ice regularly both destroys the existing local fauna and also clears new areas for colonisation, the benefit from larval dispersal to newly available sites outweighs the negative impact from increased larval mortality. Antarctic benthic communities often contain high proportions of deposit-feeding and suspension-feeding taxa, with values higher than proportions at most lower latitude sites (Arntz et al. 1994, Gutt & Starmans 1998, Starmans et al. 1999, Clarke & Johnston 2003, Clarke et al. 2004a, Gili et al. 2006, Aronson et al. 2007, Barnes & Conlan 2012). These suspension-feeders are major predators of marine invertebrate larvae (Pechenik 1987, 1999, Morgan 1995).

The Antarctic benthos contains possibly the largest differences in dispersal capacity of benthic faunas globally. This is because the very slow development rates mean the planktonic phases for many of the broadcast breeding species are much longer than those at lower latitudes, and the direct developing species alongside them have very poor dispersal capacities. Brooding species do disperse, but genetic studies have shown dispersal is limited to a few kilometres or less in, for example, the brooding Antarctic gastropod *Margarella antarctica* (Hoffman et al. 2011). Similar limited dispersal has also been shown for lower latitude species with protected development (e.g. Sherman et al. 2008, Keever et al. 2009).

Beyond larval dispersal, marine animals can drift as adults as an active process such as in the anemone *Dactylanthus antarcticus*, which inflates to large size when it has completed feeding on its soft coral prey. It then releases from the substratum and drifts until it contacts a new prey item (Peck & Brockington 2013). There have also been observations of neutrally buoyant adults of some species drifing above the seabed when they have been disturbed by ice, and this includes the colonial tunicate *Distaplia cylindrica* (J. McClintock personal communication).

One mechanism for dispersal that is possible in the polar regions that is not available elsewhere is rafting on icebergs. Seafloor debris, rocks, rubble, sediment and even boulders are often present on upturned icebergs. Living marine invertebrates have been seen amongst this debris on some icebergs, including the gastropods *Margarella antarctica* and *Nacella concinna* and the urchin *Sterechinus neumayeri* (L. Peck, pers. obs.). The frequency of this occurrence, distances travelled by rafted invertebrates and variation between species in contribution to dispersal remains to be quantified but is likely to be one of the more important mechanisms in slow-moving species with protected development to juvenile stages.

Dispersal can be achieved by other means than motile or drifting early development stages or by being carried by icebergs. Postmetamorphic stages of over 1200 marine species have been identified as being capable of dispersal attached to a range of both natural and man-made substrata (Thiel & Gutow 2005). Natural floating substrata that have aided dispersal of attached species for millions of years include macroalgae, pumice and wood, the most common materials, but large animals including whales and turtles have also been used. Marine litter, especially plastics, has dramatically changed the opportunities for rafting species to disperse over the last 50–100 years (Barnes 2002, Barnes et al. 2009, Eriksen et al. 2014, Bergmann et al. 2015).

In Antarctica, marine debris is much rarer than at lower latitudes for several reasons, including the circulation of the Southern Ocean around Antarctica, isolating it from lower latitude oceans, the absence of coastal forested areas that are the source of floating debris elsewhere, and the absence of large human populations and their associated debris. Marine debris has, however, been regularly identified and collected at several sites. A survey in 2012 found unexpectedly high incidences of debris in the Southern Ocean, with plastics and plastic fragments present at around 50,000 pieces per km^2 (http://www.theguardian.com/environment/2012/sep/27/plastic-debris-southern-ocean-pristine). Marine debris deposited annually on selected Antarctic shorelines is also monitored, as is marine debris in selected bird colonies and occurrences of debris entangled on marine mammals under a CCAMLR programme (www.ccamlr.org/en/science/marine-debris). Several species have been documented attached to floating plastics in the Southern Ocean, especially bryozoans, and this includes reproductively active species (Barnes & Fraser 2003). None of the organisms identified as rafting or attached to floating debris in Antarctica are from outside the Southern Ocean, and hence, there is no evidence that alien species have used or are using this mechanism as a route to enter Antarctic waters. The reason for this has often been assumed that the sea surface freezes all the way around Antarctica in winter, and there is no unfrozen coastline for aliens to colonise and establish. With climate change, however, it has been suggested that open coastline is likely to occur before 2100 on the Antarctic Peninsula, which would change the likelihood of establishment of alien species, and this has been identified as a future risk to biodiversity (Kennicutt et al. 2014, 2015, Sutherland et al. 2015).

Egg size, fecundity, reproductive effort and life histories

The slow development rates in Antarctic marine species described above have often been associated with, where reported, large egg size and hence reduced numbers of eggs released per spawning event. The production of larger eggs at higher latitudes and colder environments has been recognised since at least the 1930s (Thorson 1936, 1950, Clarke 1985, 1993a, Pearse 1994, Collin 2003, Moran & McAlister 2009) and was part of the paradigm of reduced pelagic development and increased protected development at high latitude, called Thorson's rule that was rejected when phylogenetic considerations were taken into account (see 'Ecological implications of slow development rates' section previously). In Antarctica, large egg size, with diameters generally two to five times greater than related temperate species, was reported in the 1970s for amphipod crustaceans (Bone 1972, Bregazzi 1972) and in the 1980s and 1990s for shrimps (Clarke 1985, 1992, 1993a,b). There are many reports of large egg size for individual species in Antarctica, again generally two to five times larger than comparison with lower latitude species (Table 2).

Because of the requirement for data for fisheries purposes, studies of fish reproduction are more common than for invertebrates, and the data collected often include egg size. A trend from smaller, pelagic eggs producing smaller juveniles at low latitude to larger demersal eggs with larger juveniles at higher latitudes is well documented (Leis et al. 2013). This is despite phylogeny having a large impact on egg size, with, for example, salmonids having very large eggs in the range 2–9 mm diameter but mostly in the 2–6 mm range. Most other temperate and tropical fish have eggs in the range 0.5–4 mm diameter (Bagenal 1971, Robertson & Collin 2015). The Antarctic fish fauna is dominated by the suborder Notothenioidea, most of which produce eggs with diameters between 3 and 5 mm, similar in size to the largest produced in cool temperate latitudes and well above the mean size for all species in lower latitude regions. The most common explanation used to explain large egg size at high latitude is temperature, but at smaller, regional scales, resource availability has been demonstrated to be important with several studies showing smaller eggs are more common in regions of high food availability and larger eggs where food supplies are limited (Lessios 1990, Marko & Moran 2002, Robertson & Collin 2015).

The numbers of studies made within species are smaller than for comparisons between species, but these comparisons have also produced data showing increases in egg size with latitude. In the isopod *Ceratoserolis trilobitoides*, eggs almost doubled in size with a less than 15° increase in latitude, where egg dry mass ranged from 3.3 to 3.9 mg dry mass in sub-Antarctic South Georgia to 6.5 mg dry mass in the high Weddell Sea (Wägele 1987, Clarke & Gore 1992, Gorny et al. 1992). Within species, trends to larger egg size at higher latitude in Antarctica have also been demonstrated in the philobryid bivalves *Lissarca miliaris* (Reed et al. 2014) and *Lissarca notorcadensis* (Brey & Hain 1992), the caridean decapod *Notocrangon antarcticus* (Lovrich et al. 2005) and in some nototheniid fish (Kock & Kellerman 1991).

In a detailed study of animal size in amphipod crustaceans, Chapelle and Peck (2004) showed that not only the largest species of amphipod at any given site increased with latitude and seawater oxygen content, but the minimum size of a species also increased towards the poles, although at a smaller rate than for larger size classes. It was further demonstrated by Chapelle and Peck (2004) that minimum amphipod size across latitude correlated with the size of egg produced. It has long been suggested in amphipod crustaceans that minimum size for a species is set by egg size and the capacity to brood embryos (Mills 1967). Strong evidence to support this came from correlations between amphipod size and the numbers of eggs produced and embryos in broods, where the smallest species are the only ones producing broods of single eggs (Sainte-Marie 1991), and that in very small species, males are smaller than females (Chapelle & Peck 2004).

Futhermore, a link between reproductive mode and egg size has been recognised for nearly 100 years (Mortensen 1921, 1936, Thorson 1936). The move to more protected development and fewer species with pelagic developmental phases (Thorson's rule) seemed to be part of a consistent

Table 2 Maximum egg diameter measurements for a range of Southern Ocean marine invertebrates

Species	Maximum egg diameter (mm)	References
Polychaete worms		
Leodamas marginatus	0.58	Hardy (1977)
Laetmonice producta	0.32	Micaletto et al. (2002)
Molluscs		
Pareledone charcoti (cephalopod)	11	Kühl (1988)
Pareledone turqueti (cephalopod)	19	Kühl (1988)
Adelieledone polymorpha (cephalopod)	10	Kühl (1988)
Nuttallochiton mirandus (polyplacophoran)	0.94	Hain & Arnaud (1992)
Neomeniomorpha (solenogastre)	0.78	Hain & Arnaud (1992)
Prodoris clavigera (nudibranch)	2.1	Wägele (1988)
Tritonia challengeriana (nudibranch)	0.34 ± 0.007 (s.e.)	Woods & Moran (2008)
Tritonia tetraquetra (nudibranch)	0.102 ± 0.001 (s.e.)	Woods & Moran (2008)
Laevilitorina caliginosa (littorinid)	0.20	Simpson (1977)
Adacnarca nitens (bivalve)	0.040	Higgs et al. (2009)
Gaimardia trapesina (bivalve)	0.40	Simpson (1977)
Plaxiphora aurata (polyplacophoran)[a]	0.27	Simpson (1977)
Hemiarthrum setulosum (polyplacophoran)[d]	0.80	Simpson (1977)
Crustaceans		
Antarctomysis maxima (mysid shrimp)	1.75 (stage 1 embryo)	Siegel & Mühlenhardt-Siegel (1988)
Mysidetes (previously *Antarctomysis*) *posthon* (mysid shrimp)	0.77 (stage 1 embryo)	Siegel & Mühlenhardt-Siegel (1988)
Eusirus perdentatus (amphipod)	2.75	Klages (1991, 1993)
Ampelisca richardsoni (amphipod)	1.1	Klages (1991)
Paraceradocus gibber (amphipod)	1.7	Klages (1991)
Echinoderms		
Heterocucumis steineni (holothurian)	1.0	Gutt et al. (1992)
Psolus dubiosus (holothurian)	1.3	Gutt et al. (1992)
Odontaster validus (starfish)[a]	0.17	Bosch & Pearse (1990)
Odontaster meridionalis (starfish)[a]	0.19	Bosch & Pearse (1990)
Glabraster (previously *Porania*) *antarctica* (starfish)[a]	0.55	Bosch & Pearse (1990)
Bathybiaster loripes (starfish)[b]	0.93	Bosch & Pearse (1990)
Psilaster charcoti (starfish)[b]	0.95	Bosch & Pearse (1990)
Acodontaster conspicuus (starfish)[b]	0.70	Bosch & Pearse (1990)
Acodontaster elongatus (starfish)[b]	0.54	Bosch & Pearse (1990)
Acodontaster hodgsoni (starfish)[b]	0.55	Bosch & Pearse (1990)
Lophaster gaini (starfish)[b]	1.28	Bosch & Pearse (1990)
Macroptychaster accrescens (starfish)[c]	1.28	Bosch & Pearse (1990)
Perknaster fuscus (starfish)[c]	1.20	Bosch & Pearse (1990)
Diplasterias brucei (starfish)[d]	2.80	Bosch & Pearse (1990)
Notasterias armata (starfish)[d]	3.50	Bosch & Pearse (1990)
Sterechinus neumayeri (sea urchin)	0.20–0.21	Moore & Manahan (2007)
Sterechinus neumayeri (sea urchin)	0.15–0.17	Suckling et al. (2015)
Ascidian		
Cnemidocarpa verrucosa	0.24	Strathmann et al. (2006)
Scleractinian corals		

Continued

Table 2 (Continued) Maximum egg diameter measurements for a range of Southern Ocean marine invertebrates

Species	Maximum egg diameter (mm	References
Flabellum thouarsii	4.80	Waller et al. (2008)
Flabellum curvatum	5.12	Waller et al. (2008)
Flabellum impensum	5.20	Waller et al. (2008)

Data for echinoderms and polyplacophorans are split into the following notes:

[a] Broadcast spawning species with feeding larvae;

[b] Broadcast spawners with lecithotrophic (non-feeding) larvae;

[c] Unknown, but probably broadcast with lecithotrophic larvae; and

[d] Brooding species.

Similar data to the above categories are only available for the species shown.

global trend that was accepted until the 1990s, when detailed within taxon analyses were used to disprove the hypothesis (Bosch & Pearse 1990, Clarke 1992, 1996, Pearse 1994, Pearse & Bosch 1994). Large egg and embryo size in Antarctica was identified as part of a global trend of increase in these characteristics with latitude from tropics to polar regions in a large meta-analysis of marine invertebrate life histories (Marshall et al. 2012), and the increase in egg size with latitude and large eggs in Antarctica remains an accepted trend and requires explanation.

The explanations for larger egg size at higher latitude, lower temperature sites have been mainly ecological and developed over several decades (Thorson 1950, Arnaud 1977, Simpson 1977, Picken 1980, Jablonski & Lutz 1983, Rohde 1985, 2002, Clarke 1987b, 1993a,b, Arntz et al. 1994). These include: (1) slow development at polar temperatures means most species cannot complete development during the brief phytoplankton bloom, which pelagic planktotrophic larvae feed on, requiring a longer period for development before reaching critical stages; (2) larger size at metamorphosis might enhance survival post settlement and thus select for larger eggs and non-pelagic development; (3) slower development increases time in the water column and increases predation in this phase, suggesting longer intracapsular developmental phases without feeding, which would require larger reserves in the egg before release to the water column would be advantageous; (4) synchronising embryo hatching to the larval phase and metamorphosis to juveniles with the phytoplankton bloom is more difficult, and hence, development during the previous winter at very low food levels would be required; (5) it is easier for offspring that do not pass through a pelagic phase to settle close to parents, where habitats are likely to be favourable, and this may be more important in cold-water environments where factors like iceberg scour may have an effect; (6) pelagic larvae may suffer osmotic difficulties in summer due to dilution of Arctic and Antarctic waters by melting ice, again giving some advantage to development in winter when food supplies for larvae are low. Rohde (2002) excluded seasonality of food supply, timing of developmental events and increased predation on the basis that larger egg size and reduced incidence of pelagic development are attributes also of parasitic taxa living at high latitudes. Settling close to parents as a driver for these adaptations is also unlikely as the same attributes are shared by species where individuals live at large distances from parental stock as well as those that colonise in close proximity. It is further unlikely that osmotic stress plays a role as species living at depths beyond the effects of melting ice have similar levels of reduced pelagic development as shallow species. An ecological reason thus still needs to be agreed upon.

It is possible that there may be a physiological explanation for the increased egg size at low temperatures, and this might also explain why there is reduced pelagic development, as larger egg size is correlated with protected development. There are three factors that would lead to increased egg size at low temperature from physiological consideration. First, that development rates are slowed more at low temperature than routine or standard metabolic rates, where development rates in brooding gastropod molluscs were five to ten times slower than temperate species, but oxygen consumption in

bivalve molluscs was only two to three times slower (Peck 2016, Figure 8). Because of this difference, the proportion of overall costs during development devoted to maintenance will be significantly higher. Extending the development period by five times but increasing maintenance metabolism 2-fold increases overall metabolic costs by 2.5 times. Slowing development by an order of magnitude and slowing maintenance metabolism by a factor of three increases overall metabolic costs by 3.3 times. These extra costs need to be met either by more food intake and/or stored reserves over the whole development period in planktotrophic developers, or from greater stored reserves in species with protected development. This analysis would lead to the prediction that, on average, increase in egg size at low temperature would be greater in species with protected development than broadcast spawners, as the option of increased overall food intake is not possible. An increased requirement for food during pelagic development may also be a driver towards protected development, especially in highly seasonal environments where food supplies are only available for restricted periods during the year.

The second physiological explanation for larger egg size is through the demonstration that it is more difficult to produce fully functional proteins at low polar temperatures because of problems with stability, or at the synthesis stage (Peck 2016, plus earlier section in this review on 'Protein synthesis, retention and folding'). The high levels of ubiquitination measured in Antarctic marine species (Todgham et al. 2007, Shin et al. 2012) suggest that during development a higher proportion of the full protein complement will be held in a cycle of ubiquitination, degradation and resynthesis than in temperate species. Under these circumstances, greater quantities of amino acids in the egg would allow protein synthesis to continue while significant amounts are cycling through degradation. Another way of overcoming some of these problems would be to change the balance of free amino acids and fully synthesised proteins in the egg, reducing the need to synthesise protein *de novo* in the early embryo stages. This hypothesis is yet to be tested, but in fish, a correlation between protein content, and reduced free amino acid content with increasing egg size has been reported (Rønnestadt & Fyhn 1993).

Third, Van der Have and de Jong (1996) evaluated changes in cell size and cell number during development of ectotherms. They concluded that growth, as increase in cell size and differentiation, as opposed to change in numbers of cells is affected differently by temperature. For a given stage of development, the number of cells present is roughly similar in different species, and the outcome of larger eggs is larger cells and hence larger size at metamorphosis in Antarctic marine species. Chapelle and Peck (1999, 2004) and Peck and Chapelle (2003) demonstrated that maximum size attained by amphipods across the globe was highly correlated with ambient oxygen levels in the environment, and Peck and Maddrell (2005) demonstrated that when oxygen levels are reduced, maximum size is lower, and cell sizes are smaller in *Drosophila melanogaster*. Levels of dissolved oxygen in seawater increase with latitude such that the concentration of dissolved oxygen at 0°C is 1.82 times higher than at 30°C. Diffusion distances for oxygen supply into developing embryos is described by the Fick equation (Dejours 1981), and a main driver of this is the concentration gradient between external environment and site of oxygen use. For a salinity of 35, the higher concentration of oxygen in polar oceans at 0°C (347.9 μmol kg^{-1}) compared to a tropical ocean at 30°C (190.7 μmol kg^{-1}) should allow eggs and embryos to be around 1.8 times larger in diameter and, hence, around six times heavier (Peck & Chapelle 1999). It thus seems that cell size relations with temperature and oxygen would suggest egg, embryo and adult size should increase at lower temperatures and, hence, with latitude. As oxygen and temperature covary in seawater, both relationships may be a result of a single underlying mechanistic explanation, that Chapelle and Peck (1999, 2004), Peck and Chapelle (2003) and Peck and Maddrell (2005) attributed to oxygen supply limitations.

The corollary of large egg size is smaller numbers of eggs released at each spawning event, and there are data that support this contention. Reports on this topic include studies on fish (La Mesa et al. 2008), mysid shrimps (Siegel & Mühlenhardt-Siegel 1988), gastropod and bivalve molluscs (Simpson 1977, Reed et al. 2014), nudibranch molluscs (Wägele 1988, Woods & Moran 2008), and caridean shrimps (Gorny et al. 1992, Clarke 1993a, Arntz et al. 1994). As larger eggs are generally correlated with fewer eggs produced in Antarctic species, a related question then emerges around

how much energy and other resources are invested in reproduction and how high latitude species compare with those in temperate or tropical regions.

Reproductive effort

All organisms acquire energy and use it for a variety of purposes. The analysis of what organisms do with this energy often involves the construction of energy budgets based on the energy equation of Winberg (1956), elucidated well by Kleiber (1961). The equation states: consumption equals the sum of somatic and gonadal growth, metabolic costs and waste products. On this basis the proportion of an individual's available energy put into reproduction, the reproductive effort (RE) can be calculated (e.g. Clarke 1987b). RE is not easy to measure because it involves not only the investment in gametes and other reproductive tissues but also the metabolic costs of synthesis and energy used in activities associated with reproduction, some of which can be costly. Even this assessment does not include potential future losses that might be incurred from an investment in reproduction that increases the likelihood of mortality (e.g. Stearns 1992). Much more frequently reproductive output (RO) is measured as the change in gonad mass across spawning periods or the collection of released gametes combined with assessments of gonad and/or gamete energy contents. RO is very useful in that it allows both temporal and spatial comparisons to be made. Several of the studies listed previously have shown a decrease in not only the number of eggs produced per year by Antarctic species, but a reduction in the mass of body tissue devoted to reproduction, reduced RO.

As RE is measured in relation to the energy taken in by an organism (absorbed by an animal), and both somatic growth (see 'Growth' section previously) and metabolic rates are lower in Antarctica than in temperate and tropical regions, the comparison of RE with warmer-water species is less clear. Furthermore, Antarctic marine species generally live much longer than warmer-water relatives (Peck et al. 2006b) and are reproductively active over a longer period. Because of this, RE needs to be considered across the whole lifetime of an individual (Clarke 1987a). Lifetime RE is further complicated by the need to include not only the energy allocated to reproduction each year, but also the likelihood of surviving to that age, or including an estimate of the average age that individuals in a given population will survive to (e.g. Myers 2002). Very few studies of polar species have calculated lifetime RE, but Clarke (1987b) made this calculation for the Northern hemisphere deep-water shrimp *Pandalus borealis*. This species has a very wide geographic range spanning mean annual temperatures ranging from 0°C to around 10°C. When the calculation of RE was made assuming no change in metabolic costs due to temperature, RE increased from the colder to warmer sites, but when metabolic costs were remodelled to vary with temperature following Arrhenius predictions (see later section on Energy use, oxygen consumption and metabolic rate), there was no change in lifetime RE across the whole range inhabited by the shrimp (Figure 9).

Few studies have looked at RE differences between the sexes, but the assumption is usually that females invest more in reproduction than males because of the larger effort put into making an egg than sperm, and that in species with parental care, females are usually the primary carers. Females are also usually used in studies where RE is assessed because it is easier to collect eggs released during spawning and, hence, to quantify energy invested than it is to collect sperm released by males (e.g. Clarke 1979, Gremare & Olive 1986, Hess 1993, Brante et al. 2003, Béguer et al. 2010). In the few studies where direct comparisons have been made, however, results have suggested male RE is either similar to female RE or is greater. For example, Vahl and Sundet (1985) concluded that males have higher RE than females in the Iceland scallop *Chlamys islandica*, and Morricone (1999) showed that gonad index (measured as the mass of gonad compared to the foot) was higher in males than females prior to spawning and decreased more on spawning in males in the limpet *Nacella deaurata* in Tierra del Fuego. In Antarctica, Tyler et al. (2003) measured changes in gonad size in the scallop *Adamussium colbecki*, and a similar analysis on the starfish *Odontaster validus* also showed RE was higher in males than females (Grange et al. 2007).

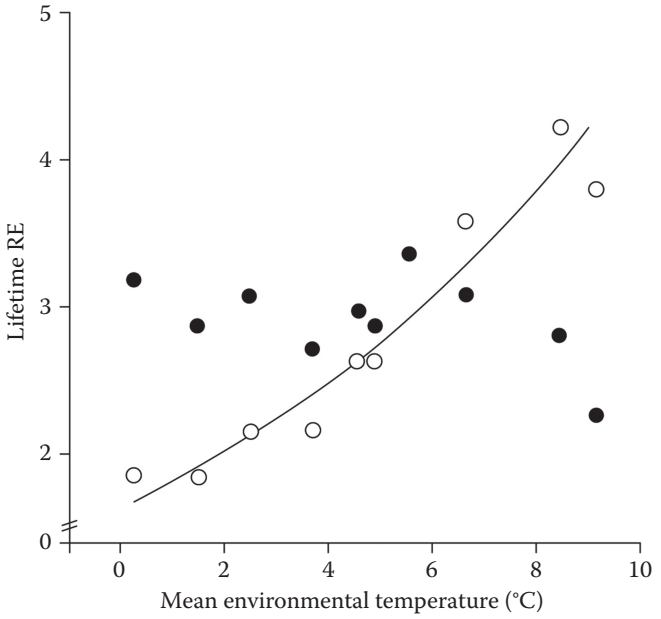

Figure 9 Lifetime reproductive effort in relation to mean environmental temperature for the caridean shrimp *Pandalus borealis*. Open symbols denote data calculated without allowing for variation in standard metabolic rate with temperature. Line fitted to Ln transformed data for both variables but shown as linear plot. Closed symbols denote data calculated assuming standard metabolic rate varies with temperature as in Clarke (1987b). There is no significant trend in the dark data. (Figure redrawn from Clarke, A. 1987b. *Marine Ecology Progress Series* **38**, 89–99.)

However, where studies of reproductive cycles have been conducted for several years, large interannual differences in RE have been identified. In a four-year analysis of reproduction in the brittle star *Ophionotus victoriae*, RO was measured as the decrease in gonad mass on spawning, and this changed by at least 5-fold between years, although the variation may be higher than this because in 1997 an estimate of 12% reduction in gonad mass was used, compared to over 80% in 1999, and the 12% value was not significantly different from zero (Grange et al. 2004). There were also very large differences, around an order of magnitude, between years in the relative size of the gonads, at peak just prior to spawning, in this species (Figure 10). Very large differences in gonad mass both between sites and between years for standard-sized animals were reported for the urchin *Sterechinus neumayeri* (Brockington et al. 2007). Large interannual differences in gonad size just prior to spawning were also reported for the Antarctic scallop *Adamussium colbecki* from Terra Nova Bay by Chiantore et al. (2002), but differences in maximum gonad size between years were smaller and not significant in the starfish *Odontaster validus* and the brittle star *Ophionotus victoriae*. This was, however, only a two-year study, and as can be seen from Figure 10, a longer investigation may be needed to see the large variations reported by Grange et al. (2004).

Variation in RO between years was much lower in the starfish *Odontaster validus*, where the changes in gonad index in the largest years were 2.25 times higher than the smallest years for females and 1.7 times for males (Grange et al. 2007). In a four-year study of the predatory nemertean *Parborlasia corrugatus*, there were no notable interannual differences in reproductive characters, and the authors reported that there was almost no variation in oocyte size between years in this species, which is very unusual in these types of investigation. It should, however, be noted that in *P. corrugatus*, as is typical for nemertean worms, it is not possible to separate gonads from other body tissues, and the gonad is not a discrete tissue, which precludes the measurement of a gonad index

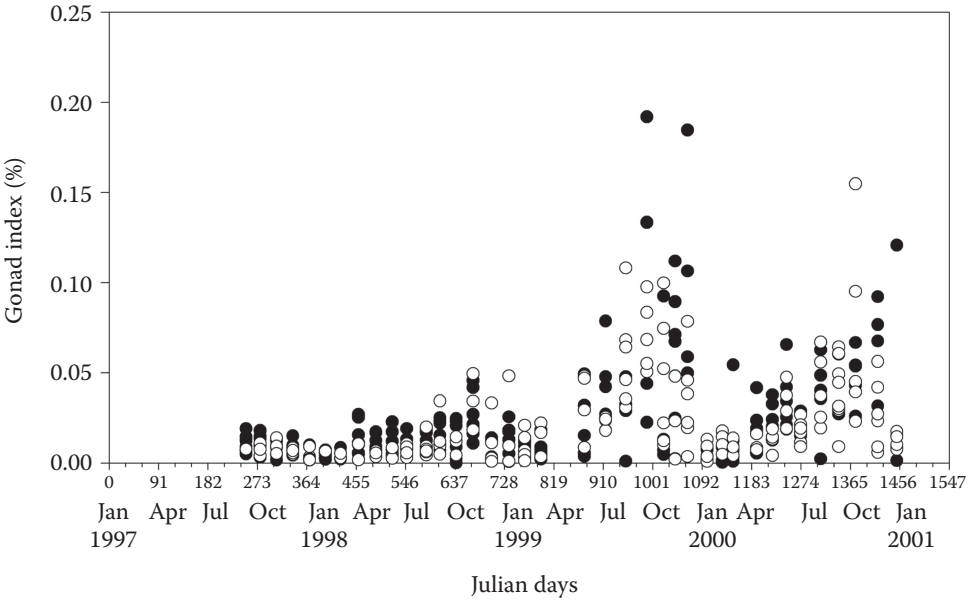

Figure 10 *Ophionotus victoriae* gonad index (the wet mass of the gonad relative to the volume of the disc for male (●) and female (○) brittle stars between August 1997 and December 2000. Note the marked difference (at least 5-fold) in change in gonad index, and hence mass of gametes released on spawning between years. (From Grange, L.J. et al. 2004. *Marine Ecology Progress Series* **278**, 141–155.)

or calculations of RO and RE. Few, if any, other studies have carried out interannual evaluations of reproductive characters over periods of more than three years.

Although the data are limited, it is notable that there were stronger interannual signals in the reproductive biology of the filter-feeding scallop than the omnivores studied by Chiantore et al. (2002). Furthermore, the brittle star *Ophionotus victoriae* and *Odontaster validus*, both of which are omnivores (McClintock 1994), had stronger interannual effects on their RO than the predatory nemertean *Parborlasia corrugatus* (Grange et al. 2004, 2007, 2011a). This difference across trophic groups would be expected from considerations of the effects of seasonal and interannual variation in resource availability and quality in different levels of the food web (Dunbar 1970, Clarke 1983, 1988, 1991). Similar differences in the impact of seasonal and interannual environmental factors on different trophic levels have been noted in other physiological characteristics such as feeding biology and oxygen consumption (e.g. Obermüller et al. 2010). Spatial variation in food supply has also been identified as a factor influencing biological characteristics, including growth and reproduction in populations of marine invertebrates on either side of McMurdo Sound (Dayton et al. 1969, 1970, Dayton 1990). These data have led authors to suggest that the primary mechanism for differences in interannual variation in reproductive characters between trophic groups is likely food availability.

Of interest here is that the timing of reproductive cycles appears to be markedly influenced by light regime. Pearse and Bosch (2002) conducted a series of elegant experiments on the common circumpolar omnivorous starfish *Odontaster validus* that demonstrated that gametogenic cycles could be shifted 180° out of phase by manipulating light regime. When specimens were held in a light regime that was six months out of phase, spawning occurred almost exactly six months later than in the wild, and this change was completed within a year.

There is a clear need to improve understanding of patterns of RE in Antarctic marine species, how it varies compared to species at lower latitudes, and also how it varies within the Southern Ocean and the factors determining the variation. Reproduction of many species is very likely to

be affected by long-term cycles in the environment such as the Southern Annular Mode (SAM) and other factors such as El Niño. These are overlaid on long-term environmental change such as the Antarctic Peninsula warming that occurred over the last half of the twentieth century. Studies collecting data over periods in excess of 10 years, or repeat studies at decadal intervals, similar to the multiple year analyses reported by Chiantore et al. (2002) and Grange et al. (2004, 2007, 2011a), are needed to identify effects of these cycles and trends. There is also a need to improve understanding of differences between male and female RE, both in Antarctica and in other oceans around the world, and to identify if the balance of RE between the sexes varies with global region. RE is a major factor affecting life histories of animals that dictates success or failure of a species in a given environment.

Life-history theory

Understanding of life histories and the development of life-history theory during the 1950s and 1960s was based around the concept of trade-offs in the allocation of resources and the impact on fitness of diverting resources into one direction over another (Medawar 1952, Williams 1957, Hamilton 1966). Current life-history theory models were developed initially by Gadgil & Bossert (1970). The classic trade-off identified in life-history theory is that between investment in the individual's own survival and investment in offspring (Charnov & Krebs 1973, Stearns 1992, Kaplan & Gangestad 2005), and this trade-off varies with a range of factors including age and ecological context (Hoyle et al. 2008). Other important trade-offs occur as well, a prime example being the one between number of offspring and investment per propagule.

The trade-off between investment in individual offspring and numbers of offspring is a central part of life-history theory (Vance 1973, Smith & Fretwell 1974). David Lack first placed life histories in an evolutionary context (for animals with parental care) when working on birds. Lack (1947) hypothesised that natural selection will favour the clutch size that produces the most offspring that survive. It should be noted that this trade-off is very unlikely to be independent of other trade-offs, including reproductive investment versus parental survival and offspring size versus offspring survival. From this it is clear that there might be several interlinked 'optimum' solutions to the trade-off between offspring number and offspring size that also vary with external environmental conditions (Stearns 1989, 1992, Walker et al. 2007). Since then the field has developed to say that the number of offspring that survive and reproduce should be optimised, and that where adult resources are finite, which is generally true for animals, then number and size of embryo produced directly trade-off.

Many authors over several decades have stressed that early-stage survival and performance strongly influence population dynamics in marine and aquatic systems (Thorson 1946, Strathmann 1985, Roughgarden et al. 1988, Pechenik 1999, Moran & Emlet 2001, Underwood & Keough 2001, Marshall et al. 2006, 2012). As seen earlier, there is a very common if not universal trend towards larger egg sizes at higher latitudes, and it is clear that greater investment per egg, and hence individual offspring, is the optimum life-history solution in Antarctica, and this likely maximises embryonic and larval survival to juvenile stages. The reasons for this remain to be identified but could be due to problems making proteins at low temperature (Peck 2016), or for reasons given earlier around slowed development rates and overall energy requirements. The final outcome in terms of importance to life histories would be to enhance early-stage survival and hence overall fitness.

Longevity and age at first reproduction

Longevity and age at first reproduction are key life-history traits. They allow generation time and number of years over which an individual reproduces to be calculated. In marine environments, data for these two characteristics are often best quantified and understood for fish because of their value, for example, in setting catch limits in fisheries. In Antarctica, data are sparse for invertebrates but

available for several fish species and good for some, for example, *Notothenia coriiceps* (Kock 1992), *Dissostichus eleginoides* (Kock et al. 1985).

Temperate fish usually mature at ages between one and four years. Sole has a 50% age at first reproduction of 1.7–2.5 years (Mollet et al. 2013); for haddock, this is three years, whiting two years and cod three to five years (Hunter et al. 2015). Arruda et al. (1993) reported seven goby species in the Ria de Aveiro lagoon, Portugal, all mature at less than one year of age, while O'Brien et al. (1993) showed that 14 of 19 species of finfish investigated on the Georges Bank reached maturity in less than 2.5 years, and only one required more than five years. A few species take longer, and the sea bass *Dicentrarchus labrax* requires three to six years to reach maturity in North Wales (Carroll 2014). Antarctic fish generally take much longer than temperate species to become mature. *Notothenia coriiceps, N. rossii, Chaenocephalus aceratus* and *Gobionotothen gibberifrons* all require six to eight years to reach maturity, and *Pleuragramma antarctica* and *Trematomus eulepidotus* need seven to nine years (Kock 1992). *Dissostichus eleginoides* does not mature before it is 8–10 years old (Kock et al. 1985), *Trematomus bernacchii* reaches maturity at around 10 years (Gon & Heemstra 1990), and *Dissostichus mawsoni* needs 13–17 years to achieve maturity (Parker & Grimes 2010). Most of the previous species live to between 15 and 30 years, with later-maturing species having greater longevity (Gon & Heemstra 1990). Smaller Antarctic species generally mature earlier and have less longevity. *Lepidonotothen* (formerly *Nototheniops*) *nudifrons* reaches maturity at four to five years (Radtke & Hourigan 1990), *Harpagifer antarcticus* lives to nine years of age (Daniels 1983) and matures at around five years, or 55% of maximum age (La Mesa & Eastman 2012), and Kock and Kellerman (1991) estimates that most small notothenioids in the pack-ice zone live for less than 10 years and begin spawning at three to four years.

Most fish species achieve maturity between 30%–40% of maximum age and 50%–80% of maximum size (Kock 1992, He & Stewart 2001). Antarctic species, therefore, reproduce over many years and for longer periods, on average, than warmer water fish. This increases lifetime RE compared to temperate and tropical species. Reduced numbers of gametes released decreases RE relatively, but large egg size may offset the decrease. Calculating lifetime RE is, therefore, not a trivial exercise.

Data are generally poorer for longevity and age at first reproduction for Antarctic marine invertebrates. The Antarctic scallop *Adamussium colbecki* lives for more than 10 years and becomes mature at between six and seven years of age (Cattaneo-Vietti et al. 1997). The large infaunal bivalve *Laternula elliptica* lives up to 36 years (Philipp et al. 2005), begins to produce gonads at 30–40 mm length, aged four to five years, but does not begin reproducing until around nine to ten years of age (Urban & Mercuri 1998, Clark et al. 2013). In brooding bivalves *Mysella* (previously *Kidderia*) *subquadrata* at Palmer station matures at 23–27 months post fertilisation, 18–22 months after juveniles are released from broods (Shabica 1974), whereas the smallest brooding female of *Adacnarca nitens* in the Weddell Sea is around 3.5–4 years old, and 50% brooding is thus not reached until individuals are at least five years of age (Higgs et al. 2009). The common limpet *Nacella concinna* begins to produce gonads with mature gametes at 18–20 mm length at Rothera Point, Adelaide Island (S. Morley, personal communication), which from growth rate data at the same site equates to four to five years of age (Clarke et al. 2004b). In the brachiopod *Liothyrella uva*, broods are first seen in individuals around 31 mm in length (Meidlinger et al. 1998), which equates to an age around 17–18 years (Peck et al. 1997b). Seasonal changes in body mass associated with reproduction in the sea urchin *Sterechinus neumayeri* at Rothera Point, Adelaide Island become apparent at a test diameter of around 15 mm (T. Souster, pers. comm.). From growth rate data from the same site, this equates to an age of eight to nine years (Brey et al. 1995a, Brockington 2001a). The reviews of the biology and reproduction of the amphipods have concluded that polar species are characterised by slow growth, great longevity and deferred maturity (Sainte-Marie 1991, Johnson et al. 2001). Evidence for this includes the Antarctic *Paramoera walkeri* which lives for up to four years and matures at 19 months of age (Rakusa-Suszczewski 1972, Brown et al. 2015), *Eusirus perdentatus* which lives for five to eight years and matures at three years (Klages 1993), and

Orchomenella franklini which lives for three years and begins reproducing after two years (Baird & Stark 2013). Most warmer-water marine invertebrate species mature in less than a year, and tropical species often have more than one generation per year.

One species where maturation has been stated to be early, and contrary to the usually identified situation of deferred maturity, is in the pennatulid sea pen *Malacobelemnon daytoni* (Servetto et al. 2013). In this species, which grows to over 120 mm rachis length, a measure of overall size (López-González et al. 2009), the smallest mature colony was 15 mm long. Octocorals from different regions have been reported to mature at between 2 and 13 years of age (Coma et al. 1995). One remaining issue with the observation of early maturation in *M. daytoni* is that there are no data on its growth rate, and although the size for maturity is small, it is possible that like other Antarctic octocorals growth is very slow (e.g. Peck & Brockington 2013), which would extend the age at first or 50% maturity.

Overall maturity appears to be delayed in Antarctic fish and invertebrates. Data are not strong enough to be definitive on how much it is slowed, but in most cases, the slowing appears to be in the range 2-fold to 10-fold.

Energy use, oxygen consumption and metabolic rate

A basic requirement for all organisms is to use energy to perform the biological functions necessary for life across all their life-history stages. This is true from the molecular level where gene expression requires energy to locomotion in whole animals. The ability to perform these functions and the rate at which they are carried out ultimately depend on an adequate energy supply. In this context, all organisms transform energy. Photosynthesising groups (plants, cyanobacteria, etc.) transform light energy into chemical energy. Animals predominantly consume energy in the form of biomass and use it in a variety of ways to maintain their body tissues, to grow, to reproduce, to produce defences, in activity, and so forth. These processes can be aggregated into an energy budget:

$$C - F = P_s + P_r + R + U + M \text{ (following Peck et al. 1987b)}$$

where C = food consumed, F = faeces produced, P_s = somatic growth, P_r = reproductive investment, R = respiration, U = excretion, and M = mucus production. This form of the energy budget was chosen to emphasise that in some groups non-standard components can be large parts of the budget. In the case shown, the budget was formulated for a gastropod mollusc, *Haliotis tuberculata*, where mucus accounted for up to nearly 30% of the energy consumed (Peck et al. 1987b). There are other cases where an unusual term has been included in the energy budget, including a third growth or productivity component in crustaceans to represent the energy lost as cast exoskeletons during moulting (e.g. Luxmoore 1985).

There have been very few energy budgets constructed for Antarctic marine species, and none of these have measured all of the parameters of the budget at the same time. They have combined published data for some parts of the budget with new measurements. There are clearly some problems with these approaches, as the studies that data were collated from were carried out at different times and sometimes different places. The only study to date that measured all of the major components of the energy budget was Luxmoore (1985) who studied the carnivorous isopod *Paraserolis* (previously *Serolis*) *polita* at Signy Island. Assimilation efficiency (=absorption efficiency) on a diet of the amphipod *Cheirimedon femoratus* was 80%, which is similar to other carnivorous isopods (Luxmoore 1985). The study covered more time than any other Antarctic energy budget investigation as measurements were made every month for two years. Data were size-corrected and expressed as energy values for the whole population in Borge Bay, Signy Island, South Orkney Islands. Energy consumption was estimated from measurements of absorption efficiency multiplied by the sum of all other components of the energy budget. Energy consumed was estimated at 289 J m^{-2} yr^{-1}, somatic growth accounted for

78 J m^{-2} yr^{-1}, reproductive growth 24 J m^{-2} yr^{-1}, losses through moulted skeleton 13 J m^{-2} yr^{-1}, oxygen consumption 108 J m^{-2} yr^{-1}, ammonia excretion 9 J m^{-2} yr^{-1}, and faecal production 58 J m^{-2} yr^{-1}. The largest components of the budget were somatic growth and oxygen consumption, and somatic growth cost over three times as much energy as reproductive growth.

Kowalke (1998) carried out a broad-scale analysis of energetics of two Antarctic sponges, four ascidians and the bivalve mollusc *Laternula elliptica,* all of which are sessile suspension-feeders. He estimated energy consumption from measurements of pumping rate combined with assessments of the energy content of suspended material in the water around his target species, which was dominated by phytoplankton in summer months and resuspended benthic particulate material in winter. He used published values for respiration and somatic and gonadal production to calculate energy budgets. One drawback of this approach is that there was a large discrepancy (25%–30% for the bivalve *L. elliptica* and 52%–83% for the ascidians) between estimated annual energy intake, which may have been due to an overestimation of the amount of food available in winter. Energy budget values were expressed as summations for the populations present in Potter Cove, King George Island and were corrected for the size ranges of animals present. Populations of the bivalve *L. elliptica* allocated similar amounts of energy to respiration (480 kJ m^{-2} yr^{-1}), faecal production (436 kJ m^{-2} yr^{-1}) and somatic production (467 kJ m^{-2} yr^{-1}), but less on reproductive production (324 kJ m^{-2} yr^{-1}). These proportions would, however, be expected to vary if population demography were different. In three of the four ascidian species, *Ascidia challengeri, Cnemidocarpa verrucosa* and *Molgula pedunculata*, faecal egestion accounted for over twice as much energy used as respiration and somatic growth, and reproductive growth accounted for only a small part of the budget. In the fourth species, *Corella eumyota*, respiration and somatic growth each accounted for around 40%–45% of the energy used, while faecal egestion and reproductive growth were smaller at 7.0%–7.5% each.

Aguera et al. (2015) calculated a dynamic energy budget (DEB) for the starfish *Odontaster validus* using predominantly published data from sites in the Ross Sea and Antarctic Peninsula and collected in different years, up to more than 30 years apart. The budget showed similar levels of reproductive investment as temperate seastars, the ability to mobilise reserves rapidly, very slow growth, only reaching maximum size after 35 years and beginning to reproduce after seven years. It did not, however, reflect the very large interannual reproductive output measured in this species by Grange et al. (2007). A similar approach was used to produce a DEB for the large infaunal bivalve *Laternula elliptica*, again based on literature, data collected at a range of sites and over multiple years by Aguera et al. (2017). They described *L. elliptica* as having a 'metabolism specifically adapted to low temperatures, with a low maintenance cost and a high capacity to uptake and mobilise energy, providing this organism with a level of energetic performance matching that of related species from temperate regions'. These are the first budgets of this type, and it will be interesting to see the variation in findings from future exercises similar to this on other Antarctic taxa, as *L. elliptica* is one of the largest and fastest growing bivalves from this region.

For fish, Everson (1970b) produced an energy budget for *Notothenia neglecta* (now *coriiceps*) in Borge Bay, Signy Island, South Orkney Islands. He determined age (and hence growth from von Bertalanffy size to age relationships) from scale and otolith ring assessments, somatic production from annual changes in body mass, and reproductive production from changes in gonad mass on spawning. Oxygen consumption was assessed at the same time on the same population but reported elsewhere (Ralph & Everson 1968). Amounts of energy consumed were estimated as proportions of energy used in respiration and growth ($1.25 \times (P_s + P_r + R)$), and faecal production and nitrogen excretion calculated as 20% of energy consumed. On this basis, growth was slow, and the main component of the energy budget was respiration, which accounted for more than 25 times the energy used in somatic and reproductive growth combined and nearly four times as much as the energy lost in faeces and nitrogen excretion.

Brodte et al. (2006) also investigated energetics in a fish, but they studied the non-notothenioid Antarctic eelpout *Pachycara brachycephalum*. Growth was measured at different temperatures in

laboratory trials along with respiration, nitrogen excretion and body condition. Faecal production was calculated from an equation relating food intake and temperature for brown trout by Elliott (1976). *Pachycara brachycephalum* inhabits deeper waters where the temperatures are a few degrees warmer than shallower Antarctic sites, so rates of growth (etc.) are not as slow as for several of the shallower notothenioids. The paper compared the Antarctic species with a temperate eelpout *Zoarces viviparus* from the North Sea where temperatures at collection were 17.5–19.5°C. Both species were fed *ad libitum* with cockle meat (*Cerastoderma edule*) on every second day but had very low absorption efficiencies (∼7%–25% for *Pachycara brachycephalum* and ∼2%–9% for *Zoarces viviparus*). Values for carnivorous fish are usually in the range 60%–90% and for herbivorous fish 40%–75% (Wooton 2012). Measurements were made at 0°C, 2°C, 4°C and 6°C, and energy used in growth, oxygen consumption, ammonia excretion and faecal production was ∼15%–30% greater than energy consumed at 2°C and 4°C. In the temperate species, 50%–85% of absorbed energy was used in metabolism, whereas in the Antarctic species, this was 45%–75% (Brodte et al. 2006). The Antarctic species also grew faster than the temperate species in this study at these low temperatures.

Energy budgets may be more difficult to obtain for cold-water species because of their slow growth rates (Peck 2016), extreme seasonality of the environment where some species cease feeding for several months in winter, and other aspects of physiology can be highly seasonal (Gruzov 1977, Whitaker 1982, Clarke 1988, Clarke et al. 1988, Clarke & Peck 1991, Pearse et al. 1991, Arntz et al. 1994, Barnes & Clarke 1995, Brockington et al. 2001, Jazdzewski et al. 2001, Fraser et al. 2002, 2004, Barnes & Peck 2005, Morley et al. 2007, 2016c, Obermüller et al. 2010, 2013). The very large interannual variation in biology, presumably caused by long-term variations in food supply quality and quantity, and evidenced by very large interannual variation in reproduction (e.g. Grange et al. 2004) adds further to the complexity. This means that all energy budgets in polar regions need to be evaluated regularly during the year and over several years to cover all of these aspects. However, the lack of good data for energy budgets for Antarctic marine species requires attention, and good studies in this will likely advance understanding of differences compared to lower latitude species and also trade-offs during periods of stress or environmental change.

Energy budget theory has developed over the last 20 years into the field of dynamical energy budgeting where the static 'snapshot' of most previous energy budget studies that calculated the budget for a set moment in time was extended to follow the changes of the energy fluxes through an organism over time and in its full formulation over the full life cycle of that organism (Kooijman 2000). This approach has recently been applied to the Antarctic starfish *Odontaster validus* (Aguera et al. 2015) and infaunal bivalve mollusc *Laternula elliptica* (Aguera et al. 2017), as described earlier. The dynamic energy budget approach has distinct advantages in that it is mechanistically based and allows analyses of seasonal and ontogenetic changes in energy use, can identify critical times when energy may be limiting, and can interpolate from stage to stage and time to time using a set of well-developed equations. Its main drawback is the requirement for large amounts of data on several aspects of the biology of an organism at the same time, and for several parts of the life cycle, and these need to be repeated at different times of the year to allow for seasonal aspects to be covered, all of which require non-trivial levels of effort and expertise. A major element of all energy budgets is the cost of maintenance of the organism and the costs of activities. These are usually measured via oxygen consumption.

Oxygen consumption, metabolic cold adaptation and metabolism

All of the major processes in an energy budget (covering all of the energy used by the organism) have an associated metabolic cost accrued when ATP is used in that process. In fully aerobic conditions, this can be measured via oxygen consumption (MO_2), and oxygen consumption is a measure of the immediate energy requirement under these conditions. Following the rationale laid out in Clarke (1987a), the energy budget then becomes:

$$C = \boxed{F} + \begin{bmatrix} P_s \\ + \\ R_s \end{bmatrix} + \begin{bmatrix} P_r \\ + \\ R_r \end{bmatrix} + \boxed{R_m} + \boxed{R_a} + \boxed{U} + \boxed{M}$$

where R_s represents the respiratory costs associated with somatic production, R_r is the respiratory costs of reproductive production, R_m is maintenance metabolic cost and R_a is respiratory costs associated with activity. From the previous equation, it is clear that measured oxygen uptake in an organism is a complex entity made up of several costs ($R_s + R_r + R_m + R_a$) from a range of sources (Clarke 1987a).

There have been many investigations of whole-animal oxygen consumption in Antarctic marine invertebrates and fish. These include: amphipods (e.g. Opalinski & Jazdzewski 1978, Rakusa-Suszczewski 1982, Chapelle et al. 1994, Chapelle & Peck 1995, Doyle et al. 2012, Gomes et al. 2013, 2014); isopods (e.g. Belman 1975, Luxmoore 1984, Robertson et al. 2001); the nemertean *Parborlasia corrugatus* (Clarke & Prothero-Thomas 1997, Davison & Franklin 2002, Obermüller et al. 2010); bivalves (Ralph & Maxwell 1977, Davenport 1988, Ahn & Shim 1998, Kowalke 1998, Pörtner et al. 1999b, Peck & Conway 2000, Brockington 2001a, Peck et al. 2002, Heilmayer & Brey 2003, Heilmayer et al. 2004, Pörtner et al. 2006, Morley et al. 2007, Cummings et al. 2011); gastropods (Ralph & Maxwell, 1977, Houlihan & Allan 1982, Peck 1989, Peck & Veal 2001, Fraser et al. 2002, Harper & Peck 2003, Obermüller et al. 2010, Morley et al. 2012a, Watson et al. 2013, Peck et al. 2015b, Suda et al. 2015); cephalopods (Daly & Peck 2000, Oellermann et al. 2012); bryozoans (Peck & Barnes 2004, Barnes & Peck 2005); brachiopods (Peck et al. 1986a,b,c, 1987a, 1997a,b, Peck 1989, 1996); ascidians (Kowalke 1998, Torre et al. 2012); sponges (Kowalke 1998, Gatti et al. 2002, Morley et al. 2016b); cnidarians (Torre et al. 2012, Henry & Torres 2013); echinoids (Belman & Giese 1974, Brockington & Peck 2001, Watson et al. 2013); asteroids (Belman & Giese 1974, Peck et al. 2008, Obermüller et al. 2010); holothurians (Fraser et al. 2004); and ophuiroids (Obermüller et al. 2010).

Studies of resting or routine MO_2 date back to the early 1960s (e.g. Wohlschlag 1963, 1964, Hemmingsen et al. 1969, Everson & Ralph 1970, Holeton 1970, Wells 1978, 1987, White et al. 2012). MO_2 in Antarctic fish has also been measured in relation to several other factors, including feeding (e.g. Johnston & Battram 1993, Boyce & Clarke 1997, Sandblom et al. 2012); effects of temperature (e.g. Johnston et al. 1991); acclimation of metabolism to altered environmental conditions, especially elevated temperature (e.g. Wilson et al. 2002, Robinson & Davison 2008, Strobel et al. 2012, Enzor et al. 2013, Enzor & Place 2014, Peck et al. 2014, Morley et al. 2016c); field levels of activity and seasonality (Campbell et al. 2008, Obermüller et al. 2010); antioxidant and reactive oxygen species production (Abele & Puntarulo 2004, Heise et al. 2004, Benedetti et al. 2008, Mueller et al. 2011, Enzor & Place 2014, Almroth et al. 2015); and the functioning of reversible oxygen binding pigments in oxygen delivery (e.g. Davino et al. 1994, di Prisco et al. 2002, Cheng & Detrich 2007, Verde et al. 2008, 2011, Cheng et al. 2009a,b, Giordano et al. 2010, 2012a, 2015).

MO_2 increases across latitudes towards the tropics, and as temperature increases, in fish (Clarke & Johnston 1999) and invertebrates (Peck & Conway 2000, Peck et al. 2006b, Peck 2016). Early in the last century, Krogh (1916) recognised that polar cold-blooded animals are active at low temperatures, but temperate ectotherms are not when cooled to similar temperatures. This led him to propose the hypothesis that polar species should have elevated metabolic rates to overcome the effects of low temperature. The first studies on metabolic rates in Antarctic ectotherms supported this idea, and this led to the concept of 'metabolic cold adaptation' (MCA) (Scholander et al. 1953, Wohlschlag 1964). Studies of several molecular and cellular processes have also showed compensation for low temperature in high latitude species, for example, elevated mitochondrial ATP synthesis capacity (Sommer & Pörtner 2004), increased enzyme activities (Crockett & Sidell 1990), greater mitochondrial volume density in fish muscles (Johnston et al. 1998, Guderley 2004, Lurman *et al*. 2010a,b), and microtubule assembly (Pucciarelli et al. 1997, 2013, Detrich et al. 2000).

Note that for some of these adaptations some taxa do not follow the trend, for instance adaptation to low temperature allows Antarctic clams of the genus *Laternula* to bury at the same rate as temperate congeners, but this is achieved through having larger burying muscles and not through increases in mitochondrial content of the muscle, as seen in fish swimming muscles, which in the Antarctic species are the same, or lower than temperate and tropical clams (Morley et al. 2009b,c). More recent whole-animal research on MO_2, primarily investigating within species trends, evaluating populations living at different latitudes and temperatures, provided further support for MCA (e.g. Hodkinson 2003, Schaefer & Walters 2010, Gaitán-Espitia & Nespolo 2014). These findings mainly show that populations living at higher latitudes and cooler temperatures have higher metabolic rates (and usually higher cellular process rates such as enzyme activity) than populations or congeners living at warmer temperatures when both are measured at the same temperature. When measured at their normal habitat temperature, the colder populations and species have lower metabolic rates than their warmer counterparts. The same outcome of lower physiological rates, mainly MO_2 at lower temperatures, was the finding of studies comparing large numbers of species across tropical to polar latitudes in fish (Clarke & Johnston 1999) and bivalve molluscs (Peck & Conway 2000, Peck 2016), both of which showed the change in MO_2 with temperature matched Arrhenius predictions, with Q_{10} values predominantly in the range two to three. These latter studies argued strongly against the MCA hypothesis, and within species, MCA studies have recently concluded that while there is some compensation of metabolism, evolutionary adaptation and phenotypic thermal plasticity appear insufficient to fully compensate for the thermodynamic effects of reduced temperature (e.g. White et al. 2012). Thus, it seems that while some compensation is evident in Antarctic marine species in certain cellular processes, and in some aspects of whole-animal metabolism, it is insufficient to move large-scale comparisons of oxygen consumption with temperate and tropical species outside Arrhenius expectations. It should be noted here, however, that there is good evidence for MCA in terrestrial insects (Addo-Bediako et al. 2002) and the difference between terrestrial and marine animals in this respect remains to be explained.

Beyond comparisons of routine, basal or standard metabolism, valuable comparisons of abilities to raise metabolic rates to do work in marine animals are also possible. In Antarctic marine species, research in this area has mainly been on the rise in metabolism after feeding.

Specific dynamic action of feeding (SDA) and metabolic scope

Metabolic rates of animals rise after consuming food. They stay high for a period and then return to pre-feeding levels. The postprandial rise and fall of metabolism is called the specific dynamic action of feeding (SDA) or the heat increment of feeding (HIF). This phenomenon has been known since the first half of the twentieth century when it was identified in domesticated animals (Brody 1945). The rise in metabolism is usually assessed via oxygen consumption, which in fully aerobic conditions is a proxy for proximate energy use and comprises the total costs of processing food (handling and digestion) and a variety of postabsorptive processes. These include the breakdown and synthesis of proteins, transport of absorbed materials, storage and growth (Peck 1998, Secor 2009, Khan et al. 2015). Studies manipulating diets with materials that are not absorbed, such as cellulose, indicated that only 5%–30% of the SDA is used in handling food and digestion (Tandler & Beamish 1979, Carefoot 1990), and some studies showed food handling accounted for less than 3% of the metabolic rise (Cho & Slinger 1979). Other studies further showed protein synthesis can form a large part of the SDA (e.g. Houlihan et al. 1995). Furthermore, studies injecting amino acids into animals showed that an SDA was produced of similar size to a meal with the same amino acid content (Brown & Cameron 1991, Peck 1998). This also suggests the major components of the SDA are post absorptive. The conclusion from all of these studies is that in most cold-blooded species the largest portion of the rise in metabolism after feeding is in postabsorptive processes, mainly in protein turnover.

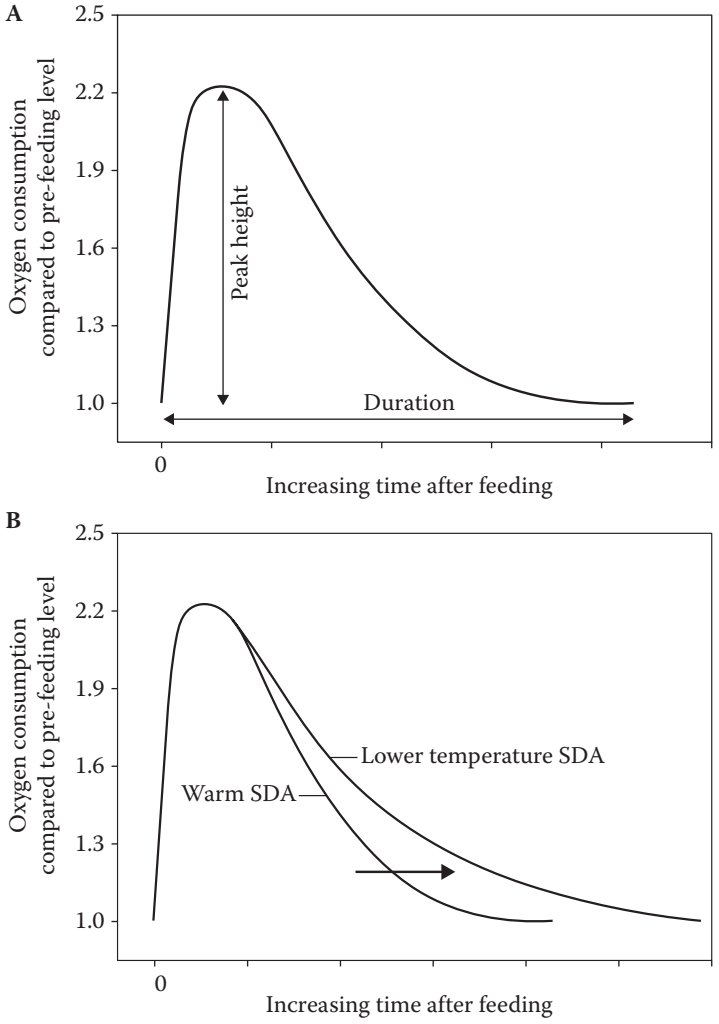

Figure 11 An idealised representation of the Specific Dynamic Action of feeding (SDA). (A) Oxygen consumption by an idealised animal following feeding. MO_2 rises to a peak, after which it declines back to pre-feeding levels. Peak height is measured as a factorial multiplier of pre-feeding MO_2. In the example given here, the peak is 2.2 times higher than the pre-feeding MO_2. When SDA studies are carried out, the usual statistics quoted are the factorial peak height and the duration, which is the time from the beginning of the rise above pre-feeding MO_2 to when oxygen consumption returns to that level). 0 shows the day when animals were fed. (B) Figure demonstrating that at lower temperatures factorial peak height is the same as in warmer SDAs, but the duration is extended. (Modified from Peck, L.S. 2016. *Trends in Ecology and Evolution* **31**, 13–26.)

There are two main aspects of the SDA that are usually reported. These are peak height and the duration of the rise in metabolism (Figure 11). Peak height is usually expressed as the factorial rise above the pre-feeding standard or routine metabolic rate where a doubling of metabolism after feeding produces an SDA peak height of x2 and a trebling produces one of x3. In most marine ectotherms, the SDA peak rise is in the range two to four (Peck 1998), but some species can have much higher values than this, with a value of 45 reported for Burmese pythons eating a Thomson's gazelle (Secor & Diamond 1995). This is similar to the maximum aerobic scopes for racehorses, which are the highest reported for any vertebrate (Birlenbach & Leith 1994). The duration of the SDA is the time from the initial rise in metabolism after feeding to the return to pre-feeding levels.

The area under the curve is called the SDA coefficient. It represents the total amount of energy used in digestive and postabsorptive processes associated with a feeding event.

There have been several investigations of SDA in a range of Antarctic marine species. These include fish (Johnston & Battram 1993, Boyce & Clarke 1997, Brodeur et al. 2002, Vanella et al. 2010, Sandblom et al. 2012), amphipods (Chapelle et al. 1994) and isopods (Robertson et al. 2001), rhynchonelliform brachiopods (Peck 1996), nemertean worms (Clarke & Prothero-Thomas 1997), limpets (Peck & Veal 2001) and starfish (Peck et al. 2008). These studies all demonstrated that the peak heights of the SDAs measured were similar to those of related or ecologically similar species from lower latitudes, but the SDA duration was markedly extended. Peck (2016) took this analysis further and compared SDA characteristics for marine invertebrates and fish across the globe from the tropics to the polar regions. He showed that peak heights did not vary with latitude or temperature (Figure 12A), but SDA duration increased as temperature decreased at higher latitudes (Figure 12B). He further demonstrated that the increase in SDA duration matched expected Arrhenius relationships for the effect of temperature on biological systems for temperate and tropical species, but the durations for extreme low temperatures, around or below 0°C, in the polar regions were markedly longer than they should be. They were significantly above predicted values for polar temperatures from the Arrhenius relationship for temperate and tropical species (Figure 12C).

This slowing of process rate for the SDA to levels well below that expected from Arrhenius temperature relationships for temperate and tropical species is very similar to that seen for growth (Figure 3) and embryonic development (Figure 8). It emphasises that marine species living at low polar temperatures around or below 0°C experience extra difficulties with physiological processes that require significant protein synthesis, and it highlights that problems with protein synthesis or folding are the likely cause of these dramatic slowing of rates (Peck 2016). The impact of adaptation to low temperature on performance of the above biological functions is clear and dramatically reduces their rates compared to warmer-water species. A major function not yet considered is whole-animal activity. This is important in a number of ecological contexts, including foraging, predator–prey interactions, reproductive behaviours and competition.

Activity

The rate at which activity is carried out is rarely measured in polar marine invertebrates and fish. The studies that have been conducted show activity is usually carried out much more slowly than in temperate and tropical species, and in general, Antarctic species are 2–10 times slower than temperate species living in 10–15°C warmer conditions (Figure 13). These have been previously reviewed in Peck (2002a), Pörtner (2002a) and Peck et al. (2006b). Some examples are: clap frequency in the Antarctic scallop *Adamussium colbecki* was measured to be performed at approximately 50% the rate of temperate scallops (Bailey et al. 2005); Antarctic bivalve molluscs and anemones require between 5 and 10 times longer than related or ecologically similar temperate species when burying (Ansell & Peck 2000, Peck et al. 2004a); average pumping rates, when feeding, were 15–50 times slower in Antarctic sponges, ascidians, and the bivalve mollusc *Laternula elliptica* than related or ecologically similar temperate species (Kowalke 1998); the Antarctic predatory snail *Trophonella longstaffi* takes 28 days to drill through the shell of its prey and complete a meal, compared to 10–12 days for temperate predatory snails (Harper & Peck 2003); the limpet *Nacella concinna* routinely walks at speeds of 0.13–0.25 mm s^{-1}, and 0.25–1.0 mm s^{-1} during escape responses from predators, rates that are on average just over half as fast as temperate limpets (Peck et al. 1993, 2006b, Peck, 2002a, Markowska & Kidawa 2007); the spatangoid urchin *Abatus ingens* moves through sediment at 0.3–1.95 cm h^{-1} on average, with maximum speeds of 1.1–3.3 cm h^{-1} (Thomson & Riddle 2005), which compares with the temperate *Echinocardium cordatum* that moves at 2.0–8.0 cm h^{-1} and lives at temperatures between 6°C and 15°C (Buchanan 1966); and locomotion speeds in the Antarctic starfish *Odontaster validus* were measured at 0.06–0.55 mm s^{-1} (McClintock et al. 2008), which

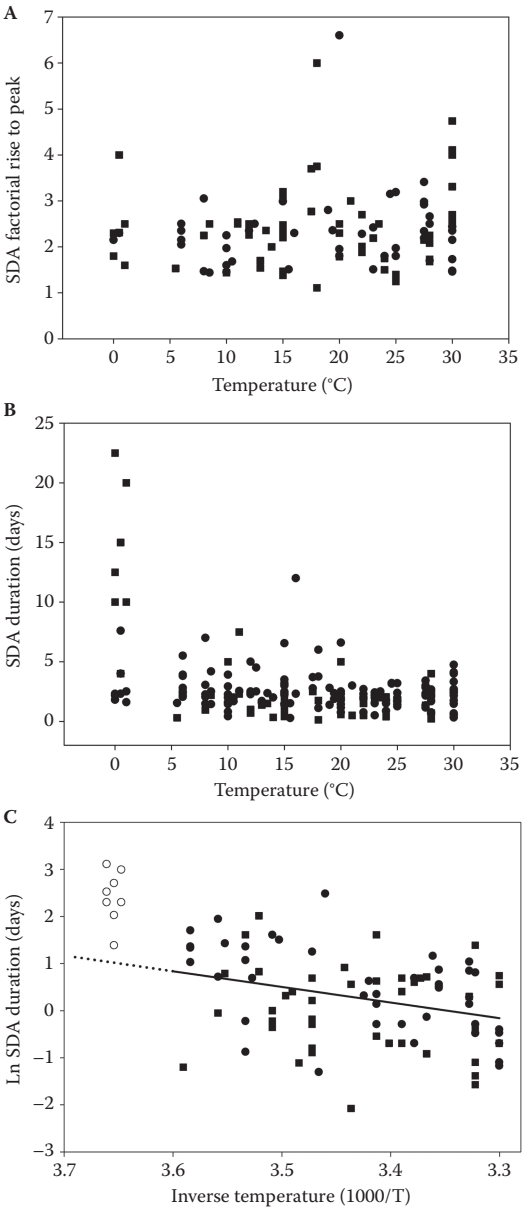

Figure 12 Specific Dynamic Action of feeding (SDA) data for marine invertebrates and fish at normal habitat temperatures from the tropics to the poles. (A) SDA peak height (factorial peak increase in MO_2 over pre-feeding level). There is no significant relationship with temperature ($FP = 0.232 + 0.009\ T$, $r^2 = 0.00$, $F_{1,110} = 0.85$, $P = 0.358$, $VIF = 1.00$). (B) SDA duration (days: the time taken from the initial rise in MO_2 after feeding to the return to pre-feeding levels). (C) An Arrhenius plot of SDA duration. The solid line represents the relationship for temperate and tropical species (Ln SDA (days) $= -11.13 + 3.32(1000/K)$; $r^2 = 0.107$, $F = 10.4$, $P < 0.0001$, 88 d.f.); the dotted line shows the extension of the relationship for tropical and temperate species to polar temperatures. In all plots, each data point represents a single species, and where the literature contains more than one record, the value plotted is the mean for duration and temperature. Closed symbols are for temperate and tropical species living at mean temperatures above 5°C; open symbols are for polar species living permanently near or below 0°C; • = marine invertebrates; ■ = marine fish. (Figure from Peck, L.S. 2016. *Trends in Ecology and Evolution* **31**, 13–26.)

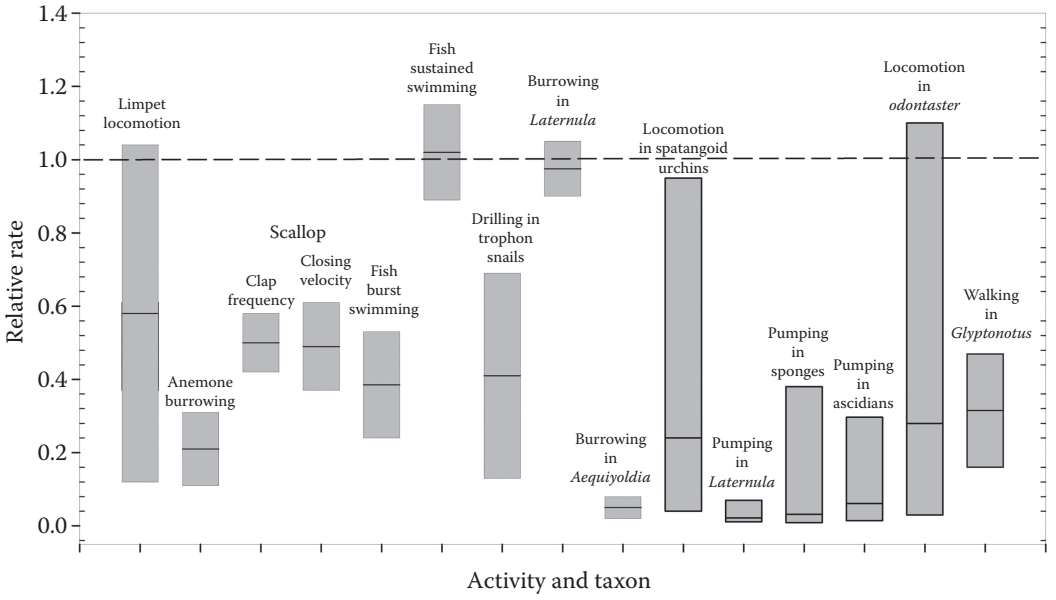

Figure 13 Rates of accomplishing various activities for a range of Antarctic marine invertebrates compared with related or ecologically similar temperate species. The hatched line indicates representative rates for temperate species and is set at a value of 1. Data sources for comparisons of limpet locomotion, anemone burrowing, scallop and fish swimming, and burrowing in bivalve molluscs are all taken from Peck (2002a) and Peck et al. (2004a, 2006b). Data for drilling in the predatory snail *Trophonella longstaffi* are from Harper and Peck (2003); for pumping of water in association with feeding currents from Kowalke (1998); for locomotion in spatangoid urchins from Thomson and Riddle (2005); for locomotion in the starfish *Odontaster validus* from McClintock et al. (2008); and walking in the isopod *Glyptonotus antarcticus* from Young et al. (2006a). Boxes show the full range of values, with the midline indicating the mean. (Figure based on Peck, L.S. et al. 2004a. *Polar Biology* **27**, 357–367 and Peck, L.S. et al. 2006b. *Biological Reviews* **81**, 75–109.)

compares with data for temperate species that usually fall in the range 0.5–2 mm s^{-1}, with some species over 20 mm s^{-1} (echinoblog.blogspot.co.uk, accessed 6 Feb 2016).

To date, only two whole-animal activities have been identified in Antarctic marine invertebrates and fish that appear fully compensated for temperature. One is in Notothenioid fish where sustained swimming is maintained at the same speed (as number of body lengths per second) as temperate species. This temperature compensation is supported by an increase in the numbers of mitochondria in the red muscles. The polar species have roughly twice as many mitochondria per gram of muscle tissue as temperate species, but this is only in red, not white muscle (Johnston et al. 1998). The second activity fully compensated for low temperature is burrowing in the infaunal Antarctic clam *Laternula elliptica*. In this species, the adaptation that allows the activity to be performed at similar rates as temperate and tropical congeneric species has been identified. It is not via an increase in mitochondria to improve energy generation but by an increase in size of the muscle that is used for burying, the foot, which is around two to three times larger than in warmer-water congeners (Morley et al. 2007, 2009b,c).

Although the data are limited, there are some patterns worth noting in Figure 13. Excluding the two activities where temperature compensation has been identified, and a mechanism explaining the compensation described (sustained swimming in fish and burrowing in *Laternula elliptica*), six of the seven remaining activities involving whole-animal movement (locomotion, burying, walking and swimming) are, on average, two to five times slower than rates for temperate species living at 10–15°C. Drilling by the predatory snail *Trophonella longstaffi* is also within this range. Slowing

of this magnitude matches expected temperature effects on biological systems, which should be in the range of one to four times for a 10°C change in temperature (Peck 2016). The only activities outside this range are those for water pumping, which are all from one study (Kowalke 1998), and the comparison for burying in the small infaunal bivalve *Yoldia* (now *Aequiyoldia*) *eightsii* (Peck et al. 2004a). Both of these are much slower than expected, being on average more than 10 times slower than temperate species. These findings require further study to verify they are slowed by this amount. If they are slowed more than other activity comparisons, then it would be difficult to explain why burying in one bivalve species (*Laternula elliptica*) should be fully temperature-compensated while another species living in the same habitat is slowed more than expected, and other activities based around muscular contraction (walking, swimming) are slowed by the expected amount. The extra slowing for pumping in bivalve molluscs, ascidians and sponges (Kowalke 1998), is an activity based around ciliary pumping mechanisms, and if verified, these findings would suggest that there is an extra impact of low temperature on such mechanisms. Viscosity of seawater increases as temperatures fall to values around 0°C (Peck 2016), and this has been cited in the past as a major factor affecting swimming in organisms using cilia for propulsion, for example, ciliates and protists (Beveridge et al. 2010) and also in marine invertebrate larvae (Podolsky & Emlet 1993, Chan 2012). A similar effect on ciliary feeding pumps would explain the markedly lower pumping rates in Antarctic sponges, ascidians and bivalve molluscs observed by Kowalke (1998) and could be a low temperature constraint on this feeding mechanism.

Temperature affects the rate at which cellular biochemical and biological processes proceed (Hochachka & Somero 2002, Peck 2016). In whole animals, physiologies generally speed up to an optimum temperature and then decline above this before failure. There is also a hierarchical arrangement where complexity of organisation reduces the optimum and maximum temperature for function with cellular functions continuing to higher temperatures (Pörtner 2002a, Pörtner et al. 2007, 2012). There have been very few studies of activity of Antarctic marine invertebrates and fish when temperatures are reduced to values below 0°C. One such was an investigation of walking and righting in the isopod *Glyptonotus antarcticus* and the amphipod *Paraceradocus gibber* (Young et al. 2006a). In both species, walking speed increased consistently between −2°C and +5°C, when experiments were halted to avoid reaching the thermal limit. In contrast, there was no significant relationship between the time required to right when turned over in *Glyptonotus antarcticus* at temperatures between −2°C and +5°C. There have been many studies where data have been collected in positive temperatures. These have produced variable results, with some showing a decline in capability with temperature, but others showing an increase. Those that show an increase include the study by Young et al. (2006a) above on *G. antarcticus* and *Paraceradocus gibber*. The starfish *Odontaster validus* has also been reported to demonstrate an increase in activity rate with temperature. The time required to right when turned over decreases up to 7.5°C, but turning rate then slows markedly before the animal's upper thermal limit at around 10°C (Peck et al. 2008). However, Kidawa et al. (2010) found that increasing temperature from 0°C to 5°C reduced the number of individuals capable of righting and also slowed responses to food, food odour and rate of locomotion. Of the species showing declining activity rates with temperature, swimming in the scallop *Adamussium colbecki* and righting in the limpet *Nacella concinna* are very temperature sensitive, with a complete loss of capability at temperatures between 2°C and 5°C in both species (Peck et al. 2004b). Locomotion in *N. concinna*, in populations at its northern limit in South Georgia is, however, fastest at 2°C but continues until temperatures reach 14°C (Davenport 1997). Reburying when removed from sediment declines markedly between 0°C and 5°C in the infaunal clam *Laternula elliptica*, with large animals losing the ability to bury at lower temperatures than small ones, and all sizes incapable of reburying above 5°C (Peck et al. 2004b). The isopod *Paraserolis* (previously *Serolis*) *polita* exhibits declining rates of righting with increasing temperature between 0°C and 5°C (Janecki et al. 2010). Reduced salinity also slowed the rate of righting in *P. polita*, and the salinity effect was stronger at higher temperatures.

Investigations of the effect of temperature on the performance of activity and other physiological processes are important, because although there has been significant research on absolute temperature limits in several species, the relationship between absolute limits and limits for performing functions is poorly understood, especially in terms of diversity and differences between species. A few studies do exist, and research has demonstrated that upper temperature limits to successful fertilisation (>50%) of eggs in the starfish *Odontaster validus* and the bivalve *Laternula elliptica* were around 5°C and 6°C, respectively (Grange et al. 2011b). Normal early embryo development declined markedly to values below 50% at 2–3°C in the urchin and 6–8°C in the starfish, and for surviving larvae, development rate was not affected by elevated temperature up to 5.7°C (the maximum temperature tested) in the urchin and between 7°C and 9°C in the starfish. Similar, though less extensive data were obtained for the same species by Stanwell-Smith and Peck (1998), and these values are lower than upper temperature limits for acute warming experiments (1°C day^{-1}) for adults of these species (Peck et al. 2009a) but are similar to limits at slow rates of warming (1°C $month^{-1}$) of 3–4°C for *Sterechinus neumayeri* and 6°C for *Odontaster validus* (Peck et al. 2009a), and adult upper temperature limits for acclimation of similar or slightly lower values (Peck et al. 2014). At least in some Antarctic species, temperature limits for rates of development thus seem to be similar to adult limits at slow, ecologically more relevant rates of warming. Data for the limpet *Nacella concinna* show that duration tenacity, the time an individual can stay attached to a surface against an applied force, declines by 50% between 0°C and 5°C (Morley et al. 2012a), but radula rasping while eating continued to temperatures between 10°C and 12°C (Morley et al. 2014). Both of these experiments were carried out at a rapid, acute rate of warming of 0.2°C h^{-1}, and at the slower but still rapid rate of warming of 1°C day^{-1}, adult thermal maxima were between 11°C and 12°C. In an acute warming experiment involving the starfish *Odontaster validus*, the rate at which an individual righted itself when turned over increased from 0°C to 8°C but declined rapidly when warmed at around 10°C, and the proportion of animals feeding when offered food was 100% between 0°C and 6°C but declined to below 50% between 8°C and 10°C (Peck et al. 2008). In the same experiments, adult thermal limits (50% survival) were between 12°C and 15°C. In the infaunal clam *Laternula elliptica*, 50% of individuals lose the capacity to rebury when removed from sediment at 3°C, and 50% of individuals of the limpet *Nacella concinna* failed to right when turned over at the same temperature when warmed at 0.1°C h^{-1}. In the scallop *Adamussium colbecki*, there was a complete loss of capacity to swim, a high-energy activity, when temperatures were raised to between 1°C and 2°C (Peck et al. 2004b). At a slower rate of warming, which should lower thermal limits (Peck et al. 2009a, 2014), *Nacella concinna* had an upper lethal temperature (50% survival) of 11–12°C and *Laternula elliptica* of 14–15°C (Peck et al. 2009a).

Differences between whole-animal upper temperature limits and essential biological functions vary markedly amongst functions and between species. The differences between species in the effect of temperature on functions will, however, dictate many of the changes in community and ecosystem structure that will occur in the coming decades because they will be one of the main influences on critical ecological factors such as competition and predation. Small differences in relationships between performance and temperature will bear heavily on competitive and predator–prey outcomes in a warming world. Despite this, the relationships between loss of critical function and upper survival limit on warming remains very poorly understood in all but a very small number of species in Antarctica, and globally.

Temperature, power and crushing predators

As seen previously, temperature has a marked effect on the performance of several physiological attributes of marine ectotherms, including oxygen consumption and activity that appear to follow Arrhenius predictions in Antarctic species and development, growth and postprandial processes associated with feeding that are slowed beyond expected levels. The performance of animal muscles

is also affected by temperature, which affects many aspects of behaviour. As noted previously, some of these have specific adaptations to overcome temperature limitations such as burying in the clam *Laternula elliptica* and sustained swimming in fish, whereas most, including burst swimming in fish, do not (Figure 13). It is generally accepted that the force generated by muscles does not vary with temperature because the force generated is dependent on the number of cross bridges involved in the contraction of the muscle. Observations, however, suggest that in ectotherms there may be a small increase in force generated by muscles at higher temperatures when measured at normal habitat temperatures, and the increase may be as much as 10% for each 10°C rise in temperature (Shadwick & Lauder 2006). Rate characteristics such as the time involved in force development, the cycle time of cross bridges in muscles and relaxation time vary to a much greater extent with temperature (Johnson & Johnston 1991, Shadwick & Lauder 2006). The outcome of changes in these characteristics is that power generation varies with temperature (Wakeling & Johnston 1998). In fish muscles, power generation increases by around 2.5 times for each 10°C rise in temperature from polar to tropical species (Figure 14), which is in line with expected Arrhenius temperature effects.

Muscle power increases with muscle diameter and, hence, muscle mass. To fully compensate for a reduction in power output as temperature decreases along the lines shown in Figure 14, a muscle would have to increase its mass by around 2.5 times for every 10°C drop in temperature, or to produce the same power, an Antarctic ectotherm would need a muscle over 15 times larger than a tropical species at 30°C.

Force may often be thought of as the important criterion limiting the ability of durophagous predators to complete a successful attack on prey items. Power is the rate of doing work, and work is force times distance moved. Force exerted by muscle does not vary with temperature, but power

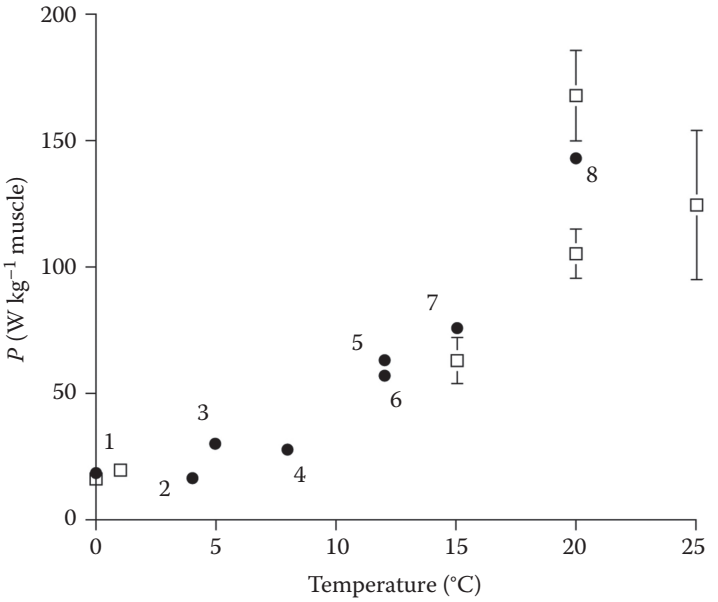

Figure 14 Fish muscle mass-specific power output with environmental ambient temperature. Open symbols denote data for *Notothenia coriiceps* and *Notothenia rossii* from Antarctica, *Myoxocephalus scorpius* from the North Sea, *Scorpaena notata* and *Serranus cabrilla* from the Mediterranean and *Paracirrhites forsteri* from the Indo-West-Pacific. Numbers with filled circles denote data for: 1 *Notothenia coriiceps* from Franklin and Johnston (1997); 2 and 4 *Gadus morhua* from Moon et al. (1991) and Anderson and Johnston (1990); 3, 6 and 7 *Myoxocephalus scorpius* from Altringham and Johnston (1990), James and Johnston (1998) and Wakeling and Johnston (1998); 5 *Pollachius virens* from Altringham et al. (1993); and 8 *Scorpaena notata*. (Figure from Wakeling, J.M. & Johnston, I.A. 1998. *Journal of Experimental Biology* **201**, 1505–1526.)

does (Wakeling & Johnston 1998). During the handling phase of an attack, crushing predators such as reptant decapods will often apply force several times to identify the best position for an attack before applying full force (Hughes & Seed 1995). Two main ways that durophagous crustaceans attack their prey are either by direct crushing or by chipping or cutting the shell edge and inserting chelae (Elner & Hughes 1978). The former is generally used for small prey and the latter for larger prey (Ameyaw-Akumfi & Hughes 1987). These predators have also been observed applying pressure multiple times to a prey bivalve, up to 200 times in a method termed a pressure pulse attack that is thought to weaken shells by producing microfractures (Boulding & Labarbera 1986). Larger prey have significantly higher rewards per unit effort for predators and should be taken preferentially (MacArthur & Pianka 1966). However, durophagous crustaceans often take less preferred prey on energy maximisation criteria because of other factors such as potential damage to claw crushing surfaces (Smallenge & Van der Meer 2003). Large size has also been identified as a refuge from predation because the prey organism grows beyond the size that the predator can successfully attack (e.g. Harper et al. 2009).

Reductions in muscle performance at low temperature, such as slower cross-bridge cycling time and relaxation, that result in reduced power output, are likely important factors in the absence of durophagous predators such as brachyuran crabs in Antarctica (Aronson et al. 2007). The 'picking' method of feeding by the lithodid crabs that are present in Antarctica requires less force and power to make successful attacks. The power versus temperature relationship shown in Figure 14 would suggest that power limitation is likely to preclude crushing predators from Antarctic waters for many decades, if not centuries to come. The forces and power that predators can exert are two of the factors affecting how robust skeletons of their prey need to be, and this has clear implications for life at low temperature in the Southern Ocean.

Shell thickness and energy budgets

Antarctic marine ectotherms have often been described as having thin or small shells (Arnaud 1977, Vermeij 1978, Arntz et al. 1994, Aronson et al. 2007, McClintock et al. 2009). Early studies noted that bivalve molluscs tend to be smaller in the polar regions (Nicol 1964, 1966) and have less ornate shells (Nicol 1967), and that gastropod molluscs also have smaller shells at high latitudes (Graus 1974). These findings have been more recently identified as part of a global trend of decreasing skeleton size from tropical to polar latitudes in groups with external shells (rhynchonelliform brachiopods, bivalve and gastropod molluscs) and also in echinoid urchins (Watson et al. 2012). Decreasing skeleton size with latitude, therefore, appears to be a general trend across a wide range of taxa and not limited to molluscs.

Two main hypotheses have been proposed to explain the decrease in skeleton size towards the poles. The first is that on physical environmental and energetic considerations the cost of shell production increases towards the poles. Most marine ectotherm skeletons are made from calcium carbonate ($CaCO_3$). As temperature decreases in the sea, the solubility of calcium carbonate increases (Revelle & Fairbridge 1957). As a consequence, the saturation state of $CaCO_3$ (Ω_{CaCO3}) in seawater decreases, where saturation state is defined as: the product of the concentrations of dissolved calcium and carbonate ions in seawater divided by their product at equilibrium. At lower temperatures, the ions used to make skeletons are more soluble, and more thermodynamic work is required to remove them from seawater. This has been proposed by several authors to be the possible reason why skeletons are smaller at high latitude because it increases the energy needed to complete shell production (Graus 1974, Vermeij 1978, Clarke 1983, Clarke 1990, Clarke 1993c, Vermeij 1993). This argument has been combined with the poleward decrease in metabolic rates in marine ectotherms described earlier, and elsewhere (e.g. Peck 2016), to show not only should the costs of building skeletons increase in real terms at lower temperatures, but this effect should be greater in relation to metabolic costs (Clarke & Johnston 1999, Peck & Conway 2000, Watson et al. 2017).

The second major hypothesis to explain the observed latitudinal variation in skeleton size is that it is caused by changes in predation pressure. Direct evidence for latitudinal gradients in predation pressure is limited (e.g. Vermeij 1978), although recently Harper and Peck (2016) completed the first global-scale analysis of predation pressure by evaluating repairs from shell damage caused by durophagous predators from tropical to polar latitudes. They demonstrated that the incidence of repaired shell damage, and hence durophagous predation pressure, declines towards the poles. There are some examples covering smaller geographic scales that appear to show levels of predation pressure are higher at lower latitudes (Paine 1966, MacArthur 1972). Furthermore, durophagous predators such as brachyuran crustaceans and fish are missing from, or are rare in, shallow nearshore habitats (<100 m depth) in Antarctica (Aronson & Blake 2001, Clarke et al. 2004a, Aronson et al. 2007), being restricted to areas with seawater temperatures above 0°C (Griffiths et al. 2013). One reason put forward for the absence of brachyurans in Antarctica, in addition to muscle power constraints cited earlier, is that reptant decapod crustaceans have a high haemolymph magnesium ion concentration compared to other crustaceans. Magnesium ions act as a narcotic for many marine invertebrates, and if, as has been shown for some species, extracellular magnesium increases with decreasing temperature (Morritt & Spicer 1993), the narcotising effect may remove them from sites permanently at 0°C and below (Frederich et al. 2000, 2001), making them unable to inhabit Antarctic shallow coastal waters.

Recently Watson et al. (2017) compared the energetic cost of making skeleton with those of respiration and growth, which are two of the major components of the energy budget. The costs of making skeletons in bivalve and gastropod molluscs were small as proportions of the energy budget, being 0.4%–7.4% of the total calculated budget in gastropod molluscs and 0.2%–3.4% in bivalve molluscs. Costs were greater at higher latitudes than in warmer sites, and predicted ocean acidification effects raised cost estimates to over 10% of the total energy budget by the end of the century in polar gastropods. The conclusion drawn by Watson et al. (2017) was that both cost and durophagous predation pressure might be major drivers of skeleton size in bivalve and gastropod molluscs. Data are insufficient to separate out the effects of predation and cost on skeleton size, but similar trends of reduced skeleton size towards the poles exist in other taxa. For example, in echinoid urchins the impact of durophagous predators is very different across latitudes from the effect of crushing predators on bivalve and gastropod molluscs. Overall, more work is needed to identify conclusively the factors controlling skeleton size variation with latitude and the reason for small skeletons in Antarctica. It is still not possible to exclude calcification costs or predation as the main factor in any taxon.

Seasonality

Seasonality is often overlooked in investigations of adaptation and effect of environment on organism biology. Seasonality is caused by variations in the incident energy arriving at the Earth's surface through the year, which is approximated by day length, but also varies in some regions with seasonal weather patterns and cloud cover. There is little variation in this factor in tropical latitudes but very great variation in the polar regions, where periods of 24 hours of sunlight in summer are counterbalanced with periods of 24 hours of dark in winter. This pattern is caused by the tilt of the Earth.

Variations in climate and small changes in seasonality over long time periods are caused by three main factors. These are: wobbles in the Earth's rotational axis, called axial precession, which produces a 23,000-year cycle in incident light energy arriving at the surface; changes in the tilt angle of the Earth, called obliquity, which gives a 41,000-year cycle in incident radiation; and changes in the shape of the Earth's orbit, called eccentricity, which results in 100,000-year and 400,000-year cycles in incident radiation (Zachos et al. 2001).

Over geological time, some aspects of current seasonality are as strong as or possibly stronger than previous periods (Clarke & Crame 2010). This is especially so in the polar regions because

the poles are currently isolated. In the Arctic, a small ocean is nearly surrounded by land, and in the Antarctic, a large continent is isolated by a circulating ocean that has a strong temperature discontinuity with other oceans at the polar frontal zone (PFZ). Up until approximately 34 mya, the poles were less isolated because large amounts of energy were moved to the high latitudes by ocean currents, and the polar regions were significantly warmer than today (Florindo & Siegert 2009). This resulted in less ice at the poles, and coastal ice and sea ice are large drivers of the current seasonality in the polar regions, making conditions more extreme in these respects now than in most previous geological periods (De Conto et al. 2007). Most previous geological periods saw the distribution of continents in one or two large masses, including Pangea and Gondwana, where one or both poles had little terrestrial continental cover, even when there were polar land masses that were continuous with lower latitude continents.

The minimum and maximum extent of sea ice around Antarctica vary markedly between years. In the last 30–40 years, the satellite era, Antarctic sea ice in a typical year has varied from a minimum of around 3×10^6 km^2 to a maximum around 18×10^6 km^2 (http://earthobservatory.nasa.gov/Features/WorldOfChange/sea_ice_south.php). The largest maximum extent was 20.1×10^6 km^2, which was reached in September 2014. The growth and recession of around 15×10^6 km^2 of sea ice annually has a dramatic effect on the seasonality of the ocean beneath. Sea ice reduces the amount of light penetrating into the water column and reduces mixing due to wind.

This extreme variation in some aspects of the physical environment contrasts with the temperature stability that characterises the Southern Ocean. Sea temperatures are possibly the most stable of any ocean on Earth. At high Antarctic sites (e.g. McMurdo Sound), mean annual temperature variation is less than 0.5°C, and the most variable sites recorded to date (e.g. Signy Island, South Orkney Islands) have annual ranges around 4.5°C (Barnes et al. 2006a).

Seasonality is a major structuring characteristic for ecology, adaptation biology and biodiversity in Antarctica (Clarke 1988). One of the most obvious impacts on organisms of the intense seasonality in light and ice cover in Antarctica is the effect on primary productivity, and this strong signal of seasonality propagates through the food web. Phytoplankton blooms tend to be more intense in Antarctica in nearshore environments, where chlorophyll (Chl) standing stock levels average 10–15 mg m^{-3} for up to three months, and peak values can exceed 30 mg m^{-3} (Clarke & Leakey 1996, Clarke et al. 2008). In offshore areas, Chl levels in blooms typically reach values around an order of magnitude lower than this, but in some areas, such as the ice edge and in polynyas, productivity levels are often twice as high, or more than in open ocean blooms (Arrigo et al. 2015). In offshore blooms, productivity is limited by nutrient availability, often iron (Boyd et al. 2012), whereas in coastal polynyas, melting ice shelves increase iron availability, enhancing productivity. In a recent study of 46 polynyas, this factor explained more than twice as much variation in productivity as any other factor (Arrigo et al. 2015).

The main part of nearshore phytoplankton blooms is often dominated by large diatoms and colonial phytobionts of the microphytoplankton (Clarke et al. 2008), which peak between early December and mid-March. The main part of the nanophytoplankton bloom (5–20 μm diameter) follows a similar time course, but there is detectable productivity between September and June, and their Chl concentration during the summer averages around only 0.5–1.0 mg m^{-3}, more than an order of magnitude less than that in the larger diatom fraction. The small nanophytoplankton bloom (2–5 μm diameter) also lasts between September and June but achieves peak Chl levels of only 0.2–0.4 mg m^{-3} (Clarke et al. 2008).

The intense seasonality of ice and phytoplankton above 5-μm diameter, led Clarke (1988) to suggest there should be periods of low activity in terms of growth and other physiological attributes in winter, and biological activity in at least primary consumers should be linked to the short summer period of main phytoplankton biomass. This idea was part of a larger hypothesis on the impact of seasonality on organism biology, namely the seasonality hypothesis, which posits that seasonal signals should be stronger in primary consumers than predators or scavengers less directly dependent

on algal productivity (Clarke 1988). It also argues that as seasonality in light regime becomes more extreme towards the poles then seasonal limitation of organism biology should be stronger at higher latitudes, which has been observed to be the case (Clarke & Peck 1991). There are also very strong seasonal signals in the Antarctic in marine benthic community development through a combination of intense seasonality of reproductive cycles and recruitment/establishment on surfaces (e.g. Bowden 2005, Bowden et al. 2006, 2009).

The combination of the idea of seasonal limitation of biological capacity with observations that superficially appear in conflict with the hypothesis, of high biomass and biodiversity (Gutt et al. 1992, Clarke & Johnston 2003, Gutt et al. 2013a), has led to the suggestion that there is an Antarctic paradox. Support for a paradox has also cited work that shows: some Antarctic taxa grow to very large size; some groups reproduce and grow at similar rates to temperate taxa (e.g. Teixidó et al. 2004); that there are sediment 'food banks' of large amounts of primary productivity that settle on the seabed, not consumed by pelagic organisms that are available for months over spring, summer and autumn on some parts of the continental shelf (Mincks et al. 2005); tidal and ice associated water movements that resuspend sediment material in winter making it available for benthic suspension-feeders (Peck et al. 2005, Smith et al. 2006); some Antarctic benthic suspension-feeders consume small particles whereas their temperate relatives consume zooplankton (Orejas et al. 2003); some suspension-feeders feed throughout the year (Barnes & Clarke 1994, 1995); and there have been observations of unusual feeding behaviours such as in the upright nephtheid soft coral *Gersemia antarctica*, that supplements suspension-feeding by bending its whole body to deposit feed on benthic organisms in surface sediments (Slattery et al. 1997).

Seasonality of feeding

Most of the observations used to support the idea of a seasonality paradox do not conflict with the idea that seasonality constrains the biology of many of the organisms living there. In fact, some of these observations could be used to support seasonal constraints. For instance, the finding that some suspension-feeding groups consume small particles instead of zooplankton is support for the idea that seasonal limitations of availability of suitable food sources have forced these taxa to move to alternative food supplies. Similarly, the suspension-feeders that feed all year round (Barnes & Clarke 1994, 1995) feed on the smaller size fractions, again possibly because of seasonal restrictions in the availability of larger size fractions that would be consumed in less seasonal environments. Furthermore, the dramatic sedimentation events that result in high levels of organic material in sediments could be evidence that the intensity of seasonality is so strong that the normal processes where much of the organic material produced in the water column is broken down before reaching the seabed are overwhelmed. Reproduction and growth reported at similar rates to temperate species are often small number comparisons, and where large numbers are considered, the fastest Antarctic rates may be similar to temperate species elsewhere, but they are significantly slower than the fastest temperate and tropical species, although care is needed when making comparisons of rates (Peck 2016). Most of the arguments about resuspension of food in winter due to currents do not apply to the very large number of organisms living on most rock surfaces, and this effect is primarily one of sediment dwelling species.

Very strong effects of seasonality on the biology of Antarctic marine invertebrates and fish are evident from a very large number of studies, some of which have been reviewed in Clarke (1988), Arntz et al. (1994) and Peck et al. (2006b). In one of the earliest studies of seasonality, Gruzov (1977) showed that while the biomass of detritivores and omnivores did not noticeably vary from summer to winter, large changes in numbers of species consuming plankton occurred (e.g. some hydroids), and some species entered a state of diapause in winter (e.g. the holothurian *Oswaldella antarctica*).

Part of the seasonality limitation hypothesis is that effects would be expected to be stronger in taxa directly dependent on primary productivity (herbivores) as opposed to detritivores, omnivores

and carnivores. As noted earlier, a few benthic marine species have been demonstrated to feed throughout the year (Barnes & Clarke 1994, 1995, Obermüller et al. 2010). However, in the majority of species, feeding either ceases in winter or is markedly curtailed. This has been noted for the sea urchin *Sterechinus neumayeri* (Brockington 2001a, Brockington et al. 2001), for the sea cucumber *Heterocucumis steineni* (Fraser et al. 2004), and for the infaunal bivalve mollusc *Laternula elliptica* (Ahn et al. 2001, Morley et al. 2007). In an extensive year-round study of suspension-feeding taxa at Signy Island, Barnes and Clarke (1995) found that of 10 bryozoan species studied, one fed throughout the year, and the other nine ceased feeding for periods between one and five months in winter. They also showed that a hydroid and a suspension-feeding polychaete ceased feeding for one month each year, while the holothurian *Cucumaria georgiana* stopped for between three and five months. Fraser et al. (2002) showed that the limpet *Nacella concinna* feeds all year round, but there was still a very large decrease in feeding (as estimated from faecal egestion of freshly caught individuals) to a value only around 10%–15% that of summer feeding levels. All of the species mentioned previously are either directly dependent on primary productivity or are grazers or omnivores that consume large amounts of phytodetritus. The seasonal signal in feeding is very strong, such that over 95% of species that directly consume phytoplankton, benthic microalgae or macroalgae cease feeding in winter, and those that do continue feeding in winter consume only a small fraction of the amounts eaten in summer.

There have been few investigations of year-round feeding in higher trophic level groups in Antarctica. Obermüller et al. (2010), however, studied seasonal variation in feeding and metabolic characteristics in three carnivores and two omnivores near Adelaide Island, Antarctic Peninsula. Feeding rate varied significantly with season in the sponge-eating nudibranch *Doris kerguelenensis* and the predator/scavenger amphipod *Paraceradocus miersi*. There was no seasonal signal in feeding in the predatory fish *Harpagifer antarcticus* and nemertean *Parborlasia corrugatus*, and the scavenging brittle star *Ophionotus victoriae*. Other studies on the predatory fish *Harpagifer antarcticus* and *Notothenia coriiceps* found that acclimating them to winter light regimes resulted in lower food intake even when excess food was available (Targett 1990, Johnston & Battram 1993, Coggan 1996).

Seasonality of activity, metabolism and growth

The strength of seasonal signals in other aspects of the biology than feeding varies markedly. The Antarctic fish *Notothenia coriiceps* has been identified as entering a low activity state in winter similar to hibernation in some mammals (Campbell et al. 2008). Gruzov (1977) noted a marked decline in activity, growth and metabolism of several groups of marine invertebrates near Myrny Station, on the Zukov Islands in the Davis Sea, which he described as similar to diapause. Species noted to exhibit very large seasonal activity changes included the hydroid *Oswaldella antarctica*, the holothurian *Staurocucumis turqueti* (previously *Cucumaria spatha*) and the alcyonarian *Eunephthya* sp., although Gruzov (1977) did note that this phenomenon is widespread beyond the previous examples, especially in holothurians and sponges.

Many studies have shown strong seasonality of growth in Antarctic fish (e.g. Everson 1970b, Kawaguchi et al. 1989, Casaux et al. 1990, Targett 1990, Coggan 1996, 1997, La Mesa & Vacchi 2001) and invertebrates (e.g. Arntz et al. 1994, Brethes et al. 1994, Barnes 1995, Barnes & Clarke 1998, Peck et al. 2000, Ahn et al. 2003, Heilmayer et al. 2005, Bowden et al. 2006, Peck & Brockington 2013). One unusual finding was that the brachiopod *Lioythyrella uva* grew five times faster in winter than summer in shell growth but increased mass in summer, not winter, when reserves were laid down as protein in the outer mantle (Peck et al. 1997b). This was interpreted as minimising overall annual energy costs by separating growth from feeding periods. Some studies have shown only small differences in growth rates between summer and winter in Antarctic marine invertebrates, such as in juveniles of the infaunal deposit feeding bivalve mollusc *Yoldia* (now *Aequiyoldia*) *eightsii*

at Signy Island, where seasonal differences in growth were not significant in specimens less than 10 mm in length (Peck et al. 2000). The explanation for this was year-round availability of food. This argument, however, should also apply to many scavengers and carnivores, for example, fish that do show strong seasonality in growth.

Growth can be difficult to assess in many species, especially soft-bodied animals such as sea anemones or jellyfish. One approach is to quantify changes in the total amount of protein in the animal with time. Many authors have argued that in the soft tissues of most animal species growth occurs mainly through the synthesis and retention of proteins, and that process exceeds degradation of proteins that are either malformed or have come to the end of their useful life (e.g. Fraser & Rogers 2007). The seasonality of protein synthesis has been measured across the year in some Antarctic marine species and has been shown to be highly seasonal, for example, in the holothurian *Heterocucumis steineni* (Fraser et al. 2004) and the limpet *Nacella concinna* (Fraser et al. 2007). These data are in line with studies showing growth to be seasonal in many marine species and they support the strong links between protein synthesis and growth, although it should also be noted that protein synthesis is essential for many other functions that are not growth related, such as protection from freezing or responding to environmental stress.

Seasonal studies of metabolic rates in Antarctic ectotherms have generally demonstrated strong seasonal signals. The data on seasonal changes in oxygen consumption in predators and primary consumers/grazers are summarised in Figure 15. Summer to winter changes in oxygen consumption have a smaller range in predators (1.1–2.2) than primary consumers/grazers (0.8–5.8). Predators generally feed throughout the year (Obermüller et al. 2010), and this is one of the differences between higher and lower trophic levels in the seasonality hypothesis (Clarke 1988). Some primary consumers/grazers have also been shown to feed year-round on benthic productivity, for example, the limpet *N. concinna* (Obermüller et al. 2011, 2013) and in suspension-feeders on nano or picoplankton, for example, the bryozoan *Arachnopusia inchoata* (Barnes & Clarke 1995), which may explain some of the lower seasonal changes for primary consumers in Figure 15. The seasonal change shown for the scallop *Adamussium colbecki* may also be underestimated as in this study standard or starved oxygen consumption was measured (Heilmayer & Brey 2003), and feeding usually increases metabolic rates in marine invertebrates by 2 to 3 times (Peck 2016). The differences between Antarctic primary consumers/grazers and predators in the impact of season on metabolic rates shown in Figure 15 are not significant (data not normal after Ln, double Ln, arcsin or SQRT transforms, Kruskal Wallis $H = 2.68$, $P = 0.10$).

With increasing amounts of data gathered on seasonality and its impact on metabolic rates, it is now becoming clear that there is a signal in all trophic groups. It does not appear to be stronger in primary consumers than secondary consumers, as predicted by the seasonality hypothesis, but that other factors, such as year-round food availability for some species mean that comparisons of trophic levels may not be assessing groups where seasonal effects differ the most.

Seasonality of body mass and composition

Several studies have documented seasonal variation in body mass and proximate composition in Antarctic marine species. The brachiopod *Liothyrella uva* has strong seasonal cycles in tissue mass and also in total protein, carbohydrate and lipid composition (Peck et al. 1987a, Peck & Holmes 1989). The strongest cycle was in protein. Oxygen-to-nitrogen ratios from respiration and excretion studies were used to show this species fuels its metabolism predominantly from protein (Peck et al. 1986c, 1987b). Furthermore, seasonal protein stores have been identified in temperate brachiopods (James et al. 1992). The authors concluded that protein was being used as the seasonal storage material in *L. uva*. In the large infaunal bivalve *Laternula elliptica*, there were strong seasonal cycles in organic mass, protein and lipid, and these cycles differed between tissues (Ahn et al. 2003). Large mass changes occurred in muscle, gonads and digestive gland during spawning, and protein

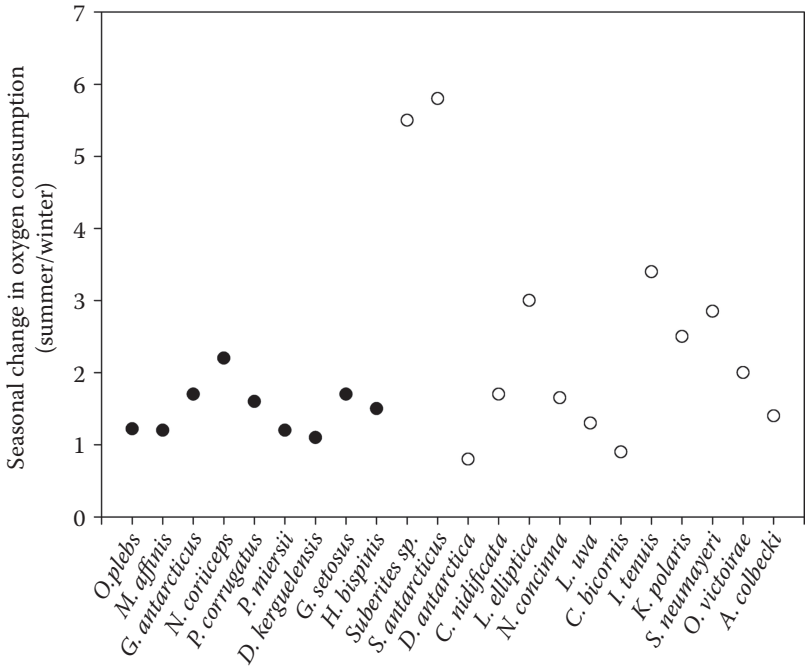

Figure 15 Seasonal changes in oxygen consumption for polar predators and primary consumers/grazers. Data shown are the factorial change from summer to winter. Data are for the primary consumers: rhynchonelliform brachiopod *Liothyrella uva* (Peck et al. 1986c, 1987a, 1997a,b), the infaunal bivalve *Laternula elliptica* (Brockington 2001b, Morley et al. 2007), the scallop *Adamussium colbecki* (Heilmayer & Brey 2003), the bryozoans *Camptoplites bicornis*, *Isosecuriflustra tenuis* and *Kymella polaris* (all Barnes & Peck 2005), the sponges *Suberites* sp., *Sphaerotylus antarcticus*, *Dendrilla antarctica* and *Clathria nidificata* (all Morley et al. 2016c), and the limpet *Nacella concinna* (Fraser et al. 2002). In the grazers, the sea urchin *Sterechinus neumayeri* (Brockington & Peck 2001) and the brittle star *Ophionotus victoriae* (Obermüller et al. 2010). Predatory species shown are the amphipods *Abyssorchomene* (previously *Orchomene*) *plebs* (Rakusa-Suszczewski 1982) *Gammarus setosus* (Weslawski & Opalinski 1997) and *Paraceradocus miersi* (Obermüller et al. 2010), the isopod *Glyptonotus antarcticus* (Janecki & Rakusa-Suszczewski 2006), the sponge-eating nudibranch *Doris kerguelenensis*, the nemertean *Parborlasia corrugatus* and the fish *Harpagifer bispinis* (all Obermüller et al. 2010). Data for the fish *Notothenia coriiceps* are from Campbell et al. (2008). Lehtonen (1996) studied seasonal metabolic rates in the Arctic benthic amphipod *Monoporeia affinis*, and these data are included to make the comparison one of polar species and not just Antarctic. Open symbols denote primary consumers and grazers, closed symbols denote predatory species. (Figure modified and redrawn from Morley, S.A. et al. 2016c. *Biodiversity* **17**, 34–45.)

was again identified as the main overwintering reserve, accounting for 60% of the energy used in winter compared to 20% each for lipid and carbohydrate. Pearse and Giese (1966a,b) also noted high-protein and low-carbohydrate contents in a survey of the biochemical composition of seven species of benthic marine invertebrates from McMurdo Sound. Cycles in organic content have been noted in the limpet *Nacella concinna,* with summer levels being around twice those of winter levels (Fraser et al. 2004), in the urchin *Sterechinus neumayeri* (Brockington & Peck 2001), and in three bryozoan species (Barnes & Peck 2005), although the seasonal changes in the bryozoans were small. Heilmayer and Brey (2003) found no seasonal change in soft tissue mass from summer to winter in the scallop *Adamussium colbecki*, which is surprising as this is a suspension-feeding bivalve, and the expectation is that species dependent for their nutrition on the highly seasonal short-duration phytoplankton bloom should exhibit strong seasonal signals in their body composition and mass.

It should be noted that much stronger seasonal signals in mass and proximate composition are seen in some pelagic species, especially some herbivorous crustaceans, and these signals are much stronger in high-latitude sites than in temperate or tropical regions (Clarke & Peck 1991). For example, calanoid copepods can be more than 50% lipid at the end of summer (Båmstedt 1986). Metabolic rates and activity levels in pelagic invertebrates are also generally higher than in benthic species, and it has been argued that these characteristics increase the impact of seasonality on their biology, resulting in stronger seasonal signals in mass and body composition (Clarke & Peck 1991). Whole-animal adaptations and responses to seasonal signals are underpinned by adaptations within the cells of the animals being studied.

Cellular level adaptations

When temperature changes, selection is expected to favour organisms maintaining their physiological functions at rates as close to those at the higher temperature as is feasible and consistent with maximising reproductive fitness (Clarke 1991, 2003, Hochachka & Somero 2002). They can do this by using three general mechanisms that affect the proteins involved in metabolomics processes: by modulating the intracelleular milieu, by using the cytosol to reduce the effects of the temperature alteration on protein reactivity; to use different protein variants or isoforms that have better thermal characteristics at the new temperature and/or by changing the concentrations of reactants, usually enzymes, in cells (Hochachka & Somero 2002). Most studies in this area have been on single factors in cells, or single proteins, especially enzymes (Clarke 2003). They have in some cases, however, shown strong links between protein function and whole-animal capacities or performance (e.g. Neargarder et al. 2003).

Although understanding in this field of general cellular adaptations is far from complete, patchy and still controversial in many areas, there are some well described adaptations and hypotheses. One of these is the imidazole alphastat hypothesis first proposed by Reeves (1972). This hypothesis is based around the premise that protein function is optimised by the modulation of intracellular and extracellular pH. This is achieved, at least in part, by using imidazole groups to buffer the temperature induced changes. Overall imidazole and protein ionisation are held at constant levels, which maintains cellular functions (Pörtner et al. 1998, Burton 2002). The alphastat hypothesis is generally well accepted, and there are far more studies supporting it than against, but some authors have argued strongly against its generality on several grounds (e.g. Heisler 1986), and some studies reported data that do not support alphastat (e.g. Taylor et al. 1999). Alphastat is portrayed as a universal mechanism for adaptation of cellular function as temperature varies. There are, however, many factors beyond this that assist with adaptation or acclimation to altered temperature.

Another general mechanism that has received significant levels of research and support is the modulation of the composition of cell membranes. Alterations in lipid composition occur when temperature changes the optimum balance between flexibility and rigidity in the liquid-crystalline membrane bilayer and also between lipid phases including gel and crystalline, sometimes called lamellar and non-lamellar phases. The process of increasing levels of unsaturated fatty acids in membranes at lower temperature has been documented in species across the globe and is often seen in acclimation to temperature change. The general principle is that the levels of unsaturated fatty acids increase in cell membranes at lower temperature, a process called 'homeoviscous adaptation' (Dey et al. 1993, Hazel 1995). Increased levels of unsaturated fatty acids in cellular membranes have been reported for Antarctic fish (reviewed in Verde et al. 2006). Logue et al. (2000) studied membrane fatty acid composition in 17 species of fish from across the globe, including four from Antarctica (*Pagothenia borchgrevinki*, *Trematomus bernacchii*, *Dissostichus mawsoni* and *Lycodichthys dearborni*) and one from the sub-Antarctic South Georgia (*Notothenia neglecta*, now *N. coriiceps*). By assessing the fluorescence anisotropy of a probe (1,6-diphenyl-1,3,5-hexatriene), they identified that there was a high level of temperature compensation in membrane static order (a measure of fluidity or viscosity) in the Antarctic

species. The membranes in the synaptosomes (neuronal synapses, or nerve cell junctions, isolated for research purposes) of the Antarctic fish were, however, less fluid than predicted from first principles, and temperature compensation was only partial and not complete. It may be that perfect compensation of membrane fluidity is not possible, and on this basis, low-temperature adaptation of many membrane related processes are, at best, imperfect. Data are very limited on the relative functioning of membrane associated processes versus those within the cell milieu, but the compensation of cytochrome c oxidase in the Antarctic eelpout is less well compensated for temperature than citrate synthase, which is not membrane associated (Hardewig et al. 1999a), and a similar imperfect adaptation of membrane related processes was also found for Arctic cod (Lucassen et al. 2006).

Changing fatty acid composition in membranes has been shown to affect proton leak in mitochondria and, hence, the costs of maintaining these organelles (Porter et al. 1996, Brookes et al. 1998). It also affects the functioning of membrane-embedded proteins such as membrane pumps to a greater or lesser extent and other functions such as the electron transport chain. Imperfect compensation for temperature would thus be expected to have significant effects on the functioning of many cellular processes in Antarctic ectotherms.

It is interesting to note here that the fatty acid profiles of marine mammals, both pinnipeds and cetaceans, are consistent with the temperature-related adaptations seen in ectotherms. Thus, the superficial, colder layers of the skin in seals, walruses and whales are enriched in unsaturated fatty acids, whereas the deeper, warmer layers are enriched in saturated fatty acids and long-chain monounsaturated fatty acids (Fredheim et al. 1995, Best et al. 2003, Bagge et al. 2012). These changes in composition are usually interpreted as being related to dietary or storage functions, but at least one author has identified a potential functional relationship with temperature (Strandberg et al. 2008).

Several specific adaptations have been identified in Antarctic marine ectotherms. Some of them, such as antifreeze in fish, are general low-temperature adaptations seen in both poles, and some have only been identified in Antarctic species, but this is likely a function of the age of the available habitat and isolation from other faunas. Some of the main cellular and physiological adaptations are described below.

Antifreeze

The most well-known adaptation of marine species to polar waters is the production of antifreeze to overcome the problem of their tissues freezing. The temperature of the seawater in much of the Southern Ocean is below −1°C, for at least parts of the year and at the highest latitude marine sites for most of the year (Barnes et al. 2006a). This poses problems for organisms that have body fluids that freeze at temperatures close to 0°C. Vulnerable species can respond to this type of challenge in one of two ways, allowing their extracellular body fluids to freeze (freeze tolerant), or to employ mechanisms to ensure body fluids do not freeze (freeze avoidance) (Lee & Denlinger 1991, Duman 2015). Antarctic marine species studied to date use a variety of methods to avoid freezing. Marine invertebrates have body fluid concentrations similar to seawater and so should not freeze until the water around them freezes. Antarctic marine invertebrates might, therefore, be expected to have few problems as long as they avoid solid ice. Many species, however, live in close contact with ice, with some even using ice as their main habitat, feeding off epontic productivity (e.g. Wiedenmann et al. 2009) and using ice as a refuge from predation (Thomas & Diekmann 2010), and this also includes some fish species (DeVries & Wohlschlag 1969). In these conditions, very small ice crystals are often present in seawater, and there is a need to inhibit their growth in tissues and cells.

Antarctic fish have a significant problem living in these conditions because water-based solutions with solute concentrations similar to their body fluids freeze at temperatures between −0.5°C and −1.0°C (Eastman & DeVries 1986, Peck 2015). Early studies of high latitude Southern Ocean fishes demonstrated that the freezing point of their circulating fluids was below −2°C, and the extra freezing resistance was due to the presence of antifreeze glycoproteins (AFGP) in their blood serum

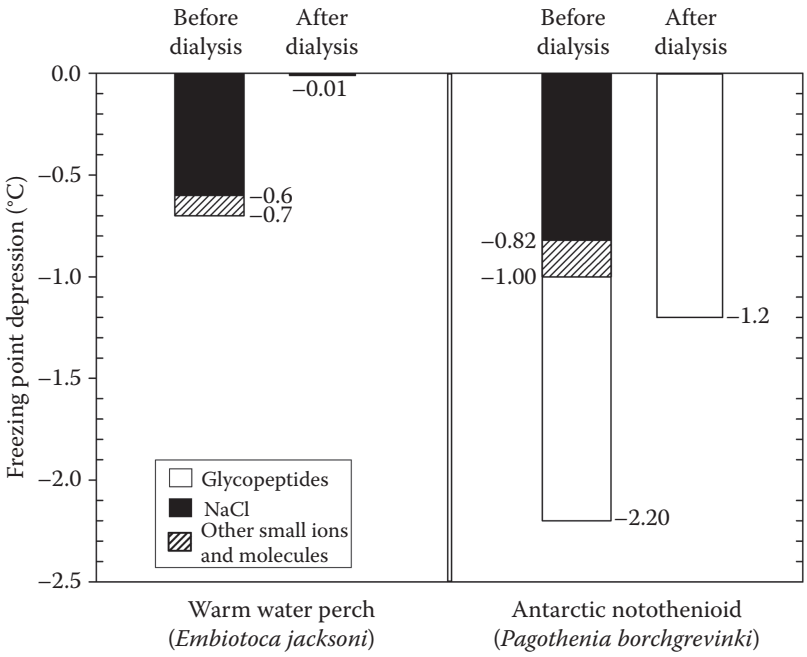

Figure 16 The effect of NaCl, other small ions and molecules, and glycopeptides on the freezing point of blood plasma from a warm-water fish (the perch *Embiotoca jacksoni*) and an Antarctic notothenioid (*Pagothenia borchgrevinki*). The higher salt content of the plasma of *P. borchgrevinki* produces a larger freezing point depression than in the warm-water *E. jacksoni*, but over half the freezing point depression in the Antarctic species is due to glycoproteins. The higher salt concentration in Antarctic fish plasma gives an extra 0.3°C freezing point depression over the temperate perch, but a further 1.2°C is added by the presence of AFGP molecules. These extra lowerings of the freezing point seem small, but they make Antarctic fish safe in an environment where temperatures rarely fall below −2°C. (Figure from Peck, L.S. 2015. *Journal of Experimental Biology* **218**, 2146–2147.)

(DeVries & Wohlschlag 1969, DeVries 1971). Antarctic fish also have higher solute concentrations in their blood (osmotic concentration of 550–625 mOsm kg^{-1}) than temperate and tropical fish (320–380 mOsm kg^{-1}). This higher concentration of low-molecular-weight solutes accounts for around half of the total freezing point depression (to around −1.1°C), with the rest (to just below −2°C) accounted for by the action of AFGPs (Figure 16) (Eastman & DeVries 1986).

A surprising number of Antarctic marine invertebrate species inhabit the intertidal (Waller et al. 2006a, Waller 2013) where they can be exposed to temperatures much lower than the freezing point of seawater. In a study of 11 intertidal species, Waller et al. (2006b) showed their 50% freezing points ranged from −5.5°C in the limpet *Nacella concinna* to −23.1°C in the marine mite *Rhombognathus gressitti*, and freezing point depression was inversely correlated with size. Further investigation of eight species of intertidal invertebrates showed only three had different freezing points between intertidal and subtidal populations, and one of these three, the copepod *Tigriopus angulatus*, had a lower freezing point in the subtidal population. One species studied by Waller et al. (2006b), the nemertean *Antarctonemertes valida*, showed evidence of the presence of antifreeze proteins through thermal hysteresis of the supercooling point of its haemolymph. Thermal hysteresis is the separation of the freezing point and the melting point of a liquid. It is characteristic of antifreeze proteins and glycoproteins and is not seen when the freezing point is lowered by the addition of solutes.

More recent research showed that the mucus secreted by the limpet *Nacella concinna* contributed to freezing resistance, possibly because its high viscosity inhibits ice crystal proliferation (Hawes

et al. 2010). These studies show that Antarctic marine invertebrates have freezing points well below those expected from knowledge of their body fluid solute concentrations, but the evidence suggests few have antifreeze proteins because of the lack of thermal hysteresis. Identifying the mechanisms conferring this extra freezing resistance requires further research.

Over the last 20 years, the rapid development of molecular and 'omics' technologies have had a marked impact on understanding antifreeze mechanisms and the evolution of antifreeze molecules. This has aided in understanding the biodiversity and evolution of antifreeze mechanisms with AFGPs now known globally from insects, frogs, plants, bacteria, ciliates, diatoms and copepods as well as fish (Kiko 2010, Storey & Storey 2013, Duman 2015, Pucciarelli et al. 2015).

Many different-size isoforms of antifreeze glycoproteins have been identified in Antarctic notothenioid fishes. They are encoded in large families of polyprotein genes (Chen et al. 1997). These large gene families arose by gene duplication, enabling the synthesis of large quantities of protective antifreeze glycoproteins and antifreeze proteins. Fourteen antifreeze glycoprotein polyprotein genes have now been identified. They each encode multiple (up to 30–40) antifreeze glycoprotein molecules. This emphasises how important this adaptation was in the evolution of Antarctic fishes (Nicodemus-Johnson et al. 2011).

Antifreeze glycoproteins in notothenioid fish evolved from a pancreatic trypsinogen serine protease progenitor following duplications of a coding element between intron one and exon two of the trypsin gene (Chen et al. 1997). It is now accepted that this was a critical evolutionary step that gave a great advantage to notothenioid fish over other taxa as the Southern Ocean cooled to subzero temperatures. Structurally almost identical antifreeze glycoproteins have been found in some Arctic gadoids (DeVries & Cheng 2005), but they arose from a different evolutionary route. The precursor for the Arctic AFGP gene is not known, but it did not derive from a trypsin-like gene (Cheng & Chen 1999, Near et al. 2012).

In excess of the AFGPs of Antarctic notothenioids, four different types of antifreeze proteins (AFP) that work in a similar way to the AFGPs, inhibiting ice crystal growth, have been identified in fish around the globe (DeVries & Cheng 2005, Davies 2014). Type I AFPs were identified first in *Pseudopleuronectes americanus*, the American flounder, but have subsequently been found in other flounder species and some sculpins (Duman & DeVries 1976, Graham et al. 2013). The taxonomic diversity suggests type I AFPs have evolved independently on several occasions. Type II AFPs are present in smelt, herring and the sea raven. They are globular, and some need calcium ions to be active, whereas other forms do not. This variation in action has been suggested to indicate different routes of evolution are involved (e.g. Ewart et al. 1998). Type III AFPs have been identified in zooarcid fish from Antarctica and also from the northern hemisphere. There are two forms of this group of AFPs, one that does not appear to produce a thermal hysteresis effect but produces a larger hysteresis when both forms are combined (Nishimiya et al. 2005). Type III AFP seems to have evolved from a sialic acid precursor (Cheng & DeVries 1989, Baardsnes & Davies 2001). Type IV AFP was first identified in *Myoxocephalus octodecemspinosus*, the long-horned sculpin by Deng et al. (1997). Transcripts of type IV AFP have now been found in *Carassius auratus*, the carp and *Danio rerio*, the zebrafish, both of which are freshwater fish, which should not need to be protected against freezing, but the AFP appears important in developmental processes (Xiao et al. 2014).

In addition to the AFGPs that Antarctic notothenioids produce, many fish in this group also produce an AFP that lacks carbohydrate and is around 15 kDa in size (Jin 2003, DeVries 2004, Yang et al. 2013). This AFP has little thermal hysteresis on its own, but when it is present in combination with the AFGPs, the thermal hysteresis effect is doubled. Because of this enhancing effect, the protein was called an antifreeze-potentiating protein (AFPP). To achieve the full thermal hysteresis effect seen in Antarctic fish plasma, both the AFPP and the AFGPs need to be present because the AFGPs and the AFPP bind to different parts of the growing ice crystal.

All AFPs and AFGPs work in the way that DeVries (1971) proposed, which was later confirmed by Raymond and DeVries (1977) in what is now called the adsorption-inhibition mechanism. Ice crystals

grow when water molecules attach to the surface plane of the crystal. AFPs and AFGPs slow or halt the growth by adsorbing on to the crystal surface at specific sites where growth is preferred, which is usually on a prism plane. Once attached, water molecules are precluded from attaching to the ice crystal at these sites, and growth can only occur in regions between the AF(G)P molecules in non-preferred sites (Raymond & DeVries 1977, Raymond et al. 1989, Knight et al. 1991, Duman 2015). The regions between attached AF(G)Ps have a high radius of curvature. The curvature of a surface affects many factors such as the stability of small droplets and the growth of small crystals in what is known as the Kelvin effect (Berg 2010), which contributes to inhibition of further growth of ice crystals. Different molecules often adsorb onto different surfaces, and the strength of the thermal hysteresis (and the freezing point depression) depends on the site of adsorption. The mechanism that binds the AFPs or AFGPs to the crystal surface was first thought to be via hydrogen bonding to oxygen in the ice lattice (DeVries 1971, DeVries & Cheng 1992, Sicheri & Yang 1995). This hypothesis is based on the presence of repeat structures in the AFP and AFGP molecules. More recent work has indicated that another mechanism may be important too, and this involves the organisation of water molecules into a crystal-like arrangement around more hydrophobic residues. The 'organised' water then freezes to the ice crystal surface, adhering the AFP or AFGP at the same time (Jia & Davies 2002, Garnham et al. 2011, Davies 2014, Sun et al. 2014). Some studies have suggested that both mechanisms may be used and their importance varies between AFPs and also between AFGPs (Ebbinghaus et al. 2012, Meister et al. 2013, 2014). An interesting outcome of antifreeze molecules binding to ice crystals to stop them growing is that this process seems to inhibit melting of ice crystals in positive temperatures such that they can become super-heated (Cziko et al. 2014).

There is significant developmental and ecological variation in antifreeze properties of Antarctic fishes. Thus, in a study of the larvae of three Antarctic fish species, one, *Pagothenia borchgrevinki* had larvae with high levels of AFPs, similar to those in adults, but the other two, *Gymnodraco acuticeps* and *Pleuragramma antarctica*, had larvae that did not contain any AFPs or AFGPs but still did not freeze in significantly subzero temperatures. It was argued that protection seems to be gained from a physical barrier around the larva from the integument and a reduction in susceptible external tissues such as gills (Cziko et al. 2006). Analyses of samples collected in recent ecological surveys have identified that blood serum antifreeze activity of Antarctic *Trematomus* fishes varies across habitat temperature and depth (Jin & DeVries 2006, Fields & DeVries 2015). The mechanisms for achieving this variability are still to be identified.

The evolution of antifreeze molecules was thus a step that allowed fish species to succeed in polar marine conditions. A very wide range of AFPs and AFGPs has been identified in fish across the globe, and several types can occur in a single species. They have evolved many times from different sources and via different routes. The remarkable similarity of AFGPs across fish species, especially Antarctic and Arctic species that are only distantly related, is one of the best known examples of convergent evolution.

Tubulins

One of the best described examples of a molecular-level adaptation to low temperature in polar seas is in tubulins and their polymerisation into microtubules. Microtubules are polymers that perform a cytoskeletal function in the cells of all eukaryotes. They are involved in a very wide range of physiological and structural processes including cell division, maintaining the shape of cells, transport within cells, secretion, cell motility, the mitotic spindle, centrioles, basal bodies, cilia and cell polarisation. They are especially important in neuronal tissues and for neuronal function. Microtubules are composed of α- and β-tubulin heterodimer subunits joined together into linear protofilaments. A single microtubule contains 10–15 protofilaments that are linked laterally in the construction of a hollow cylinder 24-nm diameter (Rusan et al. 2008). Microtubules are polar structures because of the way the $\alpha\beta$ heterodimers are arranged. They also have different rates of

polymerisation at each end because of this arrangement. Protofilaments are structured with the β-tubulin monomer aligned towards the plus, faster growing end, and the α-tubulin monomer at the other slower-growing end. There is a third isoform γ-tubulin that is important as a template in microtubule assembly. Microtubules also have associated heterogeneous proteins (microtubule-associated proteins or MAPs) attached to their surfaces.

When microtubules polymerise, structured water is released from sites where the subunits make contact (Correia & Williams 1983). Polymerisation is also entropically driven. Because of these factors, microtubule assembly and polymerisation are temperature sensitive (Detrich 1998). In mammals, microtubule assembly functions best at temperatures near 37°C, and they depolymerise at temperatures around or below 15°C, whilst in temperate fish, microtubules also depolymerise at temperatures below 5°C (Detrich & Overton 1986). Microtubules of Antarctic fish are stable at all marine temperatures experienced in the Southern Ocean, down to below −2°C (Detrich et al. 1987). They also polymerise at subzero temperatures (Detrich 1991). The low-temperature stability and polymerisation of microtubules in Antarctic fish is achieved by changes in the sequence of the tubulin proteins that increases the flexibility of domains that are involved in contact between dimers, and these substitutions occur post translationally (Wallin & Stromberg 1995, Detrich et al. 2000). This is probably particularly important to the low-temperature polymerisation of tubulins (Shearwin & Timasheff 1992, Detrich 1998). Other potentially important factors are changes to the hydrophobic properties of the dimer surfaces (Detrich et al. 2000) and changes in the electrostatic properties of tubulin dimers to reduce repulsion (Detrich 1998).

With regard to other species, much recent work has focussed on identifying and characterising tubulins in the Antarctic ciliate *Euplotes focardii*. Genes for one α-tubulin and three β-tubulins were first identified in the 1990s (Miceli et al. 1994, 1996). Subsequently, a fourth β-tubulin was discovered in this species (Pucciarelli et al. 2009). *Euplotes focardii* has been described as being exceptionally rich in microtubules, and several genes encoding tubulins have been characterised. Three isotypes of β-tubulin have been identified in this species that have small sequence substitutions compared to the β-tubulin of the temperate *E. crassus*. These changes increase the flexibility of the tubulin protein (Chiappori et al. 2012). Each isotype exhibits different flexibility in regions involved in lateral and longitudinal contact phases when microtubules assemble.

Recent studies on tubulins in Antarctic species have focussed on the folding mechanism and the factors involved in obtaining successful folding to the functional microtubule. In *E. focardii*, this has included the analysis of the role of chaperonins and co-factors in the folding process (Pucciarelli et al. 2013). Cuellar et al. (2014) investigated the role of the cytosolic chaperonin (CCT) in tubulin folding in the Antarctic fish *Gobionotothen gibberifrons* and concluded that the folding cycle of CCT is 'partially compensated at their habitat temperature, probably by means of enhanced CP-binding affinity and increased flexibility of the CCT subunits'. Overall, it appears that there are many adaptations to facilitate the production of microtubules at low temperature in Antarctic marine species, that full compensation for temperature is probably not achieved, and that a significant part of the adaptation is achieved from amino acid substitutions that increase flexibility of the proteins involved.

Haemoglobin and oxygen transport

To biologists not familiar with Antarctic marine species, one of the most surprising and difficult adaptations to account for is the absence of red blood cells and haemoglobin in the channichthyid icefish. This trait was noted in the early part of the twentieth century by naturalists visiting Antarctica and was described scientifically by Ruud (1954) who, when he first heard of the fish that had clear blood on a visit to South Georgia over 30 years before, was initially sceptical of their existence. Haemoglobinless fish evolved in the evolutionary long-term, low-temperature habitats in the seas around Antarctica, where the oxygen concentration in seawater is 1.8–1.9 times higher than tropical seawater, and metabolic rates are around 10–25 times lower than species living at 30°C

(Clarke & Johnston 1999, Peck & Conway 2000). The condition has been described in 16 species, all members of the family Channichthyidae, or crocodile icefish. This phenotype is not possible at higher temperatures where minimum, basal, metabolic rates and costs are higher because of the Arrhenius effects of temperature on biological reaction rates.

The lack of haemoglobin in channichthyid blood means oxygen is carried only in solution, and the blood is only capable of carrying around 10% of the oxygen of red-blooded relatives (Holeton 1970, Cheng & Detrich 2012). The haemoglobinless condition has been described as maladaptive, disadaptive or disadvantageous (e.g. Montgomery & Clements 2000). Adaptation via natural selection would argue, however, that when functional haemoglobin was lost there must have been a strong selective advantage for this trait to have persisted, or that the trait arose under conditions where selection pressures were relaxed and has then persisted with little selection pressure acting against (Cheng & Detrich 2012). The argument that the loss of haemoglobin may have occurred under conditions of low selection pressure is supported by the fact that the channichthyids are sedentary and sluggish. They evolved from an ancestor with these characteristics that diverged from their nearest relatives the dragon fishes (Bathydraconidae) around 6–12 mya (Near et al. 2012, Verde et al. 2012a). On the basis of genetic data, the channichthyids diversified and lost myoglobin genes sometime during the last 2–5.5 mya when there were ice ages and Antarctica had periodic ice-sheet extensions and contractions (Bargelloni et al. 2000, Sidell & O'Brien 2006). This would have produced conditions where deep fjords were periodically available for colonisation by a relatively depauperate fish fauna, leading to conditions of low selection pressure (Sidell & O'Brien 2006, Cheng & Detrich 2012). This is further supported by phylogenetic analyses that suggest the loss of genes for haemoproteins occurred on four separate occasions in the channichthyid lineage (Near et al. 2006, Sidell & O'Brien 2006). The other alternative, that there may have been selective advantages with the loss of haemoglobin, has been relatively poorly investigated. Channichthyid blood viscosity has been identified as being significantly lower than that of red-blooded notothenioids (Egginton 1996, Egginton et al. 2002, 2006, Kock 2005, Garofalo et al. 2009). The viscosity of the icefish *Chaenocephalus aceratus* is around 3.3–3.5 centipoises (cP) at normal habitat temperatures compared to 5.5–6.0 cP for the red-blooded *Notothenia coriiceps* (Egginton 1996). Temperate fish blood viscosity increases more than 80% when temperatures are decreased from 25°C to 5°C (Sidell & Hazel 1987). Antarctic fish blood is made more viscous by the increase in osmolarity to around twice those of temperate fish, from raised solute concentrations, and by the presence of AFPs and AFGPs, which are essential for fish to live at significantly subzero temperatures (Egginton et al. 2006). Further increases in viscosity will occur in the presence of small ice crystals beginning to grow around nuclei when temperatures are near the freezing point of the fish blood. It may be that under these conditions channichthyid icefish with low-viscosity blood have an advantage over red-blooded species.

If the very strong reduction in the ability to carry oxygen around the body in channichthyids is disadaptive and persists because of a lack of selection pressure, we would expect to see impacts on a range of life-history traits from growth rate to reproductive investment. There are good data for the latter. Kock et al. (2000) measured gonad index (GI) in four species of haemoglobinless channichthyids and 10 species of red-blooded nototheniids and concluded that all species had GI values of 20%–25% at spawning with the exception of *Lepidonotothen squamifrons*, a species with haemoglobin, which has a lower value. Kock and Kellerman (1991) measured GI in three species of channichthyid and 12 species of nototheniid. The mean GI for the former was 19.28% (s.e. = 3.71) and for the latter was 19.33% (s.e. = 2.36). There is thus little support from these data that the lack of haemoglobin puts overall restrictions on the balance between energy intake and energetic costs in channichthyids compared to red-blooded nototheniids.

The evolution of this trait in channichthyids has produced a range of other adaptations to compensate for the reduced oxygen-carrying capacity of the blood (Verde et al. 2012b, 2011, di Prisco & Verde 2015). At the cellular level, these include increased densities of mitochondria in the muscle cells of the heart of channichthyids (O'Brien et al. 2000), where mitochondria account for 36% of the cell volume in *Chaenocephalus aceratus*, which does not express myoglobin in its

muscle tissues, compared to 20% in *Chionodraco rastrospinosus*, a channichthyid that does express myoglobin, and only 16% in *Gobionotothen gibberifrons*, a red-blooded notothenioid. Of the 16 Antarctic channichthyids that are haemoglobinless, six completely lack myoglobin in their muscles (Grove et al. 2004, Sidell & O'Brien 2006, O'Brien 2016). Myoglobin is thought to have a critical role in the storage and diffusion of oxygen in cells (Wittenberg & Wittenberg 2003), and it was described as an 'essential hemoprotein in striated muscle' (Ordway & Garry 2004). The finding that all channichthyids lack myoglobin in their striated muscle (Grove et al. 2004), and that some lack it in heart muscle as well (Moylan & Sidell 2000, Sidell & O'Brien 2006), changed the appreciation in this field. As the lack of oxygen-binding proteins has been argued as a disaptation and negative in terms of animal fitness (e.g. Montgomery & Clements 2000), it is interesting that it has recently been suggested that the loss of these oxygen carriers reduces levels of oxygen damage in cells and tissues and may provide a benefit in terms of reduced costs for the repair of proteins following reactive oxygen species (ROS) damage (O'Brien 2016).

To compensate for the reduction in oxygen-carrying capacity of the blood of haemoglobinless fish, it is further thought that an increase of mitochondrial density may play a role. In this case, oxygen delivery would be enhanced via diffusion through the lipids in mitochondrial membranes. This would also increase ATP production because the folding of the internal surfaces, the cristae density, is lower in haemoglobinless species, which reduces the capacity for oxidative phosphorylation (O'Brien et al. 2000, 2003, O'Brien 2016). This would be offset to some degree by more efficient oxygen supply through the lipids in membranes.

At the tissue level, haemoglobinless species have large hearts that pump four to five times as much blood, and they have a total blood volume two to four times that of red-blooded species (Hemmingsen 1991). The heart itself is composed of spongy myocardium infused with a high density of capillaries, and it pumps at lower pressure than hearts of red-blooded fish, but pumps a large volume with each contraction. The output of the heart is generally accepted in these species to be regulated by heart rate, with stroke volume (volume of haemolymph pumped per heart contraction) varying little (Axelsson et al. 1992). Haemoglobinless fish have capillaries that have diameters around 1.5 times greater than red-blooded relatives, and Egginton et al. (2002) concluded that wider capillaries are essential for the maintenance of tissue oxygenation in the absence of respiratory pigments. They also have lower numbers of circulating blood cells and high lipid contents in the plasma compared to temperate species (Davison et al. 1997), which are also thought to be adaptations to low temperature and high environmental oxygen concentrations, especially increased blood viscosity and slowed biochemical reactions (Farrell & Steffensen 2005, Campbell et al. 2009).

Resistance to blood flow is governed by two main factors, the viscosity of the circulating fluid and the characteristics of the blood vessels (Dejours 1966, Schmidt-Nielsen 1997). The rate of liquid flow in tubes is described by Poiseille's equation:

$$Q = \Delta p \frac{\pi}{8} \frac{r^4}{l\eta} = \frac{p}{R}$$

where Q = rate of fluid flow; Δp = the pressure drop along the tube (p = pressure); r = tube radius; l = tube length; η = viscosity; and R = resistance). The important relationships in this equation are that resistance to flow is proportional to the length of the tube and to viscosity, and it is inversely proportional to the fourth power of the radius. Increasing capillary diameter in haemoglobinless fish by $\times 1.5$ thus reduces resistance to flow more than 5-fold, that is, to less than 20% of the resistance of the narrower capillaries. Water viscosity increases at lower temperatures and more than doubles as temperature is reduced from 30°C to 0°C. Furthermore, it changes more at low temperatures, around and below 0°C, than at higher temperatures. Many of the attributes of haemoglobinless fish blood can thus be interpreted as adaptations to allow increased blood flow and overcome problems of increased viscosity and capillary resistance in a low-temperature world, where the likelihood of the presence

of micro ice crystals, that also increase fluid viscosity, is high. Recent studies have further suggested that the loss of Hb and Mb, their associated NO-oxygenase activity and subsequent elevation of nitric oxide (NO) levels up to twice those observed in red-blooded notothenioids (Beers et al. 2010), may explain the unique cardiovascular and physiological traits evolved in icefish to assure higher blood volume and cardiac output (Sidell & O'Brien 2006), thus posing the question whether other globin family members (neuroglobin and citoglobin) might compensate such losses in icefish.

Neuroglobin and cytoglobin

Haemoglobin has been known as a component of animal blood, and associated with oxygen transport since the mid-nineteenth century (Hoppe-Seyler 1864, Fenn & Rahn 1964). Myoglobin has been recognised as important in oxygen relations in vertebrate muscles for over 50 years and was one of the first molecules to have its 3-dimensional structure elucidated using X-ray diffraction techniques (Kendrew et al. 1958). Two other members of the superfamily of globins have recently been identified in vertebrates: neuroglobin, which is present in the central and peripheral components of the nervous system; and cytoglobin, which is present in all major tissues. Both were discovered by the same team around the turn of the century (Burmester et al. 2000, 2002). The functions of these molecules remain to be fully elucidated, but neuroglobin probably has at least some oxygen delivery or scavenging related role, as it confers protection from hypoxic neuronal injury *in vitro* and ischaemic cerebral injury *in vivo* in mice (Sun et al. 2001, Greenberg et al. 2008).

Recently the genes for neuroglobin (Cheng et al. 2009a,b, Boron et al. 2011, Giordano et al. 2012a) and cytoglobin (Shin et al. 2012) have been discovered in Antarctic fish. Neuroglobin is a 17-kDa monomeric hexa-coordinated hemoprotein with the classical globin folding pattern. It has a high oxygen affinity (in the range of typical myoglobin values (half saturation pressure $P_{50} = 0.9–2.2$ Torr (0.12–0.29 kPa))). Cytoglobin is a 21-kDa hemoprotein with the same globin folding pattern and oxygen affinity in the myoglobin-like range of 1 Torr (0.13 kPa). Antarctic fish neuroglobin and cytoglobin have been shown to bind oxygen and carbon monoxide reversibly. They also have high oxygen affinity, which is similar to that of human cytoglobin, but the high oxygen affinity means they are unlikely to be involved in oxygen transport (Giordano et al. 2015, Verde et al. 2011). Other globins, including globin X and Y, found in teleosts, have not been found so far in Antarctic fish (Giordano et al. 2015). Neuroglobin has been found in the haemoglobinless channichthyids, most of which also lack myoglobin. It has been hypothesised that their retention in this group is likely to be associated with protection of nervous tissues from nitrosative effects and oxidative damage to tissues in the oxygen-rich waters of the Southern Ocean (Giordano et al. 2015). One other way that the function and importance of cytoglobins has been studied is through their genes and gene expression.

Cytoglobin (Cygb) genes are expressed in all vertebrate tissues, in a range of species. Cygb concentration is higher in the brain, eyes, skeletal muscles, heart and liver than other tissues (Burmester et al. 2002, Fordel et al. 2004). Cygb functions in cells and tissues are poorly described to date, but several possible roles have been suggested. These include: nitrite reduction and nitric oxide (NO) generation during anaerobiosis (Li et al. 2012); regulation of intracelluar NO concentrations (Liu et al. 2012); oxygen supply to the respiratory chain in mitochondria (Kawada et al. 2001, Hankeln et al. 2005), and during the synthesis of collagen (Schmidt et al. 2004), and to protect cells against oxidative stress (Li et al. 2007). There are many stresses that animals face, both in the Antarctic and elsewhere. There is a range of responses to stresses, but the most well known are possibly the heat shock response (HSR) and mechanisms to reduce or repair damage from reactive oxygen species. These are discussed below.

Stress responses: the HSR and reactive oxygen species

The heat shock response (HSR) is the only response to stress identified in organisms that has been claimed to be universal (Gross 2004). The HSR classically involves the production of heat shock

proteins (HSP) in response to a thermal challenge (Gross 2004). They are also, however, produced in response to a wide range of other stressors, including dehydration in plants and insects (Feder & Hofmann 1999). The HSP family of proteins is large, and there are many forms that differ among species. They have a wide range of functions, which include helping misfolded proteins to reach their functional state or to return to that state if it is lost. They have also been recognised to assist in the identification of degraded proteins and to have a role in the regulation of their removal from the cell. This process is an important part of the prevention of the formation of cytotoxic aggregates in cells (Parsell & Lindquist 1993). The best studied of the HSP proteins are the HSP70 proteins, so called because they are the 70 kDa family.

At the start of this millennium, Hofmann et al. (2000) made a surprising discovery when investigating the HSR in Antarctic fishes. When they warmed *Trematomus bernacchii*, the expected classic HSR was not elicited; HSP70 production did not increase when they raised temperatures beyond its normal temperature range. This was the first time such an HSR had not been demonstrated on warming beyond normally experienced temperatures in any multicellular organism more complex than a hydroid (La Terza et al. 2001, 2004, 2007). Studies that followed showed that the majority of Antarctic fishes lack the ability to increase HSP70 production when challenged with any of the commonly used stressors (Tomanek 2010, Beers & Jayasundara 2014). The reason for this lack of HSR is thought to be due to a mutation in the *hsp70* gene, specifically in its promoter region that inhibits the binding and following transcription of HSF1 (Buckley et al. 2004). All Antarctic fish do, however, constitutively express at high levels the inducible form of the HSP70 protein that is usually subject to an increase in production in response to stress in all non-Antarctic invertebrates and fish (Place & Hofmann 2005, Clark et al. 2008a).

Antarctic marine invertebrates differ from the fish in that they exhibit a range of HSP70 responses following exposure to heat stress. A few studies have found an HSR in some species, while others have reported a lack of increase in HSP production in Antarctic invertebrate species when warmed. Recently the sea urchin *Sterechinus neumayeri* was shown to increase HSP70 in response to exposure to 3°C temperatures for 48 hours (González et al. 2016). Two molluscs, the clam *Laternula elliptica* and the limpet *Nacella concinna*, both exhibited an HSR, but an increase in production of a range of HSPs only occurred in experiments when temperatures were raised to 8–10°C and 15°C, respectively, with no HSR at lower temperatures (Clarke et al. 2008). These temperatures are well above any that *Laternula elliptica* and *Nacella concinna* have been exposed to for millions of years. The possibility that there might be a functional need for an HSP in these species was later shown in the limpet when the induction of several members of the HSP70 family was demonstrated to occur during the tidal cycle in individuals living in the intertidal (Clark et al. 2008c) and also in association with the spring thaw of sea ice and exposure over highly extended periods to low levels of warming (Clark & Peck 2009b). To date, only one species of invertebrate has not been shown to exhibit an HSP70 HSR, the starfish, *Odontaster validus* (Clark et al. 2008b). However, these heat shock experiments only evaluated the HSR using *hsp70* genes cloned by degenerate polymerase chain reaction (PCR). Thus, it is likely that not all members of the HSP70 family were identified. In the same series of experiments, no HSR was detected in the amphipod *Paraceradocus miersi*, (Clark et al. 2008b), but subsequent thermal challenges using discovery-led next-generation sequencing (NGS) did in fact reveal the possession of a thermally inducible form of HSP70 (Clark et al. 2016). In the Antarctic krill *Euphausia superba* and *E. crystallorophias*, gene duplication events were shown to have occurred that produced several forms of HSP70 but even so change has to have only resulted in a weak HSR (Cascella et al. 2015).

In a recent study using acute warming of 1°C h^{-1}, Clark et al. (2016) showed that the HSR varied markedly between six different species of Antarctic marine invertebrate, with each species having its own response to warming. They used a combined transcriptomic and metabolomics approach to evaluate the response to acute warming and demonstrated that the upregulation of the production of members of the HSP70 family occurred in three species, (the amphipod *Paraceradocus miersi*, the rhynchonelliform brachiopod *Liothyrella uva* and the bivalve mollusc *Laternula elliptica*), whereas in three others (the

gastropod mollusc *Marseniopsis mollis*, the holothurian *Cucumaria georgiana* and the bivalve mollusc *Aequiyoldia eightsii*), there was no indication of any change in HSP70 production at this particular rate of thermal change. This work demonstrated that the response varies with the challenge applied.

Interestingly, numerous HSP family gene duplications have been identified in Antarctic marine species, including in krill, which indicates an ongoing requirement for their production. The hypothesis that living in polar marine conditions where temperatures are permanently around or below 0°C requires constitutively high expression of one or more *hsp70* genes is still the main paradigm in this area of science.

Antarctic marine species have been noted for nearly two decades to have elevated resting or constitutive levels of the proteins involved in pathways conferring resistance to, and providing protection from, damage from reactive oxygen species (ROS), primarily superoxide dismutase (SOD), catalase and the glutathione enzymes (Abele & Puntarulo, 2004, Chen et al. 2008, Clark et al. 2010, 2011). This is explained as an adaptation to living in polar marine environments, where ambient oxygen levels are the highest in the world's oceans, and the capacity for body fluids to carry dissolved oxygen is the highest on Earth, making the organisms living there more vulnerable to ROS damage than those from lower latitudes. In their study of the effects of acute warming on six Antarctic marine invertebrates, Clark et al. (2017) found that none of them produced the expected response to reactive oxygen damage, with no detectable upregulation of pathways conferring resistance as evidenced by expression levels of SOD, catalase or glutathione enzyme genes. Previous research on bivalves focussed on SOD and the pro-oxidative product malondialdehyde (MDA) in Antarctic bivalve molluscs (*Adamussium colbecki* and *Aequiyoldia eightsii*) had shown that SOD levels decreased, but MDA levels increased when the animals were warmed (Regoli et al. 1997, Abele et al. 2001). MDA is often used as an indicator of oxidative stress because it is part of the signalling system deciding cell survival or death (Ayala et al. 2014). Because of this, the increase in MDA combined with a decrease in SOD with warming was explained via an evolutionary maximisation of the antioxidant system to cope with the very high levels of oxygen in the ambient environment, but this came with a reduction in thermal stability of the antioxidant system. It has been suggested that these could be 'examples of species-specific enhanced sensitivity of critical enzymes which directly impact on organism physiology and survival' (Clark et al. 2017). Antarctic marine species are often thought to have evolved fine-scale adaptation to extreme low temperature conditions because of the long evolutionary period, in excess of 10 million years, they have evolved in isolation from lower latitude faunas (Clarke & Crame 1992). Despite this, recent work has questioned whether the proteins of Antarctic marine ectotherms are fully adapted to temperatures around and below 0°C (Peck 2016, Clark et al. 2017).

It is the specific adaptations to any environment that produce the cellular and physiological attributes of all species, and these adaptations enhance or constrain their capacities to respond to change in the environment. The fine-scale, and often unique, adaptations described for Antarctic marine species previously will dictate their future success or failure.

Impacts of environmental change

The discussion so far has concentrated on adaptations to the Antarctic environment at the whole-animal and cellular levels. The cryosphere is being increasingly affected by climate change, and it might be expected that cold-adapted endemic polar species may be particularly vulnerable (Somero & DeVries 1967, Peck 2002a,b, Peck et al. 2006a,b, 2009a,b, 2014, Pörtner et al. 2007, 2012).

Human-driven environmental change is a global phenomenon, with clear impacts on biodiversity in all regions of the Earth (UNEP 2012). The areas of most rapid change to date have been in the polar regions where the fastest rates of regional warming on Earth have been reported. This warming has been accompanied by dramatic loss of sea ice and recession of coastal glaciers and ice shelves (IPCC 2014). In Antarctica, many regions have not exhibited significant change over the last 50–100 years, but the Antarctic Peninsula has seen some of the fastest change over the last 50 years (Turner et al. 2009). The atmospheric warming on the peninsula may be less now than in the past (Turner

et al. 2016), but coastal ice is still receding, and oceanic systems are still in flux (Cook et al. 2016). In parts of this region, air temperatures increased by over 3°C in the last half of the twentieth century, and sea temperatures to the west of the Peninsula increased by 1°C over the same period (Meredith & King 2005). The major challenges that marine species face from the current environmental change in the polar regions comes from three main sources: increased temperature, ocean acidification and altered levels of sea ice and iceberg scour in the benthos, although salinity (Clark & Peck 2009a,b) and hypoxia (Tremblay & Abele 2016) have also been noted as potentially important stressors.

Responding to change at the level of the organism

Organisms can respond to changes in their environment in a large number of ways that vary across process scales from cellular and molecular to community and ecosystem, and these responses vary with the scale of the change in spatial and temporal contexts (Figure 17). The various responses can be classified across scales. Within cells, biochemical buffering is at the smallest scale, and beyond this, gene expression and phenotypic plasticity through physiological flexibility buffer changes that occur over hours to weeks. At larger scales still, gene frequency alterations and selection in populations work alongside behavioural modifications. At slow rates of change, evolutionary gene modification and speciation are important responses. These are the more mechanistic types of response that organisms can have, and processes involving ecological interactions and migration have effects across these scales.

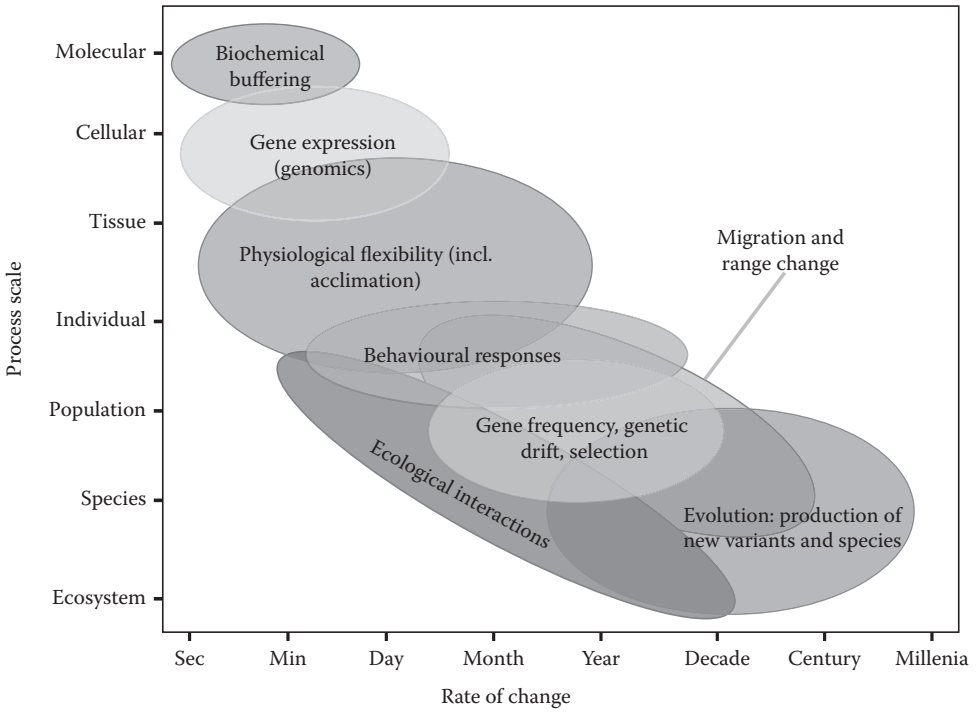

Figure 17 Schematic diagram of biological responses to changes in the environment in relation to the rate of change and the scale of process involved. In mechanistic processes, at the smallest scales biochemical buffering is entrained. This is followed by a cascade of processes through gene expression, phenotypic plasticity and population gene frequency modification through to evolutionary change. Phenotypic plasticity links mechanistic process understanding with ecological and evolutionary responses. (Figure redrawn from Peck, L.S. 2011. *Marine Genomics* **4**, 237–243.)

The type of response an organism produces varies depending on the rate of environmental change. Immediate responses required to survive rapid change often result in an increase in energy demand for muscle contraction or homeostasis. In marine invertebrates this is fuelled from phospho-L-arginine (PLA) stores in cells (e.g. Bailey et al. 2003, Morley et al. 2009a), whilst in vertebrates, the energy store is creatine phosphate (Nakayama & Clarke 2003). The size of PLA or creatine phosphate stores are one of the limitations of capacities to respond to rare rapid environmental change over short timescales of seconds to minutes, such as when seawater is heated by volcanic activity and escape responses are needed for survival. On the scale of seconds to weeks or months, several processes can have effects. Gene expression and its modulation through post translational processes such as epigenetic mechanisms are important in whole-organism responses, including those involved in stress such as the heat shock response (Gross 2004, Clark & Peck 2009a), in damage repair (Sleight et al. 2015), or in longer-term processes such as seasonal changes in the lower lethal temperature limit of the intertidal snail *Littorina brevicula* (Chiba et al. 2016) and thermal acclimation (e.g. Heinrich et al. 2012, Ravaux et al. 2012). Some of these mechanisms can persist for long periods when epigenetic factors can, at least temporarily, fix a gene expression level (Metzger & Schulte 2016, Putnam et al. 2016, Clark et al. 2018). Phenotypic plasticity is effective over a very large range of timescales from changes in heartbeat rate driven by adrenergic changes in fish (Farrell et al. 2009) to seasonal or life-history changes such as the modulation of activity (e.g. Morley et al. 2007, Aguzzi & Sarda 2008, Oystein 2012), metabolic or growth rates (e.g. Bayne 2004, Obermüller et al. 2010, 2011), or the production of antifreeze (e.g. Cheng & Detrich 2007).

Responses at the population level can be affected by modifications of the genepool from mutation or, more likely, gene flow within and between populations. Genome level responses are also dictated by life-history factors including generation time, population size, number of embryos produced per reproductive event and ocean currents (for connectivity between separate populations). In viruses and microbes, nucleotide substitution rates can be very rapid, and evolutionary change can occur in days to weeks (Peel & Wyndham 1999, Duffy et al. 2008). However, decades may be required in species with few offspring per reproductive event and long generation times such as elephants, some Antarctic marine invertebrates such as brachiopods (Peck 2008) and bivalve molluscs (Román-González et al. 2017), and whales (Jackson et al. 2009). The different responses shown in Figure 17 thus cover a range of process scales and rates of change that are much wider than the response of any single species or population, as different taxa can have very different timescales of response. Climate change-driven alterations to the environment are at the slower end of the range of rates of change seen in Figure 17, and it might be expected that only the processes relevant at decadal or longer timescales might be important when considering responses to climate change. Several authors, however, including Pörtner et al. (2007, 2012), Helmuth (2009) and Peck (2011) have emphasised that processes at shorter timescales produce a cascade of responses that play a large part in determining outcomes at larger scales. It is not only a question of population persistence but also one of maintaining reproductive fitness and being able to produce future generations. These factors are also of great importance when identifying sensitivities that are important to making future predictions.

Somero (2010, 2012, 2015), amongst other authors, argued that the most important responses organisms have to confer survival and maintain fitness in a climate change context are flexibility of the phenotype (often called phenotypic plasticity) via acclimatisation of physiological processes and via alteration of the genepool in populations, genetic adaptation. It is the former that is thought to be particularly important in long-lived species with long generation times. Organisms with very short generation times and rapid reproductive processes need less phenotypic plasticity to survive as their ability to modify their genetic complement is high, and their response is to produce new variants and not survive as individuals. Conversely, when generation times are long, including many Antarctic marine species, there will be a strong requirement for phenotypic plasticity via mechanisms such as acclimatisation to allow survival until adequate genetic adaptation can be achieved (Peck 2011).

Ecological change

In Antarctica the effects of reduced sea ice and increased levels of iceberg scour, mainly recorded in the Antarctic Peninsula region, have been predominantly evaluated as ecological impacts. They have primarily been assessed in terms of ecological outcomes and responses (e.g. Lipps et al. 1979, Gutt & Starmans 1998, 2011, 2015, Peck et al. 1999, 2010a, Riddle et al. 2007, Bertolin & Schloss 2009, Barnes & Souster 2011, Ducklow et al. 2012, 2013, Fillinger et al. 2013, Cape et al. 2014, Sahade et al. 2015, Barnes 2016, Hauquier et al. 2016).

Studies here have, for instance, demonstrated that climate-related warming has been accompanied by strengthening of winds on the Antarctic Peninsula, and this has reduced sea ice extent and duration (Spence et al. 2017). Some authors support the idea that the oceanic warming has been produced by the development of stronger southern hemisphere mid-latitude winds that assist the movement of warmer offshore waters onto the continental shelf (Martinson et al. 2008, Spence et al. 2014). An alternative explanation has, however, come from fine-scale models that suggest the heat transfer could be due to mesoscale eddies and tides (Stewart & Thompson 2013, Flexas et al. 2015). This heat transfer resulted in an increase in the ice-free period on the Bellingshausen side of the peninsula by over three months per annum between 1979–1980 and 2010–2011 (Stammerjohn et al. 2008, 2012). Amongst other effects, the loss of sea ice was attributed to be the cause of a reduction in the numbers of krill present in the region over a similar period (Atkinson et al. 2004), as sea ice is an important overwintering resource for this species (Flores et al. 2012). Recent work has also emphasised the importance of nearshore fjords for overwintering in krill (Cleary et al. 2016), and these fjords are experiencing rapid change, especially on the west Antarctic Peninsula where these environments have warmed, and the majority of glaciers have retreated significantly in the last 50 years. It is difficult to see how animals such as krill can adapt to reduced sea ice, even with altered behaviours, when they rely on it for food and shelter in the critical juvenile period over winter.

Ice shelf loss and coastal glacier retreat are, however, not only affecting those species that rely on them for overwintering, but they are markedly changing the productivity and biodiversity in these areas (Peck et al. 2010a, Barnes 2015). Ice shelf loss has increased areas of open water and seabed, where a major biotic response has been the development of new productivity and biological communities and ecosystems (Arrigo et al. 2008, Peck et al. 2010a, Gutt et al. 2013b, Constable et al. 2014, Barnes 2015). The effects of this enhanced productivity on new and surrounding communities has yet to be fully evaluated.

Sea ice loss and increased coastal glacier and ice shelf retreat have also resulted in an increase in the frequency of iceberg impacts on the seabed on the Antarctic Peninsula, which has removed biota in recent decades and is limiting the capacity for biological communities to grow and sequester carbon (Barnes DKA et al. 2014a, Barnes 2016). It is not possible for the animals inhabiting these sites to adapt to such catastrophic events, and with their slow development, Antarctic animals will recolonise these devastated areas more slowly than when similar events (e.g. bottom trawling, volcanic eruptions) take place in temperate or tropical regions of the globe. Beyond ecological analyses of the impacts of changes in sea ice and iceberg scour, the other two major problems identified with global change in the Southern Ocean, rising temperatures and ocean acidification, have received considerable attention from the science community. These have been evaluated from ecological, physiological and genetic approaches, and here adaptation is more likely. These two factors are analysed in more detail below.

Rising temperatures

There have been many studies of physiological capacities to respond to temperature stress in Antarctic marine species over recent decades on a very wide range of different taxa, including fish (e.g. Macdonald & Montgomery 1982, Hardewig et al. 1999b, Hofmann et al. 2000, 2005,

Wilson et al. 2001, 2002, Podrabsky & Somero 2006, Franklin et al. 2007, Robinson & Davison 2008, Bilyk & DeVries 2011, Strobel et al. 2012, Todgham et al. 2017), molluscs (Peck 1989, Urban & Silva 1998, Pörtner et al. 1999b, 2006, Peck et al. 2002, 2004a, Clark et al. 2008a,b, Morley et al. 2010, 2011, 2012a,b,c, Reed et al. 2012, Reed & Thatje 2015), echinoderms (Stanwell-Smith & Peck 1998, Clark et al. 2008b, Peck et al. 2008, 2009b, Morley et al. 2012b, 2016c), amphipods (Young et al. 2006a,b, Clark et al. 2008b, Doyle et al. 2012, Gomes et al. 2013, 2014, Clusella-Trullas et al. 2014, Faulkner et al. 2014, Schram et al. 2015b), isopods (Whiteley et al. 1996, 1997, Robertson et al. 2001, Young et al. 2006a,b, Janecki et al. 2010, Clusella-Trullas et al. 2014, Faulkner et al. 2014), brachiopods (Peck 1989, 2008, Peck et al. 1997a), sponges (Fillinger et al. 2013), and macroalgae or phytoplankton (Montes-Hugo et al. 2009, Schloss et al. 2012). There have also been many assessments of the effects of elevated temperature using a larger-scale approach, both experimentally and using field observations identifying multispecies response or evaluating community, ecosystem or overall biodiversity level responses (e.g. Fraser & Hofmann 2003, Peck et al. 2004b, 2010b, 2013, Aronson et al. 2007, Clarke et al. 2007, Barnes & Peck 2008, Schofield et al. 2010, Richard et al. 2012, Gutt et al. 2015, Morley et al. 2016a, Clark et al. 2017).

The vast majority of these studies have shown that Antarctic marine ectotherms have poor capacities to survive elevated temperatures in experiments, when compared with lower latitude species, which was first identified in the 1960s (Somero & DeVries 1967). Antarctic fish have generally higher capacities to tolerate warming in laboratory experiments than invertebrates (e.g. Podrabsky & Somero 2006, Franklin et al. 2007, Robinson & Davison 2008, Bilyk & DeVries 2011), and some invertebrates have possibly the poorest reported abilities to survive experimentally elevated temperatures of any marine species on Earth, including the brachiopod *Liothyrella uva* (Peck 1989), the brittle star *Ophionotus victoriae* (Peck et al. 2009b) and the bivalve mollusc *Limopsis marionensis* (Pörtner et al. 1999b), amongst several others.

Very recently some of the first *in situ* warming experiments have been deployed in Antarctica to assess the effects of warming on natural field communities of biofouling organisms (Ashton et al. 2017b). This study used an embedded heating system to raise the temperature of the surface and overlying boundary layer of water of settlement panels by 1°C or 2°C above ambient. The experiment ran for nine months, and, except for temperature, all other environmental variables were unchanged. All warming treatments produced large changes in the assemblage structure, with a pioneer species of bryozoan *Fenestrulina rugula* dominating in warmed conditions. Growth rates of the common species present nearly doubled for a 1°C warming, indicating that some transition had occurred in the organisms' physiology because this level of effect is well beyond any possible direct effect of temperature on enzyme mediated biological systems, as the Q_{10} for growth was ~1000. This unexpected effect of warming could possibly be related to the problems associated with protein synthesis at low temperature discussed in the earlier section on 'Growth'. Ashton et al. (2017b) found that a warming of 2°C produced variable results between species, and this may indicate that the more sensitive taxa were nearing their thermal limits.

Rates of warming

One early confounding factor in assessing whether Antarctic marine species were generally more sensitive to warming in experiments was that experimental protocols varied between laboratories. Such experiments also do not mimic real-time temperature changes. Thus, a major factor here is the rate of warming used in experiments. This factor has been recognised for a longer period in experiments on terrestrial species and is known as the rate hypothesis reviewed by Terblanche et al. (2011). In Antarctic marine species, Peck et al. (2009a,b) demonstrated a marked effect of rate of warming in experiments on thermal limits. In a study assessing upper temperature limits in 14 species from six phyla at warming rates from 1°C day^{-1} to 1°C $month^{-1}$, they showed that thermal maxima were 2.5–8 times lower at the slowest rate of warming than the fastest (Figure 18). However,

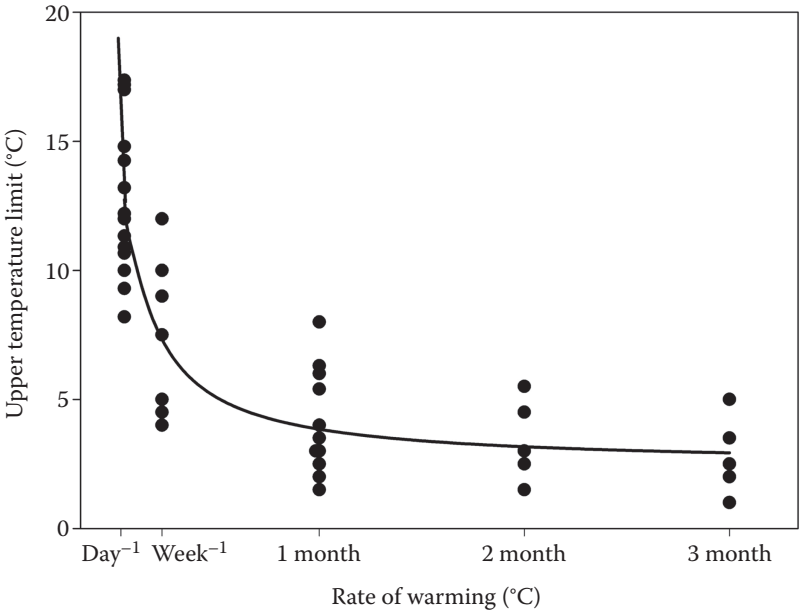

Figure 18 Upper temperature limit (CT_{max}) values for 14 species of Antarctic marine invertebrates at different rates of warming. Figure updated and adapted from Peck et al. (2014). Upper temperature limits quoted are values above the current average summer maximum temperature (1.0°C at the study site).

these results using several rates of warming also enabled, for the first time, extrapolation to long-term survival temperatures. This is particularly important in long-lived Antarctic species, where husbandry of species is often unknown or poorly understood, and it is not possible to keep many of them long-term in aquaria. In this case, more rapid thermal challenge experiments are essential, and upper thermal limits can be used as proxies for predicting the difference in resiliences or sensitivity between species and, therefore, enable modelling of future biodiversity change.

Demonstrating a relationship between the rate of warming in experiments and the upper temperature limits of species, as shown in Figure 18 and modelled by Richard et al. (2012), is of great importance when linking laboratory experiments with field observations or predictions. Sunday et al. (2011, 2012) showed there is a link between upper temperature limits and range boundaries in ectothermic animals, and the link is stronger in marine than terrestrial species. There is further a general consensus that including mechanistic biological capacities, through the use of physiological and phenotypical characteristics, into models predicting future consequences of climate change is an important step (e.g. Pennisi 2005, Gaston et al. 2009, Helmuth 2009, Peck et al. 2009a, Morley et al. 2016a). Variation in the assessment of upper temperature limits of the order seen in Figure 18 is a significant factor that can provide large errors when making predictions of climate impacts on biotas, including mechanistic traits, and one that needs to be included when making models to provide such predictions. Further important factors in the development of this macrophysiological approach that need to be quantified and allowed for include the various ways in which different aspects of phenotypic plasticity affect range shifts in response to environmental change (e.g. Chown et al. 2010, Sunday et al. 2012). Interactions between this and the effects of different rates of change are likely to be complex (Chown et al. 2009, Clusella-Trullas et al. 2011, 2014, Faulkner et al. 2014).

An additional way of analysing rate of warming data (as shown in Figure 18) and the relationship to environmental change is to use the data obtained from different rates of warming to estimate the difference between the long-term physiological temperature limit and the current maximum or

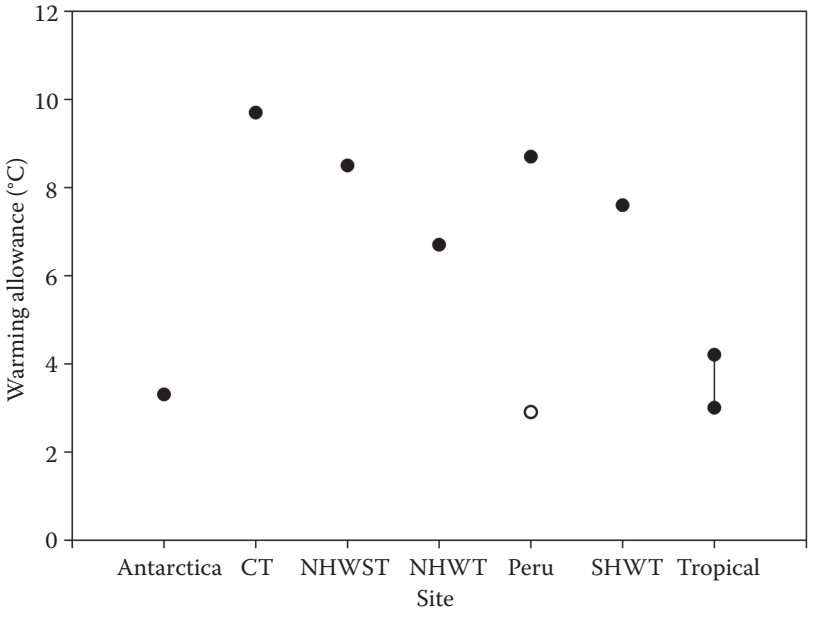

Figure 19 Warming allowances for multispecies assessments at seven sites from polar to tropical latitudes. Warming allowance here is the difference between long-term CT_{max} (see Figure 18) and the maximum environmental temperature at the site studied (°C). The sites range from Antarctica to Singapore (tropical) with abbreviations following Richard et al. (2012) and Peck et al. (2014): CT = cold temperate site (west coast of Scotland); NHWST = northern hemisphere warm shallow temperate site (depths less than 5 m); NHWT = northern hemisphere warm temperate site (deeper than 5 m; South of France and west coast of the United States); Peru (depths deeper than 5 m); and SHWT = southern hemisphere warm temperate (all depths deeper than 5 m). The line between the points for tropical data indicate the range of values, whilst the closed circle in the Peru data indicates the warming allowance outside an El Niño year, and the open symbol is for data in an El Niño. (Figure redrawn from Peck, L.S. et al. 2014. *Journal Experimental Biology* **217**, 16–22.)

mean temperatures experienced in the environment. This gives a measure of the buffer provided by the phenotypic plasticity of the population or species to warming and has been termed the warming tolerance by Deutsch et al. (2008), or the warming allowance by Richard et al. (2012). When this approach is used to compare Antarctic with temperate and tropical marine species, a pattern of small allowances in Antarctica and the tropics and larger allowances in temperate regions is apparent (Figure 19).

Figure 19 shows that Antarctic and tropical marine ectotherms have a warming allowance around 3–4°C above currently experienced maximum environmental temperatures, whereas for temperate species, this is around or more than double these values. Interestingly, in Peru, outside an El Niño, the warming allowance is around 9°C, but during an El Niño, where there are usually large mortalities in many species, it is around 3°C and similar to Antarctic and tropical species, suggesting both the very low and high-latitude species are living close to their thermal limits. However, the El Niño effect is slightly different from the tropics and poles, in that this, whilst a regular event, is infrequent and random enough that the animals are not able to adapt to the elevated temperatures it causes and as such can be viewed along similar lines to corrosive upwelling events that cause similar devastation along the US coast (Feely et al. 2008).

Having established that Antarctic marine cold-blooded species have restricted temperature limits compared to temperate species and poor capacities to respond to warming, it is now important to understand the mechanisms they can employ to resist, or respond to warming.

Mechanisms of resistance to warming

There have been many studies attempting to produce a synthetic, mechanistic understanding of the responses of marine species to warming environments or to provide an integrative evaluation of those responses (e.g. Pörtner 2001, 2002a,b, 2006, Peck 2002a,b, 2005a,b, 2011, Pörtner et al. 2005a,b, 2007, 2012, Peck et al. 2009a, 2014, Somero 2010, 2012, Ingels et al. 2012), and many of these have included understanding of Antarctic species or been built upon research carried out in Antarctica. Furthermore, the development of modern molecular methods has allowed analyses of resistance to warming at a finer scale than previously and allows a focus on specific mechanisms such as the heat shock response, the electron transport chain or anaerobic processes (e.g. Huth & Place 2016a,b, Clark et al. 2017, Enzor et al. 2017).

The most commonly cited and prevalent current theory on the mechanisms dictating resistance to warming is the oxygen and capacity limited thermal tolerance (OCLTT) hypothesis that was developed from the earlier oxygen limitation hypothesis initially proposed by Hans Pörtner (Pörtner et al. 2000, 2004, Pörtner 2001, 2002a,b, Pörtner & Farrell 2008). This hypothesis suggests that there is an optimal temperature window for an organism to function in and that at either side of this window a point is reached where performance declines because of aerobic (oxygen supply) constraints (Figure 20). The points where performance declines are called the pejus (=getting worse) thresholds (T_p in Figure 20), and these are identified by a decline in whole-animal aerobic scope (Pörtner et al. 2012). The loss of performance is attributed to the balance of oxygen demand and supply moving away from the optimal position. With continued warming or decrease in temperature, the aerobic scope eventually falls to zero when the upper or lower critical threshold temperatures (T_c in Figure 20) are reached. These points can be identified by the accumulation of anaerobic end products in cells and tissues, such as succinate in marine invertebrates and lactate in vertebrates. These effects are posited to occur before more severe physiological temperature effects such as membrane disruption or protein denaturation, which occur closer to the temperature of death (T_d in Figure 20).

The OCLTT paradigm was based around several pieces of information, many of which were obtained in studies of Antarctic marine species. These included the finding that upper critical temperatures are characterised by the accumulation of anaerobic metabolic end products such as succinate, for example, in the bivalves *Limopsis marionensis* (Pörtner et al. 1999b), *Laternula elliptica* (Peck et al. 2002) and *Adamussium colbecki* (Bailey et al. 2003), and in fish in the eelpout *Pachycara brachycephalum* (Van Dijk et al. 1999). These data were supported by findings that showed the capacity to perform activity declined before critical thresholds were achieved and well before upper lethal temperatures were reached. This was a demonstration that aerobic scope declines as temperature is progressively increased, and it was demonstrated in Antarctic species for, amongst others, burying in the clam *Laternula elliptica* and righting in the limpet *Nacella concinna* (Peck et al. 2004b), where in both species 50% of the population lost the ability to perform the activity being tested when warmed to between 2°C and 3°C, and none were capable of burying or righting, respectively, at 5°C. In the scallop *Adamussium colbecki*, increased temperature had an even stronger impact on its ability to swim, a higher energy activity requiring greater aerobic scope, with complete failure at 2°C (Bailey 2001, Bailey et al. 2005). Furthermore, the Antarctic fish *Pagothenia borchgrevinki* survives up to 11°C when warmed acutely. Its swimming performance is, however, more tightly limited, with its fastest swimming speed only observed between 1°C and 2°C, followed by a progressive decline in speed under further warming such that maximum speed at 7°C is only 50% that at 2°C (Wilson et al. 2002). Other Antarctic fish are likely to be similarly, or more, limited in their ability to maintain activity, as *P. borchgrevinki* appears to be less sensitive to elevated temperature than other species (Seebacher et al. 2005, Bilyk & DeVries 2011). A progressive loss of the capacity to perform aerobic activity with raised temperature is in line with predictions from the OCLTT hypothesis because it should reflect progressive reduction in aerobic scope or

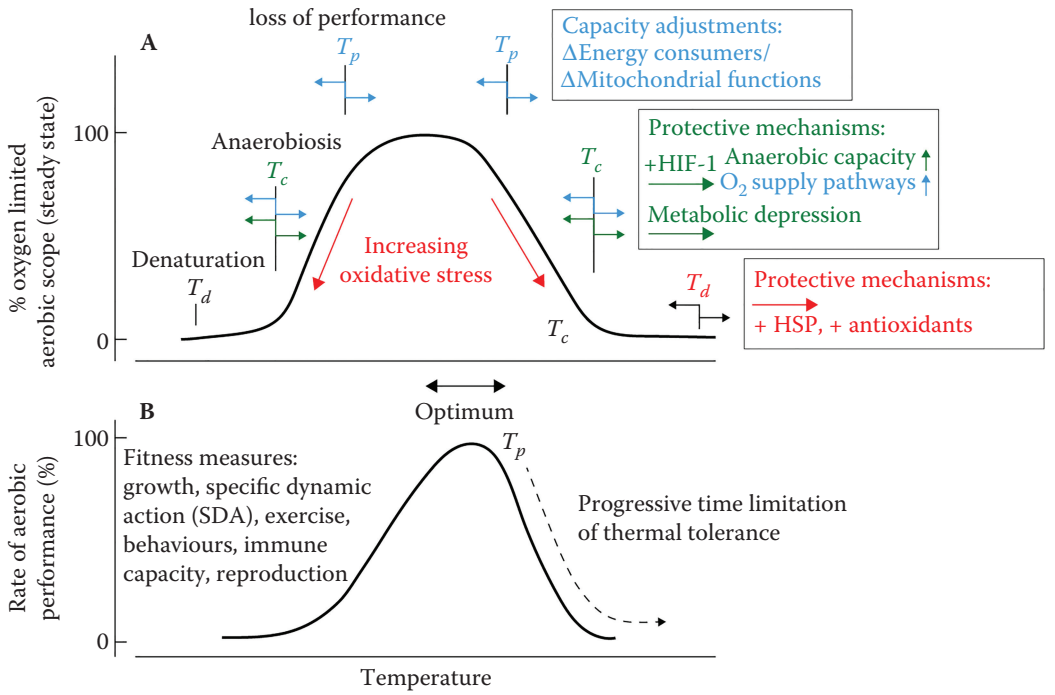

Figure 20 Schematic diagram of concept of oxygen limited thermal tolerance (following Pörtner et al. 2000, 2004, Pörtner 2001, 2002a,b). (A) An optimum temperature range is flanked by zones of progressive loss of aerobic scope. The start of these zones of progressive decline in capacity is denoted by T_p, the pejus threshold. Beyond the pejus zone is where aerobic scope declines to zero and anaerobic end products begin to accumulate. This zone is entered at the critical threshold, T_c and survival beyond T_c is time limited, depending on the rate of accumulation of anaerobic products and the species tolerance to these products. T_d denotes the zone where death occurs in the short term. All of these thresholds can shift when phenotypic plasticity mechanisms are entrained or from genetic adaptation. Boxes denote typical physiological and molecular mechanisms that dominate in each zone. (B) A typical aerobic performance curve, where whole-animal maximum scope and performance is usually asymmetric, with the peak of the curve nearer the upper T_p. (Figure modified from Figure 13.6 in Pörtner, H.O. et al. 2012. In *Antarctic Ecosystems: An Extreme Environment in a Changing World*, A. Rogers et al. (eds). Wiley Interscience, 379–416.)

capacity. Another strong support for this paradigm was obtained from studies that showed varying oxygen levels in seawater affected the upper temperature limits. Thus, when oxygen concentrations in seawater were increased, upper temperature limits and the capacity to burrow were increased, and both decreased when oxygen concentrations were lowered, in the clam *Laternula elliptica* (Peck et al. 2004b, 2007a, Pörtner et al. 2006). Several later studies provided further support for OCLTT. In Antarctica, these included that the concentration of haematocrit (the amount of haemoglobin) circulating in the blood was strongly correlated with temperature limits in five species of Antarctic fish (Beers & Sidell 2011).

Outside the Antarctic literature progressively more reports have been published that question the validity of OCLTT as a universal overarching concept explaining thermal limits (e.g. Ejbye-Ernst et al. 2016, Verberk et al. 2016). This has been especially the case in insects, where studies investigating low-temperature limits do not support the paradigm, and investigations of upper-temperature limits show stronger support in water-respiring species than air-breathing taxa (e.g. Klok et al. 2004, Stevens et al. 2010, Boardman & Terblanche 2015, Verberk et al. 2016, Shiehzadegan et al. 2017). Studies on other taxa have also questioned the universality of the hypothesis including

in the snake *Python regius* (Fobian et al. 2014), the toad *Rhinella marina* (Overgaard et al. 2012), the freshwater shrimp *Macrobrachium rosenbergii* and several fish species (e.g. Clark T. et al. 2013, Norin et al. 2014, Wang et al. 2014, Lefevre et al. 2016).

In the Antarctic literature some studies have reported data not consistent with OCLTT. Clark et al. (2017) investigated the molecular responses to warming at 1°C h^{-1} by analysing complementary metabolomics and transcriptomic data, at temperatures close to their upper limits in six marine invertebrate species. Responses were diverse, with only two of the six species showing evidence of the accumulation of anaerobic end products, whilst only three increased expression of HSP70, the classical heat shock response. Each species appeared to have its own molecular response profile, and the conclusion drawn was there is no overall unifying mechanism determining temperature limits. Further to this, Devor et al. (2016) showed that increasing the oxygen content of seawater did not affect the upper thermal limits of either red-blooded or haemoglobinless Antarctic fishes.

As discussed earlier, the rate of warming in experiments markedly affects the upper temperatures to which marine species can survive. There is also mounting evidence that the mechanisms setting these upper temperature limits differ at different rates of warming. Several studies of Antarctic fish and crustaceans at rapid rates of warming (1°C h^{-1} or faster) have cast doubt on OCLTT. These have been based around evaluations of the functions of nervous systems showing failure, of at least some parts at similar temperatures to the whole-animal upper temperature limits. In fish, there is evidence that conduction at central nervous system (CNS) synapses fails in *Pagothenia borchgrevinki* near their upper limits (Hochachka & Somero 2002). In another study on the same species, specimens produced a sharp increase in the release of acetylcholine (a neurotransmitter) at neuromuscular junctions at temperatures between 12°C and 14°C, which is near this species' upper-temperature limit at the rate of warming used (Macdonald & Montgomery 1982). A similar finding of failure of neuromuscular junction function at temperatures near to whole-animal upper limits was reported for the Antarctic amphipod *Paraceradocus gibber* and the isopod *Glyptonotus antarcticus* (Young 2004, Young et al. 2006b). This was also shown in molecular evaluations of the potential mechanism behind failure for *Paraceradocus miersi* when warmed at 1°C h^{-1} (Clark et al. 2016).

As previously noted, many studies have provided support for OCLTT, and these have predominantly been conducted at rates of warming between 1°C h^{-1} and 1°C $week^{-1}$. However, since the most relevant rates of warming in the sea in relation to responses to climate change (those involving acclimatory responses) are much slower than this, and at slower rates of change, support for OCLTT has been limited. Several studies at medium and especially at slow rates of warming have suggested that other mechanisms rather than oxygen supply might be important in setting temperature limits. These include: (1) a limited capacity of the antioxidant system in Antarctic species to combat damage from reactive oxygen, resulting in the accumulation of toxic oxidised proteins such as protein carbonyls (Regoli et al. 1997, Abele et al. 2001, Powell et al. 2005, Heise et al. 2007, Clark et al. 2013); (2) high-temperature sensitivity of critical enzymes limits function of essential pathways at higher temperatures (Clark et al. 2016); (3) limitation of energy reserves, where increased maintenance costs exceed energy acquisition (e.g. Sørensen & Loeschcke 2007, Peck et al. 2010b, 2014) and (4) key processes are slowed at low temperature, which results in the observed very long times required for acclimation in Antarctica (Peck et al. 2014) and the poor acclimation of a range of cellular processes sets limits.

The first of the mechanisms, limitation of the antioxidant system, describes an imbalance between increased production of toxic metabolic end products from increased levels of oxidative damage at elevated temperatures and the ability of the cellular mechanisms involved to break these products down. As cells and tissues become energetically compromised during prolonged heat exposure, for example, protein turnover starts to shut down as an energy saving strategy (Hochachka et al. 1996). This produces a depression in metabolic rate, and under these conditions, cells may fail to remove efficiently cellular oxidative damage products, such as protein carbonyls (oxidised proteins) and malondialdehyde (MDA), which is a biomarker of oxidative stress and an initial product of lipid

peroxidation. Accumulation of these products occurs as metabolic rates decline and autophagic, and proliferative activities become reduced (summarised by Philipp & Abele 2010). This results in a progressive increase in toxic end products in cells until a level is reached that the organisms can no longer tolerate, and apoptosis dominates the cellular processes (Powell et al. 2005, Zhang et al. 2008).

The second is a direct limitation of metabolic function by limited capacities of key enzymes. Experimental studies on the environmental stress response of *Aequiyoldia eightsii* and the scallop *Adamussium colbecki* indicated that whilst MDA levels increased in response to oxidative stress, levels of the antioxidant enzyme superoxide dismutase were decreasing (Regoli et al. 1997, Abele et al. 2001). At the time, it was suggested that whilst Antarctic species may have maximised the activity of their antioxidant system to work at near freezing temperatures to combat the associated high oxygenation levels, this came with a trade-off of reduced thermal stability (Abele et al. 2001). In similar studies, the thermal denaturation of enzymes involved in the Krebs cycle have been suggested as the underlying cause of the accumulation of succinate as a stress metabolite (Van Den Thillart & Smit 1984, Michaud et al. 2008). This field of investigation is expanding due to the rapid advances in sequencing technologies, which allow for the evaluation of thousands of genes in any one species when subjected to different environmental stressors. In the study of six different marine invertebrates warmed at 1°C h^{-1}, as described previously, different responses were seen in each species. Whilst it was impossible to narrow down organism failure to one specific enzyme or group of enzymes, it was noteworthy that in the bivalve *Aequiyoldia eightsii,* the metabolite *O*-propionyl carnitine was produced, which is involved in fatty acid and energy metabolism. This chemical is critical for the induction of antioxidant defence against lipid peroxidation in mammals, which is cytotoxic (Sayed-Ahmed et al. 2001). Hence, although limited in number, these studies show that there is species-specific enhanced sensitivity of critical enzymes, which may directly impact on organism physiology and survival.

The third mechanism for temperature limitation, via insufficiency of energy reserves, can work in two main ways: (1) As temperature increases metabolic rates in ectotherms rise, the minimum maintenance costs rise, usually increasing by a factor of two to three for every 10°C of warming (Peck 2016). Increased temperature increases the rate at which, for instance, digestive enzymes function and the rate at which food can be processed, but these changes will be small and only affect resource gained over part of the year. If overall resource availability does not change, or changes to a very small extent, and there is little or no ability to increase resources gained, then an increase in maintenance metabolic costs reduces energy available for other functions such as growth or reproduction, and such reductions can prejudice long-term survival of populations; (2) The interplay between resource availability, seasonality and increased costs could have specific impacts. Most Antarctic primary consumers feed on the summer phytoplankton bloom, which is only available for a short period each year (Clarke 1988, Clarke & Leakey 1996, Ducklow et al. 2013, Venables et al. 2013). In response to the low food availability in winter, many Antarctic species stop feeding and markedly reduce metabolic rates in winter, sometimes to a hypometabolic state (Barnes & Clarke 1994, 1995, Brockington & Peck 2001, Barnes & Peck 2005, McClintock et al. 2005, Morley et al. 2016c), and this winter hypometabolic state is not limited to primary consumers, having been observed in fish (Campbell et al. 2008), bivalve molluscs (Morley et al. 2012a), and brittle stars and nudibranch molluscs (Obermüller et al. 2010). Seasonality of primary production is primarily driven by light and nutrient availability, and these factors are not likely to change significantly the duration of food availability for primary consumers in the Southern Ocean over the coming decades of climate warming, although changes in ice cover are likely to have large effects (see sections on 'The intertidal and sea ice', and 'Ecological change'). The warming of the environment will, however, increase the metabolic energy costs of the overwintering period, and if stored reserves are insufficient, then capacity to exploit the following season's productivity could be reduced, or survival may be compromised during the winter.

The final potential mechanism for temperature limitation is the requirement for long periods for Antarctic marine species to acclimate their physiology to altered conditions. Studies of long-term exposure to raised temperature have been undertaken in Antarctic fish (Bilyk & DeVries 2011), and

there is evidence that even after prolonged periods acclimation is incomplete in cardiorespiratory capacity (Egginton & Campbell 2016), which would reduce resistance to warming. In the invertebrates, very long periods, between three and nine months, have been reported as required to complete acclimation in Antarctic marine invertebrates (Peck et al. 2009b, 2010b, 2014, Morley et al. 2011, 2016c, Suckling et al. 2015). Such long periods required to complete acclimation mean that physiological mechanisms are not optimised for several months when seasons change. Although for the next 100 years winter sea temperatures in Antarctica's shallows will still be close to the freezing point of seawater, winters will be shorter and summer maxima higher. Hence, exploitation of altered conditions, especially as the annual temperature range will increase with a warmer sea, may not be possible as the animals are almost permanently in the process of acclimating their physiology.

One reason why acclimation might require longer to complete in Antarctic species is the reported lack of ability to modulate the fatty acid saturation of cellular membranes when animals are warmed. Gonzalez-Cabrera et al. (1995), held two notothenioid fish species, *Trematomus bernacchii* and *Trematomus newnesi*, for five weeks at 4°C and showed that, although some physiological characteristics such as serum osmolarity and Na^+/K^+-ATPase activity changed over time, there was no alteration of cell membrane fatty acid saturation. Further to this, Macdonald et al. (1988) found that the release of acetylcholine from synaptic vesicles increased markedly at temperatures above 6°C in the fish *Pagothenia borchgrevinki*. As noted previously by Young (2004) and Young et al. (2006b), failure of neuromuscular junctions also occurred at temperatures near upper thermal limits in two Antarctic marine crustaceans. A failure of mitochondrial function was reported at significantly lower temperatures in Antarctic fish than temperate species by Weinstein and Somero (1998) and Strobel et al. (2013), and mitochondrial failure at the lowest reported temperature for any marine species (9°C) was reported by Pörtner et al. (1999a) for the Antarctic clam, *Laternula elliptica*. These were both identified by a sharp change in slope of an Arrhenius regression of rate of oxygen consumption versus temperature for the mitochondria. Pörtner et al. (2007, 2012) interpreted these results as indicating that the absence of acclimation could be due to the evolutionary loss or malfunction of one or more of the enzyme systems needed to restructure lipids in membranes when animals are warmed. Many of the previous failures can be explained by an uncontrolled increase in membrane fluidity, and loss of control of membrane fluidity would affect a very wide range of cellular functions from pumping of ions for homeostasis to depolarisations for nervous conduction.

It is currently unclear which of the previous mechanisms is the most important in limiting any given species' capacity to resist or survive environmental warming, and as concluded by Clark et al. (2017), for resistance to rapid warming, different factors may be the most important in limiting different species, and there might not be a single overriding paradigm. The factor dictating survival might depend on both intrinsic factors such as levels of phenotypic plasticity or extrinsic factors such as rising temperature increasing costs with little increase in resource availability, and these factors will differ between species because of, for instance, different trophic requirements, activity levels, life histories, and so forth. It is likely that one or more of the mechanisms described will impact fitness in the majority of Antarctic marine species, and possibly all of the mechanisms will need to be assessed for a wide range of species before a reliable mechanistic understanding of the responses to environmental change can be obtained for Antarctic marine species.

Effects of age and life-history stage on resistance to warming

Thermal windows differ across life-history stages (Pechenik 1987, Pörtner & Farrell 2008, Philipp & Abele 2010, Peck 2011, Clark et al. 2013, Peck et al. 2013). They are often quoted to be narrowest in early developmental stages (Vernon 1900, Spicer & Gaston 1999), and it has been suggested that thermal constraints in early life stages might be a major factor limiting geographical distributions (Andronikov 1975, Pechenik 1999, Byrne 2011, 2012, Karelitz et al. 2017). Recent studies have especially emphasised the sensitivity of larval stages (Przeslawski et al. 2015, Karelitz et al. 2017, Clark pers. comm.).

In Antarctica, the effects of temperature on development of embryos and larvae have been studied for over four decades, with research primarily on echinoderms and molluscs (Pearse 1969, Bosch et al. 1987, Clarke 1992, Stanwell-Smith & Peck 1998, Peck et al. 2006a, 2007b, 2016a). The major finding is that temperature has a much more marked effect on development rates at temperatures around or below zero than in warmer areas, that temperature is the main criterion slowing development in Antarctic species (Hoegh-Guldberg & Pearse 1995), and that problems associated with protein synthesis are probably a major factor (Peck 2016). In the urchin *Sterechinus neumayeri*, for example, development rate of eggs and embryos increased monotonically between −2°C and +0.2°C but did not increase at temperatures above this (Stanwell-Smith & Peck 1998). Mortality, on the other hand, was low and stable between −2°C and +1.7°C, above which it increased rapidly. There was thus a window between +0.2°C and +1.7°C where development was at its fastest and mortality low. Two other species studied, the starfish *Odontaster validus* and *O. meridionalis*, had different patterns, with development rate in both increasing monotonically across the temperature range studied (−2°C to +3°C). Mortality was different between the starfish species studied, with *O. meridionalis* having a linear increase in mortality across the temperature range, from around 5% to 20%, whereas *O. validus* had constant mortality between 10% and 15% across the range. For all three species, levels of mortality of the eggs and embryos were well below the normally quoted 50% in thermal tolerance studies, so the upper temperature limit for eggs and embryonic development was well above 3°C. Upper temperature limits at slow rates of warming have been measured for adult *Sterechinus neumayeri* as between 4°C and 5°C (Peck et al. 2014), and at around 7°C for adult *Odontaster validus* (Peck et al. 2008). These results show that there are marked differences in the temperature relationships for development in Antarctic marine species, and there may not be a universal pattern or difference between early life stages and adult temperature limits, but that for some at least, temperature limits to early stage development are similar to those of adults in Antarctic marine species. So far, only a single study has been conducted on the effects of pressure on the urchin *Sterechinus neumayeri* that showed increasing pressure reduced the thermal windows of development for eggs and embryos (Tyler et al. 2000).

Most research on temperature limits in the past has compared early stages with adults either at similar rates of warming, or where adults have been warmed acutely. On these measures, early life stages are generally thought to be more sensitive to elevated temperature (e.g. Storch et al. 2011, Collin & Chan 2016). As seen previously, however, temperature limits for embryonic development are close to the long-term limits, or limits at slow rates of warming for at least some of the Antarctic species studied. There may thus be a perceived difference because relevant rates of warming have not been used for each life-history stage in the comparisons. Thus, if we take into account the numbers of cell divisions involved, where early stages are conducting cell division at rates much faster than later life stages, then a comparison with long-term limits at slow rates of warming for adults would be the most appropriate, and the differences between thermal limits of early and later life-history stages might not be as extreme as often perceived. This would argue for a limiting mechanism at the cellular level where problems accumulate with cell division or metabolic processes that run faster in early stages than adults and hence would argue in favour of mechanisms that explain temperature limitation from the accumulation of toxic end products or accumulated molecular damage.

At developmental stages between larvae and adults, there have been several studies of thermal tolerance and resistance to warming in juveniles or early juveniles of Antarctic marine invertebrates. The general conclusion in most of these studies is that juveniles are more resistant to warming than adults. Thus, in a study of four Antarctic species (*Laternula elliptica, Sterechinus neumayeri, Odontaster validus* and *Heterocucumis steineni*) warmed at rates between 1°C h^{-1} and 1°C every 3 days, Peck et al. (2013) showed that early juveniles either had the same or higher upper temperature limits than large adults. Peck et al. (2007a) further showed that juveniles of the clam *Laternula elliptica* maintained the ability to rebury into sediment at higher temperatures than adults. In other studies on Antarctic marine species, juveniles have been found to be more resistant than adults to a range of environmental stressors. In *Laternula elliptica*, small individuals were less impacted than

large adults by disturbance from increased sedimentation, and survival after injury (Philipp et al. 2011). In the same species, the immune system performed better in juveniles than adults in response to physical damage and starvation (Husmann et al. 2011), and again in *L. elliptica*, juveniles were more resistant to hypoxia than adults (Clark et al. 2013).

These whole-animal results were supported by evidence from several molecular analyses. For example, a study of haemocytes and siphon tissue that showed stronger upregulation in juveniles than adults of genes involved in antioxidant defence (*Le*-SOD and *Le*-catalase), wound repair (*Le*-TIMP and *Le*-chitinase), and stress and immune response (*Le*-HSP70, *Le*-actin, and *Le*-theromacin) (Husmann et al. 2014). Additionally, in a study of resistance to warming in *L. elliptica*, younger individuals had a more robust response, as demonstrated by a strong upregulation of transcripts of chaperones and antioxidants, not seen in adults (Clark et al. 2016). In that study, Clark et al. (2016) also showed that as individuals aged the proportion of their body allocated to muscle progressively declined, which may partly explain the lack of activity in older animals. These studies of responses to elevated temperature and other stresses all support the disposable-soma-theory of ageing: in long-lived species that reproduce many times, resources are diverted from tissue maintenance to reproduction progressively with age (Abele et al. 2009), and this leaves them less capable of responding to environmental insults.

In addition to the physical effects of warming on different species, there is a significant but underexplored consequence of the increased development rates that are a consequence of warming. That is, species with a pelagic phase, either as larvae or buoyant eggs, will experience a decrease in dispersal potential as the larval developmental phase is passed through more rapidly. Consequences are likely to differ between species and also depend on distances between habitable environmental patches and current regimes, but in *Sterechinus neumayeri*, raising the temperature from −2°C to +0.5°C reduces the time from egg fertilisation to settlement from over 120 days to under 90 days, or a 25%–30% reduction. Similar reductions in larval lifetime would likely remove some current dispersal routes for several or many species. This is clearly an area that needs more investigation in the future.

Resistance to altered temperature is the most studied environmental factor in relation to predicted future change, and it is often cited as the most important factor in this respect. However, the most recent investigations have involved combined evaluations of the impacts of altered temperature and carbonate saturation on larval development (e.g. Karelitz et al. 2017). The main conclusions of this type of work are that development rates increase with temperature, but that mortality and developmental abnormality increases markedly above a certain temperature. The two combined produce an optimal temperature window for development. This is discussed in more detail below.

Ocean acidification and organismal responses

Changing ocean chemistry

Human outputs of CO_2 since the industrial revolution have increased global temperatures by absorbing radiation from the Earth that would otherwise have passed out of the atmosphere. A second major consequence is that around 30% of the CO_2 released has been absorbed by the oceans, which has resulted in a decrease of ocean pH of around 0.1 units, and the major part of this change has occurred in the last 50 years (Caldeira & Wickett 2003, 2005, IPCC 2014). Carbonate solubility varies strongly with pH, temperature and pressure, with higher solubility at lower pH, higher pressure and lower temperature. Thus, for the same amounts dissolved per unit seawater and the same concentrations, the solubility state is lower in all three cases. This results in the deep oceans being undersaturated and the polar oceans having lower carbonate saturation at the surface than oceans at lower latitudes (Orr et al. 2005, Fabry et al. 2009). Future predictions are that acidification will continue to be strongest in the polar regions, especially in Antarctica such that surface waters will be undersaturated for aragonite, the more soluble of the common forms of carbonate, by the middle of this century (Figure 21, McNeil & Matear 2008, Feely et al. 2009a,b, 2012). This undersaturation will occur first in winter, which has

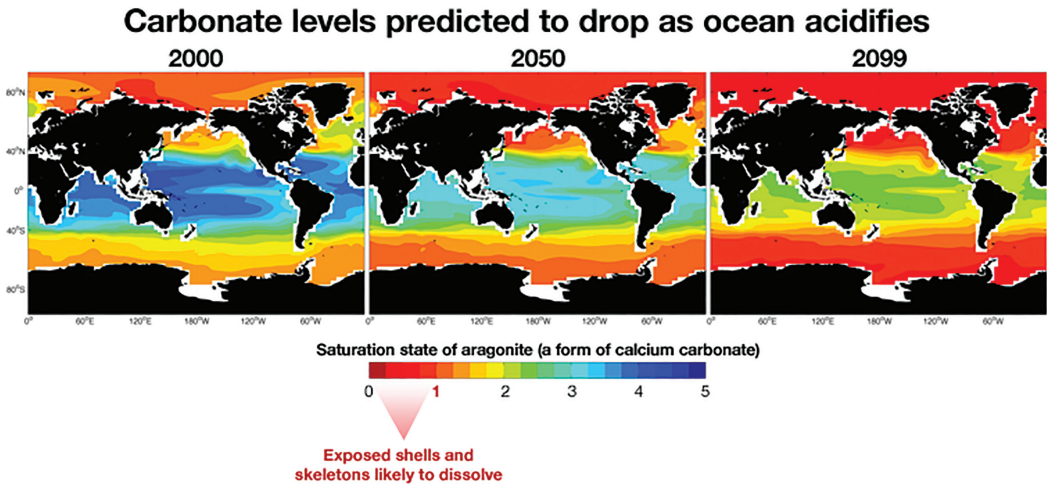

Figure 21 Model derived saturation states for aragonite in the world's oceans for 2000, 2050 and 2099. Where aragonite saturation is below 1, it is undersaturated, and materials made of this form of $CaCO_3$ should dissolve. (Figure produced by Woods Hole Oceanographic Institution based on Feely, R.A. et al. 2009a. *Oceanography* **22**, 36–47.)

colder conditions than summer, and there is already a seasonal signal in carbonate saturation in the Southern Ocean (McNeil et al. 2011, Hauri et al. 2016, Legge et al. 2017).

General predictions are that as carbonate solubility increases organisms will need to expend more energy to extract this essential material from seawater, and species heavily dependent on carbonates to make skeletons, such as molluscs, echinoderms and crustaceans, will be particularly at risk. Indeed, trends in skeletons across latitudes have also been observed that are consistent with higher solubility of carbonates at higher latitudes (e.g. Watson et al. 2012, 2017), and in an observational study, Sewell and Hoffmann (2011) using an analysis of depth ranges and calcification of Antarctic echinoderms concluded with the prediction that future acidification will produce a shallowing of the carbonate compensation depth (the depth at which the solubility (Ω) of $CaCO_3 = 1$ and below this it dissolves), which will remove heavily calcified forms from progressively shallower depths. In this respect, these groups in the polar regions can be viewed as likely being the first to suffer from acidification effects and as 'a canary in the mine' type of indicator of ecosystem state or health. Given the importance of Antarctica as the place where acidification is predicted to show its effects first, it is surprising that more research has not been carried out on the impact it is having, or will have, on Southern Ocean species. From a Web of Science search in September 2017, nearly 6000 papers have been published on ocean acidification in international scientific journals, but fewer than 250 of these include material on Antarctica.

The importance of Antarctic studies in a global context has been highlighted by several authors and a range of reasons quoted. Thus Whiteley (2011) stated 'The species most at risk [from ocean acidification] are exclusively marine and have limited physiological capacities to adjust to environmental change. They are poor iono- and osmoregulators and have limited abilities to compensate for acid–base disturbances. The problems are compounded in slow-moving, relatively inactive species because they have low circulating protein levels and low buffering capacities. Species living in low-energy environments, such as deep-sea and polar habitats, are particularly vulnerable, because they are metabolically limited with respect to environmental change'. This is the generally accepted position in ocean acidification research. However, despite the perceived importance of polar research and the seeming vulnerability of its fauna, there are relatively few publications and data are scarce.

Global responses to ocean acidification

Early investigations of the effects of altered pH generally found strongly negative effects on organisms of acidified conditions, especially in groups such as corals (e.g. Hoegh-Guldberg 1999, Raven et al. 2005, Kleypas et al. 2006, Hoegh-Guldberg et al. 2007, Kuffner et al. 2008, Kroeker et al. 2010, 2013). This area of research particularly expanded after the publishing of the seminal paper 'The other CO_2 problem' (Doney et al. 2009). Studies around this time on the effects of lowered pH on early life stages usually reported particularly large negative impacts (e.g. Kurihara & Shirayama 2004, Kurihara et al. 2007, Dupont et al. 2008, Watson et al. 2009). The majority of research in this field to date has concentrated on temperate species and studies range from field observations, for example in pteropods (Bednaršek et al. 2012), through laboratory manipulations to historical evaluations of skeletons in sediments (e.g. Mackas & Galbraith 2012) or from museum collections (Cross et al. 2018). The most frequent approach has primarily been based on laboratory manipulations and evaluating responses in terms of survival, integrity of skeletal structures or evaluations of physiological mechanisms such as metabolism or acid–base regulation (e.g. Gazeau et al. 2007, 2011, McDonald et al. 2009, Melzner et al. 2009a,b, 2011, Beniash et al. 2010, Talmage & Gobler 2010, Welladsen et al. 2010, Baumann et al. 2012, Comeau et al. 2012a, Ziveri et al. 2014).

Many of the earlier studies suffered from being short-term, acute exposures, and this problem began to be highlighted in the field around 2011 (e.g. Byrne 2011, Whiteley 2011). Whilst short-term studies may be useful in highlighting the differences in resilience between species, progressively more research has been conducted using longer-term exposures of weeks to months. Many of these have reported greatly reduced or no measureable effects of lowered pH on marine species in adult resistance (e.g. Coleman et al. 2014, Hazan et al. 2014, Cross et al. 2015, 2016), energetics (Morley et al. 2016c), reproductive characteristics (Havenhand & Schlegel 2009, Parker et al. 2012, Suckling et al. 2015, Munday et al. 2016, Runge et al. 2016), and embryonic and larval development (e.g. Suckling et al. 2014a,b, Bailey et al. 2016). These studies demonstrate that the impacts of acidification are much less when long-term exposures are used, and negative reproductive effects are lessened greatly when parental broodstock are conditioned for long periods before spawning (e.g. Suckling et al. 2015). One step further on from long-term studies is that of multigenerational effects. To date, very few studies have investigated the capacities of species to respond to acidified conditions across generations, and generally, significant adaptation is found in most of these studies (reviewed in Sunday et al. 2014, Stillman & Paganini 2015). In microbes, performance returns to normal levels within a few cell divisions (e.g. Collins 2012, Lohbeck et al. 2013). In multicellular animals, the requirement for such research has been highlighted, although data are very limited (e.g. Munday et al. 2013, Reusch 2014, Sunday et al. 2014). In the very few multigenerational studies conducted, performance of animals held in acidified conditions returns to levels very similar to that of individuals held in control conditions in only a few generations, and this has been demonstrated in the marine polychaete *Ophryotrocha labronica* (Rodríguez-Romero et al. 2016) and the sea urchin *Psammechinus miliaris* (Suckling & Clark pers. comm.), but there may also be lasting subtle effects such as impaired learning and altered neurotransmitter and retinal function (Nilsson et al. 2012, Chivers et al. 2014, Chung et al. 2014, Lai et al. 2015, Roggatz et al. 2016). An unusual very recent approach has been to investigate skeletons of marine calcifiers from samples collected over the last 120 years from museum specimens. In such a study, Cross et al. (2018) showed that oceanic changes since the early 1900s have had no discernible effect on shell structure or chemistry using a wide range of analytical techniques. Another unusual, very recent approach assessed changes in shell shape (Telesca et al. 2018) and composition (Telesca pers. comm.) in mussels of the genus *Mytilus* from sites across 3980 km of coastline stretching from the Arctic to the Mediterranean Sea and showed that seawater pH had a very small effect on these keystone bivalve and that temperature salinity and food supply were the major drivers. The only change detected in the study was a 3% increase in shell density. Furthermore, studies at the molecular level have shown significant amounts of genetic variability in response to ocean acidification (Pespeni et al. 2013a,b), which may promote resilient populations.

Another more recent development in the field is to investigate multiple species, or community-level responses to acidification. Here studies have generally shown that some species are negatively impacted by lowered seawater pH, others are affected little by conditions predicted up to 2100, while some species have improved performance in altered conditions (e.g. Dijkstra et al. 2011, Hale et al. 2011, Peck et al. 2015a, Schram et al. 2017). There has also been a move to study multifactorial effects, primarily combined with temperature but also with other factors such as salinity. These investigations have usually found that temperature has a larger impact on the biology of the studied species than acidification (e.g. Wood et al. 2010, Noisette et al. 2014, 2015, Collard et al. 2016, Zhang et al. 2016, Glandon & Miller 2017, Karelitz et al. 2017).

The impacts of acidification on marine calcifiers that reduce skeletal integrity are often discussed in the context of predator/prey interactions and poorer abilities to defend against, especially, crushing predators. Such discussions usually ignore likely impacts on the predators, where data are generally more limited, but impacts could be greater on durophagous predators because their skeletons are more soluble, and their skeletons dissolve faster in exposures to acidified conditions in general than their molluscan prey (E.M. Harper, personal communication). The crushing molars on the dactylus pivot point of crab and lobster chelae are the hardest and most carbonate-dense structures in either crustacean or molluscan skeletons. It is likely that they will, therefore, be more difficult to make in a future high CO_2 world than less calcium-dense structures. Further to this, recent research has demonstrated that when Antarctic macroalgae are held in altered conditions, their ability to deter amphipod herbivores remains unchanged, despite there being changes in their biochemical composition (Schram et al. 2017). More research is needed on crustacean predators and their likely future under climate change to better inform debate on predator/prey interactions in the coming decades.

Despite the increasing number of studies demonstrating that impacts of acidification are much less when long-term exposures are used and multiple generations examined, there are species differences. In some species, there are rapid adaptations to altered pH conditions across generations, but there are still species where acidification has significant negative impacts and areas, such as predation pressure, where there are very few data. The current challenge is to identify which species are being, and will be, negatively impacted in future and how that will affect ecosystem stability and the capacity of the oceans to provide services for human societies.

Ocean acidification in Antarctica

In a similar fashion to studies at lower latitudes, several Antarctic studies have reported negative impacts of ocean acidification. This was especially so for the early research where laboratory exposures to altered pH were rapid and acute. Again, as understanding improved and experiments have become more sophisticated, more recently laboratory-based research has used longer-term exposures and often reported smaller impacts, or none at all, for mid- or end-century predicted conditions. Recent studies involving more than one environmental stressor have also usually found acidification to have a smaller impact than other factors, especially temperature (e.g. Huth & Place 2016a,b, Enzor et al. 2017).

Enzor et al. (2017) working on Antarctic fish, using modern molecular methods, showed that temperature had a much larger effect on animal physiologies and capacity to acclimate than altered pH, but there was a small combined effect beyond that of temperature alone. In a 42- to 56-day acclimation experiment, they demonstrated that *Pagothenia borchgrevinki* was able to acclimate its oxygen consumption and aerobic capacity to temperatures around 4°C and a pCO_2 of 1000 μatm, but *Trematomus newnesi and T. bernacchii* only achieved partial compensation, indicating there were energetic limitations or compromises. Temperature is usually identified as the major factor in experiments on Antarctic fish species when more than one variable is considered. There are, however, very large differences in the responses to multiple environmental stressors between Antarctic fish species that have been observed at molecular, cellular, tissue and whole-animal levels

(e.g. Huth & Place 2016a,b). This echoes the work identifying species-specific responses and species-specific factors setting limits to warming in Antarctic marine invertebrates (Clark et al. 2017).

Most of the polar, and more specifically Antarctic, work on altered seawater chemistry has focussed on sea urchins, as these are very easy to maintain in aquaria and spawn. Recent laboratory investigations have focussed on multiple stressors and attempted to identify the relative impact of acidification and any synergistic effects. Ho et al. (2013) conducted fertilisation experiments on the urchin *Sterechinus neumayeri* at temperatures 2°C and 4°C above, and 0.2–0.4 pH units below, ambient. They found that temperature and sperm concentration affected fertilisation rates, but acidification did not. Ericson et al. (2012) studied fertilisation and early development in the same species and concluded that both attributes were highly resistant to altered pH and temperature conditions over the coming decades, but that predicted conditions for 2100 and beyond had measureable negative effects for both temperature and pH and their interactions. Similar conclusions were earlier drawn by Ericson et al. (2010) for both *S. neumayeri* and the nemertean *Parborlasia corrugatus*, where in both species fertilisation and early development were not noticeably affected by a pH decrease of 0.3–0.5 units. In a later study on *Sterechinus neumayeri*, Yu et al. (2013) also found very limited effects of near future acidification conditions (to 2100) on early development, and Clark et al. (2009) found that embryonic and larval development in *S. neumayeri* is more resilient to future predicted acidification conditions than in urchins from lower latitudes. In an investigation on the Subantarctic urchin *Arbacia dufresnii*, Catarino et al. (2012) concluded there was no measurable effect on embryo or larval morphology or behaviour of lowered pH (to 7.7 or 7.4), and the only identified impact was a slowing of development rate. There have been several investigations of combined impacts of predicted climate-driven alterations to temperature and acidification on Antarctic species. These have predominantly reported significant temperature but only mild or no effects of acidification. This has been demonstrated for early development in the urchin *Sterechinus neumayeri* (Byrne et al. 2013, Kapsenberg & Hofmann 2014). More recently, Karelitz et al. (2017) came to similar conclusions for the urchin *S. neumayeri* and the starfish *Odontaster validus*, that elevated temperature has a far greater impact on embryo and larval development then lowered pH, that there is little synergistic effect, and that temperature will have far more impact on future distributions than acidification of the oceans in these species. Similarly, in the infaunal bivalve mollusc *Laternula elliptica*, Bylenga et al. (2015) showed there was little effect of altered pH on fertilisation and early development, but elevated temperature (from −1.6°C to −0.5°C) had a positive effect across all pH treatments. In the single stressor experiment on the starfish *Odontaster validus*, Gonzalez-Bernat et al. (2013) reported negative effects of lowered pH on larval survival at end-century predicted conditions but not in near future conditions. They also reported small negative impacts on fertilisation success in end-century conditions but only at low-sperm concentrations. It thus seems that from the limited number of species studied, Antarctic urchins are resistant to predicted acidification conditions to the end of the century and possibly beyond.

In terms of the impacts on adults, Cummings et al. (2011) studied the effects of lowered pH on the bivalve *Laternula elliptica* and found significantly higher basal metabolic rates and more indication of stress as indicated by HSP70 expression after 21 days. They further found no significant differences between altered pH treatments and controls after 120 days in HSP70 expression or animal condition, but basal metabolism was elevated. They suggested that long-term increased costs could have large impacts on survival of the species. Further to this, McClintock et al. (2009) showed that shells of three dead mollusc and one dead brachiopod species suffered significant dissolution within 35 days of exposure to pH 7.4. Schram et al. (2014) found that altered pH and elevated temperatures to predicted end-century levels had no measurable effect on righting responses in the limpet *Nacella concinna* or the gastropod *Margarella antarctica*. Further to this, Schram et al. (2016a) found little or no effect of the same conditions on shell morphology, proximate body composition, growth or net calcification in the same species. One study at least, however, has reported stronger acidification than temperature effects at end-century conditions. Schram et al. (2016b), working on the macroalgal associated amphipods *Gondogeneia antarctica* and *Paradexamine fissicauda*, identified a range of

sublethal effects caused by elevated temperature and lowered pH, but the latter produced a large increase in mortality in both species. As discussed in the previous section on 'Global responses to ocean acidification', our knowledge of predator–prey interactions in a high CO_2 world is poor. However, in Antarctica, this point might be different from lower latitudes because of the lack of durophagous predators (e.g. Aronson et al. 2007), but skeletal integrity and strength is likely to be important here in defence against drilling predators such as the snail *Trophonella shackletoni* and also against the abundant soft-bodied predators including starfish, anemones and nemertean worms.

A few studies in Antarctica have assessed the impacts of altered pH on macroalgae, which are important in their own right but also serve an extra key function as community habitats. Schoenrock et al. (2015) studied combined end-century temperature and acidification effects on *Desmarestia anceps* and *D. menziesii* and found no negative responses to either stressor in either species. The species did, however, respond differently, which led the authors to conclude that future change could alter algal community structure and, hence, communities associated with and dependent on macroalgae. After this, Schoenrock et al. (2016) showed that amongst the macroalgae crustose fleshy species responded better to altered conditions than calcified species, again suggesting significant change in community structure is likely in the coming decades.

Responses to altered environments can require very long periods in Antarctic marine invertebrates as acclimation to elevated temperature can take three to nine months (Peck et al. 2009b, 2010b, 2014, Bilyk and DeVries 2011), and acidified conditions can extend this period (Suckling et al. 2015). Thus, long-term studies are paramount in these species to ensure they are fully acclimated to the altered conditions, as stated in the previous section 'Global responses to ocean acidification' on temperature, and to allow evaluations of realistic responses to predicted environmental change. For example, *Laternula elliptica* requires very long times to complete shell repair after damage (Sleight et al. 2015), and hence, it is likely that some of the results obtained in the study by Cummings et al. (2011) may have differed if longer times had been allowed for full acclimation. In fact, long-exposure experiments on Antarctic brachiopods showed that they are able to repair shell damage and also produce new growth in end-century pH conditions at the same rates as animals in controls (Cross et al. 2015). Similarly, in a two-year exposure study of reproduction in the urchin *Sterechinus neumayeri*, Suckling et al. (2015) showed that up to eight months might be required for adults to acclimate fully their metabolism to altered pH and temperature, and embryo and larval development were significantly enhanced in altered conditions when the parents had been exposed to end-century conditions for 17 months as opposed to six months. In the same species, Morley et al. (2016c) found no effect of lowered pH (-0.3 and -0.5 units) or elevated temperature (2°C) on the growth of somatic or reproductive tissue, or scope for growth after 40 months of exposure. In general, even though the number of species studied to date is small, these very long-term exposures show at least some Antarctic marine species have the potential for significant phenotypic plasticity to respond to altered pH.

In contrast to shallow-water species, research on some pelagic taxa has consistently demonstrated negative impacts of acidification. Thus, Bednaršek et al. (2012) showed that Southern Ocean pteropods have significant dissolution of their shells that is consistent with increased carbonate solubility in the region. A similar result was also demonstrated for pteropods in low-pH upwelling water in California (Bednaršek et al. 2014). Other studies have demonstrated measurable impacts of acidification on pteropods in experiments (Lischka et al. 2011) and from observations of changes in latitude and time (Comeau et al. 2012b). However, more recently, Peck et al. (2016b,c) have cast some doubt on how important some of these observations are as they showed that in healthy animals the external protein covering on pteropod shells, the periostracum, and internal repair mechanisms can provide a powerful defence against dissolution at reduced pH. They further showed that individuals that have damaged periostracum, either from earlier failed predation attacks or from handling in experiments, suffer significant dissolution that can be confused with dissolution from altered conditions, *per se*. Other Antarctic pelagic species investigated include copepods (Bailey et al. 2016), where acidification had little or no effect on development of early life stages, and krill where

Kawaguchi et al. (2011) found no effect on embryos and larvae of elevating CO_2 to 1000 μatm but found negative impacts at 2000 μatm. In a microcosm-based community-level study, Tarling et al. (2016) showed that exposure to pCO_2 levels of 750 and 1000 μatm altered the community balance, and the interaction between copepods and their dinoflagellate prey was particularly affected. It should be noted that all of the pelagic experimental studies, because of restrictions to shipboard experiments, have been short-term, often with large changes to levels of pCO_2 in the system to values beyond those predicted for the year 2100, and as seen for benthic species, increasing the duration of exposure significantly alters the outcomes of experimental trials. The future challenge will be the development of longer-term trials in pelagic species.

In summary, there are very few long-term studies in Antarctic species. Where these have been performed, they generally show resilience. However, to date we have no knowledge of the underlying genetics of either skeletal production, what makes a more resilient animal or indeed and what proportion of the population may contain genes that confer resilience. These are clearly targets for future research.

Summary and conclusions

Biodiversity in the Southern Ocean is much higher than would be expected from standard texts on global biodiversity that highlight the trend of reducing diversity with latitude. This high Antarctic biodiversity is particularly evident in the benthos, where it is estimated that as many as 17,000–20,000 species of invertebrate are likely living on the Antarctic continental shelves. The fauna has evolved in isolation from other continents and continental shelves, and a range of unique adaptations has been produced, the most well known of which are antifreeze in fish, an absence of red blood cells in channichthyid fish, the absence of the standard heat shock response in several species and large size in some taxa. There are likely many more subtle changes that are opaque to the methods used to assess adaptations in the past, but that will be uncovered in the coming years because of the rapid improvement in the 'omics' technologies and the explosion of their use on Antarctic species in the last five years.

As well as many cellular and physiological adaptations being different in Antarctic marine species, life histories and physiological rates are generally slower than those at lower latitudes. Some traits such as growth and embryo/larval development are slowed well beyond the normal expected effects of temperature on biological systems. This has been attributed to problems associated with the manufacture of proteins at low temperatures, which is carried out at rates around eight times slower than in temperate species. This problem has also been suggested to play a role in the observation that Antarctic marine species also generally have larger eggs than those at lower latitude, and there seems to be a general trend of larger eggs in lower temperature habitats. One factor suggested to be potentially important in making proteins more difficult to synthesise in Antarctica is increased viscosity effects on protein folding at temperatures near or below 0°C. Increased viscosity has also been proposed in this review as possibly implicated in pumping rates slowed beyond expected temperature effects in Antarctic filter feeders. This contrains feeding abilities but also has strong implications for all ciliary-based activity at polar temperatures, including swimming in marine invertebrate larvae and sperm and protists. A further viscosity-related point that needs attention is the possibility that the absence of haemoglobin in channichthyid icefish might give advantages at low subzero temperatures when blood viscosity is raised further by the presence of small ice crystals and the attendant antifreezes.

Slower physiological rates appear to be linked to lower capacities for activity and to perform work. This has been suggested to be the possible cause for the lack of crushing predators in Antarctic marine habitats, as power production in muscles is related to environmental temperature. It is suggested here that predation patterns in Antarctica may also differ from lower latitudes as they are dominated by soft-bodied, engulfing predators such as starfish, nemertean worms and anemones. This means predation would differ in kind from tropical to polar regions and makes assessments of predation pressure across latitudes more complex than considered in previous studies.

Global environmental change is a major issue for biologists and ecologists across the planet. It is particularly important in polar regions because the most rapid change has occurred in these areas in recent decades. In Antarctica, rapid change has been confined mainly to areas on and around the Antarctic Peninsula, where air temperatures rose by around 3°C in the last half of the twentieth century, and to the west of the Antarctic Peninsula, where sea temperatures at the surface increased by 1°C in the same time. Other areas of Antarctica have not warmed significantly, and this has been explained by the tight wind patterns around the continent. The ozone hole has contributed to the tightening and strengthening of the circumpolar westerly winds around Antarctica in the last century, which may have helped to keep the east Antarctic from warming (Marshall 2003, Barnes EA et al. 2014b, https://legacy.bas.ac.uk/met/gjma/sam.html). The future strength of the circumpolar westerlies and hence their impact on temperature in east Antarctica is affected both by the filling of the ozone hole and global CO_2 concentrations. These opposing effects have different outcomes in different Intergovernmental Panel on Climate Change (IPCC) model predictions (Barnes EA et al. 2014b). Some predictions indicate there will be more rapid warming in east and parts of west Antarctica, which would expand considerably the potential area where ecosystems are under threat.

Two main challenges for organisms in the Southern Ocean from climate change have been identified: warming and ocean acidification. There are two main ways organisms can respond effectively to such change, by coping with the plasticity of their phenotype and adapting their genetic make-up to make them more fit for the new conditions. Antarctic marine species appear to have poor capacities to respond to environmental warming compared to temperate species and in this respect are similar to tropical species. Unlike both temperate and tropical species, however, they need very long periods to reset their physiology after a change in temperature, requiring up to as much as nine months to acclimate. This means their ability to cope, through phenotypic plasticity, with fluctuations in temperatures is less than species living elsewhere. Their long generation times and production of larger, but fewer eggs when they spawn are also both factors reducing their likelihood of either generating mutations that are beneficial in increasing survival or exchanging useful genes between populations.

In the context of ocean acidification, calcification, especially to produce skeletons, has a greater energetic cost for high latitude marine species than those living at lower latitudes because CO_2 and carbonate solubility is higher in colder waters, which reduces carbonate availability. This cost is even greater when assessed in relation to the animal's overall energy budget because metabolic and growth rates fall markedly at temperatures below 0°C, but costs of calcification do not. Evidence for this is seen in the trend for marine calcifiers to have smaller skeletons in colder waters. Furthermore, taking into account regional impacts of climate change, carbonate ion availability will reach critical levels of undersaturation in polar oceans before areas at lower latitudes. Data suggest, however, that Antarctic marine species have better than expected capacities to resist altered seawater pH, and that temperature is likely to be a greater challenge for many species than acidification, at least until the end of this century. In this context, there is a fundamental need for long-term studies of organismal responses to change over several months to years. There is a further need for research incorporating transgenerational effects. Such studies should incorporate temperature, altered pH, oxygen and salinity amongst other factors, as well as working at higher ecological scales incorporating several species or working at the community or assemblage level. There are, however, many unknowns, and each species has different responses to change. The data are too poor to be able to identify which species are most vulnerable to change and if any of these are crucial to continued ecosystem functioning. This is the challenge for the future.

Long-term studies over decadal scales are needed to identify changes in physiological processes, especially reproductive effort and success, in Antarctic marine species. Data to date show large interannual variation. However, identifying trends, the role of natural cycles such as Southern Oscillation Index (SOI) or El Niño-Southern Oscillation (ENSO), or the effects of extreme years is essential to predicting impacts of future change, and this is not possible without very long-term data.

In addition, future change will also bring the collapse of ice shelves and coastal glaciers, which will expose new areas of coastal ocean to sunlight for primary production, both in the water column or, in shallower areas, on the seabed itself. This will allow new communities to establish, and at least in the short-term, overall levels of biomass in the Southern Ocean are likely to increase due to these processes. It could also affect the dispersal capabilities of many species, as it has been suggested here that transport on icebergs is a likely important mechanism for gene flow in the sedentary or slow moving benthos that brood their offspring, and these species dominate assemblages on the Antarctic seabed. There is much uncertainty over future changes in the physical marine environment, especially in relation to frequency of iceberg scour, currents and circulation patterns, so detailed predictions of biodiversity responses are not possible. It is highly likely, however, that if and when there is ice-free coastline year-round in Antarctica, the prospects for the establishment of non-native species will rise dramatically.

Overall, the marine life in the Antarctic is characterised by a unique cold-adapted fauna. Much current research has concentrated on the effects of change on marine invertebrates which are integral to the Antarctic food web and Antarctic marine ecology. Changes to the numbers and the balance of these invertebrates will significantly impact commercial fisheries, the ecology of marine protected areas (MPAs) and the populations of the charismatic larger animals (seals, whales, albatrosses, etc.) on which much of the burgeoning tourist industry is based. However, we currently do not know if the ecology of the polar regions critically hinges on one or two or even a handful of species. There are insufficient data at present for any level of certainty. However, with the emergence of new technologies, we are now in a better position than ever before to unlock the secrets of Antarctic marine life. These developments are rapidly changing our abilities to obtain information, produce and interrogate models, and test and erect hypotheses. This is especially so in the 'omics' technologies, where a revolution in understanding seems to be happening now. Dramatic improvements in understanding are also likely from the use of unmanned vehicles such as drones and gliders and the increasing sophistication of satellite imaging and analysis.

In terms of the science to be done in Antarctica in the coming decades, there are more questions and challenges now than ever before. The future may be daunting in many respects for many marine species, with the prospects of large negative impacts from climate change, but it also holds very exciting times for science in Antarctica, especially in understanding adaptations and improving the knowledge base from the use of novel technologies.

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