COMMENTARY

Why might they be giants? Towards an understanding of polar gigantism

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Summary

Beginning with the earliest expeditions to the poles, over 100 years ago, scientists have compiled an impressive list of polar taxa whose body sizes are unusually large. This phenomenon has become known as 'polar gigantism'. In the intervening years, biologists have proposed a multitude of hypotheses to explain polar gigantism. These hypotheses run the gamut from invoking release from physical and physiological constraints, to systematic changes in developmental trajectories, to community-level outcomes of broader ecological and evolutionary processes. Here we review polar gigantism and emphasize two main problems. The first is to determine the true strength and generality of this pattern: how prevalent is polar gigantism across taxonomic units? Despite many published descriptions of polar giants, we still have a poor grasp of whether these species are unusual outliers or represent more systematic shifts in distributions of body size. Indeed, current data indicate that some groups show gigantism at the poles whereas others show nanism. The second problem is to identify underlying mechanisms or processes that could drive taxa, or even just allow them, to evolve especially large body size. The contenders are diverse and no clear winner has yet emerged. Distinguishing among the contenders will require better sampling of taxa in both temperate and polar waters and sustained efforts by comparative physiologists and evolutionary ecologists in a strongly comparative framework.

Introduction

'...as the dredge cleared the surface, we saw it full and overflowing with every form of sea life it is possible to imagine… most conspicuous of all were the giant sea-spiders, red in color, and from 6 to 7 inches across the legs.'

From *South with Mawson* by C. F. Laserson, zoologist on the 1911–1914 Australasian Expedition (Laserson, 1947).

For well over a century, zoologists and explorers to the poles have observed that organisms there can reach remarkably large sizes. Early explorers from the Antarctic, such as Laserson from the Australasian expedition, wrote in their populist travel journals about the giant animals obtained from nearshore marine dredging (Laserson, 1947); the organisms collected by these expeditions were written up in scientific journals of the day (e.g. Eights, 1856; Hodgson, 1905; Dall, 1907). Sea spiders the size of dinner plates, and other bizarre life discovered by these explorers, added to the mystery and excitement surrounding the Antarctic continent and helped to fuel the Heroic Age of Antarctic Exploration.

From a biologist's perspective, polar gigantism fascinates because it is bizarre, and because gigantism is a potentially powerful tool for understanding the physical, ecological and evolutionary principles that govern the evolution of body size. Body size is a key determinant of how organisms interact with their environments (Hildrew et al., 2007), and understanding the evolution of body size has been a central focus of evolutionary biology (Roff, 1992; Stearns, 1992; Blanckenhorn, 2000). That polar giants occur in many distantly related taxa indicates that gigantism has evolved independently many times, suggesting that some master mechanism drives the pattern (Chapelle and Peck, 1999). This has in turn led to questions about patterns of absence, i.e. why some polar groups contain no giants. By 'going to extremes', biologists hope to understand factors that drive evolution in the ecosphere in general.

Though gigantism has also been reported from terrestrial organisms [e.g. lichens (Øvstedal and Smith, 2001)], we focus on organisms from the marine environment because the terrestrial Antarctic fauna is comparatively sparse, whereas the polar oceans are home to a fauna that is rich and often strange. In terms of multiple metrics, conditions in polar oceans are extreme. Polar oceans are the coldest large bodies of water on earth, with temperatures at the freezing point of seawater (–1.8°C) during winter in the Arctic and year-round near the continental coast and ice shelves of the Southern Ocean (Clarke, 2003). Polar ectotherms, which do not produce substantial metabolic heat, move, grow, feed and reproduce at body temperatures so cold that temperate and tropical relatives would be torpid or even frozen solid. Numerous metabolic, biochemical, life history and physiological adaptations have been described that help polar ectotherms to function at these temperatures (e.g. DeVries, 1988; Clarke, 1991; Clarke, 1998).

Polar environments have other unique characteristics. Above the Arctic and Antarctic circles, day length cycles annually between 0 and 24h, driving dramatic annual cycles of productivity and, therefore, food availability for filter and
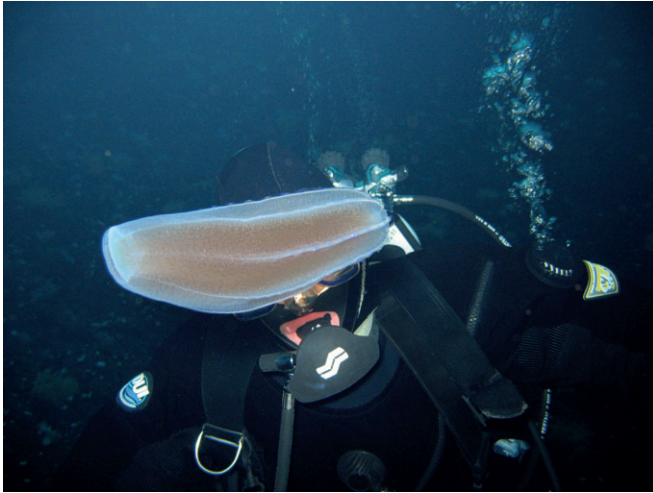
Fig. 1. Diver A. L. Moran behind a large beroid ctenophore, near McMurdo Station, Antarctica. Photo by B. Miller.

Fig. 2. Diver S. Rupp pictured near McMurdo Station, Antarctica, amongst specimens of the glass sponge *Anoxycalyx jouboni*. Photo by R. Robbins.

suspension feeders (Clarke, 2003). This cycle of feast and famine has been linked to unusually slow growth rates, enhanced resistance to starvation, and reduced ecological competition (Lindstedt and Boyce, 1985; Cushman et al., 1993; Arnett and Gotelli, 2003). Seawater in the Southern Ocean is also rich in O_2 and silica (Ragueneau et al., 2000), and building shells and other calcium carbonate structures is both more difficult and more energetically expensive in the cold (McClintock et al., 2009). Organisms in the Antarctic have evolved in relative isolation under these conditions for millions of years, making the Antarctic a 'natural laboratory for tackling fundamental questions' (Clarke, 2003). Below, we explore the links between the physical, chemical and biological environments of polar seas and the evolution of gigantism.

Who are the giants?

Polar gigantism has been reported among many taxa of marine organisms, including copepods (Hop et al., 2006), pteropod molluscs (Weslawski et al., 2009), cephalopod molluscs (Rosa and Siebel, 2010), ctenophores (Barnes, 2005) (Fig. 1), chaetognaths (MacLaren, 1966), foraminiferans (Mikhalevich, 2004), amphipod crustaceans (DeBroyer, 1977), isopod crustaceans (Menzies and George, 1968; Luxmoore, 1982), sponges (Fig. 2) (Dayton and Robillard, 1971), polychaete annelids (Hartman, 1964), echinoderms (Dahm, 1996) and pycnogonids (sea spiders; Fig. 3) (Child, 1995). Polar gigantism has also been reported from the fossil record [trilobites (Gutiérrez-Marco et al., 2009)]. We first discuss definitions of 'gigantism' and explore how common this phenomenon is in polar systems.

Clearly gigantism is relative, requiring comparison with other related taxa. In early studies of isopod and tanaid crustaceans, Wolff (Wolff, 1956a; Wolff, 1956b) noted that the largest species within genera occurred in the Antarctic and the deep sea. Arnaud (Arnaud, 1974), in what is still the most extensive review of polar gigantism, reported the lengths of the largest polar organisms while acknowledging that size must be considered in the context of each phylogenetic group. Other polar researchers have applied more quantitative criteria; DeBroyer (DeBroyer, 1977) categorized a species as giant if it was at least twice as large as the mean body size in its genus, and Chapelle and Peck (Chapelle and Peck, 1999)

if its body length was in the top 5% for its taxon within a particular habitat.

Although there is no universal definition of polar gigantism, comparative evidence that it exists is strong, at least in some taxonomic groups. Perhaps the clearest example comes from amphipods in the suborder Gammaridae, shrimplike crustaceans that are diverse and that contain close relatives living in both polar and non-polar regions (DeBroyer, 1977; Gomes et al., 1993). DeBroyer (DeBroyer, 1977) analyzed gammarid body sizes and found strong evidence for large body size at the poles, particularly in the Antarctic; 31% of species in the Southern Ocean had body lengths >2× larger than the mean body size of their genus, compared with 28% in the Arctic, 21% in the deep sea and 0.8% in the tropics. Thus, although giants occur in most habitats, they are more common at the poles. In isopods of the cosmopolitan genus *Serolis*, maximum body size increased with latitude and no small-bodied species occurred in the Southern Ocean (Fig. 4) (Luxmoore, 1982).

Although the literature contains many other references to gigantism, few examples have been analyzed in a comparative context. Gigantism among pycnogonids is frequently cited (e.g. Dell, 1972; Arnaud, 1974; Child, 1995; Clarke and Johnston, 2003) and would be a good subject for additional comparative work because sea spiders are found worldwide, yet are abundant and diverse in the Southern Ocean (Child, 1995; Munilla and Soler-Membrives, 2009). The largest pycnogonids occur in the polar oceans and the deep sea (Arnaud and Bamber, 1988). Glass sponges (Class Hexactinellida) provide another spectacular example (Dell, 1972): the barrel sponge *Anoxycalyx (Scolymastra) jouboni* can reach 2 m in height and 1.5 m in diameter (Dayton and Robillard, 1971). The ribbon worm *Parbolasia corrugatus* can reach 2 m in length and 100 g in body mass (Davison and Franklin, 2002), making it among the world's largest nemerteans by mass (Arnaud, 1974), and at least 14 species of polychaete worms (phylum Annelida) from the Antarctic have body lengths >10 cm (Hartmann, 1964), including *Ophioglycera eximia*, which reaches 76 cm. However, although these examples are spectacular, demonstrating gigantism *via* the comparative method has been impossible in many cases because of low taxon sampling and a lack of detailed phylogenies.

Fig. 3. Giant Antarctic sea spider (phylum Pycnogonidae), probably *Colossendeis megalonyx*, photographed near McMurdo Station, Antarctica. The gloved finger of a diver is visible at the bottom left. Photo by B. Miller.
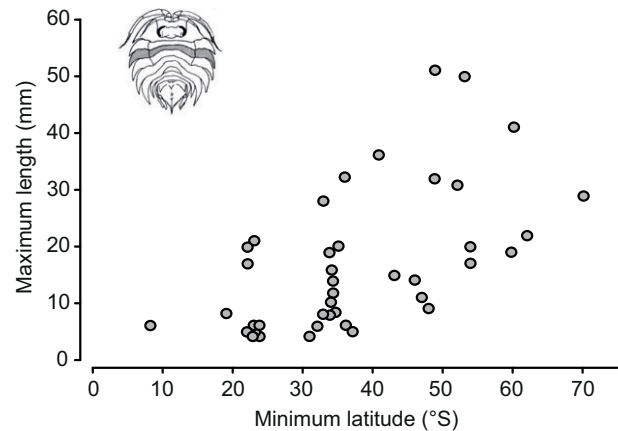

Fig. 4. Variation in size with latitude of isopod crustaceans in the genus *Serolis*. Maximum length of adult males of the 41 species that occur at depths of <200 m plotted against their minimum recorded latitude. Spearman's rank correlation coefficient, r^2=0.650 (*P*<0.001). [Redrawn and reprinted from *J. Exp. Mar. Biol. Ecol.* **56**, Luxmoore, R. A., Moulting and growth in serolid isopods, p. 82. Copyright (1982), with permission from Elsevier.]

Many other major groups lack giants or even trend towards high-latitude nanism (unusually small body size). In the bivalve molluscs (clams, scallops and oysters), Nicol (Nicol, 1967) found no high-latitude species, towards either pole, that he considered large. In fact, many are unusually small [<10 mm in length (Nicol, 1967)]. Prosobranch gastropod molluscs (shelled snails) also lack giants at the poles, and tend to be small in the Antarctic (but not the Arctic) (Arnaud, 1974). Other groups that lack giants, or that tend towards polar dwarfism, include scaphopod molluscs (tusk shells) (Arnaud, 1974), chitons (class Polyplacophora) (Arnaud, 1974), fish (Andriashev, 1965; Knox, 2007) and brachiopods (Arnaud, 1974; Peck and Harper, 2010). Moreover, even higher taxa that contain polar giants may have subgroups that do not. For example, in the amphipod family Lyssianasidae – which is in the suborder Gammaridae, discussed above as containing giants – polar species are not unusually large compared with cold-temperate species. High-latitude species tend to be larger than average, but this trend is driven by a lack of large-bodied species in the tropics rather than the presence of giants at the poles (Steele, 1983).

This diversity of examples demonstrates that studying polar gigantism is a two-part problem. The first is to determine whether polar gigantism is systematic or represents excessive attention paid to a few unusual taxa. In part, this issue stems from a historic paucity of studies on polar taxa, and of taxonomic specialists working on Antarctic groups (Arnaud, 1974). Likewise, polar waters have historically been poorly sampled, particularly deeper zones (Griffiths et al., 2009); however, substantial international efforts have recently been made to further explore and describe the biological diversity of the Southern Ocean [e.g. the Census of Antarctic Marine Life, part of the International Polar Year research effort; described in Griffiths et al. (Griffiths et al., 2011)]. New focus on the diversity and relatedness of polar organisms, combined with modern systematic and comparative methods, will provide new tools for detecting gigantism, or the lack thereof.

The second part of the problem is to determine, for taxa that show polar gigantism, whether some common factor drives, or allows, evolution of large body size or, instead, whether many factors contribute idiosyncratically in different taxa. The rest of our review focuses on this second problem. Many hypotheses have been suggested to explain polar gigantism, and these provide a large set of alternative but non-exclusive potential mechanisms.

Why might they be giants?

Like other biogeographic patterns, polar gigantism likely will defy simple explanatory frameworks. One set of theories invokes biophysical and physiological explanations; these focus on the effects of unusual levels of environmental factors in polar environments, particularly temperature, oxygen and carbonate chemistry. A second set of ideas invokes biogeographic and ecological explanations, which draw historical links between polar oceans and other regions that share taxa, or which invoke unusual ecological conditions at the poles. A third set focuses on developmental plasticity and evolution. These explanations tend to analyze life history trade-offs between growth, fecundity and mortality associated with latitudinal changes in competition and predation, temperature and resource availability. Not all possible mechanisms are mutually exclusive. We agree with Angilletta et al. (Angilletta et al., 2004) that any broad theory of body size will have to be multivariate, in the sense that multiple factors probably contribute to gigantism in taxon-dependent ways. This prognosis could be viewed as gloomy, but it likely reflects the messy, historical, contingent nature of biology better than any simpler alternative.

Below we organize the discussion around the three levels of analysis outlined above, with caveats. The first is that several of the ideas (e.g. the temperature–size rule) do not fit readily into our organizational scheme because they integrate elements from across levels of biological organization; for convenience, we discuss the temperature–size rule in the section on developmental plasticity and evolution. Second, most of the ideas focus on temperature. A temperature-centered approach is appropriate: cold, stable temperatures are a dominant characteristic of polar marine habitats, temperature has pervasive effects on all biological processes, and most studies to date have focused on temperature as a causal agent. Nevertheless, it is not certain that low temperature has driven polar gigantism either alone or in interaction with other factors. Therefore, third, we also consider a smaller set of non-temperature hypotheses.
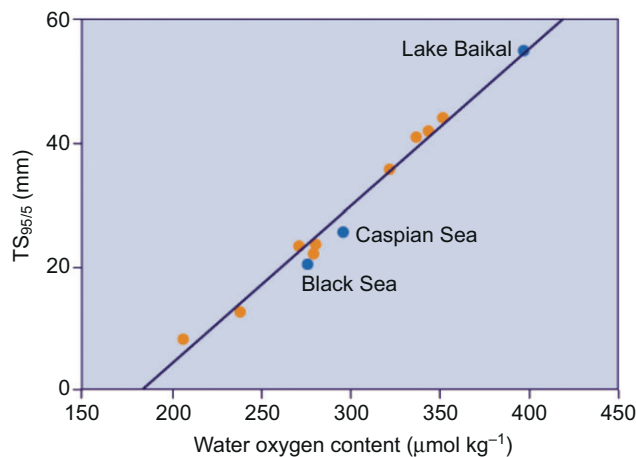
Fig. 5. The relationship between water oxygen content (at 100% saturation) and body size of the largest 5% of species of amphipod crustaceans in a given habitat (TS$_{95/5}$). Orange circles are marine sites; blue circles are reduced-salinity sites. Reprinted with permission from Macmillian Publishers Ltd: *Nature*, Chapelle, G., and Peck, L. S., Polar gigantism dictated by oxygen availability, pp. 114-115, Fig. 2b, 1999.

Biophysical and physiological explanations
Oxygen hypothesis

The oxygen hypothesis, proposed by Chapelle and Peck (Chapelle and Peck, 1999), states that polar gigantism stems from high oxygen availability coupled with low metabolic rates. The authors surveyed maximum body sizes in collections of amphipod crustaceans from different habitats, finding that the size of 'giants' in each locality – defined as the largest 5% of species in each habitat – correlated strongly with potential oxygen availability determined from water temperature (Fig. 5). They concluded that 'maximum potential size is limited by oxygen availability'. The oxygen hypothesis has received considerable attention (see McClain and Rex, 2001; Chapelle and Peck, 2004; Woods and Moran, 2008; Woods et al., 2009; McClain and Boyer, 2009; Klok et al., 2009; Verberk and Bilton, 2011; Verberk et al., 2011) and also considerable support in some taxa, particularly amphipods (e.g. Chapelle and Peck, 2004). Moreover, there is a substantial subset of literature suggesting that atmospheric O_2 and organismal body size have been linked through history (for a review, see Payne et al., 2011). However, even among the gammarid amphipods, which are poster children for polar gigantism, many polar representatives are tiny, and only a small fraction of taxa reach very large sizes even in regions of the highest oxygen availability (Chapelle, 2001; Chapelle and Peck, 2004). Thus, the main effect of the high ratio of oxygen availability to demand at cold temperatures is to increase the window of body sizes into which lineages diversify, rather than to drive the evolution of large body sizes. Other factors must be invoked to explain selection for large body size.

One appeal of the oxygen hypothesis is that it is experimentally tractable, in that it can be directly tested by assessing whether large-bodied organisms perform worse in hypoxia than small-bodied ones. Such a prediction follows naturally from the oxygen hypothesis, which implies that large-bodied organisms are closer to some upper limit in body size beyond which oxygen supplies would become inadequate. In one experimental test, Peck et al. (Peck et al., 2007) found that larger-bodied Antarctic clams had reduced burying performance in hypoxia compared with smaller

conspecifics. By contrast, Woods et al. (Woods et al., 2009) used a righting assay to assess whether large-bodied Antarctic pycnogonids performed worse in hypoxia than small-bodied pycnogonids. In this case, the data said otherwise: regardless of body size, all pycnogonids performed worse in hypoxia, and there was no hint of size dependence in the effects.

The straightforward interpretation of the data of Woods et al. (Woods et al., 2009) is that they reject the oxygen hypothesis. However, a more nuanced interpretation is possible. In particular, although cold temperatures and plentiful oxygen may have allowed the repeated evolution of gigantic Antarctic pycnogonids, there has been superimposed on those events a process of coadaptation by different, linked components of the respiratory system, and trade-offs among multiple costs and benefits of having cuticles of some particular permeability. Pycnogonids obtain oxygen *via* diffusion directly across the chitinous exoskeleton, and diffusion is facilitated through pits and channels that make up >30% of the cuticular surface (Davenport et al., 1987). The lack of any size-dependent effects of hypoxia on performance might be explained by selection acting to reduce the 'excess' oxygen diffusion capacity of small polar pycnogonids, perhaps to increase resistance to predators or buckling forces, or to protect them from excessively high levels of internal oxygen, which could produce damaging reactive oxygen species. Conversely, in the evolutionary trajectory from small to large body sizes, perhaps giant pycnogonids obtain adequate oxygen, even when working hard, through cuticles that have evolved to be especially permeable to oxygen. These outcomes could be interpreted as reflecting either symmorphosis (the idea that organismal form and function are closely matched across levels of biological organization) or size-dependent shifts in the relative value of the costs and benefits of having a particular cuticular permeability.

The links between body size, environmental oxygen availability and performance have been used to argue that as marine and aquatic environments warm, small body size will be favored and giants will be among the first to disappear (Chapelle and Peck, 2004; Daufresne et al., 2009; Pörtner, 2010). Our arguments above, however, imply that temperature-dependent physiological systems (that is, essentially all systems) are more co-adapted to each other than they are to the size of the organism. Thus, there is no simple prediction possible about the relationship between size and vulnerability, at least with respect to individual organisms (rather than evolving lineages) and physical aspects of the environment such as temperature or oxygen availability.

Carbonate and silica chemistry in Antarctic waters

Polar seas, in particular the Southern Ocean, have unusual carbonate and silica chemistry, possibly affecting which taxa attain giant sizes. Some marine taxa use silica in their skeletons, including both the single-celled diatoms and radiolarians and the multicellular 'glass' sponges (phylum Porifera, class Hexactinellidae). Silica is often limiting in tropical and subtropical waters, but is more abundant in the Southern Ocean because of upwelling of silica-rich deep water (Ragueneau et al., 2000). Plentiful silica may contribute to the large size of silica-based organisms such as the giant Antarctic glass barrel sponge, *Anoxycalyx (Scolymastra) jouboni* (Arnaud, 1974). However, the availability of silica does not lead to gigantism in all silicaceous organisms; though the shells of Antarctic radiolarians are more heavily silicified than the shells of warm-water relatives, their cell sizes are no larger (Lazarus et al., 2009).

Why don't some other groups of organisms attain giant sizes at the poles? The answer may also be determined by ocean chemistry, particularly levels of calcium carbonate ($CaCO_3$). The solubility of CO_2 increases with decreasing temperature, and, by taking up more CO_2, cold waters become relatively more acidified. In turn, cold water and acidification enhance the dissolution of $CaCO_3$, potentially making calcification difficult and costly at cold temperatures (reviewed in Doney et al., 2009). This problem is most acute in the Southern Ocean, where temperatures are <0°C year-round, dissolved CO_2 is high and there is little input of carbonate from freshwater runoff. In this corrosive environment, animals with skeletons based on $CaCO_3$, such as echinoderms, shelled molluscs and stony corals, may be limited to small sizes by the high metabolic expense of building and maintaining their skeletons (Arnaud, 1974). Some groups, such as the shelled molluscs, indeed lack polar giants, and Antarctic animals with calcareous skeletons are often thin and fragile compared with their temperate relatives. However, other calcifying groups such as the echinoderms have large Antarctic representatives [e.g. the starfish *Megapteraster* (Arnaud, 1974)]. An alternative explanation for fragile calcareous exoskeletons is the lack of durophagous (crushing) predators in the Southern Ocean (Aronson et al., 2009).

Biogeographic and ecological explanations
Monsters from the deep

Many authors have noted that taxa from the polar oceans, particularly the Southern Ocean, share common evolutionary histories with taxa from the deep sea (Zinsmeister and Feldmann, 1984; Clarke, 2003). 'Abyssal gigantism' occurs in some of the groups also noted for polar gigantism, including pycnogonids, isopods, and amphipods. Does polar gigantism reflect invasion of the Southern Ocean by large-bodied animals from the deep sea? Perhaps, but the evolutionary history of the benthic Southern Ocean fauna is complex, likely with movement in both directions (shelf to deep and *vice versa*) (Brandt et al., 2007a; Strugnell et al., 2011). As data from the recent ANDEEP program, which samples the deep-water fauna of the Southern Ocean, are analyzed (e.g. Brandt et al., 2007b), such links, if present, should become apparent.

We suggest that the explanation that polar giants are 'monsters from the deep' is less than satisfying, because although it provides a proximate evolutionary explanation, it also pushes off the mechanistic explanation into other biomes: why then do large-bodied individuals evolve in abyssal zones? Abyssal waters share some features of polar waters, such as cold and stable temperatures, but other evolutionary forces that shape body size in the two regions likely differ and lead to contrasting outcomes in the two habitats; e.g. although gigantism is common among deep-sea shelled gastropods (McClain and Rex, 2001), it is not in polar regions (Arnaud, 1974).

Starvation resistance and the seasonal availability of resources

In polar seas, primary production fluctuates circannually, from high in the summer to virtually zero in the winter. Compared with small animals, large animals may resist starvation better (Cushman et al., 1993; Arnett and Gotelli, 2003), which may drive the evolution of large size in environments that impose intermittent starvation (Ashton, 2002; Blackburn et al., 1999). Strong seasonality may also limit the total number of species that an environment can support, which may alleviate interspecific competition, at least during periods when resources are available (Geist, 1987; Blackburn et al., 1999; Zeveloff and Boyce, 1988). Among polar ectotherms, however, metabolic rates are extremely low (Clarke, 1983) and even very small animals can live for months without feeding (Shilling and Manahan, 1994). Likewise, organisms that are most likely to be affected by low productivity in winter are filter feeders that rely on phytoplankton. In at least some groups of filter feeders, however, such as bivalves, polar gigantism has not been observed; in fact, this group tends towards nanism (Arnaud, 1974). Thus, resource availability does not provide an overarching framework for polar gigantism.

Latitudinal changes in resource quality

The quality of food resources for herbivores may increase with latitude (e.g. Bolser and Hay, 1996), and this may be related to latitudinal patterns of body size (for a review, see Ho et al., 2010). This hypothesis was tested by Ho et al. (Ho et al., 2010), who found that herbivorous ectotherms from a range of habitats (marine, terrestrial) in the Northern Hemisphere grew to larger sizes when reared on high-latitude diets. We know of no direct tests of this idea with polar organisms. In general, Antarctic macroalgae (which are the food of many herbivores in regions where ice cover does not preclude macroalgal growth) have stronger chemical defenses than do Arctic algae (Amsler et al., 2005), suggesting that this hypothesis is more relevant to northern than to southern polar gigantism.

Interspecific interactions

The Southern Ocean has a particularly unusual faunal composition. This region saw the onset of oceanic cooling and glaciation that likely scoured the continental shelves periodically beginning in the early Miocene, reducing regional diversity and eliminating some groups that are common elsewhere in the Southern Hemisphere (Anderson, 1999; Brandt, 2005). In particular, durophagous predators – such as sharks, skates and decapod crustaceans that break hard-shelled prey – have been absent from the Southern Ocean since the Eocene (Aronson et al., 2009). In their place, the most important predators now are asteroids, nemertean worms, isopods, amphipods, crustaceans and pycnogonids (Aronson et al., 2009), and this shift may have selected some lineages for larger body size (Barnes and Arnold, 2001).

The island rule of biogeography (Foster, 1964; Case, 1978) provides a framework for understanding the ecological factors driving the evolution of body size when animals invade novel, isolated habitats. When species invade islands, small mammals often evolve larger sizes whereas large-bodied taxa tend to shrink (Foster, 1964; reviewed in Millien and Damuth, 2004). The island rule cannot be explained by oxygen or temperature, because these rarely differ between islands and nearby mainlands. Rather, island gigantism is generally attributed to an escape from mainland predators and competitors, whereas nanism has been ascribed to reduced resource availability on islands (Foster, 1964). The Southern Ocean has many island-like characteristics: it is physically isolated and physiologically distinct, and many taxa have undergone ecological release from historical predators and competitors. We suggest that such factors, coupled with the raising of the ceiling on possible body sizes by the high ratio of oxygen supply to demand, may have led to the evolution of giants in many taxa. However, as on islands, most Antarctic taxa are neither giants nor dwarfs (Case, 1974).

Developmental and evolutionary explanations
Latitudinal gradients in body size and the temperature–size rule

Any temperature-related explanation must articulate the relationship between polar gigantism and two better-known patterns: latitudinal gradients in body size and the temperature–size

rule. Latitudinal gradients in body size represent a generalization of Bergmann's rule, which states that, within genera of endothermic vertebrates, species at higher latitudes tend to have larger body sizes (Bergmann, 1847; Watt et al., 2010). Bergmann proposed that larger individuals, with smaller surface-area-to-volume ratios, could more easily maintain high, stable body temperatures in cold environments. In general, ectotherms do not face similar thermoregulatory problems. However, many ectothermic taxa nevertheless show similar latitudinal gradients in body size (Angilletta and Dunham, 2003; Walters and Hassall, 2006; Pincheira-Donoso et al., 2008; Wilson, 2009; Lee and Boulding, 2010). Because Bergmann's rule applies specifically to endothermic vertebrates (Watt et al., 2010), we refer to the broader pattern, which includes ectotherms, as 'the latitude–size rule'.

Clearly, polar gigantism could be a high-latitude endpoint of the latitude–size rule applied to marine species; therefore, general explanations for this pattern may, in the end, also explain polar gigantism. Despite a broad search for explanatory mechanisms, no consensus has emerged. The four primary contenders, which partially overlap hypotheses outlined above, are that latitude–size clines reflect: (1) artifacts of phylogenetic history, because at high latitudes, large-bodied lineages are more likely to establish and diversify; (2) size-dependent variation between species in rates of migration or ability to establish in new areas; (3) variation in resistance to starvation (see above); and (4) variation in ability of species to conserve or dissipate heat (Cushman et al., 1993; Gaston and Blackburn, 2000). The latter mechanism, although plausible for terrestrial ectotherms (in air), is unlikely to be important for most marine ectotherms, which are essentially always in thermal equilibrium with their surroundings.

Polar gigantism and the latitude–size rule are both related to the temperature–size rule proposed by Atkinson (Atkinson, 1994; Atkinson, 1996), which focuses on developmental plasticity in response to rearing temperature. It is now evident that ectotherms growing in colder temperatures tend to reach larger final body sizes than do conspecifics in warmer temperatures (see Atkinson and Sibly, 1996; Atkinson et al., 2006; and references therein). In a broad review, Atkinson (Atkinson, 1994) found that in >80% of species, organisms grew larger when reared in cooler temperatures, in some cases by large margins. A string of papers in the past 20 years has sought to explain this pattern in satisfactory theoretical terms. Most of the models hinge on the idea that rate processes involved in growth or differentiation, or that the rates of growth, predation and fecundity, are differentially sensitive to temperature (reviewed by Angilletta et al., 2004; see also Perrin, 1995; Angilletta, 2009; Arendt, 2011). However, there is a more general reason to suspect that the temperature–size rule cannot not explain polar gigantism fully: the magnitude of the temperature–size rule within species does not appear, in general, to be large enough to account for the observed evolutionary differences in body size among species, with the caveat that there are few data available for evaluating this claim quantitatively.

Cold-driven selection for large offspring size

Another, less obvious form of gigantism common in polar waters is found in eggs, embryos and larvae. Thorson (Thorson, 1950) and Rass (Rass, 1935) first identified this biogeographic trend, in which marine invertebrates and fish at high latitudes produce fewer, larger offspring than their relatives elsewhere. 'Thorson's rule' (Mileikovsky, 1971), as it is now called, ascribes this pattern to evolutionary shifts from planktotrophy (having larvae that require exogenous food to complete development) to lecithotrophy (larvae

that can complete development without exogenous particulate food); lecithotrophy may be advantageous in polar climates because of long developmental times coupled with extreme seasonality in food availability (Thorson, 1950; Laptikhovsky, 2006). Even among planktotrophs, however, egg size tends to be large in polar regions (Thorson, 1950; Marshall, 1953). Rass (Rass, 1935) and Laptikhovsky (Laptikhovsky, 2006) point out that cold temperatures induce fish and invertebrates to produce larger eggs (plasticity); this is one oft-cited component of the temperature–size rule. Large egg size may also reflect selection for increased maternal provisioning to offset: (1) a poor or seasonally brief feeding environment (Thorson, 1950; Marshall, 1953), (2) greater competition in polar environments (Alekseev, 1981), or (3) the prolonged development that occurs at cold temperatures (Marshall, 1953).

Polar 'embryo gigantism' appears to be considerably more widespread than adult gigantism; for example, although the eggs and larvae of Antarctic fish are large in general (Marshall, 1953; and others reviewed in Knox, 2007), to our knowledge the adults of Antarctic fish are not considered large (see Marshall, 1953; Johnston et al., 2003). Among polar nudibranchs, eggs and embryos can be dramatically larger than those of temperate relatives (Woods and Moran, 2008), but sizes of adults are only modestly so. Comprehensive comparative studies are still lacking, but this pattern suggests that selection, plasticity or their combination act strongly on oogenesis to increase the size of eggs, larvae and juveniles in polar environments. Polar gigantism among embryos provides a rich but unmined context for testing theories of optimal offspring size (e.g. Smith and Fretwell, 1974; Yampolsky and Scheiner, 1996; Fox and Czesak, 2000). Note that this pattern (relatively larger embryos compared with adults) runs counter to the developmental effects of temperature across stages: Forster et al. (Forster et al., 2011) showed that developmental temperature generally had greater effects on adult size than on offspring size. This mismatch further undermines the possibility that the temperature–size rule accounts generally for polar gigantism (see preceding section).

Conclusions

The extreme, constant cold of polar marine environments has been implicated in many unusual traits, including gigantism, extreme stenothermality, freeze tolerance and changes in oxygen carrying and storage capacity. In general, these traits are interpreted as adaptive, though we do not always understand the underlying factors that have driven their evolution, or whether some may be 'disaptations' allowed by polar conditions (Sidell and O'Brien, 2006). Of polar phenomena, gigantism may be the most complex to unravel because body size is so central to ecological and evolutionary processes.

Our review has broken the problem of polar gigantism into two major issues. The first is, surprisingly, to determine even how common polar gigantism is. Although there are many convincing reports of polar giants, it remains unclear whether these examples reflect a few attention-grabbing outliers or more pervasive shifts in distributions of body size. Resolving this issue will require systematic sampling of species and body sizes in phylogenetic contexts. The second problem is to link patterns of body size to explanatory mechanisms. We distinguish at least eight major hypotheses above; each deserves additional theoretical and experimental work. Finally, looming above the set of individual hypotheses is the meta-problem of whether just one hypothesis will emerge as dominant or, alternatively, whether multiple hypotheses contribute to the pattern in taxon- and context-dependent ways. The

way forward, we think, is to view these possibilities as opportunities: understanding the factors underlying polar gigantism will both shed light on the fundamental processes underlying body size evolution and provide insight into the challenges that polar organisms will face during future climate change.

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