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PERSPECTIVES

Why polar gigantism and Palaeozoic gigantism are not equivalent: effects of oxygen and temperature on the body size of ectotherms

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Summary

1. Organisms of gigantic proportions inhabited the world at a time of a hyperoxic prehistoric atmosphere (Palaeozoic gigantism). Extant giants are found in cold polar waters, with large quantities of dissolved oxygen (polar gigantism). Oxygen is usually deemed central to explain such gigantism. Examples of one category of gigantism are often cited in support of the other, but novel insights into the bioavailability of oxygen imply that they cannot be taken as equivalent manifestations of the effect of oxygen on body size.

2. Recently, the availability of oxygen has been shown to be lower in cold waters, despite greater oxygen solubility. Consequently, gigantism in cold, oxygenated waters and gigantism in an oxygen-pressurized world are fundamentally different: Palaeozoic gigantism likely arose because of greater oxygen availability, while polar gigantism arises in spite of lower oxygen availability.

3. The traditional view of respiration focuses on meeting the challenge of extracting sufficient amounts of oxygen, which essentially is a toxic gas. We present a broader perspective, which specifically includes risks of oxygen poisoning. We discuss how challenges pertaining to balancing oxygen uptake capacity and risks of oxygen poisoning are very different for animals breathing either air or water.

4. We propose a novel explanation for polar gigantism in aquatic ectotherms, arguing that their larger body size represents a respiratory advantage that helps to overcome the larger viscous forces in water. Being large helps organisms to balance the opposing risks of asphyxiation and poisoning, especially in colder, more viscous, water. This results in a selection for larger sizes, with polar gigantism as the extreme manifestation. Hence, a larger size provides respiratory benefits to water-breathing ectotherms, but not terrestrial ectotherms. This can explain why clines in body size across temperature and latitude are stronger in aquatic ectotherms.

Key-words: Bergmann's rule, boundary layer, cost of breathing, oxygen limitation, oxygen toxicity, respiration, respiratory control, symmorphosis, temperature-size rule, viscosity

Oxygen and gigantism

Gigantism has long fascinated biologists and the role of oxygen has captured the minds of many researchers. This interest is not surprising given that body size is a primary corollary of key life-history traits such as fecundity,

mortality and growth rates, thus governing the way organisms interact with their environment (Peters 1983; Hendriks 1999; Brown *et al.* 2004; Hildrew, Raffaelli & Edmonds-Brown 2007). Of course, numerous other factors (e.g. temperature, length of growing season, food quality and quantity) are known to affect body size (e.g. Chown & Gaston 2010; Moran & Woods 2012), but oxygen may shift or push the boundaries of size distribution set by

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these other factors, with organisms attaining gigantic proportions accordingly. So, here we focus on situations where other factors already favour large size, and where elevated oxygen has been argued to either remove a final constraint or further drive the evolution of larger bodies. Most examples of gigantism fall into one of two categories, in each of which the dominant view is that oxygen is causally related to large body sizes. The first category, Palaeozoic gigantism, draws on a fossil record of giant arthropods and other animal groups coinciding with times of a hyperoxic and hyperdense prehistoric atmosphere; an oxygen-pressurized world (e.g. Graham *et al.* 1995). The second category, polar gigantism, draws on examples of gigantic ectotherms found in the icy polar waters, capable of holding large quantities of dissolved oxygen (e.g. Chapelle & Peck 1999; Woods *et al.* 2009). In both cases, the pattern seems straightforward enough: larger body sizes are associated with more oxygen. Mechanisms of decreased oxygen uptake and increased oxygen transport distance are used to explain how oxygen can set an upper limit to body size. The lower surface area to volume ratio in larger-sized organisms makes it more challenging for oxygen uptake to meet whole-body oxygen demand. Furthermore, once inside the body, oxygen needs to be transported over larger distances. Examples of one category of gigantism are often cited in support of the other (Chapelle & Peck 1999; Spicer & Gaston 1999; Harrison, Kaiser & VandenBrooks 2010; Payne *et al.* 2011). But can they really be taken as equivalent manifestations of the effect of oxygen on body size?

Polar gigantism in an oxygen low

Recent research shows the bioavailability of oxygen to be lower in cold waters, despite greater oxygen solubility (Verberk *et al.* 2011). The reason for this is that the diffusivity of oxygen decreases with decreased water temperature, which outweighs the increase in solubility (Dejours 1981; Woods 1999; Verberk *et al.* 2011). Consequently, and counter to received wisdom, the amount of oxygen that diffuses per time unit is lower in the cold, despite oxygen being dissolved in greater quantities, reducing an organism's capacity to take up oxygen (oxygen supply). Observed oxygen shortages in warmer habitats do not arise from lower oxygen concentrations, but instead through organismal oxygen demand exceeding supply (Atkinson, Morley & Hughes 2006; Woods & Moran 2008; Verberk *et al.* 2011; Fig. 1). A lower bioavailability of oxygen in the cold invalidates the usual explanation of high external availability of oxygen accounting for polar gigantism (Chapelle & Peck 2004). Instead, reduced organismal oxygen demand at cold temperatures may allow larger body size (Makarieva, Gorshkov & Li 2005; Verberk *et al.* 2011). Under this new view, oxygen supply can be higher in colder waters, but only when expressed relative to demand (Woods *et al.* 2009; Verberk *et al.* 2011).

Polar gigantism fits with the general pattern that across aquatic species, cold conditions also favour larger species

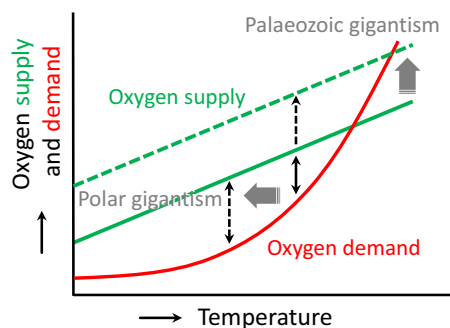


Fig. 1. Oxygen supply and demand as a function of temperature. If oxygen sets limits to the body size that an organism can attain, then larger ratios of oxygen supply relative to demand would allow for larger body sizes. Higher ratios can explain both Palaeozoic gigantism and polar gigantism. However, the higher ratio comes about via *increased* oxygen supply in an oxygen-pressurized world (upward grey arrow) and via *decreased* oxygen demand in the polar waters (sideward grey arrow). Note that environmental availability of oxygen rises in both air and water with increased temperature, so the larger ratios alone cannot explain observed discrepancies in size responses between aquatic and terrestrial ectotherms.

(Daufresne, Lengfellner & Sommer 2009), giving rise to latitudinal clines and abyssal clines in their body size (Timofeev 2001; Moran & Woods 2012; Jamieson *et al.* 2013). This latitudinal pattern across species is accompanied by a similar pattern within species of individuals attaining larger body sizes when reared at cooler temperatures (Atkinson 1994; de Queiroz & Ashton 2004), which is referred to as the temperature-size rule or TSR (Atkinson & Sibly 1997). While notable exceptions exist to both patterns (see e.g. Ashton 2002; Berke *et al.* 2013), the pattern of increases in body size with cool conditions seems especially strong in aquatic ectotherms, both across species (Daufresne, Lengfellner & Sommer 2009) and within species (Forster, Hirst & Atkinson 2012). By contrast, the largest representatives of terrestrial ectotherm taxa tend to inhabit the tropics (Makarieva, Gorshkov & Li 2005). So, can we explain such differences between the aquatic realm and the terrestrial realm (see Webb 2012) and are they related to differences in oxygen dynamics?

Both on land and in water, lower temperatures give rise to higher ratios of oxygen supply to demand. Yet, the discrepancy between aquatic and terrestrial ectotherms in, for example, their latitudinal size clines suggests that while increased ratios may be necessary for polar gigantism in water, they are not sufficient, and there must be an additional factor selecting for or permitting larger body sizes in cold waters. Could this be related to the fact that breathing under water is much more challenging than breathing air?

Balancing the risk of asphyxiation with the risk of oxygen poisoning

While oxygen can be good for generating the energy that supports most animal life, one can have too much of a

Box 1. Oxygen toxicity

Oxygen free radicals or reactive oxygen species can cause loss of function and damage within a cell, a situation referred to as oxidative stress. Although low levels of reactive oxygen species may be necessary for normal functioning as regulatory mediators in signalling processes (Droge 2002; Boardman *et al.* 2012), oxidative stress contributes to senescence and ultimately death (Fenn, Henning & Philpott 1967; Fridovich 1998; Lane 2002). Consequently, oxygen delivery and utilization have to be tightly regulated to balance the generation of energy and the production of toxic oxidants. For example, insects alter their breathing pattern abruptly to avoid oxygen toxicity (Hetz & Bradley 2005; but see Boardman *et al.* 2012), while during development, they can alter their tracheal volumes in response to rearing oxygen, regulating internal oxygen levels (VandenBrooks *et al.* 2012). Reversible binding of oxygen by respiration pigments also stabilizes oxygen levels. In this light, it is perhaps not surprising that evolutionary innovations in haemoglobin did not only occur during times of low oxygen, but also during times of high oxygen (Powell 2010). Mutant mice whose haemoglobin had better oxygen delivery capacity partook more actively in running activity, possibly as a last resort to downregulate cellular oxygen concentration (Shirasawa *et al.* 2003; Matsumoto *et al.* 2007). Additionally, temperature-induced differences in oxygen utilization altered the effects of ambient oxygen availability on fruit fly growth and survival (Frazier, Woods & Harrison 2001). Oxygen toxicity, even in normoxic conditions, has been reported for aquatic invertebrates (Fox & Taylor 1955) and mutant mice (Wicks *et al.* 2009). These mice could not express the anti-oxidant superoxide dismutase and suffered from increased oxidative damage, having a reduced life span under normoxia, but not hypoxia. So, oxygen can be toxic, even at relatively low levels, making tight regulation important. But precisely because of this tight regulation and effect of detoxifying antioxidants, oxygen toxicity is frequently masked.

good thing; high levels of oxygen are toxic (Box 1). Consequently, an animal must be able to reduce the risk of oxygen toxicity, while at the same time retaining sufficient scope for oxygen uptake across different levels of activity. These go hand in hand: increasing the capacity for oxygen uptake will likewise increase the risk of oxygen poisoning. Temperature and atmospheric pressure affect this balancing act very differently for organisms breathing in air or water (Table 1, Hypothesis 1) and consequently have different implications for polar gigantism and Palaeozoic gigantism.

One of the main differences between aquatic and aerial respiration is that water is much more dense and viscous than air, which together raise the costs of breathing or the mechanical power (J s^{-1}) needed to ventilate respiratory surfaces; the difference in density (kg m^{-3}) is 800-fold, and the difference in viscosity (Pa s) is 60-fold at 15 °C (Dejours 1981). In addition, the oxygen content of water is lower than air, which further increases costs of breathing (Makarieva *et al.* 2008). For instance, in rainbow trout, the oxygen cost associated with forced convection of water is about 10% of the total metabolism under resting conditions (Jones & Schwarzfeld 1974), which is about an order of magnitude greater compared with humans (Scheid 1987). The greater work involved in forced convection of dense, viscous water compared with air can explain why aquatic organisms rely on cutaneous respiration to a greater extent compared with terrestrial organisms (Table 1; Box 2). In contrast, many terrestrial animals have impermeable skins, an adaptation to reduce water loss. They mostly use lungs or tracheal systems to force convection of air.

The higher reliance on cutaneous respiration and the higher costs involved in forced convection of water, limits the capacity of water breathers to regulate oxygen uptake.

Compared with air-breathing organisms, they have fewer opportunities to balance risks of too little oxygen (asphyxiation) with those of too much oxygen (toxicity) without incurring large energetic costs, and hence, they are more susceptible to effects of low and high oxygen (Table 1; Verberk & Bilton 2011).

Box 2: Cutaneous respiration

Given the greater difficulty of forced convection of dense, viscous water compared with air, cutaneous respiration is a cheap way of taking up oxygen for aquatic ectotherms. Accordingly, many aquatic ectotherms use cutaneous oxygen uptake to some extent. For instance, damselfly nymphs can lose gills and still survive, provided the water is well oxygenated (Eriksen 1986). In crustaceans, gill excision does not impair oxygen uptake at low temperatures (Spicer & McMahon 1994). Furthermore, fish larvae breathe through their skin, which is rich in capillaries to extract oxygen from the water in a counter current fashion (Pauly 2010). Even adult fish rely on cutaneous respiration, accounting for 30% of the total metabolism under resting conditions (Feder & Burggren 1985). Thus, under circumstances of low activity or favourable conditions, aquatic ectotherms meet part of their oxygen demand by cutaneous oxygen uptake.

Advantages of large body size in cold water versus an oxygen-pressurized world

Oxygen has been hypothesized to become limiting at larger sizes (von Bertalanffy 1960), because when size increase

Table 1. List of hypotheses underpinning oxygen-related gigantism in water, the underlying mechanisms and their predictions backed up with evidence. For each hypothesis, recommendations for future experiments are also given

Proposed hypothesis	Mechanism	Prediction	Evidence	Future tests
H1. Regulation of oxygen supply to avoid both toxicity and asphyxiation is more difficult/costly in water than in air.	There is far less oxygen available in water, while the costs of moving water over respiratory surfaces are higher because water is much denser and more viscous than air.	<ol style="list-style-type: none"> Oxygen-based mechanisms will affect water-breathing ectotherms more than air-breathers <ol style="list-style-type: none"> Increased oxygen demand in warm environments will reduce optimal size more in water- than in air-breathers as the former cannot readily increase oxygen uptake. Hyperoxia will act more forcefully in driving evolutionary size increases in water- than in air-breathers by alleviating the higher costs associated with oxygen uptake and via enhanced oxygen toxicity. Tegument breathing avoids costly ventilation of gills and will therefore be widespread in aquatic ectotherms, even in large species and especially in species found in running waters. Across aquatic species, cold conditions exclude small species. Also supports H1. The scaling exponent of metabolism is temperature dependent in water breathers. As boundary layers will restrict gas exchange especially in smaller organisms with low Reynolds numbers, scaling exponents should be higher in cold water. 	<ol style="list-style-type: none"> Latitudinal size clines are opposite in terrestrial and aquatic ectotherms (e.g. Makarieva, Gorshkov & Li 2005; Verberk <i>et al.</i> 2011; Moran & Woods 2012). This also supports H3. Palaeozoic gigantism during oxygenation events is documented especially for aquatic ectotherms (Braddy, Poschmann & Tetlie 2008; Verberk & Bilton 2011) Even large fish rely partly on cutaneous respiration, despite operculum-enclosed gills which allow for efficient (but costly) forced convection of water (e.g. Feder & Burggren 1985). 	Test if the magnitude of effect of oxygen levels on physiological responses related to oxygen limitation (e.g. growth, heat tolerance) depends on their respiratory control: Poor regulators (e.g. tegument breathers) should show larger responses than good regulators and air-breathers.
H2. In cold, viscous water, gas exchange is compromised in small aquatic gas exchangers.	Cold, viscous water increases the thickness of boundary layers (reducing oxygen supply), while also increasing the effort required for ventilation (oxygen demand). These viscosity impacts are less for larger water-breathing organisms.	<ol style="list-style-type: none"> Across aquatic species, cold conditions exclude small species. Also supports H1. The scaling exponent of metabolism is temperature dependent in water breathers. As boundary layers will restrict gas exchange especially in smaller organisms with low Reynolds numbers, scaling exponents should be higher in cold water. 	<ol style="list-style-type: none"> Small fish species are absent in cold waters (Pauly 1998). In several fish species, the scaling exponent increases with decreasing temperatures (Killen, Atkinson & Glazier 2011; Ohlberger <i>et al.</i> 2012). 	Test if increased viscosity reduces growth and respiration in water-breathing ectotherms: Larger organisms should be less affected by increases in viscosity.
H3. Regulation of oxygen supply to avoid both toxicity and asphyxiation becomes easier for larger organisms in cold, viscous water.	Regulating oxygen uptake is more difficult in cold water where the higher viscosity reduces oxygen uptake and increases ventilation costs. Larger organisms can attain a greater range of <i>Re</i> helping them to balance asphyxiation and toxicity risks.	<ol style="list-style-type: none"> Polar giants are selected for as a large body helps to better regulate their oxygen budget. Consequently, gigantism should be absent in polar groups with a respiratory system that already allows for good respiratory control. 	<ol style="list-style-type: none"> Across species, organisms are larger in cold water (Daufresne, Lengfellner & Sommer 2009). H3 is also supported by evidence 1a and 3, above. Polar gigantism seems to be especially common in animal groups which rely on cutaneous respiration, thus having poor respiratory control (see text). 	Test if large organisms have better respiratory control than small organisms and if this difference becomes larger in colder, more viscous water.

is isometric, respiratory surface areas scale allometrically ($\propto M^{2/3}$) and are insufficient to meet the isometrically increasing demand of metabolizing body mass ($\propto M^1$) beyond a certain threshold size. Although the exact values of these scaling relationships may be more variable, the hypothesis still assumes that when expressed as mass-specific rates on a double-logarithmic plot, as in Fig. 2, oxygen supply (uptake capacity) would have a more negative slope than oxygen demand (maintenance metabolism) (Atkinson, Morley & Hughes 2006). According to this model, maximum body size can be explained from the balance between oxygen supply and oxygen demand (Fig. 2), the difference between them being aerobic scope or scope for growth (von Bertalanffy 1960). Cold conditions slow down chemical reactions involved in metabolism more than diffusion rates, and these kinetic effects result in higher ratios of oxygen supply to demand (Woods 1999; Atkinson, Morley & Hughes 2006; Verberk *et al.* 2011; Fig. 1). Thus, oxygen supply and demand will converge at a larger maximum size under cold conditions (compare Fig. 2a,b). While terrestrial ectotherms can easily increase ventilation rates, aquatic animals face higher costs of ventilation and rely more on cutaneous respiration (Box 2) and may therefore be more prone to oxygen shortage under warm conditions. Consequently, increased oxygen demand in warm environments may reduce optimal size more in water- than in air-breathers (Daufresne, Lengfeller & Sommer 2009; Table 1, Hypothesis 1).

Focussing now on aquatic ectotherms and how cold conditions favour large body sizes (polar gigantism), two additional, related arguments can be made. Both hypotheses are related to the viscosity of water, which doubles between 25 and 0 °C (Box 3). The higher viscosity of cold water increases the thickness of boundary layers enveloping respiratory surfaces and increases drag resistance. Increased drag results in higher energy expenditure when generating water currents necessary for respiration or feeding and during locomotion. Hypothesis 2 recognizes that larger organisms are relatively less influenced by viscosity of water (e.g. copepods experience viscous forces in water similar to a human swimming in tar). The higher viscosity of cold water will increase the costs of breathing (increase drag and hence ventilation costs) and decrease the capacity for oxygen uptake (increase boundary layer thickness), thus decreasing aerobic scope for all sizes, but especially for small-bodied organisms (compare Fig. 2c,d). The challenge of overcoming viscous forces is summarized by the dimensionless Reynolds number (Re), which is proportional to the length and speed of an organism and inversely related to viscosity (Box 3). The effects of Re on costs of ventilation (and boundary layer thickness) produce a nonlinear scaling relationship between body mass and oxygen demand (and between body mass and oxygen supply) (Fig. 2; Box 3; Vogel 1996). The result is that oxygen supply and demand may intersect twice, converging towards both minimal and maximal sizes and that increasing viscosity narrows the window of permissible body sizes (com-

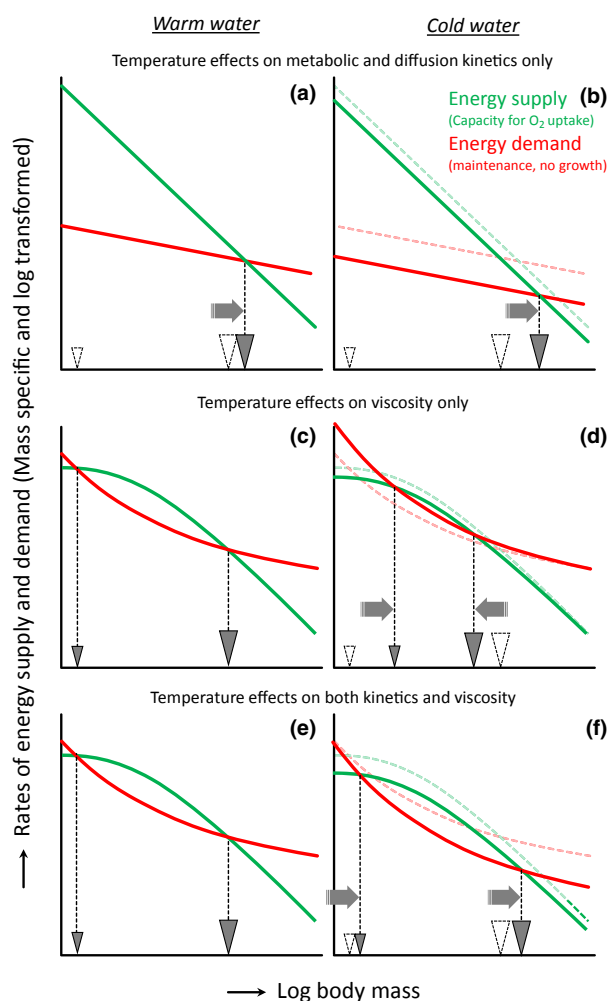


Fig. 2. Schematic representation of how rates of oxygen uptake and oxygen demand change with body mass thus setting limits to maximum or minimum size (indicated by filled triangles). Oxygen demand reflects maintenance costs. Warm water conditions (a,c,e) are indicated separately from cold water conditions (b,d,f). For ease of comparison, warm water conditions are given as broken lines and open triangles in the corresponding cold water conditions. The factorial scope for growth is shown by double-headed arrows, which is the factor by which energy supply exceeds demand or maintenance costs. Temperature effects on chemical metabolic processes and physical diffusion processes are indicated separately (a,b) and in combination with temperature-induced viscosity effects (e,f). Increased viscosity results in thicker boundary layers and more drag (c,d), but the effects scale nonlinearly; small organisms are affected more (Box 3). Hence, oxygen supply and demand lines are curved. The warm condition with full effects of temperature (e) is taken as a reference for maximum and minimum size (open triangles). Kinetic effects only (a,b) result in increased maximum size, while making no statement about minimal size. Viscosity effects only (c,d) result in both selection against small size and reducing maximum size in the cold (in effect reducing the size window). In combination, kinetic and viscosity effects (e,f) result in both selection against small size and increasing maximum size in the cold (shifting the size window).

pare Fig. 2c,d). At small sizes, thick boundary layers preclude effective oxygen uptake and relatively high energy expenditure is needed to overcome drag effects. Thus, there

Box 3. Water viscosity, boundary layers and drag effects

Effects of water viscosity have been mainly studied in relation to swimming, where viscous drag forces reduce swimming performance (Fuiman & Batty 1997). Viscosity becomes more important in cold water (von Herbing 2002) and in smaller organisms (Podolsky & Emler 1993; Müller, Stamhuis & Videler 2000; Larsen, Madsen & Riisgård 2008; Beveridge, Petchey & Humphries 2010). Swimming efficiency increases rapidly with increasing body size, as mass-specific energetic costs decline (Kaufmann 1990). Thus, to escape viscosity effects, strong selection on fish larvae to increase body length has been proposed, which is consistent with larval elongation in many species (Müller & Videler 1996).

Cold, viscous water will not only challenge forced convection (increase costs of breathing) but also increase the thickness of a boundary layer enveloping respiratory surfaces (decrease oxygen uptake). Such boundary layers can significantly impede gas exchange: In fish gills, diffusion resistance of boundary layers could be 5–10-fold that of the gill membrane itself and may account for up to 80–90% of the total diffusion resistance to oxygen transfer from water to blood (Hills & Hughes 1970). Consequently, such boundary layers can become depleted of oxygen. An experiment by Pinder & Feder (1990) illustrates this depletion: immobilized frogs (of *c.* 200 g) placed in fully saturated, still water experienced virtual anoxia, as the partial pressure of oxygen immediately adjacent to the skin dropped to only 2 kPa.

Flow regimes are highly dependent on the Reynolds number (Re), which is the ratio of inertial to viscous forces and consequently quantifies the relative importance of these two types of forces for given flow conditions. Re is proportional to the length of the organism (or organ) along the flow route of the adjacent fluid L , the relative velocity of the fluid relative to the organism (or organ) U , and the density of the fluid ρ , and is inversely proportional to the dynamic viscosity of the fluid μ :

$$Re = (\rho UL)/\mu \quad \text{eqn 1}$$

Larger aquatic animals have the advantage of being much less affected by boundary layers and drag effects, as expressed by their higher Re (Statzner & Holm 1989). Drag is reduced as flow becomes non-laminar (e.g. the occurrence of attached vortices or von Karman vortex trails). Yet, this effect is not linear (Vogel 1996); drag reductions become increasingly smaller at a larger body size and higher Re . This causes a reduction in mass-scaling of maintenance metabolism with increased body size, which is visualized in Fig. 2 schematically by the upwards-concave curve of oxygen demand, rather than a straight line. The thickness of the boundary layer at a given distance away from the leading edge also scales nonlinearly with Re . As diffusion rate is inversely proportional to the boundary layer thickness (diffusion distance), increasing Re will promote oxygen diffusion, especially at low Re , and then less strongly at high Re . Therefore, oxygen supply is visualized by a negatively sloping curve, with a slope strongly influenced by the scaling of respiratory surface area.

seems to be a penalty for being small in colder water and smaller fish species are indeed more predominant in the tropics (Fig. 2 in Pauly 1998). Moran & Woods (2012) similarly note that polar 'embryo gigantism' appears to be considerably more widespread than adult gigantism. Since viscosity effects are stronger for smaller life stages, this could provide an additional selection pressure for large offspring size in polar waters, giving offspring a head start to escape viscosity effects. In isolation, the increased viscosity of cold water will also reduce maximum body size, but since kinetic effects simultaneously increase the ratio of oxygen supply relative to demand (Fig. 2a,b), maximum size may be increased in cold water (compare Fig. 2e,f). As the influence of viscosity effects is diminished at larger sizes, cold water is hypothesized to select for larger minimal size through viscosity effects while enabling larger maximal size through kinetic effects (Table 1, Hypothesis 2, see also Box 4).

A third reason for growing larger in cold water combines both previous hypotheses, suggesting that larger-bodied organisms can better regulate their oxygen budget, especially in cold, viscous water. Increasing ventilation effort, resulting in thinner boundary layers and enhanced

oxygen transfer, may help to avert asphyxiation as long as the extra oxygen taken up exceeds the oxygen expended in increasing the ventilation activity. The higher viscosity of cold water increases ventilation costs and decreases oxygen transfer, lowering an organism's ventilatory efficiency (ratio of extra oxygen gained from increasing ventilation activity above a reference routine level relative to the oxygen expended in this increased ventilation). For example, small animals with low Re incur large respiratory costs upon active ventilation, which may not be compensated for by gains in oxygen uptake (e.g. high gill movement may have the effect of circulating water within the boundary layer, but not refreshing the boundary layer with water from outside). Given that viscosity effects are diminished at larger sizes, ventilatory efficiency increases with body mass (Fig. 3), reaching a plateau at very high Re , when viscosity effects are negligible (arrows in Fig. 3). The key points are that the efficiency curve rises to a higher efficiency in the cold and that the curve continues to rise in the cold beyond the size at which the curve has flattened out in the warm (because the same Re is reached at a larger size in the cold). Maximum efficiency is higher in the cold because cold water can hold more oxygen than warm

water (Verberk *et al.* 2011). For large organisms, supplying the same volume of new water to the gills requires only slightly more ventilatory effort in the cold, but this same volume contains much more oxygen in cold water (solubility of oxygen in water almost doubles between 30 and 0 °C). Being able to greatly alter their oxygen uptake through ventilation gives large organisms, but not small organisms much improved regulatory ability in cold water compared with warm water (Table 1, Hypothesis 3). Ventilatory efficiency could thus select for increasingly larger body sizes in cold water, leading to polar gigantism. Lower temperatures may similarly drive the increases in body size observed in the cold waters of the deep sea (McClain & Rex 2001; Timofeev 2001; Hunt & Roy 2005; Moran & Woods 2012; Jamieson *et al.* 2013). Such abyssal gigantism could likewise be explained by viscosity effects conferring large-bodied animals with an improved regulation of their oxygen budget.

Based on hypothesis 3, animals whose respiratory system already allows for good regulation will be less likely to display polar gigantism. Indeed, polar groups which contain no giants (e.g. fish, bivalve molluscs and the morphologically similar brachiopods; Moran & Woods 2012) happen to be similar in having enclosed gills which they can ventilate using forced convection of water, likely giving them enhanced respiratory control. The Antarctic colossal squid (*Mesonychoteuthis hamiltoni*), a cephalopod, would seem an exception, but the thin skin of cephalopods, especially squid, has been suggested to be an important accessory organ for oxygen uptake: up to 60% of the oxygen budget in the squid's mantle tissue is taken up cutaneously (Pörtner 1994). *M. hamiltoni* has greatly enhanced lateral fins making this species probably even more reliant on cutaneous respiration. In the cold water where this species occurs (Rosa & Seibel 2010), the poor respiratory control resulting from reliance on cutaneous respiration (Box 2), would trigger the respiratory advantage of being large.

In contrast to the cold water situation, there is no similar respiratory advantage from having a large body size on land, as temperature does not appreciably alter the viscosity of air (Montgomery 1947). This difference between breathing in water or in air may at least partly explain the occurrence of giant aquatic ectotherms in the cold, while the largest terrestrial ectotherms have been found in the tropics (Makarieva, Gorshkov & Li 2005; Verberk *et al.* 2011; Moran & Woods 2012). In an oxygen-pressurized world, the higher partial pressure of oxygen enables organisms both in air and water to allocate more resources to body size increment as fewer resources are required for respiratory structures and ventilation (Owerkowicz, Elsey & Hicks 2009). Increases in atmospheric oxygen may push back body size constraints by alleviating costs associated with oxygen uptake and especially in water breathers such costs are higher. Additionally, increases in oxygen could enhance oxygen toxicity especially for small aquatic organisms, as they are inherently poor regulators due to the high

costs of regulating oxygen uptake (Verberk & Bilton 2011; Fig. 2c) and favour the evolution of increased size.

In summary, cold water *reduces* oxygen bioavailability while increasing the respiratory benefits of having a larger body size, whereas in an oxygen-pressurized world, the oxygen availability is *increased*, thereby decreasing asphyxiation risks and increasing toxicity risks which in turn can increase selection for a larger body size (Fig. 1). Thus, although still related to oxygen, the mechanisms driving or allowing increases in body size are distinct in polar and Palaeozoic gigantism: examples of polar gigantism cannot be taken as support for Palaeozoic gigantism. Moreover, the principles operating for terrestrial and aquatic ectotherms are fundamentally different.

Implications

The perspective of balancing toxicity and asphyxiation risks presented here may be key to understanding gigantism in aquatic organisms via costs associated with regulating oxygen uptake. It also informs the related discussion concerning symmorphosis (Woods *et al.* 2009) and helps explain respiratory adaptations to different flow regimes.

SYMMORPHOSIS

The hypothesis of oxygen limitation posits that oxygen sets an upper ceiling to body size, which implies that larger organisms should be more susceptible to hypoxia, or conversely, that smaller organisms should have excess capacity for oxygen uptake. The alternative possibility is that of symmorphosis: an organism's capacity to take up oxygen is matched to its oxygen requirements, irrespective of size. To test among these ideas, Woods *et al.* (2009) investigated the effect of hypoxia on pycnogonids of different

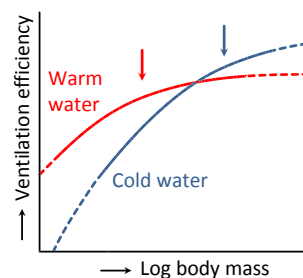


Fig. 3. Schematic representation of how ventilatory efficiency changes with body size in warm water and cold water. Ventilatory efficiency is defined as the ratio of the percentage of extra oxygen gained from increased ventilation above a reference routine level relative to the percentage of extra oxygen expended in increasing ventilation activity. The higher viscosity of cold water increases ventilation costs and decreases oxygen transfer, lowering an organism's ventilatory efficiency. Given that viscosity effects are diminished at larger sizes, ventilatory efficiency increases with body mass, reaching a plateau at very high *Re*. Arrows indicate the point at which curves start plateauing. Body sizes outside the size window are indicated by broken lines.

Box 4. The temperature-size rule (TSR)

For aquatic ectotherms, oxygen uptake capacity has been proposed to limit growth or aerobic scope (von Bertalanffy 1960; Perrin 1995; Atkinson, Morley & Hughes 2006; Pauly 2010; Forster, Hirst & Atkinson 2012). According to this idea, growth is proportional to the energy that remains after accounting for energy expenditure towards catabolism or maintenance (actually, non-growth metabolism):

$$d\omega/dt = \text{anabolism} - \text{catabolism} = \eta\omega^m - \kappa\omega^n \quad \text{eqn 2}$$

in which ω is the body mass of an organism, η and κ are coefficients of anabolism and catabolism, respectively, and m and n are constants. Equating aerobic scope to energy budget (i.e. assuming no anaerobic metabolism), capacity for oxygen uptake scales with gill surface ($m < 1$), while maintenance costs scale isometrically ($n \approx 1$). Hence, towards larger sizes, aerobic scope declines and growth would eventually stop when all energy is allocated towards maintenance (anabolism = catabolism). If temperature differentially affects the coefficients of anabolism and catabolism (η and κ), catabolism could be relatively lower in the cold, liberating energy towards growth. This would imply that growth efficiency increased upon cooling; yet, in a meta-analysis, Angilletta & Dunham (2003) found no evidence for this. Instead, Angilletta & Dunham (2003) suggested that the mass exponents themselves could differ in thermal sensitivity (m and n), which they supported using empirical evidence from six ectotherms (three fish and three crustaceans, all of them aquatic). Moreover, intraspecific scaling exponents decreased with temperature in several fish species (Killen, Atkinson & Glazier 2011; Ohlberger *et al.* 2012). Despite this empirical evidence, no mechanistic explanation existed for why these mass exponents should differ with temperature. Such a mechanism is provided by Hypothesis 2 (Table 1). The increase in viscosity with cooling entails greater respiratory costs especially for small-bodied organisms, while the thicker boundary layers will decrease oxygen supply (Fig. 4). By contrast, larger organisms are affected by viscosity to a much lesser degree (Box 3). Note that in this hypothesis (mass-specific), oxygen consumption decreases both with cooling and with larger size as is widely recognized (Pauly 2010). In cold water, aquatic ectotherms will grow slower initially, but as scope for growth declines less with size, they end up growing to a larger final size. Note that this mechanism only operates for metazoans beyond a certain size. Makarieva *et al.* (2008) predict 1 mg fresh weight as a critical size beyond which convection of water and the associated costs of breathing come into force. Very small organisms (<1 mg fresh weight) will be able to supply oxygen by diffusion and live in a medium dominated by viscosity and laminar flow; their body size may not be oxygen limited, nor will increases in their body size change their viscosity dominated flow regime. Intriguingly, this size threshold is very close to the 0.1 mg dry weight above which the TSR has been found to start acting more forcefully in aquatic ectotherms (Forster, Hirst & Atkinson 2012). It would be interesting to investigate the role of viscosity in the TSR and explore the size range over which viscosity affects the TSR (Forster, Hirst & Atkinson 2012).

size. They found no size difference in how well different-sized pycnogonids coped with hypoxia, consistent with the idea of symmorphosis. However, performances of pycnogonids were tested only under cold conditions and they used large experimental tanks which – similar to the situation in the field – would have provided plenty of opportunities for boundary layers to form. Peck *et al.* (2007) found that hypoxia reduced the burial performance of the Antarctic clam *Laternula elliptica*, especially in larger individuals. Intriguingly, this interaction between size and oxygen disappeared at low temperatures, where performances of large individuals increased relative to small individuals for the different oxygen treatments. These findings are thus consistent with our Hypothesis H3 that in cold, more viscous water, large organisms can better regulate their oxygen budget compared with small organisms.

The costs associated with maintaining elaborate respiratory structures in any animal might seem but a small price to pay given the large advantages of having high aerobic scope for growth, reproduction and hence organismal fitness: a greater capacity to take up oxygen (overdesigned respiratory system) would do away with asphyxiation risks. However, having an overdesigned respiratory system

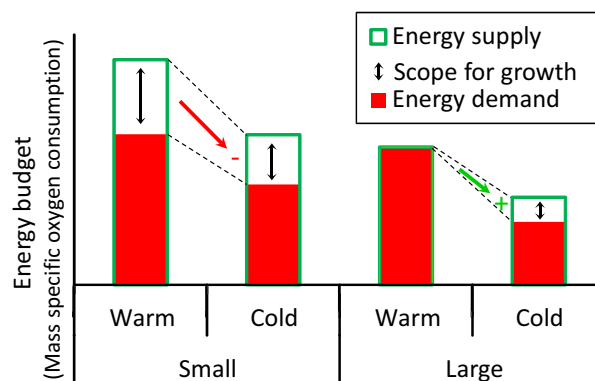


Fig. 4. Differences in mass-specific oxygen consumption as a measure of energy budget in small and large aquatic ectotherms in cold and warm waters. Energy is allocated either towards maintenance or growth (in the large ectotherms in warm water, all energy is allocated towards non-growth, maintenance metabolism). Note that scope for growth decreases in small individuals upon cooling, but increases in large individuals.

comes at the high price of oxygen toxicity. Thus, symmorphosis could perhaps be better explained from the balance between toxicity risks and risks of asphyxiation, rather

than from the balance between the gains of aerobic scope against the costs of maintaining excess capacity for oxygen uptake. Thus, the balancing act of toxicity and asphyxiation risks presented here can reconcile oxygen limitation and symmorphosis.

RESPIRATORY ADAPTATIONS

The need to regulate oxygen uptake seems much reduced in running-water ectotherms, especially compared with their counterparts in standing waters. In running waters, flow results in a continuous, high supply of oxygen by improved aeration of water and by a reduced thickness of boundary layers, whereas standing waters are characterized by much larger diel fluctuations in oxygen and temperature. This fits with the observation that invertebrate species found predominantly under high flow, typically have smaller or no gills. In these conditions, the risk of a smaller gill area is reduced as there are no profound oxygen minima. At the same time, such decreased gill area helps reduce the risk of oxygen toxicity. Note also that other advantages associated with small gills (e.g. reduced infection risks) are not expected to vary consistently along the running–standing water divide. Another way to detoxify oxygen is by adopting higher metabolic rates (food resources permitting), and indeed, controlled measurements of oxygen consumption rates in running-water invertebrates are consistently higher than those of their standing-water counterparts (Fox, Simmonds & Washburn 1935; Hynes 1970). Susceptibility to having either too much or too little oxygen thus seem pronounced in aquatic ectotherms with poor regulatory capacity; potential risks can be traced back to morphological and physiological differences of these aquatic ectotherms inhabiting waters with different flow regimes.

THE TEMPERATURE-SIZE RULE

The temperature-size rule describes that individuals attain larger body sizes when reared at cooler temperatures than when reared at warmer temperatures (Atkinson & Sibly 1997). In contrast to the parallel effect of altered resource supply on both growth rate and adult body size, lower temperatures result in slower growth but to a larger final size. Many explanations have been offered for this life-history puzzle (Angilletta & Dunham 2003). Lower metabolic maintenance costs in the cold relative to oxygen supply, as first proposed by von Bertalanffy (1960) could explain growth towards larger sizes, at least in aquatic ectotherms (von Bertalanffy 1960; Perrin 1995; Pauly 2010). However, to also explain the lower growth rates observed in the cold, growth efficiency should decrease with increasing temperatures (see Box 4); yet, this is not supported by the available data (Angilletta & Dunham 2003). We suggest that in addition to cold-inhibition of enzymatic function that would reduce growth efficiency in all environments, larger aquatic organisms have relatively

lower costs of breathing (less drag) and retain relatively higher capacity for oxygen uptake (smaller boundary layers) in the more viscous, cold water. As a result, aerobic scope or excess oxygen, which can be used to perform work and grow, starts out lower in cold water but declines less rapidly with size, leading to slower growth to a larger final size (Fig. 2; Fig. 4).

Conclusions

In conclusion, the mechanisms driving or allowing increases in body size are distinct in polar and Palaeozoic gigantism, even though they may still be related to oxygen. The bioavailability of oxygen is lower in cold, viscous water, but there are respiratory benefits of having a larger body size. In contrast, the bioavailability of oxygen is higher in an oxygen-pressurized world, which selects for larger body sizes as it decreases asphyxiation risks and increases toxicity risks. Thus, examples of polar gigantism cannot be taken as support for Palaeozoic gigantism.

Challenges of ensuring sufficient oxygen uptake while avoiding oxygen poisoning are very different for animals breathing in air or water. This suggests that some macrophysiological rules (especially those pertaining to an oxygen-mediated mechanism) cannot be readily transferred between the aquatic and the terrestrial realm. In both prehistoric and polar gigantism, trends for large body size seem to be more pronounced in water. The perspective of balancing toxicity and asphyxiation risks presented here offers a new explanation for polar gigantism, arguing that a larger body size represents a respiratory advantage, providing a positive selection for large body size in cold water. Combining respiration physiology (costs of respiration and ventilation) and hydrodynamics (viscosity and boundary layers) improves our understanding of patterns in ectotherm body size over a latitudinal or temperature range. Differences in density and viscosity can explain the discrepancy in latitudinal size clines between aquatic and terrestrial ectotherms, while temperature-driven changes in scaling exponents of metabolic rate shed new light on the life-history puzzle of the TSR.

Future research would be profitably directed to elucidating how the balance between oxygen poisoning and maintaining capacity for oxygen uptake is affected by changes in viscosity and hyperoxia. A comparative approach quantifying size responses to either viscosity, oxygen toxicity or both in a range of organisms differing in respiratory control would seem particularly fruitful (Table 1).

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