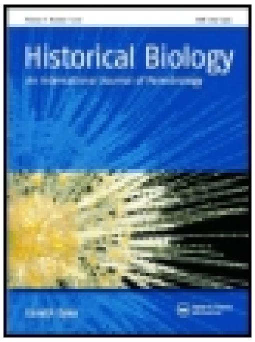

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The evolution of gigantism in active marine predators

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ABSTRACT
A novel hypothesis to better understand the evolution of gigantism in active marine predators and the diversity of body sizes, feeding strategies and thermophysiologies of extinct and living aquatic vertebrates is proposed. Recent works suggest that some aspects of animal energetics can act as constraining factors for body size. Given that mass-specific metabolic rate decreases with body mass, the body size of active predators should be limited by the high metabolic demand of this feeding strategy. In this context, we propose that shifts towards higher metabolic levels can enable the same activity and feeding strategy to be maintained at bigger body sizes, offering a satisfactory explanation for the evolution of gigantism in active predators, including a vast quantity of fossil taxa. Therefore, assessing the metabolic ceilings of living aquatic vertebrates and the thermoregulatory strategies of certain key extinct groups is now crucial to define the energetic limits of predation and provide quantitative support for this model.

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Introduction

Body size is a key biological trait for all organisms, being a crucial determinant of different physiological, anatomical, ecological, and life history parameters (Peters 1983; Calder 1984). The influence of body size goes beyond the individual level, reaching multiple scales of organization and affecting the structure and dynamics of ecological networks (with implications for food web stability, the patterning of energy fluxes, and the responses to perturbations; see Woodward et al. 2005). For these reasons, the evolution of gigantism has long been a topic of considerable interest among biologists. As a consequence, numerous hypotheses have been proposed to explain the mechanisms underlying this phenomenon (e.g. Cope's rule, Bergman's rule, Rensch's rule, Island rule), as well as disentangling the constraining factors that limit maximum sizes in animals (Alexander 1998; Burness et al. 2001; Freedman & Noakes 2002; Hone & Benton 2005; Makarieva et al. 2005a, 2005b, 2006; Vermeij 2016).

Vertebrates hold the records for the biggest sizes within all the habitats and ecological niches that they occupied during the Phanerozoic (Alexander 1998; Vermeij 2016). Among gigantic vertebrates, those inhabiting marine environments achieve (or achieved in the past) the biggest sizes ever recorded (Alexander 1998; McClain et al. 2015). Interestingly, there is a clear tendency for the largest swimming vertebrates to be slow filter feeders, whereas active predators are always notably smaller (Alexander 1998; Cavin 2010; Friedman et al. 2010; note that this fact is also evident in invertebrates, e.g. Vinther et al. 2014; Klug et al. 2015). Some authors have tried to explain this pattern in terms of optimal prey-size selection for enhancing capture rates (Webb & De Buffrénil 1990; Domenici 2001). However, such suggestions do not seem to offer a complete explanation since they are unable to elucidate the eventual evolution of gigantism in some predators, or to explain why this pattern occurs at a different size range for each metabolic level. Namely, the biggest endothermic predators are much bigger than their ectothermic counterparts, and the same can be said for slow filter feeders. Accordingly, among living taxa, the sperm whale (*Physeter macrocephalus*) and the Greenland shark (*Somniosus microcephalus*) are the biggest predatory vertebrates with endothermic and ectothermic metabolism respectively. However, the first one is four times bigger than the second one (McClain et al. 2015). Similarly, the biggest endothermic filter-feeding vertebrate, the blue whale (*Balaenoptera musculus*), exceeds in more than 10 m the maximum length of its ectothermic equivalent, the whale shark (*Rhincodon typus*) (McClain et al. 2015). Given this scenario, here we provide a novel view that entails a more comprehensive understanding of the diversity of body sizes, feeding strategies and thermophysiologies of extinct and living aquatic vertebrates, considering that mass-specific metabolic rate can act as a constraining factor of the activity level and feeding strategy. From this perspective, we propose that shifts towards higher metabolic levels, promoted by different extrinsic or intrinsic factors, allow a similar activity and feeding strategy to be sustained at bigger body sizes, offering a satisfactory and more holistic explanation for the evolution of gigantism in active predators.

Unravelling the relationship between body size, feeding strategy and thermophysiology in aquatic vertebrates

Recently, Makarieva et al. (2005a, 2005b, 2006) assessed the effects of metabolic rate on body size providing new clues

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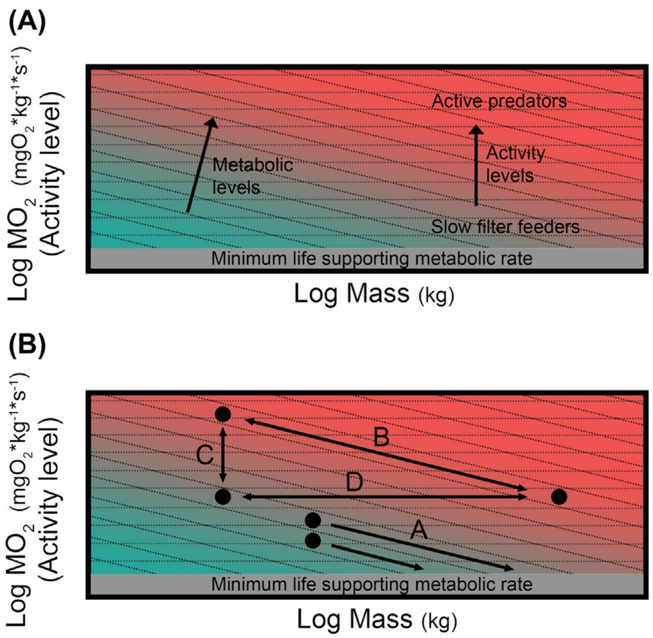
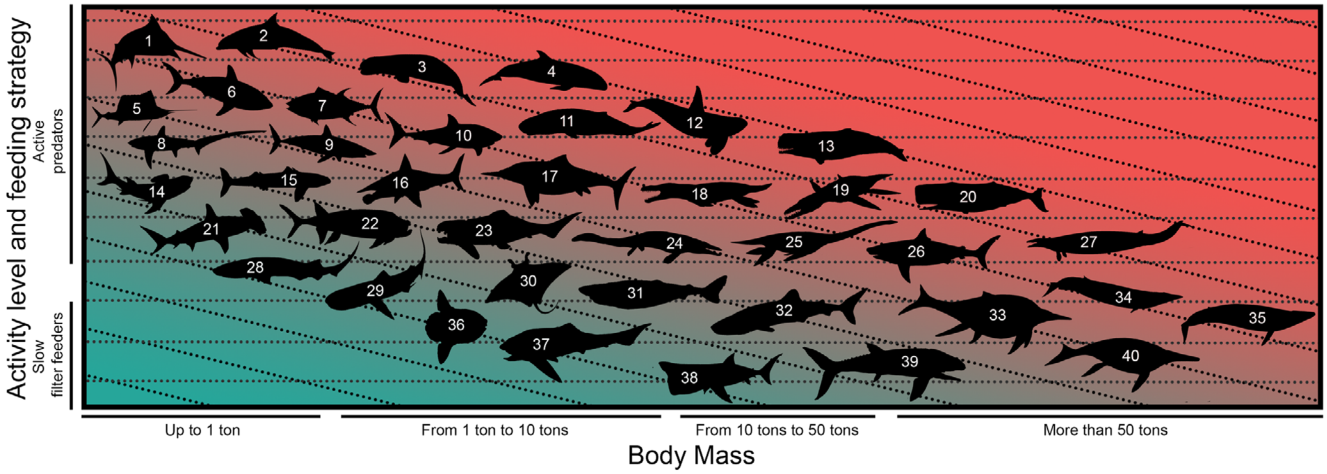


Figure 1. (A) Explanatory diagram showing the relationship between body mass (*X* axis), metabolic rate (≈ activity level) (*Y* axis) and metabolic level (with bluish and reddish tones in the online version representing lower and higher metabolic levels, respectively). (B) Relative positions and possible movements within this theoretical space implying changes in body mass, activity and metabolic levels.

that could shed some light on the above mentioned scenario. Physiological viability of living taxa is limited by a critical minimum value of mass-specific metabolic rate, which is extremely similar for all living organisms (Makarieva et al. 2006) (Figure 1(A)). Given that the mass-specific metabolic rate decreases with increasing body size, larger size is not physiologically sustainable once this limit has been reached (Makarieva et al. 2005a, 2005b). Interestingly, higher metabolic levels, promoted for example by high ambient temperatures or high oxygen concentrations, imply bigger potential body sizes as this critical minimum value is reached at larger body mass (compare the two hypothetical taxa of case A in Figure 1(B)) (Makarieva et al. 2005a, 2005b). Based on their ideas, we make some other predictions considering that concrete values of metabolic rate act also as a limiting factor for the activity level and feeding strategy in animals (Peterson et al. 1990; Hammond & Diamond 1997). These are: (1) activity will decrease when body size increases within each metabolic level (case B in Figure 1(B)); (2) when comparing similar-sized individuals, those with higher metabolic levels will display more active lifestyles (case C in Figure 1(B)); and (3) when comparing organisms with similar activity levels, those with higher metabolic levels will reach larger body sizes (case D in Figure 1(B)).

In this context, the diversity of body sizes, feeding strategies and thermophysiologies of extinct and living aquatic vertebrates can be much better explained (Figure 2). The high energetic requirements derived from an active predatory lifestyle could account for the notorious body size differences between aquatic predators and filter-feeders of the same metabolic level. According to prediction (1) outlined above, it is expected that as body mass increases past some threshold value, the energetic costs of a predatory lifestyle become too high and only less active lifestyles (i.e. filter feeding) are physiologically possible (Figure 3(A)). Similarly, differences in metabolic level may also satisfactorily explain why endothermic predators and endothermic



1 *Xiphias gladius* ^{me}
2 *Tursiops truncatus* ^{ed}
3 *Delphinapterus leucas* ^{ed}
4 *Pseudorca crassidens* ^{ed}
5 *Istiophorus albicans* ^{me}
6 *Lamna ditropis* ^{me}
7 *Thunnus thynnus* ^{me}
8 *Alopias vulpinus* ^{me}
9 *Isurus oxyrinchus* ^{me}
10 *Carcharodon carcharias* ^{me}
11 †*Brygmophyseter shigensis* ^{ed}
12 *Orcinus orca* ^{ed}
13 †*Livyatan melvillei* ^{ed}
14 †*Stethacanthus altonensis* $^{me?}$
15 †*Cladoselache fyleri* $^{me?}$
16 †*Helicoprion bessonovi* $^{me?}$
17 †*Ophthalmosaurus icenicus* ^{me}
18 †*Kronosaurus queenslandicus* ^{me}
19 †*Pliosaurus funkei* ^{me}
20 *Physeter macrocephalus* ^{ed}
21 *Sphyrna lewini* ^{ec}
22 †*Xiphactinus audax* $^{me?}$
23 †*Dunkleosteus terrelli* $^{me?}$
24 †*Tylosaurus proriger* ^{me}
25 †*Mauisaurus haasti* ^{me}
26 †*Otodus megalodon* $^{me?}$
27 †*Basilosaurus cetoides* ^{ed}
28 *Hexanchus griseus* ^{ec}
29 *Megachasma pelagios* ^{ec}
30 *Manta birostris* $^{me?}$
31 *Somniosus microcephalus* ^{ec}
32 *Rhincodon typus* ^{ec}
33 †*Shonisaurus popularis* ^{me}
34 *Balaenoptera physalus* ^{ed}
35 *Balaenoptera musculus* ^{ed}
36 *Mola mola* ^{ec}
37 †*Titanichthys clarkii* ^{ec}
38 *Cetorhinus maximus* ^{ec}
39 †*Leedsichthys problematicus* ^{ec}
40 †*Shastasaurus sikanniensis* ^{me}

Figure 2. Diversity of body masses, feeding and thermoregulatory strategies of living and extinct aquatic vertebrates (ed, endotherm; ec, ectotherm; me, mesotherm; cross sign denotes an extinct taxon). The existence of active predatory and fast-swimming lifestyles among different extinct groups of gigantic chondrichthyans (e.g. Symmoriidae, Cladoselachidae, Eugeneodontiformes or Otodontidae; outlines 14–16 and 26), osteichthyans (e.g. Xiphactinidae; outline 22) and placoderms (e.g. Dunkleosteidae; outline 23) might be indicative of high metabolic levels and is compatible with the existence of meso/endothermy.

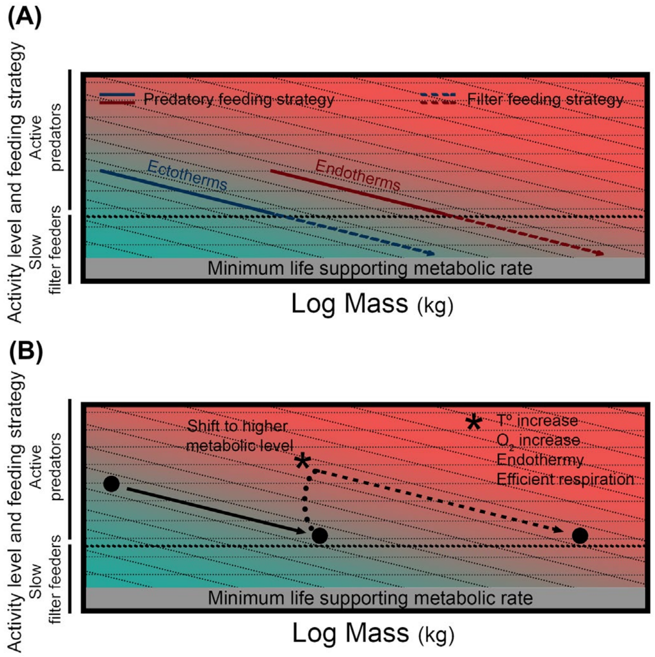


Figure 3. (A) Diagram showing how endothermic aquatic vertebrates, situated in higher metabolic levels, can reach bigger potential body sizes than their ectothermic analogues. (B) Visual explanation of how shifts towards higher metabolic levels, mediated by different factors, contribute to maintaining a predatory lifestyle at bigger body sizes.

filter-feeders are bigger than their ectothermic analogues. Taking into account our prediction (3) outlined above, this could be because endothermic animals have higher metabolic levels than ectothermic animals of the same size, allowing them to afford the energetic costs of a given feeding strategy at bigger body sizes (Figure 3(A)).

A common nexus for the main promoting factors of big body sizes in active predators

The gigantism of many extinct and living predators has been related to different extrinsic and intrinsic factors.

Among extrinsic factors, the presence of comparatively high oxygen levels has been proposed several times as the promoter of the big body sizes of some extinct predatory animals (e.g. Graham et al. 1995; Chown & Gaston 2010 and references therein). The mid-Palaeozoic (Carboniferous and Devonian) oxygenation event has been linked with the gigantism of various marine invertebrate groups, such as the orthoceratids or eurypterids (Klug et al. 2015) (but also foraminifers; Graham et al. 1995; Payne et al. 2012), as well as terrestrial flying and non-flying arthropods (Graham et al. 1995; Dudley 1998, 2000; Harrison et al. 2010). In a similar way, another peak in atmospheric oxygen during the Cretaceous has been suggested as the trigger of gigantism in some other insect groups (Dudley 1998). Interestingly, body size of living insects is constrained by oxygen availability (Peck & Maddrell 2005; Harrison et al. 2006, 2010; Kaiser et al. 2007). In this sense, several works (Harrison et al. 2006; Kaiser et al. 2007; Klok & Harrison 2009; Zhao et al. 2010) have recently provided empirical evidence supporting the idea that hyperoxia enables bigger body sizes in different extant arthropods (although see Woods et al. 2009). Dahl and Hammarlund (2011) suggested that low atmospheric oxygen pressure could act as an evolutionary barrier for big body sizes in early vertebrates, and they linked the gigantism of some armoured fishes (placoderms) with the high oxygen levels of the Devonian.

The rise of ambient temperatures has also been proposed as a possible extrinsic reason for the gigantism of some extinct vertebrate predators including snakes (e.g. the python *Titanoboa* (Head et al. 2009)) and lizards (Head et al. 2013). In addition, temperature could have played a major role in the giganstism of other vertebrates that lived in the tropics during greenhouse periods, such as some Cretaceous or Miocene crocodylomorphs (Sereno et al. 2001; Aguilera et al. 2006). The effect of ambient temperature on increasing body size have recently been examined in a considerable number of living taxa, including arthropods, annelids, molluscs and vertebrates (Makarieva et al. 2005b). However, increases in body sizes due to higher ambient temperatures are only expected to occur in terrestrial poikilotherms (Makarieva et al. 2005a, 2005b).

Regarding intrinsic factors, the evolution of mechanisms that allow highly efficient respiration has also been linked to the gigantism of some air-breathing predatory vertebrates. Thus, one of the most representative examples in this sense could be the evolution of avian-like respiratory systems in pterosaurs (Claessens et al. 2009; Ruxton 2014) and saurischian dinosaurs (O'Connor & Claessens 2005; Sander et al. 2011). The recent description of unidirectional airflow in crocodilians suggests that this might have been another relevant factor involved in the gigantism of some crocodylomorphs (see above). In fact, the high similarity between bird and crocodilian respiratory systems supports the idea that unidirectional airflow is the ancestral condition for all archosaurs (Schachner et al. 2013; Farmer 2015a), a group that comprises numerous examples of gigantic predators other than non-avian dinosaurs, pterosaurs or crocodylomorphs (including for example several basal forms, Turner & Nesbitt 2013; or the more derived 'terror birds', Alvarenga et al. 2011). Differences in body size between mammals and dinosaurs during the Mesozoic have also been attributed to differences in their respiratory efficiency, and it has been suggested that non-unidirectional airflow system of mammals could have been a competitive disadvantage (Farmer 2015b). Similarly, Ruxton (2011) proposed that the higher respiratory efficiency of air-breathing aquatic vertebrates over water-breathing taxa could explain the body size differences between marine mammals and fishes.

Finally, the evolution of anatomical structures and physiological mechanisms that allow heat generation and/or retention can be considered as another intrinsic factor that promotes bigger potential body sizes (Vermeij 2016). Supporting this idea, the biggest living fishes with an active predatory lifestyle are mesotherms (Dickson & Graham 2004). This factor could be involved in the gigantism of some extinct vertebrate predators where endothermy or mesothermy has recently been confirmed, including dinosaurs (Amiot et al. 2006; Pontzer et al. 2009; Eagle et al. 2011), ichthyosaurs, plesiosaurs and mosasaurs (Bernard et al. 2010; Harrell et al. 2016). The big sizes and active lifestyles presupposed for a considerable number of extinct aquatic vertebrates suggest that the occurrence of endothermy or mesothermy could have been more common in the past than expected (see fossil taxa with question marks in Figure 2).

In sum, several disparate factors seem to facilitate independently, or in combination, the acquisition of gigantic sizes in predatory animals. However, to date, the common mechanisms underlying this phenomenon have never been addressed. The new perspective here proposed allows integration of most previous hypotheses into a common context when considering that all these factors induce rises in metabolic rate. Therefore, a shift to higher metabolic levels, regardless of the underlying promoting cause, implies that similar mass-specific metabolic rates, activity levels and feeding strategies can be maintained at bigger body sizes. The evolution of gigantism in predators could then be understood and interpreted in a more holistic way as a phenomenon closely linked with physiological or environmental changes that allowed the animals to cope with the increased energetic costs of active predation at unusually large body sizes (Figure 3(B)).

Conclusions

The relationship between body size and metabolic rate has repeatedly been studied with body size considered as an independent variable. However, Makarieva et al. (2005a, 2005b, 2006) have recently suggested that metabolic rate could be an important constraining factor of the maximum body size of animals and plants. Following this idea, our proposal considers metabolic rate as a key determinant factor for body size, activity level and feeding strategies in aquatic vertebrates. Then, given that mass-specific metabolic rate decreases when the body mass increases, we hypothesize that active predation is unaffordable once a given body mass is reached and only less active lifestyles and feeding strategies (e.g. filter feeding, scavenging, etc.) are physiologically sustainable above this size. However, this limit is reached at different body sizes depending on the thermoregulatory strategy and, ultimately, metabolic level; endothermic predators can reach bigger potential body sizes than their ectothermic analogues. Interestingly, shifts towards higher metabolic levels, promoted by different intrinsic or extrinsic factors, can enable the same activity level and feeding strategy to be maintained at bigger body sizes, offering a satisfactory explanation for the evolution of gigantism in active predators.

Future perspectives

This theoretical approach opens the door to a good deal of possible studies that could shed light onto the ideas here proposed. In this sense, assessing the metabolic ceilings of living aquatic vertebrates is now crucial to define the energetic limits of predation and to provide quantitative support for this model. Fortunately, the recent development of techniques that allow the study of the energetics of large marine vertebrates offers a wide range of possibilities in this regard (Payne et al. 2015). On the other hand, progress in histological techniques (Zehbe et al. 2010) and temperature-sensitive isotopic fractionation applications (Bernard et al. 2010; Eagle et al. 2010, 2011) enables the study of physiological traits in fossil taxa in an increasingly reliable way (Vermeij 2015). Hence, assessment of the thermoregulatory strategies of certain key extinct groups could provide essential data for completing and interpreting the diversity of body sizes, thermophysiologies and feeding strategies of aquatic vertebrates, as well as contributing to a better understanding of the mechanisms involved in the evolution of gigantism in predators.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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