

COMMENTARY

The evolution of foraging capacity and gigantism in cetaceans

J. A. Goldbogen^{1,*} and P. T. Madsen^{2,3}

ABSTRACT

The extant diversity and rich fossil record of cetaceans provides an extraordinary evolutionary context for investigating the relationship between form, function and ecology. The transition from terrestrial to marine ecosystems is associated with a complex suite of morphological and physiological adaptations that were required for a fully aquatic mammalian life history. Two specific functional innovations that characterize the two great clades of cetaceans, echolocation in toothed whales (Odontoceti) and filter feeding in baleen whales (Mysticeti), provide a powerful comparative framework for integrative studies. Both clades exhibit gigantism in multiple species, but we posit that large body size may have evolved for different reasons and in response to different ecosystem conditions. Although these foraging adaptations have been studied using a combination of experimental and tagging studies, the precise functional drivers and consequences of morphological change within and among these lineages remain less understood. Future studies that focus at the interface of physiology, ecology and paleontology will help elucidate how cetaceans became the largest predators in aquatic ecosystems worldwide.

KEY WORDS: Scaling, Odontocetes, Mysticetes, Diving, Filter feeding, Echolocation

Introduction

Researchers have long recognized the importance of body size in biology. The influence of scale is omnipresent throughout an animal's life history and its impact determines a diverse range of processes, ranging from organismal performance to ecological niche (Peters, 1983; Schmidt-Nielsen, 1984; Vermeij, 2016). Most importantly, body size acts as a primary driver and allometric constraint of metabolism such that larger animals generally exhibit lower mass-specific metabolic rates (Weibel and Hoppeler, 2005; West et al., 2002; White et al., 2009). Nevertheless, extremely large body size (i.e. gigantism) comes at the cost of high absolute food requirements (Croll et al., 2006; Williams, 2006), but also confers a suite of advantages, including reduced cost of transport (Alexander, 2005; Williams, 1999) and the ability to fast for extended periods of time (Castellini and Rea, 1992; Lindstedt and Boyce, 1985; Millar and Hickling, 1990), which together enhance migratory capacity (Watanabe et al., 2015). An additional benefit of gigantism is improved anti-predator defense and, therefore, decreased predation risk (Ford and Reeves, 2008; Sinclair et al., 2003). However, with rising anthropogenic disturbance and pressures worldwide (McCauley et al., 2015), many large animals are now facing

increased extinction risk despite having protected status (Payne et al., 2016; Ripple et al., 2017).

The largest animals of both the past and present tend to be vertebrate filter feeders in marine ecosystems (Alexander, 1998; Friedman et al., 2010; Vermeij, 2016). Filter feeding in vertebrates is characterized by the engulfment of prey-laden water into the oropharyngeal cavity followed by the filtration of large numbers of organisms suspended in the fluid (Goldbogen et al., 2017; Motta et al., 2010; Paig-Tran et al., 2013; Rubenstein and Koehl, 1977; Sanderson et al., 2016; Sanderson and Wassersug, 1990; Werth, 2000b; Werth and Potvin, 2016). Swimming-induced dynamic pressures power engulfment in aquatic vertebrates (Vogel, 1994), but the specific flow pathways and mechanisms of prey capture likely vary among the recognized modes of filter feeding (Goldbogen et al., 2017; Paig-Tran et al., 2013; Sanderson et al., 2001, 2016; Sanderson and Wassersug, 1993). Most species filter feed at relatively low speeds with mouth agape, allowing water and prey to enter the mouth and then pass through an oral filter before exiting the oropharyngeal cavity (Simon et al., 2009; Werth, 2004; Werth and Potvin, 2016). In contrast, rorqual whales (Balaenopteridae; see Glossary) engulf large volumes intermittently at high speeds and then start filtration after the mouth has closed (Goldbogen et al., 2017). Although many vertebrate filter feeders exhibit large body size, we note that this foraging strategy is also exhibited by many smaller species, such as anchovies and sardines. These species can form extremely large aggregations, filter feed at lower trophic levels, and collectively accumulate a tremendous amount of biomass in upwelling habitats (Cury et al., 2000). Interestingly, much larger intermittent filter feeders, such as humpback whales, feed on these types of fish when oceanographic conditions permit (Fleming et al., 2015). With one filter feeder eating another, this trophic linkage reflects the rapid flux of energy through productive ecosystems from very small plankton to the largest whales.

Filter feeding contrasts with particulate feeding (Fig. 1), where prey is targeted and captured individually, and these foraging mechanisms result in divergent energetic efficiencies by affecting the rate of prey intake, the prey types that can be targeted and the mechanical costs of feeding (Carey and Goldbogen, 2017; James and Probyn, 1989; Sanderson and Cech, 1992). We note that this feeding mode characterization is more general than other behavioral frameworks that aim to define behavioral components of foraging such as prey capture, manipulation and processing (Hocking et al., 2017b; Kienle et al., 2017; Marshall and Goldbogen, 2015). Although filter feeders such as baleen (see Glossary) whales (Mysticeti) and whale sharks (*Rhincodon typus*) are the largest extant marine vertebrates, some particulate feeders have also evolved very large body sizes, suggesting that gigantism can evolve for different reasons and in response to a variety of environmental forces (Lindberg and Pyenson, 2006). Classic examples of gigantic particulate feeders include white sharks (*Carcharodon carcharias*) and sperm whales (*Physeter macrocephalus*) in modern oceans. Moreover, several extinct lineages of gigantic particulate feeders (i.e. *Leviathan melvillei*

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Glossary**Baleen**

A keratinous filtering apparatus exhibited by extant baleen whales (Mysticeti), comprising transverse plates that fray on their lingual edge exposing tubules that act to retain prey as water exits the mouth.

Continuous ram filter feeding

A specific foraging mode exhibited by bowhead whales and right whales; Whales feed at slow speeds with mouth gape, allowing water to pass by baleen and exiting at the back corners of the mouth.

Crown cetacean

A crown group includes all living species and their ancestors back to the most recent common ancestor and all descendants of that ancestor even if extinct.

Edentulous

Toothless.

Flow sensing

Some marine mammals (i.e. pinnipeds) use specialized whiskers, or vibrissae, to track hydrodynamic signatures without the use of other sensory modalities.

Gingiva

The gums.

Lunge feeding or engulfment feeding

A dynamic feeding process in rorqual whales that involves the engulfment and subsequent filtration of a large volume of prey-laden water.

Pinniped

Amphibious, carnivorous marine mammals that include 'eared' seals (Otariidae), 'earless' seals (Phocidae) and walrus (Odobenidae).

Positive allometry

The disproportionate scaling of a parameter or process that is greater than what is expected by isometry (i.e. proportional increase).

Raptorial

Predatory, primarily with the use of teeth in odontocetes to seize prey.

Rorqual

Term used to describe members of a family of baleen whales (Balaenopteridae) that are characterized by lunge feeding, a unique filter feeding mode that is facilitated by a complex suite of anatomical adaptations.

Stem odontocete

A stem group is a paraphyletic group of extinct species, typically falling outside the crown group.

Suction feeding

A feeding mode characterized by the generation of negative pressure via oropharyngeal expansion to pull in fluid and suspended prey.

and *Carcharocles megalodon*) are also represented in the fossil record (Lambert et al., 2010; Pimiento and Balk, 2015). However, the largest animals among all the ocean giants, specifically in terms of body mass, are represented by several extant cetacean species (Lockyer, 1976). Although filter feeding likely represents the ancestral state of vertebrates (Sanderson and Wassersug, 1993), there is mounting evidence that filter feeding has secondarily evolved from particulate feeding [i.e. via raptorial (see Glossary) or suction prey capture mechanisms] in multiple independent lineages and ultimately led to large body size in both mammals and fishes (Friedman, 2012; Friedman et al., 2010; Geisler et al., 2017; Hocking et al., 2017a; Pyenson, 2017).

The evolutionary transitions from particulate feeding to filter feeding in aquatic vertebrates have followed similar trajectories in different lineages (Friedman, 2012). For example, the parallel morphological changes in both whales and bony fishes (i.e. pachycormiform teleosts) consisted of a reduction (and ultimate loss or near-complete loss) of dentition followed by an increase in body size (Friedman, 2012). Interestingly, the evolutionary innovation of filter feeding in mysticetes, which probably

occurred approximately 30 Mya (Geisler et al., 2017; Pyenson, 2017), did not result in an immediate increase in extreme body size; rather, gigantism evolved in multiple baleen whale lineages much more recently (<5 Mya), during the Plio-Pleistocene (Pyenson, 2017; Pyenson and Vermeij, 2016; Slater et al., 2017). The evolution of gigantism in toothed whales (Odontoceti) is less clear, but a broad outline of body size through deep time in this clade suggests a more gradual increase in size since the origin of echolocation (Pyenson, 2017; Pyenson and Sponberg, 2011). Within the clade that comprises sperm whales and their extinct relatives (Physeteroidea), phylogenetic comparative analyses suggest that very large body size also evolved independently in multiple lineages (Boersma and Pyenson, 2015; Lambert et al., 2015). However, the precise timing and the mode of body size evolution among odontocetes remain poorly understood.

Predator-prey interactions at the extremes

The body size of both toothed whales and baleen whales is generally many orders of magnitude larger than their prey (Domenici, 2001; Webb and De Buffrénil, 1990), with some exceptions in specific populations of deep-diving toothed whales that target giant squid or for some killer whales ecotypes that cooperatively hunt baleen whales (Clarke, 1996; Lindberg and Pyenson, 2006). This has important implications for the dynamics that govern the interaction between predator and prey, largely owing to larger animals being less maneuverable than smaller ones (Howland, 1974). Specifically, the scaling of control surfaces relative to body mass and volume indicates that larger animals should have diminished unsteady locomotor performance, thereby yielding lower acceleration and maneuvering capacity (Domenici, 2001; Vogel, 2008; Webb and De Buffrénil, 1990). Because smaller prey should more easily evade larger predators, large aquatic vertebrates have evolved different strategies to efficiently capture smaller prey, such as the use of suction feeding (see Glossary) (Bloodworth and Marshall, 2005; Hocking et al., 2013; Kane and Marshall, 2009; Werth, 2000a), high-speed attacks (Aoki et al., 2012; Marras et al., 2015; Aguilar Soto et al., 2008), ambush-like attack trajectories (Goldbogen et al., 2017, 2013; Huvneers et al., 2015), bulk filter feeding mechanisms with an enlarged engulfment apparatus (Goldbogen et al., 2010; Werth, 2004), coordinated feeding in groups (Benoit-Bird and Au, 2009; Wiley et al., 2011) or the use of appendages (i.e. tails or flukes) that can reach higher accelerations than the main body (Domenici et al., 2000, 2014; Oliver et al., 2013). Alternatively, larger animals can forage in dark environments using echolocation or flow-sensing (see Glossary) structures to gain a sensory advantage on their prey (Hanke et al., 2012; Johnson et al., 2004; Madsen et al., 2005, 2007; Miller et al., 2004). Such low-light habitats can generally occur at any depth at night or, conversely, at any time at extreme depths. However, deep habitats provide large endothermic predators access to prey that may be more vulnerable in the oxygen minimum zone (i.e. physiologically compromised and less able to avoid predation), thereby increasing foraging success (Gilly et al., 2013; Naito et al., 2017) via carefully orchestrated prey-specific approaches in concert with suction feeding (Madsen et al., 2013).

High quality prey often can be found deep in the ocean, so access to this remote habitat is essential to maximize foraging efficiency (Benoit-Bird et al., 2016; Friedlaender et al., 2016; Greene et al., 1988). Air-breathing predators must therefore evolve the capacity to dive longer and deeper to exploit these resources (Halsey et al., 2006; Hochachka, 2000; Miriceta et al., 2013). Diving capacity is influenced by the magnitude of body oxygen stores, the rate of

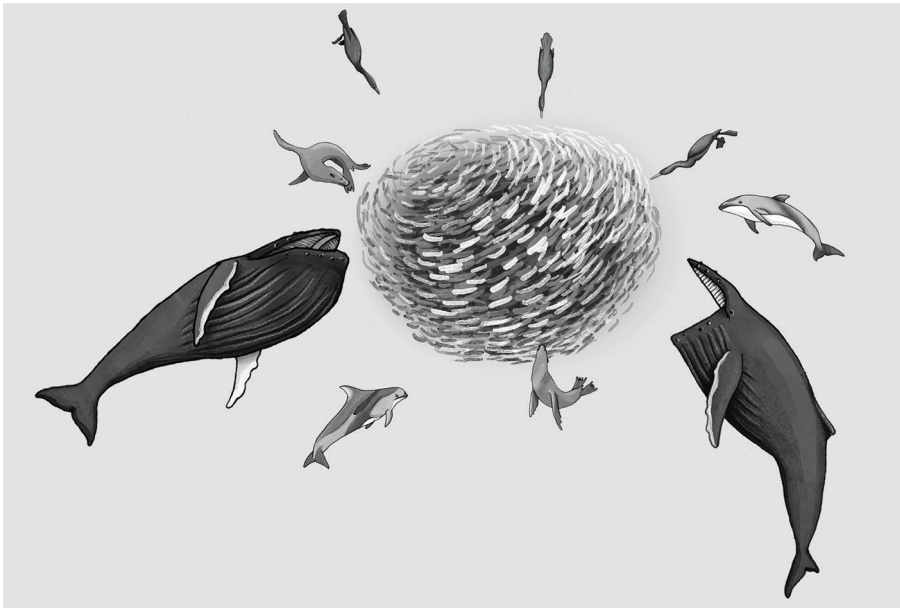


Fig. 1. Illustration of different marine vertebrates exploiting a bait ball of forage fish. Among these species are many particulate feeders (e.g. cormorants, sea lions and dolphins), those that are largely limited to capturing one prey at a time. This contrasts with bulk filter feeding, characterized by the engulfment of large numbers of prey in a single mouthful, here represented by a humpback whale. Illustration by Alex Boersma.

oxygen usage and tolerance for low oxygen (Ponganis, 2015; Ponganis et al., 2011). Factors that influence oxygen storage include body size (Hudson and Jones, 1986), myoglobin content (Mirceta et al., 2013; Noren and Williams, 2000) and a wide range of mechanisms for tolerating low oxygen (Meir et al., 2009; Zenteno-Savin et al., 2010). The rate of oxygen usage is influenced by activity (Martín López et al., 2015; Williams et al., 2000), body condition (Miller et al., 2016), muscle design (Velten et al., 2013) and cardiovascular responses during a breath-hold dive (Ponganis et al., 2011). Despite the wide range of factors that influence diving capacity among diving birds and mammals, diving capacity generally increases with body size (Halsey et al., 2006). This follows from body oxygen stores being generally isometric (Hudson and Jones, 1986) and the metabolic rates exhibiting negative allometry (Uyeda et al., 2017; White et al., 2009), thereby making diving capacity increase by approximately $(\text{mass})^{0.3}$ (Halsey et al., 2006). However, departures from this general trend may be further influenced by ecological factors, physiological adaptations and behavioral specializations (Ponganis, 2015). Nevertheless, the enhanced diving capacity and, by extension, increased foraging capacity, namely the ability to access and efficiently exploit high quality prey patches, represents a fundamental advantage of large body size in breath-hold divers.

Potential drivers of gigantism in toothed whales

How, when and why did cetaceans evolve their high performance foraging capacity and how does this correspond to the evolution of gigantism? In toothed whales (Fig. 2A), it has been hypothesized that echolocation first evolved for nocturnal epipelagic foraging on diel vertically migrating cephalopods (Lindberg and Pyenson, 2007). Alternatively, stem odontocetes (see Glossary) may have first developed enhanced active auditory scene assessment or echo-ranging acoustic behavior in order to navigate. This ability could then be subsequently adapted to detect large prey or prey aggregations, providing selection pressure for increasingly sophisticated biosonar mechanisms and increased body size for deep-ocean foraging. Recent research has shown that the earliest cetaceans (i.e. stem cetaceans or archeocetes that are not members of Neoceti: Mysticeti+Odontoceti) exhibited unremarkable hearing specializations (neither ultrasonic nor infrasonic) compared with

extant species (Geisler, 2017; Mourlam and Orliac, 2017). Nevertheless, unsophisticated echolocation should theoretically work for the normal hearing range of medium-sized mammals (Fenton and Ratcliffe, 2014). Paleontological and comparative studies suggest that biosonar evolved early in odontocetes and played a major role in the radiation and overall ecological success of this clade (Churchill et al., 2016; Geisler et al., 2014; Madsen and Surlykke, 2013; Park et al., 2016). Therefore, echolocation probably preceded the evolution of gigantism in odontocetes (Fig. 2A,B). The ability to exploit prey in low-light conditions would bolster nocturnal epipelagic foraging and the progressive exploration of deeper habitats. Either scenario would have selected for a suite of physiological mechanisms that enhance diving capacity, especially large body size and body plans that minimize the costs of diving (Pabst et al., 2016; Velten et al., 2013), in order to optimize foraging in mesopelagic and, ultimately, bathypelagic ecosystems (Fais et al., 2015). We hypothesize that these selective pressures led to the independent evolution of gigantism in multiple odontocete lineages including sperm whales (Physeteridae) and beaked whales (Ziphiidae), where the largest of them, the sperm whale (*Physeter macrocephalus*), spend nearly half of their lives at depths in excess of 500 m (Miller et al., 2004; Watwood et al., 2006).

Potential drivers of gigantism in baleen whales

The gradual increase in toothed whale body size since the Oligocene is markedly different than the much more recent (i.e. Pliocene-Pleistocene) and perhaps punctuated evolution of gigantism in baleen whales (Pyenson and Sponberg, 2011; Pyenson and Vermeij, 2016; Slater et al., 2017). Although extant baleen whales are edentulous (see Glossary) and use a keratinized oral filter as an obligate feeding mechanism (Goldbogen et al., 2017; Pivorunas, 1979; Szewciw et al., 2010; Thewissen et al., 2017; Werth, 2013), there are several well-described tooth-bearing mysticetes that currently represent the earliest known of all neocetes (Neoceti: Mysticeti+Odontoceti) or crown cetaceans (see Glossary) (Lambert et al., 2017). Because baleen does not readily fossilize, with notable exceptions (Esperante et al., 2008; Gioncada et al., 2016; Marx et al., 2017), it is difficult to infer precisely when filter feeding evolved (Fig. 2A). Two largely competing hypotheses disagree on

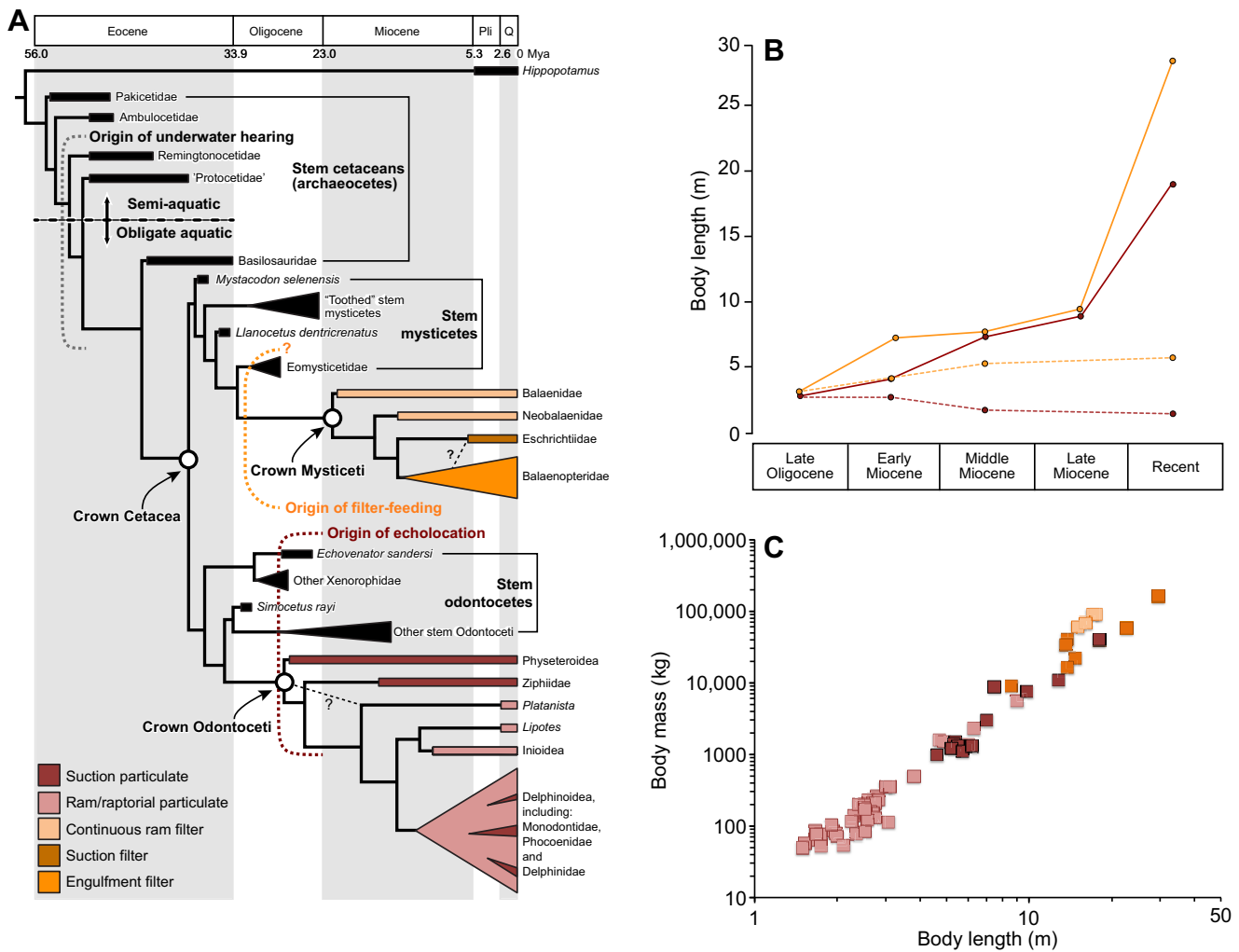


Fig. 2. Body size variation, evolutionary relationships and inferred feeding mode among cetaceans. (A) Cetacean phylogeny and inferred feeding mode for extant species. Modified from Pyenson (2017). (B) A broad estimate of body size evolution for mysticetes (orange) and odontocetes (red) over the past 25 million years. Maxima and minima are shown by the solid and dashed lines, respectively. Modified from Pyenson and Sponberg (2011). (C) Approximate length–mass relationships among extant cetaceans. Rorqual whales (Balaenopteridae) and gray whales (Eschrichtiidae), dark orange; Balaenidae, light orange; beaked whales (Ziphiidae) and sperm whales (Physeteridae), dark red; river dolphins (Platanista, Lipotes, Iniioidea) and smaller toothed whales (Delphinoidea), light red. Some estimates may be close to observed maxima, whereas others are estimates based on length–mass relationships from closely related species (Bigg and Wolman, 1975; Bloch et al., 2012, 1996; Bloch and Zachariassen, 1989; Cabbage and Calambokidis, 1987; Folkens and Reeves, 2002; George, 2009; Kenyon, 1961; Lockyer, 1976; Omura et al., 1955; Perryman and Lynn, 2002; Read and Tolley, 1997; Velten et al., 2013).

whether tooth loss preceded the evolution of baleen (Marx et al., 2016; Peredo et al., 2017) or whether toothed mysticetes possessed both teeth and baleen simultaneously for millions of years before the ultimate loss of teeth (Deméré et al., 2008; Geisler et al., 2017). Comparative morphological analyses suggest that early toothed mysticetes were not able to filter feed using their teeth, unlike what is observed in some pinnipeds (see Glossary) such as leopard seals (Hocking et al., 2013). The early-tooth-loss hypothesis suggests that stem mysticetes evolved a dedicated suction feeding capacity, which led to tooth loss, and then baleen later evolved from enlarged gingiva (see Glossary) (Geisler, 2017; Marx et al., 2016; Peredo et al., 2017). This hypothesis is consistent with the observation of reduced dentition in odontocetes that exhibit high-performance suction feeding compared with close relatives (Werth, 2006). Although key fossils suggest that raptorial feeding preceded filter feeding independent of suction-feeding specializations (Geisler et al., 2017), experimental evidence in modern cetaceans demonstrates that different prey-capture mechanisms are not

mutually exclusive and may be used together or in sequence for a given feeding morphology (Marshall and Goldbogen, 2015).

Despite the dearth of information available to better understand the early origins of mysticetes, it is thought that obligate filter feeding evolved in the early Oligocene (Pyenson, 2017), and then specialized filter feeding modes [i.e. intermittent ram filter feeding in rorqual whales and continuous ram filter feeding (see Glossary) in balaenid whales] evolved in the early Miocene, approximately 20 million years and 15 million years before the evolution of gigantism (Slater et al., 2017), respectively. The clade-wide shift in the mode of body size evolution is temporally linked to the onset of intensified glaciation and upwelling (Lawrence et al., 2006; Marlow et al., 2000; Slater et al., 2017). Both oceanographic processes are well-known drivers of prey abundance and patchiness in modern feeding hot spots for baleen whales (Croll et al., 2005; Nowacek et al., 2011). Wind-driven upwelling in temperate ecosystems brings cold, nutrient-rich deep water into the light-receiving photic zone, thereby causing a trophic cascade and an overall increase in productivity of planktonic

organisms such as krill (Santora et al., 2011). With the influx of bioavailable iron from glacial runoff and ice sheet melting (Bhatia et al., 2013; Hawkings et al., 2014), the enhanced overall productivity is predicted to increase prey abundance (Meire et al., 2017). Although it has yet to be rigorously demonstrated, an increase in overall prey abundance should lead to greater patchiness given the tendency of animals to form aggregations (Parrish and Edelman-Keshet, 1999). Also, if resources (i.e. primary productivity) become heterogeneously distributed (Martin, 2003), then prey for whales (i.e. zooplankton to forage fish) may also become patchy and be further modulated by large-scale oceanographic forcing (Cotté and Simard, 2005). Increased patchiness will result in a higher density of prey engulfed by baleen whales, thereby increasing the overall energetic efficiency of foraging (Goldbogen et al., 2011; Hazen et al., 2015). Furthermore, greater patchiness is associated with larger size classes of krill (Décima et al., 2010), thus baleen whales that target such patches will likely benefit from higher prey energy densities (Lee et al., 2006).

It is thought that the increased productivity, patchiness and prey densities that resulted from Plio-Pliocene ocean dynamics provided mysticetes with an evolutionary pathway towards greater body sizes (Slater et al., 2017). Interestingly, a large raptorial shark predator, *Carcharocles megalodon*, apparently went extinct at this same climatic transition in deep time (Collareta et al., 2017; Pimiento and Clements, 2014), which may have provided release from predation and further facilitated gigantism in mysticetes. Alternatively, resistance to predation could have been a driver for larger body sizes in baleen whales. Nevertheless, it is not clear that *C. megalodon* preyed on baleen whales (Collareta et al., 2017), given that modern great white sharks (*Carcharodon carcharias*) typically scavenge on dead baleen whales (Curtis et al., 2006), rather than actively prey on baleen whales (Taylor et al., 2013). Researchers argue that the now extinct giant raptorial sperm whale (*L. melvillei*) of the Miocene preyed on small to medium-sized mysticetes and thus occupied the same ecological niche as extant transient killer whales (*Orcinus orca*) (Lambert et al., 2010). Killer whale attacks on multiple baleen whale species have been well documented (Ford and Reeves, 2008), although most attacks target small species or calves and thus may not represent a major force of predation (Ford and Reeves, 2008; Mehta et al., 2007).

If adult individuals of large, extant baleen whales are largely free from predation pressure, then their foraging performance across scale may reflect differences in foraging efficiency that selected for larger body size. The engulfment apparatus of baleen whales exhibits positive allometry (see Glossary) whereby larger whales possess relatively larger skulls, jaws and baleen (Goldbogen et al., 2012, 2010; Pyenson et al., 2013). In intermittent ram filter feeders (i.e. lunge filter feeding), specifically rorqual whales (Balaenopteridae), this pattern of relative growth is also observed in the dimensions of the hyper-extensible oropharyngeal cavity that is lined with specialized groove blubber (Shadwick et al., 2013). As a consequence, the mass-specific engulfment capacity in rorquals increases with body size (Goldbogen et al., 2012, 2010). Thus, for every feeding event, larger whales can enhance their foraging capacity by increasing the amount of prey captured. However, because lunge feeding (see Glossary) is a dynamic event with a large mouth aperture presented to flow at high speed, large amounts of water are accelerated and high drag is incurred (Goldbogen et al., 2007; Potvin et al., 2009; Simon et al., 2012). Despite the high energetic costs that result from increased drag during feeding, the overall efficiency of the feeding lunge is high so long as the density of the targeted prey patch is also high (Goldbogen et al., 2011).

However, the high costs of feeding will limit diving capacity, which likely explain the relatively lower foraging dive durations of the largest rorquals (i.e. blue and fin whales) compared with other large whales (Acevedo-Gutierrez et al., 2002; Croll et al., 2001). The cost of a lunge is largely determined by the size of the engulfed water mass, but also the maximum speed just prior to mouth opening (Cade et al., 2016; Goldbogen et al., 2011; Potvin et al., 2009, 2012). Because large whales lunge at higher speeds and have greater mass-specific engulfment capacities, the combined cost progressively limits dive capacity that should otherwise be granted by large body size (Goldbogen et al., 2012). For example, the relatively high cost of feeding in blue whales is estimated to be approximately 60% of the total cost of a foraging dive (Goldbogen et al., 2011). By contrast, the cost of feeding in minke whales is predictably very low because of the very low mass-engulfment capacity, and thus is close to that for steady swimming (Blix and Folkow, 1995; Potvin et al., 2012). An additional cost of relatively larger gulps in bigger whales is that a greater proportion of the limited dive time must be devoted to the purging and filtration of the engulfed water (Goldbogen et al., 2012). Consequently, there is an inverse relationship between the number of lunges per dive and engulfment capacity, such that smaller whales take many small gulps and larger whales take fewer big gulps (Friedlaender et al., 2014). It follows that larger rorquals appear to be forfeiting their diving capacity for enhanced foraging capacity, and this predictably increases the energetic efficiency of feeding at larger sizes (Friedlaender et al., 2014; Goldbogen et al., 2012, 2011, 2010).

Concluding remarks

The mechanisms driving the evolution of gigantism and foraging capacity in cetaceans remains poorly understood. Here we provide different hypotheses that can be tested in future comparative studies. We posit that toothed whales evolved gigantism because echolocation allowed for the progressive invasion of the deep ocean that required larger size and enhanced diving capacity. In contrast, filter-feeding baleen whales evolved gigantism in response to recent changes in the ocean that provided high-quality prey patches, thereby resulting in increased foraging efficiency at greater whale sizes that could, in turn, support such extremes in body mass. With the advent of biologging tag technology, our ability to quantify the diving and foraging performance of cetaceans in their natural environment has greatly increased in the past two decades. The next great challenge is to integrate data from individual studies to test mechanistic hypotheses regarding form, function, physiology and ecology across scales. Specifically, we need to better understand the energetics of foraging and how it compares between particulate-feeding odontocetes and filter-feeding mysticetes. Furthermore, we need to test whether the estimated energetic efficiency of foraging increases with body size in both lineages and by what magnitude. Although direct oxygen consumption measurements cannot yet be made on cetaceans in natural environments, a comparative analysis of feeding rates and foraging performance in species ranging from the small harbor porpoise to the huge blue whale will provide key insights into the physiology and functional ecology of cetaceans. Moreover, these studies will clarify the processes that may have driven body size evolution in a group of mammals that ultimately led to the largest animals ever.

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Competing interests

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