

How Whales Dive, Feast, and Fast: The Ecophysiological Drivers and Limits of Foraging in the Evolution of Cetaceans

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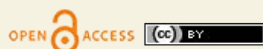
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Keywords

body size, scaling, gigantism, diving, foraging, predator–prey

Abstract

Whales are an extraordinary study group for questions about ecology and evolution because their combinations of extreme body sizes and unique foraging strategies are unparalleled among animals. From a terrestrial ancestry, whales evolved specialized oceanic foraging mechanisms that characterize the two main groups of living cetaceans: echolocation by toothed whales and bulk filter feeding by baleen whales. In toothed whales, lineage-specific increases in body size, enhanced diving capacity, and echolocation enable them to hunt the most abundant prey on the planet: deep-sea fish and cephalopods. Even greater body size increases, along with filter feeding and fasting capacity, permit large baleen whales to migrate long distances and exploit epipelagic patches of schooling prey, such as krill or fish, which are highly abundant but ephemeral. For both groups, prey abundance and distribution limit foraging performance, yielding divergent energetic niches that have shaped their convergent evolution to gigantism.

1. INTRODUCTION

As early as Galileo Galilei (Galileo 1638), scholars interested in the diversity of life hypothesized that the physical environment might constrain biological shape and size (Gould 1992). Over the past few centuries, investigators of these physical constraints questioned whether scaling changes in anatomical proportions or behavior have encountered fundamental limits at both smaller and larger sizes (Alexander 1998). Mammals provide an interesting test case for such questions about the evolution of form and function: They span body sizes ranging from 3-g shrews and bats to 150-ton whales; they inhabit vastly different physical environments, including land, air, and water; they share the same body plan, physiology, and reproductive modes; and they are, at most organismal scales, accessible as living animals or as museum vouchers, sometimes with extensive fossil records.

Many studies on mammalian constraints and size limits focus on terrestrial species, revealing that, for example, proportionally thicker bones evolve with increasing body size (Dick & Clemente 2017). Interestingly, shape change alone cannot support the mechanical demands of extreme body weight without trade-offs in locomotor performance (Dick & Clemente 2017). Despite such scale-dependent constraints, terrestrial mammals evolved gigantism multiple times over the course of geologic time, particularly as herbivores (Saarinen et al. 2014). However, even the largest land animals, whose maximum size may be limited ultimately by food intake (Burness et al. 2001) rather than the biomechanics of limbs, are much smaller in mass than the largest whales alive today (Vermeij 2016).

Whales (crown Cetacea) are a group of marine mammals that includes over 80 extant species, all of which spend their entire lives in water (**Figure 1**). Although most living species are marine, spanning polar to equatorial waters, a few lineages are exclusively riverine (Kaschner et al. 2012). All of today's whales are descended from extinct and much smaller semiaquatic ancestors that had weight-bearing limbs 50 million years ago (Ma) (Thewissen 2013). Within approximately 10 million years, the ancestors of today's cetaceans evolved a set of adaptations for obligate aquatic life, including the reduction of hind limbs in favor of tail-propelled swimming, modified forelimbs as control surfaces for swimming, and many changes to the skull and jaws for sensing, breathing, and feeding in the water.

Today's cetacean species belong to one of two different subgroups: filter-feeding baleen whales (Mysticeti) and echolocating toothed whales (Odontoceti). Odontocetes are characterized by their ability to use echolocation to target prey throughout the water column (Jensen et al. 2018, Wisniewska et al. 2016); some species lack teeth, and others have reduced tooth counts, yet all of their ancestors possessed teeth (Fitzgerald 2006). By contrast, mysticetes resorb tooth buds in utero (Peredo et al. 2017) and instead use a complex, keratinized structure called baleen, which hangs from the roof of their mouth, to filter prey in large quantities (Goldbogen et al. 2017).

Living cetaceans are especially interesting from a scaling perspective because they exhibit a nearly 5,000-fold range in mass across their extremes (Lockyer 2007), from 30-kg harbor porpoises (*Phocoena phocoena*) to 150,000-kg blue whales (*Balaenoptera musculus*). Today, extinction risk is only loosely correlated with extremes in body size: Some cetacean species at both size extremes, such as the small vaquita (*Phocoena sinus*) and the giant North Atlantic right whales (*Eubalaena glacialis*), are imperiled by ship strike, bycatch, and entanglement (D'agrosa et al. 2000, Stewart et al. 2021). Still other species, such as humpback whales (*Megaptera novaeangliae*) and fin whales (*Balaenoptera physalus*), are recovering successfully from industrial whaling, which decimated global populations, especially during the twentieth century (Rocha et al. 2014).

Apart from their impressive breadth and extremes in organismal size, the abundance of whales has been important for human society. For thousands of years, whales were resources to be consumed, either for their meat, fat (i.e., oil), skeletons, or baleen. In the past 1,000 years, the exploitation of whales was directly connected with mercantile and colonial economies;

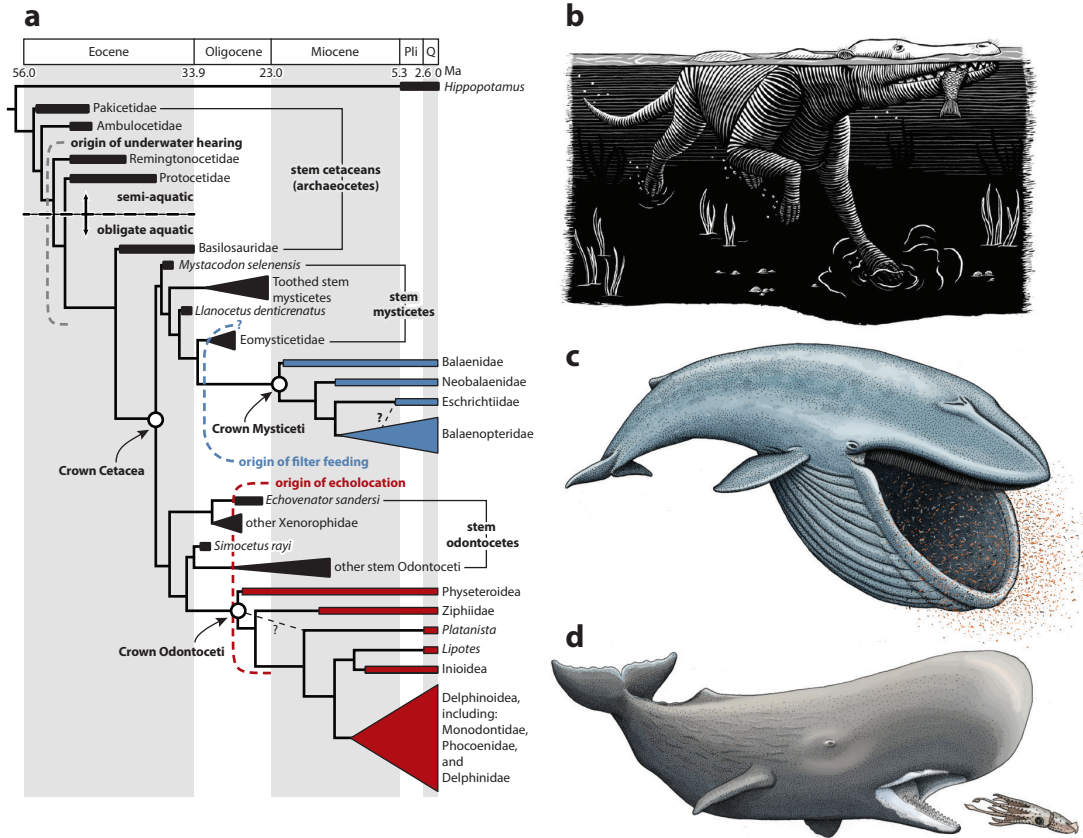


Figure 1

Evolutionary relationships among cetaceans. (a) Cetacean phylogeny showing major evolutionary transitions and taxonomic groups. (b) *Pakicetus*. (c) Blue whale (largest baleen whale) lunge feeding on krill. (d) Sperm whale (largest toothed whale) suction feeding on a cephalopod. Abbreviations: Ma, million years ago; Pli, Pliocene; Q, Quaternary. Illustrations in panels b–d provided by Alex Boersma with permission.

approximately 200 years ago, whaling was a foundation for several national economies prior to the rise of petroleum as a fuel. In the past half century, there has been a notable shift from the economics of whales as resources of consumption to granting them bona fide legal protection to now having immense conservation value, especially for a multi-billion-dollar whale watching industry (Burnett 2012, Durfort et al. 2022, Savoca et al. 2021).

Notably, industrial whaling in the twentieth century was one of the greatest removals of animal biomass in human history, killing 2–3 million large whales. This reduction in biomass rendered most large whale populations a small percentage of their preexploitation state (Rocha et al. 2014), although calibration of the data for these states prior to whaling is difficult to validate beyond inference and incomplete historical data (Alter et al. 2012). Recent advances in at-sea technology offer ways to study in great detail whale physiology, behavior, ecology, and life history. For example, their large size and specialized foraging mechanisms give whales access to prey that are unevenly distributed in space and time (Goldbogen et al. 2019), and in many cases, these prey patches represent some of the most abundant ocean biomass on the planet. Like many other marine mammals, whales are ocean navigators and sentinels that reflect ocean processes on long-lived mammalian

time scales, exceeding a century in some species (Dietz et al. 2021, George et al. 1999, Hazen et al. 2019, Trumble et al. 2013). However, their enormous size—orders of magnitude larger than other marine mammals—suggests an ability to have disproportionate impacts on food webs and ocean health (Estes et al. 2006, Kanwisher & Ridgway 1983, Katona & Whitehead 1988).

The mechanisms that drove the ecological and evolutionary success of whales are important for predicting their fate during the Anthropocene. As bycatch, pollution, climate change, and biodiversity loss accelerate, the consequences of these activities remain difficult to predict, and hence mitigate, in pelagic ecosystems (Santora et al. 2020, Whitehead et al. 2008). Whales and their ecosystems operate at scales of time (centuries) and space (ocean basins) that are similarly hard to understand because these interactions unfold across vast, complex environments and beyond human lifetimes and instruments (Mansouri et al. 2021, Winfield et al. 2020). The rate and magnitude of ocean change will have a profound impact on these ocean giants, and conversely, the rate and mode of the recovery or decline of whale populations will play major roles in the functioning of future ocean ecosystems.

By addressing a series of questions, this review explores the principles that govern the drivers and limits of foraging and body size in whales. Here we use the term drivers to mean a set of conditions, both abiotic and biotic, that promoted the evolution of morphological and physiological adaptations. Conversely, limits are constraints imposed by the scaling of physiological and/or ecological processes. We examine the body size evolution of cetaceans in a comparative context to understand the exceptional gigantism of the largest whales. We argue that the scaling of physiological processes provided two evolutionary pathways to gigantism: (a) the extreme breath-hold diving capacity conferred by large body size, which allowed toothed whales to access stable and abundant populations of fish and squid in the deep sea, and (b) the extreme filter feeding and fasting abilities of larger baleen whales, which allowed them to rapidly consume abundant but seasonally ephemeral food. The evolution of gigantic whales generated predator–prey interactions at extreme scales that have profound implications for the energetic efficiency of foraging in the largest of mammals. Specifically, we posit that the size structure and ephemerality of prey communities impose different drivers and limits on body size that depend on the foraging adaptations that distinguish toothed whales from baleen whales. Lastly, we pose several questions that relate to the consequences of extreme body size in increasingly urbanized ocean ecosystems.

2. WHAT ARE THE EVOLUTIONARY TRAJECTORIES OF WHALE BODY SIZE?

Among all mammals, whales are most closely related to other even-toed, hoofed mammals (Artiodactyla) such as deer, cattle, pig, sheep, and camels. Their closest living relatives are hippos (**Figure 1**). Outwardly, today's whales lack many of the traits shared among artiodactyl mammals (e.g., grinding teeth, weight-bearing limbs, hind limbs, toes, and hooves). Moreover, the body size range of living whales far exceeds the group-wide size range of any of their close living relatives. The large morphological gap between whales and other land mammals today can be explained by the whale fossil record, which spans just slightly more than 50 million years (Pyenson 2017). The oldest fossil relatives that are more closely related to whales than other artiodactyls, such as *Indohyus* and *Pakicetus*, possess key structures in the basicranium, related to the middle ear bones, allying these small semiaquatic four-legged species with today's cetaceans (Nummela et al. 2004). The fossil record of the first 10 million years of whale evolution shows increasing amphibious adaptations via sequential changes in the skeleton, especially for locomotion in water but also in sensory and feeding systems (Thewissen & Williams 2002). This first phase of whale evolutionary history encompasses the entire transition from terrestrial to ocean ecosystems, spanning body

sizes between those of domestic dogs to the first obligately aquatic whales, such as *Basilosaurus* (Gingerich 1998), which was as large as today's killer whales (*Orcinus orca*; approximately 5 tons). The second phase of whale evolution occurred in the past ~40 million years, encompassing all of their diversification once they became fully aquatic, including the extinction of the earliest whales, the appearance of foraging adaptations such as extreme gigantism (100 tons), echolocation, filter feeding, and the multiple reinvasions of freshwater ecosystems (Pyenson 2017).

Although fossil whale skeletons are incomplete, some measurements of their skulls provide reliable estimates for reconstructing their body size (Pyenson & Sponberg 2011). This method is convenient, given the adequacy of the cetacean fossil record (Uhen & Pyenson 2007) and the diagnostic value of skulls for determining taxonomic identity and phylogenetic relationships (Fordyce & de Muizon 2001). The fossil record provides direct evidence for past evolutionary states that are otherwise unobtainable, and one of the fundamental insights for body size evolution is that no fossil whale species was larger than its living relatives. For example, the minimum and maximum estimates of the largest fossil sperm whale, *Liopytan melvillei* (~13–17 m) are comparable to extant sperm whales (*Physeter macrocephalus*) but still smaller than the largest records (19 m) for this living species (Lambert et al. 2010, Lockyer 1976); moreover, killer whales (*Orcinus orca*), Baird's beaked whales (*Berardius bairdii*), and the largest species of rorqual whales (Balaenopteridae), gray whales (*Eschrichtius robustus*), and bowhead and right whales (Balaenidae) are all larger than any of their respective fossil relatives (Bianucci et al. 2016, 2022; Bisconti et al. 2021; Slater et al. 2017). The second major insight from the fossil record is that gigantism (body lengths exceeding 10 m) evolved multiple times: Toothed whales and baleen whales independently evolved gigantism, even within subclades (e.g., Bisconti et al. 2021). Third, while some cetacean lineages show trends toward dwarfism over geologic time (Bisconti et al. 2021, Sander et al. 2021), broader trends indicate gigantism evolving over the same time range. The repeated, independent evolution of gigantism across several cetacean clades suggests that common factors influenced the evolution of body size (Pyenson et al. 2014, Slater et al. 2017).

In the broadest view, the evolutionary history of cetaceans parallels other tetrapod lineages with terrestrial ancestry that have invaded ocean ecosystems since the end of the Permian, over 250 Ma. These lineages, including marine reptiles such as ichthyosaurs, plesiosaurs, mosasaurs, penguins, and sea turtles, show similar converging bauplans (body plans) and ecomorphologies that can be identified in many of today's marine mammals, such as forelimbs modified as flippers to form efficient, wing-like control surfaces for high-performance maneuvers in water (Kelley & Pyenson 2015). After the end of the Cretaceous (66 Ma), both cetacean ancestors and sirenian ancestors were the first mammalian lineages to independently undergo similar morphological transformations in their transition from land to sea, both starting approximately 50 Ma (Domning 2001, Gingerich 2005). Later, in the last half of the Cenozoic era (30 Ma to present), other marine mammals adapted to life at sea in various capacities, as seen in the amphibious lifestyles of pinnipeds (seals and sea lions), arctoid bears, mustelids (otters and their relatives), and extinct sea sloths or the unique aquatic adaptations of the extinct desmostylians (Berta 2017).

Some marine mammal clades, such as pinnipeds (Churchill et al. 2015), show weak trends toward gigantism in their diversification from smaller ancestors; the largest pinniped ever was a fossil walrus relative, *Pontolis magnus*, at over 4 m in body length, but it was well within an order of magnitude in size of the earliest pinnipeds. However, no other marine mammal lineage evolved the absolute size extremes of extant cetaceans. Sirenians, which have had a similarly long evolutionary history as whales, reached a size maximum with the historically extinct Steller's sea cow (*Hydrodamalis gigas*), at approximately 9 m in length and 8–10 tons (Domning 1978, Estes et al. 2016). Interestingly, both cetaceans and sirenians show a delayed increase in body size evolution (Pyenson & Vermeij 2016): Unlike mammals on land or ichthyosaurs in Mesozoic oceans, whales

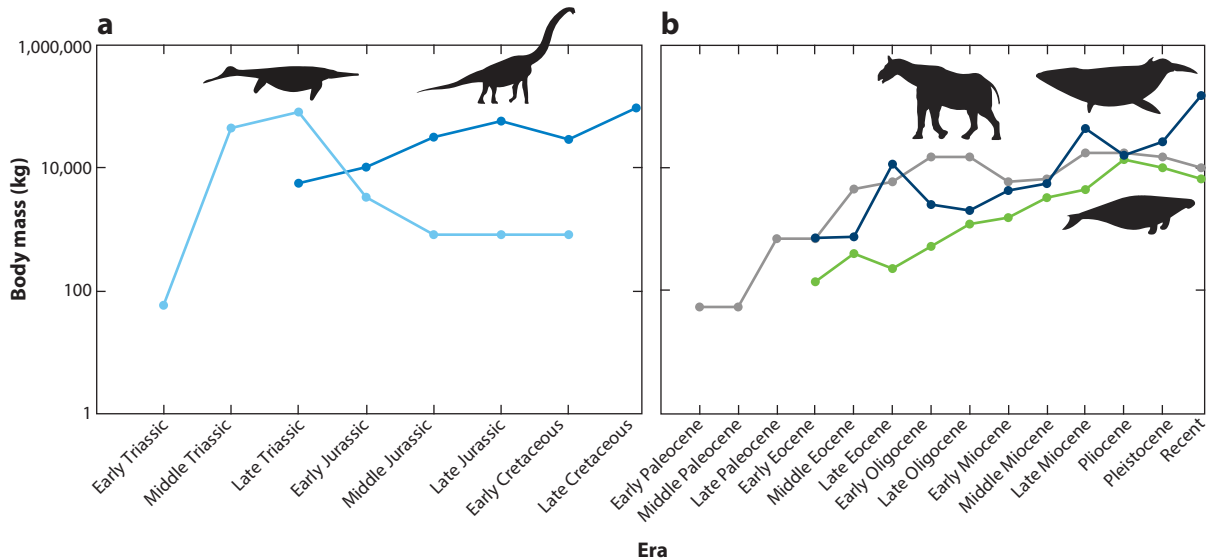


Figure 2

Maximum tetrapod body size on land and in the sea for the past 250 million years. (a) Maximum body size of ichthyosaurs (light blue line; Ichthyosauria) and sauropod dinosaurs (dark blue line; Sauropodomorpha) in the Mesozoic. (b) Maximum body size for land mammals (gray line), sirenians (green line), and cetaceans (dark blue line) in the Cenozoic. Panel a created using data on ichthyosaurs from Gutarra et al. (2019) and Sander et al. (2021) and data on dinosaurs from Benson et al. (2018). Panel b created using land mammal data from Saarinen et al. (2014); sirenian data from Pyenson & Vermeij (2016), using the combined mass equation from Sarko et al. (2010); and cetacean data from Gingerich (1998) and Pyenson & Vermeij (2016), with corresponding equations from Pyenson & Sponberg (2011) and Silva & Downing (1995).

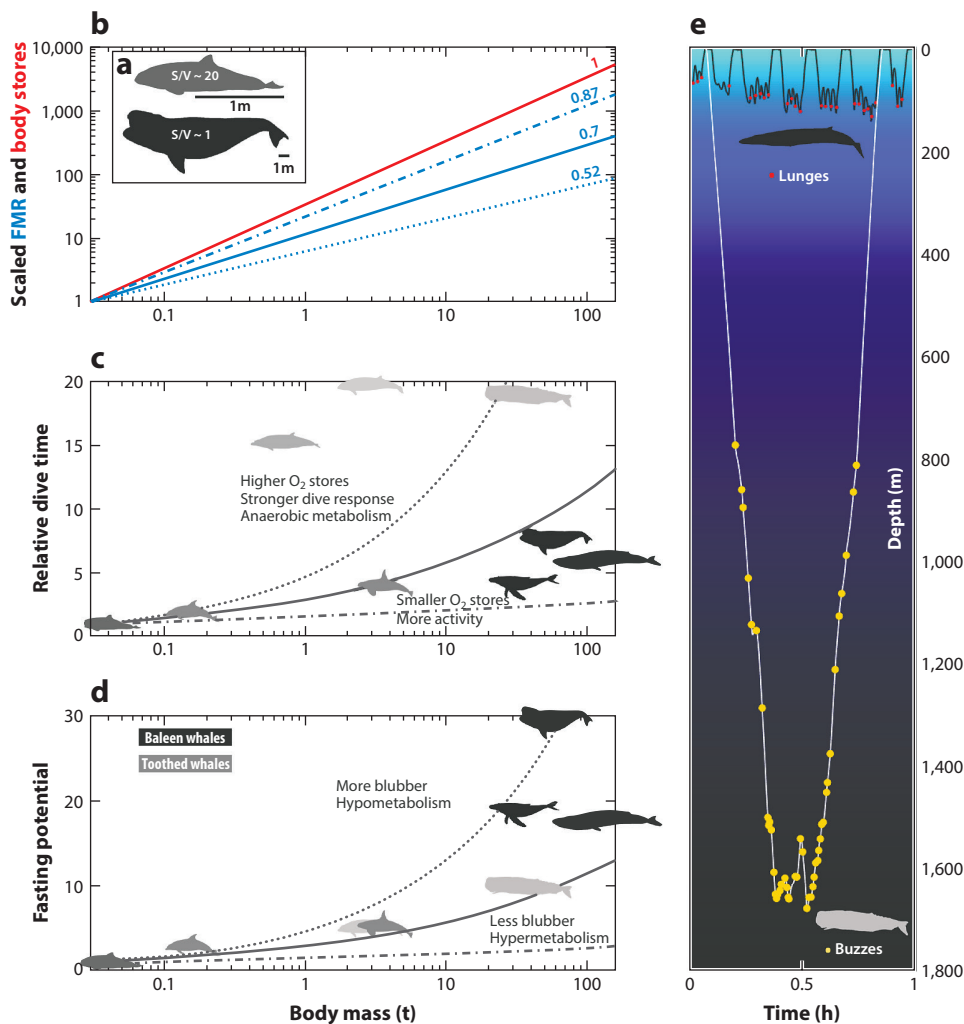
and sirenians both took over 90% of their evolutionary history to achieve the maximum sizes observed in today's extremely large species (Sander et al. 2021, Slater et al. 2017) (Figure 2).

Compared with ichthyosaurs and other marine reptiles, mammals adapting to life in water faced at least an order of magnitude greater mass-specific food requirements as endotherms, requiring sensory and locomotor capabilities that would improve hunting capabilities by the same magnitude. The higher metabolic rates associated with endothermy enabled higher sustained swim speeds and longer migratory distances that could ultimately enhance foraging efficiencies (Watanabe et al. 2015). Therefore, the independent evolution of larger body sizes in marine mammals reflects not only a release from the constraints of supporting body weight but also scale-dependent physiological and energetic advantages to meet these challenges (Gearty et al. 2018). Greater food availability in the ocean was probably one of the most important drivers for cetaceans to invade the ocean in the first phase of their evolution; the subsequent evolution of foraging and physiology adaptations during the second phase of their evolution allowed whales to evolve the largest body sizes in the history of animal life (Lindberg & Pyenson 2006).

3. WHAT ARE THE PHYSIOLOGICAL CONSEQUENCES OF BODY SIZE CHANGES IN WHALES?

Porpoises (Phocoenidae) include the smallest whales, but they have adult body weights (approximately 30 kg) larger than >95% of all terrestrial mammal species (Smith & Lyons 2011). This lower size limit is likely imposed by the physiological problem of keeping small bodies warm in water (Ahlborn & Blake 1999), a medium that has a heat conductivity 25 times higher than air and a

much higher heat capacity (Denny 1993). Smaller endothermic animals face the thermoregulatory consequences of large ratios between their surface area, over which heat is lost, and the volume of their heat producing core (**Figure 3a**) (Ryg et al. 1993). Consequently, small whales must either live in warm tropical waters, employ insulating blubber layers so large that they eventually impede efficient locomotion, or maintain very high mass-specific metabolic rates to produce enough heat to offset heat loss (Ahlborn & Blake 1999). This problem is extreme for newborns: For example, 8-kg porpoise calves born in the icy waters off Greenland must have very high metabolic rates to stay warm, resulting in large nursing costs for their mothers (Rojano-Doñate et al. 2018). All smaller aquatic mammals at high latitudes such as river otters, beavers, musk rats, and small pinnipeds are amphibious; they venture into water only for foraging between extended periods on land, where they can also give birth and nurse their young in a medium of lower heat conductivity. Thus, the lower size limit for whales as obligate aquatic endotherms is likely set by the mass-specific costs of keeping small bodies warm in water (Ahlborn & Blake 1999, Kanwisher & Sundnes 1965).



(Caption appears on following page)

Figure 3 (Figure appears on preceding page)

Scaling of foraging, diving, and fasting capacity with body size in cetaceans. (a) A 30-kg porpoise and a 100-ton right whale exhibit a 20-fold difference in the surface-to-volume ratio (S/V). The porpoise must have a high mass-specific FMR to stay warm, whereas the right whale cannot freeze no matter how cold the water is and therefore does not need elevated mass-specific FMR to stay warm. (b) Scaled FMR against cetacean body mass (M , in tons) normalized to a 0.03-ton porpoise using slopes of 0.52, 0.7, or 0.87 from published literature (*blue lines*). The red line depicts the isometric relationship (M^1) between body stores of oxygen or blubber against body mass. (c) Because body oxygen stores scale isometrically and the rate at which they are used (FMR) scales hypoallometrically ($M^{0.7}$) during diving, diving capacity scales with $M^{0.3}$ (*solid line*). A whale that is 1,000 times heavier should be able to hold its breath eight times longer. Different scaling of FMR with body mass can enhance (*dotted line*) or diminish (*dot-dash line*) diving capacity. Dive times can also be modulated by activity levels (e.g., locomotor gaits, feeding rates), ecological factors (e.g., prey distribution), and other physiological adaptations (e.g., myoglobin concentration and level of dive response). (d) Because blubber stores scale isometrically (M^1) and the rate at which they are used (FMR) scales hypoallometrically ($M^{0.7}$), fasting potential also scales with $M^{0.3}$. A whale that is 1,000 times heavier should be able to live off its blubber reserves 8 times longer. Variation in scaling of FMR with body mass can enhance (*dotted line*) or diminish (*dot-dash line*) fasting potential. The y-axis values in panels b–d are nondimensional, reflecting scaled values relative to those of the smallest whale, a 0.03 ton harbor porpoise. (e) Dive profiles of a 30-ton sperm whale hunting single prey with echolocation (buzz, *yellow dots*) during a 50-min dive and a 45-ton fin whale lunge feeding on schooling small prey (*red dots*) during several 8-min dives. Abbreviations: FMR, field metabolic rate; M , mass; S/V, surface-to-volume ratio. Panel e provided by Simone Videsen with permission.

Depending on the water temperature, whales of several hundred kilograms (e.g., many dolphin species belonging to Delphinidae) can still face thermoregulatory challenges in high-latitude and temperate waters. However, larger dolphins have the advantage compared to smaller toothed whales (i.e., porpoises) because they need proportionally less blubber (as a percentage of lean body mass) to provide the same amount of absolute insulation per area of body surface. When whales reach a size of approximately 1 ton, they are likely within their thermoneutral zones (where the metabolic rate is independent of water temperature) (Ryg et al. 1993). Accordingly, the seasonally thick blubber layers (up to 70 cm) in large whales, such as in right whales, function as long-term energy stores rather than as needed insulation (Lavigne et al. 1990) because of the very low surface-to-volume ratios, close to unity, in these rotund giants (**Figure 3a**). The mass-specific costs of staying warm in water are hence much lower for larger whales than smaller whales, and this fundamental consequence of scaling dictates the extraordinary fasting ability in the former (Millar & Hickling 1990) and the constant high mass-specific feeding requirements of the latter (Kanwisher & Sundnes 1965).

The field metabolic rate (FMR), which reflects the combined energy turnover per unit time of a wild animal, generally scales with body mass to the power of approximately 0.7 for mammals (Nagy 2005). It is an open and highly debated question whether such scaling also applies to marine mammals (Williams & Maresh 2015). Because whales of increasingly larger size spend less energy on thermoregulation and locomotion (due to the lower cost of transport) (Williams 1999), proposed estimates of FMR body-mass scaling coefficients may be as low as 0.52 (Boyd & Hoelzel 2002), implying that large whales have five times lower food requirements (**Figure 3b**) than predicted from terrestrial mammals (Nagy 2005). If FMR instead follows the scaling observed in smaller carnivorous mammals (0.87) (Williams et al. 2020), large whales may have extreme food requirements that are five times higher than predicted from terrestrial mammals (Nagy 2005) (**Figure 3b**). We do not currently have the field data to resolve this debate despite its critical importance for understanding the ecological roles of whales. Therefore, we chose a coefficient of 0.7 in this section to explore the scaling implications of gigantism in whales, while also including other suggested coefficients for comparison.

Although larger whales need much more food than smaller whales in absolute amounts, larger whales need proportionally less food per unit mass because of the negative allometry of metabolic rate. This scale-dependent physiological consequence has likely played an important role in the evolution and ecology of whales. **Figure 3b** shows that a 30,000-kg whale, which weighs 1,000 times more than a 30-kg porpoise, needs only 125 times as much food ($1,000^{0.7} = 125$). Consequently, a small porpoise must catch 25–30 times its own body mass in prey per year, whereas a 30-ton whale may need only 3–4 times its own body mass in prey per year. Therefore, smaller toothed whales must catch fish prey of approximately 8% of their body weight on average every day, year-round (Rojano-Doñate et al. 2018). Large baleen whales on average catch a similar percentage of their own body weight per day (Savoca et al. 2021, Videsen et al. 2023) but meet their yearly food requirements by doing so in just 3–4 months of successful foraging (Lockyer 2007). This means that large baleen whales can wait for food to aggregate seasonally in time and space, whereas small whales must find food regularly throughout the year. However, under circumstances in which large prey is not abundant enough or when it is not possible to catch small prey in large quantities, only small marine mammals can thrive, owing to their smaller absolute food requirements. Although small whales have higher mass-specific FMRs than large whales, their absolute smaller food requirements allow them to use a greater diversity of less prey-dense food niches than larger whales. Therefore, lineages being under selection to enhance energy intake in different foraging niches may be a driver for elevated speciation rates (Gearty et al. 2018), such as those observed in smaller toothed whales (McGowen 2011). In contrast, baleen whales exhibit relatively lower generic diversity since the Plio-Pleistocene boundary ~ 2.6 Ma.

An additional advantage conferred by large size is generated by a favorable ratio between body stores and the rates at which they are consumed (Millar & Hickling 1990). Body stores of both fat and oxygen generally scale isometrically with body mass such that the maximum amount of oxygen or blubber that can be stored per kilogram is a fixed fraction of lean body mass (**Figure 3b**). Because the rates of oxygen consumption, during both diving and blubber consumption (i.e., while fasting), scale hypoallometrically with mass to the power of 0.7, and the stores of oxygen and blubber scale isometrically to the power of 1, the capacity to perform aerobic breath-hold dives (as well as to fast) consequently scale with body mass to the power of 0.3 (**Figure 3c,d**). Therefore, a 30-ton sperm whale should breath-hold dive 8 times ($1,000^{0.3}$) longer than a 30-kg porpoise simply because it is 1,000 times heavier, and it therefore consumes oxygen 8 times slower per unit body mass. There are additional adaptations, such as diving hypometabolism via a stronger dive response and larger oxygen stores per unit body mass (Ponganis 2015), that further enhance aerobic breath-hold capabilities beyond what is conferred by large body size. Therefore, a 50-min dive by a 30-ton sperm whale is perhaps no more extraordinary than a 3-min dive by a 30-kg porpoise. However, a crucial distinction is that a 3-min dive does not provide enough time to effectively forage on prey in the deep sea. It follows that large body sizes are a defining characteristic of >20 species of toothed whales that regularly forage in meso- and bathy-pelagic prey layers (**Figure 3d,e**).

Gigantism alone does not confer extraordinary diving abilities. For example, from first principles, large baleen whales between 50 and 150 tons should also be able to perform breath-hold dives of an hour or more (**Figure 3c**). However, the selective advantages for the evolution of such prolonged breath holds were likely not imposed because their prey are found in epipelagic waters (<200–300 m), especially in the photic zone, which represent foraging depths that are only 10–15 body lengths for large baleen whale species like blue whales and fin whales and are therefore easily accessible (**Figure 3d,e**). Therefore, we argue that the evolutionary pathways to gigantism in baleen whales were not driven by a need for extreme diving capabilities but rather mainly influenced by the selective forces associated with efficient foraging on ephemeral and seasonal

giga-patches of prey in epipelagic waters (Slater et al. 2017). Such temporally brief but spatially dense feasts with high feeding rates allow larger baleen whales to quickly build substantial lipid stores because of the differential scaling of stomach volume (isometry) and FMR (hypoallometry). In contrast, smaller whales require a larger proportion of their stomach capacity to support higher mass-specific metabolic rates, allowing for less ingested energy per time to be allocated to body stores. Interestingly, gastrointestinal lengths appear to scale with negative allometry (Williams 2006), which may track with FMR scaling in cetaceans and other marine mammals (Williams et al. 2001). Although smaller whales may be able to digest food faster because of a relatively longer intestinal track, larger whales should be able to store relatively more energy from a full stomach as blubber because of lower mass-specific metabolic rates.

Cetaceans in good body condition have typical blubber stores of some 25% of body mass, and in large balaenids it may reach 45% at the end of the feeding season (Omura et al. 1969). Body size and lipid stores are direct proxies for realized prey abundance, as well as the needed length of the foraging season (Brodie 1975). However, because of the scaling of FMR with mass, the depletion rate of these energy stores during fasting varies dramatically across scale. Large whales can fast off the same relative blubber store (as a percentage of lean body mass) at least an order of magnitude longer than small cetaceans (**Figure 3d**), and they can prolong such fasting by lowering their activity budget (Bejder et al. 2019). In contrast, smaller cetaceans in cold water face a dramatic negative feedback loop during fasting because a thinner blubber layer requires a higher FMR to stay warm, which in turn consumes more blubber when starving (Rojano-Doñate et al. 2018). Based on metabolic rate and blubber measurements, even well-nourished porpoises may starve to death in cold waters in less than 10 days (Kastelein et al. 1997). Therefore, smaller toothed whales must feed regularly to meet their high mass-specific metabolic rates, and they cannot rely on their blubber stores to search for food for extensive periods of time.

The extraordinary fasting ability of large baleen whales enables them to exploit extremely patchy seasonal prey aggregations that may be available only for a few months of the year. This is a typical pattern in capital breeding life history strategies, where the energy for reproduction is procured before birth and nursing of the calf (Pirotta et al. 2018). Right whales, for example, in excellent body condition can survive entirely on their blubber stores for more than a year, which also leads to the horrific observations of prolonged suffering before death when entangled in fishing gear that often allows them to breathe but not feed sufficiently or at all (van der Hoop et al. 2017). A shortened foraging season frees up much of the year to migrate to less productive, warmer waters to give birth to their calves and engage in complex, often vocally mediated, mating behaviors (Tyack & Whitehead 1983). A capital breeding life history and longitudinally oriented migrations likely lessen the predation pressure from killer whales, which are much more abundant at productive high-latitude feeding grounds (Corkeron & Connor 1999). Such breeding migrations are well documented in humpback whales, gray whales, and right whales. These migrations involve fasting mothers that not only survive on their own blubber stores while migrating and growing a fetus but also mobilize their blubber stores to nurse a growing calf before migrating back to the feeding grounds with their calf while still fasting (Christiansen et al. 2016). Consequently, many larger baleen whales undergo dramatic changes in their body mass of more than 30% in a year between a maximum when leaving the feeding grounds and a minimum when returning from the breeding grounds after up to 9 months of essentially fasting while nursing a calf (Christiansen et al. 2018).

In contrast, all toothed whales are income breeders, for which the energy for nursing the calf with milk is fully or partially fueled by concurrent foraging. Smaller toothed whale mothers must catch up to twice as much fish as normal to fuel their own metabolism and the production of milk needed for the growth and metabolism of their offspring (Kastelein et al. 1997). It follows

that smaller whales cannot move from prey-rich feeding grounds to low-productivity breeding areas with fewer predators to give birth and nurse a calf. Consequently, some whale species have evolved other antipredator behaviors such as acoustic crypsis or social defenses to constantly navigate soundscapes of fear where tonal sounds trigger very strong antipredator responses (Aguilar de Soto et al. 2012, Aguilar Soto et al. 2020, Miller et al. 2022, Morisaka & Connor 2007). Such responses to killer whale sounds, for example, predispose some cetacean species to costly behavioral or even deadly physiological reactions (i.e., cessation of foraging, energetic flight responses, or decompression sickness) in response to tonal human-made sounds (i.e., 1- to 4-kHz naval sonar) in the same frequency band (Miller et al. 2022).

The benefits of whale gigantism discussed above are more pronounced for lower scaling coefficients of FMR with mass because it increases the ratio between stores and the rates at which they are depleted (**Figure 3b–d**). Thus, if the FMR of larger whales is lower than what would be predicted based on extrapolations from terrestrial mammals, the advantages over smaller cetaceans in terms of dive times, foraging efficiency, and fasting potential are larger. Conversely, if large cetaceans have higher FMRs than standard scaling would predict, the advantages of gigantism are smaller. It is therefore critically important to develop reliable but noninvasive techniques to estimate the FMRs of large whales at sea to understand how they can feast and fast in anthropocene oceans (McHuron et al. 2022).

4. WHAT ARE THE ENERGETIC CONSTRAINTS OF EXTREME PREDATOR–PREY SIZE RATIOS?

As filter-feeding and echolocating whales independently evolved increasingly larger body sizes, they faced a fundamental ecological problem: Large prey are much less abundant than smaller prey in the ocean. Consequently, at larger body sizes, whales must increasingly rely on catching larger quantities of relatively smaller prey or become more efficient at catching the few large prey species that are available (Goldbogen et al. 2019). Rare examples of the latter include mammal-eating killer whales that cooperatively hunt baleen whales, other toothed whales, and pinnipeds (Ford & Reeves 2008) and false killer whales (*Pseudorca crassidens*) that target large fish. In the fossil record, a similar phenomenon likely occurred for the extinct sperm whale relatives, such as *Livyatan melvillei*, whose diet may have included small baleen whales in the Miocene (Lambert et al. 2010). However, most echolocating toothed whales hunt individual prey that are typically 3–4 orders of magnitude smaller than themselves (**Figure 4a**). Porpoises, for example, may in some areas eat more than 2,000 small fish per day, spending large proportions of their time foraging to locate and catch each small prey item individually using echolocation (Wisniewska et al. 2016).

Larger toothed whales also catch their prey individually but do so in the largest ecosystem on the planet, the mesopelagic deep scattering layer, where larger and more nutritional prey are carefully detected and selected in a sea of low energy organisms (Arranz et al. 2011, Tønnesen et al. 2020). Sperm whales rarely consume giant squid (Clarke 1996, Whitehead 2003) but rather target deep sea cephalopods and fish weighing 1–8 kg using a very powerful long-range sonar system enabled by a hypertrophied sound-producing nose (Møhl et al. 2003). Their reliance on high feeding rates, enabled by long-range echolocation, on relatively small prey explains how the very largest toothed whales can meet their energetic demands in the deep sea (Goldbogen et al. 2019). By contrast, pilot whales (*Globicephala* spp.) are medium-sized odontocetes that target larger prey in rich upwelling areas using high-speed chases (Aguilar Soto et al. 2008). More than 20 beaked whale species (Ziphiidae) inhabit vast swaths of the world's deep oceans by catching 20–50 small-to medium-sized prey per dive, interspersed by protracted periods of shallower, nonforaging dives (Goldbogen et al. 2019, Madsen et al. 2013). To feed at such high rates in the mesopelagic prey

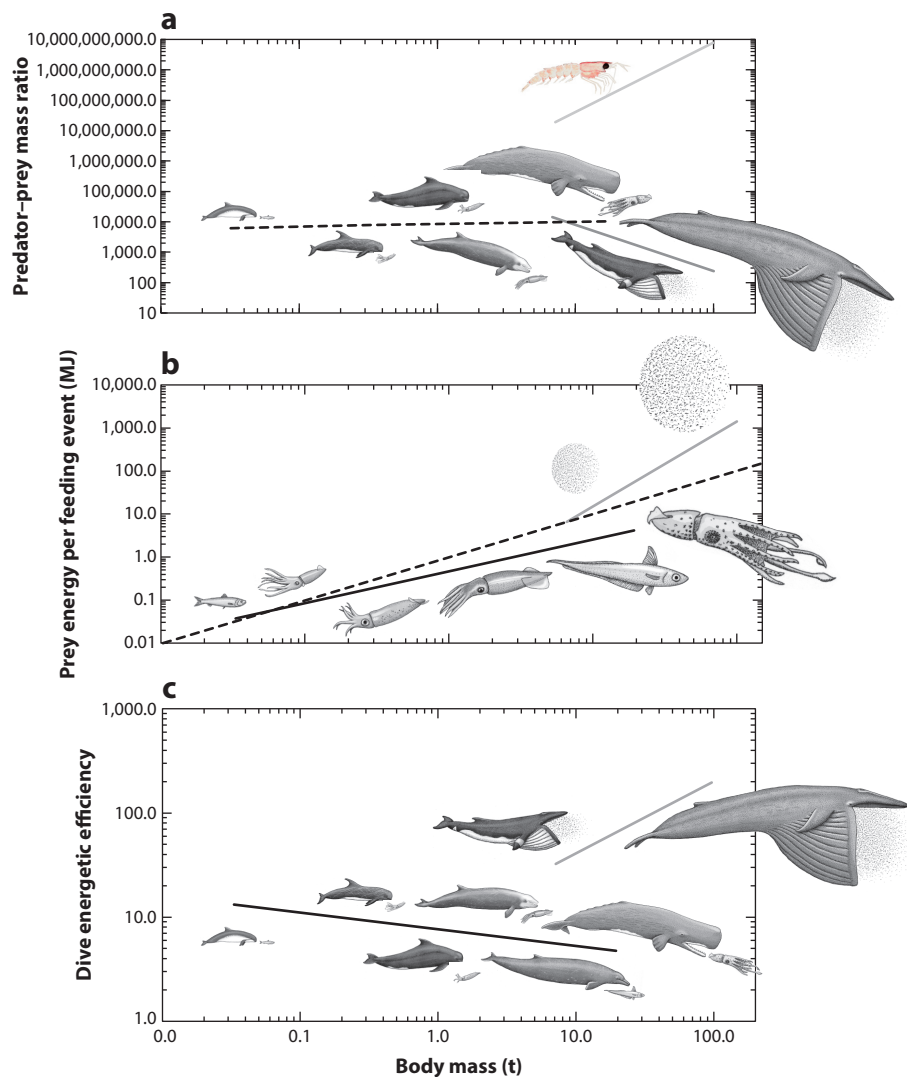


Figure 4

Scaling of predator-prey energetics. (a) Predator-prey mass ratios are relatively invariant with increasing predator size in toothed whales (black dashed line), whereas lunge feeding rorqual whales exhibit increasing ratios relative to individual krill (light gray line) or decreasing ratios relative to patches of krill that can be engulfed (dark gray line). (b) The amount of energy potentially acquired during each feeding event departs from isometry (dashed line). Prey captured by toothed whales exhibit negative allometry (solid black line), whereas krill patches engulfed by rorqual whales exhibit positive allometry (gray line). (c) Assuming metabolic rate scales with body mass to the power 0.45, the energetic efficiency of foraging dives appears to decrease with body size in toothed whales (black line) but increases with body size in rorqual whales (gray line). Figure created using data from Goldbogen et al. (2019). Data for balaenids not shown for clarity. Krill illustration in panel b provided by Mehr Kumar with permission, and illustrations of feeding cetaceans and their prey in panels a–c provided by Alex Boersma with permission.

layer, deep-diving toothed whales faced strong selection pressures to evolve larger body size and achieve long dive durations, along with the long-range detection and discrimination capabilities offered by powerful echolocation (Jensen et al. 2018). Echolocation is hypothesized to have first evolved in low-visibility waters and later been honed for foraging on deep-sea prey at depths beyond the photic zone (Lindberg & Pyenson 2006). Interestingly, the emergence of large body size in lineages of deep-diving odontocetes occurred ~15 million years after the appearance of the oldest echolocating odontocetes in the Oligocene.

At the upper extreme of body mass, large baleen whales live off tiny prey that are 6–10 orders of magnitude smaller than themselves. Right whales and bowhead whales (*Balaena mysticetus*) that weigh 30–70 tons forage strictly on copepods, each individually weighing less than 10 mg (Fortune et al. 2020). They feed by continuously filtering volumes of prey-laden water at slow and steady speeds less than 1 m/s (Simon et al. 2009). Large balaenid whales can filter 100 m³ of water per minute across 2–4-m-long baleen plates, using continuous ram filter feeding, capturing up to 60,000 copepods/min (>500 grams wet weight/minute) when targeting dense prey patches (Simon et al. 2009, van der Hoop et al. 2019). This foraging strategy allows them to increase blubber thickness in just a few months of feeding (George et al. 2015) and then effectively fast off these fat reserves for the remainder of the year. How their intestinal systems adapt to such protracted epochs of feast and famine is unknown. Their narrow food niche of copepods and a highly specialized feeding mechanism serves balaenid whales well in healthy and stable marine ecosystems, but if copepods under environmental change fail to form predictable and dense aggregations, such a strategy becomes maladaptive. This could be particularly acute when combined with other stressors (Christiansen et al. 2020), especially considering a consistent lack of recovery in many populations after the end of whaling.

Rorqual baleen whales (Balaenopteridae), such as blue whales and humpback whales, evolved a specialized filter feeding mode called lunge feeding, which differs from the balaenid continuous ram filtration in that rorqual engulfment and filtration phases are decoupled in time (Goldbogen et al. 2017, Werth et al. 2018). Rorquals accelerate to high speed (2–5 m/s) to open their mouths (Cade et al. 2016, Simon et al. 2012) and engulf discrete volumes of water that are commensurate with the whale's own body size in larger species (Kahane-Rapport & Goldbogen 2018). Filtration begins after the whale closes its mouth around the engulfed water, leaving a relatively small area of baleen through which the engulfed water is purged from the oral cavity, keeping the filtered prey inside the mouth (Goldbogen et al. 2017). Because of the scaling differences between baleen area and engulfment volume, the time required to filter engulfed water increases allometrically with body size, reaching up to 80 seconds in the largest blue whales (Kahane-Rapport et al. 2020). In contrast, one of the smallest lunge filter feeders, the Antarctic minke whale (*Balaenoptera bonaerensis*), exhibits filter times of approximately 10 seconds (Kahane-Rapport et al. 2020), resulting in the highest measured lunge rates of any rorqual (Cade et al. 2023, Friedlaender et al. 2014). Long filtration times in larger rorquals yield relatively higher prey intake despite executing only a few lunges per foraging dive (Goldbogen et al. 2019, Kahane-Rapport et al. 2020). Despite the high drag required for lunge feeding, the overall foraging costs are low relative to the energy gained (Videsen et al. 2023), thereby conferring high foraging efficiency (energy gained versus energy spent while foraging) (Goldbogen et al. 2019, Gough et al. 2022).

The evolution of different feeding modes among cetaceans results in distinct foraging niches across body size. First, the scaling of prey energy obtained during each feeding event departs from isometry because of differences in intake mechanism and the discrepancy between the relative sizes of predator and prey (Goldbogen et al. 2019). Although larger toothed whales feed on absolutely larger prey, they are not proportionally larger (**Figure 4b**), and thus the energy intake per feeding

event exhibits negative allometry (Goldbogen et al. 2019). In contrast, larger rorquals have relatively greater engulfment capacities (Kahane-Rapport et al. 2020) and therefore exhibit positive allometry in energy intake per feeding event when targeting krill (Goldbogen et al. 2019, Gough et al. 2022). Because the number of feeding events is ultimately constrained by time available in the prey layer at depth, larger toothed whales have predictably lower energetic efficiencies at the scale of individual foraging dives (**Figure 4c**). In contrast, gigantism provides an advantage for bulk filter feeding because epipelagic prey patches are much larger than can be engulfed on a given dive or even a series of dives (Cade et al. 2021). These profound differences in foraging efficiencies between the largest toothed whales and rorquals may explain their differences in reproductive potential: Large rorquals may have calves every 2–4 years, whereas large toothed whales may have calves every 5–7 years and employ allo-nursing for even longer (Whitehead 2003).

5. CONCLUSION

Whales interest a broad range of biologists because their large size makes them relevant for understanding the limits and possibilities of biology. With body lengths as great as 30 m and body masses over 150 tons, cetaceans rank as the largest vertebrates to have ever evolved on the planet, making them profoundly relevant for comparative questions about the allometry of life history, physiology, organismal growth, energetics, and animal movement. Understanding how whales grow and maintain their superlative size was once the territory of theory; today, advances in remote sensing and biologging have allowed researchers to collect in situ data to test fundamental hypotheses about the functionality of extremes in animal biology.

Both the mechanisms that drive the ecological and evolutionary success of whales and the factors that limit their foraging are important for knowing their fate during the Anthropocene. As climate change, pollution, and biodiversity loss accelerate, changes to ocean ecosystems threaten the prevalence of both key prey items and whale lineages that have become hyperspecialized in diet, distribution, or body size. Blue whales, for example, specialize on krill, and without the presence of this prey in sufficient densities and abundances, it is unclear how they can sustain their enormous body size. All of the largest toothed whales, from beaked whales to sperm whales, critically rely on the vast mesopelagic prey layers, but how are they affected when such deep ecosystems are slated for increased trawling and sea-floor mining? To what degree does whale watching offer a noninvasive way for whales to exist in increasingly industrialized oceans? Whales operate at time and space scales that are hard to appreciate and understand; their lives unfold in big, complex environments and at time scales sometimes beyond human lifetimes. The rate and magnitude of ocean change will have an impact on ocean giants, and we need to know their response and resilience to human encroachment to inform much needed conservation measures, which may play critical roles in future ocean health and productivity.

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