

# How do feeding biomechanics, extreme predator–prey size ratios and the rare enemy effect determine energetics and ecology at the largest scale?

Jeremy A. Goldbogen\* and David E. Cade

## ABSTRACT

The most recent and largest radiation of marine filter feeders are edentulous baleen whales (Mysticeti) that use keratinized racks of fringed and matted baleen to filter zooplankton (e.g. krill) or small schooling fish (e.g. anchovies, sardines). Rorqual whales (Balaenopteridae) exhibit the greatest size range among mysticetes and employ a unique lunge-feeding mechanism whereby engulfment and filtration are temporally decoupled. As a result, lunge feeding confers the ability to rapidly engulf large prey aggregations, such as krill or schooling fish, followed by a prolonged filter phase. In contrast, engulfment and filtration occur at the same time in all other gigantic filter feeders (e.g. basking sharks, whale sharks) at slow speeds. Although lunges in rorquals occur at higher speeds, the extreme predator–prey ratios at play suggest that whales may not be able to overcome the escape abilities of scattering prey. These types of prey have been engaged in evolutionary arms races with smaller predators for tens of millions of years prior to the rise of today's ocean giants. Extant rorqual whales evolved gigantism only in the last few million years; thus, they represent rare enemies of small prey such that flight responses may be delayed until escape is less likely. Data from whale-borne movement-sensing tags, looming stimulus experiments and stomach contents suggest a potential trade-off in capture efficiency for different prey types (e.g. fish versus krill) with increasing whale body size. Such constraints likely shaped the ecology and energetics of foraging at the largest scales.

**KEY WORDS:** Foraging, Scaling, Energetics, Filter feeding, Predator–prey, Cetaceans

## Introduction

Comparative physiologists have long predicted that the largest animals experience several problems related to the isometric scaling of body morphology and the negative allometry of metabolic rate (Alexander, 1998; Krogh, 1934). The largest animals tend to be marine filter feeders and this ecomorphology has evolved repeatedly in several fish and mammal lineages (Friedman et al., 2010). In most of these lineages, engulfment and filtration occur simultaneously at slow and relatively steady speeds (Potvin and Werth, 2017; Simon et al., 2009; Werth, 2004; Werth and Potvin, 2016). Given isometric morphology, the power required for filtration should scale such that larger filter feeders will have to swim faster and use a greater proportion of their energy intake to generate the required filtration

pressures (Alexander, 1998). Following this logic, larger filter feeders would experience a decrease in the energetic efficiency of feeding. However, the scaling of feeding morphology in the largest and most recent radiation of gigantic filter feeders, rorqual whales (Mysticeti: Balaenopteridae), departs significantly from isometry (Goldbogen et al., 2012, 2010). Specifically, rorquals exhibit positive allometry of the engulfment apparatus, including bony (skull length and width, jaw length) and soft tissue elements (the expandable ventral groove blubber), such that larger rorquals have relatively greater engulfment capacities (Goldbogen et al., 2010; Kahane-Rappaport and Goldbogen, 2018).

The complex suite of anatomical and biomechanical adaptations enables rorquals to temporally decouple engulfment and filtration in a unique filter-feeding mode called lunge feeding. Lunge feeding is characterized by a three-step foraging mechanism (Goldbogen et al., 2017): (1) acceleration to high speed (Simon et al., 2012); (2) engulfment of a large volume of prey-laden water (Shadwick et al., 2013); (3) filtration of water out of the mouth past a keratinized oral filter called baleen (Werth, 2013). Although engulfment capacity scales with positive allometry (Kahane-Rappaport and Goldbogen, 2018), baleen area scales with negative allometry (Werth et al., 2018), which forces larger whales to extend their filtration times during breath-hold dives (Kahane-Rappaport et al., 2020). Filtration time, the equivalent of handling time in other predators, is inversely related to lunge-feeding frequency, an energetic trade-off that shaped the ecology and evolution of foraging among rorqual species (Kahane-Rappaport et al., 2020). Hydro-mechanical models of lunge feeding indicate that the cost of engulfment is proportional to the magnitude of the engulfed water, suggesting that feeding costs scale with positive allometry (Potvin et al., 2009, 2012). However, the swimming and feeding kinematics are diverse among rorqual species (Cade et al., 2016; Gough et al., 2022, 2021; Potvin et al., 2021; Segre et al., 2022), suggesting that the energetics of this behavior, and how it scales with body size, is much more complicated than what can be predicted from first principles and thus warrants continued study (Goldbogen et al., 2019; Potvin et al., 2021, 2012).

The problem of how animals feed on the move is important because it has a direct impact on organismal fitness. Laboratory studies offer powerful experimental approaches to understanding multiple aspects of foraging (Carrillo and McHenry, 2016; Ishikawa et al., 2022; Johansen et al., 2020; McHenry et al., 2009; Soto et al., 2015). However, this approach may unnaturally limit the amount of movement that can occur during feeding events. In contrast, investigations in the wild using biologging or remote sensing technologies provide natural conditions but likely preclude experimental control. Locomotion is required for many foraging mechanisms and strategies, not only to find food but also to capture maneuverable and energy-rich prey (Williams et al., 2014; Wilson

Hopkins Marine Station, Oceans Department, Stanford University, 120 Ocean View Blvd, Pacific Grove, CA 93950, USA.

\*Author for correspondence (jergold@stanford.edu)

 J.A.G., 0000-0002-4170-7294

et al., 2018). In some aerial species such as swifts, animals can obtain potential energy from the physical environment (wind), and then convert this to kinematic energy in order to capture prey while gliding (Hedrick et al., 2018). However, most animals must use power generated from locomotor muscles to capture prey (Camp and Brainerd, 2014; Camp et al., 2015; Wilson et al., 2013) and balance the cost of hunting with the potential benefit of successful prey capture (Williams et al., 2014). In the dense aquatic environment, most adept swimmers are streamlined to reduce drag and increase the efficiency of locomotion (Vogel, 1994); however, several groups have convergently evolved filter-feeding mechanisms that require a substantial departure from a streamlined body form as they ram through the water column to engulf and filter large volumes of water (Sanderson and Wassersug, 1993). Thus, ram filter feeding predictably incurs a high cost from the energy lost due to drag (Carey and Goldbogen, 2017; Potvin and Werth, 2017; Werth and Potvin, 2016). If the cost of the feeding event is high, then the aggregate energy content of engulfment prey must be higher. This may be why rorquals evolved large engulfment capacity, which should allow energy intake to far exceed energy expended, but only if sufficient prey densities are targeted (Goldbogen et al., 2011; Hazen et al., 2015).

### Prey selection

Prey resources are often ephemeral and patchily distributed in the marine environment, manifesting hierarchically as dense patches within lower density patches (Kotliar and Wiens, 1990). Such a dynamic, heterogeneous prey-scape has important consequences for marine predators, especially filter feeders, which rely on dense patches of prey (Benoit-Bird, 2024). If prey were equally distributed throughout the ocean, energy intake may not substantially exceed the high cost of filter feeding and thus these foragers would face an 'energetic knife-edge' (Sims, 1999). Consequently, filter feeders must select high-density prey patches (Hazen et al., 2015; Sims and Quayle, 1998) and small-bodied prey types that are less likely to escape an enlarged engulfment apparatus (Domenici, 2001). High-speed lunge feeding by rorqual whales enables feeding on schools of forage fish that have high-speed escape abilities (Cade et al., 2020). Nevertheless, most rorqual species also feed on patches of small-bodied plankton such as krill that appear to have limited escape speeds and disordered escape behaviors (Hamner and Hamner, 2000). The largest rorqual species, the blue whale (*Balaenoptera musculus*), only feeds on krill, whereas smaller rorqual species such as minke whales (*Balaenoptera acutorostrata*) and humpback whales (*Megaptera novaeangliae*) exhibit a greater diversity of prey preferences and often feed on agile fish. Although it has not been comprehensively studied, these data suggest a scale-dependent constraint on prey capture that could shape their dietary preferences.

Understanding how body size influences prey preference has important consequences for the energetic niches occupied by the largest filter feeders as well as the potential ecological and evolutionary constraints they face in dynamic prey-scapes. The fossil record indicates that baleen whales evolved edentulous feeding tactics at relatively small (3–8 m in total body length) body sizes prior to the evolution of baleen (Peredo et al., 2018; Pyenson, 2017). However, this size range is still much larger than most predators, which tend to feed on one prey at a time (Goldbogen and Madsen, 2018) and have a much longer co-evolutionary history with schooling fish. It is thus likely that early whales took advantage of 'the rare enemy effect' whereby the thresholds at which schooling fish disperse in response to a looming stimulus are too delayed to

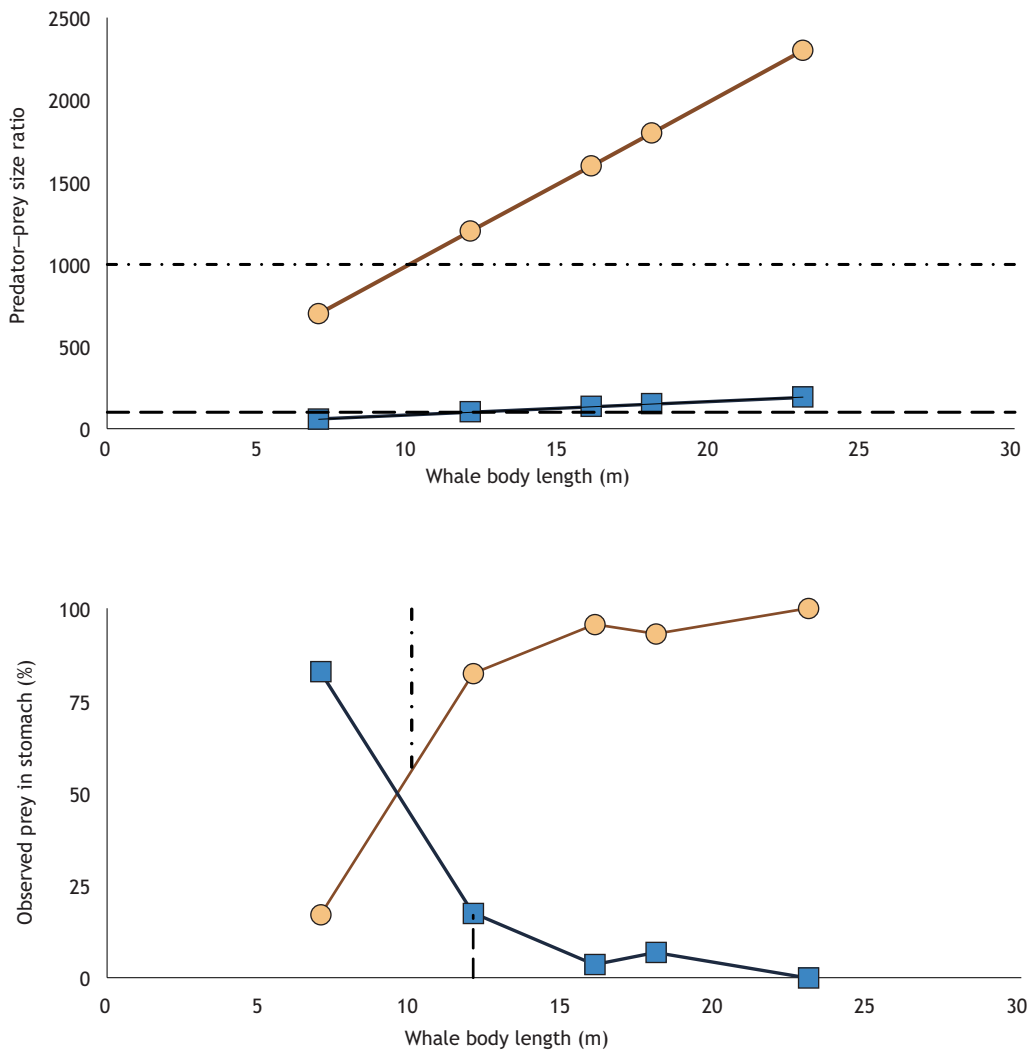
avoid engulfment by these unfamiliar, large predators (Cade et al., 2020). This delay could have led to the evolution of retention mechanisms, such as baleen, that would keep engulfed prey inside the mouth when teeth are lacking (Peredo et al., 2018). Fossil evidence indicates a clade-wide evolutionary shift to gigantic body sizes (>10 m total body length) during an era of intensified upwelling in the ocean (Marlow et al., 2000; Slater et al., 2017). Wind-driven upwelling facilitates an upward trophic cascade (wind>upwelled nutrient-rich deep water>phytoplankton>zooplankton) and the eventual formation of abundant and dense fish schools and krill patches (Benoit-Bird et al., 2019), a hallmark of baleen whale foraging ecology known as 'wind to whales' (Croll et al., 2005). It is hypothesized that the additional enhancements in efficiency offered by lunge filter feeding in concert with intensified upwelling facilitated the evolution of larger whale size via highly efficient exploitation of abundant and dense prey (Slater et al., 2017).

When predators are similar in size to their prey, or up to 10 times larger than their prey (predator–prey size ratio, or PPSR= $10^0$ – $10^1$ ; see Fig. 1A), capture can occur when  $v > \sqrt{r}$ , where  $r$  is the predator–prey ratio of turning radii and  $v$  is the predator–prey ratio of speed (Domenici, 2001; Howland, 1974; Webb and De Buffrénil, 1990). At greater size differences between predator and prey (PPSR $\approx 10^2$ ), as in humpback whales foraging on anchovies (Fig. 1A), the predator should require attack speeds that are 10 $\times$  prey escape speeds (Cade et al., 2020). However, humpback whales can capture anchovies by using mouth-opening lunge speeds of  $3.8 \pm 0.7$  m s $^{-1}$  (mean $\pm$ s.d.), approximately 60% higher than mean anchovy escape speeds (Cade et al., 2020). In previous work, virtually approaching stimuli based on humpback whale tag-measured speed profiles were used to determine looming thresholds (LTs) that elicit anchovy escape (Cade et al., 2020). Predator–prey simulations using LT data suggest that humpback whales could capture 30–60% of an anchovy school because their apparent size (from the fish's perspective) does not exceed their response threshold until after mouth opening (Cade et al., 2020).

At greater size differences, large baleen whales foraging on small zooplankton such as krill represent PPSR $\approx 10^3$ . This size difference suggests that prey no longer have a maneuverability advantage because of the relative size of the predator's mouth, requiring predator detection at thousands of body lengths away and an escape speed of hundreds of body lengths per second (Domenici, 2001; Webb and De Buffrénil, 1990). Our *in situ* observations (Goldbogen et al., 2017) indicate that krill do not respond to lunging blue whales at depth (Fig. 1B), suggesting krill LTs may not be exceeded or they occur so late that the krill only initiate escape as they are being engulfed. These data advance the hypothesis that the scaling of predator–prey interactions constrains foraging performance and limits the ability of filter feeders to capture certain types of prey. The null hypothesis is that rorquals will not suffer from decreased capture efficiency when foraging on fish. However, stomach contents data (Nemoto, 1970; Tamura and Fujise, 2002) support an alternative hypothesis: that smaller rorquals are more likely to feed on more agile prey such as fish, whereas larger rorquals target less agile zooplankton such as krill (Fig. 1B).

### Prey escape

From the smallest rorquals, minke whales ( $\sim 7$  m), to the largest, blue whales ( $\sim 25$  m), the predator–prey size ratios range from about 100 to over 1000 when targeting fish (i.e. anchovy) or krill, respectively. We hypothesize that whales across their full body size range can capture a greater proportion of a krill patch than a fish school because of the different escape response abilities between



**Fig. 1. Scaling of predator–prey interactions.** (A) Theoretical predator–prey size ratios (PPRS) calculated for rorquals across scale feeding on krill (orange: length, 1 cm) or anchovy (blue: length, 12 cm). (B) The proportion of rorqual stomachs (Nemoto, 1970; Tamura and Fujise, 2002) with less agile prey (krill or similarly small prey such as copepods: orange) compared with more agile prey (forage fish; blue). Theoretical predator–prey size (with respect to length) ratios (PPRS) are shown for two values by dot-dash and dashed lines. The dot-dash line indicates a PPRS of 1000 when whales feed on krill whereas the dashed line reflects a PPRS of 100 when whales feed on forage fish.

fish and krill (Hamner and Hamner, 2000; O’Brien, 1987). This is consistent with the observation that in some areas where krill is exceptionally abundant, such as the Southern Ocean, all rorqual species big and small feed on krill whereas other predators in the same area may not (Laws, 1977). The positive allometry of feeding morphology means that the area of the mouth projected to flow is relatively greater in larger whales (Kahane-Rappoport and Goldbogen, 2018), which should increase the catch of smaller and less agile prey such as krill even in the absence of complex maneuvering. Whales experience a decrease in maneuverability with increasing body size (Segre et al., 2022), so smaller rorquals should have higher catch efficiencies when targeting fish. However, the time scale of the whale’s gape angle cycle could scale in different ways when feeding on different prey, thereby setting up a complex interaction space for whales and their prey (Potvin et al., 2010).

### Intermediate foraging strategies

If larger rorquals can better exploit small prey such as krill and smaller rorquals can more effectively capture fish, then intermediate-sized rorquals (10–15 m in body length) may have the advantage of more flexible foraging strategies by leveraging a sufficient catch performance among multiple prey types. Rorquals are not a speciose group, but there are several species that occupy an intermediate size range (Lockyer, 1976). Humpback whales occupy this size class and there is a well-documented range of foraging strategies and prey

preferences among humpback whale populations. Interestingly, many of these strategies, such as bubble-net feeding (Wiley et al., 2011), lobtail feeding (Allen et al., 2013), trap feeding (McMillan et al., 2019) and side-roll feeding on the sea floor (Ware et al., 2013), negate or limit the escape response of prey and in doing so may ameliorate any whale size-dependent constraints. In addition, humpback whales often extend their relatively long (~30% body length) flippers out on either side of the mouth during lunges, potentially to redirect prey into the mouth (Cade et al., 2020). Humpback whale prey preferences often switch between krill and fish when oceanographic conditions favor the abundance of one prey over another (Fleming et al., 2015), further reinforcing their characterization as a generalist predator. Such a foraging strategy may reflect the complex and dynamic oceanography that has played out during the evolutionary history of rorquals (Pyenson, 2017).

Other intermediate-sized rorquals, such as Bryde’s whales (*Balaenoptera brydei/edeni*) and sei whales (*Balaenoptera borealis*) also exhibit flexible foraging strategies. Like humpback whales, Bryde’s whales in some areas also evolved strategies that counter fish escape responses or redirect fish trajectories into the whale’s mouth. Such is the case for the bizarre tread-water feeding behavior in Bryde’s whales in the Gulf of Thailand (Iwata et al., 2017). The whale is vertically oriented in the water column with its mouth agape at approximately 90 deg and positioned just above the water surface (Iwata et al., 2017). The fluke is then oscillated back and forth,

somehow causing fish to jump out of the water and into the whale's mouth (Iwata et al., 2017). The sister taxon to *B. brydei/edeni*, sei whales (*B. borealis*) are morphologically divergent from rorquals in that they share some similarities with the balaenid whales (bowhead whales, *Balaena mysticetus*; right whales, *Eubalaena* sp.) that are continuous ram filter feeders, or the so-called skim feeders that filter and engulf simultaneously at slow and steady speeds (Simon et al., 2009; Werth, 2004). Sei whales have more strongly arched rostra, longer baleen plates, greater baleen area and finer baleen fringes compared with all other rorquals (Brodie and Vikingsson, 2009; Werth et al., 2018). Although these adaptations are reminiscent of balaenid foraging morphology, they still possess all the essential anatomical innovations required for lunge feeding, including ventral groove blubber (Shadwick et al., 2013), an invertible tongue (Lambertsen, 1983) and an extensible oropharyngeal cavity (Goldbogen et al., 2017). Biologging data show that sei whales exhibit biomechanically distinct lunge-feeding and skim-feeding behaviors, presumably to be used interchangeably for different prey types and distributions (Segre et al., 2021). These traits distinguish sei whales as a functional intermediate and ecologically flexible species among rorquals, exhibiting intermediate body sizes.

There are a few baleen whale species that are not lunge-feeding rorquals but provide useful comparisons within both ecomorphological and phylogenetic contexts. In particular, the intermediate-sized gray whale (*Eschrichtius robustus*) is nested within a paraphyletic Balaenopteroidea (rorquals+gray whale) (Árnason et al., 2018) and lacks the necessary morphological adaptations for lunge feeding as observed among rorquals. Gray whales lack an extensive ventral groove system that characterizes all rorquals (Shadwick et al., 2013) and instead possess a few (2–6) ventral pleats coupled with a well-developed hyolingual apparatus for suction feeding (Werth, 2000, 2007). This contrasts with the largely hydraulic, ram-based feeding in rorquals (Potvin et al., 2009). Either gray whales reflect an ancient generalist foraging morphology shared among stem balaenopteroids or their derived features evolved to exploit coastal prey. Gray whales are well known to suction feed on littoral benthic invertebrates (Cacchione et al., 1987; Johnson and Nelson, 1984; Oliver and Slattery, 1985). If gray whales are morphologically specialized for feeding on invertebrates in the seafloor, it is interesting that they can sometimes feed at the sea surface, including on fish (Webber et al., 2024). Dietary flexibility despite specialized feeding morphology could be another example of Liem's Paradox (Liem, 2015), and accordingly a jack-of-all-trades foraging ability could have helped gray whales cope with changes in sea level that limited critical coastal habitats multiple times during the Pliocene (Pyenson and Lindberg, 2011).

In many of the cases above, intermediate-size rorqual whale species have evolved several strategies that limit prey escape and in doing so they may be able to circumvent any scale-dependent constraints associated with the predator–prey interactions that occur within the water column. Such an approach may have allowed many rorqual species to opportunistically benefit from unique foraging niches and distinct trophic positions among populations. In South Africa, Bryde's whales eat more fish inshore relative to offshore, where krill is mostly consumed (Best, 2001). The offshore population appears to have had a higher reproductive rate (Best, 2001), which may reflect favorable energetics that result from both more abundant prey and a predictably higher capture efficiency for krill as we hypothesized above. If true, this provides evidence for how the scaling of predator–prey interactions can influence the fitness of individuals and the health of populations. The phenomenon of

extraordinary krill abundance has been documented in many different oceans and rorqual species, presenting as whale super groups that can quickly form and dissipate as oceanographic conditions change (Cade et al., 2021a,b; Nowacek et al., 2011). Such examples from modern whales and whale ecosystems suggest that deep time changes in the abundance of krill or fish could provide the necessary conditions for the evolution of different filter-feeding strategies among body size classes (Slater et al., 2017).

### Filling the knowledge gaps

There are multiple, cross-disciplinary research areas that could clarify the mechanisms that govern the interactions between predators and prey at these scales. First, the continued deployment of high-resolution movement sensing and video tags on additional whale species and populations would determine the speeds and maneuvers used to capture different size prey (Cade et al., 2016). Second, the integration of active sonar systems tuned to the detection of patchy prey into biologging tags would provide complementary information on prey distribution as well as the nature, timing and efficacy of prey response (Goulet et al., 2019; Lawson et al., 2015). Third, laboratory-based stimulus experiments on whale prey (Cade et al., 2020) that incorporate tag-derived data could provide insight into how whales capture prey in different ecological contexts (dark versus light habitats) and different predator–prey scenarios (small versus big prey; slow versus agile prey). Lastly, the energetic consequences of these different foraging styles can be evaluated using biomechanical and physiological models that incorporate tag data over time scales that correlate with the temporal scales of feeding (Potvin et al., 2021; Videsen et al., 2023). The synthesis of data across these research areas could provide unique insight into how whales evolved prey preferences and different ecological niches at the largest sizes (Goldbogen et al., 2019).

The role of whales as major consumers in the world's oceans will ultimately be constrained by the predator–prey interactions explored in this Commentary. The summed outcome of these interactions at seasonal to annual scales will determine the flux of energy across trophic levels and influence globally important biogeochemical processes. An integrated approach is needed to fully understand the mechanisms that determine the margin between life and death for schooling prey when targeted by their gigantic, rare enemies – rorqual whales.

### Acknowledgements

We thank the JEB community for organizing and hosting the symposium that encouraged this work. We also thank two anonymous reviewers for their constructive feedback.

### Competing interests

The authors declare no competing or financial interests.

### Special Issue

This article is part of the special issue 'Integrating Biomechanics, Energetics and Ecology in Locomotion', guest edited by Andrew A. Biewener and Alan M. Wilson. See related articles at [https://journals.biologists.com/jeb/issue/228/Suppl\\_1](https://journals.biologists.com/jeb/issue/228/Suppl_1).

### References

- Alexander, R. M. (1998). All-time giants: the largest animals and their problems. *Palaeontology* **41**, 1231–1245.
- Allen, J., Weinrich, M., Hoppitt, W. and Rendell, L. (2013). Network-based diffusion analysis reveals cultural transmission of lobe-tail feeding in humpback whales. *Science* **340**, 485–488. doi:10.1126/science.1231976
- Árnason, Ú., Lammers, F., Kumar, V., Nilsson, M. A. and Janke, A. (2018). Whole-genome sequencing of the blue whale and other rorquals finds signatures for introgressive gene flow. *Sci. Adv.* **4**, eaap9873. doi:10.1126/sciadv.aap9873
- Benoit-Bird, K. J. (2024). Resource patchiness as a resolution to the food paradox in the sea. *Am. Nat.* **203**, 1–13. doi:10.1086/727473

- Benoit-Bird, K. J., Waluk, C. M. and Ryan, J. P.** (2019). Forage species swarm in response to coastal upwelling. *Geophys. Res. Lett.* **46**, 1537-1546. doi:10.1029/2018GL081603
- Best, P. B.** (2001). Distribution and population separation of Bryde's whale *Balaenoptera edeni* off southern Africa. *Marine Ecology-Progress Series* **220**, 277-289. doi:10.3354/meps220277
- Brodie, P. and Vikingsson, G.** (2009). On the feeding mechanisms of the sei whale (*Balaenoptera borealis*). *J. Northwest Atl. Fish. Sci.* **42**, 49-54. doi:10.2960/J.v42.m646
- Cacchione, D., Drake, D., Field, M. and Tate, G.** (1987). Sea-floor gouges caused by migrating gray whales off northern California. *Cont. Shelf Res.* **7**, 553-560. doi:10.1016/0278-4343(87)90021-5
- Cade, D. E., Friedlaender, A. S., Calambokidis, J. and Goldbogen, J. A.** (2016). Kinematic diversity in rorqual whale feeding mechanisms. *Curr. Biol.* **26**, 2617-2624. doi:10.1016/j.cub.2016.07.037
- Cade, D. E., Carey, N., Domenici, P., Potvin, J. and Goldbogen, J. A.** (2020). Predator-informed looming stimulus experiments reveal how large filter feeding whales capture highly maneuverable forage fish. *Proc. Natl. Acad. Sci. U.S.A.* **117**, 472-478. doi:10.1073/pnas.1911099116
- Cade, D. E., Fahlbusch, J. A., Oestreich, W. K., Ryan, J., Calambokidis, J., Findlay, K. P., Friedlaender, A. S., Hazen, E. L., Seakamela, S. M. and Goldbogen, J. A.** (2021a). Social exploitation of extensive, ephemeral, environmentally controlled prey patches by supergroups of rorqual whales. *Anim. Behav.* **182**, 251-266. doi:10.1016/j.anbehav.2021.09.013
- Cade, D. E., Seakamela, S. M., Findlay, K. P., Fukunaga, J., Kahane-Rapport, S. R., Warren, J. D., Calambokidis, J., Fahlbusch, J. A., Friedlaender, A. S., Hazen, E. L. et al.** (2021b). Predator-scale spatial analysis of intra-patch prey distribution reveals the energetic drivers of rorqual whale super-group formation. *Funct. Ecol.* **35**, 894-908. doi:10.1111/1365-2435.13763
- Camp, A. L. and Brainerd, E. L.** (2014). Role of axial muscles in powering mouth expansion during suction feeding in largemouth bass (*Micropterus salmoides*). *J. Exp. Biol.* **217**, 1333-1345. doi:10.1242/jeb.095810
- Camp, A. L., Roberts, T. J. and Brainerd, E. L.** (2015). Swimming muscles power suction feeding in largemouth bass. *Proc. Natl. Acad. Sci. USA* **112**, 8690-8695. doi:10.1073/pnas.1508055112
- Carey, N. and Goldbogen, J. A.** (2017). Kinematics of ram filter feeding beat-glide swimming in the northern anchovy *Engraulis mordax*. *J. Exp. Biol.* **220**, 2717-2725. doi:10.1242/jeb.158337
- Carrillo, A. and McHenry, M. J.** (2016). Zebrafish learn to forage in the dark. *J. Exp. Biol.* **219**, 582-589. doi:10.1242/jeb.128918
- Croll, D. A., Marinovic, B., Benson, S., Chavez, F. P., Black, N., Ternullo, R. and Tershy, B. R.** (2005). From wind to whales: trophic links in a coastal upwelling system. *Mar. Ecol. Prog. Ser.* **289**, 117-130. doi:10.3354/meps289117
- Domenici, P.** (2001). The scaling of locomotor performance in predator-prey encounters: from fish to killer whales. *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* **131**, 169-182. doi:10.1016/S1095-6433(01)00465-2
- Fleming, A. H., Clark, C. T., Calambokidis, J. and Barlow, J.** (2015). Humpback whale diets respond to variance in ocean climate and ecosystem conditions in the California Current. *Glob. Change Biol.* **22**, 1214-1224. doi:10.1111/gcb.13171
- Friedman, M., Shimada, K., Martin, L. D., Everhart, M. J., Liston, J., Maltese, A. and Triebold, M.** (2010). 100-million-year dynasty of giant planktivorous bony fishes in the mesozoic seas. *Science* **327**, 990-993. doi:10.1126/science.1184743
- Goldbogen, J. A. and Madsen, P. T.** (2018). The evolution of foraging capacity and gigantism in cetaceans. *J. Exp. Biol.* **221**, jeb166033. doi:10.1242/jeb.166033
- Goldbogen, J. A., Potvin, J. and Shadwick, R. E.** (2010). Skull and buccal cavity allometry increase mass-specific engulfment capacity in fin whales. *Proc. R. Soc. B Biol. Sci.* **277**, 861-868. doi:10.1098/rspb.2009.1680
- Goldbogen, J. A., Calambokidis, J., Oleson, E., Potvin, J., Pyenson, N. D., Schorr, G. and Shadwick, R. E.** (2011). Mechanics, hydrodynamics and energetics of blue whale lunge feeding: efficiency dependence on krill density. *J. Exp. Biol.* **214**, 131-146. doi:10.1242/jeb.048157
- Goldbogen, J. A., Calambokidis, J., Croll, D., McKenna, M. F., Potvin, J., Pyenson, N. D., Schorr, G., Shadwick, R. E. and Tershy, B. R.** (2012). Scaling of lunge feeding performance in rorqual whales: mass-specific energy expenditure increases with body size and progressively limits diving capacity. *Funct. Ecol.* **26**, 216-226. doi:10.1111/j.1365-2435.2011.01905.x
- Goldbogen, J. A., Cade, D. E., Calambokidis, J., Friedlaender, A. S., Potvin, J., Segre, P. S. and Werth, A. J.** (2017). How baleen whales feed: the biomechanics of engulfment and filtration. *Ann. Rev. Mar. Sci.* **9**, 367-386. doi:10.1146/annurev-marine-122414-033905
- Goldbogen, J. A., Cade, D. E., Wisniewska, D. M., Potvin, J., Segre, P. S., Savoca, M. S., Hazen, E. L., Czapanskiy, M. F., Kahane-Rapport, S. R., DeRuiter, S. L. et al.** (2019). Why whales are big but not bigger: physiological drivers and ecological limits in the age of ocean giants. *Science* **366**, 1367-1372. doi:10.1126/science.aax9044
- Gough, W. T., Smith, H. J., Savoca, M. S., Czapanskiy, M. F., Fish, F. E., Potvin, J., Bierlich, K. C., Cade, D. E., Di Clemente, J., Kennedy, J. et al.** (2021). Scaling of oscillatory kinematics and Froude efficiency in baleen whales. *J. Exp. Biol.* **224**, jeb237586. doi:10.1242/jeb.237586
- Gough, W. T., Cade, D. E., Czapanskiy, M. F., Potvin, J., Fish, F. E., Kahane-Rapport, S. R., Savoca, M. S., Bierlich, K. C., Johnston, D. W., Friedlaender, A. S. et al.** (2022). Fast and furious: energetic tradeoffs and scaling of high-speed foraging in rorqual whales. *Integr. Org. Biol.* **4**, obac038. doi:10.1093/iob/obac038
- Goulet, P., Guinet, C., Swift, R., Madsen, P. T. and Johnson, M.** (2019). A miniature biomimetic sonar and movement tag to study the biotic environment and predator-prey interactions in aquatic animals. *Deep Sea Res. Oceanogr. Res. Papers* **148**, 1-11. doi:10.1016/j.dsr.2019.04.007
- Hamner, W. M. and Hamner, P. P.** (2000). Behavior of Antarctic krill (*Euphausia superba*): schooling, foraging, and antipredatory behavior. *Can. J. Fish. Aquat. Sci.* **57**, 192-202. doi:10.1139/f00-195
- Hazen, E. L., Friedlaender, A. S. and Goldbogen, J. A.** (2015). Blue whales (*Balaenoptera musculus*) optimize foraging efficiency by balancing oxygen use and energy gain as a function of prey density. *Sci. Adv.* **1**, e1500469. doi:10.1126/sciadv.1500469
- Hedrick, T. L., Pichot, C. and de Margerie, E.** (2018). Gliding for a free lunch: biomechanics of foraging flight in common swifts (*Apus apus*). *J. Exp. Biol.* **221**, jeb186270. doi:10.1242/jeb.186270
- Howland, H. C.** (1974). Optimal strategies for predator avoidance: relative importance of speed and maneuverability. *J. Theor. Biol.* **47**, 333-350. doi:10.1016/0022-5193(74)90202-1
- Ishikawa, K., Wu, H., Mitarai, S. and Genin, A.** (2022). Effects of prey density and flow speed on plankton feeding by garden eels: a flume study. *J. Exp. Biol.* **225**, jeb243655. doi:10.1242/jeb.243655
- Iwata, T., Akamatsu, T., Thongsukdee, S., Cherdskujai, P., Adulyanukosol, K. and Sato, K.** (2017). Tread-water feeding of Bryde's whales. *Curr. Biol.* **27**, R1141-R1155. doi:10.1016/j.cub.2017.09.045
- Johansen, J. L., Akanyeti, O. and Liao, J. C.** (2020). Oxygen consumption of drift-feeding rainbow trout: the energetic tradeoff between locomotion and feeding in flow. *J. Exp. Biol.* **223**, jeb220962. doi:10.1242/jeb.220962
- Johnson, K. R. and Nelson, C. H.** (1984). Side-scan sonar assessment of gray whale feeding in the Bering Sea. *Science* **225**, 1150-1152. doi:10.1126/science.225.4667.1150
- Kahane-Rapport, S. R. and Goldbogen, J. A.** (2018). Allometric scaling of morphology and engulfment capacity in rorqual whales. *J. Morphol.* **279**, 1256-1268. doi:10.1002/jmor.20846
- Kahane-Rapport, S. R., Savoca, M. S., Cade, D. E., Segre, P. S., Bierlich, K. C., Calambokidis, J., Dale, J., Fahlbusch, J. A., Friedlaender, A. S., Johnston, D. W. et al.** (2020). Lunge filter feeding biomechanics constrain rorqual foraging ecology across scale. *J. Exp. Biol.* **223**, jeb224196. doi:10.1242/jeb.224196
- Kotliar, N. B. and Wiens, J. A.** (1990). Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos* **59**, 253-260.
- Krogh, A.** (1934). Physiology of the blue whale. *Nature* **133**, 635-637. doi:10.1038/133635a0
- Lambertsen, R. H.** (1983). Internal mechanism of rorqual feeding. *J. Mammal.* **64**, 76-88. doi:10.2307/1380752
- Laws, R. M.** (1977). Seals and whales of the Southern Ocean. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **279**, 81-96. doi:10.1098/rstb.1977.0073
- Lawson, G. L., Hückstädt, L. A., Lavery, A. C., Jaffré, F. M., Wiebe, P. H., Fincke, J. R., Crocker, D. E. and Costa, D. P.** (2015). Development of an animal-borne "sonar tag" for quantifying prey availability: test deployments on northern elephant seals. *Anim. Biotelemetry* **3**, 22. doi:10.1186/s40317-015-0054-7
- Liem, K. F.** (2015). Adaptive significance of intra- and interspecific differences in the feeding repertoires of cichlid fishes. *Am. Zool.* **20**, 295-314. doi:10.1093/icb/20.1.295
- Lockyer, C.** (1976). Body weights of some species of large whales. *ICES J. Mar. Sci.* **36**, 259-273. doi:10.1093/icesjms/36.3.259
- Marlow, J. R., Lange, C. B., Wefer, G. and Rosell-Melé, A.** (2000). Upwelling intensification as part of the Pliocene-Pleistocene climate transition. *Science* **290**, 2288-2291. doi:10.1126/science.290.5500.2288
- McHenry, M., Feitl, K., Strother, J. and Van Trump, W.** (2009). Larval zebrafish rapidly sense the water flow of a predator's strike. *Biol. Lett.* **5**, 477-479. doi:10.1098/rsbl.2009.0048
- McMillan, C. J., Towers, J. R. and Hilderling, J.** (2019). The innovation and diffusion of "trap-feeding," a novel humpback whale foraging strategy. *Mar. Mamm. Sci.* **35**, 779-796. doi:10.1111/mms.12557
- Nemoto, T.** (1970). Feeding pattern of baleen whales in the ocean. In *Marine Food Chains* (ed. J. H. Steele), pp. 241-252. Berkeley: University of California Press.
- Nowacek, D. P., Friedlaender, A. S., Halpin, P. N., Hazen, E. L., Johnston, D. W., Read, A. J., Espinasse, B., Zhou, M. and Zhu, Y.** (2011). Super-aggregations of krill and humpback whales in Wilhelmina bay, Antarctic peninsula. *Plos One* **6**, e19173. doi:10.1371/journal.pone.0019173
- O'Brien, D. P.** (1987). Description of escape responses of krill (Crustacea, Euphausiacea), with particular reference to swarming behavior and the size and proximity of the predator. *J. Crustac. Biol.* **7**, 449-457. doi:10.2307/1548294
- Oliver, J. S. and Slattery, P. N.** (1985). Destruction and opportunity on the sea floor: effects of gray whale feeding. *Ecology* **66**, 1965-1975. doi:10.2307/2937392

- Peredo, C. M., Pyenson, N. D., Marshall, C. D. and Uhen, M. D.** (2018). Tooth loss precedes the origin of baleen in whales. *Curr. Biol.* **28**, 3992-4000.e2. doi:10.1016/j.cub.2018.10.047
- Potvin, J. and Werth, A. J.** (2017). Oral cavity hydrodynamics and drag production in Balaenid whale suspension feeding. *Plos One* **12**, e0175220. doi:10.1371/journal.pone.0175220
- Potvin, J., Goldbogen, J. A. and Shadwick, R. E.** (2009). Passive versus active engulfment: Verdict from trajectory simulations of lunge-feeding fin whales *Balaenoptera physalus*. *J. R. Soc. Interface* **6**, 1005-1025. doi:10.1098/rsif.2008.0492
- Potvin, J., Goldbogen, J. A. and Shadwick, R. E.** (2010). Scaling of lunge feeding in rorqual whales: An integrated model of engulfment duration. *J. Theor. Biol.* **267**, 437-453. doi:10.1016/j.jtbi.2010.08.026
- Potvin, J., Cade, D. E., Werth, A. J., Shadwick, R. E. and Goldbogen, J. A.** (2021). Rorqual lunge-feeding energetics near and away from the kinematic threshold of optimal efficiency. *Integr. Org. Biol.* **3**, obab005. doi:10.1093/iob/obab005
- Potvin, J., Goldbogen, J. A. and Shadwick, R. E.** (2012). Metabolic expenditures of lunge feeding rorquals across scale: implications for the evolution of filter feeding and the limits to maximum body size. *Plos One* **7**, e44854. doi:10.1371/journal.pone.0044854
- Pyenson, N. D.** (2017). The ecological rise of whales chronicled by the fossil record. *Curr. Biol.* **27**, R558-R564. doi:10.1016/j.cub.2017.05.001
- Pyenson, N. D. and Lindberg, D. R.** (2011). What happened to gray whales during the Pleistocene? The ecological impact of sea-level change on benthic feeding areas in the North Pacific Ocean. *Plos One* **6**, e21295. doi:10.1371/journal.pone.0021295
- Sanderson, S. L. and Wassersug, R.** (1993). Convergent and alternative designs for vertebrate suspension feeding. In *The Skull: Functional and Evolutionary Mechanisms*, Vol. 3 (ed. J. Hanken and B. K. Hall), pp. 37-112. Chicago: University of Chicago Press.
- Segre, P. S., Weir, C. R., Stanworth, A., Cartwright, S., Friedlaender, A. S. and Goldbogen, J. A.** (2021). Biomechanically distinct filter-feeding behaviors distinguish sei whales as a functional intermediate and ecologically flexible species. *J. Exp. Biol.* **224**, jeb238873. doi:10.1242/jeb.238873
- Segre, P. S., Gough, W. T., Roualdes, E. A., Cade, D. E., Czapanskiy, M. F., Fahlbusch, J., Kahane-Rappaport, S. R., Oestreich, W. K., Bejder, L., Bierlich, K. C. et al.** (2022). Scaling of maneuvering performance in baleen whales: larger whales outperform expectations. *J. Exp. Biol.* **225**, jeb243224. doi:10.1242/jeb.243224
- Shadwick, R. E., Goldbogen, J. A., Potvin, J., Pyenson, N. D. and Vogl, A. W.** (2013). Novel muscle and connective tissue design enables high extensibility and controls engulfment volume in lunge-feeding rorqual whales. *J. Exp. Biol.* **216**, 2691-2701. doi:10.1242/jeb.081752
- Simon, M., Johnson, M., Tyack, P. and Madsen, P. T.** (2009). Behaviour and kinematics of continuous ram filtration in bowhead whales (*Balaena mysticetus*). *Proc. R. Soc. B Biol. Sci.* **276**, 3819-3828. doi:10.1098/rspb.2009.1135
- Simon, M., Johnson, M. and Madsen, P. T.** (2012). Keeping momentum with a mouthful of water: Behavior and kinematics of humpback whale lunge feeding. *J. Exp. Biol.* **215**, 3786-3798. doi:10.1242/jeb.071092
- Sims, D. W.** (1999). Threshold foraging behaviour of basking sharks on zooplankton: life on an energetic knife-edge? *Proc. R. Soc. Lond. B Biol. Sci.* **266**, 1437-1443. doi:10.1098/rspb.1999.0798
- Sims, D. W. and Quayle, V. A.** (1998). Selective foraging behaviour of basking sharks on zooplankton in a small-scale front. *Nature* **393**, 460-464. doi:10.1038/30959
- Slater, G. J., Goldbogen, J. A. and Pyenson, N. D.** (2017). Independent evolution of baleen whale gigantism linked to Plio-Pleistocene ocean dynamics. *Proc. R. Soc. B* **284**, 20170546. doi:10.1098/rspb.2017.0546
- Soto, A., Stewart, W. J. and McHenry, M. J.** (2015). When optimal strategy matters to prey fish. *Integr. Comp. Biol.* **55**, 110-120. doi:10.1093/icb/icc027
- Tamura, T. and Fujise, Y.** (2002). Geographical and seasonal changes of the prey species of minke whale in the Northwestern Pacific. *ICES J. Mar. Sci. J. Conseil* **59**, 516-528.
- Videsen, S. K. A., Simon, M., Christiansen, F., Friedlaender, A., Goldbogen, J., Malte, H., Segre, P., Wang, T., Johnson, M. and Madsen, P. T.** (2023). Cheap gulp foraging of a giga-predator enables efficient exploitation of sparse prey. *Sci. Adv.* **9**, eade3889. doi:10.1126/sciadv.ade3889
- Vogel, S.** (1994). *Life in Moving Fluids: The Physical Biology of Flow*. Princeton, NJ: Princeton University Press.
- Ware, C., Wiley, D., Friedlaender, A. S., Weinrich, M., Hazen, E. L., Bocconcelli, A., Parks, S. E., Stimpert, A. K., Thompson, M. A. and Abernathy, K.** (2013). Bottom side-roll feeding by humpback whales (*Megaptera novaeangliae*) in the southern Gulf of Maine, U.S.A. *Mar. Mamm. Sci.* **30**, 494-511. doi:10.1111/mms.12053
- Webb, P. W. and De Buffrénil, V.** (1990). Locomotion in the biology of large aquatic vertebrates. *Trans. Am. Fish. Soc.* **119**, 629-641. doi:10.1577/1548-8659(1990)119<0629:LITBOL>2.3.CO;2
- Webber, M. A., Keener, W., Markowitz, T. M., Chamberlin, D., Allen, D. D., Lane, R. S., Slaathaug, J. M., Rodriguez, P. N., Goerge, K. and O'Hern, J.** (2024). Fish feeding and rapid foraging behavior switching by gray whales (*Eschrichtius robustus*) in California. *Aquat. Mamm.* **50**, 132-151. doi:10.1578/AM.50.2.2024.132
- Werth, A. J.** (2000). Feeding in marine mammals. In *Feeding: Form, Function and Evolution in Tetrapod Vertebrates* (ed. K. Schwenk), pp. 475-514. New York, NY: Academic Press.
- Werth, A. J.** (2004). Models of hydrodynamic flow in the bowhead whale filter feeding apparatus. *J. Exp. Biol.* **207**, 3569-3580. doi:10.1242/jeb.01202
- Werth, A. J.** (2007). Adaptations of the cetacean hyolingual apparatus for aquatic feeding and thermoregulation. *Anat. Rec. Adv. Integr. Anatomy Evol. Biol.* **290**, 546-568. doi:10.1002/ar.20538
- Werth, A. J.** (2013). Flow-dependent porosity and other biomechanical properties of mysticete baleen. *J. Exp. Biol.* **216**, 1152-1159. doi:10.1242/jeb.078931
- Werth, A. J. and Potvin, J.** (2016). Baleen hydrodynamics and morphology of cross-flow filtration in balaenid whale suspension feeding. *Plos One* **11**, e0150106. doi:10.1371/journal.pone.0150106
- Werth, A. J., Potvin, J., Shadwick, R. E., Jensen, M. M., Cade, D. E. and Goldbogen, J. A.** (2018). Filtration area scaling and evolution in mysticetes: trophic niche partitioning and the curious cases of sei and pygmy right whales. *Biol. J. Linn. Soc.* **125**, 264-279. doi:10.1093/biolinnean/bly121
- Wiley, D., Ware, C., Bocconcelli, A., Cholewiak, D. M., Friedlaender, A. S., Thompson, M. and Weinrich, M.** (2011). Underwater components of humpback whale bubble-net feeding behaviour. *Behaviour* **148**, 575-602. doi:10.1163/000579511X570893
- Williams, T. M., Wolfe, L., Davis, T., Kendall, T., Richter, B., Wang, Y., Bryce, C., Elkaim, G. H. and Wilmers, C. C.** (2014). Instantaneous energetics of puma kills reveal advantage of felid sneak attacks. *Science* **346**, 81-85. doi:10.1126/science.1254885
- Wilson, A. M., Lowe, J. C., Roskilly, K., Hudson, P. E., Golabek, K. A. and McNutt, J. W.** (2013). Locomotion dynamics of hunting in wild cheetahs. *Nature* **498**, 185-189. doi:10.1038/nature12295
- Wilson, A. M., Hubel, T. Y., Wilshin, S. D., Lowe, J. C., Lorenc, M., Dewhirst, O. P., Bartlam-Brooks, H. L., Diack, R., Bennitt, E. and Golabek, K. A.** (2018). Biomechanics of predator-prey arms race in lion, zebra, cheetah and impala. *Nature* **554**, 183-188. doi:10.1038/nature25479