
Minke whale feeding rate limitations suggest constraints on the minimum body size for engulfment filtration feeding

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Supplementary Information

Supplementary Box 1- Metabolic scaling exponent

There are reasonable debates as to the most appropriate metabolic scaling exponent, and the empirical work cited found scaling exponents ranging from 0.63 to 1⁹⁵⁻¹⁰⁴. Although metabolic rate has never been explicitly measured in baleen whales, of the two most commonly cited exponents, 0.67 and 0.75, we use the higher one as both larger animals generally^{102,103} and artiodactyls specifically¹⁰⁴ tend to have higher metabolic scaling exponents. Indeed, in order to account for mysticetes in the energy surplus model of Gearty et al.³⁰, an adjustment of the intake rate exponent from 0.71 to 0.78 was required. For our calculations, smaller intake rate scaling exponents would steepen the slope, implying minke whales would be further underperforming expectations, while larger intake rate scaling exponents would have the opposite implication.

Supplementary Box 2- Seasonal variation

Due to the temporal constraints on feeding, the negative scaling of feeding rates with body size at night combined with the neutral scaling during the day imply that the diel difference between nighttime and daytime feeding rates within foraging bouts was greater for small whales than for large whales (Fig 2i). Within AMW, daytime feeding rates for a 5 m AMW were 24% of the nighttime rates, while daytime feeding rates for a 9 m AMW were 41% of the nighttime rates. At the larger end of the rorqual whale size scale, a 22 m blue whale daytime feeding rate is 75% of the nighttime rate (Fig 2i). Under the assumption that the feeding rates and proportion of day and night feeding we observed would be maintained throughout the course of a nominal foraging season from Nov 1 to May 1, model results suggest that AMW feeding in our study area at the observed rates would not start performing more lunges at night than during the day until Feb 1 (Extended Data Fig 8b) and continue doing so for the remainder of the season.

From Nov 19 to Jan 24, when it never gets completely dark at our field site in the West Antarctic Peninsula (Extended Data Fig 8), if prey conditions, and, consequently, feeding rates, were the same as what we observed in late summer, our model suggests that whales > 7 m could account for the lost prime foraging time by foraging longer during the day, but smaller whales could not. As an extreme example, a whale of theoretically small size (3 m) would have to feed 42.5 hrs/day during the day to account for the lost ideal foraging time. Under alternative assumptions about the caloric value of lunges performed in surface-associated nighttime krill patches compared to daytime krill patches, that relationship changes somewhat (Extended Data Fig 8d). However, deep lunges would have to be 2.5 times as calorie-rich as shallow lunges in order for the theoretical 3 m whale to match its autumn intake rates by feeding 100% of its time. At that day:night calorie/lunge ratio, a 5 m whale would have to spend more than 22.7 hours per day feeding during the peak daylight time of year (Extended Data Fig 8d).

Supplementary Box 3- Strategies to overcome filter feeding minimum size constraints in neonates

A filter feeding minimum size constraint suggests two alternate strategies for juvenile forms of obligate filter-feeding species: 1) birth young at or above the minimum body size for suspension feeding, or 2) for some initial stage young must adopt an alternate feeding strategy. The limited data on neonate and juvenile members of filter feeding fish species seem to support these predictions. Manta and devil rays (*Mobula* sp.) and basking sharks (*Cetorhinus maximus*) give live birth to some of the largest neonates of all fish¹⁰⁵⁻¹⁰⁸, which is likely to approximate the MSC of these species. Whale shark neonates, however, have been measured at less than 0.5 m¹⁰⁹, but have underdeveloped gill filtering structures¹¹⁰ and filtering pads¹¹¹, and observations of younger individuals typically highlight more flexible foraging behavior, including suction feeding^{112,113}. Little is known about the feeding habits of megamouth sharks (*Megachasma pelagios*); however, the only recorded individual caught by commercial longline was a juvenile specimen (190 cm total length), indicating that this individual was likely scavenging on particulate prey¹¹⁴.

Supplementary Box 4- The effect of depth, density and seasonality on prey and feeding rate

As the density of krill within prey patches increases, rorqual whales increase their feeding rates to take advantage of high-quality food^{48,90,91,115}. Given this trend, the 3-4 times greater feeding rates of AMW in shallow water (Fig 1b,c) are likely to indicate higher prey density per lunge, implying that the diel patterns we observe may underestimate the relative importance of nighttime feeding in relation to daytime feeding for small whales. Modeling results suggest that if prey behavior were to remain constant throughout the year (deep during the day, shallow at night), the extended day lengths in polar regions during the summer would be a critical environmental factor that limits engulfment filtration feeding at AMW body size. At the latitude of our study, if feeding rates and foraging durations were consistent throughout the year, total night lunges could exceed day lunges for 69% of the year (Extended Data Fig 8); however, for the majority of time AMW spend in the foraging region the sun is above the horizon – e.g. in our study area there is no true darkness from Nov 19 to Jan 24. If the observed feeding rates and diel proportions were maintained during midsummer, a 9 m whale would only perform 73% of the total lunges over 24 hrs we observed during the study period, while a 5 m whale would only perform 56% and a theoretical 3 m whale would only perform 44%.

Typical diel vertical migration patterns are often modified in polar summers, however. For instance, in a comparative seasonal study on West Antarctic Peninsula krill, summer krill in the 1993 season were found to be more abundant in near-surface waters than in the fall¹¹⁶. Recent video evidence has shown that small swarms of krill at the surface may still be dense¹¹⁷, suggesting that while larger animals like humpback whales may have to use herding strategies like bubble net feeding to aggregate smaller groups^{117,118}, smaller animals like AMW may still be able to take advantage of small, dense patches. Because shallow feeding during our study period was tightly coupled with night feeding, our model of seasonal total feeding (Extended Data Fig 8) based on the proportion of night feeding could also be interpreted as a proportion of shallow feeding, demonstrating the greater dependence of shallow prey patches for smaller whales and supporting the suggestion that environmental conditions with surface-associated krill patches would be necessary to support small whales currently, and support their evolution in prehistoric oceans.

Other regions of the world also at times support productive surface patches of krill. In the Taranaki Bight, New Zealand, blue whales have been associated with krill patches that were densest in shallow (< 20 m) waters¹¹⁹, and in the Gulf of St. Lawrence, Canada, blue whales feeding at night on shallow prey had feeding rates twice as high as during the day⁹¹ coincident with shallow, dense prey patches¹²⁰. These areas do not, however, currently support abundances of krill-feeding minke whales, suggesting that surface patches in these regions are not consistent enough to make engulfment filtration feeding worthwhile at small body sizes (Supplementary Box 5).

Supplementary Box 5- Temporal constraints on rorqual whale feeding

In rorqual whales, large body size minimizes the effects of the biomechanical, physiological and environmental constraints on feeding rate. Physiologically, increased oxygen stores coupled with lower mass-specific metabolic rate allow for longer and deeper dives in larger animals^{35,121}, increasing the time available for foraging at depth (Fig 4, Extended Data Fig. 5) or the oxygen available for metabolically expensive tasks like lunge feeding^{35,53}.

Biomechanically, increased engulfment capacity in larger animals allows for proportionally greater intake with every lunge, minimizing the overall number of lunges needed for a given intake. Accordingly, fewer lunges implies that the total time devoted to size-invariant constraints like approach and search time is decreased in larger animals. Conversely, smaller animals spend more total time searching for and approaching prey patches than do large ones.

Of the three phases of lunge feeding (acceleration, engulfment, and filtration), filtration time is the most dynamic, with the steepest relationship to body size (Fig 3) and the largest overall effect on lunge time. Due to the inflated buccal cavity and associated increased drag, the energetic cost of powered progress during filtration is high, so decreasing filter time increases the time available for other behaviors. Accordingly, small whales have relatively more baleen surface area which serves to decrease filter time^{37,64,70}. However, as body size decreases, reductions in filter time have a proportionally lower effect on overall lunge time, leaving little scope to increase lunge rates by decreasing filter times (Extended Data Fig 6). The only way, then, for small animals like AMW to substantially increase their overall intake is to decrease the search time between lunges or to increase the amount of time actively foraging, both tactics limited by diurnal and seasonal temporal constraints as well as prey distribution patterns.

The amount of time available for foraging decreases with dive depth in AMW (Fig 4). Larger animals like blue whales, in contrast, can proportionally increase foraging time by decreasing surface time between dives, requiring only 32-51% of the time at the surface that an AMW does for a given dive length⁽⁵³⁾, Extended Data Fig 5). When feeding near the surface, however, whales can combine breathing/recovery with the filtration and/or search phases (utilizing specialized oral plugs to keep water out of the gastrointestinal tract¹²²), nearly removing the surface interval restriction as well as the transit time to depth, thereby allowing for ultra-high foraging rates in near-surface feeding (typically at night) (Fig 1b) that increase inversely with size (Fig 2g,j). The physiological constraints on dive duration relative to surface recovery time act more on smaller whales than larger whales (Fig 4), serving to limit the daytime (deep) feeding rates generally (Fig 2j), and explaining the observed lack of relationship between AMW daytime feeding rates and body length (Fig 5).

Supplementary References

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