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Integrative Approaches to the Study of Baleen Whale Diving Behavior, Feeding Performance, and Foraging Ecology

JEREMY A. GOLDBOGEN, ARI S. FRIEDLAENDER, JOHN CALAMBOKIDIS, MEGAN F. MCKENNA, MALENE SIMON, AND DOUGLAS P. NOWACEK

For many marine organisms, especially large whales that cannot be studied in laboratory settings, our ability to obtain basic behavioral and physiological data is limited, because these organisms occupy offshore habitats and spend a majority of their time underwater. A class of multisensor, suction-cup-attached archival tags has revolutionized the study of large baleen whales, particularly with respect to the predatory strategies used by these gigantic bulk filter feeders to exploit abundant oceanic resources. By integrating these data with those from other disciplines, researchers have uncovered a diverse and extraordinary set of underwater behaviors, ranging from acrobatic diving maneuvers to extreme feeding events during which whales engulf volumes of prey-laden water that are much larger than their own body. This research framework not only improves our knowledge of the individual performance and behavior of these keystone predators but also informs our ability to understand the dynamics of complex marine ecosystems.

Keywords: animal behavior, marine biology, natural history, locomotion, integrative biology

The extreme body size of mysticetes is a testament to their ecological role as bulk feeders on mass quantities of zooplanktonic resources. All baleen whale species (suborder Mysticeti) feed by filtering prey-laden water through racks of keratinized baleen plates that hang down from the rostrum. By feeding in bulk on aggregations of zooplankton and fish, mysticetes exhibit one of the most energetically efficient foraging strategies among marine organisms (Goldbogen et al. 2011). There are three modes of filter feeding observed among baleen whales (Werth 2000): (1) continuous ram feeding by bowhead and right whales (family Balaenidae, or *balaenids*), (2) suction feeding by gray whales (*Eschrichtius robustus*), and (3) intermittent ram feeding or lunge feeding by rorqual whales (family Balaenopteridae, or *balaenopterids*). During continuous ram feeding, balaenid whales swim through patches of prey at slow, steady speeds with their mouth agape, thereby forcing water past the exposed baleen plates. In contrast, lunge feeding in rorquals is characterized by the engulfment of a large volume of prey-filled water at high speed, followed by the filtering of the engulfed water with the mouth closed. Gray whales are thought to

depress their tongue to suck in prey and water, often along the seafloor, to feed on benthic invertebrates. Despite these vastly different filter-feeding modes, baleen whales are generally considered opportunistic feeders that exploit dense prey patches whenever they are present (Werth 2001).

Until recently, much of what was known about how whales feed was limited to opportunistic observations at the sea surface or functional inferences from anatomical dissection (Werth 2000). The advent of animal-borne tags enables the remote, fine-scale measurement of behavior during foraging dives, during which researchers are unable to study animals directly. These data have not only dramatically increased our understanding of whale feeding behavior but have also increased our knowledge of how foraging performance relates to broader ecological and evolutionary processes (Friedlaender et al. 2009, Goldbogen et al. 2012, Potvin et al. 2012). Here, we highlight a body of work that uses multi-sensor tags to investigate the kinematics and foraging behavior of the world's largest whales. Specifically, we focus on the feeding performance of baleen whales and discuss how the integration of these complex data sets with knowledge from

other disciplines has led to major insights into the evolutionary ecology of gigantism in the marine environment.

Animal-borne tags take on many different forms and exhibit a wide variety of sensor modalities, ranging from high-resolution behavior loggers (Nowacek et al. 2001, Miller et al. 2004, Goldbogen et al. 2006, Simon et al. 2009) to satellite-linked tags that provide tracking data over large spatial and temporal scales (Bailey et al. 2009, Durban and Pitman 2011). Although a wide variety of animals have borne these devices across this technological spectrum, the majority of biologging studies have involved sea birds, cetaceans, and pinnipeds (Ropert-Coudert et al. 2010). Large-scale projects that have integrated techniques and sensor suites across taxa have provided a wealth of information on habitat use and animal migration at the scale of ocean basins (Block et al. 2011, Costa et al. 2012). At the scale of individual foraging dives, accelerometer-equipped tags have revealed the fine-scale details of animal behavior within the context of energy use and acquisition (Gleiss et al. 2011, Goldbogen et al. 2012). In combination with other sensors, such as stereo hydrophones and magnetometers, archival tags have now become powerful tools to simultaneously quantify animal behavior and the acoustic environment at extremely high resolution (Johnson et al. 2009).

The foraging behavior of toothed whales has been well characterized using multisensor tags, especially with regard to acoustic communication and echolocation (Johnson et al. 2009). The logistic implementation of these devices is not trivial and typically requires considerable field efforts with the coordination of multiple research vessels and large research teams. Prior to its deployment, each tag is equipped with suction cups for attachment and a VHF (very high frequency) radio transmitter for animal tracking and tag retrieval. The tag is affixed to the end of a several-meter-long fiberglass or carbon fiber pole and placed on the whale's back as it surfaces (figure 1). When tags are deployed on focal animals, researchers often obtain complementary data, such as prey field distribution and abundance, using active hydroacoustic systems, as well as prey type from plankton net tows (Croll et al. 1998, Goldbogen et al. 2008, Friedlaender et al. 2009, Hazen et al. 2009, Nowacek et al. 2011). This type of information on prey provides an important ecological context for the whale's foraging behavior, and it also helps inform estimates of how much prey is consumed during each foraging dive.

Although research on large whales presents a range of logistic challenges, mysticetes represent a model group with which to study biomechanics, foraging ecology, and energetics in a natural context. Because feeding is a crucial component of baleen whale life history, tagging operations in many temperate and polar latitudes are bound to capture a series of foraging bouts. As large apex predators that target resources at relatively low trophic levels, baleen whale physiology is honed for the efficient exploitation of patchily abundant prey. However, foraging effort at depth is ultimately limited by the amount of oxygen stores within the body, the rate at which oxygen is depleted during a dive,



Figure 1. Deploying a suction-cup digital tag to a surfacing blue whale. Photograph: Jeff Foster. The photograph was taken under National Marine Fisheries Service permit no. 14534.

and the lowest tolerable level of oxygen in the body. Because high-quality prey patches may be deep, by virtue of the diurnal vertical migration exhibited by zooplankton aggregations, whales must balance the metabolic costs of diving against the potential for very high energy gain from acquired prey in the deep ocean. Moreover, the feeding mechanism of some baleen whale species necessitates complex fluid-structure interactions and predictably high drag costs that will influence an animal's energy budget. Therefore, a complete understanding of foraging in baleen whales, as in all marine animals, requires an integration of biomechanics, energetics, diving physiology, and behavioral ecology.

Tagging gigantic bulk filter feeders: Fine-scale foraging behavior

Before the arrival of multisensor tags, researchers had investigated only dive depth as a first approximation of describing behavior. The earliest measurement of diving depth in a baleen whale was made by a capillary-tube pressure gauge, which recorded only the maximum pressure experienced, attached using a harpoon to a fin whale (Scholander 1940). The development of time-depth recorders made for more-systematic investigations of diving depth in many marine mammals, by measuring depth continuously as a function of time, ever since its inception in the 1960s (Kooyman 1966, 2004). The first time-depth recorder deployments revealed important insights into the routine behavior of foraging

baleen whales using different data collection modalities, including acoustic telemetry (Winn et al. 1995), satellite-linked (Mate et al. 2007), and archival tags (Panigada et al. 1999, Croll et al. 2001, Calambokidis et al. 2007). These studies demonstrated that baleen whales—rorquals in particular—exhibit much shorter dive depths and breath holds than would be expected from their body mass alone (Croll et al. 2001), a phenomenon that is unique among diving animals and related directly to their extreme feeding behavior (Goldbogen 2010).

As tag technology evolved to include more-complex sensor suites, our ability to understand fine-scale foraging behavior at depth dramatically increased. Right whales (*Eubalaena glacialis*) were the first baleen whale species studied with multisensor acoustic tags. This study used accelerometer signals to determine the whale's body pitch

angle and locomotor gait (gliding versus active swimming strokes) during diving (Nowacek et al. 2001). Right whales exhibited a descent powered by steady swimming and a primarily gliding ascent (Nowacek et al. 2001). This choice of swimming gait reinforces the fact that right whales are positively buoyant, a characteristic that made this species so prone to exploitation and depletion during the nineteenth-century commercial whaling operations. A more recent tagging study on bowhead whales (*Balaena mysticetus*) revealed the same basic fluking patterns (figure 2) that were observed in right whales (Simon et al. 2009), a result consistent with the low fineness ratio (stocky body shape) and fatty body condition generally shared by all balaenids (Woodward et al. 2006).

Unlike the gliding gaits adopted during ascent and descent, the bottom phase of balaenid foraging dives exhibit a higher

proportion of continuous swimming (Woodward 2006, Simon et al. 2009). The kinematic data provided strong evidence that continuous ram filter feeding is powered in part by hydraulic, flow-induced pressures. However, a flow tank study using scaled models showed that hydrodynamic pressures (i.e., the Bernoulli and Venturi effects) must also drive the filtration process (Werth 2004). This hydrodynamic effect is generated by the unique morphology of the balaenid filter-feeding apparatus: The anterior opening of the mouth (where water flows in) is much larger than where the water exits the mouth posteriorly (Werth 2004). Such a feeding mechanism predictably increases filtration performance and concomitantly reduces drag on the body (Werth 2004) but, as a trade-off, requires a slower swimming speed during foraging (Simon et al. 2009). It is not surprising, therefore, that swimming speeds during the bottom phase of a dive (0.8 meters [m] per second), during which feeding predictably occurs, were significantly lower than those during ascent or descent (1.3–1.6 m per second) (Simon et al. 2009). With large, high-aspect-ratio control surfaces (flukes and flippers) and a bulky body shape, balaenids appear to be optimized for these slow, steady swimming speeds that are required for their ram filter feeding strategy (Woodward et al. 2006).

Rorquals represent an extraordinarily contrasting case to bowhead and right whales in several different aspects.

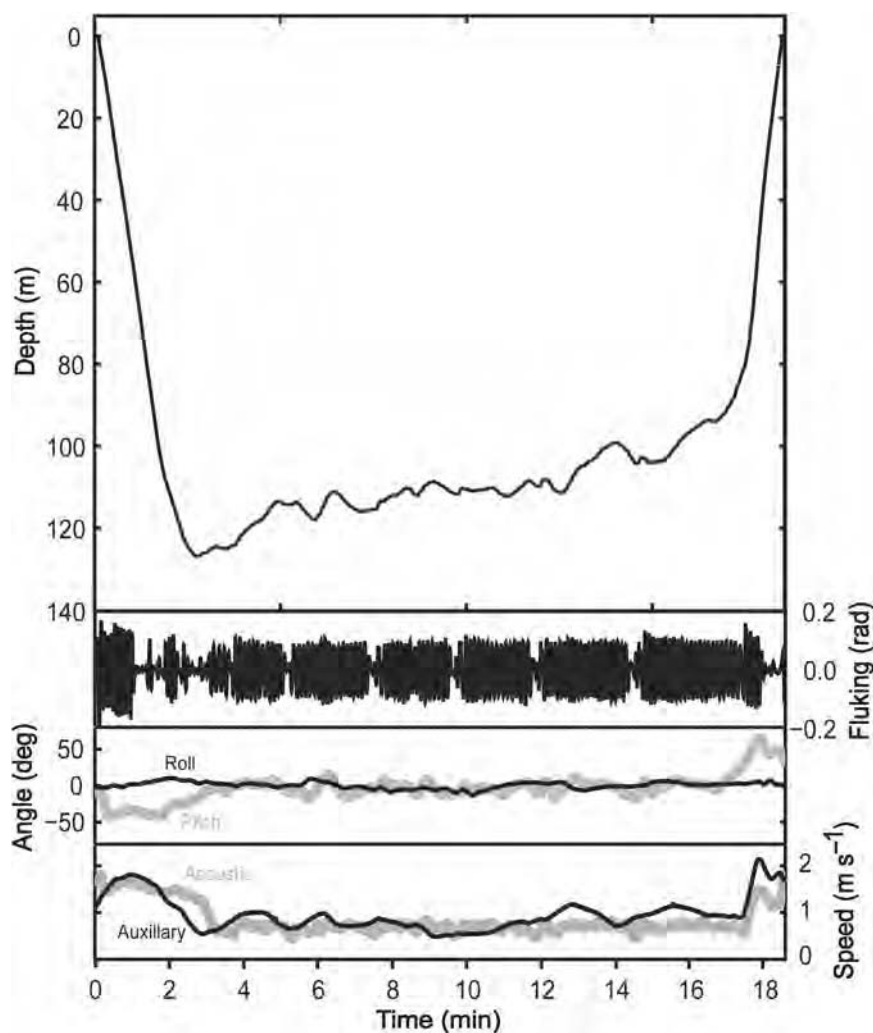


Figure 2. Kinematics of a bowhead whale foraging dive. Virtually continuous ram feeding is exhibited during the bottom phase of the dive. Two estimates for speed are shown: the speed estimated from flow noise (the gray line) and that estimated from the angle-corrected depth rate (the black line). Abbreviations: deg, degree; m, meters; min, minutes; rad, radians; s^{-1} , per second. Source: Adapted from Simon and colleagues (2009).

Kinematic data from digital tags attached to foraging rorquals reveal the opposite choice of locomotor gait during diving (figure 3). Specifically, rorqual foraging dives are characterized by a gliding descent, several lunges at depth, and an ascent that is powered by steady swimming strokes (figure 3; Goldbogen et al. 2006, 2011, Woodward 2006, Ware et al. 2011). Because of their negative buoyancy, rorquals can readily glide to depth, a common locomotor strategy exhibited by many marine mammals for energetically efficient diving (Williams et al. 2000). Gliding gaits are also observed in between lunges at depth, which are generally associated with the purging phase as engulfed water is filtered out of the buccal cavity. In cases in which lunges involve vertical excursions from beneath a prey patch, a gliding gait is apparently used to reposition the body for another lunge and also

to help regain the momentum that was lost during a lunge (Goldbogen et al. 2011).

The mechanics of the body during lunges indicate a dynamic feeding strategy in which the body undergoes several cycles of rapid speed changes (Goldbogen et al. 2006, Woodward 2006, Doniol-Valcroze et al. 2011, Goldbogen et al. 2011, Ware et al. 2011, Simon et al. 2012). A typical rorqual lunge is characterized by an initial acceleration to high speed, a deceleration phase, and a primarily gliding phase at a relatively low speed of approximately 1 m per second while the engulfed water is filtered (Simon et al. 2012). Substantial rolling behavior has been recorded during lunges in humpback and fin whales (Goldbogen et al. 2006, Stimpert et al. 2007), with the greatest roll moment occurring at maximum speed during lunge feeding (Goldbogen

et al. 2006). Considering that maneuvers in other animals involve temporal coupling of roll with yaw and pitch moments, the changes in body orientation observed during lunges may simply occur as the whale modifies its trajectory to engulf a prey patch. Alternatively, a roll could function to reposition the engulfment apparatus to ensnare prey next to a boundary (Goldbogen et al. 2006), such as the seafloor or the sea surface (Hain et al. 1995, Friedlaender et al. 2009, Hazen et al. 2009, Ware et al. 2011, Wiley et al. 2011), and it may also represent a strategy that enhances capture success by anticipation of the direction of prey escape (Potvin et al. 2010).

Putting tag data to use:

Quantifying feeding performance

Despite the vastly different diving and feeding kinematics that are observed between balaenids and balaenopterids, they share a common feeding mechanism that uses baleen to filter prey from engulfed water. For a given density of prey, therefore, the amount of food that can be processed is determined by engulfment performance or the *filter rate* (the volume of water filtered by baleen per unit of time). By integrating kinematic data from digital tags with the morphological dimensions of the mouth, researchers have estimated the amount of prey-laden water processed by these large, bulk filter-feeding predators. The first approach was developed for rorqual lunge feeding, an engulfment mechanism that is facilitated by a complex suite of physiological

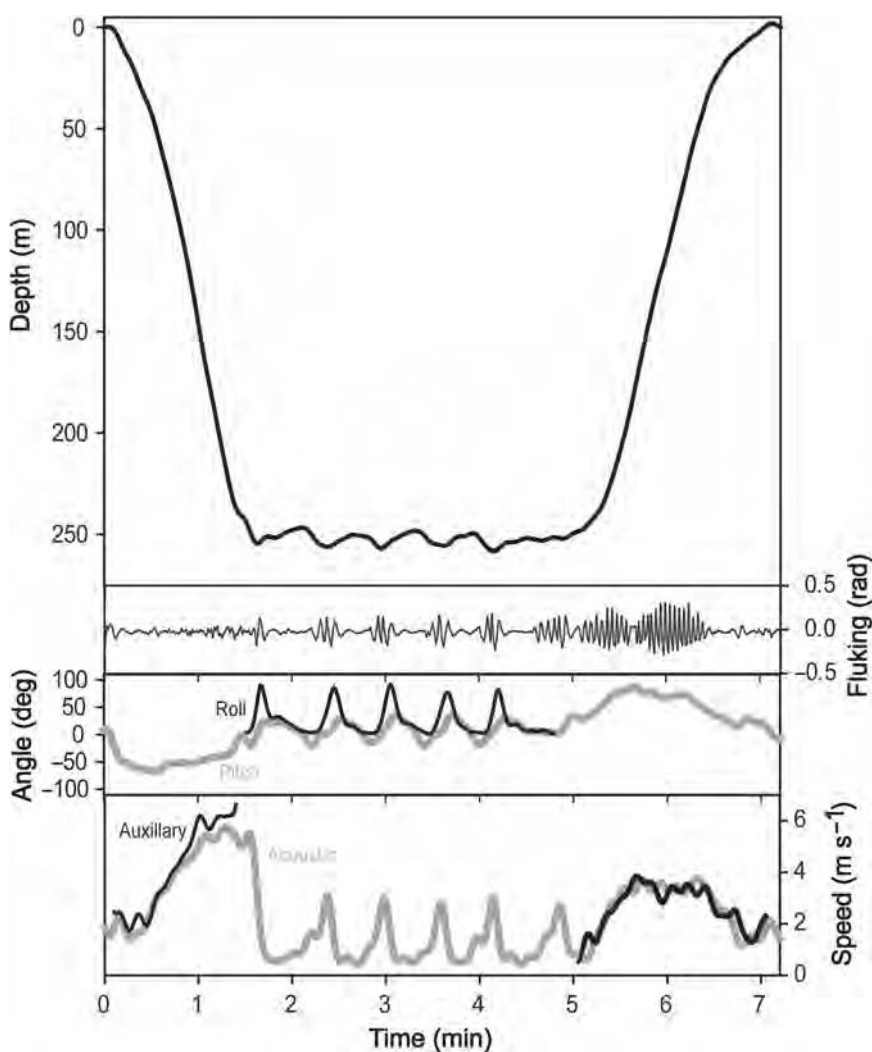


Figure 3. Kinematics of a fin whale foraging dive. The first of six lunges occurs at the end of the descent phase. Two estimates for speed are shown: the speed estimated from flow noise (the gray line) and that estimated from the angle-corrected depth rate (the black line). Abbreviations: deg, degree; m, meters; min, minutes; rad, radians; s^{-1} , per second. Source: Adapted from Goldbogen and colleagues (2006).

adaptations (Goldbogen 2010, Pyenson et al. 2012). In particular, these whales have hyperexpandable throat pouches that enable the engulfment of large volumes of prey and water. The engulfment process is dynamic and involves a complex coordination of mouth opening and closing movements relative to the acceleration of the body.

To model this process, researchers first invoked a simple, quasisteady hydrodynamic model of engulfment in fin whales (Goldbogen et al. 2007). This method relied on the premise that the dimensions of the skull and mandibles define the effective mouth area through which water enters the buccal cavity. Gape angle controls how much mouth area is exposed to flow, such that greater gape angles increase the projected area of the mouth. The volume engulfed, therefore, is simply the product of the projected mouth area and the displacement of the body, which is derived from the speed data. The calculated engulfment volume for an adult fin whale was estimated as 60–80 cubic meters (m^3), a volume greater than the whale's own body size (Goldbogen et al. 2007). Such estimates have generally been consistent with estimates of engulfment capacities based on simple geometric approximations of the buccal cavity (Goldbogen et al. 2010), as well as advanced models that account for complex hydrodynamic phenomena (Potvin et al. 2009, 2010, Goldbogen et al. 2011).

Because lunges occur one after another at the bottom of deep foraging dives, the duration in between each lunge (called the *interlunge interval*), represents the time required to filter and purge the engulfed water mass. The interlunge interval has been similar among studies in different geographic regions in both humpbacks (Ware et al. 2011, Goldbogen et al. 2012, Simon et al. 2012) and blue whales (Woodward 2006, Doniol-Valcroze et al. 2011, Goldbogen et al. 2011) foraging on krill, which suggests that this parameter is indeed representative of the time required to process the engulfed water mass before another lunge can be performed. However, studies of humpback whales foraging on more-elusive schooling fish, such as capelin, have revealed longer interlunge intervals (Simon et al. 2012), which may indicate either longer prey handling times or the increased time needed to find the next fish school to attack. Engulfment volume divided by the interlunge interval yields the *volumetric flow rate*, or the volume of engulfed water that is filtered per unit of time. This parameter appears to be approximately the same (around 2 m^3 per second) among rorqual species of different sizes (Goldbogen et al. 2012), but bowhead whales appear to be capable of significantly higher filter rates of approximately 3 m^3 per second (Simon et al. 2009). The filter rates in balaenids can be calculated as the product of projected mouth area and speed (Simon et al. 2009), assuming that there is no bow wave directly in front of the mouth aperture (Werth 2004).

The differences in filter performance observed between rorquals and balaenids may reflect preferences in prey type or differences in distribution or abundance, which in turn influence life history and ecological niche. Given their

relatively high maximum lunge speeds of 2–4 m per second (Goldbogen et al. 2012), balaenopterids may be more effective at exploiting agile prey, such as fish or krill, that exhibit well-known escape responses (O'Brien 1987, Domenici 2001). The obligatory filter phase in between lunges allows for some movement in the water column, albeit at low speed, which thereby increases the probability of locating a higher-quality prey patch for the next lunge. For these reasons, rorqual lunge feeding may also be better suited for dense, patchily distributed prey aggregations. Because rorquals engulf a discrete volume of water, the energetic efficiency of the lunge is reliant on extremely dense prey aggregations (Goldbogen et al. 2011). In contrast, balaenids generally exhibit slow ram feeding speeds of less than 1 m per second (Simon et al. 2009), which limits their prey options primarily to slow-moving copepods. As a trade-off, continuous ram feeding with a gigantic filtration system will be limited virtually only by dive time. Therefore, the balaenid feeding strategy is predictably more effective for diffuse (yet still abundant) zooplankton layers, although greater food density will also return substantial energetic benefits.

A comparison of long-term, continuous foraging behavior between rorquals and balaenids reveals significant differences in feeding performance (figure 4). At the same approximate foraging depth, a blue whale exhibited more than twice as many dives (23 dives) per unit of time (relatively shorter dive durations) than did a bowhead whale (10 dives). Even though these two taxa are roughly in the same body-size class (more than 50,000 kilograms) and should exhibit similar diving capacities, these differences are probably due to the relatively higher cost of intermittent lunge feeding than of continuous ram feeding (Acevedo-Gutiérrez et al. 2002). Rorquals lunge at high speeds, which range from 2 to 4 m per second, with their mouths agape. Because the balaenid feeding strategy operates at a relatively lower energetic cost (Nousek-McGregor 2010) than that of rorquals (Goldbogen et al. 2011, 2012), foraging time at depth is maximized, and therefore, a balaenid can process more prey-laden water than a balaenopterid of a similar size can. In this example, the bowhead whale filtered an estimated $18,000 \text{ m}^3$ in 2.7 hours—more than twice as much as the blue whale did (approximately 9000 m^3)—during the same amount of time. Nevertheless, despite the major energetic costs required for lunge feeding and the negative consequences that it has for diving capacity (limiting dive time and forcing a return to the sea surface), rorquals benefit by having the ability to feed on relatively agile and elusive prey. In contrast, bowhead and right whales have a more economical feeding strategy that enables higher filter-feeding rates but at a cost of their being limited to relatively nonevasive prey types.

The volumetric filter rate distributed over the effective baleen filter area gives an estimate of flow speed past the baleen. In fin whales, this value is predicted as 0.7–0.9 m per second, which is remarkably similar to that of continuously ram filter-feeding bowhead whales (Simon et al. 2009). At these flow speeds, baleen fringes appear to

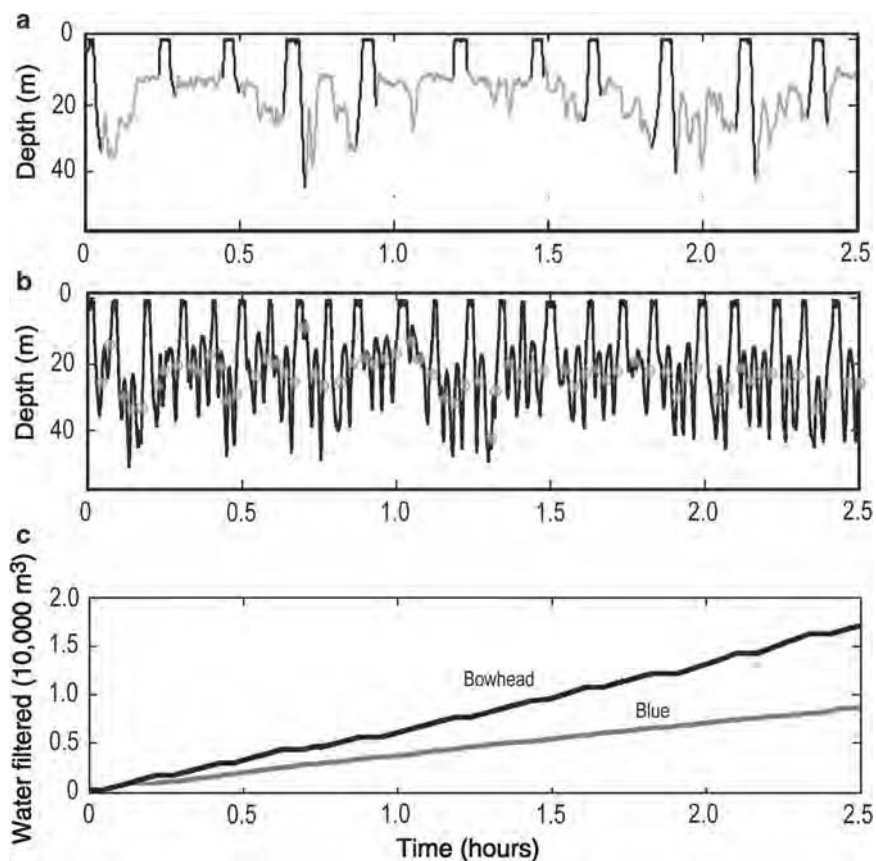


Figure 4. Comparison of diving behavior and filtration performance between continuous ram feeding in a bowhead whale and intermittent (lunge) feeding in a blue whale. Dive profiles for a bowhead whale (a) and for a blue whale (b) feeding at the same approximate depth. The estimated water filtered as a function of time is shown for each species (c). Abbreviations: m, meters; m^3 , cubic meters.

operate at intermediate Reynolds numbers ($Re = 500\text{--}700$; Goldbogen et al. 2007). The Reynolds number is a non-dimensional parameter that describes the character of fluid flow (inertial forces relative to viscous forces), and similarities in these values in different systems suggest that the hydrodynamics of those systems are also comparable (Vogel 1994). Interestingly, filter-feeding fishes, which employ a high-throughput and efficient cross-flow filtration mechanism, function at about the same flow speeds and Reynolds numbers (0.4–0.7 m per second, $Re = 150\text{--}600$; Sanderson et al. 2001). A comparison of these data suggests that baleen acts as a cross-flow filter rather than, as is often assumed, a dead-end sieve (Goldbogen et al. 2007), although experimental data from flow tank studies are needed to test these predictions (as was suggested by Werth [2004]). Such a mechanism should increase the efficiency of filtration and help avoid the logistic problem of removing prey lodged in baleen and the reduced flow rates that would result from it (Werth 2001). Therefore, despite vastly different morphological adaptations required for distinct filter feeding modes, baleen whales appear to be unified by the same hydrodynamic principles of particle capture.

Linking whale foraging behavior to prey abundance and distribution

Although biologging tags have advanced our fundamental knowledge of the underwater behavior of baleen whales, linking this information with environmental measures can offer greater insights into the interactions between predators and prey across ocean ecosystems. Because of their large body size, baleen whales require vast quantities of prey, and their feeding morphology is highly adapted for this purpose (Werth 2000, 2007, Woodward et al. 2006, Pyenson et al. 2012). By combining tagging efforts with concurrent quantitative measures of the distribution, abundance, and behavior of their prey, we can further understand the complex relationships between baleen whales and their environment (Croll et al. 1998, 2005). This information can play a fundamental role in understanding how perturbations to these ecosystems, ranging from climate change to human exploitation of marine resources, affect keystone predators (Wiedenmann et al. 2011).

The kinematic patterns described previously provide insights into how different baleen whales satisfy particular ecological niches. Although the fusiform shape of the largest rorqual whales (i.e., blue and fin whales) aids in high-speed lunging, particularly on small prey, the large oar-like flippers unique to humpback whales increase their maneuverability and allow for a broad range of unique feeding behavior (Woodward et al. 2006). Superimposed on these constraints associated with mechanical design is the strong effect of body size, especially when considered against the size of the targeted prey (Domenici 2001). Specifically, as animals increase in size, they become much less maneuverable, and this decreases their ability to capture elusive prey. These differences in maneuverability and swimming performance may influence the exploitation of particular prey types (Goldbogen et al. 2010, 2012), which also differ in their ability to escape oncoming predators (Potvin et al. 2010). For example, the extreme size of blue whales means that their maneuverability is severely decreased, and as a consequence, they are limited to very small prey (i.e., krill; Goldbogen et al. 2010, 2011, 2012). In contrast, the impressive agility and cooperative hunting behavior of humpback whales enable the efficient exploitation of larger, more mobile species (i.e., fish; Friedlaender et al. 2009, Hazen et al. 2009, Wiley et al. 2011). Despite the patterns underlying these prey preferences, all rorqual species, regardless of

body size or mechanical design, have been known to feed on krill. Although this common prey preference may be due to the high occurrence or abundance of krill across ocean ecosystems, how and when different baleen whale species prefer particular prey types within any given geographic region is virtually unknown.

Recent studies have begun to link foraging behavior with metrics of prey availability in order to better understand predator–prey interactions and how they fluctuate over different temporal and spatial scales. For example, the humpback whales of Stellwagen Bank produce bubble nets only during daylight hours and target aggregations of fish (e.g., sand lances) that are both in the upper portion of the water column and oriented vertically (Friedlaender et al. 2009, Hazen et al. 2009). Sand lances can be found feeding in the water column during daylight hours but retreat to the sandy seafloor at night for shelter. Humpback whales are able to respond to these daily changes in prey behavior by adopting bottom-feeding strategies at or near the seafloor when sand lances burrow. When sand lances are found both near the surface and at the bottom, humpback whales are able to switch between bubble-net and bottom feeding from dive to dive, giving the whales the greatest opportunity to maximize their energetic gain per unit of time.

In most cases, prey are distributed in discrete patches that whales feed on until the prey's density or biomass falls below a crucial threshold, below which it is not energetically efficient for the whales to continue feeding (Goldbogen et al. 2011). Biologging tags have enabled researchers to investigate how whale foraging behavior can be predicted by optimal-foraging theory (Doniol-Valcroze et al. 2011), according to which behavior is driven by the balance between the energy gain from acquired prey and the costs of diving to and from a prey patch. More-detailed studies in which tag studies are combined with dedicated efforts to determine the prey–field environment around feeding whales are now under way to provide insight regarding the decisions that whales make to optimize their feeding efficiency in the face of the costs associated with diving and foraging (Friedlaender et al. 2011, Nowacek et al. 2011). In the Antarctic, humpback whales alter the depth of their feeding bouts with the diel movements of their prey (Antarctic krill, *Euphausia superba*) and target denser layers of krill on deeper dives (Friedlaender et al. 2011, Nowacek et al. 2011, Ware et al. 2011). Such information on feeding behavior and the ecological relationships between baleen whales and their prey would not be possible without the advances in multisensor biologging tags and the integrative approaches described above to determine feeding performance and filtration rates.

The energetic efficiency of bulk filter feeding

The ability of marine mammals to assimilate energy from the environment during foraging is needed for a variety of vital life functions, including locomotion, growth, and reproduction (Costa and Williams 1999). For baleen whales, the energetic efficiency of bulk filter feeding is considered the

primary mechanism that can help maintain their extreme body size (Goldbogen et al. 2010). However, filter feeding is only efficient if sufficiently dense prey patches can be targeted and adequately exploited (Goldbogen et al. 2011). As the largest animals on earth, blue whales exhibit the greatest absolute metabolic demands, and their foraging behavior is strongly driven by the depth of dense krill patches (figure 5). The ability to exploit these high-quality prey aggregations at depth is ultimately limited by a whale's breath-hold capacity, a characteristic that generally increases with body size across all animals. For example, the extreme size of blue whales is associated with a limited dive capacity because of the high energetic cost required to lunge feed (Potvin et al. 2009, 2010). As a direct result, the number of lunges that can be performed during a dive is decreased, and therefore, the energetic efficiency is also decreased. Because larger rorquals engulf relatively larger gulps of water during each lunge (Goldbogen et al. 2010), the relative cost of feeding is also increased and, consequently, diving capacity is progressively decreased in larger body-size classes (Goldbogen et al. 2012). In other words, large rorqual whales forfeit their ability to dive longer and deeper in favor of a greater mass-specific engulfment capacity, a result that is directly due to the greater relative size of their skull and buccal cavity. By taking in a volume of water that is increasingly greater than their own body size, the energetic efficiency of feeding becomes very high, which in blue whales can be several orders of magnitude higher than that of other marine mammals (Goldbogen et al. 2011) but only if high-quality prey patches can be engulfed. However, if prey is diffuse and very deep, foraging efficiency is severely diminished, and the advantages of bulk filter feeding are effectively nullified.

High-quality prey patches may occur anywhere in the water column, but those resources (e.g., krill) may often be deep, because they undergo their diel vertical migrations to avoid predators. Therefore, the effect of prey-patch depth is a major factor with which foraging baleen whales must contend when seeking to maximize energetic efficiency. In blue whales, the number of lunges performed within a given dive increases with prey-patch depth but only up to a depth at which the costs of diving and lunge feeding begin to limit both optimal foraging behavior (Doniol-Valcroze et al. 2011) and what may be physiologically possible (Goldbogen et al. 2011). Consequently, the energetic efficiency of a given foraging dive will be independent of the foraging depth (figure 6a), so long as the prey density is also independent of depth. Alternatively, if prey density increases with depth, the energetic benefits of feeding at depth will likely greatly exceed the costs associated with deep diving (figure 6b). What these models fail to account for, however, are the increased recovery times required at the sea surface following deeper dives. Such a factor will predictably decrease foraging efficiency, simply because more time must be devoted to recovery rather than to more feeding. Therefore, future research efforts to estimate foraging efficiency should extend our integrated approach to account for a multiplicity of

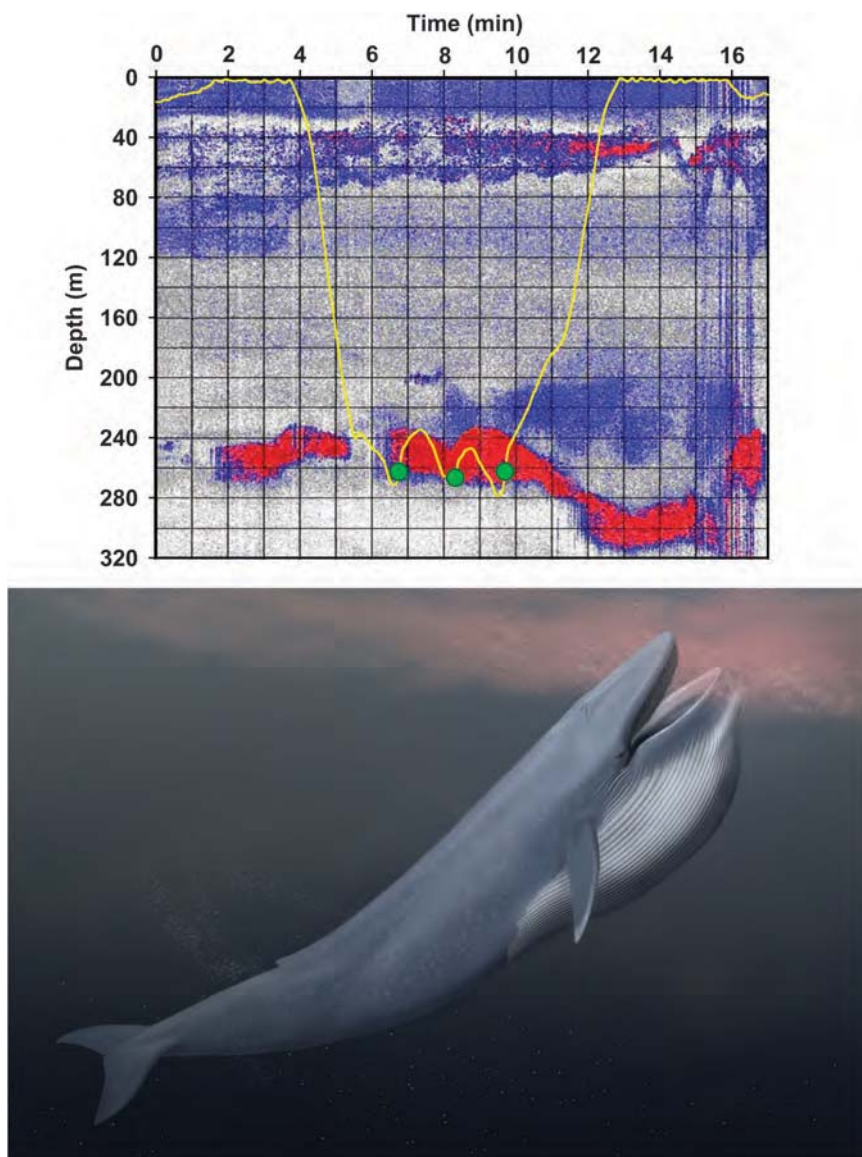


Figure 5. Example of a blue whale foraging dive (in yellow) superimposed on krill distribution and density data (the upper panel). The red, blue, and white indicate high-, medium-, and low- (i.e., none) density krill patches, respectively. The green circles highlight when lunges occur at the bottom of the foraging dive. The lower panel is an illustration of a blue whale as it begins to open its mouth and lunges into a dense krill patch from below. Abbreviations: m, meters; min, minutes. Illustration: Carl Buell.

factors that can significantly affect a whale's energy budget (Potvin et al. 2012).

Understanding foraging efficiency is not only crucial for understanding the ecology of baleen whales, but it also has major implications for explaining body-size evolution and the energetic limits to body size (Potvin et al. 2012). Several baleen whale species represent the largest of all living animals, and the fossil record suggests that present-day whales are much bigger than their ancestors. For these reasons, researchers have a unique opportunity to study how animals function at the upper extreme of body mass and to

investigate whether whales may be able to achieve even larger body sizes. Using an energetic approach, McNab (2009) argued that the balance between available energy resources and energy use should impose an upper limit on body size. Such a process also implies that the high abundance of resources in the marine environment compared with terrestrial ecosystems provides an explanation for the larger size of marine mammals relative to that of terrestrial mammals (McNab 2009). Furthermore, the high energetic efficiency of bulk filter feeding in baleen whales could also explain why baleen whales can be larger than toothed whales (Goldbogen et al. 2010). Remarkably, the energy and power requirements of lunge feeding are expected to increase disproportionately in the very largest body-size classes (Potvin et al. 2012), which would result in decreased diving capacity and reduced access to prey patches at depth (Goldbogen et al. 2012). As a consequence, the energetic efficiency of foraging in the largest rorquals will predictably decrease, and larger rorquals may be competitively inferior with respect to resource acquisition. Such a phenomenon would impose an energetic limit or a power limit on the evolution of larger body sizes in this clade (Potvin et al. 2012). If this is the case, it is somewhat paradoxical that the mechanism that promotes gigantism in baleen whales may also limit maximum body size and may therefore explain why no animal is larger than today's blue whale.

Conclusions

Biologging studies generate complex time-series data sets that necessitate considerable analytical efforts. The data themselves serve as powerful descriptors of behavior as a first approximation, but novel methods are required to provide an estimate for parameters that can be directly quantified (e.g., energy expenditure and prey consumption) in other biological systems. For example, by integrating kinematic data from digital tags with the morphological data of the engulfment apparatus, an estimate of the filter rate can be obtained for baleen whales (Goldbogen et al. 2007, Simon et al. 2009). In addition, techniques must be developed for accurately determining the size of a tagged whale to improve the efficacy of modeling and simulation efforts. By incorporating

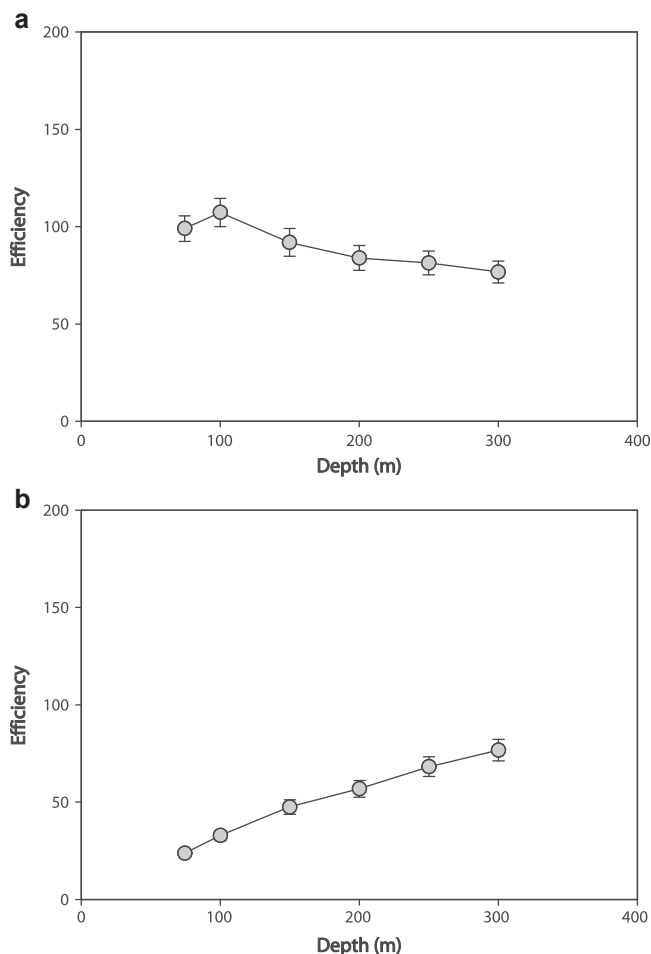


Figure 6. Estimated efficiency of blue whale foraging dives if krill density (a) remains constant with depth or (b) increases with depth. Abbreviation: m, meters.

these data into novel hydromechanical models—specifically for large rorqual whales—researchers have determined the forces required for engulfment (Potvin et al. 2009, 2010). In turn, this methodology informs the estimation of feeding-energy budgets, a fundamental concept in baleen whale foraging ecology and life history (Goldbogen et al. 2011, 2012). And when they are linked to quantitative measures of prey, ecological relationships between baleen whales and their environment become more lucid (Friedlaender et al. 2009, Hazen et al. 2009, Nowacek et al. 2011). However, these types of models and relationships must be continually modified and updated as tag technology advances to produce higher-resolution and multidimensional data sets that may uncover novel insights into behavioral processes. As our precision in measuring individual animal movements increases, it is crucial to adapt or augment existing environmental sampling tools (e.g., echosounders) to measure variables at the scales relevant to whale behavior.

The proliferation of archival tag studies has prompted a variety of advanced analytical methods, including statistical

approaches that have been proposed for data exploration, such as the *k*-means clustering of accelerometer signals in order to generate time-series ethograms (Sakamoto et al. 2009). Given their multidimensional complexity, however, the types of computational approaches that are required to sufficiently analyze tag data may transcend modern statistics, and differences may be distinguished only by the human visual system (Hurley and Oldford 2011). In fact, customized software packages are now being used to help elucidate complex behavioral patterns through the visualization of the underwater orientation and movement of tagged whales in three-dimensional spaces (e.g., TrackPlot; Ware et al. 2011, Wiley et al. 2011). Overarching all these data streams and analytics is the need to directly observe the tagged animal and its environment in order to fully investigate foraging ecology. This evolution of animal-borne video systems provides a powerful visual context of both predator and prey, as well as a confirmation of the behavioral states interpreted from a suite of archival tag sensors (Davis et al. 1999, Calambokidis et al. 2007). Furthermore, efforts must be made to merge different tag modalities (e.g., archival, satellite, telemetry) that measure parameters at different temporal and spatial scales. Ultimately, the wide range of data streams, mechanistic models, and statistical analyses must all be integrated into high-throughput visualization software so that biologists can efficiently process and analyze these data.

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