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SHORT COMMUNICATION

Feeding rates and under-ice foraging strategies of the smallest lunge filter feeder, the Antarctic minke whale (*Balaenoptera bonaerensis*)

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ABSTRACT

Body size and feeding mode are two fundamental characteristics that determine foraging performance and ecological niche. As the smallest obligate lunge filter feeders, minke whales represent an ideal system for studying the physical and energetic limits of filter feeding in endotherms. We used multi-sensor suction cup tags to quantify the feeding performance of Antarctic minke whales. Foraging dives around and beneath sea ice contained up to 24 lunges per dive, the highest feeding rates for any lunge-feeding whale. Their small size allows minke whales access to krill in sea-ice environments not easily accessible to larger baleen whales. Furthermore, their ability to filter feed provides an advantage over other smaller sympatric krill predators such as penguins and seals that feed on individual prey. The unique combination of body size, feeding mechanism and sea-ice habitat of Antarctic minke whales defines a previously undocumented energetic niche that is unique among aquatic vertebrates.

INTRODUCTION

Body size is one of the most important physiological parameters that determine the energetics of foraging in air-breathing marine vertebrates. Large body size in particular confers a variety of physiological advantages that increase foraging efficiency, including a lower cost of transport and enhanced diving capacity (Halsey et al., 2006; Williams, 1999). However, as predators increase in size they also experience decreased acceleration and maneuvering performance, both of which may limit foraging success (Domenici, 2001). Predators at the upper extreme of body mass must therefore exhibit specialized morphology to increase maneuvering performance (Miklosovic et al., 2004) or foraging strategies (i.e. cooperative foraging, corralling, tail slaps) that do not involve whole-body attacks (Domenici, 2001). Furthermore, many large-bodied predators have evolved bulk-filter feeding modes that are designed to exploit aggregations of prey items that are smaller by several orders of magnitude.

Bulk filter feeding is predictably efficient, but only when dense prey patches are exploited (Goldbogen et al., 2011). Because these high quality prey patches often occur deep in the water column, the rate of resource extraction is ultimately limited by the predator's

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diving capacity. As the largest predators, bulk-filter-feeding baleen whales (Mysticeti) should exhibit extensive dive durations when foraging. However, several rorqual whale species (Balenopteridae) exhibit severely limited dive durations because their bulk-filter-feeding mechanism is energetically costly (Goldbogen et al., 2012). This lunge-feeding mechanism involves the intermittent engulfment of large volumes of prey-laden water, a process that incurs tremendous amounts of drag and energy expenditure that is largely proportional to the size of the engulfed water mass (Goldbogen et al., 2011). The engulfment structures that determine engulfment capacity (skull, mandibles, ventral pouch) scale allometrically with body size such that larger rorqual whales have greater mass-specific engulfment capacity (Goldbogen et al., 2010). As a consequence, each lunge performed by larger rorquals incurs a greater mass-specific energetic cost that progressively limits dive capacity (Goldbogen et al., 2012).

The mechanical scaling effects imposed on the rorqual lunge-feeding mechanism predictably play a major role in influencing foraging energetics, ecological niche and life history in these gigantic filter feeders. Rorquals not only rank among the largest animals of all time, but also vary significantly in body size from 5 m long minke whales (*Balaenoptera acutorostrata*) to blue whales (*Balaenoptera musculus*) over 30 m long. Although the size-dependent trade-off between feeding performance and diving capacity is well known in larger whales, how they manifest at the smallest scale is poorly understood. Minke whales are a unique test for this hypothesis because they occupy a body size range where lunge feeding may have evolved (Pyenson and Sponberg, 2011). Therefore, understanding the feeding performance and diving behavior of minke whales can provide important insights into the ecology and evolution of bulk filter feeders. Here we present the first dive data from tag deployments on Antarctic minke whales (*Balaenoptera bonaerensis* Burmeister 1867) foraging on Antarctic krill (*Euphausia superba*) and quantify dive capacity and feeding performance of the smallest lunge-feeding whale.

RESULTS AND DISCUSSION

We recorded a total of 2831 feeding events during 649 foraging dives from tag records. The mean (±s.e.) dive depth and duration for each of two whales was 18±5 m and 1.4±0.4 min, respectively, reaching maximums of 105±1 m and 7.2±3.2 min. Both whales maintained a very high level of feeding activity and performed up to 22±2.82 lunges per dive. At a feeding rate of 102±6 lunges h^{-1}, and an engulfment volume of 1.9 m^3, each whale processed ~193±12 m^3 of prey-laden water per hour. The number of lunges per dive and dive duration generally increased with depth (Fig. 1A), although a *k*-means cluster analysis revealed three significantly different foraging dive types: short surface dives (Fig. 1C), long shallow dives (Fig. 1E) and long deep dives
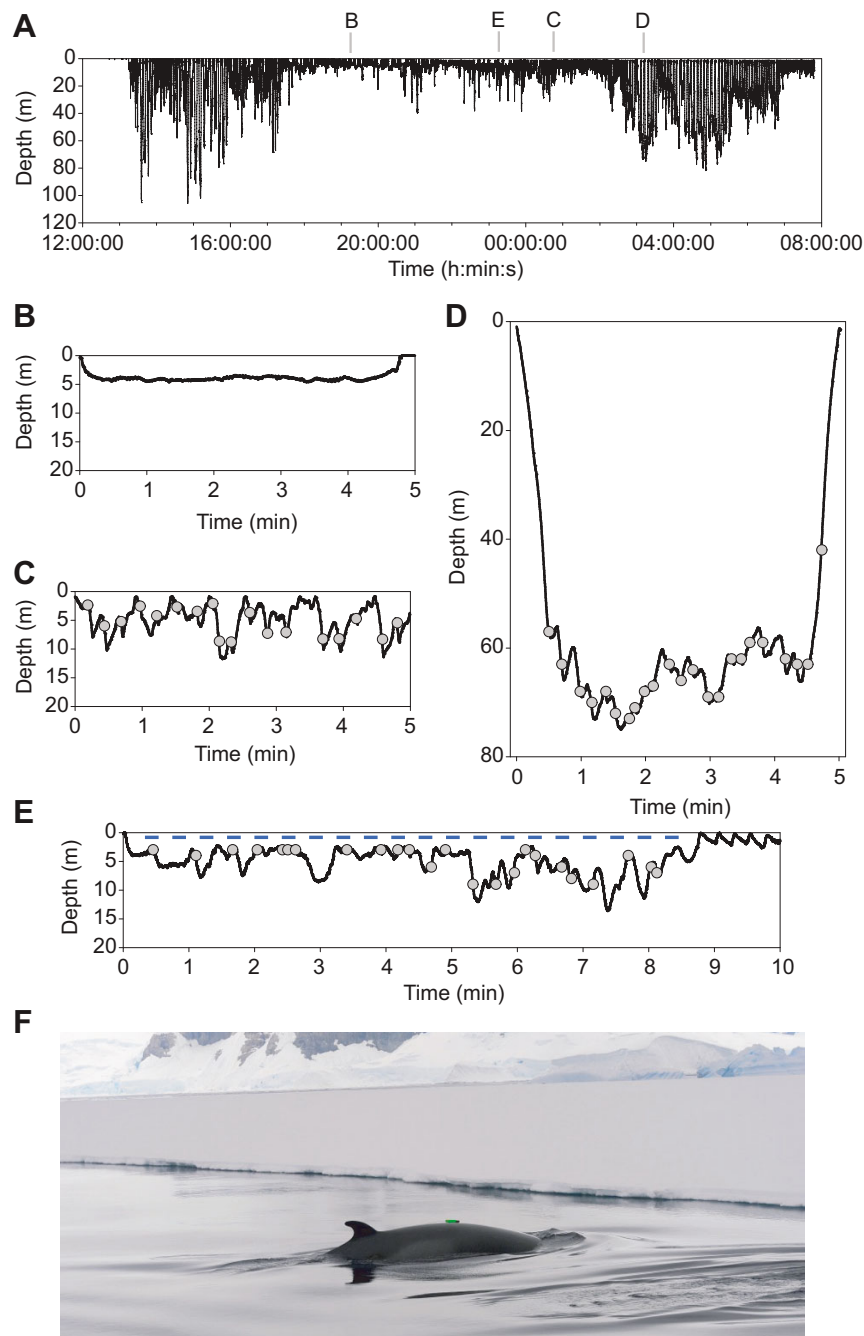
Fig. 1. Time–depth profile and feeding performance for an Antarctic minke whale. (A) The entire time depth profile of over 18 h. (B) An example of a shallow, non-feeding dive. (C) A series of short and shallow feeding dives (grey circles indicate feeding lunges). (D) An example of a long, deep feeding dive. (E) A long, shallow feeding dive presumably under sea ice. The dashed blue line indicates the typical depth of sea ice in the region and reveals that in this single dive the whale lunges several times in direct proximity to the underside of the sea ice. (F) A tagged Antarctic minke whale approaching and diving under sea ice (bottom).

(Fig. 1D). Across both whales, shallow dives accounted for 73% of all dives, but only 34% of the lunges occurred in these short dives. Shallow and longer dives accounted for most of the feeding effort, 40% of all lunges (Table 1).

The foraging behavior of Antarctic minke whales is characterized by extremely high feeding rates and relatively shallow dives (<100 m) compared with other, larger baleen whales. Our analyses suggest that high lunge frequency, defined by the number of lunges performed per dive, occurs when minke whales target krill under sea ice. This notion was confirmed by our direct observations of whales diving underneath sea ice that link temporally with periods in the tag data that show the occurrence of such dives. These observations highlight the importance of sea ice in structuring the foraging behavior of minke whales because a significant proportion of their diving costs includes extended excursions under sea ice (Fig. 1E).

Although this feeding mode has never been described before, this behavior represents a high proportion of foraging effort.

Our results indicate that minke whales take advantage of the sea ice habitat unlike all other baleen whales because their small size provides the increased maneuverability required to navigate in and around ice in search of krill. In addition, the ability to bulk filter feed, compared with other krill predators that are single-item (e.g. penguins) (Watanabe and Takahashi, 2013) or suction/small-batch filter feeders (e.g. leopard and crabeater seals) (Hocking et al., 2013), provides enhanced foraging capacity during extended dives under sea ice. This foraging strategy contrasts with that of larger rorqual whales in the Southern Ocean that are limited to the relatively ice-free continental shelf (humpback and fin whales) or offshore (humpback, fin and blue whales) waters (Friedlaender et al., 2011; Friedlaender et al., 2009; Johnston et al., 2012).

Table 1. Dive parameters and feeding rates for three distinct Antarctic minke whale foraging strategies including open-water (short, shallow and long, deep) and under-sea-ice approaches

Dive type	Time (min)	Depth (m)	Lunges	% of total dives	% of total lunges	P Dive depth versus lunges	Dive time versus lunges
Whale 1							
Short, shallow	0.9±0.6	13.1±7.7	2.4±1.6	76.7	77.3	<0.0001	0.03
Under ice	3.4±0.7	21.2±9.1	8.3±5.3	20.0	11.6	0.35	<0.0001
Long, deep	5.6±1.8	54.3±18.2	13.0±4.4	3.3	11.1	0.77	<0.0001
Whale 2							
Short, shallow	0.7±0.46	7.0±6.9	1.9±1.2	5.4	23.2	0.0004	<0.0001
Under ice	2.9±0.6	39.0±14.8	8.2±3.1	79.1	41.6	0.001	0.005
Long, deep	4.2±0.37	59.5±20.5	15.4±2.6	15.5	35.2	0.39	0.77

Values are means ± s.d. for dive metrics, and *P*-values are given for relationships between dive depth versus lunges and dive time versus lunges.

As the smallest rorqual, minke whale feeding performance is limited by its relatively small feeding apparatus (Nakamura et al., 2012), yielding an engulfment capacity that is no more than 70% of body mass. In contrast to large rorquals, which typically execute a small number of extremely large gulps (100–150% of body mass) of water during long dives (Goldbogen et al., 2012), minke whales perform a high number of very small gulps. Minke whales can make over 20 lunges per dive, substantially more than any other rorqual whale (Fig. 2). Hydro-mechanical models of engulfment suggest that minke whales are able to execute such a high number of lunges per dive because the energetic cost of each lunge is very low, with power requirements that are comparable to steady swimming (Potvin et al., 2012). Low feeding costs should help minke whales maximize dive duration, a key advantage when exploiting krill beneath sea ice. Although most minke whale dives were relatively short and shallow (Fig. 1C, Table 1), we observed maximum dive durations of 9.4 min, commensurate with the breath-hold durations observed in some of the largest rorquals during foraging dives (Goldbogen et al., 2012).

The extended dive capacity, high lunge feeding rates and relatively small body size of minke whales facilitate below-ice krill foraging, supporting an energetic niche not explicitly observed in any other sympatric krill predator, including other whales, seals, penguins and seabirds (Friedlaender et al., 2011; Friedlaender et al.,

2009). Moreover, the morphological adaptations for lunge feeding at a size exhibited by minke whales enable the exploitation of krill resources that are largely unavailable to other baleen whales (e.g. humpback whales) (Friedlaender et al., 2006; Friedlaender et al., 2009; Friedlaender et al., 2011). Despite being limited to relatively small gulps of prey-laden water, minke whales can feed at high rates at a relatively low energetic cost. This feeding strategy should confer high energetic efficiency for dense, patchily distributed prey, but in a more adaptable way compared with larger rorquals that are committed to larger gulps that take longer to filter and process (Goldbogen et al., 2012). Although our data help clarify the relationship between body size and foraging performance in bulk filter feeders, future studies should focus on adaptable foraging strategies in response to different conditions (prey types and densities) in order to better understand the link between feeding biomechanics and dynamic ecological niches.

Minke whales are found in all major oceans in relatively high abundances, yet little empirical data on their behavior exist for any region. Despite being the most numerous cetacean in the Southern Ocean and the subject of a contentious lethal sampling program, no efforts were made to directly study the underwater behavior of these important predators (Gales et al., 2005). Because of the logistical constraints of working in and around sea ice in a remote environment, the difficulty of approaching whales closely enough for tagging, and the only recent advancement of multi-sensor tag technology, data on Antarctic minke whale behavior remained elusive. While we report on a limited sample size, we believe the long duration of the deployments and the amount of foraging behavior measured combined with the novelty of data for the species is sufficient to make the inferences we have reported.

MATERIALS AND METHODS

Non-invasive multi-sensor, archival recording tags (Acousonde, acousonde.com) were attached to minke whales in Wilhelmina Bay, Antarctic Peninsula, using a 6 m carbon fiber pole from a 6.3 m inflatable boat. The tags record pressure, temperature, acceleration and magnetic field along three orthogonal axes at 10 Hz, are positively buoyant and contain a VHF transmitter for tracking and tag recovery. We deployed tags on two minke whales in February 2013 for 18 and 8 h, respectively. Each tagged whale was part of a large group of six to 40 whales feeding in and around large floes of pack ice and adjacent to and under fast ice in the bay. We followed tagged whales during daylight hours and recorded whale locations at the surface using a GPS and laser range finders. We also recorded the sea-ice environment around the tagged whale (% of ice cover), and specifically if the whale dove under or emerged from underneath sea ice to temporally link these with dive data from tags (Fig. 1).

Using previously published methods, we determined the depth and timing of feeding lunges from acceleration, depth rate and fluking dynamics.
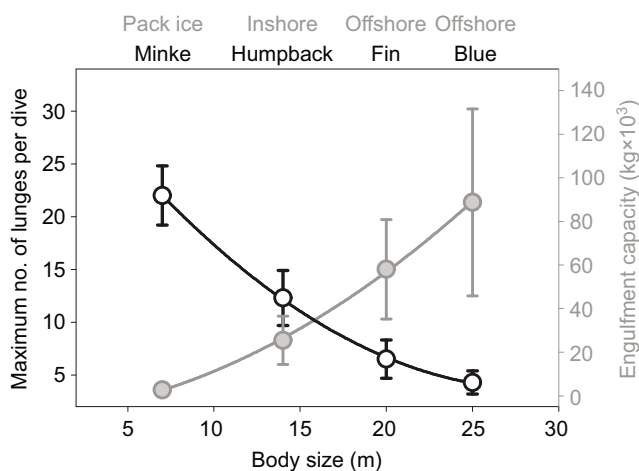

Fig. 2. Engulfment capacity and maximum number of lunges per dive with respect to body size in four krill-feeding baleen whale species. Antarctic minke whales lunge more frequently and filter less water than any other rorqual whale, a trend that generally reflects ecological niche (inshore to offshore distribution). Data for blue, fin and humpback whales are from Goldbogen et al. (Goldbogen et al., 2012).

Specifically, we determined the presence of a lunge by visually inspecting the norm of the jerk signal (Simon et al., 2012), which represents the rate of acceleration experienced by the whale-borne tag across all three-orthogonal axes of the accelerometer. Lunges were clearly distinguished from active bouts of fluking during non-feeding swimming by a jerk threshold greater than 20 m s^{-3}. Lunges also typically involved rapid changes in depth rate and a bout of fluking that were distinct from surfacing events.

For each dive we calculated the number of lunges, total dive time, mean lunge depth and maximum dive depth. Using morphometric information of the engulfment apparatus (Goldbogen et al., 2010; Potvin et al., 2010), we estimated the maximum engulfment capacity for an average-sized adult minke whale and estimated the cumulative amount of water and prey processed over time (Goldbogen et al., 2012; Goldbogen et al., 2013). We performed k-means cluster analysis to define three classes of dives based on dive time, dive depth and number of lunges. Means of all predictor variables were compared using t-tests for significant differences. We then performed linear regressions of lunge counts per dive against dive time and then against dive depth for each cluster to determine significant relationships.

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Author contributions
A.S.F., D.P.N., A.J.R., D.W.J., and N.G. conceived of, designed, and conducted the experimental research. A.S.F., and J.A.G. performed analyses and interpretation of the findings being published. All authors contributed to the drafting and revising of the article.

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