

# Extreme diel variation in the feeding behavior of humpback whales along the western Antarctic Peninsula during autumn

A. S. Friedlaender<sup>1,\*</sup>, R. B. Tyson<sup>1</sup>, A. K. Stimpert<sup>2</sup>, A. J. Read<sup>1</sup>,  
D. P. Nowacek<sup>1,3</sup>

<sup>1</sup>Division of Marine Science and Conservation, Duke University Marine Laboratory, 135 Duke Marine Lab Road, Beaufort, North Carolina 28516, USA

<sup>2</sup>Naval Postgraduate School, Department of Oceanography, 833 Dyer Road, Monterey, California 93943, USA

<sup>3</sup>Department of Electrical and Computer Engineering, Pratt School of Engineering, Duke University, Durham, North Carolina 27708, USA

**ABSTRACT:** Most humpback whale *Megaptera novaeangliae* populations partition their time between prey-rich feeding and prey-deficient breeding/calving regions. How these whales feed and optimize the consumption of prey resources prior to long-distance migrations and fasting is largely unknown. We deployed multi-sensor tags on humpback whales around the western Antarctic Peninsula to describe their daily activity patterns late in the feeding season to test the hypothesis that feeding behavior varies over the diel cycle so as to maximize energy intake and limit energy expenditure. Dives were assigned to a behavioral state (feeding, resting, traveling, exploring) to determine hourly rates and to build an ethogram of activity patterns. Our results show a distinct diel pattern of whales feeding exclusively at night. Feeding depth was deeper around sunrise/sunset and shallower (~50 m) at night, consistent with diel vertical prey movement. Shallow feeding dives typically contained a single feeding lunge, a strategy known to increase feeding efficiency and maximize intake rates by maintaining proximity to the surface and reducing the energetic costs of deep diving. The lack of feeding during daytime may indicate prey being too deep for efficient foraging. Our results add information where currently there is a paucity of data describing how baleen whales optimize feeding behavior, specifically in relation to prey distribution and movement, to fuel their extraordinary energetic requirements necessary for growth, migration, and reproduction. Understanding behavioral patterns and predator/prey dynamics in rapidly changing marine environments, like the Antarctic Peninsula, is critical for understanding how these changes will affect ecosystem structure and function.

**KEY WORDS:** Humpback whale · Foraging ecology · Tagging · Antarctica

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## INTRODUCTION

Migratory animals conduct seasonal, and often synchronized, movements between spatio-temporally discrete and ephemeral ecological regions (Greenberg & Marra 2005). Typically, such animals spend a portion of their annual cycle in a resource-rich region to replenish and build up energy reserves

in anticipation of migration to a distant and often resource-deficient region (Dingle 1996). Baleen whales use the energy gained on feeding grounds to help support energetically costly behaviors such as reproduction and the growth of dependent calves. Time and behavior on feeding grounds must be optimized so animals can acquire energy for the entire year, and whales may maximize their daily energetic in-

\*Email: asf7@duke.edu

puts by feeding on high densities of prey, feeding often, and/or expending as little energy as possible to find and consume prey.

Like other mysticetes, humpback whales *Megaptera novaeangliae* have evolved unique morphological adaptations to feed on small, patchy prey. All balaenopterid whales (e.g. blue, fin, humpback, and minke) engulf large volumes of prey-rich water in a flexible and extendible buccal cavity and sift out prey through comb-like baleen. Their lunging feeding behavior is energetically costly because it involves a series of high-energy locomotor maneuvers to accomplish (Acevedo-Gutiérrez et al. 2002, Potvin et al. 2009, Goldbogen et al. 2012). The energetic cost of this feeding strategy is worthwhile, however, because balaenopterid whales can engulf a volume of prey-laden water that may equal up to two-thirds of their body mass in one lunge (Pivorunas 1979, Brodie 1993). Over time, this strategy has allowed baleen whales to evolve into the largest predators on the planet (Williams 2006, Goldbogen et al. 2011). The relatively recent development of multi-sensor recording tags that sample animal movements at high frequencies has allowed researchers the opportunity to better understand the kinematics and energetic costs associated with this unique feeding strategy and test ecological hypotheses relating to predator–prey interactions (e.g. Goldbogen et al. 2008, 2011, Friedlaender et al. 2009, Hazen et al. 2009).

Humpback whales use nearshore waters off the western side of the Antarctic Peninsula as one of several feeding areas around the continent. This region supports a large population of Antarctic krill *Euphausia superba* that forms the primary prey for a large guild of predators, including whales, penguins, and seals. During summer, krill are generally distributed broadly across the continental shelf, occurring in discrete patches (<1 km in length) in the upper reaches (<100 m) of the water column (Nicol 2006). In autumn, adult krill move into bays and fjords, where they coalesce into large, dense aggregations (Nowacek et al. 2011) prior to the formation of winter sea ice. Sea ice algal communities act as a food resource for juvenile krill (Nicol 2006), and importantly for adult krill, ice cover provides them with protection from air-breathing predators, including baleen whales. The distribution of humpback whales in Antarctic waters is tightly coupled to that of krill throughout the feeding season (Friedlaender et al. 2006), and high densities of whales have been found associated with large aggregations of krill late in the Antarctic feeding season (Nowacek et al. 2011, Johnston et al. 2012).

To date, however, little is known specifically about diel variation in the behavior of humpback whales during their feeding season. Humpbacks are a major predator of krill and the most abundant mysticete whale in the nearshore waters of the Antarctic Peninsula (e.g. Johnston et al. 2012), so information on their feeding behavior may provide insights into the coupling of predators and prey in this region and, specifically, help us to understand how these whales optimize consumption of prey resources prior to long-distance migrations.

The development of multi-sensor data logging tags and associated analytical tools has revolutionized our ability to infer feeding behavior of whales using both kinematic and acoustic information (e.g. Goldbogen et al. 2008, Ware et al. 2011, Simon et al. 2012). We deployed multi-sensor tags on humpback whales on the western side of the Antarctic Peninsula to describe their daily activity patterns late in the feeding season. Specifically, we tested the hypothesis that humpback whales vary their feeding behavior over the diel cycle to maximize energy intake and limit energy expenditure in anticipation of long-distance migrations.

## MATERIALS AND METHODS

### Whale tagging

In May 2009 and 2010, we deployed multi-sensor suction-cup tags (digital acoustic recording tags, DTAGs; Johnson & Tyack 2003) on humpback whales in Wilhelmina Bay, on the western Antarctic Peninsula, to measure their underwater movements and behaviors. These small (10 × 20 cm), lightweight (<200 g), pressure-tolerant tags have been used with increasing frequency in studies of cetacean behavior and ecology over the past decade (e.g. Johnson et al. 2009). Each tag contains temperature and pressure sensors as well as 3-axis accelerometers and magnetometers, can record sounds at sampling rates up to 192 kHz, and is powered by a rechargeable lithium-ion battery. All non-audio sensors are sampled at 50 Hz, and data are stored on the tag using standard flash memory. The tag is equipped with a VHF beacon that transmits whenever the tag/whale is at the surface, allowing us to track the whale's location. The tag also contains a release mechanism that can be programmed to relieve suction to the silicon cups at a predetermined time or after a specified deployment period. The tag contains syntactic floatation; after the tag

releases from the whale, it floats and is retrieved, and the data are offloaded to a laptop computer via an infrared USB download mechanism.

We deployed tags with a programmed release time of 24 h on whales during daylight hours. We used a 6 m Zodiac Mark V inflatable boat powered with a Yamaha 40 hp 4-stroke engine to approach animals. In all cases, we approached whales either at idle speed or using paddles after the engine had been turned off. Approaches were typically made from a perpendicular angle or from behind the whale at a 45° angle so as not to position the boat over the whale's flukes. We deployed tags using a 6 m carbon-fiber pole with a customized housing that held the tag. Tags were placed on the dorsal surface of the whale or high on the flank, forward of the dorsal fin. The reactions of whales to tagging events ranged from none to moderate, with the most typical response being an accelerated dive upon deployment that we considered to be minor. All of the whales in this study were either resting or traveling when they were tagged, and as in other regions, the whales appeared to return to their pre-tagging behavior within 1 to 2 dives (less than 20 min) (Nowacek et al. 2004, Hazen et al. 2009). This was confirmed from focal individual follows of tagged whales. In the present study, we use data collected only from whales more than 2 yr old. Matthews (1937) indicated that Antarctic humpback whales become independent in their second year (for both males and females). Any pair of whales in which one whale was substantially larger would likely be a mother with a 1 yr old calf. In this study, we did not use tag data from any whales deemed to have been dependent calves. As humpback whales are weaned towards the end of their first year, we considered any whale other than a dependent calf to be at least 2 yr old.

Once a tag was deployed, the boat remained close to the whale, taking care to remain far enough away so as not to influence its behavior (>100 m). For the remaining daylight hours after tagging, we conducted a focal individual follow with continuous sampling of behavioral states (Altmann 1974). On each surfacing, we collected information on the time, location (from a hand-held GPS), behavioral state of the whale, and group size. Behavioral states included resting, traveling, socializing, and feeding. At least once during each surfacing interval, we used Leica Vector IV laser range finders to estimate the position of the tagged whale in relation to the boat by measuring both range and bearing to the whale at the surface. We used this information to triangulate the position of the whale. After dark, tagged whales

were tracked using VHF antennas and receivers from a large research vessel (ARSV 'Laurence M Gould' in 2009 and RVIB 'Nathaniel B Palmer' in 2010) until the following morning, when the small boat was redeployed to continue focal follows, or until the tag fell off the whale.

### Data analysis

We first processed data from the tags in Matlab™ using tools developed to calibrate tag sensors. We then imported sensor data into Trackplot, a customized visualization software package developed for projecting and analyzing tag-derived data (Ware et al. 2006). Trackplot uses time, depth, pitch, roll, and heading data to generate a continuous graphical ribbon indicating the position and orientation of the whale in 3 dimensions (Ware et al. 2006). We defined a dive as any time the tag was submerged below a depth of 3 m. Using accelerometer data and flow noise from the acoustic record, we identified individual lunges or feeding events based on changes in the accelerometer signal in correlation with flow noise from the tag's acoustic record, similar to Goldbogen et al. (2008), Ware et al. (2011), and Tyson et al. (2012). We excluded possible lunges shallower than 3 m due to interference from surface interactions (i.e. abrupt changes in flow noise when the whale surfaced). Thus, we built a database in which every dive was coded as feeding or non-feeding, based on the presence or absence of feeding events, and recorded the number, depth, time, and location of each feeding event. All dive records and presumed lunges were assessed by 2 of the authors (A. S. Friedländer and R. B. Tyson), who helped develop the lunge-detecting algorithm, for accuracy. If there was disagreement, the presumed lunge in question was removed from our analyses, similar to Ware et al. (2011).

The DTAG does not provide an estimate of its location, so we relied on positional fixes from laser range finders as described above (see Ware et al. 2011 for details on the method). We used positional fixes to anchor the track of the whale in Trackplot to known locations and estimated movement of the whale between these fixes assuming a constant speed of travel ( $1 \text{ m s}^{-1}$ ). Once all of the positional fixes were linked to surfacing events, we could estimate an approximate position of individual lunges from the dive record, along with their time and depth.

To build an ethogram of behaviors for the tagged whales, we developed behavioral classifications based on maximum dive depth, duration, and the

presence or absence of feeding lunges. Dive profiles generated by time–depth recording tags have long been used to characterize marine mammal diving behavior and dive types (Kooyman 1968, Lesage et al. 1999). More recently, additional sensors added to these tags have provided novel information about the behavior of animals during dives, and these data have further refined our ability to categorize marine mammal behavior during dives (Davis et al. 2003). We defined the following behavioral states: resting, traveling, exploring, and feeding. Resting dives were <10 m in depth with no feeding lunges. Traveling dives occurred between 10 and 50 m in depth without feeding events; traveling is not expected to occur above 10 m, as this would increase traveling costs because of wave drag (Lighthill 1971, 1978). Exploratory dives occurred >50 m deep but without feeding events. Finally, we defined feeding as any dive with one or more lunges. To test whether our classification scheme was representative of the behavior of the whales, we performed a *k*-means clustering test using 3 clusters and normal mixtures, with dive time, maximum depth, and duration as parameters for non-feeding dives. The results of this exploratory analysis indicate that our classification scheme represents significantly different types of dives that are naturally partitioned, which matched our *a priori* classifications (Table 1).

We used this information to describe the frequency and timing of these behavioral states over the course of a 24 h period for all whales tagged in the study. To determine if there were diel patterns in whale behavior, we determined the number of each dive type by hour for each whale. These were pooled together and divided by the number of whales tagged in that hour to generate a normalized hourly rate of dives in each behavioral state. We then coded these as being during either day or night, based on local sunrise/sunset times, and compared the overall dive rate for each behavioral state for day versus night using pooled *t*-tests. Resting behavior can occur at the surface (<3 m depth) and may not be represented in the dive record based on how we classified dives, so we augmented the tag records to find times when then

Table 1. *Megaptera novaeangliae*. Differences in dive metrics for non-feeding dives. *A priori* behavioral states were based on dive depth: resting (<10 m), traveling (10 to 50 m), and exploring (>50 m). Values in parentheses are SD. *k*-means clustering was performed to corroborate these classifications. Each dive type was significantly different from one another at the  $p < 0.05$  level between dive duration and depth between behavioral states within a *priori* and *k*-means clustering methods

Dive type	N	<i>A priori</i> classification		<i>k</i> -means clustering	
		Dive duration (min)	Dive depth (m)	Dive duration (min)	Dive depth (m)
Resting	936	0.54 (0.03)	5.4 (0.4)	0.6	7.4
Traveling	663	2.48 (0.04)	21.1 (0.6)	3.2	29.5
Exploring	171	4.84 (0.09)	85.1 (1.1)	6.1	88.8

Table 2. *Megaptera novaeangliae*. Digital acoustic recording tags (DTAG) deployment records from Wilhelmina Bay for 2009 to 2010. Tag durations and feeding dive metrics are shown for each whale, including number of foraging dives, number of lunges, lunges per dive, and lunge rate per hour

Year	Whale ID	Tag duration (h)	No. of foraging dives	No. of lunges	Mean no. of lunges dive <sup>-1</sup>	SD	Lunge rate h <sup>-1</sup>
2009	122b	18.4	433	635	1.47	1.13	34.4
2009	127a	24.6	90	382	4.29	2.85	15.5
2009	148a	25.2	248	603	2.43	2.08	23.9
2009	152a	22.3	518	882	1.70	1.68	39.6
2010	132a	23.1	97	317	3.27	2.60	13.7
2010	133a	22.2	103	393	3.82	1.92	17.7
2010	139a	20.6	296	851	2.88	1.93	41.2
2010	151a	24.6	160	573	3.58	2.03	23.3
2010	144a	21.1	307	943	3.07	1.76	44.6

tagged whales remained at the surface uninterrupted for >10 min. We considered this to be logging or resting behavior.

## RESULTS

We tagged 9 humpback whales in Wilhelmina Bay in 2009 ( $n = 4$ ) and 2010 ( $n = 5$ ), yielding a total of 202 h, 14 min, 24 s of tag data (Table 2). The tags were deployed between 18:45 and 25:38 h. The whales were tagged between 08:42 and 14:28 h local time, GMT – 5 h.

Based on the presence of 1 or more lunges, we identified 2252 feeding dives from all tagged whales, averaging 250.2 (SD = 153.8) per whale. The number of feeding events (lunges) ranged between 317 and 943 per whale, averaging 619.9 (SD = 231.6) per whale. The average rate of lunges per hour was 28.2 (SD = 11.8). Whales in 2009 averaged 625.5 (SD = 204.68) lunges per whale, compared to 615.0 (SD = 275.00) for whales in 2010. These numbers were not

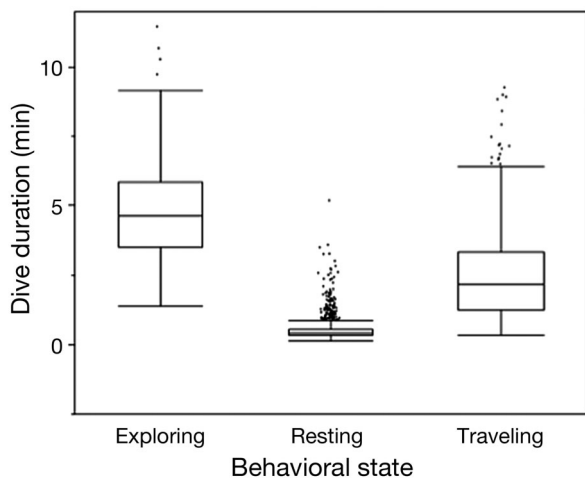


Fig. 1. *Megaptera novaeangliae*. Median values (horizontal line), 25 and 75% quartiles (box) and SE (whiskers) in dive duration across non-feeding behavioral states. Outlier points are staggered to show their frequency

significantly different (Welch's  $t$ -test,  $p = 0.95$ ). In 2009, whales averaged 28.4 (SD = 10.75) lunges  $h^{-1}$ , while whales in 2010 averaged 28.1 (SD = 14.00). Feeding lunge rates did not differ between years (Welch's  $t$ -test,  $p = 0.98$ ).

A total of 1770 non-feeding dives were recorded and categorized as exploring ( $n = 171$ ), resting ( $n = 936$ ), and traveling ( $n = 663$ ). Exploratory dives averaged 4.8 min in duration (SD = 1.76) and had a mean maximum dive depth of 79.5 m (SD = 30.36). Resting dives averaged 0.60 min in duration (SD = 0.49) and

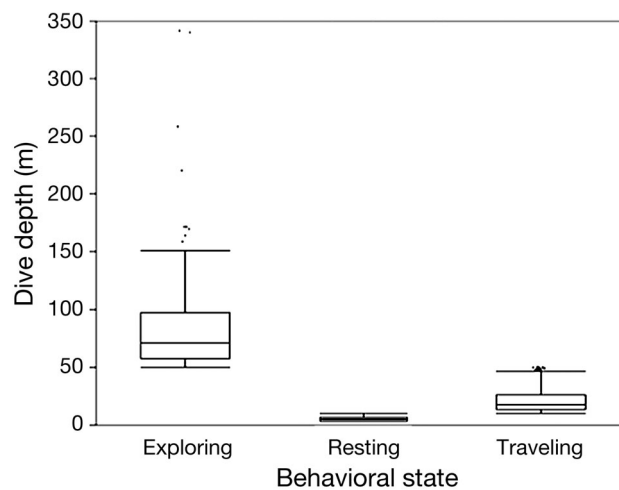


Fig. 2. *Megaptera novaeangliae*. Median values (horizontal line), 25 and 75% quartiles (box) and SE (whiskers) in dive depth across non-feeding behavioral states. Outlier points are staggered to show their frequency

5.2 m in depth (SD = 1.89). Traveling dives averaged 2.6 min in duration (SD = 1.60) and 21.6 m in depth (SD = 10.51). The 3 clusters determined from the  $k$ -means clustering described in 'Materials and methods' had average dive durations of 6.1, 0.6, and 3.2 min and average depths of 88.8, 7.4, and 29.5 m, respectively. These 3 classes of dives were all significantly different from each other and corroborate our *a priori* classification categories (Figs. 1 & 2).

Travel and resting dives occurred throughout the day and night (Fig. 3). Exploratory dives also occurred throughout the day and night but were largely absent between 16:00 and 21:00 h. There were no significant differences in the dive rates for any non-feeding behavioral state between day and night. Exploratory dives averaged 0.93 (0.18 SE) dive  $h^{-1}$  during daytime and 0.62 (0.11 SE) dive  $h^{-1}$  during nighttime and were not significantly different ( $p < 0.15$ ). Resting dive rates were not significantly different ( $p < 0.3$ ) between day and night, averaging 3.3 (1.2 SE) and 4.7 (0.5 SE) dives  $h^{-1}$ , respectively. Similarly, traveling dive rates were not significantly different ( $p < 0.77$ ) between day and night, averaging 2.7 (0.6 SE) and 2.5 (0.3 SE) dives  $h^{-1}$ , respectively.

Exploring and feeding behavior included several dives that were deeper than any previously reported for humpback whales (276 m, Hamilton et al. 1997). Sixteen feeding dives and 2 exploratory dives were  $>350$  m, with the deepest, a feeding dive, reaching 388 m.

Feeding dives showed a distinct diel pattern. Significantly more feeding dives occurred during nighttime than during daylight hours ( $p < 0.0008$ ): 8.24

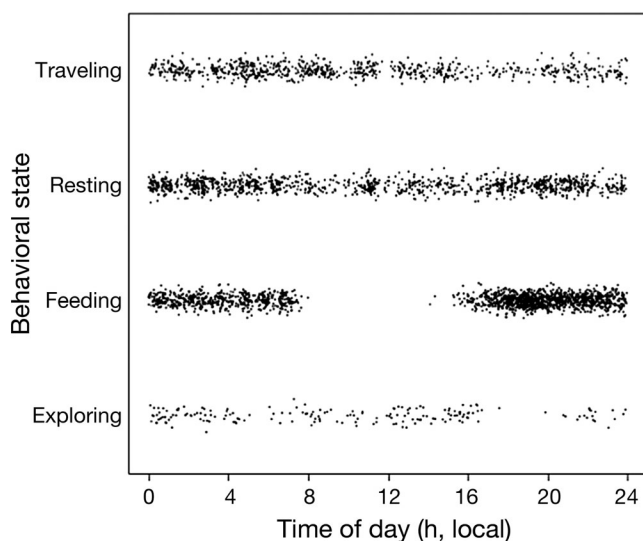


Fig. 3. *Megaptera novaeangliae*. Frequency and temporal distribution of all dives categorized by behavioral state for all tagged whales ( $n = 9$ ) from 2009 to 2010 in local time (GMT - 5 h). Individual dives are staggered along the vertical axis for each behavioral state to show the density of points

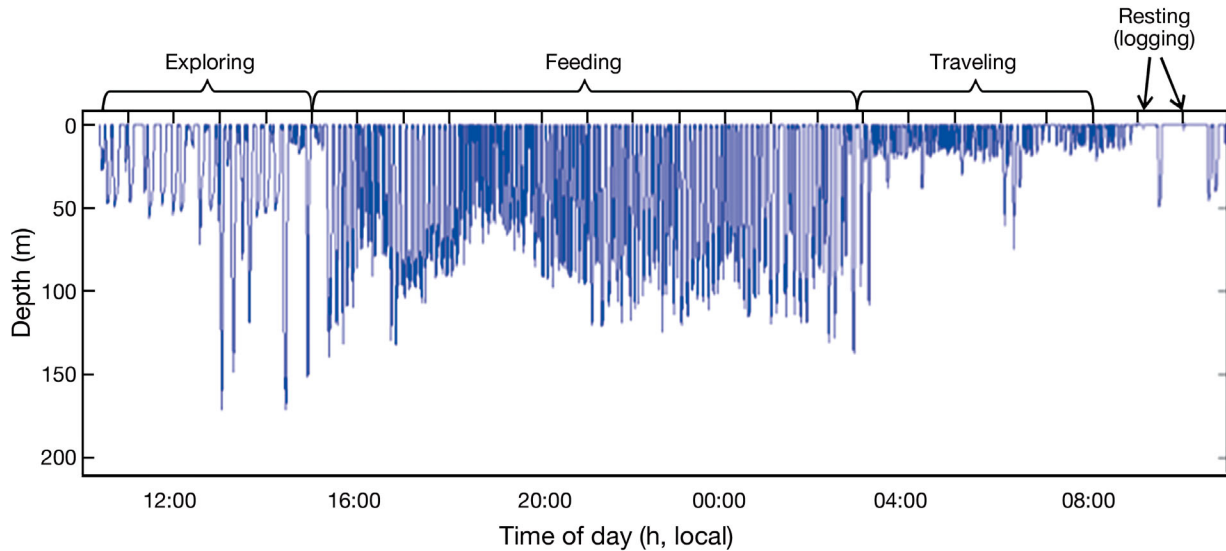


Fig. 4. *Megaptera novaeangliae*. Representative dive profile for a humpback whale tagged in Wilhelmina Bay (Mn151a, 13 to 14 May 2010). Behavioral states are marked, including an extended feeding bout during afternoon and night, traveling in the early morning, extended surface (resting or logging) periods during daylight hours, and exploratory dives in early afternoon prior to feeding

(1.0 SE) and 0.25 (1.7 SE) dives  $h^{-1}$ , respectively (Fig. 4 shows a representative dive record). No feeding dives occurred between 08:00 and 14:00 h. When considering all whales, the frequency of feeding dives overall increased from 14:00 to 19:00 h and then decreased until 06:00 h, nearly ceasing by 07:00 h (Fig. 5). The depth of feeding events also shows a distinct diel pattern (Fig. 6), with the first feeding dives in late afternoon occurring relatively deep in the water column, several greater than 300 m. One whale made 2 feeding dives in the 14:00 h period. All other whales began feeding during the 15:00 h period (sunset). The first feeding dives occurred in the 14:00 h period and were both made by the same whale. Feeding was first observed in more than one animal during the 15:00 h period

(after sunset), and we consider this to be the typical initiation of feeding for animals in the study area at this time of year. The average depth of feeding lunges from 15:00 to 17:00 h was 146 m (SE = 40.8), before decreasing to 49 m (SE = 2.75) from 18:00 to 04:00 h and then increasing to 93 m (SE = 10.2) by 07:00 h. The average depth of feeding dives over a 24 h period was 55 m, with 25 and 75% quartiles of 15 and 80 m, respectively. We also found a distinct pattern in the number of lunges per dive; more than half (55%) of the feeding dives contained a single lunge, and the frequency of feeding dives decreased as the number of lunges per dive increased. A similar percentage (57.7%) of feeding dives occurred in the upper 50 m of the water column, and the percentage of feeding dives decreased with increasing depth.

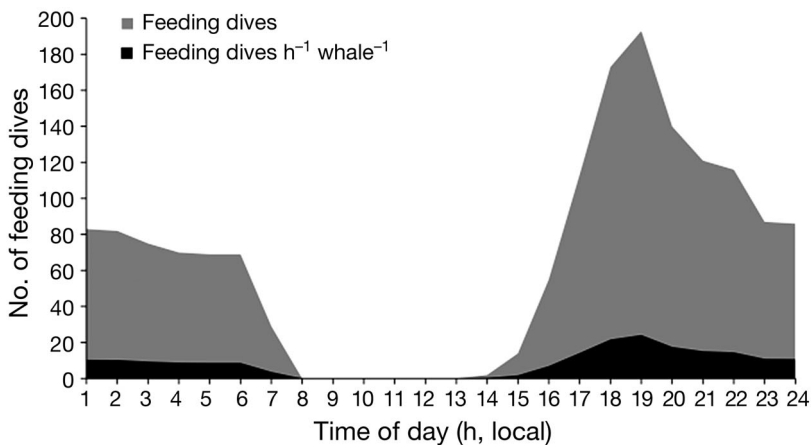


Fig. 5. *Megaptera novaeangliae*. Frequency (grey) and rate (black) of feeding dives per hour standardized by the number of whales tagged during each hour

With respect to extended surface intervals that would not be evident from our classification of dives from tag data, we found 35 instances where whales were continuously at the surface (shallower than 3 m) for >10 min between dives. These resting or logging periods were significantly more common during day than night hours ( $p < 0.0001$ ). Most (30/35) of these events occurred between 05:00 and 15:00 h and were generally associated with traveling or resting behavior (23/35). Of the 5 instances when long-duration surfacing occurred at night, 4 occurred during foraging bouts (Fig. 7).

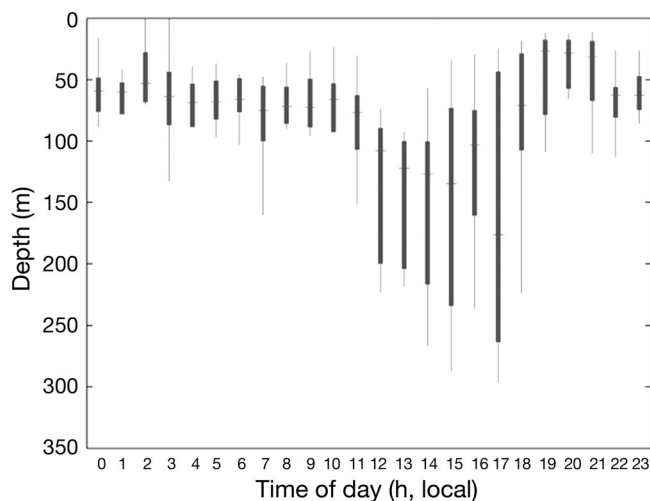


Fig. 6. *Megaptera novaeangliae*. Hourly median values (horizontal line), 25 and 75% quartiles (box) and SE (whiskers) in humpback whale depth of feeding dives in Wilhelmina Bay

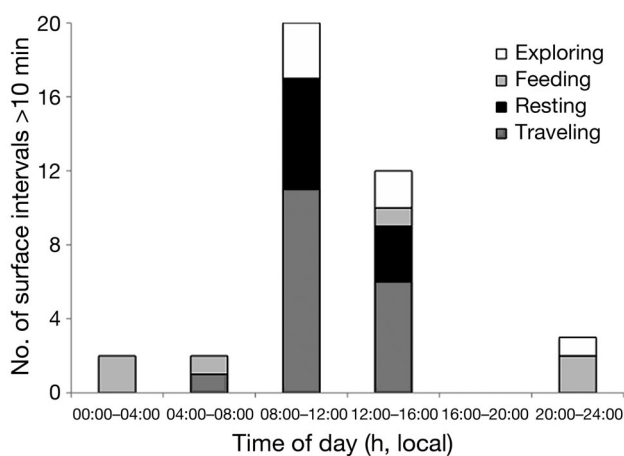


Fig. 7. *Megaptera novaeangliae*. Timing and behavioral state associated with extended (>10 min) surface intervals. Behavioral state was determined as that in which the whale was found on the dive prior to logging

## DISCUSSION

Our results provide detailed information on the underwater behavior and daily activity patterns of humpback whales in Antarctic waters to support our hypothesis that whales feed in a diel manner. All of the tagged whales in our study exhibited similar diel feeding behavior late in the feeding season, presumably just prior to migration to low-latitude, prey-deficient breeding/calving grounds. We believe that the observed feeding pattern is linked to the behavior of their prey, Antarctic krill, and maximizes energy intake versus expenditure. By limiting the amount of time and energy spent diving when prey are deeper

and instead feeding at relatively shallow depths, the whales may be maximizing their feeding rates and potentially their feeding efficiency.

All of the whales in our study began feeding near dusk, continued feeding until the following morning, and ceased feeding soon after sunrise. During daylight hours, the whales typically rested at the surface, often logging for over 2 h at a time. During these resting periods, the whales may have been processing ingested food from the previous night. In early afternoon, before sunset, the whales often made a series of deep exploratory dives interspersed with deep feeding dives. These deep exploratory dives may provide the whales with information on the distribution and structure of prey vertically beneath them. The whales then began relatively uninterrupted foraging until the following morning, before ceasing and returning to resting and traveling. Although we found no significant changes in the rates of non-feeding dives from day to night, there is a period of time prior to when the whales begin feeding in late afternoon when exploratory dive frequency increases, and after the whales begin feeding after sunset, very few exploratory dives occur. This suggests that search effort to locate prey patches before feeding is profitable, and once the whales begin feeding, they do so in a high quality patch that they are able to forage on consistently.

Previous work on humpback whales on a North Atlantic feeding ground in mid-summer has shown that whales feed throughout the day and night, altering their foraging strategies in response to changes in the behavior and distribution of prey (Friedlaender et al. 2009, Hazen et al. 2009). Our results show changes in feeding depths from afternoon into night and vice versa that are consistent with diel vertical movement of prey in the water column (Zhou & Dorland 2004). Nowacek et al. (2011) describe the unique oceanographic properties and prey availability in this study region during autumn. A massive krill swarm (>2 million t) occurred in Wilhelmina Bay and in some places reached a vertical thickness of 200 m, typically in deep water (>400 m). The central mass of the krill layer migrated vertically at night into the upper 50 m of the water column (Espinasse et al. 2012), making access to prey substantially easier for the whales during this time.

The majority of shallow (<50 m) feeding dives in our study included a single lunge, a strategy that is thought to increase efficiency by allowing the whale to remain close to the surface, reducing the energetic costs of diving (Kramer 1988, Carbone & Houston 1996, Doniol-Valcroze et al. 2011). Deep-

feeding dives, in contrast, were much more likely to contain multiple feeding lunges (Ware et al. 2011). In these ways, the whales appear to be maximizing their energetic intake through the timing of behavioral state changes and feeding at times when the energetic costs associated with deep diving are minimized.

Optimal foraging theory suggests that the energetic costs of accessing prey by air-breathing predators scale with the depth of prey, so the whales should behave in ways such that the energy obtained per dive increases with feeding depth (Mori 1998, Thompson & Fedak 2001). In blue whales *Balaenoptera musculus* (Doniol-Valcroze et al. 2011) and Antarctic humpback whales (Ware et al. 2011, Tyson et al. 2012), the number of lunges per dive increases with dive depth. However, until recently, little information has been available to test whether there is a relationship between feeding depth relative to the vertical distribution of prey. Our results provide evidence that humpback whales in Antarctica limit the energetic costs associated with diving by feeding primarily in the upper 50 m of the water column during the night, when prey have migrated towards the surface.

Johnston et al. (2012) reported that the density of whales in Wilhelmina Bay and surrounding areas during the autumn of 2009 was the highest ever reported for humpback whales. This abundance of whales is directly related to the availability of prey, which is partially mediated by the absence of sea ice. In autumn, humpback whales exploit krill that have moved inshore in large aggregations but are not yet covered by the sea ice that will later protect them from air-breathing predators (Nowacek et al. 2011). This represents the final opportunity for whales to acquire the energy necessary for migration, breeding, and (in the case of females) calf provisioning, so the behaviors we describe may be critical to the successful completion of their annual cycle. Our observations depict how humpback whales manage their daily behavior to limit energy expenditure and maximize their energetic gains.

For migration to increase fitness, departure from one habitat must occur before its resource quality has declined below a threshold where net energy gain is positive (Dingle & Drake 2007). Such is the case for humpback whales feeding in the waters around the western Antarctic Peninsula. However, there is still much to be learned about the timing of migrations in relation to the availability of prey and the spatial distribution of whales late in the feeding season. Humpback whales undergo one of the longest migra-

tions of any mammalian species (Stevick et al. 2011), and to fuel this remarkable life history strategy, they feed in regions that contain extraordinarily rich prey resources.

Future work should examine how interannual variation in the onset of annual sea ice cover affects both the availability of prey and the foraging success and distribution of humpback whales (and other krill predators) in this region, which is rapidly warming (Vaughan et al. 2003). In the northwestern Atlantic, there is evidence that rapid climate change can modify the timing of sea ice cover, phytoplankton blooms, and presence of apex predators. A temporal mismatch of these biotic and abiotic constituents can have significant negative effects on the abundance of the biological components, which in turn impacts the foraging success and survivability of marine mammals (Laidre et al. 2008, Moore & Huntington 2008). Over the short term, delays in the onset of ice cover may extend the feeding season for growing populations of humpback whales around the Antarctic Peninsula. Over the longer term, prospects for the foraging ecology of these whales are less clear because of the uncertain effects of climate change on prey populations.

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#### LITERATURE CITED

- Acevedo-Gutiérrez A, Croll DA, Tershy BR (2002) High feeding costs limit dive time in the largest whales. *J Exp Biol* 205:1747–1753
- Altmann J (1974) Observational study of behavior: sampling methods. *Behaviour* 49:227–267
- Brodie PF (1993) Noise generated by the jaw actions of feeding fin whales. *Can J Zool* 71:2546–2550
- Carbone C, Houston AI (1996) The allocation of time over the dive cycle: an approach based on aerobic and anaerobic respiration. *Anim Behav* 51:1247–1255
- Davis RW, Fuiman LA, Williams TM, Horning M, Hagey W (2003) Classification of Weddell seal dives based on 3 dimensional movements and video-recorded observations. *Mar Ecol Prog Ser* 264:109–122
- Dingle H (1996) Migration: the biology of life on the move.



- Oxford University Press, New York, NY
- Dingle H, Drake VA (2007) What is migration? *Bioscience* 57:113–121
- Doniol-Valcroze T, Lesage V, Giard J, Michaud R (2011) Optimal foraging theory predicts diving and feeding strategies of the largest marine predator. *Behav Ecol* 22: 880–888
- Espinasse B, Zhou M, Zhu Y, Hazen EL and others (2012) Austral fall–winter transition of mesozooplankton assemblages and krill aggregations in an embayment west of the Antarctic Peninsula. *Mar Ecol Prog Ser* 452:63–80
- Friedlaender AS, Halpin PN, Qian SS, Lawson GL, Wiebe PH, Thiele D, Read AJ (2006) Whale distribution in relation to prey abundance and oceanographic processes in the western Antarctic Peninsula shelf waters. *Mar Ecol Prog Ser* 317:297–310
- Friedlaender AS, Hazen EL, Nowacek DP, Halpin PN and others (2009) Diel changes in humpback whale feeding behavior in response to sand lance *Ammodytes* spp. behavior and distribution. *Mar Ecol Prog Ser* 395:91–100
- Goldbogen JA, Calambokidis J, Croll DA, Harvey JT and others (2008) Foraging behavior of humpback whales: kinematic and respiratory patterns suggest a high cost for a lunge. *J Exp Biol* 211:3712–3719
- Goldbogen JA, Calambokidis J, Oleson E, Potvin J, Peyenson ND, Schorr G, Shadwick RE (2011) Mechanics, hydrodynamics and energetics of blue whale lunge feeding: efficiency dependence on krill density. *J Exp Biol* 214:131–146
- Goldbogen JA, Calambokidis J, Croll D, McKenna MF and others (2012) Scaling in lunge feeding performance in rorqual whales: mass-specific energy expenditure increases with body size and progressively limits diving capacity. *Funct Ecol* 26:216–226
- Greenberg R, Marra PP (eds) (2005) *Birds of two worlds: the ecology and evolution of migration*. Johns Hopkins University Press, Baltimore, MD
- Hamilton PK, Stone GS, Martin SM (1997) Note on a deep humpback whale dive near Bermuda. *Bull Mar Sci* 61: 491–494
- Hazen EL, Friedlaender AS, Thompson MA, Ware CR, Weinrich MT, Halpin PN, Wiley DN (2009) Fine-scale prey aggregations and foraging ecology of humpback whales *Megaptera novaeangliae*. *Mar Ecol Prog Ser* 395: 75–89
- Johnson M, Tyack PL (2003) A digital acoustic recording tag for measuring the response of wild marine mammals to sound. *IEEE J Ocean Eng* 28:3–12
- Johnson MP, Aguilar De Soto N, Madsen PT (2009) Studying the behaviour and sensory ecology of marine mammals using acoustic recording tags: a review. *Mar Ecol Prog Ser* 395:55–73
- Johnston DW, Friedlaender AS, Read AJ, Nowacek DP (2012) Initial density estimates of humpback whales *Megaptera novaeangliae* in the inshore waters of the western Antarctic Peninsula during the late autumn. *Endang Species Res* 18:63–71
- Kooyman GL (1968) An analysis of some behavioral and physiological characteristics related to diving in the Weddell seal. *Antarct Res Ser* 11:227–261
- Kramer DL (1988) The behavioral ecology of air breathing by aquatic animals. *Can J Zool* 66:89–94
- Laidre KL, Stirling I, Lowry LF, Wiig O, Heide-Jorgensen MP, Ferguson SH (2008) Quantifying the sensitivity of Arctic marine mammals to climate-induced habitat change. *Ecol Appl* 18:S97–S125
- Lesage V, Hammill MO, Kovacs KM (1999) Functional classification of harbor seal (*Phoca vitulina*) dives using depth profiles, swimming velocity, and an index of foraging success. *Can J Zool* 77:74–87
- Lighthill MJ (1971) Large-amplitude elongated-body theory of fish locomotion. *Proc R Soc Lond B Biol Sci* 179: 125–138
- Lighthill J (1978) *Waves in fluids*. Cambridge University Press, Cambridge
- Matthews LH (1937) The humpback whale, *Megaptera nodosa*. *Discov Rep* 17:7–92
- Moore SE, Huntington HP (2008) Arctic marine mammals and climate change: impacts and resilience. *Ecol Appl* 18:S157–S165
- Mori Y (1998) Optimal choice of foraging depth in divers. *J Zool* 245:279–283
- Nicol S (2006) Krill, currents, and sea ice: *Euphausia superba* and its changing environment. *Bioscience* 56:111–120
- Nowacek DP, Johnson MP, Tyack PL (2004) North Atlantic right whales (*Eubalaena glacialis*) ignore ships but respond to alerting stimuli. *Proc Biol Sci* 271:227–231
- Nowacek DP, Friedlaender AS, Halpin PN, Hazen EL and others (2011) Super-aggregations of krill and humpback whales in Wilhelmina Bay, Antarctic Peninsula. *PLoS ONE* 6:e19173
- Pivorunas A (1979) The feeding mechanisms of baleen whales. *Am Sci* 67:432–440
- Potvin J, Goldbogen JA, Shadwick RE (2009) Passive versus active engulfment: verdict from trajectory simulations of lunge-feeding fin whales *Balaenoptera physalus*. *J R Soc Interface* 6:1005–1025
- Simon M, Johnson M, Madsen PT (2012) Keeping momentum with a mouthful of water: behavior and kinematics of humpback whale lunge feeding. *J Exp Biol* 215: 3786–3798
- Stevick PT, Neves M, Johansen F, Engel M, Allen J, Marccondes M, Carlon C (2011) A quarter of a world away: female humpback whale moves 10,000 km between breeding areas. *Biol Lett* 7:299–302
- Thompson D, Fedak MA (2001) How long should a dive last? A simple model of foraging decisions by breath-hold divers in a patchy environment. *Anim Behav* 61:287–296
- Tyson RB, Friedlaender AS, Ware C, Stimpert AK, Nowacek DP (2012) Synchronous mother and calf foraging behavior in humpback whales *Megaptera novaeangliae*: insights from multi-sensor suction cup tags. *Mar Ecol Prog Ser* 457:209–220
- Vaughan DG, Marshall GJ, Connolley WM, Parkinson C and others (2003) Recent rapid regional climate warming on the Antarctic Peninsula. *Clim Change* 60:243–274
- Ware C, Arsenault R, Wiley D, Plumlee MD (2006) Visualizing the underwater behavior of humpback whales. *IEEE Comput Graph Appl* 26:14–18
- Ware C, Friedlaender AS, Nowacek DP (2011) Shallow and deep lunge feeding of humpback whales in fiords of the west Antarctic Peninsula. *Mar Mamm Sci* 27:587–605
- Williams TM (2006) Physiological and ecological consequences of extreme body size in whales. In: Estes JA, DeMaster DP, Doak DF, Williams TM, Brownell RL (eds) *Whales, whaling and ocean ecosystems*. University of California Press, Berkeley, CA, p 191–201
- Zhou M, Dorland RD (2004) Aggregation and vertical migration behavior of *Euphausia superba*. *Deep-Sea Res II* 51: 2119–2137