

Foraging behavior of humpback whales: kinematic and respiratory patterns suggest a high cost for a lunge

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SUMMARY

Lunge feeding in rorqual whales is a drag-based feeding mechanism that is thought to entail a high energetic cost and consequently limit the maximum dive time of these extraordinarily large predators. Although the kinematics of lunge feeding in fin whales supports this hypothesis, it is unclear whether respiratory compensation occurs as a consequence of lunge-feeding activity. We used high-resolution digital tags on foraging humpback whales (*Megaptera novaengliae*) to determine the number of lunges executed per dive as well as respiratory frequency between dives. Data from two whales are reported, which together performed 58 foraging dives and 451 lunges. During one study, we tracked one tagged whale for approximately 2 h and examined the spatial distribution of prey using a digital echosounder. These data were integrated with the dive profile to reveal that lunges are directed toward the upper boundary of dense krill aggregations. Foraging dives were characterized by a gliding descent, up to 15 lunges at depth, and an ascent powered by steady swimming. Longer dives were required to perform more lunges at depth and these extended apneas were followed by an increase in the number of breaths taken after a dive. Maximum dive durations during foraging were approximately half of those previously reported for singing (i.e. non-feeding) humpback whales. At the highest lunge frequencies (10 to 15 lunges per dive), respiratory rate was at least threefold higher than that of singing humpback whales that underwent a similar degree of apnea. These data suggest that the high energetic cost associated with lunge feeding in blue and fin whales also occurs in intermediate sized rorquals.

Key words: diving, foraging, whale.

INTRODUCTION

Baleen whales (Mysticeti) are obligate filter feeders, using keratinized plates of baleen to filter small zooplankton from ingested water. Three modes of filter-feeding have been observed among living mysticetes (Werth, 2000): (1) skim or continuous ram feeding (Balaenidae), (2) suction feeding (Eschrichtiidae) and (3) intermittent ram or lunge feeding (Balaenopteridae). Lunge feeding only occurs in Balaenopteridae (rorquals), a group that is characterized by a reduced tongue and a series of longitudinal grooves of highly extensible, elastic blubber located on the ventral side of the body (Orton and Brodie, 1987). During a lunge, rorquals accelerate toward prey and lower their mandibles, exposing the oral cavity to oncoming flow. Drag is generated, causing expansion of the ventral groove blubber around a large volume of water and prey (Goldbogen et al., 2007). The high drag generated during engulfment dissipates the kinetic energy of the body, and as a result, the next lunge requires acceleration from rest. The forces required to repeatedly accelerate the body demands more energy compared with maintaining constant speed; therefore, the number of lunges executed during a dive is predicted to have a significant effect on the energetic cost of foraging.

Lunge feeding occurs not only at the sea surface, but also apparently at any depth where prey is particularly abundant (Calambokidis et al., 2008). However, regardless of depth, rorqual

foraging dives are limited to very short durations despite their large body size (Croll et al., 2001; Croll et al., 2005; Dolphin, 1988; Goldbogen et al., 2006; Panigada et al., 1999), a characteristic that typically enables longer diving in a wide range of air-breathing vertebrates (Halsey et al., 2006; Schreer and Kovacs, 1997). The energetic cost of lunge feeding is hypothesized to be the cause of low dive durations observed among larger rorquals, such as blue and fin whales (Acevedo-Gutierrez et al., 2002; Croll et al., 2001). This limited diving capacity contrasts with the longer dives of bowhead whales (Krutzikowsky and Mate, 2000), which are nearly as massive but ram feed continuously – a feeding strategy that has been considered more efficient (Acevedo-Gutierrez et al., 2002). Dive profiles of blue and fin whales (*Balaenoptera musculus*, *B. physalus*) provide support for this hypothesis, demonstrating an increase in post-dive recovery time when more lunges are performed at depth (Acevedo-Gutierrez et al., 2002). Further support is provided by the detailed kinematics of these lunges at depth, which indicate a rapid deceleration of the body due to the high drag experienced during engulfment (Goldbogen et al., 2006; Goldbogen et al., 2007).

However, it is unknown whether respiratory rate is increased during these extended post-dive surface periods, and previous methods to detect lunges have relied on subjective analysis of dive profiles (Acevedo-Gutierrez et al., 2002; Blix and Folkow, 1995)



Fig. 1. A tagged humpback whale. The bioacoustic probe was equipped with silicon suction cups for attachment and a flotation device to facilitate recovery.

or have assumed that whales perform only one lunge per dive (Dolphin, 1987b). The methods to determine the number of lunges during a foraging dive have since been developed (Goldbogen et al., 2006), and in this study we build on those efforts by recording breathing events for tagged humpback whales from kinematic and acoustic data. Because rorquals breathe once upon surfacing (Brodie, 2001), this serves as a way to determine the number of breaths

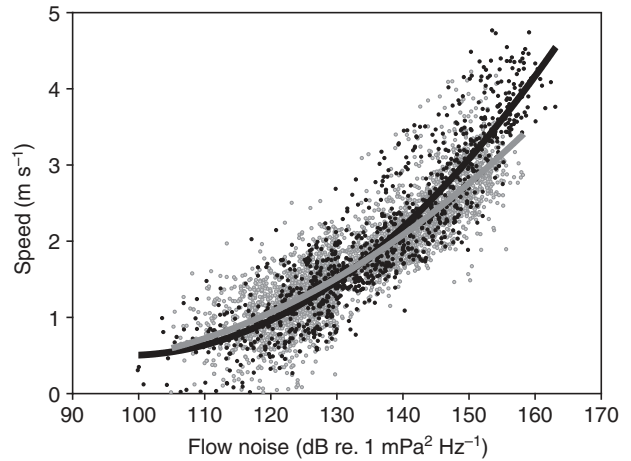


Fig. 2. Flow noise increases with body speed. The relationship between flow noise, measured by the hydrophone, and speed, calculated from the kinematics of the body, is shown for each whale (MnA, gray; MnB, black) during steep glides ($-30 \text{ deg.} \leq \text{pitch} \leq 30 \text{ deg.}$). The relationship between flow noise and body speed was consistent among whales; each line represents a quadratic regression through the data from each whale (MnA, $r^2=0.76$; MnB, $r^2=0.84$).

between dives. The number of breaths taken after a dive is important because it provides information on the oxygen deficit and carbon dioxide build up that has occurred during a dive (Boutillier et al.,

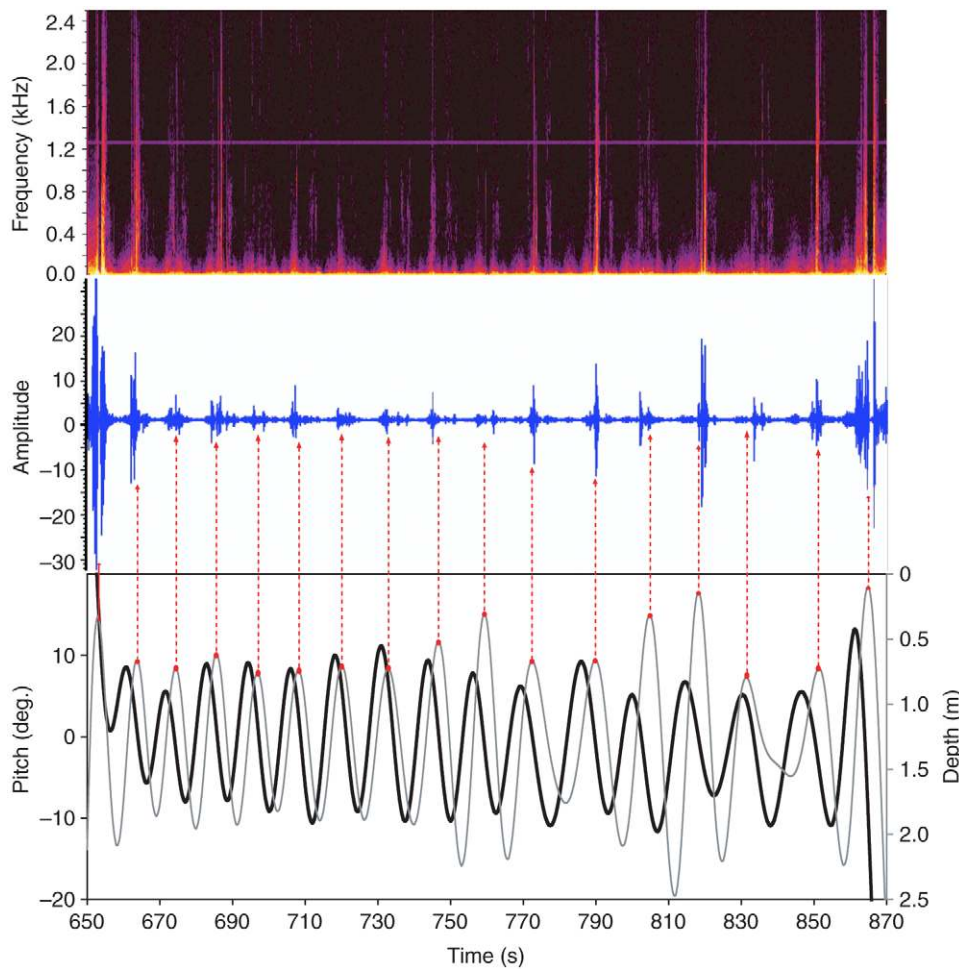


Fig. 3. Detection of breaths during a surface interval. We interpreted the cyclic kinematic (bottom panel) and repeatable acoustic (top two panels) patterns during surface intervals as a series of breaths. As the tag breaks the surface, a signal was evident in both the waveform (middle panel) and spectrogram (top panel). These events (marked by dashed red arrows) coincided with minima in the dive profile (gray trace) and were phase coupled with the body pitch record (black lines), such that dive profile minima occurred when the body was level (pitch=0 deg.). Here we show a 3.7 min surface interval with 17 breaths following a foraging dive that included 15 lunges at depth (the dive shown in Fig. 4).

2001; Kooyman et al., 1971). Thus, if lunge feeding is energetically costly, we would expect respiratory compensation when this activity is superimposed on apnea.

In this study we show that humpback whales required longer dives to perform more lunges at depth and that these lunges were targeted toward the shallowest part of the densest krill layer. Lunge frequency was significantly correlated with post-dive surface time and post-dive respiratory frequency. When compared with data for singing humpback whales (Chu, 1988), foraging whales exhibited severely limited dive durations and increased respiratory rates. These data suggest that the high foraging costs associated with lunge feeding in blue and fin whales also occur in intermediate sized rorquals.

MATERIALS AND METHODS

The tag

We attached high-resolution digital tags to the backs of surfacing humpback whales at different locations off the central coast of California (Fig. 1). A 5.3 m Rigid-Hulled Inflatable Boat (RHIB) was used in conjunction with the R/V *John Martin* (Moss Landing Marine Laboratory, CA, USA) to visually locate humpbacks. The RHIB was used to approach surfacing whales from behind and tags were applied to the dorsal surface of the whale with a 4 m fiberglass pole, as previously described (Goldbogen et al., 2006; Oleson et al., 2007). Once tagged, researchers on the R/V *John Martin* would begin tracking the whale to collect hydroacoustic data (see 'Hydroacoustic prey-field mapping' below). The high-resolution digital tag (Bioacoustic Probe; Greeneridge Sciences, Goleta, CA, USA) contains a pressure transducer, hydrophone and a two-axis accelerometer (Burgess et al., 1998; Goldbogen et al., 2006). The tag is equipped with silicon suction cups for attachment and a flotation device to facilitate tag recovery after the tag falls off the whale. Depth, flow noise and two-dimensional body acceleration (body pitch and swimming strokes) were recorded by the tag (Goldbogen et al., 2006).

Using flow noise to determine lunges and breaths

The flow noise recorded by the hydrophone generates information on the whale's speed at any given point of a dive (Goldbogen et al., 2006) and also pinpoints when a lunge occurs (Calambokidis et al., 2008). We established a relationship between flow noise and speed by: (1) measuring the body velocity from kinematic data (vertical velocity divided by the sine of body pitch angle) during steep glides ($-30 \text{ deg.} \leq \text{pitch} \leq 30 \text{ deg.}$), and (2) calculating the root-mean-square sound pressure (50 Hz $1/3$ octave band). We used this relationship to calculate the speed of the whale throughout each dive (Fig. 2). This is advantageous because the speed calculated from body kinematics is inaccurate when body pitch is close to zero (Goldbogen et al., 2006), which is the typical orientation of the whale during lunges. Speed profiles were low-pass filtered (0.2 Hz finite impulse response filter) to remove any noise associated with lift production by the fluke.

An excursion below a depth greater than one body length ($>10 \text{ m}$) was considered a dive. A dive was considered a foraging dive if a lunge was detected. The presence of a lunge was confirmed by the following criteria (Goldbogen et al., 2006; Goldbogen et al., 2007): (1) a bout of fluking associated with a distinct speed maximum (determined from flow noise), and (2) continued swimming throughout the lunge, particularly during the deceleration phase. The rapid deceleration during continued fluking is characteristic of the high drag experienced during lunge feeding.

Following each dive, the amount of time the whale spent at the surface was recorded, defined as the time between the whales' first

Table 1. Dive data summary for tagged humpback whales

Whale	Date (m/d/yr)	Foraging dives recorded	Dive duration (min)	Maximum dive depth (m)	Descent duration (min)	Average descent speed (m s^{-1})	Average descent angle (deg.)	Proportion of descent gliding (%)	Number of lunges per dive*	Ascent duration (min)	Average ascent speed (m s^{-1})	Average ascent angle (deg.)
MnA	9/28/04	43	7.7±2.0	139±29	1.3±0.4	1.7±0.2	-57±8	47±18	8±4 (16)	1.6±0.4	1.4±0.2	56±11
MnB	9/28/04	15	7.9±1.5	156±25	1.1±0.1	1.5±0.4	-60±8	50±14	6±3 (10)	2.0±0.9	1.5±0.3	55±19

Values are means ± s.d. *Maximum value given in parentheses.

Table 2. Lunge data summary for tagged humpback whales

Whale	Date (m/d/yr)	Number of lunges	Maximum velocity (m s^{-1})	Lunge duration (s)	Time between consecutive lunges (s)	Change in pitch during lunge (deg.)	Body pitch at jaw opening (deg.)
MnA	9/28/04	362	2.7 ± 0.3	15 ± 1	18 ± 6	48 ± 22	0 ± 22
MnB	9/28/04	89	2.3 ± 0.6	16 ± 3	25 ± 5	55 ± 28	-16 ± 24

Values are means \pm s.d.

and last breath. A breath could be detected in two ways (Fig. 3): (1) an acoustic signal when the tag breaks the water surface, and (2) a phase relationship between undulations in the dive profile and body pitch angle. We determined the number of breaths taken before and after a dive. Following previously described methods (Goldbogen et al., 2006), other diving parameters were recorded during each phase of a dive, including dive duration, maximum dive depth, body angle, gait transition depth, and glide time.

Prey-field distribution and relative density

When a whale surfaces and dives a 'footprint' is left on the water surface because of the water displaced by the moving body. When possible, we navigated the R/V *John Martin* directly from one surface location ('footprint' series) to the next. Along this route, acoustic backscatter by depth was recorded using a Simrad EK60 (Strandpromenaden, Horten, Norway) digital scientific echosounder operating at 38, 120 and 200 kHz. The echosounder operated at a pulse length of 1024 μs pinging every 2 s along the route. These data allowed us to generate a prey-field map that shows the relative density and distribution of zooplankton as a function of time and

depth (Croll et al., 2005). We then superimposed the synchronized dive profiles onto the corresponding prey-field maps. We calculated relative density of krill aggregations as a function of depth by integrating nautical area scattering coefficient ($\text{m}^2 \text{target nautical mi}^{-2}$) values every $15 \text{ s} \times 10 \text{ m}$ along the path of the foraging whale (Croll et al., 2005). We also determined prey type with targeted zooplankton net tows that consisted of 333 micron nets on a tucker trawl.

Statistics

All parameters were tested for normality and homoscedacity before performing statistical tests. An overall significance level of 0.05 was used. We used least-squares linear regression to determine the relationship between diving parameters. We used analysis of covariance (ANCOVA) to test whether lunge frequency has a significant effect on the relationship between dive duration and respiratory frequency or surface recovery time.

RESULTS

During the summer of 2004 and 2005, 18 taggings were attempted off the coast of central California. Here we report data from two

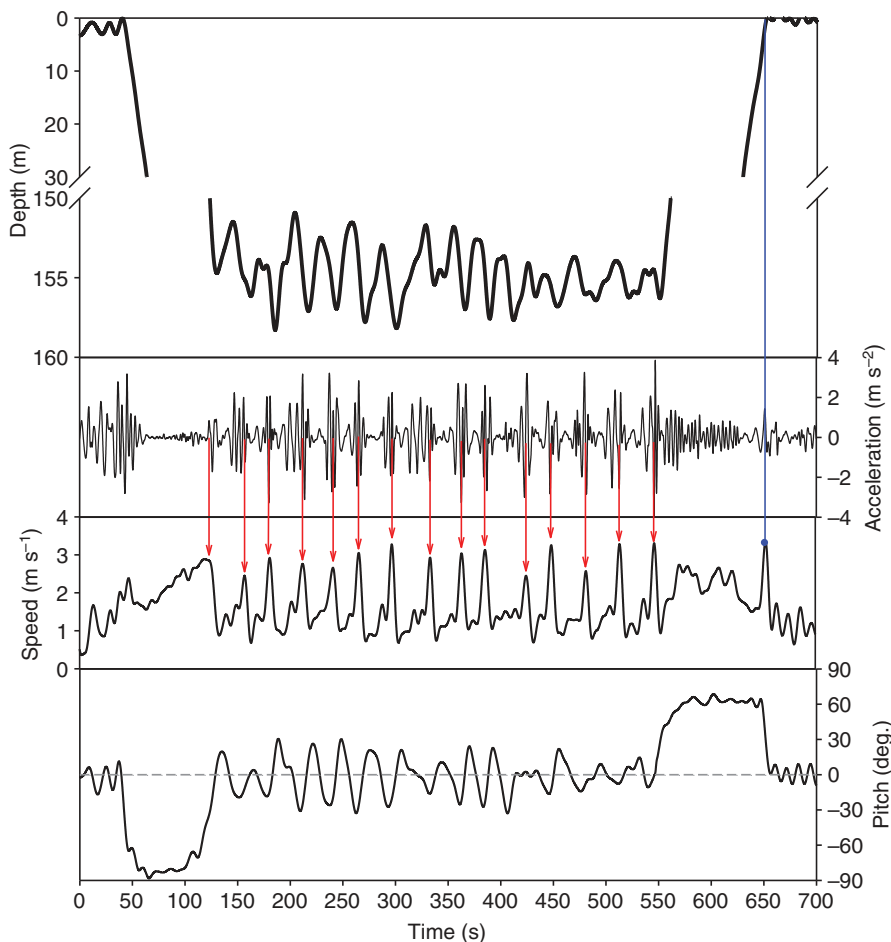


Fig. 4. Kinematics of foraging dives. Swimming strokes (acceleration), speed and pitch angle are shown for a foraging dive (whale MnA). Foraging dives consisted of a gliding descent and an ascent powered by steady swimming. Lunges at the bottom of each dive are marked by speed maxima and bouts of fluking. Each lunge is identified by a red arrow and highlights how the deceleration phase of each lunge occurs during continued swimming, which is a defining characteristic of a lunge. The vertical blue line marks a speed maximum that is not considered a lunge because it is associated with the tag breaking the sea surface. Also note how each lunge occurs when the body is approximately horizontal (dashed line).

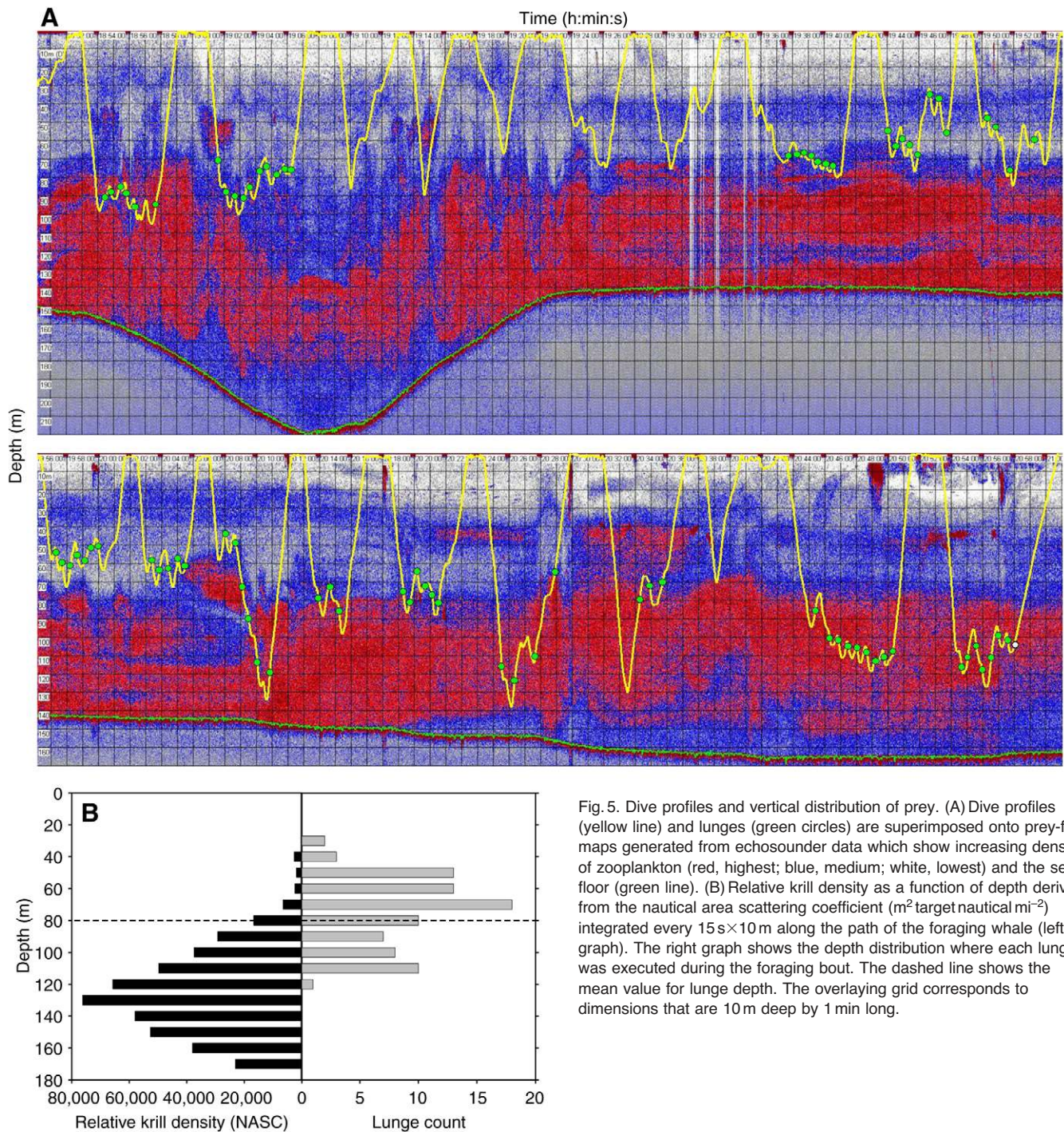


Fig. 5. Dive profiles and vertical distribution of prey. (A) Dive profiles (yellow line) and lunges (green circles) are superimposed onto prey-field maps generated from echosounder data which show increasing density of zooplankton (red, highest; blue, medium; white, lowest) and the sea floor (green line). (B) Relative krill density as a function of depth derived from the nautical area scattering coefficient (m^2 target nautical mi^{-2}) integrated every $15\text{ s} \times 10\text{ m}$ along the path of the foraging whale (left graph). The right graph shows the depth distribution where each lunge was executed during the foraging bout. The dashed line shows the mean value for lunge depth. The overlaying grid corresponds to dimensions that are 10 m deep by 1 min long.

long tag deployments (Tables 1 and 2) on foraging humpback whales off Point Reyes, California ($38^{\circ}09'\text{N}$, $123^{\circ}20'\text{W}$): the whale known as MnA performed 43 foraging dives and 362 lunges (over approximately 8 h), whereas whale MnB executed 15 foraging dives and 89 lunges (over approximately 5 h). Tags were typically attached near the dorsal fin and as such the lateral inclination of the tag did not allow us to determine body roll systematically for either individual.

The kinematics of humpback foraging dives were similar to that previously described for fin whales (Goldbogen et al., 2006). These characteristics included a gliding descent, several lunges at depth, and an ascent powered by steady swimming (Fig. 4). Speed of the

body gradually increased throughout these gliding descents, which is indicative of negative buoyancy. On ascent, speed was relatively constant and similar in magnitude with respect to a variety of swimming animals of different sizes (Sato et al., 2007). The integration of dive profiles and prey distribution maps showed how lunges were directed towards the upper boundary of dense aggregations of prey (Fig. 5). Prey was identified as krill (94% *Euphausia pacifica*, 6% *Thysanoessa spinifera*) by zooplankton net tows. The foraging behavior of each whale appeared to be serially correlated, where deeper, longer dives occurred in bouts (Fig. 6).

Foraging dives that included more lunges at depth were associated with longer dive durations (Fig. 7A; MnA, $y=0.473x+3.716$,

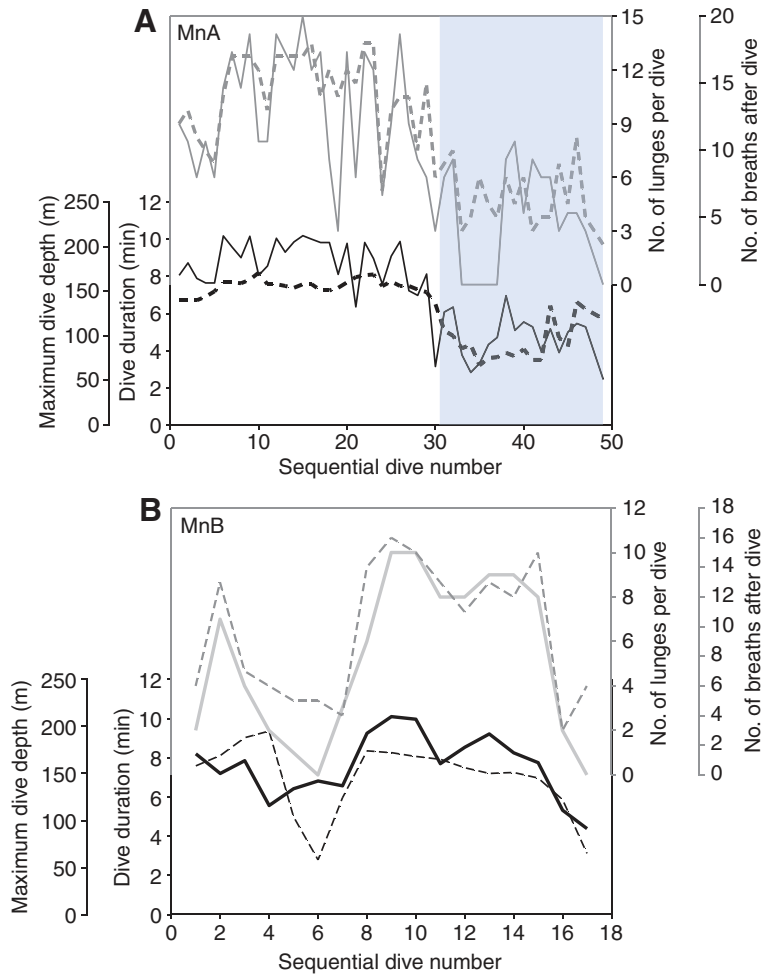


Fig. 6. Time series of diving behavior. Dive duration (thin black line), maximum dive depth (dashed black line), lunge frequency (thin gray line), and post-dive breaths (dashed gray line) are shown as a function of sequential dive number for whale MnA (A) and MnB (B). Dives 31–49 are shown with hydroacoustic data in Fig. 5 (light blue box).

$r^2=0.77$, $P<0.001$; MnB, $y=0.358x+5.719$, $r^2=0.65$, $P<0.001$). We found a significant relationship between the number of lunges per dive and the number of breaths taken directly after that corresponding dive (Fig. 7B; MnA, $y=1.130x+3.733$, $r^2=0.83$, $P<0.001$; MnB, $y=0.831x+5.245$, $r^2=0.63$, $P<0.001$). There was also a significant relationship between lunge frequency and the number of breaths taken before the dive, but the relationship was considerably weaker (MnA, $y=0.8x+5.527$, $r^2=0.41$, $P<0.001$; MnB, $y=0.618x+6.873$, $r^2=0.33$, $P<0.001$). We found a significant relationship between lunge frequency and post-dive surface time (Fig. 7C; MnA, $y=0.294x+1.928$, $r^2=0.52$, $P<0.001$; MnB, $y=0.19x+1.329$, $r^2=0.43$, $P<0.001$). There was also a significant relationship between lunge frequency and the steepness of ascent after the lunge bout (Fig. 7D; MnA, $y=2.93x+29.127$, $r^2=0.73$, $P<0.001$; MnB, $y=4.776x+26.464$, $r^2=0.72$, $P<0.001$) and descent on the subsequent dive (Fig. 7D; MnA, $y=-1.457x-43.972$, $r^2=0.42$, $P<0.001$; MnB, $y=-2.51x-43.5436$, $r^2=0.66$, $P<0.001$).

DISCUSSION

In a series of studies, Dolphin (Dolphin, 1987a; Dolphin, 1987b; Dolphin, 1987c; Dolphin, 1988) tracked diving humpback whales and their prey with an echosounder. He found that deeper dives resulted in an increase in post-dive surface time and respiratory frequency (Dolphin, 1987c). For some of these deep dives, the echosounder trace indicated feeding behavior when whales swam through patches of krill in a sinusoid-like fashion [see figure 1C of Dolphin (Dolphin, 1987c) and also figure 1b of Dolphin (Dolphin,

1987b)]. These vertical undulations at the bottom of each dive are reminiscent to the patterns in the dive profile that we observe here (Fig. 4). From his data, Dolphin concluded that the energetic cost of foraging was determined by dive depth, and therefore dive duration, which was influenced by the spatial distribution and density of target prey patches (Dolphin, 1988).

Here we build on these studies with more detailed kinematic data from high resolution digital tags. These data, combined with a more complete understanding of how these whales feed (Goldbogen et al., 2007) allow us to define actual lunge-feeding events (Fig. 4) and establish a more appropriate metric for evaluating the energetic costs of foraging in rorquals. For example, Dolphin (Dolphin, 1987b) assumed that humpback whales performed only one lunge per dive, whereas we show that humpbacks are capable of executing up to 15 lunges per dive (Fig. 3B). Furthermore, by highlighting where these lunges occur at the bottom of a dive, we are able to demonstrate how bouts of lunges are directed towards dense krill patches (Fig. 5). These results are consistent with video footage from Crittercam studies on foraging blue whales that show lunges occurring within dense krill aggregations (Calambokidis et al., 2008).

Theory predicts that a predator's optimal foraging depth is always shallower than the depth of highest prey density (Mori, 1998). Our results support these predictions because humpback whales executed lunges at the upper-most boundary of dense krill patches (Fig. 5), rather than dive deeper in search of higher density patches. It is not clear how rorquals are able to detect this increase in prey density with depth. Researchers suggested echolocation as a possible

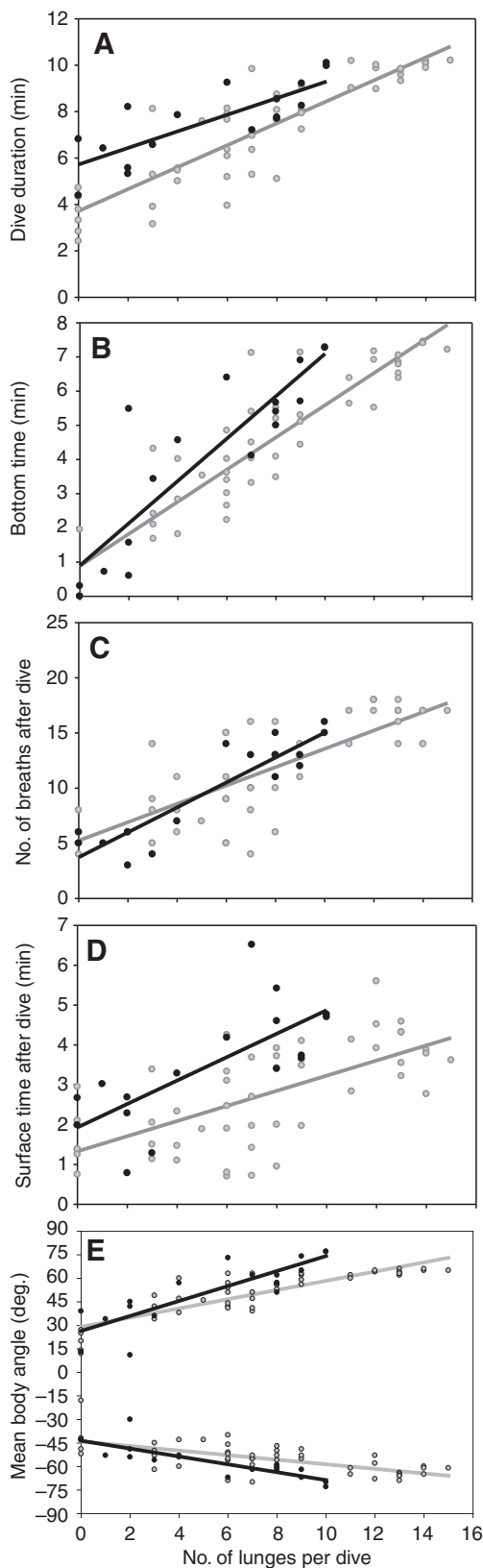


Fig. 7. Respiratory and kinematic parameters associated with lunge frequency. (A) Foraging dives that involved more lunges required longer dive durations (MnA, $r^2=0.77$, $P<0.001$; MnB, $r^2=0.65$, $P<0.001$) and (B) more bottom time (MnA, $r^2=0.83$, $P<0.001$; MnB, $r^2=0.77$, $P<0.001$). (C) A significant correlation was found between the number of lunges executed per dive and the number of post-dive recovery breaths (MnA, $r^2=0.83$, $P<0.001$; MnB, $r^2=0.63$, $P<0.001$). (D) Post-dive surface time increased with lunge frequency (MnA, $r^2=0.52$, $P<0.001$; MnB, $r^2=0.43$, $P<0.001$). (E) Lunge frequency was associated with a steeper ascent following the lunge bout (D; MnA, $r^2=0.73$, $P<0.001$; MnB, $r^2=0.72$, $P<0.001$) and a steeper descent during the subsequent dive (D; MnA, $r^2=0.42$, $P<0.001$; MnB, $r^2=0.66$, $P<0.001$). Black lines, MnB; gray lines, MnA.

(Ogawa and Shida, 1950; Slijper, 1979). Thus, a rorqual may decide to continue descent until it swims into a sufficiently dense prey patch, as indicated by the number of hits against such sensory structures.

Our data suggest that lunge frequency may be an indication of prey patch quality. When krill is abundant, humpbacks should attempt as many lunges as possible and return to the surface at steep body angles (Fig. 7E). A steeper trajectory during a dive should enhance bottom time and the opportunity to execute more lunges at depth (Fig. 7B). By contrast, when prey patch quality is poor, the dive is terminated early and the ascent to the surface, as well as the descent on the next dive, occurs at shallower body angles (Fig. 7E). For example, note the drop in the depth of the densest krill layer between the second and third dive of Fig. 5, which is then followed by several non-foraging dives. Shallow body angles during diving will expand the horizontal area covered and thereby increase the likelihood of locating a better prey patch (Sato et al., 2004). This may explain why dives that involved fewer lunges were not relatively longer (Fig. 7A), but instead were terminated early because of poor prey patch quality. It also suggests that in most cases dive duration is under behavioral control rather than limited physiologically (Spurling et al., 2007; Thompson and Fedak, 2001), except where prey patch is very good and maximum exploitation of the patch is desired (i.e. the most lunges possible).

The respiratory patterns associated with lunge frequency for humpback whales support the hypothesis that lunge feeding is energetically costly. Foraging dives with more lunges were followed by a longer surface interval (Fig. 7D) and more breaths during that interval (Fig. 7C). Dolphin (Dolphin, 1987c) also showed respiratory compensation with increasing dive depth and duration (Dolphin, 1987c), which was probably related to lunge frequency, based on our observations (Figs 6 and 7). Other diving cetaceans in controlled experimental conditions, such as bottlenose dolphins and the beluga, also increase respiratory frequency after longer dives (Shaffer et al., 1997; Williams et al., 1999). This type of respiratory adjustment is a hallmark of increased ventilation that occurs between dive bouts for a variety of birds and mammals (Andrews et al., 2000; Butler and Jones, 1997). Ventilation is the product of respiratory frequency and tidal volume, and both of these parameters increase in concert with longer dive durations (Kooyman et al., 1971). Increased ventilation is necessary because of the oxygen deficit and accumulation of carbon dioxide acquired during submergence (Boutilier et al., 2001). The rapid replacement of oxygen stores throughout the body is further facilitated by an increased heart rate during these surface intervals (Andrews et al., 1997; Thompson and Fedak, 1993).

If lunge feeding is energetically costly and consequently limits maximum dive time, there should be respiratory compensation (number of post-dive breaths) when this type of activity is superimposed on apnea (dive duration). We can provide indirect

mechanism after discovering click trains and buzzes associated with night-time feeding behavior (Stimpert et al., 2007), but such signals were not detected during the day time foraging bouts presented here. Alternatively, rorquals may be able to mechanically sense prey *via* tactile hairs or vibrissae located on the rostrum and mandibles

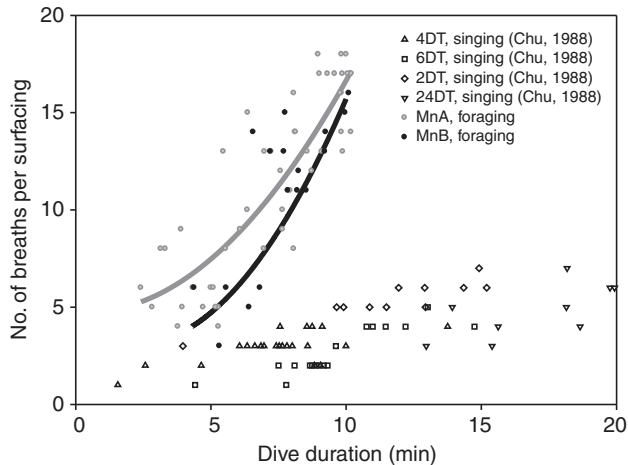


Fig. 8. Relationship between dive duration and respiration rate for singing and foraging humpbacks. Data for foraging whales are for MnA (gray circles) and MnB (black circles) and data for four singing humpback whales are shown as open symbols (Chu, 1988). Dive duration increased with the number of breaths taken after that dive (MnA, $y=5.450-0.409x+0.155x^2$, $r^2=0.77$, $P<0.001$; MnB, $y=4.085-0.908x+0.207x^2$, $r^2=0.62$, $P=0.005$). Note that the longest singing dives (20 min) are approximately twice as long as the longest foraging dives (10 min). Also, at dive durations of 10 min, the number of breaths taken is three times higher during foraging.

evidence for high feeding costs by comparing diving and respiratory data between singing (Chu, 1988) and foraging humpback whales (Fig. 8); maximum dive durations of singing humpback whales were 20 min, approximately twice that for foraging humpback whales. At the highest lunge frequencies (10–15 lunges per dive), the number of post-dive breaths is at least triple the value observed in singing humpbacks that undergo similar dive durations (Chu, 1988). However, analysis of covariance does not reveal lunge frequency to be a significant cofactor for this relationship within each individual whale, which is the result of the colinearity and asymptotic nature of these dive parameters. Thus more data is needed to firmly conclude that the increased respiratory rate during foraging is due to the energetic cost of lung feeding rather than an extended breath hold.

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REFERENCES

- Acevedo-Gutierrez, A., Croll, D. A. and Tershy, B. R. (2002). High feeding costs limit dive time in the largest whales. *J. Exp. Biol.* **205**, 1747–1753.
- Andrews, R. D., Jones, D. R., Williams, J. D., Thorson, P. H., Oliver, G. W., Costa, D. P. and LeBoeuf, B. J. (1997). Heart rates of northern elephant seals diving at sea and resting on the beach. *J. Exp. Biol.* **200**, 2083–2095.
- Andrews, R. D., Costa, D. P., Le Boeuf, B. J. and Jones, D. R. (2000). Breathing frequencies of northern elephant seals at sea and on land revealed by heart rate spectral analysis. *Respir. Physiol.* **123**, 71–85.
- Blix, A. S. and Folkow, L. P. (1995). Daily energy-expenditure in free-living minke whales. *Acta Physiol. Scand.* **153**, 61–66.

- Boutilier, R. G., Reed, J. Z. and Fedak, M. A. (2001). Unsteady-state gas exchange and storage in diving marine mammals: the harbor porpoise and gray seal. *Am. J. Physiol. Regul. Integr. Comp. Physiol.* **281**, R490–R494.
- Brodie, P. F. (2001). The mechanics of cetacean respiration: the significance of rapid gas exchanges in a selectively tuned system, with emphasis on the porpoises (*Balaenoptera* sp.). In *Secondary Adaptations of Tetrapods to Life in Water* (ed. J. M. Mazin and V. de Buffrenil), pp. 353–362. Munchen, Germany: Verlag.
- Burgess, W. C., Tyack, P. L., Le Boeuf, B. J. and Costa, D. P. (1998). A programmable acoustic recording tag and first results from free-ranging northern elephant seals. *Deep Sea Res. Part II Top. Stud. Oceanogr.* **45**, 1327–1351.
- Butler, P. J. and Jones, D. R. (1997). Physiology of diving of birds and mammals. *Physiol. Rev.* **77**, 837–899.
- Calambokidis, J., Schorr, G. S., Steiger, G. H., Francis, J., Bakhtiari, M., Marshall, G. and Oleson, E. (2008). Insights into the underwater diving, feeding, and calling behavior of blue whales from a suction-cup attached video-imaging tag (Critercam). *MTS J.* **31**, 15–25.
- Chu, K. C. (1988). Dive times and ventilation patterns of singing humpback whales (*Megaptera novaeangliae*). *Can. J. Zool.* **66**, 1322–1327.
- Croll, D. A., Acevedo-Gutierrez, A., Tershy, B. R. and Urban-Ramirez, J. (2001). The diving behavior of blue and fin whales: is dive duration shorter than expected based on oxygen stores? *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* **129**, 797–809.
- Croll, D. A., Marinovic, B., Benson, S., Chavez, F. P., Black, N., Ternullo, R. and Tershy, B. R. (2005). From wind to whales: trophic links in a coastal upwelling system. *Mar. Ecol. Prog. Ser.* **289**, 117–130.
- Dolphin, W. F. (1987a). Dive behavior and estimated energy-expenditure of foraging humpback whales in Southeast Alaska. *Can. J. Zool.* **65**, 354–362.
- Dolphin, W. F. (1987b). Prey densities and foraging of humpback whales, *Megaptera novaeangliae*. *Experientia* **43**, 468–471.
- Dolphin, W. F. (1987c). Ventilation and dive patterns of humpback whales, *Megaptera novaeangliae*, on their Alaskan feeding grounds. *Can. J. Zool.* **65**, 83–90.
- Dolphin, W. F. (1988). Foraging dive patterns of humpback whales, *Megaptera novaeangliae*, in Southeast Alaska: a cost-benefit-analysis. *Can. J. Zool.* **66**, 2432–2441.
- Goldbogen, J. A., Calambokidis, J., Shadwick, R. E., Oleson, E. M., McDonald, M. A. and Hildebrand, J. A. (2006). Kinematics of foraging dives and lunge-feeding in fin whales. *J. Exp. Biol.* **209**, 1231–1244.
- Goldbogen, J. A., Pyenson, N. D. and Shadwick, R. E. (2007). Big gulps require high drag for fin whale lunge feeding. *Mar. Ecol. Prog. Ser.* **349**, 289–301.
- Halsey, L. G., Butler, P. J. and Blackburn, T. M. (2006). A phylogenetic analysis of the allometry of diving. *Am. Nat.* **167**, 276–287.
- Kooyman, G. L., Kerem, D. H., Campbell, W. B. and Wright, J. J. (1971). Pulmonary function in freely diving weddell seals, *Leptonychotes weddellii*. *Respir. Physiol.* **12**, 271–282.
- Krutzkowsky, G. K. and Mate, B. R. (2000). Dive and surfacing characteristics of bowhead whales (*Balaena mysticetus*) in the Beaufort and Chukchi seas. *Can. J. Zool.* **78**, 1182–1198.
- Mori, Y. (1998). Optimal choice of foraging depth in divers. *J. Zool.* **245**, 279–283.
- Ogawa, T. and Shida, T. (1950). On the sensory tubercles of lips and oral cavity in the sei and fin whale. *Sci. Rep. Whales Res. Inst.* **3**, 1–16.
- Oleson, E. M., Calambokidis, J., Burgess, W. C., McDonald, M. A., LeDuc, C. A. and Hildebrand, J. A. (2007). Behavioral context of call production by eastern North Pacific blue whales. *Mar. Ecol. Prog. Ser.* **330**, 269–284.
- Orton, L. S. and Brodie, P. F. (1987). Engulfing mechanics of fin whales. *Can. J. Zool.* **65**, 2898–2907.
- Panigada, S., Zanardelli, M., Canese, S. and Jahoda, M. (1999). How deep can baleen whales dive? *Mar. Ecol. Prog. Ser.* **187**, 309–311.
- Sato, K., Charassin, J. B., Bost, C. A. and Naito, Y. (2004). Why do macaroni penguins choose shallow body angles that result in longer descent and ascent durations? *J. Exp. Biol.* **207**, 4057–4065.
- Sato, K., Watanuki, Y., Takahashi, A., Miller, P. J. O., Tanaka, H., Kawabe, R., Ponganis, P. J., Handrich, Y., Akamatsu, T., Watanabe, Y. et al. (2007). Stroke frequency, but not swimming speed, is related to body size in free-ranging seabirds, pinnipeds and cetaceans. *Proc. R. Soc. Lond., B, Biol. Sci.* **274**, 471–477.
- Schreer, J. F. and Kovacs, K. M. (1997). Allometry of diving capacity in air-breathing vertebrates. *Can. J. Zool.* **75**, 339–358.
- Shaffer, S. A., Costa, D. P., Williams, T. M. and Ridgway, S. H. (1997). Diving and swimming performance of white whales, *Delphinapterus leucas*: An assessment of plasma lactate and blood gas levels and respiratory rates. *J. Exp. Biol.* **200**, 3091–3099.
- Slijper, E. J. (1979). *Whales*. London: Cornell University Press.
- Sparling, C. E., Georges, J. Y., Gallon, S. L., Fedak, M. and Thompson, D. (2007). How long does a dive last? foraging decisions by breath-hold divers in a patchy environment: a test of a simple model. *Anim. Behav.* **74**, 207–218.
- Stimpert, A. K., Wiley, D. N., Au, W. W. L., Johnson, M. P. and Arsenault, R. (2007). 'Megapclicks': acoustic click trains and buzzes produced during night-time foraging of humpback whales (*Megaptera novaeangliae*). *Biol. Lett.* **3**, 467–470.
- Thompson, D. and Fedak, M. A. (1993). Cardiac responses of gray seals during diving at sea. *J. Exp. Biol.* **174**, 139–164.
- Thompson, D. and Fedak, M. A. (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.
- Werth, A. J. (2000). Feeding in marine mammals. In *Feeding: Form, Function and Evolution in Tetrapod Vertebrates* (ed. K. Schwenk), pp. 475–514. New York: Academic Press.
- Williams, T. M., Haun, J. E. and Friedl, W. A. (1999). The diving physiology of bottlenose dolphins (*Tursiops truncatus*) I. Balancing the demands of exercise for energy conservation at depth. *J. Exp. Biol.* **202**, 2739–2748.