

High feeding costs limit dive time in the largest whales

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Summary

Large body size usually extends dive duration in air-breathing vertebrates. However, the two largest predators on earth, the blue whale (*Balaenoptera musculus*) and the fin whale (*B. physalus*), perform short dives for their size. Here, we test the hypothesis that the foraging behavior of these two species (lunge-feeding) is energetically expensive and limits their dive duration. We estimated the cost of lunge-feeding in both species using an approach that combined attaching time/depth recorders to seven blue whales and eight fin whales and comparing the collected dive information with predictions made by optimality models of dive behavior. We show that the rate at which whales recovered from a foraging dive was twice that of a non-foraging dive and that the cost of foraging relative to the cost of travel to and from the prey patch was 3.15 in

blue whales (95% CI 2.58–3.72) and 3.60 in fin whales (95% CI 2.35–4.85). Whales foraged in small areas (<1 km²) and foraging bouts lasted more than one dive, indicating that prey did not disperse and thus that prey dispersal could not account for the limited dive durations of the whales. Despite the enormous size of blue whales and fin whales, the high energetic costs of lunge-feeding confine them to short durations of submergence and to areas with dense prey aggregations. As a corollary, because of their limited foraging time under water, these whales may be particularly vulnerable to perturbations in prey abundance.

Key words: foraging, diving, feeding costs, blue whale, *Balaenoptera musculus*, fin whale, *Balaenoptera physalus*.

Introduction

Large body size allows air-breathing vertebrates to increase their oxygen stores and thus prolong underwater foraging duration (Hochachka and Somero, 1984; Kooyman, 1989). The largest air-breathing vertebrates are the blue whale (*Balaenoptera musculus*) and the fin whale (*B. physalus*). Adult blue whales average 24.7 m in length and 92 671 kg in mass, adult fin whales average 21.2 m in length and 52 584 kg in mass (Nishiwaki, 1950). Nonetheless, these two whales spend no more time under water than smaller species diving to similar depths (Croll et al., 2001).

Oxygen is a limiting factor in air-breathing vertebrates, and some marine mammals, including the blue whale, glide during a dive, a behavior that appears to reduce oxygen consumption (Williams et al., 2000; Davis et al., 2001; Nowacek et al., 2001). The amount of time that a diver is able to remain under water relying solely on its oxygen stores is called the theoretical aerobic dive limit (TADL) and is calculated by estimating the oxygen stores and diving metabolic rate of a species, usually on the basis of body mass (Kooyman, 1989; Boyd, 1997). The TADLs of blue and fin whales are 31.2 and 28.6 min, respectively, yet their foraging dives average only 7.8 and 6.3 min (Croll et al., 2001); the largest predators on earth have the shortest dive durations relative to their TADL.

Three hypotheses may explain the discrepancy between measured and predicted dive durations in blue whales and fin whales. (i) Prey are found in shallow waters and thus dive durations are short. This is because in most circumstances dive duration is positively correlated with dive depth (Kramer, 1988; Houston and Carbone, 1992). However, blue whales and fin whales generally forage on prey aggregations at depths greater than 100 m (Panigada et al., 1999; Croll et al., 2001). (ii) Prey disperse quickly, forcing whales to feed elsewhere (Croll et al., 2001). However, euphausiids maintain dense aggregations for several days, even when whales are foraging in the area (Simrad and Laroie, 1999). (iii) The rate of energy expenditure is greater amongst foraging blue whales and fin whales than for other divers. This could result from lunge-feeding, which may be an energetically expensive behavior that consumes much oxygen and limits blue whales and fin whales to dives that are of shorter duration than their TADL (Croll et al., 2001).

Blue and fin whales feed by lunging forward to engulf water that contains prey, such as small (<4 cm) euphausiid crustaceans (Kawamura, 1980). Prey items are filtered through keratinized plates called baleen. When lunging, the mouth and throat engulf a mass of water representing nearly 70% of the

whale's body mass per lunge (Pivorunas, 1979) (see Fig. 1). The fast forward swimming motion of the whale and the displacement of the tongue, which invaginates to form a hollow structure, force water and prey into the mouth (Lambertsen, 1983). When euphausiids have been engulfed, the lower jaw is closed and water is forced through the baleen (Pivorunas, 1979). When feeding at the surface, whales breathe immediately after each lunge; however, when feeding at depth, they lunge up to eight times before coming to the surface to breathe (Tershy et al., 1993; Croll et al., 2001). Lunging has been termed 'the largest biomechanical action in the animal kingdom' (Brodie, 1983). However, the cost of lunge-feeding has not been measured.

We estimated the cost of lunge-feeding by attaching time/depth recorders (TDRs) to seven blue whales and eight fin whales and comparing the observed dive behavior with predictions made by optimality models of diving (Houston and Carbone, 1992). Animals increasingly deplete their oxygen stores as the cost of a dive increases and therefore need more time to replenish oxygen stores at the surface after the dive (Kooyman et al., 1980). Costs are measured in oxygen utilized; however, we indirectly estimated the costs of lunge-feeding by measuring the time needed to recover at the surface after a dive. Specifically, we examined the prediction that the recovery time of blue whales and fin whales after a dive, measured to normalize for dive duration as the rate of increase in time spent at the surface as dive duration increased, would be positively related to the number of lunges per dive. If this were true, a lunging-costly model should provide the best fit to the observed dive durations.

Materials and methods

Remote-sensing techniques

To collect data on lunge behavior and dive duration, we attached TDRs to seven blue whales (*Balaenoptera musculus*) and eight fin whales (*B. physalus*) along the coasts of Baja California, Mexico, and California, USA. We followed the methodology described in Croll et al. (1998). Briefly, tags were attached to the dorsal surface of the whale 2–3 m caudal of the blowhole using a compound crossbow. They were deployed from a small skiff (<7 m). Each tag had three components: (i) a TDR (Wildlife Computers, Redmond, USA), (ii) a VHF radio transmitter (Advanced Telemetry Systems, Isanti, USA) to track the tagged whale, and (iii) a radio-activated release mechanism (Jamie Stamps, Livermore, USA). Time and depth were logged at 1 s intervals. Upon tagging, each whale was followed in a 15 m vessel at a distance of 100–200 m to record its location with a global positioning system (GPS) every time it came to the surface.

Once the tag had been released from the whale, we localized it with the directional VHF system. Dive data were analyzed using software provided by the TDR manufacturer (Dive Analysis, Wildlife Computers). We

considered individual whales to be independent observations and calculated the median values of dive parameters for each. We defined a dive as any period under water at depths of 20 m or greater and a surface interval as the post-dive duration at depths of 2 m or less. The software Dive Analysis automatically calculated mean ascent and descent rates of dive.

In a profile of time *versus* depth, an upward movement of 8 m or more followed by a downward movement characterized certain dives. (Fig. 1A). Whales move significantly faster during the ascent portion than during the descent portion of such excursions, each of which lasts less than 1 min (Croll et al., 2001; present study). In addition, the depth of such vertical excursions corresponds with regions of densely aggregated euphausiids (Croll et al., 1998). Thus, following Croll et al. (2001), each such excursion was counted as a foraging lunge; whales were considered to be foraging if the profile of time *versus* depth showed one or more lunges during the dive (Fig. 1A) and non-

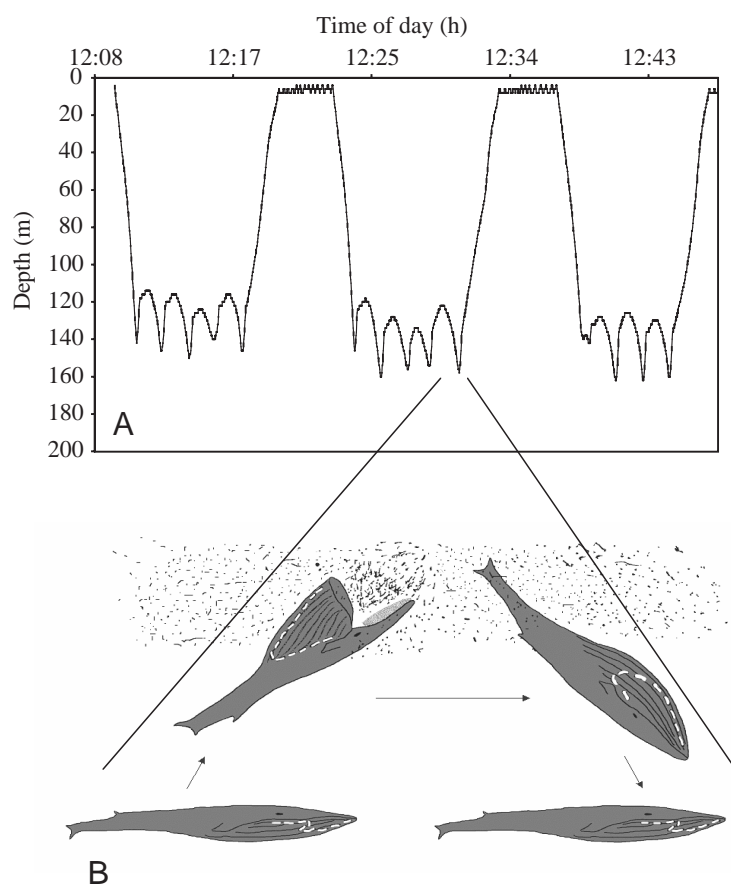


Fig. 1. Lunge-feeding in blue whales and fin whales. (A) A series of three foraging dives. Each spike at the bottom represents a lunge. (B) Representation of one vertical lunge at depth. During a vertical lunge, whales move significantly faster during the ascent than during the descent (Croll et al., 2001), and underwater video recordings indicate that whales lunge upside-down (J. Calambokidis, personal communication, Cascadia Research Collective, 218½ West Fourth Avenue, Olympia, WA 98501, USA). Thus, the whale is depicted upside-down and lunging upwards, with the dashed line indicating the invagination of the tongue. Modified from Berta and Sumich (1999).

foraging if no lunges were recorded. Because *Balaenoptera* whales have been observed lunging horizontally at the surface (Tershy et al., 1993), it is possible that such horizontal lunges also occur at depth. However, in a profile of time *versus* depth, it would not be possible to discern whether a whale lunged horizontally. Thus, we only analyzed non-foraging dives in which the whale dived directly to depth and returned to the surface without spending time at depth (Croll et al., 2001).

Recovery time at the surface

To assess whether whales incurred a cost by lunge-feeding, we employed the rate of increase of the time spent recovering at the surface as dive duration increases. This rate was defined as the slope *b* of the fitted lines between dive duration and time at the surface after the dive. The higher the value of the slope, the longer the time that the whale spent recovering at the surface as dive duration increased. In this manner, we discarded the confounding effect of dive duration since longer dives require more time at the surface (Kooyman, 1989). We divided the slope of foraging dives by the slope of non-foraging dives and thus defined relative rates of increase of the time spent recovering at the surface. We tested with an order of heterogeneity test the prediction that as the number of lunges per dive increased these relative rates would also increase. An order of heterogeneity test allows comparison of three or more populations against simply ordered alternative hypotheses (Rice and Gaines, 1994). It is a directional test that allowed us to detect differences in the relative rate of the time needed to recover among distinct lunge classes from expected lowest (zero lunges) to expected highest (four lunges).

Optimality models

We compared the observed values of dive duration with the values predicted by optimality models assuming either a metabolic cost of feeding or no cost of feeding (Houston and Carbone, 1992), which we termed the lunging-costly and the no-cost models, respectively. The optimality models employ foraging time at different water depths as currency. Thus, we added predicted foraging time and observed travel time to obtain theoretical dive durations, which were compared with the observed dive durations obtained from TDR data. Travel time was the time that a whale spent moving to and from the surface and was calculated by subtracting the foraging time (defined as the time spent at depths greater than 75% of the maximum depth of dive) from the dive duration. Two equations maximizing foraging time in divers allowed us to obtain predicted foraging

time for both the no-cost and the lunging-costly models (Houston and Carbone, 1992):

$$(s^*) = [K(1 - e^{-\alpha s}) - (m_1 \tau_i)] / (\tau + s^*) \tag{1}$$

defines optimal surface time, and:

$$t^*_i = [K(1 - e^{-\alpha s^*_i}) - (m_1 \tau_i)] / m_2 \tag{2}$$

defines optimal foraging time, where $K=31.2$ min or 28.6 min, the TADL of blue and fin whales, respectively (Croll et al., 2001), α is exchange rate of oxygen at the surface (dimensionless)=0.5 (half the rate of oxygen use while diving;

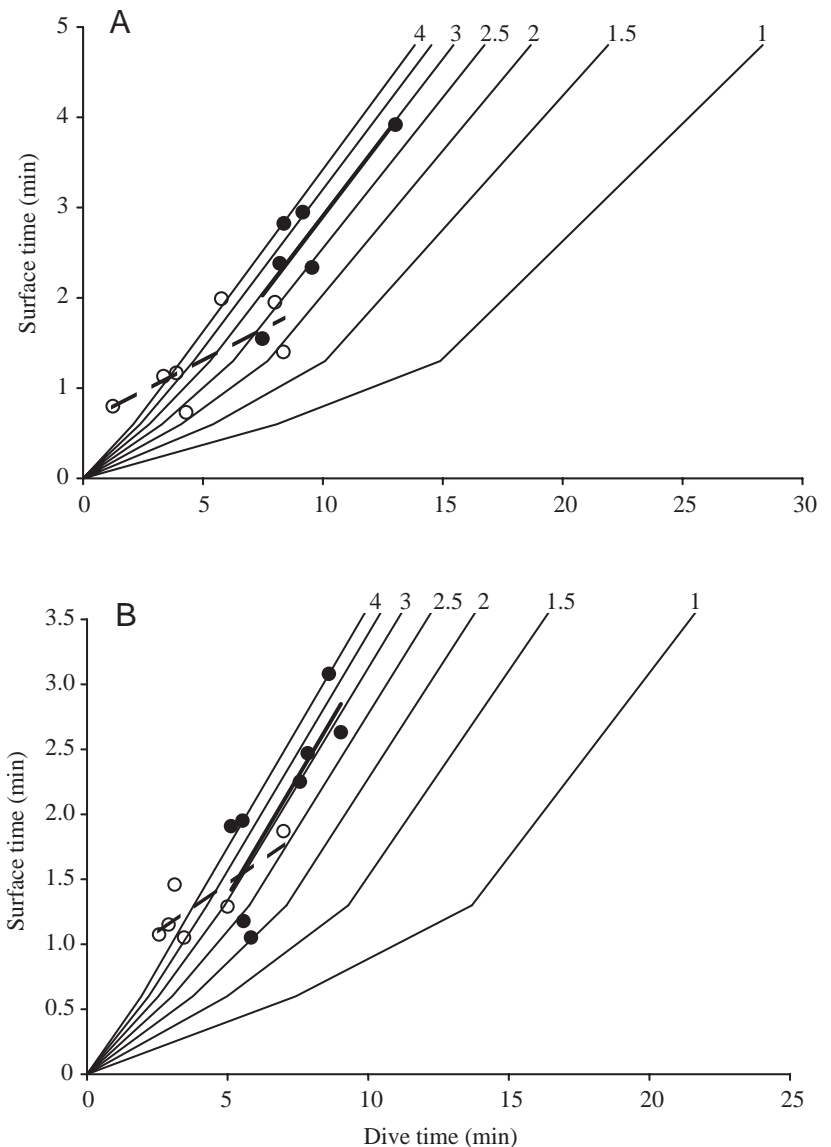


Fig. 2. Time spent at the surface relative to dive duration. (A) Blue whales; (B) fin whales. For clarity, we depict only non-foraging dives and three-lunge foraging dives. The different slopes between non-foraging and foraging dives indicate that lunge-feeding incurred a cost. Dashed lines, open circles, non-foraging dives; bold solid lines, filled circles, three-lunge foraging dives. The thin solid lines indicate the predicted surface time according to different values of the cost of foraging relative to the cost of traveling to and from the prey patch. Note that for three-lunge foraging dives the relative cost of foraging appears to be 3 for both species.

Houston and Carbone, 1992), m_1 is the rate of use of oxygen while diving (dimensionless)=1 (the proportion of the metabolic rate employed to estimate K ; Houston and Carbone, 1992), m_2 is the rate of use of oxygen while foraging, τ is travel time to and from the prey patch, s is surface time and t is foraging time. An asterisk indicates the optimal value of a variable.

Because these are optimality models, the subscript 'i' indicates that different values of time spent recovering at the surface (s) correspond to different travel times (τ). To obtain the predicted foraging time for the no-cost model, we defined m_2 as 1, i.e. the cost of foraging equals the cost of traveling to and from the prey patch (Houston and Carbone, 1992). To obtain the predicted foraging times for the lunging-costly model, we solved for m_2 to obtain the cost of foraging relative to the cost of traveling to and from the prey patch. We obtained a common cost for foraging dives by randomly selecting only one foraging dive from each individual.

Results

Post-dive surface intervals increased rapidly with increasing number of lunges per dive normalized for dive duration, indicating that lunge-feeding exacted an energetic cost on the whales (blue whales, zero lunges, $b=0.14$, $P=0.073$; one lunge, $b=0.14$, $P=0.328$; two lunges, $b=0.29$, $P=0.043$; three lunges, $b=0.35$, $P=0.025$; four lunges, $b=0.37$, $P=0.098$; fin whales, zero lunges, $b=0.20$, $P=0.017$; one lunge, $b=0.16$, $P=0.132$; two lunges, $b=0.30$, $P=0.001$; three lunges, $b=0.37$, $P=0.014$; four lunges, $b=0.41$, $P=0.035$) (Fig. 2). The relative rate of increase of the time spent recovering at the surface also increased with number of lunges per dive indicating that, as the number of lunges per dive increased, the two whale species spent more time recovering at the surface (order of heterogeneity test, blue whales, $OH=0.57$, $P=0.036$; fin whales, $OH=0.67$, $P=0.017$) (Fig. 3).

One-lunge dives had a similar relative rate of increase of the time spent recovering at the surface to non-foraging dives (Fig. 3). Thus, they were different from the rest of the foraging dives. We hypothesize that this is because whales exerted the least effort per lunge when lunging once; because of this, we continued the analysis only for dives with two or more lunges per dive. Lunge velocity and distance increased in blue whales from $1.5\pm 0.90\text{ m s}^{-1}$ and $24.0\pm 11.37\text{ m}$ ($N=6$), respectively, in dives with one lunge to $2.6\pm 0.95\text{ m s}^{-1}$ and $34.7\pm 8.07\text{ m}$ ($N=6$), respectively, in dives with two or more lunges (means \pm s.d.; paired t -test; distance, $t_5=-3.08$, $P=0.027$; velocity, $t_5=-4.47$, $P=0.007$). Similarly, lunge velocity and distance increased in fin whales from $1.5\pm 0.37\text{ m s}^{-1}$ and $17.3\pm 6.57\text{ m}$ ($N=8$) to $1.8\pm 0.31\text{ m s}^{-1}$ and $23.3\pm 2.83\text{ m}$ ($N=8$) (means \pm s.d.; paired t -test, distance, $t_7=-2.39$, $P=0.048$; velocity, $t_7=-2.61$, $P=0.035$).

The optimality models provided a good fit to the observed foraging time for dives with two or more lunges (Fig. 4). The relative cost of foraging was 3.15 for blue

whales and 3.60 for fin whales (blue whales, 95 % CI 2.58–3.72, $r^2_{\text{obs-pred}}=0.624$; fin whales, 95 % CI 2.35–4.85, $r^2_{\text{obs-pred}}=0.615$). In all cases, the observed foraging time was far shorter than that predicted by the no-cost model (Fig. 4). Whales foraged at depths greater than 100 m: maximum depth of dive averaged $132.0\pm 48.87\text{ m}$ in blue whales and $102.0\pm 40.77\text{ m}$ in fin whales during two-lunge dives ($N=4$ blue whales, $N=8$ fin whales), $157.3\pm 33.27\text{ m}$ in blue whales and $113.3\pm 36.00\text{ m}$ in fin whales during three-lunge dives ($N=6$ blue whales, $N=8$ fin whales) and $150.3\pm 52.09\text{ m}$ in blue whales and $109.8\pm 34.62\text{ m}$ in fin whales during four-lunge dives (means \pm s.d.) ($N=7$ blue whales, $N=5$ fin whales).

Absolute differences between predicted and observed dive durations were smaller in the lunging-costly model than in the no-cost model for dives with two or more lunges (paired t -test; blue whales, two lunges, $t_3=-9.94$, $P=0.002$; three lunges, $t_5=-15.55$, $P<0.001$; four lunges, $t_6=-10.91$, $P<0.001$; fin whales, two lunges, $t_7=-15.03$, $P<0.001$; three lunges, $t_7=-10.81$, $P<0.001$; four lunges, $t_4=-3.68$, $P=0.021$) (Fig. 5).

Whales increased their vertical speed at the beginning of each lunge, suggesting that the costs of lunge-feeding were related to the effort needed to accelerate their large body. The vertical speed of blue whales at the beginning of a lunge averaged $1.3\pm 0.39\text{ m s}^{-1}$ and at the mid-point of the ascent it had increased to $2.9\pm 0.85\text{ m s}^{-1}$, up to a maximum of 4.0 m s^{-1} (means \pm s.d., paired t -test, $t_6=-5.51$, $P=0.002$). The vertical speed of fin whales at the beginning of a lunge averaged $2.3\pm 1.66\text{ m s}^{-1}$ and at the mid-point of

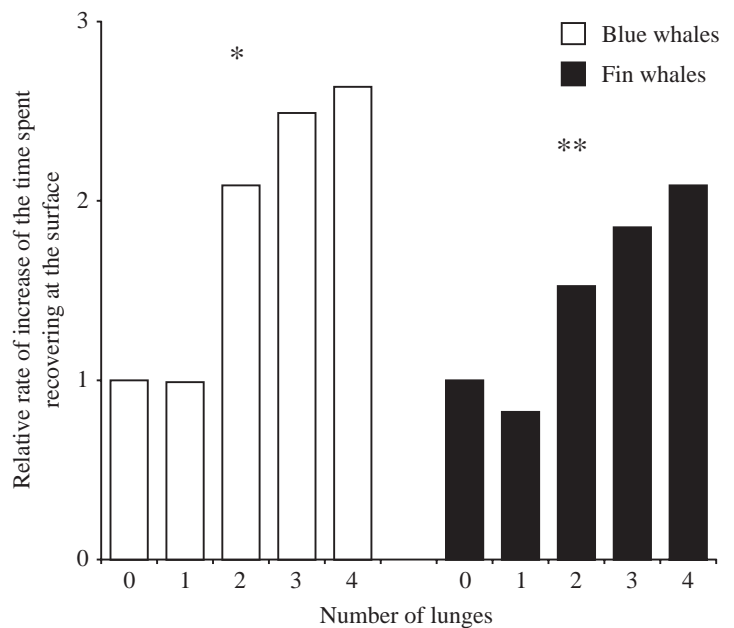


Fig. 3. The relative rate of increase of the time spent recovering at the surface after a dive significantly increased with the number of lunges per dive. That is, whales spent more time recovering at the surface as the number of lunges per dive increased. By definition, zero-lunge dives are non-foraging dives. * $P<0.05$, ** $P<0.01$.

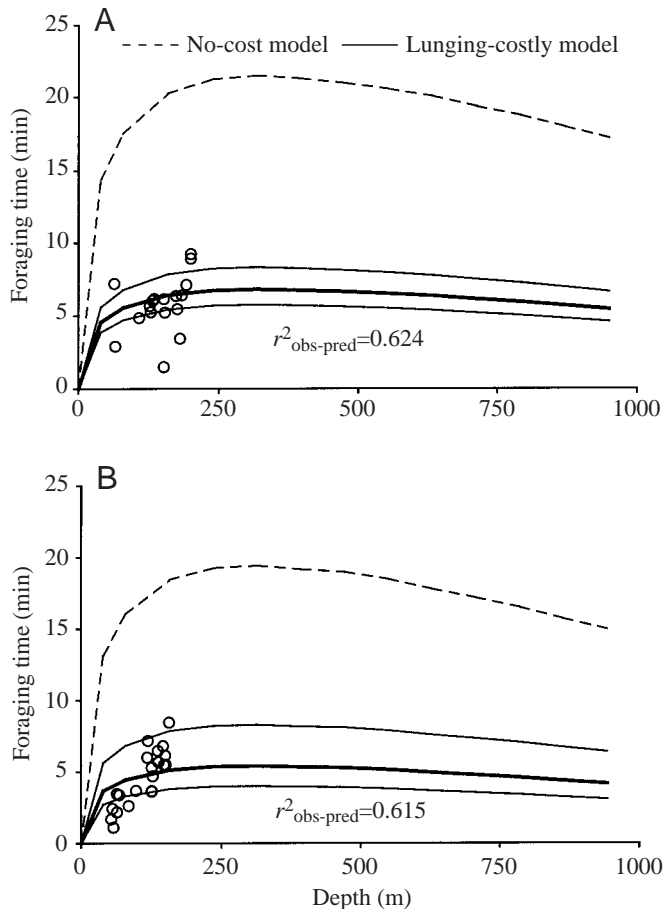


Fig. 4. Foraging time relative to dive depth. Open circles indicate observed foraging times for dives with two or more lunges. The solid lines indicate the predicted foraging time $\pm 95\%$ CI according to the lunging-costly model. The broken line indicates the predicted foraging time according to the no-cost model. Values of r^2 are for the lunging-costly models. (A) Blue whales. On the basis of the lunging-costly model, the cost of foraging relative to the cost of travel to and from the prey patch was 3.15 (95% CI 2.58–3.72). (B) Fin whales. On the basis of the lunging-costly model, the cost of foraging relative to the cost of travel to and from the prey patch was 3.60 (95% CI 2.35–4.85).

the ascent it had increased to $5.0 \pm 3.16 \text{ m s}^{-1}$, up to a maximum of 10.7 m s^{-1} (means \pm S.D., paired t -test, $t_7 = -4.08$, $P = 0.005$). The ascent phase of lunges averaged $34.2 \pm 13.49 \text{ s}$ and $32.9 \pm 6.74 \text{ s}$ in blue whales and fin whales, respectively (means \pm S.D., $N = 7$ blue whales, $N = 8$ fin whales for all values in paragraph).

Foraging in both whale species occurred in areas smaller than 1 km^2 for extended periods, suggesting that the prey did not disperse. The distance between foraging dives averaged $525.4 \pm 144.98 \text{ m}$ and $895.7 \pm 198.09 \text{ m}$ in blue whales and fin whales, respectively (means \pm S.D., $N = 5$ blue whales, $N = 5$ fin whales). Foraging bouts consisted of 9.1 ± 8.90 dives and 10.9 ± 10.15 dives in blue whales and fin whales, respectively (means \pm S.D., $N = 7$ blue whales, $N = 8$ fin whales).

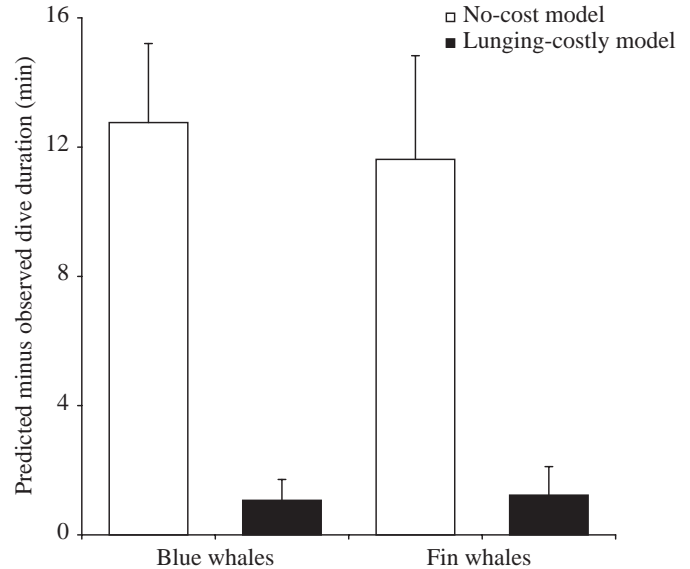


Fig. 5. The lunging-costly model predicted dive duration better than the no-cost model for dives with two or more lunges. Thus, we combined those dives in the graph for clarity. Error bars indicate S.D. ($N = 7$ for blue whales, $N = 8$ for fin whales).

Discussion

Our data support the hypothesis that lunge-feeding is energetically expensive and limits foraging time and dive duration in blue whales and fin whales. Lunge-feeding incurred a cost in the two species as measured by the rate of increase of the time spent recovering at the surface (Figs 2, 3). This cost was similar for both whale species and estimated to be three times larger than the cost of traveling to and from the prey patch (Fig. 4). In addition, this cost best explained the observed foraging times and dive durations (Figs 4, 5). We suggest that the high costs of lunge-feeding were due to the increases in speed sustained for approximately 30 s during the ascent phase of a lunge in combination with the drag created by moving the open mouth through the water at speeds above 3 m s^{-1} . The similar costs of one-lunge dives and non-foraging dives can be explained by the reduced effort incurred by whales when lunging only once during a dive. Thus, one-lunge dives may have represented exploratory dives in which whales assessed whether the concentration of prey was large enough to warrant foraging. This suggests that a foraging threshold occurs in these whales (Croll et al., 1998; Simrad and Laroie, 1999).

Non-foraging dives of blue whales and fin whales were shorter than foraging dives. However, this is an expected result since, when not foraging, whales are merely traveling from one prey patch to another, presumably not attempting to maximize the time spent under water, and performing shallow dives between 20 and 30 m in depth (Croll et al., 2001). Even if a diver is attempting to maximize time spent foraging, the rate of energetic gain or energetic efficiency optimality models predict a positive relationship between dive duration and dive depth (Kramer, 1988; Houston and Carbone, 1992). This prediction is supported by empirical evidence (for a review,

see Schreer and Kovacs, 1997). The only exception to this positive relationship between dive duration and dive depth occurs when the cost of foraging is smaller than the cost of travel (Houston and Carbone, 1992), which was clearly not the case for blue whales and fin whales.

The horizontal distances that blue whales and fin whales covered while foraging are well within the size of euphausiid aggregations (approximately 5000–10 000 m in one dimension) upon which the whales typically feed (Croll et al., 1998; Simrad and Laroie, 1999). This result, and the observation that consecutive foraging bouts consisted of more than one dive, indicates that prey did not disperse and that whales were foraging on the same aggregation of euphausiids.

In view of the high cost of lunge-feeding, large whales that do not employ this mechanism should dive for longer than blue whales or fin whales. This prediction is supported by data from bowhead whales (*Balaena mysticetus*). Adult bowhead whales average 48 250 kg in mass, 48 % less than blue whales (Croll et al., 2001), yet they spend more time foraging under water (1.5–2 times) and less time recovering from a dive (0.5 times) than blue whales diving to comparable depths (Dorsey et al., 1989; Krutzikowsky and Mate, 2000). Bowhead whales are able to reduce their feeding costs by maintaining a constant depth and a consistent stroke rate and by burst-and-glide swimming (Nowacek et al., 2001). In addition, bowhead whales are slow swimmers, and a close relative, the right whale (*Balaena glacialis*), averages only 0.7 m s⁻¹ when feeding at depth (Goodyear, 1995). In contrast, during each lunge, blue whales and fin whales accelerate their large bodies to reach remarkable speeds, frequently changing depths and moving against the force of gravity. We hypothesize that the feeding costs of bowhead whales are low because of their energy-saving behaviors and because they move more slowly than blue whales and fin whales.

High feeding costs have been shown to maintain populations of endangered species at low levels (Gorman et al., 1998). Blue whales are a critically endangered species despite a decade of moratorium on commercial whaling (Clapham et al., 1999). Factors involved in the slow recovery of blue whales may include their small population size after whaling was banned (Clapham et al., 1999), their dependence on euphausiids as food (Kawamura, 1980), the long-term negative trend in the abundance of euphausiids in relation to changes in global climate (Loeb et al., 1997; Siegel et al., 1998) and the high costs of lunge-feeding.

Lunge-feeding is an impressive biomechanical event that comes at a high energetic cost. At the physiological level, it limits foraging time and dive duration despite the fact that blue whales, and presumably fin whales, glide during a dive, thus saving energy (Williams et al., 2000). At the ecological level, it confines blue whales and fin whales to areas with dense prey aggregations and may make them particularly vulnerable to perturbations in prey abundance. Paradoxically, the behavior that allows these whales to exploit the patchy and ephemeral resources of the ocean limits them to short foraging dives in productive regions such as submarine canyons or the Southern

Boundary of the Antarctic Circumpolar Current (Croll et al., 1998; Tynan, 1998).

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