Scaling of lunge-feeding performance in rorqual whales: mass-specific energy expenditure increases with body size and progressively limits diving capacity

Jeremy A. Goldbogen*,[1], John Calambokidis[1], Donald A. Croll[2], Megan F. McKenna[3], Erin Oleson[4], Jean Potvin[5], Nicholas D. Pyenson[6], Greg Schorr[1], Robert E. Shadwick[7] and Bernie R. Tershy[3]

[1]*Cascadia Research Collective, 218½ W. 4th Ave, Olympia, Washington 98501, USA;* [2]*Department of Ecology and Evolutionary Biology, Center for Ocean Health, 100 Shaffer Road, University of California, Santa Cruz, California 95060, USA;* [3]*Scripps Institution of Oceanography, University of California, San Diego, 9500 Gilman Dr., La Jolla, California 92093, USA;* [4]*Pacific Islands Fisheries Science Center, 2570 Dole Street, Honolulu, HI 96822-2396, USA;* [5]*Department of Physics, Saint Louis University, 3450 Lindell Boulevard, St. Louis, Missouri 63103, USA;* [6]*Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, PO Box 37012, MRC 121, Washington, DC 20013-7012, USA; and* [7]*Department of Zoology, University of British Columbia, #4200-6270 University Blvd., Vancouver, British Columbia, Canada*

Summary

1. Diving capacity generally increases with body size both within and among taxanomic groups because of the differential scaling between body oxygen stores and metabolic rate.

2. Despite being some of the largest animals of all time, rorqual whales exhibit very short dive times relative to other large divers because of the high energetic costs incurred during lunge feeding. This mode of filter feeding requires high drag for the engulfment of large volumes of prey-laden water, and the magnitude of both drag and engulfment volume is largely determined by the size and shape of the skull.

3. The positive allometry of rorqual skulls increases mass-specific engulfment capacity in larger whales, but the energetic requirements of feeding are also predicted to increase and thus further limit diving capacity.

4. To test the hypothesis that the energetic cost of a lunge is disproportionately higher in larger rorquals, we compared diving and lunge-feeding performance among three different-sized species (blue, fin and humpback whales) foraging on krill.

5. Our hydrodynamic analyses indicate that the mass-specific energy expenditure will increase with body size if rorquals lunge at length-specific speeds (in body lengths per second) that are independent of body size, a condition that is supported by tag data.

6. Although the absolute time required to filter each volume of water increased with body size, maximum dive duration and depth were not significantly different among species. As a consequence, the maximum number of lunges executed per dive decreased with body size.

7. These data suggest that, unlike all other true divers, adult rorqual species do not exhibit a positive relationship between body size and diving capacity. Larger rorquals forfeit diving capacity for greater engulfment capacity, a trade-off that favours the efficient exploitation of patchily dense prey aggregations. Such a trade-off may underlie different foraging strategies associated with resource partitioning, life history and ecological niche.

Key-words: allometry, balaenopteridae, diving, drag, energetics, engulfment, filter feeding, rorqual, scaling, whale

Introduction

Body size is a prime determinant of how animals function at all levels of biological organization (Schmidt-Nielsen 1984).

*Correspondence author. E-mail: jgoldbogen@gmail.com

Scale effects on the efficiency of metabolic rate (White, Blackburn & Seymour 2009), as modulated by lifestyle (Sibly & Brown 2007) and activity (Suarez & Darveau 2005), determine the rate at which animals acquire and expend energy. The size dependence of metabolic rate, where larger animals generally exhibit lower mass-specific rates of metabolism, represents a major constraint that influences how animals interact with their environment (Peters 1983). Large body size necessitates high absolute energetic requirements, but it also grants low relative rates of production (energy use per unit body mass) and therefore many physiological and ecological advantages. Such size-related functional constraints ultimately shape animal behaviour, performance and life history (Dial, Greene & Irschick 2008). Although many aspects of vertebrate ecology are explained in this context, relatively little is known about how these body size trade-offs affect specific activities in their natural environment – particularly at the extreme upper limit of body mass.

The largest vertebrates of all time are predominately suspension filter feeders in the marine environment and include baleen whales (Werth 2000), elasmobranchs (Sanderson & Wassersug 1993) and bony fishes (Friedman *et al.* 2010). By feeding in bulk on patchy, but dense prey patches, this strategy confers high energetic efficiency and thus supports the maintenance of extremely large body size (Goldbogen *et al.* 2011). Unlike filter-feeding fishes (Gleiss, Norman & Wilson

2011), however, the extent to which baleen whales can exploit prey at depth is limited by their breath-hold diving capacity. The ability to dive longer and therefore deeper is determined by the level of oxygen stores within the body, the rate of oxygen consumption (i.e. metabolic rate) and hypoxemic tolerance (Kooyman 1989; Butler & Jones 1997). Diving capacity generally increases with body size because larger animals deplete their oxygen stores, which are assumed to be isometric (Lasiewski & Calder 1971; Hudson & Jones 1986), at a lower mass-specific rate than smaller animals (Butler & Jones 1982; Halsey, Butler & Blackburn 2006). Such enhanced diving capacity, therefore, should confer an advantage to larger whales by (i) enabling access to deeper and potentially higher quality (i.e. denser) prey and (ii) allowing longer dives and therefore more time to search for and exploit prey patches.

Electronic tagging studies (Fig. 1a,b) have shown that some baleen whale species, such as bowhead whales *Balaena mysticetus* (Balaenidae), exhibit dive durations that are consistent with their large body size (Krutzikowsky & Mate 2000). However, similar studies on large rorquals (Balaenopteridae) indicate a very limited dive capacity for blue, fin and humpback whales, where dive times are roughly half of that predicted by body size (Croll *et al.* 2001; Goldbogen *et al.* 2008; Doniol-Valcroze *et al.* 2011). The discrepancy between balaenids and balaenopterids is attributed to the energetic consequences associated with the different filtering modes employed by each family (Acevedo-Gutierrez, Croll & Tershy 2002). Balaenids
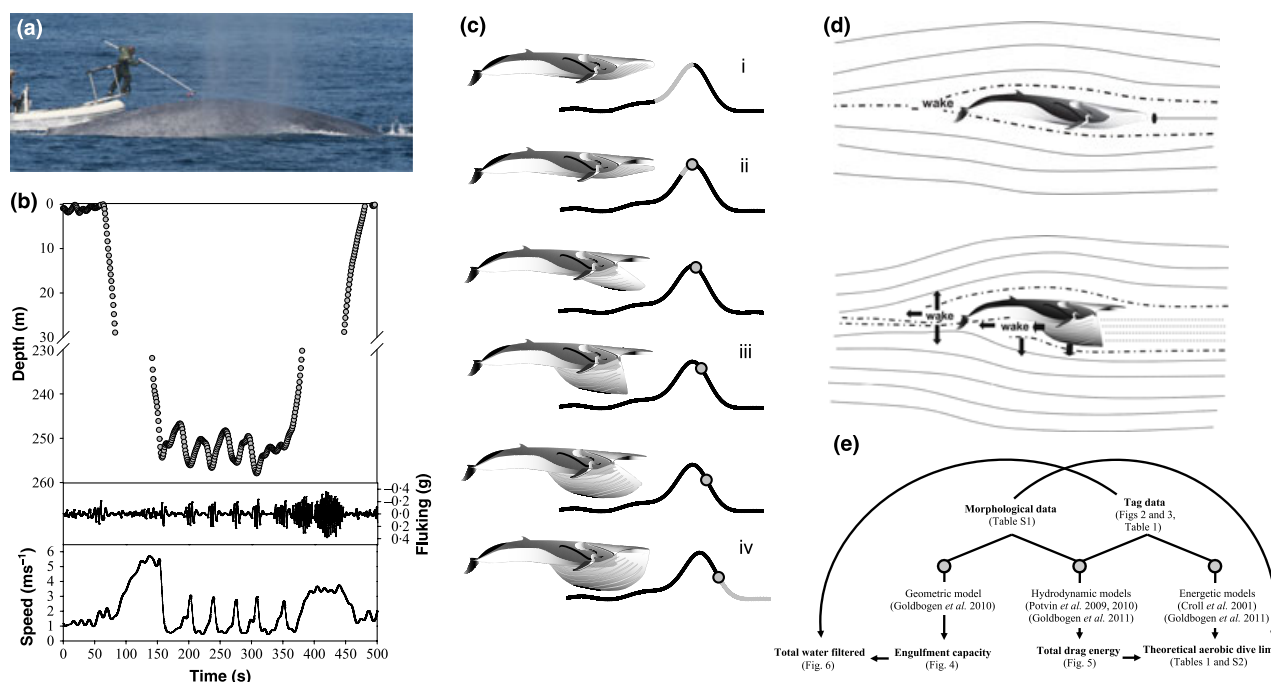
Fig. 1. Methodology and analytical approach. (a) Deploying an acoustic tag on a surfacing blue whale. (b) An example of a fin whale foraging dive that includes six lunges (one lunge at the end of descent) at depth. (c) Predicted changes in gape angle during a single fin whale lunge: (i) pre-engulfment acceleration, (ii) the beginning of engulfment at mouth opening at (or just prior to) maximum velocity, (iii) maximum gape and (iv) the end of engulfment at mouth closure and the beginning of the purging phase. Black lines show the velocity profile of a single lunge. Grey lines highlight different phases of the lunge, and grey dots show the progression of gape angle changes along the velocity profile. (d) Theoretical changes in flow during engulfment for external flow (solid lines), near boundary flow (thick dotted and dashed lines) and internal flow (thin dashed grey lines). Drag acting on a lunge-feeding whale consists of shape drag from external flow around the body and engulfment drag from the acceleration of fluid inside the mouth (internal flow). (e) Flow chart for the different data sets and modelling used in this study.

capture prey using continuous ram filtration at slow, steady speeds (Werth 2004; Simon *et al.* 2009). In contrast, balaenopterids are lunge feeders that intermittently engulf large volumes of prey and water. This bulk filter-feeding strategy is a dynamic process that involves extremely high drag (Goldbogen, Pyenson & Shadwick 2007); the work required to overcome high drag during lunge feeding at depth causes a rapid depletion in body oxygen stores and thus limits dive time.

Lunge feeding consists of three phases: pre-engulfment, engulfment of water and prey, and the purging or filtering of engulfed water (Fig. 1c). During pre-engulfment, the whale accelerates to high speed. At maximum velocity, or just prior to, the whale begins to open its mouth to extremely large gape angles, thereby allowing a flux of water into the mouth and the expansion of the buccal cavity. During engulfment, the tongue inverts and expands into a capacious sac that contains the engulfed water mass (Lambertsen, Ulrich & Straley 1995). The extensible buccal cavity is bounded by several well-developed muscle layers and elastic blubber that comprise the ventral groove system (Orton & Brodie 1987).

Unsteady hydrodynamic models of lunge feeding suggest that the inflation of the buccal cavity is resisted (i.e. slowed down) and controlled by the eccentric contraction of the muscles associated with the ventral groove blubber (Potvin, Goldbogen & Shadwick 2009). Such a mechanism implies, by virtue of action–reaction, that the engulfed water mass is gradually accelerated forward in the direction of the lunge. The acceleration of engulfed fluid from inside the mouth produces a novel source of drag, as shown in Fig. 1d), in addition to that generated from flow around the body (Potvin, Goldbogen & Shadwick 2009). The net drag acting on a rorqual rapidly dissipates the kinetic energy of the body as the jaws close around the engulfed water (Goldbogen *et al.* 2006; Goldbogen, Pyenson & Shadwick 2007). Because multiple lunges occur one after another at the bottom of deep foraging dives, the rorqual must re-accelerate from a lower speed to execute the next lunge. The mechanical work required to (i) accelerate the body prior to engulfment, (ii) accelerate the engulfed water during engulfment and (iii) swim against drag as the mouth is agape at high speed, represent major sources of energy expenditure during lunge feeding (Potvin, Goldbogen & Shadwick 2010). This energetic cost is thought to accelerate the depletion of oxygen stores at depth, thus limiting the maximum duration of a dive in large rorquals (Acevedo-Gutierrez, Croll & Tershy 2002).

The magnitude of the engulfed water mass and the amount of drag sustained during a lunge are primarily determined by the projected area of the mouth aperture (Goldbogen, Pyenson & Shadwick 2007). The morphology of the skull (i.e. the size and shape of the mandibles) delimits mouth area and thus represents a key factor in the mechanics of lunge feeding (Potvin, Goldbogen & Shadwick 2009). The duration and magnitude of the forces at play during lunge feeding, in turn, ultimately determine the energy expenditure of engulfment (Potvin, Goldbogen & Shadwick 2010). Morphometric analyses have demonstrated that the dimensions of the engulfment apparatus (skull, mandibles and ventral groove blubber that bounds the extensible buccal cavity) are positively allometric, whereby the dimensions of these structures become relatively larger in bigger animals (Goldbogen, Potvin & Shadwick 2010). By having larger skulls and buccal cavities relative to body size, rorquals significantly enhance their mass-specific engulfment capacity. However, physical principles indicate that the energy required to lunge feed will increase because drag will be sustained over longer distances (Potvin, Goldbogen & Shadwick 2010). Therefore, it is predicted that increased foraging costs will progressively limit diving capacity in larger rorquals (Goldbogen, Potvin & Shadwick 2010). To test this hypothesis, we compared diving and lunge-feeding performance (during deep foraging dives directed at krill) among blue whales (*Balaenoptera musculus*), fin whales (*Balaenoptera physalus*) and humpback whales (*Megaptera novaeangliae*), which vary in mean body size. Our analysis is based on the use of tag data and morphological data, combined with unsteady hydrodynamic modelling, to investigate the kinematics, dynamics and energetics of engulfment *per se*, as performed previously in a study of blue whale lunge-feeding efficiency in relation to krill density (Goldbogen *et al.* 2011).

Materials and methods

Our analytical approach integrated a combination of previously published data sets and mechanistic models to examine the scaling of lunge-feeding energetics and dive capacity in rorqual whales. The approach is summarized in the diagram shown in Fig. 1e and supporting details are provided in Appendix S1 (see Supporting Information). There are two sources of data in this paper: morphological data and tag data. We used three different types of models: geometric, hydrodynamic and energetic. Geometric models were used to estimate engulfment capacity based on morphological data (Goldbogen, Potvin & Shadwick 2010). Hydro-mechanical models provided an estimate for the amount of drag required for engulfment and the amount of energy expended during a lunge (Potvin, Goldbogen & Shadwick 2009, 2010; Goldbogen *et al.* 2011). Our hydro-mechanical models took into account a significant range of lunge speeds (±2 standard deviations) that were determined from the tag data. Estimates of energy expenditure were integrated with tag data and morphological data to calculate the theoretical aerobic dive limit (TADL) with and without lunge-feeding costs (Croll *et al.* 2001).

MORPHOLOGY, ALLOMETRY AND ENGULFMENT CAPACITY

Body dimensions were obtained for each species as a function of body length from the *Discovery Reports* (Mackintosh & Wheeler 1929; Matthews 1937). Body mass data were compiled from a variety of studies (Mackintosh 1942; Quiring 1943; Nishiwaki & Oye 1951; Ash 1953; Lockyer 1976; Lockyer & Waters 1986; Víkingsson, Sigurjónsson & Gunnlaugsson 1988). It is noted that these studies span different geographical ranges, which may exhibit small differences in body size (Gilpatrick & Perryman 2008). The complied data sets here, therefore, represent global averages for a generalized rorqual species. The morphometric data from these investigations were digitized by hand, and allometric relationships for each morphological parameter were established using reduced major axis regressions (Table S1, Supporting Information). Derived morphological parameters, such

as mouth area and frontal body area (greatest maximum projection), were obtained using simple geometric calculations from direct morphological measurements (Goldbogen, Potvin & Shadwick 2010). These allometric equations were used to calculate the value of each morphological parameter for a particular sized rorqual that was investigated in our hydrodynamic models (see below).

We estimated engulfment capacity posterior and anterior to the temporomandibular joint, namely the sections of the buccal cavity that extending posteriorly to the end of the ventral groove system and anteriorly to the rostrum, using the following equation and the morphology of the engulfment apparatus (Goldbogen, Potvin & Shadwick 2010):

$$\frac{M_w}{M_c} = \frac{\rho_w \frac{\pi}{3} L_0 \left(X_{jd} L_{jaw} \right) \left(\frac{1}{2} w_{head} \right)}{M_c} \qquad \text{(eqn 1)}$$

This expression relates the mass of the engulfed water (M_w) and whale (M_c) with the density of sea water (ρ_w), the resting length of the ventral groove blubber (L_0), mandible length (L_{jaw}), the width of the skull (W_{head}) and body mass (M_c). The jaw disarticulation factor X_{jd} accounts for the increase in mouth area associated with the rotation and shape of the mandibles (Lambertsen, Ulrich & Straley 1995).

TAG DATA

We applied high-resolution acoustic tags (Fig. 1a) to the backs of surfacing blue, fin and humpback whales during the summer and fall months in the Pacific Ocean off the California coast (Goldbogen *et al.* 2006; Oleson *et al.* 2007; Goldbogen *et al.* 2008, 2011). Tagging operations occurred between 2002 and 2007 for blue whales, 2004–2009 for humpback whales and only 2003 for fin whales. The tags contained a two-axis accelerometer, pressure transducer and a hydrophone. Acoustic data were sampled at 2048 Hz, whereas hydrostatic pressure and acceleration were sampled at 1 Hz. Tags were equipped with suction cups for attachment and a float to facilitate tag recovery. Each whale was approached from behind in a rigid-hulled inflatable boat, and then, the tags were applied to each whale's back using a pole. We obtained data with the acoustic tags for four humpback whales (76 foraging dives, 682 lunges), seven fin whales (28 foraging dives, 122 lunges) and 28 blue whales (203 foraging dives, 682 lunges) during the summer months in the Pacific Ocean off the California Coast. Based on the available evidence (i.e. scat, echosounder data), all of these tagged whales were feeding on krill during deep foraging dives (Goldbogen *et al.* 2006, 2008, 2011).

We used the flow noise measured by the hydrophone to estimate swimming speed during dives (Goldbogen *et al.* 2006). Swim speed data, along with the detection of active swimming strokes from the accelerometer, allowed us to determine when lunges occurred at the bottom of foraging dives (Fig. 1b,c). These lunges almost invariably were temporally linked with vertical undulations in the dive profile (Goldbogen *et al.* 2006, 2008, 2011). To supplement our data set from the acoustic tags, we incorporated dive data from time–depth recorders that were attached to surfacing blue and fin whales during the summer months from 1995 to 1999 off the California coast and Baja California (Croll *et al.* 2001). These tags provided additional data on dive duration, depth and the number of lunges per dive (Acevedo-Gutierrez, Croll & Tershy 2002). Data from these tags were obtained for 10 additional fin whales and 10 additional blue whales. However, data for filter time (time in between each lunge at depth) were only available from the acoustic tag because it required higher-resolution sampling to estimate the duration of the lunge and also pinpoint exactly when the lunge occurred.

HYDRODYNAMIC DRAG AND ENERGY EXPENDITURE: GENERAL APPROACH

The mechanics and energetics of the pre-engulfment and engulfment phases were analysed using an updated version of the unsteady hydrodynamic model of Potvin, Goldbogen & Shadwick (2009, 2010), as recently described by Goldbogen *et al.* (2011). In this approach, the deceleration of a lunging whale of body mass is computed *via* Newton's second law, as resulting from the combined action of fluke thrust, weight-adjusted buoyancy and drag. This scheme parses the drag force into two components (Fig. 1d): engulfment drag and shape drag. Engulfment drag is caused by cavity wall musculature pushing (*via* eccentric contraction) and accelerating forward the engulfed mass. Shape drag is generated by flow moving outside and around the whale's body. Engulfment drag is predominantly an active process (i.e. muscle-powered), whereas shape drag can have *both* active and passive components.

Passive shape drag occurs whenever the (external) flows are deflected by a body of fixed shape. However, passive shape drag may be increased when the body changes shape as a result of the flows' pressure being exerted on it, as with inflating parachutes. *Active* shape drag would arise, on the other hand, whenever the flows are deflected by a body deforming under the action of an internal agent that is independent of flow dynamics, as with muscle in animals or with hydraulic piston activation in aircraft (for spoiler or flaps deployment, for example). In the case of lunge-feeding rorqual whales, active shape drag would arise whenever the tail, flukes and/or any other body parts are being flexed to act as hydrodynamic brakes rather than as lift and thrust devices. Evidence for the use of active shape drag during lunge feeding has not been demonstrated, but such action from the flippers may be required to cancel the nose-down pitch moment that must arise during engulfment (Cooper *et al.* 2008).

The hydrodynamic model provides equations of motion for both pre-engulfment and engulfment phase, with the former including the purging phase of the previous lunge (Fig. 1c). From these equations of motion, we estimated the energy budget for the whale's motion relating the overall change of a whale's kinetic energy during both pre-engulfment and engulfment, to the gains accrued through fluking thrust and the losses incurred through both engulfment and shape drag. Details of this energy budget, including a new assessment of the contributions by active drag, are provided in Appendix S1 of the Supporting Information. The model was adapted for a wide range of body sizes within each species (body length from the tip of the snout to the notch of the flukes): humpback whales from 11 to 15 m, fin whales from 18 to 23 m and blue whales from 22 to 27 m. We tested the sensitivity of the model to multiple input parameters including maximum lunge speed and drag coefficient. Other input parameters, including those related to gape angle dynamics, were predicted from first principals and were corroborated by video footage of rorquals performing lunges at the sea surface (Potvin, Goldbogen & Shadwick 2010). The model output for energy expenditure was then used in coordination with an estimate of diving metabolic rate (DMR) to calculate a TADL following the methods established in previous studies (Shaffer *et al.* 1997; Croll *et al.* 2001).

IMPACT OF LUNGE-FEEDING COSTS ON THEORETICAL AEROBIC DIVE LIMIT

Croll *et al.* (2001) calculated a TADL for blue and fin whales based on available oxygen stores and allometric predictions of DMR. We repeated this analysis for humpback whales using the same methods by Croll *et al.* (2001) and Shaffer *et al.* (1997). This approach incorporated

a multitude of physiological parameters and scaling relationships from previous studies (Lenfant, Johansen & Torrance 1970; Lockyer 1976; Ridgway *et al.* 1984; Goforth 1986; Kooyman 1989; Boyd & Croxall 1996; Noren & Williams 2000; Williams *et al.* 2000). We then superimposed our estimates for the energetic cost of lunge feeding onto the allometric predictions of DMR to recalculate TADL for all three species (Table S2, Supporting Information). We converted mechanical energy to metabolic energy using an estimate of bulk efficiency of 0·25 (Ahlborn 2004) and propulsive efficiency. Propulsive efficiency was tuned (assigned) to reflect both morphological design and a realistic range of published values (Fish & Rohr 1999). Accordingly, we ranked each species according to three morphological indicators of unsteady locomotor performance that will have a major influence on the propulsive efficiency (rank 1–3, 3 = highest performance)/fluke aspect ratio, total fluke area/total body area and total fluke area$^{1/2}$/Body volume$^{1/3}$. A morphological profile that is more efficient at unsteady locomotor manoeuvres (i.e. lunge feeding) will exhibit a lower fluke aspect ratio and higher values for both total fluke area/total body area and total fluke area$^{1/2}$/body volume$^{1/3}$ (Woodward, Winn & Fish 2006).

STATISTICS

All parameters were log transformed and tested for normality and equal variance before running statistical tests, which used an overall significance level of 0·05. For each parameter, we computed mean values and associated standard deviations within each species. We then used a one-way ANOVA to test for significant differences among species, followed by the Student–Newman–Keuls (SNK) method as a multiple comparison procedure.

Results

DIVING PERFORMANCE

Foraging behaviour in all species often involved continuous foraging bouts at depth (Fig. 2). Summary statistics for basic
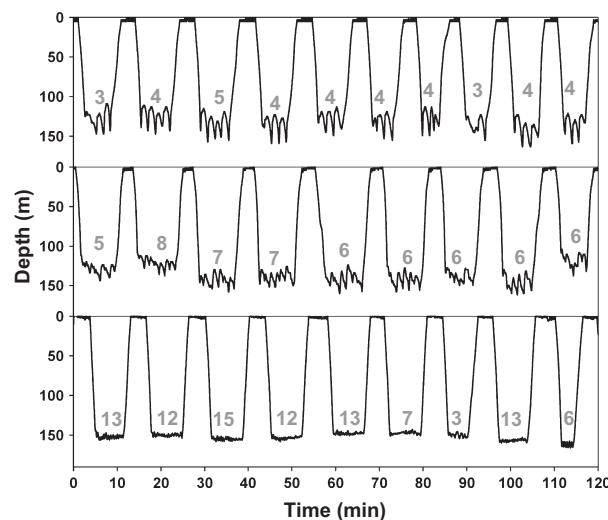

Fig. 2. Continuous foraging bouts at the same approximate depth in three different rorqual whales. Dive profiles for a blue (upper panel), fin (middle panel) and humpback whales (lower panel). Grey numbers above the bottom phase of each dive represent the number of lunges performed during each dive.

foraging dive parameters are given in Table 1. Individuals performed lunges at a wide range of depths, which, on average, were not significantly different among species (Fig 3a, $P = 0·564$, one-way ANOVA). Maximum dive depth was also not significantly different among all three species (Fig. 3a, $P = 0·993$, one-way ANOVA). Average dive duration in fin whales was significantly shorter than both blue (Fig. 3b, $P < 0·001$, SNK) and humpback whales ($P = 0·023$, SNK); however, there was no significant difference in average dive duration between blue and humpback whales ($P = 0·856$, SNK). Maximum dive duration was not significantly

Table 1. Summary statistics for diving capacity, lunge feeding performance and model output. Values derived from tag data (see text) represent the mean across individuals

Parameter	Humpback whale	Fin whale	Blue whale
Tag data: diving capacity, lunge feeding and filter performance			
Number of tagged whales	4	17	38
Average dive duration (min)	9·6 (2·1)	7·0 (1·4)	9·8 (2·0)
Maximum dive duration (min)	11·3 (1·5)	9·3 (3·1)	11·6 (1·8)
Average dive depth (m)	189 (74)	170 (70)	190 (58)
Maximum dive depth (m)	214 (76)	211 (58)	211 (54)
Average number of lunges per dive	9·1 (1·8)	3·9 (1·4)	3·3 (1·2)
Maximum number of lunges per dive	12·3 (2·6)	6·5 (1·8)	4·3 (1·1)
Maximum lunge speed (m s^{-1})	2·3 (0·1)	3·0 (0·4)	3·7 (0·4)
Maximum lunge speed (L_{body} s^{-1})	0·164 (0·008)	0·150 (0·022)	0·147 (0·017)
Filter time between lunges (s)	13 (3)	28 (4)	55 (10)
Filter rate (m^3 s^{-1})	2·2 (0·5)	1·8 (0·2)	2·0 (0·4)
Hydrodynamic and energetic model output			
Mechanical energy required for engulfment (J kg^{-1})	2·4	4·0	5·7
Mechanical energy required for a single lunge (J kg^{-1})	4·9	8·4	12·1
Total mechanical energy required for lunges at depth (kJ)	2608	3953	6723
Total metabolic energy required for lunges at depth (l O$_2$)	837	1788	3041
Theoretical aerobic dive limit (TADL) without lunge feeding costs (min)	22·1	27·6	30·1
TADL with lunge feeding costs (min)	11·74	10·96	11·67

One standard deviation about the mean is given in parentheses. Values generated from hydrodynamic, mechanical and bioenergetic models correspond to the average body size for each species (Table S2).
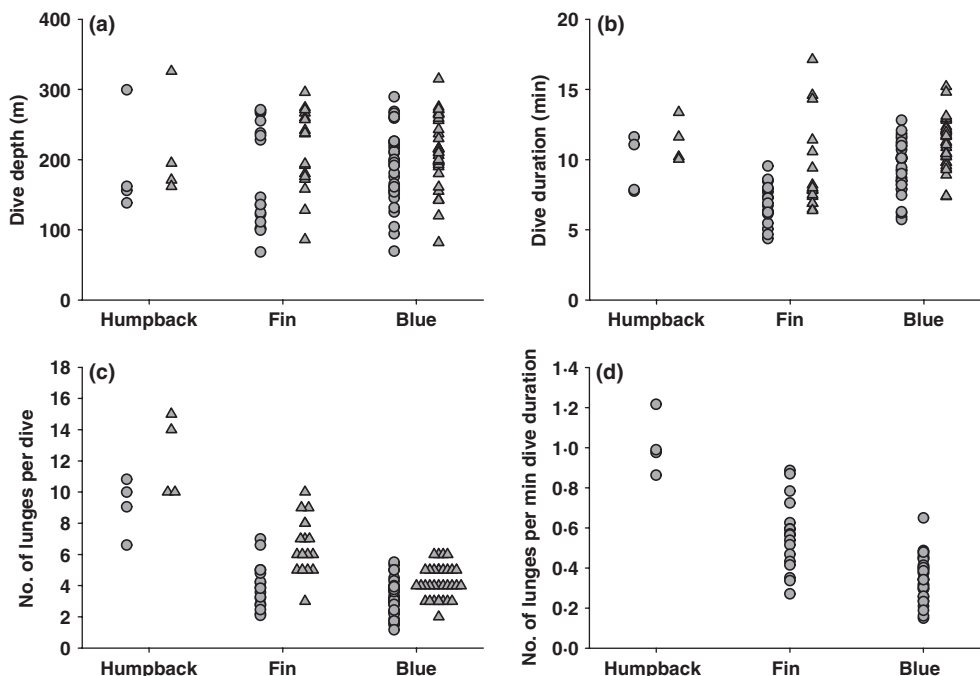
Fig. 3. Comparison of diving parameters among species. Dive depth (a), dive duration (b), lunge frequency (number of lunges per dive) (c), and lunge frequency normalized to dive duration (d) for humpback (Mn, $n = 4$), fin (Bp, $n = 17$) and blue whales (Bm, $n = 38$). Each circle represents the average value for each individual. Upward triangles correspond to maximum values for each individual. Symbols for maximum lunge frequency were offset, and all others are 35% transparent, to show overlapping values.

different among species (Fig. 3b; $P > 0.05$, one-way ANOVA). The deepest single foraging dive for any individual was 326 m, 296 m and 315 m for humpback, fin and blue whales, respectively. The longest foraging dive for any individual humpback, fin and blue whale was 13·4, 17·1 and 15·2 min, respectively.

The average number of lunges performed by humpback whales was significantly higher than both fin and blue whales (Fig. 3c, $P < 0.001$, SNK), but there was no difference between blue whales and fin whales ($P = 0.088$, SNK). However, the average number of lunges executed *per minute dive duration* was significantly different among species and decreased with increasing body size (Fig. 3d; $P < 0.001$, SNK). The maximum number of lunges performed per dive (lunge frequency) was also significantly different among species and decreased with increasing body size (Fig. 3c; $P < 0.001$, SNK). The highest number of lunges recorded for any individual humpback, fin and blue whale was 15, 10 and 6, respectively.

The duration between each lunge at depth (excluding the deceleration and acceleration phase of each lunge), or the time needed to purge and filter the engulfed water before the next lunge is executed, was significantly different among species ($P < 0.001$, SNK). Filter time was 13 ± 3 s for humpback whales, 28 ± 4 s for fin whales and 55 ± 10 s for blue whales. Filter rate, calculated by dividing the volumetric engulfment capacity estimated for an average size whale for each species (Humpback: $L_{body} = 14$ m, $V_{cavity} = 28$ m^3; Fin: $L_{body} = 20$ m, $V_{cavity} = 50$ m^3; Blue:

and $L_{body} = 25$ m, $V_{cavity} = 110$ m^3) by the filter time value, was 2·2 ± 0·5 m^3 s^{-1} for humpback whales, 1·8 ± 0·2 m^3 s^{-1} for fin whales and 2·0 ± 0·4 m^3 s^{-1}. If these body size and engulfment volume estimates are representative of the tagged whales, filtration rate will be independent of body size ($P = 0.304$, one-way ANOVA) despite a predicted increase in filter area associated with the positive allometry of the skull.

ALLOMETRY OF MORPHOLOGICAL DIMENSIONS AND ENGULFMENT CAPACITY

The scaling of body mass (M) with respect to body length (L_{body}) was significantly different than isometry ($M = L_{body}^3$) within each species (Table S1). Over the range of body sizes that are obligate lunge feeders (humpback, 8–15 m; fin, 12–24 m; and blue, 15–28 m) from weaning to maximum length (Huang, Chou & Ni 2009), each species is expected to have a different mean mass. The dimensions of the engulfment apparatus (length of gape L_{gape}, lateral projected length of the jaw L_{jaw} and width of the skull w_{head}) were positively allometric, and therefore, mouth area also exhibited positive allometry. Similar to previous results in fin whales (Goldbogen, Potvin & Shadwick 2010), a relatively larger buccal cavity (defined by the length of the ventral groove system L_{VGB}, which was also positively allometric) coupled with greater mouth area increased engulfment capacity and mass-specific engulfment capacity in each species (Fig. 4).
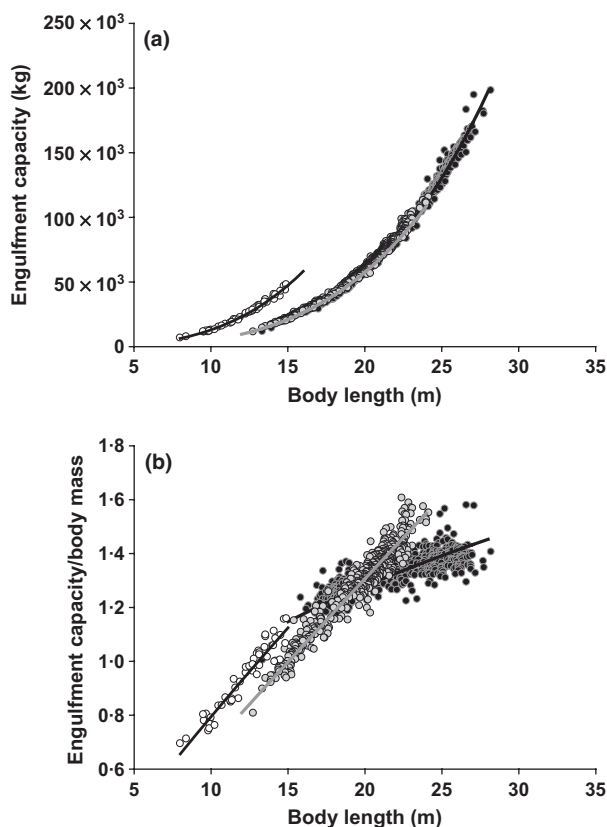
Fig. 4. Relationship between engulfment capacity (M_w) and body length (L_{body}). (a) Engulfment capacity was positively allometric in blue whales (black circles: $M_w = 1.023 L_{body}^{3.65}$, $r^2 = 0.99$, $P < 0.005$), fin whales (grey circles: $M_w = 1.604 L_{body}^{3.51}$, $r^2 = 0.99$, $P < 0.005$) and humpback whales (white circles: $M_w = 8.0094 L_{body}^{3.21}$, $r^2 = 0.99$, $P < 0.005$). (b) Mass-specific engulfment capacity, a non-dimensional parameter that is equal to engulfment capacity divided by body mass, was positively allometric in blue whales (black circles: $M_{ms} = 0.412 L_{body}^{0.37}$, $r^2 = 0.68$, $P < 0.005$), fin whales (grey circles; $M_{ms} = 1.311 L_{body}^{0.94}$, $r^2 = 0.94$, $P < 0.005$) and humpback whales (white circles: $M_{ms} = 0.1106 L_{body}^{0.86}$, $r^2 = 0.93$, $P < 0.005$).

LUNGE-FEEDING PERFORMANCE: HYDRODYNAMICS AND ENERGETICS

Maximum lunge speed was significantly different among species and increased with ranked body size (Table 1, $P < 0.001$, SNK). These values were 2.3 ± 0.1 m s^{-1} for humpback whales, 3.0 ± 0.4 m s^{-1} for fin whales and 3.7 ± 0.4 m s^{-1} for blue whales. Assuming an average body length for each species (humpback: $L_{body} = 14$ m; fin: $L_{body} = 20$ m; and blue: $L_{body} = 25$ m), we divided speed by body length to obtain maximum lunge speed in body lengths per second (humpback: $V_n = 0.164 \pm 0.008$ L_{body} s^{-1}; fin: $V_n = 0.150 \pm 0.022$ L_{body} s^{-1}; and blue: $V_n = 0.147 \pm 0.017$ L_{body} s^{-1}), which was not significantly different among species ($P = 0.276$, one-way ANOVA). Variation of the specific speed with respect to body size was discussed in the context of prey capture by Potvin, Goldbogen & Shadwick (2010). For the hydrodynamic and energetic models, we explored a significant range in observed lunge speeds (± 2 standard deviations) for

humpback whales ($1.8–3.0$ m s^{-1}), fin whales ($2.1–4.1$ m s^{-1}) and blue whales ($3.1–4.1$ m s^{-1}).

Higher lunge speeds together with an increase in projected mouth area resulted in relatively higher peak drag forces (mass-specific total drag, f_d^{tot}) in larger rorquals, but only for lunge-feeding simulations where V_n was independent of body size. These values ranged from 0.6 N kg^{-1} in the smallest-sized humpback to 1.2 N kg^{-1} in the largest-sized blue whale; the average estimate for all sizes of rorquals (interspecifically) was 0.9 ± 0.2 N kg^{-1}. Because we did not know the precise length of tagged whales, we explored other possibilities where V_n would vary systematically with body size (but still within the range of speeds estimated from the tag data): (i) V_n is independent of body size, (ii) V_n increases with body size and (iii) V_n decreases with body size. Under the two scenarios where V_n exhibits size dependence, mass-specific peak total drag was approximately the same for different size rorquals. These values were 1.0 ± 0.4 and 1.1 ± 0.3 N kg^{-1} when V_n increased and decreased with body size, respectively. Therefore, the magnitude of the f_d^{tot} was generally insensitive to systematic variations in V_n with respect to body size.

The magnitude and duration of drag forces that were sustained during engulfment provided an estimate of the energy used to lunge feed. The mass-specific energy expenditure of engulfment due to drag ($\Delta q_d \equiv (\Delta Q_{drag}^{engulfment} + \Delta Q_{drag}^{shape})/M_c$), which includes both engulfment drag and shape drag, increased with body size (among species) regardless of the relationship between V_n and body size (Fig. 5). It is noted that even if peak drag forces were relatively the same among species (V_n increase or decrease scenarios), those forces were sustained for longer distances because engulfment requires more time in larger rorquals (Potvin, Goldbogen & Shadwick 2010). The total drag energy increased with increasing relative lunge speed within each species and larger species exhibited higher energy expenditures at any given relative lunge speed (Fig. 5).

INTEGRATING LUNGE-FEEDING COSTS INTO THE THEORETICAL AEROBIC DIVE LIMIT

We calculated TADL for blue, fin and humpback whales with and without lunge-feeding costs (Table S2). Without lunge-feeding costs, TADL for each species was approximately two to three times longer than the maximum durations of foraging dives presented here (Fig. 3). In contrast, maximum dive times of humpback whales during singing dives (20 min) (Chu 1988) were much closer to our predicted TADL (22 min). Our hydrodynamic analyses provided an estimate for the amount of mechanical energy required for lunge feeding during a foraging dive. Mechanical energy was converted to metabolic energy using bulk and propulsive efficiency values. Propulsive efficiency reflected a ranking of three morphological parameters that indicate unsteady locomotor performance (rank: 1–3, 3 = highest performance). A sum of these ranks suggests that humpback whales (rank sum = 9) are more efficient at lunge feeding than both blue (rank sum = 5) and fin whales (rank
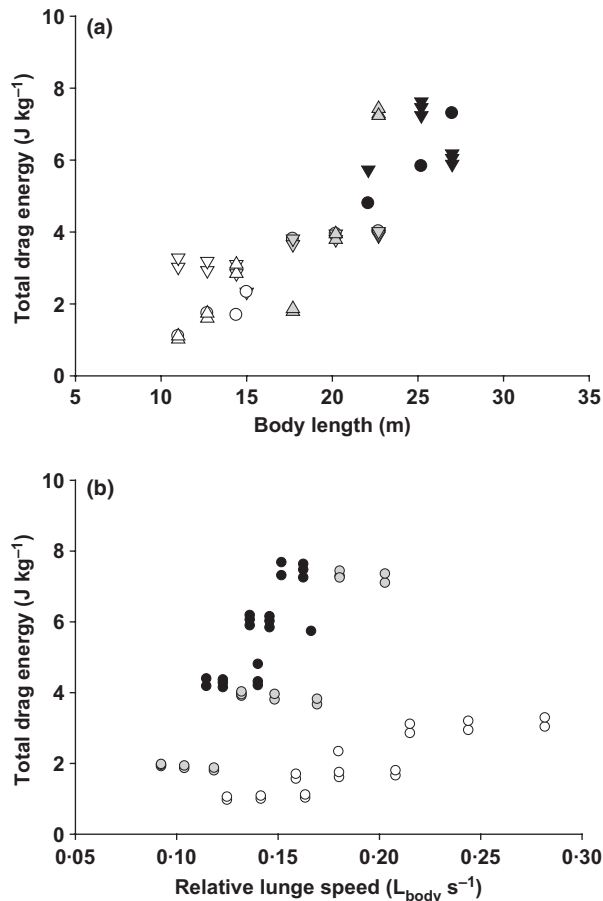
Fig. 5. Relationship between body length (L_{body}) and the mass-specific energy expenditure of engulfment. (a) Values generated from 59 lunge-feeding simulations for humpback (white symbols), fin (grey symbols) and blue whales (black symbols) are shown for three different size classes within each species. The total drag energy generally increases with body size for different scenarios of relative lunge speed (V_n): (i) V_n is independent of body size (circles), (ii) V_n increases with body size (upward triangles) and (iii) V_n decreases with body size (downward triangles). Multiple points at a given body length represent variations in drag coefficient (see text) and relative lunge speed. (b) Mass-specific drag energy generally increases with relative lunge speed within each species.

sum = 5). We assigned propulsive efficiency values for humpback whales (0·91) that reflected this greater unsteady locomotor capacity relative to blue and fin whales (0·86). These values, which are within the range of published values for propulsive efficiency in other cetaceans (Fish & Rohr 1999), generated a TADL that was within one standard deviation of the observed maximum dive times (Fig. 2).

Discussion

Ever since the first deployment of a time–depth recorder on a marine mammal (Kooyman 1966), diving capacity has been a fundamental concept in diving physiology. The ability to dive longer and deeper is an essential component of foraging success and ecological function in a host of marine mammals and birds. In general, larger animals have greater diving capacity (Butler & Jones 1982; Halsey, Butler & Blackburn 2006)

because body oxygen stores scale isometrically (Lasiewski & Calder 1971; Hudson & Jones 1986) and oxygen depletion rates scale negatively with body size (White, Blackburn & Seymour 2009); however, there is considerable variation around this trend because of differences in behaviour, physiology and performance. For example, rorqual whales represent some of the largest divers of all time, but they exhibit relatively short dive durations because of the high energetic demands of their unique lunge-feeding strategy (Acevedo-Gutierrez, Croll & Tershy 2002). Here, we investigated diving and lunge-feeding performance among three differently sized rorqual species foraging on krill. Our results suggest that, unlike all other taxonomic groups of true divers, diving capacity does not increase with body size within rorquals because of the scaling of lunge-feeding costs. Larger rorquals are morphologically optimized to increase mass-specific engulfment volume, but this enhanced capacity comes at a relatively higher energetic cost that progressively limits dive time.

SCALING OF LUNGE-FEEDING ENERGETICS

Our analyses indicated that the energetic cost of a lunge was positively allometric, whereby the cost of engulfment was relatively higher in larger rorquals (Fig. 5). We attributed this result to the positive allometry of the engulfment apparatus (skull and buccal cavity), which effectively increased mouth area and engulfment capacity relative to body size (Table S1, Fig. 4). Relatively more mouth area increased the two components of drag that occur during a lunge (Potvin, Goldbogen & Shadwick 2009): (i) *shape drag* from the flow around the mouth and body, and (ii) *engulfment drag*, which arises from the acceleration of engulfed fluid from inside the mouth. Both types of drag were generally increased because of the relative increase in projected mouth area, but drag was greater in larger rorquals because lunge speed significantly increased with body size (Table 1). Higher drag forces sustained for greater periods of time resulted in elevated energy expenditures during engulfment in larger rorquals.

The scaling of lunge-feeding costs was generally not affected by differences in relative lunge speed (V_n). This relationship remained robust if V_n varied in a systematic way within the range of speed values estimated from the tag data. Because the precise lengths of tagged whales were unknown, there were three possibilities: (i) V_n was independent of body size, (ii) V_n increased with body size or (iii) V_n decreased with body size. Under each condition, the relative cost of engulfment increased with body size (Fig. 5a). Based on the average size whale predicted for each species in this study (humpback: L_{body} = 14 m; fin: L_{body} = 20 m; and blue: L_{body} = 25 m), the tag data supported the condition that V_n was independent of body size (Table 1), which yielded a mass-specific cost of engulfment in blue and fin whales that was approximately three- and two-fold higher than humpback whales, respectively (Fig. 5a).

Within each species, the relative cost of engulfment tended to increase with increasing V_n (Fig. 5b). Moreover, the

relative cost appears to increase much more rapidly with V_n in larger rorquals. These simulations suggest that whales (large size whales in particular) could save energy if they lunged at lower speeds. However, our tag data indicated that absolute lunge speed increased significantly with body size such that the relative speed was independent with body size (Table 1). One possible explanation for this result is that a higher speed is required to generate enough dynamic pressure and completely expand the buccal cavity. However, our simulations of lunge feeding suggest that the same-sized water mass can be engulfed at much lower speeds. This is possible because engulfment appears to be an active process whereby the inflation of the buccal cavity is actively resisted by the eccentric contraction of the muscles associated with the ventral groove blubber (Potvin, Goldbogen & Shadwick 2009). Therefore, the same size volume of water can be engulfed at a lower speed if less resistance is generated by the muscles of the buccal cavity. By invoking action–reaction, less resistance to flow inside the mouth yields a lower acceleration of the engulfed water mass. As a consequence, less drag is sustained and engulfment would require lower energy expenditure. Therefore, based on purely theoretical grounds and simulation data, it appears that engulfment is physically possible at much lower speeds than those exhibited by tagged whales.

An alternative explanation for the positive relationship between body size and absolute lunge speed is that larger rorquals are less manoeuvrable and thus require higher attack speed to successfully capture a significant proportion of a krill patch (Potvin, Goldbogen & Shadwick 2010); Physical principles predict that unsteady locomotor performance, such as the ability to manoeuvre and accelerate, should decrease with increasing body size in aquatic vertebrates (Webb & Debuffrenil 1990; Domenici 2001; Vogel 2008). Such mechanical scaling effects will arise in rorquals because of the differential scaling of body mass relative to control (flippers) and propulsion (flukes) surfaces (Goldbogen, Potvin & Shadwick 2010); Such an effect, in addition to other physiological constraints (Tershy 1992), has been hypothesized as a driving factor in what determines prey preferences in different-sized rorquals. Another detrimental consequence of size on foraging performance is that krill may be able to visually detect larger whales from a greater distance away. This facilitates the early onset and the magnitude of the escape response (Costa 2009; Cooper & Stankowich 2010) and thus may decrease foraging efficiency (O'Brien 1987). However, rorquals may be able to avoid visual detection if they lunge from beneath a krill patch where there is a lack of back-welling light (Calambokidis et al. 2007; Goldbogen et al. 2011). This type of ambush strategy, together with increased attack speed and greater mouth area, should minimize the rapid expansion of krill patches during a lunge and increase the proportion of krill captured.

SCALING OF DIVING CAPACITY IN RORQUALS

The cost of lunge feeding scaled in such a way that it became a greater proportion of DMR in larger rorquals. In this way,

relatively higher energetic demands in larger rorquals deplete body oxygen stores at a greater rate and therefore progressively limit dive time. These arguments suggest that the scaling of lunge-feeding costs effectively negates the diving capacity enhancements which are typically granted by large body mass. Despite this cost being significant in magnitude relative to the cost of diving *per se*, lunge feeding is predicted to remain energetically efficient overall if sufficiently dense patches of krill can be located and exploited (Goldbogen et al. 2011). Therefore, we suggest that there is a trade-off between mass-specific engulfment capacity and the energetic cost of a lunge, where the former increases the energetic efficiency of lunge feeding and the latter limits diving capacity. Because the magnitude of each factor emerges from complex scaling interactions (morphology, predator–prey interactions and biomechanics), we suggest that the effect of size on lunge-feeding performance has a major influence on rorqual foraging ecology.

Limited dive times and longer filter times in larger rorquals resulted in a decrease in lunge frequency (lunges per dive) with increasing body size (Fig. 3c). As a result, the total (cumulative) volume of water processed and filtered during a typical 10-min foraging dive will eventually stop increasing with body size and then decrease at the upper extreme of body mass in blue whales (Fig. 6). This trend, which is illustrated here up to the largest known blue whale length that has associated weight data ($L_{body} = 29.5$ m; Lockyer 1976), was estimated from linear and allometric equations that relate body length with lunge frequency, i.e. number of lunges per dive ($f_{max} = -0.8187 L_{body} + 26.434$), and engulfment capacity (Fig. 4), respectively. The rapid drop in total water filtered occurs because the number of predicted lunges approaches zero at larger body sizes. If these scaling relationships are accurate, then blue whales longer than 25.5 m will have no advantage over smaller whales with regard to the overall energetic efficiency of deep foraging dives. Such an effect is
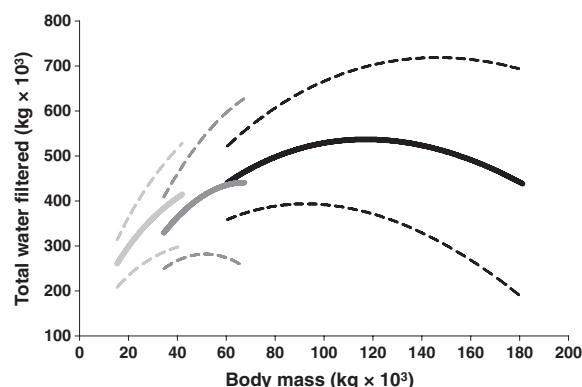
Fig. 6. Total water engulfed and filtered during a typical deep foraging dive. Predicted values are shown for blue (black), fin (dark grey) and humpback whales (light grey) as a function of body mass. Values were predicted based on morphology (Fig. 4) and observed lunge frequency maxima (Fig. 3c). Lunge frequency was assumed to decrease interspecifically and intraspecifically with body size within the observed range of values. Solid and dashed lines represent average and one standard deviation, respectively.

predicted despite larger whales being able to swim slightly faster (Watanabe *et al.* 2010) at a relatively lower cost (Williams 1999) during the ascent and descent phases of foraging dives. However, Southern Hemisphere blue whale whales, which are significantly larger than eastern North Pacific blue whales (Gilpatrick & Perryman 2008), may have an advantage over smaller rorquals at targeting denser, larger krill patches with greater mouth area and more capacious buccal cavities.

The decrease in lunge-feeding performance in larger rorquals will be disadvantageous if deep krill patches are low in density, which would then cause lunge feeding to be less efficient. Consequently, a greater proportion of energy intake must be used to pay for relatively higher lunge-feeding costs. Because larger rorquals possess greater mass-specific engulfment capacity, they could lunge at shallower depths to increase energetic efficiency (i.e. less energy spent diving). In this way, the scaling of lunge-feeding costs may influence the choice of foraging depth for different-sized rorquals (Goldbogen, Potvin & Shadwick 2010). Limited support for this hypothesis is provided from a study on sympatric rorquals, where minke whales (*Balaenoptera acutorostrata*; size range: L_{body} = 5–11 m) foraged on deeper krill than humpback whales (Friedlaender, Lawson & Halpin 2009). Although we do not expect the trends reported here (for deep dives directed at krill) to apply to rorquals foraging on fish aggregations or at shallow depths (Stimpert *et al.* 2007; Alves *et al.* 2009; Friedlaender *et al.* 2009; Hazen *et al.* 2009; Ware, Friedlaender & Nowacek 2010), rorquals of different size may be more effective at exploiting certain combinations of prey type, size, depth, patchiness and/or density. However, other benefits to larger body size such as lower mass-specific locomotor costs enhancing long-distance migratory abilities may also drive selection for larger body size (Croll, Tershy & Newton 2008). More studies are needed that examine the relationship between morphology, performance and ecology in rorquals. Such an approach will elucidate the role that lunge feeding has played in the ecological diversification in a clade of the largest vertebrates ever to have lived.

Acknowledgements

References

Acevedo-Gutierrez, A., Croll, D.A. & Tershy, B.R. (2002) High feeding costs limit dive time in the largest whales. *Journal of Experimental Biology*, **205**, 1747–1753.

Ahlborn, B.K. (2004) *Zoological Physics*, 2nd edn. Springer-Verlag, Berlin.

Alves, F., Dinis, A., Cascão, I. & Freitas, L. (2010) Bryde's whale (*Balaenoptera brydei*) stable associations and dive profiles: new insights into foraging behavior. *Marine Mammal Science*, **26**, 202–212.

Ash, C.E. (1953) Weights of Antarctic humpback whales. *Norsk Hvalfangsttid*, **42**, 387–391.

Boyd, I.L. & Croxall, J.P. (1996) Dive durations in pinnipeds and seabirds. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **74**, 1696–1705.

Butler, P.J. & Jones, D.R. (1982) The comparative physiology of diving in vertebrates. *Advances in Comparative Physiology and Biochemistry*, **8**, 179–364.

Butler, P.J. & Jones, D.R. (1997) Physiology of diving of birds and mammals. *Physiological Reviews*, **77**, 837–899.

Calambokidis, J., Schorr, G.S., Steiger, G.H., Francis, J., Bakhtiari, M., Marshal, G., Oleson, E.M., Gendron, D. & Robertson, K. (2007) Insights into the underwater diving, feeding, and calling behavior of blue whales from a suction-cup-attached video-imaging tag (CRITTERCAM). *Marine Technology Society Journal*, **41**, 19–29.

Chu, K.C. (1988) Dive times and ventilation patterns of singing humpback whales (Megaptera-Novaeangliae). *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **66**, 1322–1327.

Cooper, W.E. & Stankowich, T. (2010) Prey or predator? Body size of an approaching animal affects decisions to attack or escape. *Behavioral Ecology*, **21**, 1278–1284.

Cooper, L.N., Sedano, N., Johansson, S., May, B., Brown, J.D., Holliday, C.M., Kot, B.W. & Fish, F.E. (2008) Hydrodynamic performance of the minke whale (*Balaenoptera acutorostrata*) flipper. *Journal of Experimental Biology*, **211**, 1859–1867.

Costa, G.C. (2009) Predator size, prey size, and dietary niche breadth relationships in marine predators. *Ecology*, **90**, 2014–2019.

Croll, D., Tershy, B.R. & Newton, K. (2008) Filter feeding. *Encyclopedia of Marine Mammals*, 2nd edn (eds W.F. Perrin, B. Wursig & J.G.M. Thewissen), pp. 421–425. Academic Press, Burlington, MA.

Croll, D.A., Acevedo-Gutierrez, A., Tershy, B.R. & Urban-Ramirez, J. (2001) The diving behavior of blue and fin whales: is dive duration shorter than expected based on oxygen stores? *Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology*, **129**, 797–809.

Dial, K.P., Greene, E. & Irschick, D.J. (2008) Allometry of behavior. *Trends in Ecology & Evolution*, **23**, 394–401.

Domenici, P. (2001) The scaling of locomotor performance in predator-prey encounters: from fish to killer whales. *Comparative Biochemistry and Physiology a-Molecular and Integrative Physiology*, **131**, 169–182.

Doniol-Valcroze, T., Lesage, V., Giard, J. & Michaud, R. (2011) Optimal foraging theory predicts diving and feeding strategies of the largest marine predator. *Behavioral Ecology*, **22**, 880–888.

Fish, F.E. & Rohr, J.J. (1999) Review of dolphin hydrodynamics and swimming performance. *SPAWARS System Center Technical Report*. San Diego, CA.

Friedlaender, A.S., Lawson, G.L. & Halpin, P.N. (2009) Evidence of resource partitioning between humpback and minke whales around the western Antarctic Peninsula. *Marine Mammal Science*, **25**, 402–415.

Friedlaender, A.S., Hazen, E.L., Nowacek, D.P., Halpin, P.N., Ware, C., Weinrich, M.T., Hurst, T. & Wiley, D. (2009) Diel changes in humpback whale *Megaptera novaeangliae* feeding behavior in response to sand lance *Ammodytes* spp. behavior and distribution. *Marine Ecology-Progress Series*, **395**, 91–100.

Friedman, M., Shimada, K., Martin, L.D., Everhart, M.J., Liston, J., Maltese, A. & Triebold, M. (2010) 100-million-year dynasty of giant planktivorous bony fishes in the mesozoic seas. *Science*, **327**, 990–993.

Gilpatrick, J.W. & Perryman, W.L. (2008) Geographic variation in external morphology of North Pacific and Southern Hemisphere blue whales (*Balaenoptera musculus*). *Journal of Cetacean Research Management*, **10**, 9–21.

Gleiss, A.C., Norman, B. & Wilson, R.P. (2011) Moved by that sinking feeling: variable diving geometry underlies movement strategies in whale sharks. *Functional Ecology*, **25**, 595–607.

Goforth, H.W. Jr (1986) Glycogenolytic responses and force production characteristics of a bottlenose dolphin (*Tursiops truncatus*), while exercising against a force transducer. PhD thesis, University of California, Los Angeles, CA.

Goldbogen, J.A., Potvin, J. & Shadwick, R.E. (2010) Skull and buccal cavity allometry increase mass-specific engulfment capacity in fin whales. *Proceedings of the Royal Society B-Biological Sciences*, **277**, 861–868.

Goldbogen, J.A., Pyenson, N.D. & Shadwick, R.E. (2007) Big gulps require high drag for fin whale lunge feeding. *Marine Ecology-Progress Series*, **349**, 289–301.

Goldbogen, J.A., Calambokidis, J., Shadwick, R.E., Oleson, E.M., McDonald, M.A. & Hildebrand, J.A. (2006) Kinematics of foraging dives and lunge-feeding in fin whales. *Journal of Experimental Biology*, **209**, 1231–1244.

Goldbogen, J.A., Calambokidis, J., Croll, D., Harvey, J., Newton, K., Oleson, E., Schorr, G. & Shadwick, R.E. (2008) Foraging behavior of humpback whales: kinematic and respiratory patterns suggest a high cost for a lunge. *Journal of Experimental Biology*, **211**, 3712–3719.

Goldbogen, J.A., Calambokidis, J., Oleson, E., Potvin, J., Pyenson, N.D., Schorr, G. & Shadwick, R.E. (2011) Mechanics, hydrodynamics and energetics of blue whale lunge feeding: efficiency dependence on krill density. *Journal of Experimental Biology*, **214**, 131–146.

Halsey, L.G., Butler, P.J. & Blackburn, T.M. (2006) A phylogenetic analysis of the allometry of diving. *American Naturalist*, **167**, 276–287.

Hazen, E.L., Friedlaender, A.S., Thompson, M.A., Ware, C.R., Weinrich, M.T., Halpin, P.N. & Wiley, D.N. (2009) Fine-scale prey aggregations and foraging ecology of humpback whales *Megaptera novaeangliae*. *Marine Ecology-Progress Series*, **395**, 75–89.

Huang, S.-I., Chou, L.-S. & Ni, I.-H. (2009) Comparable length at weaning in cetaceans. *Marine Mammal Science*, **25**, 875–887.

Hudson, D.M. & Jones, D.R. (1986) The influence of body mass on the endurance to restrained submergence in the pekin duck. *Journal of Experimental Biology*, **120**, 351–367.

Kooyman, G.L. (1966) Maximum diving capacities of the Weddell Seal, *Leptonychotes weddelli*. *Science*, **151**, 1553–1554.

Kooyman, G.L. (1989) *Diverse Divers: Physiology and Behavior*. Springer-Verlag, Berlin.

Krutzikowsky, G.K. & Mate, B. (2000) Dive and surfacing characteristics of bowhead whales (*Balaena mysticetus*) in the Beaufort and Chukchi seas. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **78**, 1182–1198.

Lambertsen, R., Ulrich, N. & Straley, J. (1995) Frontomandibular stay of balaenopteridae – a mechanism for momentum recapture during feeding. *Journal of Mammalogy*, **76**, 877–899.

Lasiewski, R.C. & Calder, W.A. (1971) Preliminary allometric analysis of respiratory variables in resting birds. *Respiration Physiology*, **11**, 152–166.

Lenfant, C., Johansen, K. & Torrance, J.D. (1970) Gas transport and oxygen storage capacity in some pinnipeds and sea otter. *Respiration Physiology*, **9**, 277.

Lockyer, C. (1976) Body weights of some species of large whales. *Ices Journal of Marine Science*, **36**, 259–273.

Lockyer, C. & Waters, T. (1986) Weights and anatomical measurements of Northeastern Atlantic fin (*Balaenoptera physalus*, Linnaeus) and sei (*B. borealis*, Lesson) whales. *Marine Mammal Science*, **2**, 169–185.

Mackintosh, N.A. (1942) The southern stocks of whalebone whales. *Discovery Reports*, **22**, 197–300.

Mackintosh, N.A. & Wheeler, J.F.G. (1929) Southern blue and fin whales. *Discovery Reports*, **1**, 257–540.

Matthews, L.H. (1937) The humpback whale, *Megaptera nodosa*. *Discovery Reports*, **22**, 197–300.

Nishiwaki, M. & Oye, T. (1951) Biological investigation on blue whales (*Balaenoptera musculus*) and fin whales (*Balaenoptera physalus*) caught by the Japanese Antarctic whaling fleets. *The Scientific reports of the Whales Research Institute. Tokyo, Japan*, **5**, 91–167.

Noren, S.R. & Williams, T.M. (2000) Body size and skeletal muscle myoglobin of cetaceans: adaptations for maximizing dive duration. *Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology*, **126**, 181–191.

O'Brien, D.P. (1987) Description of escape responses of krill (Crustacea, Euphausiacea), with particular reference to swarming behavior and the size and proximity of the predator. *Journal of Crustacean Biology*, **7**, 449–457.

Oleson, E.M., Calambokidis, J., Burgess, W.C., McDonald, M.A., LeDuc, C.A. & Hildebrand, J.A. (2007) Behavioral context of call production by eastern North Pacific blue whales. *Marine Ecology-Progress Series*, **330**, 269–284.

Orton, L.S. & Brodie, P.F. (1987) Engulfing mechanics of fin whales. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **65**, 2898–2907.

Peters, R.H. (1983) *The Ecological Implications of Body Size*. Cambridge University Press, Cambridge, UK.

Potvin, J., Goldbogen, J.A. & Shadwick, R.E. (2009) Passive versus active engulfment: verdict from trajectory simulations of lunge-feeding fin whales *Balaenoptera physalus*. *Journal of the Royal Society Interface*, **6**, 1005–1025.

Potvin, J., Goldbogen, J.A. & Shadwick, R.E. (2010) Scaling of lunge feeding in rorqual whales: an integrated model of engulfment duration. *Journal of Theoretical Biology*, **267**, 437–453.

Quiring, D.P. (1943) Weight data on five whales. *Journal of Mammalogy*, **24**, 39–45.

Ridgway, S.H., Bowers, C.A., Miller, D., Schultz, M.L., Jacobs, C.A. & Dooley, C.A. (1984) Diving and blood oxygen in the white whale. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **62**, 2349–2351.

Sanderson, S.L. & Wassersug, R. (1993) Convergent and alternative designs for vertebrate suspension feeding. *The Skull: Functional and Evolutionary Mechanisms* (eds J. Hanken & B.K. Hall), pp. 37–112. University of Chicago Press, Chicago, IL.

Schmidt-Nielsen, K. (1984) *Scaling: Why Is Animal Size So Important?* Cambridge University Press, Cambridge.

Shaffer, S.A., Costa, D.P., Williams, T.M. & 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. *Journal of Experimental Biology*, **200**, 3091–3099.

Sibly, R.M. & Brown, J.H. (2007) Effects of body size and lifestyle on evolution of mammal life histories. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 17707–17712.

Simon, M., Johnson, M., Tyack, P. & Madsen, P.T. (2009) Behaviour and kinematics of continuous ram filtration in bowhead whales (*Balaena mysticetus*). *Proceedings of the Royal Society B-Biological Sciences*, **276**, 3819–3828.

Stimpert, A.K., Wiley, D.N., Au, W.W.L., Johnson, M.P. & Arsenault, R. (2007) 'Megapclicks': acoustic click trains and buzzes produced during night-time foraging of humpback whales (*Megaptera novaeangliae*). *Biology Letters*, **3**, 467–470.

Suarez, R.K. & Darveau, C.A. (2005) Multi-level regulation and metabolic scaling. *Journal of Experimental Biology*, **208**, 1627–1634.

Tershy, B.R. (1992) Body size, diet, habitat use, and social-behavior of Balaenoptera whales in the Gulf of California. *Journal of Mammalogy*, **73**, 477–486.

Víkingsson, G.A., Sigurjónsson, J. & Gunnlaugsson, T. (1988) On the relationship between weight, length and girth dimensions in fin and sei whales caught off Iceland. *Report of the International Whaling Commission*, **38**, 323–326.

Vogel, S. (2008) Modes and scaling in aquatic locomotion. *Integrative and Comparative Biology*, **48**, 702–712.

Ware, C., Friedlaender, A.S. & Nowacek, D.P. (2010) Shallow and deep lunge feeding of humpback whales in fjords of the West Antarctic Peninsula. *Marine Mammal Science*, **27**, 587–605.

Watanabe, Y.Y., Sato, K., Watanuki, Y., Takahashi, A., Mitani, Y., Amano, M., Aoki, K., Narazaki, T., Takashi, I., Minamikawa, S. & Miyazaki, N. (2010) Scaling of swim speed in breath-hold divers. *Journal of Animal Ecology*, **80**, 57–68.

Webb, P.W. & Debuffrenil, V. (1990) Locomotion in the biology of large aquatic vertebrates. *Transactions of the American Fisheries Society*, **119**, 629–641.

Werth, A.J. (2000) Feeding in marine mammals. *Feeding: Form, Function and Evolution in Tetrapod Vertebrates* (ed. K. Schwenk), pp. 475–514. Academic Press, New York, NY.

Werth, A.J. (2004) Models of hydrodynamic flow in the bowhead whale filter feeding apparatus. *Journal of Experimental Biology*, **207**, 3569–3580.

White, C.R., Blackburn, T.M. & Seymour, R.S. (2009) Phylogenetically informed analysis of the allometry of mammalian metabolic rate supports neither geometric nor quarter-power scaling. *Evolution*, **63**, 2658–2667.

Williams, T.M. (1999) The evolution of cost efficient swimming in marine mammals: limits to energetic optimization. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, **354**, 193–201.

Williams, T.M., Davis, R.W., Fuiman, L.A., Francis, J., Le Boeuf, B.L., Horning, M., Calambokidis, J. & Croll, D.A. (2000) Sink or swim: strategies for cost-efficient diving by marine mammals. *Science*, **288**, 133–136.

Woodward, B.L., Winn, J.P. & Fish, F.E. (2006) Morphological specializations of baleen whales associated with hydrodynamic performance and ecological niche. *Journal of Morphology*, **267**, 1284–1294.

Supporting Information

Additional supporting information may be found in the online version of this article.

Appendix S1. Hydrodynamic drag and energy expenditure: mathematical model.

Table S1. Scaling of body dimensions and engulfment capacity with respect to body length.

Table S2. Values used in the calculation of the theoretical aerobic dive limit (TADL).

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.