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## Rorqual whale (Balaenopteridae) surface lunge-feeding behaviors: Standardized classification, repertoire diversity, and evolutionary analyses

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### ABSTRACT

Rorqual whales (Family: Balaenopteridae) are the world's largest predators and sometimes feed near or at the sea surface on small schooling prey. Most rorquals capture prey using a behavioral process known as lunge-feeding that, when occurring at the surface, often exposes the mouth and head above the water. New technology has recently improved historical misconceptions about the natural variation in rorqual lunge-feeding behavior yet missing from the literature is a dedicated study of the identification, use, and evolution of these behaviors when used to capture prey at the surface. Here we present results from a long-term investigation of three rorqual whale species (minke whale, *Balaenoptera acutorostrata*; fin whale, *B. physalus*; and blue whale, *B. musculus*) that helped us develop a standardized classification system of surface lunge-feeding (SLF) behaviors. We then tested for differences in frequency of these behaviors among the three species and across all rorqual species. Our results: (1) propose a unified classification system of six homologous SLF behaviors used by all living rorqual whale species; (2) demonstrate statistically significant differences in the frequency of each behavior by minke, fin, and blue whales; and (3) provide new information regarding the evolution of lunge-feeding behaviors among rorqual whales.

**Key words:** rorqual whale, Balaenopteridae, feeding behavior, lunge-feeding, surface feeding, evolution, minke whale, fin whale, blue whale.

Rorqual whales (Family: Balaenopteridae) are the world's largest predators and sometimes feed near or at the sea surface on concentrations of relatively small schooling fishes, krill, or squid (*e.g.*, Sears 1983, Schoenherr 1991, Corkeron *et al.* 1999, Friedlaender *et al.* 2009, Kot *et al.* 2009). Most rorquals feed by opening their mouth

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widely and accelerating through these concentrations until prey and water quickly fill their expandable ventral pouch (Pivorunas 1979; Lambertsen 1983; Orten and Brodie 1987; Goldbogen *et al.* 2006, 2007, 2008). The mouth then closes nearly all the way as musculature and viscoelastic material properties of the pouch and tongue squeeze water back out the mouth through a set of baleen plates that trap prey for consumption (Pivorunas 1979, Lambertsen 1983, Kot 2005, Potvin *et al.* 2009). This process is collectively known as lunge-feeding and when it occurs near the surface it often exposes the mouth and head above the water (*e.g.*, Heithaus and Dill 2009, Kot 2009). Surface lunge-feeding (SLF) behavior is the result of a shallow foraging process containing a series of complex behavioral choices (see Fig. 1). Reasons why rorquals feed at the surface include opportunistic encounters with prey in this location, exploitation of prey along oceanographic fronts (Johnston *et al.* 2005, Kot 2005, Doniol-Valcroze *et al.* 2007), and prey-corralling techniques associated with the air-sea boundary (Hain *et al.* 1982, Lynas and Sylvestre 1988, Hoelzel and Stern 2000, Wiley *et al.* 2011).

Increasingly advanced data collection technology has helped improve historical misconceptions about the natural variation in rorqual lunge-feeding behavior from a time when the minke whale (*Balaenoptera acutorostrata* Lacépède, 1804) was believed

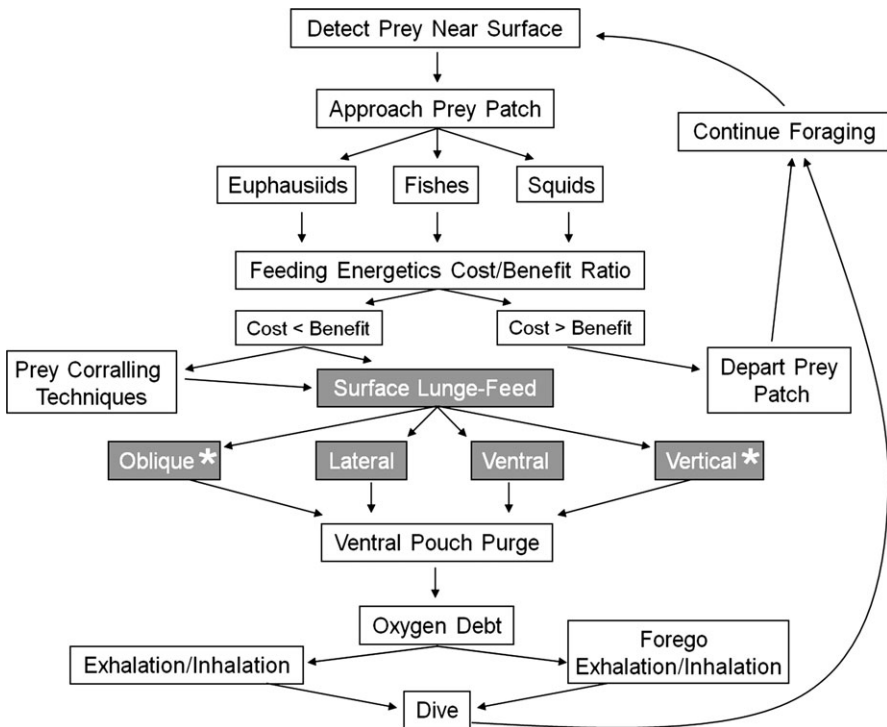


Figure 1. Flow chart showing major components of the rorqual whale foraging behavior process. Multiple arrows radiating from a node represent choices including different surface lunge-feeding behaviors (shaded boxes). Asterisks (\*) indicate feeding behaviors that expose the blowholes above the surface, allowing a rapid exhalation and inhalation during the lunge, possibly increasing foraging efficiency.

to feed similarly to the much larger fin whale (*Balaenoptera physalus* Linnaeus, 1758; Stewart and Leatherwood 1985), and the fin whale was thought to feed similarly to the humpback whale (*Megaptera novaeangliae* Borowski, 1758; Tomilin 1957; Gaskin 1976). Researchers using image-based methods, including from aircraft, began to identify discrete feeding behaviors used by individual rorqual species (e.g., Jurasz and Jurasz 1979, Gaskin 1982, Hain *et al.* 1982, Sears 1983, Horwood 1987, Lynas and Sylvestre 1988, Hoelzel *et al.* 1989). Recent use of animal-borne data loggers has now generated what is likely the most accurate information about the variability in lunge-feeding behavior among the rorquals (Croll *et al.* 2001; Acevedo-Gutierrez *et al.* 2002; Goldbogen *et al.* 2006, 2008, 2011, 2013; Calambokidis *et al.* 2007; Friedlaender *et al.* 2009; Hazen *et al.* 2009). Collectively this body of work demonstrates that rorquals use a variety of lunge-feeding behaviors. However, missing from the literature is a dedicated investigation into the identification, use, and evolution of these behaviors used specifically at the sea surface, an ecological barrier important for capturing prey by rorquals.

Adding to this deficiency is the need for standardized terminology that systematically describes and categorizes different SLF behaviors. For hundreds of years studies published in the popular and scientific literature described these behaviors broadly and with inconsistent terminology (e.g., Théodat Sagard 1632 in Winn and Winn 1985, Bonnaterre 1789, Andrews 1909). Some recent studies continue to use such vague, somewhat interpretable, and different terminology to describe the same behaviors (e.g., Yochem and Leatherwood 1985, McDonald *et al.* 2005). This use of inconsistent terminology potentially creates communication problems among investigators of whale behavior. For example, some descriptions of “lateral lunge feeding” (Jurasz and Jurasz 1979) are similar to “side-feeding” (Watkins and Schevill 1979, Gaskin 1982, Yochem and Leatherwood 1985, Edds and Macfarlane 1987), “side lunge-feeding” (McDonald *et al.* 2005), “feeding on their sides” (Stewart and Leatherwood 1985), and “horizontal lunges at the surface” (Wenzel *et al.* 1988). Further demonstrations of inconsistency include the separation of lunge-feeding from other feeding behaviors such as “side- and lunge-feeding” (Yochem and Leatherwood 1985, Evans 1990) and “rolling and side-lunging” (Edds and Macfarlane 1987). Some investigators distinguish SLF altogether from feeding behavior near the surface but associated with sea birds (Hoelzel *et al.* 1989, Hoelzel and Stern 2000, Robinson and Tetley 2007).

Some of the most detailed terminology about SLF comes from studies in the western North Atlantic (Watkins and Schevill 1979, Gaskin 1982, Sears 1983, Edds and Macfarlane 1987). These were some of the first to classify rorqual SLF behavior by variation in body orientation yet they lack standardization and consistency. Researchers in eastern Canada have modified some of this terminology to describe new behaviors (Lynas and Sylvestre 1988, Kuker *et al.* 2005, Kot *et al.* 2009) but other useful terminology from this area only appears in limited availability on web sites, in tourist information leaflets, and in unpublished proceedings at regional scientific conferences (e.g., Koster and Tschertter 2006, Tschertter and Morris 2007).

Here we present comparative results from a long-term series of field observations that allowed us to develop a standardized classification system of rorqual whale SLF behaviors. We applied this system to test for differences in frequency of these behaviors among our three study species and across all extant rorqual species, and then reconstructed the evolution of each behavioral type. The aim of this investigation was to establish a behavioral baseline that will improve communication among

investigators and facilitate future whale behavior research, including understanding about the evolution of rorqual whale surface feeding behaviors.

## METHODS

### *Field Observations and Image Analyses*

To identify different SLF behaviors, we obtained and analyzed data from field observations, digital photography, and video of surface feeding *B. acutorostrata*, *B. physalus*, and blue whales (*Balaenoptera musculus* Linnaeus, 1758). Data were collected during the summers of 1999–2008 in the Gulf of St. Lawrence, Canada, where most effort used 4.6–7.3 m rigid-hull inflatable boats; alternatively, some work was conducted from helicopters and sailboats. When unfavorable sea conditions prohibited offshore effort, we obtained video from terrestrial locations where rorquals were sometimes observed feeding near shore. Sample sizes of each species were determined using standard photographic identification techniques (Hammond *et al.* 1990, Sears *et al.* 1990) and then applied to statistical tests.

All video of feeding whales was recorded with Sony MiniDV camcorders (Sony Corp., Tokyo, Japan) and uploaded onto a laptop computer for review with Adobe Premiere Pro 2.0 software (Adobe Systems, Inc., San Jose, CA). Clips of feeding sequences were generated for individuals and then grouped by species. Each clip was analyzed using slow playback (35% real time) to identify feeding anatomy, body angles, and body orientations during feeding. Noticeable differences in these allowed us to develop categories of discrete feeding behavior types. Even though some investigators define surface feeding as when a rorqual opens its mouth within the upper 3 m of water (Jurasz and Jurasz 1979), we based our behavioral and kinematics descriptions on lunges exhibiting an open mouth and a distended ventral pouch at or above the surface. Most of our observations featured an open mouth in pursuit of fishes or krill leaping above the surface, indicating that the whales were feeding. It is also possible that the whales could have been lunging with opened mouths for other purposes including communication, parasite removal, play, and displays of annoyance or excitement (Clapham 2009). However, these behaviors do not typically involve an open mouth, although *B. acutorostrata* has been shown to use nonfeeding gulps for communication or display (Arnold *et al.* 2005). What is not likely is that these lunges involved aggression because the whales were clearly chasing prey, and aggression such as “inflated head lunges” (Baker and Herman 1984) typically happens during breeding periods when feeding is not believed to occur (Dawbin 1966). It is also not likely that these lunges involved thermoregulation because evidence suggests that mysticetes conserve heat, not expend it, through their mouth (Heyning and Mead 1997).

### *Statistical Testing of Behavioral Frequencies*

Frequencies of each feeding behavior were comparatively tested among *B. acutorostrata*, *B. physalus*, and *B. musculus* using proportion and count data. All statistical tests were conducted using IBM SPSS Statistics 19 software (IBM Corp., Armonk, NY). Prior to testing, normality of all data was tested using Shapiro-Wilk tests. Levene’s test was used to determine the assumption of equal variance. Kruskal-Wallis tests were used to test for statistically significant differences ( $P < 0.05$ ) in mean

frequency (proportions) of each feeding behavior in the three study species. Chi-square analyses tested for significant differences between observed proportions (% total) of feeding behaviors and the expectation of equally distributed proportions (null hypothesis). Count and proportion data were used to compare frequencies of the combinations of SLF behaviors exhibited by individual *B. acutorostrata*, *B. physalus*, and *B. musculus*. All procedures helped test our two main hypotheses: (1) rorqual whales use SLF behaviors in different proportions that are statistically significant, and (2) each rorqual whale species uses a different suite of these behaviors.

#### *Diversity Score Index*

A diversity score index was developed to measure the diversity of behaviors exhibited by all balaenopterid species, also including the Antarctic minke whale (*Balaenoptera bonaerensis* Burmeister, 1867), sei whale (*Balaenoptera borealis* Lesson, 1828), Bryde's whale (*Balaenoptera edeni* Anderson, 1878), Omura's whale (*Balaenoptera omurai* Wada *et al.* 2003), and humpback whale. Observational data from our three study species were combined with information from published descriptions of feeding behaviors in all living rorqual species. We measured the quantity of behaviors exhibited per species using a simple scoring system of 0 = Absence, 1 = Presence, and 0.5 = Hypothesized Presence. Total scores provided a measure of surface feeding behavioral diversity for each taxon.

Efforts were made to validate our total scores by minimizing bias from individual reviewers. This involved comparing our scores with those from two anonymous whale researchers that reviewed a series of random samples from our previously scored video clips. Results demonstrated little discrepancy between the reviewers' classification of different lunge-feeding types and our own. Scores were 100% consistent for *B. acutorostrata* and *B. physalus* across all reviewers, and 64% consistent for *B. musculus*. Therefore, a higher quality selection of lunge-feeding video sequences (*e.g.*, less blur and more visible feeding anatomy above the surface) were then chosen and analyzed for *B. musculus*.

#### *Evolutionary Analysis*

The evolutionary history of each SLF behavior within Balaenopteridae was evaluated under the assumptions of Maximum Parsimony (MP) and Maximum Likelihood (ML). Each of the six lunge-feeding types was encoded as absent (0) or present (1) in a character matrix for all eight balaenopterid species (Bannister 2009). Behaviors classified as a "hypothesized presence" were encoded as unknown/missing (?) to account for uncertainty and the effect on ancestral node reconstruction. Mesquite v2.71 software (Maddison and Maddison 2009) was used to trace the behavioral evolution using the phylogeny of Balaenopteridae (after McGowen *et al.* 2009) and forcing it to be monophyletic relative to the gray whale (*Eschrichtius robustus* Lilljeborg, 1861), which represented the nonSLF outgroup taxon. Mesquite was also used to calculate the number of steps (*n*) and a consistency index (CI) for MP analyses, and proportional likelihoods (PL) for ML analyses. Reconstructions with "hypothesized presence" recoded to presence were also considered.

## RESULTS

Our results identified six homologous SLF behaviors used in different proportions and combinations by *B. acutorostrata* ( $n = 62$ ), *B. physalus* ( $n = 10$ ), and *B. musculus* ( $n = 39$ ), based on 250 h of video data containing 3,617 SLF events. Table 1 summarizes our proposed standardized classification scheme for the six SLF behaviors. Upright body orientations at oblique angles (pitch) above the surface were classified as oblique lunges (OL). Lateral orientations were classified as lateral lunges, with right lateral lunges (RL) and left lateral lunges (LL) representing right and left orientations, respectively. Inverted orientations were classified as ventral lunges, with clockwise ventral lunges (CWVN) and counterclockwise ventral lunges (CCWVN) representing body rolling direction (with the whale's rostrum facing a clock) leading to an upright position for breathing. Upright rolling typically occurred after inverted and lateral lunges. Lastly, vertical body orientations were classified as vertical lunges (VT). Figure 2 includes photographs of rorquals performing some of these behaviors.

Results from Kruskal-Wallis tests showed statistically significant differences in mean proportions (%) for all lunge-feeding behaviors, except VT (Table 2). Chi-square tests also supported significant differences between observed proportions and the expectation of equally distributed proportions for each behavior, except VT (Fig. 3). All six behaviors were used in relatively different proportions (including in absence) by the three species, suggesting discrete SLF behavioral repertoires (Fig. 4). *Balaenoptera acutorostrata* used all six behaviors as part of their repertoire with OL, RL, and CCWVN comprising 94.5% of our total observations. *Balaenoptera physalus* used four of the six behaviors as part of their repertoire with RL comprising 96% of our observations. *Balaenoptera musculus* used four of the six behaviors with RL, LL, CWVN, and CCWVN comprising 90% of the observations. Statistical tests allowed us to reject our null hypotheses that rorqual whales use surface feeding behaviors in similar proportions, and with similar behavioral repertoires.

Sums of diversity scores demonstrated an order of behavioral repertoire diversity across all eight species of Balaenopteridae. *Balaenoptera acutorostrata* measured the highest score and *B. omurai* was the lowest (Table 3). Intermediate scores formed the remaining list of species in order of decreasing diversity. Calculated scores for *B. acutorostrata*, *B. physalus*, and *B. musculus* were very similar when using observational data or data from descriptive accounts in the literature. This validated the accuracy of our method for determining repertoire diversity in species we did not observe.

Count data also showed that individuals of the three species used different proportions (%) of specific combinations of behaviors during feeding bouts (Fig. 5; note symbols associated with nomenclature). For individuals using one behavior, 6 of 6 (100%) *B. physalus* used RL, 16 of 23 (70%) *B. acutorostrata* used OL, and 5 of 12 (42%) *B. musculus* used CCWVN. When individuals used two behaviors, 7 of 11 (64%) *B. musculus* used a combination of CWVN + CCWVN, 2 of 4 (50%) *B. physalus* used RL + CCWVN, and 8 of 27 (30%) *B. acutorostrata* used both OL + RL and RL + CCWVN combinations equivocally (both 30%). When using combinations of three behaviors, 6 of 7 (86%) *B. musculus* used RL + CWVN + CCWVN and 4 of 7 (57%) *B. acutorostrata* used OL + RL + CCWVN. When using four behaviors, 2 of 2 (100%) *B. acutorostrata* used OL + RL + CCWVN + VT and 8 of 8 (100%) *B. musculus* used RL + LL + CWVN + CCWVN. No *B. physalus* used more than two behaviors and no *B. acutorostrata* or *B. musculus* used more than four.

Figure 6 represents the evolutionary history of SLF behaviors in Balaenopteridae with reconstructions including hypothesized presence (see Table 4). Both OL and RL

Table 1. Rorqual whale surface lunge-feeding (SLF) behaviors and descriptions.

SLF behavior	Nomenclature	Symbol	Description
I	Oblique Lunge	OL	Forward trajectory from a feeding whale that is approximately 45° with the sea surface (similar to the surfacing trajectories observed underwater by Williamson (1972). This oblique angle (body pitch) varies from 10° to 75°. Re-entry typically lands on the mental (chin) region and is thought to aid purging of the pouch (Lynas and Sylvestre 1988). Photographs of whales at the end of VT sometimes appear similar to OL ( <i>e.g.</i> , fig. 4b in Jurasz and Jurasz 1979). Therefore, interpretation of still images can be difficult for the untrained observer, and require more information about moving anatomy found within video footage.
IIa	Right Lateral Lunge	RL	Forward trajectory from a feeding whale that occurs at a low angle with the sea surface while the right flank of the whale remains generally downward and in the water. An axial, counterclockwise roll (rostrum facing a clock) that exposes the blowholes for a rapid breath may occur before the animal descends below the surface. Constant or accelerated motion is typically seen for some distance at the surface before any rolling occurs. This motion helps distinguish RL from CCWVN.
IIb	Left Lateral Lunge	LL	Forward trajectory from a feeding whale that occurs at a low angle with the sea surface while the left flank of the whale remains generally downward and in the water. An axial, clockwise roll that exposes the blowholes for a rapid breath may occur before the animal descends below the surface. Constant or accelerated motion is typically seen for some distance at the surface before any rolling occurs. This motion helps distinguish LL from CWVN lunges.
IIIa	Clockwise Ventral Lunge	CWVN	Forward trajectory from a feeding whale that occurs from an inverted position and usually at a low angle with the sea surface before an axial, clockwise roll occurs. The angle may reach up to about 45°, which is typical for smaller and juvenile animals. The roll may expose the blowholes for a breath. The latter stage of ventral lunges may appear similar to lateral lunges, especially in the larger rorqual species, but can be distinguished by a mostly continued rolling motion throughout the lunge.
IIIb	Counterclockwise Ventral Lunge	CCWVN	Forward trajectory from a feeding whale that occurs from an inverted position and usually at a low angle with the sea surface before an axial, counterclockwise roll occurs. Similar to CWVN, the angle may reach up to about 45°, which is typical for smaller and juvenile animals. This rolling direction may also expose the blowholes for a breath.
IV	Vertical Lunge	VT	Near vertical (76° to 90°) trajectory from a feeding whale that is above the surface and typically falling forward onto its chin. Some whales may fall backward on top of their head, or laterally onto either side of their head. The mouth often closes rapidly during the ascent of the vertical lunge.



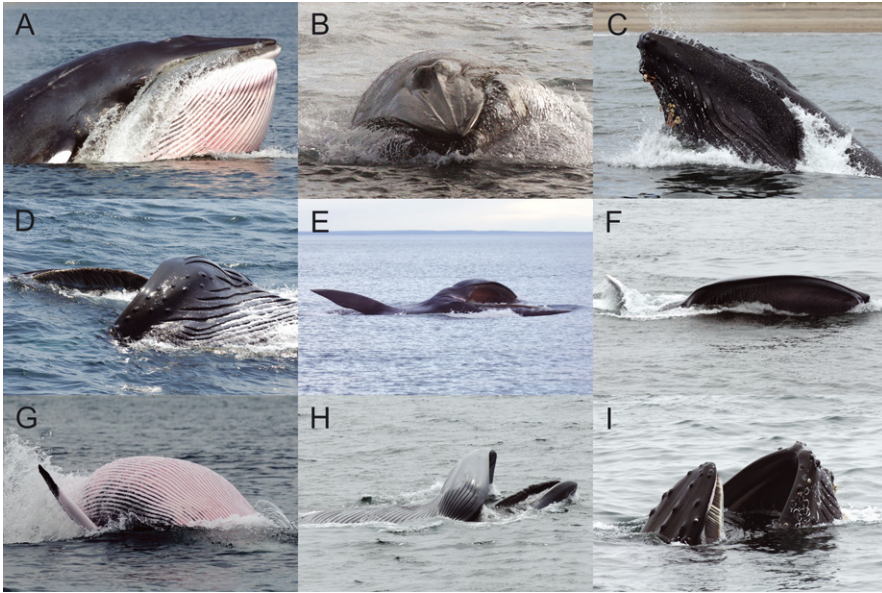


Figure 2. Photographs of rorqual whales exhibiting different surface lunge-feeding behaviors: *B. acutorostrata* with oblique lunge (A), *B. edeni* with oblique lunge (B), *M. novaeangliae* with oblique lunge (C), *M. novaeangliae* with a right lateral lunge (D), *B. physalus* with right lateral lunge (E), *B. musculus* with right lateral lunge (F), *B. acutorostrata* with counterclockwise ventral lunge (G), *B. musculus* with counterclockwise ventral lunge (H), *M. novaeangliae* with vertical lunge (I). Photo credit: B. Kot/MICS (A, C–I) and Carlos Olavarria (B; used with permission).

Table 2. Mean ( $\pm$  SE) proportion values (%) for each lunge-feeding behavior by *B. acutorostrata*, *B. physalus*, and *B. musculus*. Results from Kruskal-Wallis tests showed statistically significant differences ( $P < 0.05$ ) in these mean values for all feeding behaviors except vertical lunges. Dashes (–) indicate feeding behaviors not observed for a species.

Feeding behavior	<i>B. acutorostrata</i> ( $n = 62$ )	<i>B. physalus</i> ( $n = 10$ )	<i>B. musculus</i> ( $n = 39$ )	$P$
Oblique Lunge	45% $\pm$ 5%	6% $\pm$ 6%	–	<0.01
Right Lateral Lunge	23% $\pm$ 4%	85% $\pm$ 8%	26% $\pm$ 5%	<0.01
Left Lateral Lunge	0.6% $\pm$ 0.5%	–	8% $\pm$ 3%	<0.01
Clockwise	2% $\pm$ 1%	–	19% $\pm$ 4%	<0.01
Ventral Lunge				
Counterclockwise	20% $\pm$ 3%	7% $\pm$ 7%	46% $\pm$ 5%	<0.01
Ventral Lunge				
Vertical Lunge	4% $\pm$ 2%	0.07% $\pm$ 0.07%	–	0.135

behaviors (Fig. 6A, B) are shared among all balaenopterids and were highly supported as present in the most recent common ancestor (MRCA) of Balaenopteridae ( $n = 1$ , CI = 1.000, PL = 0.932, clade 1). OL (Fig. 6A) in *B. bonaerensis*, *B. omurui*, and *B. musculus* was classified as hypothesized presence. This behavior was highly supported as present in the MRCA of clade 2 (*B. borealis* to *B. physalus*; PL = 0.988).

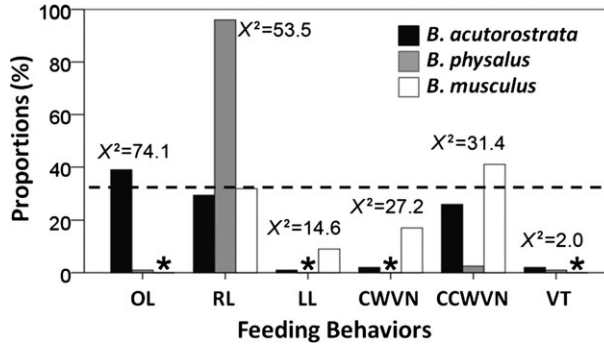


Figure 3. Proportions (%) of six homologous surface lunge-feeding behaviors by 62 *B. acutorostrata* (closed bar), 10 *B. physalus* (shaded bar), and 39 *B. musculus* (open bar) observed in this study. Chi-square tests ( $\chi^2$ ) showed statistically significant differences between observed proportions and the expectation of equally distributed proportions (null hypothesis) for each behavior, except vertical lunges (VT). Dashed line references the expected proportion value (33.3%) for each behavior. Asterisks (\*) within the triplicate clusters identify whale species not observed using that feeding behavior. See Table 1 for descriptions of the abbreviated feeding behavior categories along the x-axis.

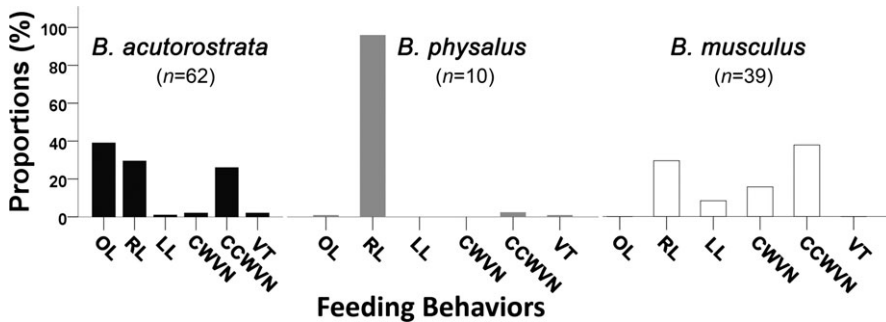


Figure 4. Surface lunge-feeding behavioral repertoires of *B. acutorostrata*, *B. physalus*, and *B. musculus* observed in this study. Bar graphs show proportions (%) of some or all of the six homologous feeding behaviors comprising each repertoire. See Table 1 for descriptions of the abbreviated feeding behavior categories along the x-axis.

RL (Fig. 6B) was classified as hypothesized presence for *B. bonaerensis*, *B. borealis*, and *B. omurai*. This behavior was highly supported as present in the MRCA of clade 1 (PL = 0.992) and of clade 3 (comprised of *B. borealis* to *B. musculus*; PL = 0.996). The most parsimonious scenario is the presence of both behaviors in *B. bonaerensis*, *B. borealis*, *B. omurai*, and *B. musculus*. MP analysis supported a single loss ( $n = 2$ , CI = 0.500) of LL (Fig. 6C) in *B. omurai*, however, this was not supported in ML analyses, with equivocal results (PL = 0.500). Recoding from hypothesized presence to presence in *B. bonaerensis*, *B. borealis*, and *M. novaeangliae* increased the MRCA PL to 0.846 (clade 1), 0.934 (clade 2), and 0.925 (clade 4; *B. borealis* to *B. omurai*), respectively, for presence of LL (results not shown) and supported a single loss in *B. omurai* (MRCA PL = 0.757). The reconstruction of CWVN (Fig. 6D) showed that presence or absence was equivocal in MP ( $n = 2$ , CI = 0.500), but with a higher likelihood of

Table 3. Known surface lunge-feeding behaviors used by all rorqual species. A diversity score index (SI) is assigned to each species according to known feeding behavior presence (dark shaded box: score = 1), absence (open box: score = 0), and hypothesized presence (light shaded box: score = 0.5). Numbers in the cells refer to the references listed below the table.

Species	OL	RL	LL	CWVN	CCWVN	VT	SI
<i>B. acutorostrata</i>	9	4	4	8	8	11	6.0
<i>B. physalus</i>	3	3	3		10	5	5.5
<i>B. musculus</i>		12	12	10	12	13	5.5
<i>M. novaeangliae</i>	6	3				6	4.5
<i>B. edeni</i>	2	14	14			1	4.5
<i>B. bonaerensis</i>							3.0
<i>B. borealis</i>	7						2.0
<i>B. omurai</i>							2.0

References: 1. Gaskin 1972; 2. Gaskin 1976; 3. Gaskin 1982; 4. Gill *et al.* 2000; 5. Goldbogen *et al.* 2006; 6. Hain *et al.* 1982; 7. Jefferson *et al.* 2008; 8. Koster and Tschertter 2006; 9. Kot *et al.* 2009; 10. BWK, RS, DZ, and MSG, unpublished data; 11. Lynas and Sylvestre 1988; 12. Sears 1983; 13. RS, unpublished data; 14. Tershy and Wiley 1992. See Table 1 for descriptions of the abbreviated feeding behavior categories along the x-axis.

presence in the balaenopterid MRCA based on the ML (PL = 0.664) reconstruction. A loss of CWVN was indicated for the MRCA of clade 4 (PL = 0.748). Recoding from hypothesized presence to presence in *B. bonaerensis*, *M. novaeangliae*, and *B. physalus* increased the PL of the MRCA of clade 1 and clade 4 to 0.798 (present) and 0.845 (absent), respectively (results not shown). The most parsimonious scenario for CCWVN (Fig. 6E;  $n = 2$ ; CI = 0.500) and VT (Fig. 6F;  $n = 2$ , CI = 0.500) suggested presence in the balaenopterid MRCA. However, this was found to be equivocal by ML (PL = 0.500). A single loss of both behaviors was indicated in *B. borealis*, with MP and ML unable to reconstruct the MRCA of clade 3. Recoding from hypothesized presence in *B. bonaerensis*, *B. edeni*, *B. omurai*, and *M. novaeangliae* for CCWVN, and *B. bonaerensis* and *B. omurai* for VT, supported a single loss in *B. borealis* that diverged from a MRCA that most likely exhibited both behaviors (PL = 0.8112).

## DISCUSSION

### *Standardized Behavioral Classification System*

This investigation allowed us to propose a unified behavioral classification system of standardized terminology and descriptions for different SLF behaviors used by rorqual whales. Our descriptions followed the level of detail by Hain *et al.* (1982) and were based on variants of upright, lateral, inverted, and vertical body orientations, relative to the sea surface, using modified terminology from Jurasz and Jurasz (1979) and Lynas and Sylvestre (1988). We used expansions of these terms, consistent descriptors, and new information about body rolling direction to form the system. Application of this system allowed us to comparatively test for differences in behavioral variability and evolutionary history regarding the specialized feeding adaptations used by rorqual whales to capture schooling prey in bulk near the sea surface. Ultimate explanations for this variability involve 12–28 million years (Jackson *et al.* 2009) of selective pressures adapting each species for a distinct repertoire of surface feeding behaviors.

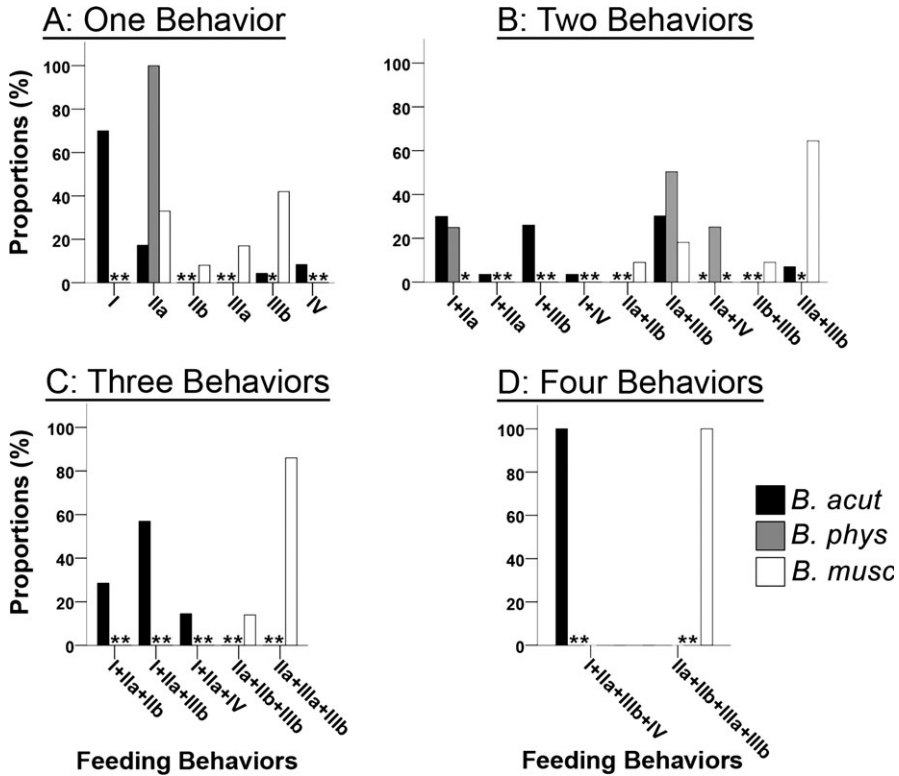


Figure 5. Proportions (%) of the combinations of surface lunge-feeding behaviors used by individual *B. acutorostrata* (closed bar), *B. physalus* (shaded bar), and *B. musculus* (open bar) when one (A), two (B), three (C), and four (D) different behaviors were used during a feeding bout. Individual *B. acutorostrata* and *B. musculus* were not observed using more than four feeding behaviors while *B. physalus* were not observed using more than two. Roman numerals represent each feeding behavior (see Table 1).

#### Behavioral Repertoires: Identification and Diversity Among Rorquals

Use of our classification system provided evidence that each rorqual species uses a discrete suite of SLF behaviors that we identified as a behavioral repertoire. The magnitude of behaviors present or hypothesized as present in each repertoire represented a measure of behavioral diversity for each species. *Balaenoptera acutorostrata*, one of the most globally distributed piscivores and zooplanktivores (Horwood 1990, Reeves *et al.* 2002), demonstrated the most diverse SLF behavioral repertoire (Table 3). *Balaenoptera physalus* and *B. musculus*, also historically cosmopolitan (prior to commercial whaling), demonstrated slightly less diverse feeding repertoires, despite the mostly stenophagous diet on krill in *B. musculus* (Nemoto 1970). *Megaptera novaeangliae* and *B. edeni* exhibited intermediate levels of diversity, while *B. bonaerensis*, *B. borealis*, and *B. omurai* exhibited the least. Collectively this information creates a behavioral diversity gradient across all rorqual species, suggesting that *B. acutorostrata* is the most generalized surface feeder while *B. omurai* is the most specialized.

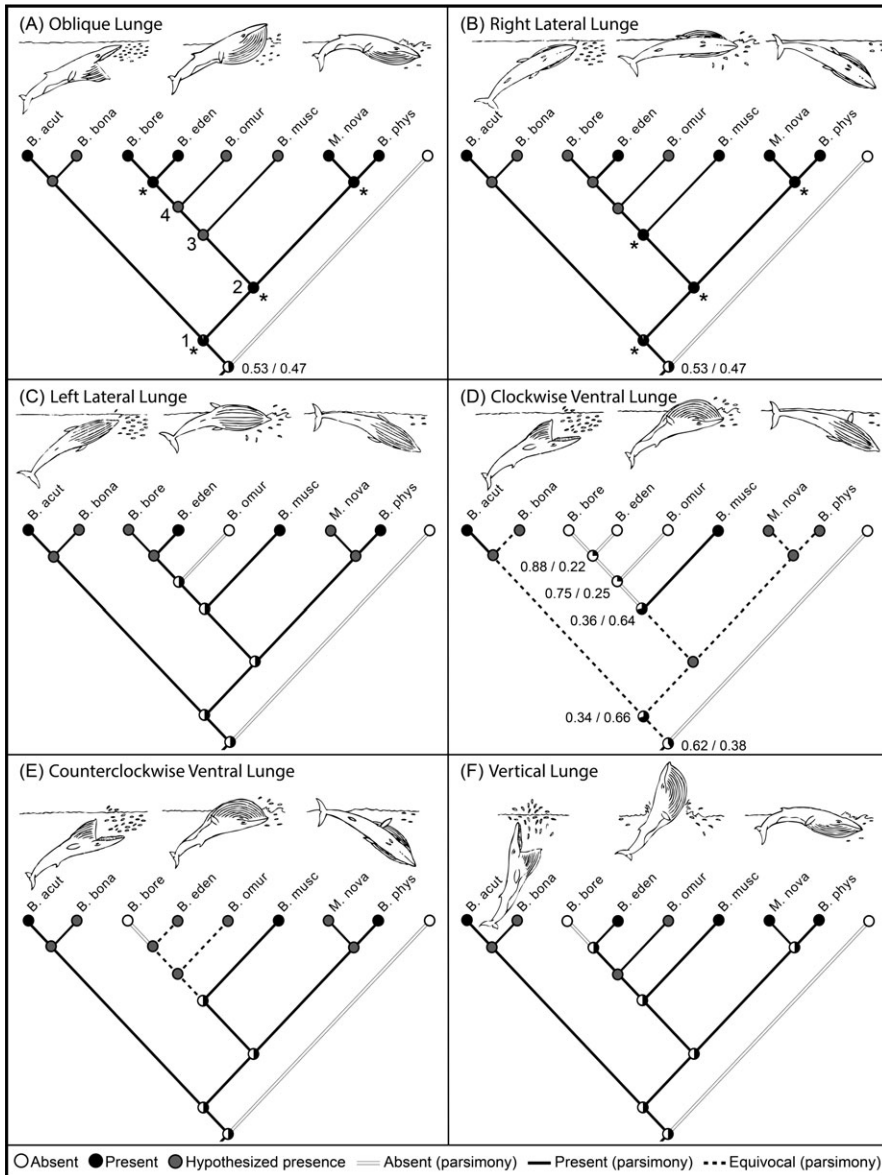


Figure 6. Reconstruction of the evolution of the six lunge-feeding behaviors based on Parsimony (branches) and Maximum Likelihood (absent/present proportional likelihood values at nodes; \* >0.95) optimality criteria. Clades 1–4 are identified in box A and apply to all reconstructions (boxes A–F). Phylogeny of Balaenopteridae is after McGowen *et al.* (2009) and forced to be monophyletic, with gray whales (*E. robustus*) representing an outgroup taxon. Sketches illustrate left-to-right feeding sequences for each behavior and the small elliptical shapes represent targeted prey such as schooling fish.

Table 4. Lunge-feeding behavior character matrix used to trace the evolutionary history in Balaenopteridae (Fig. 6) under the Parsimony and Maximum Likelihood optimality criteria. 0 = absent; 1 = present; 1\* = hypothesized presence (encoded as ? in separate analyses to evaluate the effect on ancestral node reconstruction; see results for further discussion). See Table 1 for descriptions of the abbreviated feeding behavior categories along the x-axis.

Species	OL	RL	LL	CWVN	CCWVN	VT
<i>B. acutorostrata</i>	1	1	1	1	1	1
<i>B. physalus</i>	1	1	1	1*	1	1
<i>B. musculus</i>	1*	1	1	1	1	1
<i>M. novaeangliae</i>	1	1	1*	1*	1*	1
<i>B. edeni</i>	1	1	1	1	1*	1
<i>B. bonaerensis</i>	1*	1*	1*	1*	1*	1*
<i>B. borealis</i>	1	1*	1*	0	0	0
<i>B. omurai</i>	1*	1*	0	0	1*	1*
<i>E. robustus</i>	0	0	0	0	0	0

Decreased maneuverability of *Balaenoptera* vs. *Megaptera* may have contributed to differences in our diversity scores (Woodward *et al.* 2006). A paucity of known information about the feeding behaviors of *B. bonaerensis* and *B. omurai* (Jefferson *et al.* 2008) may have also biased their scores due to their recent distinctions as new species (Rice 1998, IWC 2001, Wada *et al.* 2003, Sasaki *et al.* 2006). However, based on known SLF information from the closely related *B. acutorostrata*, although a more dedicated piscivore (Sergeant 1963), we hypothesized that *B. bonaerensis* also uses all six feeding behaviors. Our frequency data indicated that OL, RL, and CCWVN may be the most important behaviors for rorquals to efficiently capture prey near the sea surface. Test results showing right-handed lateralized behavior (see below) support this evidence.

#### Individual Behavioral Differences

Results from count data demonstrated that individual *B. acutorostrata*, *B. physalus*, and *B. musculus* used one to four of the six homologous behaviors (Fig. 7). Although Kruskal-Wallis and chi-square tests showed that *B. acutorostrata* used all six behaviors, our count data showed that no individual whale from each species used more than four in its repertoire. Individual *B. acutorostrata* and *B. musculus* used up to four different behaviors while individual *B. physalus* used one or two.

#### Evidence of Behavioral Lateralization

Further application of the classification system allowed us to test for behavioral lateralization among *B. acutorostrata*, *B. physalus*, and *B. musculus* using SLF behaviors with right and left components. Results from chi-square tests showed significant differences in the frequency of right-handed vs. left-handed lateral and ventral lunges (Table 5). Similar right-handedness is known in *B. physalus* and *M. novaeangliae* (Tershy and Wiley 1992, Clapham *et al.* 1995, Canning *et al.* 2011) but we provide new evidence for this in *B. acutorostrata* and *B. musculus*. Explanation for lateralization in *B. physalus* is attributed to their asymmetric pigmentation (Mitchell 1972, Brodie 1977, Gambell 1985, Tershy and Wiley 1992), however, *B. acutorostrata* and *B. musculus* lack any such obvious asymmetries. Further explanation comes from

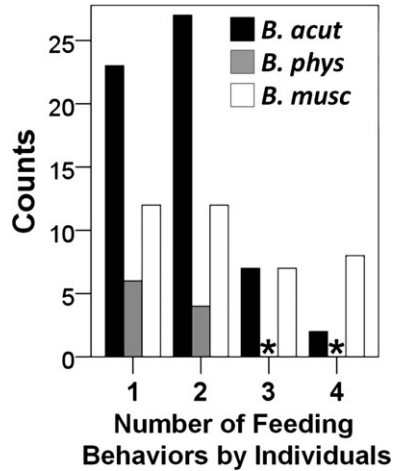


Figure 7. Counts of individual *B. acutorostrata*, *B. physalus*, and *B. musculus* that used one to four different surface lunge-feeding behaviors. No whales were observed using more than four of the six identified behaviors.

Table 5. Results from behavioral lateralization tests for *B. acutorostrata*, *B. physalus*, and *B. musculus*. Chi-square tests ( $\chi^2$ ) showed statistically significant differences in the use of right-handed (favoring the right side) *vs.* left-handed (favoring the left side) lateral and ventral lunge-feeding behaviors. See Table 1 for descriptions of the abbreviated feeding behavior categories along the x-axis.

Species	(Right) RL	(Left) LL	$\chi^2$	<i>P</i>	(Right) CCWVN	(Left) CWVN	$\chi^2$	<i>P</i>
<i>B. acutorostrata</i>	96	2	90	0	85	7	66	<0.01
<i>B. physalus</i>	185	0	185	0	5	0	5	<0.01
<i>B. musculus</i>	130	36	53	0	166	69	40	<0.01

recent evidence that behavioral lateralization is widespread across many vertebrate animals, and suggests that predators including mammals may be able to exploit the predictability of behavior from population-level lateral biases in prey (Vallortigara and Rogers 2005). Various teleost fishes prefer right turns to inspect predators from their right side (De Santi *et al.* 2001), indicating a potential feeding advantage for a pursuing rorqual that would likely turn to the right or favor its right side as part of its repertoire of lateralized feeding adaptations.

#### Evolution of SLF Behaviors

Explanations for the evolution of surface feeding behaviors in rorqual whales involve ecological, physiological, and other selective pressures adapting each species for a suite of efficient feeding maneuvers specialized for engulfing prey at the sea surface. Some of these pressures likely include preferred diet, prey availability, prey density, competition for prey, foraging habitat, and oceanographic conditions. Our evolutionary reconstructions demonstrated OL and RL as synapomorphies with the most common ancestor in clade 2 (Fig. 6A, B), as well as in all of Balaenopteridae

(clade 1). Body rolling may assist with visual processing of prey fields because roqual eyes are laterally positioned (Goldbogen *et al.* 2013) yet, given our evidence that OL behavior (nonrolling) is frequently exhibited by some species (*e.g.*, *B. acutorostrata*) and is present in all balaenopterids, nonrolling behaviors could be advantageous for tracking prey directly forward of a feeding roqual. Explanations for presence of RL in all balaenopterids can be explained by their known tendency to exhibit right-handed behavioral lateralization (Clapham *et al.* 1995, Canning *et al.* 2011; Table 5, this study) and to help prevent prey from escaping through a roqual's palatalmandibular gaps when using OL (Potvin *et al.* 2010). However, the current lack of field observations (*e.g.*, not limited to published literature) for the presence of right-handed CCWVN behavior in *B. bonaerensis*, *B. edeni*, *B. omurai*, and *M. novaeangliae* weakens this evidence (Fig. 6E).

Lost CWVN, CCWVN, and VT traits in *B. borealis* may be due to this species' ability to facultatively skim-feed when zooplankton (*e.g.*, copepods) is abundant at the surface (Horwood 2009); sometimes they continue using this method even if opportunities exist to lunge-feed on schooling fishes nearby (Watkins and Schevill 1979). Perhaps the forward pressure wave generated by an accelerating roqual prior to SLF tends to scatter smaller zooplankton like copepods, resulting in a less efficient prey capture tactic than skim-feeding. *Balaenoptera musculus* may be able to skim prey off the surface (Winn and Winn 1985) and, if krill concentrations are low, so can *B. bonaerensis* (Horwood 1987, 1990). Perhaps skim-feeding plays a larger role in the plasticity and evolution of roqual SLF behaviors than is currently understood.

Our statistics indicated that LL was the second least frequent behavior among roquals (Fig. 3, 4) yet it remained present in all species, except *B. omurai* (Fig. 6C). Given the paucity of existing behavioral data for *B. omurai*, we recognize the limitations in determining any of its behaviors. However, to include it in this study we categorized its SLF behaviors as hypothesized presence using behaviors from its close relative *B. edeni* that exhibits morphological and geographical range similarities (Sasaki *et al.* 2006, Yamada 2009); we also included the assumption that they exhibit right-handed behavioral lateralization like most other roqual species (as discussed above).

The presence or absence of CWVN was equivocal (MP), with a slightly higher likelihood for presence among Balaenopteridae. However, a loss was indicated for *B. borealis*, *B. edeni*, and *B. omurai* (clade 4; Fig. 6D). Except for the loss of CCWVN and VT traits in *B. borealis*, the presence or absence in the MRCA (clade 1; Fig. 6E, F) was equivocal due to uncertainty of CCWVN being present in *B. bonaerensis*, *B. edeni*, *B. omurai*, and *M. novaeangliae*. Improving the documentation of these behaviors among these species would likely support the presence and exhibition of both traits, as these behaviors appear to play important roles in the feeding repertoires of roquals. Although shared among most balaenopterids (Fig. 6E), VT were used the least among our three observed study species (Fig. 3, 4). Perhaps this behavior is used under certain prey conditions (*e.g.*, rapidly fleeing fish schools) when the most energetic SLF behavior (see below) is most effective to capture fast swimming prey from below. Low observed frequency of this behavior could also be explained by its relatively high energetic cost among the six SLF behaviors (BWK, RS, DZ, and MSG, unpublished data).

Preferred prey likely contributes major selective pressures toward the evolution of individual SLF behaviors in roqual whales. Literature involving these preferences by each roqual species, including detailed stomach content analyses from during commercial whaling efforts, is extensive and therefore not included here. However, we



refer the reader to the Literature Cited section in our study for some specific information on preferred prey by most of the rorquals, and to Pauly *et al.* (1998) and Barros and Clarke (2009) for more general information.

### *Greater Behavioral Variability at the Surface than at Depth*

Our feeding behavior diversity scores for *B. physalus*, *M. novaeangliae*, and *B. musculus* were higher at the surface than at depth, concluded after determining underwater scores from published accounts that used data loggers attached to rorquals (Table 6). Similar to our observations of body rolling during ventral lunges by surface feeding *B. musculus*, recent work by others has demonstrated that *B. musculus* feeding at depth also perform 360° body rolls during underwater ventral lunges, but with a frequency of 10% (Goldbogen *et al.* 2013) *vs.* our observed frequency of 59%. If complete body rolls assist with visual detection and engulfment of prey in the low ambient light at depth (Goldbogen *et al.* 2013), it is plausible that increased visual acuity in near-surface lighting would allow rorquals to use more lunging behaviors at the surface because lateral lunges incorporate partial rolling ( $\leq 180^\circ$ ), and both OL and VT have upward trajectories that position backlit prey against downwelled sunlight.

Lunge-feeding is energetically costly and limits dive times (Acevedo-Gutierrez *et al.* 2002), suggesting that more time can be used for foraging rather than diving to reach prey at depth (Goldbogen *et al.* 2011, Ware *et al.* 2011). Therefore, having more time to feed could also afford rorquals the use of higher behavioral variation at the surface, including use of the more energetically taxing feeding behaviors. Less dependence on behaviors that allow simultaneous breathing (*e.g.*, OL and VT) could promote higher behavioral variability when feeding at the surface (see asterisks in Fig. 1). This supports why 90% of *B. physalus* and 100% of *B. musculus* in our observations used feeding behaviors not allowing breaths (lateral and ventral lunges). With the exception of individual whales (mostly *B. acutorostrata*) using OL that allow breaths, most whales rolled upright to breathe after each or every other lunge. Even though rorqual foraging efficiency is suggested to be similar at the surface as it is at depth (Goldbogen *et al.* 2011, Ware *et al.* 2011), we provide new evidence that feeding behavior at the surface is relatively more variable.

### *Lunge-Feeding Energy*

In combination with high variability in the choice of surface feeding behaviors, rorquals in our observations also demonstrated high variability in the energy

Table 6. Known at depth lunge-feeding behaviors used by *B. physalus*, *M. novaeangliae*, and *B. musculus*. A diversity score index (SI) is assigned to each species according to known feeding behavior presence (dark shaded box: score = 1), absence (open box: score = 0), and hypothesized presence (light shaded box: score = 0.5) from studies using dataloggers (see references below). See Table 1 for descriptions of the abbreviated feeding behavior categories along the x-axis.

Species	OL	RL	LL	CWVN	CCWVN	IV	SI
<i>B. physalus</i>			2		2	2	4.0
<i>M. novaeangliae</i>	3	4	4			4	4.0
<i>B. musculus</i>	5			6	1		3.0

References: 1. Acevedo-Gutierrez *et al.* 2001; 2. Goldbogen *et al.* 2006; 3. Goldbogen *et al.* 2008; 4. Canning *et al.* 2011; 5. Goldbogen *et al.* 2011; 6. Goldbogen *et al.* 2013.

of their lunges. Highly energetic lunges were conspicuously faster and exposed more anatomy above the surface than less energetic lunges, with the most intense generating enough momentum to carry at least half the body above the surface. The least energetic did not expose an open mouth, yet the distended pouch remained visible, above the surface (similarly noted by Watkins and Schevill (1979)). Despite these qualitative determinations, it was clear that the consistent order of decreasing energy by feeding type was vertical, oblique, ventral, and lateral lunges. These differences were likely motivated by variability in hunger state or compensatory behavior (e.g., lunging acceleration) in response to specific prey escape maneuvers. Twice during our study we observed different *B. acutorostrata* performing unusually energetic CCWVN where momentum from chasing capelin (*Mallotus villosus*) tilted the peduncle and flukes 3–4 m above the surface, temporarily upending their bodies into a near-vertical position. *Megaptera novaeangliae* are known to feed with similarly energetic lunges (e.g., oblique, lateral, and vertical) but have also been observed rising slowly up to the surface with their mouth open (Hain *et al.* 1982).

Our observations support previous evidence that highly energetic SLF behavior in *B. acutorostrata* is associated with piscivory (Lynas and Sylvestre 1988). We also observed *B. physalus* and *B. musculus* using highly energetic lateral and ventral lunges when feeding on krill along oceanographic fronts, although others have observed *B. physalus* feeding more rapidly on fishes than krill (Tomilin 1957). Early commercial whalers described intensely feeding *B. physalus* with “supreme indifference” to boat presence, even when markers (1–3 ft metal darts) were shot into the whales’ backs (Gunther 1949). Our observations of feeding *B. acutorostrata*, *B. physalus*, and *B. musculus* often showed similar levels of apparently focused behavior.

### Bubble Production

All three species in our field observations sometimes produced bubbles that rose up to the surface. Some of these may have assisted in concentrating prey (e.g., Hain *et al.* 1982, Lynas and Sylvestre 1988, Kuker *et al.* 2005, Tschertner and Morris 2007, Wiseman 2008) but others appeared when lunge-feeding was not observed, perhaps as a form of communication as suggested by Pryor (1986). *Megaptera novaeangliae* are widely known for producing single and multiple bubbles while lunge-feeding at the surface (e.g., Hain *et al.* 1982) and, during rapid prey chases, so are *B. physalus* that sometimes produce a single 30–50 cm diameter bubble (Watkins *et al.* 1981). We observed *B. physalus* produce single bursts of air and they most often appeared at the surface prior to RL. As the bubble reached the surface, the whale’s rostrum became visible about 10 m ahead (Fig. 8). It is unclear what mechanism produced this bubble yet, judging by its position as the whale moved underneath, it may be associated with the sound-producing cavitation known to occur when *B. physalus* open their jaws (Watkins *et al.* 1981, Brodie 1993).

We also observed *B. acutorostrata* and *B. musculus* produce 1–3 bubbles during some surface feeding bouts. These typically occurred between consecutive lunges and whether or not the blowholes rose above the surface to intake air. Whatever the mechanism, some rorquals produce bubbles that frighten prey into higher concentrations (Sharpe and Dill 1997), thereby suggesting that breath-holding may help maintain stealthy approaches toward prey patches before bubbles are deployed. Recent evidence also demonstrates that *B. edeni* in the Caribbean Sea produce bubble curtains



Figure 8. Video frame of a *B. physalus* performing a right lateral lunge just after a single, subsurface bubble was produced (A). The whale is lunging to the right and the tip of the rostrum (B) is surfacing approximately 10 m ahead of the bubble. The bubble production mechanism may be associated with the sound-producing cavitation known to occur when *B. physalus* open their jaws (Watkins *et al.* 1981, Brodie 1993). Photo credit: B. Kot/MICS.

somewhat similar to *M. novaeangliae*, with observations and photographs suggesting their function is associated with subsurface feeding.<sup>2</sup>

### *Synchronous Lunging*

The majority of our observations involved single whales feeding independently. However, we also observed individual episodes from two *M. novaeangliae* and two *B. musculus* feeding next to each other in synchrony. The *M. novaeangliae* fed together, in parallel and in the same direction on a krill patch. The *B. musculus* also fed together and in parallel on krill, but with their mouths toward each other with the tips of their mandibles moving past within 10 m. Synchronous surface feeding by rorquals is known in groups of *M. novaeangliae* (Hain *et al.* 1982), and in duplicate and triplicate by *B. physalus* (Reeves *et al.* 2002, Aguilar 2009), but very little is known about individuals of any species lunging against each other. If deliberate, this behavior may be a novel tactic to improve individual prey capture efficiency under certain prey conditions.

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<sup>2</sup>Personal communication from Sébastien Greaux, OMMAG, rue hegesippe Legitimus, beauport, 97117 Port Louis, Guadeloupe, September 2013.

## LITERATURE CITED

- Acevedo-Gutierrez, A., D. A. Croll and B. R. Tershy. 2002. High feeding costs limit dive time in the largest whales. *Journal of Experimental Biology* 205:1747–1753.
- Aguilar, A. 2009. Fin whale *Balaenoptera physalus*. Pages 433–437 in W. Perrin, B. Würsig and J. G. M. Thewissen, eds. *Encyclopedia of marine mammals*. 2nd edition. Academic Press, San Diego, CA.
- Andrews, R. C. 1909. Observations on the habits of the finback and humpback whales of the eastern North Pacific. *Bulletin of the American Museum of Natural History* 26:213–216.
- Arnold, P. W., R. A. Birtles, S. Sobtzyck, M. Matthews and A. Dunstan. 2005. Gulping behavior in rorqual whales: Underwater observations and functional interpretation. *Memoirs of the Queensland Museum* 51:309–332.
- Baker, C. S., and L. M. Herman. 1984. Aggressive behavior between humpback whales (*Megaptera novaeangliae*) wintering in Hawaiian waters. *Canadian Journal of Zoology* 62:1922–1937.
- Bannister, J. L. 2009. Baleen whales (Mysticetes). Pages 80–89 in W. Perrin, B. Würsig and J. G. M. Thewissen, eds. *Encyclopedia of marine mammals*. 2nd edition. Academic Press, San Diego, CA.
- Barros, N. B., and M. R. Clarke. 2009. Diet. Pages 311–316 in W. Perrin, B. Würsig and J. G. M. Thewissen, eds. *Encyclopedia of marine mammals*. 2nd edition. Academic Press, San Diego, CA.
- Bonnaterre, A. 1789. Tableau encyclopédique et méthodique des trois regnes de la nature, dédié et présenté à M. Necker, Ministre d'Etat, et Directeur Général des Finances. *Cétologie* 4:1–28 (seen in Winn and Winn 1985).
- Brodie, P. F. 1977. Form, function, and energetic in Cetacea: a discussion. Pages 45–48 in R. J. Harrison, ed. *Functional anatomy of marine mammals*. Academic Press, New York, NY.
- Brodie, P. F. 1993. Noise generated by the jaw actions of feeding fin whales. *Canadian Journal of Zoology* 71:2546–2550.
- Calambokidis, J., G. S. Schorr, G. H. Steiger, *et al.* 2007. Insights into the underwater diving, feeding, and calling behavior of blue whales from a suction-cup-attached video-imaging tag (Critttercam). *Marine Technology Society Journal* 41:19–29.
- Canning, C., D. Crain, T. S. Eaton, Jr., *et al.* 2011. Population-level lateralized feeding behavior in North Atlantic humpback whales, *Megaptera novaeangliae*. *Animal Behaviour* 82:901–909.
- Clapham, P. J. 2009. Humpback whale *Megaptera novaeangliae*. Pages 582–585 in W. Perrin, B. Würsig and J. G. M. Thewissen, eds. *Encyclopedia of marine mammals*. 2nd edition. Academic Press, San Diego, CA.
- Clapham, P. J., E. Leimkuhler, B. K. Gray and D. K. Mattila. 1995. Do humpback whales exhibit lateralized behavior? *Animal Behaviour* 50:73–82.
- Corkeron, P., P. Ensor and K. Matsuoka. 1999. Observations of blue whales feeding in Antarctic waters. *Polar Biology* 22:213–215.
- Croll, D. A., A. Acevedo-Gutierrez, B. R. Tershy and J. Urban-Ramirez. 2001. The diving behavior of blue and fin whales: Is dive duration shorter than expected based on oxygen stores? *Comparative Biochemistry and Physiology Part A* 129:797–809.
- Dawbin, W. H. 1966. The seasonal migratory cycle of humpback whales. Pages 145–170 in K. S. Norris, ed. *Whales, dolphins and porpoises*. University of California Press, Berkeley, CA.
- De Santi, A., V. A. Sovrano, A. Bisazza and G. Vallortigara. 2001. Mosquitofish display differential left- and right-eye use during mirror-image scrutiny and predator-inspection responses. *Animal Behaviour* 61:305–310.
- Doniol-Valcroze, T., D. Bertheaux, P. Larouche and R. Sears. 2007. Influence of thermal fronts on habitat selection by four rorqual whale species in the Gulf of St. Lawrence. *Marine Ecology Progress Series* 335:207–216.

- Edds, P. L., and J. A. F. Macfarlane. 1987. Occurrence and general behavior of balaenopterid cetaceans summering in the St. Lawrence estuary, Canada. *Canadian Journal of Zoology* 65:1363–1376.
- Evans, P. G. H. 1990. *The natural history of whales and dolphins*. Facts on File, Inc., New York, NY.
- Friedlaender, A. S., E. L. Hazen, D. P. Nowacek, *et al.* 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.
- Gambell, R. 1985. Fin whale *Balaenoptera physalus*. Pages 171–192 in S. H. Ridgway and R. Harrison, eds. *Handbook of marine mammals*. Academic Press, London, U.K.
- Gaskin, D. E. 1972. Whales, dolphins, and seals, with special reference to the New Zealand region. St. Martin's Press, New York, NY.
- Gaskin, D. E. 1976. The evolution, zoogeography and ecology of Cetacea. *Oceanography and Marine Biology—An Annual Review* 14:247–346.
- Gaskin, D. E. 1982. *The ecology of whales and dolphins*. Heinemann Press, London, U.K.
- Gill, A., B. R. Fairbairns and R. S. Fairbairns. 2000. Some observations of minke whale (*Balaenoptera acutorostrata*) feeding behaviors and associations with seabirds in the coastal waters of the Isle of Mull, Scotland. *European Research on Cetaceans* 13:61–64.
- Goldbogen, J. A., J. Calambokidis, R. E. Shadwick, E. M. Oleson, M. A. McDonald and J. A. Hildebrand. 2006. Kinematics of foraging dives and lunge-feeding in fin whales. *Journal of Experimental Biology* 209:1231–1244.
- Goldbogen, J. A., N. D. Pyenson and R. E. Shadwick. 2007. Big gulps require high drag for fin whale lunge feeding. *Marine Ecology Progress Series* 349:289–301.
- Goldbogen, J. A., J. Calambokidis, D. A. Croll, *et al.* 2008. Foraging behavior of humpback whales: Kinematics and respiratory patterns suggest a high cost for a lunge. *Journal of Experimental Biology* 211:3712–3719.
- Goldbogen, J. A., J. Calambokidis, E. Oleson, J. Potvin, N. D. Pyenson, G. Schorr and R. E. Shadwick. 2011. Mechanics, hydrodynamics and energetics of blue whale lunge feeding: Efficiency dependence on krill density. *Journal of Experimental Biology* 214:131–146.
- Goldbogen, J. A., J. Calambokidis, A. S. Friedlaender, *et al.* 2013. Underwater acrobatics by the world's largest predator: 360° rolling manoeuvres by lunge-feeding blue whales. *Biological Letters* 9:20120986.
- Gunther, E. R. 1949. The habits of fin whales. *Discovery Reports* 25:113–142.
- Hain, J. H. W., G. R. Carter, S. D. Kraus, C. A. Mayo and H. E. Winn. 1982. Feeding behavior of the humpback whale, *Megaptera novaeangliae*, in the western North Atlantic. *Fishery Bulletin* 80:99–108.
- Hammond, P. S., S. A. Mizroch and G. P. Donovan. 1990. Report of the workshop on individual recognition and the estimation of cetacean population parameters. Report of the International Whaling Commission (Special Issue 12):3–17.
- Hazen, E. L., A. S. Friedlaender, M. A. Thompson, C. R. Ware, M. T. Weinrich, P. N. Halpin and D. N. Wiley. 2009. Fine-scale prey aggregations and foraging ecology of humpback whales *Megaptera novaeangliae*. *Marine Ecology Progress Series* 395:75–89.
- Heithaus, M. R., and L. M. Dill. 2009. Feeding strategies and tactics. Pages 414–422 in W. Perrin, B. Würsig and J. G. M. Thewissen, eds. *Encyclopedia of marine mammals*. 2nd edition. Academic Press, San Diego, CA.
- Heyning, J. E., and J. G. Mead. 1997. Thermoregulation in the mouths of feeding gray whales. *Science* 278:1138–1139.
- Hoelzel, A. R., and S. J. Stern. 2000. *Minke whales*. Voyageur Press, Stillwater, MN.
- Hoelzel, A. R., E. M. Dorsey and S. J. Stern. 1989. The foraging specializations of individual minke whales. *Animal Behaviour* 38:786–794.
- Horwood, J. 1987. *The sei whale: Population biology, ecology and management*. Croom Helm, London, U.K.
- Horwood, J. 1990. *Biology and exploitation of the minke whale*. CRC Press, Boca Raton, FL.

- Horwood, J. 2009. Sei whales *Balaenoptera borealis*. Pages 1069–1071 in W. Perrin, B. Würsig and J. G. M. Thewissen, eds. Encyclopedia of marine mammals. 2nd edition. Academic Press, San Diego, CA.
- IWC (International Whaling Commission). 2001. Annex U. Report of the working group on nomenclature. Journal of Cetacean Research and Management 3 (supplement): 363–365.
- Jackson, J. A., C. S. Baker, M. Vant, D. J. Steel, L. Medrano-Gozález and S. R. Palumbi. 2009. Big and slow: Phylogenetic estimates of molecular evolution in baleen whales (suborder Mysticeti). Molecular Biology and Evolution 26:2427–2440.
- Jefferson, T. A., M. A. Webber and R. L. Pitman. 2008. Marine mammals of the world: A comprehensive guide to their identification. Academic Press, London, U.K.
- Johnston, D. W., L. H. Thorne and A. J. Read. 2005. Fin whales (*Balaenoptera physalus*) and minke whales (*Balaenoptera acutorostrata*) exploit a tidally-driven island wake ecosystem in the Bay of Fundy. Marine Ecology Progress Series 305:287–295.
- Jurasz, C., and V. P. Jurasz. 1979. Feeding modes of the humpback whale, *Megaptera novaeangliae*, in Southeast Alaska. The Scientific Reports of the Whales Research Institute, Tokyo 31:69–83.
- Koster, S., and U. Tschertner. 2006. Lateralisation of minke whales (*Balaenoptera acutorostrata*) whilst surface feeding in the St. Lawrence Estuary, Canada. Abstract from the 20th Conference of the European Cetacean Society, 2–7 April 2006, Gdynia, Poland.
- Kot, B. W. 2005. Rorqual whale surface-feeding strategies: Biomechanical aspects of feeding anatomy and exploitation of prey aggregations along tidal fronts. M.A. thesis, University of California, Los Angeles, CA. 80 pp.
- Kot, B. W. 2009. Rorqual whale (*Balaenopteridae*) lunge-feeding behaviors, processes and mechanisms. Ph.D. thesis, University of California, Los Angeles, CA. 219 pp.
- Kot, B. W., C. Ramp and R. Sears. 2009. Decreased feeding ability of a minke whale (*Balaenoptera acutorostrata*) with entanglement-like injuries. Marine Mammal Science 25:706–713.
- Kuker, K. J., J. A. Thomson and U. Tschertner. 2005. Novel feeding tactics of minke whales, *Balaenoptera acutorostrata*, in the Saguenay-St. Lawrence National Marine Park. Canadian Field Naturalist 119:214–218.
- Lambertsen, R. H. 1983. Internal mechanism of rorqual feeding. Journal of Mammalogy 64:76–88.
- Lynas, E. M., and J. P. Sylvestre. 1988. Feeding techniques and foraging strategies of minke whales (*Balaenoptera acutorostrata*) in the St. Lawrence River estuary. Aquatic Mammals 14:21–32.
- Maddison, W. P., and D. R. Maddison. 2009. Mesquite: A modular system for evolutionary analysis, version 2.71. Available at <http://mesquiteproject.org>.
- McDonald, M. A., J. A. Hildebrand, S. M. Wiggins, D. Thiele, D. Glasgow and S. Moore. 2005. Sei whale sounds recorded in the Antarctic. Journal of the Acoustical Society of America 118:3941–3945.
- McGowen, M. R., M. Spaulding and J. Gatesy. 2009. Divergence date estimation and a comprehensive molecular tree of extant cetaceans. Molecular Phylogenetics and Evolution 53:891–906.
- Mitchell, E. D. 1972. Whale pigmentation and feeding behavior. American Zoologist 12:60.
- Nemoto, T. 1970. Feeding pattern of baleen whales in the ocean. Pages 241–252 in J. H. Steele, ed. Marine food chains. University of California Press, Berkeley, CA.
- Orton, L. S., and P. F. Brodie. 1987. Engulfing mechanics of fin whales. Canadian Journal of Zoology 65:2898–2907.
- Pauly, D. A., W. Trites, E. Capuli and V. Christensen. 1998. Diet composition and trophic levels of marine mammals. ICES Journal of Marine Science 55:467–481.
- Pivorunas, A. 1979. The feeding mechanisms of baleen whales. American Scientist 67:432–440.

- Potvin, J., J. A. Goldbogen and R. E. Shadwick. 2009. Passive versus active engulfment: Verdict from trajectory simulations of lunge-feeding fin whales *Balaenoptera physalus*. *Journal of the Royal Society Interface*. doi:10.1098/rsif.2008.0492.
- Potvin, J. J., J. A. Goldbogen and R. E. Shadwick. 2010. Scaling of lunge feeding in rorqual whales: An integrated model of engulfment duration. *Journal of Theoretical Biology* 267:437–453.
- Pryor, K. 1986. Non-acoustic communicative behavior of the great whales: Origins, comparisons, and implications for management. Report of the International Whaling Commission (Special Issue 8):89–96.
- Reeves, R. R., B. S. Stewart, P. J. Clapham and J. A. Powell. 2002. Guide to marine mammals of the world. Alfred A. Knopf, New York, NY.
- Rice, D. 1998. Marine mammals of the world. Society for Marine Mammalogy Special Publication Number 4.
- Robinson, K. P., and M. J. Tetley. 2007. Behavioral observations of foraging minke whales (*Balaenoptera acutorostrata*) in the outer Moray Firth, north-east Scotland. *Journal of the Marine Biological Association of the United Kingdom* 87:85–86.
- Sasaki, T., M. Nikaido, S. Wada, T. K. Yamada, Y. Cao, M. Hasegawa and N. Okada. 2006. *Balaenoptera omurai* is a newly discovered baleen whale that represents an ancient evolutionary lineage. *Molecular Phylogenetics and Evolution* 41:40–52.
- Schoenherr, J. 1991. Blue whales feeding on high concentrations of euphausiids around Monterey Submarine Canyon. *Canadian Journal of Zoology* 69:583–594.
- Sears, R. 1983. A glimpse of blue whales feeding in the Gulf of St. Lawrence. *Whale Watcher* 17:12–14.
- Sears, R., J. M. Williamson, F. Wenzel, M. Bérubé, D. Gendron and P. W. Jones. 1990. The photographic identification of the blue whale (*Balaenoptera musculus*) in the Gulf of St. Lawrence, Canada. Report of the International Whaling Commission (Special Issue 12):335–342.
- Sergeant, D. E. 1963. Minke whales, *Balaenoptera acutorostrata* Lacépède of the western North Atlantic. *Journal of the Fisheries Research Board of Canada* 20:1489–1504.
- Sharpe, F. A., and L. M. Dill. 1997. The behavior of Pacific herring schools in response to artificial humpback whale bubbles. *Canadian Journal of Zoology* 75:725–730.
- Stewart, S. S., and S. Leatherwood. 1985. Minke whale *Balaenoptera acutorostrata*. Pages 91–136 in S. H. Ridgway and R. Harrison, eds. *Handbook of marine mammals*. Academic Press, London, U.K.
- Tershy, B. R., and D. M. Wiley. 1992. Asymmetrical pigmentation in the fin whale: A test of two feeding related hypotheses. *Marine Mammal Science* 8:315–318.
- Tomilin, A. G. 1957. Mammals of the USSR and adjacent countries. Volume 9. Cetacea. Israel Program for Scientific Translations, Jerusalem, 1967. 717 pp. (NTIS No. TT65-500867).
- Tscherter, U., and C. Morris. 2007. Individual site fidelity and novel feeding strategies of minke whales: A summary of research results. Pages 14–22 in K. Robinson, P. Stevick, and C. D. MacLeod, eds. *Proceedings of the workshop: An integrated approach to non-lethal research on minke whales in European waters*. European Cetacean Society Special Publication Series No. 47.
- Vallortigara, G., and L. J. Rogers. 2005. Survival with an asymmetrical brain: Advantages and disadvantages of cerebral lateralization. *Behavioral and Brain Sciences* 28:575–633.
- Wada, S., M. Oishi and T. K. Yamada. 2003. A newly discovered species of living baleen whale. *Nature* 426:278–281.
- Ware, C., A. S. Friedlaender and D. P. Nowacek. 2011. Shallow and deep lunge feeding of humpback whales in fjords of the West Antarctic Peninsula. *Marine Mammal Science* 27:587–606.
- Watkins, W. A., and W. E. Schevill. 1979. Aerial observation of feeding behavior in four baleen whales: *Eubalaena glacialis*, *Balaenoptera borealis*, *Megaptera novaeangliae*, and *Balaenoptera physalus*. *Journal of Mammalogy* 60:155–163.

- Watkins, W. A., K. E. Moore, D. Wartzok and J. H. Johnson. 1981. Radio tracking of finback (*Balaenoptera physalus*) and humpback (*Megaptera novaeangliae*) whales in Prince William Sounds, Alaska. *Deep-Sea Research* 28A:577–588.
- Wenzel, F., D. K. Mattila and P. J. Clapham. 1988. *Balaenoptera musculus* in the Gulf of Maine. *Marine Mammal Science* 4:172–175.
- Wiley, D., C. Ware, A. Bocconcelli, D. Cholewiak, A. Friedlaender, M. Thompson and M. Weinrich. 2011. Underwater components of humpback whale bubble-net feeding behavior. *Behaviour* 148:575–602.
- Williamson, G. R. 1972. The true body shape of rorqual whales. *Journal of Zoology* 167:277–286.
- Winn, L. K., and H. E. Winn. 1985. *Wings in the sea: The humpback whale*. University Press of New England, Hanover, NH.
- Wiseman, N. 2008. Genetic identity and ecology of Bryde's whales in the Hauraki Gulf, New Zealand. Ph.D. dissertation, University of Auckland, Auckland, New Zealand. 231 pp.
- Woodward, B. L., J. P. Winn and F. E. Fish. 2006. Morphological specializations of baleen whales associated with hydrodynamic performance and ecological niche. *Journal of Morphology* 267:1284–1294.
- Yamada, T. K. 2009. Omura's whale *Balaenoptera omurai*. Pages 799–801 in W. Perrin, B. Würsig and J. G. M. Thewissen, eds. *Encyclopedia of marine mammals*. 2nd edition. Academic Press, San Diego, CA.
- Yochem, P. K., and S. Leatherwood. 1985. Blue whale *Balaenoptera musculus*. Pages 193–240 in S. H. Ridgway and R. Harrison, eds. *Handbook of marine mammals*. Academic Press, London, U.K.

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