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Feeding performance by sympatric blue and fin whales exploiting a common prey resource

ARI S. FRIEDLAENDER,¹ Marine Mammal Institute, Hatfield Marine Science Center, Oregon State University, 2035 Marine Science Drive, Newport, Oregon 97365, U.S.A. and Southall Environmental Associates, Inc. 9099 Soquel Drive, Suite 8, Aptos, California 95003, U.S.A.; JEREMY A. GOLDBOGEN, Department of Biology, Hopkins Marine Station, Stanford University, Pacific Grove, California 93950, U.S.A.; ELLIOTT L. HAZEN, UC Santa Cruz–Long Marine Laboratory, Institute of Marine Sciences, 100 Shaffer Road, Santa Cruz, California 95060, U.S.A. and NOAA Southwest Fisheries Science Center, Environmental Research Division, 1352 Lighthouse Ave., Pacific Grove, California 93950, U.S.A.; JOHN CALAMBOKIDIS, Cascadia Research Collective, 218½ W. 4th Avenue, Olympia, Washington 98501, U.S.A.; BRANDON L. SOUTHALL, Southall Environmental Associates, Inc. 9099 Soquel Drive, Suite 8, Aptos, California 95003, U.S.A. and UC Santa Cruz–Long Marine Laboratory, Institute of Marine Sciences, 100 Shaffer Road, Santa Cruz, California 95060, U.S.A.

A major focus in macroecology is to understand the mechanisms that drive differences in habitat, morphology, and behavior in closely related species (Brown 1995). Within this paradigm, energy use and prey acquisition play a fundamental role in affecting behavior, especially with respect to foraging patterns and predator-prey interactions. Because resources may occur in discrete regions and are often limited, sympatric organisms that feed in similar ways partition resources, when they are limited, both to avoid competition and maximize energy gain (Pianka 1974, Schoener 1983). Baleen whales (Mysticeti) comprise more than a dozen species that have evolved a bulk-filter feeding strategy that enables the efficient exploitation of low trophic level oceanic resources. Although mysticetes are opportunistic predators that feed on diverse prey types, from schooling fish to small copepods, many sympatric baleen whale species, including blue (*Balaenoptera musculus*) and fin whales (*Balaenoptera physalus*), target the similar resources. What remains unknown, however, is whether resources are partitioned when baleen whales and prey overlap in both time and space.

¹Corresponding author (e-mail: ari.friedlaender@oregonstate.edu).

Blue and fin whales, co-occur in the summer months off the central California coast to feed on ephemeral krill (*Euphausia pacifica* and *Thysanoessa spinifera*) patches. As the two largest living animals on the planet, they require vast quantities of food to support their energy demands (Goldbogen *et al.* 2011). Recent evidence suggests that sympatric baleen whales may partition resources vertically. Friedlaender *et al.* (2009a) found significant differences in the depth of prey patches around sightings of humpback (*Megaptera novaeangliae*) and minke (*Balaenoptera bonaerensis*) whales in Antarctic waters, yet no direct quantitative data on the distribution of prey exist concurrent to tag-derived data on the feeding depths and behavior of sympatric baleen whales. Recent studies have documented the foraging behavior and kinematics of blue and fin whales independently, enhancing our understanding of these ocean predators (Goldbogen *et al.* 2006, 2011), but no study has simultaneously assessed the foraging behavior of these species feeding in close proximity on a common prey resource.

In August 2012, we deployed multi-sensor archival suction-cup tags concurrently on two (one adult and one juvenile) blue and one fin (adult) whale feeding in sympatry, and used scientific echosounders to quantify the distribution and abundance of available prey resources. We tested the hypothesis that sympatric baleen whale species partition resources through species-specific behaviorally-mediated foraging behavior.

Digital acoustic recording tags (DTAGs, Johnson and Tyack 2003) were initially deployed on the juvenile blue and the adult fin whale feeding within 1.5 km of each other. These short-term, suction-cup-attached tags contain 3-axis accelerometers, magnetometers, and pressure and temperature sensors that sample at 50 Hz. High-resolution dive profiles were generated and feeding lunges were determined using methods described previously (Goldbogen *et al.* 2006, Ware *et al.* 2010). A Wildlife Computers Mark-10 satellite-linked time-depth recording tag was deployed on the adult blue whale in the area approximately 5 h later. The time-depth profiles for the two whales outfitted with DTAGs were analyzed to determine dive depth, dive duration, and the number of feeding lunges per dive per whale. Ascent and descent rates were also calculated for each dive. Data from the Mark-10 tag were used for comparisons of dive depths between species. Nonparametric statistical comparisons across species were made (Wilcoxon rank-sum tests) to test for differences in mean rates and depths.

Krill schools are inherently patchy (Santora *et al.* 2011) and thus were characterized using an adaptive survey protocol, including six adaptive 1 km transects surrounding the foraging whales (Friedlaender *et al.* 2009b, Hazen *et al.* 2011). These transects were designed to pass close to the whales (<500 m) and continue orthogonally before turning the ship and returning to the whale's location from a different angle. The resulting pattern resembles a clover-leaf when completed around a stationary whale, but more of a saw-tooth pattern when whales are in transit (see Hazen *et al.* 2011 for specific details regarding this survey method). Data were collected within the context of a controlled sound exposure experiment conducted in parallel with the current study (for details see Southall *et al.* 2012).

We used 38 and 120 kHz SIMRAD EK60 echosounders calibrated with a tungsten-carbide sphere of known target strength (TS) (Foote *et al.* 1987). Mapped prey schools were detected using the SHAPES school detection algorithm (5 m linking distance) within Echoview 5 (<http://www.myriax.com>) incorporating a -75 dB threshold (Coetzee 2000). We used a mean adult krill length of 28 mm from the literature (Santora *et al.* 2011) and published target strength-length relationships

(Lawson *et al.* 2006) to calculate a krill target strength estimate of -75.0 dB (*e.g.*, Watkins and Brierley 2002) to convert acoustic backscatter to estimates of krill density (Simmonds and MacLennan 2005). We also examined the difference in scattering between the 120 kHz and 38 kHz data to ensure schools were consistent with krill scattering properties (Watkins and Brierley 2002).

DTAGs were deployed at 1200 and 1250 local time for 19.6 and 19.7 h, respectively on the fin and blue whale. Based on continuous focal animal behavior follows (that began approximately 30 min prior to tagging) (*e.g.*, Altmann 1974), we did not observe any change in behavior due to tagging. The second blue whale was tagged at 1705 local time in close proximity to the other whales (<2 km) while it too was feeding, and it continued to feed after tag deployment, which lasted until 1945. Feeding depths for all whales were relatively consistent during daylight hours until becoming shallower in early evening, suggesting diel vertical movement of prey (*e.g.*, Hewitt and Demer 2000, Simard and Sourisseau 2009) (Fig. 1). At night, both tagged whales remained shallower than 15 m, with no indication of feeding. The fin whale began shallow feeding before sunrise, while the blue whale showed no indications of feeding before the tag released the following morning.

During the entirety of their concurrent feeding bout, the blue whale fed significantly deeper, and for significantly longer average dive durations than the fin whale

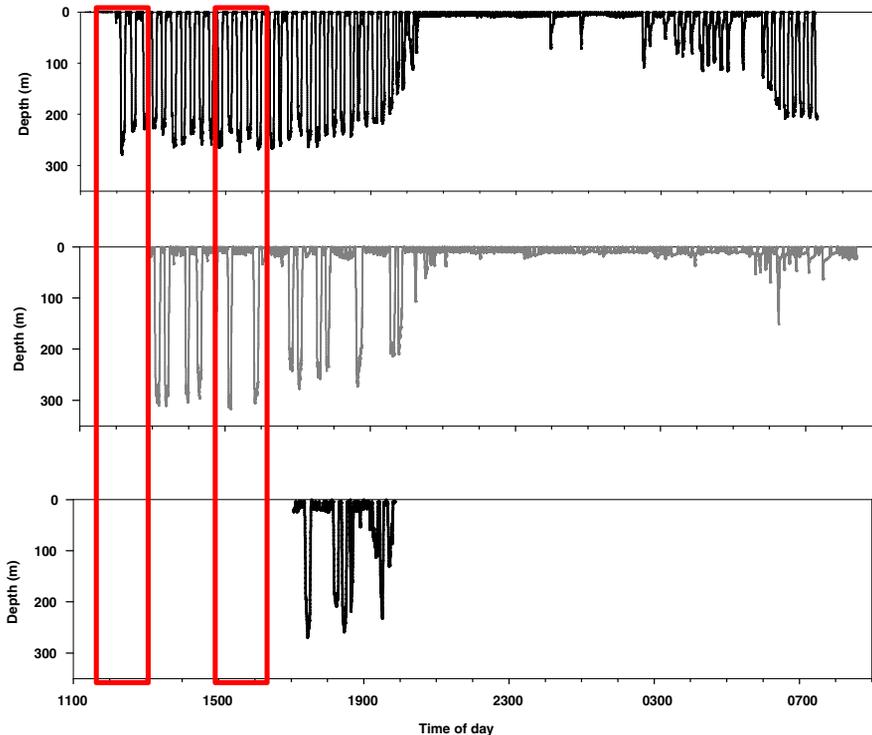


Figure 1. Time-depth dive profiles for the fin (top) and blue (middle and bottom) whales tagged with multi-sensor recording tags. The time periods of prey mapping is highlighted with the rectangles.

(Table 1, Fig. 2). However, the fin whale executed more feeding dives and significantly more feeding lunges per dive (6.1 *vs.* 2.4) than the blue whale. The blue whale executed up to four lunges per dive while the fin whale performed up to eight per dive. Using published metrics for engulfment capacity from Goldbogen *et al.* (2011), we estimate that the fin whale filtered 5.5 times more water by volume than the blue whale over the period of their concurrent feeding (Fig. 2). Both whales had similar dive ascent (2.9 and 2.8 m/s) and descent rates (2.0 and 2.0 m/s). These feeding and kinematic rates are consistent with those measured independently for adult representatives of each species in previous research (see Table 1).

Six discrete krill patches were found near (<1 km) the feeding locations of whales between 230 and 249 m, ranging in density from 101 to 3,740 krill/m³ with detailed school parameters shown in Table 2. Two patches contained low densities (mean 119.25 krill/m³), two had moderately higher densities (mean 367.18 krill/m³), and two were an order of magnitude denser (mean 3,521.08 krill/m³). The mean depth of krill patches had similar maximum values (mean = 277 m; ANOVA $P = 0.87$), and varied but had insignificant differences in patch height (mean = 37 m; ANOVA $P = 0.65$) based on *t*-tests (Table 2).

Before behavioral response experiments and when prey patch information was first collected (1200–1315), the whales were feeding separately, approximately 2 km apart (Fig. 3). During this time, the feeding depth of the first tagged blue whale (308 m, 5.4 m SD) was significantly deeper ($P < 0.0002$) than fin whale feeding depth (242 m, 6.3 m SD). After the sound exposure experiment, and when prey was mapped a second time (1500–1615), the tagged blue and fin whales were feeding in closer proximity (<500 m) to each other. From the period after the playback, when prey mapping was conducted and all tagged whales were in closer proximity to each other, until 1900 when both whales changed their feeding depths perceptibly, blue (260 m, 7.6 SD) and fin whale (249 m, 4.2 SD) feeding depth was not significantly different (ANOVA, $P = 0.2$) (Fig. 1). Any transient responses of the tagged whales to sound exposure (as in Goldbogen *et al.* 2013) before the second period of prey mapping did not appear to affect the feeding depth of the tagged whales during the period of our measurements.

Table 1. Comparison of foraging dive metrics (with standard deviations) of a sympatric blue whale and fin whale (* $P < 0.01$, ** $P < 0.0001$, *** $P < 0.002$). Previously published dive metrics for blue and fin whales are shown for qualitative comparison. From this study, we recorded 14 and 34 foraging dives from DTAG data for the blue whale and fin whale, respectively.

	Blue whale (this study)	Fin whale (this study)	Mean blue (Goldbogen <i>et al.</i> 2011, 2012)	Mean fin (Goldbogen <i>et al.</i> 2011, 2012)
Dive duration (min)	9.5 (1.4)	8.3 (1.5)*	9.8 (2.0)	7.0 (1.4)
Dive depth (m)	277 (37)	231 (49)**	190 (58)	170 (70)
Number of lunges per dive (mean)	2.4 (1.1)	6.1 (1.5)***	3.3 (1.2)	3.9 (1.4)
Number of lunges per dive (maximum)	4	8	4 (1)	7 (2)
Mean descent speed (m/s)	2.9 (0.3)	2.8 (0.3)	2.6 (0.5)	3.7 (0.4)
Mean ascent speed (m/s)	2.0 (0.3)	2.0 (0.2)	1.6 (0.5)	2.4 (0.3)

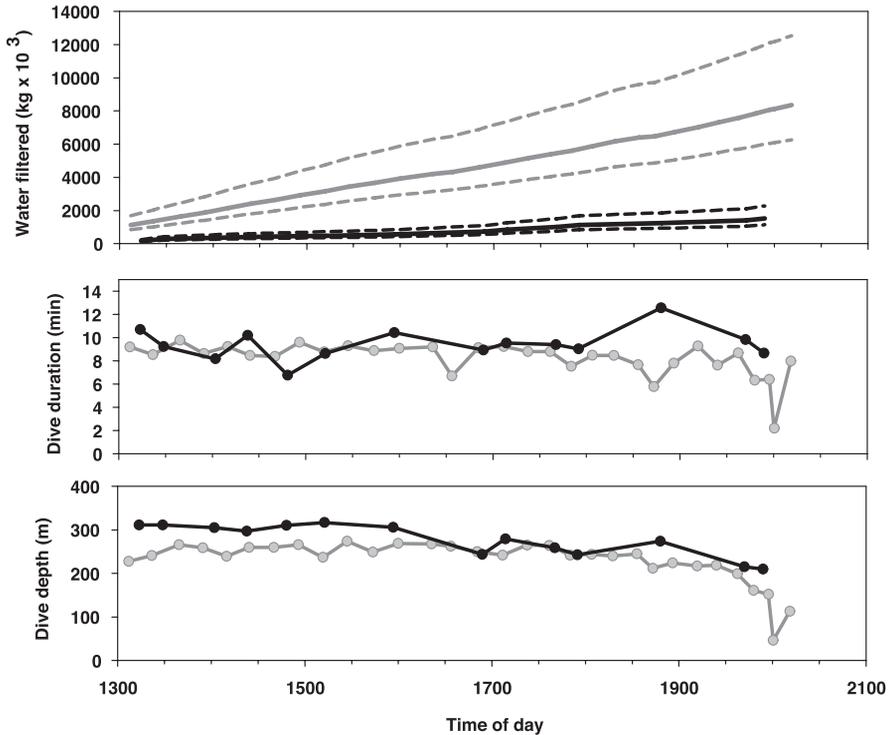


Figure 2. Feeding performance for the fin (gray line) and blue (black line) whales tagged with multi-sensor suction cup tags during concurrent feeding bouts. Estimates of water filtered and processed (top) are based on the number of lunges inferred from tag data and the engulfment models for similar body size (18 m). Solid lines represent the performance estimate for a similar body size of each species and the dashed lines reflect adult body size range (fin, 16–20 m; blue, 20–24 m). Dive duration (middle) and maximum dive depth (bottom) of each species is also shown (taken from Goldbogen *et al.* 2012). Each point represents a single dive in the middle and bottom panel.

Over the course of the day, the feeding depth of the juvenile blue whale was significantly deeper (ANOVA, $P < 0.001$) when it was feeding alone when prey mapping was done before playback experiments *vs.* after the experiment when prey was mapped a second time and the blue whale was in close proximity to the fin whale. Conversely, the fin whale remained in the same general area throughout the day and its feeding depth did not change significantly (ANOVA, $P = 0.15$) from when it was feeding alone when prey was measured before exposure experiments *vs.* after the experiments and when the blue whale had moved into close proximity (< 500 m). Similarly, no changes were detected in feeding depth with the second tagged blue whale feeding in the same area.

Our results indicate that the feeding behaviors of blue and fin whales may be mediated by the depth of prey and species-specific behaviors, including the number of lunges per dive, rather than by the presence of and potential for competitive interactions with other whales. We found that when blue and fin whales were feeding independently and likely on different prey patches, their feeding depths were significantly

Table 2. Metrics for krill patches measured in the depth range of feeding blue and fin whales. Patch types are named relative to the density of krill observed in each. Mean and standard deviations are given for patch density, depth, height, top and bottom depth of patches.

Patch type	Density (krill/m ³)	Mean depth (m)	Mean height (m)	Mean patch top depth (m)	Mean patch bottom depth (m)
Low	119.25 (15.56)	245.00 (2.83)	34.50 (28.99)	210.50 (26.16)	279.50 (31.82)
Medium	367.18 (26.36)	230.50 (0.71)	40.00 (42.43)	191.00 (43.84)	270.50 (41.72)
High	3,521.08 (309.73)	245.50 (4.95)	36.00 (18.38)	210.00 (24.04)	281.50 (14.34)

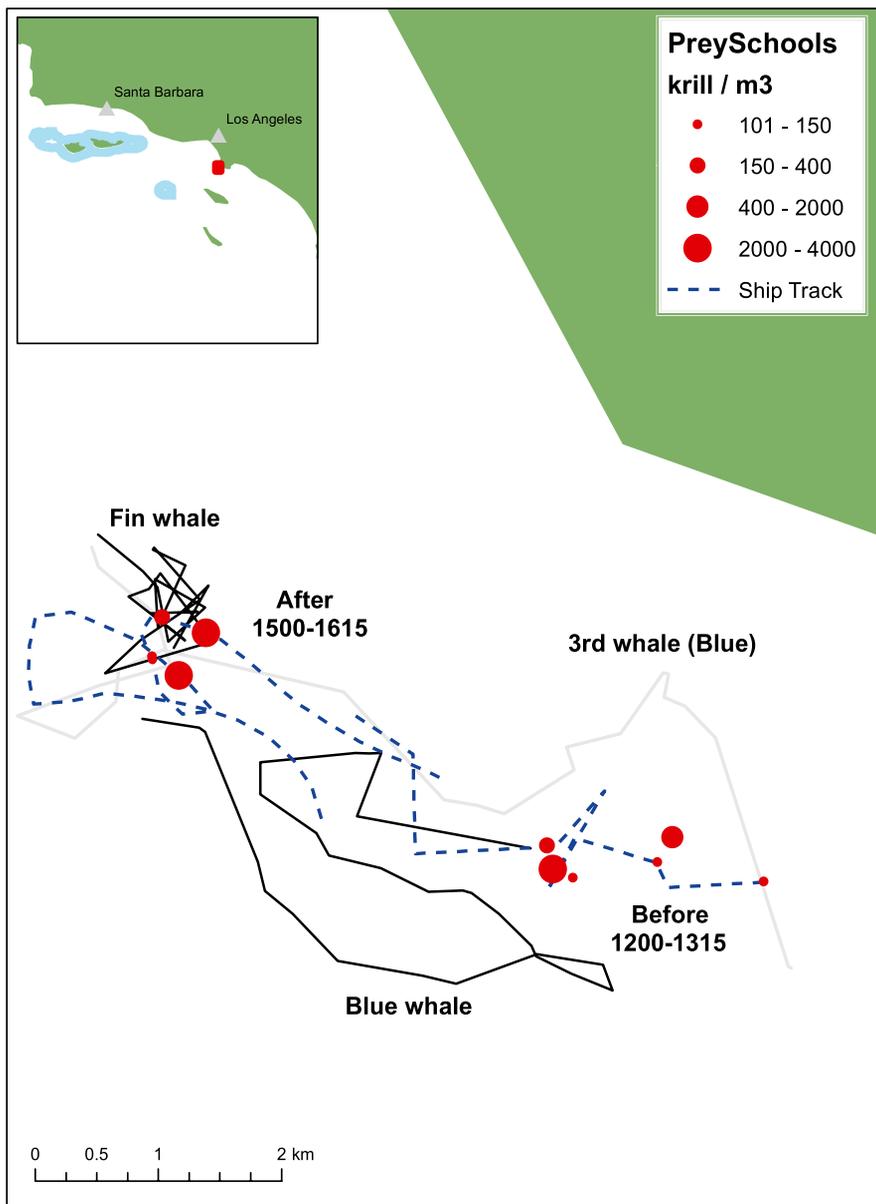


Figure 3. Map showing the movements of the tagged blue and fin whales as well as the distribution and density of prey patches measured (in black). The times reflect the two bouts of prey mapping before and after controlled exposure experiments. The track of the "blue whale" indicates the whale was feeding alone to the southeast initially and moved northwest ultimately, ending up in close proximity to the "fin whale" when focal follow observations ceased. The track of the second blue whale tagged, "3rd whale," shows spatial proximity to the other two tagged whales, but was tagged after the prey mapping (in gray).

different. This could reflect the overall depth of the prey patches that each whale was targeting. However, based on their spatial proximity the blue whale (and a second tagged whale) may have moved into close proximity to the fin whale and presumably fed on the same prey patch as the fin whale, there was no significant difference in the feeding depth between the whales. As the fin whale remained relatively stationary throughout this time, feeding on the same patch, it is possible that the addition of the blue whales to the feeding bout did not affect either whale's feeding behavior.

Our data provide initial data indicating species-specific differences in feeding behavior that have previously been documented separately for each species and that may hold true when these whales are feeding in sympatry. In our example, blue and fin whales do not partition resources by feeding at significantly different depths when targeting the same patch. The mean depths of krill patches in the range of the feeding whales were not related to patch density, *e.g.*, shallow patches were not less dense.

It is noteworthy that the daily behavioral patterns of both Dtagged whales were similar, suggesting that they share similar prey requirements and limitations to profitable foraging. When changes in feeding depth do occur, as seen with diminishing light conditions, both whales changed feeding depths simultaneously to likely track the vertical migration of krill towards the sea surface. Both whales fed continuously during the day, ceasing at night when krill were either no longer available to be preyed upon by being targeted visually (*e.g.*, Goldbogen *et al.* 2012) or no longer present in sufficient densities to reward feeding (Piatt and Methvan 1992, Goldbogen *et al.* 2011). Both the tagged blue and fin whale then spent the night near the surface and did not feed again until the following morning. This pattern varies from those observed in the autumn for Antarctic humpback whales that feed almost exclusively at night when krill becomes available near the water's surface (Ware *et al.* 2010), but is similar to blue whale behavior in the North Atlantic (Doniol-Valcroze *et al.* 2011). Such differences could reflect a combination of key physiological and environmental factors such as cost of transport, which is predictably lower in larger whales (Williams *et al.* 1999), and temporal and spatial variations in prey density and behavior. This suggests that both blue and fin whales making deep feeding dives on the most dense prey patches represents an optimal strategy (*e.g.*, Mori 2002, Doniol-Valcroze *et al.* 2011), whereas smaller humpback whales that have a relatively higher cost of transport may be able to meet maximized energetic gain by exploiting surface krill patches at night, even if prey density is relatively lower at the sea surface.

Prey distribution and abundance is a primary driver of baleen whale distribution and feeding behavior (*e.g.*, Croll *et al.* 2005, Friedlaender *et al.* 2006) at broad spatial scales. In our study of sympatric blue and fin whales, despite the overall similarities in the dive profiles, we found differences in feeding performance (*e.g.*, lunge frequency) that may represent unique predatory strategies that minimize competition yet maximize energy gain. More dedicated work in this respect may also elucidate species-specific differences in the kinematics of feeding that may better inform our observations. Understanding how sympatric species coexist and extract a common resource in relation to one another provides critical information for future research and conservation efforts. For instance, direct knowledge of the energetic needs and demands of these predators is essential to accurately assess potential risks posed from behavioral responses to anthropogenic sounds common in the southern California bight (*e.g.*, sonar, vessels) that may disrupt feeding at critical times or occur chronically throughout their lifetimes (Goldbogen *et al.* 2013). It is crucial that more directed and dedicated research efforts are made to study the feeding behavior of sympatric whales in combination with quantitative measures of prey at the spatial and temporal

scales at which these whales feed. Both tagging and prey mapping have become relatively commonplace techniques in marine mammal science, and the analytical tools now exist to facilitate a better understanding of the complex ecological relationships between marine mammals and their prey.

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