

BODY SIZE, DIET, HABITAT USE, AND SOCIAL BEHAVIOR OF *BALAENOPTERA* WHALES IN THE GULF OF CALIFORNIA

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Four sympatric species of whales in the genus *Balaenoptera* were studied May 1983–April 1986 in the Canal de Ballenas, Gulf of California, Mexico. Most data were collected on the two most abundant species, Bryde's whale (*B. edeni*), ca. 13,000 kg and fin whale (*B. physalus*), ca. 47,000 kg. Bryde's whales fed primarily on schooling fish and were most abundant in summer and autumn when schooling fish are concentrated in the study area. Fin whales were only observed feeding on euphausiids, and were most abundant in winter and spring when euphausiids are abundant throughout the Gulf of California. Bryde's whales fed more at dawn and dusk, whereas fin whales fed throughout the day. Bryde's whales were relatively resident to the study area, rarely traveled in groups, and frequently fed alone or in small aggregations. Fin whales, in contrast, were relatively transient, passing through the study area and lingering only to feed; they traveled in larger groups and fed in larger aggregations, within which there were coordinated groups of two to four individuals. These results, coupled with limited data on the blue whale (*B. musculus*), ca. 80,000 kg, and minke whale (*B. acutorostrata*), ca. 5,000 kg, are interpreted in light of theories that relate body size to diet, habitat use, and social behavior in better-studied terrestrial mammals.

Key words: *Balaenoptera*, behavior, diet, habitat use, Gulf of California

Body size is one of the most important determinants of metabolic rate, digestive efficiency, and total caloric requirements (Peters, 1983; Schmidt-Nielsen, 1984). Such physiological constraints can, in turn, have a strong influence on diet, which may ultimately shape most aspects of ecology and behavior. Comparative studies of different-sized ungulates (Clutton-Brock et al., 1980; Jarman, 1974), primates (Clutton-Brock and Harvey, 1977), ground squirrels (Armitage, 1981), canids (Bekoff et al., 1981), and sea ducks (Aythyinae, Goudie and Ankney, 1986) suggest that within taxonomic groups, smaller species feed on higher-quality food than larger species, and their food is found in smaller, less-concentrated, and more spatially and temporally predictable patches. These and similar studies also have shown that smaller species also tend to be found in less-open habitat, to have smaller home

ranges, and to be less social than larger species. This general relationship between body size, diet, habitat use, and sociality previously has not been examined in a comparative study of different-sized baleen whales.

In the Gulf of California, four species of *Balaenoptera* whales, Bryde's (*B. edeni*), ca. 13,000 kg, fin (*B. physalus*), ca. 47,000 kg, blue (*B. musculus*), ca. 80,000 kg, and minke (*B. acutorostrata*), ca. 5,000 kg, are seasonally sympatric. In this paper I present data on their diet, habitat use, and social behavior, which suggest that these largest of all animals exhibit some of the same-size-based behavioral and ecological traits as better-studied terrestrial animals.

MATERIALS AND METHODS

The three most important oceanographic features of the study area (Fig. 1) were described by Roden (1964), Alvarez-Borrego (1983), Alvarez

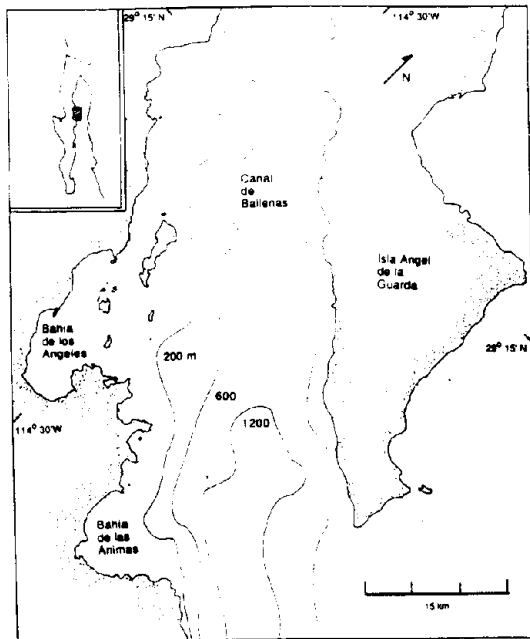


FIG. 1.—The study area. Notice the two relatively shallow bays, numerous rocky islands and points, and the deep water between Isla Angel de la Guarda and Baja California.

et al. (1984), and Tershy et al. (1991): extreme-spatial habitat variability with points, islands, and shallow bays adjacent to pelagic waters; extreme-temporal habitat variability with temperate water conditions ($\geq 14^{\circ}\text{C}$) and prevailing northwest winds in winter and spring, and tropical water conditions ($\leq 28^{\circ}\text{C}$) with southeast winds in summer and autumn; strong tidal currents (≤ 3 m/s), which mix the water column keeping photic-zone nutrient levels high enough to sustain year-round primary productivity comparable to major-upwelling zones. This mixing also causes sea-surface temperatures in the Canal de Ballenas to be 2–5°C lower than the rest of the Gulf of California (Badan-Dangon et al., 1985).

In the study area, Bryde's and fin whales were sighted with roughly equal frequency (about once every 5 h of boat time). Blue and minke whales were sighted less than once per 100 h of boat time (Tershy et al., 1990). Thus, most data are from Bryde's and fin whales.

My assistants and I observed Bryde's, fin, blue, and minke whales during 2,700 h of research in May–September 1983, April–September 1984, April–December 1985, and January–April 1986

(Tershy et al., 1990). The primary goal was to encounter as many individual whales as possible by using a consistent search method in which we ran our 4.2-m skiff in a straight line at planing speed (ca. 17 km/h) for 5–10 min, then shut off the engine for 15 min to listen for the blows or exhalations of whales and conduct a 360°-binocular scan. We made no attempt to randomize the search effort on a daily basis. However, on a weekly basis we covered most of the study area and all three major habitat types (Tershy et al., 1990). Throughout the day we counted all cetaceans sighted, regardless of distance from our skiff (Tershy et al., 1991).

When a whale was sighted, we attempted to approach to within 100 m and recorded the following data: its location by triangulation off nearby landmarks with a handheld sighting compass; the group size or number of aggregated whales; the behavior as either traveling or feeding (at the surface or apparent feeding at depth). Following Wilson (1975), we defined an aggregation as a number of individuals gathered in the same place, but without obvious internal organization, and a group as a set of animals remaining together for a period of time while interacting with one another to a distinctly greater degree than with other conspecifics. In practice, two or more animals swimming within 50 m of each other engaged in the same behavior at the same time with coordinated swimming and respiratory behavior were considered members of the same group. About 33% of the individual Bryde's and fin whales, and all blue and minke whales were distinctive enough to individually identify from photographs of their dorsal fins and dorsal surfaces (Tershy et al., 1990).

We attempted to determine the taxa of the whale's prey (fish or planktonic invertebrates) by direct observation of prey entering the mouth of lunging whales, and by analysis of fecal samples collected with a handheld plankton net and then examined under a dissecting scope for either fish scales and bones, or hard parts of invertebrates. When whales were feeding in mixed-species aggregations with planktivorous birds and elasmobranchs, we assumed that the whales also were feeding on planktonic invertebrates. When whales were in mixed-species feeding aggregations with piscivorous birds, elasmobranchs, and large fish, we assumed that the whales were feeding on fish.

When several widely separated whales were sighted at the same time, we counted the whales, recorded the size of each group, and first at-

tempted to approach the largest group, or, if all groups were of equal size, the closest. When two species of whale were sighted, we first attempted to approach the species sighted less often in the past 2 weeks.

Statistical tests follow Zar (1984). I used a non-parametric Mann-Whitney test with a normal approximation, Z , for $n > 19$ to test for differences between Bryde's and fin whales in the median: size of feeding aggregation; distance of feeding locations to shore and to previous feeding locations; days between subsequent identifications of individuals; number of identifications per individual; traveling size of group. I used chi-square goodness-of-fit or contingency tests to detect differences between Bryde's and fin whales in the: proportion of days when feeding was observed; the diurnal distribution of feeding events; and, the proportion of feeding whales compared with traveling whales that were resighted within 1 month. I used simple-linear regression and a Student's t -test to determine the significance of the relationship between seasonal distributions of common dolphins (*Delphinus delphis*) and Bryde's whales. To test the relationship between body size and a measure of residency in the four species of *Balaenoptera* studied, I conducted a log-log regression (Peters, 1983) of body mass (derived from equations in Lockyer, 1976) and average number of identifications per individual in each species (from Tershy et al., 1990), excluding known females to correct for the tendency of females to be more resident (Tershy et al., 1990).

Using the compass bearings, I plotted the position of each feeding location, by hand, on a 1:50,000 scale map. For each species I then measured the distance from each feeding location to the closest previous feeding location from the same field season, and to the closest shoreline including islands (any error in plotting locations should be equally distributed between the two species). There are no detailed charts for the study area, and we did not record water depth in the field.

RESULTS

Bryde's whales preyed on small schooling fish, such as the Pacific sardine (*Sardinops sagax*) and thread herring (*Opisthonema*), in 88.6% of 88 feeding events, and zooplankton in 11.4%. Fin whales preyed on zooplankton, such as the euphausiid *Nyc-*

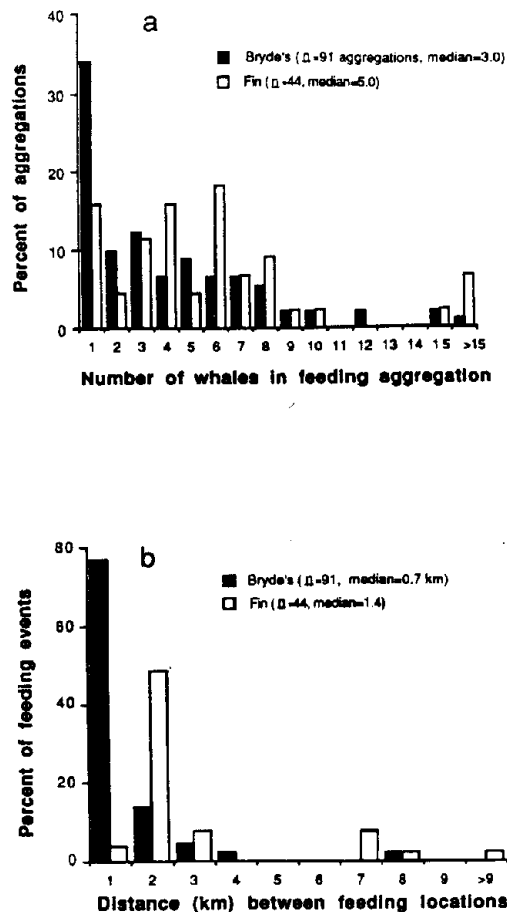


FIG. 2.—Minimum feeding-aggregation sizes for Bryde's (*Balaenoptera edeni*) and fin (*B. physalus*) whales in the Gulf of California, 1983–1986 (a). Nearest distances between locations where feeding was observed for Bryde's and fin whales (b).

tiphanes simplex, in all 30 feeding events (B. R. Tershy, in litt.).

Bryde's whales fed on a higher proportion of the days they were sighted (82 of 136 days, 60%) than did fin whales (41 of 116 days, 35%; $\chi^2 = 7.98$, $P < 0.005$). Bryde's whales had smaller feeding aggregations than fin whales (Bryde's, $n = 91$ feeding events, median = 3.0 whales; fin, $n = 44$, median = 5.0; $Z = 2.44$, $P < 0.002$; data were recorded as minimum number of whales and, therefore, underestimate the sizes of larger feeding aggregations; Fig. 2a). The distance between within-year feeding locations was

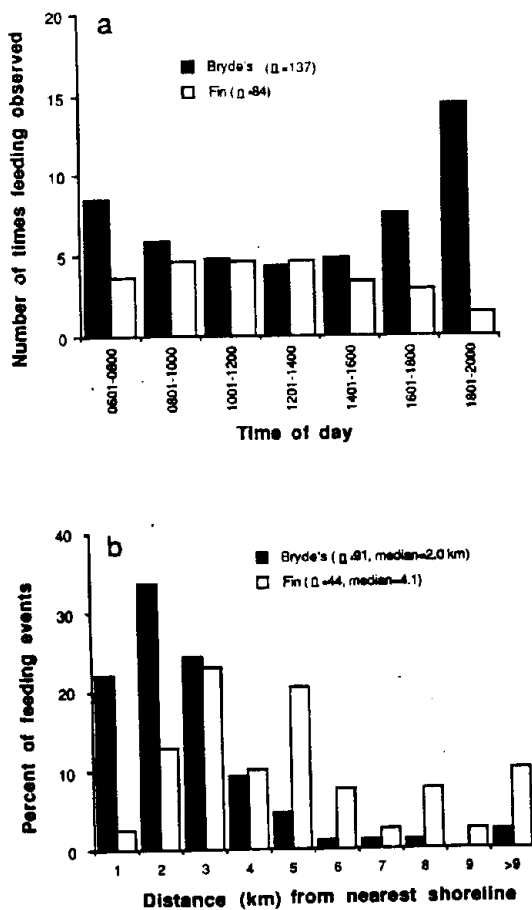


FIG. 3.—The diel distribution of feeding events for Bryde's (*Balaenoptera edeni*) and fin (*B. physalus*) whales in the Gulf of California, 1983–1986 (a). Distances of Bryde's and fin whale feeding events from the nearest shoreline (b).

less for Bryde's whales than for fin whales (Bryde's, $n = 91$ feeding locations, median = 0.7 km between feeding locations; fin, $n = 44$, median = 1.4; $Z = 4.428$, $P < 0.003$), which suggests that Bryde's-whale feeding locations were more clumped (Fig. 2b).

For fin whales, the ratio of feeding events observed in each of the seven 2-h time intervals between 0600 and 2000 was equal to the ratio of hours of boat observations in each time interval ($n = 84$ 2-h time blocks with feeding, $\chi^2 = 4.7$, $P < 0.75$). This was not true for Bryde's whales ($n = 137$, $\chi^2 = 21.676$, $P < 0.005$), which fed more at dawn

and dusk (Fig. 3a). In both species, whales stopped lunging, and feeding aggregations began to disperse shortly after sunset.

Bryde's whales fed closer to shore than fin whales (Bryde's, $n = 91$ feeding events, median = 2.0 km from nearest shoreline; fin, $n = 44$, median = 4.1; $Z = 5.316$, $P < 0.002$). More than 80% of Bryde's whale feeding events were within 3 km of the nearest shoreline, while >80% of all fin whale feeding events were ≥ 3 km from the nearest shoreline (Fig. 3b).

Both species were seen in the study area throughout the year. However, Bryde's whales were most abundant in summer and autumn, and mean number sighted per hour per week was positively correlated with water temperature (Tershy et al., 1990). The mean numbers of Bryde's whales and piscivorous common dolphins sighted per week were positively correlated ($r = 0.81$, $d.f. = 52$, $t_1 = 10.0$, $P < 0.001$, for 1984 and 1985 combined). Fin whales, in contrast, were most abundant in winter and spring, and mean number sighted per hour per week was negatively correlated with water temperature (Tershy et al., 1990).

Bryde's and fin whales were sighted with about the same frequency; however, the daily mean number of Bryde's whale sighted per hour was more evenly distributed than the daily mean number of fin whales sighted per hour (Bryde's, $\bar{X} = 0.22$ sightings/h, $CV = 113\%$; fin, $\bar{X} = 0.23$, $CV = 236\%$, for 1985 and 1986 combined). Within each of the field seasons, individually identified fin whales were resighted most often within 1 day, but Bryde's whale resightings were more evenly distributed over time (Bryde's, $n = 106$ resightings, median = 9.0 days between sightings; fin, $n = 60$, median = 2.0 days; $Z = 15.85$, $P < 0.002$). Feeding fin whales were resighted more often within the next 31 days (39.7% of 73 feeding whales) than fin whales only observed traveling (1.0% of 80 traveling individuals; $\chi^2 = 18.40$, $P < 0.001$). Bryde's whale resightings, in contrast, were independent of behavior (43.4% of 146 feeding individuals resighted com-

pared with 38.2% of 55 traveling whales resighted; $\chi^2 = 0.06$, $P > 0.5$). Finally, individual Bryde's whales were sighted significantly more often than individual fin whales (Bryde's, 142 individuals, 1.9 identifications per individual; fin, 148 individuals, 1.2 identifications per individual; $Z = 1.77$, $P < 0.04$).

When all four species of *Balaenoptera* in the study area were compared, the smaller minke and Bryde's whales appeared to be less transient than larger fin and blue whales. Body mass of the species was significantly related to the average number of sightings of an individual for each species ($r = 0.97$, slope = 0.36, $t = 5.91$, $P = 0.025$).

Bryde's whales were more solitary than fin whales. Excluding females with young, 93% of traveling Bryde's whales were solitary, while >60% of traveling fin whales were observed in groups of two to 10 individuals (Bryde's, $n = 195$ groups, 201 whales, median = 1.0; fin, $n = 197$ groups, 323 whales, median = 2.0; $Z = 19.84$, $P < 0.002$; Fig. 4). Bryde's whales formed smaller feeding aggregations than fin whales (Fig. 2a), within which individual Bryde's whales acted independently. Fin whales, in contrast, spent 65–95% of their time in coordinated groups of two to four (B. R. Tershy, in litt.).

DISCUSSION

Bryde's whales fed primarily on fish, while fin whales only were observed feeding on euphausiids. The fish species that Bryde's whales preyed on have a maximum swimming speed of 150 cm/s (Beamish, 1978), while the 10–25-mm euphausiids that fin whales preyed on probably were slower than 100 cm/s (the maximum speed recorded for the 40–55-mm long *Euphausia superba*—Hamner et al., 1983). The fish that Bryde's whales preyed on also are higher in caloric content (1.1–1.5 kcal/kg—V. D. Sidwell, in litt.), than are euphausiids (0.98 kcal/kg—Chu, 1982).

Although we collected no direct data on prey distribution or behavior, we can make

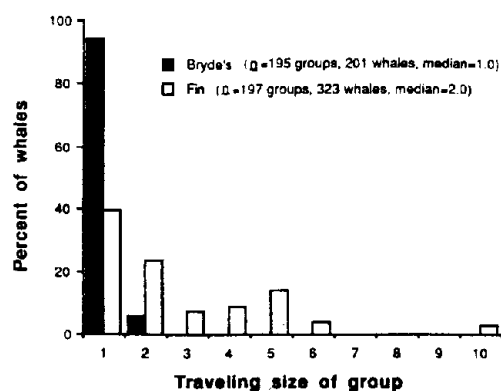


FIG. 4.—Group sizes of traveling Bryde's (*Balaenoptera edeni*) and fin (*B. physalus*) in the Gulf of California, 1983–1986.

inferences based on the behavior of the whales. Bryde's whales were observed feeding on a higher percentage of the days they were sighted than were fin whales. If Bryde's and fin whales had an equal ability to find suitable patches of prey, and an equal probability of feeding whenever these patches were found, then the difference in feeding rate between the two species may indicate the more-consistent presence of prey patches suitable to Bryde's whales.

The number of Bryde's whales at a feeding event was less than the number of fin whales (Fig. 2a); that the mean number of each species sighted per hour was nearly equal suggests that the size of the fish patches that Bryde's whales fed on were smaller than the size of the krill patches that fin whales fed on, or perhaps that patches of fish were more ephemeral. The size of feeding aggregations or groups is grossly proportional to the size of prey patches in many animals, including invertebrates (Antezana and Ray, 1984; Gillespie, 1987; Stuart, 1986), rodents (Lovegrove and Wissel, 1988), primates (Reynolds and Reynolds, 1965; Turnbull, 1962; van Lawick-Goodall, 1968), and delphinids (Würsig, 1986).

The relative close proximity of Bryde's whale feeding locations (Fig. 2b) suggests that the concentrations of fish they fed on were more spatially predictable than the concentrations of krill that fin whales con-

sumed. Thus, Bryde's whales fed on fish that are fast and nutritious and appeared to be in small spatially and temporally predictable patches. Fin whales, in contrast, fed on krill that are relatively slow and less nutritious, and appeared to be in large spatially and temporally less-predictable patches.

The different times of day that the two species fed (Fig. 3a) may be related to the antipredation mechanisms of their respective prey. Bryde's whales fed more often at dawn and dusk, when some species of fish school less cohesively (Glass et al., 1986), and are less able to detect predators (Munz and McFarland, 1973; Pitcher and Turner, 1986). Fin whales, in contrast, fed throughout the day with a slight, nonsignificant peak during midday. Euphausiids school and possibly detect predators by rheotaxis (Hamner, 1984; Hamner et al., 1983), thus, their predator avoidance may be less dependent on light levels.

Bryde's whales were most abundant in the Canal de Ballenas in summer and autumn. The Pacific sardine and, to a lesser extent, the thread herring were the most-abundant schooling fish in the Gulf of California during the study period (Lluch-Belda et al., 1986). They were the most conspicuous and probably the most common prey of Bryde's whales in the study area (B. R. Tershy, in litt.). Pacific sardines are a temperate species that breeds in winter and spring in cold-upwelled water along the eastern Gulf south of the study area. In summer when the water warms, adult sardines swim northward, and eggs and larvae are advected northward (Hammann et al., 1988; Lluch-Belda et al., 1986). Thus, in late summer, most of the Pacific sardines in the Gulf are concentrated in the relatively cool waters of the study area. Thread herring, a more-tropical species, also are most abundant in the study area during late summer when they expand their range northward (Lluch-Belda et al., 1986). Bryde's whales, like the commercial sardine fleet (Lluch-Belda et al., 1986), probably made limited north-south migrations following the sardine and herring concentrations into and out of the study area.

Fin whales were most abundant in the Canal de Ballenas in winter and spring. The most abundant euphausiid in the Gulf is the temperate *Nyctiphanes simplex* (Brinton and Townsend, 1980; Brinton et al., 1986; Lapota and Losee, 1984). This species forms larger, more-concentrated swarms than the other Gulf euphausiids (E. Brinton, pers. comm.) and appears to be the primary prey of fin whales throughout the Gulf (B. R. Tershy, in litt.). Data on seasonal distribution and abundance are few, but adult *N. simplex* breed and are most abundant in winter and spring when cooler waters prevail. In summer, as water temperatures in the Gulf rise, *N. simplex* stops breeding, adults die off, and abundance is substantially lower (E. Brinton, pers. comm.; Brinton and Townsend, 1980). Pelagic red crabs (*Pleuroncodes planipes*), another potentially significant prey for fin whales, have a similar seasonal distribution (E. Brinton, pers. comm.). It is likely that fin whales migrate into the Gulf in winter and spring when *N. simplex* is abundant, but that most individuals leave during summer and autumn (Tershy et al., 1990). Several species of large rays (Mobulidae) prey primarily on *N. simplex* in the Gulf and have a seasonal distribution similar to fin whales (Notobartolo di Sciara, 1988).

It is unlikely that the seasonal movements of fin and Bryde's whales in the study area are determined by breeding migrations. No mating behavior was seen in the study area. Fin-whale females with young made up $\leq 1\%$ of the population in the study area, while Bryde's whales appeared to give birth throughout the year, based on the size distribution of young (Tershy et al., 1990).

Bryde's whales were relatively resident to the study area, and solitary (Figs. 2b and 4). Fin whales, in contrast, were transient, passing through the study area and lingering only to feed, traveled in groups of two to 10 individuals, and frequently formed large feeding aggregations. These differences may be due to differences in the distribution and behavior of their respective prey. The fish that Bryde's whales fed on were faster swim-

mers, higher in caloric content, and appeared to be in more abundant, smaller, more spatially and temporally predictable patches than the euphausiids that fin whales fed on.

Jarman (1974) proposed a gradient in food quality, patch size, and spatial/temporal distribution along which antelope vary their residency patterns and sociality. At one extreme, food is high quality and patches are small and predictable in time and space. These food patches are exploited by small antelope, such as dikdiks (*Rhynchotragus*), which have relatively low total caloric requirements, high metabolic rates, and low food retention times. Intraspecific competition at these patches is relatively high, and these antelope are solitary or in intersexual pairs, and resident to small home ranges from which they attempt to exclude conspecifics. At the other extreme, food is low quality and patches are large and unpredictably distributed in time and space. These patches are most often exploited by large antelope like cape eland (*Taurotragus oryx*), which have higher total-caloric demands, lower metabolic rates, and longer retention times. Here intraspecific competition for food is relatively low, and these antelope are gregarious, roam over a large area, and make no attempt to defend territories.

In antelope, the relationship between body size, diet, and behavior occurs over a 250-fold range of body mass (Jarman, 1974), and is partially dependent on scaling of rumen size, food retention time, and digestive efficiency (Demment and Van Soest, 1985). However, similar relationships between body size, diet, and behavior have been found in a number of other groups with smaller differences in body size and carnivorous, omnivorous, or frugivorous diets (Bekoff et al., 1981; Clutton-Brock, 1974; Fleming, 1991; Jarman and Southwell, 1986; Lovegrove and Wissel, 1988). My data on Bryde's and fin whales in the Canal de Ballenas are consistent with the relationship between body size, diet, habitat use, and social behavior first proposed by Jarman (1974). The correlation between body mass

and average number of identifications per individual in the four species I studied also is consistent with Jarman's model.

Many aspects of the natural history of blue and minke whale also are consistent with a size-based relationship between diet, habitat use, and social behavior in *Balaenoptera*. In the study area (B. R. Tershey, in litt.), in the southern Gulf of California (Gendron, 1990), and in other parts of the world (Gaskin, 1982; Kawamura, 1980) blue whales feed almost exclusively on euphausiids. Blue whales usually are found well offshore (Evans, 1980; Tomilin, 1967), often travel in groups, and form large feeding aggregations (Schoenherr, 1988; Tomilin, 1967; Yochem and Leatherwood, 1985), within which individuals form coordinated feeding groups of two to four (B. R. Tershey, in litt.). Unfortunately, since 1930 populations of blue whales have been so severely reduced (Chapman, 1974) that differential abundance makes it impossible to accurately compare gregariousness in fin and blue whales.

Minke whales in the northern hemisphere primarily feed on small schooling fish (Gaskin, 1982; Kawamura, 1980), but also feed on larger fish such as mature Arctic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*—Jönsgard, 1982). They are usually seen close to shore (Omura and Sakiura, 1956; Perkins and Whitehead, 1977; Piatt et al., 1989) and alone or in small aggregations (Dorsey, 1983; Edds and Macfarlane, 1987). Off the coast of Washington, where individually identified minke whales have been intensively studied, Dorsey (1983) observed three exclusive adjoining ranges in an area of ca. 600 km². In the northern hemisphere, minke whales are clearly the most solitary, most near-shore, and the most piscivorous of the *Balaenoptera*.

In Antarctic waters, blue, fin, and minke whales feed on euphausiids (Gaskin, 1982), while in many parts of the Atlantic, such as Witless Bay, Nova Scotia, both fin and minke whales feed on schooling fish (Piatt et al., 1989). In these areas, body size may influence the size and density of the prey

patch that different-sized whales can efficiently exploit (J. Piatt, pers. comm.) rather than the prey species.

The differences in diet, habitat use, and social behavior of *Balaenoptera*, the largest of all animals, appear to be consistent with size-related trends found in better-studied terrestrial animals. The application of these size-related studies of terrestrial animals to *Balaenoptera* can help guide research on unknown aspects of their behavioral ecology such as social organization and mating systems.

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