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whales in the Gulf of California, Mexico**

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San Jose State University, 1993

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

A Thesis

Presented to

The Faculty of the Department of Marine Sciences

San Jose State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

Bernie Russell Tershy

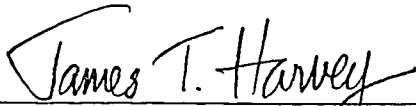
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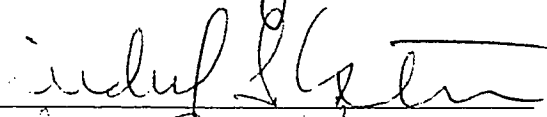
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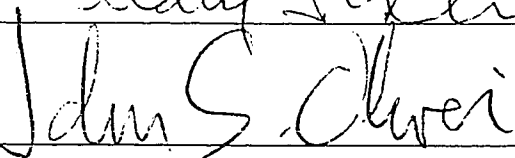
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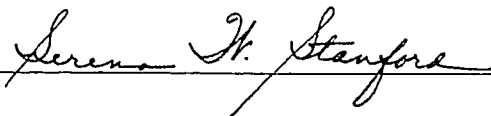
  
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## ABSTRACT

### BODY SIZE, DIET, HABITAT USE, AND SOCIAL BEHAVIOR OF BALAENOPTERAN WHALES IN THE GULF OF CALIFORNIA, MEXICO.

by Bernie R. Tershy

Four sympatric whale species in the genus Balaenoptera were studied between May 1983 and April 1986 in the Canal de Ballenas, Gulf of California, México. Most data were collected on the two most abundant species, the Bryde's whale (B. edeni), ~13,000-kg weight, and fin whale (B. physalus), ~47,000-kg weight. Bryde's whales fed primarily on schooling fish, and were most abundant in summer and fall when schooling fish were concentrated in the study area. Fin whales were observed feeding only on euphausiids, and were most abundant in winter and spring when euphausiids were 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), ~80,000-kg, and minke whale (B. acutorostrata), ~5,000-kg, are interpreted in light of theories which relate body size to diet, habitat use, and social behavior in better studied terrestrial mammals.

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## INTRODUCTION

In this thesis I present the summation of a three years of field work on four sympatric species in the genus Balaenoptera, in the Canal de Ballenas, Gulf of California. In an earlier publication (Tershy et al. 1990b) my co-authors and I presented basic natural history data on the abundance, seasonal distribution, and population composition of these four congeners. In a second publication (Tershy et al. 1993a) we presented basic natural history data on the diet and feeding behavior of the two most common species. This thesis is the summary publication (Tershy 1992), which combines the data presented in the first two publications with additional data, and examines them in relation to the large body of literature on scaling theory. The thesis follows the format of the *Journal of Mammalogy*, the journal in which it was printed.

Data for several other short papers were also collected during my thesis research. Because these papers may also be of interest to readers of this thesis, I cite them here, and briefly explain their relationship to each other. Tershy et al. (1993c), Tershy and Breese (1990), and Tershy et al. (1990a) discussed the relative abundance and seasonal distribution of seabirds in the Canal de Ballenas, and some of the behavioral and ecological interactions among species. Breese and Tershy (1993), Edds et al. (1993), Tershy and Breese (1991), Tershy and Wiley (1992), and Tershy et al. (1993b) presented data on the relative abundance and seasonal distribution of cetacea in the Canal de Ballenas, and their behavior. Finally, Tershy et al. (1991) presented data that indicated a relationship between the movements of marine mammals and birds, and the physical oceanography of the Canal de Ballenas.

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 affect most aspects of ecology and behavior. Comparative studies of different sized ungulates (Jarman, 1974; Clutton-Brock et al., 1980), primates (Clutton-Brock and Harvey, 1977), ground squirrels (Armitage, 1981), canids (Bekoff et al., 1981), and sea ducks (Goudie and Ankney, 1986) indicated 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. 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 among body size, diet, habitat use, and sociality has not been examined previously in a comparative study of different-sized baleen whales.

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

## STUDY AREA AND METHODS

The three most important oceanographic features of the study area (Fig. 1) are: described by Roden (1964), Alvarez-Borrego (1983), Alvarez et al.(1984), and Tershy et al. (1991): (1) extreme spatial variability with points, islands, and shallow bays adjacent to pelagic waters; (2) extreme temporal variability, with temperate water conditions (as low as 14°C) and prevailing northwest winds in winter and spring, and tropical water conditions

(as high as 28°C) and southeast winds in summer and fall; and (3) strong tidal currents (0-3-m/sec), which mix the water column keeping nutrient levels in the photic zone 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 less 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., 1990b). Thus Bryde's and fin whales were sampled more frequently.

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., 1990b). Whales were located 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<sup>-1</sup>) for 5 or 10-min, shut of the engine for 15-min listening for the blows or exhalations of whales, and conducting a 360° binocular scan. We made no attempt to randomize the search effort on a daily basis. On a weekly basis however, we covered most of the study area and all 3 major habitat types (Tershy et al., 1990b). Throughout the day, we counted all cetaceans sighted, regardless of distance from the skiff (Tershy et al., 1991).

When a whale was sighted, we approached to within 100-m and recorded the following data: its location by triangulation using nearby landmarks and a handheld sighting compass; 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., 1990b).

To determine taxa of whale prey (fish or planktonic invertebrates) I observed prey entering the mouth of lunging whales, and analyzed fecal samples collected with a hand-held plankton net. Feces were examined under a dissecting scope for either fish scales and bones, or invertebrate hard parts. When whales were feeding in mixed-species aggregations with planktivorous birds and elasmobranchs, we assumed whales were also feeding on planktonic invertebrates. When whales were in mixed-species feeding aggregations with piscivorous birds, elasmobranchs, and large fish, we assumed whales were feeding on fish (Tershy et al., 1993a).

When several widely separated whales were sighted at the same time, we counted the whales, recorded the size of each group, and approached the largest group, or if all groups were of equal size, the closest. When two species of whale were sighted, we approached the species sighted less often in the past 2 weeks.

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 of the median feeding aggregation size, distance of feeding locations from shore and from previous feeding locations, days between subsequent identifications of individuals, number of identifications per individual, and, group size of whales engaged in traveling behavior. 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,

proportion of feeding whales vs traveling whales resighted within one 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 Balaenoptera species studied, I did a log-log regression (Peters 1983) of body mass (derived from equations in Lockyer, 1976) and mean number of identifications per individual in each species (Tershy et al., 1990b). I excluded known females because females appear to be more resident (Tershy et al., 1990b).

Using compass bearings, I plotted the position of each feeding location, by hand, on a 1:50,000 scale map. For each species, I measured distance from each feeding location to the closest previous feeding location 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

Diet.--Bryde's whales preyed on small schooling fish, such as the Pacific sardine (Sardinops sagax) and thread herring (Opisthonema sp.), in 88.6% of 88 feeding events, and zooplankton in 11.4%. Fin whales preyed on zooplankton, such as the euphausiid Nyctiphanes simplex, in all 30 feeding events (Tershy et al., 1993a.).

Habitat use: feeding.--Bryde's whales fed on a greater 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 under estimate the sizes of larger feeding aggregations; Fig. 2a). The distance between within year feeding locations

was 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 intervals ( $n=84$  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 all Bryde's whale feeding events were within 3 km of the nearest shoreline, while > 80% of all fin whale feeding events were  $\geq 3$  km from the nearest shoreline (Fig. 3b).

Habitat use: seasonal distribution.--Bryde's and fin whales were seen in the study area throughout the year. Bryde's whales However, were most abundant in summer and fall, and mean number sighted per hour per week was positively correlated with water temperature (Tershy et al., 1990). Mean numbers of Bryde's whales and piscivorous common dolphins (*Delphinus delphis*) sighted per week were correlated positively ( $r=0.81$ ,  $d.f.= 52$ ,  $t_1= 10.0$ ,  $P<0.001$ , 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 correlated negatively with water temperature (Tershy et al., 1990b).

Habitat use: residency patterns.--Bryde's and fin whales were sighted with about the same frequency (Tershy et al., 1990), however, the daily mean number of Bryde's whale sighted per hour was more evenly distributed throughout the year 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 1985/86). Within each field season, individually identified fin whales were resighted most often within 1 day, but Bryde's whale resightings were more evenly distributed through 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 traveling fin whales (1.0% of 80 traveling individuals;  $X^2=18.40$ ,  $P<0.001$ ). Bryde's whale resightings, in contrast, were independent of behavior (43.4% of 146 feeding individuals resighted vs 38.2% of 55 traveling whales resighted;  $X^2=0.06$ ,  $P>0.5$ ). Lastly, 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 less transient than larger fin and blue whales. Species body mass was significantly related to the average number of sightings of an individual for each species ( $t=0.97$ , slope=0.36,  $t=5.91$ ,  $P=0.025$ ).

Social behavior.--Bryde's whales were more solitary than fin whales. Excluding cows with calves, 93% of traveling Bryde's whales were solitary, whereas > 60% of traveling fin whales were observed in groups of 2-10 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 2-4 (Tershy et al., 1993a).



## DISCUSSION

Diet.--Bryde's whales fed primarily on fish while fin whales were only observed feeding on euphausiids. The fish species that Bryde's whales preyed have a maximum swimming speed of 150 cm/sec (Beamish, 1978), whereas the 10-25-mm euphausiids that fin whales ate probably swim slower than 100 cm/sec (the maximum speed recorded for 40-55-mm long Euphausia superba; Hamner et al., 1983). Fishes that Bryde's whales were greater in caloric content (1.1-1.5 kcal/kg, Sidwell, 1981) than are euphausiids (0.98 kcal/kg, Chu, 1982).

Although I collected no data on prey distribution or behavior, I can make inferences based on the behavior of the whales. Bryde's whales were observed feeding on a greater percentage of days they were sighted than fin whales. If Bryde's and fin whales had an equal ability of finding suitable patches of prey and an equal probability of feeding whenever these patches were found, then the difference in feeding rates between the two species may indicate the more consistent presence of prey patches suitable to Bryde's whales.

The size of fish patches Bryde's whales fed on may have been smaller, or more ephemeral, than krill patches used by fin whales because fewer Bryde's whales were in feeding aggregations than fin whales, even though their relative abundances were similar. Size of feeding aggregations or groups is grossly proportional to the size of prey patches in many animals, including invertebrates (Antezana and Ray, 1984; Stuart, 1986; Gillespie, 1987), rodents (Lovegrove and Wissel, 1988), primates (Turnbull, 1962; Reynolds and Reynolds, 1965; van Lawick-Goodall, 1968), and delphinids (Würsig, 1986). The relative close spacing of Bryde's whale feeding locations (Fig. 2b) indicated that the concentrations of fish they fed on were more spatially predictable than the concentrations of krill eaten by fin whales. Thus, Bryde's whales fed on fish that were fast and nutritious, and appeared to be in small spatially and temporally predictable patches. Fin whales, in

contrast, fed on krill that were relatively slow and less nutritious, and appeared to be in large spatially and temporally less-predictable patches.

Habitat use: feeding.--The different times of day 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 mid day. Euphausiids school and possibly detect predators by rheotaxis (Hamner et al., 1983; Hamner, 1984); therefore, predator avoidance may be less dependent on light levels.

Habitat use: seasonal distribution.--Bryde's whales were most abundant in the Canal de Ballenas in summer and fall when Pacific sardine and thread herring were the most abundant schooling fish in the Gulf of California (Lluch-Belda et al., 1986). They were the most conspicuous and probably most common prey of Bryde's whales in the study area (Tershy et al. 1993a). Pacific sardines are a temperate species, which breed 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 (Lluch-Belda et al., 1986; Hammann et al., 1988). 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 movements 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; Lapota and Losee, 1984; Brinton et al., 1986). This species forms larger, more-concentrated swarms than the other Gulf euphausiids (E. Brinton, pers. comm.), and is the primary prey of fin whales throughout the Gulf (Tershy et al. 1993a). 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 increase, N. simplex stop breeding, adults die off, and abundance is substantially less (Brinton and Townsend, 1980; E. Brinton, pers. comm.). Pelagic red crabs (Pleuroncodes planipes), another potentially significant prey for fin whales, have a similar seasonal distribution (E. Brinton pers. comm.). It is possible that fin whales migrate into the Gulf in winter and spring when N. simplex is abundant, but that most individuals leave during summer and fall (Tershy et al., 1990b). Several species of large rays (family 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 seasonal movements of fin and Bryde's whales in the study area was determined by breeding migrations. No mating behavior was seen in the study area. Fin whale cows with calves composed  $\leq 1\%$  of the population in the study area, whereas Bryde's whales apparently gave birth throughout the year, based on the size distribution of calves (Tershy et al., 1990b).

Residency patterns and social behavior.--Bryde's whales were relatively resident to the study area, and solitary (Figs. 2b, 4). Fin whales, in contrast, were transient, passing through the study area and lingering only to feed, traveled in groups of 2-10 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 swimmers, 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 sp.), which have relatively low 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 where they attempt to exclude conspecifics. At the other extreme, food is low quality and patches are very large and unpredictably distributed in time and space. These patches are most often exploited by large antelope like cape eland (Taurotragus oryx), which have greater 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 do not 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 rumin 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 (Clutton-Brock, 1974; Bekoff et al., 1981; Jarman and Southwell, 1986; Lovegrove and Wissel, 1988; Fleming, 1991). 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 study species is also consistent with Jarman's model.

Many aspects of blue and minke whale natural history also are consistent with a size-based relationship between diet, habitat use, and social behavior in Balaenoptera. In the study area (Tershy et al., 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 are usually found well offshore (Tomilin, 1967; Evans, 1980), 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 2-4 (Tershy et al., 1993a). 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 feed primarily on small schooling fish (Kawamura, 1980; Gaskin, 1982) but also feed on larger fish such as mature Arctic cod (Gadus morhua) and haddock (Melanogrammus aeglefinus, Jönsgard, 1982). Minke whales 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 Washington State, where individually identified minke whales have been intensively studied, Dorsey (1983) observed three exclusive adjoining ranges of three individuals in an area of about 600 km<sup>2</sup>. In the northern hemisphere, minke whales are clearly the most solitary, near-shore, and piscivorous of the Balaenoptera.

In the Antarctic, blue, fin, and minke whales feed on euphausiids (Gaskin 1982), whereas 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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## FIGURE CAPTIONS

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.

Fig. 2.-- Minimum feeding-aggregation sizes of Bryde's (Balaenoptera edeni) and fin (B. physalus) whales in the Gulf of California, 1983-86 (A). Nearest distances between locations where feeding was observed for Bryde's and fin whales (B).

Fig. 3.-- The diel distribution of feeding events for Bryde's (Balaenoptera edeni) and fin (B. physalus) whales in the Gulf of California, 1983-86 (A). Distances of Bryde's and fin whale feeding events from the nearest shoreline (B).

Fig. 4.--Group sizes of traveling Bryde's (Balaenoptera edeni) and fin (B. physalus) in the Gulf of California, 1983-86.

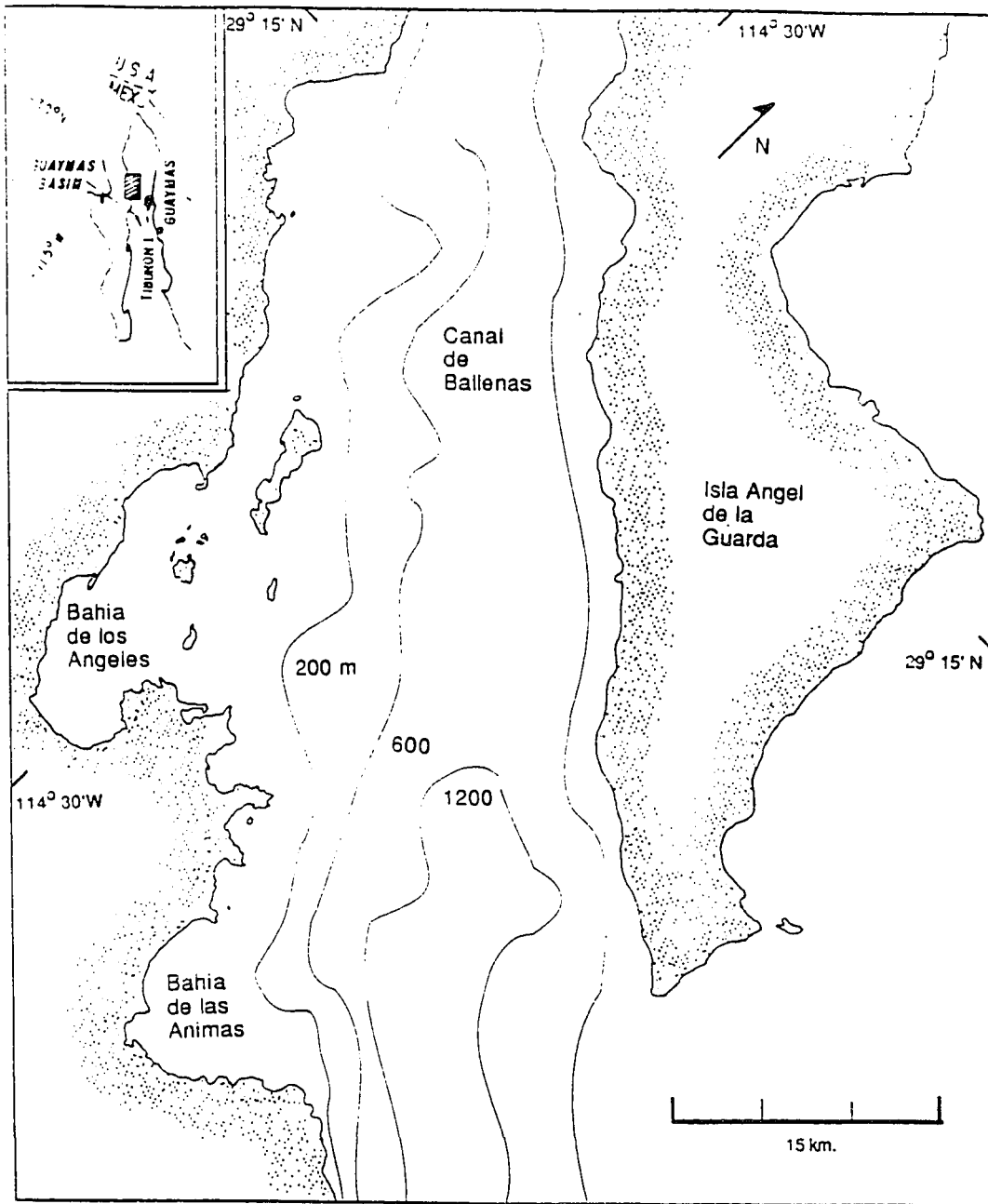


Fig. 1

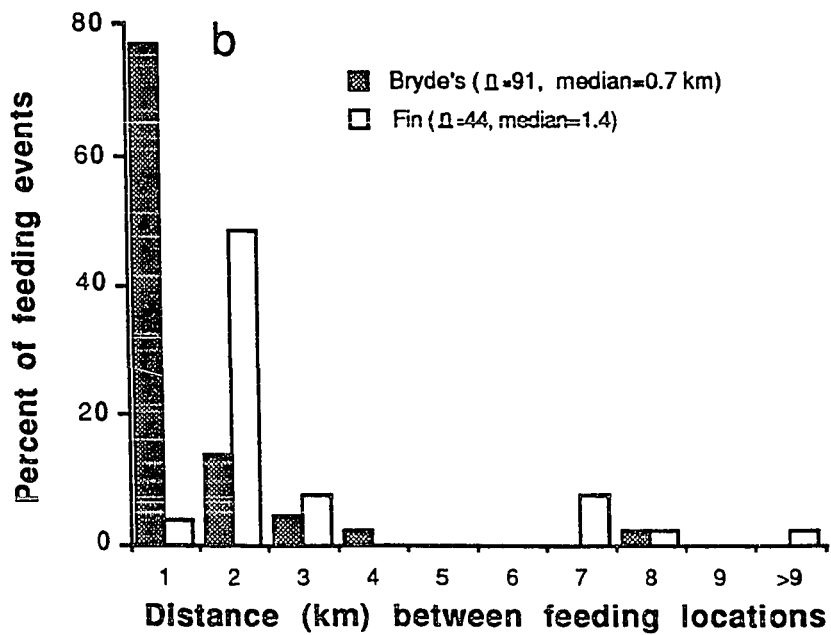
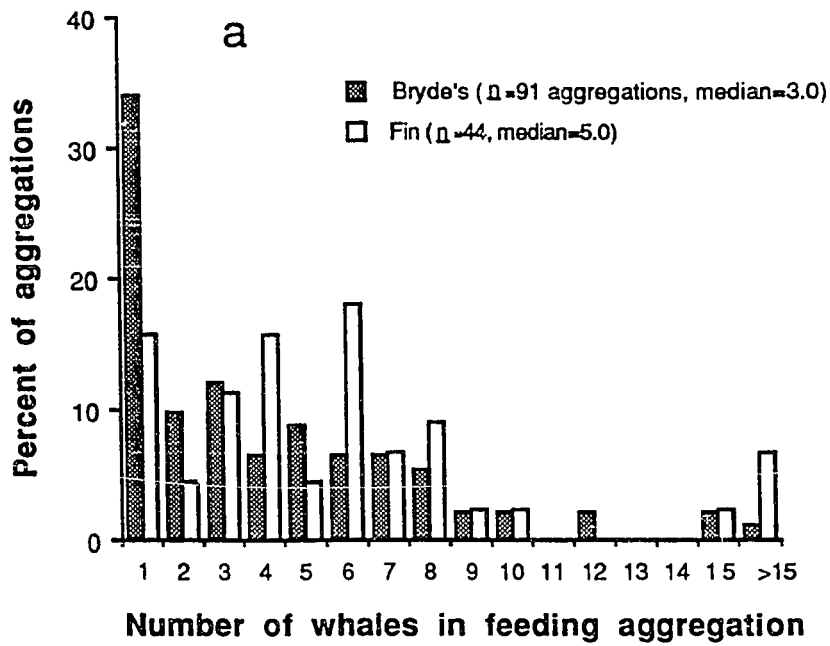


Fig. 2

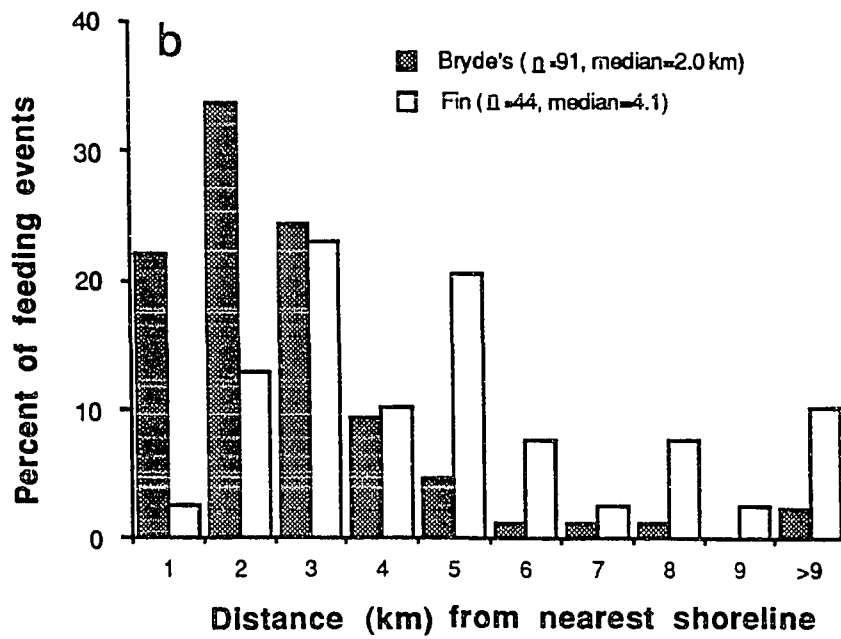
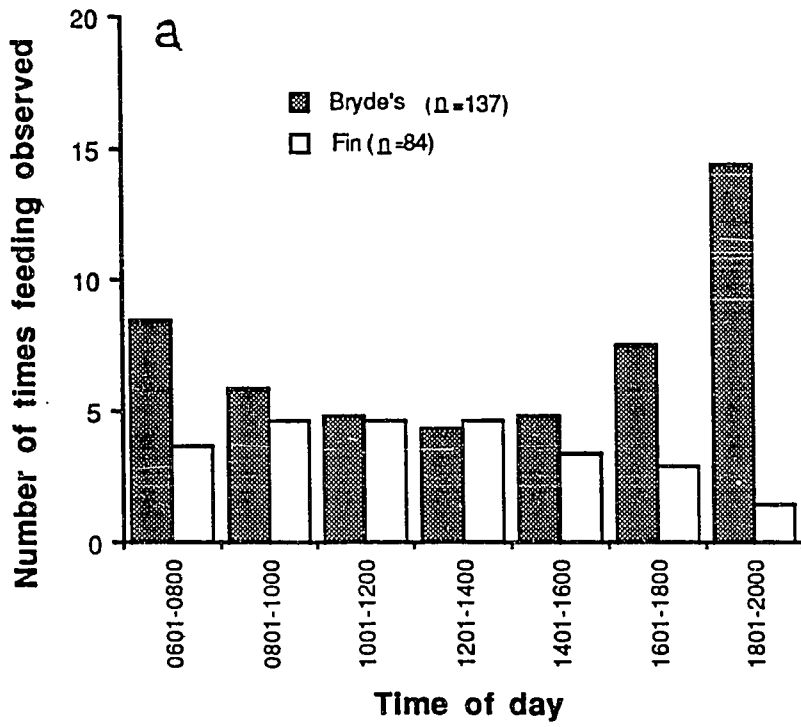


Fig. 3



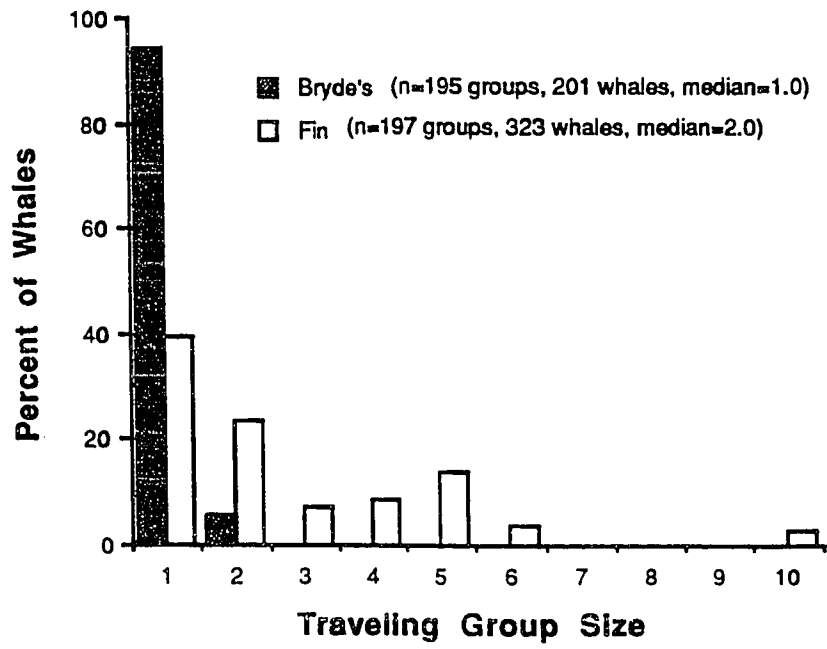


Fig. 4