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Habitat Partitioning by Three Species of Dolphins in Santa Monica Bay, California

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Abstract.—Habitat partitioning by bottlenose dolphins (*Tursiops truncatus*), short-beaked common dolphins (*Delphinus delphis*), and long-beaked common dolphins (*D. capensis*), were assessed during 178 surveys conducted between 1997–2000 in Santa Monica Bay, California. Bottlenose dolphins were found year-round within 0.5 km from shore in 80.0 % of the sightings (n = 137) but they were also found in deeper waters further offshore. The two common dolphin species were observed year-round (n = 83) far from shore and near escarpments; they were sympatric but never seen in mixed schools. This study suggests that habitat partitioning in the bay probably relates to resource partitioning among three dolphins species with roughly similar ecological needs.

Interspecific investigations of odontocete behavioral ecology are rare (Polacheck 1987; Selzer and Payne 1988; Shane 1994; Gowans and Whitehead 1995) and no such studies have been conducted in the Southern California Bight. Studies in Santa Monica Bay (Fig. 1; Bearzi 2005) have found that it is inhabited year-round by three relatively abundant cetaceans: the bottlenose dolphin (*Tursiops truncatus*), the short-beaked common dolphin (*Delphinus delphis*), and the long-beaked common dolphin (*D. capensis*). This investigation examines spatial distribution and habitat partitioning of these three species in the bay between 1997–2000.

Similar species that co-occur are thought to compete for resources unless they occupy different physical locations and/or feed on different prey (Roughgarden 1976). Along the California coast, short-beaked and long-beaked common dolphins are seldom seen close to shore, whereas populations of bottlenose dolphins occur inshore year-round (Carretta et al. 1998; Forney and Barlow 1998; Hansen 1990; Defran and Weller 1999). The genus *Delphinus* has been observed associated with characteristic offshore bathymetric features such as escarpments and submarine canyons (Evans 1974; Polacheck 1987; Selzer and Payne 1988; Gaskin 1992; Gowans and Whitehead 1995). This study correlates the distributions of bottlenose dolphins, short-beaked common dolphins and long-beaked common dolphins with the environmental features of Santa Monica Bay to describe habitat use and inter-specific aggregations of these species.

Species Distributions

The genus *Tursiops* is found widely in temperate and tropical waters. Populations of bottlenose dolphins are known to inhabit pelagic waters as well as coastal

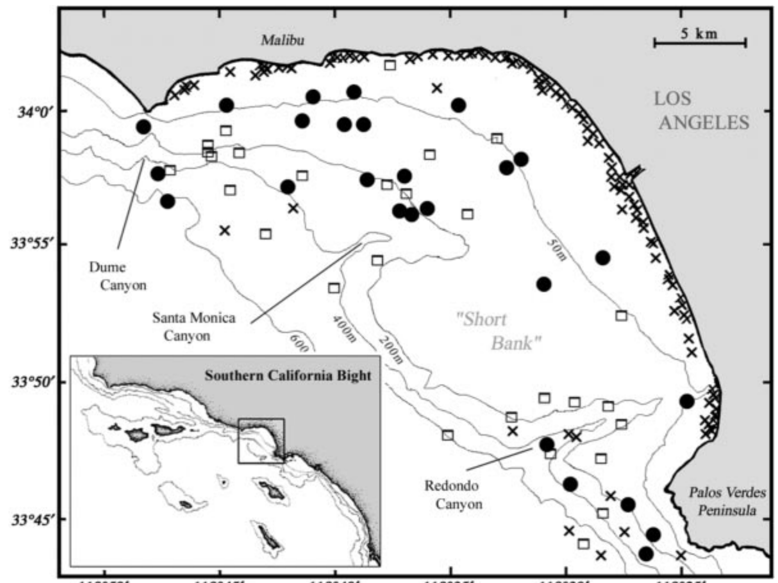

Fig. 1. The study area and the distribution of bottlenose dolphins (×), short-beaked common dolphins (●), and long-beaked common dolphins (□) in the bay. Each symbol represents initial GPS coordinates of sightings. Sightings outside the bay and sightings of *Delphinus* spp. not recognized at the species level were excluded from this map. Submarine canyons (Dume, Santa Monica, Redondo) and escarpments/slopes (Palos Verdes continental slope, west of Los Angeles slope, south of Malibu montain slope) include respectively sightings located no farther than 0.4 km from each side of the canyons and the isobaths, and 1.8 km from the centers of the slopes. Flat areas and plateaus include all the sightings observed in these locations. Submarine canyons are indicated by the three lines.

areas, including bays and tidal creeks (Leatherwood et al. 1983). These populations also show morphological, osteological and molecular differentiations (LeDuc and Curry 1998; Rossbach and Herzing 1999). Coastal forms of bottlenose dolphins exist in many areas of the world (e.g., Shark Bay, Western Australia: Connor and Smolker 1985; the Firth of Tay, Scotland: Wilson 1995; Sarasota Bay, Florida: Scott et al. 1990; Wells 1991; Argentine Bay, Argentina: Würsig 1978; Croatia, Mediterranean Sea: Bearzi et al. 1999). Coastal populations usually live within 0.5 km of shore in schools of 1–25 individuals, sometimes residing in a specific area, while pelagic populations are found in larger groups of 25 to several thousand individuals ranging widely in the open ocean (Scott and Chivers 1990; Bearzi et al. 1999; Defran and Weller 1999; Bearzi 2005).

Long-term studies on free-ranging bottlenose dolphins in the Southern California Bight have been focused mostly along the San Diego coastline (less than 1 km from shore; Defran and Weller 1999). In 1996, a preliminary series of cetacean surveys in the waters of Santa Monica Bay determined that bottlenose dolphins could be found there in all seasons (Bearzi 2005).

Common dolphins (*Delphinus* spp.) also have a wide distribution in tropical and temperate waters. In the eastern North Pacific, there are two separate species of common dolphins, the short-beaked and the long-beaked common dolphin, distinguished morphometrically by Heyning and Perrin (1994) and genetically by

Rosel et al. (1994). In the Southern California Bight the two species occur sympatrically (Heyning and Perrin 1994; Rice 1998).

These dolphins usually live in large schools that can reach thousands of individuals (Cockcroft and Peddemors 1990; Klinowska 1991). Evans (1975) and Bruno et al. (2002), however, suggested that the basic social unit for common dolphins contains less than 30 individuals. Information on occurrence, distribution, and abundance have been collected for this genus in central and southern California (Evans 1975; Dohl et al. 1986; Forney and Barlow 1998), but no information on these animals was previously available for Santa Monica Bay.

Materials and Methods

Study Area

The Santa Monica Bay study area (approximately 460 km^2, Fig. 1) is a shallow shelf bounded by the Palos Verdes Peninsula to the South (33°45′N, 118°24′W), Point Dume to the North (33°59′N, 118°48′W) and the edge of the continental shelf to the West. The bottom habitat of the bay includes sandy soft sediments inshore and silts along slopes and canyons. This study area contains three submarine canyons: Dume and Redondo canyons begins in shallow water, whereas Santa Monica Canyon begins at a depth of about 100 m at the edge of the continental shelf. A shallow shelf, known as ‘‘short bank’’, located between Santa Monica Canyon and Redondo Canyon extends as a plateau from the 50-m contour and is characterized by patchy areas of exposed bedrock, rock pinnacles, gravel, and mixed sediments (Terry et al. 1956). The mean depth of the bay is about 55 m and the maximum depth 450 m. Normal water surface temperatures range from 11 to 22°C. During the 1997–98 El Niño, three peaks of sea surface temperature (SST) anomalies, with an increase in temperature of +2°C, were evident in May–June 1997, September–October 1997 and August 1998 (Nezlin et al. 2003).

Data Collection and Analysis

Regular surveys were conducted from January 1997 to December 2000 (Table 1), with an average of 3.5 surveys per month ($n = 178$). Inshore and offshore surveys, defined respectively as surveys conducted at a distance from shore ≤0.5 km and at a distance offshore >0.5 km, were carried out from a 7-m powerboat in the morning and early afternoon.

The number of kilometers surveyed in all different locations of the bay—including submarine canyons (Dume, Santa Monica, Redondo), escarpments/slopes (Palos Verdes continental slope, west of Los Angeles slope, south of Malibu montain slope), flat areas and plateaus—was calculated to determine the evenness in the coverage of the study area using a grid comprised of 82 3.7×3.7 km cells (Bearzi 2003). Using Student's t-test for independent samples, no significant difference was observed in surveying the different locations ($t = 1.92$, $df = 28$, $P > 0.05$). Differences in distribution among species in relation to the bathymetry of the bay were evaluated comparing their positions (initial GPS coordinates of dolphin sightings) among eight different isobaths from 0 to 600 m using a finer grid comprised of 2.5×2.5 km cells and calculating the total number of sightings in each cell (Bearzi 2003).

Data were collected with laptop computers and occasionally with tape record-

Table 1. Number of surveys, summary of research effort, and sighting frequencies (sightings/hour) of the three most observed cetacean species in Santa Monica Bay between 1997–2000.

	1997	1998	1999[a]	2000[b]	Total
Surveys					
Inshore surveys	5	17	12	6	40
Offshore surveys	23	3	5	4	35
Combined inshore/offshore surveys	11	38	27	27	103
Total number of surveys	39	58	44	37	178
Research Effort					
Hours spent in the field	144	224	178	149	695
Hours spent searching for dolphins	110	136	130	105	481
Hours spent with the three species	26	80	53	41	200
Hours spent with *Delphinus* spp.	9	17	18	19	63
Hours spent with *T. truncatus*	17	63	35	22	137
Sightings*	29	87	57	47	220
Tursiops truncatus					
Number of sightings	19	61	33	24	137
Sighting frequency (sightings/hour)	0.13	0.27	0.19	0.16	0.20
Delphinus spp.**					
Number of sightings	10	26	24	23	83
Sighting frequency (sightings/hour)	0.07	0.12	0.14	0.15	0.12
Delphinus capensis					
Number of sightings	2	13	11	10	36
Sighting frequency (sightings/hour)	0.01	0.06	0.06	0.07	0.05
Delphinus delphis					
Number of sightings	6	7	6	6	25
Sighting frequency (sightings/hour)	0.04	0.03	0.03	0.04	0.04
N of 5-min samples	295	1,065	698	525	2,583

[a, b] no data collection in Dec 1999 and Oct 2000.
* one mixed school of different species is counted as one sighting.
** this calculation includes *Delphinus* spp. not recognized at the species level.

ers. When dolphins were spotted, data on number of animals and behavior were recorded at 5-min intervals throughout the sighting (Bearzi 2003).

The majority of the observations were conducted with Beaufort scale 2 or less, sea state 0 and visibility $>$300 m. The dolphins' position and speed ($\pm$30 m from the boat) were approximated to the boat's position using a GPS. The boat's speed was reduced in the presence of dolphins and sudden speed or directional changes were avoided.

To distinguish between short-beaked and long-beaked common dolphins, researchers took close-up photographs of the animals' lateral foresection. Color photos were taken with 35-mm cameras equipped with 75–300-mm lenses using slide film (64-200 ISO). During the sighting, researchers also videotaped the animals' lateral foresections and recorded their behavior with Hi8-mm and Mini DV Video Camcorders. Photos and videos were reviewed in laboratory for the species identification based on body features described by Heyning and Perrin (1994).

A *dolphin school* was defined as all dolphins in continuous association with each other and within visual range of the survey team (Weller 1991). *Aggregation* referred to distances between one or more individuals of two different species being less than 100 m.

Data analyses were performed using Statview 5.02 and Grapher 3.02; data on species distribution were plotted with Arcview GIS 3.2 and Surfer 6.02.

Results

Field Effort

Data were collected during 40 inshore surveys, 35 offshore surveys, and 103 combined inshore/offshore surveys in the bay; the survey coverage between 1997 and 2000 totaled 9,526 km. A total of 446 h were spent searching for cetaceans in good weather conditions (Beaufort scale $\leq$2) and 35 h in unfavorable conditions (Beaufort scale $>$2). A total of 137 h (64.0 % of total sighting time) were spent with bottlenose dolphins during 137 sightings, lasting on average 64 min (range 3–262 min), and a total of 63 h (29.4 % of total sighting time) were spent with short-beaked and long-beaked common dolphins during 83 sightings, lasting on average 51 min (range 5–185 min; Table 1).

Occurrence, Sighting Frequencies and Distribution

Bottlenose dolphins were most frequently sighted year-round (62.3 % of the sightings; n = 220) generally inshore (80.0 %), followed by long-beaked and short-beaked common dolphins (respectively 16.4 % and 11.4 % of the sightings; Table 1, Fig. 2a). The two species of common dolphins were spotted only eight times (9.6 %) in inshore waters.

Sightings/effort for the three species in the years 1997–2000 and during different seasons are illustrated in Figs. 2a,b,c. Long-beaked common dolphins were slightly more abundant than short-beaked common dolphins in the years 1998–2000, although the difference in sighting number was not significant among the four years (long-beaked common dolphins: 59.0 %, short-beaked common dolphins: 41.0 %, n = 61; χ^2 = 1.33, df = 1, P $>$ 0.05; Table 1).

The distribution of the three species in relation to the bathymetry is presented in Fig. 1. Species distribution differed significantly according to depth (χ^2 = 92.09, df = 7, P $<$ 0.001), with bottlenose dolphins inhabiting mostly inshore waters (0–50 m deep) and the two species of common dolphins being more frequent in deeper waters. The distribution of short-beaked common dolphins versus long-beaked common dolphins also differed significantly with depth (χ^2 = 21.19, df = 7, P $<$ 0.001), with short-beaked common dolphins showing a broader distribution, mostly between the 50–100 m isobaths (Fig. 1). All species showed a significant preference for canyons, escarpments, and slopes (χ^2 = 22.41, df = 5, P $<$ 0.001). No significant difference was observed between short-beaked and long-beaked common dolphins in terms of their proximity to canyons (Dume, Santa Monica, Redondo) and escarpments/slopes (continental slope, west of Los Angeles slope, south of Malibu mountain slope; χ^2 = 1.95, df = 5, P $>$ 0.05; Fig. 1).

Short-beaked and long-beaked common dolphins did not aggregate together, although both species aggregated with other cetaceans. In offshore waters, common dolphins were observed twice in mixed schools with other cetacean species; once with Pacific white-sided dolphins (*Lagenorhynchus obliquidens*), and once with minke whales (*Balaenoptera acutorostrata*). In inshore waters, both common

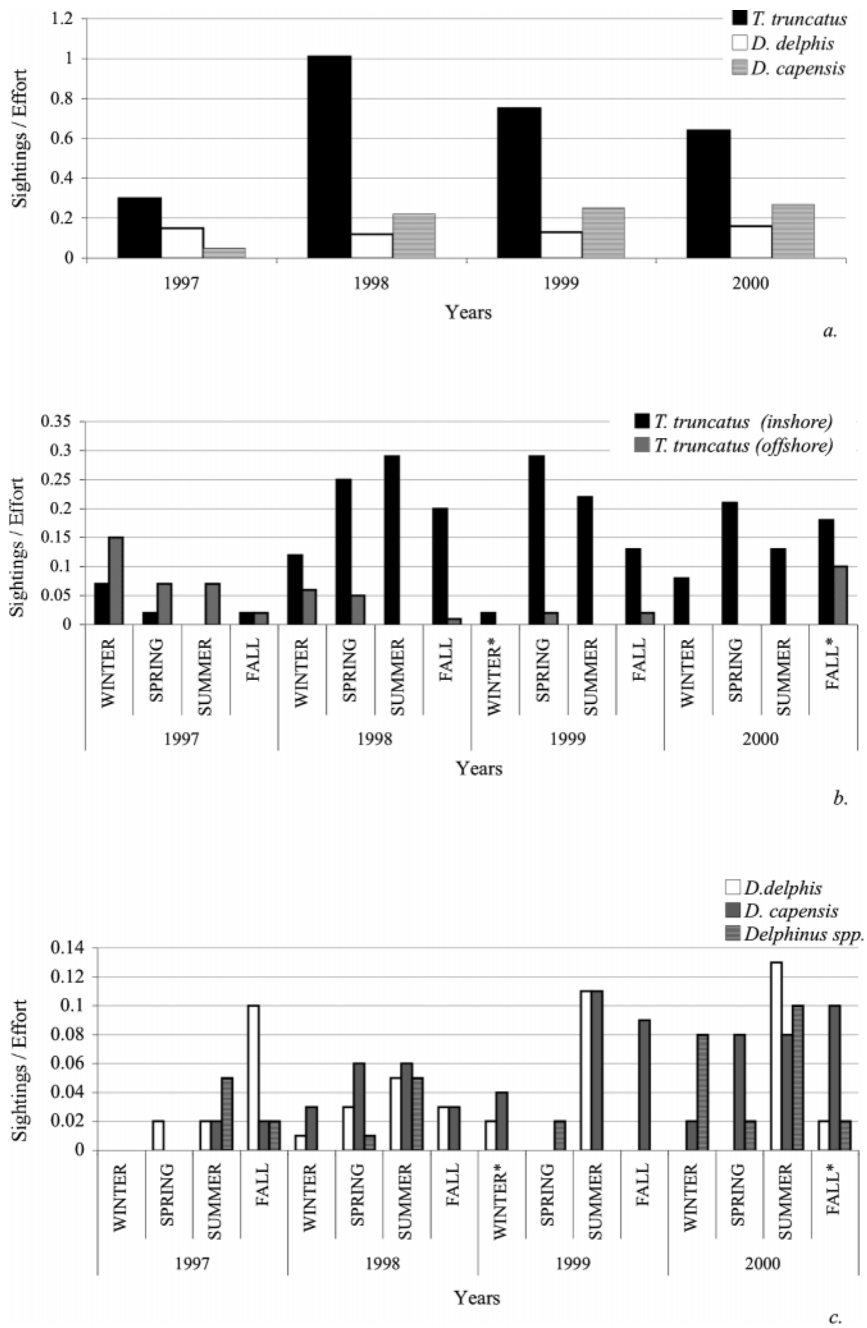

Fig. 2a,b,c. (a) Sightings/effort for the three species observed in the bay during the years 1997–2000, (b) sightings/effort for *T. truncatus* observed during inshore and offshore surveys and, (c) sightings/effort for *D. capensis*, *D. delphis*, and *Delphinus* spp. (animals recognized only at genus level). In figures 2b,c, the years were divided into four seasonal categories: Winter (December–February), Spring (March–May), Summer (June–August), and Fall (September–November). No data was collected in December 1999* and October 2000*.

dolphin species were observed 87.5 % of the sightings (n = 7) in mixed schools with coastal bottlenose dolphins.

Discussion

Bottlenose dolphins were most often observed in Santa Monica Bay, generally sighted within 0.5 km of shore, as is the case along the San Diego coastline (Defran and Weller 1999). The occurrence of *Delphinus* spp. in Santa Monica Bay was also consistent with reports for other areas of the California coast (Southern California Bight: Norris and Prescott 1961; Leatherwood et al. 1988; Bonnell and Dailey 1993; California coast: Forney and Barlow 1998). In the bay, both species of common dolphins were sighted year-round and mostly offshore with similar distributions.

Long-term studies on inshore bottlenose dolphins suggest that their distribution may be related to the distribution and abundance of nearshore prey (Defran and Weller 1999). Stomach content show that 74.0 % of their prey were either surf-perches (*Embiotocidae*) or croakers (*Scianidae*) (Norris and Prescott 1961; Walker 1981; Hanson and Defran 1993). These prey species occur year-round in shallow coastal waters of the Southern California Bight (Cross and Allen 1993). The year-round abundance of bottlenose dolphins in Santa Monica Bay may be explained by a year-round presence of nearshore prey (Deets and Roney 1999; California Department of Fish and Game 2000; Bearzi 2005).

The more-offshore sightings of short-beaked and long-beaked common dolphins may be related to different prey preferences (Table 2). For short-beaked common dolphins, Evans (1975) found their main prey in the Bight was anchovies (*Engraulis mordax*) whereas Fitch and Brownell (1968) and Schwartz et al. (1992) reported that squid (family *Gonatidae* and *Loligo opalescens*) and Pacific whiting (*Merluccius productus*) were their primary prey. All these prey species are primarily pelagic inhabitants of the Bight (California Department of Fish and Game 2000). In Santa Monica Bay, therefore, inshore bottlenose dolphins and the two species of common dolphins differ both in distribution and prey preference. I suggest that the habitat partitioning of these species is a consequence of prey specialization and competition for resources in inshore waters.

The three species distributions did overlap, however near Redondo Canyon and the continental slope south of Palos Verdes Peninsula (Fig. 1); these areas are the deepest and steepest features in the bay (Dartnell and Gardner 2004). Upwelling of highly oxygenated and nutrient-rich water was found over the San Pedro shelf and eddy-like features near the slopes in the southern half of Santa Monica shelf were also observed (Hickey 1992, 1993). These oceanographic features are optimal for mixing of nutrients that would provide rich feeding grounds for dolphins. Anchovies are known to concentrate in submarine canyons and escarpments in areas of upwelling (Mais 1974; Hui 1979). This potential abundance of prey was likely to allow the three species to coexist in the same areas.

Other locations of the bay near canyons, escarpments and slopes show a significantly higher number of sightings than flat areas and plateaus. These results show interesting parallels with white-sided dolphins (*Lagenorhynchus acutus*) and short-beaked common dolphins along the continental shelf of northeastern United States (Selzer and Payne 1988), and various odontocetes near a submarine canyon on the Scotian Shelf (Gowans and Whitehead 1995). Other authors have also

Table 2. Diet of *T. truncatus* and *Delphinus* spp. in Southern California waters. N = nearshore prey, O = offshore prey, B = prey present in both, inshore and offshore waters (e.g., different seasons, different life stages, etc.).

Prey	Habitat	*T. truncatus*[1]	*Delphinus* spp.[2]
Walleye surfperch (*Hyperprosopon argenteum*)	N	X	
Pile surfperch (*Damalichthys vacca*)	N	X	
Black surfperch (*Embiotoca jacksoni*)	N	X	
Shiner surfperch (*Cymatogaster aggregatus*)	N	X	
White surfperch (*Phanerodon furcatus*)	N	X	
Barred surfperch (*Amphistichus argenteus*)	N	X	
Blacksmith (*Chromis punctipinnis*)	N	X	
Spotfin croaker (*Rancador stearnsi*)	N	X	
Kelp bass (*Paralabrax clathratus*)	N	X	
Smelts (*Osmeridae*)	N	X	X
Queenfish (*Seriphus politus*)	N	X	X
California halibut (*Paralichthys californicus*)	B	X	
Yellowfin croaker (*Umbrina rancador*)	B	X	
White croaker (*Genyonemus lineatus*)	B	X	
California corbina (*Menticirrhus undulates*)	B	X	
Specklefin midshipman (*Porychthys myriaster*)	B	X	
Octopoteuthidae	B	X	
Plainfin midshipman (*Porychthys notatus*)	B	X	X
Cusk eel (*Ophidiidae*)	B	X	X
Jack mackerel (*Trachurus symmetricus*)	B	X	X
Northern anchovy (*Engrualis mordax*)	B	X	X
Market squid (*Loligo opalescens*)	B	X	X
Sardine (*Sardinops coerulea*)	B		X
Pacific mackerel (*Scomber japonicus*)	B		X
Pacific whiting (*Merluccius productus*)	O		X
Northern lampfish (*Stenobrachius leucopsarus*)	O		X
Bonito (*Sarda chiliensis*)	O		X
California Smoothtongue (*Bathylagus stilbius*)	O		X
Pacific pompano (*Peprilus simillimus*)	O		X
Lanternfish (*Myctophidae*)	O		X
Medusafish (*Icichthys lockingtoni*)	O		X
Onychoteuthidae	O		X
Gonatus sp.	O		X

[1] Walker 1981; Hanson and Defran 1993 (for coastal populations). Data from stomach contents.
[2] Norris and Prescott 1961; Fitch and Brownell 1968; Evans 1975; Schwartz et al. 1992; Bonnell and Dailey 1993; M. Bearzi pers. obs. Data from stomach contents and fish scale collection.

reported the presence of the genus *Delphinus* along sea floor reliefs, submarine canyons and escarpments (Evans 1974; Hui 1979; Polacheck 1987; Selzer and Payne 1988; Gaskin 1992; Gowans and Whitehead 1995), showing that undersea topography, rather than water depth, is the most significant physical feature influencing the distribution of common dolphins.

In Santa Monica Bay, the two species of common dolphins have the same preference for the same escarpments, slopes and submarine canyons, but short-beaked common dolphins show a less-defined distribution, predominantly between the 50–100 m isobaths. The year-round co-occurrence of these species in the study area over four years may be related to productive feeding grounds, rich enough in prey to support their feeding requirements. This is suggested by the relatively high amount of time spent feeding or diving (about 30.0 % of total time; Bearzi

2003) in comparison to data reported by Neumann (2001) for the Bay of Plenty, New Zealand (17.0 % of total time).

Shifts in abundance of long-beaked and short-beaked common dolphins were observed since the last century in southern California waters (Banks and Brownell 1969; Heyning and Perrin 1994). In this study, long-beaked common dolphins were the more common in the bay starting from 1998, at the end of the 1997–1998 El Niño, showing a pattern similar to the one previously observed by Heyning and Perrin (1994). These authors suggested that environmental factors may be more advantageous to one or the other species at different times. However, differences in habitat use between short-beaked and long-beaked common dolphins are complex, considering the similar diet of the two species (Fitch and Brownell 1968; Schwartz et al. 1992; Ohizumi 1998). In the southern California waters, stomach content analyses showed that short-beaked common dolphins feed more on squid, a prey usually caught at depth during the day or at surface at night, than do long-beaked common dolphins (Schwartz et al. 1992). Decreased squid abundance during the last two El Niño events (California Department of Fish and Game 2000) could partially explain the greater number of short-beaked common dolphins before both El Niño events and the decrease in number after these events.

Although short-beaked and long-beaked common dolphins were both sighted in similar locations of the bay, confirming a sympatric micro-range, no occurrence of these two taxonomically close species in mixed schools was ever observed. The slight difference in diet could indicate a separation of ecological niches reducing the occurrence of direct competition for food resources when the dolphins are sympatric. Different preferences in prey for sympatric dolphins were observed by other authors (Das et al. 2000; Hale et al. 2000). Gowans and Whitehead (1995) explained the co-occurrence of species either by a superabundance of food or by a slightly different diet that may eliminate a competitive pressure between the species.

Conclusions

Spatial habitat partitioning by different dolphin species has rarely been described in detail (Selzer and Payne 1988; Gowans and Whitehead 1995). This study provides a description of habitat partitioning by three species of dolphins in Santa Monica Bay. Bottlenose dolphins were found year-round in shallow waters, clearly separated from the distribution of short-beaked and long-beaked common dolphins, but they were also observed occasionally in deeper waters over the continental shelf and pelagic waters outside the bay. Short-beaked and long-beaked common dolphins were found year-round in the bay but mostly far from shore. Both common dolphin species were sighted in areas of complex underwater topography. Although they were observed in similar locations of the bay, confirming their sympatric range, these two species were never seen in mixed schools.

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