CALIFORNIA SEA LIONS USE DOLPHINS TO LOCATE FOOD

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Aggregations by 3 species of dolphins (the bottlenose dolphin [*Tursiops truncatus*], the short-beaked common dolphin [*Delphinus delphis*], and the long-beaked common dolphin [*Delphinus capensis*]) and California sea lions (*Zalophus californianus*) were investigated in Santa Monica Bay, California. Groups were followed and observed during 201 boat-based surveys conducted in 1997–2001 documenting that sea lions were aggregated in 18.6% of the sightings with bottlenose dolphins (150 bottlenose dolphin sightings) and in 45.9% of the sightings with 1 of the 2 species of common dolphins (98 common dolphin sightings). Aggregations of bottlenose dolphins and sea lions were observed in inshore (<500 m from shore) and offshore (>500 m) waters, whereas common dolphins and sea lions were observed only in offshore waters. These aggregations were often recorded feeding near escarpments and submarine canyons, showing a striking preference for these bathymetric features. The results show that sea lions spend a significant amount of time following dolphins, sea lions initiate aggregation and departure from dolphin schools, these aggregations occur more often than is expected by chance, and no aggressive behavior between sea lions and dolphins was ever observed at or near the surface. I argue that sea lions may take advantage of the superior food-locating abilities of dolphins. This paper provides the 1st detailed description of mixed-species aggregations and habitat usage by 3 dolphin species and sea lions.

Key words: bottlenose dolphin, California sea lion, long-beaked common dolphin, mixed-species aggregations, short-beaked common dolphin, social parasitism

Interspecific aggregations are documented from fish (see Lukoschek and McCormick [2002] for a review) and birds (Dolby and Grubb 1998; Morse 1970, 1977) to mammals such as ungulates, primates, and cetaceans (see Stensland et al. [2003] for a review). In cetaceans, mixed-species groups are reported for more than 30 species (see Frantzis and Herzing [2002] for a review) in different marine habitats (Au and Perryman 1985; Norris and Prescott 1961; Perrin et al. 1973; Polacheck 1987; Reilly 1990; Saayman et al. 1972; Selzer and Payne 1988; Shane 1995; Würsig and Würsig 1980).

The recognized theoretical justifications for these aggregations are the foraging advantages and predator avoidance gained by the species involved, although other explanations such as reproductive and social advantages cannot be excluded (Stensland et al. 2003). The function and benefit of these mixed-species groups are usually not tested in the field (Stensland et al. 2003). The goal of this paper is to better understand the reasons for aggregations of 3 species of delphinids and sea lions.

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Cetacean and pinniped aggregations are mentioned by several authors (Fink 1959; Gallo Reynoso 1991; Leatherwood 1975; Shane 1994; Suryan and Harvey 1998; Würsig and Würsig 1980), but detailed descriptions of these mixed-species aggregations have not yet been attempted. Further, no studies have been conducted on this subject in the Southern California Bight, the region of the Pacific Ocean off southern California where the coastline curves inward.

Santa Monica Bay, which lies within the Bight (Fig. 1), is inhabited year-round by 3 relatively abundant dolphin species (bottlenose dolphin [*Tursiops truncatus*], short-beaked common dolphin [*Delphinus delphis*], and long-beaked common dolphin [*D. capensis*]) and 1 regularly observed species of pinniped (California sea lion [*Zalophus californianus*]—Bearzi 2003). The high and year-round presence of these species in the bay offers an excellent opportunity to investigate sea lion and dolphin aggregations and their habitat use.

Coastal populations of bottlenose dolphins usually live within 1 km of shore (Defran and Weller 1999) in small schools of 5–25 individuals, sometimes residing in a specific area, whereas offshore populations are found in larger schools in the open ocean (Connor et al. 2000). Long-term studies on bottlenose dolphins for the Southern California Bight have focused mostly on inshore populations (Bearzi 2005a; Defran et al. 1999).
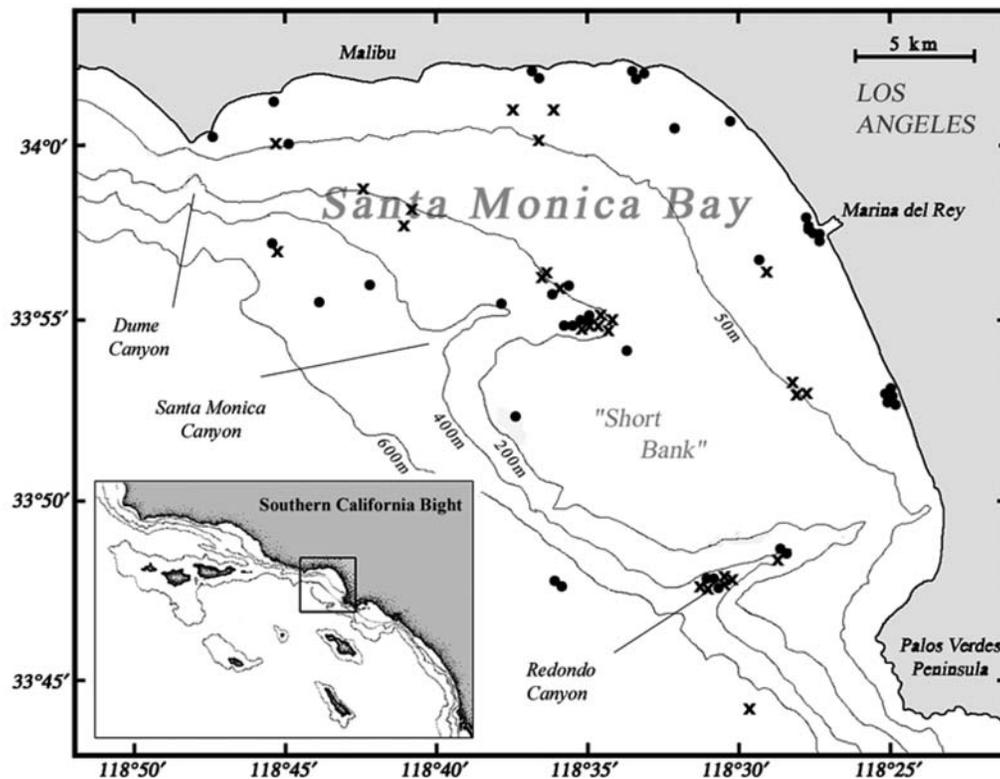
Fig. 1.—The study area in Santa Monica Bay, California, lying within the Southern California Bight (inset). Symbols indicate the distribution of bottlenose dolphins (•) and 2 species of common dolphins (×) in aggregations with California sea lions during surface-feeding activities in the bay. Each symbol represents initial GPS coordinates of feeding effort during a sighting.

Short-beaked common dolphins and long-beaked common dolphins occur sympatrically in the Southern California Bight (Heyning and Perrin 1994) and generally live in large schools that can reach thousands of individuals (Cockcroft and Peddemors 1990; Klinowska 1991). However, Evans (1994) and Bruno (2001) suggested that the basic social unit of common dolphins contains fewer than 30 individuals. Inshore populations of short-beaked common dolphins have been described for the Southern California Bight (Evans 1975), although the ecology of offshore populations is still unknown (Rice 1998). In Santa Monica Bay, both common dolphin species were observed near escarpments and submarine canyons mostly in pelagic waters, separated from the distribution of coastal bottlenose dolphins found mostly in shallow waters within 0.5 km of shore (Bearzi 2005c).

At sea, California sea lions can be observed alone or in small groups when foraging on schooling fish (Riedman 1990). This species is the most abundant pinniped in the Southern California Bight (Bonnell and Dailey 1993) and its ecology is well known both for local rookeries and at sea (Antonelis et al. 1984, 1990; Bonnell and Ford 1987; Lowry et al. 1990; Stewart and Yochem 2000).

This paper suggests that the 3 species of delphinids and the sea lions aggregate in the study area to attain foraging benefits. The hypothesis I am testing is that sea lions take advantage of the superior ability of dolphins to locate food. Dolphins use echolocation as a principal means of locating prey (Norris 1969), whereas sea lions rely mostly on their vision (Levenson

and Schusterman 1997, 1999). Sea lions may have a better chance of finding resources that are patchily distributed in the open ocean by exploiting the more sophisticated food-finding ability of dolphins.

To test the hypothesis, I first examined species of pinnipeds and dolphins found in aggregations, number of animals involved in aggregations, and stability of mixed-species groups. Then, using focal group observational data, I investigated whether aggregations are food-based, considering the behavior of the 3 species of dolphins and sea lions during joint activities; whether dolphins and sea lions feed together at the same time; under which circumstances dolphins and sea lions associate and break apart; whether, based on surface observations, dolphins and sea lions use similar techniques during foraging and feeding activities; and whether mixed-species aggregations of dolphins and sea lions feed in specific locations in the bay. (Note: in this study, short-beaked common dolphins and long-beaked common dolphins are usually discussed together as common dolphins, considering their sympatry in the study area and the similarities in their behavioral patterns [see Bearzi 2005b].)

Seabirds are perhaps another important component of feeding activities of mixed groups of dolphins and sea lions. However, sea lions were recorded approaching dolphin schools in total absence of seabirds (birds were completely absent from the field of view during 10 of a total of 45 dolphin sightings where approach by 1 species was clearly observed), showing that sea lions may seek dolphins without using birds as a clue.

An ongoing study is investigating the role of seabirds in these mixed-species aggregations.

MATERIALS AND METHODS

Study area.—Santa Monica Bay (approximately 460 km^2; Fig. 1) is 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 bay contains 3 submarine canyons: Dume and Redondo canyons, which start in shallow waters (<50 m), and Santa Monica Canyon, which begins at a depth of about 100 m at the edge of the continental shelf. A shallow shelf between Santa Monica Canyon and Redondo Canyon extends as a plateau from the 50-m contour (Dartnell 2000). The typical depth is 60–70 m and the maximum depth is 400–500 m. Surface temperatures range from 11°C to 22°C (July–December: 16–22°C; January–June: 11–17°C).

Data collection and analyses.—Surveys were conducted from January 1997 to August 2001 (March–December 1997 and January–August 2001; no data were collected in December 1999, October 2000, and July 2001), with an average of 3.5 days on the water per month ($n = 201$) and a total of 52 h spent with pinniped and dolphin aggregations (Table 1).

Inshore (distance from shore < 500 m) and offshore (distance from shore > 500 m) routes were carried out in the morning and early afternoon usually with sea condition <2 on the Beaufort wind-force scale. Routes, planned for an even coverage of the bay throughout the study period, were covered from a 7-m-long power boat (1997–2000) and a 10-m-long power boat (2001) at an average speed of 18 km/h (Bearzi 2003).

Data were collected with laptop computers. When dolphins were spotted, species, number of animals, data on behavioral states and events, group formation, boat disturbance, and association with other species were recorded for 5-min periods throughout the sighting (Bearzi 2003; Table 2). Behavior of groups was studied using a focal-group following protocol with scan sampling (Altmann 1974; Mann 1999); animals were always scanned left-to-right or right-to-left from the beginning to the end of a school to include all individuals. Groups were always monitored for >25 min during a sighting and behaviors or individuals sampled were limited to those that could be reliably or consistently recorded (Mann 1999). The protocol included a decision rule to always stay with the larger group when 1 or more animals left the initial focal group.

Position and speed of dolphins were both estimated relative to the boat's position ± 30 m using a global positioning system (GPS, Garmin 76, Ramsey, Hampshire, United Kingdom). Sightings of sea lions during search for dolphins were recorded, with description of their behavioral states and events (Table 2), and GPS positions.

Groupings and activities were recorded. Groupings were categorized as being associations or aggregations. An association was defined as a grouping in which pinnipeds and dolphins were <100 m apart in a 5-min sampling period; when the individuals were about 1 m apart, it was categorized as a close association. An aggregation was defined as a continuous association between sea lions and dolphins for ≥10 min, with the 2 groups displaying similar activities during at least part of the sighting. Behavior was classified as states and events, defined following Altmann (1974).

Number of animals, behavior, and group formation were estimated when the boat was <50 m from a dolphin school. During mixed-species associations, data on type of aggregations (including behaviors displayed by each species during approach, interaction, and separation), distances between pinnipeds and dolphin focal group, and pinniped species and number were recorded. At least 10 min were

TABLE 1.—Number of boat surveys and summary of research effort in Santa Monica Bay, California, for the years 1997–2001.

Data collection parameters	1997	1998	1999	2000	2001	Total
Boat surveys						
Inshore (<500 m from shore)	5	17	12	6	4	44
Offshore (>500 m from shore)	23	3	5	4	4	39
Combined inshore and offshore	11	38	27	27	15	118
Total number of boat surveys	39	58	44	37	23	201
Research effort						
Hours spent with pinniped and dolphin aggregations	7	12	6	10	17	52
Hours spent with bottlenose dolphins and California sea lions	2	8	1	1	1	13
Hours spent with both species of common dolphins and California sea lions	3	4	5	9	16	37
Total n of 5-min behavioral samples collected	295	1,065	698	525	490	3,073

spent with the animals before defining an aggregation. Color photographs (transparencies) were taken with 35-mm Canon EOS1N and A2 cameras equipped with 75–300 mm lenses (Lane Success, New York, New York). During the sighting, researchers also videotaped the animals' behavior with a Canon Hi8mm Video Camcorder or Canon GL1 Digital Camcorder. Photos and videos were cataloged and reviewed for species identification and to determine the nature and length of aggregations. This study was conducted under the guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998). Fieldwork was carried out under the current laws of California and the General Authorization for Scientific Research issued by the National Oceanic and Atmospheric Administration (file 856-1366, Silver Spring, Maryland).

Responses to potential disturbance involving the research boat and the mixed-species aggregations also were considered. In a total of 76 aggregations, animals showed no response to the approach or pass-by of the boat in 88.2% of the sightings ($n = 67$); approach and bowride were observed in 7.9% and 3.9% of the sightings, respectively, whereas avoidance was never observed.

Data analyses were performed using Statview 5.02 (Statview Software, Cary, North Carolina), Statistica 6.0 (Statsoft, Orlando, Florida), and Grapher 3.02 (Golden Software, Golden, Colorado); data on species distribution were plotted with Arcview GIS 3.2 (ESRI, Redlands, California) and Surfer 6.02 (Rockware, Golden, Colorado) software. To analyze differences between group sizes of mixed-species aggregations versus dolphin school group sizes without sea lions, sightings were chosen to be independent. Only 1 sighting per day was considered to avoid pseudoreplication. Because variances of group sizes were large, statistical distributions of group sizes using the chi-square method were compared. To obtain patterns of statistical distribution, each sample was tabulated with intervals of 5. To establish correlations between behavior of the 3 dolphin species and behavior of sea lions during joint activities, a Spearman rank correlation on 4 subsets of data representing the 4 behavioral states was used.

To determine whether mixed-species aggregations fed in specific locations in the bay, a chi-square test was used to compare the number of sightings of aggregations near submarine canyons and escarpments, slopes, and bottom reliefs (considered areas of striking bathymetry) versus the number of sightings of aggregations near flat areas, plateaus, and inshore waters.

TABLE 2.—Definitions of the most important behavioral states and events, group formation, and boat disturbance (for the entire list of definitions see Bearzi [2003]).

Behavior	Description
Behavioral states	
Travel	Moving steadily in 1 direction during the 5-min sampling period
Diving	No steady directional movement; dives longer than 30 s occurring during the 5-min sampling period
Surface-feeding	Obvious feeding activities performed close to water surface (Shane 1990); dolphins often seen catching fish by pursuing them parallel to water surface or moving in circle and diving in same small area; birds usually concentrated over dolphins (Bearzi et al. 1999) during the 5-min sampling period
Socializing	Some or all group members in almost constant physical contact with one another and often displaying surface behaviors; no steady directional movement (Shane 1990) during the 5-min sampling period
Playing	Any activity that incorporates use of a foreign object during the 5-min sampling period
Additional categories used to describe pinniped behavior	
Swimming	Moving without a precise direction at any speed and without leaping
Resting	Nostrils at or close to the surface; body sloping downward at an angle, rising to surface to breathe
Thermoregulating	Hind and foreflippers extend above surface or any other hind- or foreflipper position extend above surface but not as in jugging
Porpoising	Leaping from water in a shallow arch, reentering headfirst (Peterson and Bartholomew 1967)
Bottling	A posture sometimes assumed by a pinniped resting in water: head extended above surface while rest of body submerged vertically under water
Jugging	Both hind flippers and 1 foreflipper extend above surface (Riedman 1990)
Following fishing boat	Following fishing boat while trawling at 0−300 m from stern
On buoys, on rocks	Thermoregulation, resting, or other behavior displayed on buoys
Behavioral events (aerial behavior—from Weaver 1987)	
Head up	Exposure of foresection of body at surface in a near-vertical or vertical position, remaining briefly stationary
Leap	Airborne forward progress of at least 1 body length while in dorsal position (but repetitive instances of leaping are referred to as porpoising)
Spyhop	Brief vertical or near-vertical elevation of the body with head-up exposure of foresection
Swims	Swims through water
Porpoising	Repetitive performance of abrupt lunges over water surface between shallow submergences during rapid forward progress in dorsal position
Group formation (modified from Shane 1990)	
Tight	Dolphins generally <1 body length apart
Loose	Dolphins generally 1−5 body lengths apart
Dispersed	Dolphins generally >5 body lengths apart
Variable	Dolphins irregularly spread; or a group that meet >1 of above criteria
Convergent	Joining of ≥1 subgroups to the focal group
Boat disturbance (modified from Würsig et al. 1998)	
Avoidance	Animals move away from vessel or appear to dive in response to vessel
No response	Animals show no apparent response relative to approach or pass-by of vessel
Approach	Animals move toward vessel during at least part of observation period
Bowride	Special case of an approach response (animals swim near bow of the boat)

RESULTS

Field effort and number of sightings.—In 249 h observing 314 groups of dolphins encountered during 305 sightings, 52 h (20.9% of total time) were recorded observing aggregations of dolphins and sea lions (Table 1). On average, 28 min (range = 10–60 min) were spent with bottlenose dolphin and sea lion aggregations and 45 min (range = 10–305 min) were spent with both common dolphin species and sea lion aggregations.

Bottlenose dolphins were the most frequently sighted species, followed by the 2 species of common dolphins (Table 3). Bottlenose dolphins were sighted in 49.2% of the total sightings

($n = 150$); short-beaked common dolphins and long-beaked common dolphins were both seen in 32.1% of the total sightings ($n = 98$). The California sea lion was the most abundant pinniped in the bay (77.8%, $n = 957$), followed by the Pacific harbor seal (*Phoca vitulina richardsi*) and the northern elephant seal (*Mirounga angustirostris*), sighted in 18.6% ($n = 178$) and 0.6% ($n = 6$) of the observed cases, respectively.

Species of pinnipeds and dolphins found in aggregations and number of animals involved in aggregations.—In Santa Monica Bay, sea lions are regularly found with bottlenose dolphins and 2 species of common dolphins year-round; these aggregations occur for a longer duration than expected by

TABLE 3.—Number of dolphin sightings, sea lion sightings, associations and aggregations in Santa Monica Bay.

Counts and frequencies	1997[a]	1998	1999	2000	2001[a]	Total
No. dolphin sightings[b]	41	108	66	54	36	305
No. common dolphin[c] sightings	10	26	24	23	15	98
Common dolphin sighting frequency (sightings/h)	0.07	0.12	0.14	0.15	0.15	0.12
Short-beaked common dolphin						
No. sightings	6	7	6	6	7	30
Sighting frequency (sightings/h)	0.04	0.03	0.03	0.04	0.07	0.04
Long-beaked common dolphin						
No. sightings	2	13	11	10	5	41
Sighting frequency (sightings/h)	0.01	0.06	0.06	0.07	0.05	0.05
No. bottlenose dolphin sightings	19	61	33	24	13	150
Bottlenose dolphin sighting frequency (sightings/h)	0.13	0.27	0.19	0.16	0.13	0.19
No. pinnipeds counted during search for dolphins[d]	172	332	135	245	73	957
No. California sea lions	150	299	115	109	72	745
No. California sea lion sightings during dolphin sightings (at >100 m)[e]	20	69	32	32	27	180
No. pinniped and dolphin associations (at <100 m)[f]	16	61	31	30	26	164
No. bottlenose dolphin and sea lion associations	5	37	7	4	3	56
No. common dolphin and sea lion associations	6	12	15	17	20	70
No. other dolphins and sea lion associations	5	4	1	4	1	15
No. pinniped and dolphin aggregations[g,h]	12	28	16	13	12	81
No. bottlenose dolphin and sea lion aggregations	4	18	4	1	1	28
No. common dolphin and sea lion aggregations	6	7	10	11	11	45
No. other dolphins and sea lion aggregations	2	3	1	1	0	7

[a] 1997, from May to December (only for pinnipeds observations); 2001 from January to August.
[b] One mixed-species school is counted as 1 sighting.
[c] Individuals not recognized at species level.
[d] Generic pinnipeds not recognized at species level.
[e] California sea lion was the only pinniped observed during dolphin sightings at >100 m. Numbers refer to effective sightings that may have had >1 animal.
[f] Associations of dolphins with harbor seals.
[g] Aggregations of dolphins with harbor seals.
[h] One dolphin sighting may have had >1 aggregation with pinnipeds. Only 1 aggregation with pinnipeds per day was considered to avoid pseudoreplication.

chance (Table 3). Results for associations and aggregations are presented separately.

Pinnipeds were found in association with dolphins in 164 of the observed cases (53.8% of 305 dolphin sightings) in the years 1997–2001; of these, 28.0% were close associations. The pinniped species seen most often in association was the California sea lion (86.0%, n = 141), followed by the Pacific harbor seal (14.0%, n = 23). Elephant seals were never observed in association with dolphins. California sea lions were associated primarily with the 2 species of common dolphins and secondarily with bottlenose dolphins. Of a total of 98 sightings of the 2 species of common dolphins, sea lions were found in association during 70 (71.4%) of the total sightings; of a total of 150 bottlenose dolphin sightings, sea lions were associated during 56 (37.3%) of the total sightings (Table 3).

In the years 1997–2001, 81 aggregations that included both dolphins and pinnipeds were observed (26.6% of the total 305 dolphin sightings). Of a total of 98 sightings of short-beaked common dolphins and long-beaked common dolphins, sea lions were found in aggregations during 45 of the total sightings (45.9%); of a total of 150 bottlenose dolphin sightings, sea lions were seen in aggregations during 28 of the total sightings (18.6%; Table 3). Pacific harbor seals were rarely sighted in aggregations with bottlenose dolphins (1.2%, n = 1), and never observed in aggregation with the 2 species of common dolphins.

Stability of mixed-species groups.—Mixed groups of dolphin species and sea lions in associations and aggregations were present year-round over the entire study period (Fig. 2). Average group sizes observed for dolphins in associations and aggregations with sea lions are listed in Table 4. Sea lions
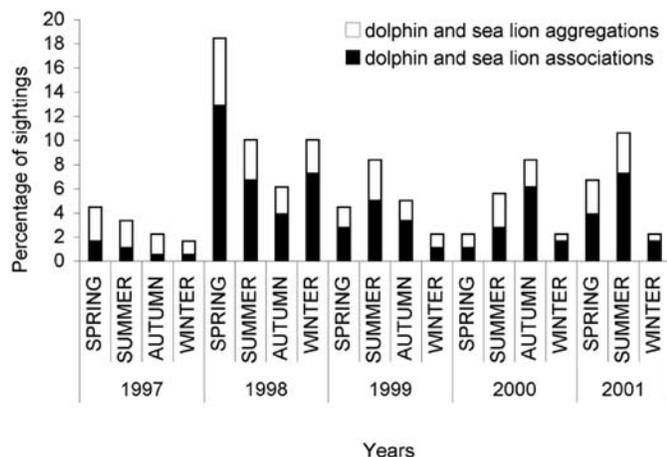
Fig. 2.—Seasonal distribution of dolphins associated and in aggregations with California sea lions in 1997–2001. Data on the 3 species of dolphins were combined to simplify the figure. Percentage of sightings was divided into 4 seasonal categories: winter (December–February), spring (March–May), summer (June–August), and autumn (September–November).

observed in absence of dolphins had a mean group size that was between group sizes observed for aggregations and associations (sea lion mean group size = 2.09, range = 1–50, n = 741 sea lion sightings in absence of dolphins). For bottlenose dolphins, a significant difference was observed between group sizes of mixed-species aggregations versus dolphin school group sizes without sea lions (χ^2 = 59.16, $d.f.$ = 5, P < 0.0001; normalized and tabulated with intervals of 5), with larger group sizes observed for animals in aggregations. For short-beaked and long-beaked common dolphins, no significant difference was observed between group sizes of mixed-species aggregations versus dolphin school group sizes without sea lions (χ^2 = 9.80, $d.f.$ = 20, P < 0.97; normalized and tabulated with intervals of 25).

A significant difference was observed between group sizes of California sea lions found in aggregations with dolphins (Table 4) versus California sea lions not observed in aggregations ($\bar{X}$ = 3.51, t = 4.43, $d.f.$ = 84, P < 0.001), with aggregations of these animals showing larger group sizes. Of a total of 73 aggregations, the group size of sea lions changed substantially during each of 68 observation periods (93.1% of the observed cases). Mean group size for sea lions was 4.5 animals during 26 mixed-species aggregations (35.6% of the observed cases). An increase in sea lion group size from

TABLE 4.—Group sizes of dolphins and sea lions found in aggregations or associations in the years 1997–2001.

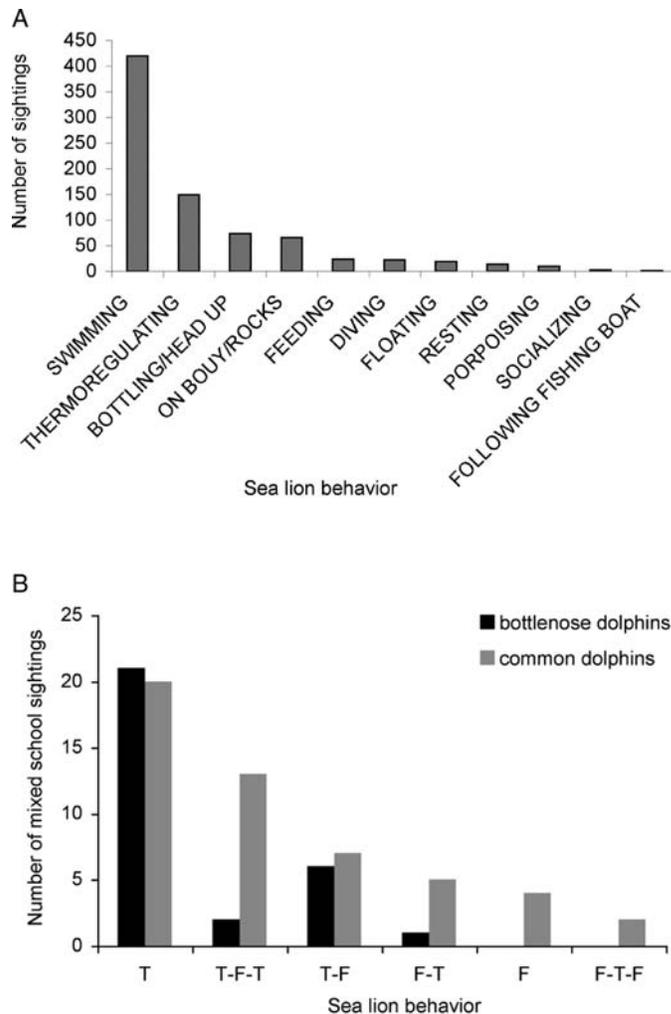|	Aggregations			Associations[a]		
Species	$\bar{X} \pm SE$	Range	n	$\bar{X} \pm SE$	Range	n
California sea lion	4.51 ± 0.79	1–50	85	1.43 ± 0.19	1–9	46
Bottlenose dolphin	11.31 ± 0.90	3–25	29	9.57 ± 0.67	1–40	99
Common dolphin species	84.06 ± 12.45	3–500	50	76.47 ± 16.47	1–570	38

[a] Associations do not include aggregation data.

Fig. 3.—A) Behaviors of California sea lions in the absence of dolphins in 1997–2001. B) Behaviors of sea lions in aggregations with bottlenose dolphins and common dolphins. Abbreviations: T = traveling, F = surface-feeding. T-F-T, T-F, and F-T indicate sequences of behavioral states. (Single behavioral states and behavioral state sequences are mutually exclusive categories.)

the beginning to the end of sightings was observed, with a range of 1–35 sea lions joining the schools.

Mean duration of a dolphin school sighting was 74.73 min (SE = 6.24, range = 10–270 min, n = 76) and mean length of a mixed-species sighting was 37.17 min (SE = 4.59, range = 10–270 min, n = 76). Sea lions were seen together with dolphins for more than half of dolphin sightings (55.7% of the time, n = 76).

Behavior of the 3 species of dolphins and sea lions during joint activities.—Behavior of sea lions in aggregation with dolphins was analyzed to determine correlations of behavior of sea lions with behavior of dolphins during the most frequently observed behavioral states: diving, traveling, surface-feeding, and socializing. Sea lions and dolphins did not show a statistical correlation of behaviors during short-term associations in the 4 behavioral states, except for travel (Spearman's R = 0.52, $d.f.$ = 1.94, P < 0.05, n = 12). In aggregations, however, these species displayed a high and significant correlation during 3 of 4 activities (surface-feeding: Spearman's R = 0.80, $d.f.$ = 11.70,

$P < 0.001$, $n = 81$; traveling: Spearmans's $R = 0.77$, $d.f. = 10.724$, $P < 0.001$, $n = 81$; socializing: Spearman's $R = 0.42$, $d.f. = 0.37$, $P > 0.05$, $n = 81$; diving: Spearman's $R = 0.35$, $d.f. = 3.36$, $P < 0.001$, $n = 81$). Sea lions, in the absence of dolphins, spent most of their time swimming (52.0% of the sightings, $n = 807$ sea lion sightings in absence of dolphins) and thermoregulating (18.5% of the sightings; Fig. 3A). They were occasionally observed diving (2.7%), surface-feeding (2.9%), and socializing (0.4%).
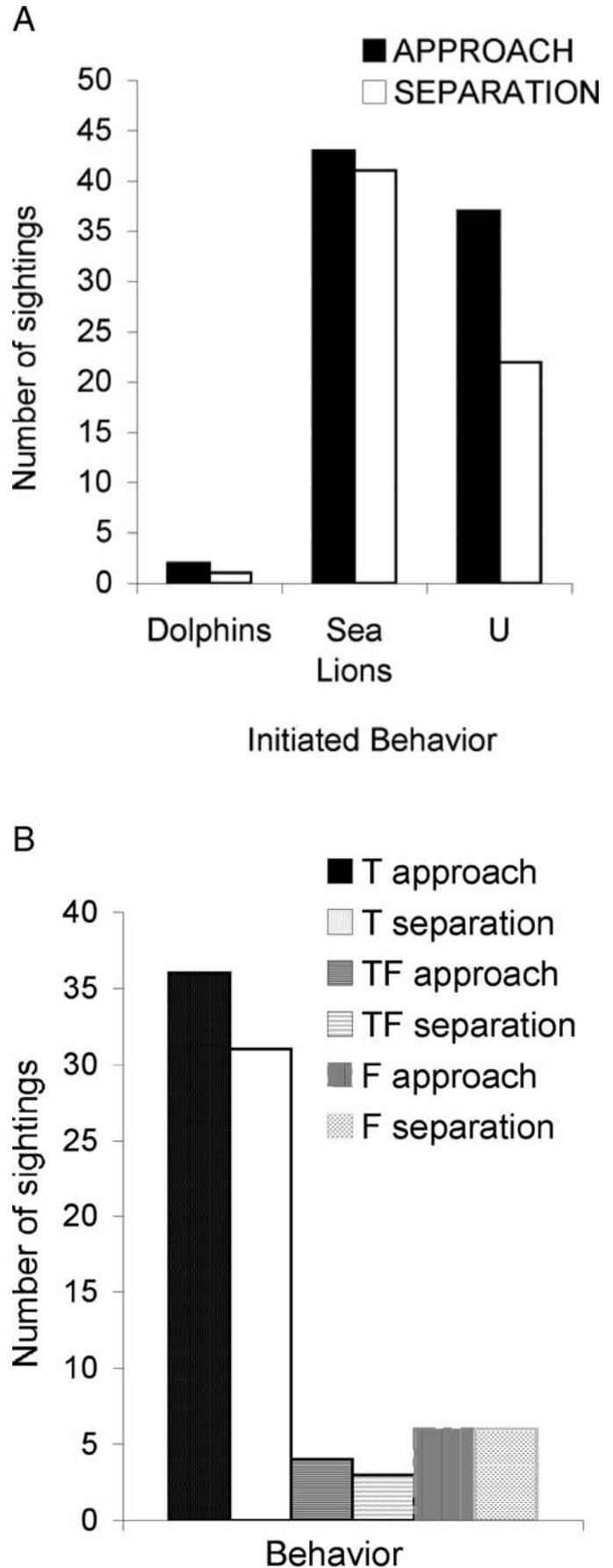
Do dolphins and sea lions feed together at the same time?— Sea lions and dolphins were observed feeding at the same time. Sea lions were observed spending a similar amount of time traveling together with bottlenose dolphins and both common dolphin species (bottlenose dolphins: 27.4% of sighting time; short-beaked common dolphins and long-beaked common dolphins: 28.8% of sighting time). Of a total of 73 mixed-species sightings, sea lions were found surface-feeding or in combined feeding and traveling activities with dolphins 54.8% of the observed cases showing a significant amount of time spent in these activities in comparison to sea lion groups observed feeding alone (2.9%; Figs. 3A and 3B). From surface observations and video analysis, sea lions were clearly seen to start surface-feeding activities in synchrony with dolphins 81.6% of the observed cases ($n = 49$ sightings).

Single and sequential behavioral states displayed by sea lions in aggregations with bottlenose dolphins and the 2 species of common dolphins during traveling and surface-feeding activities are shown in Fig. 3B. California sea lions were seen spyhopping and raising the head out of the water (head up) while following a dolphin school in 83.6% of the observed cases (58.9% with the 2 species of common dolphins; 24.6% with bottlenose dolphins, $n = 73$ observations). During observations of aggregations, sea lions also were seen changing their behavioral states in synchrony with dolphin schools and displaying behaviors similar to the dolphins in 89.0% of the observed cases ($n = 73$ observations).

Circumstances under which dolphins and sea lions associate and break apart.—Sea lions appeared to both initiate and terminate aggregations with dolphins. Video behavioral sequence analyses for the bay show that sea lions tend to approach dolphins mostly during traveling and that dolphins usually do not approach or separate from sea lions.

Of a total of 45 dolphin sightings where approach by 1 species was clearly observed, sea lions moved toward dolphins in 95.5% of the observed cases. Similar results were observed for separation, with sea lions moving away from dolphins in 97.6% of the observed cases ($n = 42$; Fig. 4A).

It was mostly during traveling that sea lions approached dolphins and separated from them (80.0% and 73.3% of

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FIG. 4.—Approaches to ($n = 82$) and separations from ($n = 64$) groupings of dolphins and sea lions, showing A) which group initiated approaches and separations, and B) behaviors observed during approaches and separations. Abbreviations: U = not known whether it was a dolphin or a sea lion that initiated approaches and separations, T = traveling, TF = travel-feeding, F = surface-feeding activities.

TABLE 5.—Number of sightings of bottlenose dolphins and common dolphins in aggregation with sea lions during surface-feeding activities in relation to bottom topography of Santa Monica Bay, California. Submarine canyons include sightings located ≤0.4 km from each side of the canyons and isobaths, and bottom reliefs and slopes include those ≤1.6 km from centers of slopes. Flat areas and plateaus include all the sightings observed in these locations.

Bottom topography	Bottlenose dolphins and sea lions	Common dolphins and sea lions	Total
Submarine canyons			
Dume	0	0	0
Santa Monica	5	6	11
Redondo	5	6	11
Escarpments, slopes, and bottom reliefs	7	12	19
<500 m from shore	19	0	19
Plateau ("short bank")	2	0	2
Other flat areas in Santa Monica Bay	2	4	6

observations, respectively); approach and separation during travel-feeding and feeding activities was seldom observed (respectively 7.1% and 9.5% for approach and separation during travel-feeding, and 14.3% for both approach and separation during feeding; Fig. 4B).

Do dolphins and sea lions use similar techniques during foraging and feeding activities?—Based on surface observations of feeding activities during 7 mixed-species aggregations with bottlenose dolphins, California sea lions displayed the same behavior as dolphins with dives concentrated exclusively where prey was encircled. California sea lions observed during surface-feeding activities in 37 mixed-species aggregations with common dolphins also were seen skimming to catch the prey in synchrony with dolphins (16.2%) and displaying similar diving patterns. During feeding activities in aggregations, California sea lions always were seen extending the head above the surface at least once during each sighting. On a total of 73 mixed-species sightings, aggressive behavior among these marine mammal species was never observed at or near the surface. Opportunistic observations using an underwater video camera during feeding activities of mixed-species groups seemed to support the lack of aggressive behavior among these animals.

Do mixed-species aggregations of dolphins and sea lions feed in specific locations in the bay?—Distribution and number of sightings of the 4 species in aggregations during surface-feeding activities and in relation to the bathymetry of the bay illustrate that these aggregations show a preference for canyons and slopes (Fig. 1; Table 5). A significant difference between number of sightings of aggregations of feeding dolphins and sea lions in proximity of submarine canyons and escarpment, slopes, bottom reliefs versus the number of sightings of aggregations of feeding dolphins and sea lions near flat areas, plateaus, and inshore waters was observed ($\chi^2 = 27.96$, $d.f. = 5$, $P < 0.001$), with aggregations showing a preference for canyons and slopes. Aggregations of bottlenose dolphins and sea lions at less than 500 m from shore were frequently seen

(27.9%, $n = 68$ sightings) but neither common dolphin species were observed in aggregations with sea lions in inshore waters. No significant difference in number of aggregations with sea lions and bottlenose dolphins versus aggregations with sea lions and both common dolphin species was observed in proximity of canyons, slopes, and escarpments ($t = 1.58$, $d.f. = 3$, P 0.05).

DISCUSSION

Species of pinnipeds and dolphins found in aggregations, number of animals involved in aggregations, and stability of aggregations.—In Santa Monica Bay, sea lions are regularly found with the 3 species of dolphins year-round. These aggregations seem to have a functional advantage for at least 1 of the species. Average group sizes observed for the 3 dolphin species in aggregations with sea lions are larger in comparison to those observed for dolphin schools with no sea lions; sea lions also tend to be found in larger groups during aggregations with dolphins.

Dolphins typically live in schools that are not permanent units of a specific size (Norris and Dohl 1980). The term fission–fusion is used to include those societies in which individuals form temporary groups that frequently aggregate or separate into bigger or smaller units (Wilson 1977). The definition of fission–fusion society usually refers to animals such as the bottlenose dolphin and the common dolphins with a low predatory pressure that use patchy food resources variable in space and time (Scott and Cattanach 1998). These fluid societies of dolphins—like the societies of other mammal species such as primates—allow individuals to select their group size and habitat depending on activity and ecological conditions (Gygax 2002; Stensland et al. 2003). Dolphin species that inhabit open areas with patchy resources usually form large groups (Scott and Cattanach 1998; Wells et al. 1999; Zemel and Lubin 1995) and opportunities for multispecies aggregations of marine mammals at sea increase where prey and habitat overlap (Norris and Dohl 1980).

A variety of advantages of foraging in a group have been suggested for many species (see Stensland et al. [2003] for list of species) including dolphins (Kenney 1990; Norris and Prescott 1961; Scott and Chivers 1990). A high concentration of food can facilitate the fusion of different social units for mutual protection and prey detection until the resource is reduced or exploited. In contrast, a more uniform food distribution and a smaller amount of prey may induce competition among conspecifics for limited resources (Weller 1991; Würsig 1986).

Like dolphins, sea lions are particularly flexible in their foraging strategies; they can forage alone or in cooperative groups depending on type and distribution of food resources (Riedman 1990; Wells et al. 1999). Sea lions feed in bigger groups in presence of large fish schools and when resources are patchily distributed (Fiscus and Baines 1966).

Behavior of the 3 species of dolphins and sea lions during joint activities.—Sea lions were frequently seen raising their heads out of the water, spyhopping, and adjusting their routes to locate and track dolphin schools; leaping behavior also was

adopted by sea lions in the study area to approach common dolphins that had suddenly increased their speed in pelagic waters. Aggression between sea lions and dolphins was never observed at or near the surface in the study area, as also reported by Gallo Reynoso (1991) for short-beaked common dolphins and sea lions in the Gulf of California.

Do dolphins and sea lions feed together at the same time?— In Santa Monica Bay, dolphins and sea lions were observed feeding together at the same time. Pinniped groups are known for foraging with feeding dolphins and seabirds. Common dolphins are most frequently observed feeding in association with sea lions (*Zalophus*) and harbor seals (*P. vitulina*—Gallo Reynoso 1991; Wells et al. 1981), followed by bottlenose dolphins, Pacific white-sided dolphins (*Lagenorhynchus obliquidens*), and dusky dolphins (*Lagenorhynchus obscurus*— Leatherwood 1975; Würsig and Würsig 1980). Tarasevich (1957) suggests that aggregations tend to form when 2 species feed on the same prey resources. In southern California waters, mixed-feeding schools often prey on anchovies or squid schools, as reported by Norris and Dohl (1980). In these waters, the California sea lion feeds opportunistically on a variety of prey items and shows several diet similarities that overlap with the most common prey consumed by the 2 common dolphin species and bottlenose dolphins, also known as opportunistic species (Antonelis et al. 1984; see Bearzi [2003] for list of prey species consumed by the 4 marine mammal species and the degree of overlap in diet). The overlap in prey items commonly found in the Southern California Bight (California Department of Fish and Game 2000) is reflective of the formation of mixed-feeding aggregations in the study area, as suggested by Tarasevich (1957).

Circumstances under which dolphins and sea lions associate and break apart.—Sea lions' initiation and termination of foraging and feeding with dolphins does not necessarily provide compelling evidence that they "seek" dolphins considering that the foraging range of different species may overlap when food is abundant and available. However, several important factors suggest that sea lions may take advantage of the ability of the 3 species of dolphins to locate food in Santa Monica Bay and that these encounters are not casual, including the amount of time spent by sea lions following dolphins (not vice versa) during traveling before the commencement of feeding activities, the frequent use by sea lions of spyhopping and head-up behaviors for route adjustments when following dolphins (apparently to avoid losing them), and the time spent together feeding (in comparison to the time that sea lions dedicate to feeding activity when they are not in mixed-species groups). Sea lions join a dolphin school during traveling, exploit the same or similar food resources, and break away from dolphins immediately after feeding.

Do dolphins and sea lions use similar techniques during foraging and feeding activities?—In Santa Monica Bay, sea lions in aggregations with dolphins were observed encircling their prey and diving at depth like bottlenose dolphins, but they were also seen adopting other hunting techniques such as pursuing schooling fish close to the surface and skimming to snatch the prey, a method frequently used by both species of

common dolphins in the study area. Similar opportunistic observations where sea lions and porpoises adopt similar techniques are reported by Fink (1959) for aggregations of harbor porpoises (*Phocoena phocoena*) and California sea lions, in which porpoises continually encircle sardine schools keeping the prey concentrated, whereas sea lions attack the periphery of the school.

Do mixed-species aggregations of dolphins and sea lions feed in specific locations in the bay?—The distribution of the 4 species in mixed-species aggregations during surface-feeding activities is related to the bathymetry of the bay and it reflects the habitat preference of the odontocete component of the mixed-species groups (Bearzi 2005c), showing that dolphins are the primary factor affecting the observed distribution. Mixed-species aggregations of bottlenose dolphins and sea-lions occur most commonly in feeding areas located in inshore waters, near Santa Monica and Redondo canyons and slopes, versus flat areas and plateaus. Aggregations of common dolphins and sea lions are absent along shore but show the same preference for feeding grounds located near the 2 canyons and slopes versus flat areas and the continental shelf plateaus.

Presumably, the high concentration of mixed-species aggregations in proximity to these canyons and the continental slope is associated with the striking bathymetry of these regions, optimal locations for coastal upwelling and mixing of nutrients and, consequently, areas rich in prey for marine mammals (Bearzi 2003). Anchovies (*Engraulis mordax*), a common prey of short-beaked common dolphin in the Bight (Evans 1975), for instance, are known to concentrate in areas of upwelling and mixing of nutrients (Hui 1979; Mais 1974). Common dolphins in other areas around the world are known to take advantage of productive areas of upwelling (Gaskin 1992) and other marine mammal multispecies aggregations along seafloor relief, submarine canyons, and escarpments are known (Gowans and Whitehead 1995; Hui 1979; Selzer and Payne 1988). The interannual differences of dolphins associated and in aggregations with sea lions observed during the study period seem to reflect the general distribution of dolphins observed for the years 1997–2001 (Bearzi 2003), with a higher presence of animals in 1998.

Do sea lions take advantage of the superior ability of dolphins to locate food?—Functional explanations for the formation of mixed-species groups usually include 2 categories: foraging advantages and predator avoidance. In this study, aggregations seem to occur for foraging advantages for at least 1 of the participating species.

It is difficult to know whether association is best classified as parasitic, commensalistic, or symbiotic, but my observations in Santa Monica Bay seem in accord with the social parasitism concept developed by Norris and Prescott (1961), where many species are thought to associate with other species with superior food-locating abilities (Norris and Dohl 1980; Shane 1994). Riedman (1990) and Würsig et al. (1994) invoke social parasitism as an explanation for those species that are able to locate food, and for other species, such as pinnipeds, birds, tuna, or dolphins, that join the original feeders. Gallo Reynoso

(1991) reported that sea lions gain benefit from cooperative feeding with dolphins.

In Santa Monica Bay, sea lions may take advantage of the prey-detection ability of dolphins and use their visual clues to locate dolphins in the open ocean. This may explain the occurrence of frequent spyhop and head-up behaviors displayed by sea lions when looking for dolphins as well as leaping behavior, perhaps used not only to increase speed but also to gain a better viewing perspective. Dolphins use echolocation as a principal means of locating prey (Norris 1969). Pinnipeds cannot hear the echolocation clicks of dolphins (Richardson et al. 1995) but they can see well in air and water (Schusterman 1972). Sea lions are thought to use vision to orient and locate their prey (Levenson and Schusterman 1997, 1999) and actively search prey patches (Feldkamp et al. 1989). Animals in the pursuit of food may learn from others the location of food that occurs in unpredictable patches that are large enough to be shared (Ward and Zahavi 1973).

This paper does not discuss the possibility that sea lions may actively follow bird aggregations instead of dolphins to find food. In fact, sea lions were observed approaching dolphins in the complete absence of seabirds, which supports the hypothesis that sea lions may take advantage of the prey-detection ability of dolphins.

Sea lions in Santa Monica Bay seem to gain more significant advantages than do dolphins from aggregation with dolphin schools, but dolphins may also profit by sharing resources, considering that aggression between these species was never observed at or near the surface. A high presence of predators in a feeding ground rich in prey can, for instance, encourage the prey schooling behavior, facilitating the capture of food for both predators (Magurran 1990; Norris and Johnson 1994; Similä and Ugarte 1993). Pinnipeds also may use vision to locate prey by watching for bird aggregations (Riedman 1990). Dolphins may hear the pinnipeds and join them. Even if dolphins only occasionally join sea lions, it may still be to their advantage to be cooperative.

Did the mixed-species groups in the bay form for gaining antipredator advantages?—The defense of feeding grounds or food patches also may favor group formation, enhancing protection from predators such as sharks (Dolby and Grubb 1998; Norris and Schilt 1988; Scott and Cattanach 1998). However, predator presence must be relatively high in order for the mixed-species aggregations to be formed for antipredatory reasons (Stensland et al. 2003). In Santa Monica Bay, the presence of predators near mixed-species aggregations was never observed from the surface (Bearzi 2003), excluding the predator-avoidance hypothesis.

ACKNOWLEDGMENTS

LITERATURE CITED

ALTMANN, J. 1974. Observational study of behavior: sampling methods. Behaviour 49:227–267.

ANIMAL CARE AND USE COMMITTEE. 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. Journal of Mammalogy 79:1416–1431.

ANTONELIS, G. A., JR., C. H. FISCUS, AND R. L. DELONG. 1984. Spring and summer prey of California sea lions, *Zalophus californianus*, at San Miguel Island, California, 1978–79. Fishery Bulletin 82:67–76.

ANTONELIS, G. A., B. S. STEWART, AND W. F. PERRYMAN. 1990. Foraging characteristics of female northern fur seals (*Callorhinus ursinus*) and California sea lions (*Zalophus californianus*). Canadian Journal of Zoology 68:150–158.

AU, D. W. K., AND W. L. PERRYMAN. 1985. Dolphin habitats in the eastern tropical Pacific. Fishery Bulletin 83:623–643.

BEARZI, M. 2003. Behavioral ecology of the marine mammals of Santa Monica Bay, California. Ph.D. dissertation, University of California, Los Angeles.

BEARZI, M. 2005a. Aspects of the ecology and behaviour of bottlenose dolphins (*Tursiops truncatus*) in Santa Monica Bay, California. Journal of Cetacean Research and Management 7:75–83.

BEARZI, M. 2005b. Dolphin sympatric ecology. Marine Biology Research 1:165–175.

BEARZI, M. 2005c. Habitat partitioning by three species of dolphins in Santa Monica Bay, CA. Southern California Academy of Science Bulletin 104:113–124.

BEARZI, G., E. POLITI, AND G. NOTARBARTOLO DI SCIARA. 1999. Diurnal behavior of free-ranging bottlenose dolphins in the Kvarnerić (northern Adriatic Sea). Marine Mammal Science 15:1065–1097.

BONNELL, M. L., AND M. D. DAILEY. 1993. Marine mammals. Pp. 604–681 in Ecology of the Southern California Bight (M. D. Dailey, D. J. Reish, and J. W. Anderson, eds.). University of California Press, Berkeley.

BONNELL, M. L., AND R. G. FORD. 1987. California sea lion distribution: a statistical analysis of aerial transect data. Journal of Wildlife Management 51:13–20.

BRUNO, S. 2001. Il metodo della fotoidentificazione applicato allo studio della struttura sociale del delfino comune (*Delphinus delphis* Linneo, 1758) nel Mar Ionio orientale. B.A. thesis, Universita' degli Studi di Padova, Padova, Italy.

CALIFORNIA DEPARTMENT OF FISH AND GAME. 2000. Review of some California fisheries from 1999: market squid, dungeness crab, sea urchin, prawn, abalone, groundfish, swordfish and shark, ocean salmon, nearshore finfish, Pacific sardine, Pacific herring, Pacific mackerel, reduction, white seabass, and recreational. Report California Cooperative Oceanic Fisheries Investigations (CalCOFI) 41:8–25.

COCKCROFT, V. G., AND V. M. PEDDEMORS. 1990. Seasonal distribution and density of common dolphins *Delphinus delphis* off the southeast coast of southern Africa. South African Journal of Marine Science 9:371–377.

CONNOR, R. C., R. S. WELLS, J. MANN, AND A. J. READ. 2000. The bottlenose dolphin: social relationships in a fission–fusion society. Pp. 91–126 in Cetacean societies: field studies of dolphins and whales (J. Mann, R. C. Connor, P. L. Tyack, and H. Whitehead, eds.). University of Chicago Press, Chicago, Illinois.

DARTNELL, P. 2000. Predicted seafloor facies of central Santa Monica Bay, California. Report for Santa Monica Bay Restoration Project

and Foundation. United States Geological Survey, Menlo Park, California.

DEFRAN, R. H., AND D. W. WELLER. 1999. Occurrence, distribution, site fidelity, and school size of bottlenose dolphins (*Tursiops truncatus*) off San Diego, California. Marine Mammal Science 15:366–380.

DEFRAN, R. H., D. W. WELLER, D. L. KELLY, AND M. A. ESPINOSA. 1999. Range characteristics of Pacific coast bottlenose dolphins (*Tursiops truncatus*) in the Southern California Bight. Marine Mammal Science 15:381–393.

DOLBY, A. S., AND T. C. GRUBB, JR. 1998. Benefits to satellite members in mixed-species foraging groups: an experimental analysis. Animal Behaviour 56:501–509.

EVANS, W. E. 1975. Distribution, differentiation of populations, and other aspects of the natural history of *Delphinus delphis* Linnaeus in the northeastern Pacific. Ph.D. dissertation, University of California, Los Angeles.

EVANS, W. E. 1994. Common dolphin, white-bellied porpoise *Delphinus delphis* Linnaeus, 1758. Pp. 191–224 in Handbook of marine mammals. Vol. 5 (S. H. Ridgway and R. Harrison, eds.). Academic Press, San Diego, California.

FELDKAMP, S. D., R. L. DELONG, AND G. A. ANTONELIS. 1989. Diving patterns of California sea lions, *Zalophus californianus*. Canadian Journal of Zoology 67:872–883.

FINK, B. D. 1959. Observation of porpoise predation on a school of Pacific sardines. California Fish and Game 45:216–217.

FISCUS, C. H., AND G. A. BAINES. 1966. Food and feeding behavior of Steller and California sea lions. Journal of Mammalogy 47:195–200.

FRANTZIS, A., AND D. L. HERZING. 2002. Mixed-species associations of striped dolphins (*Stenella coeruleoalba*), short-beaked common dolphins (*Delphinus delphis*) and Risso's dolphins (*Grampus griseus*) in the Gulf of Corinth (Greece, Mediterrenean Sea). Aquatic Mammals 28:188–197.

GALLO REYNOSO, J. P. 1991. Group behavior of common dolphins (*Delphinus delphis*) during prey capture. Anales Instituto de Biologia, Universidad Nacional Autonoma de Mexico, Mexico, Series Zoologica 62:253–262.

GASKIN, D. E. 1992. Status of the common dolphin, *Delphinus delphis*, in Canada. Canadian Field-Naturalist 106:55–63.

GOWANS, S., AND H. WHITEHEAD. 1995. Distribution and habitat partitioning by small odontocetes in the Gully, a submarine canyon on the Scotian Shelf. Canadian Journal of Zoology 73:1599–1608.

GYGAX, L. 2002. Evolution of group size in the superfamily Delphinodea (Delphinidae, Phocoenidae and Monodontidae); a quantitative comparative analysis. Mammal Review 32:295–314.

HEYNING, J. E., AND W. F. PERRIN. 1994. Evidence for two species of common dolphins (genus *Delphinus*) from the eastern north Pacific. Contributions in Science, Natural History Museum of Los Angeles County 442:1–35.

HUI, C. A. 1979. Undersea topography and distribution of dolphins of the genus *Delphinus* in the Southern California Bight. Journal of Mammalogy 60:521–527.

KENNEY, R. D. 1990. Bottlenose dolphins off the northeastern United States. Pp. 369–386 in The bottlenose dolphin (S. Leatherwood and R. R. Reeves, eds.). Academic Press, San Diego, California.

KLINOWSKA, M. 1991. Dolphins, porpoises and whales of the world: the IUCN red data book. IUCN, Gland, Switzerland.

LEATHERWOOD, S. 1975. Some observations of feeding behavior of bottle-nosed dolphins (*Tursiops truncatus*) in the northern Gulf of Mexico and (*Tursiops* cf *T. gilli*) off southern California, Baja California, and Nayarit, Mexico. Marine Fisheries Review 37:10–16.

LEVENSON, D. H., AND R. J. SCHUSTERMAN. 1997. Pupillometry in seals and sea lions: ecological implications. Canadian Journal of Zoology 75:2050–2057.

LEVENSON, D. H., AND R. J. SCHUSTERMAN. 1999. Dark adaptation and visual sensitivity in shallow and deep-diving pinnipeds. Marine Mammal Science 15:1303–1313.

LOWRY, M. S., C. W. OLIVER, C. MACKY, AND J. B. WEXLER. 1990. Food habits of California sea lions *Zalophus californianus* at San Clemente Island, California, 1981–86. Fishery Bulletin 88:509–521.

LUKOSCHEK, V., AND M. I. MCCORMICK. 2002. A review of multi-species foraging associations in fishes and their ecological significance. Proceedings of the 9th International Coral Reef Symposium 1:467–474.

MAGURRAN, A. E. 1990. The adaptive significance of schooling as an anti-predator defense in fish. Annales Zoologici Fennici 27:51–66.

MAIS, F. 1974. Pelagic fish surveys in the California current. California Department of Fish and Game Fish Bulletin 162:1–79.

MANN, J. 1999. Behavioral sampling methods for cetaceans: a review and critique. Marine Mammal Science 15:102–122.

MORSE, D. H. 1970. Ecological aspects of some mixed species foraging flocks of birds. Ecological Monographs 40:119–168.

MORSE, D. H. 1977. Feeding behavior and predator avoidance in heterospecific groups. BioScience 27:332–339.

NORRIS, K. S. 1969. The echolocation of marine mammals. Pp. 391–423 in The biology of marine mammals (T. H. Andersen, ed.). Academic Press, New York.

NORRIS, K. S., AND T. P. DOHL. 1980. The structure and function of cetacean schools. Pp. 211–261 in Cetacean behavior: mechanism and functions (L. M. Herman, ed.). Krieger Publishing Company, New York.

NORRIS, K. S., AND C. M. JOHNSON. 1994. Schools and schooling. Pp. 232–242 in The Hawaiian spinner dolphin (K. S. Norris, B. Würsig, R. S. Wells, and M. Würsig, eds.). University of California Press, Berkeley.

NORRIS, K. S., AND J. H. PRESCOTT. 1961. Observations on Pacific cetaceans of Californian and Mexican waters. University of California Publications in Zoology 63:291–402.

NORRIS, K. S., AND C. R. SCHILT. 1988. Cooperative societies in three-dimensional space: on the origins of aggregations, flocks, and schools, with special reference to dolphins and fish. Ethology and Sociobiology 9:149–179.

PERRIN, W. F., R. R. WARNER, C. H. FISCUS, AND D. B. HOLTS. 1973. Stomach contents of porpoise, *Stenella* spp., and yellowfin tuna, *Thunnus albacares*, in mixed-species aggregations. Fishery Bulletin 71:1077–1092.

PETERSON, R. S., AND G. A. BARTHOLOMEW. 1967. The natural history and behavior of the California sea lion. Special Publication 1, The American Society of Mammalogists.

POLACHECK, T. 1987. Relative abundance, distribution and inter-specific relationship of cetacean schools in the eastern tropical Pacific. Marine Mammal Science 3:54–77.

REILLY, S. B. 1990. Seasonal changes in distribution and habitat differences among dolphins in the eastern tropical Pacific. Marine Ecology Progress Series 66:1–11.

RICE, D. W. 1998. Marine mammals of the world: systematics and distribution. Special Publication 4, The Society of Marine Mammalogy, Allen Press, Inc., Lawrence, Kansas.

RICHARDSON, W. J., C. R. GREENE, C. I. MALME, AND D. H. THOMSON. 1995. Marine mammals and noise. Academic Press, San Diego, California.

RIEDMAN, M. 1990. The pinnipeds: seals, sea lions, and walruses. University of California Press, Berkeley.

SAAYMAN, G. S., D. BOWER, AND C. K. TAYLER. 1972. Observations on inshore and pelagic dolphins on the south-eastern cape coast of South Africa. Koedoe 15:1–24.

SCHUSTERMAN, R. J. 1972. Visual acuity in pinnipeds. Pp. 469–492 in The behavior of marine mammals. Vol. 2. Vertebrates (H. E. Winn and B. L. Olla, eds.). Plenum Press, New York.

SCOTT, M. D., AND K. L. CATTANACH. 1998. Diel patterns in aggregations of pelagic dolphins and tunas in the eastern Pacific. Marine Mammal Science 14:401–428.

SCOTT, M. D., AND S. J. CHIVERS. 1990. Distribution and herd structure of bottlenose dolphins in the eastern tropical Pacific Ocean. Pp. 387–402 in The bottlenose dolphin (S. Leatherwood and R. R. Reeves, eds.). Academic Press, San Diego, California.

SELZER, L. A., AND P. M. PAYNE. 1988. The distribution of white-sided (Lagenorhynchus acutus) and common dolphins (Delphinus delphis) vs. environmental features of the continental shelf of the northeastern United States. Marine Mammal Science 4:141–153.

SHANE, S. H. 1990. Behavior and ecology of the bottlenose dolphin at Sanibel Island, Florida. Pp. 245–265 in The bottlenose dolphin (S. Leatherwood and R. R. Reeves, eds.). Academic Press, San Diego, California.

SHANE, S. H. 1994. Occurrence and habitat use of marine mammals at Santa Catalina Island, California from 1983–1991. Bulletin of the Southern California Academy of Sciences 93:13–29.

SHANE, S. H. 1995. Relationship between pilot whales and Risso's dolphins at Santa Catalina Island, California, USA. Marine Ecology Progress Series 123:5–11.

SIMILÄ, T., AND F. UGARTE. 1993. Surface and underwater observations of cooperatively feeding killer whales in northern Norway. Canadian Journal of Zoology 71:1494–1499.

STENSLAND, E., A. ANGERBJÖRN, AND P. BERGGREN. 2003. Mixed species groups in mammals. Mammal Review 33(3–4):205–223.

STEWART, B. S, AND P. K. YOCHEM. 2000. Community ecology of Channel Islands pinnipeds. Pp. 413–420 in Proceedings of the Fifth Symposium on the Biology of the California Islands, Santa Barbara, California (D. R. Browne, K. L. Mitchell, and H. W. Chaney, eds.). Minerals Management Service, United States Department of the Interior, Washington, D.C.

SURYAN, R. M., AND J. T. HARVEY. 1998. Tracking harbor seals (Phoca vitulina richardsi) to determine dive behavior, foraging activity, and haul-out site use. Marine Mammal Science 14:361–372.

TARASEVICH, M. N. 1957. Comparison of the composition of herds of aquatic and amphibious mammals. VNIRO 33:199–218.

WARD, P., AND A. ZAHAVI. 1973. The importance of certain assemblages of birds as ''information centres'' for food-finding. Ibis 115:517–534.

WEAVER, A. C. 1987. An ethogram of naturally occurring behavior of bottlenose dolphins, Tursiops truncatus, in southern California waters. M.S. thesis, San Diego State University, San Diego, California.

WELLER, D. W. 1991. The social ecology of Pacific coast bottlenose dolphins. M.S. thesis, San Diego State University, San Diego, California.

WELLS, R. S., D. J. BONESS, AND G. B. RATHBUN. 1999. Behavior. Pp. 324–422 in Biology of marine mammals (J. E. Reynolds III and S. A. Rommel, eds.). Smithsonian Institution Press, Washington, D.C.

WELLS, R. S., B. G. WÜRSIG, AND K. S. NORRIS. 1981. A survey of the marine mammals of the upper Gulf of California, Mexico. Marine Mammal Commission, Washington, D.C., Final Report PB81-168791:1–41.

WILSON, E. O. 1977. Sociobiologia: la nuova sintesi. Zanichelli Editore, Bologna, Italy.

WÜRSIG, B. 1986. Delphinid foraging strategies. Pp. 347–359 in Dolphin cognition and behavior: a comparative approach (R. J. Schusterman, J. A. Thomas, and F.G. Wood, eds.). L. Erlbaum Associates, Hillsdale and London, United Kingdom.

WÜRSIG, B., S. K. LYNN, T. A. JEFFERSON, AND K. D. MULLIN. 1998. Behaviour of cetaceans in the northern Gulf of Mexico relative to survey ships and aircraft. Aquatic Mammals 24:41–50.

WÜRSIG, B., R. S. WELLS, AND K. S. NORRIS. 1994. Food and feeding. Pp. 216–231 in The Hawaiian spinner dolphin (K. Norris, B. Würsig, R. Wells, and M. Würsig, eds.). University of California Press, Berkeley.

WÜRSIG, B., AND M. WÜRSIG. 1980. Behavior and ecology of the dusky dolphin, Lagenorhynchus obscurus, in the south Atlantic. Fishery Bulletin 77:871–890.

ZEMEL, A., AND Y. LUBIN. 1995. Inter-group competition and stable group sizes. Animal Behaviour 50:485–488.