

Aspects of the ecology and behaviour of bottlenose dolphins (*Tursiops truncatus*) in Santa Monica Bay, California

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ABSTRACT

The occurrence, distribution, site fidelity, group size and behaviour of common bottlenose dolphins (*Tursiops truncatus*) were assessed during a photo-identification study conducted between 1997–2001 in Santa Monica Bay, California. Bottlenose dolphins occurred year-round in the bay and were encountered on 56.8% of all surveys (n , total surveys=211). This species was found in waters within 0.5km of shore in 80.0% of the sightings ($n=157$), but sometimes found in deeper waters further offshore (>0.5km). No correlations between anomalies in sea surface temperatures during the 1997–98 El Niño event and sighting frequencies were observed. Group sizes varied significantly between schools observed inshore and offshore in the bay, with the largest groups sighted offshore. A total of 290 dolphins were individually photo-identified based on long-term natural marks on their dorsal fins. Forty-four individuals (15.2%) were encountered in both inshore and offshore waters, showing no exclusive fidelity to inshore waters. The low resighting rates of known individuals provided little evidence of long-term year-round site fidelity for Santa Monica Bay, revealing a range greater than the chosen study area. Several individuals, however, were resighted over one or two year periods, generally during more than one season. This suggested that these dolphins were highly mobile within the inshore waters of the Southern California Bight but they also spent time foraging and feeding in Santa Monica Bay, probably due to the presence of submarine canyons within this area. The behavioural budget for this species showed a predominance of activities characterised by travel and dive-travel (69.0%) and feeding (5.0%), indicating a fairly high proportion of time devoted to searching for prey and feeding in the study area.

KEYWORDS: SURVEY-VESSEL, SOCIAL, BEHAVIOUR, FEEDING, HABITAT, SCHOOL SIZE, DISTRIBUTION, MOVEMENTS, PHOTO-ID, EL NIÑO, CONSERVATION

INTRODUCTION

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 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). The frequent presence of bottlenose dolphins along the coastline has made this one of the best studied cetacean species in the world.

Long-term studies on free-ranging bottlenose dolphins in the Southern California Bight have been focused mostly along the San Diego coastline (less than 1km from shore; Defran and Weller, 1999). In 1996, a preliminary series of cetacean surveys in the waters of Santa Monica Bay revealed that bottlenose dolphins could be found there throughout the year, making the area suitable for a long-term study of the social ecology and behaviour of this species. This is an area of conservation interest because of possible habitat degradation due to the adjacent metropolis of Los Angeles. It is also of interest due to the large effects of some El Niño events¹ on dolphin distribution reported elsewhere along the California coast (e.g. Wells *et al.*, 1990; Bonnell and Dailey, 1993). This five-year (1997–2001) longitudinal study represents the first attempt to describe the occurrence, distribution, site fidelity, group size and behaviour of bottlenose dolphins in Santa Monica Bay using an observational approach and systematic photo-identification.

MATERIALS AND METHODS

Study area

The Santa Monica Bay study area (approximately 460km², 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 bay contains two shallow water submarine canyons (Dume and Redondo) and one deeper canyon, the Santa Monica Canyon. This begins at a depth of about 100m, at the edge of the continental shelf. The bay has a mean depth of about 55m and a maximum depth 450m. A shallow shelf between the Santa Monica and Redondo Canyons extends as a plateau from the 50m contour. The study area is characterised by mild temperatures, short rainy winters and long, dry summers. Normal water surface temperatures range from 11 to 22°C although during the 1997–98 El Niño, three peaks of sea surface temperature (SST) anomalies were evident: May–June 1997, September–October 1997 and August 1998, with an increase in temperature of +2°C above the norm (Nezlin *et al.*, 2003).

Data collection and analysis

Surveys were conducted from January 1997 to December 2001 (Table 1), with an average of 3.5 surveys per month ($n=211$). Inshore (distance from shore <500m) and offshore (>500m) surveys were carried out in the morning and early afternoon. Boat surveys were conducted from a 7m (1996–2000) and a 10m (2001) powerboat at an average speed of 18km h⁻¹. The number of kilometres spent at the different bathymetric locations in the bay (grid comprising of 82 3.7 × 3.7 units) was calculated to determine the evenness in the coverage of the study area. No significant difference was observed in surveying the different locations ($t=1.92$, $DF=28$, $P > 0.05$).

¹ El Niño is an irregular climatic phenomenon that results in *inter alia* abnormally warm sea temperatures in the eastern tropical Pacific (e.g. see www.elnino.noaa.gov).

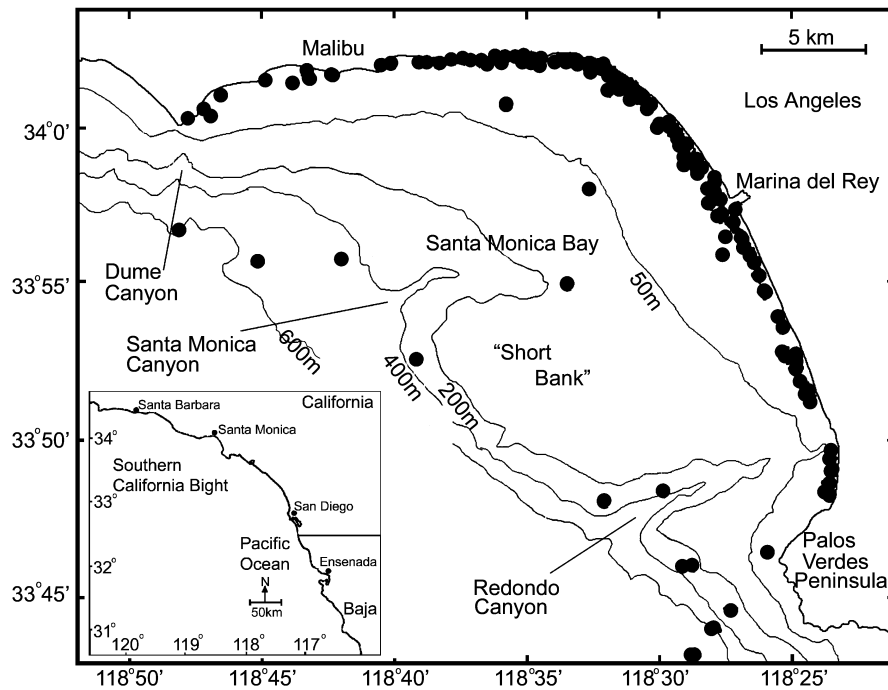


Fig. 1. The study area and the distribution of bottlenose dolphins in the bay. Each symbol (●) represents initial GPS coordinates of sightings.

Table 1

Number of surveys and summary of research effort in Santa Monica Bay for the years 1997-2001.

	1997	1998	1999	2000	2001	Total
Surveys						
Inshore surveys	5	17	12	6	7	47
Offshore surveys	23	3	5	4	6	41
Combined inshore/offshore surveys	11	38	27	27	20	123
Total number of surveys	39	58	44	37	33	211
Research effort						
Hours spent in the field	144	224	178	149	137	832
Hours spent searching for cetaceans	110	136	130	105	82	563
Hours spent with cetaceans	34	88	48	44	55	269
Hours spent with bottlenose dolphins	18	65	32	19	20	154
Total N of 5 min behavioural samples	295	1,065	698	525	675	3,258
N of 5 min behavioural samples for bottlenose dolphins	134	814	368	262	187	1,765

Data were collected with laptop computers and occasionally with tape recorders. When dolphins were seen, data on the number of animals, size classes and behaviour (Table 2) and aggregation with other species were recorded at five minute intervals throughout the sighting. The number of dolphins and size classes were additionally verified later through photo-identification analyses.

The majority of observations (91.7%) were conducted in good conditions (Beaufort scale ≤ 2 , sea state 0 and visibility $> 300\text{m}$). The dolphins' positions and speeds ($\pm 30\text{m}$ from the boat) were approximated to the boat's position using a GPS. Boat speed was reduced in the presence of dolphins and sudden speed or directional changes were avoided.

Photo-identification followed the methods of Würsig and Jefferson (1990) and Bearzi *et al.* (1997). For each sighting, an attempt was made to photograph all individuals present in the group. Colour photos were taken with 35mm cameras

equipped with 75-300mm lenses using slide film (64-200 ISO). During the sightings, researchers also videotaped and recorded the animals' behaviour with Hi8 mm and Mini DV Video Camcorders.

Behavioural data collected opportunistically from July to December 1996 (58 hours of field observations) provided a framework of information to design the behavioural sampling procedures systematically adopted from January 1997 (Bearzi, M., 2003). Videos and photographs were reviewed in a laboratory to validate field observations.

Of over 21,500 cetacean pictures taken in the years 1997-2001, 11,909 were of bottlenose dolphins. Of these, 797 were scanned and matched using a computer-assisted identification system (*Finscan*; Kreho *et al.*, 1999). During matching, marks and scars likely to have been inflicted by sharks were also documented. Adult individuals consistently accompanied by a calf over a two-month period were assumed to be females.

Table 2

Definitions of size classes, group formation, physical contact, surfacing mode, directional behaviour, behavioural states and boat disturbance.

Size classes (from Bearzi <i>et al.</i>, 1997, modified)	
Adult	Dolphins approximately 2.7-3.2m long.
Calf	A dolphin estimated to be one half the length or less of an adult, that swam next to an adult so as to be touching it at most times and that is always accompanied by an adult during the course of the observation.
Group formation (from Shane, 1990a, modified)	
Tight	Dolphins generally less than one body length apart.
Loose	Dolphins generally between 1-5 body lengths apart.
Dispersed	Dolphins generally more than 5 body lengths apart.
Variable	Dolphins irregularly spread; or a group that meet more than one of the above criteria.
Convergent	The joining of one or more subgroups to the focal group.
Physical contact	
None	No physical contact among individuals is observed during the 5 min sample.
Occasional	Physical contact among two or more individuals is occasionally observed during a 5 min sample.
Regular	Consistent physical contact among some individuals (less than one half of the total group size) is observed during a 5 min sample, while the other group members are engaged in other activities.
Intense	Consistent physical contact among the majority of the group members is observed during a 5 min sample.
Unknown	Impossible to determine (e.g. the majority of the animals are diving or feeding at depth and their behaviour is not observable).
Surfacing mode	
Calm	Most surfacing is slow and does not produce foam or water turbulence.
Active	Most surfacing is fast and produces foam or water turbulence.
Variable	Both calm and active surfacing consistently occur during 5 min sample.
Directional behaviour	
None	No directional heading and geographical movement during a 5 min sample.
Poor	Changes of direction and short stops may occur during a 5 min sample, although consistent geographic movement does occur.
Straight	Steady directional heading and geographic movement during a 5 min sample.
Zig-zagging	Continuous zig-zagging movements during a 5 min sample.
Behavioural states	
Travel	Moving steadily in one direction (Shane, 1990a) during the 5 min sample.
Dive	No steady directional movement; dives longer than 30 sec occurring during the 5 min sample.
Feeding	Obvious feeding activities performed close to the water surface (Shane, 1990a); dolphins are often seen catching fishes by pursuing them parallel to the water surface or moving in circle and diving in the same small area; birds usually concentrated over the dolphins (Bearzi <i>et al.</i> , 1999) during the 5 min sample.
Socialise	Some or all group members in almost constant physical contact with one another, oriented towards one another and often displaying surface behaviours; no steady directional movement (Shane, 1990a) during the 5 min sample.
Play	Any activity that incorporates the use of a 'foreign object' during the 5 min sample.
Milling	Moving in varying directions in one location, but showing no surface behaviours and no apparent physical contact between individuals; usually staying close to the surface (Shane, 1990a) during the 5 min sample.
Others	Any other behaviour not included in the above list.
Boat disturbance (Würsig <i>et al.</i>, 1998, modified)	
Avoidance	When an individual or focal group moved away from the vessel or appeared to dive in response to the vessel.
No response	The animal/s showed no apparent response relative to the approach or pass-by of the vessel.
Approach	The animal/s moved toward the vessel during at least part of the observation period.
Bowride	Special case of an approach response.

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. For sighting frequency analysis, different sightings of the same individual during the same day were considered only once to avoid pseudo-replication.

Definitions

Aggregation refers to distances between one or more individuals of two different species being less than 100m, and *close aggregation* as instances when the distance between one or more individuals of two different species was about 1m. A *mixed group* is an interspecific group of cetaceans in continuous aggregation with each other for at least 10 minutes, displaying similar activities at least during part of the aggregation.

A *focal group* is any group of animals (of the same species) observed in association, moving in the same direction and usually engaged in the same activity (Shane, 1990a). Groups of animals not belonging to the observed focal group and spotted at distance were recorded but their numbers were excluded from group size calculations.

A *dolphin school* is one where all dolphins (of the same species) are in continuous association with each other and within visual range of the survey team (Weller, 1991).

A *behavioural state* is defined as a broad category of activities, such as feeding behaviour, that integrates a number of individual behaviour patterns into a recognisable pattern (Table 2; Weaver, 1987). *Mating* refers only to copulation occurring between individuals of different sexes.

RESULTS

Field effort

Data were collected during 47 inshore surveys, 41 offshore surveys and 123 combined inshore/offshore surveys in the bay for the years 1997-2001. A total of 516h was spent searching for cetaceans in good weather conditions (Beaufort scale ≤ 2), while 269h were spent observing 331 cetacean groups encountered during sightings lasting on average 40 minutes (range 2-266 minutes); 157 bottlenose dolphin schools were photographed during sightings lasting, on average, about one hour (mean=59.6 minutes, SD=41.97, SE=3.38, range 3-266 minutes, $n=154$; Table 1).

Occurrence, distribution and site fidelity

The bottlenose dolphin was the species most frequently sighted year-round (48.5%, $n=157$ schools) in Santa Monica Bay. Sighting of only a single school per day was most common (62.0% ($n=131$) of all survey days ($n=211$)). Multiple schools, which ranged between two and six schools, were sighted on 12.3% ($n=26$) of all survey days.

The sighting frequencies (sightings per hour) and the total sightings for this species are presented in Table 3 and Fig. 2a. The presence of other groups not included in the focal groups was recorded during 9.6% of the sightings ($n=15$). A significant difference in the number of sightings was observed ($t=4.1$, $DF=4$, $P<0.05$), with more sightings during 1998 than in all other years. A significant difference in the sighting numbers was also observed by season (Winter: Jan-Mar, Spring: Apr-Jun, Summer: Jun-Sep, and Autumn: Oct-Dec) for each of the five years (1997: $t=3.6$, $DF=3$, $P<0.05$; 1998: $t=8.9$, $DF=3$, $P<0.001$; 1999: $t=6.7$, $DF=3$, $P<0.001$; 2000: $t=10.2$, $DF=3$, $P<0.001$; 2001: $t=15.6$, $DF=3$, $P<0.001$). In 1997, 2000 and 2001, the sightings were more frequent during winter whereas in 1998 and 1999 they were more frequent in spring and summer.

Table 3

Sighting frequency (sightings/hour) of bottlenose dolphins in the bay for the years 1997-2001.

	1997	1998	1999	2000	2001	Total
Number of sightings	19	61	33	24	20	157
Sighting frequency	0.13	0.27	0.19	0.16	0.14	0.19

The presence of calves was recorded during 43.3% of the sightings ($n=61$) with a range of 1-6 calves per sighting (mean=1.0, $SD=1.12$, $SE=0.09$, $n=141$).

Bottlenose dolphins were observed with other cetacean species in 11.5% of the 157 sightings: common dolphins, *Delphinus delphis* or long-beaked common dolphins, *D. capensis*, 50.0% of mixed sightings, $n=9$; Risso's dolphins, *Grampus griseus*, 33.3%, $n=6$; Pacific white-sided dolphins, *Lagenorhynchus obliquidens*, 5.5%, $n=1$; common minke whales, *Balaenoptera acutorostrata*, 5.5%, $n=1$; and gray whales, *Eschrichtius robustus*, 5.5%, $n=1$. All mixed groups were observed in offshore waters except one aggregation with a single common dolphin and one with a single gray whale that occurred in inshore waters.

The potential effects of the 1997-98 El Niño were examined by comparing percentages of bottlenose dolphin sightings to variations in sea surface temperature and variations in surface chlorophyll (Fig. 2a,b,c). Visual inspection of the data suggested no apparent correlations between temperature changes brought about by the 1997-98 El Niño event and changes in bottlenose dolphin occurrence in the study area.

To identify distinct individual dolphins for the study area, matching procedures focused on 138 sightings (87.9% of total bottlenose dolphin sightings). A total of 290 distinct individuals (36.4% of total identified and resighted individuals, $n=797$) were recognised in the study area between 1997-2001.

The discovery curve (rate at which new individual dolphins were identified) is presented in Fig. 3. Most individuals were first identified during 1998. The number of new identifications gradually decreased after this year but has not yet levelled off.

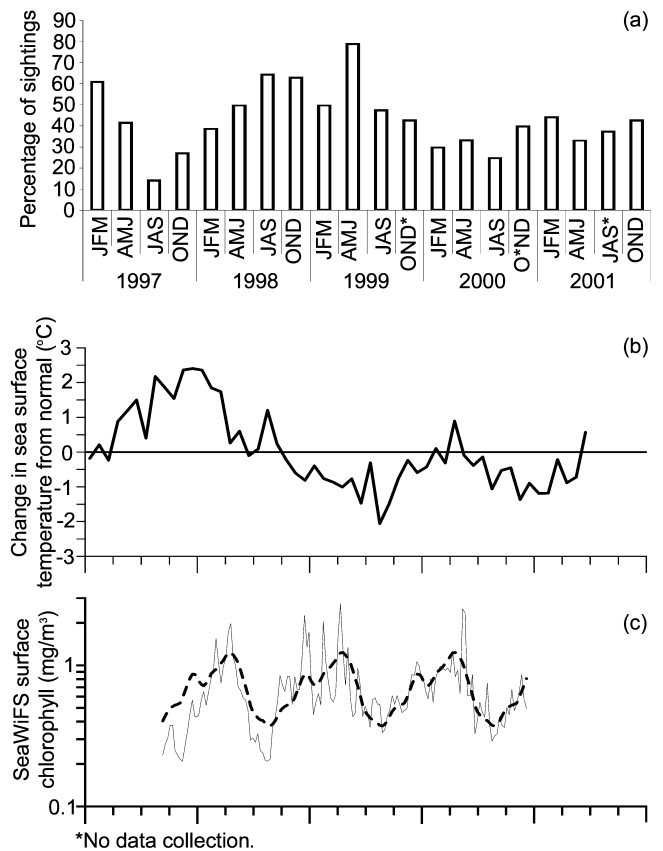


Fig. 2a,b,c. (a) Percentages of total bottlenose dolphin sightings recorded during 3-month periods (Jan-Mar, Apr-Jun, Jul-Sep, Oct-Dec) in Santa Monica Bay. (b) Variations of sea surface temperature anomalies during January 1997 – July 2001 for Santa Monica Bay based on Pathfinder AVHRR SST data (courtesy of N. Nezlin). (c) Variations of remote-sensed surface chlorophyll during 1997-2000 for Santa Monica Bay. The dashed line indicates averaged over the entire period of observations seasonal cycle (from Nezlin *et al.*, 2003).

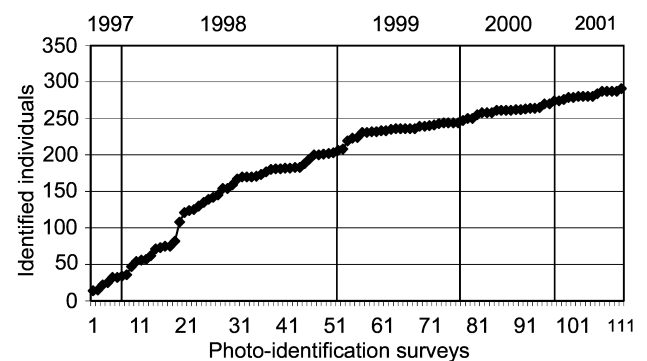


Fig. 3. Cumulative rate of identification of new individuals over time ('rate of discovery') in the years 1997-2001 for Santa Monica Bay.

The sighting frequencies for the identified dolphins ranged up to 15 days (mean=2.8, $SD=2.18$, $SE=0.12$, $n=290$; Fig. 4); 38.0% ($n=111$) were sighted only once while 22.0% were sighted five or more times. The identified individuals were observed over a one or two year period (mean=1.6, $SD=0.81$, $SE=0.04$, range 1-4, $n=290$), generally during more than one season, indicating a low degree of site fidelity as far as Santa Monica Bay is concerned. The majority of the individuals were sighted during spring in the years 1998-2001 and during winter in 1997 (see Bearzi, M., (2003) for a complete list of identified and resighted individuals during different seasons in the years 1997-2001).

Among the 290 catalogued individuals, 43 (14.8%) were classified as female. No significant differences between seasons in the number of calves sighted were observed (DF=3, $t=3.83$, $P > 0.05$).

The distribution of bottlenose dolphins in relation to the bathymetry of the bay is presented in Fig. 1. The species was found regularly in inshore waters (<500m; 79.6%, $n=157$), most often within 50-100m of the shoreline, and less often in offshore waters (>500m) near submarine canyons and escarpments. To determine whether identified individuals exclusively frequented inshore waters as reported by other authors (Hansen, 1990; Hanson and Defran, 1993), the numbers of individuals observed both in inshore and offshore waters were determined. Most individuals (80.0%, $n=157$) were observed within 500m of shore; 36 individuals were seen only in offshore waters up to 15 miles from the coast (12.4%); but 44 individuals (15.2%) were sighted both in inshore and offshore waters.

No marks and scars that could clearly be attributed to sharks were observed, although a few individuals carried unusual wounds that might have been caused by either predatory attack or severe physical contact (e.g. rocks, boat propellers, etc.). No interactions between sharks and bottlenose dolphins were seen; killer whales, another potential predator of dolphins (Würsig and Würsig, 1979), were rarely observed in the bay and never in inshore waters.

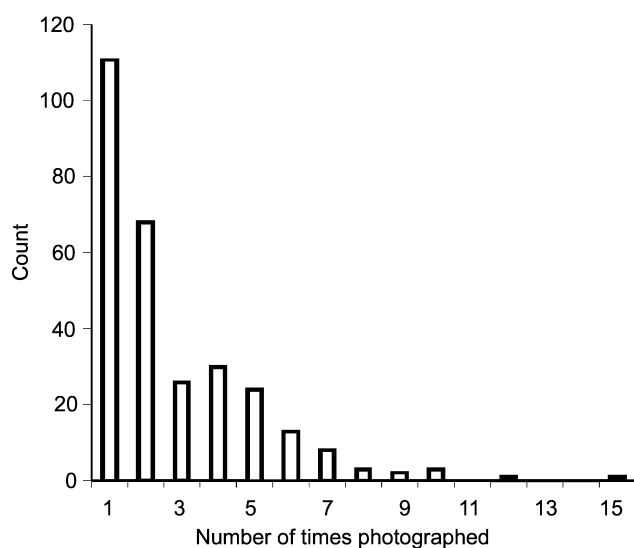


Fig. 4. Sighting frequencies for dolphins identified from 1997 to 2001.

Group sizes and group formations

Mean group sizes for inshore and offshore bottlenose dolphin schools inhabiting the study area are compared with group sizes reported by other authors in Table 4. The mean group size of inshore schools (8.8) was significantly different from offshore schools (15.0) with the largest groups observed offshore (mean difference=5.7, $t=2.81$, DF=29, $P < 0.001$). Single animals constituted 3.4% of the samples ($n=5$).

The most frequent group formation observed was *variable* (inshore schools: 67.5% of the 5 minute samples; offshore schools: 79.0% of the 5 minute samples, $n=253$ calculated on a subset of data selected at random), followed by *tight* (inshore schools: 18.2% of the 5 minute samples; offshore schools: 10.3%), *dispersed* (inshore schools: 6.5%; offshore schools: 8.3%) and *loose* (inshore schools: 7.6%; offshore schools: 2.0% of the 5 minute samples). No

significant difference was observed between inshore and offshore schools for the four group formation categories ($t=0.01$, DF=3, $P > 0.05$).

Table 4

Group sizes for inshore and offshore bottlenose dolphin schools in Santa Monica Bay and mean group sizes reported by other authors.

	Mean	SD	SE	N	Min.	Max.
Bottlenose dolphins	10.1	7.60	0.63	145	1	57
Inshore (<500m from shore)	8.8	5.31	0.49	115	1	35
Offshore (>500m from shore)	15.0	12.05	2.20	30	1	57

	Mean	Sources
Bottlenose dolphins	19.8	Defran and Weller (1999), Southern California, inshore dolphins.
	18	Hansen (1990), Southern California, offshore dolphins.
	10	Scott and Chivers (1990), Eastern tropical Pacific Ocean, inshore dolphins.

Behavioural patterns

The behavioural budget recorded for bottlenose dolphins is presented in Table 5 and Fig. 5. The budget shows a predominance of *Travel* (49.0%; n 5 minute sample=1,757) and *Dive-Travel* (20.0%) activities. *Feeding* was observed in 5.0% of the sightings, also in association with other activities such as *Travel-Feeding*: 4.5%), *Socialise* (*Feeding-Socialise*: 4.5%) and *Dive* (*Dive-Feeding*: 1.5%).

Table 5

Overall behavioural state budget recorded for bottlenose dolphins in Santa Monica Bay. Behavioural state data at less than 99.5% level were not included in the table. A hyphen between two behavioural states refers to activities performed simultaneously by different focal group individuals during 5 min sample (e.g. dive-travel, socialise-travel, etc.). A comma between two behavioural states refers to activities performed by different focal group individuals to express consecutive behaviours occurring during 5 min sample (e.g. travel, feeding means travel followed by feeding).

Behavioural states	No. of 5 min samples	Frequency distribution of observed behaviour	Total 5 min samples states
Travel	861	49.01	1,757
Dive-travel ^a	351	19.98	
Feeding	87	4.95	
Feeding-travel	78	4.44	
Socialise-travel	78	4.44	
Dive	37	2.10	
Socialise	34	1.93	
Dive, travel ^b	31	1.76	
Travel, feeding	29	1.65	
Dive-feeding	27	1.54	
Travel, dive	24	1.36	
Feeding-socialise	19	1.08	
Travel, socialise	18	1.02	
Socialise, travel	15	0.85	
Dive-travel-feeding	11	0.62	
Dive-socialise	10	0.56	
Travel-milling	9	0.51	

^aSimultaneous behaviour occurring during 5 min sample. ^bConsecutive behaviour occurring during 5 min sample.

A significant difference was observed in the behaviour patterns observed (Fig. 5) over the five years of study ($\chi^2=154.78$, DF=36, $P < 0.001$), with most travel and dive-travel recorded in 1998-99 and most feeding observed in 1997 and 2000.

Bottlenose dolphins travelled at an average speed of 4.3 km h^{-1} (mode=1.8, SD=2.56, SE=0.07, range 0.9–16.6, $n=1,107$ from subset of 5 minute samples data selected at random). Offshore schools travelled at a significantly higher speed than inshore schools (offshore: mean=5.8, SD=1.29, SE=0.04, $n=118$ from subset of data selected at random; inshore: mean=4.2, SD=1.80, SE=0.16, $n=118$; mean difference=2.2, DF=117, $t=13.47$, $P < 0.001$). During travelling, the surfacing mode was usually *calm* for both inshore and offshore schools (73.9% of the total sightings) or *variable* (25.5%); *active* surfacing was observed only rarely (0.6%).

To determine potential differences between the behavioural states of bottlenose dolphins during the El Niño years *versus* a random period of normal temperatures, different behavioural states were compared over 11 months of increased and normal sea surface temperature (high SST: June 1997–April 1998; normal SST: June 1999–April 2000). No significant difference was observed between the most common behavioural states seen during years of high SST versus normal years ($\chi^2 = 63$, DF = 56, $P > 0.05$).

Physical contact among two or more individuals in a school was recorded to be *occasional* 21.6% of the time during 5 minute samples ($n=1,515$), *regular* 3.4% of the time and *intense* 2.8% of the time. Mating behaviour was only recorded during 14 sightings (8.9%, $n=157$) in the study period.

DISCUSSION

Occurrence, distribution and site fidelity

The bottlenose dolphin was the species most often observed in Santa Monica Bay, followed by long-beaked common dolphins and common dolphins (Bearzi, M., 2003; see also Bonnell and Dailey, 1993; Forney and Barlow, 1998). Other cetaceans were occasional or rare inhabitants of the bay (Bearzi, M., 2003).

The distribution of bottlenose dolphins in the study area was largely within 500m of shore, in agreement with prior observations off the San Diego coastline (Defran and Weller, 1999; Defran *et al.*, 1999). However, they were also occasionally observed aggregating offshore near submarine canyons and escarpments (Fig. 1), where prey may be relatively more abundant (Hui, 1979). In Santa Monica Bay, bottlenose dolphins and the two common dolphin species generally differed both in distribution and prey preference, which has been suggested to be due to habitat partitioning, as a consequence of prey specialisation and competition for resources in inshore waters (Bearzi, M., 2003).

El Niño, is a pole-ward propagation of nutrient-poor warm water along the coast of Western America caused by a break-down of trade wind circulation (Tomczak and Godfrey, 1994). It usually reduces primary productivity throughout most of the coastal Eastern Pacific (Cane, 1983) and has been correlated with shifts in the distribution of

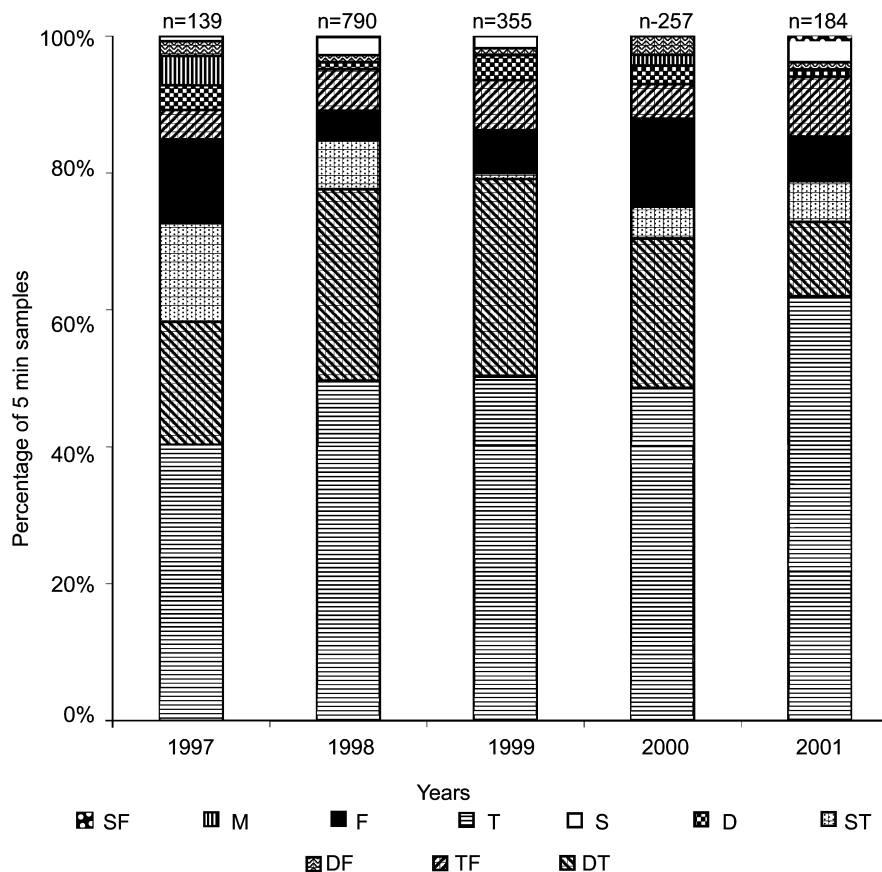


Fig. 5. Behavioural budget computed for the 10 most common patterns of activities during the study period. T=Travel, DT=Dive-Travel, ST=Socialise-Travel, F=Feeding, TF=Travel-Feeding, D=Dive, M=Milling, DF=Dive-Feeding, S=Socialise, SF=Socialise-Feeding. These behaviours include activities performed simultaneously and in sequence by different focal group individuals during 5 minute sample.

marine mammals and their prey (Shane, 1995a; b; Defran *et al.*, 1999; Hill, 1999). By contrast, La Niña is characterised by upwelling-favourable trade winds that restore levels of primary productivity (Chavez *et al.*, 1999). In the present study: (1) bottlenose dolphins occurred throughout the period, including during the strong 1997-1998 El Niño and the following La Niña events of 1998-2001; and (2) the number of bottlenose dolphin sightings peaked during the winter months in the years 1997, 2000 and 2001 and during spring and summer in 1998 and 1999, showing a high number of sightings during the El Niño event.

During the 1982-83 El Niño coastal bottlenose dolphins off San Diego were observed to extend their range to central and Northern California; this was believed to be a response to prey abundance fluctuations (Wells *et al.*, 1990; Dailey *et al.*, 1993). No systematic data were collected that would suggest a similar northward migration of coastal dolphins during the 1997-98 event, but K.J. Dudzik (pers. comm.) observed a slight decline in numbers of this species along the San Diego coastline at this time that may have contributed to the high numbers of dolphin sightings in Santa Monica Bay. The apparent lack of severe effects may be explained by prey abundance during these years for the Southern California Bight. Whilst the 1997-98 El Niño event had a dramatic negative affect on several important fisheries (e.g. decreases in squid and anchovy catches), some fisheries including the Pacific sardine (*Sardinops sagax*), white seabass (*Atractoscion nobilis*) and splitnose rockfish (*Sebastes diploproa*), showed improved catches in the Santa Monica Bay area (California Department of Fish and Game, 2000). Bottlenose dolphins are opportunistic species that feed on different prey, based on availability and abundance (Bearzi, G. *et al.*, 1999). During the El Niño years, bottlenose dolphins may have fed on species that were more abundant in Santa Monica Bay, eliminating the need to leave the study area.

The rate at which previously unidentified dolphins were discovered in the study area increased most rapidly in 1998 (when effort was highest). The discovery curve of new individuals for this study was comparable to the trend reported for Southern California (Weller, 1991; Defran and Weller, 1999), but it was in contrast with some other studies around the world where asymptotes were recorded over shorter periods of time (Wells, 1986; Ballance, 1990).

The number of identified dolphins in the study area was lower than the number reported for the San Diego area, approximately 140km to the south ($n=290$, this study, vs $n=373$, Defran and Weller, 1999), but given the discovery curve shown in Fig. 3, it is probable that not all dolphins had been identified by the end of this study in 2001.

The variability in bottlenose dolphin sightings and the generally low individual sighting frequencies were consistent with data from San Diego (Defran and Weller, 1999). The variations in time between many of the resightings of identified dolphins in Santa Monica Bay suggested that the area represents part of a larger 'home range'² within the California coast. Defran *et al.* (1999) reported that 58.0% ($n=120$) of a total population of 207 individuals exhibited back-and-forth movements over 470km of coastline between three discrete regions where photo-identification studies were conducted: Santa Barbara and Orange County, California; and Ensenada, in Baja California, Mexico, with no evidence of site fidelity to any

particular area. These authors concluded that the high mobility of dolphins within a relatively narrow coastal zone reflected the extremely dynamic nature of this coastal ecosystem and the associated patchy distribution of food resources available (Dailey *et al.*, 1993). Previous work has also shown that movements by bottlenose dolphins were more evident where temperature and prey abundance fluctuate seasonally (Wells *et al.*, 1990; Bräger *et al.*, 1994).

In Santa Monica Bay, located between Santa Barbara and San Diego (see Fig. 1), most of the identified individuals were not observed year-round, showing the absence of a strong residency pattern. This suggests that they belonged to the same highly mobile and behaviourally flexible open coastal population observed by Defran *et al.* (1999), but has not yet been confirmed by comparing the two photo-id catalogues. However, in Santa Monica Bay: (1) at least some individuals appeared to utilise the area on a seasonal basis; and (2) the overall proportion of dolphins sighted only once in the bay (38.0%; n surveys in 1997-2001=211) was significantly lower than the proportion reported in other areas along the California coast (71.0% Orange County, 69.0% Ensenada, 53.0% Santa Barbara, n surveys in 1981-1989=241; Defran *et al.*, 1999), showing some degree of fidelity by bottlenose dolphins to Santa Monica Bay.

Although most identified individuals were observed within 500m of shore, some of the same individuals were also observed in offshore waters (>1km from shore). This contrasts with data reported for the Southern California waters where dolphins were almost always encountered within 1km of shore, showing a high fidelity to a 'coastal corridor' between 10 and 30m depths, with no matching between inshore and offshore individuals (Shane, 1994; Defran and Weller, 1999; Defran *et al.*, 1999). Although bottlenose dolphins in Santa Monica Bay also showed a preference for a coastal corridor, they did not adhere to a rigorous 1km boundary. This may be due to the different bathymetry and oceanography of the two study areas. Presumably, the presence of the same individuals in both inshore and offshore waters for Santa Monica Bay was related to the presence of submarine canyons and escarpments (Dartnell, 2000), which are optimal features for mixing of nutrients and consequently are rich in prey for dolphins. On the contrary, the San Diego area showed different oceanographic characteristics. There, the open coastal waters were relatively dynamic with a substantial variability in water temperature and, consequently, in abundance and composition of patches of prey over years or decades (Dailey *et al.*, 1993; Defran *et al.*, 1999). Weller (1991) reported that these variations were responsible for the behavioural flexibility demonstrated by bottlenose dolphins to changes in habitat ecology along the Southern California coastline.

In conclusion, the bottlenose dolphins of Santa Monica Bay appear to exhibit similar movements to the dolphin population of the open coastal waters of the San Diego area but they also showed some characteristics common to individuals living in more protected areas. They exhibited some degree of site fidelity, inshore-offshore movements (Connor and Smolker, 1985; Wells *et al.*, 1987; Bearzi, G. *et al.*, 1997) and an apparent indifference to El Niño shifts.

Group sizes and group formations

There was a substantial range in observed group sizes for bottlenose dolphins in Santa Monica Bay (range 1-57 individuals). The results of this study are similar to the findings of Hansen (1990) and Scott and Chivers (1990;

² Home range was defined following Burt (1943) as that area traversed by the individual in its normal activities of food gathering, mating and caring for young.

Table 4). The higher difference in group size for inshore dolphins reported by Defran and Weller (1999) off San Diego in comparison to this study may be due to the use of dissimilar methodologies and definitions.

Bottlenose dolphins showed an increased group size from inshore to offshore waters, in agreement with the findings of Defran and Weller (1999) for Southern California. A similar trend for this species was observed by Scott *et al.* (1990) in Florida waters, where school sizes increased with water depth. As suggested by Wells *et al.* (1980), larger group sizes may benefit from cooperative feeding on patchy, rich food resources found in deeper habitats. In Santa Monica Bay, the increase in group size from inshore to offshore waters was perhaps a response to a patchy distribution and abundance of prey (Dailey *et al.*, 1993). Some authors have suggested that predation may be responsible for increased group sizes in dolphins (e.g. Norris and Dohl, 1980; Norris and Schilt, 1988; Scott and Cattanch, 1998). However, the low numbers of scars inflicted by sharks on identified individuals and the low number of predators observed at the surface in the study area suggested that predation pressure was not a major factor in determining group size.

Offshore bottlenose dolphins were also often found in aggregations with other cetaceans, which effectively increased school size. The presence of mixed species aggregations in offshore feeding grounds rich in prey can promote schooling behaviour of prey and facilitate the capture of food for one or both predators (Magurran, 1990; Similä and Ugarte, 1993; Norris and Johnson, 1994).

Although bottlenose dolphin schools showed a *variable* group formation, with no significant difference observed between inshore and offshore schools, inshore groups were sighted more often in a *tight* group formation than offshore groups. The *tight* formation is possibly related to a different feeding strategy used by dolphins when food is less patchily distributed (Wells *et al.*, 1980).

Behavioural patterns

Behavioural data collected for bottlenose dolphins in Santa Monica Bay were similar to those reported for the San Diego coastline (Hanson and Defran, 1993). In both areas, bottlenose dolphins spent a fairly high amount of time travelling (this study: 69.0% travel plus dive-travel; San Diego: 63.0% travel plus dive-travel). Feeding activities were observed 19.0% of the time near San Diego and 16.0% in Santa Monica Bay. Different methodologies and definitions probably account for the minor differences in behaviour recorded in the two areas. The relatively high proportion of behavioural states such as travel and feeding across seasons is likely to have been related to a year-round occurrence of prey, as also reported by Hanson and Defran (1993). Although feeding at the surface was observed occasionally, the rather large amount of time spent dive-travelling and diving may have been related to food searching or feeding activities not directly observed by the researchers (Bearzi, G. *et al.*, 1999). The significantly greater amount of travel and dive-travel recorded during the years 1998-99 for the study area may have been linked to an increased need to forage for prey, which had become more patchily distributed during those two years.

Bottlenose dolphins in Santa Monica Bay were regularly observed travelling in a *calm* surfacing mode and at speeds usually lower in comparison to those calculated for bottlenose dolphins in other areas worldwide (this study: 4.3km h⁻¹; Würsig and Würsig, 1979: 6.1km h⁻¹; Shane, 1990a: 5.5km h⁻¹; Bearzi, G. *et al.*, 1999: 7.1km h⁻¹). Considering that travelling has the primary function of

locating food and conspecifics (Shane, 1990b), bottlenose dolphins in the study area may have travelled at lower speed to inspect shallow waters and forage for prey along the shore. In addition, a recurrent transition among behaviours indicative of foraging were often observed (Table 5), suggesting a consistent effort devoted to feeding-related activities, as also reported by Bearzi *et al.* (1999). Other behavioural activities unrelated to foraging and feeding were occasionally seen year-round during the study period, with irregular physical contact and mating observed mostly during socialising.

Bottlenose dolphins spent most of their time moving along favourite 'corridors' within 50 metres of shore, as also recorded by Defran and Weller (1999). Frequent direction changes along the coastline were often observed, which are likely to be related to prey movements. Dolphin travel activities were often followed by feeding activities in spots that may have reflected the presence of demersal prey on sand flats. On a larger scale than the study area, Defran *et al.* (1999) showed the high mobility of inshore bottlenose dolphins along the California coast is probably due to a shift in prey distribution. It is likely that the same dolphins frequented both the San Diego coastline and the study area following prey distribution.

ACKNOWLEDGEMENTS

The manuscript was improved through review by W. Hamner, J. Heyning, G. Grether, B. Schlinger, P. Mendel and G. Bearzi. Field research was funded by Ocean Conservation Society, the UCLA Mentor Research Program Fellowship and the Coastal Environmental Quality Graduate Fellowship. Special thanks to C. Saylan, the Los Angeles Dolphin Project assistants (particularly K. Jones, L. Openshaw and D. Osell), N. Nezlín, Maptech, Trimble Navigation and ESRI. Fieldwork was carried out under the current laws of California and the General Authorisation for Scientific Research issued by NOAA (File No. 856-1366).

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Date received: April 2004.

Date accepted: October 2004.

