

Ecology and comparison of coastal and offshore bottlenose dolphins (*Tursiops truncatus*) in California

Maddalena Bearzi^{A,B}, Charles A. Saylan^A and Alice Hwang^A

^AOcean Conservation Society, PO Box 12860, Marina del Rey, CA 90295, USA.

^BCorresponding author. Email: mbearzi@earthlink.net

Abstract. Populations of coastal and offshore bottlenose dolphins (*Tursiops truncatus*) are considered to differ ecologically, with implications for their protection and management. We assessed occurrence, distribution and behaviour of coastal and offshore populations of dolphins during a photo-identification study in Santa Monica Bay and nearby areas (1997–2007). Bottlenose dolphins occurred year-round and were encountered on 44.2% of all surveys ($n = 425$). We photo-identified 647 individuals; of these, 375 (58.0%) were coastal (<1 km from shore), 241 (37.2%) offshore (1–65 km from shore) and 31 were both (4.8%). Dolphins mostly travel (69.0%) and travel-dive (61.5%), with offshore dolphins socialising more (22.6%) than coastal. There were low re-sighting rates for both coastal and offshore dolphins. Low re-sighting rates of coastal individuals provide little evidence of year-round site fidelity, suggesting their range is greater than the study area. Several individuals were re-sighted between and over 1-year periods, often foraging. This suggests that coastal dolphins: (1) are highly mobile within inshore waters, but spend time foraging in the study area; and (2) range >1 km from shore, contrary to what has been previously reported.

Additional keywords: behaviour, conservation, distribution, feeding, habitat, occurrence, photo-identification.

Introduction

Common bottlenose dolphins (*Tursiops truncatus*; hereafter bottlenose dolphins) are top predators and, as such, useful bio-indicators of the health and status of the marine environment (Wells *et al.* 2004; Torres *et al.* 2008). A better understanding of dolphin populations both in coastal and offshore waters – including their ecological comparison and knowledge of their ranging patterns – is crucial to protect cetacean species (Fury and Harrison 2008) and for making conservation and management decisions for proposed Marine Protected Areas (MPAs; Wilson *et al.* 2004).

The genus *Tursiops* occurs in both temperate and tropical waters. Populations inhabit pelagic waters as well as coastal areas (Leatherwood *et al.* 1983). These populations exhibit morphological, osteological and molecular differences (LeDuc and Curry 1998; Rossbach and Herzing 1999; Fazioli *et al.* 2006). In the eastern North Pacific Ocean, a coastal (inhabiting waters <1 km from shore) and offshore (inhabiting waters >1 km from shore) population of bottlenose dolphins is recognised based on morphology, photo-identification and aerial surveys (Walker 1981; Defran and Weller 1999; Carretta *et al.* 2006). Coastal dolphins have less genetic variability than offshore dolphins. Genetic differentiation in mitochondrial DNA and microsatellite loci indicates long-term separation (Lowther 2006). There are currently ~320 coastal bottlenose dolphins (Dudzick *et al.* 2005) and the offshore population is estimated to be ~3000 individuals within the United States Exclusive Economic Zone (Carretta *et al.* 2006). Long-term studies of free-ranging bottlenose dolphins in the Southern California Bight (SCB) have focussed mostly near San Diego (less than 1 km from shore; Defran and

Weller 1999). Offshore dolphins are poorly studied worldwide (Silva *et al.* 2008) and, in SCB, they are considered a separate population based on photographic and genetic evidence (Shane 1994; Lowther 2006).

This long-term study (1997–2007) on bottlenose dolphins off Southern California waters is a new ecological comparison between coastal and offshore populations, providing data on the previously unstudied behavioural ecology of the offshore bottlenose dolphin population, and revising previous literature stating these populations are entirely spatially separate in Southern California waters. Understanding the ecology and dynamics of these coastal and offshore dolphins off California waters – as well as their site fidelity and spatial overlap – is useful not only for any decision making process for proposed MPAs in the area, but also findings that have implications for future genetic and population studies (Lowther 2006).

Materials and methods

Study area

The Santa Monica Bay study area (~460 km²) 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 escarpment to the west. The bay contains three submarine canyons: Dume and Redondo Canyons head in shallow water (50 m), whereas Santa Monica Canyon begins at a depth of ~100 m. The mean depth is ~55 m and the maximum depth 450 m. Surveys were also conducted outside Santa Monica Bay, both along the coast (at 0.5 km from shore) to the south (33°43'N, 118°15'W) and to the north (34°5'N, 119°6'W), and in pelagic

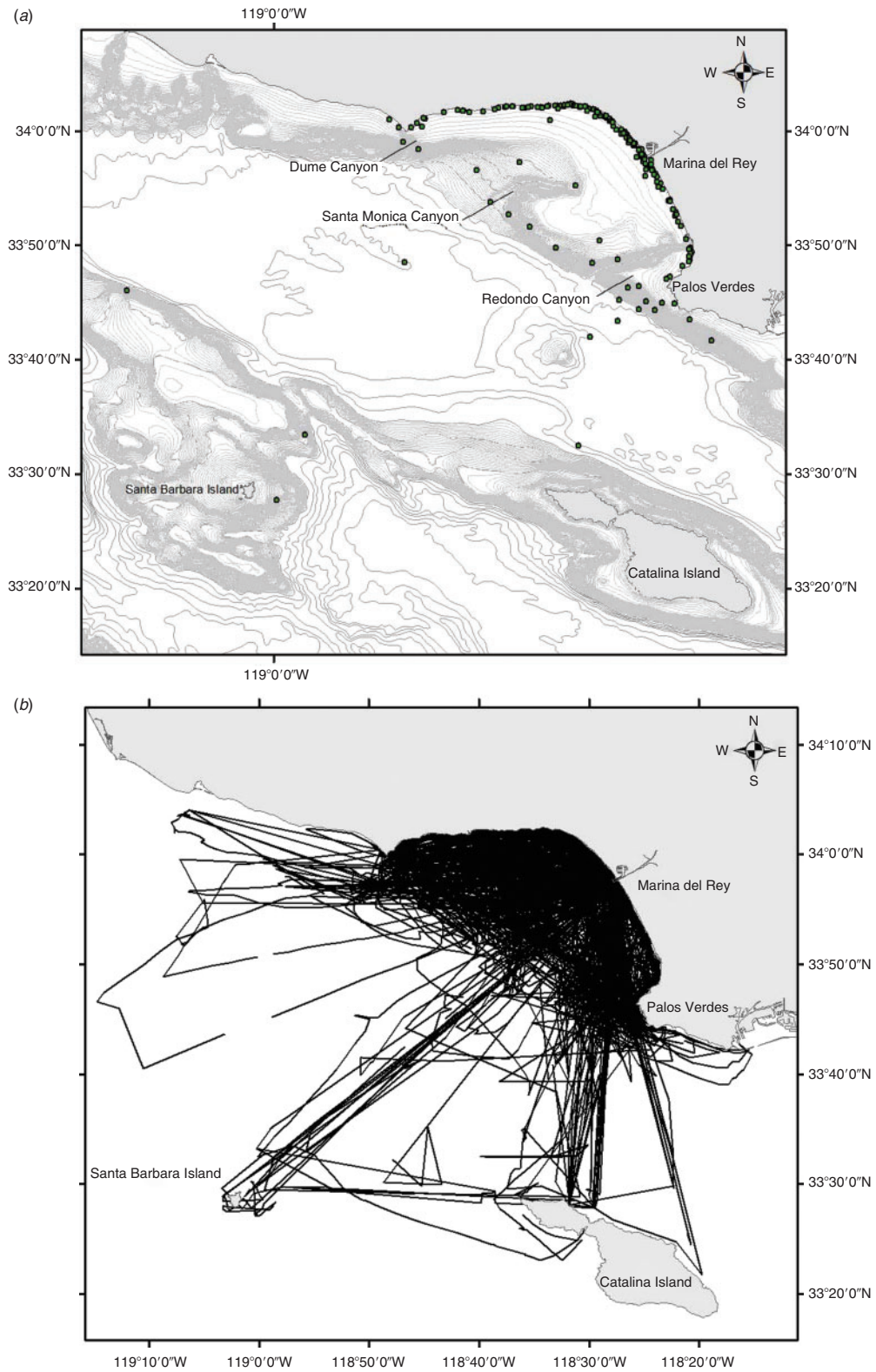


Fig. 1. (a) The study area and the distribution of coastal and offshore bottlenose dolphins. Each symbol represents initial GPS coordinates of photo-identified bottlenose dolphin sightings. (b) The total survey effort in the study area for the years 1997–2007.

waters off Catalina (33°23'N, 118°41'W) and Santa Barbara Islands (33°27'N, 119°3'W) up to 65 km offshore (Fig. 1a).

The bay has mild temperatures, short rainy winters and long, dry summers. Normal water surface temperatures range from 11 to 22°C. During the 1997–1998 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 (Nezlin *et al.* 2003).

Data collection and analysis

Surveys were conducted from February 1997 to June 2002 and from June 2005 to July 2007 for an average of 5.2 days per month ($n = 425$, Table 1). Inshore (distance from shore up to 1 km) and offshore (distance from shore >1 km) routes were followed in the morning and early afternoon with winds of Beaufort scale 2 or less, sea state of 0 (no sea swells) and visibility >300 m. Routes were planned to allow an even coverage of the bay (Fig. 1b). Surveys were done from 7-m (1997–2000) and 10-m powerboats (2001–2002, 2006–2007) and a 17-m sailboat (2005), moving at an average speed of 18 km h⁻¹. The dolphins' position and speed (± 30 m from the boat) were approximated to the boat's position using a GPS. When dolphins were observed, data on the number of animals and behaviour (Bearzi 2005a) with other species were recorded at 5-min intervals. The number of dolphins was verified later using photo-identification analysis. Photo-identification followed the methods of Würsig and Jefferson (1990) and Bearzi *et al.* (1997). For each sighting of dolphin groups, we attempted to photograph all individuals. Colour photographs were taken with 35-mm Canon 1N (Canon, Lake Success, NY, USA) cameras equipped with 75–300-mm lenses, and a digital camera 10D equipped with a 400-mm lens (Canon, Lake Success, NY, USA). We also videotaped the animals with Canon Hi8 mm or Canon GL1 Digital Video Camcorders. Behavioural data collected from July to December 1996 (58 h of field observations) provided a framework for the design of sampling procedures systematically, which were adopted beginning January 1997 (Bearzi 2003). For 1997–2002, 810 images were scanned and matched using a computer-assisted identification system (*Finscan*; Kreho *et al.* 1999). For 2005–2007, 464 digital images were catalogued and matched using ACD See software and techniques described by Mazzoil *et al.* (2004; modified).

T-tests were used to assess seasonal and annual differences in sighting numbers. Chi-square tests were used to determine how behavioural budgets differed between coastal and offshore dolphins and across years. The basic assumptions of normality and independence were met. Data analyses were performed using Statview 5.0 (SAS Institute, Cary, NC, USA) and Microsoft Excel 2003 (Microsoft Corporation, Redmond, WA, USA); data on species distribution were plotted with ArcGis version 9.2 (ESRI, Redland, CA, USA). For sighting frequency analysis, different sightings of the same individual during the same day were considered only once. Since no genetic analysis was performed, data for coastal and offshore bottlenose dolphins were divided based on their distance from shore: all bottlenose dolphins observed during coastal surveys 0.5 km from shore (which includes animals occasionally observed up to 1 km from shore) were considered coastal; all bottlenose dolphins observed during surveys at >1 km from shore were considered offshore.

A *dolphin school* was defined as all dolphins in continuous association with each other and within visual range of the survey team (Weller 1991) and a *focal group* was defined as any group of animals 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 number was excluded from group size calculation. A *behavioural state* was defined as a broad category of activities, such as feeding behaviour, that integrates several individual behaviour patterns into a recognisable pattern (Weaver 1987; for definitions see Bearzi 2005a).

Results

Field effort

Data were collected during 204 inshore and 221 offshore surveys (Table 1). A total of 823 h were spent searching for cetaceans in good weather conditions. A total of 400 h were spent observing 509 dolphin groups for an average of 50 min (range 1–263 min); 221 bottlenose dolphin schools were encountered. Coastal bottlenose dolphin sightings lasted on average 59 min (s.d. = 38.94, range 3–262 min, $n = 175$); offshore dolphin sightings lasted on average 57 min (s.d. = 43.02, range 4–166 min, $n = 40$) (Table 2).

Occurrence, distribution and site fidelity

In coastal waters, bottlenose dolphins were the species most frequently sighted year-round (84.1%, $n = 180$ schools). Only one school was encountered on 48.0% of all survey days (98 of 204). Multiple schools (range = 2–6) were sighted on 17.7% ($n = 36$) of all inshore surveys. In offshore waters, dolphins were sighted less often (14.0%, $n = 41$ schools; Table 2). Only one school was encountered on 15.4% of offshore survey days (34 of 221). Multiple schools (range = 2–5) were only sighted during two offshore surveys. For both coastal and offshore dolphins, the presence of other groups not included in the focal groups occurred during 18.1% of sightings ($n = 40$).

The sighting frequencies (sightings h⁻¹) and the percentage of total sightings for coastal and offshore dolphins are presented in Table 2 and Fig. 2. There was a significant difference between years in the number of sightings of coastal dolphins ($t_8 = 3.60$, $P = 0.007$), with more sightings during 1998 than all other years. A significant difference in number of sightings was also recorded for offshore dolphins ($t_8 = 3.5$, $P = 0.008$), with more sightings during 1997 than all other years.

A significant difference in sighting numbers was observed within the four seasonal categories for 7 out of the 9 years; no difference was found in 2002 and 2006 (Table 3). In 1997, 2000 and 2007, sightings were more frequent during winter months; in other years, more frequent in spring and summer. For coastal dolphins, a significant difference in sighting numbers within the four seasonal categories was observed for 5 out of the 9 years. In 1998, 1999 and 2007, coastal dolphin sightings occurred more frequently during spring and summer; in 2000 and 2001, more frequently in winter. For offshore dolphins, there was no significant difference in sighting numbers within the four seasonal categories for any of the years (Table 3).

Table 1. Number of surveys and summary of research effort in Santa Monica Bay and adjacent areas for the years 1997–2002 and 2005–2007
BD, bottlenose dolphins

	1997	1998	1999	2000	2001	2002	2005	2006	2007	Total
Surveys										
Inshore surveys	16	55	39	33	27	9	3	14	8	204
Offshore surveys	34	41	32	31	26	12	7	28	10	221
Total number of surveys	50	96	71	64	53	21	10	42	18	425
Research effort ^A										
Hours spent in the field	144	224	178	149	137	73	68	194	56	1223
Hours spent searching for cetaceans	110	136	130	105	82	44	48	134	34	823
Hours spent with cetaceans	34	88	48	44	55	29	20	60	22	400
Hours spent with BD ^B	18	65	32	19	20	7	9	28	15	213
Hours spent with coastal BD	8	56	27	12	17	4	6	17	12	159
Hours spent with offshore BD	10	9	5	7	3	3	3	11	3	54
N of 5-min behavioural samples for all cetaceans	295	1065	698	525	675	396	265	638	234	4791
N of 5-min behavioural samples for BD	134	814	368	262	187	100	115	297	163	2409

^AInshore and offshore surveys conducted during the same day were considered as two separate surveys. ^BData on research effort for 2002 are calculated on a total of 17 surveys. No data were collected: December 1999, October 2000, July 2001, September 2001, July 2005, December 2005, May 2006, February–April 2007.

Table 2. Number of sightings and sighting frequency (sightings h⁻¹) of bottlenose dolphins for 1997–2002 and 2005–2007
BD, bottlenose dolphins

	1997	1998	1999	2000	2001	2002	2005	2006	2007	Total
N bottlenose dolphin sightings	20	61	34	22	20	7	10	29	18	221
Sighting frequency	0.14	0.27	0.19	0.15	0.14	0.10	0.15	0.15	0.32	0.18
N coastal BD sightings	7	58	32	16	18	6	6	21	16	180
Sighting frequency	0.05	0.26	0.18	0.11	0.13	0.08	0.39	0.47	0.55	0.15
N offshore BD sightings	13	3	2	6	2	1	4	8	2	41
Sighting frequency	0.09	0.01	0.01	0.04	0.01	0.01	0.06	0.05	0.07	0.03

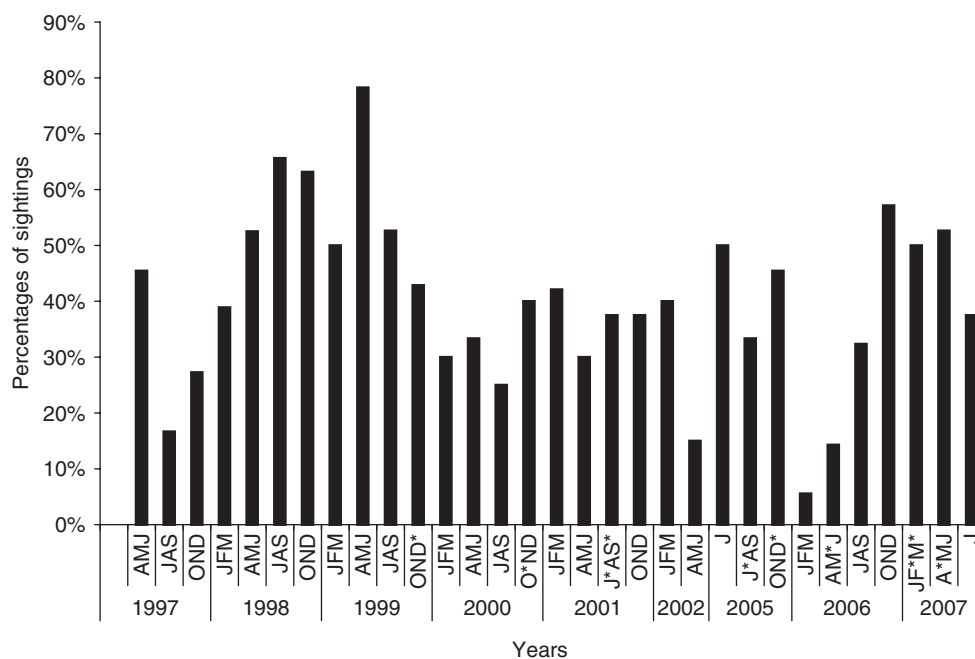


Fig. 2. Percentages of total bottlenose dolphin sightings recorded during 3-month periods (January–March, April–June, July–September, October–December) in Santa Monica Bay and adjacent areas. *, no data collection.

Table 3. Difference in sighting numbers for coastal and offshore bottlenose dolphins within the four seasonal categories (Winter: January–March, Spring: April–June, Summer: June–September and Fall: October–December) between 1997–2002 and 2005–2007

	1997	1998	1999	2000	2001	2002	2005	2006	2007
Combined coastal and offshore									
t	3.6	8.9	6.7	10.2	15.6	2.2	8.6	2.4	10.0
df.	3	3	3	3	3	1	2	3	2
P	0.031	0.003	0.005	0.002	0.001	0.272	0.013	0.096	0.010
Coastal									
t	2.7	7.7	5.5	8.4	7.6	1.7	1.8	2.2	4.9
df.	3	3	3	3	3	1	2	3	2
P	0.075	0.005	0.012	0.004	0.005	0.344	0.217	0.110	0.039
Offshore									
t	1.7	1.6	1.4	1.8	1.6	1	1.8	2.4	2
df.	3	3	3	3	3	1	2	3	2
P	0.182	0.211	0.261	0.169	0.211	0.500	0.217	0.096	0.189

Calves were recorded in 42.0% of the sightings ($n = 86$; range 1–6; mean = 2.0, s.d. = 1.0, $n = 205$). Calves were recorded during 37.2% of coastal sightings ($n = 64$; range 1–6; mean = 1.6, s.d. = 0.92, $n = 172$). During offshore surveys, calves were seen 66.7% of the time ($n = 22$) with a range of 1–4 calves per sighting (mean = 2.0, s.d. = 0.90, $n = 33$). For both coastal and offshore bottlenose dolphins, a significant difference in the number of calf sightings among seasons was observed ($t_3 = 8.93$, $P = 0.003$), with more calves sighted in the spring than in the other three seasons.

This species was found regularly in coastal waters (<500 m; 84.1%, $n = 180$ schools), most often within 10–100 m from shore, and less often in offshore waters (>500 m; 18.6%, $n = 41$ schools). Offshore bottlenose dolphins had a preference for submarine canyons and the escarpments between Santa Monica and Redondo Canyon and off Palos Verdes (67.7%, $n = 21$ of 31 identified individuals). Outside the bay, bottlenose were mostly concentrated near escarpments off Santa Barbara and Catalina Islands (12.9%, $n = 4$) (Fig. 1a).

To identify distinct coastal and offshore individual dolphins, matching procedures focussed on 195 sightings (88.2% of total bottlenose dolphin sightings, $n = 221$). A total of 647 distinct individuals (50.8% of total identified and re-sighted individuals, $n = 1274$) were recognised. 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 inshore and offshore were calculated. Three hundred and seventy-five (58.0%) out of the 647 identified individuals were recorded only in coastal waters, 241 (37.2%) were seen only in offshore waters, but 31 individuals were seen in both coastal and offshore waters (4.8%). Of these 31 individuals, the majority (90.3%, $n = 28$) were sighted offshore only once, 2 (6.4%) were observed offshore twice and 1 (3.2%) was seen offshore four times. The distance from shore of the 31 individuals observed both in coastal and offshore waters varied between 3 and 5 km from the coast (19.3%, $n = 6$) to >15 km offshore (22.6%, $n = 7$). Most of these individuals, however, were recorded along the Santa Monica Bay escarpment and near submarine canyons (71%, $n = 22$). Further, three individuals (9.7%) were observed in offshore schools of different composition (range 2–4 schools).

Many individuals were first identified during 1998, and the number of new identifications gradually decreased (Fig. 3a, b). Beginning in 2005, however, the overall number of new individuals sharply increased, and has continuously risen since. The majority of offshore individuals were newly identified during 2005–2006, while the highest increase in new coastal dolphins was observed in 2007.

Sighting frequencies for identified dolphins ranged up to 15 days (mean = 1.97, s.d. = 1.86, $n = 647$; available as an Accessory Publication to this paper in Accessory Publication 1); 63.1% ($n = 408$) were sighted only once while 9.4% ($n = 61$) were sighted five or more times. For coastal dolphins, 50.7% ($n = 190$) were sighted only once, while most offshore dolphins (90.5%, $n = 218$) were sighted once. The number of sightings within seasons and years for identified individuals in coastal and offshore waters is presented in Accessory Publication 2.

Behavioural patterns

The time budget of bottlenose dolphins was predominantly *Travel* (42.2%; n 5-min samples = 2381) and *Travel-dive* (24.5%). *Feeding* was observed in 4.0% of sightings, also in association with other activities such as *Travel* (*Travel-feeding*: 5.9%), *Dive* (*Dive-feeding*: 1.3%) and *Socialise* (*Feeding-socialise*: 0.9%). The behaviour of coastal and offshore dolphins differed significantly ($\chi^2_9 = 32.22$, $P = 0.001$), with more *Travel-dive* observed in coastal schools, and more *Travel-socialise* and *Travel-dive-socialise* observed in offshore schools. The overall behavioural budget recorded for coastal and offshore bottlenose dolphins is presented in Accessory Publication 3.

The cumulative behavioural budget – computed for the six most common patterns of activities – is shown in Fig. 4. There was a significant difference in behaviour between years ($\chi^2_{40} = 383.39$, $P = 0.001$), with most *Travel* and *Travel-dive* recorded in 1998, 1999 and 2007, most *Feeding* observed in 1997 and 2000, most *Travel-feeding* observed in 2002 and most *Travel-socialising* observed in 2006.

Bottlenose dolphins travelled at an average speed of 4.5 km h⁻¹ (mode = 1.8, s.d. = 2.57, range 0.9–16.6, $n = 1250$ from subset of 5-min data samples selected at random). Offshore schools travelled faster than coastal schools (offshore: mean = 6.2, s.d. = 3.02, $n = 150$ from subset of data selected

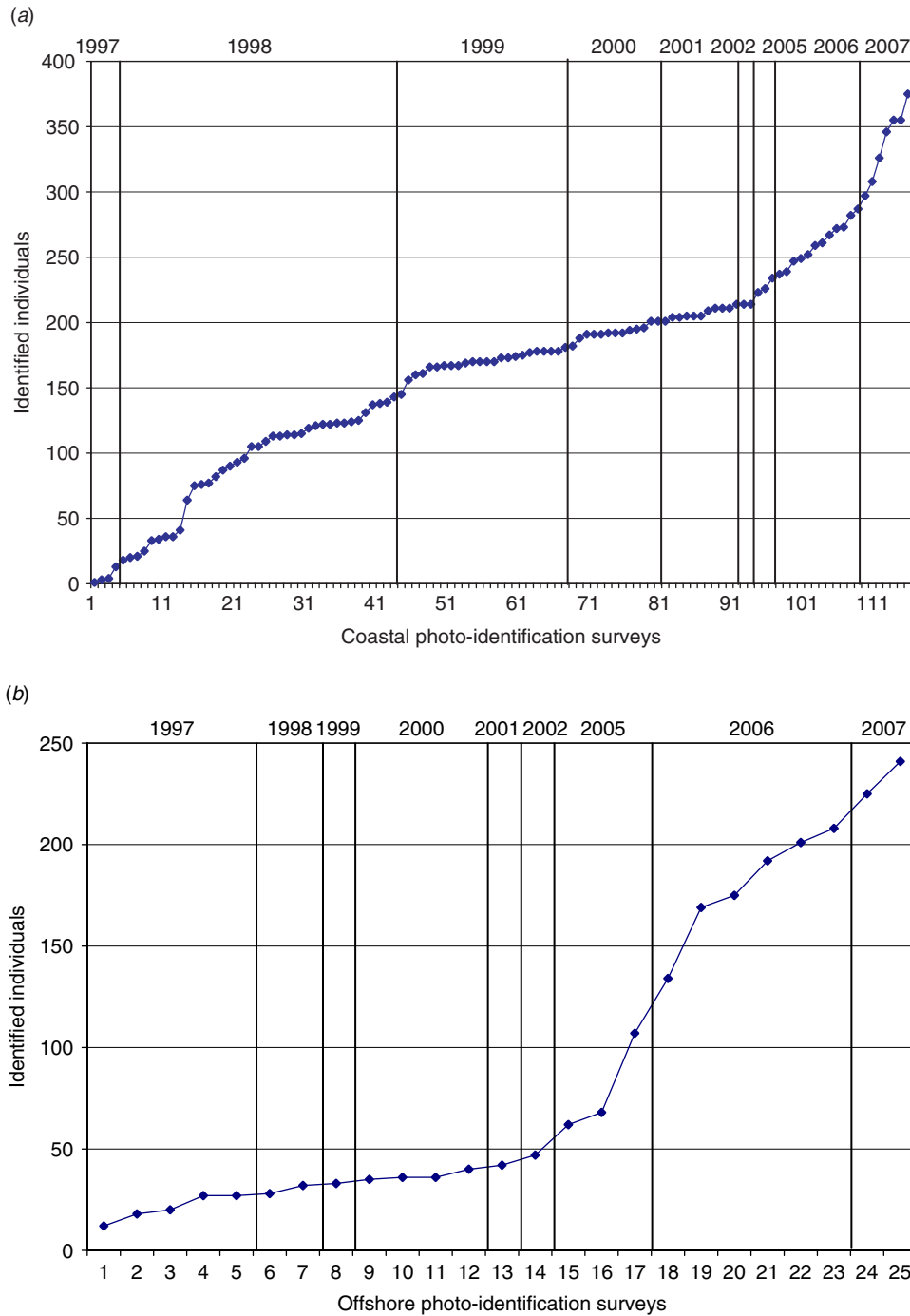


Fig. 3. Rate of identification of new coastal (a) and offshore (b) bottlenose individuals over time ('rate of discovery') in the years 1997–2007 for Santa Monica Bay and adjacent areas.

at random; coastal: mean = 4.0, s.d. = 2.26, $n = 150$; mean difference = 2.1, $t_{149} = 7.58$, $P = 0.001$).

Discussion

Occurrence, distribution and site fidelity

The bottlenose dolphin was the most commonly observed species in Santa Monica Bay, as previously recorded for the SCB

(Bonnell and Dailey 1993; Carretta *et al.* 2006). The occurrence and distribution of coastal dolphins was mostly within 500 m from shore, largely in agreement with observations off the San Diego coastline (Defran and Weller 1999; Lang 2002; Dudzik *et al.* 2005). This differs, however, from Southern California reports suggesting coastal dolphins occur only less than 1 km from shore. These reports imply high fidelity to a 'narrow coastal corridor' at depths of 10–30 m (Shane 1994; Defran and

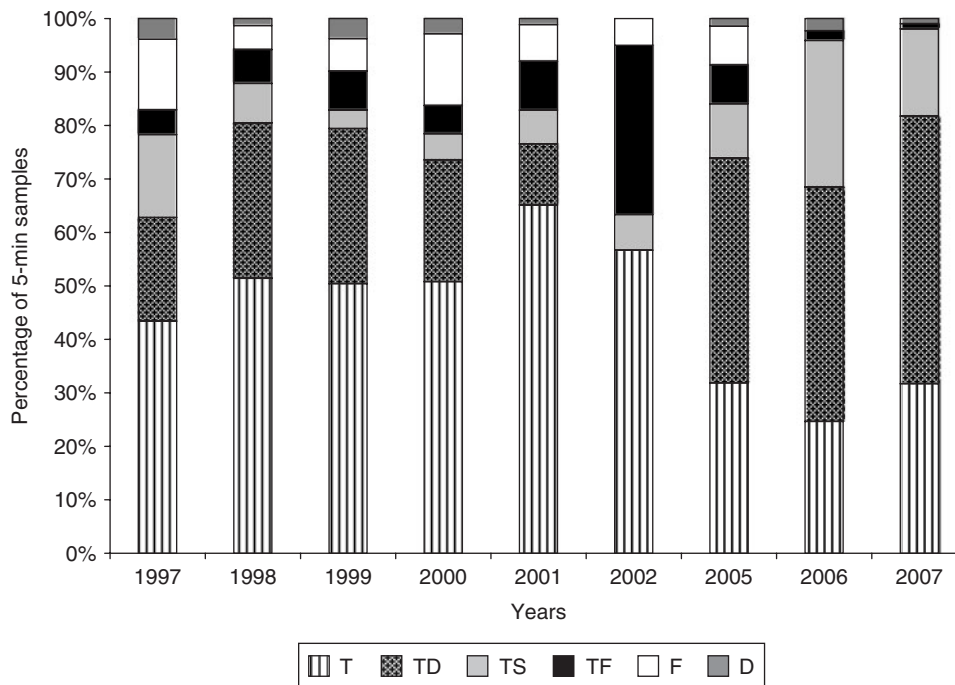


Fig. 4. Behavioural budget computed for the six most common patterns of activities during the study period for combined coastal and offshore bottlenose dolphins. T, Travel; TD, Travel-Dive; TS, Travel-Socialise; TF, Travel-Feeding; F, Feeding; D, Dive. These behaviours include activities performed simultaneously by different focal group individuals during 5-min samples.

Weller 1999; Defran *et al.* 1999), with no overlap between coastal and offshore individuals (Schultz *et al.* 1988; DeDecker *et al.* 1999). In the present study, 31 photo-identified coastal individuals were observed in offshore waters up to 15 km from shore. Further, several individuals preferred canyons and escarpments. The dissimilar bathymetry and oceanography of the two areas may explain some of the observed differences. Likely, the presence of the same individuals both inshore and offshore in Santa Monica Bay and adjacent areas is related to the presence of submarine canyons and escarpments (Dartnell 2000; Bearzi 2005b), optimal features for mixing of nutrients and consequently rich in prey for dolphins (Hui 1979). In contrast, the San Diego area has different oceanographic characteristics with open coastal waters being relatively unstable and dynamic with a substantial variability in water temperature and, consequently, in abundance and type of prey over years or decades (Dailey *et al.* 1993; Defran *et al.* 1999). Weller (1991) reported these variations were responsible for dolphins' behavioural flexibility relative to changes in habitat.

Schultz *et al.* (1988) and DeDecker *et al.* (1999) suggested that coastal animals follow a narrow corridor less than 1 km from shore and do not mix with offshore animals. Offshore dolphins were usually >4 km from shore along California and Baja, ranging as far north as Oregon and Washington (Carretta *et al.* 2006; Lowther 2006). Our data are consistent with previous observations but some individuals photo-identified offshore were also observed at less than 500 m from shore, and *vice-versa*, showing no restrictions to either the offshore waters or a 4-km boundary.

The significant difference in sighting numbers for both coastal and offshore dolphins and the seasonal differences observed

for coastal dolphins is likely related to prey distribution and abundance and the presence of the 1997–1998 El Niño (Bearzi 2005a). El Niño usually reduces primary productivity throughout most of the coastal Eastern Pacific (Cane 1983) and is correlated with shifts in distribution of marine mammals and their prey (Shane 1995a, 1995b; Defran *et al.* 1999; Hill 1999). We found that dolphins occurred throughout the 1997–1998 El Niño and the following La Niña. The lack of severe effects driven by warm-water incursions on this species may be explained by the opportunistic feeding habits of bottlenose dolphins (Bearzi *et al.* 1999). During the 1997–1998 El Niño event, some fisheries decreased in SCB but others improved; prey items such as Pacific sardine (*Sardinops sagax*), white seabass (*Atractoscion nobilis*) and splitnose rockfish (*Sebastes diploproa*) were among the species in which catches increased (California Department of Fish and Game 2000). Offshore animals exhibited no apparent seasonality in distribution as reported by Carretta *et al.* (2006) for California waters.

The common presence of calves in spring agrees with Scott *et al.* (1990) for the West coast of Florida, although seasonal peaks may vary by area. Worldwide, calves are known to be born throughout the year (Hansen 1990).

The rate at which previously unidentified dolphins were discovered increased mostly in 2005–2007. For coastal dolphins, the rate increased mostly in 1998 and 2007. For 1997–2002, the rate of discovery curve for newly identified coastal dolphins was comparable to the trend for Southern California (Defran and Weller 1999; Lang 2002; Dudzik *et al.* 2005), but it contrasts with other studies where asymptotes occur over shorter periods of time (Wells 1986; Campbell *et al.* 2002;

Zolman 2002). After appearing to approach a possible asymptote in 2002, however, many new individuals were identified during 2005–2007, likely due to a hiatus in the study, but also to a change in distribution due to oceanographic conditions. D. Maldini (pers. comm.) recorded a sharp increase of newly photo-identified dolphins in 2006–2007 near Monterey. For offshore dolphins, the rate at which new individuals were identified increased mostly in 2005–2007, likely due to identification of a limited number of offshore dolphins in previous years. This trend is comparable to what Speakman *et al.* (2006) reported along the Atlantic coast where dolphins appear to be short-term or infrequent visitors, or transients. The number of identified coastal dolphins was comparable to the number reported for the San Diego area, 140 km to the south ($n = 375$, the present study, *v.* $n = 373$, Defran and Weller 1999).

The variability in coastal dolphin sightings and the low individual sighting frequencies were generally consistent with data from San Diego (Defran and Weller 1999). The variation in time between many re-sightings of identified coastal dolphins in Santa Monica Bay suggested that the area represents part of a larger home range within the California coast. Defran *et al.* (1999) reported that 58.0% ($n = 120$) of 207 individuals exhibited back-and-forth movements over 470 km of coastline, with no evidence of fidelity to any particular area. The high mobility of dolphins within a relatively narrow coastal zone reflected the dynamic nature of this coastal ecosystem and the associated patchy distribution of food resources (Dailey *et al.* 1993). Previous work also suggested that bottlenose dolphins made more movements where temperature and prey abundance fluctuate seasonally (Wells *et al.* 1990; Bräger *et al.* 1994).

In Santa Monica Bay, most identified coastal individuals were not observed year-round and the proportion of coastal dolphins sighted only once in the bay (50.7%) was comparable to the proportion reported in other areas along the California coast (69.0% Ensenada, 71.0% Orange County, 53.0% Santa Barbara; Defran *et al.* 1999), indicating the absence of a strong residency pattern and the likelihood of belonging to the same highly mobile and behaviourally flexible open coastal population. In the bay, however, some individuals used the area on a seasonal basis, showing some degree of fidelity to the study area. The low re-sighting rates and lack of seasonality exhibited by offshore bottlenose dolphins suggests little or no site fidelity to the study area, as reported by previous studies for the SCB (Carretta *et al.* 2006; Lowther 2006).

Behavioural patterns

Our behavioural data are comparable to studies for the San Diego area (Hanson and Defran 1993), with bottlenose dolphins travelling most of the time. Feeding was seen more often near San Diego (19.0% of the time) than in the study area (13.2%), possibly due to differences in methodologies and definitions of 'feeding'. Surface feeding was occasionally observed. The rather large amount of time spent travel-diving and diving may have been also related to food searching or feeding activities, which cannot be directly observed (Bearzi *et al.* 1999). The significantly greater amount of travel and travel-dive recorded during the years 1998–1999 may have been linked to an increased need to forage for prey, which had become more patchily distributed

during those 2 years (Bearzi 2005a). The significantly greater amount of travel-socialise and travel-dive-socialise observed in offshore dolphins as compared with coastal dolphins may be related to a greater need for cooperative feeding strategies in pelagic waters (Rossbach and Herzog 1999).

Travel speeds lower than those calculated for bottlenose dolphins in other areas were recorded (the present study: 4.5 km h⁻¹; Würsig and Würsig 1979: 6.1 km h⁻¹; Shane 1990a: 5.5 km h⁻¹). Bottlenose dolphins were likely to travel at lower speed to forage in shallow waters considering that travel has, among its main functions, the purpose of locating food (Shane 1990b). Offshore dolphins travelled at higher speeds than coastal, possibly due to increased water depth resulting in different foraging strategies (Rossbach and Herzog 1999).

Coastal dolphins spent most of their time moving along favourite 'corridors' within 50 m from shore, as also recorded by Defran and Weller (1999), Lang (2002) and Dudzik *et al.* (2005). Frequent direction changes along the coastline were often observed in relation to prey movements. Travel activities were often followed by feeding in spots that may have reflected the presence of demersal prey on sand flats (Navarro and Bearzi 2007; M. Bearzi, pers. obs.). On a larger scale than the study area, Defran *et al.* (1999) showed the high mobility of coastal dolphins along the California shoreline, probably due to a shift in prey distribution. It was likely that the same dolphins frequented both the San Diego coastline and the study area following prey distribution. Offshore dolphins showed frequent directional changes and short stops, which may also have been related to prey movements, as well as increased socialising activities. The apparent high mobility of offshore dolphins suggests they may belong to the same population of dolphins ranging from Baja California to Washington reported by Carretta *et al.* (2006).

Implications for conservation and management

New insights on coastal and offshore bottlenose dolphins for Santa Monica Bay and adjacent waters show that: (1) the spatial overlap between the two populations previously considered completely separate, (2) the year-round presence of animals near shore and in proximity of canyons and escarpments and (3) the time spent by these animals foraging in the study area are significant factors to take into account in any decision-making process for the conservation and management of marine resources in the area. Bottlenose dolphins are apex predators and vulnerable to indirect threats, such as chemical pollution, acoustic pollution and marine debris (Simmonds and Hutchinson 1996; Fury and Harrison 2008). Direct anthropogenic effects on these marine mammals are difficult to assess, but dolphins bioaccumulate toxins and may suffer immunological and reproductive disorders as a consequence (Simmonds and Hutchinson 1996). Coastal dolphins are particularly susceptible to harmful threats as they inhabit regions where pollution is usually abundant (Curry 1997; Wang *et al.* 1999). Coastal animals in the Eastern North Pacific are also known to have the highest levels of DDT concentration of all marine mammals, which seriously affects reproductive rate (Hansen 1990).

To protect and manage any cetacean species, it is important to determine its population boundaries and potential gene flow across those boundaries (Dizon 2002). These boundaries can be

initially determined by geographic distribution, behaviour and morphology and, later on, sibling species and subspecies can be distinguished using molecular genetic analysis (Lande 1991; Tezanos-Pinto *et al.* 2009). The present study offers new insights on the occurrence, distribution and behaviour of coastal and offshore dolphins. Further, it emphasises the need for genetic analysis studies on photo-identified individuals in the study area to better understand the differentiation between coastal and offshore bottlenose dolphin forms, and the need for conservation and management of these animals.

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