

## The behaviour and feeding ecology of the Pacific coast bottlenose dolphin, *Tursiops truncatus*

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### Abstract

An activity budget was determined for Pacific bottlenose dolphins (*Tursiops truncatus*) in a 0.5 km wide by 32 km long study area located in the coastal waters of north San Diego County during daylight hours. Twelve months of cliff-based behaviour sampling accumulated 213 hrs of direct observation on 73 dolphin schools. Behaviour was documented through instantaneous samples of focal group activity taken at 3 min intervals, evenly distributed across time of day and season. The overall proportion of time spent in each of the five behaviour states was: travel (63%), feed (19%), social (12%), play (3%) and rest (3%), and 90% of all dolphin activity occurred within 0.25 km of shore. Dolphin behaviour proportions were relatively constant across seasons except for an increase in social activity during the summer. Feeding time increased during the early morning and late afternoon; during periods of high tide current; and in ocean border, reef, and estuary habitats. Distributions of travel time were inversely related to feeding across diurnal, tide, and habitat type analyses. Variations in the temporal and spatial distribution of feeding were integrated with a review of the trophic relations and availability of 25 dolphin prey fish. Our interpretation of these data placed primary emphasis on seasonal and diurnal temporal cycles, tide currents, and habitat features which affect dolphin prey directly, while secondary emphasis was placed on the coastal distribution of prey species nutrients.

### Introduction

Photoidentification studies of Pacific coast bottlenose dolphins (*Tursiops truncatus*) within the San Diego study area between 1981-1983 (Hansen, 1990) and 1984-1989 have recently been summarized (Defran and Weller, in prep; Hansen and

Defran, 1990). These data provide evidence for little year round or seasonal site fidelity among dolphins within the San Diego study. Further resights of dolphins photographed in the San Diego Study area at Santa Barbara, Orange County, and Ensenada suggests that Pacific coast bottlenose dolphins are highly mobile within the Southern California Bight, and that many of these individuals travel significant distances along this coastline (Defran *et al.*, 1986; Weller and Defran, 1989). The mobility and range characteristics of individual Pacific coast bottlenose dolphins are in marked contrast to the high degree of geographic fidelity displayed by coastal bottlenose dolphins in Sarasota, Florida (Irvine *et al.*, 1981; Scott *et al.*, 1990; Wells, 1978, 1986; Wells *et al.*, 1980; Wells *et al.*, 1987) as well as in Golfo San José, Chubut, Argentina (Würsig, 1978; Würsig and Harris, 1990; Würsig and Würsig, 1977, 1979).

Little is known about the global or local ecological variables that affect the distribution of coastal bottlenose dolphins within the Southern California Bight. An exception is the warm water El Niño event of 1982-1983. Reports by Wells *et al.* (1990) and Defran *et al.* (1991) suggest that the El Niño shifted the normal range of the population from the coastal waters of Los Angeles as far north as Santa Barbara, California. For a subset of these dolphins, the shift has extended as far north as the Monterey Bay area of north central California. Wells *et al.* (1990) suggested that changes in the distribution of dolphin prey fish, associated with the northern incursion of warm water, were probably the primary factor leading to the dolphins' shift in distribution.

Even less is known about the impact of local ecological variables on short-term behaviour states, such as traveling, feeding, and socializing in the Pacific coast bottlenose dolphin. Activity budgets compiled on several other coastal populations of bottlenose dolphins suggest that the availability of prey associated with diurnal, tide, and habitat variables exerts a strong influence on the organization

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of behaviour (Ballance, 1992; Saayman *et al.*, 1973; Würsig and Würsig, 1979). Shane's (1990b) comparative assessment of bottlenose dolphins in Aransas Pass, Texas and Sanibel Island, Florida indicates that differences in feeding behaviour between these populations are consistent with the prey ecology unique to each study area. In addition, behavioural studies of coastal populations of spinner (*Stenella longirostris*), dusky (*Lagenorhynchus obscurus*), and humpback (*Sousa chinensis*) dolphins have also demonstrated the importance of foraging demands in shaping the temporal and spatial distributions of dolphin activity (Norris and Dohl, 1980a; Saayman and Tayler, 1979; Würsig and Würsig, 1980).

Systematic and quantitative methods for sampling dolphin behaviour are essential to determining the effects of ecological variables on the budgeting of dolphin activity, both within a population and for comparative analysis between populations. As recently as 1979, however, Saayman and Tayler (1979: 167) noted that comprehensive studies of free-ranging dolphin behaviour '... were virtually non-existent and the available information must be extracted from diverse and fragmentary observations scattered in the literature.' The application of traditional behaviour sampling techniques (Altmann, 1974) to the quantification of behaviour in free-ranging dolphins (e.g., Acevedo, 1991; Ballance, 1992; Shane 1990a, b) is, therefore, a recent and needed development.

With these theoretical and methodological considerations in mind, the current research was designed to evaluate how San Diego dolphins budget their activity in relation to the ecological features of their habitat. The immediate background for this work was the development of a detailed and illustrated ethogram for San Diego dolphins (Weaver, 1987). This description of the dolphins' behavioural repertoire determined the elements used for defining the functional behavioural states of travel, feed, social, play, and rest for the current study. In turn, these states were analyzed as a function of diurnal, tide, and habitat variables. The prey ecology of Pacific coast bottlenose dolphins was also reviewed in order to interpret relationships between factors affecting prey availability at multiple trophic levels and observed patterns of dolphin behaviour.

## Methods

### Study Area

The study area was a narrow 16 km<sup>2</sup> coastal strip in San Diego County, California, U.S.A., that extends 31.8 km from Scripps Pier at the south boundary (32°52'00"N) to South Carlsbad at the north

boundary (33°07'30"N), and to 0.5 km offshore (Fig. 1). Water depth where dolphins have been observed ranges from 1 m nearshore to 6 m along the offshore boundary. Steep cliffs interspersed with low-lying flat areas border the shoreline. Beaches are variable in composition and range from gently sloping sand, to rock outcrop, and estuary mouth. Numerous submerged reefs and sea-grass flats are within 0.5 km of shore. Dense beds of giant kelp (*Macrocystis pyrifera*) border about 50% of the study area and are located about 0.5 km offshore (North and Hubbs, 1968) (Fig. 2).

The north San Diego County shoreline is exposed to the full force of the surf, which averages 1 m in height. Tides are semi-diurnal with a mean range of 1.2 m (U.S. Dept. of Commerce, 1987-1988 tide tables). During the study, ocean temperatures ranged from a mean low of 13°C in the winter to a high of 21°C in the summer (Scripps Institute of Oceanography, Marine Life Research Group, 1988-1989 water temperature tables). Winds are predominantly from the west northwest, light to still in the morning (0-8 km/hr), often becoming gusty in the afternoon (8-20 km/hr).

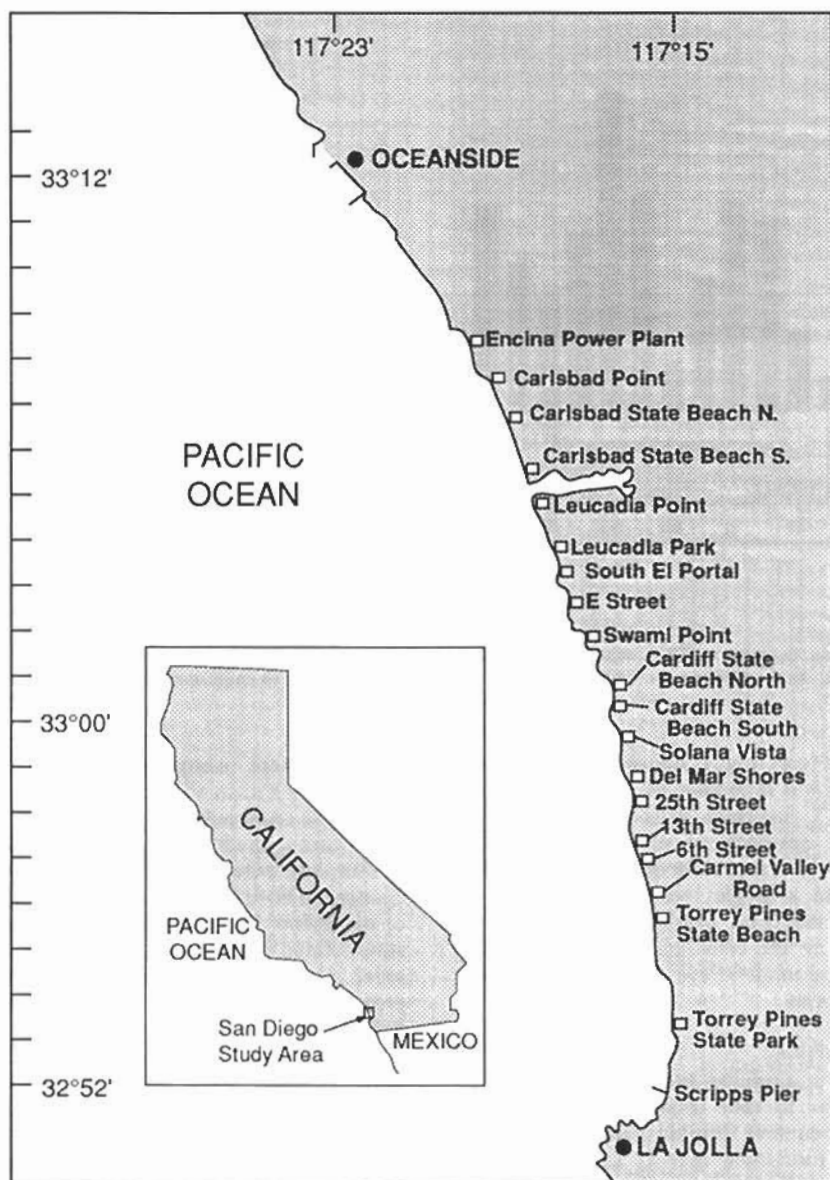
### Materials

A light truck was used for transportation between observation points. Small hand-held 7 × 35 Bushnell binoculars were used for searching and close range observation, and larger tripod mounted zoom 7-20 × 50 Minolta binoculars were used for long-range observation. An electronic cycling timer with a beeper was used for timing instantaneous sampling intervals and for keeping time of day. All ecological variables, search information, and behavioural observations were recorded on prepared forms.

### Research Effort

Prior to formal data collection, a five-month pilot study was conducted to develop and refine the research methodology. Formal data collection began in April 1988 and ended March 1989. One hundred and twenty surveys were conducted involving 426 hrs in the field, of which 213 hrs were spent in direct observation of dolphins. Once located, dolphins were tracked and observed for periods of 33 min to 9.3 hrs.

During the course of data collection, each quarter of the year was sampled relatively evenly. Within each quarter, further effort was directed to sampling dolphin behaviour evenly across all daylight hours. Representative sampling of all daylight hours was accomplished by keeping careful records on the temporal distribution of dolphin observation time. This information was then used to direct observation effort to periods of the day that were lacking in data within each month. These measures



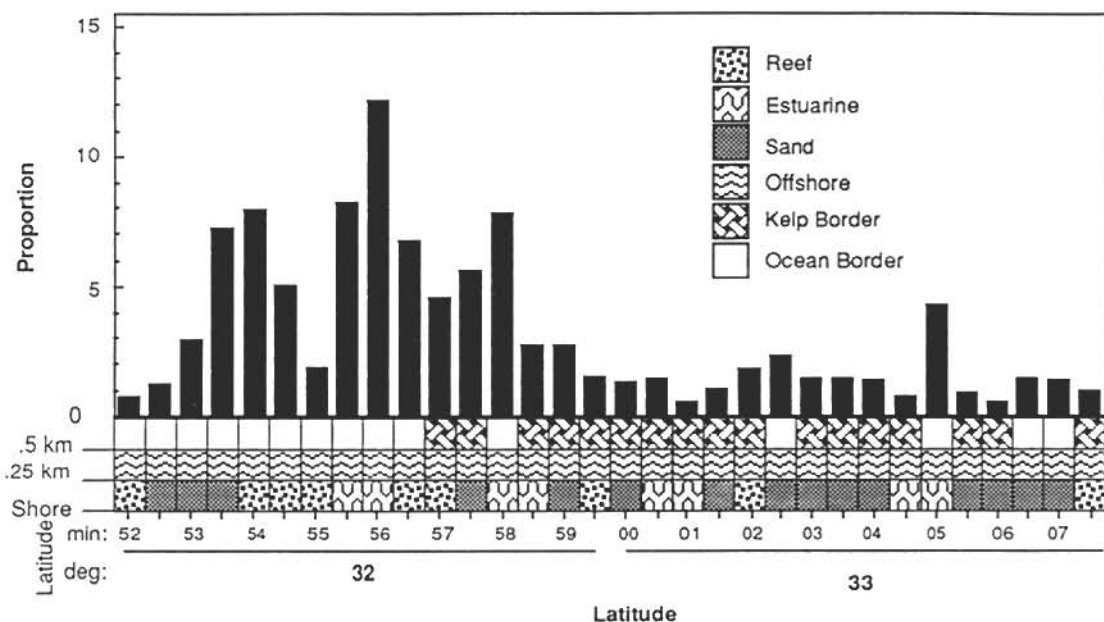
**Figure 1.** Map of the San Diego study area. Inset shows the location of the study area along the California coast. The study area extends from Scripps Pier at the south boundary ( $32^{\circ}52'00''\text{N}$ ,  $117^{\circ}15'00''\text{W}$ ) to South Carlsbad at the north boundary ( $33^{\circ}08'30''\text{N}$ ,  $117^{\circ}22'00''\text{W}$ ). Locations of the 19 land-based observation points are indicated with open squares.

were taken to avoid a data set with a disproportionate number of data records representing any given season or time of day.

#### Land Surveys

Dolphins were located through a systematic search from 19 land-based observation points (Fig. 1). The

portion of the study area that can be viewed from each observation point varies depending on the site's elevation and geographic obstructions in the field of view. Differences in distance between adjacent observation points reflect differences in the view afforded by each site. In portions of the study area with a low elevation or convex curvature in the



**Figure 2.** Schematic depiction of reef, estuary, sand, offshore, kelp border, and ocean border habitat types within the San Diego study area. Bars represent the overall percent of time dolphins spent in each section.

coastal contour (e.g., Fig. 1, between 6th street and 25th streets), it was necessary to space observation points closely. Conversely, at Torrey Pines State Park, with an elevation of 91 m and an unobstructed view, a 5.6 km section of the coast could be monitored from a single location. Surveys were usually conducted from south to north. At each observation point the coastline was systematically scanned with the unaided eye and binoculars for a minimum of 3 min.

#### *Behavioural Sampling*

Once located, a modified form of instantaneous sampling similar to that used by Shane (1990a) was used to document dolphin behaviour. In this procedure the functional activity of focal groups was recorded at 3 min intervals, which allowed adequate time for both observation and the recording of dolphin activity. A focal group was defined as the aggregation of dolphins viewed within the field of the binoculars during the course of an observation interval. Focal groups, rather than focal individuals, were sampled because established methods for identifying individual dolphins (Scott *et al.*, 1990) were not feasible from our land-based observation sites. Further, dolphins near each other generally engaged in the same types of behaviours at the same time so that focal group behaviour was characteristic of individual behaviour (Ballance, 1992).

The present sampling scheme differed from Shane's (1990a) in that all functional categories of behaviour recorded were based on an aggregate of observations made during the observation interval. A sampling criterion was employed to account for changes in both focal group size and the probability of observing a behavioural event. Specifically, one state-related event per five dolphins was required to score a state for a 3 min interval. When a focal group engaged in more than one behaviour state during an observation period, mixed behaviour states were recorded (Shane, 1990a). Mixed states were recorded when different individuals in the focal group were simultaneously engaged in different behaviour states, and when the behavioural state of the group changed during the observation interval. During a single observation interval, at most three states were combined to create a mixed state.

The sampling procedure occurred as follows: 1) dolphins were sighted and the cycling timer was set, 2) the dolphins were observed for a 3 min interval, 3) when the timer sounded, the time was noted, and 4) behavioural variables were recorded. This procedure was repeated and continued for as long as the dolphins were in observational range. When the observer could no longer distinguish the occurrence of behavioural events, he relocated in the appropriate direction to continue observation. An effort was made to remain with the same focal

group of dolphins during the course of a day's observation.

#### *Behavioural Measures*

The ethogram compiled by Weaver (1987) provided the basis for defining the behavioural states of travel, feed, social, play, and rest operationally. The particular events associated with each state were similar to those used in other dolphin behaviour assessments (Ballance, 1992; Saayman *et al.*, 1973; Saayman and Tayler, 1979; Shane, 1990b; Shane *et al.*, 1986). Travel was characterized by the uniform directional movement of focal group individuals, with a rhythmic pattern of surfacing followed by shallow submergence. Feeding involved variable directional movement of focal group individuals with frequent steep and rapid diving, often exposing the fluke or tail stock. Social behaviour also involved variable directional movement, but in combination with bodily contact and splashing among conspecifics, display of the ventral surface while swimming or stationary, chase of one conspecific by another, and various aerial leaps and displays. Play consisted primarily of surfing on waves, but also included dragging kelp on the leading edge of the dorsal fin. Rest was characterized by a pronounced and diminished lack of activity and included floating and very slow movement.

Additional recorded variables included dolphin group formation, position along the coast, distance from shore, and direction of movement. Group formation was characterized by: 1) whether or not the school was partitioned into subgroups, 2) the shape of the focal group as either wide or round, and 3) an estimate of the average dispersion (in dolphin lengths) of individuals within the focal group. The dolphin's north-south position parallel to the coast was recorded as occurring in one of 32 consecutively numbered 30 sec latitude sections, which when corrected to compensate for the curvature of the coastline measure 0.93 km apart (Fig. 2). Distance from shore was estimated as either: 1) within 0.25 km of shore (nearshore), 2) between 0.25 and 0.5 km from shore (offshore), and 3) greater than 0.5 km from shore. These distance estimates were aided by habitat features such as the location of kelp beds, which begin at approximately 0.5 km from shore, and the area beyond where waves begin to form, which is approximately 0.25 km from shore. The dolphin's direction of movement was characterized as either north, south, variable, or stationary.

#### *Statistical Analysis*

Diurnal and tide effects on the percent of time dolphins spent in each behaviour state were analyzed with a one-factor randomized groups

analysis of variance (ANOVA). A  $2 \times 3$  randomized groups ANOVA was used to analyze the effects of habitat features on the percent of time spent in each behaviour state. Planned comparisons examined specific diurnal, tide, and habitat effects. Descriptive global behaviour proportions are provided for evaluation of seasonal effects, patterns of group formation, some habitat effects, and for population comparisons of overall percentages of time spent in each behaviour state.

Behavioural records compiled on focal group activity were pooled for the observations used in the analyses of diurnal, tide, and habitat effects. Most observations represent data pooled across a month. Any month with less than 3 hrs of accumulated sampling records in any one of four defined periods of the day was combined with the pooled data of another month from the same season. The four periods of the day include: 1) early morning (dawn-0859), 2) late morning (0900-1159), 3) early afternoon (1200-1459), and 4) late afternoon (1500-dusk). Three months fell short of the 3 hr criterion and were combined, resulting in a total of nine observations for the entire data set.

The absence of individual identification for the subjects observed raises concerns about the independence of the observations used in our diurnal, tide, and habitat ANOVAs. Long-term photoidentification data documenting low frequency sighting patterns of individual dolphins in the San Diego study area (Defran and Weller, in prep) along with sightings of these same dolphins at other locations across the Southern California Bight lessens the severity of this problem. For example, 23% of the 373 individuals photographed during 146 boat-based surveys carried out between 1984-1989 were sighted only one time, and 66% were sighted less than one time per year. Even the most frequently photographed subset of this sample had very low sightings per opportunity ratios. These low individual sighting frequencies were consistent with the highly varied field estimates of total dolphins in the study area (abundance) and school size. We believe it is unlikely, therefore, that the pooled observations represent a small subset of groups composed of repeatedly sampled individuals. Rather, it is likely that the observations represent a quasi-random cross section of the population of dolphins that frequent the San Diego study area, with a negligible degree of statistical dependence between the pooled observations.

Individual scores which constitute the variance for each ANOVA were derived by sorting each pooled observation by the levels of the respective diurnal, tide, or habitat variable and then within each level, sorting by behaviour state. Nine

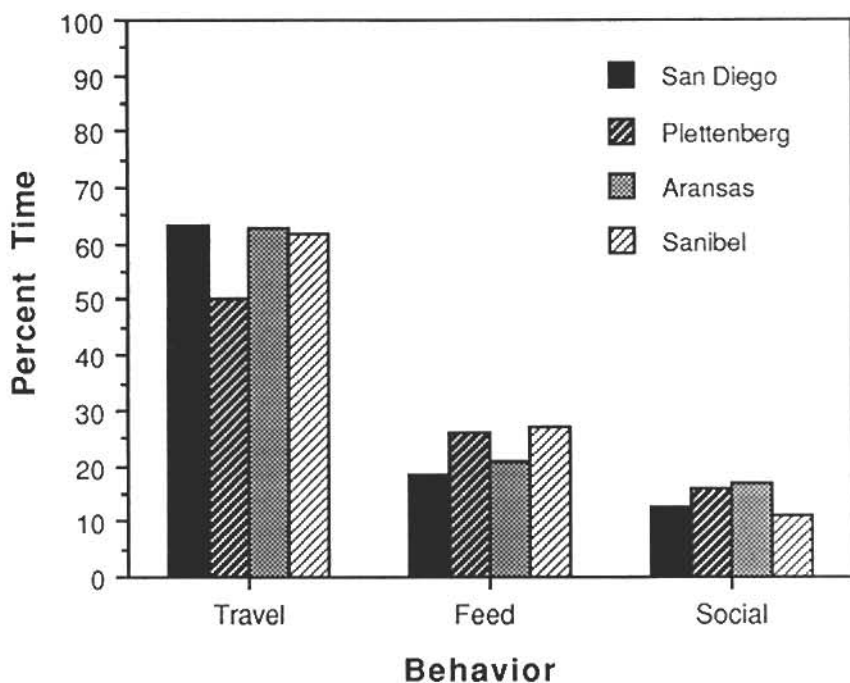


Figure 3. Percent of time bottlenose dolphins spent traveling, feeding, and socializing in the San Diego, Plettenberg Bay, Aransas Pass, and Sanibel Island study areas (Saayman & Tayler, 1979; Shane, 1986).

behaviour states were recorded: 1) travel, 2) feed, 3) social, 4) travel/play, 5) travel/rest, 6) travel/feed, 7) travel/social, 8) travel/feed/social, and 9) feed/social. For each score, mixed behaviour categories (numbers 4-9 above) were reduced to the five core states: travel, feed, social, play, and rest. Mixed states with two core state components, such as travel/feed, were treated as one half of a record (1.5 min) for each of the two states. The mixed state category of travel/feed/social was treated as one third of a record (1 min) for each core state component. Once reduced, the percent of time associated with each core state was calculated. For example, if in the analysis of diurnal effects (with 4 levels of time of day), one of the pooled observations had 75 sampling records (225 min) for the early morning level of the time of day variable (dawn-0859), with 50 travel records (150 min), the early morning travel score for the observation would be 66%. Apart from the overall proportion of time devoted to each behaviour, all descriptive data and analyses are restricted to travel, feeding, and social behaviour. Presentations of behavioural data are expressed in proportions, but these were arc-sine transformed when subjected to statistical analysis.

## Results

### Behaviour State Proportions

The proportion of dolphin time spent in each state provides a baseline for the evaluation of percentages associated with the specific analyses presented below, and for comparisons between populations (Fig. 3). San Diego dolphins spent the greatest amount of time in travel. Intermediate percentages were spent in feeding and social behaviour. Play (3%) and rest (3%) accounted for the lowest percentages of dolphin time. To compare the present data with Shane's (1986) Sanibel Island, Florida data, overall frequencies associated with her mixed behaviour categories of 'Travel/Feed' and 'Social Travel' were partitioned into their core components of travel, feed, and social behaviour. This treatment of the Sanibel Island data differs from Shane's (1990b) comparative assessment, in which the core component of travel in these mixed states was lumped with feeding and socializing.

### Seasonal Effects

For a descriptive assessment of seasonal effects, global percentages of traveling, feeding, and social behaviour were calculated as a function of: 1)

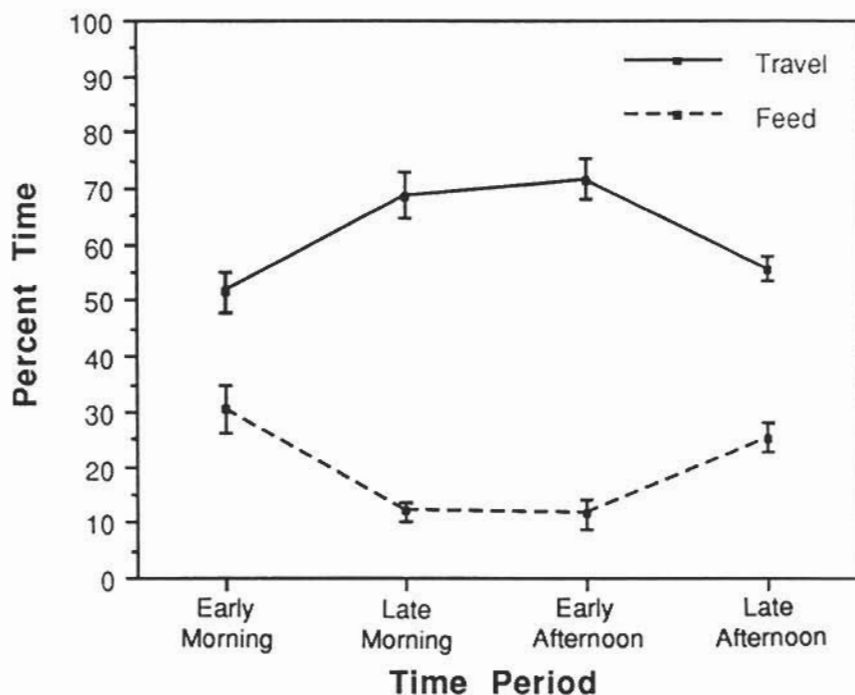


Figure 4. Mean percent of time dolphins spent traveling and feeding as a function of early morning, late morning, early afternoon, and late afternoon day periods. Vertical bars represent standard errors.

spring (March, April, May), 2) summer (June, July, August), 3) fall (September, October, November), and 4) winter (December, January, February). Travel was greatest in the winter at 67%, with a narrow range in variation for fall through spring percentages (59–62%). Seasonal percentages of feeding also displayed little variation with a spring high of 20% and a fall low of 17%. Social activity showed the greatest seasonal variability with a peak at 18% during summer and a low of only 5% during the winter; moderate social percentages were observed for fall (13%) and spring (15%).

#### Diurnal Effects

Diurnal effects were evaluated as function of the four day-periods previously defined. Time spent traveling ( $F=7.11$ ;  $df=3,32$ ;  $P<0.01$ ) and feeding ( $F=9.13$ ;  $df=3,32$ ;  $P<0.01$ ) differed significantly as a function of day period (Fig. 4). During the two midday periods (late morning and early afternoon) time spent in travel was significantly greater than in either the early morning or late afternoon ( $P<0.05$ ). The diurnal distribution of feeding time was inversely related to travel, with significantly

greater feeding time in the early morning and late afternoon than in either midday period ( $P<0.05$ ).

#### Tide Effects

Tide effects were evaluated as a function of four tide categories: 1) low tide (one hour before and after low tide), 2) high tide (one hour before and after high tide), 3) ebb tide (the interval of receding tide between high and low tides), and 4) flood tide (the interval of increasing tide between low and high tides). Social behaviour was relatively invariant across the tide categories, and differences, were statistically non-significant. Variation in traveling and feeding was also nonsignificant, but displayed a pattern consistent with being affected by changes in tide current. Travel was greater during high and low tide states (low tide current), with feeding showing an inverse pattern (Fig. 5).

The effect of tide current on traveling and feeding was analyzed by combining ebb and flood tide states to create a category of high tide current, and combining high and low tide states to create a category of low tide current. Feeding time was significantly greater during periods of high tide current than during low tide current ( $F=5.02$ ;

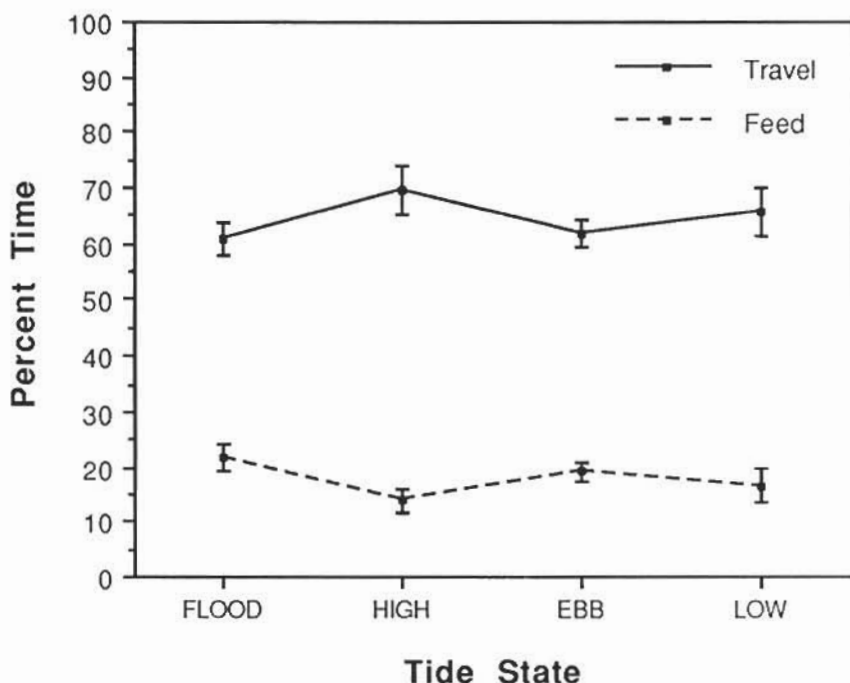


Figure 5. Mean percent of time dolphins spent traveling and feeding as a function of flood, high, ebb, and low tide states. Vertical bars represent standard errors.

$df=1,32$ ;  $P<0.05$ ). Effects of tide current on travel were nonsignificant.

#### Habitat Effects

Dolphin behaviour was evaluated as a function of six habitat types identified within the San Diego study area: 1) offshore, 2) estuary, 3) reef, 4) sand, 5) kelp border, and 6) ocean border. The study area was divided into 64 equivalent sections (measuring 0.25 km by 0.97 km) which were classed according to their habitat characteristics (Fig. 2). All sections between 0.25 km and 0.5 km from shore were classed as offshore area; while sections within 0.25 km and shore were classed as nearshore. Nearshore sections within 0.97 km on either side of an estuary mouth were classed as estuary. Nearshore sections in which the predominant substrate type was rock were classed as reef, and those in which the predominant substrate was sand were classed as sand. Kelp border area included near and offshore sections in which the offshore boundary (0.5 km from shore) of the study area was adjacent to kelp beds. Ocean border area included near and offshore sections in which the offshore boundary of the study area was open ocean.

Ninety-nine percent of all dolphin behaviour took place within 0.5 km of shore, with 90% of all

activity occurring within 0.25 km of shore. This pattern of nearshore fidelity is not likely to be the result of methodological constraints on observing dolphins from shore because in over 200 hrs of direct observation: 1) dolphins were easily observable at distances greater than 0.5 km from shore although this was rare (<1% of all observation time), 2) the dolphins' overall progression of movement was always parallel to the coast, and 3) dolphins were never observed to leave the study area by heading offshore, even though observations were often terminated by dolphins leaving the study area at the northern and southern boundaries. Although slightly less than half of the study area (47%) was ocean border, dolphins spent 70% of their time in ocean border habitat type (Fig. 2). Even between  $32^{\circ}57'00''N$ – $33^{\circ}07'30''N$ , where the predominant border type is kelp, ocean border areas show relative increases in the overall percent of time dolphins spent in these areas (Fig. 2).

A  $2 \times 3$  ANOVA design was used to analyze the effects of offshore border type (kelp and ocean) and nearshore habitat type (estuary, reef, and sand) on the percent of time spent traveling, feeding, and socializing. The main effect of border type on travel time was significant ( $F=7.86$ ;  $df=1,48$ ;  $P<0.01$ ) with greater travel occurring in kelp than in ocean



**Table 1.** Mean percent of time dolphins spent in nearshore traveling, socializing, and feeding, and the overall percent of time spent in offshore feeding as a function of kelp and ocean border types, and estuary, reef, and sand habitats

	Estuary	Reef	Sand	Mean
<b>NEARSHORE</b>				
Travel				
Kelp	60.88	77.73	71.06	69.89
Ocean	54.71	53.32	61.78	56.60
Mean	57.79	65.52	66.42	
Social				
Kelp	9.42	7.17	8.50	8.36
Ocean	13.96	13.91	16.31	14.73
Mean	11.69	10.54	12.40	
Feed				
Kelp	15.77	10.08	13.08	12.98
Ocean	21.20	27.11	8.92	19.08
Mean	18.48	18.59	10.99	
<b>OFFSHORE</b>				
Feed				
Kelp	22.41	28.10	32.15	27.55
Ocean	38.37	35.53	19.30	31.07
Mean	30.39	31.82	25.73	

border types (Table 1). There was a significant simple effect of greater travel in kelp than in ocean border reef areas ( $P < 0.05$ ). The main effect of border type on feeding approached significance ( $P = 0.06$ ) and the simple effect of greater feeding in ocean than in kelp border reef areas was significant ( $P < 0.01$ ). Nearshore habitat type exerted a significant main effect on feeding behaviour ( $F = 4.33$ ;  $df = 2,48$ ;  $P < 0.05$ ) with greater feeding in both estuary and reef, than in sand areas ( $P < 0.05$ ). There was a significant interaction ( $F = 7.16$ ;  $df = 2,48$ ;  $P < 0.01$ ) between nearshore habitat and border type, with greater feeding in kelp than in ocean border sand areas (Table 1). Finally, border type had a significant main effect on time spent in social behaviour ( $F = 8.06$ ;  $df = 1,48$ ;  $P < 0.01$ ) with greater social time occurring in ocean than in kelp border types (Table 1).

Of the 9% of dolphin time spent offshore, slightly more than half was spent in kelp (54%), with slightly less in ocean border areas (46%). However, when offshore time was partitioned by association with border and nearshore habitat type, the greatest amount of time was spent in kelp border sand areas (32%), the least amount of time was spent in kelp border estuary areas (7%), with intermediate percentages (13–19%) associated with all other nearshore habitat and border type

combinations. While offshore, 47% of all time was spent traveling, 31% was spent feeding, and 19% was spent in social behaviour. In comparison to the percentages associated with these behaviours for the entire data set, traveling in offshore areas was reduced while feeding and social behaviour were increased. A breakdown of offshore feeding by adjacent border and nearshore habitat type reveals a distribution roughly parallel to that of the nearshore analysis of habitat features described above (Table 1).

A final comment concerns the absence of other cetaceans within the study area. Bottlenose dolphins were the only small cetaceans, but not the only marine mammals, observed in the study area on a regular basis. Individuals and occasional pairs of sea lions (*Zalophus californianus*) and, less commonly, harbor seals (*Phoca vitulina*) were observed throughout the year. Other cetacean species were seasonally or occasionally observed about 1 km or more offshore from the study area, including schools of Pacific white-sided dolphins (*Lagenorhynchus obilquidens*) and common dolphins (*Delphinus delphis*) and December–March migrating gray whales (*Eschrichtius robustus*).

#### Group formation

The size of the 73 schools we observed was highly variable with a mean of 35 individuals and a standard deviation of 22.4. Group formation was analyzed by calculating the overall percent of time spent in each behaviour state as a function of subgroup presence, focal group shape, and focal group dispersion. Dolphin schools were comprised of subgroups during a greater percent of travel, feed, and social time (Fig. 6A). During feed and social, focal groups were almost exclusively in a round shape, but during travel, focal groups were round and wide about equally often (Fig. 6B). In each behaviour state, focal group dispersion estimates of less than two dolphin lengths accounted for a greater percent of dolphin time. However, while feeding, the amount of time dolphins spent more and less dispersed, respectively, was nearly evenly divided (Fig. 6C).

## Discussion

#### Behaviour State Proportions

Of the three most frequently observed behaviour states, dolphins spent the greatest amount of time in travel, an intermediate amount of time feeding and the least time in social activity. These proportions were similar to those of comparable behaviour states reported for humpback dolphins in Plettenberg Bay, Africa and for bottlenose dolphins in Aransas Pass, Texas and Sanibel Island, Florida

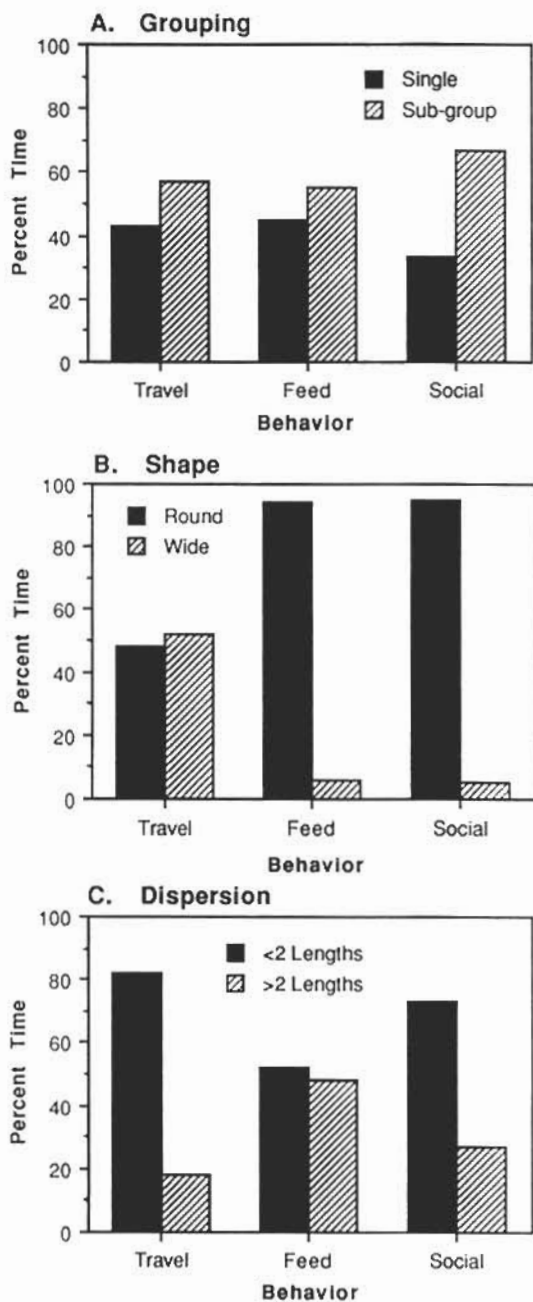


Figure 6. Mean percent of time dolphins spent traveling, feeding, and socializing as a function of A. Grouping, B. Shape, and C. Dispersion variables.

(Saayman and Tayler, 1979; Shane, 1986) (Fig. 3). Parallels between these behaviour state proportions across studies are noteworthy considering the differences associated with methodology, habitat, and

population parameters (see reviews by Ballance, 1990; Shane *et al.*, 1986).

#### Prey Species Ecology

Seasonal, diurnal, tide, and habitat effects of behaviour state and group formation results are interpreted relative to the ecology of fish preyed upon by Pacific coast bottlenose dolphins. twenty-five prey fish were identified for review from two stomach content analyses on Pacific coast bottlenose dolphins (Norris and Prescott, 1961; Walker, 1981). Most of the fish species reviewed exhibit spring through summer spawning, and of the 19 species for which information on spawning migration was attained, only two (*Menticirrhus undulatus* and *Paralabrax clathratus*) exhibit seasonal offshore movement (Feder *et al.*, 1974; Fitch and Lavenberg, 1971; 1975; Love *et al.*, 1984; North and Hubbs, 1968).

Table 2 summarizes each fish by: 1) the percent of the frequency of occurrence of each fish found in dolphin stomach contents, 2) dietary preference, 3) diet activity cycle, and 4) habitat preference. Percentages calculated for the number of each fish in dolphin stomach contents were based on values derived by combining the frequency of occurrence of fish found across both stomach content analyses. These percentages are used as a crude index of the importance of each fish as prey for the Pacific coast bottlenose dolphin (Table 2). Species of the families Embiotocidae (surf perches, numbers: 6-12) and Sciaenidae (croakers, numbers: 18-23), comprised 75% of the fish identified (Walker, 1981).

The dietary preference of each fish is characterized as either planktonic or benthic. Species with a diet consisting primarily of zooplanktonic organisms, taken directly from the water column, were classed as planktonic. The benthic category includes those species which usually take relatively immobile prey from benthic substrate. Sixty-eight percent of the summarized dolphin prey fish are benthic feeders, and nearly all of these species are regular inhabitants of middle to bottom depths. Diving-intensive feeding for San Diego dolphins (Behaviour Measures section), is consistent with the middle to bottom depth ranges preferred by most of their prey. The habitat preferences of the reviewed fish include open sand, rocky reef, kelp forest, nearshore surf, and estuary areas.

This list of prey species is not comprehensive; it excludes invertebrate species because it is difficult to determine whether an invertebrate was consumed directly by a dolphin or secondarily by a prey fish. Pacific coast bottlenose dolphins probably consume some invertebrate species, particularly squid (*Loligo opalescens*), which are seasonally abundant in the nearshore waters of southern California.

Table 2. Summary of 25 prey fish of the Pacific coast bottlenose dolphin by percent of occurrence of each fish found in dolphin stomach contents, dietary preference, diel activity cycle, and habitat preference

No.	Species (Common name)	Stomach Content	Dietary Preference	Activity Cycle	Habitat Preference	Reference*
1.	<i>Atherinopsis californiensis</i> (Jacksmelt)	0.37	planktonic	N.A.	sand	2), 11)
2.	<i>Porichthys myriaster</i> (Specklefin midshipman)	3.74	benthic	nocturnal	sand, rock	2), 4), 11)
3.	<i>Porichthys notatus</i> (Plainfin midshipman)	9.36	benthic	nocturnal	sand, rock	2), 4), 11)
4.	<i>Paralichthys californicus</i> (California halibut)	1.87	benthic	diel	sand	2), 3), 7), 10), 11)
5.	<i>Trachurus symmetricus</i> (Jack mackerel)	0.75	planktonic	diurnal	N.A.	2), 3), 5), 11)
6.	<i>Amphistichus argenteus</i> (Barred surfperch)	4.12	benthic	N.A.	sand, rock, surf	2), 3), 9)
7.	<i>Cymatogaster aggregatus</i> (Shiner surfperch)	1.12	planktonic	nocturnal	sand, kelp, estuary	2), 4), 5), 7), 9)
8.	<i>Damalichthys vacca</i> (Pile surfperch)	1.12	benthic	diurnal	sand, rock, kelp	2), 5), 11)
9.	<i>Embiotoca jacksoni</i> (Black surfperch)	0.37	benthic	diurnal	sand, rock, kelp, estuary	2), 4), 5), 7), 10), 11)
10.	<i>Hyperprosopon argenteum</i> (Walleye surfperch)	14.98	planktonic	nocturnal	sand, rock, kelp, surf	2), 5), 6), 7), 11)
11.	<i>Phanerodon furcatus</i> (White surfperch)	4.87	benthic	diurnal	sand, rock, kelp	2), 9), 10), 11)
12.	<i>Rhacochilus toxotes</i> (Rubberlip surfperch)	0.75	benthic	N.A.	sand, rock, kelp	2), 3), 10), 11)
13.	<i>Oxyjulis californica</i> (Senorita)	0.37	planktonic	diurnal	sand, rock, kelp	2), 4), 5), 6), 10), 11)
14.	<i>Otophidium scrippsii</i> (Cusk-eel)	1.12	benthic	nocturnal	sand, rock	4), 11)
15.	<i>Atherinops affinis</i> (Topsmelt)	0.75	planktonic	N.A.	sand, rock, kelp	2), 9), 10), 11)
16.	<i>Pleuronichthys coenosus</i> (C-O turbot)	0.75	benthic	diel	sand, rock, kelp	2), 5), 7), 11)
17.	<i>Chromis punctipinnis</i> (Blacksmith)	3.00	planktonic	diurnal	sand, rock, kelp	2), 3), 5), 6), 10), 11)
18.	<i>Cynoscion nobilis</i> (White seabass)	0.37	benthic	nocturnal	sand, rock, surf	2), 3), 10), 11)
19.	<i>Genyonemus lineatus</i> (White croaker)	17.98	benthic	N.A.	sand, kelp	1), 8), 9), 11)
20.	<i>Menticirrhus undulatus</i> (California corbina)	7.12	benthic	N.A.	sand, surf, estuary	2), 3), 9), 11)
21.	<i>Ranccador stearnsi</i> (Spotfin croaker)	2.25	benthic	N.A.	sand, rock, surf	2), 11)
22.	<i>Seriplus politus</i> (Queenfish)	18.35	planktonic	nocturnal	sand, rock, surf	1), 2), 5), 6), 9), 11)
23.	<i>Umbriina rancador</i> (Yellowfin croaker)	1.50	benthic	nocturnal	sand, rock, surf, estuary	1), 2), 5), 7), 11)
24.	<i>Paralabrax clathratus</i> (Kelp bass)	2.25	benthic	diurnal	sand, rock, kelp	2), 5), 7), 10), 11)
25.	<i>Synodus lucioceps</i> (California lizardfish)	0.75	benthic	N.A.	N.A.	3), 11)

\*1) Eschmeyer, Herald & Hammann, 1983; 2) Feder *et al.*, 1974; 3) Fitch & Lavenberg, 1971; 4) Fitch & Lavenberg, 1975; 5) Hobson *et al.*, 1981; 6) Hobson & Chess, 1976; 7) Hobson & Chess, 1986; 8) Love *et al.*, 1984; 9) Norris & Prescott, 1961; 10) North & Hubbs, 1968; 11) Walker, 1981

### Seasonal Effects

A decrease in social and associated mating activity during winter was the only descriptively pronounced seasonal effect on behaviour. Other temperate latitude coastal dolphin populations display spring, summer, or fall increases in either calving or social activity. Humpback dolphins in Plettenberg Bay, Africa were reported to have more births during the summer (Saayman and Tayler, 1979). In Matagorda Bay, Texas and near Sarasota Bay, Florida bottlenose dolphins showed increased calving during spring and summer, and spring through early fall respectively (Gruber, 1981; Scott *et al.*, 1990). In Aransas Pass, Texas, the mating activity of bottlenose dolphins peaked during the spring and summer (Shane, 1990b). In contrast to these spring through fall social activity and calving peaks, bottlenose dolphins at Sanibel Island, Florida, socialized more during the fall and winter (Shane, 1990b).

Shane (1990a) suggests that seasonal variation in dolphin behaviour might be expected in relation to seasonal changes in water temperature and prey abundance. Summer mating by San Diego dolphins may be adaptive because the dolphin's one-year gestation period would translate to summer calving (Tavolga and Essapian, 1957). By calving in summer, new mother-calf pairs would expend less energy on thermoregulation because of warmer average water temperatures in summer (21°C) and fall (18°C) than during winter (13°C) and spring (16°C) (Scripps Institute of Oceanography, Marine Life Research Group, 1988-1989 water temperature tables).

The seasonal constancy observed for traveling and feeding may be related to the year round presence of prey fish in the dolphins' nearshore habitat. Only two prey fish were found to move seasonally offshore during spawning where they may become inaccessible to the dolphins as prey. Further, long-term cycles expressed across years, such as coastal warming associated with El Niño events, may be more important than annual cycles in affecting the long-term organization of Pacific coast bottlenose dolphin behaviour (Hansen and Defran, 1990; Wells *et al.*, 1990).

### Diurnal Effects

San Diego dolphins fed more during the early morning and late afternoon (crepuscular periods) with greater travel occurring during the midday hours (Fig. 4). A similar diurnal distribution of traveling and crepuscular feeding has been described for humpback dolphins in Plettenberg Bay, Africa (Saayman and Tayler, 1979) and for bottlenose dolphins in Aransas Pass, Texas (Shane, 1990b). Further, the diurnal distributions of feeding activity documented for other dolphin populations

have paralleled the diel activity patterns of their prey. Dusky dolphins in Golfo San Jose, Chubut, Argentina were reported to move further from shore and feed during the early afternoon. Würsig and Würsig (1980) suggested that dusky dolphins may have concentrated feeding during the day because schools of southern anchovy (*Engraulis ringens*) were dispersed and less accessible during the night.

Prey species of the Pacific coast bottlenose dolphin were examined for diel activity cycles that might account for increased crepuscular dolphin feeding. Most of the species reviewed are active either diurnally or nocturnally (Table 2). During crepuscular periods, many of these fish are in transition between habitats associated with resting and feeding modes (Hobson *et al.*, 1981; Hobson and Chess, 1986). San Diego dolphins may feed more during the early morning and late afternoon because during crepuscular transition fish are more accessible and susceptible to capture. This hypothesis is supported by the diel distribution of feeding activity for large piscivorous fish of tropic and sub-tropic latitudes (such as groupers) which are reported to feed opportunistically at all times, but concentrate feeding during crepuscular periods (Hobson, 1968; Hobson, 1974; Stark and Davis, 1966).

The present observations, restricted to the day, do not preclude the potential importance of nocturnal feeding activity by San Diego dolphins. A number of the San Diego dolphins' prey fish are nocturnally active and may be exploited by the dolphins during the night (Table 2). Nocturnal feeding was reported for spinner dolphins in Kealahou Bay, Hawaii, which became active in the late afternoon before moving offshore to feed at night on prey associated with the rise of the deep scattering layer (Norris and Dohl, 1980a).

### Habitat and Tide Effects

San Diego dolphins spent most of their time within 0.25 km of shore and in areas exposed to the open ocean, a finding consistent with the exclusive inshore boat-based and aerial survey sighting accounts between 1981-1989 (Defran and Weller, in prep; Hansen, 1990). When present in ocean border areas, they fed more and traveled less, with the exception of increased feeding in kelp border sand areas. They also fed more in reef and estuary areas and less in sand areas across border type (Table 1). Further, feeding activity was increased during periods of greater tide current (Fig. 5). Other coastal dolphin populations have shown patterns of feeding in association with specific geographic features, marine currents, and tide states. In Aransas Pass, Texas, bottlenose dolphins concentrated feeding in areas with a bottom topography of

high relief and steep ledges (Shane, 1977). At Sanibel Island, Florida, dolphins fed in protected shallow bay waters with strong currents, sea grasses, and mangrove lined shores (Shane, 1990a). Bottlenose dolphins in Bahia Kino, Mexico usually fed near estuaries (Ballance, 1992). Finally, hump-back dolphins in Plettenberg Bay, Africa increased feeding during flood tides and in areas of exposed coast with a rocky reef substrate (Saayman and Tayler, 1979).

In the San Diego study area, increased feeding in reef and estuary areas is consistent with the dolphin prey associated with these habitats. The greater overall dolphin time and increased feeding in ocean border latitudes (Fig. 2; Table 1), however, seems counter-intuitive. It is likely that the kelp forest harbors an abundance of prey that is consumed by the Pacific coast bottlenose dolphin (Feder *et al.*, 1974) (Table 2). Tide currents and habitat features which affect the cycling of ocean borne and estuary nutrients in the San Diego dolphins' nearshore habitat may have an important influence on the distribution and availability of dolphin prey. Zooplanktivorous prey fish may be directly affected by currents and habitat features that influence nearshore zooplankton distribution. The availability of benthic dolphin prey fish may be affected, however, by nearshore nutrient cycling through secondary trophic relations (current-carried nutrients affecting availability of benthic prey of dolphin prey fish).

Tide currents can affect the distribution of zooplankton in temperate rocky reef communities (Bray, 1980; Bray *et al.*, 1981). In the San Diego study area where kelp forest borders the coast, algae could prevent current-carried nutrients from entering the nearshore food web. If so, nearshore areas exposed to the open ocean and greater nutrient flow would be biologically richer. Areas such as reefs and estuaries, which are inherently rich with prey, would further benefit from more current-carried nutrients. A process analogous to the kelp forest acting as a filter to current-carried nutrient occurs in some reef communities. Along the windward face of Davis reef in western Australia, zooplanktivorous fish are reported to create a 'wall of mouths' that remove most of the current-carried zooplankton from the water column before it impinges upon the reef itself (Hamner *et al.*, 1988). At Naples Reef off the coast of Santa Barbara, California, the blacksmith (*Chromis punctipinnis*), a prey fish of the Pacific coast bottlenose dolphin, is reported to feed at tide incursions of reefs and kelp beds in order to take advantage of increased zooplankton availability (Bray, 1980).

The stapes and hanging fronds of the kelp forest may impede the dolphins' acoustic and visual

sensory systems as well as swimming and diving activities associated with efficient predation. San Diego dolphins may not often exploit the kelp beds directly because prey in the kelp are harder to find and catch than in nearshore areas exposed to the open ocean. Further, some of the prey fish that inhabit the kelp during the day move onto open sandy areas at night to feed on nocturnally active zooplankton and may be more accessible to the dolphins at this time (Hobson and Chess, 1976).

It is not clear why feeding increased in kelp border sand areas and while dolphins were offshore. Offshore feeding in kelp border portions of the study area may reflect dolphins exploiting fish associated with the leeward fringe of the kelp beds. In the case of increased feeding in kelp border sand areas, the leeward fringe of the kelp beds may offer better opportunities for foraging than nearshore sand areas. This hypothesis is supported by data which show that over one third of all offshore activity occurred in offshore sections bordered by kelp and adjacent to nearshore sand habitat (Fig. 2). This proposal, however, does not account for increased feeding in ocean border offshore areas.

#### Group Formation, School Size

San Diego dolphins usually traveled in a wider (abreast) than long formation and in comparably large schools. Our land-based estimates of school size averaged 35 individuals, which was higher than boat-based estimates previously reported for dolphin schools in this area (mean: 19.8) between 1984-1989, but were similar to boat-based estimates recorded during the present study period (Defran and Weller, in prep.; Defran, personal communication). All these values are considerably larger than those reported for coastal dolphin populations within the more protected Florida and Texas study sites and are similar to those reported for more open habitats (see reviews by Ballance, 1990; Shane *et al.*, 1986). Both traveling abreast and the formation of larger schools have been hypothesized to enhance the efficiency with which cetaceans encounter prey species, especially in more open habitats such as our study area (Norris and Dohl, 1980b; Würsig, 1986).

Surfing by San Diego dolphins accounted for the majority of behaviour recorded as play and may have been related to feeding. While surfing on larger waves, a rank of up to 30 dolphins would at times ride abreast in a swell. As the wave would break nearshore, the dolphins would often temporarily submerge out of sight. Twice while dolphins were surfing in this manner, brown pelicans (*Pelecanus occidentalis*) were observed plunge diving near the dolphins. Given that several of the dolphins' important prey items inhabit the surf (Table 2), surfing abreast may be a strategy for

feeding on fish available in this area. Bottlenose dolphins have been reported surfing, in a manner similar to that described for the San Diego study area, along the coast of Florida, in Plettenberg Bay, Africa, and Aransas Pass, Texas (Caldwell and Fields, 1959; Saayman *et al.*, 1973; Shane, 1977).

In conclusion, the present data provides strong evidence that, at least during the day and within a subset of their range, Pacific coast bottlenose dolphins remain exclusively close to shore and are the solitary cetacean species regularly occupying this niche. Within this nearshore habitat, the availability of dolphin prey associated with diurnal, tide, and habitat variables was interpreted as an important influence on the short-term organization of behaviour in San Diego dolphins. The available literature on the ecology of the Pacific coast bottlenose dolphins prey fish permitted a high level of detail in speculating upon relationships between dolphin behaviour and factors affecting prey availability at multiple trophic levels. We do not view these proposed relationships as the final word on the feeding ecology of San Diego dolphins. As behavioural research continues on the Pacific coast bottlenose dolphin in this and other study areas, some of the currently proposed relationships may well be replaced with better-informed views. We hope that the current work will function as a heuristic for this research.

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