BEHAVIOR AND ECOLOGY OF THE DUSKY DOLPHIN, *LAGENORHYNCHUS OBSCURUS*, IN THE SOUTH ATLANTIC

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ABSTRACT

Dusky dolphins were present in Golfo San José, Chubut, Argentina, during most of the year, with a seasonal low in abundance during winter and a high in summer. The presence of the prey species southern anchovy, *Engraulis anchoita*, appeared to affect seasonal movements.

Surface feeding was highly visible and birds also fed on fish schools which dolphins herded to the water surface. Surface feeding occurred mainly in spring and summer in the study area, and in late summer and fall in more oceanic waters near the mouth of the bay. This surface feeding pattern corresponded with the presence of southern anchovy.

Dolphins moved in small groups of about 15 individuals while resting in early morning and while looking for food in late morning. Group sizes increased during surface feeding as groups joined existing feeding activity. Because surface feeding occurred mainly around noon and early afternoon, group sizes increased at those times. Dives were longer before and during feeding, and shorter while resting. During spring, summer, and fall nights, dives were shorter, leading to the possibility that dolphins were resting at those times. The nonsurface feeding period corresponded with nighttime dispersal of southern anchovy schools. Dolphins moved in shallow water while resting and in deeper water while surface feeding. Near shore resting may be a predator-avoidance mechanism.

Most aerial behavior occurred during surface feeding, with behavior before and during surface feeding related to either herding and confining prey or possible communication of neighboring groups. Postfeeding aerial displays were assumed to serve a social function.

Calves were born mainly in the summer.

Recently there has been an increase in the number of studies of movements and migration patterns, behavior, and ecology of dolphins. Most of this work has consisted of long-term observations of the bottlenose dolphin, *Tursiops* sp. (Caldwell et al. 1965; Caldwell and Caldwell 1972; Tayler and Saayman 1972; Irvine and Wells 1972; Saayman et al. 1972, 1973; Saayman and Tayler 1973; Leatherwood 1975; Odell 1975, 1976; Castello and Pinedo 1977; Shane 1977; Würsig and Würsig 1977, 1979; Würsig 1978; Wells et al. in press; Irvine et al.[2]), but other odontocete cetaceans have received attention as well (review to 1974 by Norris and Dohl in press; Saayman and Tayler 1979, on *Sousa* sp.; Evans 1976, on *Delphinus delphis*; Norris and Dohl 1980, on *Stenella longirostris*; Gaskin et al. 1975, on *Phocoena phocoena*; Würsig in press, on *Lagenorhynchus obscurus*). This paper presents data on the yearly and daily occurrence and feeding cycles, movement patterns, general and social behavior, and ecology of the dusky dolphin, *Lagenorhynchus obscurus*, in a south Atlantic bay on the coast of Argentina.

Little information on dusky dolphins is available in the published literature. Gaskin (1968) described the distribution of these animals around New Zealand relative to sea-surface temperature, and Gaskin (1972) presented a summary of the literature. Although the genus *Lagenorhynchus* appears worldwide, populations of *L. obscurus* are confined to the Southern Hemisphere, most notably around New Zealand, South Africa, and South America. The exact northern and southern limits of the species are not known. Brownell (1965) states that dusky dolphins are distributed circumpolar to lat. 30° S, but this is disputed by Gaskin (1972). According to Rice (1977), *L. fitzroyi* is synonymous with *L. obscurus*.

More information is available on the Pacific whitesided dolphin, *L. obliquidens*. It has been described by Brown and Norris (1956), Norris and Prescott (1961), and others. A recent review of the status of this species in the eastern North Pacific

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[1] State University of New York at Stony Brook, Program for Neurobiology and Behavior; present address: Center for Coastal Marine Studies, University of California, Santa Cruz, CA 95064.

[2] Irvine, A. B., M. D. Scott, R. S. Wells, J. H. Kaufmann, and W. E. Evans. 1979. A study of the movements and activities of the Atlantic bottlenose dolphin, *Tursiops truncatus*, including an evaluation of tagging techniques. Final report for U.S. Marine Mammal Commission, Contracts MM4AC004 and MM5AC0018, 53 p.

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has been presented by Leatherwood and Reeves (1978).

MATERIALS AND METHODS

Dusky dolphins were observed at Golfo San José (Figure 1) from September 1973 through January 1974 and from July 1974 through March 1976. We made observations from shore and from a 4.5 m rubber Zodiac[3] boat powered by an 18-hp Evinrude outboard motor.

Shore observations were made through binoculars, and movement patterns of dolphin groups, ranging from six to several hundred individuals, were followed with a Kern Model DKM 1 surveyor's theodolite (see Materials and Methods in Würsig and Würsig 1979). This technique allowed us to describe where and how fast the dolphins moved during different times of day.

Observations were made from the boat by moving up to a group of dolphins and then stopping the engine. This allowed us to drift near the dolphins while taking notes on their behavior. We believe that the natural behavior of dolphins was at times affected by the presence of the boat, and therefore made an attempt to confirm all behavior seen from the boat by shore-based observations.

To get some idea of group stability over time, we spaghetti-tagged 24 individuals in conjunction with a radio-tagging study. These tags were color-coded plastic streamers lanced into the thick blubber behind the dorsal fin. For a description of the tags and tagging procedures, as well as radio-track data, see Würsig (in press).

To compare seasonal occurrence data with water temperature, we measured temperature 1 m below the surface 5-10 times per month. For uniformity, these readings were made 0.5-3 km from shore, and in the afternoon. We used a calibrated laboratory thermometer marked every 0.2° C from 5.0° to 30.0° C.

Underwater sounds made by dolphins were recorded through U.S. Navy Sonabuoy hydrophones suspended 5-10 m below the boat. They were recorded on a Sony TC800B reel-to-reel tape recorder. A complete analysis of dolphin vocalizations is not presented in this paper. However, measurements were made of approximate distance of travel before attenuation (sounds no longer picked up by the hydrophones) of certain splash sounds related to aerial behavior. During such measurements, dolphin and boat position were recorded from shore by surveyor's theodolite, thereby providing the distance from the sound source to the hydrophone.

We used standard statistical techniques to test for differences and similarities of observations. These techniques are from Sokal and Rohlf (1969) unless stated otherwise.

RESULTS

Seasonal Occurrence Pattern

On days with winds >20 km/h, it was difficult to see dusky dolphins. Of the 433 days with winds <20km/h, dolphins were seen on 251 days, or 58%. Dolphins were seen from shore during 19 of 21 mo (Figure 2a); June and July 1975 were the only months without sightings. Although the rate of sightings varied from month to month, there was an increase in sightings from late winter (August) to summer (February 1975; December 1975), and a decrease from fall to midwinter (March through June 1975). During both years, dolphins were present on over 50% of days during which observations were made from August through February, with the one exception of <50% on the days in January 1976.

Could this cycle of dolphin occurrence be related to water temperature? Figure 2b shows average surface temperature per month within 3 km of shore during the same 21-mo period. Although upon superficial examination it appears that dolphins were less often present during the coldest months, this is not strictly true. Thus, although August was the coldest month in both years, dolphins in August were present over 70% of sighting days. The rise in temperature in spring-summer 1975-76, however, occurred earlier than in 1974-75, and temperatures from September to February were 1°-2° C higher per month than in the preceding year. Dolphins were more abundant earlier in 1975-76 than in 1974-75. While "the peak" of dolphin presence occurred in January 1975, it occurred in October 1975 in the next season, with a sharp drop-off to January 1976.

Where were the dolphins during the period from March through July, when they were rarely sighted in the study area? During 19 of 24 (79%) boat trips made throughout the bay in these months, we found them in the western part of Golfo San José, closer to the mouth of the bay and

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[3] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

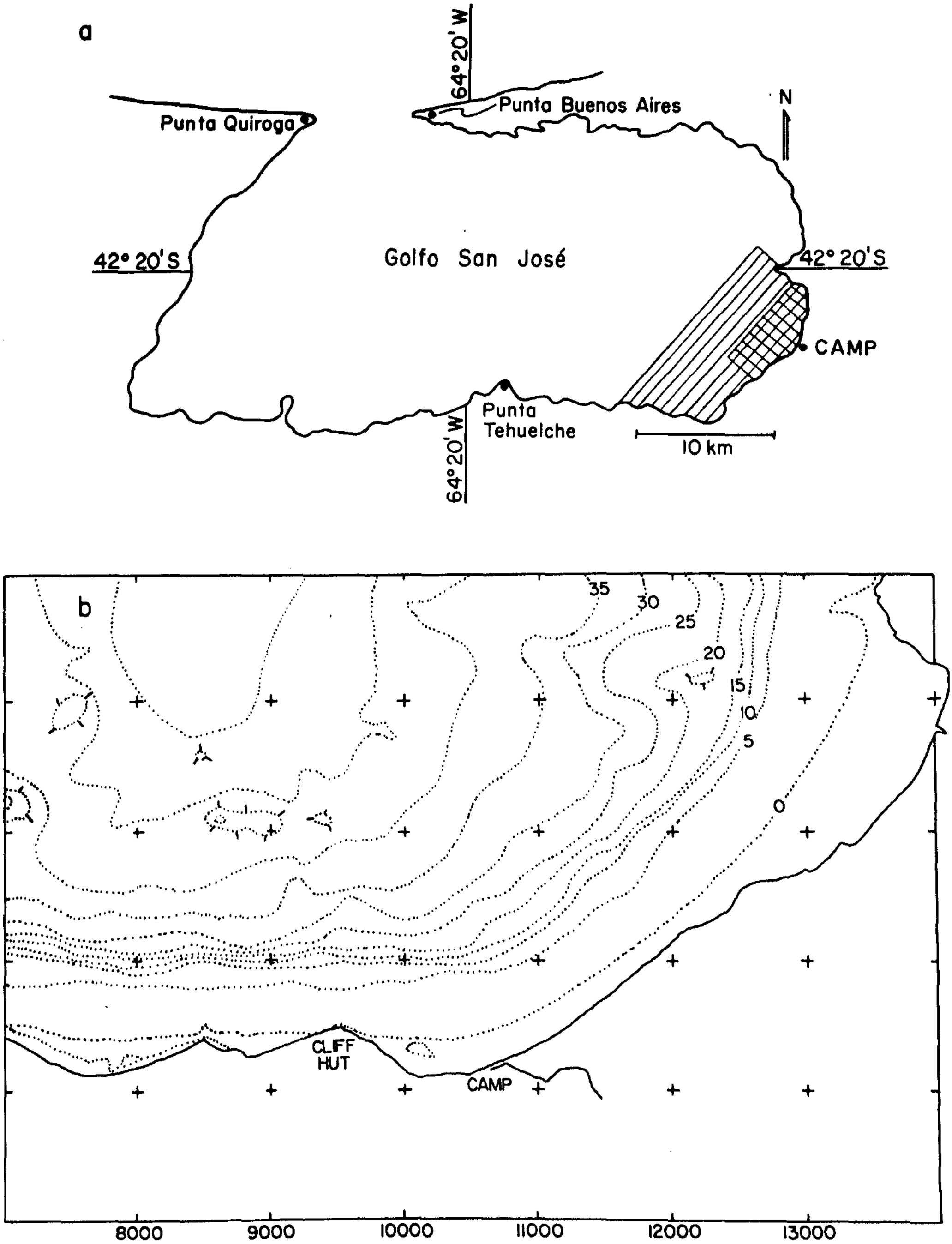

FIGURE 1.—Map of Golfo San José on Peninsula Valdés, Argentina (a). The bay is about 750 km² in area, with a 7 km wide mouth opening to the Atlantic. The lined area in the southeast portion of the bay represents the study area. The crosshatched subsection is shown in detail in b. It is a depth contour map of one-fourth of the study area. Margin numbers represent meter distances relative to a zero location on land. Crosses form 1 km squares. "Cliff Hut" and "Camp" are the locations from which most observations were made. Depth contours are in meters at mean low water (MLW). The usual distance for good observation of a moving dolphin group was at least 3 km. At a normal tide height of 5 m above MLW, water depth of 40 m was 1 km from Cliff Hut, and thus clearly visible. The map is from a larger area map which was by courtesy of Roger Payne, New York Zoological Society; Oliver Brazier, Woods Hole Oceanographic Institute; and Russ Charif, Harvard University.

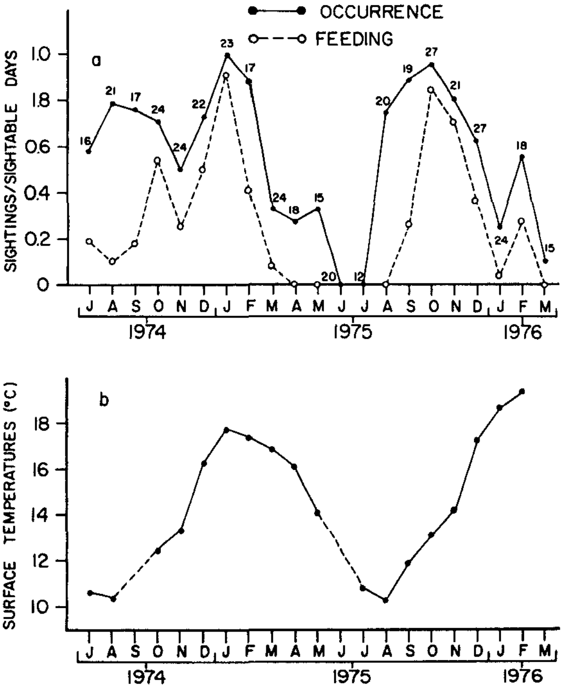

FIGURE 2.—Fraction of possible days per month on which dusky dolphins were sighted, and were seen surface feeding (a). The y-axis represents the ratio of number of days on which dolphins were sighted or were seen feeding divided by the number of days each month with winds <20 km/h (sightable days). During all sightable days, observations were made from dawn to dusk. Numbers above points represent the number of sightable days per corresponding month. Average surface temperatures within 3 km of shore during the same 21-mo period as in Figure 2a(b).

near the open ocean (Figure 1a). A large oceanic mass of water changes temperature less rapidly than nearshore shallow water, and this may have influenced the dolphin's movement, perhaps by a shift in prey location. Dolphins were found near the mouth of the bay from March through July, when temperatures in the study area dropped from 17° to 11° C (Figure 2), and it is likely that near-mouth temperatures decreased more slowly due to the influence of the open ocean water.

Although dolphins were present at the study site most of the year, and were found in Golfo San José the entire year, we did not know whether the animals were part of the same population or herd during all seasons. However, four spaghetti tags inserted in December and January were resighted in August, November, December, and January of subsequent years. This indicated that at least some of the animals were present in different seasons, and thus did not appear to migrate.

Seasonal and Daily Surface Feeding Cycles

Surface feeding of dusky dolphins was often highly visible, with birds flocking above the feeding site, allowing us to estimate from a distance when and where the dolphins were feeding on schooling fish (Figure 2a). Regardless of season, whenever dolphins were seen they were often feeding. However, in August and September 1974 and 1975, dolphins were present much of the time but little surface feeding appeared to take place. Little or no surface feeding took place in low-dolphin months of June and July and in high-dolphin months of August and September. This low in surface feeding corresponded with the lowest temperature period (about 12° C and below) of the year, possibly because fewer food fish were in the area.

When surface feeding bouts occurred, they were observed throughout the day. However, the length of feeding bouts increased as the day advanced. Feeding bouts were longest at 1500 h, then declined as evening approached (Figure 3).

Although feeding lasted longer during the afternoon (to 1500 h), there were nevertheless some long feeding bouts in the morning (Figure 4), with a significant increase in long bouts in the afternoon.

Depth of Water and Speed of Movement

Are dusky dolphins found at certain water depths and does their swimming speed vary with water depth? To answer these and similar questions, we tracked group movements by surveyor's theodolite. Figure 5a shows that they were most often tracked while in water 5-10 m deep. This peak is probably somewhat biased because observations were possible more often within about 1 km from shore, where depths of 0-30 m were found. Nevertheless, since both 0-5 m and 10-30 m depth areas approximated the area at 5-10 m, dolphins appeared to have a clear preference for traveling in water 5-10 m deep while near shore. A small but significant secondary peak also occurred at 35-45 m. Although dolphins traveled in water >65 m, this has not been represented in Figure 5a, since no water within sight was >65 m. For radio tracked movement out of sight of land see Würsig (in press).

The overall average speed was 7.7 km/h. There was a shift in speed depending upon depth of water in which the animals were traveling (Figure 6).

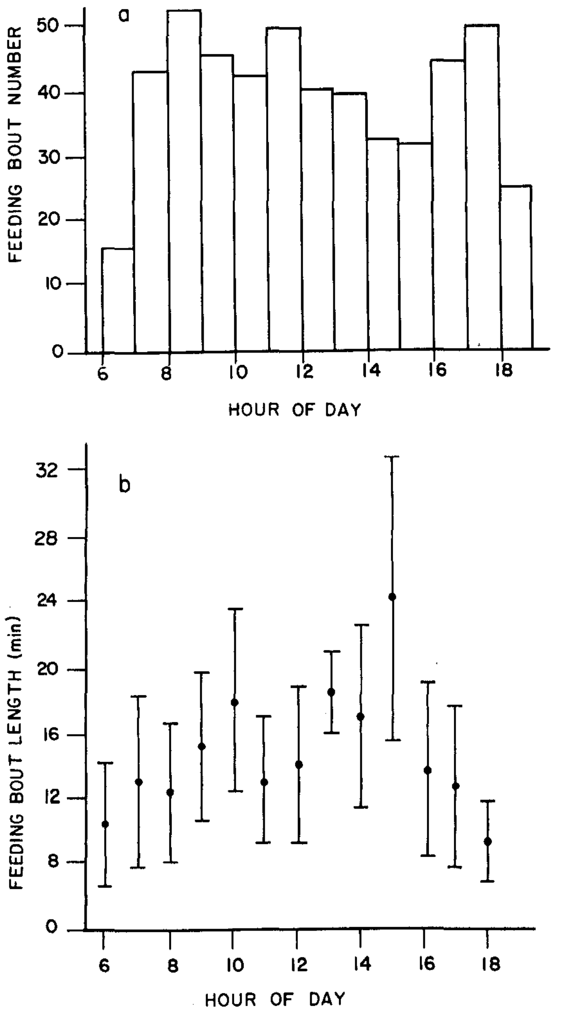

FIGURE 3.—The number (a) and mean lengths (b) of dusky dolphin feeding bouts throughout the day, summed for 21 mo from June 1974 to March 1976. Bars above and below mean feeding lengths enclose 95% confidence intervals for means.

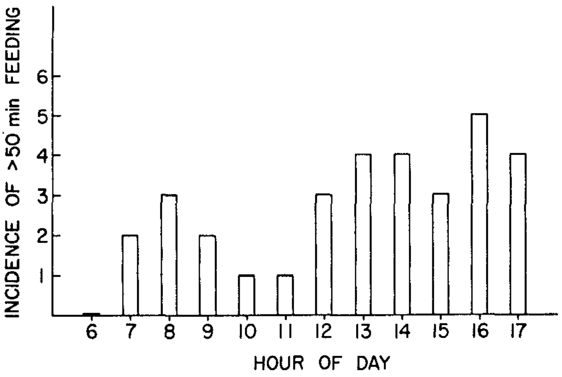

FIGURE 4.—The number of >50-min surface feeding periods of dusky dolphins during different times of day. Significantly longer surface feeding periods occurred in the afternoon (0600-1200 h = 9 or 28%; 1200-1700 h = 23 or 72%; testing equality of percentages, arc sine transformation ofr statistic t_s).

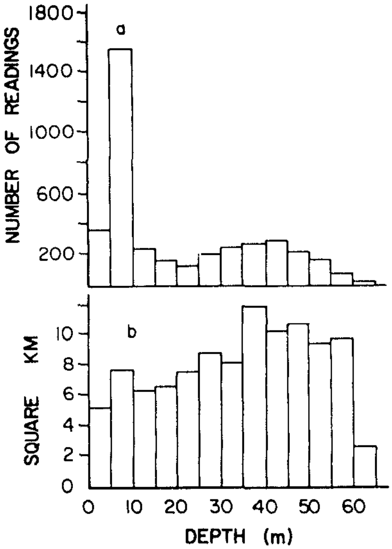

FIGURE 5.—Number of theodolite readings of dusky dolphins over depths from 2 to 65 m (a). Although most readings were at 5-10 m, a smaller peak occurred at 35-45 m which appeared to correlate with feeding activity at that depth (see text). Amount of area available in the study region as a function of water depth, at a mean tide height of 5.0 m above mean low water (b).

Groups moved at about 5 km/h in water 1-10 m, and faster in deeper water (average speed in water 55-60 m was 16 km/h). Furthermore, there was a general movement from shallow to deeper water as the day advanced (Figure 7a), and dolphins moved more rapidly in the afternoon than in the morning (Figure 7b).

Because water depth and dolphin speed were related (Figure 6), it is not surprising that dolphins, on the average, moved faster in those months in which they were in deeper water (compare Figure 8a with b). At the same time there was a strong correlation between depth and speed during different months and the amount of feeding activity during those months (compare Figure 8a with Figure 2a; correlation = 0.77, P = 0.003, Kendall coefficient of rank correlation).

Dolphin groups moved into deeper water in the afternoon in each of the 7 mo for which adequate depth versus time of day data exist (Figure 9a). In August and September, when little surface feeding occurred, and when water temperatures were lower than in summer, dolphins stayed in rela-

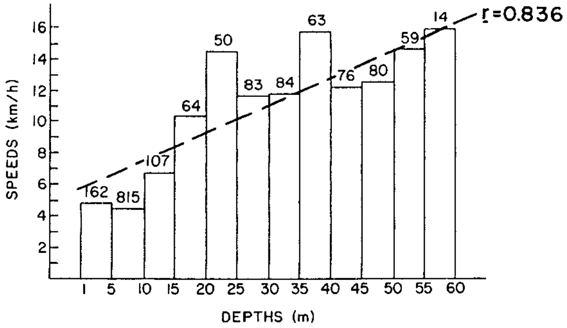

FIGURE 6.—Average speeds with which dusky dolphins traveled at different depths. The least squares regression, fit to the means shown, is statistically significant ($P<0.01$). Numbers over bars represent number of observations in that category.

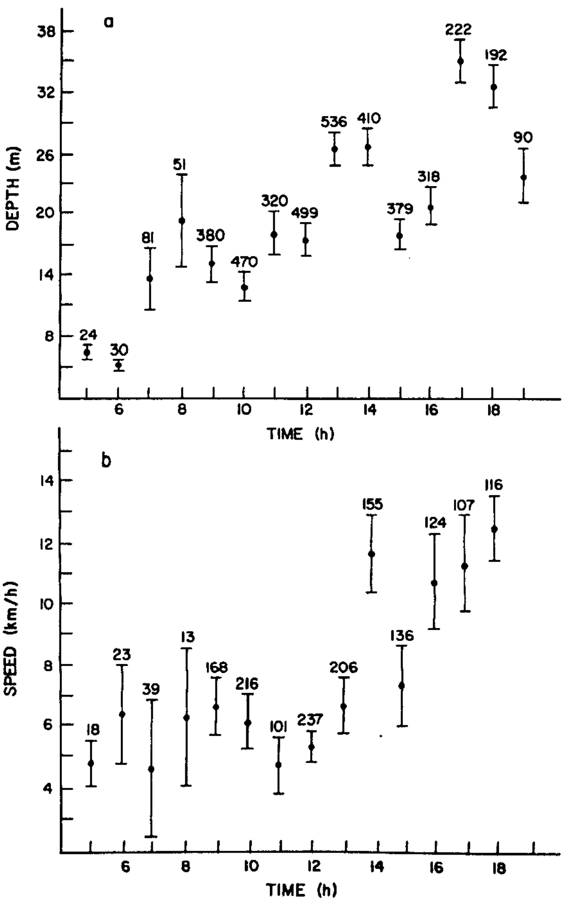

FIGURE 7.—Mean depth of water (a) and mean swimming speed (b) of dusky dolphins as a function of time of day. Bars represent 95% confidence intervals for means and numbers above bars represent the number of theodolite readings per hour interval.

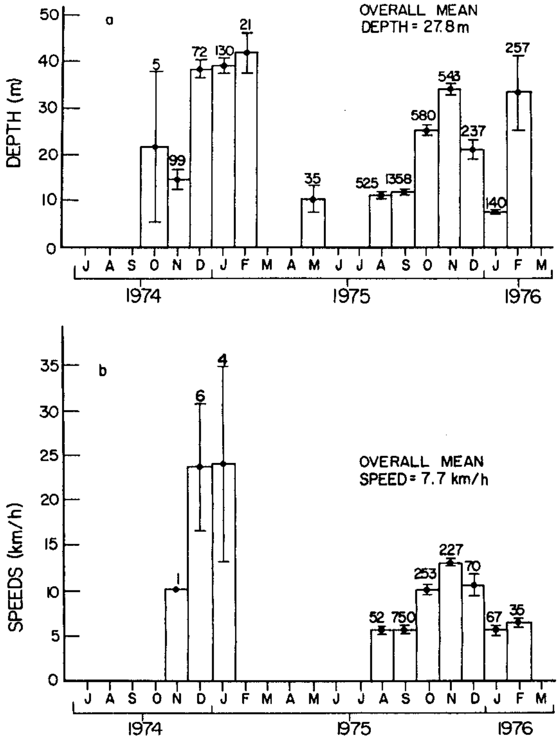

FIGURE 8.—Mean depth of water inhabited by dusky dolphins for different months (a), and mean speed of travel for dolphins for different months (b). Numbers represent number of theodolite readings obtained per month; bars represent 95% confidence intervals for means.

tively shallow water compared with the following months (Mann-Whitney U-test, $P<0.001$).

Dolphins usually moved more rapidly during afternoon than morning (Figure 9b). The increase in rapid movement per month appears related to the amount of surface feeding bouts in that month. Thus, in August 1974 and 1975 few surface feeding bouts occurred, and there was no increase in speed during the day. In September, some feeding took place, and there was a small speed increase. In October, November, December, and January much surface feeding took place during one or both years, and the afternoon speed increase was most dramatic. In February, both surface feeding and afternoon speeds were again down to pre-October levels (August, September, and February afternoon speeds are significantly different from October, November, December, and January afternoon speeds, Mann-Whitney U-test, $P<0.001$).

From these data we concluded that dolphins traveled faster at surface feeding times. This was confirmed by comparing speed data of dolphins as

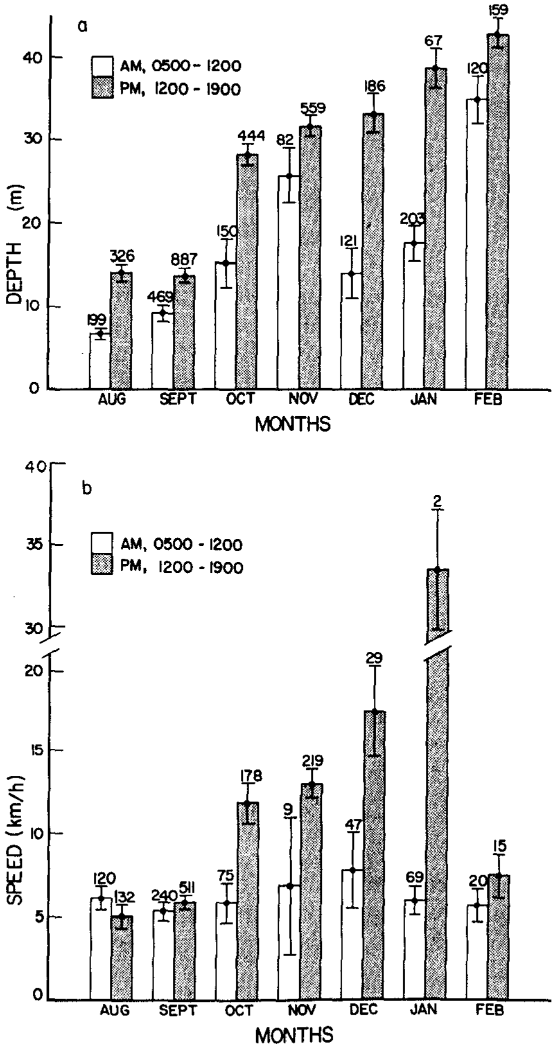

FIGURE 9.—Mean depth of water (a) and mean speed (b) of dusky dolphin travel in mornings versus afternoons, separated into those months for which adequate data are available. The lines above and below bars represent 95% confidence intervals for means, and numbers represent number of theodolite readings. During August and September, dolphins were found in significantly shallower water than during the spring and summer months of October-February (Mann-Whitney U-test, $P<0.001$). During August and September, dolphins also moved significantly slower than October through January (Mann-Whitney U-test, $P<0.001$). Almost all speed increases in these months took place in the afternoon.

they moved with no feeding bouts present in the area, and as they moved near feeding bouts (Table 1). The mean speed without feeding bouts was 6.3 km/h, while speeds around feeding bouts averaged about 15 km/h.

Dusky dolphins spent more time in deeper water when surface feeding. Furthermore, the depth of water in which surface feeding occurred increased as the summer season advanced (Figure 10). Thus the mean depth of feeding bouts during September was 21 m, but by February dolphins were surface feeding in waters 41 m deep. Since it is a general rule (and confirmed for Golfo San José by Pizzaro (1976), and pers. obs.) that deeper offshore water is cooler than shallow nearshore water in summer, this change in preferred feeding locations may represent a change in movement patterns of fish upon which the dolphins were feeding. We caught fish from schools on which the dolphins were feeding on 15 separate occasions, and identified the species composing such schools in the field about 50 more times. In all cases, the fish were southern anchovy, *Engraulis anchoita*. These fish are found in deeper water during summer in a nearby coastal area, where they are netted by fishermen (Mermoz[4]), and we suspect that they move into deeper water in summer in the present study area as well.

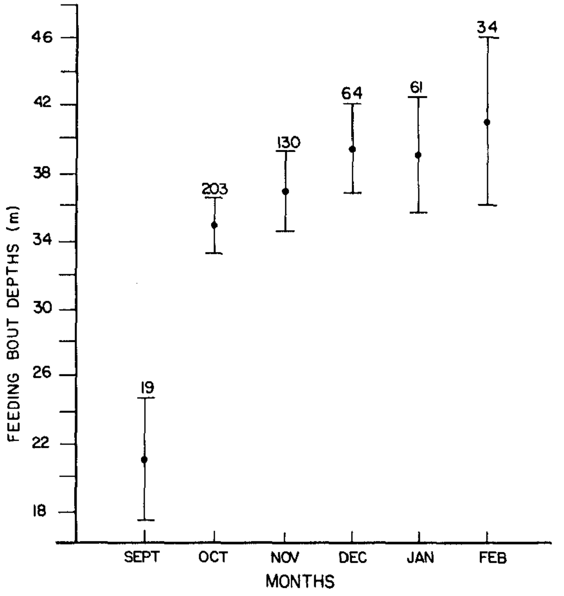

FIGURE 10.—Mean depth of dusky dolphin surface feeding bouts during different months. Bars above and below means represent 95% confidence intervals for means. Numbers above bars represent the number of theodolite readings of feeding bouts per month.

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[4] J. Mermoz, research scientist, Museo de Ciencias, Buenos Aires, Argentina, pers. commun. 1975.

TABLE 1.—Average speeds of dusky dolphins not associated with feeding, and associated with feeding activity. The difference in speed between no feeding activity seen (row 1) and speed around feeding activity (rows 2, 3, and 4) is significant ($P<0.001$, t'-test of equality of means when variances are assumed to be heteroscedastic).

Row	Category	Average speed (km/h)	Standard deviation	Theodolite readings (n)
1	No feeding activity seen	6.3	2.35	1,390
2	Dolphins not associated with feeding activity in the area	15.3	3.46	72
3	Movement towards feeding activity	13.7	3.43	88
4	Movement out of feeding activity	15.6	3.52	109

Relationships of Group Sizes, Feeding, and Aerial Behavior

For the purposes of this paper, we defined a group as a number of animals that are swimming together and moving as a unit (but not necessarily all pointed in the same direction). Individuals of a group were usually within visual range and certainly within acoustic range of at least some conspecifics. Group sizes varied from 6 to about 300 individuals. There was a seasonal shift in group sizes. From May through September, groups with <20 animals were more common than at other times of the year (Figure 11). As stated earlier, a low in feeding bouts occurred in the southeast part of Golfo San José from March to September (Figure 2a), and we gained the impression from boat trips to the middle and western section of the bay that surface feeding there occurred with high frequency in March and April, but did not often occur anywhere in the bay from May to September. As a result, it appears that smaller groups were most abundant during the nonsurface feeding months of May to September.

There was a direct relationship between size of dolphin group and surface feeding frequency. Thus, groups with <20 individuals were found in feeding bouts only 19% of the times they were spotted, while groups with >20 animals were seen feeding more of the time (Table 2). Because a surface feeding-speed relationship was noted, it is not surprising that speed of group travel increased with increasing group size. While small groups occurred most often in the morning (and were not surface feeding), larger groups were most often associated with feeding bouts in the afternoon (Table 2).

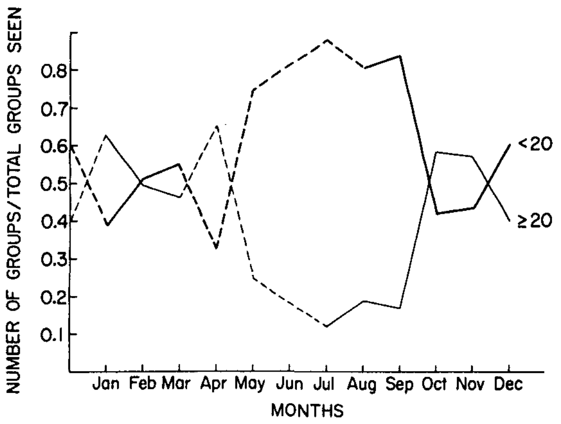

FIGURE 11.—Percentage of dusky dolphin groups with <20 individuals compared with those with ≥20 individuals, by month. Dashed lines connect one or both points with <10 groups sighted that month. October-April percentages are significantly different from those of May-September ($P<0.001$, equality of percentage test with arc sine transformation).

The larger the group size, the longer the feeding activity lasted (Table 3). The number of birds also increased with dolphin group size, and with length of feeding (Table 3). Species of birds, in approximate order of decreasing numbers, were the black-headed gull, *Larus dominicanus*; cormorants, *Phalacrocorax brasilianus* and *P. magellanicus*; terns, *Sterna* spp.; different species of Pro-

TABLE 2.—Average speed and time of day related to group size estimates, and percentage of times dusky dolphins of three different group sizes were associated with feeding activity. Groups with <20 individuals were seen feeding less frequently than larger groups ($P<0.001$, testing quality of percentages, arc sine transformation of t-statistic).

Item	Dolphin group size (estimate)		
	<20	≥20<50	≥50
Number of theodolite readings used for speed data	66	37	30
Average speed (km/h)	5.7	7.4	13.8
Standard deviation	2.30	2.60	3.45
Average time of day, Argentine local time (h:min)	10:12	13:20	14:06
Standard deviation expressed in hours and minutes	2:40	2:57	2:45
Number of times seen feeding (a)	130	177	190
Number of times seen while not feeding (b)	540	117	77
Percentage of times seen feeding during total sightings (100a/(a + b))	19	60	71

TABLE 3.—Estimated number of dusky dolphins and birds (see text) in feeding bouts of different lengths (t'-test of equality of means when variances are assumed to be heteroscedastic).

Dolphin group size	Mean length of feeding by dolphins			Mean number of birds		
	n	Mean[1]	SD	*n*	Mean[1]	SD
<10	19	6.3ns	4.42	19	75*	73.8
≥10<20	91	11.1**	12.00	91	115**	82.3
≥20<50	116	16.5**	14.38	116	163**	116.5
≥50	87	25.8	24.23	87	246	117.8

[1] ns = not significant; *$P<0.05$; **$P<0.01$.

cellariiformes; the giant petrel, *Macronectes giganteus*; and black-browed albatross, *Diomeda melanophris*. Terns were usually the first birds to begin flying over and diving into feeding dolphin groups. Then gulls and finally larger birds aggregated at the feeding area.

The most striking behavior of dusky dolphins we observed was their aerial displays. To find out why these displays occurred, we noted the frequency of this activity at different times. We saw all aerial displays described by Norris and Dohl (1980) for the Hawaiian spinner dolphin, *Stenella longirostris*. These were leaps, head-over-tail leaps, backslaps, headslaps, tailslaps, spins, and noseouts. The most "acrobatic" of these leaps was the head-over-tail leap. The spin was performed frequently by the Hawaiian spinner dolphin, but it constituted <1% of leaps in the present study. When it was seen, it was also classified as acrobatic, along with the head-over-tail leap, for further analysis.

Two other aerial displays seen in dusky dolphins were the headfirst reentry leap and its apparent variant, "humping." In the headfirst reentry, the dolphin leaped clear of the water and then arched its back strongly while flipping the tail to make a headfirst reentry. While humping, the same motion occurred except that the snout and tail did not leave the water during the body arch.

Leaps, head-over-tail leaps, backslaps, headslaps, tailslaps, and spins usually occurred in groups. That is, one animal started a particular leap, and then continued it from 3 to about 20 times. Because we could often not be certain that the same individual was performing the leaps during a leap sequence, we do not have complete quantification for this phenomenon. However, in 45 of over 1,000 leaps it was certain that the same animal leaped throughout a sequence, because we followed it visually while it swam below the surface between leaps. In all 45 instances, the leap type per sequence did not change, and a mean of 4 (SD = 2.2) leaps per sequence was performed. Although the first five or so leaps were performed with "exuberance," as animals leaped clear of the water and reentered forcefully, successive leaps were not as high, possibly as the animal tired.

The headfirst reentry and humping did not occur in sequence, but were usually performed only once by an animal within about 30 s. Because animals stayed underwater for long times between leaps, we could never be certain that the same animal leaped later on. Instead, the 30-s estimate was derived from counts of total leaps occurring in a particular group size, and must therefore be treated with caution. The headfirst reentry and humping were often performed in concert with one or two others leaping in the same manner at the same time. While all other aerial behaviors left individuals close to the water surface between leaps, the headfirst reentry and humping took them farther below the surface, and we saw them swimming out of sight at about a 75° angle.

As was described by Norris and Dohl (1980), leaps, head-over-tail leaps, backslaps, headslaps, tailslaps, and spins made noise as the animals reentered the water. That is, they created sharp bursts of sound when the animals slapped the water with their flukes or body upon reentry. Hydrophones detected the sounds underwater at approximately 0.5 km distance, but not at 1.0 km distance during four recording sessions under optimal (no wind or waves) conditions. Norris and Dohl also mentioned that sounds made by these leaps attenuate relatively rapidly, but gave no distance estimates.

Headfirst reentry and humping, however, made little or no sound above or below the water (hydrophones did not detect sound 10 m from the activity). Dolphins slid out of and into the water along their longitudinal body axis during these two leap types. Because we believe that the noise made by most leaps may be biologically meaningful, we separated them into "plain noisy" (the leap, backslap, headslap, and tailslap) and "acrobatic noisy" (head-over-tail and spin) leaps, and distinguished them from noiseless or "clean" leaps (headfirst reentries and humping). The noseout did not make noise and was often difficult to see from the boat or from shore. It was therefore not quantified.

We observed dolphins in feeding bouts for 145 h, and observed them during periods when we saw no feeding bouts for 309 h, or over twice as long. Nevertheless, we saw a significantly higher frequency of noisy and clean leaps while dolphins were surface feeding (Table 4). More noisy leaps were made during and after surface feeding than before, and those few noisy leaps which occurred before surface feeding were most often "plain" or nonacrobatic. During surface feeding, plain and acrobatic leaps occurred with about equal frequency, while after surface feeding most leaps were acrobatic. The noiseless or "clean" head-first reentry leap and humping behavior occurred more often before and during surface feeding than after surface feeding.

Our general views of behavior introduced above were as follows: When not surface feeding, dolphins usually moved in small (<20 individuals) groups (Table 2) with sporadic but relatively infrequent aerial behavior (Table 4). They usually moved slowly (about 6 km/h) at this time. Immediately previous to feeding bouts, they moved more rapidly for short periods (mean time = 6.2 min, SD = 4.53), often creating whitewater as they surged through the water at speeds >10 km/h (Table 1). We gained the impression that between such surges, they stayed underwater for longer periods than their normal diving times (mean dive time = 21 s, Würsig in press), often disappearing from sight for over 60 s. This pattern of movement lasted from a few minutes to as long as 1 h. When it stopped and dolphins were again found more often near the surface, they moved slowly and stayed in basically the same location. At this time, noiseless (clean) and noisy (plain) leaps began (Table 4). When we were near this activity in a boat, we were able to see a fish school usually 2-3 m in horizontal diameter, and 0.5 m vertical height, near the water surface.

Every time (65 occasions) the fish were observed they were southern anchovy 6-15 cm long. When we spotted the fish school near the surface, we also saw terns beginning to dive for the fish, and gulls coming from the vicinity. Plain noisy and clean leaps continued, and acrobatic leaps began to appear (Table 4). During surface feeding, many of the clean displays were composed of humping behavior. During humping, dolphins rapidly moved singly or in pairs through the fish school after coming almost vertically from deeper water, caught one to five fish in their mouths, and then descended again at a steep angle. Dolphins were also seen near and around the feeding bout nucleus, chasing and feeding on individual fish not part of the tight school.

If the surface feeding dolphins were not joined by a nearby group or groups within several minutes, the feeding bout died down. We lost sight of the fish, either because the school had been reduced by dolphins and birds or because it moved away from the surface. Often, however, other dolphin groups in the vicinity converged on the feeding bout, moving rapidly in a straight line towards the feeding birds and dolphins from as far away as 8 km, measured by theodolite on one occasion. A more usual distance was 2-3 km. As a result of this movement, the feeding bout grew larger—up to an estimated 300 dolphins and thousands of birds—and lasted for a correspondingly longer time (Table 3). Surface feeding appeared to stop when dolphins rapidly moved away from the activity, or when they began deep dives and clean leaps once again. In either case, we no longer saw the fish school. Birds stopped flying and diving in a concentrated area and settled on the water or followed

TABLE 4.—Observed incidences of aerial behavior in dusky dolphins. Numbers represent number of 15-min periods during which a particular type of leap was seen. Frequency of leaping within that period has not been quantified. "Noisy leaps, in general" represent leaps which made noise but were not separated into "plain" or "acrobatic" during data gathering. All significance testing used the equality of percentages, arc sine transformation for the statistic t_s.

Time of leaping	a Noisy leaps, in general	b Plain noisy leaps	c Acrobatic noisy leaps	d Clean leaps
A During the 15 min before feeding	24	17	0	35
B During feeding (average time of 15 min)	109	13	15	32
C During the 15 min after feeding	84	1	20	12
D Without feeding	45	22	3	25
Total	262	53	38	104

Comparisons:

Amount of noisy leaps, in general, a, associated with feeding, A-C (83%) versus without feeding, D (17%); significant difference, $P<0.001$.

Amount of noisy leaps, in general, a, before feeding, A (22%) versus after feeding, C (78%); significant difference, $P<0.001$.

Amount of noisy leaps before feeding, A, plain, b (100%) versus acrobatic, C (0%); significant difference, $P<0.001$.

Amount of noisy leaps after feeding, C, plain, b (4.8%) versus acrobatic, D (95.2%); significant difference, $P<0.001$.

Amount of plain noisy leaps, b, before feeding, A (94.4%) versus after feeding, C (5.6%); significant difference, $P<0.001$.

Amount of acrobatic noisy leaps, c, before feeding, A (0%) versus after feeding, C (100%) significant difference, $P<0.001$.

Amount of clean leaps, d, associated with feeding, A-C (76%) versus without feeding, D (24%); significant difference, $P<0.001$.

Amount of clean leaps, d, before feeding, A (74%) versus after feeding, C (26%); significant difference, $P<0.01$.

the rapidly moving dolphin group. Dolphins tended to stay together for up to several hours once groups had converged to feed, and feeding activity usually started again in these larger groups. When it did so, it lasted longer than when fewer dolphins were feeding, and therefore larger groups were more often seen in association with feeding bouts (Table 2).

Group Organization and Calving Periodicity

As mentioned previously, the most common nonfeeding group size was about 6-15 animals. In general, these groups were composed of adults, and at times included juveniles and calves. We were not able to determine sex of individuals by observing them from boat or shore, but captures of individuals prior to radio tagging (Würsig in press) demonstrated that males and females usually travelled together in these small groups. We saw small calves (about equal to or less than one-third adult size) from November through February. Furthermore, we saw "juveniles" (about one-half to two-thirds of the size of adults) or young under 1 yr of age during April-May and August-September (Table 5). The sample size was too small, however, to say definitely that young were born only during the summer, and births may have been more spread out over the year. Nevertheless, the data suggest a summer calving peak.

Although we saw small calves and young in small groups, we also saw groups of 8-20 adults and as many calves on six separate occasions. We called these groupings "nursery" groups, on the assumption that the adults may have been females, and the calves their young. During all six sightings of nursery groups, most or all other animals in the vicinity were engaged in feeding activity and aerial behavior 0.5 to several kilometers distant from the nursery group. During 12 other sightings of calves and adults, they were found in small groups in the ratio of approximately 1 calf to 10 adults and were not engaged in large-group feeding activity (although on 3 of the 12 occasions, we saw calves in small groups that were feeding). We suspect from these observations that young normally travel with adults in small groups, but when many groups coalesce to feed and socialize (see below), calves and certain adults split off at some time and form temporary nursery groups.

TABLE 5.—Sightings of calves and juvenile dusky dolphins. Incidence of calves during November to February was significantly higher than in the rest of the year ($P<0.001$, Raleigh test, Greenwood and Durand 1955).

Month	Number of sightings		Month	Number of sightings	
	Calves	Juveniles		Calves	Juveniles
Jan.	4	0	July	0	0
Feb.	1	0	Aug.	0	2
Mar.	0	0	Sept.	0	2
Apr.	0	1	Oct.	0	0
May	0	1	Nov.	2	0
June	0	0	Dec.	3	0
			Total	10	6

If there is a calving peak during the year, then most successful matings are probably also carried out in a relatively restricted time period. Most apparent copulations, consisting of rapid belly-to-belly swimming and frequent pelvic thrusts by one or both animals, appeared to take place in large groups during and after surface feeding. Most of these large groups were found in summer (Figure 11). However, it was difficult to approach small, nonsurface feeding groups, and we have few data on their underwater behavior and possible mating attempts. Although we saw some apparent mating in groups of all sizes and at all times of the year, we were not able to quantify these observations.

When we saw small groups of 6-15 animals, we usually saw many of them, up to about 30 such groups, in an area approximately 10 km in diameter. However, we were able to count these groups only under the best conditions, on a calm sea. When these groups converged to surface feed, the upper limit of group size estimate was 300 animals, and this estimate—made by different observers and at different times of year—did not vary appreciably. It thus appears that small groups made up part of a larger school or herd of animals. We do not know how stable small groups were over time, although evidence has been presented by Würsig (in press) which suggested that at least some groups remained stable over a period of at least several days, and appeared to remain together in "subgroups" of a large group during and after feeding bouts.

Interspecific Interactions

Dolphins associated with the boat at times by rapidly moving towards a moving boat from as far as 2-3 km. They would then ride the bow and stern pressure waves of the boat in characteristic dolphin fashion. This activity took place mainly when the dolphins had been surface feeding for a long time and were thus in large groups. Table 6 shows a few instances of this behavior, when we were certain whether or not the dolphins had been feeding. The data confirm the impression that dolphins which had been in or near feeding bouts approached the boat, while groups which had not been surface feeding avoided or ignored it. When the dolphins associated with the boat, a high level of acrobatic noisy leaps was also evident. Of course, it is likely that the dolphins were merely associating with the boat, and that the humans on board were irrelevant.

Dolphins also associated with the southern right whale, *Eubalaena glacialis,* and the sea lion, *Otaria flavescens,* by moving around and among them in a manner similar to that described for bottlenose dolphins (Würsig and Würsig 1979). This activity also appeared related to whether dolphins had or had not been surface feeding. Differences in behavior between "fed" and nonfeeding dolphins were striking, and we labeled them different "activity levels," following the definition of this term by Norris and Dohl (1980).

After feeding, dolphins at times balanced kelp (pieces of *Macrocystis* sp.) on their pectoral flippers. In one individual this persisted for at least 1 h. The activity of kelp-balancing, we suspect, may be termed "play."

Dolphins interacted with other odontocete cetaceans as well. Groups of from one to six killer whales, *Orcinus orca,* appeared for brief periods throughout the year (Table 7). On the six occasions when we saw them within about 1 km of dusky dolphins, the dolphins moved rapidly in a tightly bunched group away from the killer whales. On three occasions when dolphins were within 1 km of land, they moved towards the shore, and then proceeded along shore in water less than 1 m deep, the closest to shore we ever saw this species. It was reported to us by reliable observers (Jen and Des Bartlett[5]) that killer whales in our study area once surfaced within a school of dusky dolphins, with one whale dripping blood from its mouth, perhaps indicative of having actually fed on a dolphin. However, we have no conclusive evidence that killer whales habitually feed on dusky dolphins.

TABLE 6.—Number of times that dusky dolphin groups associated with the boat by orienting towards it and "bow riding," and number of times they avoided or ignored the boat; both relative to feeding activity (A significant difference from C, $P<0.01$; B significant difference from D, $P<0.001$; chi-square goodness of fit test).

Category	Moved to boat		Ignored boat	
Group not seen surface feeding	A	10	B	18
Group seen surface feeding previously on same day	C	28	D	1

TABLE 7.—The number of days per month when *Grampus griseus* and *Orcinus orca* were seen in the Golfo San José study area.

Month	*Grampus griseus*	*Orcinus orca*	Month	*Grampus griseus*	*Orcinus orca*
Jan.	6	2	July	0	0
Feb.	12	2	Aug.	0	0
Mar.	15	2	Sept.	0	3
Apr.	0	3	Oct.	7	0
May	0	1	Nov.	0	2
June	0	1	Dec.	5	5

Risso's dolphin *Grampus griseus,* associated with dusky dolphins from October through March 1974-75 and 1975-76 (Table 7). From two to six individuals consistently stayed within 1-3 km of feeding dusky dolphins during this time. It is possible that Risso's dolphins were feeding on large fish found in the vicinity of southern anchovy, but we have no data for this assumption. Whether or not the larger cetaceans were of actual help to dusky dolphins in finding food, as has been suggested by Norris and Prescott (1961) for pilot whales followed by bottlenose dolphins, and by northern right whale dolphins, is not known.

The bottlenose dolphin, *Tursiops truncatus,* was found in small groupings of 8-22 animals in the study area (Würsig 1978). They usually stayed in shallower water than did dusky dolphins, and were never observed moving in water >39 m. There was, however, some overlap in area covered by both species. On only eight occasions were both species found within 0.5 km of each other. When they were relatively close, each species continued on its previous course, and no interactions appeared to take place (although they may have been interacting by sound). This apparent lack of interaction was especially striking because both dolphin types associated with right whales and sea lions. Dusky dolphins were more abundant when bottlenose dolphins were not, and vice versa (Figure 12).

DISCUSSION

Dusky dolphins were present in Golfo San José during most or all of the year, but were located in the southeast portion, in the study area, mainly during spring and early summer. They did not

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[5] Jen and Des Bartlett, wildlife photographers, P.O. Box 17323, Tucson, AZ 85731, pers. commun. November 1974.

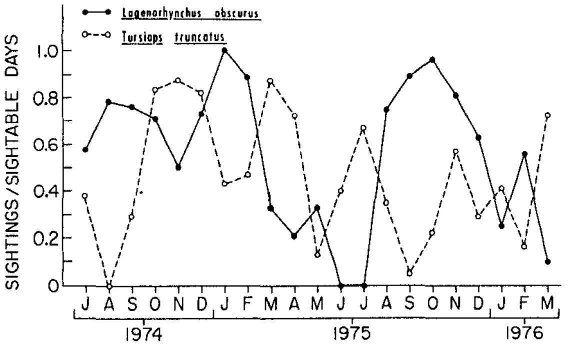

FIGURE 12.—Occurrence data from Figure 2a in conjunction with comparable data on bottlenose dolphins during the same period. The two species occurred in the study area with approximately opposite frequency, i.e., when one species was abundant, the other one was less often seen.

appear to avoid low (≈10° C) temperatures, but may have been avoiding higher (>18° C) temperatures near shore in mid- and late summer. At those times, they were found most often in cooler waters near the mouth of the bay. In Würsig (in press), it was shown that during that time they moved outside of the bay as well. Yet they did not show a well-defined seasonal migration pattern, and marked individuals were resighted in the same location during different seasons. Studies of groups of *Tursiops* sp. have indicated that degree of migration may be different for different populations. For example, bottlenose dolphins off Cape Hatteras, N. C., migrate (Mead 1975), while those of our study site did not (Würsig and Würsig 1979). Shane (1977) and Irvine et al. (see footnote 2) reported localized seasonal movements of bottlenose dolphins in the Gulf of Mexico, with differences between their East Texas and West Florida study sites. Degree of seasonally related movement probably hinges on several environmental and ecological variables, but an important factor for dolphins in temperate waters may be food availability (suggested by Norris 1967, Evans 1971, and others). Thus it seems likely that dusky dolphins moved with the food supply most of the year. The main prey item appears to be southern anchovy and we have some evidence that it is found in deeper offshore waters in spring and summer (Ciechomski 1965) and in large concentrations near the mouth of Golfo San José in late summer (Brandhorst and Castello 1971), at the same time dusky dolphins were feeding there.

Gaskin (1968) stated that dusky dolphins are present around the Hawke Bay area of New Zealand generally only in winter and spring. He related this to the presence of the cold Canterbury Current which comes close to Hawke Bay in winter and spring. Clarke (1957) and Sergeant (1962) described the seasonal migration by pilot whales as being regulated mainly by seasonal abundance of squid and certain schooling fish. Wilke et al. (1953) also found seasonal movement patterns for the Dall porpoise, *Phocoenoides dalli;* the northern right whale dolphin, *Lissodelphis borealis*; and the Pacific whitesided dolphin, *Lagenorhynchus obliquidens*. Norris and Prescott (1961) and Evans (1971) reported that the common dolphin, *Delphinus delphis,* moved closer to the shore of California in fall and winter, and moved farther offshore in spring and summer. They suggested that this movement was food related. Brown and Norris (1956) stated that whitesided dolphins off California were most often found near shore in winter and spring, and offshore in summer and fall. They also reported that the movements of the northern anchovy, *Engraulis mordax,* corresponded with the seasonal dolphin movements. Their observations of *L. obliquidens* thus agree with those of *L. obscurus* of the present study.

Frequency of feeding in the highly visible manner described, with birds flocking overhead, was seasonal. It occurred less often in winter than at other times. In winter, anchovy are found in water >100 m (which is deeper than Golfo San José), and farther north, around lat. 36°-37° S (Brandhorst et al. 1971). Thus it is probable that dolphins were not feeding on southern anchovy in winter in the study area. Yet it is not possible that mammals as small and as constantly active as dusky dolphins stopped feeding completely for several months. We can only guess that other feeding was done on prey below and not at the surface, and possibly more individually instead of as a concerted group effort. At any rate, in winter we observed very little aerial behavior and rapid movement usually attendant on surface feeding. Instead, dolphin groups consistently moved slowly and in small groups near shore. Stomach content samples would be helpful in solving this ambiguity.

Dolphins exhibited a daily feeding cycle as well. Morning surface feeding activity lasted for shorter times than in the afternoon, so that dolphins were more often seen feeding in the afternoon. They moved in shallow water (5-10 m) in the morning, but most afternoon surface feeding occurred in 35-45 m. We gained the impression that immediately before feeding, dolphins were diving for longer periods, perhaps going down deep to hunt for food. This impression was not quantified in direct association with feeding because we were unable to identify particular individuals and thus obtain length of dive records. However, we have evidence from radio-tracked dusky dolphins indicating that there is a length of dive-surface feeding time association (Würsig in press). Dive times from six dusky dolphins radio-tracked in summer showed a consistent increase in length during afternoon, with average night and morning dives about 14 s. Noon and afternoon dives rose to as high as 32 s in average duration. One animal radio-tracked in the austral winter (July-August 1974) showed no such length of dive increase in the daytime and actually surfaced more frequently in the afternoon than at other times of the day and night. This is an indication that feeding in the winter was different from feeding in the summertime. Since we believe that long dives in summer are associated with surface feeding in deeper water, it is likely that the extremely shallow and brief dives which occurred at night (Würsig in press) in summer were not associated with feeding, and that perhaps the animals were resting near the surface much of the night. This is the reverse of what was found in the common dolphin off California (Evans 1971, 1974), which dives for long periods at night—and is believed to be feeding at that time—and dives relatively shallowly during the day. Once again, this difference may be food related. While the common dolphin is thought to feed upon the deep scattering layer which rises out of deeper water enough for the dolphin to dive to it at night, no defined deep scattering layer can exist in the relatively shallow nearshore waters of the present study (Hersey and Backus 1962). Instead, dolphins feed on anchovy during the day, and move into deeper water as the day advances. Whether or not anchovy move into deeper water and are followed by the dolphin is not known. Perhaps the daily movement into deeper water was simply a consequence of being in shallow, nearshore water during night and early morning (to be discussed later), and having to go into deeper water in order to feed more efficiently. It is known that individuals of southern anchovy schools disperse during nighttime (Brandhorst and Castello 1971). This dispersal may make nighttime feeding on anchovy more difficult or impossible, and therefore dolphins may rest at night while feeding during the day in summer.

As an apparent consequence of feeding, dolphins were also found more often in deep water in spring, summer, and fall than in winter. Norris and Prescott (1961) suggested a similar movement trend for *Delphinus delphis* in California waters.

Group sizes were more often larger during the surface feeding season. The reason for this was a direct relationship between surface feeding activity and group size. Small groups usually engaged in surface feeding for only brief periods. The longer the feeding bout, the larger the number of dolphins present. Dolphins appeared to begin feeding in the morning and continued feeding through most of the afternoon; thus, there was a general increase in group size as the day advanced. The many small groups in the morning (and presumably night as well) covered a large (up to about 10 km in diameter) area, but nearest neighbors were usually no more than 0.5 km apart. We assume that they were probably within acoustic range of each other. Why did surface feeding activity last longer when dolphin numbers increased as groups joined? Perhaps larger schools of fish attract more dolphins and keep them feeding for a longer time. It is also possible that more dolphins are more efficient at herding and maintaining the fish school as a tightly clustered unit against the water surface. As an alternative explanation, it might be assumed that the small groups stopped feeding after brief periods because individuals were satiated. In a larger group, with perhaps more individuals per fish school size and more competition, this would presumably take longer. Since small schools which fed briefly were, however, seen to feed more and more as the day advanced, it seems unlikely that they had fed to satiation previously. Therefore, either larger fish schools simply attract more dolphins, or it is of direct advantage to animals to feed in larger groups, and a mechanism for telling nearby groups that herding of foodfish is in progress may have evolved. Various investigators have reported seasonal variations in group sizes, but none appear to link such variations to a particular feeding mode as in the present study. Gaskin (1972) stated that dusky dolphins off New Zealand are found in smaller schools in winter and larger ones in summer, basically the same as in our study. New Zealand dusky dolphins feed on small squid and on surface fish, but it is not clear whether their relative dependence on these prey changes seasonally.

How do other groups know about the feeding bout 0.5-1.0 km distant? It is unlikely that at that distance animals are actively echolocating on the fish school, and thus some behavior of the feeding dolphins is implicated. Perhaps underwater vocalizations serve as cues. The possibility of different sound emissions by dolphins feeding and not feeding has not yet been investigated in the present study, although Tyack (1976) found such a variation in wild bottlenose dolphins. The incidence of noisy—omnidirectional sound source—leaps increases before and during feeding, and these may provide cues to nearby dolphins. Norris and Dohl (1980) discussed the likelihood of leap sounds serving a communication function. We believe that the likelihood of such a function specifically in dusky dolphin feeding is great. If noisy leaps serve to attract or inform nearby schoolmates, and are at least in part designed to do so, this recruitment behavior may be analogous to the "drumming" recruitment of African chimpanzees, described by Reynolds and Reynolds (1965) and others. Saayman and Tayler (1979) suggested that recruitment may occur in *Sousa* sp. off South Africa as well, but they did not link it to the possibility of aerial behavior in their population.

How do groups orient towards feeding locations from a distance of more than several kilometers? Our underwater recordings of sounds created by leaps suggests that they probably do not propagate much over 1 km. Norris and Dohl (1980) also found rapid attenuation for underwater Hawaiian spinner dolphin leap sounds. But, we observed dolphins that were leaping towards a large feeding bout from as far as 8 km. One possible explanation is that at least one dolphin swam to the distant group with information about the feeding bout, a feat not unknown in the animal kingdom (von Frisch 1967, on honey bees). We have no evidence that such messenger service may take place, and suggest a possible alternative. (Although Eberhard and Evans 1962, Evans and Dreher 1962, and Dreher and Evans 1964 reported that individuals of the Pacific bottlenose dolphin, *Tursiops gilli,* have been seen detaching from a group, moving to "investigate" something, and then going back to the group. Their interpretation of scouting behavior, however, is open to speculation.) When we saw dolphins swimming towards a feeding bout from more than a few kilometers, we saw individuals leaping out of the water in high forward leaps, clearing the water by as much as three times their own length, and thus leaping as high as 4-5 m. This leaping became lower and finally subsided altogether as the animals came closer to the activity. It seems possible that dolphins are using in-air vision to orient to the feeding bout, taking the birds flying above the activity and the leaping dolphins of the activity as a cue. We present this as a tentative hypothesis because many investigators do not believe that dolphins have a high degree of long-range in-air visual acuity. Dral (1975), Herman et al. (1975), and Rivamonte (1976), however, believe that *Tursiops* sp. may have good in-air vision at infinity. Perhaps dolphins gain information about the feeding bout in some other manner, and are leaping that high and often simply as part of their rapid movement (although such high leaps are not seen during after-feeding rapid movement). The high leaps may decline when the dolphins get near the activity because they are tiring. If it should prove, however, that dolphins are capable of long-range vision, and use it in this manner, it would mean that the birds associated with dolphin feeding—up to now assumed to represent a parasitic or neutral role as they scavenge on the dolphins' herding efforts—may serve as a signal to other dolphins. Dolphin leaps would assume a similar in-air signaling function. To observers, the number of birds above an activity was a sign of the feeding activity's "success," and if dolphins can see these birds, there is no reason to assume that they could not as well gage such activity level.

Various different types of leaps and aerial displays are associated with different stages of surface feeding. What function could these leaps serve? To answer this question we will attempt to reconstruct a typical feeding bout in detail: Before surface feeding, dolphins move rapidly, and dive for long periods, indicating that they are covering a large distance and are looking for fish deeper than a few meters below the surface. Immediately before and during feeding, forward movement stops and long dives continue, interspersed with clean, noiseless leaps. During these leaps, animals reenter the water headfirst and rapidly swim down. We therefore believe that the clean leaps allow dolphins to breathe rapidly, and then forcefully and efficiently return to the depths. The humping variant of this leaping type appears similar to the headfirst surface dive employed by experienced skin divers.

As long dives decrease, a tightly bunched fish school, usually numbering several thousand fish in an area 3-5 m in diameter, is first seen at the surface. It thus appears that dolphins actively herd fish towards the surface, probably to use the surface as a wall through which the prey cannot escape. This function has also been suggested by Norris and Dohl (in press), and shown to be carried out by some large predatory fishes by Major (1976; cited by Norris and Dohl in press).

Noisy leaps, which started at some point before the fish school appeared, continue throughout surface feeding. We gained the subjective impression that these leaps occurred on the periphery of feeding bouts. This may be because breaching directly into the fish school would certainly not be of advantage in keeping it tight against the water surface. As well, it may serve to keep fish from escaping, and thus may be an acoustic or vibration "netting" effect. We often saw dolphins tailslapping rapidly (2-3 slaps/s) while moving in a tight circle around feeding bouts, and this action may further serve to keep fish from escaping (it has been described by Norris and Dohl (1980) and labeled "motorboating").

Besides the function of recruiting nearby groups to the feeding bout either purposefully or incidental to keeping fish from escaping, there is a third possibility. The splashes of noisy leaps create an underwater omnidirectional sound which may actually serve to frighten fish and cause them to school more tightly. Although work has been done on schooling relative to pressure waves (Bobbi Low[6]) as far as we know, no studies exist on sounds and fright reactions in schooling fish.

While the feeding bout continues, clean leaps and humpings continue as well, and dolphins still dive steeply. They also come up at a sharp angle, and individuals move rapidly through the bunched fish school, appearing at the other side of the school with several fish in their mouths. They then dive steeply again, and usually resume "attacks" on the fish school from below. The dolphins may stay below the fish much of the time to keep the school from escaping downward, and possibly to herd other fish to the surface to continue or prolong feeding. This is not the first indication of apparent cooperative herding and feeding in dolphins. It appears that many different species cooperate in herding, and it has been described for representatives of the genera *Orcinus, Tursiops, Sousa, Phocoena, Delphinus,* and others (see Norris and Dohl in press). Many terrestrial predators do so as well (Wilson 1975).

Acrobatic noisy leaps are most often seen during and after feeding. These may herd fish and recruit nearby groups, but they appear to require much energy and coordination which seems unnecessary just to make noise. We believe with Norris and Dohl (1980) that they may serve a "social facilitation" function, signaling a high activity level as individuals reaffirm and strengthen social and possibly sexual bonds. Saayman and Tayler (1973, 1979) describe similar high activity levels in *Sousa* sp. when two or more groups meet, and provide a similar assessment. We suggest that individual animals have taken care of the basic requirement of feeding and are now prepared to spend time socializing and "playing."

After feeding, dusky dolphins are more willing to associate with boats, human swimmers, whales, sea lions, and inanimate objects such as kelp. This may be an outgrowth of the high level of social activity at that time. Although we also saw much apparent mating after feeding, we were not able to compare it with amount of mating in small, nonsurface-feeding groups.

When many small groups coalesced to form a large one, did the smaller units remain intact or was movement of dolphins throughout the large group "random"? We saw individuals which had been spaghetti-tagged in a small group traveling together within a feeding bout a few days after tagging (Würsig in press), and thus have some indication that the small group remained intact. This agrees with data by Norris and Dohl (1980) on Hawaiian spinner dolphins. They found that there is fluidity in schools, but that small groups of 4-10 animals may be the only units with longer term continuity. We have no long-term information on group stability. However, studies of other dolphins suggest that the small-unit group composition is constantly changing (Saayman and Tayler in press, humpback dolphins; Shane 1977; Würsig 1978; Wells et al. in press, bottlenose dolphins). This flexibility in small-group composition at least superficially resembles chimpanzee group structure, and Saayman and Tayler (1979) and one of us (Würsig 1978) independently speculated that the similarity comes from feeding on unpredictable and patchy food distribution (see also Nishida 1968). If a similar group structure is found in dusky dolphins, it might be possible that individuals move randomly throughout the large after-feeding group, and that the entire group of up to 300 animals forms the more stable breeding unit or population.

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[6] Bobbi Low, professor, University of Michigan, Ann Arbor, MI 48109, pers. commun. 1976.

Captured animals were of both sexes (Würsig in press). As well, there were usually only 1 or 2 calves or small young within a group of about 15 animals, suggesting that mating is not highly polygynous. Given data from captivity (Evans and Bastian 1969 and Caldwell and Caldwell 1972 provided reviews) suggesting that promiscuity is a prominent feature of most odontocete cetaceans at least in unnatural circumstances, it is likely that the dusky dolphin social system is promiscuous as well. However, Bateson (1974) suggested rather stable relationships between some spotted, *Stenella attenuata,* and spinner dolphins for play, mating, and sleep.

We found that young were born mainly in the austral summer. If we assume an 11-12 mo gestation period (Sergeant et al. 1973 for bottlenose dolphins), most effective matings took place outside the winter season. If sexual activity continues throughout the year, then we can assume that there is a physiological change in males or females that allows conception to peak during the spring or summer. Seasonal changes in testis weight have been found for several cetacean species (for example, Ridgway and Green 1967 for *Delphinus delphis* and *Lagenorhynchus obliquidens*). It is possible that a similar physiological change may exist in dusky dolphins. This might relegate some activity appearing to serve a sexual function to the role of greeting or bond-strengthening ceremonies as has been suggested by Caldwell and Caldwell (1967), Bateson (1974), and others. We suspect, but have no definitive proof, that most mating occurs in large groups after surface feeding. Since this feeding occurs mainly in spring and summer, it correlates well with the summer calving peak. Nevertheless, if this is so, it would not invalidate the possibility of a seasonal physiological cycle, nor of "mating" at times serving a purely social function.

Groups which had about 10-20 adults and as many calves occurred at times. We saw these nursery groups mainly at the periphery of large feeding activities. They did not appear to participate in the high-activity level characteristic of large feeding bouts and after-feeding. Perhaps, when small groups feed, females with young feed and then split off as activity increases. This can be of adaptive value. Young may in this way avoid possible aggression and competition within the large feeding aggregation, and they may avoid possible predation by killer whales and sharks attracted to the activity. We saw large (3-5 m) unidentified sharks moving in dolphin feeding activity on four separate occasions, but they did not appear to bother the adult dolphins engaged in feeding.

The relationship of dusky dolphins and bottlenose dolphins was in some ways puzzling. Dusky dolphins moved in generally deeper water than bottlenose dolphins, but the two at times probably came into acoustic range of each other. Yet they did not appear to take notice of each other, although both species independently sought contact with southern right whales, sea lions, and the boat. Dusky dolphins were found in shallow water in the morning, but bottlenose dolphins were in even shallower water in the morning, then moved into intermediately deep water around noon, then into shallow water once again. It has been suggested (Würsig and Würsig 1979) that bottlenose dolphins may have been feeding on southern anchovy, the same food as that of dusky dolphins in these intermediate waters. At any rate, by that time of day, dusky dolphins were more often found in deeper water, and as a result, their food niches did not appear to overlap. As well, the two species were found with approximately opposite frequency within sight of the study area at different times of year. This suggests that one or both species may at times have actively avoided the other, although alternative explanations such as different ecological requirements may be more important.

Bottlenose dolphins moved in small groups close to shore, dusky dolphins moved in small groups while not feeding, but in larger groups around feeding time. Bottlenose dolphins appeared to spend most of their nearshore time feeding individually or perhaps in groups of two and three on large solitary fishes inhabiting nearshore rocks. Large groups are possibly not of advantage in exploiting a presumably scattered food resource. On the other hand, dusky dolphins appeared to hunt in small groups spread out over a large area, thus increasing their food-finding efficiency for a patchily distributed food resource. When food was found, they rapidly coalesced, and appeared to herd prey cooperatively, allowing more efficient feeding.

Dusky dolphins fed near the surface in deeper water in the afternoon, and moved slowly and with little activity in early morning. We suggested that the surface-feeding pattern may be associated with availability of fish at different times of day and in different areas of water. A similar change in area from nonfeeding to feeding was found for

Hawaiian spinner dolphins (Norris and Dohl 1980) and for *Sousa* sp. (Saayman and Tayler 1979). But what about the consistently shallow-water movement in the morning (and all day in winter) when dolphins did not appear to be surface feeding much of the time? Their activity level was low and they did not move rapidly. They ignored or avoided boats as well as other marine mammals. They moved in small, tight groups and we therefore gained the subjective impression that they were schooling in an almost "fishlike" manner. Because level of activity was low, objects in their paths were avoided or ignored, and schooling was tight, we believe that the dolphins were resting at this time.

There is some evidence that killer whales may prey on dusky dolphins. On three occasions when killer whales came close to dolphin groups, the dolphins moved into extremely shallow water. At the same time, they moved rapidly along shore, perhaps to avoid nearshore predation, of which killer whales are known to be capable on more stationary prey, such as elephant seals and sea lions (Norris and Prescott 1961; Tomilin 1967; pers. obs.). As well, their nearshore movement may serve to hide them from possible *Orcinus orca* echolocation, which might be confused and inefficient in very shallow water.

These observations make it likely that nearshore movement while resting is a defense against predation. In shallow water, killer whales (and possibly deepwater sharks) cannot come from below, nor from the flanking shoreline. When danger comes from the open sea, dolphins can retreat to very shallow waters in which larger predators cannot maneuver as efficiently. Norris and Dohl (1980) postulated a similar function for nearshore resting of Hawaiian spinner dolphins, suggesting that these animals possibly avoid large deepwater sharks during morning periods of low activity. Saayman and Tayler (1979) also saw *Sousa* sp. very close to shore when killer whales were near, and suggested that the dolphins might avoid predation in a similar manner. In the present population, it is possible that nearshore movement during low-activity levels may serve other functions as well, but we believe that the predator-avoidance hypothesis may be at least part of the reason.

CONCLUSION

In the preceding discussion, we attempted to link observed behavior patterns to observed or possible ecological variables. We recognize that this endeavor is highly incomplete, and that many more alternative explanations will be made available in the future. One important factor that may have been somewhat obscured in the results and discussion of behavior should be emphasized. Dolphin behavior in captivity as well as in the wild appears highly plastic and variable. For example, dusky dolphins feed on southern anchovy. Yet many species are more catholic feeders (for example, Gunter 1942, Leatherwood 1975, for *Tursiops truncatus;* and Perrin et al. 1973, for *Stenella* spp.), and it is certain that dusky dolphins engage in other feeding than surface feeding described here. We hope that future work will shed light on other feeding modes, whether subsurface feeding is done cooperatively as is surface feeding, or whether it is performed more often by single dolphins on nonaggregated prey. Such an analysis may help us understand the dramatic difference in movement patterns and general activity levels between times when dolphins feed cooperatively on the surface and when they feed in other ways.

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