BEHAVIOR AND ECOLOGY OF THE BOTTLENOSE DOLPHIN, *TURSIOPS TRUNCATUS*, IN THE SOUTH ATLANTIC

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ABSTRACT

Bottlenose dolphins observed nearshore in Golfo San José, Argentina, spent 92% of their time in water less than 10 m deep. They moved into deeper water, up to 39 m depth, mainly during midday in nonsummer for brief (16 min) periods. They moved more rapidly in deeper water, and may have been feeding on schooling fish at that time. During summer they stayed in shallow water, 2-6 m deep.

Dolphins moved parallel to shore and in consistent depth of water at almost all times. They changed direction at predictable locations and patrolled certain nearshore waters for up to several hours. Their movement was influenced by tide and by nearshore rocks.

Slow movement and apparent resting occurred mainly during the morning, while most aerial behavior, apparent sexual and social behavior, and rapid-movement feeding occurred in the afternoon.

The Atlantic bottlenose dolphin, *Tursiops truncatus*, is undoubtedly the best studied of any of the toothed cetaceans. It was successfully kept in captivity over 60 yr ago (Townsend 1914), and has since that time served as the "white rat" of cetology, with a great deal known about its behavior in captivity, but until relatively recently practically nothing known about its behavior in the wild. Long-term behavioral studies of stable bottlenose dolphin colonies in captivity were mainly carried out at Marine Studios/Marineland of Florida from the mid-1930's to mid-1950's (McBride 1940; McBride and Hebb 1948; McBride and Kritzler 1951; Essapian 1953, 1963; Tavolga and Essapian 1957; Tavolga 1966). These studies showed that bottlenose dolphins have a complex social organization, often with a male-dominated social hierarchy. From some of these studies also developed the idea that bottlenose dolphins, and other odontocete species as well, use echolocation (McBride 1956). This concept was validated by numerous workers in the 1950's and 1960's (Schevill and Lawrence 1956; Kellogg 1961; Norris et al. 1961). Other research on captive bottlenose dolphins in general (including the species *T. gilli* and *T. aduncus*, as well as *T. truncatus*) was reported by Brown and Norris (1956), Caldwell et al. (1965), D. K. Caldwell and M. C. Caldwell (1972), M. C. Caldwell and D. K. Caldwell (1972), Tayler and Saayman (1972), and Saayman et al. (1973). The

first reports of behavior in the wild consisted mainly of anecdotal information gathered opportunistically while capturing dolphins or pursuing other activities (Gunter 1942; Brown and Norris 1956; Norris and Prescott 1961; Brown et al. 1966). This led to more detailed field studies, most of which have been made within the past 10 yr, and all of which relied heavily on shore-based or small-boat operations close to shore (Saayman et al. 1972; Tayler and Saayman 1972; Irvine and Wells 1972; Saayman et al. 1973; Saayman and Tayler 1973; Shane 1977; Würsig and Würsig 1977; Castello and Pinedo 1977; Würsig 1978; Wells et al. in press; Irvine et al.[2]). At the same time, and also close to shore, behavioral investigations of other odontocete genera have been carried out. Thus, Norris and Dohl[3] studied the Hawaiian spinner dolphin, *Stenella longirostris*, Saayman and Tayler (in press) described Indian Ocean humpback dolphin, *Sousa* sp., behavior and social organization, and Würsig and Würsig[4] performed similar work on the South Atlantic dusky dolphin, *Lagenorhynchus obscurus*.

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Detailed work on the social organization of bottlenose dolphins was carried out by Irvine et al. (see footnote 2) and Wells et al. (in press). They captured many animals for tagging, and thus gained size and sex information. They found that a resident herd in the Sarasota-Bradenton area of West Florida consisted of groups whose individual membership was constantly changing by influx and efflux in a "kaleidoscopic manner." Such changes were not random, however, and several patterns of association were observed. Within a relatively stable herd occupying a well defined home range, each age and sex class frequented particular regions and interacted with other classes to varying degrees. Females of all ages and adult males ranged through the northern portion of the home range and interacted more with each other than with subadult males, which formed bachelor groups or groups with one or more adult females in the southern portion. Females with young moved throughout the home range and interacted with adult males to a lesser extent than did other females. A given group generally remained intact for only a matter of hours or days.

At least superficially similar group instability was documented for Argentine bottlenose dolphins by Würsig and Würsig (1977) and Würsig (1978), for Texas bottlenose dolphins by Shane (1977), for Hawaiian spinner dolphins by Norris and Dohl (see footnote 3), and for humpback dolphins by Saayman and Tayler (in press). These studies present the first detailed accounts of some aspects of social organization of odontocete cetaceans, and make comparisons of these animals with terrestrial mammals such as bovids and primates possible.

The present analysis of South Atlantic bottlenose dolphins represents an attempt to describe the general movement patterns, aerial and social behavior, and ecology of this population. We made no attempt to capture animals for sex and size information as we were loathe to disturb their "natural" movement and social behavior. Instead, we observed them mainly from cliffs lining the shore. Earlier, we reported on some aspects of seasonal occurrence patterns, group stability, surfacing associations, and calving seasonality of the same population discussed here (Würsig and Würsig 1977; Würsig 1978). This paper presents additional information, with the primary purpose of providing background data on the natural history of bottlenose dolphins, and hopefully also with future application to other species as further studies unfold.

MATERIALS AND METHODS

Bottlenose dolphins were observed at Golfo San José (lat. 42°23' S., long. 64°03' W.) from July 1974 through March 1976. We made observations through binoculars and a 20-power transit monocular from two points, 14 m and 46 m high at mean low water ("Camp" and "Cliff Hut," respectively, Figures 1, 2).

To describe the movements of dolphin subgroups (averaging 15 animals) which were present near the observation point anywhere from several minutes to several hours, we plotted their positions with the help of a Kern[5] model DKM1 surveyor's theodolite. The theodolite had a 20-power monocular through which the animals were followed visually. A separate eyepiece showed horizontal degrees and vertical degrees which represented the location of the dolphins, and which we read at 15 s to several-minute intervals into a cassette recorder. In the laboratory, data from the theodolite were plotted on a depth map (Figure 2), by a Hewlett-Packard Model 9830A desk calculator and plotter. Besides plotting the animals' positions, the computer program also supplied their distance from the observer, their heading in degrees relative to true north, and their speed.

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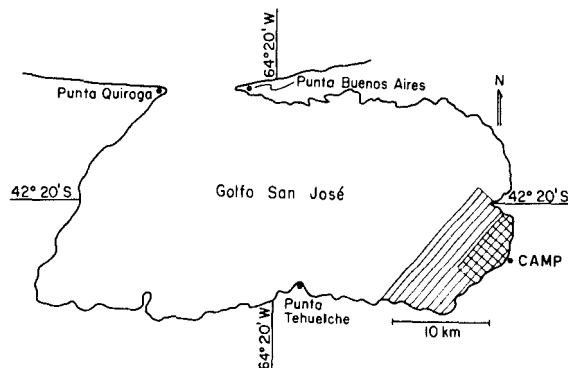

FIGURE 1.—Map of Golfo San José on Peninsula Valdés, Argentina. The bay is approximately 750 km² with a 7 km wide mouth opening to the Atlantic. The lined area in the southeast portion of the bay represents the study area. The crosshatched subsection is shown in detail in Figure 2.
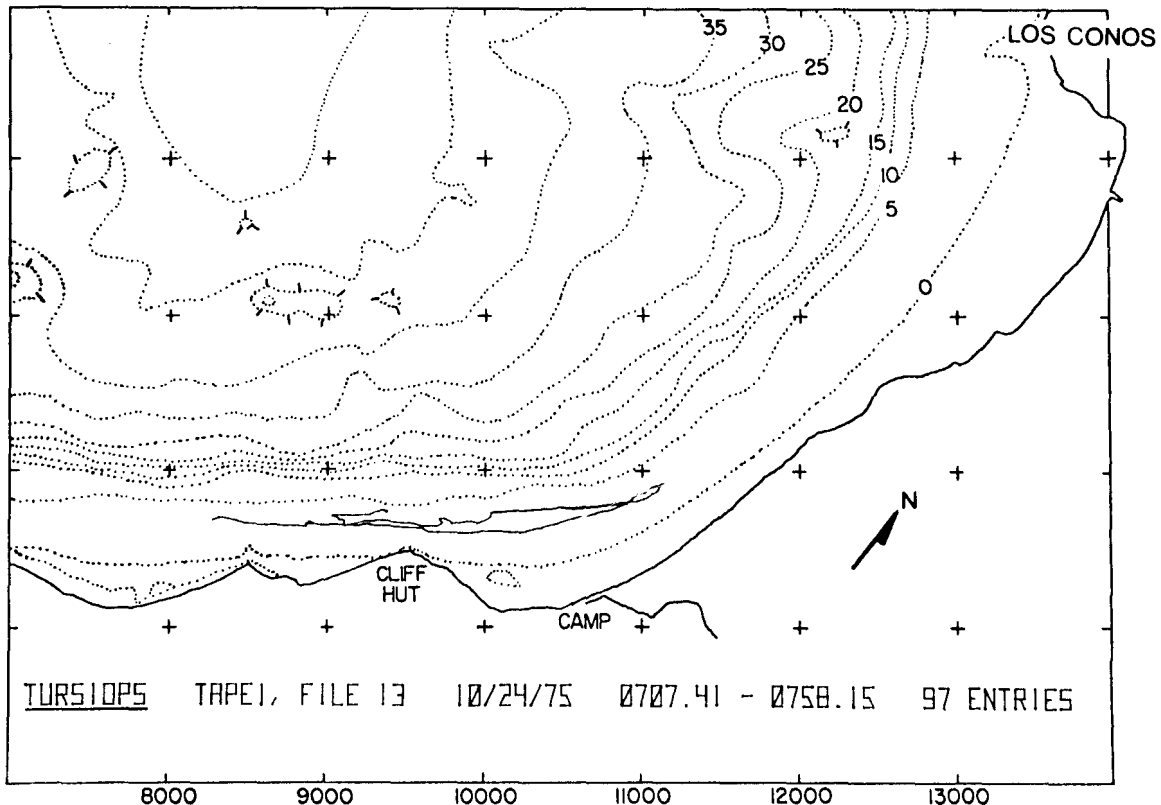
FIGURE 2.—Depth contour map of one-fourth of the study area. Margin numbers represent meter distances relative to a zero location on land. Crosses form 1 km squares. "Cliff Hut" and "Camp" are the locations from which most observations were made. Depth contours are in meters at mean low water (MLW). 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 solid line above Cliff Hut represents a sample track of a bottlenose dolphin group, and the printed information gives computer file location, date of track, time of day, and number of theodolite entries. About 200 such tracks were obtained of bottlenose dolphins during the 21-mo study. 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.

Since dolphins often did not travel in straight line, speed information from theodolite readings separated by several minutes was lower than the actual speed traveled. To minimize errors in speed calculations, only readings made within 30 s of each other were used. The accuracy of the transit ($\pm30''$ of arc) allowed for placement of position within ±100 m at 5.5 km distance.

RESULTS

Preferred Depths

To determine whether dolphins prefer a specific depth of water, and to map their movement patterns, theodolite readings were obtained whenever bottlenose dolphins came within sight-ing range of shore (1-10 km, depending on visibility). Within that range, the depth of water varied from 1 to 65 m. Bottlenose dolphins occurred 92% of the time in water <10 m deep (2,655 of 2,883 theodolite readings), within 1 km of shore (Figure 3). None were ever sighted in water >39 m. Visibility at almost all times extended to at least 3 km from shore, where water depth was 45-50 m (see Figure 1), and we consistently tracked dusky dolphins in much deeper water (Würsig and Würsig see footnote 4). Furthermore, we traversed the study area by boat in waters 1 to 10 km from shore on 109 occasions and never saw bottlenose dolphins in water >39 m. For these reasons we believe that the data for shallow nearshore travel are not biased by sighting error. In general, dolphins moved in shallow water in the morning and
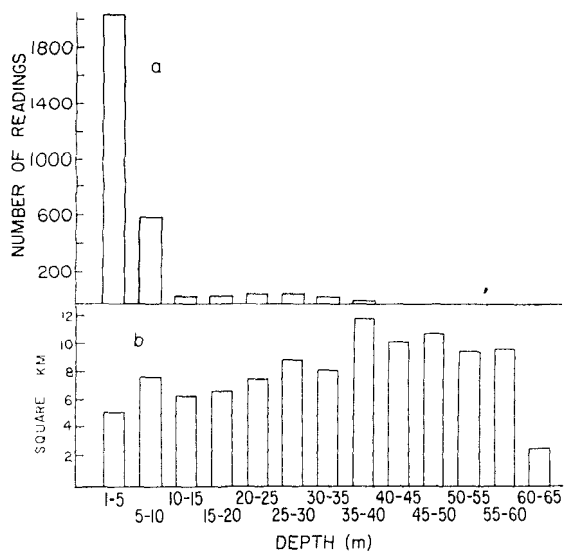
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FIGURE 3.—The number of theodolite readings of dolphins found in different depths of water (a) and the total amount of area available in the study region at different depths of water, at a mean tide height of 5.0 m above mean low water (b). Most readings were obtained in shallow water despite the fact that more geographic area was covered by deeper water. The total area used for these calculations is represented by the lined and crosshatched sections of Figure 1.

afternoon, and in deeper water around noon (Figure 4a). When deepwater movement occurred, however, it was brief (16 min average per movement in water >10 m deep, SD = 7.1, n = 230) and was interspersed with longer shallow-water travel. As a result, the increase in mean depth around noon of Figure 4a and b was not because animals consistently traveled in deeper water at those times. Instead, they more often moved for brief periods into deep water, and therefore the mean depths increase at those times. When the data were divided into months (Figure 4b, c), the nonsummer months of March, July, October, and November account for the movement into deeper water shown in Figure 3a. This trend was particularly strong for July (midwinter in Argentina), with a peak of 23 m depth at 1300 h. On the other hand, no increase in depth of water during midday took place in summer (December and January, Figure 4c). It would appear that there are predictable seasonal and daily variations in depth of water in which the dolphins move.

Speed of Movement

The overall mean speed of the dolphins calcu-

lated from the 1,545 theodolite readings made within 30 s of each other was 6.1 km/h. Speed of travel was significantly correlated with depth of water; speed was 5.7 km/h in water <10 m deep, and 13.9 km/h in deeper water (Figure 5). But, was speed directly influenced by depth of water, or was it due to distance from shore, which in general *increased with increasing depth?* To solve this ambiguity, we took random samples of 10 readings each from 1) >600 m from shore and ≥10 m depth, 2) <600 m from shore and ≥10 m depth, and 3) <600 m from shore and ≤10 m depth, and compared their speeds (Table 1). If speed were influenced by distance from shore, we would expect speeds of 1) and 2) to be different. Instead, speeds of 2) and 3) were significantly different ($P < 0.005$, Wilcoxin two-sample test, Sokal and Rohlf 1969), indicating that depth of water, not distance from shore, was probably the prime determinant of speed increase.

TABLE 1.—Samples of bottlenose dolphin speeds (kilometers per hour) in three different water conditions, selected at random from the data.

>600 m from shore ≥10 m depth	<600 m from shore ≥10 m depth	<600 m from shore <10 m depth
7.8	16.1	4.3
15.3	21.8	2.5
14.2	28.8	5.2
13.7	20.4	7.0
12.8	13.1	4.7
14.2	12.0	4.5
16.1	16.1	3.8
11.4	13.7	5.6
21.8	17.5	6.1
21.4	14.3	5.9
Mean 11.4	17.4	5.0

Speed of travel appeared uniform throughout the day (Figure 6a), but a further subdivision into months (Figure 6b, c) shows that there was an increase around noon in nonsummer months, with the average speed over 14 km/h at 1300 h during October. During December and January, no such midday peak was evident, but instead animals traveled more rapidly during late afternoon than at other times of day.

Movement Patterns

In water <10 m deep, bottlenose dolphins almost always moved parallel to the depth lines; that is, they stayed in consistent depth (Figure 7). In deeper water, movement was more random and dolphins at times rapidly crossed into different depths. Nevertheless, a tendency to follow depth contours was still present.
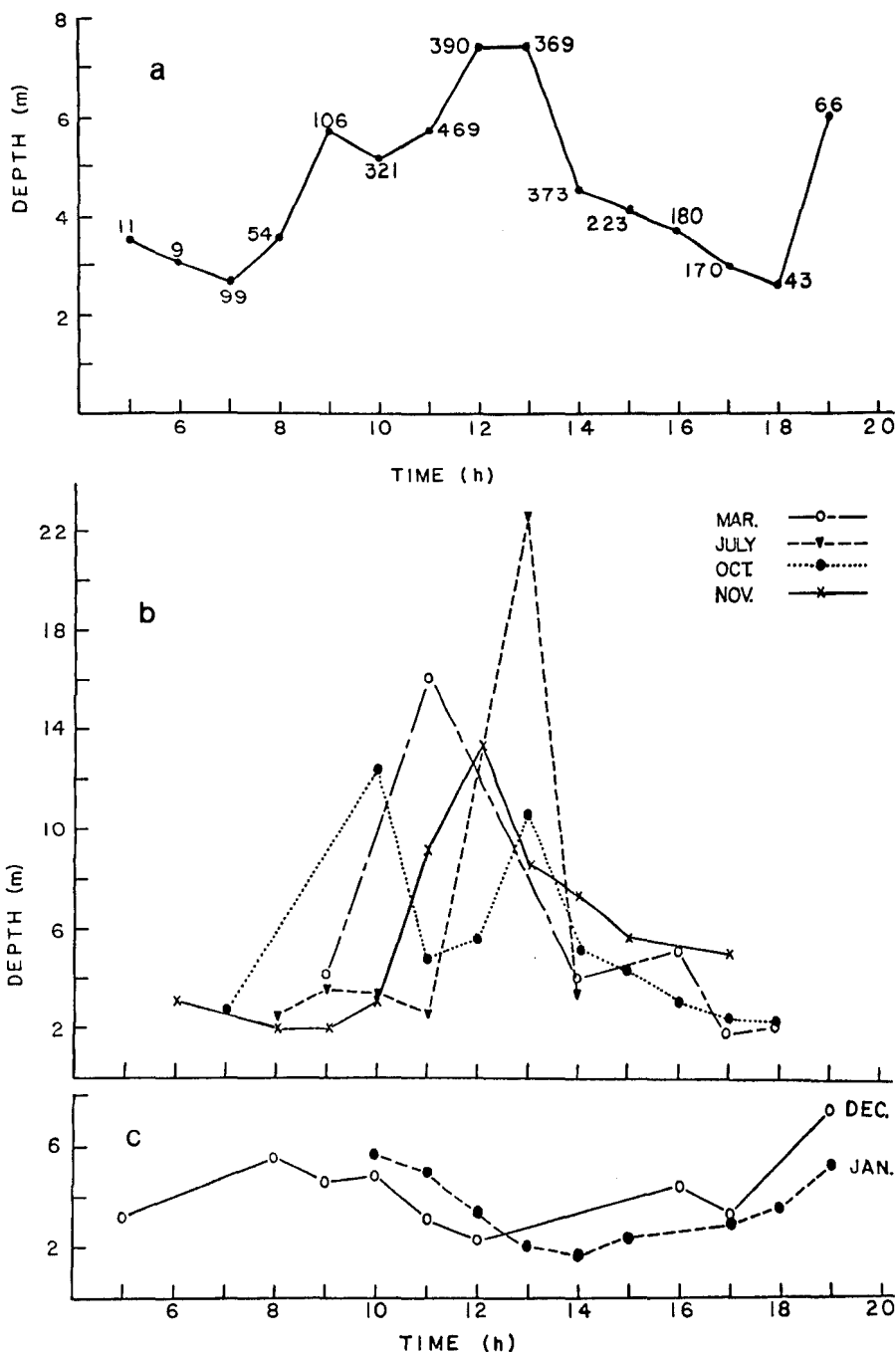
FIGURE 4.—Mean depth of water in which bottlenose dolphins were found during different times of day (a). The numbers near points represent number of theodolite readings gathered for that hour of day. The higher number of readings around midday is a result of increased work with the theodolite at that time; it does not represent an increase of dolphins in the area. Instead, the incidence of dolphin sightings was about equal for all daylight hours. These data were divided into different months (b, c). Average depths >10 m are clumped toward midday (10-13 h, $P = 0.014$, Raleigh test, Greenwood and Durand 1955). These deeper water peaks are significantly different from shallow-water travel during the rest of the day for March, July, October, and November ($P < 0.01$ in all 4 mo, Kruskal-Wallis test in lieu of one-way ANOVA, Sokal and Rohlf 1969). In December and January, dolphins stayed in shallow water all day, and this trend is different from data in b ($P < 0.001$, Mann-Whitney U test, Sokal and Rohlf 1969).
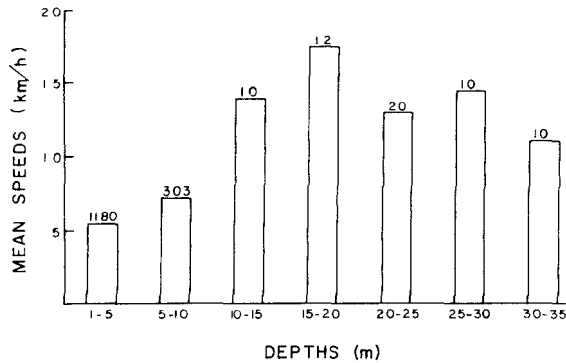
FIGURE 5.—Average speed of travel of bottlenose dolphins in different depths of water. Numbers represent number of theodolite readings per depth category for which speed information was available. Shallow-water (<10 m) speeds are significantly different from those in deeper water (P<0.01, Mann-Whitney U-test, Sokal and Rohlf 1969).

Movement of dolphins was also affected by tidal fluctuations. Animals were found in progressively shallower water as the tide ebbed. Thus, dolphins tended to remain the same distance from the high tide line. When the tide was 6 m above mean low water, dolphins were found in 9 m depth. At mean low water, they were found at a depth of 3 m (Figure 8a). At low water as the tide began to flood, the dolphins remained in shallow water (3 m) but as the tide continued to rise from 1 to 3 m, they moved into deeper water. At a tide height of 4-7 m, they moved into waters 5-10 m deep (Figure 8b). Depths over which dolphins were when flood tide was between 1 and 3 m were quite variable, indicating that the animals moved in all depths near shore at those times, and moved into deep water more often than at other tide heights. Thus, on a lowering tide, dolphins were found in progressively shallower water, while on a rising tide the reverse trend appeared, but with a dramatic interruption in this trend at tide heights of about 1-3 m. At those heights, dolphins more often moved into deep water for brief periods.

Bottlenose dolphin subgroups often moved back and forth longitudinally within a confined area near shore, thus at times staying within sight of our observation points all day. Within 0.5 km of shore, they turned (changed direction by $180° \pm 10°$) on the average every 673 m (SD = 980, n = 104), and farther than 0.5 km from shore they turned every 1,382 m (SD = 1,094 n = 11). Despite the large standard deviations in these readings, dolphins farther from shore traveled significantly longer distances before turning than when they
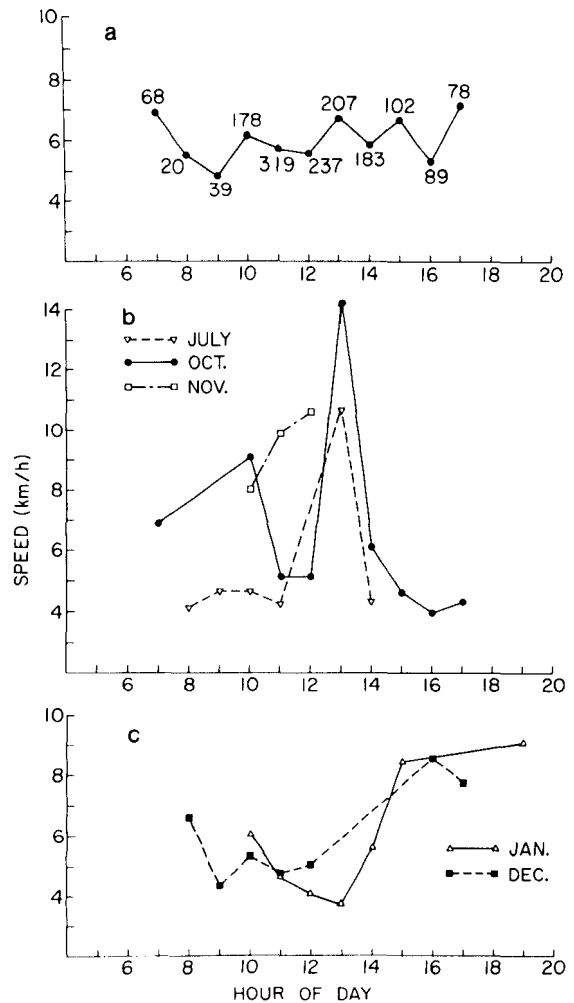

FIGURE 6.—Mean speed of travel at different times of day (a). The numbers near points represent number of theodolite readings with speed data gathered for that hour of day. These data were divided into months (b, c). In July and October, dolphins traveled faster at 1300 h than at other times, while in December and January, they traveled faster in late afternoon (P<0.01, Kruskal-Wallis test in lieu of one-way ANOVA Sokal and Rohlf 1969).

were within 0.5 km of shore (P <0.05, t-test). However, because they traveled faster when farther from shore (and in generally deeper water, see Figure 4), the time between turns was not significantly longer (mean time <0.5 km from shore = 8.8 min, >0.5 km = 10.0 min). Thus, dolphins changed direction about every 9 or 10 min. The increase in distance covered appeared to be a consequence of the greater speed in deeper water.

Changes in direction by $180° \pm 10°$ were often made at the same locations on different days, and

TYPE OF MOVEMENT IN WATER <10m DEEP

Movement	Observed	%	Expected	%
Parallel	796	77	258	25
Interm.	196	19	517	50
Perpend.	41	04	258	25
Total	1033	100	1033	100
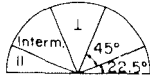
TYPE OF MOVEMENT IN WATER ≥10m DEEP

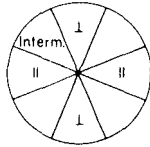| Movement	Observed	%	Expected	%
Parallel	13	38	8.5	25
Interm.	19	56	17.0	50
Perpend.	2	06	8.5	25
Total	34	100	34	100

FIGURE 7.—Movement relative to depth contours. In "parallel" movement, dolphins stayed in the same depth between theodolite readings, in "intermediate" movement they crossed contour lines at an angle, and in "perpendicular" movement they moved perpendicular to depth contours, and therefore changed depths rapidly. In shallow (<10 m) water, dolphins moved parallel to depth lines (±22.5°) significantly more than they moved perpendicular to them (±22.5°, $P < 0.001$, chi-square goodness of fit test) and in deeper (≥10 m) water this trend was weaker but still present ($P < 0.03$, test as above). The circles to the right show the divisions of movement, where parallel lines indicate movement parallel to depth lines, and an inverted T represents movement perpendicular to them. Only one-half circle is shown for shallow water because it is likely that animals near shore cannot travel into shallower water. However, the expected percentages of movement relative to depth contours remains the same in shallow and deep water.
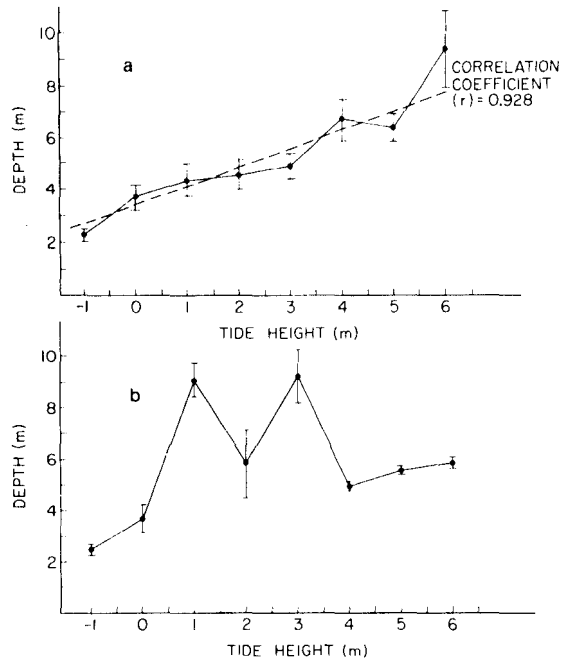

FIGURE 8.—Average depth of water in which dolphins traveled at different tide heights during a lowering (or ebb) tide (a). Bars above and below points represent 95% confidence limits. A least-squares regression line through the means shows that dolphins were found in progressively shallower water as the tide ebbed (correlation is statistically significant, $P < 0.01$). Average depth of water in which dolphins traveled at different tide heights during a rising (or flood) tide (b). The rising trend was interrupted between tides 1 and 3 m by animals more often moving into greater depth (shown by increase in mean depth and by larger 95% confidence limits, because variability increased).

therefore after a while could be predicted. Near camp there were three locations where subgroups turned more often than expected if turns were made at random ($P < 0.005$, chi-square goodness of fit test). All three of these locations were marked by rocks which were submerged during medium and high tides. When the tide was low enough to uncover these rocky areas, leaving only an even, sandy bottom covered, the preference for turning at those areas disappeared. It appears, therefore, that the animals used these rocks as underwater landmarks which, at least at times, stimulated them to change direction. It is unlikely that the dolphins turned at these locations simply to avoid bumping into the rocks, since one of the three areas was marked by rocks only 5-10 cm above the sandy substrate. All three areas formed distinct discontinuities in the bottom topography, how-

ever, and may have served as cues to turn at the boundary of the area traversed.

The tongue of land called Los Conos (Figure 2), 6 km north of camp, appeared to be the northward boundary of the present population's range. In 260 h of observation, dolphins were never observed traveling north of this point. When they were lost from sight, it was either due to bad visibility or because the animals traveled out of range in the southwest portion of the study area. In addition, when the animals were first spotted coming into the study area, they always came from the southwest, never from the north.

As was described earlier, bottlenose dolphins in the present study exhibited two distinct movements. Usually, they moved slowly and very close to shore, in shallow (<10 m deep) water. They moved for brief (16 min) periods, mainly during midday in nonsummer seasons, into deeper (>10

m) water, and moved more rapidly at that time. These two distinct movements were marked as well by a difference in group formation. While slowly traveling near shore, the dolphin subgroup was 87% of the time (226.2 h of 260 h) in a tight formation about 10-15 m wide and 50-75 m long. Because of this narrow formation, no individual was far from shore, and all were in similar depth. On the other hand, when dolphins moved into deeper water they advanced as a wider than long rank, with each animal separated from the next by as much as 25 m on its flank, yet the entire group presented one wide front. In this manner, the subgroup was able to cover a large swath of sea (up to about 300 m) as it rapidly moved ahead. During 13 of 134 times (9.7%) that rapid movement was observed, we noted 1-12 terns and at times gulls flying in front of this advancing dolphin line and diving into the water to pick up 10-15 cm long fish. We suspect that they may have been near parts of schools of southern anchovy, *Engraulis anchoita*, because of the abundance of this fish in the area. The wide front movement in deeper water may thus be a searching pattern by bottlenose dolphins for such schooling fish. When the subgroup slowed at the end of an individual-abreast run, the animals milled in different locations (122 of 134 times, 91%), giving us the impression that they were feeding in that location. However, such milling after rapid movement was usually short (60 s±30 s), and never lasted more than 5 min. At the end of milling, the subgroup usually (115 of 122 times, 94%) continued to move slowly in shallow water, but less often (7 of 122 times, 6%) began a new period of 16-min-long rapid movement in deep water.

Aerial Behavior

Aerial behavior was not as frequent in the bottlenose dolphin population we studied as in many other species of cetaceans (e.g., see Saayman and Tayler in press; Norris and Dohl see footnote 3; Würsig and Würsig see footnote 4). Individuals engaged in any form of aerial display <5% of the observed time. These displays were the 1) leap, 2) headslap, 3) noseout, 4) tailslap, and 5) kelp toss. For the sake of conformity, the aerial displays discussed below, except for 5), follow the names and descriptions of aerial behavior given for Hawaiian spinner dolphins by Norris and Dohl (see footnote 3):

1. Leaping either produced a loud sound when the animal fell back into the water onto its belly or side ("noisy leap"), or was relatively silent when the animal arched its body during the leap and reentered nose first ("clean leap"). Noisy and clean leaps occurred at any time of day when the animals were moving slowly close to shore. However, noisy leaps were most often performed by calves and subadults (calves leaped approximately 3 times as often as adults), and occurred more often in the afternoon (morning, 24 leaps in 117 h, mean = 0.21/h; afternoon, 70 leaps in 143 h, mean = 0.49/h; significant difference at $P<0.001$, testing equality of percentages, Sokal and Rohlf 1969). Clean leaps were performed only by adults and usually occurred when the group was relatively stationary in medium-deep (10 m±5 m) water. At times (about 25%, not adequately quantified for exact numbers) such leaps were attended by terns diving in the vicinity and feeding on small fish, leading to the inference that such clean leaps, which allow animals to rapidly descend headfirst, may be food-related. No daily or seasonal pattern was evident for clean leaps.

2. The headslap was seen only twice in 260 h of observation, each time performed by a subadult while the subgroup slowly moved along shore.

3. Noseouts, when dolphins poked their heads out of the water to beyond at least one eye, were about as frequent as noisy leaps and usually occurred at the same time (i.e., more often in the afternoon).

4. Tailslaps were the most frequent form of aerial behavior. They also occurred at any time during the day, but were frequent only when some disturbance occurred. Thus tailslaps were noted a) when our outboard engine was started 300-500 m from the dolphins, b) 14 of 95 times (15%) our boat initially approached a subgroup of dolphins, c) when the subgroup had been split into two adjacent groupings for several hours and then rejoined (this happened five times), and d) once when a light plane flew overhead at low altitude. In these cases, the tailslapper was always an adult, and most of the time was a large, recognizable individual who was part of a stable subunit of five individuals which consistently stayed together (dolphin no. 1 in Würsig 1978). Unlike any of the other forms of aerial behavior, which usually were performed only once by one animal at a particular time, tailslapping occurred from 10 to 20 times during one bout.

5. "Kelp tossing" usually was accompanied by high incidences of noisy leaps and noseouts. Dur-

ing kelp tossing, an animal would balance a piece of *Macrocystis* sp. on its melon or forehead, flip it to its tail with a sudden head jerk, flip it to the dorsal fin with its tail, or any variation of the above. Kelp tossing was observed nine times during the study, and lasted an average of 15 min/bout.

Social Behavior

Because most observations were done from a distance, and usually only dorsal fins were visible above the water, little insight was gained into social behavior. Nevertheless, a few major trends were apparent. When noisy leaps, noseouts, and kelp tossing occurred, animals were also often seen swimming side by side while touching, with at least one of the animals in an upside down position ("belly-up"). Viewed from directly overhead, as when the subgroup passed close beneath our observation cliff, individuals could be seen nudging each others' bodies with their snouts. As with leap frequency, most of this behavior was observed in the afternoon (12 of 17 times, 71%; significant difference from morning at $P<0.02$, testing equality of percentages, Sokal and Rohlf 1969). It appeared as well that belly-up and rubbing behavior were more frequent when two subgroups which had moved separately for several hours joined again. However, this did not happen often enough (five times in total) for statistical analysis.

Five calves were observed during the study. Each stayed close to a particular adult (see Würsig 1978), and we assume that this adult was the mother. Calves and mothers were also observed engaging in rubbing behavior with other adults.

Bottlenose dolphins associated with the southern right whale, *Eubalaena glacialis*, which were seen near shore from June through November. While moving along shore, dolphins veered from their previous path by as much as 300 m to join one or more right whales. Once with the whales, they rapidly swam back and forth across the whales' head. Whales invariably became very active when dolphins were present, blowing and "snorting" loudly in air as well as underwater. Whales also rapidly surged or lunged ahead in the direction of dolphins crossing their heads. The dolphins then rode (or surfed) on the pressure waves created by these lunges, riding along the crest of either wave cascading to the side of the whales. This association appeared to us to be play, and occurred 24 of 26 times (92%) that whales were directly in front

of the path of moving dolphins. It lasted an average of 15 min., after which the dolphins left the whales and continued in the direction in which they had been traveling before joining the whales.

Further interspecific associations occurred with the sea lion, *Otaria flavescens*, and, on one occasion, with a subadult male elephant seal, *Mirounga leonina*. The pinnipeds joined a subgroup of dolphins and traveled with it for up to 1 km, rapidly moving among the dolphins.

Dolphins also at times approached our 4.5 m rubber Zodiac boat and swam underneath the boat for brief (up to 5 min) periods. During 86 of 95 (91%) boat approaches, however, bottlenose dolphins appeared to ignore our boat, neither approaching nor avoiding it.

When winds rose above 20-30 km/h, dolphins were often observed rapidly riding down the advancing crest of waves in the surfline. It appeared that they were surfing the waves much as human surfers do, and much as dolphins did with "bow" waves of whales.

Possible Predation

We saw no direct evidence for predation on bottlenose dolphins, but one of the animals, TS (for "tiger stripes," Würsig and Würsig 1977) appeared in January 1975 with a series of scratched lines along its left dorsum. From the regularity and spacing of the lines, we believe that they were made by killer whale, *Orcinus orca*, teeth. It seems possible that this individual narrowly escaped a killer whale. Furthermore, on two separate occasions, we observed killer whales approaching within 0.5 km of bottlenose dolphins. In each case, the bottlenose dolphins rapidly swam away and toward the open sea. Their swimming was so rapid at these times that the dolphins leaped clear of the water and covered 2 or 3 times their own length out of the water during low forward leaps. Hertel (1963) suggested from mathematical models that this type of movement is most efficient for rapid surface swimming. Theodolite readings taken at these times indicate that the dolphins were moving at speeds of at least 30 km/h; however, no definitive upper limit speed information was obtained because it was difficult to follow rapidly moving animals accurately in a short-time period.

DISCUSSION

The bottlenose dolphin population studied here

spent 92% of its time in water <10 m deep, and was never seen in water >39 m during the 21-mo study. "Coastal dolphins" is therefore truly an appropriate label. Various investigators have mentioned the presence of bottlenose dolphins farther from shore and in deeper water populations distinct from the nearshore populations seen in the same general geographic area (e.g., Norris and Prescott 1961). We never saw *Tursiops* in offshore waters >3 km from land despite over 100 attempts to find them by boat in deeper water. Instead, a different animal, the dusky dolphin, *Lagenorhynchus obscurus*, was seen farther off shore during the entire year (Würsig in press; Würsig and Würsig see footnote 4).

The bottlenose dolphins studied here were almost always found in water <10 m deep; however, in autumn, winter, and spring they moved into deeper water for brief periods during midday. At that time, they sped up and moved as fast as 24 km/h. Because terns were seen feeding near such movement, and because of the wide swath of sea covered by the dolphins while rapidly advancing in this manner, we believe that during these times they were searching for and at times feeding on aggregations of schooling fish. Although adult southern anchovy are apparently not abundant in the area in winter (Brandhorst et al. 1971), juveniles are present near shore in small schools at this time (Brandhorst and Castello 1971). Similar group feeding by bottlenose dolphins has been reported on numerous occasions (Morozov 1970; Hoese 1971; Tayler and Saayman 1972; Saayman and Tayler 1973; Busnel 1973; Leatherwood 1975; Hamilton and Nishimoto 1977). We could not determine, however, whether the dolphins were actively herding fish into a tight unit against the surface of the water, as dusky dolphins are thought to do (Würsig and Würsig see footnote 4). The daily periodicity of deepwater movement during nonsummer indicates that the schooling prey of bottlenose dolphins may be more abundant in those waters during midday. However, this is at present only conjecture. At any rate, no such midday increase in speed and depth of water was evident in summer. During summer, southern anchovy are not found very often in coastal waters less than approximately 40 m deep (Ciechomski 1965; pers. obs.). Instead, these schooling fish are found in deeper (and cooler) offshore waters, where dusky dolphins feed on them. The present population, however, does not go into these deep waters in the southeast portion of Golfo San José,

and thus does not appear to have this resource available in this area during summer. Whether or not there is active competitive exclusion between bottlenose dolphins and dusky dolphins is not known.

During summer afternoons, *Tursiops* moved more rapidly and in slightly deeper water than at other times of day. We do not know whether they were cooperatively hunting and feeding on schooling fish as in the manner described above. It is possible that the animals were moving into somewhat deeper water to avoid very warm water (up to 25°C, pers. obs.) present in 0-4 m depth during hot summer weather, but as bottlenose dolphins live in warmer water elsewhere, it is more probable that their daily movement pattern was food-related.

Average speed of travel by bottlenose dolphins was 6.1 km/h. This represents one of the first times that such a speed has been reported for an undisturbed group of wild dolphins. It is similar to speed estimates made for the Indian Ocean bottlenose dolphin, *Tursiops aduncus* (9.9 km/h) and for *Sousa* sp. (4.8 km/h) during normal progression (Saayman et al. 1972; Saayman and Tayler in press). As an interesting sidelight, which may be recognized as having general significance as more population studies of dolphins unfold, bottlenose dolphins studied by Saayman et al. (1972) were usually found in deeper water while humpback dolphins were almost always found in shallow waters. While moving near shore, south Atlantic bottlenose dolphins moved roughly as fast as did humpback dolphins, and while farther from shore, they moved roughly as fast or faster than the Indian Ocean bottlenose dolphin. The same trend is true for dusky dolphins in the south Atlantic waters (Würsig and Würsig see footnote 4). A possible explanation may be that nearshore searching for food and feeding are more often functions of individuals, while deeper water prey search appears often to utilize the combined sensory abilities of the entire group as it actively echolocates for whole schools of fish. A similar pattern of dispersed individual feeding near shore and group feeding offshore has been found by Irvine, et al. (see footnote 2). The nearshore search for food requires looking in detail at the prey possibilities near rocks, plants, and on the bottom, while most efficient search in open water is likely to be facilitated by covering as large an area as possible within a small space of time. Possibly more important intraspecifically is a recent suggestion that

coastal dolphins at times rest close to shore (and move slowly while resting) to avoid deeper water predators such as sharks and killer whales (Norris and Dohl see footnote 3; Würsig and Würsig see footnote 4). They more often feed farther from shore and in deeper water, and are more active at that time.

In this study there was evidence that bottlenose dolphins near shore paid attention to bottom topography. While they in general moved over consistent water depth for brief periods, they often moved back and forth over the same bottom topography during a falling tide. As a result, they traveled in progressively shallower water as the tide receded. Furthermore, they changed direction over particular underwater landmarks, usually consisting of groups of rocks. This type of movement associated with bottom topography may be strongest while the animals are searching for bottom-dwelling prey. However, we do not know what their food was at such times. The intertidal areas in which they were traveling had abundant snails, and part of the area was covered by mussels. Mussels were especially abundant on the rocky outcroppings where dolphins turned (and at times milled or lingered for several minutes), but we have no direct evidence for feeding on shellfish. Norris and Prescott (1961) reported that *Tursiops* in California waters feed at times on hermit crabs and shellfish. Also present in and around rocks were larger—up to 1 m long—fish, *Pinguipes fasciatus*. We observed individual dolphins shaking these fish in their mouths and repeatedly tossing them into the air on three separate occasions. Although this behavior at first looked like "play" before feeding on the fish, it is likely that the dolphins were tossing and shaking them to soften the fish and possibly to separate the head from the edible body (as reported by Brown and Norris 1956). It thus appears that this fish constitutes a nearshore prey item, and it may be part of the reason that bottlenose dolphins often turned and lingered near rocks.

During intermediate flood tides dolphins traveled more often into deep water than at other tide stages. Since deepwater movement appeared correlated with group feeding on schooling fish, feeding may have occurred more often during such intermediate rising tides. We therefore suspect that schooling fish were also more often present in nearshore waters during rising tides, perhaps brought into the area from deeper water by the tidal currents. Although we have no evidence for

this postulated movement of bottlenose dolphin prey, it is a common behavior of many fish species to come in with the tide, and thus a reasonable possibility in the present case. Tide-related movements of *Tursiops* sp. have been described by McBride and Hebb (1948), Norris and Prescott (1961), D. K. Caldwell and M. C. Caldwell (1972), Irvine and Wells (1972), Shane (1977), and others. Most of these descriptions involved the movements of bottlenose dolphins into and out of coastal channels or canals and are therefore not strictly comparable with the present study. However, dolphin movement appeared often to be food-related in these studies. Saayman and Tayler (in press) found a peak in *Sousa* sp. feeding 2 h before high tide, presumably also because prey fish were being brought into their study area by the tide.

Near shore, dolphins changed direction by 180° approximately once every 700 m. This was the average distance between rocky outcroppings of cliffs. The turns often tended to keep the animals in a restricted area within sight of our observation points for several hours. When farther than 0.5 km from shore, dolphins traveled about twice the nearshore distance before turning, possibly because they encountered no rocks or outjuttings of cliffs in such deeper water. Nevertheless, because travel in one direction lasted on the average only 9 or 10 min whether near or far from shore, deeper water travel also usually kept the animals in a particular area.

Although we were able to describe the movements of bottlenose dolphins in some detail within an approximately 50 km² area, we do not know where the dolphins went when they moved out of our area. They did not travel beyond a certain point (Los Conos, Figure 2) within the study area, but at least once individuals traveled as far as 300 km away from the study site (Würsig and Würsig 1977; Würsig 1978). However, a more accurate definition of range awaits further data.

It was mentioned previously that slow movement near shore may at times be associated with feeding on large solitary fish as well as on smaller bottom-dwelling organisms. Dolphins also engaged in other activities while moving near shore. During the morning, we observed very little aerial behavior such as leaping, noseouts, belly-ups, and kelp tossing. As a result it appeared that their activity level was less during the morning than during the afternoon, and that much of the time the animals were resting as they moved back and forth close to shore. A similar pattern of rest dur-

ing morning has been reported for Hawaiian spinner dolphins by Norris (1974), Norris and Dohl (in press), and Norris and Dohl (see footnote 3) and for dusky dolphins by Würsig and Würsig (see footnote 4). Norris and Prescott (1961) also mentioned that *T. gilli* off California appears more active in the late afternoon than during the early part of the day. Why this period of rest should be concentrated in the forenoon in at least three different coastal species is not known. It contrasts in the present population with a greater amount of feeding activity in the afternoon, and it may be that schooling prey is more available in the deeper offshore waters in which these porpoises feed in the afternoon. As a result, they rest more frequently when prey is not available.

During the afternoon, activity level increased. Aerial displays were generally performed singly, however, and were often spaced in time, with only a few leaps or noseouts per hour. This amount of aerial displaying was less than for the spinner dolphins which spread out over large distances and for which the omnidirectional splashing sounds attendant to most aerial behavior is thought to serve a possible communication function (Norris 1974). Such communication would be most important when the animals are not close together as a tightly knit unit, which the present individuals were at almost all times. Nevertheless, it is still possible that noisy leaps, e.g., served to attract the attention of the rest of the subgroup in a highly efficient manner. The exact meaning, however, of these leaps is not clear.

Noseouts, belly-ups, kelp tossing, and clean leaps make little noise. These also occurred with higher frequency in the afternoon. Clean leaps, with individuals reentering the water headfirst, as has been mentioned previously, appeared to precede steep dives in intermediate and deep waters. They may be correlated with feeding on or near the bottom. Noseouts, belly-ups, and kelp tossing occurred when individuals were close together, often touching, and may be associated with "play" and copulatory activity. Especially during times when individuals moved upside down (belly-up) for 50 m or more, they were attended by one or more individuals rubbing along their flanks and dorsum. These close interpersonal associations need not necessarily indicate copulatory behavior, however. They were also performed on several occasions by adults and their small calves, and may represent a form of nonsexual social communication as has been proposed by several

other works (Caldwell and Caldwell 1967; Bateson[6]; and others). Especially significant for this hypothesis may be the fact that we observed more of these behaviors when two subgroups which had been separated for several hours or longer rejoined. Rubbing behavior and attendant aerial displays may at least in part serve a greeting function, where individuals renew and strengthen social bonds in a manner analogous to many social terrestrial mammals (for a review, see Wilson 1975).

Belly-up movement was described by Leatherwood (1975) for *T. truncatus*, and by Saayman and Tayler (in press) for *Sousa* sp. as being performed by individuals while pursuing fish near the surface of the water. Although we saw belly-up behavior only in conjunction with other behavior which we assumed to be social, it may also occur for feeding in the present population.

A final form of aerial behavior which also made a loud sound was tailslapping. It was performed at any time that the group may have been disturbed, such as upon the approach of our boat. We therefore concur with other researchers (Norris and Prescott 1961; D. K. Caldwell and M. C. Caldwell 1972) who believe that tailslapping by dolphins in general serves as a warning signal or fright reaction. It was performed with highest frequency by a large adult who was part of a "core" of individuals present throughout the 21-mo study. We suggest that this individual may have been a "leader" of the subgroup of animals, possibly dominant over other individuals. This suggestion is based only on this one behavioral pattern, however, and must therefore be treated with caution.

Dolphins associated with whales by riding on the waves created by the larger cetaceans, and rode on wind-driven waves and the pressure wave of the boat. This type of behavior has been seen in many species, and was described for dolphins riding near whales by McBride and Kritzler (1951), for dolphins riding wind-driven waves by Woodcock and McBride (1951), and for dolphins riding boat bow waves by Matthews (1948) and Woodcock (1948). Especially insightful analyses of this behavior have been provided by Scholander (1959) and Norris and Prescott (1961). They showed that dolphins could travel with less muscle movement, and therefore presumably less expenditure of

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[6]Bateson, G. The cetacean community in Whaler's Cove - Sea Life Park. Unpubl. manuscr., 16 p. Center for Coastal Marine Studies, University of California, Santa Cruz.

energy, by surfing in this manner. How much pure play (and perhaps play as a part of learning) is involved, and whether or not dolphins really ride waves to get a "free ride" to a different location are questions which remain unanswered.

In the present paper, we made an attempt to describe some of the behavior patterns which we saw most often from above the water surface, and suggested various possible functions for them. We realize, however, that most social interactions go on under water, and that dolphins probably communicate with sound at least as extensively as with observed movements. Tyack (1976) found differences in quality and quantity of sounds produced by the bottlenosed dolphins of the present study depending on whether they appeared to be feeding, socializing, or resting. Although this is a promising beginning, much more sound-behavior correlation is necessary before biological meaning can be ascribed to specific sounds.

In this paper, we have described certain movement patterns and behavior, and ascribed possible functions to them. However, the present analysis raises many more questions than it answers, and may be regarded as a first step in understanding the behavior of these animals.

ACKNOWLEDGMENTS

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