MOVEMENTS AND ACTIVITIES OF THE ATLANTIC BOTTLENOSE DOLPHIN, *TURSIOPS TRUNCATUS*, NEAR SARASOTA, FLORIDA

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ABSTRACT

A tagging-observation program was conducted to study the behavioral ecology of Atlantic bottlenose dolphins near Sarasota, Florida. Forty-seven bottlenose dolphins (24 males, 23 females) were captured, tagged, and released a total of 90 times from 29 January 1975 through 25 July 1976. Tagged animals were identified during regular boat surveys, and information was collected on all individuals and groups encountered. A total of 997 tagged or marked bottlenose dolphins were sighted. A population of bottlenose dolphins was identified in an estuarine-nearshore area extending about 40 km to the south from Tampa Bay and up to 3 km into the Gulf of Mexico. Social organization was characterized by small dynamic groups that appeared to be subunits of a larger socially interacting herd. Average group size of 688 groups was 4.8 bottlenose dolphins (standard error = 0.16). Bottlenose dolphins concentrated in different areas seasonally, possibly in response to distribution changes of important prey species. Feeding strategies of the bottlenose dolphins apparently varied according to available water depth and differed from strategies of pelagic small cetaceans. Calving apparently occurred from spring to early fall.

Until the 1970's, information on the natural history of free-ranging small cetaceans consisted primarily of chance observations (e.g., Norris and Prescott 1961). Increased interest and application of new technology have now greatly expanded our knowledge. Long-term studies of the behavior and ecology of dolphins have been conducted by researchers using boats, submersibles, aircraft, and towers or cliff-top vantage points (see review by Norris and Dohl 1980a). Biotelemetry and newly developed tagging techniques have been used extensively to gather information on delphinid movements, activities, and herd structure (Norris and Pryor 1970; Evans et al. 1971; Perrin 1975; Leatherwood and Evans 1979; Norris and Dohl 1980b). Natural marks that identify individuals have also been used as the basis for field studies of dolphins (Würsig and Würsig 1977, 1979; Shane and Schmidly[5]) as well as whales (Pike 1953; Payne 1976; Katona et al. 1979; Balcomb and Goebel[6]). Unfortunately, in most studies of free-ranging cetaceans, the age, size, and sex of herd members was usually unknown, and consequently few details about herd structure and social dynamics were collected.

The research reported here was an 18-mo tagging-observation study to collect data on movements, home range, herd structure, and habitat use of the bottlenose dolphin, *Tursiops truncatus*, near Sarasota, Fla. (lat. 27°25′ N, long. 80°40′ W). This area was chosen for several reasons: bottlenose dolphins were present throughout the year in areas where channels and islands limited their movements to predictable routes (Irvine and Wells 1972); because the area was used by many boaters, discrete use of an observation boat was not likely to affect the bottlenose dolphins' behavior; and mild weather and sheltered waters made year-round observations feasible. The study was intended to provide insights into the ecology of bottlenose dolphins in a bay-estuarine environment. This report is a revision and reanalysis of parts of Irvine et al.[7]; Wells et al. (1980)

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[5]Shane, S. H., and D. J. Schmidly. 1978. The population biology of the Atlantic bottlenose dolphin, *Tursiops truncatus*, in the Aransas Pass area of Texas. Avail. Natl. Tech. Inf. Serv., Springfield, Va., as PB-283 393, 130 p.

[6]Balcomb, K. C., III, and C.A. Goebel. 1976. A killer whale study in Puget Sound. Final Report to the National Marine Fisheries Service, Contract No. NASO-6-35330. Unpubl. rep.

[7]Irvine, A. B., M. D. Scott, R. S. Wells, J. H. Kaufmann, and W. E. Evans. 1979. Appendix A. A study of the activities and movements of the Atlantic bottlenose dolphin, *Tursiops truncatus*, including an evaluation of tagging techniques. Avail. Natl. Tech. Inf. Serv., Springfield, Va., as PB-298 042, 54 p.

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present an in-depth analysis of social behavior data from the same study.

METHODS

Study Area

The study area included inshore and coastal waters up to 3 km off the coast, extending about 40 km south from the southern edge of Tampa Bay, Fla. This area is characterized by bays and grass flats 1-4 m deep, and is protected by a series of barrier islands separated by narrow passes (Figure 1). Inshore waters, defined here as the waters between the barrier islands and the mainland, were generally protected from heavy winds and ocean swells. The Intracoastal Waterway (ICW), a boat channel between the barrier islands and the mainland, is maintained by dredging to depths of at least 2 or 3 m. Depths in the Gulf of Mexico increase gradually; the 10 m contour is about 3 km offshore (N.O.S. Chart No. 11425).

Data Collection and Analysis

We captured bottlenose dolphins using the seine net technique described by Asper (1975). We recorded the length and sex of all captured animals and then marked them with combinations of spaghetti tags, fiber glass "visual" tags, freeze brands, roto tags, and radio tags, using methods developed and tested on other small cetaceans (Norris and Pryor 1970; Evans et al. 1972). The radio tags were modified dolphin transmitters, model PT 219, of the Ocean Applied Research Corporation (OAR[8]). Transmitter signals were received on an OAR model 210 Auto-

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

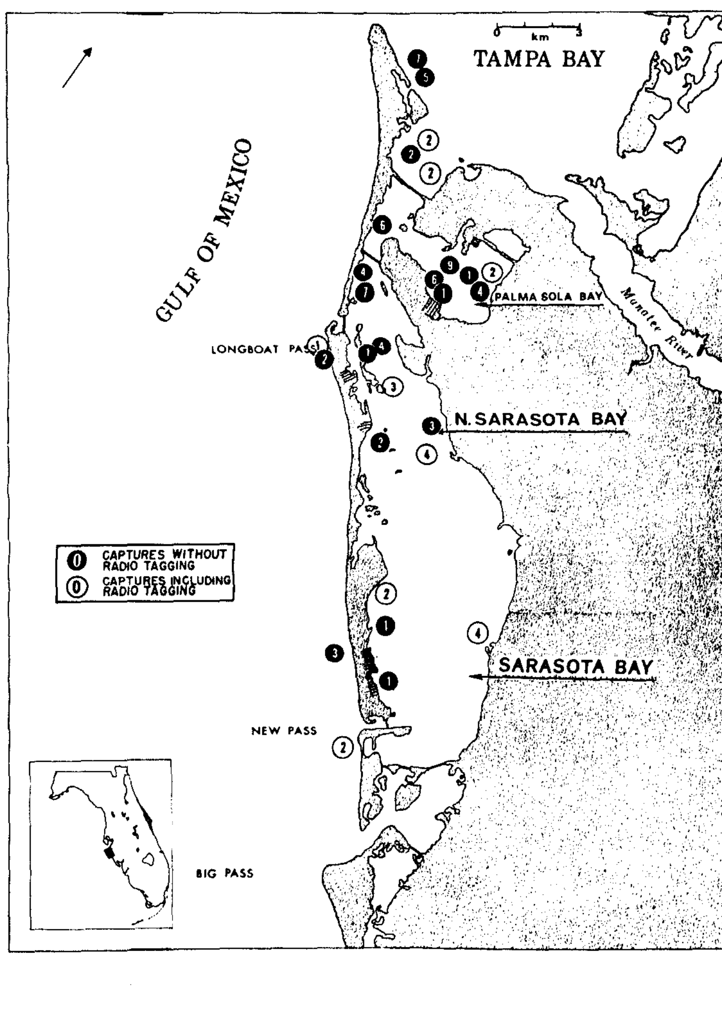

FIGURE 1.—The study area, located south of Tampa Bay near Sarasota (lat. 27°25′ N; long. 80°40′ W), Fla. The encircled numbers indicate numbers of bottlenose dolphins captured at each site.

matic Direction Finder. The tags and marking techniques used in the study were described and evaluated by Irvine et al. (footnote 7).

The boat used as a tagging platform and for surveys and radio tracking was a 7.3 m Wellcraft "Fisherman," equipped with a 3 m tuna tower. During captures, the boat was camouflaged with canvas and netting and towed to the capture site to lessen chances that tagged bottlenose dolphins might later recognize the motor sounds or visually identify the boat, and avoid it during surveys.

Radio-tagged bottlenose dolphins were usually tracked continuously for 24-48 h after installation of the radio transmitter and then relocated and tracked intermittently during the remaining life of the transmitter. As reported by Martin et al. (1971), the radio tags transmitted only when the antenna was at the surface, enabling us to measure dive times by timing the intervals between transmissions. Tracking was generally conducted from a distance and at anchor, to lessen possible influences of the tracking boat on the bottlenose dolphins' movements. Locations of radio tagged animals were determined at night by triangulation and during the day by triangulation or occasional sightings.

Boat surveys were conducted during periods when bottlenose dolphins were not being radio tracked. Surveys were conducted at least twice a week and were concentrated in northern inshore areas (Figure 2). Surveys were extended to include the Gulf of Mexico and southern inshore areas when time was allowed. Survey routes were influenced by tide and wind but were usually confined to channels or other areas >1 m deep (Figure 2).

During boat surveys and tracking trips, all dolphins sighted were counted, and tagged or marked individuals were identified if possible. Groups containing several recognizable animals were usually observed for longer periods to verify identities and associations. The distribution of sightings was therefore influenced by boat channels and by the length of time that groups were followed.

The location and direction of movement of all bottlenose dolphins sighted were noted on charts, and notes on each encounter were entered on data sheets. To correct for repeated sightings of known individuals during the same survey, we based distribution and herd size analyses on sightings more than 1 h apart. Associations between recognizable bottlenose dolphins were compiled as one sighting per group per day, but were retabulated each time the composition of a group changed. For "seasonal" analysis, the year was divided into quarters based on the beginning of field activities (29 January 1975) as follows: February, March, and April (spring); May, June, and July (summer); August, September, and October (fall); and November, December, and January (winter).

Population units were difficult to define because sea conditions and local topography usually limited sightings to nearby animals. Consequently, all bottlenose dolphins sighted within about 100 m of the boat were defined as a group. The smallest group of bottlenose dolphins observed to be closely associating and engaging in similar activities was labeled a primary group. Combinations of primary groups were labeled secondary groups. A "herd" was defined as an aggregation of bottlenose dolphins that more or less regularly occupied a given area and interacted socially with each other to a markedly greater extent than with bottlenose dolphins in adjacent areas. This definition of a herd was based on observed social interactions or associations over an extended period of time. At any given time, the members of the herd were distributed among a number of primary and secondary groups. Herds sighted during aerial surveys (e.g., Leatherwood et al. 1978) have been defined, by necessity, by proximity of animals sighted, and are probably most comparable to our definitions of primary and secondary groups.

RESULTS AND DISCUSSION

Forty-seven bottlenose dolphins (24 males, 23 females) were captured or recaptured for tagging a total of 90 times between 29 January 1975 through 25 July 1976. Ten dolphins (designated RT-1 to RT-10) were fitted with radio tags and radio tracked for up to 22 d. The total of 3,331 bottlenose dolphins sighted (Figure 3) included 2,373 during surveys (730.2 h), 529 during radio tracks (245.3 h), and 429 during capture efforts (150.8 h). Of the 997 marked bottlenose dolphins that were sighted, 781 were tagged and identifiable, 129 were tagged but unidentifiable, and 87 (distributed among 12 dolphins) were identifiable by distinctive natural marks (usually dorsal fin shape). Numerous sightings from close range suggested that tagged bottlenose dolphins did not attempt to avoid the tagging-observation boat.

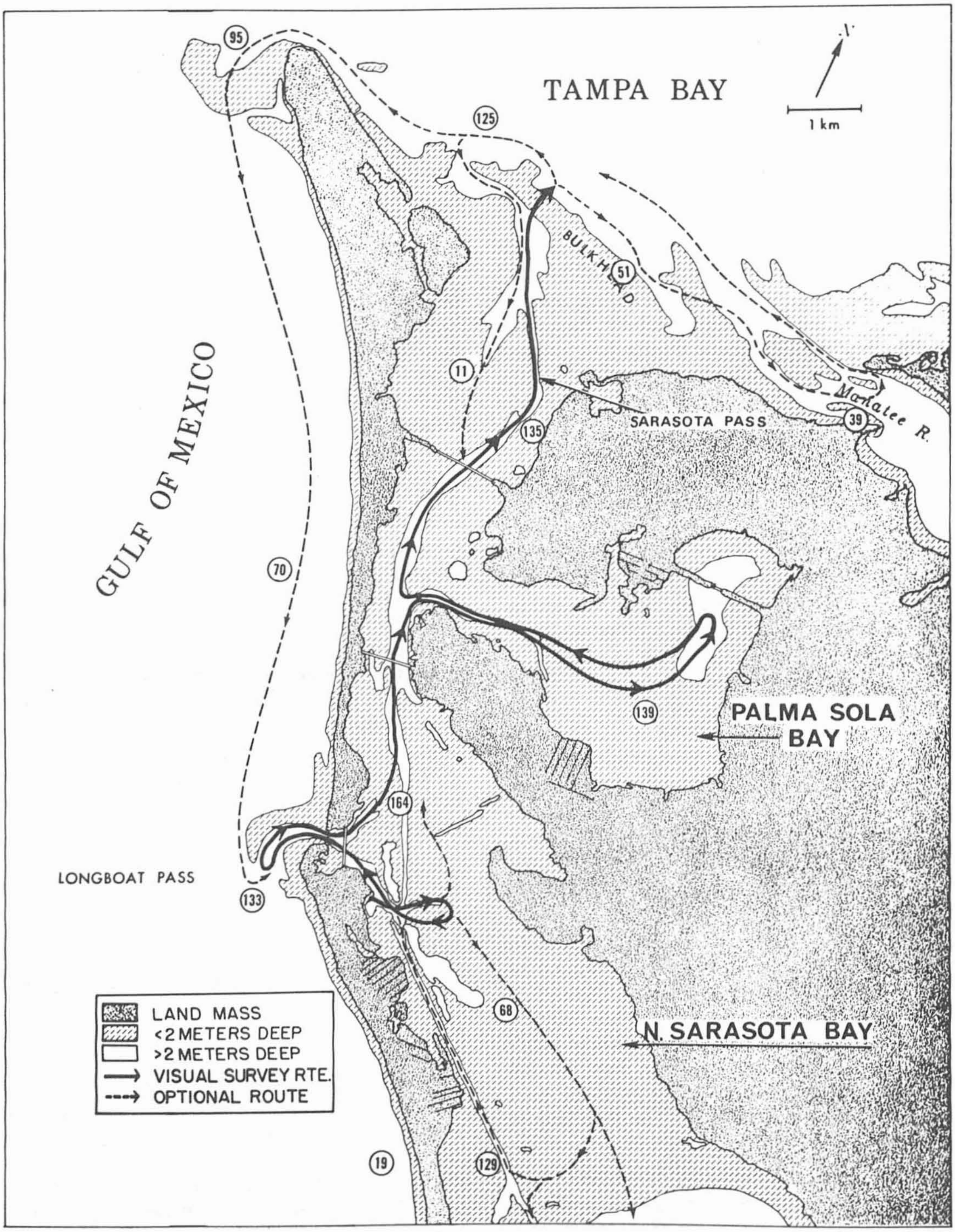

FIGURE 2.—Northern part of the study area with numerals indicating number of surveys along specific routes. Solid lines indicate usual routes. Dashed lines indicate optional routes taken when weather and time permitted. Tagged bottlenose dolphins often traveled north to the edge of Tampa (solid line route) before turning east or west (dashed line) or returning south.

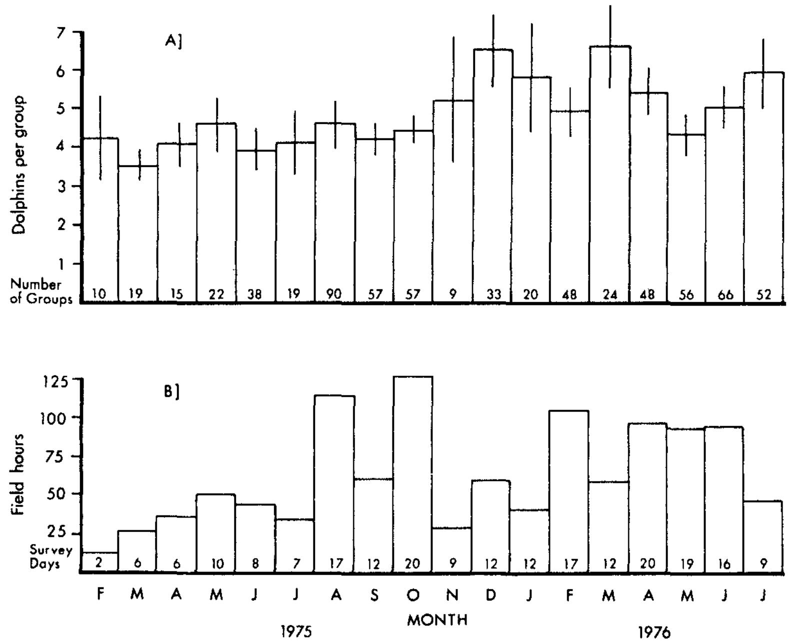

FIGURE 3.—Compilation of bottlenose dolphin sighting data by month, from boat surveys: A) Average number of dolphins sighted per group with standard error (vertical lines) and numbers of groups sighted (numerals) for each month. B) Number of field hours and boat survey days (numerals).

Home Range

Resightings of tagged bottlenose dolphins suggest that at least some were year-round residents of the study area (Figure 4). We recaptured 11 of the 12 animals tagged in 1970-71 by Irvine and Wells (1972) and identified them by freezebrands, tag scars, or dorsal fin shape—strongly implying that some bottlenose dolphins may remain in the area for several years. The existence of resident bottlenose dolphins has previously been widely proposed (Caldwell 1955; Caldwell and Golley 1965; Norris and Pryor 1970; Saayman et al. 1972; Saayman et al. 1973; Würsig and Würsig 1977, 1979; Würsig 1978; Saayman and Tayler 1979; Norris and Dohl 1980b; Shane and Schmidly footnote 5).

The home range of the bottlenose dolphins in the study area appeared to extend south from the southern edge of Tampa Bay to Big Pass (Figure 5; see also Wells et al. 1980), and to include inshore areas and waters up to 1 km into the Gulf of Mexico. No tagged bottlenose dolphins were observed more than 1 km offshore; however, survey trips rarely extended farther than 3 km offshore. At their apparent northern boundary, tagged animals terminated northerly movements at the edge of Tampa Bay by turning either east or west (Figure 2). Groups containing identifiable naturally marked bottlenose dolphins, apparently

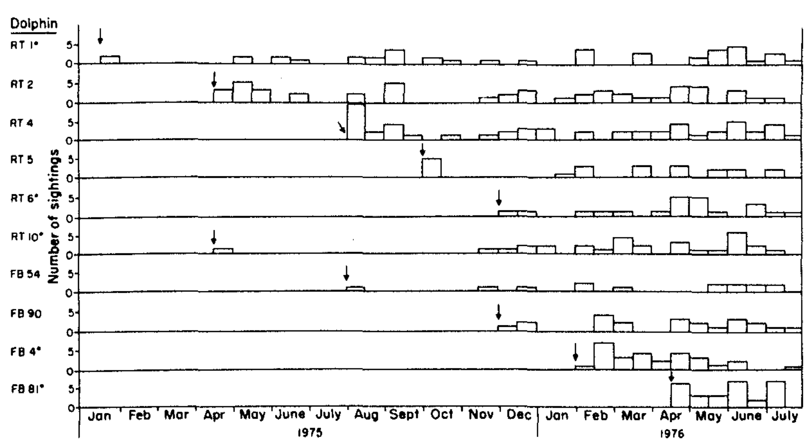

FIGURE 4.—Total biweekly sightings of selected tagged bottlenose dolphins; one sighting per day included. Twenty-three of these sightings were reported by other observers. Arrows indicate capture dates. Sighting locations of dolphins marked with an asterisk are shown in Figure 5.

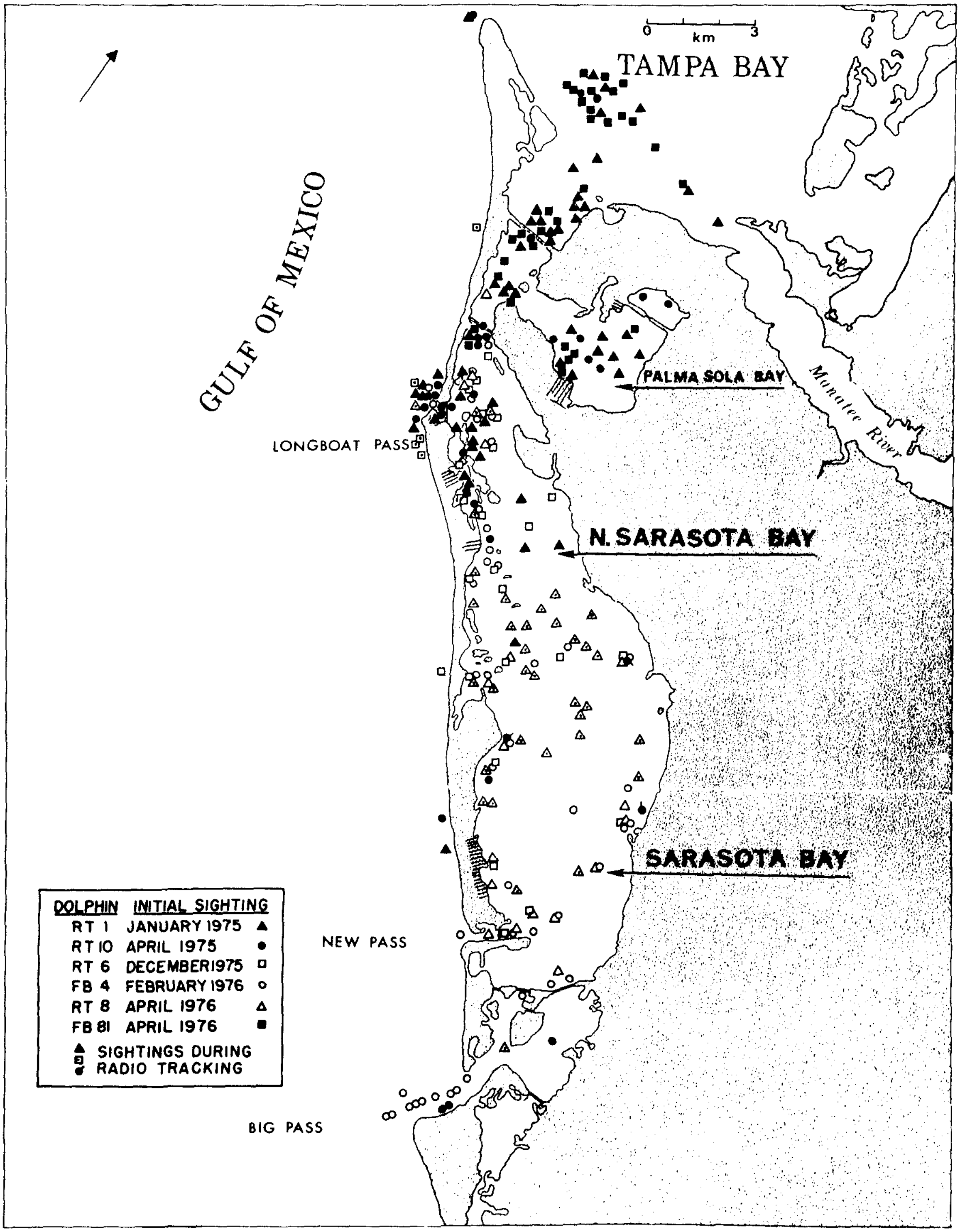

FIGURE 5.—Locations of accumulated sightings of six marked bottlenose dolphins. Sightings of these dolphins were selected to demonstrate generalized use of northern or southern parts of the study area by some animals. The home range of all tagged bottlenose dolphins in the study area extended from approximately southern Tampa Bay to Big Pass.

not belonging to the study herd, occasionally moved along the southern edge of Tampa Bay, but rarely approached tagged bottlenose dolphins and were never observed moving south in the ICW. The only tagged bottlenose dolphins known to have left the study area were two radio-tagged animals that left briefly (one moved 15 km north, the other 10 km south) on the first night after tagging. Both returned within 10 h.

The home range boundary cues used by the animals are unknown. At Tampa Bay, bottlenose dolphins might have used acoustic or visual cues associated with the sharp dropoff at the edge of Tampa Bay. Bottlenose dolphins may use landmarks to limit movements in Golfo San Jose, Argentina (Würsig and Würsig 1979), although known individuals also disappeared from the study area for 6 mo, were resighted 300 km away and then were rediscovered back in the study area 9 mo later (Würsig and Würsig 1977). Long-range movements by some group members but not by others have not been reported elsewhere; however, most studies of bottlenose dolphin home range have been conducted in restricted geographical areas with relatively few identifiable animals (see review by Norris and Dohl 1980a).

Movements and Activities

Movement patterns were similar throughout the northern part of the study area. Slow moving groups of up to six animals often spent several hours over grass flats 1-3 m deep, particularly west of the ICW north of Sarasota Pass and east of the ICW in northern Sarasota Bay (Figure 2).These groups were usually dispersed and dynamic; individuals often approached each other only occasionally, but all usually moved in the same general direction. The pace of individuals quickened at irregular intervals when apparent feeding occurred. Typically, a group of bottlenose dolphins was found in one part of the study area for several survey days, before it moved to another area, but locations and intragroup associations were generally not predictable.

Group members often converged and used channels to move between areas, usually at speeds of 2-5 km/h, although occasionally small groups in tight formation moved along the ICW at speeds exceeding 5 km/h. North-south movements of up to 30 km in a day have been observed but were not typical.

Bottlenose dolphin distribution, and perhaps abundance, differed seasonally within the home range (Figure 6). In winter, bottlenose dolphins were most abundant in passes and along the gulf shore, whereas during the warmer months relatively higher numbers were sighted in the channels and bays inshore of the barrier islands. These localized changes in bottlenose dolphin distribution may reflect changes in the distribution of food resources, or possibly seasonal changes in abundance of sharks (Wells et al. 1980).

Unlike the habitat of pelagic cetaceans, which theoretically does not restrict horizontal and vertical movements, the shallowness of many parts of our study area restricted vertical movements and thereby dictated bottlenose dolphin travel routes and influenced the structure of swimming groups. Bottlenose dolphins were only occasionally observed crossing areas <1 m deep. Bottlenose dolphins have partly beached themselves in Georgia marshes while pursuing fish (Hoese 1971), and other dolphins have been observed feeding in estimated depths of <50 cm (A. B. Irvine pers. obs.; J. S. Leatherwood[9]).

The habitat used by the bottlenose dolphins reported here appears most like that of the humpback dolphin, *Sousa* sp., observed from cliffs in South Africa (Saayman et al. 1972; Tayler and Saayman 1972; Saayman and Tayler 1973, 1979; Saayman et al. 1973) and bottlenose dolphins observed in a bay in Argentina (Würsig and Würsig 1977, 1979; Würsig 1978). In these areas, the animals also usually moved in small groups and fed individually. Although most bottlenose dolphin sightings in our study area were east of the barrier islands, tagged animals were also periodically observed near shore in the Gulf of Mexico. Bottlenose dolphins are found from well offshore into extreme shallows in the Gulf of Mexico (Leatherwood 1975; Leatherwood et al. 1978; Odell and Reynolds[10])—suggesting a distribution that is similar to that of bottlenose dolphins studied in South Africa (Saayman et al. 1972; Tayler and Saayman 1972; Saayman and Tayler 1973, 1979; Saayman et al. 1973).

Movements of bottlenose dolphins with the tides were suggested by True (1885), Gunter (1942), Irvine and Wells (1972), Würsig and Würsig

[9]S. Leatherwood, research biologist, Hubbs-Sea World Research Institute, San Diego, CA 92109, pers. commun. March 1980.

[10]Odell, D. K., and J. E. Reynolds. 1980. III, Distribution and abundance of the bottlenose dolphin, *Tursiops truncatus*, on the west coast of Florida. Avail. Natl. Tech. Inf. Serv., Springfield, Va., as PB 80-197 650, 47 p.

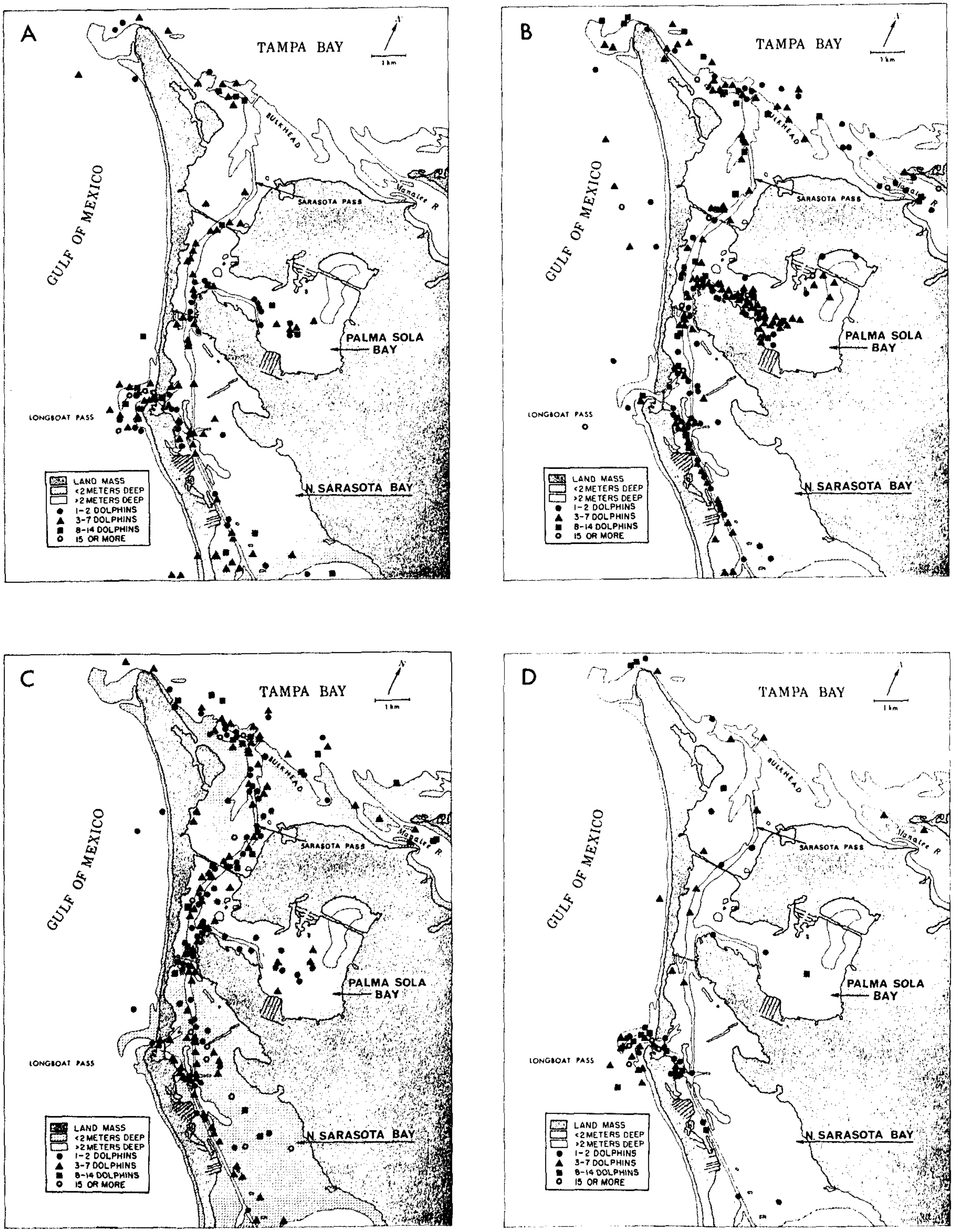

FIGURE 6.— Locations of bottlenose dolphins sighted during 3-mo periods: A) February, March, and April 1975 and 1976; B) May, June, and July 1975 and 1976; C) August, September, and October 1975; D) January, November, and December 1975, and January 1976.

(1979); however, Shane (1980) reported more movements against than with the tidal current, and Leatherwood (1979) reported seeing no relation between the bottlenose dolphin movements and tide. As indicated in Figure 7, considerably more bottlenose dolphins in our study were moving with than against the tidal currents, although the numbers of groups moving with and against the currents were almost equal. This observation suggests that larger groups of animals more often moved with the tide. The data were not analyzed statistically because a large number of animals seen were in the "milling" category, moving across the current or in irregular patterns.

The tidal current in the study area varied with physiography, but was strongest in narrow channels and passes, at times exceding 5 km/h. In Palma Sola Bay, a shallow bay with one access channel, bottlenose dolphins more often moved against than with a sometimes strong current. The animals rarely reversed direction in the Palma Sola Bay channel but often swam near the sides of the channel possibly because current velocity was reduced there.

Movement and activity patterns were not influenced by other environmental conditions in any recognizable way. Possible sun orientation, as reported for the common dolphin, *Delphinus delphis*, by Pilleri and Knuckey (1968) and Evans (1971), was not observed, although the restrictions of movements dictated by area physiography may have masked such effects. We did not detect the distinctive day-night dive interval patterns noted for other dolphin species by Evans (1971, 1974, 1975), Leatherwood and Evans (1979), Leatherwood and Ljungblad (1979), Norris and Dohl (1980b), and Würsig (in press, see footnote 11).

Social Structure

Available evidence suggests that the study area was occupied by a single discrete social unit or "herd." Groups containing naturally marked bottlenose dolphins that were seemingly not a part of this herd were repeatedly observed north, west, and south of the study area. These observations suggest that the bottlenose dolphin population on Florida's west coast may be composed of a number of distinct herds inhabiting limited geographical areas. Overlapping home ranges have also been proposed for coastal bottlenose dolphins off southern California (Leatherwood and Reeves 1978).

The uneven dispersal of sightings of bottlenose dolphins of different age and sex classes within the

[11]Würsig, B. 1976. Radio tracking of dusky porpoises (*Lagenorhynchus obscurus*) in the South Atlantic, a preliminary analysis. ACMRR Scientific Consultation on Marine Mammals, Bergen, Norway, 21 p.

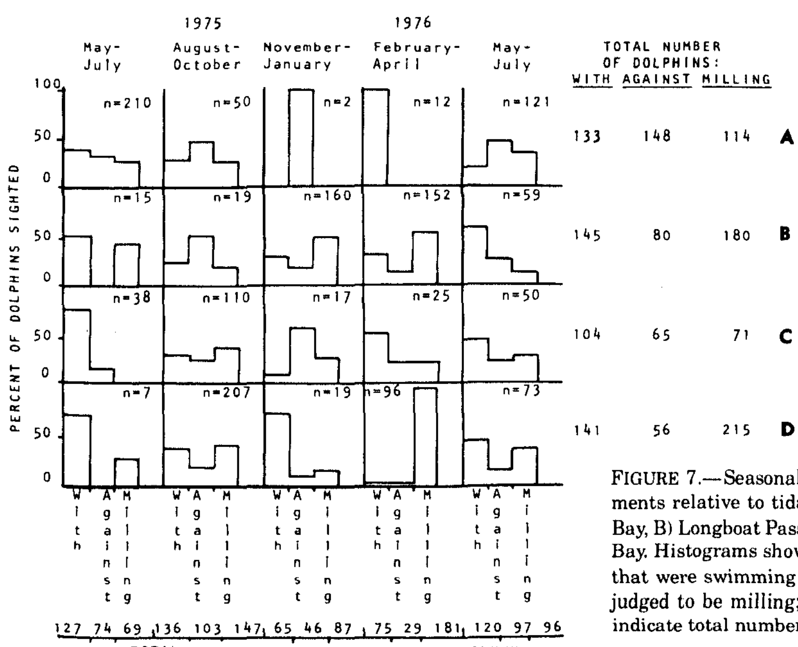

FIGURE 7.—Seasonal relationship of bottlenose dolphin movements relative to tidal flow in selected areas. A) Palma Sola Bay, B) Longboat Pass, C) Sarasota Pass, and D) North Sarasota Bay. Histograms show percent of dolphins sighted in each area that were swimming with the current, against the current, or judged to be milling; the numbers in each category and area indicate total number of dolphins seen.

study area suggested the presence of several "subherds" (Figure 5). The bulk of the tag sightings in the southern part of the study area were of the same subadult male groups, whereas cow-calf pairs were more commonly sighted in the north (Wells et al. 1980). However, some identifiable bottlenose dolphins were sighted in all parts of the study area and were associated with as many as 20 other tagged animals. Overall, we interpret the resightings of tagged animals to indicate that different age and sex classes may have favored different areas, but that social relationships were still maintained among members of the entire herd.

Bottlenose dolphins from adjacent areas that occasionally approached animals from the study herd remained for only a few minutes, and social interactions between the different groups were not observed. Various species of macropods, primates, and ungulates have similar social organizations; subgroups join to form discrete social units ("mobs," "troops," or "herds") that exhibit spatial fidelity and have little interaction with conspecifics outside the social unit (see review by Wilson 1975).

The size of the herd within the study area was difficult to determine. Boat survey results were variable, and information on bottlenose dolphin migration was unavailable. However, the lack of sightings from outside the study area, the observed movements of visually and radio-tagged dolphins, and an increase in tag sightings as the number of tags installed increased (Table 1) all suggested that the captures involved a discrete population of bottlenose dolphins. Assuming a constant population size with no emigration or immigration, we estimated that the local population contained 102 bottlenose dolphins (95% confidence limits = 90-117), using a Lincoln Index (Overton 1971) and a basis of 35 survey days (165 h), from 9 May through 9 July 1976 (Table 1). Until more data are available about this assumption, however, our population estimate must be viewed with caution.

Assuming that the group home range was 85 km^2 (Wells et al. 1980), the estimated population size suggests a density of 1.3 bottlenose dolphins/km^2. Aerial surveys indicate densities of 0.23-0.68 bottlenose dolphin/km^2 in other coastal areas of the southeastern United States (see review by Leatherwood 1979). Monthly mean bottlenose dolphin densities derived from surface survey data of Shane (1980) were 1.5-5.1 bottlenose dolphins/km^2 near Port Aransas, Tex., whereas aerial density estimates at the same area were 2.6 bottlenose dolphins/km^2 (Barham et al. 1980). The reasons for the large discrepancies between aerial and surface survey density estimates are unclear. Some animals may be counted more than once from boats, or perhaps observers in rapidly moving aircraft do not see all bottlenose dolphin groups. In any case, the differences in density estimates suggest that population estimates of bottlenose dolphins in Florida based on aerial and surface surveys may not be directly comparable.

It is not known whether the study herd remained intact throughout the year or changed composition seasonally. Tagged bottlenose dolphins that were not sighted for long periods (see Figure 4) may have lost their identifying tags, or may have left the study area, as did some bottlenose dolphins in Argentina (Würsig and Würsig 1977).

Fewer than 15% of the field sightings were of solitary bottlenose dolphins, which is an indication of the high degree of gregariousness of free-ranging bottlenose dolphins (Figure 8). Average group size (n = 688 groups) varied from 2 to 6 about an overall mean of 4.8 bottlenose dolphins/group (SE = 0.16; Figures 3A, 8). During summer 1975 and early summer 1976, groups of >40 unmarked bottlenose dolphins, probably from adjacent herds, were observed <1 km offshore in the Gulf of Mexico and within 1 km of the northern

TABLE 1.—Sightings of marked and unmarked dolphins and population size estimates, during periods from December 1975 to July 1976.

Item	17 Dec.-13 Feb.	15 Feb.-17 Mar.	20 Mar.-14 Apr.	17 Apr.-6 May	9 May-6 June	12 June-9 July
A) Number of marked dolphins	19	[1]20.75	24	[1]27.83	37	38
B) Total number of dolphins sighted	261	176	49	200	226	[2]415
C) Number of marked dolphins sighted	38	49	10	67	103	132
D) C/B	0.15	0.28	0.20	0.34	0.46	0.32
E) Estimated population size	130	74	118	83	81	119
F) 95% confidence limits	91-179	55-98	55-221	65-106	67-99	100-142

[1]Tagged dolphins were found dead on 5 March and 3 May 1976; population estimates are adjusted to account for survey days after these animals were dead.
[2]Includes 95 unmarked dolphins (in 5 groups) sighted on the periphery of the study area.

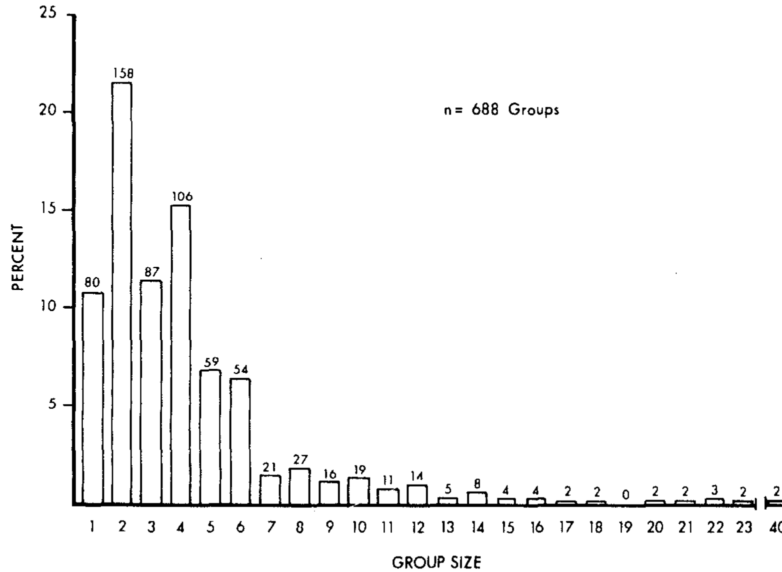

FIGURE 8.—Group size-frequency distribution. Groups were defined as all animals within about 100 m of the survey boat. Numerals indicate the number of groups in each size category.

limit of the study area in Tampa Bay. However, group size-frequency distributions did not vary significantly by month ($P>0.60$; chi-square) or season ($P>0.90$; chi-square). Group sizes were not normally distributed (Kolmogorov-Smirnov test; $P>0.05$) during 11 of the 18 mo of field activity (518 sightings), even after square root transformations (Sokal and Rohlf 1969). The lack of significant monthly trends in herd size was corroborated ($P\leq 0.35$) by a Kruskal-Wallis nonparametric analysis of variance test (Sokal and Rohlf 1969).

Social Interactions

Applying the body length-maturity relationship of Sergeant et al. (1973) we categorized each tagged bottlenose dolphin as adult or subadult. The frequencies of interactions between bottlenose dolphins of various age and sex categories are summarized in Figure 9. Adult males (246-268 cm long) associated primarily with females, apparently preferring females without calves, and were rarely observed with subadult males (210-237 cm). Subadult males were most often seen together. Adult females (235-250 cm) were sighted most often with other females. Subadult females (207-234 cm) were also frequently associated with adult females. An adult female nicknamed "Killer" (240 cm long) was usually sighted with subadult males or four adult females. Details of these observed associations are also discussed by Wells (1978) and Wells et al. (1980).

Sexually segregated groups were sighted on a number of occasions in our study and have been reported in other studies (Evans and Bastian 1969; D. K. Caldwell and M. C. Caldwell 1972; Irvine and Wells 1972; Tayler and Saayman 1972; Mead 1975; Norris and Dohl 1980a). Tavolga (1966) noted four subgroups in her detailed study of a captive colony of bottlenose dolphins at Marineland of Florida: a single adult male, adult females, subadults (mostly males), and juveniles. Miyazaki and Nishiwaki (1978) classified groups of the striped dolphin, *Stenella coeruleoalba*, into juvenile, mature mating, and mature nonmating schools, but did not report if sexual isolation occurred. Tayler and Saayman (1972) reported on the basis of five captures that subadult male bottlenose dolphins off South Africa are rarely found with "bulls" or in exclusively subadult male groups, but that captive subadult males do closely associate with bulls.

Our observations suggest that subadult males rarely interacted with bulls, but largely formed stable primary groups among themselves. Subadult males were never captured with adult males (28 captures). We observed apparent homosexual interactions within a primary group of four known subadult males during February to July 1976, but cannot verify if it is a year-round behavior. Behaviors were classified as homosexual only when an extruded penis or an apparent copulatory attempt was observed.

"Killer's" frequent association with subadult males is difficult to explain. Inasmuch as she was

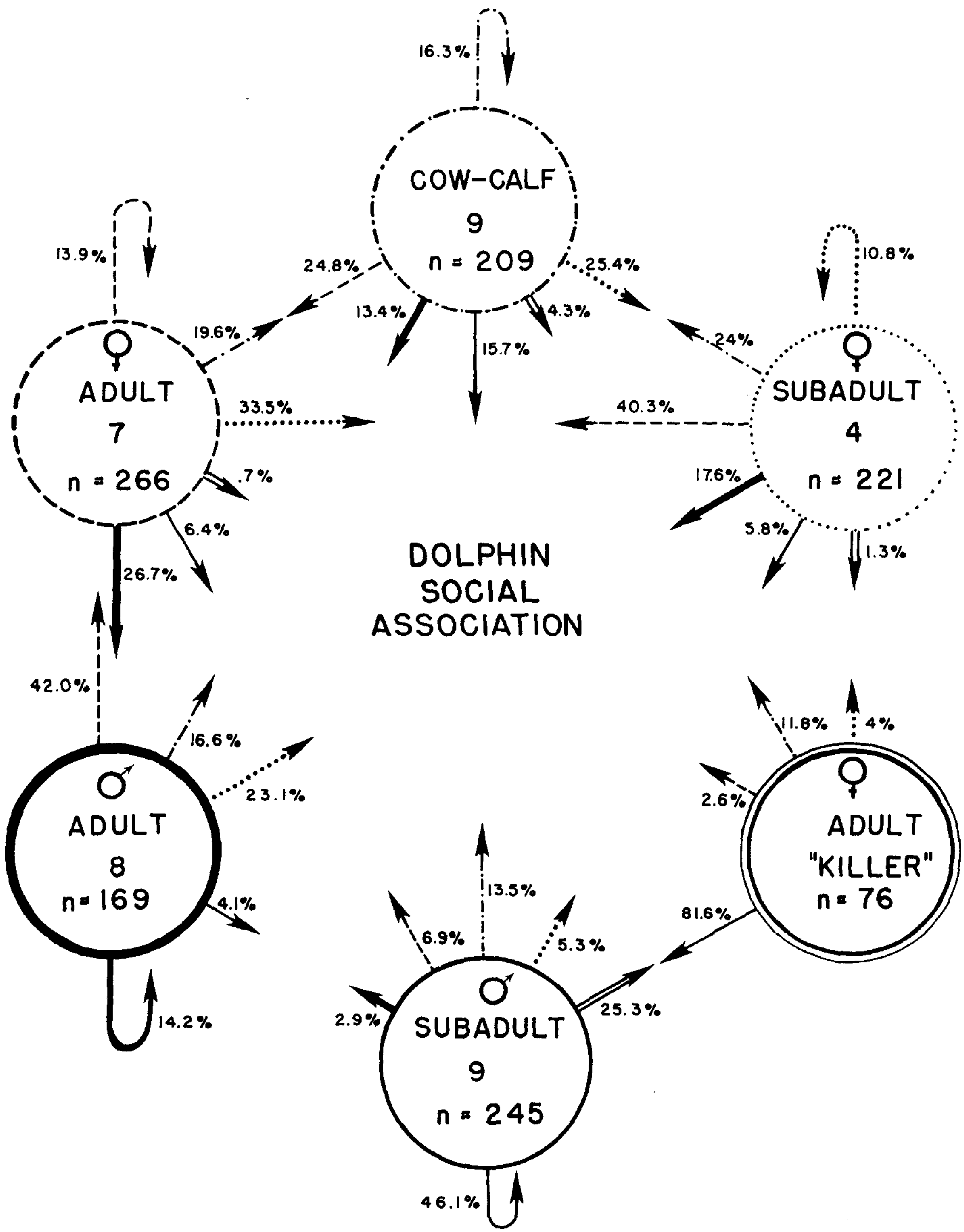

FIGURE 9.—Component social interactions among age-sex classes of known bottlenose dolphins. Sex and length were determined when the animals were captured. Age classes are based on body length-maturity data from Sergeant et al. (1973). Number of individuals is presented under each age-class. n = number of observations. Adult female "Killer" was a dolphin that had an atypical association pattern (see text).

captured and sexed several times, error in sex determination is not likely. She was occasionally seen with the same group of subadult males that had been observed engaging in homosexual activities, and on one occasion she appeared to engage in sexual activities with at least one member of that group.

The associations of longest duration involved cows and calves, although relatively prolonged aggregations of subadult males and frequent associations of adult males with adult females were noted in the spring. One calf was observed during 30 of 32 sightings of the apparent mother over a period of 15 mo, and another calf was observed with its mother on all of 20 sightings during a 9-mo period. We did not observe straying of calves, as has been noted in captivity (see review by M. C. Caldwell and D. K. Caldwell 1972) and inferred for free-ranging bottlenose dolphins in Argentina (Würsig 1978) and the Gulf of Mexico (Leatherwood[12]).

When pursued during capture attempts, calves stayed close beside their fleeing mothers, apparently being partly pulled along in the suction created by the mother's movement through the water (Norris and Prescott 1961; Norris and Dohl 1980a; Leatherwood footnote 12). While the mother was being tagged, calves remained close to the stretcher, often emitting underwater whistles audible in air. A calf released outside the net quickly became tangled in the net while attempting to return inside, where its mother was trapped. When a cow was released before her calf was freed, she invariably patroled outside the net until the calf was released. On one occasion a loud whistle from a bottlenose dolphin calf being tagged brought the mother rapidly to within 5 m of the capture net from a point about 75 m away. Apparently similar behaviors have been observed for *Stenella* sp. involved in the purse seine fishery for yellowfin tuna, *Thunnus albacares* (W. F. Perrin[13]). Close approaches by large male killer whales, *Orcinus orca*, to the outside of an enclosure containing a killer whale calf have also been observed by A. B. Irvine in Puget Sound.

Dolphins being pursued by the capture boat fled as a close-knit group often in a line abreast formation. As with bottlenose dolphins off California (Norris and Prescott 1961; Norris and Dohl 1980a) and off Louisiana (Leatherwood and Platter[14]), some bottlenose dolphins recognized the capture boat and began fleeing rapidly 400 m or more ahead of the boat. The bottlenose dolphins apparently associated the sound of the boat's engine with past captures, since naturally marked animals not previously subjected to our capture attempts did not flee. When part of a bottlenose dolphin group was encircled, the remaining members did not temporarily remain nearby, as has been reported for *Steno bredanensis* (Evans 1967), common dolphins (Pilleri and Knuckey 1968), the dusky dolphin, *Lagenorhynchus obscurus* (Würsig and Würsig 1980), and killer whales (Balcomb and Goebel footnote 6). We often observed and sometimes recaptured dolphins near earlier capture sites, suggesting that capture areas were not avoided.

Behaviors associated with the formation and maintenance of intragroup associations are not well understood. Studies of captive animals have indicated that dominance, exerted by combinations of physical posturing, aggression, and vocalization, may be important in the establishment and maintenance of social hierarchies (Tavolga 1966; M. C. Caldwell and D. K. Caldwell 1967, 1972; Evans and Bastian 1969). Most studies of captive dolphins, however, have been of <15 dolphins, often interspecifically mixed, and confined in a tank. The dominance hierarchies and social structure described for captive groups may therefore not represent the social organization of free-ranging bottlenose dolphins. For instance, the concept of microterritories suggested for captives (M. C. Caldwell and D. K. Caldwell 1972; Tayler and Saayman 1972) and presumably maintained by dominance relationships is probably not relevant to the study of wild bottlenose dolphins, which move constantly and change companions often. The small "family unit" concept proposed by McBride and Kritzler (1951) is also not compatible with our observations of dynamic group membership. Evans and Bastian (1969) proposed that the spatial consideration of primary importance to

[12]Leatherwood, S. 1977. Some preliminary impressions on the numbers and social behavior of free swimming bottlenosed dolphin calves (*Tursiops truncatus*) in the northern Gulf of Mexico. *In* S. H. Ridgway and K. W. Benirschke (editors), Breeding dolphins, present status, suggestions for the future, p. 143-167. Avail. Natl. Tech. Inf. Serv., Springfield, Va., as PB-273 673.

[13]W. F. Perrin, fishery biologist, Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92037, pers. commun. March 1980.

[14]Leatherwood, S., and M. F. Platter. 1975. Aerial assessment of bottlenosed dolphins off Alabama, Mississippi, and Louisiana. *In* D. K. Odell, D. B. Siniff, and G. H. Waring (editors), *Tursiops truncatus* Assessment Workshop, p. 49-86. Avail. Natl. Tech. Inf. Serv., Springfield, Va., as PD-291-161.

free-ranging bottlenose dolphins may be interindividual distances and ease of access to the surface for breathing. The size of the herd home range of *Tursiops truncatus*, the frequently changing group compositions, and the number of bottlenose dolphins apparently residing in the study area suggest that the social organization is very complex.

Food Resources and Feeding Behavior

Striped mullet, *Mugil cephalus*, one of the four most common fish species in the Gulf of Mexico (Gunter 1941), is thought to be the mainstay of the diet of bottlenose dolphins (Gunter 1942; D. K. Caldwell and M. C. Caldwell 1972). Seasonal movements and ranges of tagged striped mullet have been determined in several areas of the gulf coast (Idyll and Sutton 1952; Broadhead and Mefford 1956; de Sylva et al. 1956; Ingle et al. 1962). Usually, the fish remained within 32 km of the capture location, but there is little documentation of daily movements. Local commercial fishermen reported that striped mullet spawn in the Gulf of Mexico in November and remain there until spring. Bottlenose dolphin movements from inshore to gulf waters in November thus appear to be similar to those of their primary prey.

Reports by Futch (1966) and local commercial fishermen indicated that the fish movements, and therefore bottlenose dolphin feeding activities, may also be influenced by the tides. Apparently striped mullet are often found in small groups on the shallow banks of bays and estuaries during the flood tide, and gather into larger schools in deeper water as the tide begins to ebb. Dolphin movements and feeding activities cannot be directly correlated with fish distributions in our study area, but such correlations have been reported for nearshore groups of bottlenose dolphins (Würsig and Würsig 1979) and humpback dolphins (Saayman and Tayler 1979).

We surveyed potential food resources of the bottlenose dolphin by interviewing and occasionally accompanying commercial fishermen in the study area. Although striped mullet were most commonly caught, significant numbers of pinfish, *Lagodon rhomboides*; sheepshead, *Archosargus probatocephalus*; and crevalle jack, *Caranx hippos*, were also taken in the same areas. According to fishermen, local dolphins prefer striped mullet, but when striped mullet are not plentiful will eat any available fish, including the hardhead catfish, *Arius felis*, which they swallow after detaching the head. Opportunistic feeding by bottlenose dolphins has also been noted in other areas (D. K. Caldwell and M. C. Caldwell 1972; Leatherwood 1975).

The use of radio tracking data to indicate feeding behavior has been proposed for the harbor porpoise, *Phocoena phocoena* (Gaskin et al. 1975), and small pelagic cetaceans (see reviews by Leatherwood and Evans 1979). Observations of apparent feeding by tagged and untagged bottlenose dolphins in our study area, however, suggested that respiratory intervals interpreted from breaks in transmitter signals were not a valid criterion to indicate foraging for this species. We believe that the long dives associated with foraging for pelagic species are not typical in the shallow habitat of our study area, and therefore transmitted dive times were relatively uniform. Dive intervals ranged from a few seconds to 4 min 25 s, but no relations between dive intervals and time of day were detectable. Lengths of hourly dives averaged 30-40 s, but varied with location and individual bottlenose dolphin.

Feeding strategies of bottlenose dolphins appear to vary with prey abundance and depth. Large compact groups of feeding bottlenose dolphins were seen in the Gulf of Mexico, although the dispersed foraging pattern reported for common dolphins (Evans 1971, 1974, 1975) and the spinner dolphin, *S. longirostris* (Norris and Dohl 1980b), was also evident. When foraging through shallow bays and grass flats, bottlenose dolphins typically formed slow-moving, dispersed groups. Humpback dolphins off South Africa (Saayman and Tayler 1973, 1979) and bottlenose dolphins off Argentina (Würsig and Würsig 1979) also forage close to shore in small groups. Dispersed feeding would be especially effective if the dolphins stayed in acoustic contact, then responded to certain signals by converging on a concentration of fish discovered by one or more individuals. This type of convergence on food sources has been proposed for dusky dolphins (Würsig and Würsig 1980). We did not observe dolphins rapidly converging on fish schools in shallow areas, but group members did occasionally move to an area where a single dolphin had paused to feed.

Shallow-water feeding was often characterized by a rapid erratic chase that ended in a sudden tight spin or pinwheel—the process lasting 1-5 s and covering 5-20 m. Fish sometimes leaped ahead of the approaching bottlenose dolphin and were sometimes briefly observed in the bottlenose dolphin's mouth at the end of the chase. Similar behavior by feeding bottlenose dolphins has been described by Leatherwood (1975), Shane and Schmidly (footnote 5), and Shane (1980). The upside down feeding behavior reported for bottlenose dolphins (Leatherwood 1975) and humpback dolphins (Saayman and Tayler 1979) was occasionally observed. Obvious herding of fish as has been reported for several small cetaceans in nearshore areas (D. K. Caldwell and M. C. Caldwell 1972; Saayman et al. 1972; Tayler and Saayman 1972; Saayman et al. 1973; Leatherwood 1975; Saayman and Tayler 1979; Shane and Schmidly footnote 5) was not observed.

In the Gulf of Mexico (at depths of 3-6 m), rapid convergence by bottlenose dolphins within a radius of about 200 m was observed on several occasions. The bottlenose dolphins dove and remained submerged for 30-90 s in an area where no fish were obvious. Then a number of bottlenose dolphins surfaced almost simultaneously in a confined area amid large numbers of jumping striped mullet, some of which were captured in midair. Although cooperative feeding cannot be confirmed, at the very least the bottlenose dolphins were feeding on the same school of fish, and we suspect they may have herded the school at the surface in an organized way. This behavior differs somewhat from other accounts of cooperative feeding (see review by Norris and Dohl 1980a) because the fish school remained at the surface only briefly, after which the bottlenose dolphins milled in the area for 1-3 min before gradually dispersing into small groups. On one occasion, a sequence of rapid convergence on a concentrated fish school, brief intense feedings, and then dispersal into small groups was repeated three times within 45 min by 20-30 bottlenose dolphins.

Concentrated feeding at more productive areas may optimize food availability for flocking birds in the Mojave Desert (Cody 1971), and a similar strategy has been suggested for common dolphins (Evans 1971, 1974, 1975) and spinner dolphins (Norris and Dohl 1980a). These pelagic cetaceans may feed intensively, primarily after dusk and before dawn, in productive areas of the deep scattering layer before moving on. Theoretically, if the dolphins do not return to the same site for some time, the food source will replenish. In contrast, bottlenose dolphins in our study area may exert an almost constant pressure on available food resources. Inshore regions of the study area and the waters along the Gulf beaches were often traversed several times in a single day by different groups of foraging bottlenose dolphins. Evidence from captives and anecdotal accounts from commercial fishermen indicate that bottlenose dolphins also feed at night. Bottlenose dolphins may feed on different ecotypes in different geographic areas (Walker[15]), and presumably *T. truncatus* in coastal Florida have prey and feeding strategies different from bottlenose dolphins in pelagic habitats. Habitat differences are therefore important to any generalized concept of cetacean behavior and herd function. Because ecological variables influence social behavior and therefore the structure of small-cetacean herds (see reviews by Norris and Dohl 1980a; Wells et al. 1980), studies of adjacent inshore and offshore populations of bottlenose dolphins could do much to elucidate the influence of habitat on cetacean behavior.

Reproduction and Growth

Calves were defined as noticeably smaller bottlenose dolphins closely associating with a single larger animal and composed 8.2% of the bottlenose dolphins sighted. Extensive observations of tagged cow-calf pairs suggest that the above definition was generally applicable. Ten calves ($\overline{X}$ = 171 cm; SE = 9) represented 19% of all captures and recaptures. The relative number of calf sightings per month varied significantly ($P<0.0005$; chi-square contingency tables) from August 1975 to July 1976. It is not clear from the sighting data if the calves were produced during a bimodal breeding season with peaks in late spring and early fall, as suggested by Harrison and Ridgway (1971), or during a continuous breeding season with increases in activity during spring and fall. Many small cetaceans copulate throughout the year, and evidence for discrete breeding seasons is still contradictory (see review by Saayman and Tayler 1979).

Growth measurements were obtained from the repeated captures of calves and the recapture of a young individual originally captured in 1970 (Irvine and Wells 1972). Two calves were captured several times during the study; one grew from 172 to 183 cm in 13 mo, and the other from 189 to 198

[15]Walker, W. A. 1981. Geographical variation in morphology and biology of bottlenose dolphins (*Tursiops*) in the eastern North Pacific. Natl. Mar. Fish. Serv. Admin. Rep. LJ 81 03C. Unpubl. rep.

cm in 7 mo. A young bottlenose dolphin with a deformed jaw originally captured in 1970 grew from 185 to 219 cm in 5.3 yr.

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