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Randall Stewart Wells

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The dissertation of
Randall Stewart Wells
is approved:

Adrienne L. Zihlman

Dean of the Graduate Division

STRUCTURAL ASPECTS OF DOLPHIN SOCIETIES

By Randall Stewart Wells

Though the social interactions of captive dolphins have been studied extensively, little is known about the structure or structural determinants of dolphin societies in nature. I examined 3 aspects of the structure of dolphin societies: (1) the population structure of free-ranging bottlenose dolphins (*Tursiops truncatus*), (2) the patterns of composition of social units of free-ranging bottlenose dolphins, and (3) the role of sexual behavior in social interactions between captive Hawaiian spinner dolphins (*Stenella longirostris*).

The bottlenose dolphin field studies were conducted along the central west coast of Florida as part of an ongoing study begun in 1970. Photographic identification, capture, sample, mark, and release operations, and behavioral observations from small boats were used to determine dolphin ranges and social patterns during 1980-1984. Behavioral interactions in a spinner dolphin colony at Sea Life Park, Hawaii, were examined during 1979-1981 relative to reproductive hormone concentrations of the colony members.

A resident community of about 100 bottlenose dolphins was identified. Socially, this community was relatively discrete from similar adjacent units. Within the community, schools were organized on the basis of sex, age, familial relationships, and reproductive condition. Females showed strong site fidelity; some individuals were seen in the area over more than 15 years. Different female groups used different core areas. Calves remained with their mothers for 3 years or

more, before joining schools of subadults. At least some females were recruited back into their natal groups upon reaching sexual maturity. At least three generations of related females were recorded from local groups. Several males remained within their natal community upon reaching sexual maturity. Adult males mostly remained within the community range, traveling as individuals or pairs from one female school to another. However, males occasionally left the community for up to several months, suggesting a mechanism for genetic exchange between communities. A promiscuous mating system was hypothesized.

In the captive spinner dolphin colony, the amount of time spent in heterosexual swimming associations did not vary predictably relative to reproductive hormone levels. However, several classes of sexual behaviors occurred significantly more frequently when hormone levels were highest.

My involvement with this research program began in 1970. It would be impossible for me to list here everyone who has had a significant influence on me or the direction of the research over the last sixteen years. I dedicate this volume to the many participants who have helped make the research program successful, and especially to:

Ken Norris, my disseration advisor, for sharing with me his enthusiasm for delving into the mysteries of nature, and for teaching me how to ask the right questions to reveal nature's truths;

Blair Irvine, who initiated the Sarasota bottlenose dolphin research, who gave me my start in this field, and who still gives his all to the research program;

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Sue Kruse, for her insights, her support, and her patience during the prolonged gestation of this work;

The members of the Sarasota bottlenose dolphin community. My experiences with these animals over the last sixteen years have greatly enriched my life. May the knowledge gained from this research be used to help improve the quality of their lives.

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POPULATION STRUCTURE OF BOTTLENOSE DOLPHINS

INTRODUCTION

Bottlenose dolphins (*Tursiops truncatus*) are distributed continuously throughout much of the species' range. Large, contiguous or overlapping home ranges and fluid schools (Wells et al. 1980) complicate the identification of population units and assessment of their discreteness. Traditionally, individual population units of many mammals have been identified primarily through consideration of internal and external morphology of large samples of collected specimens. With the advent of legal protection for cetaceans, the need for information on population designations has become acute. This protection has also required the development of harmless approaches using living animals for obtaining the requisite information. This paper examines the results of one approach that has been developed over the past fifteen years: the integration of genetic and long-term observation data from individually distinctive free-ranging bottlenose dolphins.

There has been much confusion, historically, over species, race, and population designations for members of the genus *Tursiops*. Twenty specific names had been applied to *Tursiops* specimens from around the world by the turn of the century (Hershkovitz 1966). The accepted number of species has been revised downward in recent years, as more material has become available. One widely accepted school of thought holds that there is one species worldwide, *T. truncatus*, with sharply defined geographical races (Mitchell 1975, Rice 1977, Leatherwood and Reeves 1978, 1982, Walker 1981, Duffield et al. 1983). The races are distinguished on the basis of body length, skull measurements, tooth size and number, parasite loads, stomach contents, hematologies, and/or distribution. More taxonomic work is clearly needed.

There is general agreement that at least two forms, coastal and offshore, exist in many areas, and that primarily a single form of *T. truncatus* regularly inhabits the coastal waters of the southeastern United States. Population designations within this coastal form are problematic. In 1975, Odell, Siniff and Waring reported that "...there is no evidence to suggest that there is more than one population of *Tursiops* in Florida."

The term "population" has been defined in a number of ways. For the purposes of this paper, a population (or stock) is considered to be a single breeding unit characterized by relatively high gene flow within the unit and generally low gene flow with adjacent units (after Perrin et al. 1985). The limited ranges reported for bottlenose dolphins from several recent studies along the coast of the southeastern United States (Irvine and Wells 1972, Asper and Odell 1980, Shane 1980, Irvine et al. 1981) suggest that gene flow may be restricted at several points. Thus, a number of populations may exist along the southeastern U.S. coast.

Measurement of gene flow is not a simple matter, but recent advances are providing measures for assessing population membership, beyond the traditional comparisons described above. These techniques differ in the amount of specimen handling required and in the precision of the information they provide. Several of these techniques require specimens or biological samples. Analyses of mitochondrial DNA can provide measures of degrees of relatedness along maternal lines (Brown 1980, Ferris et al. 1981 a,b). Electrophoretic evaluation of blood proteins can provide genetic profiles using a number of different loci; large numbers of genetic profiles from one region allow estimation of gene flow (Duffield 1982, Duffield and Wells 1986). Chromosome banding patterns, from blood samples, can provide very precise measures of relatedness of individuals, but the technique is extremely expensive (Worthen 1981, Duffield et al. 1985).

Other means of assessing population membership do not require capture or handling. These include aerial photogrammetry and behavioral observations of naturally identifiable individual dolphins. Measurements from vertical photographs of dolphin schools can be used to discriminate between geographical forms which differ in length (Perryman 1980). Repeated sightings of dolphins with distinctive natural markings allow determination of home ranges and patterns of affiliation and interaction (Wursig and Wursig 1977, Norris et al. 1985). Given frequent resightings, and supplemental data from radiotracking or sightings of tagged animals (Wells 1978, Wells et al. 1980, Irvine et al. 1981, 1982), these behavioral data can be used to identify the ranges and compositions of dolphin population units. However, these behavioral data can not provide an actual measure of gene flow in the strictest sense.

The use of more than one approach increases the chances of adequately describing the structure and discreteness of a bottlenose dolphin population unit. In this study, long-term behavioral information on ranges and social associations of bottlenose dolphins along the central west coast of Florida are examined relative to genetic profiles from blood samples from many of the same dolphins, and dolphins from adjacent waters (see Duffield and Wells 1986, for details of the genetic analyses). The resulting synthesis is the first description of its kind for a population unit of small cetaceans.

METHODS

Field work with bottlenose dolphins along the central west coast of Florida was initiated in 1970, and it is still in progress. The research program has two main components: (1) temporary captures for marking, measurements, and biological sampling, and (2) observations, including radiotracking, photographic identification censuses, and focal animal behavioral observations.

Study Area

The study area extends southward approximately 160 km from St. Petersburg to Ft. Myers Beach, Florida (Figure 1). The area includes large bays such as Tampa Bay, Sarasota Bay, Gasparilla Sound, Charlotte Harbor, and Pine Island Sound, with their associated channels and shallow grassflats. These inshore waters are bounded on the west by a series of barrier islands, and communicate with the Gulf of Mexico through passes between the islands. Water depths vary from less than 1 m over the grassflats, to 10 m or more in the passes and at the western extent of the study area, about 5 km offshore of the barrier islands.

Most of the captures were concentrated in the 60 km long area off Bradenton and Sarasota. However, capture operations have been carried out from the southern edge of Tampa Bay, near Ruskin, through Pine Island Sound, near Ft. Myers Beach. Observations and photographic censuses have been conducted through the entire study area, but most of the effort has been concentrated in the area from the southern portion of Tampa Bay southward to Siesta Key off Sarasota.

Capture Operations

Dolphins were captured in the study area during 1970-1971, 1975-1976, and 1984-1985. The seine net technique described by Asper (1975) was used in each case to encircle small schools of dolphins in shallow (< 2 m deep) water. During 1970-1971, B. Irvine and I accompanied a commercial dolphin collector, and measured, sexed, tagged and released his "reject" animals. We tagged 12 dolphins in the northern half of the study area, and 18 in the southern half (Irvine and Wells 1972).

All of the captures during January 1975 - July 1976 were conducted in the northern half of the study area. Forty-seven individuals were measured, sexed, tagged and released. Ten of these dolphins carried radiotransmitters, and these were tracked for up to 22 days (Wells 1978, Wells et al. 1980, Irvine et al. 1981, 1982).

Seventy individuals were captured, measured, photographed, marked, and released during June 1984 - July 1985. Sixty of these were handled during our own June/July capture operations in the northern half of the study area. Blood samples were obtained from all of these. Estimated ages were determined from analyses of teeth from 32 individuals. Ten dolphins were tagged incidental to collection efforts by Dr. J. Sweeney in Pine Island Sound, Charlotte Harbor, and southern Tampa Bay during December 1984. Blood samples were obtained from nine of these dolphins, as well as from four other dolphins that were collected at that time. Blood samples were collected from the tail flukes of each dolphin, placed in sterile heparinized Vacutainers, and kept cool during storage and express shipment to Duffield's lab in Portland, Oregon. Electrophoretic analyses of the samples are described by Duffield and Wells (1986). Analyses of samples from June/July 1985 are still in progress; therefore, only samples collected prior to June 1985 will be considered in this report.

Observations

Observations of tagged dolphins during 1970-1971 occurred opportunistically, usually incidental to capture operations (Irvine and Wells 1972). During 1975-1976, observations were made from a 7.3 m vessel. The boat was used for radiotracking and systematic censuses over specified survey routes (Irvine et al. 1981). Photography was used extensively to confirm identifications of recognizable dolphins.

All of the new observation data reported here are the result of two kinds of efforts from small outboard powered boats (4.3 m - 5.2 m long) during April 1980 through January 1984, photographic censuses and focal animal behavioral observations. Photographic identification censuses used the survey routes established during 1975-1976 through the Bradenton-Sarasota region. These routes were expanded to include adjacent waters. All dolphin groups sighted were investigated. Date, time, location, total number of dolphins, number of calves, individual identifications, and behavioral and environmental data were recorded for each group. The dolphins' dorsal fins were photographed, using Kodachrome 64 color slide film in 35 mm cameras equipped with 200-300 mm telephoto lenses, powerwinders, and databacks. The best photographs of each individual were copied and placed in an identification catalog for subsequent comparisons. Dolphins were identified from natural markings, scars from previous tags, or freezebrands on their dorsal fins.

Focal animal behavioral observations involved moving with groups containing identifiable members for prolonged periods (typically >15 min). Behaviors of a focal dolphin and its associates were narrated into a tape recorder, and in a number of cases simultaneous hydrophone recordings of the animals' acoustic emissions were made as well. Members of groups observed in this way were also photographed to confirm identifications.

Sighting data were categorized and tabulated using the procedures of Irvine et al. (1981). Dolphins sighted within an area of approximately 100 m radius were considered for analysis purposes to be in a single school, as defined by Norris et al. (1985). "School" is thus equivalent to the term "group", as used by Irvine et al. (1981). Typically, the dolphins considered to belong to a given school were the only dolphins in sight at any given time, and they were engaged in similar activities. Sightings of dolphins were retabulated if the observations were more than one hour apart, or if the composition of a school changed. Initial school locations are presented on sighting maps.

RESULTS AND DISCUSSION

Vessel-based observations were conducted on 200 days during April 1980 - January 1984. These observations are distributed as follows: 1980 (22 days), 1981 (21 days), 1982 (77 days), 1983 (72 days), and 1984 (8 days). During this period, 1074 dolphin schools were recorded, containing a total of approximately 7806 dolphins. Four hundred sixty six individuals were identified, including 421 naturally marked dolphins and 45 previously tagged dolphins and their offspring. Of these, 116 were seen five or more times (up to 96 times); these accounted for 49% (3842 dolphins) of the total number of dolphins sighted. Data for these 116 dolphins, plus five individuals with fewer than five sightings each (one previously tagged animal, two distinctive dolphins with long sighting histories, and two calves of naturally marked females) form the basis for most of the analyses in this report (Tables 1,2,3,4).

Population Unit Definition

Two behavioral aspects are examined here to try to define population units: individual ranges of movements, and patterns of social association. Data for both of these aspects are derived from repeated sigtings of identifiable individuals. Nine of the 121 dolphins were first seen in 1970-1971; 40 were identified during 1975-1976, and the rest in 1980-1984. Of the 95 non-calves, 46 (48%) were seen in the inshore Bradenton-Sarasota waters, Tampa Bay, or the Gulf of Mexico during each of the four years of the study (Tables 1,2,3,4). These regular sighting patterns, and the movement patterns described by Irvine et al. (1981) suggested that a population unit could be defined in part on the basis of a limited geographic range, and that examination of home range patterns could be fruitful. Wells (1978) and Wells et al. (1980) showed that similar home range patterns and social association patterns were exhibited by dolphins of similar age and sex within one provisional population unit. This report expands upon these ideas through analysis of sightings over several years and from adjacent regions.

Wells (1978) determined that approximately fifteen sightings of any given dolphin from the Bradenton-Sarasota area were necessary before the size of the its home range no longer increased with each additional sighting. Seventy dolphins from Bradenton-Sarasota waters meet this criterion. The temporal regularity of sightings for these most frequently-seen individuals is indicative of the degree of residency in the areas most frequently surveyed. Forty (57%) of the seventy dolphins with at least fifteen sightings have been seen during each consecutive field session from their first identification through their last sighting (Tables 1,2,3,4). Provisional ranges were defined for the 51 dolphins with fewer than 15 sightings each, pending analyses of data collected after January 1984.

General patterns for bottlenose dolphin ranges along the central west coast of Florida are depicted in sighting maps. In broad terms, two primary "ecotypes" may be described. One ecotype included dolphins that tended to be found in deep (> approx. 4 m), open waters, and another for animals that tended to use shallow (< 4 m), complex inshore habitats. The first category included two general patterns of ranges, those of dolphins that mainly inhabited the Gulf of Mexico (Figures 2,3) and those that inhabited the deep waters of Passage Key Inlet and Tampa Bay (Figures 4,5,6). The third range pattern was exhibited by dolphins that used the shallow inshore waters near Sarasota primarily. These dolphins were categorized in finer detail as Manatee River dolphins (Figure 7), Anna Maria females (Figure 8), Palma Sola females (Figures 9,10), Sarasota females (Figures 7,11), adult males (Figure 12), transitional males (Figure 13), and subadult males (Figure 14). The sighting maps contain all of the sightings during 1980-1984 for each of the dolphins presented. Not all of the 121 dolphins are included in the maps, but each of the patterns described below is documented in the maps.

Gulf of Mexico Dolphins. All or most of the sightings of the dolphins in this category were in the Gulf of Mexico. Four of the 11 dolphins in Figures 2 and 3 were also seen occasionally inshore of the barrier islands, but 83% of the sightings of the 11 dolphins were in Gulf waters. The Gulf dolphins tended to be distributed along the length of the barrier islands, rather than concentrated at the passes. All of the dolphins were present during multiple years. Dolphin #89 was seen over a longer period than any other Gulf dolphin. It was seen repeatedly during 1975-1976 and 1980-1983, from the north end of Anna Maria Key to Siesta Key. The Gulf animals were seen from within 100 m of shore to several km offshore. Because surveys usually did not include waters south of Siesta Key or more than 5 km offshore, it is not yet possible to define boundaries for the home ranges of these animals, but we know that they were recurrent inhabitants of the waters immediately offshore of the barrier islands opposite Bradenton and Sarasota.

Passage Key Inlet - Tampa Bay Dolphins. Twenty-one non-calves were seen primarily in Tampa Bay, especially in the vicinity of Passage Key Inlet in the southwestern portion of the bay (Figures 4,5,6). Twenty of these were seen in multiple years; the remaining dolphin, #108, was identified for the first time in 1983. Three of these were first identified in the same waters in 1976. Seven of the dolphins were also seen north of a line from Egmont Key to Rattlesnake Key, thereby including the entire mouth of Tampa Bay in their ranges. However, surveys included these northern waters only 11 times, so range boundaries can not be defined. The waters near Passage Key Inlet were among the most frequently surveyed; thus, Tampa Bay sightings were inordinately clumped in that area. Bean Point Bar, to the west of the north tip of Anna Maria Key, is an exceptional area in that dolphins from a variety of regions come there to rest, especially during the winter months. In general, dolphins seen primarily in Tampa Bay tended to remain in the deeper waters and did not use the shallow grassflats and bays around the periphery of Tampa Bay to the same degree as did dolphins from the remaining categories (though they were seen in the shallow waters of Anna Maria Sound on occasion). Of particular importance for population unit designations is the lack of sightings of Passage Key Inlet - Tampa Bay (PKITB) dolphins in Palma Sola Bay, the Manatee River, and Terra Ceia Bay. Three of the PKITB dolphins were females, accompanied by calves.

The remaining categories include dolphins that use the inshore Sarasota - Bradenton waters that have been the primary study site since 1970. Because most of our marking and observation studies have occurred in these waters, more detailed information on the sexes, ages, and ranges are available for these dolphins than for the Gulf or PKITB dolphins. Thus, the following categories are more refined.

Manatee River. Six non-calves were seen repeatedly in the Manatee River - Terra Ceia Bay area (Figure 7) during 35 surveys through those waters in 1980-1984. Though these dolphins also used the shallow inshore waters to the south, they were unique in their repeated use of the Manatee River and Terra Ceia Bay shallow water regions. Two of the four adult females in Figure 7 (#79, 91) emphasized the Manatee River and Terra Ceia Bay in their daily movements, while the other two adult females (#28, 35) emphasized waters to the south. They were not seen in the deeper waters of Tampa Bay. Five of these were seen in multiple years; the sixth dolphin (#91) was first identified in 1983. Two of these were first identified several km to the south during 1975-1976.

Anna Maria Females. Seven female non-calves emphasized the waters around the northern tip of Anna Maria Key over all other areas (Figure 8). They were distinct from the PKITB dolphins in that they included Palma Sola Bay in their ranges, and they did not use the deeper waters of Tampa Bay. Like the Manatee River dolphins, there were very few sightings of the Anna Maria females off Sarasota. All of these dolphins were seen in multiple years; five were also identified in the same waters in 1975-1976. Two of these were captured in the same area and tagged in 1970-1971. Six were adult females, accompanied by calves at various times during the study.

Palma Sola Females. Fourteen adult females concentrated their activities in Palma Sola Bay and the waters around Anna Maria Key (Figures 9,10). Though their ranges were similar, these dolphins were distinguished from the Anna Maria females by their much greater emphasis of Palma Sola Bay, greater use of Sarasota waters, and less emphasis upon the waters around the north tip of Anna Maria Key. They were not found in the deeper waters of Tampa Bay, and there was only one sighting in the Manatee River. Their use of Gulf of Mexico waters was limited typically to the waters immediately adjacent to the passes. This category included the most frequently seen dolphins. All were seen in multiple years. Thirteen were also identified in the same area in 1975-1976; two of these were tagged here during 1970-1971. At least three of these females used this area as calves or subadults, and remained in the area after reaching maturity.

Sarasota Females. Three adult females swam through the shallow inshore waters off Bradenton and Sarasota, but did not clearly fit any of the previous patterns (Figure 11). Dolphin #52 was seen in multiple years around northern Anna Maria Key and Palma Sola Bay, and also around Big Sarasota Pass to the south. Dolphin #45 was mainly seen around Big Sarasota Pass and New Pass, the next inlet to the north. However, 16% of her sightings were in the vicinity of Longboat Pass, the next inlet to the north. She was seen during multiple years in the same areas, and she was originally tagged in 1976 near the northern tip of Anna Maria Key. Five of her six sightings away from the Big Sarasota Pass - New Pass area coincided with a severe red tide bloom during 1982.

Adult Males. Adult males often moved in schools independently of females, and their ranges did not appear to coincide directly with those of any particular female group in the Bradenton - Sarasota area (Figure 12). Rather, adult male ranges tended to include the ranges of several female groups. The males followed the pattern of the shallow water females, with very little use of the deeper waters of Tampa Bay or the

Gulf. Four of the seven males shown in Figure 12 have been seen in Terra Ceia Bay or the Manatee River. Six of the seven used the waters off northern Anna Maria Key. All of them have been seen in Palma Sola Bay. Only two of the seven were recorded from the waters off Sarasota, but this is probably misleading. Five other dolphins are believed to be adult males because of their large size, their consistent associations with other adult males, their degree of scarring, and their lack of accompanying calves during multiple years of observation (Dolphins #39, 40, 43, 55, 60). All five of these dolphins have numerous records from Sarasota waters, and they ranged as far north as Passage Key Inlet or Terra Ceia Bay. All of the known adult males have been seen in multiple years. Four of the adult males were tagged in the same waters in 1970-1971, and again in 1975-1976. Dolphin #27 was first recorded from the area as a young calf.

Transitional Males. Transitional males were those that made the transition from subadult, through maturing, to adult age during 1980 - 1984 (see Wells 1986 for details of age class determination). All three of these males were first tagged as subadults during 1975-1976. These males ranged through all of the waters from southern Tampa Bay to Siesta Key (Figure 13), but they utilized Palma Sola Bay to a lesser extent, and the southern waters to a greater extent, than did the adult males. The ranges of the transitional males in 1980-1984 were similar to those of the same individuals in 1975-1976.

Subadult Males. The ranges of subadult males (=subadult or maturing, Wells 1986) were similar to those of adult males in that they do not emphasize any of the particular areas that distinguish the different female groups, but rather they include the ranges of a number of the shallow water females. The subadult male ranges did not appear to be as extensive as those of the adults. They were not seen in the Manatee River or Terra Ceia Bay, but they ranged from the southern edge of Tampa Bay to Big Sarasota Pass. The subadult males used Sarasota Bay more extensively than did any other group, but the regional segregation between adult and subadult males reported by Wells et al. (1980) was not as obvious as in 1975-1976. All of the subadult males were seen during multiple years. Two of the five were captured and tagged in the same area during 1975-1976. These two were calves swimming with their mothers regularly during 1975-1976.

Annual sighting frequencies varied, depending on the sex and age of the individual. A sighting rate was calculated for each of the most frequently seen non-calf individuals of known age and sex. These data were examined for each year of study for which data from multiple censuses are available, 1980-1983. The number of sightings of each individual was divided by the number of field days that included passes through the animals' ranges. The results (Table 5) show that any given female is likely to be seen on about one out of every three field days, adult males on one out of every 6-7 field days, transitional males on one out of every 5-6 field days, and subadult males on one out of every 3 field days. The difference between values for adult males and adult females was significant (Kruskal-Wallis test with Dunn's multiple comparison, $p < 0.05$). Assuming equal sightability of males and females, this may be interpreted as indicating that adult males have broader ranges than females. Table 2 shows that some males were not seen for months at a time. Since we know that there is much overlap between male ranges and those of females, different sighting rates provide another line of evidence for males having larger ranges than females, and adult males having larger ranges than younger males. Additional support comes from 1975-1976 radiotracking results. Six males and four females were tracked. Two of the males were tracked 10-15 km to the north and to the south of the herd range, as defined by Irvine et al. (1981), but all of the females remained within the defined range.

Thus, three distinctive geographic patterns were evident for the ranges of bottlenose dolphins along the central west coast of Florida. Though there was some overlap between each of these ranges, most of the activities of the dolphins inhabiting each range occurred within regions of relatively exclusive use. Dolphins residing in any of these three ranges tended to have dolphins with similar ranges as their most frequent social associates, as shown in Table 6. Observations of schools containing residents of the same range were significantly more frequent than observations of schools including dolphins from more than one range.

Each of the three distinct assemblages of dolphins that inhabited similar ranges and that interacted socially more with each other than with adjacent assemblages was considered a "community". Because of the emphasis on geograhical and social relationships, these regional societies were similar to communities of killer whales (Bigg 1982) and chimpanzees (Goodall 1983), except that there is apparently more mixing between Tursiops communities than between killer whale communities.

The three communities that have been identified provisionally along the central west coast of Florida were distinguished as follows:

1. Gulf Community: Gulf of Mexico deep water residents, including, but not limited to, all of the dolphins depicted in Figures 2 and 3;
2. Passage Key Inlet - Tampa Bay (PKITB) Community: Passage Key Inlet - Tampa Bay deep water residents, including, but not limited to, all of the dolphins depicted in Figures 4-6;
3. Sarasota Community: Inshore, shallow water residents, including, but not limited to, the Palma Sola females, Anna Maria females, Manatee River dolphins, Sarasota females, adult males, transitional males, and subadult males depicted in Figures 7-14. The name "Sarasota" as opposed to "Bradenton" was applied because nearly all of the community members included waters off Bradenton and Sarasota within their individual ranges, whereas waters off Bradenton but not Sarasota have been used by PKITB dolphins. The adult males were tentatively placed in the Sarasota community, but their categorization was complicated by the fact that they occasionally disappeared for months at a time from the area considered to be the community's range. The various shallow water

female groupings were integrated into the Sarasota unit because their similarities in ranges and associates outweighed their differences. Collectively, these shallow water groups were much more similar to each other than they were to the Gulf or PKITB dolphins. With additional survey effort through the Gulf and Tampa Bay waters it may be possible to identify subunits such as those that comprise the Sarasota community, but such refinement is not possible with the data at hand.

To test the biological significance of these community designations, information on the genetic composition of each of the units was required. To this end, blood samples from 30 dolphins from the provisional Sarasota community, and six from southern Tampa Bay were analyzed electrophoretically (Duffield and Wells 1986). Water depth precluded use of the seine net capture technique with Gulf dolphins or dolphins in the deep water of Tampa Bay. The Tampa Bay samples were obtained from dolphins captured along the shallow southern fringe of Tampa Bay. Subsequent sightings and sighting reports of the sampled dolphins that were tagged showed the animals to remained in Tampa Bay outside of the range of the Sarasota community.

Electrophoretic analyses of five isozymes showed significant differences in gene frequencies between the Tampa Bay and Sarasota communities at three of the loci ($p=0.01$). Similar differences were found between the Sarasota community and samples from 11 dolphins from Charlotte Harbor and Pine Island Sound. Also, a unique bi-satellited chromosome marker has been reported from seven of the Sarasota community members; it has not been reported from any other *Tursiops* population (Duffield et al. 1985). In general, the Sarasota community showed a greater degree of heterozygosity than was shown in either Tampa Bay or Charlotte Harbor - Pine Island Sound. These genetic differences suggested that there was a biological significance to the behavioral community designations. However, the high degree of genetic heterozygosity indicated that the Sarasota community was not genetically isolated from other communities.

In summary, it was possible to identify at least three communities of coastal bottlenose dolphins from consideration of three criteria: individual ranges, social associations, and genetic analyses. Similar results are obtained from consideration of each criterion independently or combined. Three communities along the central west coast of Florida may be defined as follows. A Gulf community inhabits waters to the west of the barrier islands off Sarasota and Bradenton. A Passage Key Inlet - Tampa Bay community resides in Tampa Bay from at least as far east as Ruskin, westward to northern Anna Maria Key and St. Petersburg Beach. The Sarasota community inhabits the shallow inshore waters primarily to the east of the barrier islands, from Terra Ceia Bay southward to Siesta Key, off Sarasota. These ranges were used by the same individuals over many years. The ranges were not completely exclusive. Some overlap occurred along the borders, and occasional deeper penetrations of adjacent ranges by individuals have been recorded.

Community Structure

Long-term observations of the Sarasota community facilitated the characterization of some of the features of its structure. These features are site fidelity and habitat use, community size, age and sex composition, and group structure. The degree to which the structure of the Sarasota community is representative of other population units can not yet be determined. However, the presentation of the structure in this report will establish the basis for comparison as data from other population units become available.

Site Fidelity and Habitat Use. The long-term residency of many of the members of the Sarasota community is well established (Irvine et al. 1981). Tagged and naturally marked dolphins have been identified in the area over as many as 15 years. Seven (58%) of the dolphins originally tagged in the area in 1970-1971 have been seen in the area through at least mid 1985 (Dolphins #5, 7, 24, 27, 48, 58, 73). One naturally-marked dolphin (#60) first identified in 1970-1971 was seen through 1984. Thirty-two (68%) of the dolphins tagged during 1975-1976 have been seen during the 1980-1984 observations; all but one of these have been seen at least 12 times. Seventy-four percent of the previously tagged dolphins (less known mortalities prior to 1980) were identified during 1980-1984. These animals were still identifiable in spite of the fact that their tags were removed in 1976. Another four naturally-marked dolphins identified in the area in 1975-1976 were observed in 1980-1985. Twenty-seven previously tagged dolphins were observed in 1985. Again taking known and probable mortality (Dolphin #53 developed a widespread skin infection in 1982 and has not been seen since) into account, 66% of the previously tagged dolphins were seen 9-15 years after tagging. This value is probably biased downward. Three of the dolphins were young calves when first tagged in 1976, and the marked changes in fin morphology that accompany early growth may have made the animals unrecognizable between 1976 and 1980.

The members of the Sarasota community were year-around local residents. Sighting frequencies were calculated for each age/sex class during each of three seasons (April-June: 92 field days, August-November: 76 field days, December-March: 32 field days). These frequencies were calculated on the basis of number of sightings per individual per field day that included the waters used by the Sarasota community. Comparisons of sighting frequencies of the adult females, adult males, transitional males, and subadult males seen more than ten times each found no significant differences between seasons (Kruskal-Wallis test, $p > 0.05$).

All sightings of tagged or previously-tagged Sarasota dolphins during 1970-1985 have been within the inshore waters from Terra Ceia Bay to Siesta Key, and in Gulf waters within several km of the barrier islands. The only exceptions to this were the two males that were briefly radiotracked 10-15 km outside of the area during 1975-1976. The community home range as determined from data collected during 1975-1976 was shown in Figure 5 of Irvine et al. (1981). The only difference between the 1975-1976 range and the 1980-1984 range was in the inclusion of Terra Ceia Bay and the Manatee River in the latter. This difference probably existed primarily because during 1975-1976 surveys rarely included Terra Ceia Bay and the Manatee River, but it has since been found that some of the Sarasota dolphins used these waters.

Figure 15 shows sighting locations of the most frequently seen female (Dolphin #1) during 1975-1976 and 1980-1984. The extents of the ranges during those two periods were similar, but the degree of use of particular areas within the range were somewhat different. These differences may be explained as artifacts of the surveys. During 1975-1976 the surveys began near Longboat Pass, while many of the 1982-1983 surveys began in or near Palma Sola Bay, thereby increasing the frequency of coverage of those areas. Sighting distributions of males during 1975-1978 (several incidental group sightings were made in 1977-1978) and during 1980-1984 were also similar (Figure 16).

Seasonal habitat use by the Sarasota community during 1980-1984 was similar to that reported by Irvine et al. (1981). During late autumn, winter, and early spring the dolphins were concentrated around the passes, channels, and coastal Gulf waters. The dolphins were found mostly over the shallow inshore waters during the rest of the year (Figure 6 in Irvine et al. 1981).

Differential use of the Sarasota community home range by different age and sex classes was reported by Wells et al. (1980). This was manifested by subadult males using the southern waters of the range to a much greater degree than did all other classes, and by very little use of the northern waters by these young males.

This pattern was not as clear during 1980-84. The young males made extensive use of the northern waters, and dolphins believed to be adult males were seen relatively frequently in the southern waters. The patterns of greater importance appeared to involve the sizes of male vs. female ranges, as described above. The females showed a high degree of fidelity to a fairly limited area. Subadult and transitional males visited the extremes of their ranges more frequently than did females.

Adult males traveled from female school to female school. Adult males sometimes disappeared for months at a time. If the adult male patterns are extrapolated from those observed in the study area, then it seems likely that when adult males were spending time in areas outside of the ranges of the Sarasota community females, they were perhaps visiting females in other communities. Thus, the community ranges described in this report reflect those of the female segment of the community to the greatest degree, with the adult males perhaps including several communities within their ranges.

Community Size. The number of dolphins in the Sarasota community seems to have been relatively stable over many years. Irvine et al. (1981), using Lincoln Index results from 35 survey days, estimated that the Sarasota community contained 102 dolphins (95% CL = 90-117) in 1976. The 1976 estimate was based upon sightings of tagged dolphins only, not naturally marked animals. Community size estimates for 1983 were calculated in two ways. A sample of 16 survey days in September 1983 was selected. For the most direct comparison with 1976, calculations were based on 27 previously tagged dolphins that were still identifiable in September 1983. Similar calculations were made using a larger data base which included all 74 tagged and naturally-marked members of the Sarasota community and their calves in 1983. Both a Lincoln Index and the Schnabel method (as presented in Overton 1971) were used with the September 1983 data (Table 7).

The Schnabel method, designed to work with series of observations, appeared to be a better estimater than the mean of repeated Lincoln Index measurements. While the point estimates for each treatment were similar, the Schnabel estimates offered greater precision. Likewise, the larger the base of identifiable dolphins was, the more precise became the estimate. The lower 95% CL for the Schnabel estimate using previously tagged dolphins only (71) was lower than the known minimum number of dolphins based on identifications (74). Thus, the best estimate of Sarasota community size during 1983 is considered to be the Schnabel point estimate of 98 dolphins (95% CL = 89-108), based on all identifiable community members, which was essentially the same as that calculated for 1976.

Community Composition. Sex and relative age composition of the Sarasota community during September 1983 can be described, albeit incompletely, from observations and captures through 1984. Table 8 summarizes the composition of the community based on the 74 identifiable dolphins used in the community size estimate. A length-frequency distribution based on all of the dolphins handled during 1975-1976 and 1984 is presented in Figure 17.

For the purposes of Table 8, sexes were determined either from handling during captures or from repeated observations of accompaniment by calves. Age designations were based on growth layer group measurements of teeth (Hohn 1980), known birth dates, known minimum ages, or body length relative to a maturity curve based on Sarasota dolphins (see Wells 1986 for details of age class distinctions). Females were considered adult if they had been observed to be accompanied regularly by a calf, and subadult if they were seven years old or younger and not regularly associated with a larger female. Males were considered adult if they were 10 years old or older, maturing if they were 8-9 years old, and subadult if they were less than eight years old and did not associate regularly with their presumed mothers. Calves were seen on all or nearly all of their mothers' sightings. All but one of the 17 known-age calves were three years old or younger. The exception was a male that was at least seven years old and still with his presumed mother on a regular basis, behaving in this association much like younger calves. Of the two calves of unknown age, one was born before the censuses began in 1980, and the other was seen with its mother when the mother was first identified in 1981.

Group Structure. The Sarasota community was comprised of a number of schools at any given time. Age and sex were important determinants of school composition (Wells 1978, Wells et al. 1980, Irvine et al.

1981). Familial relationships can also be included as determinants of school structure, based on examination of chromosome banding patterns (Duffield et al. 1985) and repeated observations of multiple generations within schools.

Some associations between members of the same age and sex classes were more frequent than others, and the animals often shared congruent home ranges. These groups of regular associates often persisted over many years. However, groups were not discrete, permanent, or of constant composition, and not all of the community members belonged to distinguishable groups. Three kinds of groups were seen most commonly: females and young, adult males, and subadults. Group structure is described in detail elsewhere (Wells 1986), and will only be described briefly below.

The most constant groupings were females with their young calves ($\leq$ 3 years old). Seventy-nine percent (23 of 29) of the females of the Sarasota community belonged to one of three groups. Group membership for these females meant having approximately 20%-70% of their sightings in common. The most evident, and most tightly-knit female groups in the Sarasota community included Palma Sola females (14 adults: #1, 2, 4, 5, 7, 8, 9, 10 ,14, 16, 22, 23, 50, 53), Anna Maria females (seven dolphins: #21, 24, 26, 42, 47, 48, 62), and Manatee River females (two adults: #79, 91). Within these female groups, groupings were often correlated with the presence and age of calves, with calfless females remaining together, and females with young calves of similar age often swimming together. Changes in reproductive status tended to change female affiliations within groups. As many as three generations of females have been observed within the same group, and four adult females (#5, 8, 14, 23) with a unique chromosomal structure were members of the same group, suggesting that there was a high degree of relatedness between members of a given female group.

Five adult females did not fit clearly into the groups described above. Four of these females (#28, 35, 52, 68) swam often with the designated groups, and their ranges were within the community range, but their associations with any particular female or group were not sufficiently frequent to constitute group membership. One female (#45) spent most of her time in the southern portion of the community range, but when the other females were in that area she swam with them, and she occasionally traveled to the northern portion and there swam with other females as well.

Adult males swam as individuals or formed very tight groups. Typically, they swam as pairs that were together on approximately 70%-95% of their sightings. These groups were frequently seen traveling, and moved from one female school to another.

Subadults formed groups that frequently interacted with other similar groups. These groups were composed mostly of males. This was probably because females tend to mature before males and are recruited into the breeding population (and therefore back into female groups) after a much shorter period of time than were males. In at least one case, a subadult male pair was formed of similar-age males (#3, 11) whose mothers were members of the Palma Sola female group. These males have remained as a tight unit, even beyond the time when both have reached sexual maturity.

Community Discreteness

Three features are considered here: mixing between communities, emigration or dispersal, and immigration. The first is brief, with eventual return to the original community, while the last two are considered to be long-term, single direction phenomena.

Mixing. Of 679 dolphin sightings including recognizable members of the Sarasota community, 113 (17%) also included identifiable dolphins that were not considered members of the community. Of these mixed schools, 42 contained members of the PKITB community, 28 contained members of the Gulf community (Table 6), and in the remaining cases the non-Sarasota dolphins could not be assigned to a particular community. Four additional cases involved mixing between PKITB dolphins and Gulf dolphins, in the absence of Sarasota dolphins.

The frequency of occurrence of mixed schools containing Sarasota community members varied seasonally (Chi-Square = 6.31, df = 2, $p < 0.025$). Mixing occurred throughout the year, but it was more frequent than expected during August - November, and less frequent during April - July. The higher incidence of mixing coincided with the autumnal shift in habitat use, when the Sarasota dolphins used the peripheral waters more, and the shallow inshore waters less (Irvine et al. 1981). Similarly, the lowest incidence of mixing occured during the primary breeding season and when the Sarasota animals concentrated their activities in the shallow inshore waters, away from the periphery. Thus, mixing between communities was more frequent in non-breeding contexts than when genetic exchange could have been occurring.

Most of the mixing (72%) occurred around the periphery of the Sarasota community's range -- in the Gulf of Mexico, in the passes, and along the southern edge of Tampa Bay -- in the waters shared with other communities. PKITB community members ($\geq$ 5 sightings each, predominantly in Passage Key Inlet and Tampa Bay) were identified in 48% of these mixed schools along the periphery. Gulf community members ($\geq$ 5 sightings, predominantly in the Gulf) were identified in only 22% of these peripheral mixed schools. However, Gulf dolphins were identified more frequently (32%:19%) in mixed schools deep within the Sarasota community range than were PKITB animals.

Mixing involved both sexes of Sarasota dolphins, but males were involved predominantly. The sex composition of schools including members of the Sarasota community was measured for both schools which were made up of Sarasota dolphins only, and for mixed schools, in the following way. The numbers of independent (non-calf) dolphins of known sex were scored for each sighting. The compositions were assessed on the basis of whether the sightings included Sarasota males only (considered here to be those identifiable males that were tagged and seen most frequently in the Sarasota community range), Sarasota females only, or both Sarasota males and females. The compositions of schools in which the only recognizable dolphins were Sarasota community members were compared to mixed schools with a chi-square contingency test (Table 9), and were found to be highly significantly different (Chi-square = 17.71, df = 2, $p < 0.001$). Sarasota males were identified in 54% of the schools in which only Sarasota dolphins were recognized, but they were identified in 74% of the mixed schools. Conversely, Sarasota females were identified in 78% of the schools in which only Sarasota dolphins were recognized, but they were identified in only 61% of the mixed schools. There was no significant difference in the sex compositions of mixed schools during the breeding season vs. outside of the breeding season.

In summary, 17% of the schools that included Sarasota dolphins also included dolphins that were not considered members of the Sarasota community. This mixing occurred predominantly along the periphery of the Sarasota community's range, in waters shared with other communities, and mostly during the season when the Sarasota dolphins moved from their interior waters to these peripheral waters. Mixing involved both sexes, but Sarasota males were recorded from significantly more mixed schools than were Sarasota females.

Emigration. The disappearance of a regular member from a given dolphin community may indicate either emigration or mortality. In the absence of a carcass or regular sightings of the individual in a new area, it is impossible to distinguish between the two possibilities. The case then must be considered simply a loss from the community. However, knowledge of the number of regular members that have disappeared and of the number of known mortalities can provide an upper limit to the emigration rate.

Emigration from the Sarasota community was assessed by examining the yearly presence and absence data for the dolphins under observation over the longest times -- those that were first identified during 1970-1976 (Table 10). Of the 49 dolphins listed in Table 10, 30 were still in the Sarasota community in 1983. One more was reidentified as a community member during the 1984 capture and sampling project. Of the remaining 18 missing individuals, carcasses of four males have been recovered, and one female became diseased, subsequently disappeared, and is believed to have died. Three of the missing dolphins were young calves when first identified in 1976, and morphological changes in their fins, associated with growth, could have made subsequent reidentification difficult. Another dolphin, an adult male marked during our first capture in 1975, was not reidentified after the capture, probably due to tag failure. No information is available on the disappearances of the remaining nine dolphins. As we handle more of the community members, we may reidentify some of the missing dolphins.

Thus, assuming no mortalities except those noted above, a maximum of 9-13 of 49 identifiable dolphins may have emigrated during the nine year period 1975-1983, providing a rough rate of 2%-3% per year. The assumption of a mortality rate of 1% per year (5 of 49 dolphins over 9 years) is probably unrealistically low; if so, then the emigration rate could be much less than 2%-3% per year. The stability of the female segment of the community, and the differential loss from the community (Table 10) indicate that males would probably be the most frequent emigrants. In any event, emigration does not appear to be a frequent occurrence.

Immigration. One measure of immigration into the Sarasota community is the rate of addition of new dolphins to the photographic identification catalogue. Figure 18 depicts the accumulation of recognizable non-calf members of the Sarasota community from April 1980 through January 1984. The total number of dolphins increased markedly through 1980, to 52 individuals; after 1980 the rate of increase tailed off, indicating a relatively closed community. The rapid increase during the 27 field days of 1980 was assumed to be due primarily to the initial establishment of the catalogue. During 1981 - 1984, ten dolphins (3 males:2 females:5 unknown but not observed with calves) were added to the catalogue, yielding a mean rate of increase of 5.7% per year (sd = 5.51, n = 3). This rate of increase included more than just immigrants, however. One of the ten additions was a male (#73) tagged in Sarasota waters during 1970 and 1976, but not reidentified until 1982.

Very subtle markings require higher quality photographs than do other marks, which in turn may require more field time before they are added to the catalogue. One dolphin (#23) with subtle marks was added in 1982. However, she was the oldest of seven animals with a highly distinctive bi-satellited chromosome structure (Duffield et al. 1985), and all six of the other animals, presumably descended from her or her close relatives, were long-term members of the Sarasota community. This suggests that her delayed addition to the catalogue may have been an artifact of the subtlety of her markings rather than a result of recent immigration. Of the balance of the ten additions, dolphins #64, 65, 99 and 107 were distinguished on the basis of relatively subtle markings.

Changes in distinguishing characteristics may account for some of the "new" dolphins. Most fin characteristics remained constant throughout the study, as has been noted in a similar study of Hawaiian spinner dolphins, Stenella longirostris (Norris et al. 1985). Calves typically had fewer marks than older individuals; nicks and notches in the dorsal fin tend to be accumulated after separation from the mother. The transition from an unmarked calf to a distinctive independent subadult would be difficult to document. The creation of a distinctive high notch in one subadult male (#03) was clearly attributable to a bite from a conspecific. Another dolphin, #31, was 7.5 years old when first identified in 1982. His distinguishing characteristics included a high notch similar to that of #03. One dolphin (#90) added in 1983 was first identified with very fresh multiple vertical slices through its dorsal fin, presumably from a boat propellor. These cuts have since healed, but the extent of the fin mutilation has precluded determination of its identity prior to the injury.

During the 109 field days after July 1982, there was very little increase in the number of dolphins in the catalogue (Figure 18). This low rate of change was consistent with the data on stability of the community ranges and membership over the entire period 1970-1985. It seems reasonable to assume that the 91 field days up through July 1982 were required to make the initial photographic captures of the vast majority of the community members, and that the changes in the catalogue thereafter were representative of the actual dynamics of the community. If so, then the three dolphins added to the catalogue after July 1982 yield a potential immigration rate of 3.2% per year. One of these three dolphins was the mutilated dolphin #90, which may or may not have already been a member of the community before the injury. Thus, immigration into the Sarasota community appeared to be infrequent.

SYNTHESIS AND CONCLUSIONS

Behavioral data on ranges and social associations indicate the existence of at least three adjacent communities of bottlenose dolphins along the central west coast of Florida, between St. Petersburg and Sarasota. Biochemical genetic studies support this differentiation, based on samples from two of the three communities (Duffield and Wells 1985). One of these, the Sarasota community, has been the focus of research during 1970 - 1985, while the other two, the Gulf and PKITB communities, have received more peripheral attention.

The Sarasota community was composed of approximately 100 individuals. These dolphins resided primarily in shallow inshore waters, as opposed to the deeper, more open waters used by the other two communities. The Sarasota community members appeared to be permanent residents of a stable range. Females demonstrated an extremely strong degree of site fidelity within the community range. Males occasionally left the range used by the Sarasota females for up to several months. Within the community, many of the dolphins swam as members of groups based on age, sex, reproductive condition, and familial relationships. Different female groups concentrated their movements within slightly different, but overlapping, home ranges. Male groups traveled from one female group to another.

The high degree of genetic heterozygosity measured within the relatively small Sarasota community (Duffield and Wells 1985) indicated that it was not a closed reproductive unit. Several lines of evidence suggested that females were not the primary vector for genetic exchange between communities. The strong site fidelity of the adult females (measured over more than 15 years in some cases) argued against them frequently carrying genetic material between communities. One female calf and three independent subadult females have been observed to remain within the community beyond sexual maturity; none have been observed to emigrate (but long distance emigrations would not have been detected). One of the mature females first identified as a subadult and four other females of three generations carried a rare bi-satellited chromosome marker (Duffield et al. 1985), indicating a high degree of relatedness. Thus, some females and their female offspring remained with a given community for much, if not all, of their lives.

Emigration and immigration did not appear to be major driving forces for maintaining high genetic variability within communities. Thus occasions of mixing between communities during the breeding season seem to offer the greatest potential for interbreeding.

Males appeared to be the most likely vector for exchanging genetic material between communities. Sarasota males remained with the community for much, if not all of their lives. However, the males mixed more frequently than females with members of other communities, and their occasional departures from the community range no doubt placed them in contact with members of other communities.

Conversely, many of the non-calf dolphins from other communities observed in mixed schools with Sarasota females during the primary breeding season appeared to be males (based on large size, heavy scarring, and/or consistent lack of an accompanying calf). Eleven of 22 cases of mixing with Sarasota females during April through July involved these possible males from other communities (3 Gulf: 10 PKITB). These possible males have each been seen 5 - 25 times over multiple years.

How dolphins of different genders and community origins typically come into contact seems clear from the behavioral observations. However, the actual frequency of genetic exchange between communities can not be assessed without additional information on Tursiops mating systems. Wells (1986) hypothesized that the Sarasota dolphins had a promiscuous mating system, but he cautioned that available information was insufficient to accurately define the mating system or amount of genetic exchange. Such information can be derived from comparisons of the genotypes of calves, mothers, and potential fathers from blood samples.

What kind of a population unit is a community? The high degree of genetic heterogeneity in the Sarasota community, and the movements of males between communities suggest that it does not meet the criteria for being considered a population, in the strictest sense of an absolutely closed reproductive unit. According to this interpretation, the Sarasota community is likely one of a number of communities which compose a population. The limits of such a population remain unknown. The continuous distribution of _Tursiops_ around the Gulf of Mexico coast theoretically allows genetic exchange between adjacent communities. This is based on the assumptions that such communities exist outside of the central west coast of Florida, and males elsewhere travel between communities and mate outside of their natal community.

However, the population definition of Perrin et al. (1985) allows for a less-than-absolute situation. They considered a population to be a single breeding unit characterized by relatively high gene flow within the unit, and generally low gene flow with adjacent units. Depending upon interpretation, the Sarasota community could be considered to meet these criteria for a population. The available genetic samples are too limited at this time to be able to define the population status of the Sarasota community with absolute certainty.

At the very least, the females of the Sarasota community form a stable, discrete, long-term breeding unit with extremely strong ties to a particular geographic range. The society is highly structured (Wells 1986), and it is based upon bonds developed early in life and maintained over many years. In many cases familial relationships appear to form the basis of persistent social associations.

How representative is the situation along the central west coast of Florida of *Tursiops* populations elsewhere? A number of references to *Tursiops* home ranges exist in the literature, from opportunistic sightings and systematic studies. These suggest that a regular home range may be a fairly common characteristic of coastal populations. Caldwell (1955) presented the earliest evidence of residency by a bottlenose dolphin. A naturally disfigured dolphin was reported repeatedly during a two year period from the inshore waters near Cedar Key, along the northern west coast of Florida. Essapian (1962) and Caldwell and Golley (1965) reported on an albino *Tursiops* seen repeatedly in Georgia and South Carolina waters. Connor and Smolker (1985) described a group of habituated *Tursiops* along the coast of western Australia which, according to local residents, had been coming to the same area for 20 years.

Systematic studies of coastal *Tursiops* along the east coast of Florida (Asper and Odell 1980; Odell and Asper 1982), Mississippi (Solangi and Dukes 1983), Alabama (B. Goodwin, pers. comm.), Texas (Shane 1977, 1980, Shane and Schmidly 1978; Gruber 1981), California

(Hansen 1983), the Sonoran coast of Mexico (L. Ballance, pers. comm.), Patagonia (Würsig and Würsig 1977, 1979) and South Africa (Tayler and Saayman 1972; Saayman, Tayler and Bower 1973) have all found some degree of residency for identifiable individuals.

Shane (1980) defined three major home ranges near Aransas Pass, Texas which were used seasonally by some of her 21 naturally marked dolphins and year-around by others. However, she believed that the ranges of most of the dolphins extended beyond her study area. Seasonal changes in dolphin population density were noted, with the highest densities in winter. An apparent boundary between the inshore waters and the Gulf of Mexico at passes was reported.

Gruber (1981) reported on three "extended herds", each occupying its own herd range in Matagorda Bay, Texas, based on observations of twenty naturally marked dolphins. She noted that virtually no interactions between the extended herds were ever observed. One of the naturally-marked dolphins from Shane's study area 95 km to the southwest was observed near Matagorda Bay. Dolphins rarely crossed an apparent boundary between inshore waters and the Gulf.

Würsig and Würsig (1977, 1978, 1979) observed 53 naturally marked dolphins in Golfo San Jose, Argentina, over a 21 month period. They identified an apparent northward limit to the dolphins' daily movements. However, on at least one occasion individuals were observed 300 km away from their study area, and they subsequently returned to the study area months later.

Hansen (1983) identified 123 dolphins off the southern California coast, 21 of which were seen five or more times over 16 months. He considered his study area to be an important part of a home range for some of the dolphins he identified, and of decreasing importance as a home range for the other dolphins based on how often they were seen. During the 1983 El Nino warm water incursion, several of Hansen's identified dolphins were photographically identified 750 km north of their "normal" range; they subsequently returned southward several months later (R. Wells and L. Hansen, pers. observ.).

Asper and Odell (1980) and Odell and Asper (1982) captured, obtained biological samples from, and marked 76 dolphins, and carried out a resighting effort in the Indian River complex of eastern Florida during 1979-1982. Their marked animals were never seen or reported outside of the river system, and biochemical genetic studies supported their conclusion that this was a very discrete population unit. They reported that a second population unit may exist to the south.

Solangi and Dukes (1983) captured, sampled and marked 53 dolphins and conducted a resighting program in Mississippi Sound during 1982. During the study, several marked individuals were observed or recaptured in the same waters, but subsequent resighting results are not available for consideration here.

Coastal bottlenose dolphins apparently exhibit a variety of movement patterns in different areas. Home ranges with well defined boundaries have been found in a number of locations, suggesting a pattern of discreteness similar to that found off the central west coast of Florida. Physical features such as water depth and channels between land masses appear to be important criteria in defining boundaries between population units. However, seasonal changes in dolphin densities or records of exceptional movements provide additional opportunities for genetic exchange in some areas. Thus, broad extrapolation from the situation on the central west coast of Florida to other regions would not be prudent.

How do communities of bottlenose dolphins along the central west coast of Florida compare to population units of other delphinids? The bottlenose dolphin society near Sarasota appears to be intermediate between the closed societies of killer whales off Vancouver Island and the apparently more open societies of spinner dolphins off the Kona coast of Hawaii. The killer whales live in pods of extremely stable composition. Interacting pods form communities, and different communities rarely mix (Bigg 1982). In contrast, while some spinner dolphins appeared to be residents and some associations between individuals were seen repeatedly, school size and composition were quite fluid (Norris et al. 1985). Even after over 200 days in the field, new spinner dolphins continued to be added to the identification catalogue at a fairly constant rate of about one dolphin per day (Figure 47 in Norris et al. 1985). In Figure 18, the rate of accumulation of new bottlenose dolphins in the Sarasota community catalogue became nearly asymptotic after about 27 field days.

Additional data on the identities and structures of other coastal population units would be desirable for the formulation of generalizations about discreteness. In this paper, I have attempted to demonstrate the effectiveness of combining behavioral observations with information on biochemical genetic factors for obtaining these data from living <u>Tursiops</u>. With slight modifications for specific research sites, this approach should be applicable to studies of coastal bottlenose dolphins over much of the species' range.

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Table 1. Numbers of sightings of naturally-marked, non-calf dolphins per four-month-long "seasons." A-J = April-July, A-N = August-November, D-M = December-March. Left-most column containing an entry indicates the first season in which a dolphin was sighted during 1980-1984.

	1980		1981		1982			1983				
ID #	A-J	A-N	D-M	A-J	A-N	A-J	A-N	D-M	A-J	A-N	D-M	TOTAL
29		1	2		3	12	13	2	9	7	3	52
37		6	2	2	6	5	5	5	4	5	2	42
39		3	3	1	1	9	3	3	8	7	3	41
40(a)		7	2	3	1	3	8	3	6	4	4	41
43(a)		7	1	3	1	3	8	3	6	4	4	40
55	1	4				14	8	2				29
59		2	4	1	3	5	2		2	4	2	25
60(a,b)		3	2	2	2	5	3	2	1		2	22
63	1	7	2	1	7	1						19
64						2			16	1		19
65					2	6		3	5	1	1	18
69		1	4	1	2	5				2		15
71(a)		5				3			5			13
76		5				3	1		2	1		12
77		1	1		1	1	4		1	2		11
80		2				5	1	1	1			10
81		1	1			4	1		2			9
82			1			5			2	1		9
83		4			1	1	2					8
84		2			2	1	1		1	1		8
85					1	2			1	4		8
87			2		1	3	1					7
88		2	1			4						7
89(a)		2			2	1	1			1		7
90									2	4	1	7
92						4	1		1	1		7
94				1		2	1		1	1		6
95					1	1	2		1			5
96	1					1	1	2		1		6
97						3		2		1		6
98		1					2		3			6
99						1	1	3			1	6
100		1			1	1	1			2		6
101				1		3					1	5
102		1			1		2	1				5
103						2		1	1	1		5
104		1				3	1					5
105			1			3				1		5
106		2				2			1			5
107							2		2		1	5
108										4	1	5
109				1	1		1		2			5
110					1	1	1			2		5
111		1				2	1	1				5
113(a)							1		1	1		3
114(a)					1				1			2
Fld.Days	2	17	8	6	10	48	29	11	36	20	13	200

a=Identified during 1975-1976.
b=Identified during 1970-1971.

Table 2. Numbers of sightings of female dolphins per four-month-long "seasons." A-J = April-July, A-N = August-November, D-M = December-March. Left-most column containing an entry indicates the first season in which a dolphin was sighted during 1980-1984. Calves are small dolphins which regularly accompany a larger female.

	1980			1981		1982			1983			
ID #	A-J	A-N	D-M	A-J	A-N	A-J	A-N	D-M	A-J	A-N	D-M	TOTAL
Calves												
61(a)									11	5	4	20
51(a)									14	16	4	34
20(a)						9	15	3	18	16	6	67
18(a)						19	15	3	16	11	6	70
25(a)						15	8	6	16	12	2	59
15(a)						18	12	4	19	13	9	75
13(a)		3		2	3	13	10	3	22	15	6	77
Tagged Non-Calves												
21	1	10	3	2	5	10	8	4	10	7	6	66
62(b)	1	6	2	1	7					1		18
2(b)	2	5	3	1	5	25	15	3	16	11	6	92
8(b)	1	6	2	2	4	13	10	3	22	15	6	84
45(b)		7	5			7	6	6	2	1	4	38
5(b,c)	1	10	3	1	7	15	8	6	17	15	9	92
23						18	8	6	18	12	2	64
35(b)		3	2	1	7	5	1	4	10	10	1	44
14(b)	1	8		1	4	13	9	2	23	8	7	76
16(b)	1	10	2	1	5	17	4	1	19	7	7	74
53(b,d)	1	2	3		3	14	9					32
42(b)		3	1	1	3	5	5	2	7	13		40
1(b)	1	9	3	3	5	18	12	4	19	13	9	96
9(b)	1	2	3	2	2	23	15	4	19	10	1	82
7(b,c)		9		2	6	16	8	1	19	17	8	86
22(b)	2	3	2	1	3	15	5	1	21	8	4	65
28(b)		5	1	2	1	5	2	2	14	16	4	52
48(b,c)		4		2	6	4	4	3	9	4	1	37
4(b)	1	6		3	5	19	15	3	18	16	6	92
32(b)		3	6		2	9	4		14	5	4	47
10(b)	1	3	2	2	4	17	8	3	19	13	8	80
26(b)		6	3	2	7	8	6	4	12	9	2	59
52		1	2		2	2	2		13	9	3	34
24(b,c)		7	3	1	8	15	7	3	9	8	2	63
Naturally Marked Non-Calves												
47(b)		6	3	2		8	3	2	5	8	1	38
50			3		1	10	9	4	3	4	2	36
68		4		1		4		3	1	2		15
72		1	2	1	3	1		1	3	1		13
75			2		2	5	1		2			12
79		1	1			3			3	2	1	11
91									4	2	1	7
93				1	2	1		1	2			7
Fld.Days	2	17	8	6	10	48	29	11	36	20	13	200

a=Born during 1980-1984.
b=Identified during 1975-1976.
c=Identified during 1970-1971.
d=Became diseased and disappeared.

Table 3. Numbers of sightings of male dolphins per four-month-long "seasons." A-J = April-July, A-N = August-November, D-M = December-March. Left-most column containing an entry indicates the first season in which a dolphin was sighted during 1980-1984. Calves are small dolphins which regularly accompanied a larger female.

	1980			1981		1982			1983			
ID #	A-J	A-N	D-M	A-J	A-N	A-J	A-N	D-M	A-J	A-N	D-M	TOTAL
Calves												
17(a)					4	17	8	3	19	13	8	72
12(a)				2	6	16	8	1	19	17	8	77
6(a)		10	3	1	5	15	8	6	17	15	9	89
30(b)		5	2	1	6	6	1	4	10	14	2	51
86(b)		5		2								7
Non-Calves												
44		1	1		3	12	6	1	8	7		39
36			2			11	5	3	11	7	3	42
49(b)		5	1	2	3	3	6	4	8	3	1	36
31						14	3	3	21	8	2	51
3(b)		13	3	1	6	23	11	4	19	10	3	93
11(b)		11	1		5	18	8	4	20	10	3	80
38(b,c)		9	2	1	7	2	1	5	6	7	1	41
56(b)		9		1	5	4	5		2	2		28
27(b,d)		6	2	2	2	9	2	4	14	7	5	53
74			1			3	4		1	2	1	12
78						5			6			11
70						3	1		7	4		15
58(b,d)	1	5	1	1	3	1			13	1		26
112(b,d)									1			1
41	1	5			2	6	3	3	9	8	4	41
34		4	3	1	1	11	3	4	9	7	3	46
73(b,d)						2	3		1	3	3	12
Fld.Days	2	17	8	6	10	48	29	11	36	20	13	200

a=Born during 1980-1984.
b=Identified during 1975-1976.
c=Died during 1984.
d=Identified during 1970-1971.

Table 4. Numbers of sightings of calves of unknown sex per four-month-long "seasons." A-J = April-July, A-N = August-November, D-M = December-March. Left-most column containing an entry indicates the first season in which a dolphin was sighted during 1980-1984. Calves are small dolphins which regularly accompanied a larger female.

	1980		1981			1982			1983			
ID #	A-J	A-N	D-M	A-J	A-N	A-J	A-N	D-M	A-J	A-N	D-M	TOTAL
120										2		2
67									4	13		17
119						1			2	2	1	6
19						21	15	4	19	10	1	70
57						5	9	4	3	4	2	27
118					1	1		1	1			4
115				1		1			2	1		5
33				2	3	8	6	4	12	9	2	46
116			2		1	5	1		1			10
54			2	2		8	2	2	5	8	1	30
117		10										10
121		4		1		1						6
46		7	5			7	6	6	2	1	4	38
66		3	1		3	5	5					17
Fld.Days	2	17	8	6	10	48	29	11	36	20	13	200

Table 5. Sighting rates for non-calf bottlenose dolphins of known age and sex, measured over the entire period 1980-1984. Units calculated are number of sightings/individual/field day.

Class	Mean	S.D.	n
Adult Females	0.33	0.121	23
Subadult Males	0.33	0.113	5
Transitional Males	0.18	0.036	3
Adult Males	0.15	0.090	7

Table 6. Chi-square analysis of social associations between dolphins inhabiting different ranges.

	No. of Schools that Included Residents of the Sarasota Range in Association with Residents of Each of the Following Ranges:		
	Sarasota	PKITB	Gulf
Observed	610	42	28
Expected	540	97	44

Chi-Square = 46.08, df = 2, p << 0.001

	No. of Schools that Included Residents of the PKITB Range in Association with Residents of Each of the Following Ranges:		
	Sarasota	PKITB	Gulf
Observed	42	75	5
Expected	97	17	8

Chi-Square = 692.88, df = 2, p << 0.001

	No. of Schools that Included Residents of the Gulf Range in Association with Residents of Each of the Following Ranges:		
	Sarasota	PKITB	Gulf
Observed	28	5	22
Expected	44	8	4

Chi-Square = 97.19, df = 2, p << 0.001

Table 7. Community size (N) estimates for the Sarasota community in September 1983, using a Lincoln Index and Schnabel's Method.

	Lincoln Index		Schnabel Method	
Marked Animal Base	N	95% CL	N	95% CL
Previously Tagged Dolphins (M=27)	90	12-168	83	71-96
All Identifiable Dolphins (M=74)	100	69-131	98	89-108

Table 8. Sex and relative age composition of the Sarasota community in September 1983; includes identifiable dolphins only.

Sex	Age Class				
	Adults	Subadult or Maturing	Calves	Undetermined	Total
Females	26	1	7	0	34
Males	9	5	4	0	18
Undetermined	0	0	8	14	22
Total	35	6	19	14	74

Table 9. Comparison of sex compositions of sightings containing only Sarasota dolphins vs. sightings of mixed schools.

	Males Only		Females Only		Both	
Kind of Group	n	(%)	n	(%)	n	(%)
Sarasota	122	(23%)	250	(47%)	164	(31%)
Mixed	39	(39%)	26	(26%)	35	(35%)

Table 10. Yearly presence and absence records for dolphins first identified during 1970-1976. The "xx" indicates years during which an individual was observed in the Sarasota community.

			Observation		Years			
Dolphin	1970	71	75	76	80	81	82	83
Females:								
48	xx			xx	xx	xx	xx	xx
05		xx	xx	xx	xx	xx	xx	xx
07		xx	xx	xx	xx	xx	xx	xx
24		xx		xx	xx	xx	xx	xx
14			xx	xx	xx	xx	xx	xx
04			xx	xx	xx	xx	xx	xx
16			xx	xx	xx	xx	xx	xx
01			xx	xx	xx	xx	xx	xx
28			xx	xx	xx	xx	xx	xx
47			xx	xx	xx	xx	xx	xx
09			xx	xx	xx	xx	xx	xx
02				xx	xx	xx	xx	xx
45				xx	xx	xx	xx	xx
08				xx	xx	xx	xx	xx
35				xx	xx	xx	xx	xx
42				xx	xx	xx	xx	xx
22				xx	xx	xx	xx	xx
32				xx	xx	xx	xx	xx
10				xx	xx	xx	xx	xx
26				xx	xx	xx	xx	xx
53				xx	xx	xx	xx[a]	
62				xx	xx	xx		
126			xx	xx				
124				xx				
125				xx				
Males:								
58	xx		xx	xx	xx	xx	xx	xx
27	xx	xx		xx	xx	xx	xx	xx
73	xx			xx			xx	xx
112	xx			xx				xx
49			xx	xx	xx	xx	xx	xx
11			xx	xx	xx	xx	xx	xx
38			xx	xx	xx	xx	xx	xx
56				xx	xx	xx	xx	xx
03				xx	xx	xx	xx	xx
30				xx	xx	xx	xx	xx
86				xx	xx	xx		
136	xx		xx	xx				
138	xx		xx	xx				
139	xx			xx				
130			xx	xx[b]				
129			xx	xx				
137			xx	xx[b]				
132			xx					
135			xx					
131				xx				
134				xx[b]				
133				xx[b]				
127				xx				
128				xx				

[a] =Became diseased and disappeared during 1982.

[b] =Died during 1976-1977.

Figure 1. Study area along the central west coast of Florida. Shading encloses the entire area where research has been conducted, but most captures and observations have occurred off Bradenton and Sarasota.

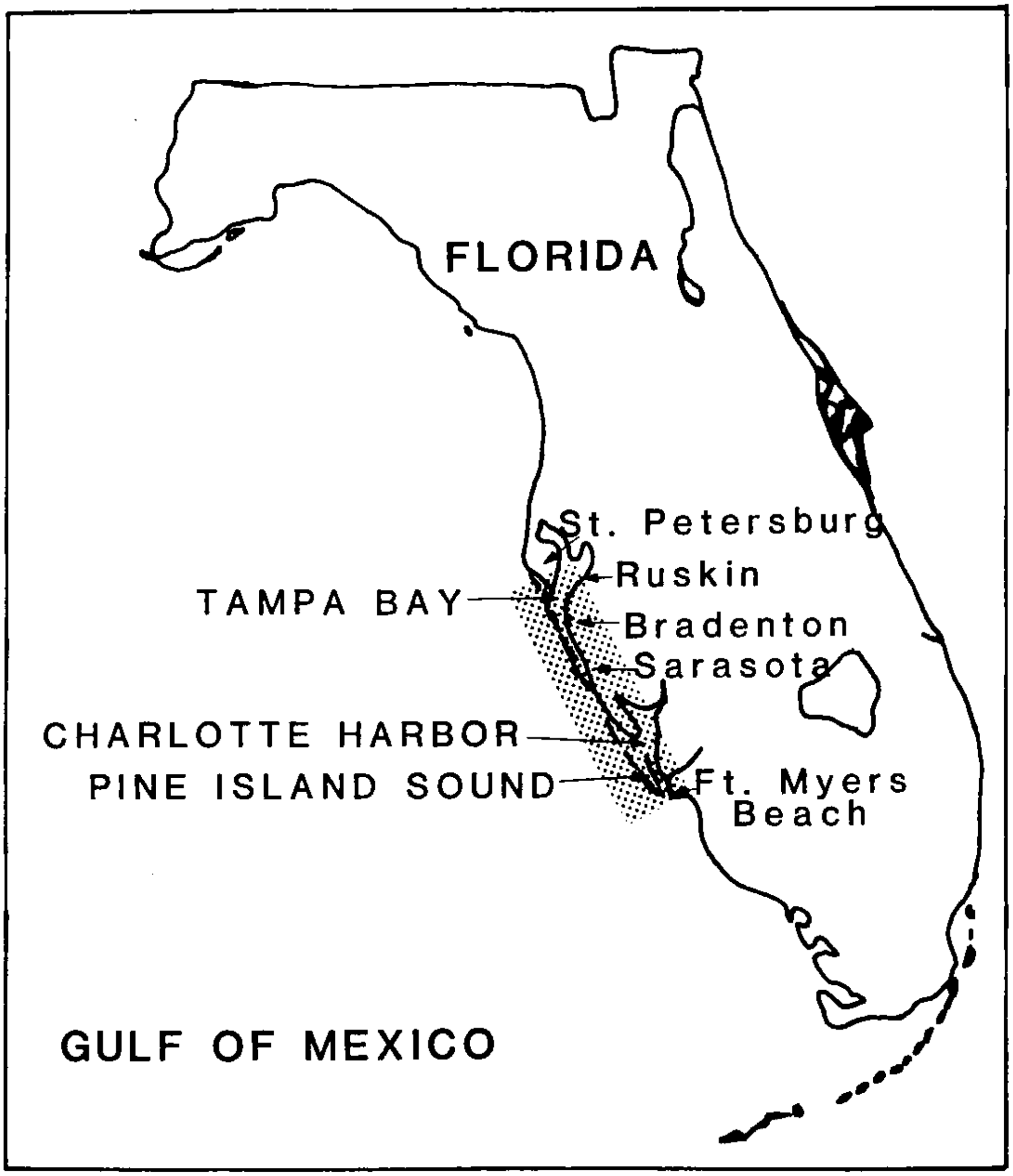

FLORIDA
St. Petersburg
Ruskin
TAMPA BAY
Bradenton
Sarasota
CHARLOTTE HARBOR
PINE ISLAND SOUND
Ft. Myers Beach
GULF OF MEXICO

Figure 2. Sightings of some of the dolphins seen primarily in the Gulf of Mexico during 1980-1983. One dolphin (#89) was also seen during 1974-1976.

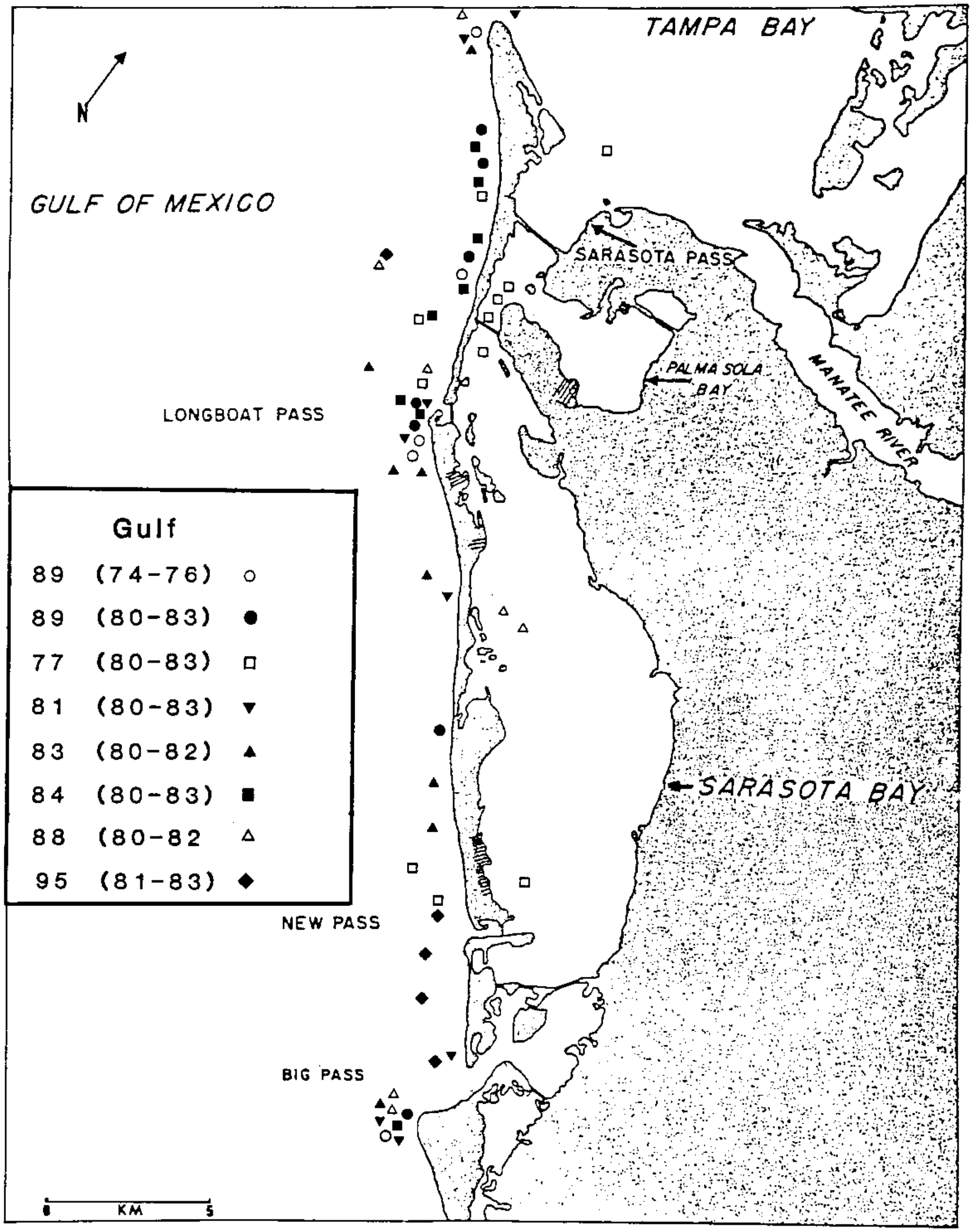

TAMPA BAY
N
GULF OF MEXICO
SARASOTA PASS
PALMA SOLA BAY
MANATEE RIVER
LONGBOAT PASS
Gulf
89 (74-76) ○
89 (80-83) ●
77 (80-83) □
81 (80-83) ▼
83 (80-82) ▲
84 (80-83) ■
88 (80-82 △
95 (81-83) ◆
SARASOTA BAY
NEW PASS
BIG PASS
0 KM 5

Figure 3. Sightings of some of the dolphins seen primarily in the Gulf of Mexico during 1980-1983.

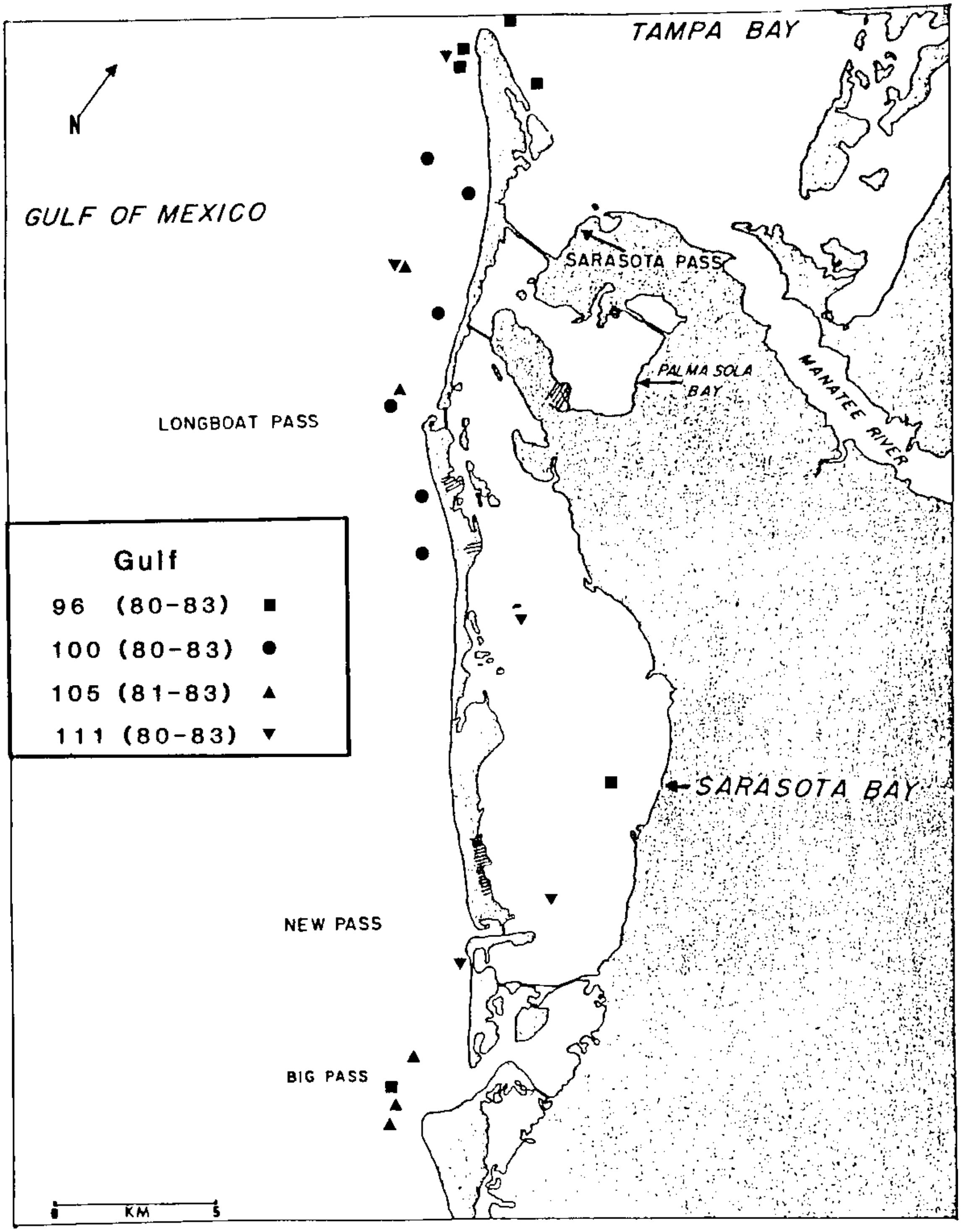

TAMPA BAY
N
GULF OF MEXICO
SARASOTA PASS
PALMA SOLA BAY
MANATEE RIVER
LONGBOAT PASS
Gulf
96 (80-83) ■
100 (80-83) ●
105 (81-83) ▲
111 (80-83) ▼
SARASOTA BAY
NEW PASS
BIG PASS
0 KM 5

Figure 4. Sightings of some of the dolphins seen primarily in Passage Key Inlet and Tampa Bay during 1975-1976 and 1980-1983.

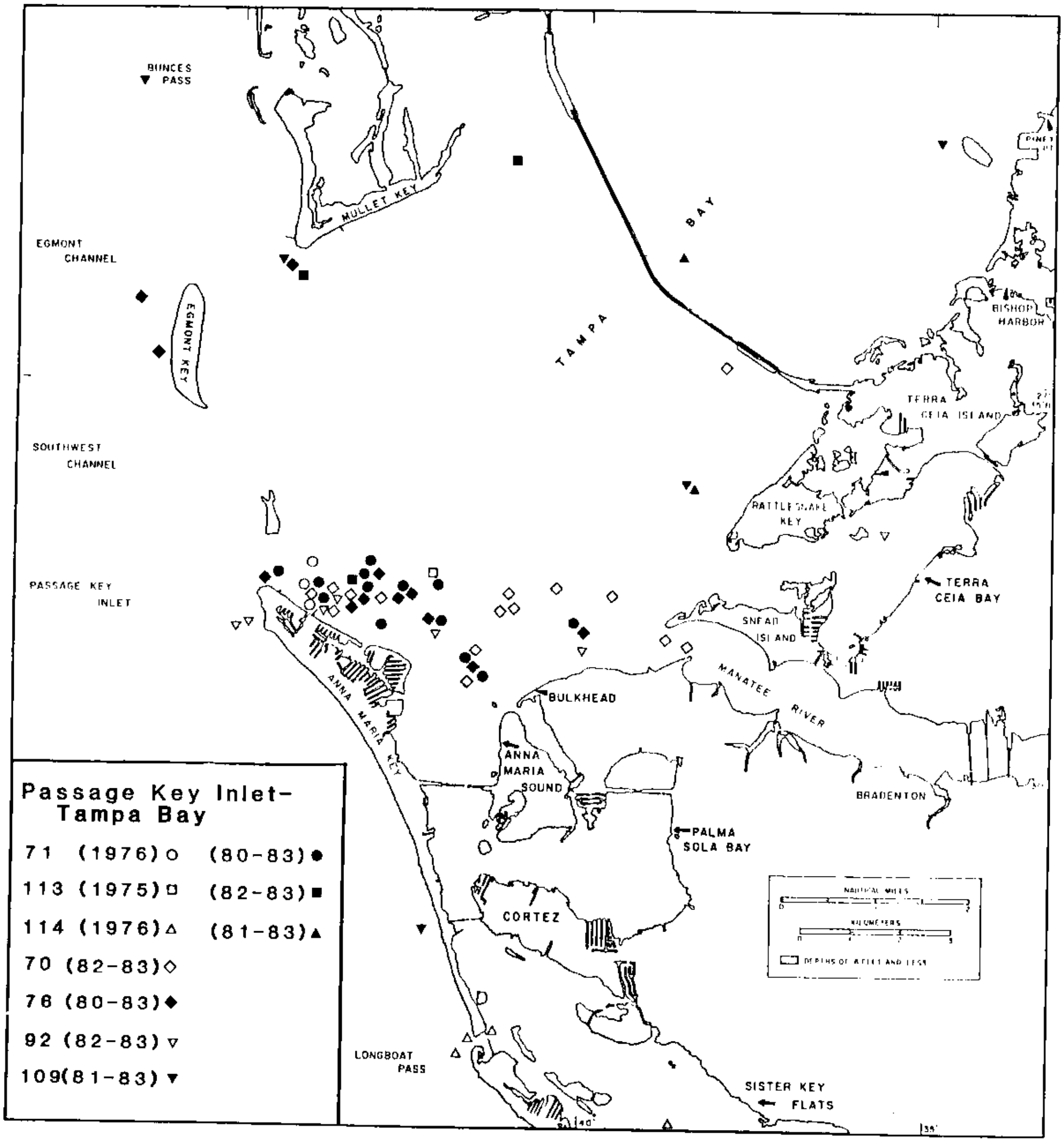

BUNCES PASS
MULLET KEY
EGMONT CHANNEL
EGMONT KEY
TAMPA BAY
SOUTHWEST CHANNEL
PASSAGE KEY INLET
BISHOP HARBOR
TERRA CEIA ISLAND
RATTLESNAKE KEY
TERRA CEIA BAY
SNEAD ISLAND
MANATEE RIVER
BULKHEAD
ANNA MARIA KEY
ANNA MARIA SOUND
BRADENTON
PALMA SOLA BAY
CORTEZ
NAUTICAL MILES
KILOMETERS
DEPTHS OF … FEET AND LESS
LONGBOAT PASS
SISTER KEY FLATS
Passage Key Inlet–Tampa Bay
71 (1976)○ (80-83)●
113 (1975)□ (82-83)■
114 (1976)△ (81-83)▲
70 (82-83)◇
76 (80-83)◆
92 (82-83)▽
109(81-83)▼

Figure 5. Sightings of some of the dolphins seen primarily in Passage Key Inlet and Tampa Bay during 1980-1984.

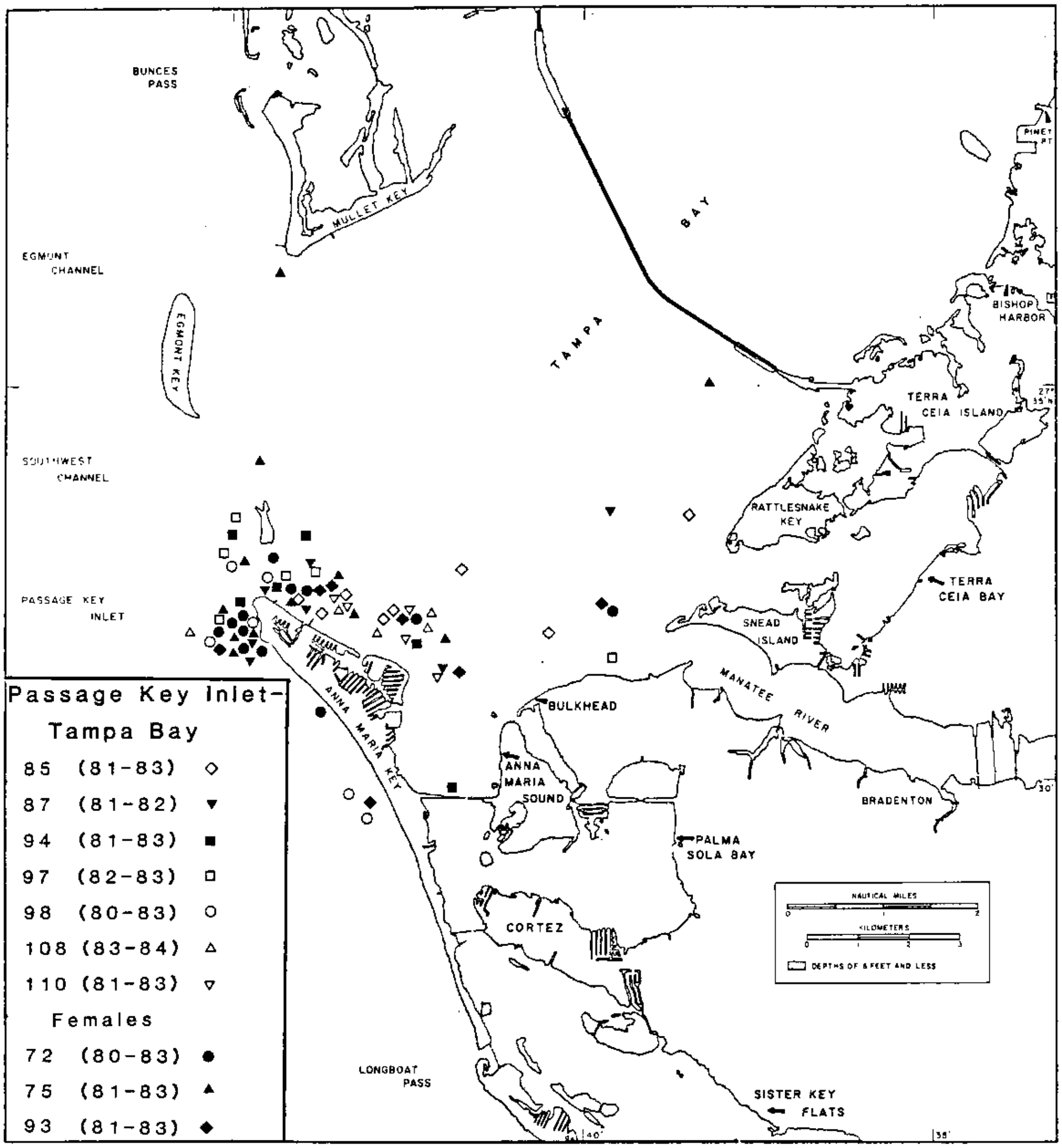

BUNCES PASS
MULLET KEY
EGMONT CHANNEL
EGMONT KEY
TAMPA BAY
PINEY PT
BISHOP HARBOR
TERRA CEIA ISLAND
27° 35'N
SOUTHWEST CHANNEL
RATTLESNAKE KEY
TERRA CEIA BAY
PASSAGE KEY INLET
SNEAD ISLAND
MANATEE RIVER
BULKHEAD
ANNA MARIA KEY
ANNA MARIA SOUND
BRADENTON
30'
PALMA SOLA BAY
CORTEZ
LONGBOAT PASS
SISTER KEY FLATS
40'
35'
NAUTICAL MILES
0
1
2
KILOMETERS
0
1
2
3
DEPTHS OF 6 FEET AND LESS
Passage Key Inlet-Tampa Bay
85 (81-83) ◇
87 (81-82) ▼
94 (81-83) ■
97 (82-83) □
98 (80-83) ○
108 (83-84) △
110 (81-83) ▽
Females
72 (80-83) ●
75 (81-83) ▲
93 (81-83) ◆

Figure 6. Sightings of some of the dolphins seen primarily in Passage Key Inlet and Tampa Bay during 1980-1984.

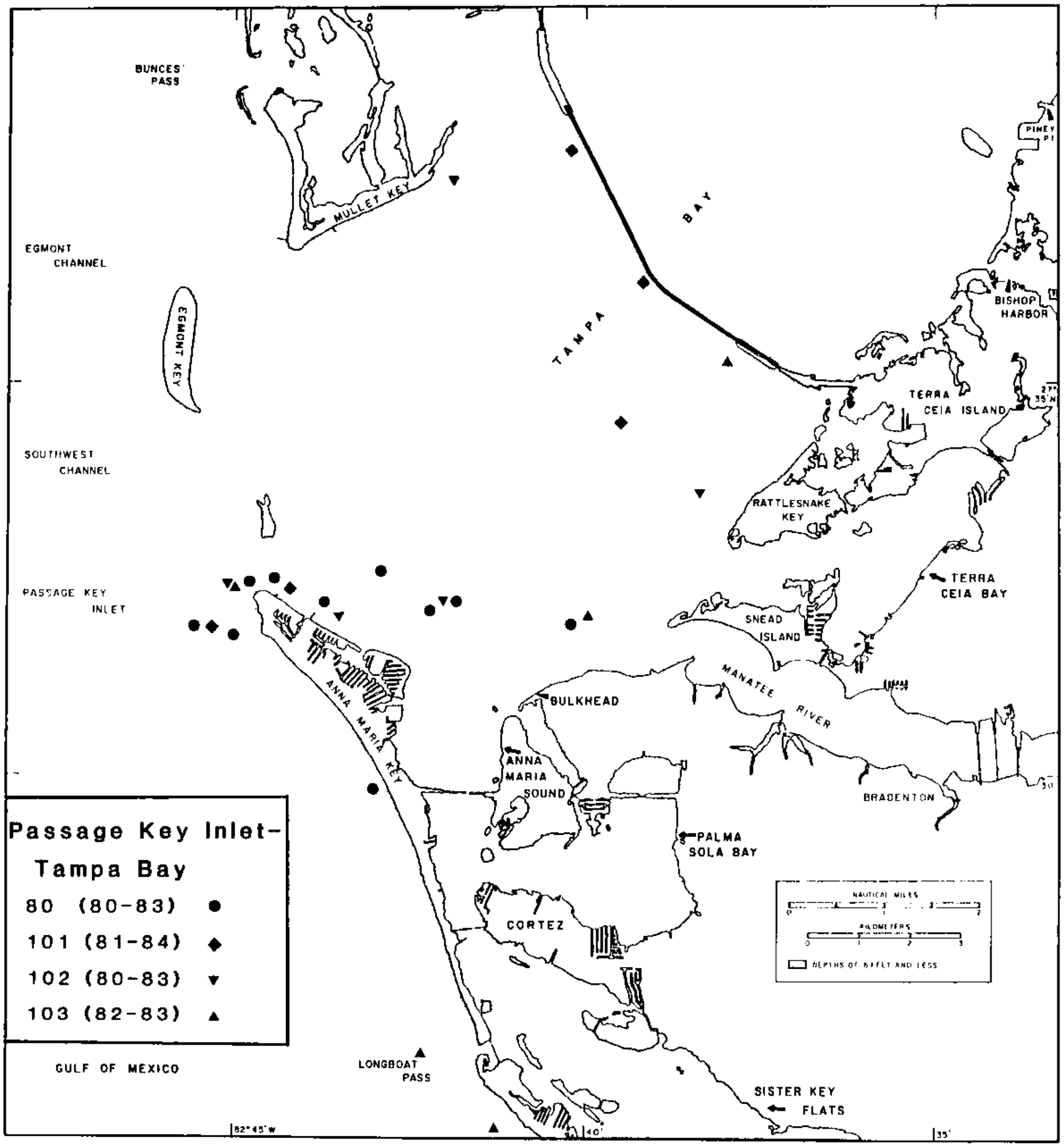
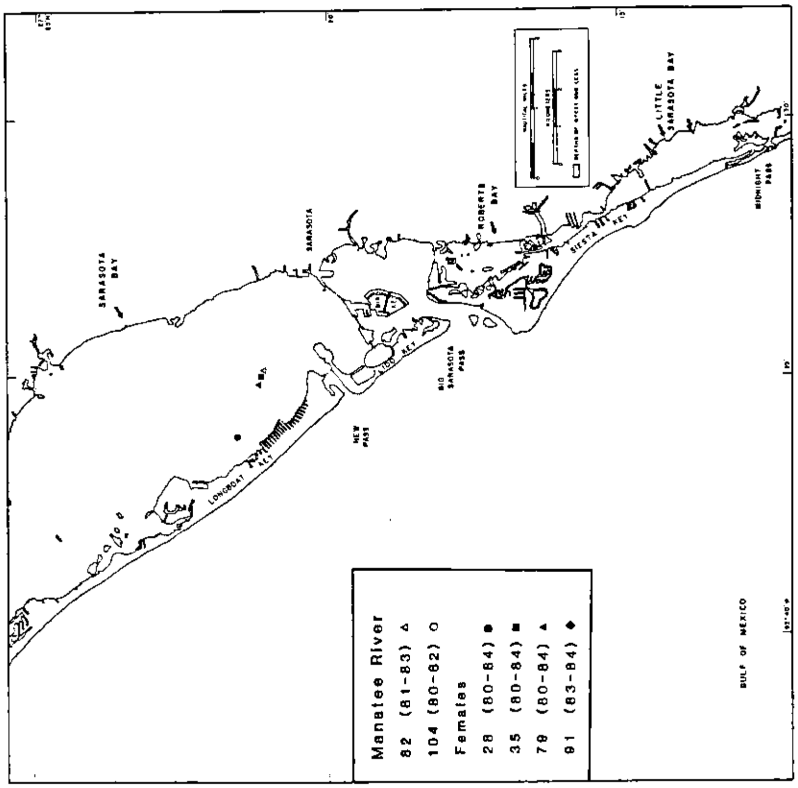

Passage Key Inlet–Tampa Bay
80 (80-83) ●
101 (81-84) ◆
102 (80-83) ▼
103 (82-83) ▲
BUNCES' PASS
MULLET KEY
EGMONT CHANNEL
EGMONT KEY
SOUTHWEST CHANNEL
PASSAGE KEY INLET
TAMPA BAY
BISHOP HARBOR
TERRA CEIA ISLAND
27° 35'N
RATTLESNAKE KEY
TERRA CEIA BAY
SNEAD ISLAND
MANATEE RIVER
BULKHEAD
ANNA MARIA KEY
ANNA MARIA SOUND
BRADENTON
PALMA SOLA BAY
CORTEZ
NAUTICAL MILES
KILOMETERS
DEPTHS OF 6 FEET AND LESS
GULF OF MEXICO
LONGBOAT PASS
SISTER KEY FLATS
82°45'W
40'
35'

Figure 7. Sightings of dolphins whose primary range included the Manatee River and Terra Ceia Bay. In this and subsequent figures, the northern section of the study area is displayed on the left, and the adjoining southern section is displayed on the right.


Manatee River
82 (81-83) △
104 (80-82) ○
Females
28 (80-84) ●
35 (80-84) ■
79 (80-84) ▲
91 (83-84) ◆
SARASOTA BAY
SARASOTA
ROBERTS BAY
LITTLE SARASOTA BAY
SIESTA KEY
MIDNIGHT PASS
BIG SARASOTA PASS
LIDO KEY
NEW PASS
LONGBOAT KEY
GULF OF MEXICO

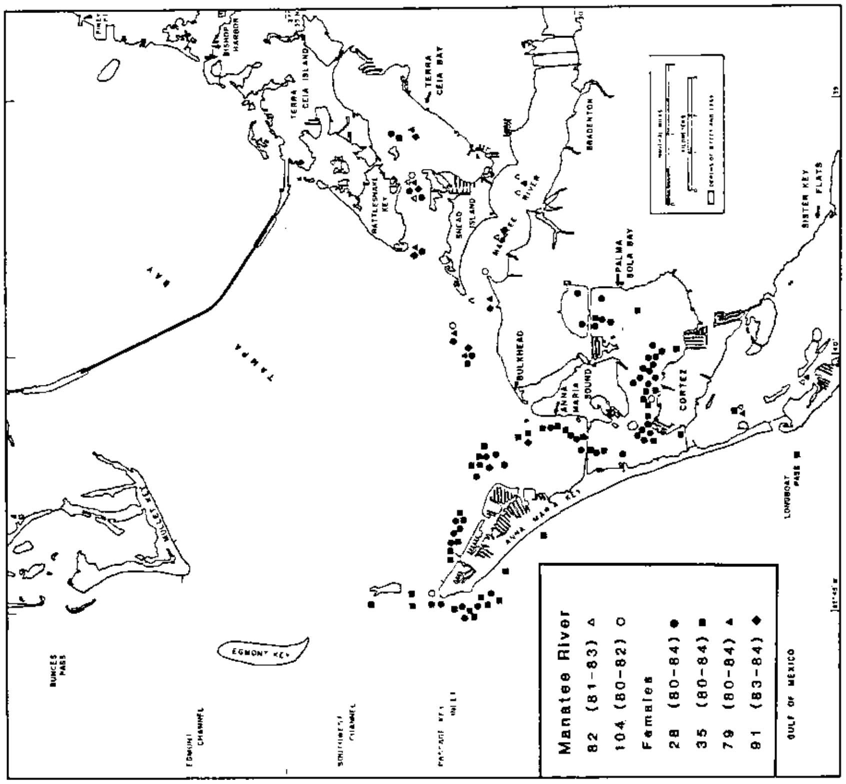
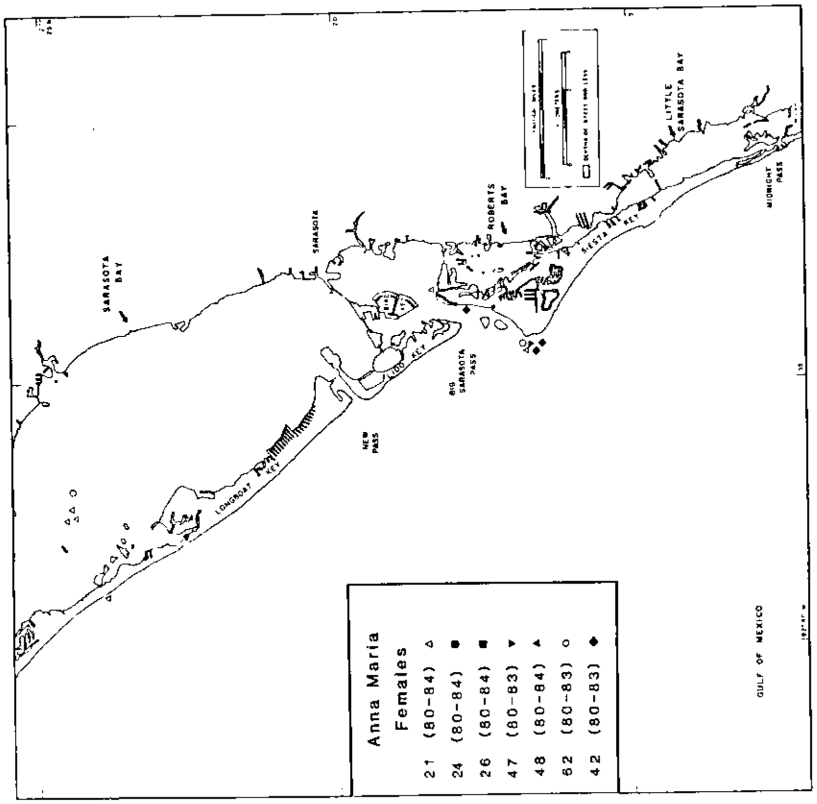

Manatee River
82 (81-83) △
104 (80-82) ○
Females
28 (80-84) ●
35 (80-84) ■
79 (80-84) ▲
91 (83-84) ◆
BISHOP HARBOR
TERRA CEIA ISLAND
TERRA CEIA BAY
RATTLESNAKE KEY
SNEAD ISLAND
MANATEE RIVER
BRADENTON
PALMA SOLA BAY
BULKHEAD
ANNA MARIA SOUND
CORTEZ
ANNA MARIA KEY
LONGBOAT PASS
SISTER KEY FLATS
TAMPA BAY
MULLET KEY
EGMONT KEY
BUNCES PASS
EGMONT CHANNEL
SOUTHWEST CHANNEL
PASSAGE KEY INLET
GULF OF MEXICO

Figure 8. Sightings of Anna Maria females during 1980-1984.


Anna Maria
Females
21 (80-84) △
24 (80-84) ●
26 (80-84) ■
47 (80-83) ▼
48 (80-84) ▲
62 (80-83) ○
42 (80-83) ◆
SARASOTA BAY
SARASOTA
ROBERTS BAY
LITTLE SARASOTA BAY
LONGBOAT KEY
LIDO KEY
NEW PASS
BIG SARASOTA PASS
SIESTA KEY
MIDNIGHT PASS
GULF OF MEXICO

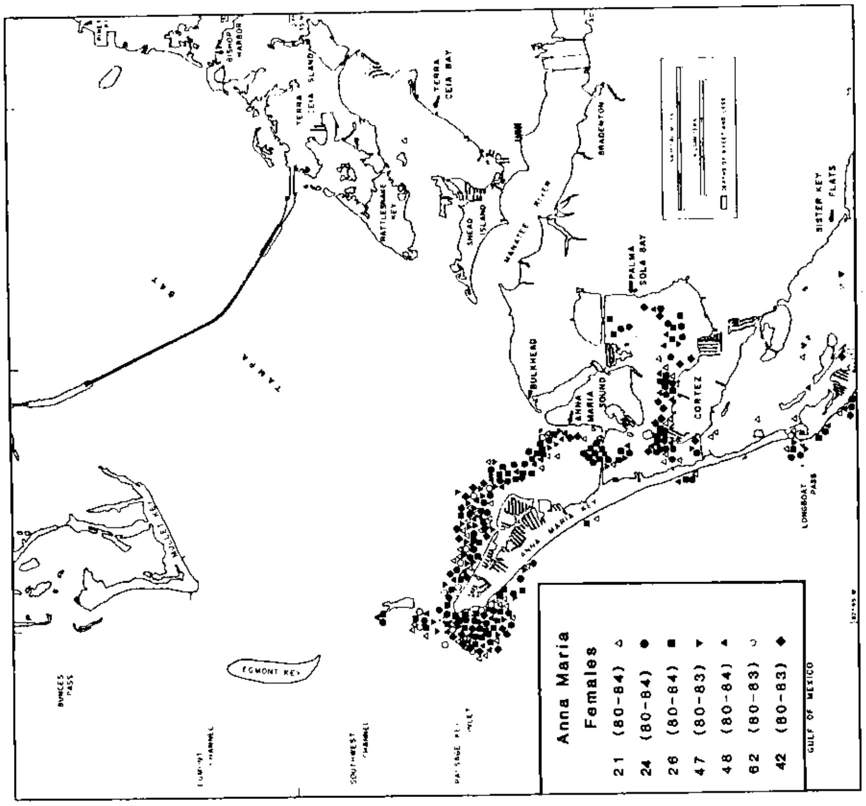
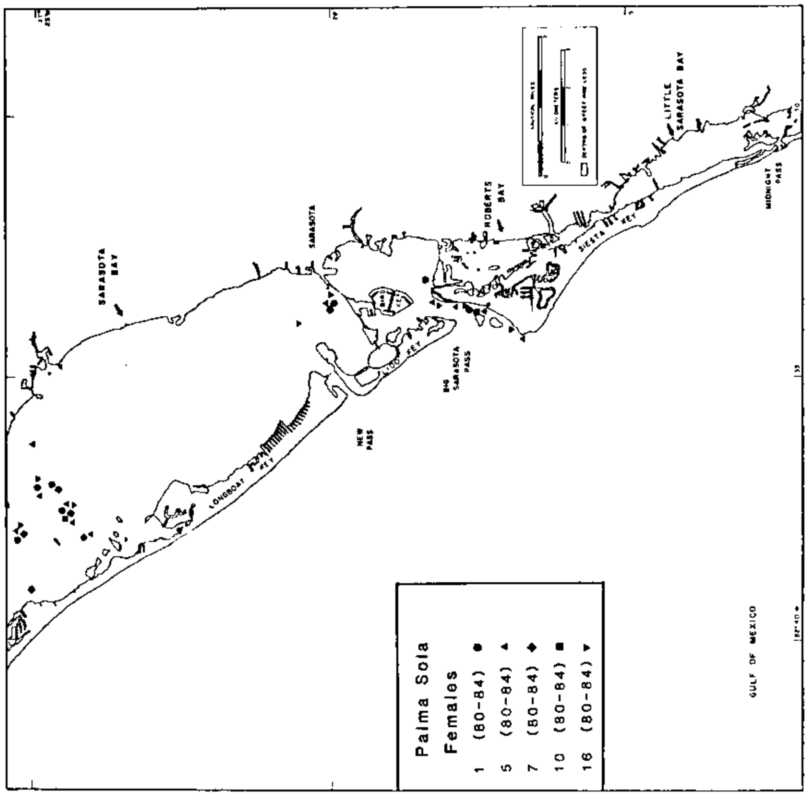

Anna Maria
Females
21 (80-84) △
24 (80-84) ●
26 (80-84) ■
47 (80-83) ▼
48 (80-84) ▲
62 (80-83) ○
42 (80-83) ◆
BISHOP HARBOR
TERRA CEIA ISLAND
TERRA CEIA BAY
BRADENTON
RATTLESNAKE KEY
SNEAD ISLAND
MANATEE RIVER
PALMA SOLA BAY
SISTER KEY FLATS
TAMPA BAY
BULKHEAD
ANNA MARIA SOUND
CORTEZ
ANNA MARIA KEY
LONGBOAT PASS
MULLET KEY
EGMONT KEY
BUNCES PASS
SOUTHWEST CHANNEL
PASSAGE KEY INLET
GULF OF MEXICO

Figure 9. Sightings of some of the Palma Sola females during 1980-1984.


Palma Sola
Females
1 (80-84) ●
5 (80-84) ▲
7 (80-84) ◆
10 (80-84) ■
16 (80-84) ▼
SARASOTA BAY
SARASOTA
ROBERTS BAY
LITTLE SARASOTA BAY
LONGBOAT KEY
NEW PASS
LIDO KEY
BIG SARASOTA PASS
SIESTA KEY
MIDNIGHT PASS
GULF OF MEXICO

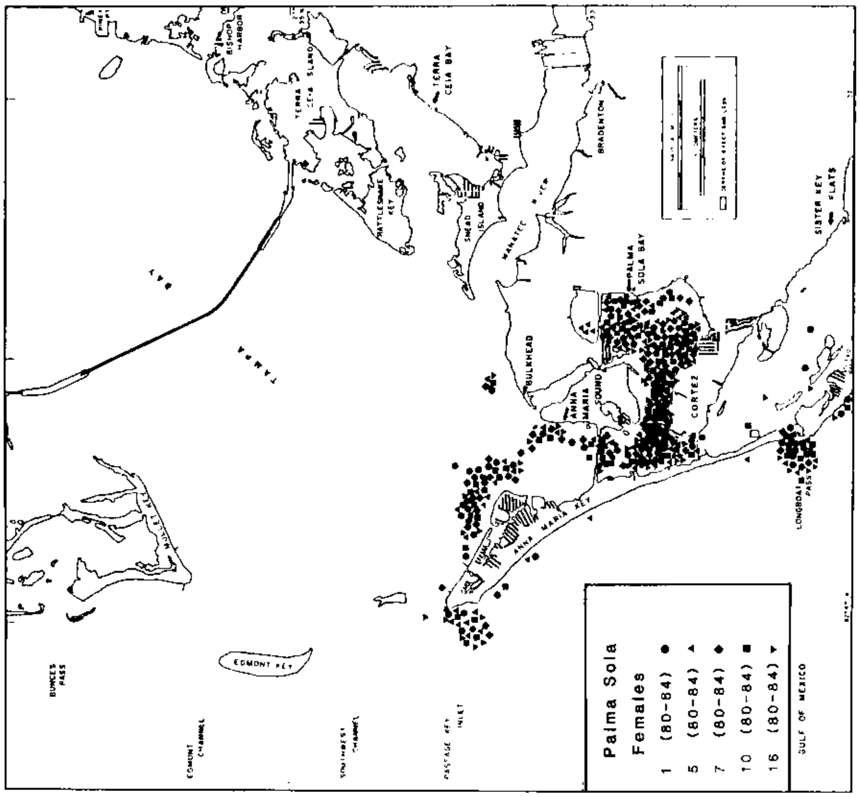
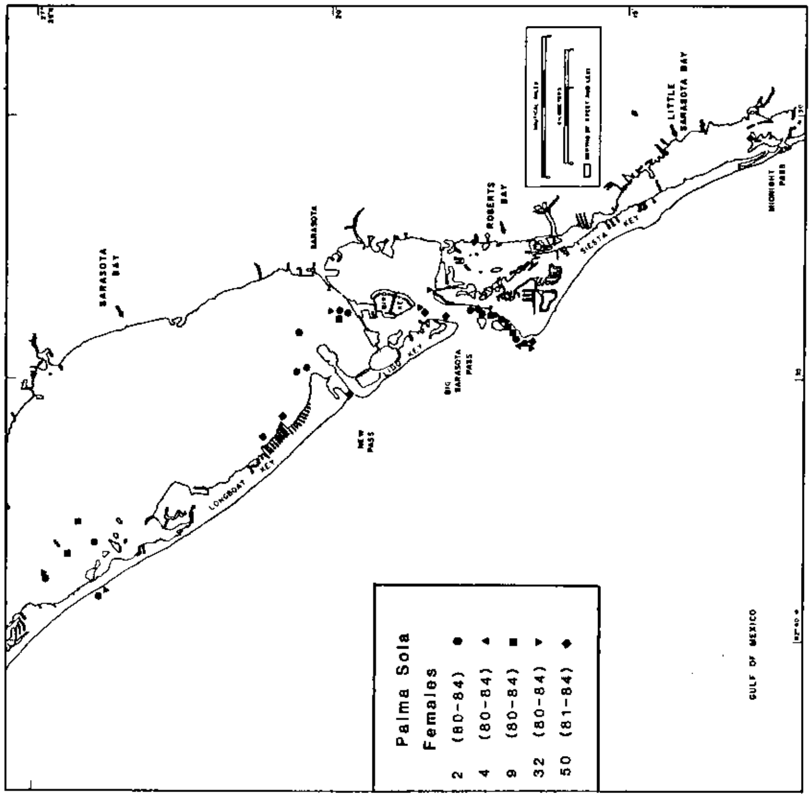

Palma Sola
Females
1 (80-84) ●
5 (80-84) ▲
7 (80-84) ◆
10 (80-84) ■
16 (80-84) ▼
BISHOP HARBOR
TERRA CEIA ISLAND
TERRA CEIA BAY
RATTLESNAKE KEY
SNEAD ISLAND
MANATEE RIVER
BRADENTON
PALMA SOLA BAY
BULKHEAD
ANNA MARIA SOUND
CORTEZ
SISTER KEY FLATS
LONGBOAT PASS
ANNA MARIA KEY
MULLET KEY
TAMPA BAY
EGMONT KEY
BUNCES PASS
EGMONT CHANNEL
SOUTHWEST CHANNEL
PASSAGE KEY INLET
GULF OF MEXICO

Figure 10. Sightings of some of the Palma Sola females during 1980-1984.


Palma Sola
Females
2 (80-84) ●
4 (80-84) ▲
9 (80-84) ■
32 (80-84) ▼
50 (81-84) ◆
GULF OF MEXICO
SARASOTA BAY
SARASOTA
ROBERTS BAY
LITTLE SARASOTA BAY
MIDNIGHT PASS
SIESTA KEY
BIG SARASOTA PASS
LIDO KEY
NEW PASS
LONGBOAT KEY

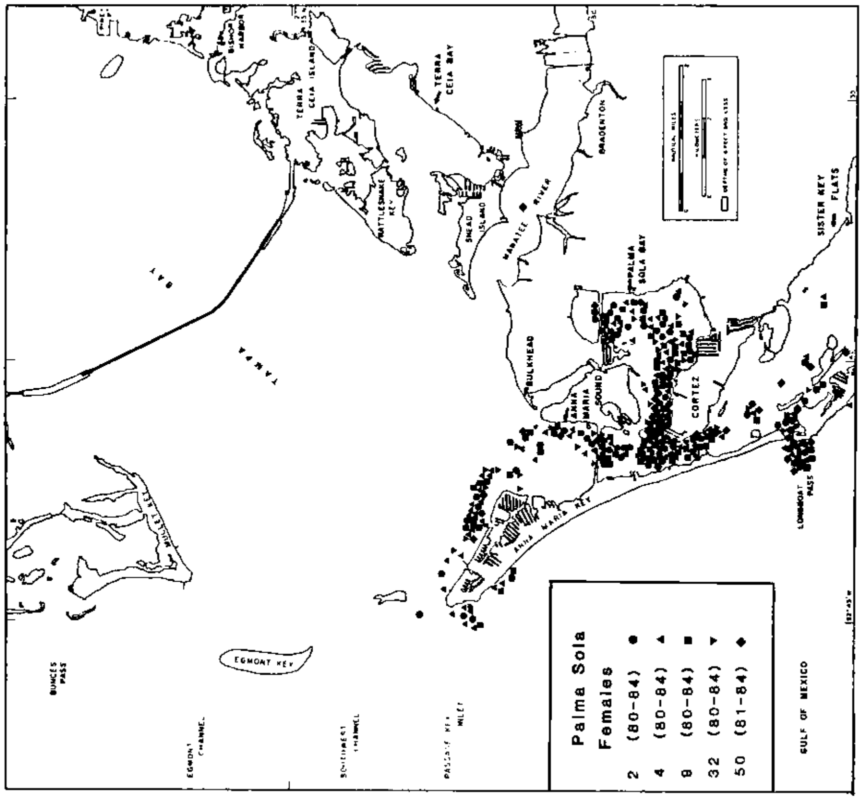
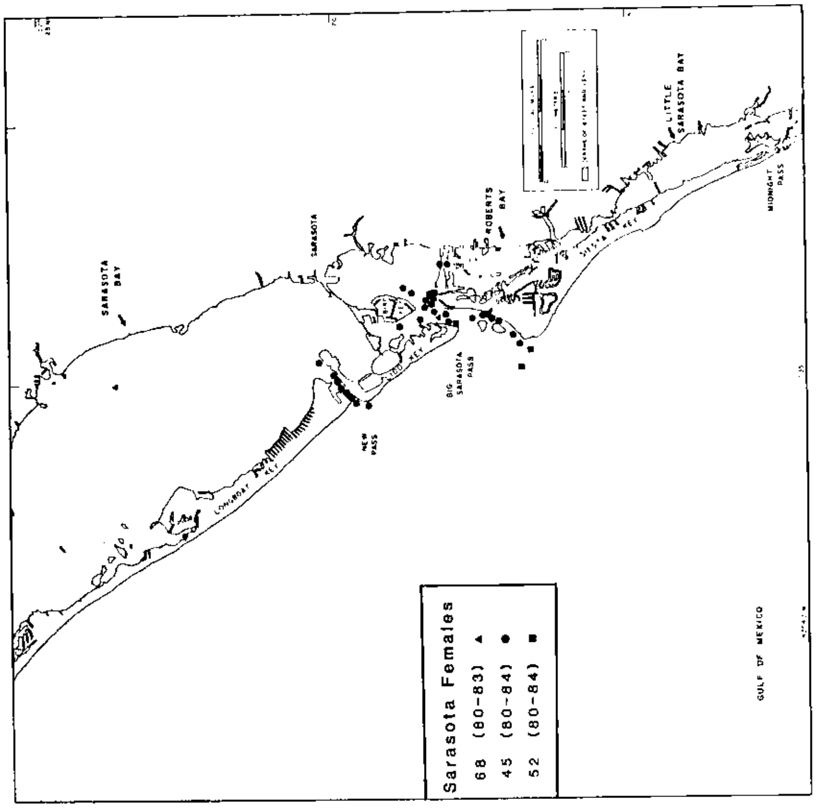

Palma Sola
Females
2 (80-84) ●
4 (80-84) ▲
9 (80-84) ■
32 (80-84) ▼
50 (81-84) ◆
GULF OF MEXICO
LONGBOAT PASS
ANNA MARIA KEY
CORTEZ
ANNA MARIA SOUND
BULKHEAD
PALMA SOLA BAY
SISTER KEY FLATS
BRADENTON
MANATEE RIVER
SNEAD ISLAND
RATTLESNAKE KEY
TERRA CEIA ISLAND
TERRA CEIA BAY
BISHOP HARBOR
TAMPA BAY
EGMONT KEY
BUNCES PASS
EGMONT CHANNEL
SOUTHWEST CHANNEL
PASSAGE KEY INLET
MULLET KEY

Figure 11. Sightings of some of the Sarasota females whose ranges did not follow any of the patterns described previously, during 1980-1984.


Sarasota Females
68 (80-83) ▲
45 (80-84) ●
52 (80-84) ■
SARASOTA BAY
SARASOTA
ROBERTS BAY
LITTLE SARASOTA BAY
MIDNIGHT PASS
SIESTA KEY
BIG SARASOTA PASS
NEW PASS
LIDO KEY
LONGBOAT KEY
GULF OF MEXICO

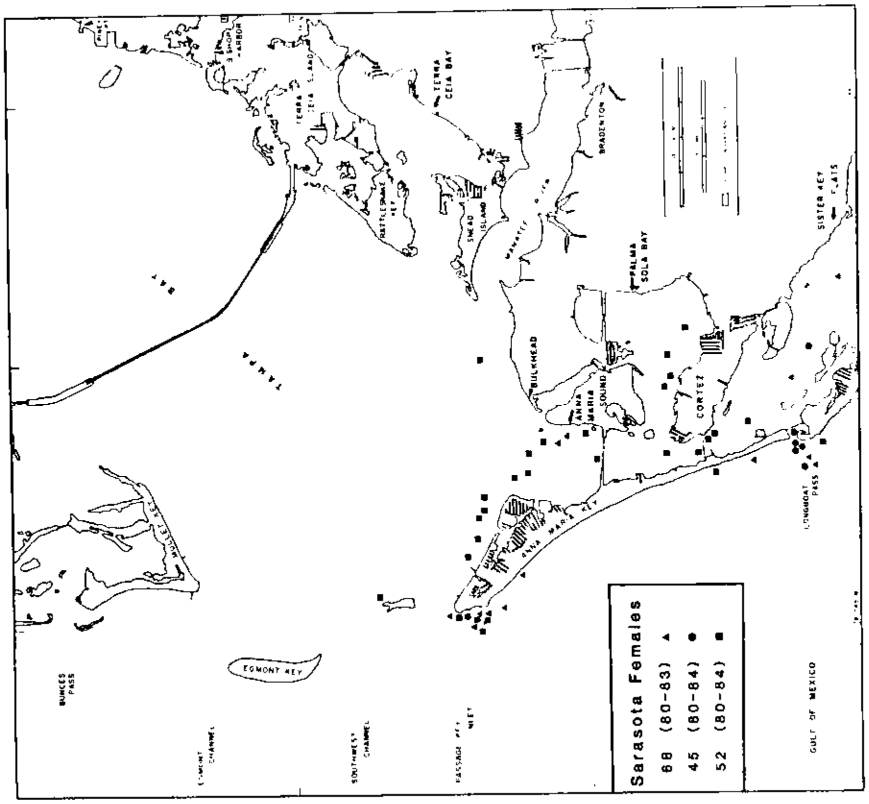
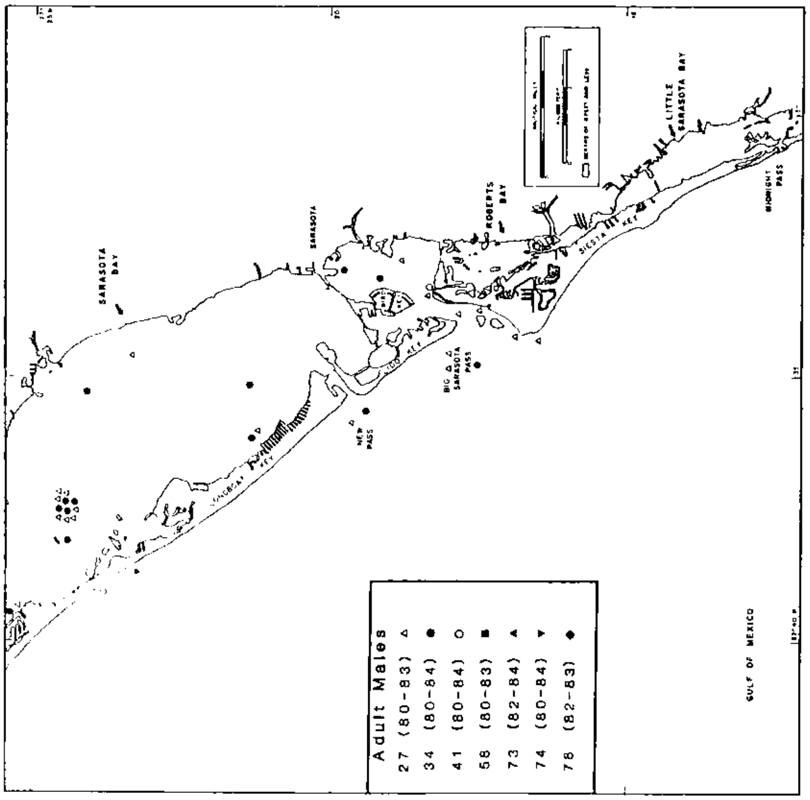

Sarasota Females
68 (80-83) ▲
45 (80-84) ●
52 (80-84) ■
BUNCES PASS
MULLET KEY
EGMONT KEY
EGMONT CHANNEL
SOUTHWEST CHANNEL
PASSAGE KEY INLET
TAMPA BAY
BISHOP HARBOR
TERRA CEIA ISLAND
TERRA CEIA BAY
RATTLESNAKE KEY
SNEAD ISLAND
MANATEE RIVER
BRADENTON
PALMA SOLA BAY
BULKHEAD
ANNA MARIA SOUND
CORTEZ
ANNA MARIA KEY
LONGBOAT PASS
SISTER KEY FLATS
GULF OF MEXICO

Figure 12. Sightings of adult males during 1980-1984.


Adult Males
27 (80-83) △
34 (80-84) ●
41 (80-84) ○
58 (80-83) ■
73 (82-84) ▲
74 (80-84) ▼
78 (82-83) ◆
SARASOTA BAY
SARASOTA
ROBERTS BAY
LITTLE SARASOTA BAY
LONGBOAT KEY
NEW PASS
BIG SARASOTA PASS
SIESTA KEY
MIDNIGHT PASS
GULF OF MEXICO

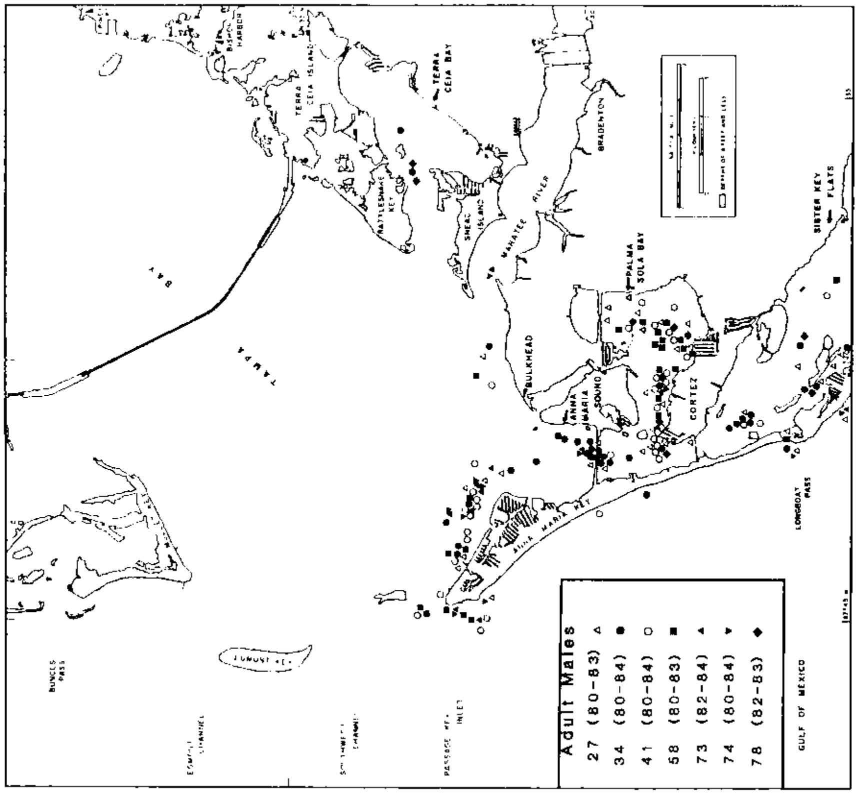

Adult Males
27 (80-83) △
34 (80-84) ●
41 (80-84) ○
58 (80-83) ■
73 (82-84) ▲
74 (80-84) ▼
78 (82-83) ◆
TAMPA BAY
TERRA CEIA ISLAND
TERRA CEIA BAY
RATTLESNAKE KEY
SNEAD ISLAND
MANATEE RIVER
BRADENTON
BULKHEAD
ANNA MARIA SOUND
PALMA SOLA BAY
CORTEZ
ANNA MARIA KEY
LONGBOAT PASS
SISTER KEY FLATS
BUNCES PASS
EGMONT KEY
PASSAGE KEY INLET
GULF OF MEXICO

Figure 13. Sightings of transitional males during 1980-1984.

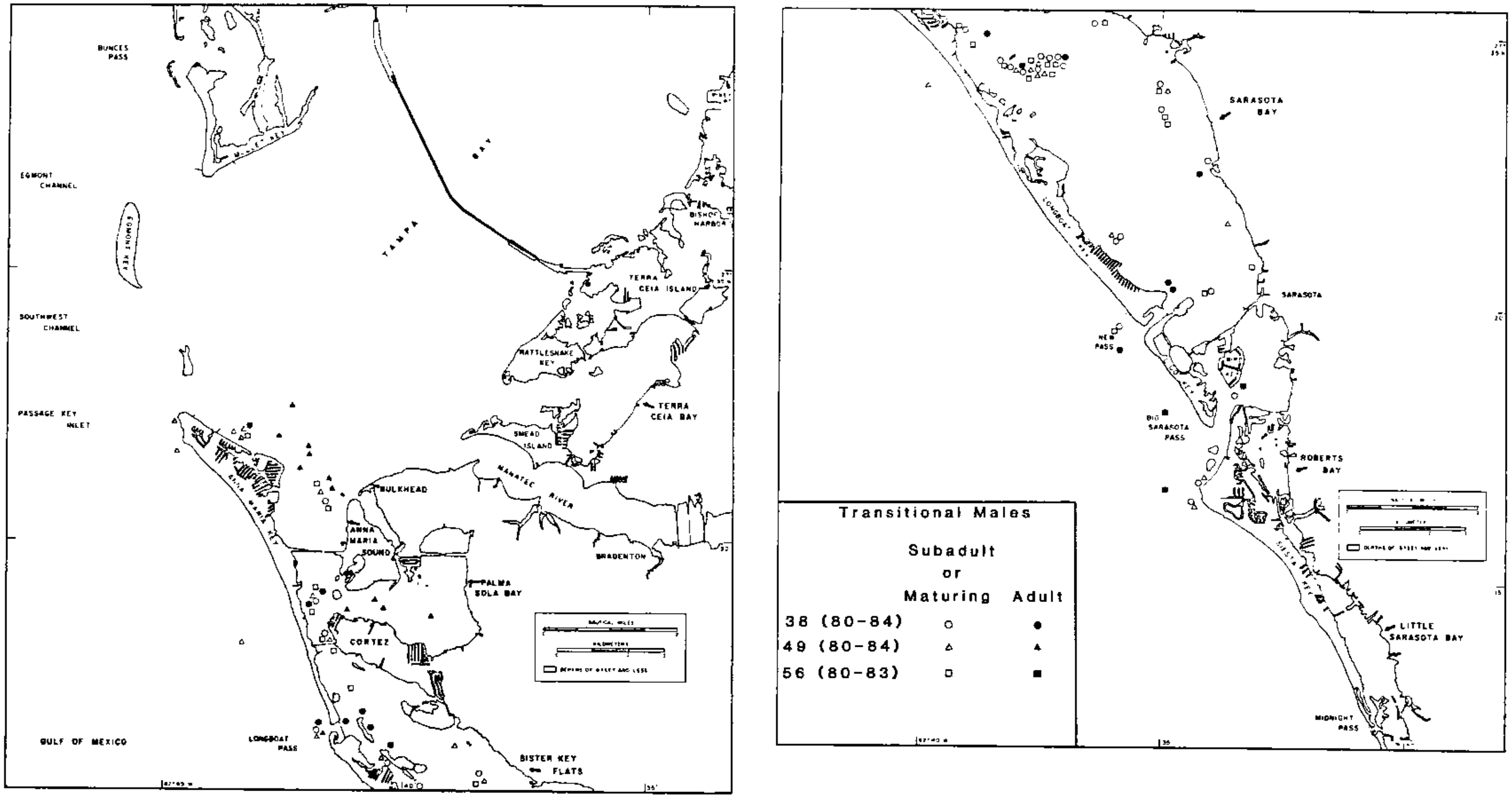
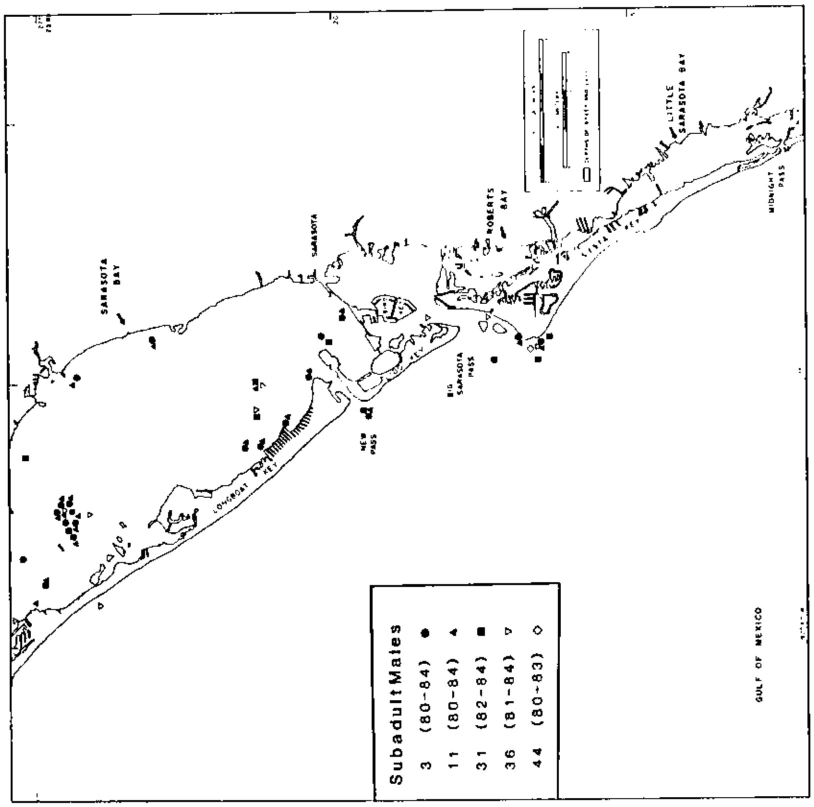

Transitional Males
Subadult or Maturing
Adult
38 (80-84) ○ ●
49 (80-84) △ ▲
56 (80-83) □ ■
BUNCES PASS
EGMONT CHANNEL
EGMONT KEY
SOUTHWEST CHANNEL
PASSAGE KEY INLET
GULF OF MEXICO
TAMPA BAY
BISHOP HARBOR
TERRA CEIA ISLAND
RATTLESNAKE KEY
TERRA CEIA BAY
SNEAD ISLAND
MANATEE RIVER
BRADENTON
BULKHEAD
ANNA MARIA SOUND
PALMA SOLA BAY
CORTEZ
ANNA MARIA KEY
LONGBOAT PASS
SISTER KEY FLATS
SARASOTA BAY
SARASOTA
LONGBOAT KEY
NEW PASS
BIG SARASOTA PASS
ROBERTS BAY
SIESTA KEY
LITTLE SARASOTA BAY
MIDNIGHT PASS

Figure 14. Sightings of subadult or maturing males during 1980-1984.


SARASOTA BAY
SARASOTA
ROBERTS BAY
LITTLE SARASOTA BAY
LONGBOAT KEY
NEW PASS
BIG SARASOTA PASS
SIESTA KEY
MIDNIGHT PASS
GULF OF MEXICO
Subadult Males
3 (80-84) ●
11 (80-84) ▲
31 (82-84) ■
36 (81-84) ▽
44 (80-83) ◇

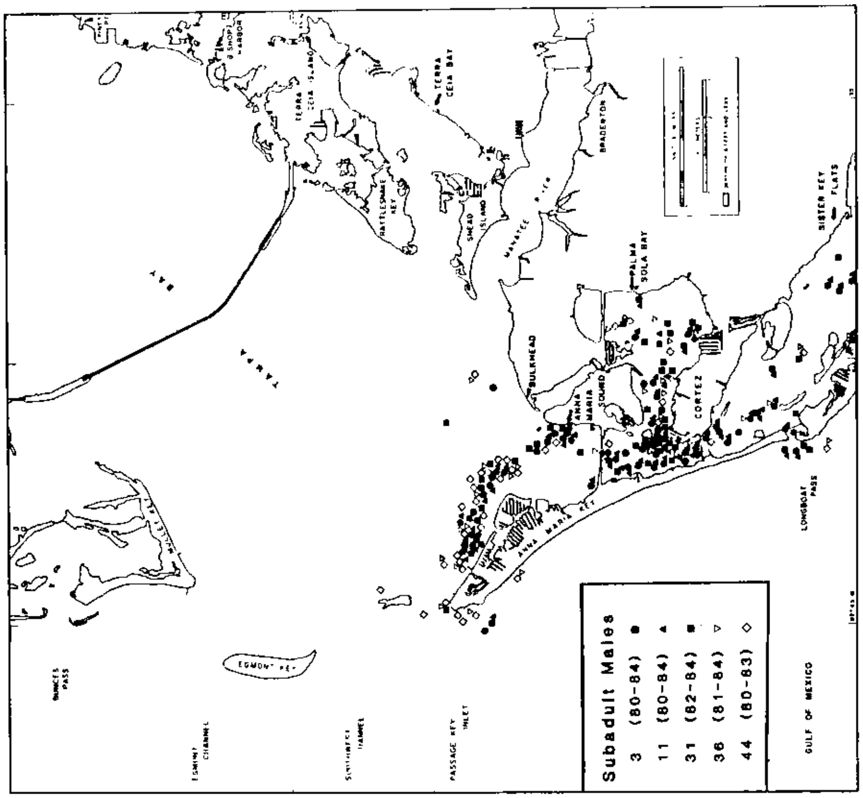

BISHOP HARBOR
TERRA CEIA ISLAND
TERRA CEIA BAY
RATTLESNAKE KEY
SNEAD ISLAND
MANATEE RIVER
BRADENTON
TAMPA BAY
MULLET KEY
BUNCES PASS
EGMONT KEY
EGMONT CHANNEL
SOUTHWEST CHANNEL
PASSAGE KEY INLET
BULKHEAD
ANNA MARIA SOUND
PALMA SOLA BAY
CORTEZ
ANNA MARIA KEY
LONGBOAT PASS
SISTER KEY FLATS
GULF OF MEXICO
Subadult Males
3 (80-84) ●
11 (80-84) ▲
31 (82-84) ■
36 (81-84) ▽
44 (80-83) ◇

Figure 15. Comparison of sightings of female dolphin #1 during 1975-1976 and 1980-1984.

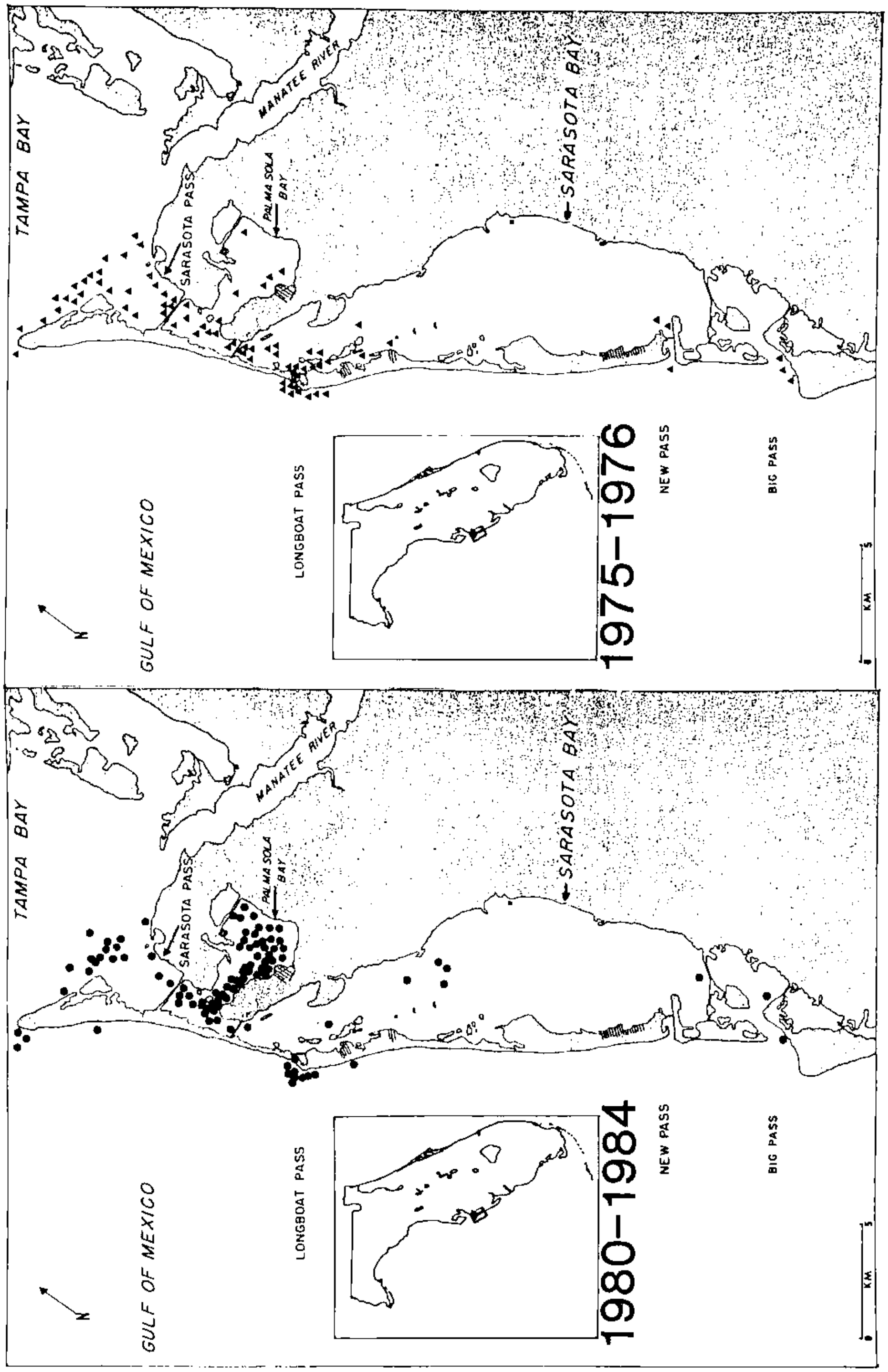

TAMPA BAY
MANATEE RIVER
SARASOTA PASS
PALMA SOLA BAY
SARASOTA BAY
GULF OF MEXICO
N
LONGBOAT PASS
NEW PASS
BIG PASS
0 KM 5
1975–1976
TAMPA BAY
MANATEE RIVER
SARASOTA PASS
PALMA SOLA BAY
SARASOTA BAY
GULF OF MEXICO
N
LONGBOAT PASS
NEW PASS
BIG PASS
0 KM 5
1980–1984

Figure 16. Comparison of sightings of males during 1975-1978 and 1980-1984.

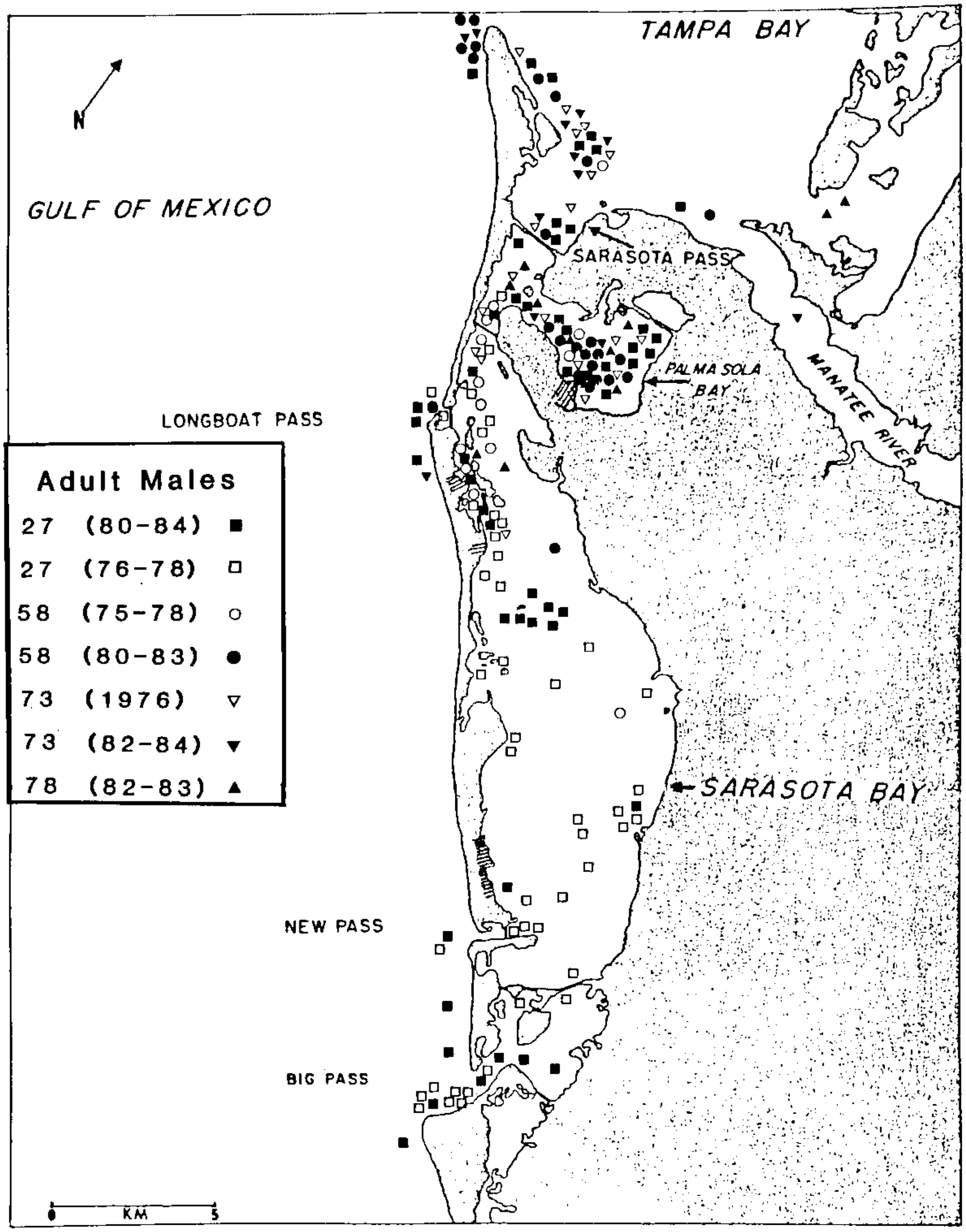

TAMPA BAY
N
GULF OF MEXICO
SARASOTA PASS
PALMA SOLA BAY
MANATEE RIVER
LONGBOAT PASS
Adult Males
27 (80-84) ■
27 (76-78) □
58 (75-78) ○
58 (80-83) ●
73 (1976) ▽
73 (82-84) ▼
78 (82-83) ▲
SARASOTA BAY
NEW PASS
BIG PASS
0 KM 5

Figure 17. Body length frequency distribution from dolphin captures during 1975-1976 and 1984.

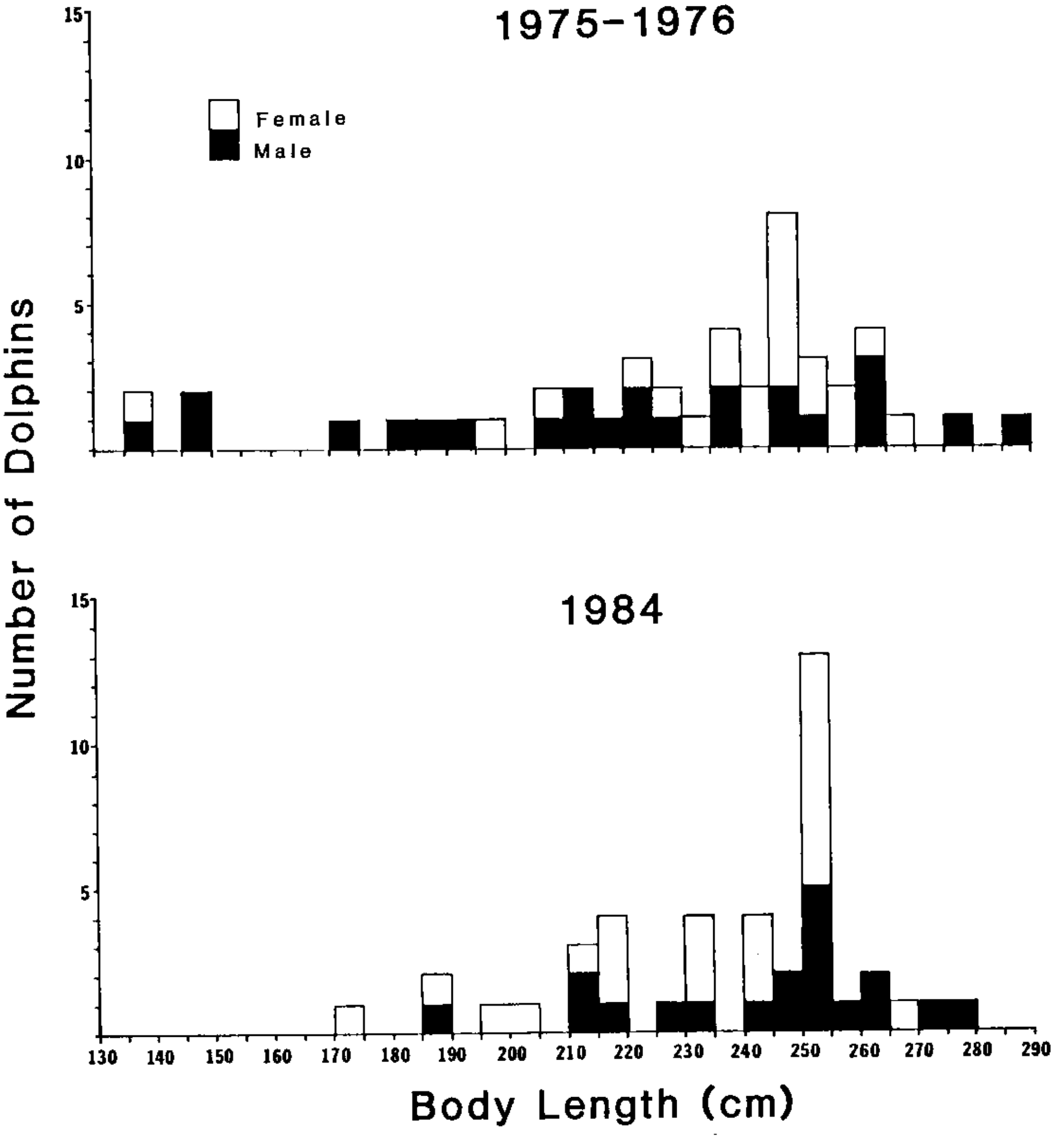
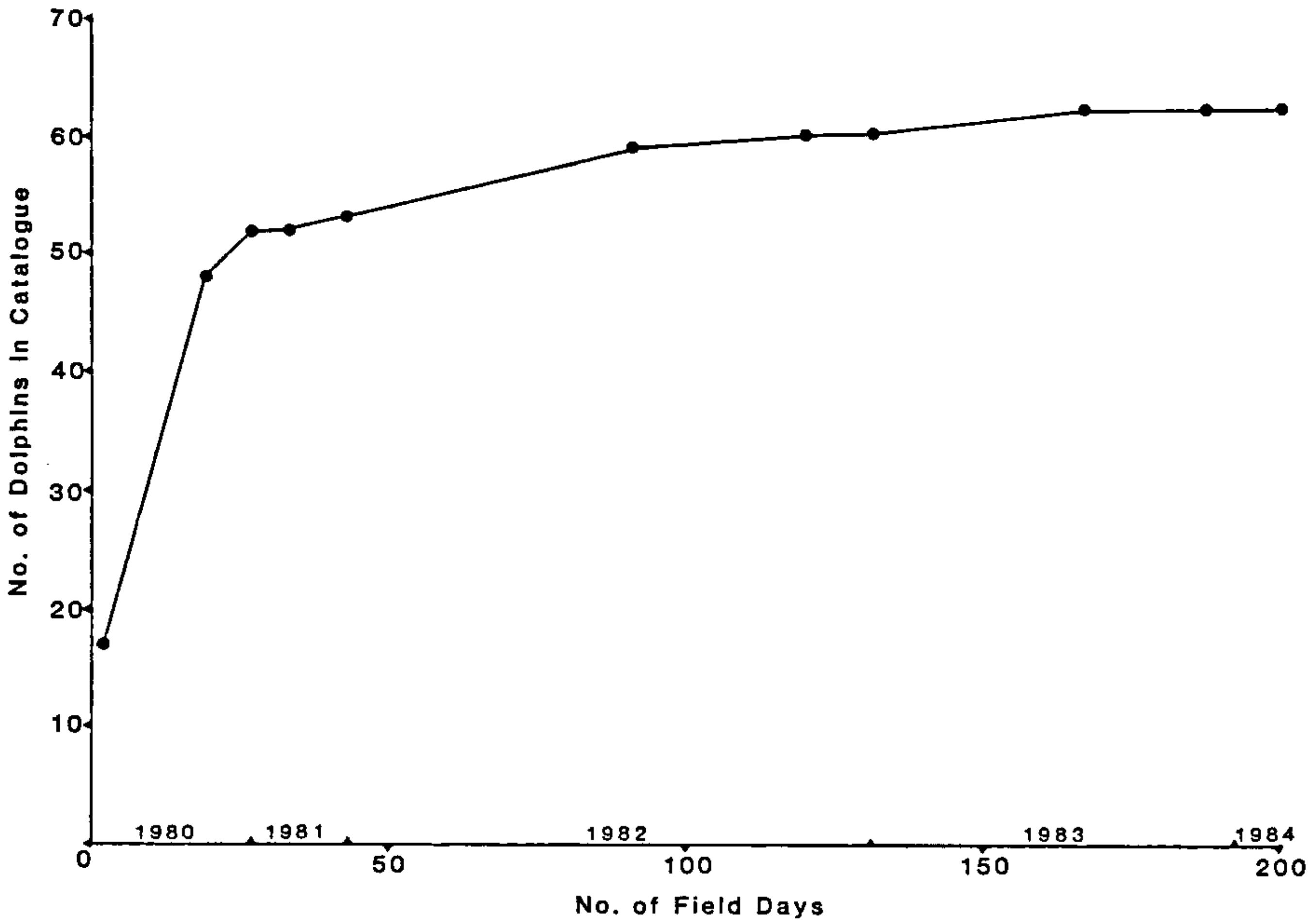

1975-1976
Female
Male
Number of Dolphins
15
10
5
1984
15
10
5
130
140
150
160
170
180
190
200
210
220
230
240
250
260
270
280
290
Body Length (cm)

Figure 18. Accumulation of identifiable dolphins in the catalogue for the Sarasota community, as a function of the number of days in the field.


70
60
50
40
30
20
10
No. of Dolphins in Catalogue
0
50
100
150
200
1980
1981
1982
1983
1984
No. of Field Days

CHAPTER TWO

THE SOCIAL STRUCTURE OF FREE-RANGING BOTTLENOSE DOLPHINS

THE SOCIAL STRUCTURE OF FREE-RANGING BOTTLENOSE DOLPHINS

1. INTRODUCTION

A description of the social structure of a species is a first step toward understanding its social organization, and ultimately, the evolutionary processes which shaped its social system. Since the mid-1960's the rapid accumulation of information from field studies of terrestrial mammals has made it possible to propose models to explain the evolution of mammalian social systems. These models have examined the species distribution of characteristics such as group size, group compositions, spatial patterns of individuals, and social interactions in relation to environmental variables (eg. Crook and Gartlan, 1966; Eisenberg et al., 1972; Clutton-Brock, 1974; Jarman, 1974; Emlen and Oring, 1977; Wrangham, 1980). Predictable patterns of organization have been found which provide insights on the adaptive significance of the social systems. Until recently, available information for cetaceans has been inadequate to allow construction of comparable models. A surge of systematic field studies of the behavior and ecology of cetaceans is beginning to provide the requisite information for examination of cetacean societies within a general mammalian context. To this end, this paper presents the results of one study of the social structure of the bottlenose dolphin, Tursiops truncatus.

Tests of hypotheses about the evolution of mammalian societies in their natural environment can be difficult. Typically, experimental manipulations of social units or their environments are either undesirable or impractical. Thus, the field researcher must take advantage of natural experiments by carefully selecting research sites to control for the variables in question, and by remaining alert for serendipitous opportunities.

The approach of longitudinal studies, in which the researcher comes to recognize the individual members of a particular social unit, has proved extremely successful in studies of a variety of terrestrial mammals. In time, information on ages, sexes, familial relationships, and life history parameters is accumulated. Such data increase precision in the definition of the contexts of social interactions. All of these factors are important in shaping social systems. The data base thus compiled over a number of years can then be used as a baseline. Any deviations from this baseline that are observed can be treated as natural experiments.

There have been few longitudinal studies of cetaceans comparable to those of many terrestrial mammals, for several reasons. Studies of the social systems of delphinid cetaceans must contend with the additional complications of working with highly mobile animals in an aquatic environment. Individual identifications often require photographs of subtle natural markings. Most delphinids lack distinctive features identifying age or sex. Much of the available information on delphinid social structure is derived from fisheries reports, where sex and age compositions of schools have been determined from collected specimens (eg. pilot whales, _Globicephala_ _macrorhynchus_, Kasuya and Marsh, 1984;

striped dolphins, Stenella coeruleoalba, Miyazaki and Nishiwaki, 1978). Observations of social associations and interactions have been made for a few species such as bottlenose dolphins (Wursig, 1978) and spinner dolphins (Stenella longirostris, Norris et al., 1985), but in most cases information on the ages, sexes, or relations of the participants has been limited. Typically, observation studies have not continued long enough to obtain correlative data on life histories and natural history.

Exceptions include several longitudinal studies of the killer whale (Orcinus orca) and the bottlenose dolphin. These studies now provide information on social patterns of identifiable individuals, many of which are of known sex, age, and lineage. Photographic identification studies of killer whales in the waters of British Columbia, Canada, were pioneered by Bigg and colleagues in the early 1970's (Bigg et al., 1976; Bigg, 1982). Their efforts were soon joined by those of Balcomb and colleagues working with killer whale pods in the adjacent waters of Puget Sound, Washington (Balcomb et al., 1980). Both studies took advantage of the predictable presence of killer whale social units, and the highly distinctive individual markings indicative of sex and age. Continuity of observations has made it possible to collect data on life histories and familial relationships, and has resulted in our present understanding of the important role of kinship in Orcinus pod structure.

Photographic identification techniques have been adapted for bottlenose dolphins as well (Wursig and Wursig, 1977). Unlike the killer whales, bottlenose dolphins offer few obvious clues to their sex, age, or lineage. However, short-term capture, sampling and release of these dolphins can provide these data. A tagging study of bottlenose dolphins along the central west coast of Florida was initiated by Irvine and Wells in 1970. Opportunistic tagging and resighting efforts during the next two years (Irvine and Wells, 1972), and systematic tagging, radiotracking, and field observation during 1975 - 1976 resulted in the description of an apparently resident social unit. Individual home ranges and social association patterns were hypothesized to be largely dependent on the age and sex of the individual, resulting in a structured society that was stable over time (Wells, 1978; Wells et al., 1980; Irvine et al., 1981).

Continued research has made it possible to test these hypotheses. If the hypotheses were to be accepted, then we would expect sex and age segregation to remain the predominant pattern over time, in spite of changes in the overall membership of the resident social unit. Likewise, we would expect particular individuals to change their movement and association patterns in predictable ways as they made transitions from one age class to the next during the process of social maturation. This chapter reports on the results of these tests from observations conducted during 1980 - 1984. In addition, it elaborates upon new findings and develops testable hypotheses about the social structure of the bottlenose dolphins.

2. METHODS

The field work with bottlenose dolphins along the central west coast of Florida, which was initiated in 1970, is still in progress. The research program has two main components: (1) temporary captures for marking, measurements, and biological sampling, and (2) observations, including radiotracking, photographic identification censuses, and focal animal behavioral observations.

2.1. Study Area

The study area extends southward approximately 160 km from St. Petersburg to Ft. Myers Beach, Florida (Figure 1). The area includes large bays such as Tampa Bay, Sarasota Bay, Gasparilla Sound, Charlotte Harbor, and Pine Island Sound, along with their associated channels and shallow grassflats. These inshore waters are bounded on the west by a series of barrier islands, and communicate with the Gulf of Mexico through passes between the islands. Water depths vary from less than 1 m over the grassflats, to 10 m or more in the passes and at the western extent of the study area, about 5 km offshore of the barrier islands. Tidal fluctuations are typically less than 1 m.

Most of the capture activities were concentrated in the 60 km long area off Bradenton and Sarasota. But some capture operations have occurred from the southern edge of Tampa Bay, near Ruskin, through Pine Island Sound, near Ft. Myers Beach. Observations and photographic censuses have been conducted through the entire study area, but most of the effort has been concentrated from the southern portion of Tampa Bay, southward to Siesta Key off Sarasota.

2.2. Capture Operations

Dolphins were captured in the study area during 1970 - 1971, 1975 - 1976, and 1984 - 1985. The seine net technique described by Asper (1975) was used in each case to encircle small schools of dolphins in shallow (< 2 m deep) water. During 1970-71, we accompanied a commercial dolphin collector, and measured, sexed, tagged and released his "reject" animals. Twelve dolphins were tagged in the northern half of the study area, and 18 in the southern half (Irvine and Wells, 1972).

All of the captures during January 1975 - July 1976 were conducted in the northern half of the study area. Forty-seven individuals were measured, sexed, tagged and released. Ten of these dolphins carried radiotransmitters, and these were tracked for up to 22 days (Wells, 1978; Wells et al., 1980; Irvine et al., 1981,1982).

Seventy individuals were captured, measured, photographed, marked, and released during June 1984 - July 1985. Sixty of these were handled during June/July capture operations in the northern half of the study area. Blood samples were obtained from all of these. Estimated ages were determined from analyses of teeth from 32 individuals. Ten dolphins were tagged incidental to the efforts of a commercial dolphin collector in the adjacent waters of Pine Island Sound, Charlotte Harbor, and southern Tampa Bay during December 1984. Blood samples were obtained from nine of these dolphins, as well as four other dolphins that were collected at that time.

Blood samples were obtained for assessment of reproductive condition and for determination of genetic relationships. The samples were collected from vessels in the fluke. Serum from one aliquot was analyzed by radioimmunoassay for concentrations of testosterone, progesterone, and estradiol by V.L. Kirby at the San Diego Zoo Research Department. Another aliquot was analyzed by D. Duffield, at Portland State University. Using electrophoresis and examination of chromosome banding patterns, familial relationships and genetic patterns in social unit membership were examined. Analyses of samples from June/July 1985 are still in progress; therefore, only samples collected prior to June 1985 will be considered in this report.

2.3. Observations

Three kinds of systematic observations were conducted. Radiotracking provided information on daily movements, activities, and social associations. Identification censuses established the membership of the resident social unit and provided information on individual ranges and social associations. Focal animal behavioral observations provided activity pattern and social interaction data.

Observations of tagged dolphins during 1970 - 1971 were opportunistic, usually incidental to capture operations (Irvine and Wells, 1972). During 1975-76, observations were made from a 7.3 m vessel. The boat was used for radiotracking and for systematic censuses over specified survey routes (Irvine et al., 1981). Photography was used extensively to confirm identifications of recognizable dolphins.

All of the new observation data reported here are the result of two kinds of efforts from small outboard powered boats (4.3 m - 5.2 m long) during April 1980 through January 1984. First, photographic censuses used the survey routes established during 1975 - 1976 through Bradenton and Sarasota waters, and these routes were expanded to include adjacent waters. Date, time, location, total number of dolphins, number of calves, individual identifications, and behavioral and environmental data were recorded for each sighting. The dolphins' dorsal fins were photographed with Kodachrome 64 color slide film in 35 mm cameras equipped with 200-300 mm telephoto lenses, powerwinders, and databacks. The best photographs of each individual were copied and placed in an identification catalog for subsequent comparisons. Dolphins were identified from natural markings, scars from previous tags, or freezebrands on their dorsal fins (Figure 2). These photographs were examined and classified three times before a sighting of a particular individual was entered into the computer data base.

Second, focal animal behavioral observations were made, involving moving with dolphin groups containing identifiable members for prolonged periods (typically >15 min). The behaviors of a focal dolphin and its associates were narrated into a tape recorder, and in a number of cases simultaneous hydrophone recordings of the animals' acoustic emissions were also made. Members of groups observed in this way were also photographed to confirm identifications.

2.4. Definitions and Data Analysis

2.4.1. Social Unit Categories

Variability in dolphin grouping patterns made classification of social units difficult. Three roughly hierarchical categories were used here. The term "school" was used as an instantaneous sampling unit. "Group" referred to a kind of stable social unit. "Community" referred to a collection of groups.

Sighting data were categorized and tabulated using the precedures of Irvine et al. (1981). Dolphins sighted within an area of approximately 100 m radius were considered to be in a single school (= group, Irvine et al., 1981). Typically, these were the only dolphins in sight at any given time, and they were engaged in similar activities. This definition is ion concordance with the usage of Norris et al. (1985, p. 33), who considered a school to be "...any aggregation of aquatic animals that swim together as a unit [see Norris and Dohl 1980]. This means that any group of dolphins that we see traveling together for long enough to make us sure they represent a cohesive unit we call a school." The terms "school" and "sighting" are used interchangably here in reference to sampling units in the field. These units are similar to small, changable units of chimpanzees known as "parties" (Goodall, 1983). They are generally unlike the stable, permanent "pods" of killer whales (Bigg, 1982). Sightings of dolphins were retabulated if the same dolphins were resighted more than one hour apart, or if the school composition changed during observations.

The term "group" is used in this paper specifically in the context of a stable social unit. As described in Section 3.2.4., regularly associating dolphins which shared congruent core areas were considered to belong to particular groups. In this context, the term "group" will be accompanied by an identifier referring to the sex, age, and/or geographical range of the members. For example, on occasion all of the members of the Anna Maria female group were observed together. At other times the members were dispersed into several smaller units, which each met the criteria for separate schools. Thus, a group maintained compositional integrity over time, while schools were ephemeral.

The Sarasota community of dolphins, as defined by Wells (1986), was composed of all of the groups (and individuals which did not clearly belong to groups) which shared large portions of their ranges and which interacted with each other to a much greater extent than with members of similar units in adjacent waters. This regional society could be considered to be a population, in the broadest sense (eg. Wilson, 1975). However, available evidence indicates that this "population" was not a closed reproductive unit, and thus not a population in the strictest sense. The term community was used because it emphasized the geographical and social relationships of the individuals. The bottlenose dolphin community was similar to that of chimpanzees (Goodall, 1983) in that the ranges of the members were largely contained within a well-defined area, and most of the activities of the members occurred within the community range, but genetic exchange occurred between communities. Killer whale communities were apparently similar to that described here for bottlenose dolphins, except different killer whale communities did not mix with each other (Bigg, 1982).

2.4.2. Dolphin Age Classes

Age classes were assigned on the basis of one or more of a variety of criteria, including known birthdate or known season of birth, analysis of growth layer groups in tooth sections (Hohn, 1980), blood serum concentrations of testosterone, progesterone, or estradiol (measured during the height of the breeding season, Irvine et al., 1981), body length relative to a maturity curve based on Sarasota dolphins, and independence from or association with a presumed mother or calf.

Calves were small dolphins regularly accompanying larger dolphins presumed to be their mothers. Calves were divided into four age classes: 0--for calves from birth through their first year, 1--from one to two years of age, 2--from two to three years of age, and 3--greater than three years old.

Two classes of immature males were identified. Subadult males were those dolphins independent of a presumed mother, who generally were less than 245 cm in length, and who were less than eight years old. Males meeting these criteria typically had testosterone concentrations of less than 1.0 ng/ml when measured during the 1984 breeding season. Because sexual maturation is a gradual process, a transitional stage was identified for the males. Maturing males were those dolphins who were independent, 245 to 249 cm long, and approximately 8 or 9 years old. During the 1984 breeding season, testosterone concentrations for dolphins meeting these criteria were typically 1.0 - 10.0 ng/ml.

Males were considered adults if they were more than 249 cm in length, and ten years old or older. Males meeting these criteria typically had testosterone concentrations greater than 10 ng/ml when measured during the breeding season in 1984. This concentration is considered to be characteristic of adult males (see Ridgway and Benirschke, 1977). Harrison and Ridgway (1971) and Harrison et al. (1972) suggested that males do not reach sexual maturity until ten years of age. Sergeant et al. (1973) reported that males from northeast Florida mature at about 12 years of age. Perrin and Reilly (1984) considered the average age at sexual maturity for males to be 11 years. Hohn (1985) cautions, however, that comparison of life history parameters produced by different studies may not be valid due to different methods of age determination and analytical techniques. Sexually mature adults were not necessarily socially mature.

Subadult females were independent young animals that had not yet been observed with a calf, and that did not produce a calf within one year of the end of the observations reported here. Subadult females were typically less than 230 cm long and less than 7 years old.

Females were classified as adult on the basis of having been seen with calves believed to be their own. Depending upon the author, sexual maturity for females is believed to occur between the ages of five and twelve years (Harrison and Ridgway, 1971; Harrison et al., 1972; Sergeant et al., 1973; Perrin and Reilly, 1984). Data from Sarasota suggest that some females matured at about six to seven years of age. Progesterone concentrations for a 6.4 year-old Sarasota female (#21) were indicative of sexual maturity. Female #02, which was tagged as a calf in 1976, was approximately 7.5 years old in 1982 (from body length vs. age curve) when she gave birth. This suggests that #02 was mature by 6.5 years of age.

Adult females were categorized by reproductive condition as (1) receptive, (2) pregnant, (3) with a calf, or (4) single, during the period when they were not accompanied by a calf. Dolphins were categorized as receptive or pregnant a posteriori, following the birth of a calf, based on a twelve month gestation period (see Ridgway and Benirschke, 1977). A female was considered to be pregnant for the twelve month period preceding birth. She was considered receptive during the season in which she became pregnant.

2.4.3. Social Association Analyses

Social associations between pairs of individuals were quantified using a Coefficient of Association (Schaller, 1972).

$$\text{Coefficient of Association} = 2J/(a+b)$$

where J = the number of joint sightings, scored once for each sighting which included both dolphin A and dolphin B

a = the total number of sightings of dolphin A

b = the total number of sightings of dolphin B

Coefficients were calculated for all possible pairs of identifiable dolphins of known sex and age. Coefficients ranged from 0.00, for two dolphins that were never seen together, to 1.00 for pairs that were always seen together.

3. RESULTS

3.1. Data Base

Most of the analyses reported here deal with data collected during April 1980 - January 1984. However, since comparisons are made to previously published data from the same population (Wells, 1978; Wells et al., 1980; Irvine et al., 1981), and because previously unpublished sightings during 1976 - 1978 are included, the entire observational data base will be described. Observations from vessels were conducted during radio tracking (1975 - 1976), and censuses (1975 - 1984). Observations occurred on 423 census days during nine years, distributed as follows: 1975 (109 days), 1976 (107 days), 1977 (6 days), 1978 (1 day), 1980 (22 days), 1981 (21 days), 1982 (77 days), 1983 (72 days), and 1984 (8 days).

During 1975 - 1978, 695 dolphin sightings containing a total of approximately 3413 dolphins were recorded. Of these, 914 were identifications of 47 tagged and 12 naturally marked dolphins. During April 1980 - January 1984, 1074 sightings were recorded, containing approximately 7806 dolphins. Four hundred sixty-six individuals were identified, including 421 naturally marked dolphins and 45 previously tagged dolphins and their offspring. Of these, 116 were seen five or more times (up to 96 times); these accounted for 49% (3842 dolphins) of all dolphins sighted. Sightings of 77 identifiable dolphins of known sex and estimated age (Tables I,II) form the data base for most of the analyses in this report. Repeated sightings of these 77 individuals accounted for 35% (3883 dolphins) of the total of 11,219 dolphins recorded during 1975 - 1984.

3.2. Characteristics of the Sarasota Bottlenose Dolphin Society

Inshore bottlenose dolphins near Sarasota, Florida constitute a resident community of approximately 100 individuals. These animals inhabited a 40 km section of coastal and associated inshore waters. This community shall be referred to as the "Sarasota community" throughout the remainder of this report. The home range of the Sarasota community has apparently remained relatively unchanged, and the community size has remained constant, from at least 1976 through 1983 (Wells, 1986).

The Sarasota community has remained relatively discrete from adjacent communities in the Gulf of Mexico and Tampa Bay in observations made to date. Mixing with identifiable residents of these adjacent communities occurred in 17% of sightings during 1980 - 1984, but annual rates of immigration and emigration appeared to be less than 2 - 3% (Wells, 1986). Thus, the vast majority of social interactions of Sarasota community members involved other long-term members of the same community.

The community is used as the framework within which the social structure is considered in this report, because of its relatively permanent residency and its discreteness from other apparently similar units. The structure of societies is strongly influenced by environmental and social pressures. The following summary of home range and social unit features will place the structure in its proper perspective.

3.2.1. Home Range Characteristics

The Sarasota community home range extended southward from the southern edge of Tampa Bay to Siesta Key, off Sarasota, Florida (Figure 3). This range included all of the shallow (typically less than 4 m deep) inshore waters to the east of the barrier island chain, and Gulf of Mexico coastal waters within approximately 1 km of shore. The inshore waters were typified by shallow, protected bays of 3 - 4 m depth (Terra Ceia Bay, Palma Sola Bay, Sarasota Bay) and included the mouth of the Manatee River. Extensive areas of highly productive grassflats of 1 - 2 m depth (Anna Maria Sound, Sister Key Flats), traversed by narrow channels of 3 m depth, exist primarily in the northern half of the home range. Narrow passes of up to 10 m depth connect the inshore and Gulf coastal waters. In the Gulf, a gently sloping sandy bottom, with occasional low (less than 1 m high) rocky reefs, gradually reaches depths of about 8 - 10 m at the western extent of the Sarasota community's typical movements. The northern border of the home range was defined by the deep (4 - 10m depth) waters of Tampa Bay.

The present Sarasota community home range, as defined by Wells (1986), differs from that described by Wells (1978), Wells et al. (1980) and Irvine et al. (1981) only in the addition of Terra Ceia Bay, at the northern extent of the inshore portion of the range. Members of the Sarasota community have been seen regularly in Terra Ceia Bay since 1980. However, since surveys through the Bay were infrequent prior to 1980, it can not be determined if this was an actual range extension, or a sampling artifact.

Long-term residency of the Sarasota community was indicated from regular resightings of a number of individuals (Wells, 1986). Seven of twelve (58%) of the Sarasota dolphins tagged during 1970 - 1971 were identified in the area during 1985. Of the 48 dolphins tagged during 1970 - 1976 (less the known mortalities), 66% were identified during 1980 - 1985, in spite of the fact that the tags had been removed in 1976. This value was probably low, as marked changes in dorsal fin morphology during early growth may have made some of the young dolphins unrecognizable between 1976 and 1980.

The Sarasota community members were year-around residents of the home range described above. Seasonal shifts in habitat use during 1975 - 1976 were described by Irvine et al (1981). During the summer months, the residents emphasized the use of the shallow grassflats during their daily activities. During the winter, the passes, channels, and shallow Gulf waters were emphasized. This pattern was maintained during 1980 - 1984. Irvine et al. (1981) and Wells et al. (1980) speculated that the shifts were due at least in part to seasonal movements of the primary prey fish, mullet (Mugil cephalus), and seasonal changes in abundance of various shark species, especially the bull shark (Carcharhinus leucas) which preys on dolphins.

3.2.2. Community Demography

The Sarasota community size seems to have been relatively stable over many years, as indicated by mark - recapture analyses. Irvine et al. (1981) estimated that the community contained approximately 102 dolphins (95% CL = 90 - 117) in 1976. In 1983, the community size was estimated to be 98 dolphins (95% CL = 89 - 108; Wells, 1986).

The study community consisted of all ages and sexes. Based on similarities in ranges and association patterns, 73 of the 77 dolphins in the data base (Tables I,II) were considered to be members of the Sarasota community (Wells, 1986). Table III summarizes the sex and age structure of the community during 1975 - 1976, and 1983 - 1984, based on that portion of the community that has been captured for age estimation, and on the observed presence of calves with females.

In both samples, the adult portion of the community appeared to be skewed towards females, while the subadult or maturing segment of the community was skewed towards males. Several factors may be contributing to these differences, assuming the relatively closed community proposed by Wells (1985). Females may tend to live longer than males. Of the individuals identified during 1975 - 1976, 88% of the females were reidentified during 1980 - 1983, while only 46% of the males were reidentified. Preliminary analyses of growth layer groups in teeth collected from 35 dolphins through 1985 found the oldest female to be approximately 44 years old, four females were over 30 years old, and four females were between 20 to 30 years of age (Mean = 17.5 yrs., n = 19). The oldest male measured to date in the community was approximately 28 years old, and only two males were older than 20 years of age (Mean = 12.3 yrs, n = 16).

Differential mortality was indicated from the few deaths of identifiable dolphins recorded to date. Carcasses of five males (2 adults:3 subadults) have been examined. Through 1985, no carcasses of identifiable females have been recovered, though one adult female (#53) developed a widespread skin disorder in 1982, and has not been seen since. However, the present samples of both teeth and carcasses are too small to be conclusive on this point. Additional tooth sample collections are planned for 1986 - 1987.

Differences in ages at sexual maturity probably accounted for some of the sex ratio differences. Females appeared to be recruited into the breeding community at an earlier age than males. If females mature earlier than males, then there should be fewer subadult females than males in the community at any given time. Assuming females have equal or longer average lifespans than males, then this would result in more adult females than males at any given time.

3.2.3 Social Unit Characteristics

The members of the Sarasota community were never all seen together in a single cohesive school. Rather, they were typically dispersed into a variety of schools distributed through the approximately 85 square km community home range, as described by Wells et al. (1980) and Irvine et al. (1981). Associations between individuals were relatively fluid, within limits. Typically, small units of persistent or frequently-recurrent associates swam through the range, often joining other similar schools for periods of minutes or hours. These schools occasionally mixed with members of adjacent communities to the north and west (17% of sightings, Wells, 1986).

This paper departs from earlier descriptions (Wells, 1978; Wells et al., 1980; Irvine et al., 1981) by examining the determinants of group structure in the detail that could only be allowed by continued long-term observations. The composition and size of social units appeared to be related to a number of factors, including sex, age, familial relationships, and reproductive condition.

3.2.3a. Composition of Schools. Sexual segregation was a marked feature of the dolphin schools observed both during 1970 through 1976 (Wells et al., 1980), and 1980 through 1984. Schools were composed typically of independent (non-calf) members of a single sex. Subgroups within schools also tended to be composed of a single sex. Social symmetry was thus allowed.

Two different samples were examined for patterns of composition. The first sample consisted of 177 sightings of Sarasota community members only, in which all of the non-calves were of known sex and estimated age. The second sample consisted of 536 sightings in which only Sarasota community members were identified, and in which age and sex data were available for at least some of the group members. Sixty-six percent of the 2745 non-calves in this sample were of known sex and estimated age.

Of the 177 sightings in the first sample, only 20% of were of mixed sex. Sixteen percent of the schools were all male, and 64% were all female. The results from this sample may be somewhat biased since the schools from which complete sex/age information was most frequently available tended to be small (Mean = 4.06 dolphins, SD = 3.585, n = 177, Range = 1 - 22).

Sexual segregation was also suggested from analysis of the second sample. Mixed sexes were observed in only 31% of the sightings. Males only were identified in 23% of the sightings; females only were identified in 46% of the sightings.

School composition was also related to individual age and reproductive condition. The first sample was analyzed for association patterns between the eight non-calf sex/age classes. Coefficients of association were calculated for each class based on the frequencies of joint occurrences within the 177 groups (Table IV). Chi-square analyses were conducted on the frequencies of joint occurrences of classes, testing the null hypothesis that associations were evenly distributed across all classes. For chi-square analysis, classes were combined on the basis of reproductive condition and age to provide sufficiently large expected frequencies in all cells to be able to proceed with the analysis (Zar, 1974). The combinations were: (1) immatures, including subadult males and females and maturing males, (2) adult males, (3) adult females without calves (singles) and receptive females, and (4) pregnant females and females with calves. The results of these analyses are summarized in Table IV. The chi-square analyses were subsequently subdivided for analysis of the relative contributions of particular classes to overall significant differences.

While associations between immatures and adults did occur, age segregation appeared to be the general rule, as suggested by Wells et al. (1980). Class associations were not evenly distributed across all classes (Table IV). Immature dolphins tended to be seen with other immatures more frequently than they were seen with any adult classes.

In the first sample, immature males were seen with an adult male and receptive females on only one occasion, on 13 July 1983. These animals interacted briefly. The sighting consisted of a young adult male trailing a single (possibly receptive) female, two receptive females, one male calf, and two maturing males. One of the receptive females (#7), with a 2 year-old male calf (#12), was approached closely by the maturing male pair, which included her 8.5 year-old son (#11). In an apparent display of aggression towards her elder son, #7 tailslapped repeatedly as he approached. Soon, #7 and #12 left the area. Thus, consideration of the associations within this anomalous school on the strict basis of sex, age, and reproductive condition was confounded by familial relationships and possible dispersive interactions within the school.

The adult male class shared its highest coefficient of association with receptive adult females (Table IV). Adult male affinities with female classes were roughly correlated with the probability of receptive females existing within the class. Affinities decreased from receptive females through single females, females with calves, and pregnant females and subadult females. Some single adult females may have been receptive, but this was not detected because they were not impregnated, or because their calves were lost. Similarly, some females with older calves may have been receptive, but they did not give birth to a viable calf one year later. By definition, pregnant or subadult females could not be considered receptive. The frequency of adult male associations with receptive and single females was much higher than that expected from the null hypothesis.

Adult male affinities for male classes were low (Table IV). While this general trend was also clear from observations outside of the first sample considered here, the extremely low values (0.00) for affinities with subadult males and other adults in Table IV appeared to be artifacts of the sample. Adult males were seen with subadult males in cases not included in the first sample. As discussed below, persistent adult male pairings resulted in some of the highest individual affinities recorded in this study. Thus, while class associations between adult males and other males may have been infrequent, they were not nonexistent.

The various classes of adult females showed relatively high affinities for each other, and low affinities for adult males and immatures of both sexes (Table IV). Amongst the adult female classes, affinities appeared to be closely related to the presence, absence, or imminence of a calf. Single adult females were most closely affiliated with receptive females, and vice versa. Pregnant females were closely affiliated with all adult females classes except receptive females. Females with calves were most closely associated with other females with calves, but they were frequently seen with the other adult female classes as well.

In summary, composition patterns for schools within the Sarasota community were related to dolphin age, sex, and reproductive condition. Immature males and females tended to be seen with other immatures more frequently than with adults of either sex. Adult males associated with receptive adult females to a greater degree than with any other class. Adult female classes tended to associate with adult females more than with any other classes, with the closest associations being between females of similar reproductive condition.

3.2.3b. School Size. The number of dolphins per school was quite variable within the Sarasota community. During 1975 and 1976, the mean value was 4.8 dolphins per sighting (Irvine et al., 1981). The mean number of dolphins per sighting during 1980 - 1984, for those schools in which only Sarasota community members were identified, was 7.04 (SD = 6.008 n = 536, Range = 1 - 39).

Numbers of dolphins per school varied significantly relative to time of day, physiography, and composition, based on earlier analyses (Wells et al., 1980). More detailed analyses of the relationships between size and composition were possible from the 1980 - 1984 data base than from the earlier data set. This resulted from improved information on ages and reproductive conditions provided from long-term observations and a capture/release program.

School size varied significantly with dolphin sex, age, and reproductive condition during 1980 - 1984. Frequency distributions for school size by age, sex, and reproductive class (Figures 4,5) were computed from the data set of all sightings that included at least one known member of the Sarasota community (Tables I,II). Differences in the numbers of dolphins per sighting were found for older age classes. There were no significant differences between male and female calves, either overall, or when subdivided by calf age class. The average number of dolphins per sighting was not significantly different for male and female subadults, but sightings containing subadults of either sex were significantly larger than those containing maturing males (Kruskal - Wallis test with Dunn's multiple comparison, $P < 0.05$). The number of dolphins per sighting for all four classes of adult females combined was significantly larger than that of adult males (Mann - Whitney $U = 65938$, $n = 199, 756$, $P < 0.01$).

Male dolphins tended to be found in progressively smaller schools from birth until they approached sexual maturity. Mean school size varied from a high of 17.80 dolphins per sighting for schools containing females with calves less than one year old, to a low value of 8.39 dolphins per sighting for maturing males (Figure 4). The two youngest male calf classes were found in significantly larger schools than were any of the non-calf male classes. The two oldest male calf classes were found in significantly larger schools than were the maturing males (Kruskal - Wallis test with Dunn's multiple comparison, $\underline{P} < 0.05$). The difference in school size between the younger calves and the adult males may be due in part to the fact that females with young calves were generally non-receptive; thus, the adult males and young calves were not together often. In contrast, mothers of older calves were more likely to be receptive, which may in part account for the similarities in school sizes for adult males and the oldest male calves. Within the male calf classes, there was a significant linear relationship between increasing calf age and decreasing number of dolphins per sighting (Figure 4; Spearman rank correlation coefficient $\underline{r} = -0.23$, $\underline{n} = 250$, $\underline{P} < 0.001$). Maturing males tended to be found in the smallest schools of any classes, with associations of three or fewer individuals being most common.

The average number of dolphins per sighting varied with age for females in a manner similar to that noted for males. Mean school size ranged from a high of 14.49 dolphins per sighting for sightings containing females with calves less than one year old, to an average value of 10.24 dolphins per sighting for females with calves of all ages (Figure 5). The two classes of the youngest female calves were found with significantly more dolphins per sighting than were adult females with calves of all ages (Kruskal - Wallis test with Dunn's multiple comparison, $\underline{P} < 0.05$). As in the case of the male calves, a significant inverse linear relationship was found between female calf age and average school size (Figure 5, Spearman rank correlation coefficient $\underline{r} = -0.11$, $\underline{n} = 329$, $\underline{P} < 0.05$). The female with calf class includes a number of females with older calves, born prior to 1980, for which no other age or sex information is available. This lends additional support to the notion of decreasing school size with calf age. Schools containing single females and/or pregnant females were also significantly larger than those of females and their calves (Kruskal - Wallis test with Dunn's multiple comparison, $\underline{P} < 0.05$). The lack of significant differences between the sizes of schools containing older calves, receptive females, and females with calves of all ages may be related in part to the inclusion of undetected receptive females in the classes involving females and calves.

In summary, bottlenose dolphin school size tended to decrease with dolphin age, until the individuals approached sexual maturity. Young calves tended to be found in the largest schools. Adult males were found in somewhat larger schools than subadult or maturing males. For females, school size was relatively constant across subadult and adult classes. However, females with calves of all ages tended to be found in somewhat smaller schools than were other non-calf females.

3.2.4. Patterns of Individual Associations

Individual dolphins were seen with a variety of associates. During 1980 - 1984, each of 38 Sarasota community non-calves was seen with an average of 60.55 different identifiable non-calves (SD = 13.866, range = 25 - 91). This total may be low, as sightings may have included some individuals that were not identified either because they lacked distinctive markings, or because they did not appear in photographs. On average, unidentified non-calves comprised 18.5% of the dolphins in the 536 sightings in which only Sarasota community members were identified.

The Sarasota community members also showed much variation in the frequency of association with particular individuals, as well as in the number of associates. As with many of the other features of the schools, the frequency of association, as described by coefficients of association, varied with sex and age.

3.2.4a. Females with Calves. Females and their young calves formed the most consistent associations within the Sarasota community. Mothers and calves were seen together in nearly every sighting of the mother during the first three to four years of the calf's life (Figure 6). The variation in the affinities shown for young calves (Figure 6) may be explained at least in part by two factors. First, newborn calves surfacing on the far side of their mothers can be difficult to see and thus may not have been recorded. Second, young calves typically lacked individually distinctive markings, and were usually identified on the basis of the female with which they were most closely associated. When young calves were swimming together in "playpens" (groups of interacting calves of similar age surrounded by their mothers), or when one female was apparently "babysitting" for another's calf, it was difficult to identify each individual calf.

Separation of the mother and calf typically occurred after three years or more. In Figure 6, the coefficients of association between mothers and calves gradually decreased after the calf reached three to four years of age, but the calves were still seen with their mothers on occasion up to at least nine to ten years of age. The precise ages at separation have been documented for four calves, but these separations occurred after the January 1984 cut-off for data included in association analyses. Thus, coefficients of association with their mothers following separation were not available. The mean age at separation for these four calves was 3.5 years ($\underline{SD}$ = 0.41).

Three years seemed to be the minimum age of separation. Only four other calves were observed to cease swimming with their mothers at less than four years of age. Two of these disappeared within the first year of life, presumably prior to weaning, and therefore they probably died. The fates of the other two remain unknown, as the separation occurred between 1976 and 1980, when few observations were made. At this writing, six other calves were still with their mothers (with coefficients of association > 0.96) more than 3.5 years after birth.

The impetus for separation of mothers and calves remains unclear. Pregnancy does not appear to be the underlying cause of separation. In two cases, mothers gave birth to a new calf within one to five months following separation. New calves were not immediately forthcoming in four other cases. In two other cases older siblings remained with their mothers following the birth of new calves.

Parent-offspring conflict was suggested by extensive toothrakes on at least two calves. Immediately prior to separation, one 3.5 year-old female calf exhibited fresh rakes over much of her dorsum anterior to her dorsal fin. The spacing between rakes (8-9 mm) was similar to that between her mother's teeth. A 4.5 year-old male calf, that was still swimming alongside his mother 17 months after the birth of a sister, showed extensive toothrakes over much of his body. However, in neither case could the mothers be definitely implicated as the sources of the rakes.

Calf age appears to be one factor involved in the ordering of schools containing females and calves. Female calves less than one year old showed a higher degree of association with other calves less than one year old than with older calves or subadults (Figure 7). A highly significant inverse correlation was found between coefficient of association and dolphin age, from newborn through subadult (Spearman rank correlation coefficient $\underline{r} = 0.60$, $\underline{t} = -7.56$, $\underline{n} = 102$, $\underline{P} < 0.001$).

The creation of a well-defined cohort of newborn calves, such as that produced by a seasonal concentration of births, would facilitate the formation of nursery schools. Calving appeared to be highly seasonal in the Sarasota community (Figure 8). Though calves may have been born throughout the year, most births occurred during the late spring through early autumn, as also shown by Irvine et al. (1981).

Reproductive seasonality appeared to be closely tied to environmental factors such as water temperature. The number of births was significantly correlated with water temperature (Spearman rank correlation coefficient $\underline{r} = 0.93$, $\underline{Z} = 3.08$, $\underline{P} < 0.001$). Births tended to occur when water temperatures exceeded 27°C, and at least 38% of the births occurred when the temperatures were in excess of 30°C. Annual water temperature cycles in the Sarasota area were highly predictable, typically ranging from lows of 13° to 14°C to highs of 30° or 31°C. The coincidence of births with the warm extreme of the thermal cycle suggests that thermoregulation requirements or associated energetic limitations may be important driving forces in determining the seasonality of reproduction. A difference between body and ambient temperatures of 7° - 10°C in the summer compared to 23° - 24°C in the winter means much less energy must be expended by the mother during the summer to maintain both her own and, indirectly, her newborn's body temperature.

The attraction between mothers with new calves may be related to a similar degree of dependency by their calves. Though precocial in terms of swimming ability at birth, newborn calves share similar limitations in their abilities, and each calf places similar energetic demands on its mother. Also, during the summer months mullet (one of the primary prey species), are abundant over the shallow grassflats frequented by the dolphins. These shallow grassflats should provide protection from large predatory sharks during the first few months of life (Wells et al., 1980).

3.2.4b. Female Associations with Females. One of the most striking features of female - female interactions was that nearly every female was seen with each other female member of the Sarasota community at some time during the study. During 1975 - 1978, 82.4% of all possible pairwise female - female associations were recorded (Figure 9). During 1980 - 1984, 95.8% of these possible associations were observed (Figure 10). The lower value from 1975 - 1978 was probably an artifact of the observation effort. Half of the females in Figure 9 were identified for the first time during the last four months of the primary 1975 - 1976 field effort, whereas all of the females in Figure 10 were observed repeatedly over multiple years.

The females were quite variable in their frequencies of association with other females. Clusters of females with higher coefficients of association with each other than with the other females are evident in Figures 9 and 10. The most obvious cluster from 1975 - 1976 included two adults, #24 and #26, and two subadults, #125 and #62. The mean coefficient of association for this cluster was 0.68 (*SD* = 0.103, *n* = 12). During 1980 - 1984, three of the four dolphins in this cluster (#24, #26, #62) were identified, and they still associated closely with each other, with a mean coefficient of association of 0.56 (*SD* = 0.124, *n* = 6). In Figure 10, these three animals appear to form the "core" assocations within a larger cluster of dolphins with similar association patterns. A second, even larger cluster was also evident in Figure 10.

The members of the clusters were examined for shared characteristics in addition to association patterns. Familial relationships were identified for six of the members of the larger of the two clusters in Figure 10. A unique marker chromosome was found in four adult females and one of their calves (#08, #14, #23, #05, #13), indicating a high degree of relatedness (Duffield et al., 1986). The mean coefficient of association between the three related females identified during 1975 - 1978 was 0.34 (SD = 0.105, n = 6). During 1980 - 1984, the mean coefficient of association for all four of these related adults was again 0.34 (SD = 0.056, n = 12). Two other females (#22 and #02) in the larger cluster were identified as a mother - calf pair in 1976. Both have given birth to new calves since 1982, and have remained in the cluster. The coefficients of association between these two females were 1.00 in 1976, and 0.31 in 1980 - 1984. The age difference between the youngest calf and the oldest adult female with the chromosome marker (30 years), the long-term presence of the dolphins in the area (since 1970 for #05), and the similarities in the coefficients of association of the adults over at least nine years, suggest that familial relationships may be important determinants in the formation of these clusters.

The females in the clusters of similar associations shown in Figures 9 and 10 typically shared congruent home ranges (Wells, 1986).

The home ranges of the members of different clusters were overlapping, but different core areas were emphasized in the animals' day-to-day activities. Wells (1986) identified particular female groups with non-overlapping core areas based on these clusters. In general, a female was considered to belong to a particular group if (1) she shared her home range with the other group members, (2) she had a coefficient of association of at least 0.31 (from the value for related females) with one or more group members, and (3) her mean coefficient of association with all of the group members was within one standard deviation of the overall mean association coefficient for all of the group members with each other. Some stable groups existed over many years. However, these groups were not discrete, permanent units of constant composition, and not all of the community members belonged to distinguishable groups. The formulation of a hard and fast definition for a less than absolute behavioral tendency is fraught with difficulty. Thus, the working definition for a group should be applied cautiously.

Two female groups were identified from the clusters in Figure 10. These two groups accounted for 78% of the females with sufficient numbers of sighting records ($\geq$ 15) to be included in Figure 10. These groups were named on the basis of the unique regions in which the activities of each group were concentrated (Figure 11). The Anna Maria female group consisted of seven identifiable non-calves: #42, #47, #48, #24, #26, #62, and #21 (Mean coefficient of association = 0.34, SD = 0.165). The Palma Sola female group consisted of 14 identifiable non-calves: #08, #14, #22, #16, #23, #10, #01, #05, #53, #07, #09, #04,

#02, and #50 (Mean coefficient of association = 0.33, SD = 0.109). Analysis using the Kruskal - Wallis test with Dunn's multiple comparison showed significant differences ($P < 0.05$) for the coefficients of association of the Anna Maria group members for each other compared to their coefficients of association for Palma Sola group members, and vice versa. The within-group coefficients of association were similar for both female groups.

A third female group within the Sarasota community was provisionally identified. The Manatee River female group consisted of two identifiable adult females (#79 and #91) with a coefficient of association of 0.92. These dolphins were not included in Figure 10 because of low numbers of sighting records (11 and 7, respectively). These two females used many of the same areas used by other groups, but they were seen most frequently to the northeast of the other groups, in the Manatee River and Terra Ceia Bay.

Five other adult females did not fit clearly into the female groups described above. Four of these (#28, #35, #52, and #68) swam often with the groups, and their home ranges were within the community range (Wells, 1986), but their associations with any particular female or group were not sufficiently frequent to constitute group membership. Female #45 spent most of her time in the southern portion of the community range, but she swam with other females when they moved through the southern range, or when she traveled to the northern range.

Members of particular female groups were rarely all present in a single school, at least in the case of a large group such as the Palma Sola females. Rather, group members often were observed in several different schools distributed through the group's range. Within these female groups, associations tended to follow patterns relating to reproductive condition. As described above, the presence and age of calves were important factors, with calfless females swimming together, and females with young calves tending to swim together. Changes in reproductive status tended to change female association patterns. For example, the associations between mother (#22) and her subadult daughter (#02) decreased from 0.77 to 0.17 after #02 gave birth to a calf. During the first year of her calf's life, the coefficients of association of #02 with two other Palma Sola female group members with young of the year (#04 and #09) increased from 0.29 and 0.39, prior to birth, to 0.57 and 0.68, respectively. Thus, while familial relationships may play an important role in determining female group membership, other factors such as reproductive condition appear to play the predominant role in determining associates within a group.

3.2.4c. Male Associations with Males. Male - male interactions were much more limited than female - female interactions. During 1975 - 1978, only 41.0% of the possible pairwise male - male associations were recorded (Figure 12). For 1980 - 1984, this figure increased to 76.2% (Figure 13). It seems likely that this increase was largely a sampling artifact, resulting from differences in duration of observation periods. Over half of the males in Figure 12 were initially identified during the final six months of the primary 1975 - 1976 field effort, whereas all of the males in Figure 13 were observed repeatedly over multiple years.

As indicated above by the analyses of class association patterns in general, the association patterns of individual males appeared to be strongly correlated with the ages of the individuals. Most male - male associations were between males of similar age. Males tended to become more restricted in their associations with other males of the same age class after the onset of sexual maturity. In both the 1975 - 1978 and 1980 - 1984 samples, adult males associated with few other adult males (40.0% and 61.9% of all possible pairwise associations, respectively). In contrast, younger males were observed in 85.7% (Figure 12) and 92.9% (Figure 13) of all possible pairwise associations with other young males. The association coefficients for individuals of each male class over the entire period 1980 - 1984 were examined with a Kruskal-Wallis test and Dunn's multiple comparison. The coefficients of association between adult males (Mean = 0.08, SD = 0.162, n = 40) were significantly ($P < 0.05$) less than those between males that matured during this period (Mean = 0.29, SD = 0.137, n = 6) or those between immature males (Mean = 0.20, SD = 0.223, n = 20). The within-age-class coefficients for the two young male categories were not significantly different from each other. From Figures 12 and 13 it is evident that the most frequent interactions between males were between small clusters of individuals of the same age classes. Younger males demonstrated a clear preference for associating with a number of other males of similar age, individual adult males showed a consistently low frequency of association with any males except a select few other adults (Figures 12, 13).

Associations between individual males of different age classes occurred, but they were infrequent. During 1975 - 1978, adult and subadult males were observed together in only 19.0% of all possible pairwise interactions. Adult males were observed during 1980 - 1984 in 73.2% of all possible pairwise associations with younger males. The mean association coefficient for the adult male interactions with other adult males was not significantly different from those for associations between adult males and either of the younger male categories. However, the within-age-class coefficients for the younger males were significantly ($\underline{P} < 0.05$) greater than their coefficients of association with adult males.

Groups of regular associates were evident for many males. The characteristics of these male groups were similar to those of the female groups. Group members moved through similar ranges (Wells, 1986). Whereas females showed a high degree of site fidelity to a relatively limited area, with occasional excursions to other areas, males visited the extremes of the community range more frequently than did females. Maturing or adult males occasionally disappeared from the normal range of the community for months at a time. Wells et al. (1980) reported a pattern of differential use of the waters of the community home range by adult males compared to subadult males. This pattern was not clearly evident during 1980 - 1984.

Adult male groups tended to be considerably smaller than female groups. Individual adult males were typically observed either as the only adult male in a school, or as a member of a persistent pair (or, in some cases, trio) of dolphins. For example, in 90.2% of his sightings adult male #41 was the only adult male identified, and in 76.9% of his sightings #58 was the only adult male identified. In contrast, relatively high coefficients of association (0.45 - 0.75) were measured for the pairings of #73 and #137, #136 and #138 during 1975 - 1976, and #73 and #74 during 1980 - 1984 (Figures 12, 13).

Pairs of closely associated adult males may have been more common than was indicated in Figures 12 and 13. Other pairs of close associates were believed to have been composed of two adult males, but the sexes and ages of some of the individuals were not confirmed. Dolphin #34, one of the largest and oldest males handled during the study, shared a coefficient of association of 0.94 with #39. Dolphin #39 was believed to be a male based on the facts that it appeared even larger than #34, it was heavily scarred, and it was not observed with a calf presumed to be its own at any time during a period of more than six years. Such large size and heavy scarring has been considered characteristic of sexually mature males (see Ridgway and Benirschke, 1977). Similarly, two other large, heavily scarred dolphins (#40 and #43) observed together consistently since 1975 and which were never seen with calves believed to be their own, shared a coefficient of association of 0.96. These two cases represented the highest coefficients of association for any pairs of dolphins in the Sarasota community, with the exception of mothers with their young calves. In another case, male #27 shared a coefficient of association of 0.55 with another large, heavily scarred dolphin that had been identified regularly since 1970, but was never with a calf of its own.

Some adult male pairs formed originally when the animals were subadults. Males were observed as members of small, persistent groups (= primary groups, Wells et al., 1980) well before they reached sexual maturity (Figures 12,13). In each case, the highest affinities were with other animals of nearly the same age. Subadult males were in schools in which only other subadult or maturing males were identified in 29.4% of the schools in which subadult males were observed. Long-lasting, closely associated pairs (with their coefficients of association) included #27 and #134 (0.71) and #56 and #133 (0.52) during 1975 - 1978, and #03 and #11 (0.80) during 1980 - 1984. The #03 - #11 pair already existed in 1980, when the dolphins were 6.5 and 5.5 years old, respectively. The mothers of these dolphins were rarely seen together during the brief time that both were identifiable in 1976, but they showed a high association coefficient (0.48) from 1980 - 1984. A persistent trio, composed of males #56 and #38 a dolphin of similar size but unknown sex, #37, had a mean coefficient of association of 0.58 (SD = 0.134) during 1980 - 1984. Unlike the adult males, all of the younger males were typically observed with a number of other males of the same age. Those males that were not part of particular groups were generally sighted with a variety of males of similar age. Groups of close associates frequently interacted with the other groups of similar age males. Extensive socializing was observed in these young male schools. The socializing bouts were manifested by much contact, simultaneous erections, chases, aerial behaviors, and splashing.

The importance of close associations to some of the individual males was suggested by two facts. First, the durations of the bonds tended to be prolonged. Dolphins #136 and #138 were observed together during 1970 - 1971 and during 1975 - 1976 (Irvine and Wells, 1972; Wells et al., 1980). Dolphins #73 and #74 were together at least from 1982 through 1985. Dolphins #56, #38, and #37 were closely associated from 1980 through 1982. The pair #38 and #37 remained closely associated until the death of #38 in 1984. Dolphins #03 and #11 have remained closely associated at least from 1980 through 1985.

Second, when one member was lost from a pair, the remaining member often formed a new bond of similar strength with another male. Adult male #73 formed a new pair with #74 following the death of his previous partner, #137. Similarly, #56 formed the trio with #38 and #37 following the death of his previous partner, #133. Likewise, #27 formed a new pair with #60 following the death of his previous partner, #134.

Speculations on the adaptive value of these male pair bonds are possible based on anecdotal field observations, but available data are insufficient to be conclusive. If some male pairs are composed of related individuals, (a possibility suggested by the fact that the mothers of at least one male pair swim in the same band), then the maintenance of the pair may serve to increase the fitness of both individuals, as in the case of lions (Schaller, 1972).

On several occasions, a male pair has been observed apparently separating an individual female from a school. One particularly intriguing incident occurred on 4 July 1985. Six dolphins, including two pairs of young adult males 10 - 13 years old and two females 7 - 10 years old moved slowly northward past our observation boat. They moved over shallow grassflats, feeding on mullet by knocking them from the water with their flukes. Two large, older adult males (#73 and #74) approached rapidly from the south. When the dolphins were resighted several minutes later, only mature female #21 from the original school was in sight, with #73 and #74. Following a brief bout of socializing culminated by tailslaps against one of the males by the female, the two males apparently chased the female at moderate speed for 2.8 km, flanking her on each side and slightly behind her or moving up alongside her. The three dolphins swam towards a feeding school of females and calves. The nursery school left the area, and the trio began feeding.

In summary, patterns of male interactions with other males apparently took either of two forms. Some adult males remained relatively isolated from other adult males, while other adult males formed close associations with a few individuals of similar age and sex, similar to those which were typical of younger males.

3.2.4d. Associations Between Females and Males. Interactions between the sexes involved most of the members of the Sarasota community

(Figures 14,15). During 1980 - 1984, 83.7% of all possible pairwise associations between males and females were recorded. There were no significant differences in the numbers of different females with which males of different ages associated.

Interactions between the sexes were less frequent than interactions within sex and age classes (Figures 14,15). The frequencies of male interactions with females varied significantly with age of the males (Kruskal - Wallis test with Dunn's multiple comparison, $\underline{P} < 0.05$). Significantly higher mean coefficients of association with females were measured for adult males (0.08, $\underline{SD} = 0.067$, $\underline{n} = 189$) and immature males (0.10, $\underline{SD} = 0.062$, $\underline{n} = 135$) than for transitional males, the males that matured during 1980 - 1984 (0.03, $\underline{SD} = 0.033$, $\underline{n} = 81$).

Interactions between subadult dolphins and members of the opposite gender of any age were relatively common. Of all groups in which subadult males were identified, 55.5% also included adult females. Of these mixed groups, 34.8% also included adult males. The co-occurrence of subadult males and adult females was independent of female reproductive seasonality (Contingency chi-square = 0.02, $\underline{P} < 0.75$).

Adult females were recorded from 44.4% sightings of groups containing maturing males. In 28.6% of these mixed sightings, adult males were also present. Frequency of sightings of maturing males with adult females was independent of female reproductive seasonality (Contingency chi-square = 1.99, $\underline{P} < 0.25$).

Individual subadult females were also seen with subadult and maturing males. During 1975 - 1978, the coefficients of association for subadult female #04 with subadult males were equal to or greater than the coefficients for the subadult males with each other (Figure 14). Similarly, during 1980 - 1984 the coefficients of association for subadult female #21 with the immature males were within the range of those of the immature males for each other.

Adult males were associated with female dolphins more frequently than were younger males, and their association frequencies were correlated with female reproductive seasonality. Adult males did not remain with any particular school of females for an extended period. Rather, they tended to move from female school to female school. Adult females were identified in 65.3% of the groups in which adult males were identified. Adult males and females were together during the May - October breeding season significantly more frequently than would be expected if the associations were distributed evenly throughout the year (Contingency chi-square = 6.04, $\underline{P} < 0.025$).

At least two very different patterns of association with females were apparent for different adult males. The resident male pattern, exemplified most clearly by #41 and #58, was characterized by associations between a single adult male with one or more females at any given time. The single male tended to remain in the limited area within which the female groups concentrated their activities. The roving male pattern, as exemplified by #34, #73 and #74, was typified by males which ranged over a large area, beyond the regions in which the largest female groups concentrated their activities. The roving males were frequently observed travelling through the channels of the community home range, spending brief periods of time with females which they encountered. Available evidence suggests that the tight multi-male units described above were characteristic of the roving male pattern, but confirmation of this will require confirmation of the sex of members of the pairs which follow this pattern, #39, #40, and #43.

The differences between these two patterns can be described best by comparing the two extreme cases for which the most sighting data were available, dolphins #41 and #34. Ninety-three percent of resident male #41's sightings were within the region used most frequently by the Anna Maria and Palma Sola female groups. Dolphin #34 ranged to the north and south of this area significantly more frequently than did #41; only 67% of his sightings were within the core areas of the main female groups (Contingency chi-square = 8.29, $\underline{P} < 0.025$). Both were large males: #41 was 266 cm long, and #34 was 273 cm long and approximately 26 years old in 1985. In 87.5% of his sightings with adult females during the breeding season #41 was the only adult male identified. In contrast, #34 shared a coefficient of association of 0.94 with #39, a presumed (but unconfirmed) adult male. Other adult males were identified in 38.9% of the schools in which #34 was with adult females during the breeding season.

The males #41 and #34 showed marked differences in their associations with females. Resident male #41 had the greatest mean coefficient of association (0.15, SD = 0.072, n = 27) for an adult male with females during 1980 - 1984. One of the lowest mean values belonged to roving male #34 (0.06, SD = 0.039, n = 27), and the difference between the two males was significant (Kruskal - Wallis test with Dunn's multiple comparison, $P < 0.05$). Resident males #41 and #58 were observed with receptive females on 26.8% and 23.1% of their sightings, respectively. In contrast, roving males #34, #73, and #74 were not observed with known receptive females during 1980 - 1984. The difference in the patterns for resident male #41 and roving male #34 was highly significant (Contingency chi-square = 15.54, $P \ll 0.001$).

During the breeding season, resident male #41 was observed with significantly more adult females per sighting (Mean = 4.82, SD = 3.316, n = 34) than was #34 (Mean = 2.17, SD = 3.621, n = 36; Kruskal - Wallis test with Dunn's multiple comparison, $P < 0.05$). In those cases when #41 was not the only adult male with a school of females, the number of females in the school was much larger than his overall mean (Mean = 8.00, SD = 2.580, n = 4). This was also true for those cases when #34 and #39 were associated with adult females and other adult males (Mean = 5.00, SD = 3.916, n = 7). These observations were suggestive of a pattern in which each single or multi- adult male unit may have typically been accompanying an optimal number of females.

In summary, associations occurred between members of all age classes of males and females. Frequencies of associations were independent of female reproductive seasonality for subadult and maturing males, but associations between adult males and females were most frequent during the breeding season. Male associations with females became less frequent as subadult males matured, but they became more frequent during adulthood. Adult males apparently engaged in at least two different patterns in their associations with adult females. Single, resident males remained in areas frequented by large numbers of females and associated with many of them. Roving multi-male groups tended to range over large areas and associated with small numbers of adult females at any given time. Only resident males have been observed with receptive females to date.

4. DISCUSSION

The data from 1980 - 1984 support the hypothesis of a stable sex and age based social structure for the Sarasota bottlenose dolphin community. In addition, improved means of recognizing familial relationships and reproductive condition have facilitated refinement of hypotheses about the structural basis of the dolphin society. The features of this society can be summarized as follows.

4.1. Social Structure Summary

The Sarasota community represents a relatively closed society (Wells, 1986). The community home range appears to be well defined and permanent. Dispersal of young out of the community has not yet been documented. Several offspring of community members have remained with the natal community through sexual maturity. Permanent immigration and emigration of of members of other age classes appears to be infrequent. However, short-term absences (days-months) from the region have been recorded for maturing and adult males.

In spite of the relatively closed nature of the community, genetic heterogeneity within the community is high (Duffield and Wells, 1986). Wells (1986) suggested that such high heterogeneity might be maintained if male movements outside of normal community ranges were a common feature of coastal bottlenose dolphin societies, and if fertile matings occurred during the excursions. Thus, Sarasota females might be expected to be impregnated by males from other communities on occasion.

This community of about 100 animals was composed of smaller assemblages of socially-interacting individuals. These groups were organized on the basis of age, sex, familial relationships, and reproductive condition. Groups of regular, long-term associates were generally of the same age and sex. Members of particular groups shared congruent ranges.

Female groups tended to be larger than male groups. One female group, at least, was composed of family members. Three generations of related females have been recorded from this group. Typically, all of the members of a particular female group did not swim together at any given time. Rather, several schools of females of similar reproductive condition were dispersed over the group's range. Different female groups had overlapping ranges, and females from different groups often swam with each other in these areas of overlap. However, different groups had different core areas in which most of their activities were concentrated.

Young dolphins remained with their natal groups for at least the first three to four years of their lives. During this time they typically swam alongside their mothers, with "babysitters," or in "playpens" with other calves, with their mothers nearby. Mothers and their calves were observed with progressively smaller numbers of animals per sighting with increasing calf age. Mothers with calves less than one year old tended to be found together more than with any other age or sex class. Male offspring were sighted with their mothers on occasion ten or more years after birth.

Upon leaving their natal groups, calves joined subadult groups. Both males and females comprised these groups, but males greatly outnumbered females. These small groups frequently swam with similar groups, interspersing bouts of traveling and feeding with intensive socializing. Subadults used much the same ranges as the adult females, but they visited the extremes of the ranges more frequently.

Upon reaching sexual maturity, some, if not all, females rejoined their natal groups. A number of close male - male associations begun as subadults or earlier were maintained through the maturing phase and into adulthood. Maturing males were found in small groups of pairs or trios.

Pairs of males formed the closest affinities of any unit except for mothers with their young calves.

Adult male groups concentrated most of their activities within the range of a single community. However, their ranges included those of a number of female groups, perhaps from more than one community. Associations between adult males and younger dolphins were infrequent. Associations between adult males and adult females were most frequent during the breeding season, and then they were most closely associated with receptive females. Adult males apparently engaged in at least two patterns of association with females. In the first, large single males resided in the areas used most extensively by the major female groups. All of the associations with presumed receptive females involved these males. The second pattern involved pairs of adult males roving through large areas, associating briefly with one or a small number of females at a time.

4.2. Mating System

The mating system of wild dolphins has defied accurate description to date. Sexual behavior, including copulation, is frequently observed under a variety of circumstances in captivity and in the wild. Both heterosexual and homosexual behavior is evident during all seasons (McBride and Hebb, 1948; Brown and Norris, 1956; Saayman and Tayler, 1977; Ostman, 1985). Copulations occur between dolphins of all age classes (Tavolga, 1966). Two-day-old male bottlenose dolphins have exhibited erections, and copulations involving dolphins within their first few months of life have been recorded (McBride and Kritzler, 1951; M. Caldwell and Caldwell, 1972). The early development of sexual behavior, many years before sexual maturity, suggests that it is quite important in the lives of the animals. However, the frequency of occurrence of sexual behavior between adults outside of the breeding season, between individuals of different species, between individuals of the same sex, and involving immature individuals indicate that sexual behavior can occur in both reproductive and non-reproductive contexts.

Descriptions of mating systems of dolphins have suffered from an inability to factor out sexual interactions occurring within strictly social contexts from those involved in reproductive contexts. Seasonal variations in reproductive condition are well documented. However, the animals exhibit few visual indications of reproductive condition. In captivity, it has been possible to monitor reproductive condition precisely through regular measurements of steroid hormone concentrations in blood (Tursiops: Kirby and Ridgway, 1984; Stenella: Wells, 1984). Thus, to define mating systems, definition of partners during coinciding periods of estrus and maximum testicular activity would be of interest. The determination of paternities through analysis of blood samples from calves resulting from these combinations would be of particular interest. Unfortunately, all of the captive experiments to date that have involved simultaneous systematic behavioral observations and hormonal measurements have occurred in situations where only a single adult male was present.

In nature, four generalized mating systems are possible: monogamy, polyandry, polygyny, and promiscuity. Ideally, identification of a mating system is based on measurements of copulation frequencies and reproductive success (LeBoeuf, 1978). These kinds of data are not yet available for free-ranging dolphins. But the mating systems may be inferred because the four mating systems differ in the patterns of relative parental investment of each sex. Because parental investment is manifested in many animals by social bonding, inferences about dolphin mating systems may be drawn from the association patterns of adults.

The Sarasota dolphins do not exhibit any patterns of long-term pair bonding between adult males and females that would be diagnostic of a monogamous system. Individual males or small groups of males typically joined larger groups of females for only brief periods. Different adult males associated with a given adult, and presumably receptive female from one day to the next.

A number of facts argue for a polygamous breeding system. The association of adult males and females mostly during the breeding season is indicative of low levels of male parental investment. Kenagy and Trombulak (1986) predicted that dolphins would exhibit extreme multi-male breeding because of their unusually large testes. They calculated relative testes size for three delphinid species (but not including *Tursiops*), and found the values to be 7.18 - 13.10 times the predicted size based on the general allometric relationship of mammalian testes mass/body mass. Their sample size was small, but the trend was consistent across five species of small odontocetes.

Members of the Genus Tursiops appeared to follow the general delphinid pattern for relative testes size. Data on testes mass and body mass for two adult male Tursiops aduncus (Ross, 1977) were used to calculate their position on a scale of relative testes size. The resulting values were 5.98 and 7.74 times the predicted values. In general, greater relative testes size is associated in mammals with multi-male breeding systems. This is apparently a result of the selective pressures of multiple inseminations, sperm competition within the female reproductive tract, spontaneous ovulations, and seasonal reproduction (Harcourt et al., 1981; Harvey and Harcourt, 1984; Kenagy and Trombulak, 1986).

The bottlenose dolphin also shows extremely high sperm concentrations in the ejaculate. Schroeder et al. (1983) reported sperm counts of up to 6.298×10^{10} sperm per cc of ejaculate for captive male bottlenose dolphins. This concentration is among the highest recorded for any mammal, and is approximately 300 times the mean concentration for humans and 100 times that of chimpanzees (Smith, 1984).

The fluid association patterns, in conjunction with the unusually high sperm producing capabilities of the bottlenose dolphins, support a polygamous mating system hypothesis for these animals. Skewed adult sex ratios and differential mortality rates relative to sex, such as those observed for the Sarasota dolphins are also characteristic of polygamous mating systems (Trivers, 1972, 1985; Ralls et al., 1980).

Polygamy is correlated with sexual dimorphism in many mammals. As Ralls et al. (1980, p. 239) state, "In species having promiscuous or polygynous mating systems, the number of matings a male may attain is potentially large and there is an increased selective premium on morphological, behavioral, and physiological characteristics that function in epigamic and intrasexual interactions directly related to mating." Some sexual size dimorphism exists in bottlenose dolphins, but it is muted in comparison with that of some other odontocetes such as pilot whales, killer whales, and sperm whales. Adult male bottlenose dolphins tend to attain greater lengths than females (D. Caldwell and Caldwell, 1972). That the dimorphism may be a result of intrasexual selection is indicated by the heightened male aggression that has been commonly reported for Tursiops reaching sexual maturity (McBride and Hebb, 1948; McBride and Kritzler, 1951; Tavolga, 1966; Norris, 1967; Caldwell and Caldwell, 1977; Wood, 1977). However, data for polygynous pinnipeds suggest that size dimorphism may not be as important in sexual selection in water as on land (Stirling, 1983).

The variability of associations between adult males and receptive females does not facilitate distinguishing between the possibilities of one male mating with multiple females or one female mating with multiple males. But, there is a strong tendency toward polygynous mating systems in the Mammalia (Eisenberg, 1981). In the extreme case, polygyny implies that a single male will control access to all of the receptive females in a group throughout the period of receptivity. Unfortunately, there are no data for the precise duration of the period of female bottlenose dolphin receptivity, though Sawyer et al. (1983) and Kirby and Ridgway (1984) reported multiple ovulations by captive female *Tursiops* during a single breeding season.

One can not rule out the possibility of a given male controlling access to a female during a relatively brief period of receptivity. In fact, captive adult males have been reported to maintain much longer associations with adult females during the breeding season than during the rest of the year (days or weeks versus minutes or hours, Tavolga and Essapian, 1957). However, given the brevity of the associations of adult males and females in the wild, and the fact that bottlenose dolphins appear to be spontaneous rather than induced ovulators (Kirby and Ridgway, 1984), it seems unlikely that a male could be assured of being present during the entire period of receptivity of a particular female. Perhaps such factors as the unrestricted movements of the females, the presence of other adult males, and/or simultaneous existence of receptive females in different schools inhibit the expression in the wild of the longer pair bonds reported from captivity.

Promiscuous and other polygamous mating systems can be distinguished on the basis of the formation of at least temporary pair bonds in the latter (Wilson, 1975, p. 327). The day-to-day changes in associations between adult male and female dolphins during the breeding season indicate that neither strict polygyny nor polyandry is the rule. Thus, we are left with promiscuity as the most likely mating system. The frequent movements of adult males from one female school to another during the breeding season suggest that the males are searching for mating opportunities. Because reproduction is roughly seasonal, and multiple ovulations per female may occur, it is likely that more than one female in the community may be receptive at any given time. Rather than investing their efforts in monopolizing access to any given receptive female, the Sarasota males appeared to be maximizing their opportunites for contact with a number of receptive females.

Promiscuous matings are not necessarily random matings. In fact, they are usually highly selective (Wilson, 1975). In theory, mating attempts by a number of males with a given female dolphin may also provide the female with opportunities to choose from a selection of males. Tayler and Saayman (1972) reported competition between adult females for attention from the adult males during the breeding season.

Observations from captivity support the hypothesis of a promiscuous mating system. Tayler and Saayman (1972, p. 21) observed a pair of captive males with females during the breeding season, and described a "...rotating, alternating kind [of mating system] lacking in permanent sexual bonds" for Tursiops aduncus. McBride (1940) reported that two adult males captured together courted the same female, and engaged in practically no fighting. In both of these accounts, dominance of one adult male over the other was well established, but both males had mating opportunities. These anecdotes are of particular interest because of the existence in the Sarasota community of closely-bonded male pairs that persist even during the breeding season.

Tests of the hypothesis of a promiscuous mating system require measurements of the relative reproductive success of males. Such measurements are possible through examination of genetic patterns from blood samples. Comparisons of results of chromosome banding pattern and electrophoretic analyses for calves, their mothers, and possible fathers can provide an indication of patterns of paternity. A demonstration of the impregnation of the receptive females in the community by a variety of males during a given breeding season would support the hypothesis of promiscuity. Additional support would be obtained if the number of calves sired by a particular male was independent of the amount of time the male associated with receptive females.

The promiscuity hypothesis would have to be re-examined relative to polygyny if, for example, all of the calves produced within a female group in a given year were sired by a single male. Bottlenose dolphins exhibit a high degree of behavioral plasticity (see Shane et al., 1986). It is possible that this plasticity could be translated into the existence of more than one mating system at any given time, as demonstrated for chimpanzees (Tutin, 1979) and other animals (Emlen and Oring, 1977). Tests of the promiscuity hypothesis are in progress at this writing. Future research will emphasize focal animal behavioral observations of males over long periods. This will allow more precise definition of periods of association with females, and examination of male - male interactions for indications that direct or indirect control of access to females may be exerted.

4.3. Rearing System

The rearing of the young appeared to be entirely the responsibility of females, and it included both maternal and allomaternal care. The parental investment of the males apparently ends with conception. Such differential investment would be expected in a promiscuous mating system, where the nature of the mating system precluded paternal identification of their own offspring. The mother-calf bond is strong, with close associations lasting several years beyond weaning.

The nursery school appears to provide a protected environment within which early post-natal development and learning occur. McBride and Kritzler (1951) observed that the parent and other adult female captive dolphins showed great solicitude for the protection of the newborn young. Leatherwood (1977) noted that subgroups containing small bottlenose dolphin calves were located away from the perimeter of free-ranging schools, and mothers shielded the young from aversive stimuli. The protective function of dolphin schools has been discussed at length by Norris and Dohl (1980) and Wells et al. (1980). As summarized by Norris and Dohl (p. 248, 1980), "The variation in school size is exactly what would be predicted if predation were the basis for the degree of schooling tendency (Williams, 1964; Hamilton, 1971)."

Nursery schools were prominent features of the Sarasota community's social structure. Schools containing the youngest calves were, on average, the largest schools observed off Sarasota. School size decreased regularly with increasing calf age (Figure 5). It may be hypothesized that this pattern might be expected if there existed an optimal school size for females without dependent calves. This optimal school size of approximately ten to twelve dolphins might be based at least in part on the need for protection from predators and mediated by resource availability. As the calves' dependency decreased and they began to contribute to the integrated functions of the schools, the overall school size decreased, but the total number of contributing members remained constant.

One measure of the effectiveness of nursery schools in protection from predation is the incidence of shark bite scarring. Of 86 dolphins examined during captures from 1975 - 1985, 22 were calves, and none of these calves exhibited obvious shark bite scars. Of the remaining non-calves, 21.9% wore obvious shark bite scars, and others were scarred in a manner suggestive of shark bites. An alternative explanation for the low incidence of scarring on calves is that these small animals were more likely to be killed than were larger dolphins when they were attacked. However, the disappearance of only two dependent calves has been documented during 1980 - 1984. In contrast, 16 calves were known to survive beyond three years of age during the same period. Thus, it seems that the nursery schools provided an effective defense against predation.

The lengthy period of close association between mother and calf beyond the 1.5 year nursing period (McBride and Kritzler, 1951) indicates that the bond is based on more than simply the nutritional needs of the calf. Norris and Dohl (1980) discussed the importance of learning in the developmental process of schooling cetaceans. Many, if not most, of the activities of every day dolphin life appear to have a learned component. The three year or longer period of the mother calf bond is likely when the calves learn or refine their knowledge of such things as echolocation, other individual and group foraging and feeding techniques (Norris and Prescott, 1961), recognition of the 100 or so other community members, home range features and limits, recognition of adjacent communities, resource distribution, predator avoidance, patterns of social interaction, and sensory integration with other school members, to name just a few.

4.4. Comparisons with Other Mammals

Beyond certain basic differences imposed by living in different media, large mammals in both aquatic and terrestrial environments face many of the same environmental pressures related to sociality. The pervasiveness of patterns of social responses to similar ecological factors both within and across taxonomic groups of terrestrial mammals (eg. Eisenberg et al., 1972; Crook et al., 1976) suggests that analogous social solutions should be exhibited by some aquatic mammals as well. Thus, it is perhaps not surprising to find that coastal bottlenose dolphins share many features of their social structure in common with a large, terrestrial carnivore such as the Serengeti lion, *Panthera leo*. Both species are top level predators in relatively open habitats. Both species engage in cooperative hunting, but for both species, prey capture is done typically on an individual basis. Increased hunting efficiency through cooperation is apparently one of the factors that has led to group formation in lions (Kleiman and Eisenberg, 1973); it is likely that the same is true for dolphins (Norris and Dohl, 1980).

Schaller (1972, p. 33) described "prides" of lions as the resident lionesses and their cubs which share the pride area and which interact peacefully. Schaller also included attending males in this definition, but his subsequent description of male behavior indicated that males could be considered separately, as in the case of the Sarasota dolphins. Much like the female groups of dolphins, different prides had ranges that overlapped, but each emphasized different core areas. Other pride features include: (1) all pride lionesses are directly related and consist of daughters, mothers, grandmothers, and pehaps another generation, (2) no matter how widely females are scattered or how frequently they meet each of the other members, they still constitute a closed social unit which strange lionesses are not permitted to join, (3) the most potent factor for drawing lionesses together is the presence of small cubs, (4) although each pride member readily associates with every other member, some, especially members of the same age and sex, are together more often than others, (5) males may be alone or together, with females or without them, (6) males often form long-lasting companionships with brothers or male pride-mates of similar age, (7) male bonds with females are not as close as with other males; male contacts with females remain casual except during courtship, (8) both nomad and resident lions inhabited the Serengeti; estrus females accept either resident or nomad males, and (9) males remain with females during the period of estrus.

Many of the pride features listed above are directly comparable to dolphin group features; other comparisons require additional data. The description of lion prides, where female group composition varied from day to day within the more permanent structure of an extended family appears to parallel dolphin group structure much more closely than do the more stable female-centered family units within kinship groups of elephants (Loxodonta africana, Douglas- Hamilton, 1973; Douglas-Hamilton and Douglas-Hamilton, 1975). More information on dolphin familial relationships and interactions are required to place the dolphin groups accurately in perspective relative to other mammalian social units.

In spite of the many similarities in their social structures, lions and dolphins apparently differ in their mating systems. Lions are polygynous, whereas bottlenose dolphins appear to be promiscuous. The marked differences may be related to several factors. First, defense of multiparous females may be a better investment for male lions than defense of the uniparous females would be in the dolphins. Second, the open habitat of the Serengeti may facilitate visual detection of competitors by males for the control of access to an estrus female lion.

Murky coastal waters and brief copulations might render such detection and defense much more difficult for bottlenose dolphins.

The apparent convergence of the social structures of dolphins and lions is intriguing. However, at our present level of knowledge about the behavioral and ecological relationships of free-ranging dolphins these comparisons are necessarily simplistic. More rigorous comparisons with lions and other mammals can lead to well founded hypotheses of the evolutionary basis of the bottlenose dolphin social system. Field studies to develop and test these hypotheses will provide a more complete understanding of the lives of these animals within a general mammalian context.

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Table I. Identifiable female bottlenose dolphins of known or estimated age.

	AGE CLASS[a]				AGE EST. BASIS[b]	NUMBER OF SIGHTINGS							
ID	70-71	75-78	80-81	82-84		75-8	80	81	82	83	84	SUM	RELATIONS[c]
124		C0			LB A	7						7	M=8
18				C0,1	LB A				34	32	4	70	M=2
61				C0	LB HA					17	3	20	M=32
20				C0,1	LB HA				24	39	4	67	M=4
2		C	S,A	A	LB HAIC	10	7	9	40	32	4	102	M=22,C=18
51				C0	LB A					33	1	34	M=28
25				C1-3	L THA				23	34	2	59	M=23
15				C0-2	LBTHA				30	38	7	75	M=1
13			C0,1	C1-3	LBTHA		3	5	23	42	4	77	M=8
62		S	S		L I	20	8	9				37	
14		S	A	A	L THI	21	9	5	22	34	6	97	
9		S	A	A	L TIC	1	3	7	38	33	1	83	C=19
125		S			L I	34						34	
21			S	S	L THI		12	9	18	24	3	66	
8		A	A	A	L T CI	20	7	8	23	42	4	104	C=124,13
45		A	A	A	L C	2	7	4	13	12	1	39	C=127,46
4		S	A	A	L THIC	38	7	8	34	39	4	130	C=20
23				A	L THC				26	36	2	64	C=25
5	A	A	A	A	L HC	16	11	11	23	41	6	108	C=128,6
35		A	A	A	L HC	1	3	10	6	24	1	45	C=30
68			A	A	L T C		4	1	4	6		15	C=121
16		A	A	A	L T C	24	11	8	21	30	4	98	C=117
53[e]		A	A	A	L C	1	3	6	23			33	C=122
42		A	A	A	L C	1	3	5	10	22		41	C=66,67
22		A	A	A	L HC	10	5	6	20	31	3	75	C=2
1		A	A	A	L THC	83	11	10	30	38	7	179	C=15
28		S	A	A	L T IC	2	5	4	7	35	1	54	C=123,51
32		A	A	A	L HC	1	3	8	13	20	3	48	C=61
126		A			L C	33						33	C=129
48	A	A	A	A	L C	1	4	8	8	16	1	38	C=86
7	A	A	A	A	L THC	37	9	8	24	40	5	123	C=11,12
10		A	A	A	L T C	20	4	8	25	38	5	100	C=3,17
26		A	A	A	L C	16	6	12	14	26	1	75	C=33
52			A	A	L HC		1	4	4	24	1	34	
24	A	A	A	A	L C	24	7	12	22	20	2	87	
47			A	A	C	9	6	5	11	16		47	C=54
50			A	A	C			4	19	12	1	36	C=57
72[d]			A	A	C		1	6	1	5		13	C=115
75[d]			A	A	C			4	6	2		12	C=116
91				A	C					6	1	7	C=120
79			A	A	C		1	1	3	5	1	11	C=119
93[d]			A	A	C			3	1	4		8	C=118

---

[a] Age classes: C0 = first year calf, C1 = second year calf, etc., S = subadult, M = maturing, A = adult.

[b] Age determinations: L = from body length, B = known date or season of birth, T = from tooth sections, H = from hormone measurements, A = regularly accompanied by presumed mother, I = independent of presumed mother, C = regularly accompanied by a calf.

[c] Relations: "M =" identifies the dolphin's mother, "C=" identifies the dolphin's calf.

[d] Considered to belong to the Passage Key Inlet - Tampa Bay community.

[e] Became diseased and disappeared in 1982.

Table II. Identifiable male bottlenose dolphins of known or estimated age.

	AGE CLASS[a]				AGE EST.	NUMBER OF SIGHTINGS							
ID	70-71	75-78	80-81	82-84	BASIS[b]	75-8	80	81	82	83	84	SUM	RELATIONS[c]
127		C			L A	1						1	M=45
128		C0			LB A	6						6	M=5
30		C	C3	C3	L HA	1	5	9	7	28	2	52	M=35
86		C	C3		L A	1	5	2				8	M=48
129		C			L A	30						30	M=126
27	C1	S	A	A	L THAI	45	7	5	11	27	3	98	
11		C0,1	S	S,M	L THAI	24	12	5	26	35	2	104	M=7
130[e]		C			L	2						2	
3		C2	S	S,M	L THAI	19	14	9	34	34	2	112	M=10
6			C0,1	C1-3	LB HA		10	9	23	41	6	89	M=5
12			C0	C1-3	LBTHA			8	24	40	5	77	M=7
17			C0	C0-2	LBT A			4	25	38	5	72	M=10
49		S	S,M	M,A	L HI	76	6	5	9	15	1	112	
131		S			L I	15						15	
56		S	S,M	M,A	L I	53	9	6	9	4		81	
132		S			L THI	1						1	
38[g]		S	S,M	M,A	L T I	31	10	9	3	18	1	72	
133[e]		S			L I	21						21	
134[e]		M			L T I	31						31	
44			S	S	L I		1	4	18	16		39	
135		M			L I	3						3	
36			S	S	L HI			2	16	23	1	42	
136	A	A			L I	13						13	
74			A	A	L HI		1		7	3	1	12	
78				A	L THI				5	6		11	
137[f]		A			L T I	52						52	
70[d]				A	L I				4	11		15	
73	A	A	A	A	L HI	19			5	6	1	31	
58		A	A	A	L HI	13	6	5	1	14		39	
138		A			L I	6						6	
112		A	A	A	L I	10				1		11	
31				S,M	L THI				17	32	2	51	
34			A	A	L T I		6	3	14	21	2	46	
139	A	A			L I	1						1	
41			A	A	L I	1	6	2	9	22	2	42	

---

[a] Age classes: C0 = first year calf, C1 = second year calf, etc., S = subadult, M = maturing, A = adult.

[b] Age determinations: L = from body length, B = known date or season of birth, T = from tooth sections, H = from hormone measurements, A = regularly accompanied by presumed mother, I = independent of presumed mother.

[c] Relations: "M =" identifies the dolphin's mother.

[d] Considered to belong to the Passage Key Inlet - Tampa Bay community.

[e] Died in 1976. [f] Died in 1977. [g] Died in 1984.

Table III. Sex and age composition of the Sarasota community during 1975 - 1976 and 1983 - 1984.

		1975 - 1976		1983 - 1984	
Class		**Males:Females**	**Total**	**Males:Females**	**Total**
Adult	No.	7:16	23	11:26	37
	%	30:70		30:70	
Subadult or Maturing	No.	9:5	14	5:1	6
	%	64:36		83:17	
Calf	No.	8:2	10	4:7	11
		80:20		36:64	

Table IV. Dolphin school composition patterns as measured by coefficients of association for classes based on age, sex, and reproductive condition. Coefficients were calculated from 177 schools of completely known composition. See text for description of the chi-square analysis.

CLASS	SUBAD. FEMALE	SUBAD. MALE	MATUR. MALE	ADULT MALE	SINGLE FEMALE	RECEP. FEMALE	PREG. FEMALE	FEM.+ CALF
SUB.FEM.	0.00	.18	.31	.10	.08	.06	.05	.05
SUB.MALE	.18	.05	.47	0.00	.17	.04	.04	.11
MAT.MALE	.31	.47	.29	.04	.10	.04	0.00	.06
AD.MALE	.10	0.00	.04	0.00	.23	.29	.10	.16
SING.FEM.	.08	.17	.10	.23	.45	.51	.23	.35
REC.FEM.	.06	.04	.04	.29	.51	.36	.11	.26
PREG.FEM.	.05	.04	0.00	.10	.23	.11	.25	.25
FEM.+CALF	.05	.11	.06	.16	.35	.26	.25	.42
CHI-SQUARE=	10.63	19.84	55.59	16.30	15.56	21.57	8.29	14.45
DF=	3	3	3	3	3	3	3	3
SIGNIF.=	P<.025	P<.001	P<.001	P<.001	P<.005	P<.001	P<.05	P<.005

Figure 1. Study area along the central west coast of Florida. Shading encloses the entire area where research has been conducted, but most captures and observations have occurred off Bradenton and Sarasota.

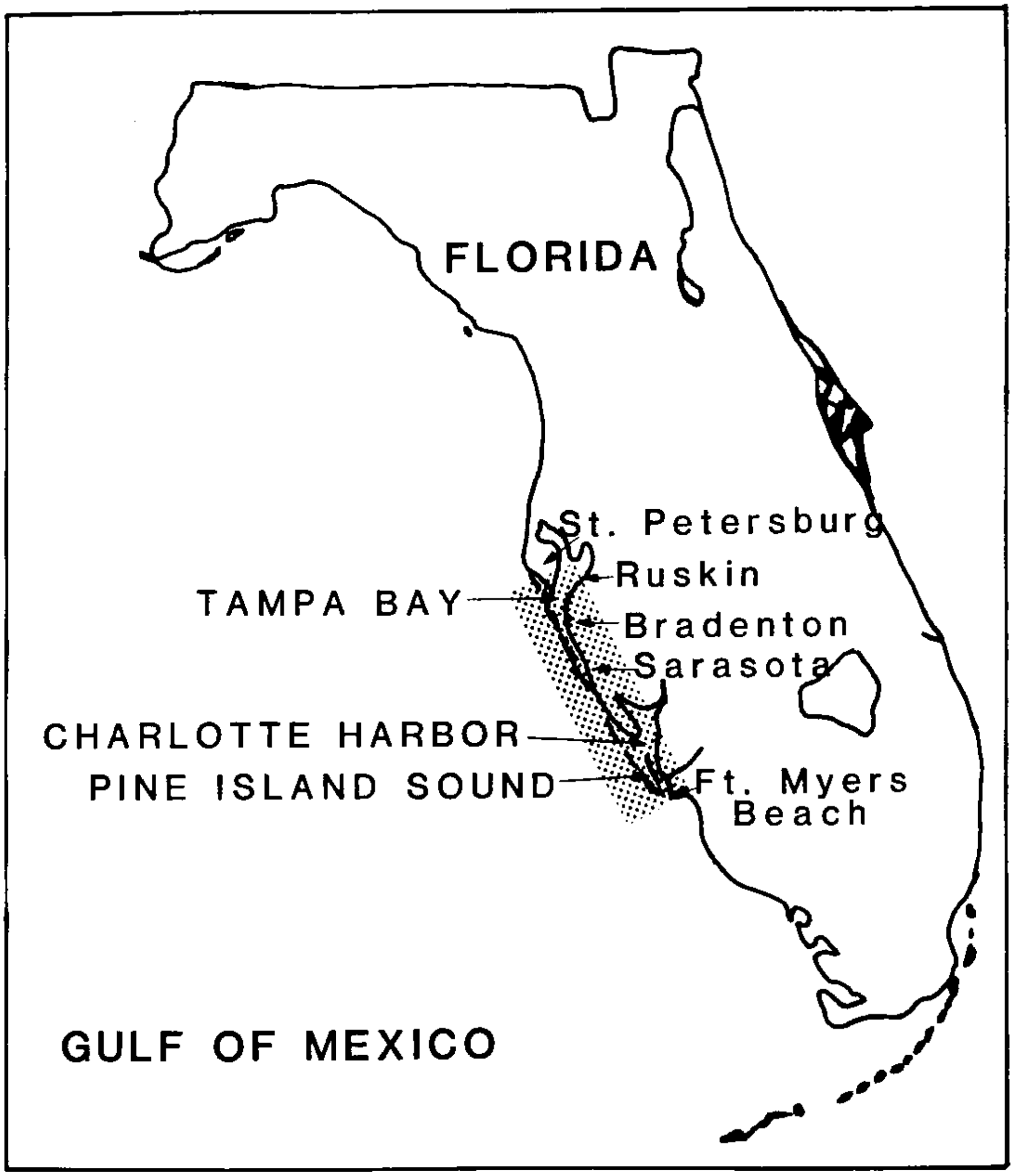

FLORIDA
St. Petersburg
Ruskin
TAMPA BAY
Bradenton
Sarasota
CHARLOTTE HARBOR
PINE ISLAND SOUND
Ft. Myers
Beach
GULF OF MEXICO

Figure 2. The notch and faint freezebrand on the dorsal fin in this 1983 photograph identify the dolphin as one that was marked as a calf in 1976. Her own calf, a yearling, surfaces alongside.

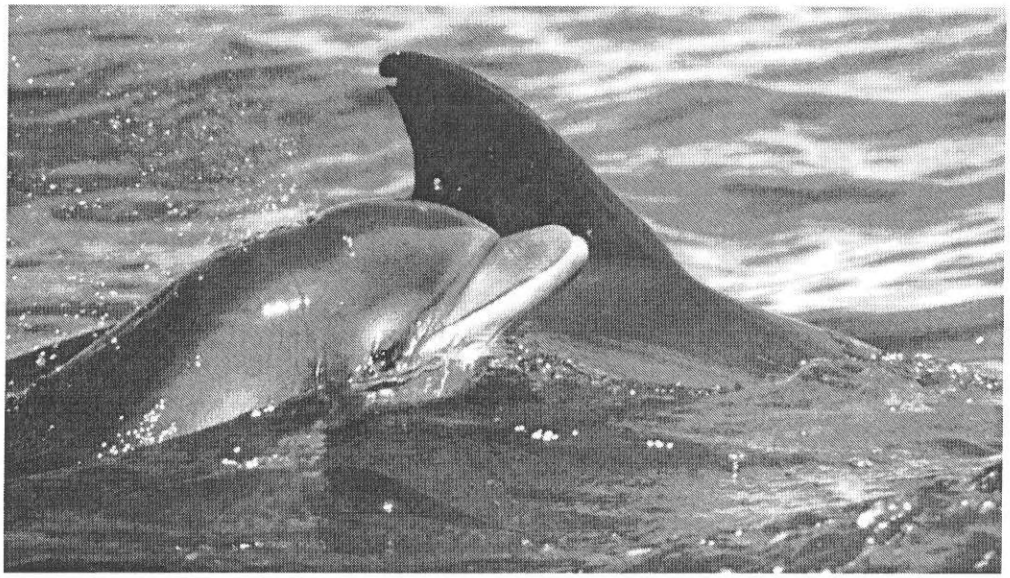
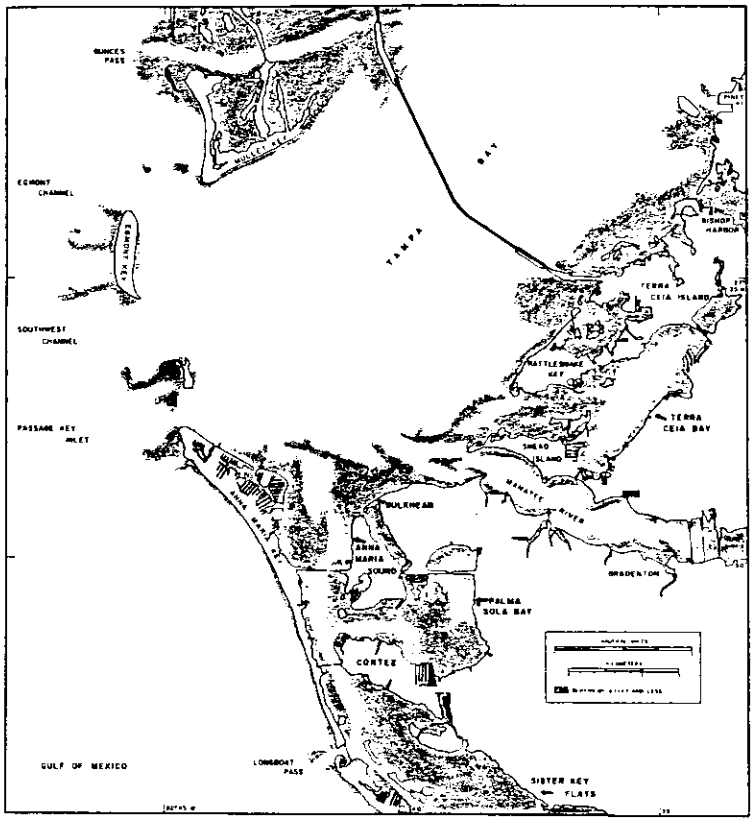


Figure 3. Details of the home range of the Sarasota population and surrounding waters. The lefthand figure shows the northern half of the primary study area, the righthand figure shows the southern half.


BUNCES PASS
MULLET KEY
EGMONT CHANNEL
EGMONT KEY
TAMPA
BAY
SOUTHWEST CHANNEL
PASSAGE KEY INLET
BISHOP HARBOR
TERRA CEIA ISLAND
RATTLESNAKE KEY
TERRA CEIA BAY
SNEAD ISLAND
MANATEE RIVER
BULKHEAD
ANNA MARIA SOUND
BRADENTON
PALMA SOLA BAY
ANNA MARIA KEY
CORTEZ
GULF OF MEXICO
LONGBOAT PASS
SISTER KEY FLATS

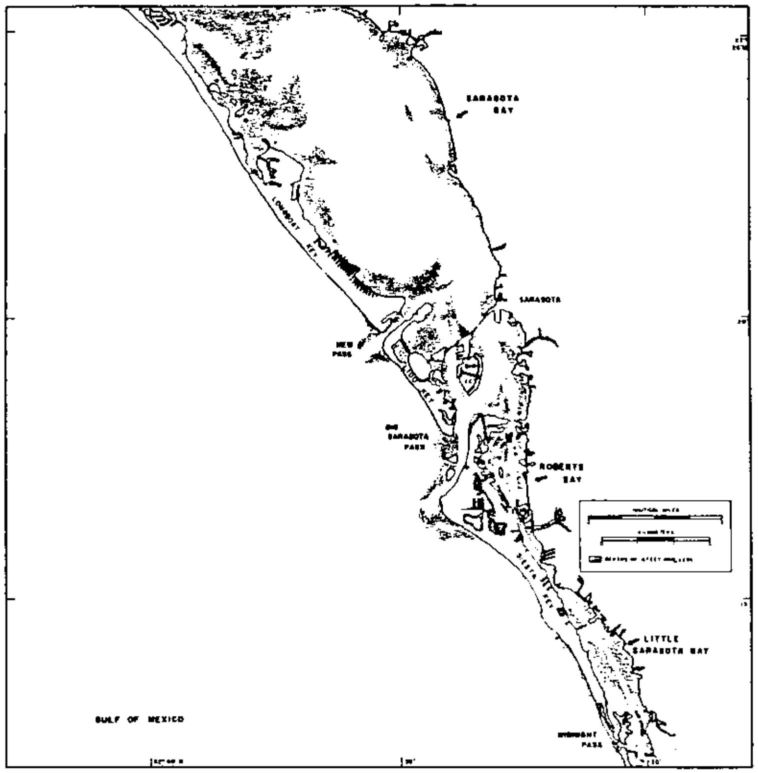

SARASOTA BAY
LONGBOAT KEY
SARASOTA
NEW PASS
LIDO KEY
BIG SARASOTA PASS
ROBERTS BAY
SIESTA KEY
LITTLE SARASOTA BAY
GULF OF MEXICO
MIDNIGHT PASS

Figure 4. Frequency distributions of the numbers of dolphins per sighting for male dolphins of different age classes. The sample size is the number of sightings which contained each age class.

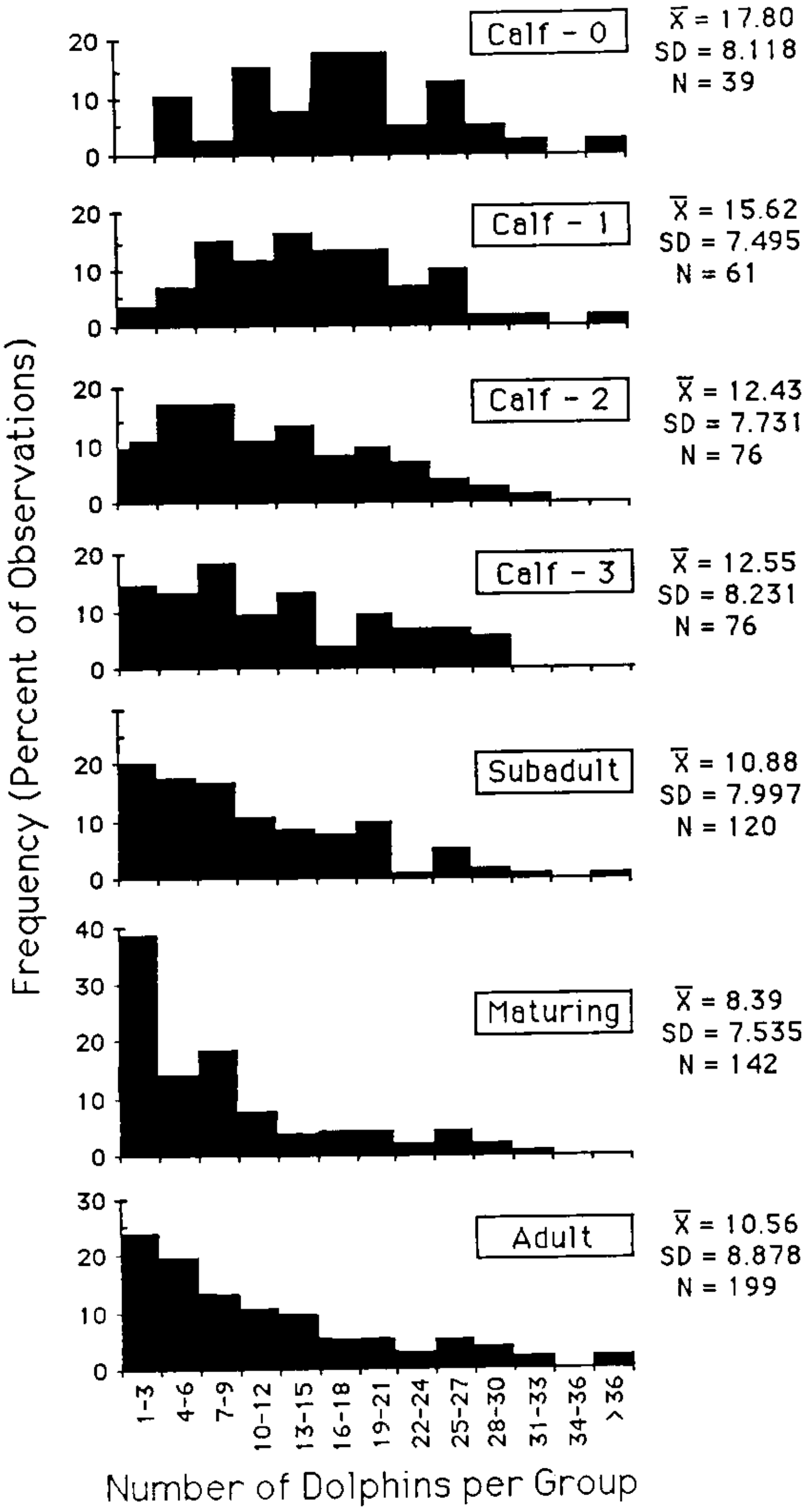

Calf - 0
X̄ = 17.80
SD = 8.118
N = 39
Calf - 1
X̄ = 15.62
SD = 7.495
N = 61
Calf - 2
X̄ = 12.43
SD = 7.731
N = 76
Calf - 3
X̄ = 12.55
SD = 8.231
N = 76
Subadult
X̄ = 10.88
SD = 7.997
N = 120
Maturing
X̄ = 8.39
SD = 7.535
N = 142
Adult
X̄ = 10.56
SD = 8.878
N = 199
Frequency (Percent of Observations)
0
10
20
30
40
1-3
4-6
7-9
10-12
13-15
16-18
19-21
22-24
25-27
28-30
31-33
34-36
>36
Number of Dolphins per Group

Figure 5. Frequency distributions of the numbers of dolphins per sighting for female dolphins of different classes of age or reproductive condition. The sample size is the number of observed groups which contained each class.

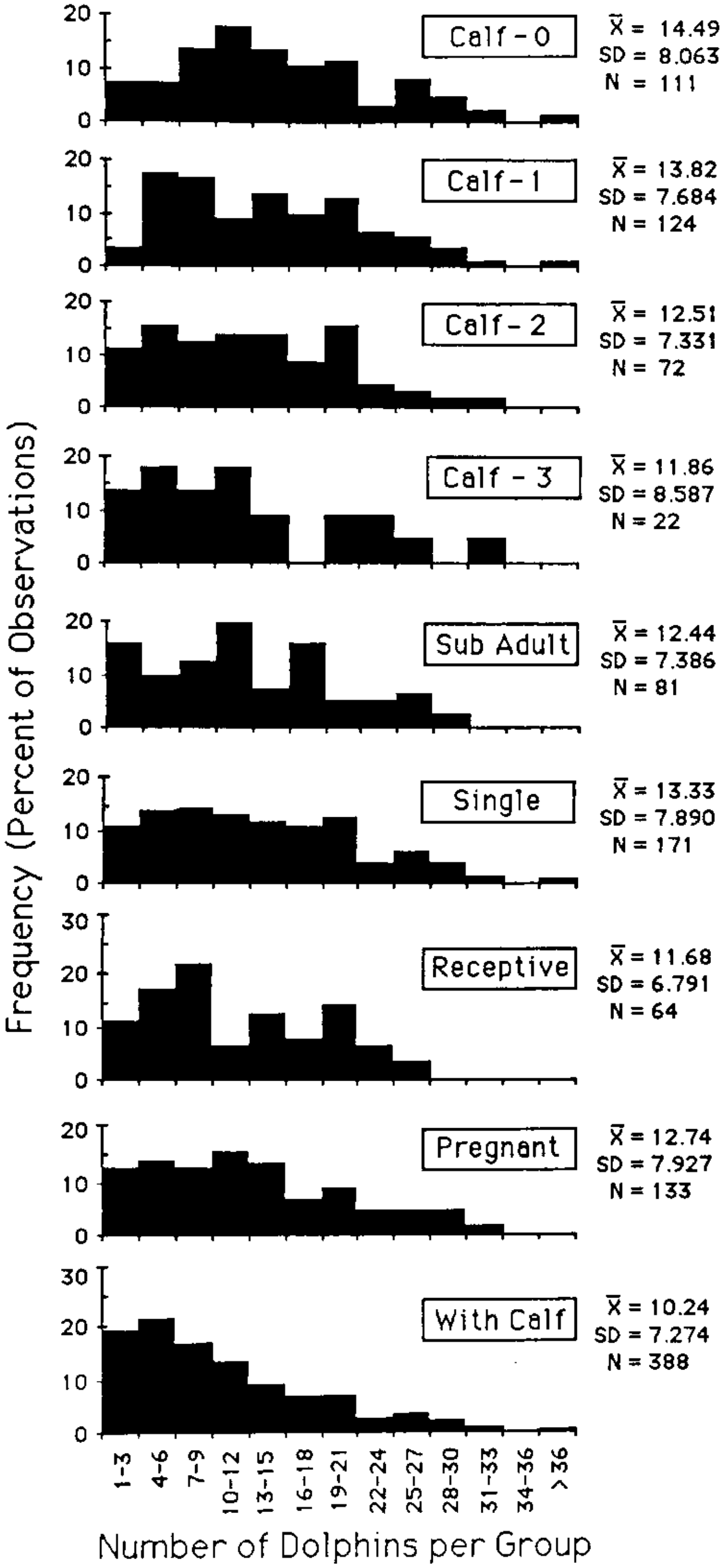

Calf - 0
X̄ = 14.49
SD = 8.063
N = 111
Calf - 1
X̄ = 13.82
SD = 7.684
N = 124
Calf - 2
X̄ = 12.51
SD = 7.331
N = 72
Calf - 3
X̄ = 11.86
SD = 8.587
N = 22
Sub Adult
X̄ = 12.44
SD = 7.386
N = 81
Single
X̄ = 13.33
SD = 7.890
N = 171
Receptive
X̄ = 11.68
SD = 6.791
N = 64
Pregnant
X̄ = 12.74
SD = 7.927
N = 133
With Calf
X̄ = 10.24
SD = 7.274
N = 388
0
10
20
30
Frequency (Percent of Observations)
1-3
4-6
7-9
10-12
13-15
16-18
19-21
22-24
25-27
28-30
31-33
34-36
> 36
Number of Dolphins per Group

Figure 6. Comparison of coefficients of association between mothers and their calves over time. Mean, standard deviation, and number of mother - calf pairs are presented for each calf age.

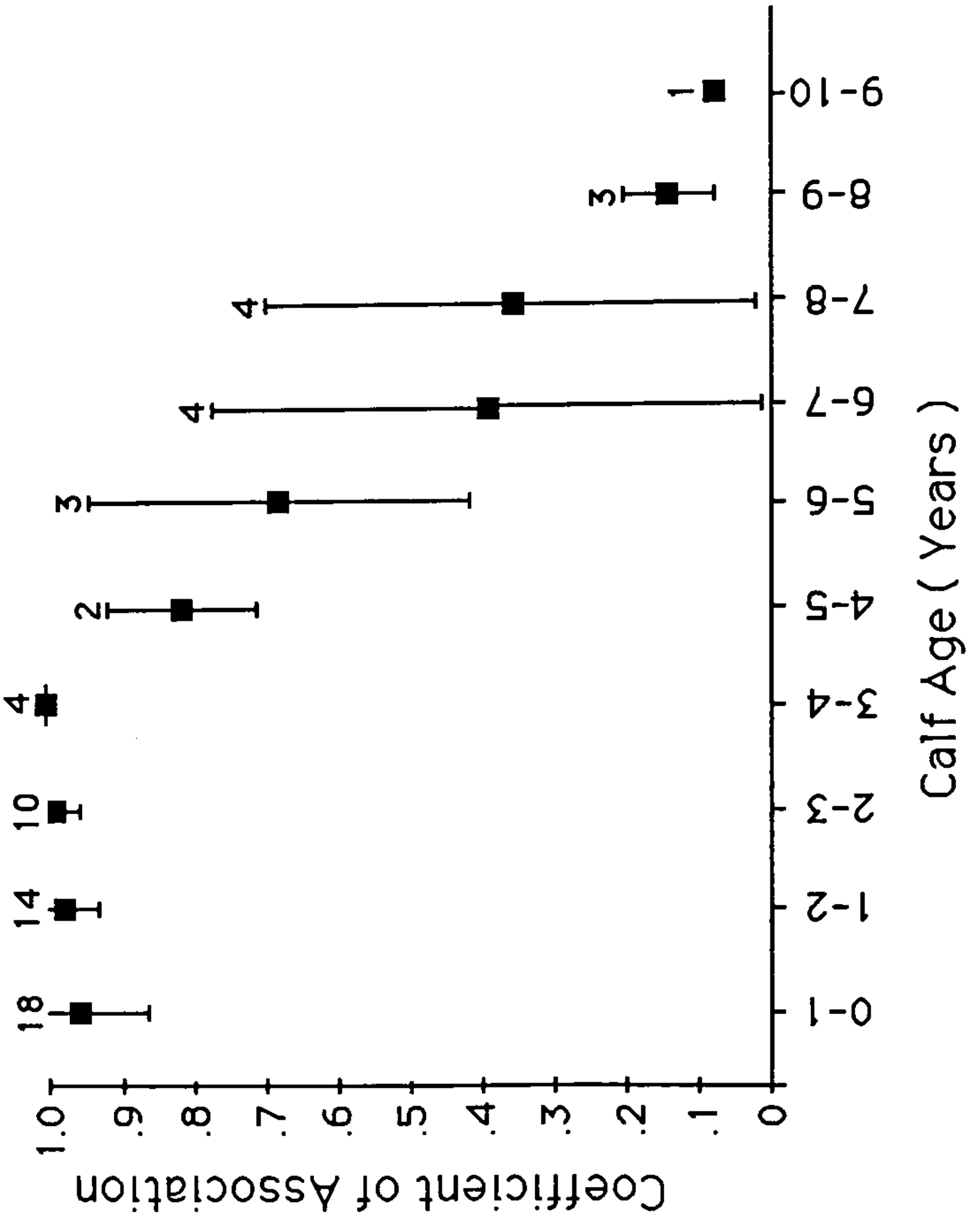

Coefficient of Association
1.0
.9
.8
.7
.6
.5
.4
.3
.2
.1
0
Calf Age (Years)
0-1
1-2
2-3
3-4
4-5
5-6
6-7
7-8
8-9
9-10
18
14
10
4
2
3
4
4
3
1

Figure 7. Mean coefficients of association of first year female calves with all other sex, age, and reproductive condition classes. Mean, standard deviation, and number of pairwise associations are presented for interactions between first year females and each other class.

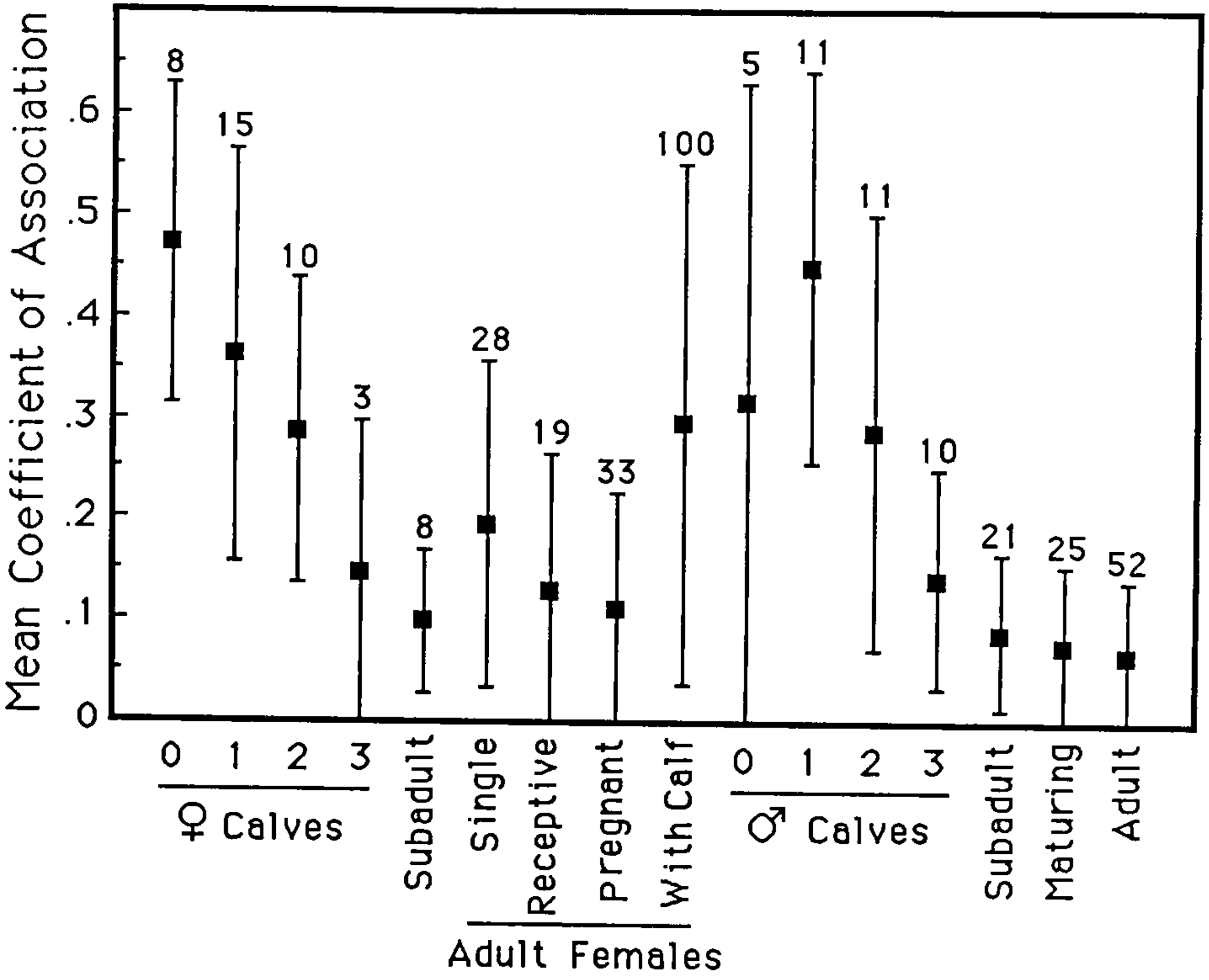

Mean Coefficient of Association
0
.1
.2
.3
.4
.5
.6
8
15
10
3
8
28
19
33
100
5
11
11
10
21
25
52
0
1
2
3
♀ Calves
Subadult
Single
Receptive
Pregnant
With Calf
Adult Females
0
1
2
3
♂ Calves
Subadult
Maturing
Adult

Figure 8. Seasonality of bottlenose dolphin births near Sarasota, Florida during 1976 - 1985, relative to month and water temperature. "Actual Births" refer to those documented within a given month. "Possible Births" were scored when the interval between the last sighting of a mother without a calf and her first sighting with a new calf spanned more than one month. A possible birth was considered to have an equal probability of occurrence at any given time during the interval. Mean water temperatures were calculated from records from Palma Sola Bay during 1975 - 1982.

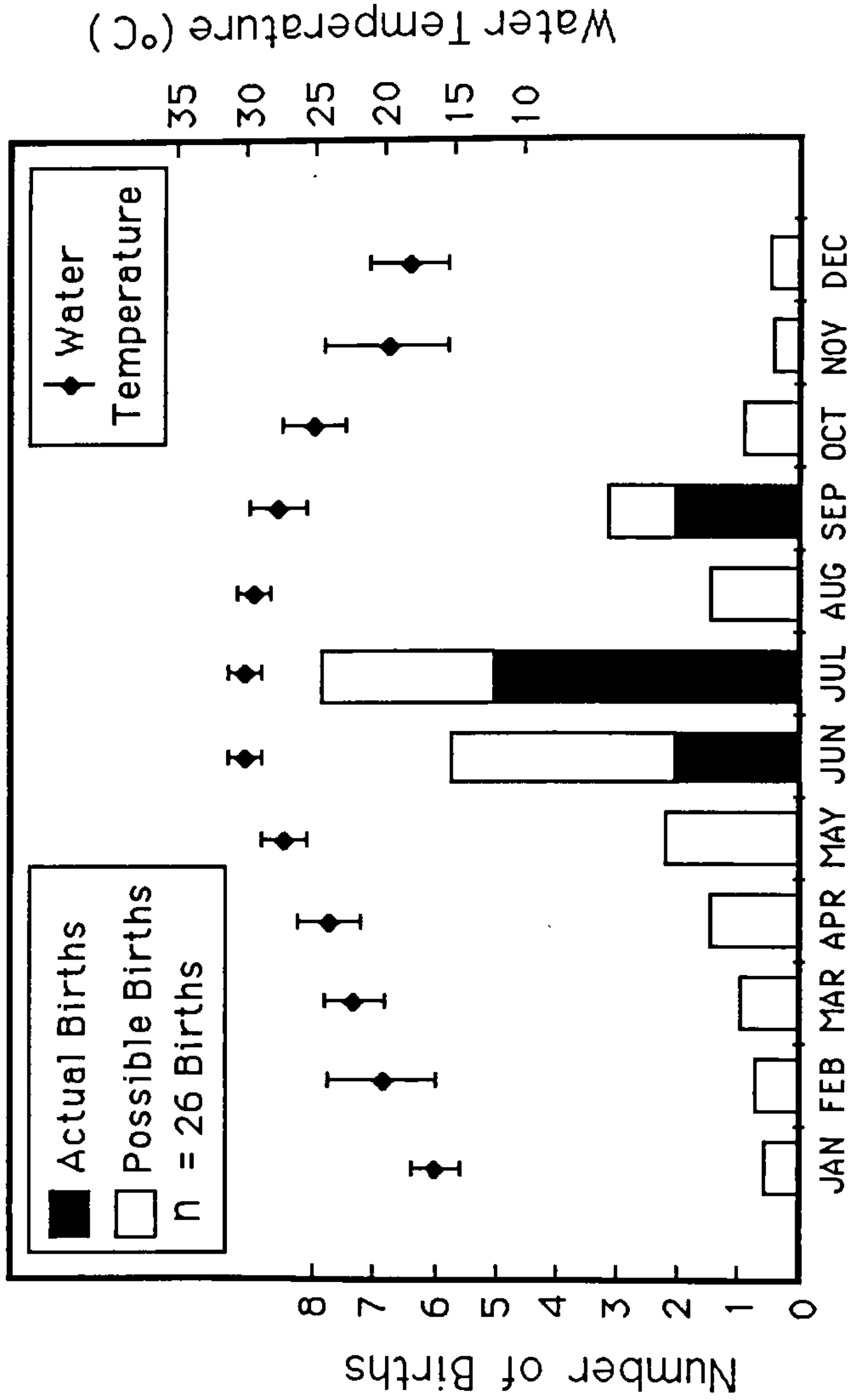
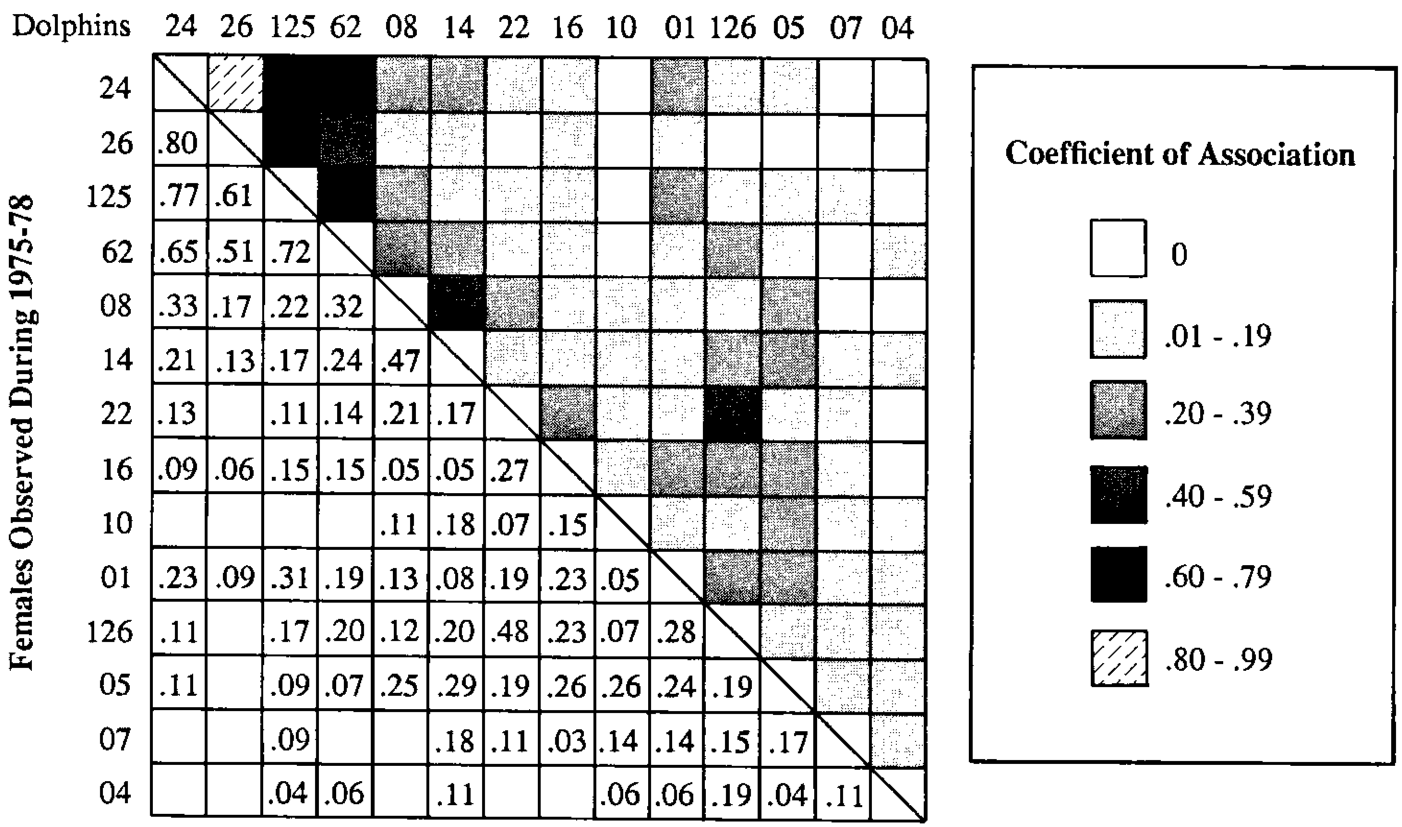

Actual Births
Possible Births
n = 26 Births
Water Temperature
Number of Births
0
1
2
3
4
5
6
7
8
Water Temperature (°C)
10
15
20
25
30
35
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC

Figure 9. Coefficients of association for pairs of female dolphins observed during 1975 - 1978. The coefficients given in the bottom half of the matrix are presented graphically with corresponding degrees of shading in the upper half.

Females Observed During 1975-78



Dolphins	24	26	125	62	08	14	22	16	10	01	126	05	07	04
24														
26	.80													
125	.77	.61												
62	.65	.51	.72											
08	.33	.17	.22	.32										
14	.21	.13	.17	.24	.47									
22	.13		.11	.14	.21	.17								
16	.09	.06	.15	.15	.05	.05	.27							
10					.11	.18	.07	.15						
01	.23	.09	.31	.19	.13	.08	.19	.23	.05					
126	.11		.17	.20	.12	.20	.48	.23	.07	.28				
05	.11		.09	.07	.25	.29	.19	.26	.26	.24	.19			
07			.09			.18	.11	.03	.14	.14	.15	.17		
04			.04	.06		.11			.06	.06	.19	.04	.11	

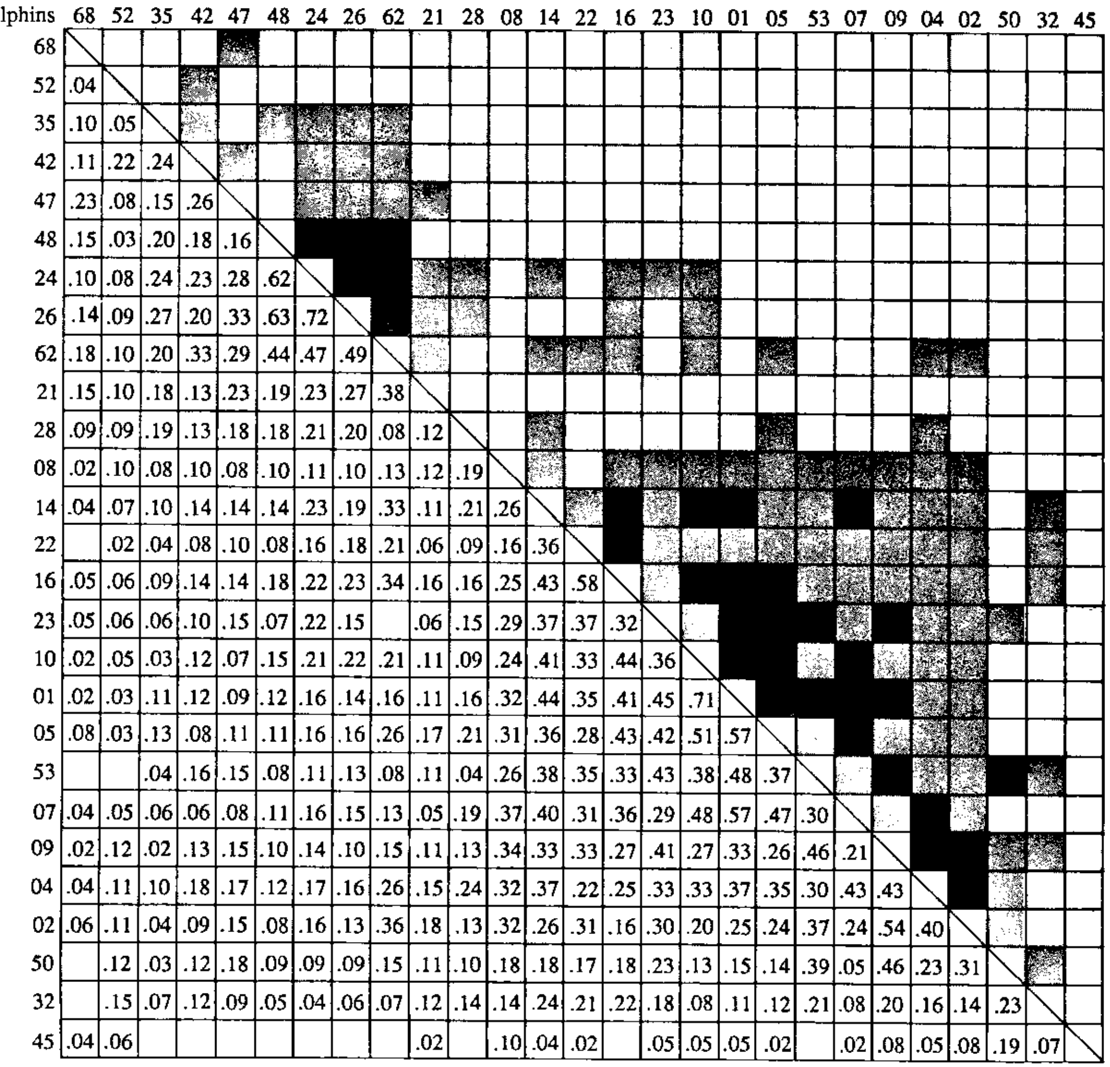
Females Observed During 1975-78

Coefficient of Association

- ☐ 0
- ░ .01 - .19
- ▒ .20 - .39
- ▓ .40 - .59
- █ .60 - .79
- ▨ .80 - .99

Figure 10. Coefficients of association for pairs of female dolphins observed during 1980 - 1984. The coefficients given in the bottom half of the matrix are presented graphically with corresponding degrees of shading in the upper half.

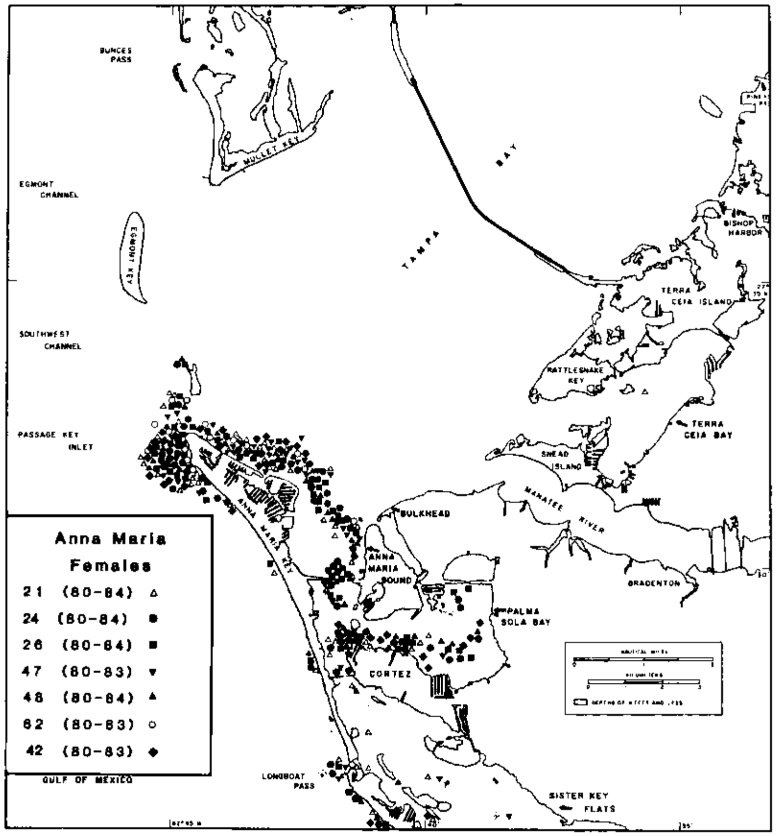
Females Observed During 1980-84



Females Observed During 1980-84

Dolphins	68	52	35	42	47	48	24	26	62	21	28	08	14	22	16	23	10	01	05	53	07	09	04	02	50	32	45
68																											
52	.04																										
35	.10	.05																									
42	.11	.22	.24																								
47	.23	.08	.15	.26																							
48	.15	.03	.20	.18	.16																						
24	.10	.08	.24	.23	.28	.62																					
26	.14	.09	.27	.20	.33	.63	.72																				
62	.18	.10	.20	.33	.29	.44	.47	.49																			
21	.15	.10	.18	.13	.23	.19	.23	.27	.38																		
28	.09	.09	.19	.13	.18	.18	.21	.20	.08	.12																	
08	.02	.10	.08	.10	.08	.10	.11	.10	.13	.12	.19																
14	.04	.07	.10	.14	.14	.14	.23	.19	.33	.11	.21	.26															
22		.02	.04	.08	.10	.08	.16	.18	.21	.06	.09	.16	.36														
16	.05	.06	.09	.14	.14	.18	.22	.23	.34	.16	.16	.25	.43	.58													
23	.05	.06	.06	.10	.15	.07	.22	.15		.06	.15	.29	.37	.37	.32												
10	.02	.05	.03	.12	.07	.15	.21	.22	.21	.11	.09	.24	.41	.33	.44	.36											
01	.02	.03	.11	.12	.09	.12	.16	.14	.16	.11	.16	.32	.44	.35	.41	.45	.71										
05	.08	.03	.13	.08	.11	.11	.16	.16	.26	.17	.21	.31	.36	.28	.43	.42	.51	.57									
53			.04	.16	.15	.08	.11	.13	.08	.11	.04	.26	.38	.35	.33	.43	.38	.48	.37								
07	.04	.05	.06	.06	.08	.11	.16	.15	.13	.05	.19	.37	.40	.31	.36	.29	.48	.57	.47	.30							
09	.02	.12	.02	.13	.15	.10	.14	.10	.15	.11	.13	.34	.33	.33	.27	.41	.27	.33	.26	.46	.21						
04	.04	.11	.10	.18	.17	.12	.17	.16	.26	.15	.24	.32	.37	.22	.25	.33	.33	.37	.35	.30	.43	.43					
02	.06	.11	.04	.09	.15	.08	.16	.13	.36	.18	.13	.32	.26	.31	.16	.30	.20	.25	.24	.37	.24	.54	.40				
50		.12	.03	.12	.18	.09	.09	.09	.15	.11	.10	.18	.18	.17	.18	.23	.13	.15	.14	.39	.05	.46	.23	.31			
32		.15	.07	.12	.09	.05	.04	.06	.07	.12	.14	.14	.24	.21	.22	.18	.08	.11	.12	.21	.08	.20	.16	.14	.23		
45	.04	.06								.02		.10	.04	.02		.05	.05	.05	.02		.02	.08	.05	.08	.19	.07	

Figure 11. Sightings of representative dolphins of the Anna Maria (left) and Palma Sola (right) female groups in the northern half of the community home range. Note the differential use of Palma Sola Bay and the waters around the northern half of Anna Maria Key.


BUNCES PASS
MULLET KEY
EGMONT CHANNEL
EGMONT KEY
TAMPA
BAY
BISHOP HARBOR
TERRA CEIA ISLAND
SOUTHWEST CHANNEL
RATTLESHAKE KEY
TERRA CEIA BAY
PASSAGE KEY INLET
SNEAD ISLAND
MANATEE RIVER
BULKHEAD
ANNA MARIA KEY
ANNA MARIA SOUND
BRADENTON
PALMA SOLA BAY
CORTEZ
LONGBOAT PASS
SISTER KEY FLATS
GULF OF MEXICO
82°45' W
Anna Maria
Females
21 (80-84) △
24 (80-84) ●
26 (80-84) ■
47 (80-83) ▼
48 (80-84) ▲
62 (80-83) ○
42 (80-83) ◆

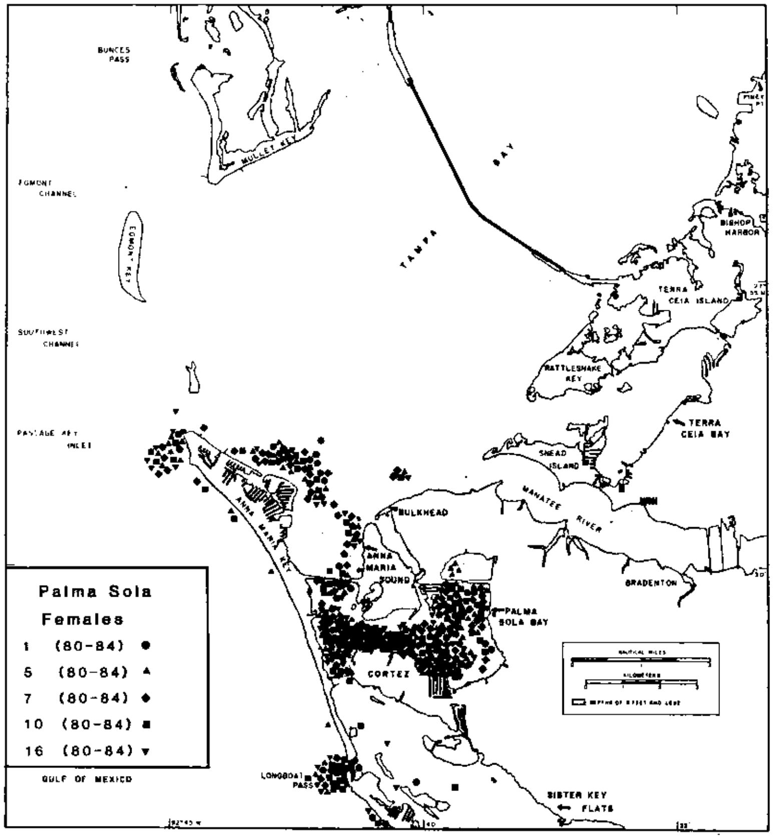
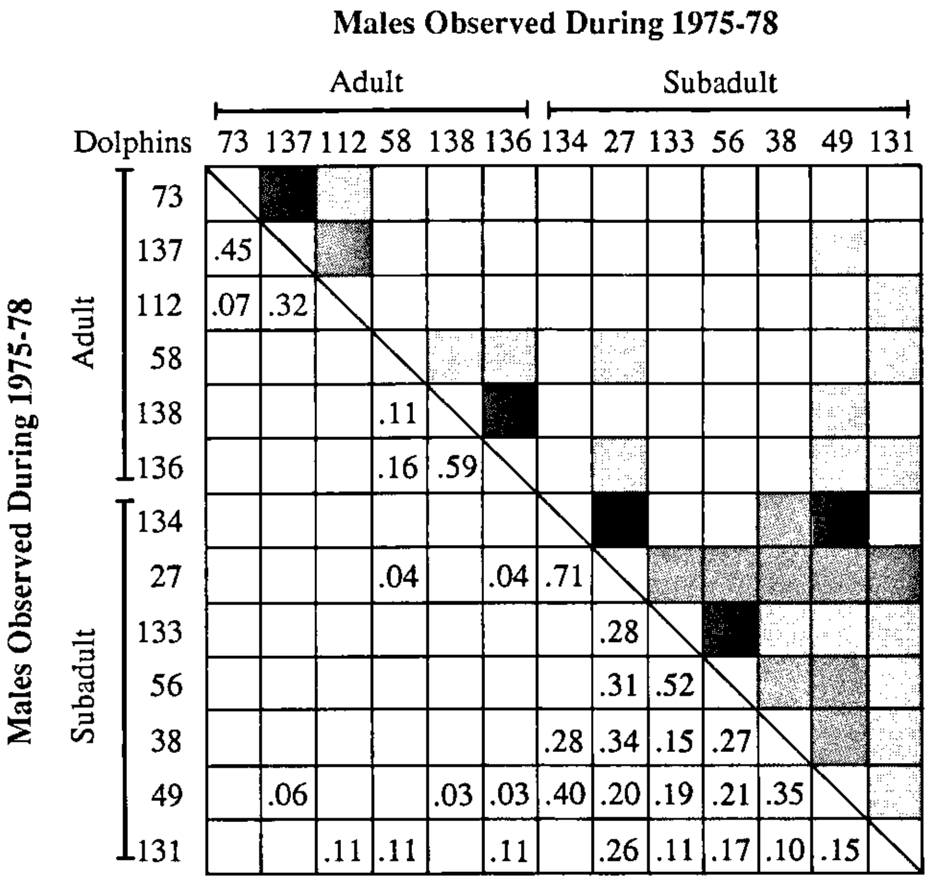

BUNCES PASS
MULLET KEY
EGMONT CHANNEL
EGMONT KEY
TAMPA
BAY
BISHOP HARBOR
TERRA CEIA ISLAND
SOUTHWEST CHANNEL
RATTLESNAKE KEY
TERRA CEIA BAY
PASSAGE KEY INLET
SNEAD ISLAND
MANATEE RIVER
BULKHEAD
ANNA MARIA KEY
ANNA MARIA SOUND
BRADENTON
PALMA SOLA BAY
CORTEZ
LONGBOAT PASS
SISTER KEY FLATS
GULF OF MEXICO
82°45' W
Palma Sola
Females
1 (80-84) ●
5 (80-84) ▲
7 (80-84) ◆
10 (80-84) ■
16 (80-84) ▼

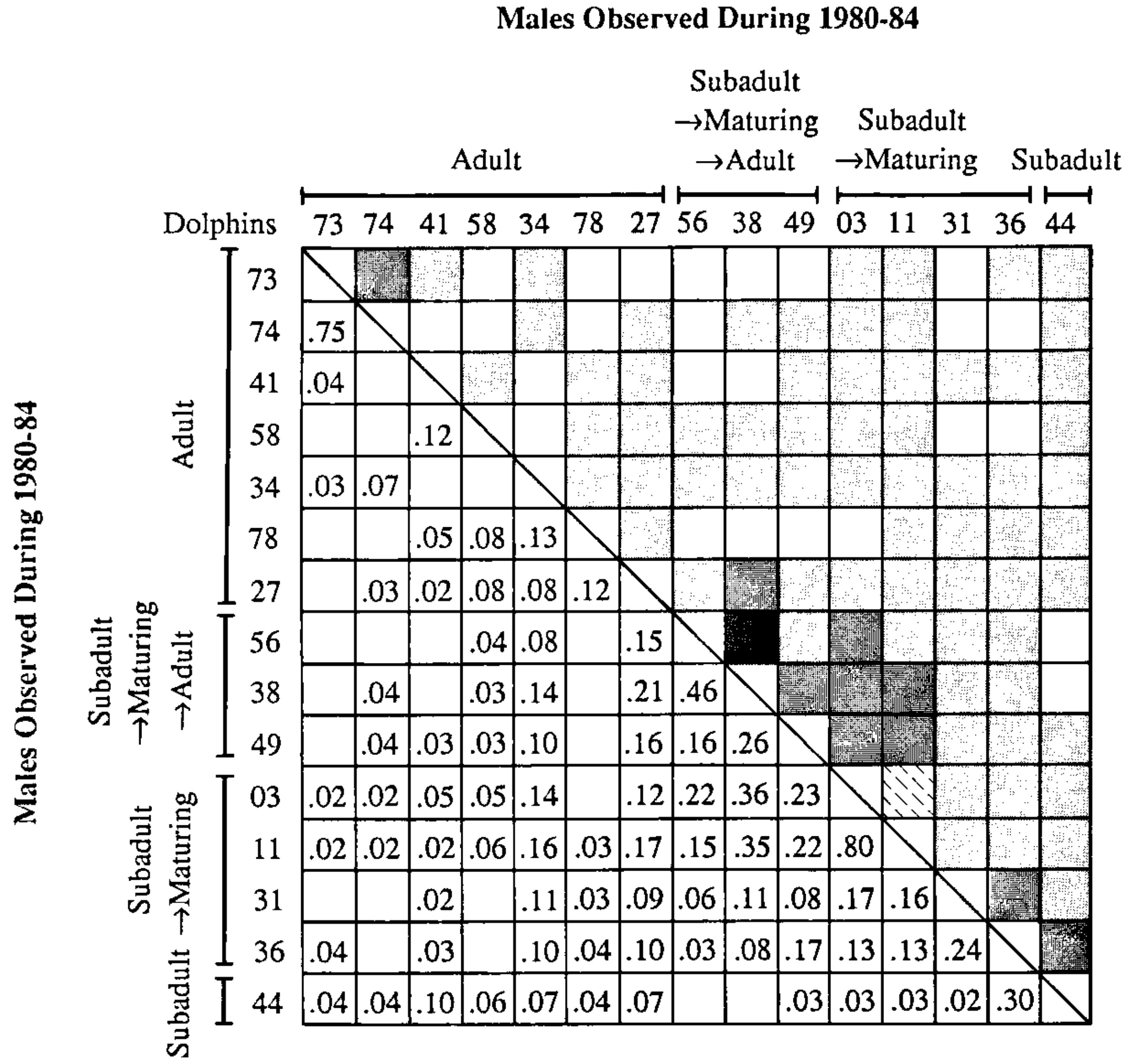
Figure 12. Coefficients of association for pairs of male dolphins observed during 1975 - 1978. The coefficients given in the bottom half of the matrix are presented graphically with corresponding degrees of shading in the upper half.



Males Observed During 1975-78

Males Observed During 1975-78	Dolphins	73	137	112	58	138	136	134	27	133	56	38	49	131
		Adult						Subadult						
Adult	73													
	137	.45												
	112	.07	.32											
	58													
	138				.11									
	136				.16	.59								
Subadult	134													
	27				.04		.04	.71						
	133								.28					
	56								.31	.52				
	38							.28	.34	.15	.27			
	49		.06			.03	.03	.40	.20	.19	.21	.35		
	131			.11	.11		.11		.26	.11	.17	.10	.15	

Figure 13. Coefficients of association for pairs of male dolphins observed during 1980 - 1984. The coefficients are overall values, based on the entire four year period. Thus, some of the calculations are for males that made transitions through more than one age class. The coefficients given in the bottom half of the matrix are presented graphically with corresponding degrees of shading in the upper half.



Males Observed During 1980-84

		Adult							Subadult →Maturing →Adult			Subadult →Maturing				Subadult
	Dolphins	73	74	41	58	34	78	27	56	38	49	03	11	31	36	44
Adult	73															
	74	.75														
	41	.04														
	58			.12												
	34	.03	.07													
	78			.05	.08	.13										
	27		.03	.02	.08	.08	.12									
Subadult →Maturing →Adult	56				.04	.08		.15								
	38		.04		.03	.14		.21	.46							
	49		.04	.03	.03	.10		.16	.16	.26						
Subadult →Maturing	03	.02	.02	.05	.05	.14		.12	.22	.36	.23					
	11	.02	.02	.02	.06	.16	.03	.17	.15	.35	.22	.80				
	31			.02		.11	.03	.09	.06	.11	.08	.17	.16			
	36	.04		.03		.10	.04	.10	.03	.08	.17	.13	.13	.24		
Subadult	44	.04	.04	.10	.06	.07	.04	.07			.03	.03	.03	.02	.30	

Males Observed During 1980-84

Figure 14. Coefficients of association for male - female pairs observed during 1975 - 1978. The high coefficients obscured by shading are as follows: 24/73=0.62, 125/73=0.61, and 04/49=0.66.

Males Observed During 1975-78

Females Observed During 1975-78

	Adult						Subadult						
Dolphin	73	137	112	58	138	136	134	27	133	56	38	49	131
24	[illegible]	.26	.06										
26	[illegible]	.26	.08										.08
125	[illegible]	.25	.06									.04	.07
62	[illegible]	.20						.07		.06	.07		.08
08	.32	.05	.07										.36
14	.25			.07		.07		.07			.04	.08	.29
22	.14	.07	.20										.10
16	.15	.09	.27	.06				.03	.05	.03			.07
10		.05	.07	.08		.08		.14					.18
01	.29	.18	.19			.09		.05				.09	.06
126	.13	.08	.26					.06	.06	.06	.03	.11	.30
05	.13							.03				.03	.16
07		.06		.05		.05		.06	.07	.03	.04	.07	.19
04				.05		.05	[illegible]	.30	.24	.16	[illegible]	[illegible]	.36

Figure 15. Coefficients of association for male - female pairs observed during 1980 - 1984.

Males Observed During 1980-84

Females Observed During 1980-84

	Adult							Subadult →Maturing →Adult			Subadult →Maturing				Subadult
Dolphins	73	74	41	58	34	78	27	56	38	49	03	11	31	36	44
68			.03	.05	.10	.10	.03			.04	.07	.06	.03	.08	.11
52			.05	.07			.09			.06	.06	.07	.03	.08	.25
35			.14	.06	.13		.02				.07	.08	.07	.19	.19
42	.04	.04	.10	.03	.02		.04				.05	.02		.15	.38
47	.08	.04	.05	.19	.07	.11	.09	.03	.03	.14	.08	.05		.19	.13
48	.08	.08	.15	.06	.12	.06	.07			.06	.05	.03	.05	.03	.16
24	.08	.08	.17	.07	.07	.07	.05			.06	.06	.04	.04	.06	.18
26	.09	.09	.10	.09	.10	.04	.04			.04	.07	.03	.04	.06	.14
62			.24	[illegible]			.14	.06	.06		.05				.29
21	.08	.05	.19	.15	.09		.12	.02	.04	.10	.23	.19	.06	.17	.19
28	.06	.03	.19	.08	.12	.04	.13		.02	.14	.07	.06	.09	.11	.11
08	.02	.02	.10	.11	.02	.08	.16	.04	.03	.05	.10	.12	.07	.07	.10
14	.05	.02	.22	.18	.08	.11	.09	.04	.03	.11	.13	.10	.09	.13	.09
22	.03		.21	.11	.04	.09	.10			.02	.17	.12	.08	.08	.04
16	.05	.02	.33	.20	.03	.06	.14	.06	.05	.07	.20	.14	.08	.04	.07
23	.05	.05	.17	.20	.08	.08	.10			.05	.13	.11	.02	.10	.10
10	.07	.04	.18	.08	.05	.10	.09	.02	.02	.03	.13	.08	.08	.02	.07
01		.02	.20	.08	.07	.09	.11	.07	.06	.05	.18	.14	.06	.05	.09
05	.04	.02	.18	.15	.07	.06	.11	.07	.06	.06	.18	.12	.07	.03	.05
53			.08	.14	.11	.22	.11	.07	.07	.04	.14	.08	.15	.13	.22
07	.04	.02	.22	.09	.06	.08	.13	.05	.05	.08	.17	.13	.10	.05	.08
09	.04	.04	.08	.04	.06	.07	.12	.02	.02	.07	.16	.14	.08	.08	.13
04	.10	.06	.18	.14	.04	.05	.14	.03	.02	.06	.16	.16	.11	.09	.08
02	.02	.02	.15	.10	.03	.09	.12		.06	.06	.14	.14	.09	.12	.12
50	.04	.04	.09	.04	.05	.09	.12			.03	.10	.10		.08	.11
32	.03		.09	.11			.08			.05	.10	.09	.07	.14	.02
45			.03				.07	.03						.06	

CHAPTER THREE

REPRODUCTIVE BEHAVIOR AND HORMONAL CORRELATES IN HAWAIIAN SPINNER DOLPHINS, *STENELLA LONGIROSTRIS*

Reproductive Behavior and Hormonal Correlates in Hawaiian Spinner Dolphins, *Stenella longirostris*

ABSTRACT

The distinction between the reproductive and social context of sexual behavior for dolphins is often difficult to make. This problem was examined through comparison of behavior patterns and steroid hormone concentrations in a captive colony of Hawaiian spinner dolphins, *Stenella longirostris.* Once every two weeks, behavioral observations were made over a 24 hour period, and blood samples were drawn for radioimmunoassay of testosterone in the male, and estradiol and progesterone in the two females. An apparent seasonal peak in testosterone was recorded for the male; possible ovulations were noted for the females. The amount of time spent in heterosexual swimming associations did not vary predictably relative to hormone levels. Genital-to-genital contact and mutual ventral presentations occurred most frequently during periods of high testosterone levels. Beak-to-genital propulsion appeared to be related to ovulatory events. All other kinds of contact, one-way ventral presentations, and chases occurred with equal frequency regardless of reproductive hormone levels, suggesting a more social context for these behaviors.

Knowledge of reproductive cycles is crucial to understanding any society of animals. The purpose of this study was to attempt to relate measurements of steroid reproductive hormone concentrations to concurrent observations of behavioral patterns in order to distinguish between reproductive and social contexts of sexual behavior in Hawaiian spinner dolphins, Stenella longirostris, and to examine the effects of reproductive condition on school structure.

Time relationships between hormonal events and the behavioral and physical correlates of reproduction are well known for other mammals. For example, close monitoring of hormone concentrations in study groups of rhesus monkeys (Macaca mulatta) has allowed precise determination of the timing of endocrine events associated with ovulations and has resulted in observations of strong correlations between mating behavior and hormone concentrations (Wilson, Gordon and Collins, 1982). Until recently there has not been an effective, harmless means of assessing the reproductive condition of dolphins. Now, radioimmunoassay analysis of steroid hormones, using small blood samples, provides a practical means of assessing reproductive conditions of both male and female dolphins. The technique has been applied to bottlenose dolphins (Tursiops truncatus) and common dolphins (Delphinus delphis) (Sawyer-Steffan and Kirby, 1980; Kirby and Ridgway, 1984). I attempt here to use a combination of radioimmunoassays and behavioral observations to see how well the two kinds of assessments support one another. Does overt sexual behavior closely track changes in blood-carried steroid hormones? Can particular behavior patterns be identified at having reproductive vs social contexts?

Delphinid social and sexual behavior has been described qualitatively for a variety of species, including bottlenose dolphins (McBride and Hebb, 1948; McBride and Kritzler, 1951; Tavolga and Essapian, 1957; Tavolga, 1972; Caldwell and Caldwell, 1972; Tayler and Saayman, 1972; Saayman, Tayler and Bower, 1973; Saayman and Tayler, 1977), common dolphins (Essapian, 1962), and members of the genus Stenella (Bateson, 1974; Norris and Dohl, 1980). Puente and Dewsbury (1976) identified and quantified the occurrence of "courtship and copulatory" patterns for bottlenose dolphins; from the frequencies they observed they determined that some patterns were more likely to be associated with copulation than were others. Several authors have recognized the importance of sexual behavior in both reproductive and social contexts (Saayman and Tayler, 1977; Norris and Dohl, 1980). Norris and Dohl state (page 845) ". . .sexual behavior and social communication are interwoven to such an extent that it is often impossible to separate true courtship and mating behavior from communicative behavior of other sorts."

METHODS

A captive colony of spinner dolphins held at Sea Life Park, Oahu, Hawaii, was sampled and observed regularly. From September 1979 until February 1980 the captive colony consisted of two males and three females ranging in estimated age from eight to sixteen years (Table 1). From February 1980 through June 1981, the colony consisted of the three oldest dolphins; Lioele, a male, and Kahe and Kehaulani, both females. Lioele had a deformity of the spine as a result of an injury incurred two years previously. While the deformity did not prevent his participation in any major class of behaviors, the intensity of his involvement was typically less than for the other dolphins. The colony was maintained strictly for research in the 25 m diameter, 3 m deep Bateson's Bay. Human contact was limited to three feedings per day and biweekly blood sampling.

Blood samples were obtained every other Wednesday from 5 September 1979 through 29 October 1980. Additional samples were collected on 22 June 1981. For blood sampling, the dolphins entered an adjoining, smaller tank which was then drained until the dolphins could be handled individually on the shallowest portion of the sloping tank floor. The dolphins were restrained by two handlers, and blood was drawn from a large, superficial vessel on the dorsal aspect of the fluke. The 24-36 cc samples were centrifuged, filtered, and frozen prior to analysis.

Steroid hormone concentrations were measured using radioimmunoassay techniques. Serum from males was analyzed for testosterone (Smith-Kline Laboratory, Honolulu, HI; sensitivity = 0.05 ng/ml); samples from females were analyzed for estradiol (Smith-Kline Laboratory, Honolulu, HI; sensitivity = 1.9 pg/ml) and progesterone (V. Kirby, San Diego Zoo; sensitivity = 33 pg/ml). Progesterone was measured from February 1980 through June 1981.

Behavioral observations were made in conjunction with each blood-sampling session. The behavioral patterns of the colony were monitored for the first ten minutes of every half hour through the twenty-four hours preceding or following hormone sampling. An observer at the side of the observation tank narrated behavioral events and times of occurrence into a tape recorder. The durations of heterosexual pairings and the frequencies of occurrence of all other behavioral patterns considered to have sexual or social connotations were measured from the transcriptions of the tapes. The durations of heterosexual pairings were measured as the periods during which the dolphins swam and surfaced synchronously within approximately 2 m of each other, engaged in similar activities, and swam approximately side by side. Other behavior patterns were scored as one occurrence as long as the participants were together and engaging in the activity. If the dolphins separated to terminate the activity or to surface to breathe, and then engaged in the activity again, two occurrences were scored. The behavior patterns were further partitioned on the basis of the role of the participant. A dolphin was classified as "giving" the behavior if it initiated or was the most active participant in a behavioral sequence; the more passive participant or the individual receiving the attentions of the "giver" was classified as the recipient. Distinctions were sometimes difficult and some of the behavior patterns involved mutual participation.

Only observations made from February 1980 through June 1981, when the colony composition was stable and when progesterone was measured, are considered here.

The distribution of durations of heterosexual pairings and frequencies of occurrence of the behavioral patterns were compared relative to the concentrations of reproductive hormones measured during the same period with a Kolmogorov-Smirnov Goodness of fit test (Zar, 1974; 0.05 level of significance). Testosterone concentrations were considered "high" if greater than 30 ng/ml, "intermediate" if between 8-30 ng/ml, and "baseline" below 8 ng/ml. "High" estradiol concentrations were those over 90 pg/ml, "intermediate" were between

50-90 pg/ml, and "baseline" were below 50 ng/ml (this categorization scheme follows that of Wilson, Gordon, and Collins, 1982). Progesterone concentrations over 3 ng/ml were considered indicative of ovulation, 1-3 ng/ml concentrations were "indeterminate," and below 1 ng/ml were "baseline" (Wilson *et al.,* 1982; Kirby and Ridgway, 1984).

RESULTS

Steroid hormone concentration

Serum testosterone measurements (Fig. 1) ranged from less than 1 ng/ml to over 60 ng/ml for the adult male (Lioele) monitored throughout the study. The values for the smaller males, Apiki and a dolphin that was tagged and released off the coast of Hawaii, were within the baseline range for Lioele (0-8 ng/ml). Lioele's testosterone titer increased significantly beginning in March 1980, reached maximum levels in June-July 1980, and returned to baseline in October 1980. A single sample from June 1981 was nearly identical to the highly elevated value from the same period during the previous year.

Estradiol concentrations were usually low or intermediate for both females (Figs. 2 and 3). Elevated estradiol values were noted for Kahe in June 1981, and for Kehaulani in October 1979 and 1980.

Progesterone concentrations were highly variable for both females (Figs. 2 and 3). The elevated progesterone values for Kehaulani in September-October 1980 suggested ovulations. The October surge in progesterone was preceded by elevated estradiol and low progesterone, perhaps indicating both the follicular and luteal phases of the cycle. Progesterone level in Kahe increased markedly in July 1980 and remained elevated at least through the end of the continuous observation period (October 1980). It was found to be elevated again in June 1981. Elevated progesterone values over prolonged periods are typically indicative of pregnancy, but no calf or aborted fetus was forthcoming.

Durations of heterosexual pairings

The amount of time spent by each dolphin swimming in association with a dolphin of the opposite sex did not appear to vary predictably with the hormone levels of any of the participants. Total time spent in each heterosexual pairing was calculated for each observation day. Comparisons of the distributions of these pair totals with the hormone concentration categories showed no significant differences from the random. In general, Lioele (♂) tended to spend more time with Kahe (♀) than with Kehaulani (♀). The mean proportion of the observation days each dolphin spent in each pairing, relative to the hormone categories, is presented in Table 2. Lioele spent the greatest proportion of time paired with females (49.8%), rather than swimming alone or in a trio, on the day when the females' progesterone concentrations were at their lowest value (1 April 1980). The next highest proportion of time in which Lioele was paired with females (36.1%) occurred on the day of Kahe's highest recorded estradiol concentration (22 June 1981). High estradiol concentrations are associated with the follicular phase of the female cycle, when estrus would be most likely to occur (Cupps, Anderson and Cole, 1969). However, as only one hormone concentration on these two dates could be considered indicative of imminent ovulation, these anecdotes are only suggestive of the possible role of female steroid hormone in influencing swimming associations.

Behavior patterns

Six patterns of behavior with potential sexual connotations were identified and scored. Each of these patterns involved interactions between pairs, as noted by Bateson (1974). The six patterns are: genital-to-genital contact, beak-to-genital propulsion, other genital contact, non-genital contact, ventral presentations, and chases. Genital-to-genital contact was scored when the genital regions of both members of the heterosexual pair were in contact with each other. Intromission was difficult to observe, but was seen as part of this pattern. Beak-to-genital propulsion, as described by Bateson (1974) and Norris and Dohl (1980), involved the placement of the tip of the rostrum of a trailing dolphin in the genital slit of another, with the flukebeats of the trailing animal propelling the pair at slow speed. Occasionally the flukes of the propelled dolphin rested on the head of the other individual. This was usually a protracted behavior, and was scored once for each period of contact between surfacings. Other genital contact included all other occasions when the genital region of one dolphin was in contact with any part of the other dolphin. This category included such behavior patterns as inserting fins in the genital slit of another dolphin, or rubbing or stroking the genital region of the other dolphin. Non-genital contact included caressing of the dolphin by another, or both simultaneously, using the pectoral fins, flukes, rostrum, head, or flanks. Typical forms of non-genital contact involved one animal raising a pectoral fin while the other dolphin rubbed on the outstretched fin (we called it "pec-whetting"). The pectoral fins of both dolphins sliced rapidly back and forth against each other. In a more passive pattern, swimming occurred with the pectoral fin of one animal in contact with the body of the other. Non-genital contact often involved an increase in swimming speed. Ventral presentations consisted of the tilting of the belly of one dolphin toward another, or tilting by both toward each other simultaneously or in rapid alternation. This behavior pattern varied from a slight tilt of one partner to one rolling over beneath another with ventrum oriented upwards. Chases generally consisted of a pair of dolphins swimming rapidly, often with one dolphin behind the other. As used here, the term "chase" does not necessarily imply that one animal was chasing the one ahead. Often the initiation of a chase was so sudden and so synchronous that it was impossible to determine whether the activity was a "chase" or a "follow."

These behavior patterns occurred with variable frequencies relative to the steroid hormone concentrations (Tables 3, 4, and 5). In general, most of the behavior patterns occurred less frequently between individuals of opposite sex than they did between the two females. All but genital-to-genital contact were observed in both heterosexual and female-female pairings.

Genital-to-Genital contact occurred only in male-female pairs. Only three occurrences of genital-to-genital contact were observed. Intromission was observed once and was believed to have occurred during the other times but could not be confirmed. Erection was not not seen at any time other than during this intromission. All the genital-to-genital contacts occurred when the male's testosterone titer was high (more than 48 ng/ml) (Kolmogorov-Smirnov $D = 0.74$, $n = 3$, $p < 0.05$).

Genital-to-genital contacts were not clearly related to female hormone concentrations, occurring at both baseline and high levels of estradiol or progesterone.

The occurrence of beak-to-genital propulsion was most closely related to the female hormone cycle. The male rarely propelled the females; there was no clear relationship between the incidence of giving or receiving propulsion and testosterone concentration. However, the highest frequency of beak-to-genital propulsion occurred during the follicular phase of the only clearly-defined ovulatory cycle observed during this study. Kehaulani propelled Lioele seven times on 30 September when her estradiol titer was the highest of the study, and when her progesterone was at a low level. This resulted in a significant difference in the occurrence of beak-to-genital propulsion relative to Kehaulani's estradiol titer $D = 0.82$, $n = 8$, $p < 0.01$).

Mutual ventral presentations, in which both the male and female tilted their bellies toward each other, were significantly related to testosterone levels ($D = 0.44$, $n = 10$, $p < 0.05$) and Kahe's estradiol concentrations ($D = 0.67$, $n = 5$, $p < 0.05$). The frequency of occurrence of mutual ventral presentations was not consistent for all the females, suggesting that the significance of Kahe's relationship may be due to the coincidental result that her highest estradiol value and Lioele's high testosterone concentrations occurred together on 22 June 1981.

No significance was found in the comparisons of the hormone concentrations and frequencies of occurrence of other genital contacts, non-genital contacts, chases or one-way ventral presentations.

DISCUSSION

Although sample sizes were small, the frequencies of occurrence of three behavior patterns appeared to be closely linked to changes in reproductive hormone levels. Genital-to-genital contact and mutual ventral presentations occurred most frequently when the male's testosterone concentrations were high. Beak-to-genital propulsion appeared to be related to ovulatory or associated events. All other contact, chases, and one-way ventral presentations were not significantly related to hormone concentrations, and presumably were typically used in more social than reproductive contexts. Dolphin copulations occur with the two participants oriented ventrum to ventrum; thus the actual mechanics of mutual ventral presentations are similar to genital-to-genital contact, and mutual ventral presentation is known to serve as a precursor behavior to copulation, for example, in Delphinus (Essapian, 1962).

Some of the behavior patterns were not correlated with hormonal events. Many delphinid courtship and copulatory patterns may be used in contexts outside of reproduction. Non-reproductive contexts may be identified when the behavior patterns occur between inappropriately-matched individuals (but it is possible that sexually-aroused individuals may use patterns with inappropriate partners). Copulations between males (Bateson, 1974), attempted matings between male calves and their mothers within several days of birth (Caldwell and Caldwell, 1972), or beak-to-genital propulsion between two females (Bateson, 1974) could scarcely be considered reproductive, yet each of the patterns have been described as a courtship pattern when engaged in by adult dolphins of different sexes. Table 6 summarizes occurrences of behavior patterns in heterosexual or homosexual pairs of dolphins of three genera and shows that most of the behavior patterns are observed in both homosexual and heterosexual combinations. Though this table sometimes suffers from a lack of observations of homosexual behavior in some of the available literature, the similarities in patterns across genera and widespread occurrence of patterns in both kinds of pairings is noteworthy. Other behavior patterns have been included in lists of courtship and copulatory patterns for *Tursiops* and *Delphinus,* such as head-butting, mouthing, leaping, vocalizing, tailslaps and headslaps. Head-butting and mouthing have not been reported for *Stenella* spp.

It may be more difficult to identify the context of behavior patterns involving heterosexual pairs of adults than of homosexual pairs, but knowledge of the reproductive condition of members of heterosexual pairs can be useful in distinguishing between reproductive and other social contexts. Puente and Dewsbury (1976) found that *Tursiops* behavior patterns they termed "courtship" occurred more frequently on days without copulations. However, all of their observations were made during the presumed breeding season (McBride and Hebb, 1948; McBride and Kritzler, 1951; Tavolga, 1966), and no data are available for comparisons with frequencies outside of the breeding season. It would be expected that behavior patterns most closely linked to reproduction would increase in frequency during the reproductive season. Similar behavior patterns observed at other times of the year or between inappropriate participants could be assumed to occur as part of the ordering of dolphin schools, or developing or maintaining relationships between individuals. Changes in the frequency of mating activity and durations of heterosexual pairings on a seasonal basis have been reported for Tursiops in several locations (McBride and Kritzler, 1948; McBride and Hebb, 1951; Tavolga, 1966; Saayman and Tayler, 1977). For example, males are reported to spend more time with females during the spring, and more copulations occur then. In one case it was reported that female-female social interactions were curtailed in the spring (Saayman and Tayler, 1977). These changes were presumed to coincide with the breeding season, but no precise measures of the reproductive condition of the involved dolphins were made.

The lack of significant relationships between duration of heterosexual pairings and hormonally determined reproductive condition differs from descriptions of Tursiops behavior, where such associations seem clear (Tavolga, 1966). This difference could be related in these observations to a possible inability of the deformed male to maintain swimming associations of long duration. It could also reflect interspecific differences in school structure. Spinner dolphins often swim in large schools of mixed sex, whereas coastal bottlenose dolphins often swim in single-sex schools that occasionally meet and mix for periods of variable length with schools of the other sex (Norris and Dohl, 1980; Wells, Irvine and Scott, 1980). The constant availability of members of the opposite sex within a school may preclude the need to change typical swimming association patterns.

Acoustic recordings have not been made consistently throughout any of the studies reported in the literature, making comparisons of occurrence of vocalizations difficult. Leaping, head-slaps and tail-slaps have been observed in the present study as "punctuation" signaling the initiation of termination of bouts of social behavior involving pairs of dolphin.

The hormonal determination of reproductive condition in males may be simpler than in females, as the period of elevated testosterone concentrations may be prolonged, as shown in Fig. 1. Ridgway and Green (1967) identified a "definite seasonal rut" in male Lagenorhynchus obliquidens and D. delphis, during which there was a significant increase in the size of the testes, prostate, and muscles associated with the reproductive organs. Perrin and Henderson (1984) observed similar changes in male spinner dolphins in the eastern tropical Pacific. Kirby and Ridgway (1984) measured significant seasonal increases in testosterone levels in male Tursiops. Very few comparative data on hormones in Stenella spp. are available. Sawyer-Steffan and Kirby (1980) reported testosterone values of 0.5 ng/ml to 6.7 ng/ml for four immature specimens killed in the tuna-seine fishery; these values were less than or equal to the baseline values for Lioele.

Female reproductive condition may be more difficult to determine because of the short-lived nature of the hormonal events surrounding ovulation. If spinner dolphins follow the typical ovulatory cycle described by Cupps, Anderson and Cole (1969), then elevated estradiol values in conjunction with low progesterone concentrations, followed by reduced estradiol levels and a progesterone surge, should define an ovulation and presumably should define the time during which behavioral estrus should occur. Measurements of estradiol surges alone are not enough to indicate imminent ovulations. Biweekly measurements of progesterone and estradiol may be insufficient to document each ovulation, as suggested by the fact that only one presumed ovulation was clearly indicated in 8.5 months of continuous measurements of two females (Fig. 3). Rather than the long breeding season suggested for the males, the breeding season for the females during one year may consist of an unknown number of brief periods of receptivity associated with multiple ovulations. Multiple ovulations per season have been suggested from the data from the tuna-seine fishery. Perrin, Holts and Miller (1977), Perrin, Coe and Zweifel (1976), and Perrin and Henderson (1984) reported variations in ovulation rates for Stenella spp. with age with the younger adults showing evidence of more (up to 4) ovulations per year. Ridgway and Kirby (1984) reported multiple spontaneous ovulations in captive D. delphis. Benirschke, Johnson and Benirschke (1980) provided evidence from the examination of ovaries of Stenella spp. that spontaneous ovulations may occur. Few hormone data are available for comparison, but Sawyer-Steffan and Kirby (1980) found progesterone and estradiol levels from their Stenella specimens to be similar to levels obtained from pregnant and non-pregnant Tursiops, and these levels are comparable to those reported here. As noted by Tayler and Saayman (1972) and Puente and Dewsbury (1976), receptivity in the female is critical to the completion of courtship patterns, and such receptivity is likely to be closely related to the reproductive condition of the female. More data are needed to document this relationship adequately.

More frequent blood sampling in association with observations of the patterns of social behavior of dolphin groups may provide more clear-cut determinations of the contexts of the observed behavior patterns and thereby provide the basis for better understanding the mechanisms utilized by delphinids in ordering their schools and developing and maintaining interindividual relationships.

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Table 1

Composition of the Sea Life Park spinner dolphin colony from September 1979 through June 1981. From February 1980 through June 1981, the colony consisted of only the three largest dolphins; only the data from this period are considered in the analyses presented in this report.

Dolphin	Sex	Length (cm)	Age* (years)	Comments
Lioele	Male	183	16	Captured 2 September 1976
Kehaulani	Female	190	12	Captured 9 September 1976
Kahe	Female	191	11	Captured 15 June 1972
Apiki	Male	172	9	Captured 27 August 1976 Died 9 February 1980
Mahealani	Female	175	8	Captured 23 May 1974 Died 13 January 1980

* Age in 1980 determined from analysis of growth layer groups in sectioned teeth (Myrick, Shallenberger, Kang and MacKay, 1984).

Table 2

Proportion of total observation time during which heterosexual pairings occurred, relative to steroid hormone concentrations. Means calculated from daily ratios of time paired:total observation time.

	Lioele with Kahe		Lioele with Kahaulani	
	Mean ± S.D.	n(days)	Mean ± S.D.	n(days)
Testosterone				
Baseline (0-8 ng/ml)	0.24 ± 0.055	4	0.02 ± 0.018	4
Intermediate (8-30 ng/ml)	0.26 ± 0.097	9	0.04 ± 0.026	9
High (>30 ng/ml)	0.18 ± 0.102	4	0.06 ± 0.028	4
Estradiol				
Baseline (0-50 pg/ml)	21.1 ± 7.44	11	3.9 ± 2.93	14
Intermediate (50-90 pg/ml)	24.8 ± 13.05	4	2.8 --	1
High (>90 pg/ml)	33.0 ---	1	4.3 ---	1
Progesterone				
Baseline (0-1 ng/ml)	24.9 ± 11.25	7	4.7 ± 2.74	12
Intermediate (1-3 ng/ml)	--- ---	0	6.5 ---	1
High (>3 ng/ml)	23.4 ± 7.16	9	1.4 ± 1.44	3

Table 3

Heterosexual behavior patterns: male relations to females (no. occurrences/hr) relative to serum testosterone conc. of the male

Female behavior patterns relative to male (Lioele)	Lioele		
	Baseline (0-8 ng/ml) n=4 days Mean ± S.D.	Intermediate (8-30 ng/ml) 26.06 hours Mean ± S.D.	High (>30 ng/ml) n=9 days Mean ± S.D.
Genital-genital contact			
Mutual	0	0	0.13 ± 0.135
Beak-to-genital propulsion			
Give	0	0.02 ± 0.053	0
Receive	0.24 ± 0.480	0	0.03 ± 0.065
Other genital contact			
Give	0	0.02 ± 0.050	0.07 ± 0.130
Receive	0.11 ± 0.210	0.01 ± 0.043	0.03 ± 0.065
Non-genital contact			
Give	0	0.03 ± 0.062	0
Receive	0.08 ± 0.165	0.13 ± 0.290	0.17 ± 0.127
Mutual	0.25 ± 0.289	0.05 ± 0.076	0.17 ± 0.168
Ventral presentation			
Give	0.04 ± 0.080	0.03 ± 0.062	0.17 ± 0.168
Receive	0.29 ± 0.300	0.12 ± 0.149	0.03 ± 0.065
Mutual	0.08 ± 0.087	0.02 ± 0.050	0.23 ± 0.167
Chases			
Give	0	0.03 ± 0.066	0
Receive	0	0	0

Table 4

Heterosexual behavior patterns: female relations to male (no. occurrences/hr) relative to estradiol of females

Behavior patterns relative to female	Kahe		
	Baseline (0-50 pg/ml) n=11 days: 76.31 hr Mean ± S.D.	Intermediate (50-90 ng/ml) n=4 days: 29.07 hr Mean ± S.D.	High (>90 pg/ml) n=1 day:7.53 hr Mean ± S.D.
Genital-to-genital contact			
Mutual	0	0	0.26 -
Beak-to-genital propulsion			
Give	0	0	0
Receive	0.02 ± 0.048	0	0
Other genital contact			
Give	0	0.03 ± 0.065	0
Receive	0	0.11 ± 0.210	
Non-genital contact			
Give	0.06 ± 0.111	0	0.13 -
Receive	0	0	0
Mutual	0.05 ± 0.074	0.17 ± 0.135	0.27 -
Ventral presentation			
Give	0.04 ± 0.067	0.14 ± 0.198	0
Receive	0.04 ± 0.069	0.13 ± 0.133	0.40 -
Mutual	0	0.07 ± 0.078	0.40 -
Chases			
Give	0	0	0
Receive	0.01 ± 0.045	0	0

Table 4, continued

Behavior patterns relative to female	Kehaulani		
	Baseline (0-50 pg/ml) n=14 days: 98.12 hr Mean ± S.D.	Intermediate (50-90 ng/ml) n=1 day: 7.53 hr Mean ± S.D.	High (>90 pg/ml) n=1 day:7.26 hr Mean ± S.D.
Genital-genital contact			
Mutual	0.01 ± 0.035	0	0
Beak-to-genital propulsion			
Give	0.01 ± 0.035	0	0.96 -
Receive	0.02 ± 0.070	0	0
Other genital contact			
Give	0.05 ± 0.089	0.03 ± 0.065	0
Receive	0.02 ± 0.051	0	0
Mutual	0.01 ± 0.037	0.03 ± 0.065	0.28 -
Ventral presentation			
Give	0.06 ± 0.098	0	0
Receive	0.13 ± 0.035	0	0
Mutual	0.04 ± 0.067	0	0
Chases			
Give	0	0	0
Receive	0	0	0

Table 5

Heterosexual patterns: female relations to male (no. occurrences/hr) relative to progesterone of the females

Behavior patterns relative to female	Kahe*		Kehaulani		
	Baseline (0-1 ng/ml) n=7 days: 49.98 hours Mean ± S.D.	High (>3 ng/ml) n=9 days: 61.58 hours Mean ± S.D.	Baseline (0-1 ng/ml) n=12 days: 84.96 hours Mean ± S.D.	Intermediate (1-3 ng/ml) n=1 day: 6.35 hours Mean ± S.D.	High (>3 ng/ml) n=4 days 28.21 hours Mean ± S.D.
Genital-to-genital contact					
Mutual	0	0.03 ± 0.090	0.01 ± 0.038	0	0
Beak-to-genital propulsion					
Give	0	0	0.09 ± 0.276	0	0
Receive	0.02 ± 0.061	0	0	0	0
Other genital contact					
Give	0.02 ± 0.049	0	0	0	0
Receive	0	0.05 ± 0.140	0.03 ± 0.083	0	0
Non-genital contact					
Give	0.05 ± 0.125	0.05 ± 0.077	0.05 ± 0.089	0	0.07 ± 0.085
Receive	0	0	0.01 ± 0.038	0.15 -	0
Mutual	0.04 ± 0.063	0.14 ± 0.120	0.02 ± 0.081	0	0.07 ± 0.078
Ventral presentation					
Give	0.06 ± 0.073	0.06 ± 0.143	0.06 ± 0.097	0.31 -	0
Receive	0.06 ± 0.076	0.09 ± 0.152	0.02 ± 0.055	0	0
Mutual	0.02 ± 0.049	0.06 ± 0.136	0.05 ± 0.071	0	0
Chases					
Give	0	0	0	0	0
Receive	0.02 ± 0.50	0	0.01 ± 0.043	0	0

*No serum progesterone concentration between 1-3 ng/ml were measured for Kahe. Serum samples on 11 June 1980 were too small for progesterone analysis; thus only 16 blood sampling days are considered for Kahe.

Table 6

Occurrence of behavior patterns within heterosexual and homosexual pairings, as observed in three delphinid genera: *Stenella* (S), *Tursiops* (T) and *Delphinus* (D)

	Sexual composition of pairs			Association with copulation	
Behavior pattern	M-F	M-M[ab]	F-F	With	Without
Genital to genital contact	STD	ST		STD	ST
Beak to genital contact	ST	S	S	ST	ST
Other genital contact	STD	ST	S	STD	STD
Non-genital contact	STD	ST	S	STD	STD
One-way ventral presentations	ST	[c]	S	ST	ST
Mutual ventral presentations	STD	[c]	S	STD	ST
Chases	ST	S	S	ST	ST

a. No observation of M-M or F-F *Delphinus* combinations were available from the literature.

b. The only available description of M-M *Stenella* combinations are reported by Bateson, 1974.

c. Ventral presentations not considered in the descriptions of Bateson, 1974.

Sources: McBride and Hebb, 1948; McBride and Kritzler, 1951; Tavolga and Essapian, 1957; Essapian, 1962; Tavolga, 1966; Caldwell and Caldwell, 1972; Tayler and Saayman, 1972; Saayman, Tayler and Bower, 1973; Bateson, 1974; Puente and Dewsbury, 1976; Saayman and Tayler, 1977; Norris and Dohl, 1980.

Figure 1. Serum testosterone concentrations for three male Hawaiian spinner dolphins.

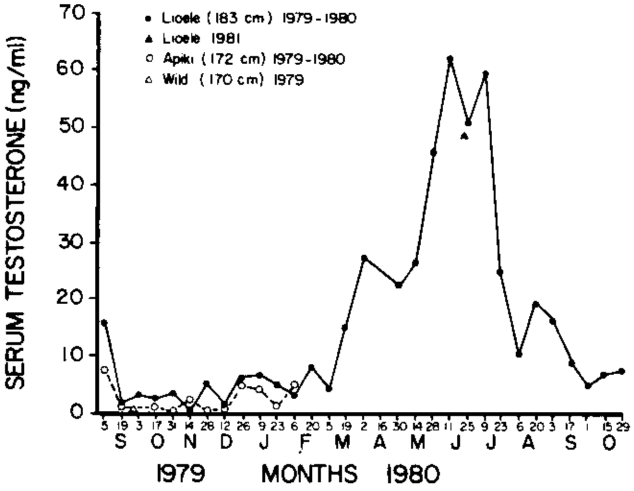

Fig. 1. Serum testosterone concentrations for three male Hawaiian spinner dolphins.

Figure 2. Serum estradiol and progesterone concentrations for female Hawaiian spinner dolphin Kahe.

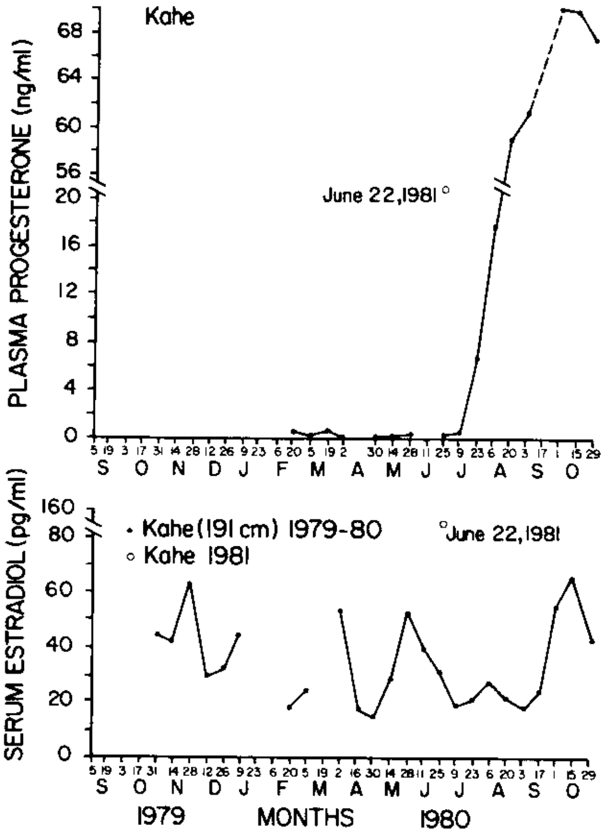

Fig. 2. Serum estradiol and progesterone concentrations for female Hawaiian spinner dolphin Kahe.

Figure 3. Serum estradiol and progesterone concentrations for female Hawaiian spinner dolphin Kehaulani.

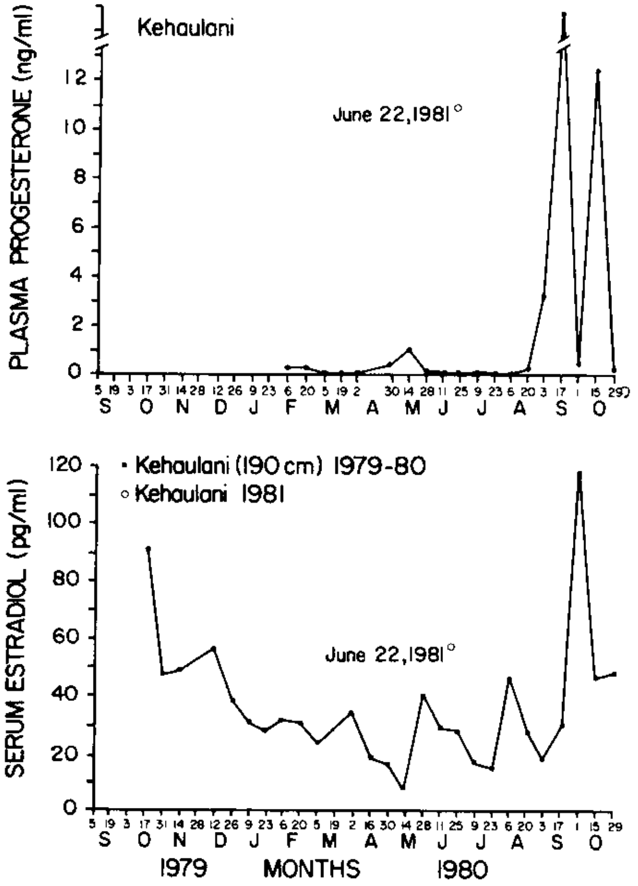

Fig. 3. Serum estradiol and progresterone concentrations for female Hawaiian spinner dolphin Kehaulani.