

**BEHAVIOR, ASSOCIATION PATTERNS AND HABITAT USE
OF A SMALL COMMUNITY OF BOTTLENOSE DOLPHINS
IN SAN LUIS PASS, TEXAS**

A Thesis

by

ERIN ELIZABETH HENDERSON

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

August 2004

Major Subject: Wildlife and Fisheries Sciences

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ABSTRACT

Behavior, Association Patterns and Habitat Use

of a Small Community of Bottlenose

Dolphins in San Luis Pass, Texas. (August 2004)

Erin Elizabeth Henderson, B.A., Drew University

Chair of Advisory Committee: Dr. Bernd Würsig

Photoidentification surveys of bottlenose dolphins (*Tursiops truncatus*) were conducted from December of 2002 through December of 2003 in Chocolate Bay, Texas, and the adjacent Gulf of Mexico area. The research represented the continuation of an ongoing study of the dolphins of this area. Behavioral sampling was carried out on a small resident community of dolphins that seasonally reside in Chocolate Bay, as well as on dolphins found along the gulf coastline. Resident dolphins had a daily behavioral pattern, with peaks of foraging activity in the morning, traveling at midday, and socializing in late afternoon. Gulf dolphins had small mean group sizes of 3.4 and were primarily observed foraging and traveling, with little socializing. When resident and gulf dolphins interacted, the mean group size increased to 12 and the proportion of social behavior increased. Association indices demonstrated no long-lasting associations among adult male dolphins, while strong associations existed between several females. Females revealed two patterns of association; they were either members of a female band with other mother-calf pairs, or were solitary with no strong affiliations with any

dolphins other than their calf. Males seemed to disperse upon maturation, which maintained the community size of approximately 35 animals. Behavioral evidence indicates the resident community is matrilineally related and composed largely of adult females and their offspring. A few adult males remain resident, while most young males disperse from the community and may rove among the gulf population. Although mating probably occurs between resident and gulf dolphins, sources of both maternity and paternity for residents need to be determined, and further behavioral work needs to be carried out to support this hypothesis.

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CHAPTER I

INTRODUCTION

Bottlenose dolphins (*Tursiops* sp.) of the family Delphinidae are found in the major oceans of the world from approximately 60° N latitude in the Atlantic Ocean and 40° N latitude in the Pacific Ocean to about 55° S latitude in the southern oceans.

Presently, two species are internationally recognized, *Tursiops truncatus* and *Tursiops aduncus*. *T. aduncus*, or the Indo-Pacific bottlenose dolphin, has a smaller distribution and is found only along the coastline in the Indian and southeastern Pacific Oceans.

This species also is slightly smaller, with a maximum length of 2.5-2.6 m. While it has the same basic gray coloration pattern as *T. truncatus*, it is also marked by ventral spotting along the belly that may extend longitudinally as the animal ages. *T. truncatus*, the common bottlenose dolphin, has a distribution that includes deep oceanic and coastal waters in the Pacific, Atlantic and Indian oceans. The common bottlenose dolphin has a larger body size (maximum lengths of 2.4-3.8 m) than the Indo-Pacific species, and has a basic gray coloration pattern with countershading (Reeves *et al.* 2002).

The common bottlenose dolphin appears to have two genetically distinct forms, referred to as “coastal” and “offshore” (Hersh and Duffield 1990; Wells *et al.* 1999). Several features can be used to distinguish the two forms. On the eastern U.S. coast, the offshore form has two separate stocks, one in the Gulf of Mexico and one in the North

This thesis follows the style and format of Marine Mammal Science.

Atlantic, and ranges between 200 and 2,000 m isobaths. This morphotype is about 15% longer than the inshore morphotype, has a shorter, wider rostrum, and smaller flippers. Relatively large body size and small appendages may be adaptations that decrease heat loss in colder deep water, whereas the smaller body size and larger flippers of the inshore form may not only assist in thermoregulation, but may be beneficial for maneuvering through shallow water (Hersh and Duffield 1990; Wells *et al.* 1999). Additionally, the offshore form has a higher hemoglobin concentration and red blood cell count, which is consistent with longer and deeper dives that are necessary for foraging in deeper waters (Hersh and Duffield 1990). Finally, parasite loads are different between the two forms, which has been shown to be a useful method of distinguishing stocks (Balbuena and Raga 1994; MacKenzie 2002). The coastal form is also found inshore, not only along the coast but also in bays and estuaries.

Male bottlenose dolphins become sexually mature between eight and twelve years of age, whereas females mature slightly earlier, between five and ten years of age. Females live to about 50 years, and males live to about 40 years (Reynolds *et al.* 2000). Females have an average interbirth interval of three to six years, with a mean of four years, although for some females it may be as brief as two years. Gestation lasts for 12 months, and weaning occurs between 18 and 30 months (Mann *et al.* 2000; Reynolds *et al.* 2000). These dolphins are relatively long lived, slow breeding animals with long-lasting social bonds, and often display high degrees of site fidelity to specific areas, although they also exhibit long distance migration patterns in some areas.

The ability of bottlenose dolphins to occur a variety of habitats makes this one of the most broadly distributed of all cetacean species, comparable to killer whales, (*Orcinus orca*). Due to their nearshore abundance on almost every continental coastline (Reeves *et al.* 2002), and the many individuals held in captivity (*i.e.* Schroeder 1990; Herman *et al.* 1993), bottlenose dolphins are one of the most studied cetacean species. Because of their diverse habitats, bottlenose dolphin behavior varies widely; so that an examination of communities in different microhabitats should provide for a better understanding of the species' ecological response to environmental variation. In addition, management plans based on observed behavior and habitat use for bottlenose dolphins might be applied, with appropriate cautions, to less common cetacean species that use similar niches.

The present study explores the home range, habitat use, behavior and association patterns of a small group of coastal bottlenose dolphins that occur in a shallow bay complex at the southwest end of Galveston Island, Texas. The objectives of this study are to:

1. Explore beyond the boundaries of the current known range to determine the outer limits of the resident population's home range;
2. Examine possible daily or seasonal behavioral trends among resident and gulf dolphins, and determine if these relate to habitat use;
3. Compare behavioral patterns between resident and gulf dolphins, and determine if and how these patterns change when the populations interact; and

4. Examine association patterns among residents to reveal the social organization of this community.

Methods to achieve these objectives include:

1. Photo-identification surveys of resident and gulf dolphins in all known areas of use as well as in previously unexplored areas;
2. Instantaneous method of recording behavioral patterns, and a behavioral comparison of time budgets among resident, gulf, and mixed groups of dolphins;
3. Compare behaviors of resident, gulf and mixed groups to areas of occurrence, time of day and season to relate behavior to habitat use.
4. Longitudinal analysis of association indices for resident dolphins.

Results from this study are described in the following four chapters: Chapter II, Occurrence Patterns; Chapter III, Behavior; Chapter IV, Association Patterns; and Chapter V, Summary and Conclusions.

CHAPTER II

OCCURRENCE PATTERNS

Introduction

The bottlenose dolphin (*Tursiops truncatus*) is one of the most cosmopolitan cetaceans, ranging in diverse habitats from the cold temperate waters of Moray Firth, Scotland (Wilson *et al.* 1997; Wilson *et al.* 1999) in the northern hemisphere and Doubtful Sound, New Zealand (Lusseau *et al.* 2003) in the southern, to the tropical waters of the Bahamas (Rossbach and Herzing 1999). They inhabit small seas and open oceans (Bearzi *et al.* 1999), coastal waters with steep cliff walls (Hanson and Defran 1993; Defran *et al.* 1999), and shallow protected bays (Wells *et al.* 1987). Their use of such wide-ranging and variable habitats is due not only to their almost-global distribution, but to the variety of prey available in each area. Occurrence and behavioral patterns have been partially attributed to movement and availability of prey (Ballance 1992; Hanson and Defran 1993; Felix 1997; Barco *et al.* 1999). Habitat use and movement patterns are also affected by other environmental factors, such as water temperature, salinity, and bathymetry. For bottlenose dolphins, depth and bathymetry have been shown to be important in selecting critical habitat areas (Wilson *et al.* 1997; Ingram and Rogan 2002; Hastie *et al.* 2003), while changes in the environment may act as a natural barrier (Würsig and Würsig 1979; Borobia *et al.* 1991). Other factors influencing distribution patterns include predation and reproduction (Connor *et al.* 2000). In open water areas, with higher risks of predation and a patchier distribution of

prey, group sizes tend to be larger, apparently to offer better protection to individuals, as well as to facilitate prey capture rates. In the protected waters offered by a bay, larger group sizes would likely be more of a hindrance, as prey are more likely to be evenly distributed and predation risks are lower relative to those of the open ocean (Norris and Dohl 1980; Shane *et al.* 1986; Defran and Weller 1999). Mothers and calves are more protected in shallow bays, whereas in open waters, larger groups may provide increased security for young calves (Scott *et al.* 1990).

Dolphin movement and distribution often has a seasonal component, which is likely related to the movement of prey and environmental conditions. In Sarasota, Florida, (Scott *et al.* 1990) dolphins occur inside bays more in warm summer months, and in passes between islands and the Gulf of Mexico (GoM) in cold winter months. This may be due to an increase in prey availability in bays in summer, as fish enter bays to spawn, as well as an increase in predation pressure in the GoM in summer. Bays also offer increased protection for new calves in spring (Scott *et al.* 1990). Similarly, the Moray Firth dolphins (Wilson *et al.* 1999) occur within the estuary in greater numbers from May to September, and in lowest numbers from October through April. Additionally, all individuals are found at their innermost extent in the estuary in mid-summer (Wilson *et al.* 1997). In the Shannon Estuary in Ireland, there is an increase in use of the outer estuary from May to September (Ingram and Rogan 2002). Off the coast of Virginia, animals occur in the bay and along the coast only from April through November (Barco *et al.* 1999). While these coastal dolphins utilize bays part of the year,

they do not seem to exhibit site fidelity to one particular area. Instead, they migrate long distances along the coastline in a seasonal pattern (Connor *et al.* 2000).

This lack of site fidelity in northwest Atlantic coastal dolphins is similar to the observed pattern on the Pacific coast of the U.S. Off the steep coastal waters of southern California, bottlenose dolphins display little residency to any given area, and instead range up and down the coastline, with sightings along the entirety of the 732 km Southern California Bight (Defran *et al.* 1999). Probably due to the open waters of this area, group sizes are large and home ranges are expansive. These patterns may also be related to patchiness of prey distribution and generally deep waters (Shane *et al.* 1986; Defran and Weller 1999). Many dolphins utilize the area, with 3,700 dolphins sighted and 424 individually identified in a seven-year study (Defran *et al.* 1999). In contrast, Wells and colleagues have been studying a group of dolphins along the west coast of Florida for 30 years. This small group of just over 100 animals exhibits a high degree of site fidelity to a relatively small (85 km^2) shallow bay system near Sarasota (Wells *et al.* 1987; Connor *et al.* 2000; Reynolds *et al.* 2000). Group size for this population is much smaller than in the open waters of California (Scott *et al.* 1990). The population in Shark Bay, Australia, another large shallow bay complex, also displays a high degree of residency (Smolker *et al.* 1992; Connor *et al.* 2000). Shark Bay is a large area, spanning $5,000 \text{ km}^2$, with about 220 animals regularly resighted, and with a core group of about 60 animals (Smolker *et al.* 1992).

This chapter explores the habitat use and range of bottlenose dolphins utilizing a part of the northwestern Gulf of Mexico coastline and the shallow bay system of San

Luis Pass/Chocolate Bay (SLP/CB) off Galveston Island, Texas. This area was first surveyed in 1990 (Henningsen and Würsig 1991); in 1995 Maze-Foley began an in-depth study of the region, and resighted 14 of the same dolphins (Maze-Foley and Würsig 1999). This work was sustained by Irwin and Würsig (in press) and low level surveys continued through 2001. It was determined that two groups of dolphins used the area; one group became designated “bay” dolphins or “residents”, while the remainder of the dolphins were considered “gulf” animals. Residents were defined as being sighted in three of four seasons (Irwin and Würsig in press). These dolphins appear to remain in the area all year long, although there is a seasonal trend similar to that in Sarasota, where dolphins use the shallow bays in summer and occur in the channel and GoM in winter (Irwin and Würsig in press; Scott *et al.* 1990; Maze-Foley and Würsig 1999). In contrast, gulf dolphins are rarely resighted, and may be moving up and down the coastline. These animals may display seasonal residency in some parts of their range, similar to the bottlenose dolphins of the northwest Atlantic coast (Barco *et al.* 1999; Connor *et al.* 2000). All populations displaying this long-term site fidelity appear to occupy areas characterized by a shallow protected bay in at least a portion of the home range.

Due to the similarities in habitat type, climate, and prey preferences between the SLP/CB population and the Sarasota population, and based on observations already made by previous researchers, I expect that the SLP/CB dolphins will display similar behaviors and habitat preferences. These dolphins have already shown seasonal use of the bay and gulf, which will be compared to fish catch data for the area to determine if a correlation between seasonal patterns and fish distribution exists. Other environmental

data will be examined as well to ascertain what, if any, factors influence the seasonal trend. This chapter will explore the limits of the range of the resident dolphins, beyond what was previously estimated. Finally, this chapter examines site fidelity patterns of residents and their persistent small population size.

Methods

Study Area

San Luis Pass and Galveston Bay are at the southwestern end of Galveston Island and the Galveston Bay Estuary, the second largest estuary in Texas (Maze-Foley and Würsig 1999). This area is $\sim 65 \text{ km}^2$ and previously was divided into four sections based on habitat characteristics: Chocolate Bay (CB), the San Luis Pass channel (SLP), West Bay (WB), and the Gulf of Mexico (GoM) (Maze-Foley and Würsig 1999; Irwin and Würsig in press). This study also includes an adjacent bay, Bastrop Bay (BB), and divides the GoM into two sections, the North GoM (NG) and South GoM (SG). It also incorporates further coastline to the south of this study area near the town of Surfside (SS) and the Surfside Shipping Channel (SC) that connects to the Intracoastal Waterway (ICW) (Fig. 1).

Both CB and BB vary in depth but are relatively shallow (CB $x = 2.98 \pm 1.978\text{m}$, BB $x = 1.30 \pm 0.529\text{m}$), and also have a generally muddy bottom topography scattered with numerous oyster reefs. CB is bisected by a shipping channel, and is bordered on the southwest by the ICW, both of which are much deeper. WB is more consistent in

depth ($x=2.33 \pm 0.577$), but is still shallow, with bottom topography of mud and silt.

The bottom topography of SLP, the channel between the GoM and WB, is marked with

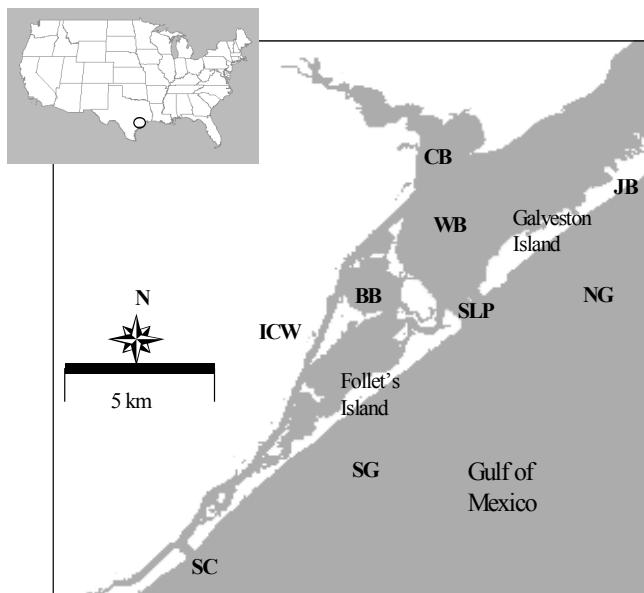


Figure 1. Map of survey areas. CB=Chocolate Bay, WB=West Bay, BB=Bastrop Bay, SLP=San Luis Pass, JB=Jamaica Beach, NG=North Gulf, SG=South Gulf, SC=Surfside Shipping Channel.

dense sand bars that shift constantly in the rapid movement of the tides, and this area is extremely shallow except during high tides ($x=1.14 \pm 0.770$). These areas are all used by small recreational vessels, whereas the ICW and CB shipping channels are regularly traversed by large barges. The two GoM sections run NE to SW along the coasts of Galveston and Follets Islands, with sandy bottoms and greater depths (NG $x=5.23 \pm$

2.242, SG $x=4.91 \pm 2.199$). Surveys in the GoM were run on two tracks, one 0.25 miles offshore and the other 0.75 miles offshore. At the southwestern edge of this study, SC is a deep channel ($x=13.10 \pm 4.737$) with considerable boat traffic, both large and small. Shrimp trawling occurs in the GoM, SC, and the channel area of CB, but cannot be accommodated by the shallow bays or SLP.

Data Collection

After a pilot study from September through November 2002, data were gathered for 13 months, from December 2002 through December 2003. A 5.1 m Boston Whaler with a 4-stroke, 200 hp motor was used to survey the study area. Every survey covered a minimum of two sections of the study area, though most studies covered three or more. Surveys were only conducted in sea states of Beaufort three or less. Previous work had determined that track lines were not suitable for this area (Irwin and Würsig in press), and so survey routes were set and followed using a Garmin 45 GPS Personal Navigator. Survey speed was maintained between 10 – 12 knots until a group of dolphins was located, then speed was reduced to match the pace of the group. Groups were defined as all dolphins in apparent association, generally doing the same behavior (Shane 1990; Bräger *et al.* 1994; Karczmarski 1999). Group composition estimates included adults, juveniles, calves, and neonates. Adult bottlenose dolphins in this area are about 2.50 – 2.65 m in length (Stolen *et al.* 2002; TMMSN¹), and calves were defined following Maze-Foley (1999) and Shane (1990) as being two-thirds or less the length of an adult,

¹ Texas Marine Mammal Stranding Network, 4700 Ave U Galveston Texas 77551, 2004.

or about 1.5 m or less. Such small dolphins continuously swimming next to or slightly behind an adult were also identified as calves. Neonates had visible fetal folds, a dark gray color, and uncoordinated surfacings (Maze-Foley and Würsig 1999; Irwin and Würsig in press). Photographs were taken of all members of each group using a Nikon D-1 Digital Camera, with an 80-400mm zoom lens (Markowitz *et al.* 2003). We stayed with each group until all members were photographed, environmental conditions worsened, or the group was lost for more than 10 minutes.

Environmental data were taken at the end of each group encounter, as well as every hour in order to compare conditions with and without dolphins present. These data included salinity, depth, Beaufort, swell, cloud cover, and wind speed and direction. Each location was also correlated with a type of bottom topography. Seasons were defined following Maze-Foley and Würsig (1999) and Irwin and Würsig (in press) as: fall (September-November), winter (December-February), spring (March-May) and summer (June-August). However, for purposes of analysis, these were combined into two periods: warm (May-October) and cold (November-April) (*e.g.* Irwin and Würsig in press).

Photo-identification

I photo-identified dolphins, mainly by using the natural markings, scars and nicks on the trailing edge of their dorsal fins (Würsig and Würsig 1977; Defran *et al.* 1990; Würsig and Jefferson 1990). Photographs of each individual were downloaded from the digital camera and examined for quality. Five categories of quality were used, each

considering the criteria of relative size of the image in the photograph, focus, parallax, contrast, and the proportion of the fin visible. Those with a category of three or higher (fair, good, or excellent) were entered into a fin-recognition assistance program called Finscan (Hillman *et al.* 2003; Markowitz *et al.* 2003). Photographs were then matched within the catalog from this study, as well as against the catalogs compiled by Irwin and Würsig (in press) and Maze-Foley and Würsig (1999) to determine status and duration of residency. It was assumed that all animals in the group had been identified if each individual in the group had four or more photographs taken per group encounter.

Resident dolphins had previously been defined by Irwin and Würsig (in press) as those animals initially sighted in three of four seasons, with continued sightings in at least two seasons. New residents in this study followed that definition and additionally had to be seen within the bay at least part of the year. However, any animal that had previously been designated a resident was automatically defined as such. Groups in this study were categorized based on the composition of its members: Resident groups consisted of all resident animals, Mixed groups consisted of both resident and gulf animals, and Gulf groups consisted of only gulf animals.

Home Range

The previously known range of the resident dolphins included CB, WB, SLP, and NG as far north as Jamaica Beach (JB) (Beier 2001; Irwin and Würsig in press). Surveys in this study extended beyond the limits of previous studies in this area, including further up CB into Chocolate Bay, further south in the GOM as far as the

Surfside Shipping Channel, the ICW from SC to CB, and BB. The apparent northern limits of the Resident group were established by Beier (2001), who surveyed the GOM along the entire length of Galveston Island, and observed residents as far north as JB (Fig 1). Therefore, that distance was not covered by this study.

Prey Data

Barros and Odell (1990) examined stomach contents of stranded dolphins along the gulf coast from Texas to Florida to determine prey preferences of dolphins in this area. While fishes were the most common prey, both cephalopods and crustaceans were discovered as well. For the Texas area, the most frequently consumed species were Atlantic croaker (*Micropogonias undulates*), sand sea trout (*Cynoscion arenarius*), brief squid, (*Lolliguncula brevis*), silver perch (*Bairdiella chrysaura*) and spot (*Leiostomus xanthurus*). Other researchers have also included mullet (*Mugil* sp.) as a major component of the diet of dolphins in this area (Gunter 1942; Shane 1990).

Catch data were gathered by NMFS from 1976-2002 in the SLP, CB and WB areas. Three methods were used to survey the fish species in the areas: bottom trawls, bag seines and cast nets. These samples were taken throughout the year to give an indication of what fish species were present seasonally in the channel and bay areas (Mark Fisher, personal communication²).

² Mark Fisher, National Marine Fisheries Services, Rockport Marine Lab, 702 Navigation Circle, Rockport TX 78382, 2003.

Analysis

Sighting Per Unit Effort (SPUE, unit = one min) was defined as the amount of time spent with dolphins divided by the total amount of time surveying the area, and was calculated for all areas to balance the survey effort with the actual amount of time spent with dolphins. Kruskal-Wallis tests were used to look for effects of Time of Day (ToD) on group encounters, as well as for seasonal effects on aspects of the environment. A logistic regression was run to determine which environmental factors significantly varied with the presence or absence of dolphins. An ANOVA was then run on each environmental factor that varied to determine where the differences were significant. A MANOVA was run to determine whether environmental features were uniform throughout all study areas, while a Dunnett's T3 post hoc test was run to establish which areas differed. Mann Whitney U tests were used to examine seasonal effects on the numbers of calves, area use by all groups, and the type of group encountered. The number of calves found in each study area was examined using Kruskal-Wallis test, while the number of calves for each group category was examined using Dunnett's T3 post hoc test. ANOVA was used to explore group size by both group category and by study area. Seasonal effects of fish occurrence were examined using chi-square analysis. All analysis was performed using SPSS for Windows Version 11.0 (SPSS 2001).

Results

Environmental Data

Preliminary surveys were conducted from September through November 2002.

From December 2002 through December 2003, 156 h were spent surveying during 38 days on the water. Of those, 28.5 h were with dolphins, for 18% SPUE. A total of 49 groups were seen on 29 of the 38 survey days, with $x = 33.32$ min/group and $x = 1.8$ groups/day. The majority of the survey time was spent in CB and SLP (32% and 20% respectively). No dolphins were ever encountered in WB or BB, while the highest SPUE was for SC (53%), where dolphins were photographed on every survey in that area (Fig 2). Each group type (Resident, Gulf, and Mixed) was seen throughout the day, with no significant effect of ToD on the type of group encountered (i.e., Residents were not seen more in the morning). Finally, all areas were surveyed throughout the day, with no bias of ToD on any particular study area.

Environmental data were gathered on 48 occasions with and 58 times without dolphin groups, and all data had a normal distribution. Depth ($p < 0.0001$), salinity ($p = 0.040$), and Beaufort ($p = 0.032$) all differed significantly with or without dolphins. Dolphins were found significantly more often in depths of 0-6m than in depths of 6m or more ($p = 0.009$). TOD, swell, and cloud cover had no effect on the presence of dolphins.

Seasonal changes also had an expected impact on environmental factors. Beaufort and depth were significantly different between warm and cold seasons ($p = 0.048$ and 0.041). Depth, salinity and swell were significantly different ($p < 0.0001$) between study areas. Depth was significantly lower in all bay areas than in gulf areas, salinity in the CB/IWW areas was significantly lower overall than in gulf and channel areas, and swell was significantly higher in gulf areas than in bay areas (Table 1).

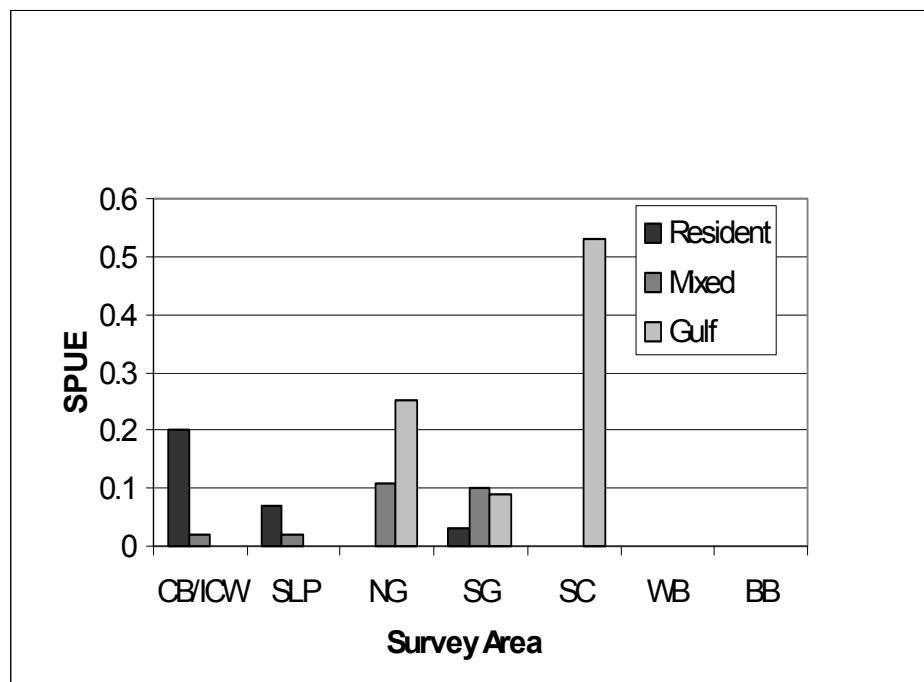


Figure 2. Sighting Per Unit Effort (SPUE) in all survey areas for all group categories. December 2002 through December 2003.

Table 1. P-values of Dunnett's T3 post hoc test comparing depth, salinity and swell by study area. A * indicates significance at the 0.05 level.

		CB	BB	WB	SLP	NG	SG	SC
Depth Salinity Swell	CB	-----	0.079	0.887	1.000	*0.014	*0.049	0.152
			0.808	0.339	*<0.001	*<0.001	*<0.001	0.999
			1.000	1.000	0.929	0.069	*<0.001	0.602
Depth Salinity Swell	BB	-----		0.385	*0.031	*<0.001	*<0.001	0.104
				1.000	0.808	0.671	0.761	0.996
				1.000	0.852	0.098	*0.003	0.998
Depth Salinity Swell	WB	-----			0.361	*0.001	*0.003	0.132
					0.856	0.741	0.823	0.999
					0.999	0.321	*0.013	0.852
Depth Salinity Swell	SL P	-----				0.089	0.188	0.167
						1.000	1.000	0.749
						0.829	*0.013	0.256
Depth Salinity Swell	NG	-----						0.227
								0.694
								*0.010
Depth Salinity Swell	SG	-----						0.281
								0.741
								*<0.001
Depth Salinity Swell	SC	-----	-----	-----	-----	-----	-----	-----

Photo-identification

In the 16 months of survey effort, 110 animals were identified with photographs of high quality. Seventy-five of these were gulf dolphins, while the remaining 35 were residents. Of the gulf dolphins, only two were resighted twice; the rest were only seen once. The gulf dolphin 0282 was seen in November 2002 in SC, and in August of 2003 just outside SC in the GOM, both times in Gulf groups. The gulf dolphin 0296 was also seen in SC in October 2002, then again in the same location over a year later, in November 2003. Of the residents, 25 were resights from previous studies, while 10 were

newly identified. Six of the new residents were calves, two were juveniles whose fins were probably not recognizable yet in previous years as calves, and two were adults. Of the original 25 residents, 11 were of the initial 14 that were identified by Henningsen and Würsig (1991) and resighted by Maze-Foley and Würsig (1999). Five calves were also seen in the Gulf groups. In Resident and Mixed groups, there were often multiple calves seen in a group, up to four at a time. In Gulf groups, on the other hand, there were only one or two calves ever present. In fact, this difference was significant between Resident and Gulf groups ($p=0.008$). Calves were seen in all study areas, and the numbers of calves were not significantly different by study area ($p= 0.057$). However, the number of calves differed between the warm and cold season, with more calves in the warm season ($p=0.027$).

Fifty-nine groups were encountered in all 16 months of surveys, 24 Gulf, 23 Residents, 8 Mixed, and 4 with unknown compositions (photographs of the entire group were not taken or considered incomplete) (Fig. 3). Thirty groups were seen in the cold season, while 29 were seen in the warm season. Of the cold-season groups, the majority of groups seen were Gulf ($N=18$), whereas only eight were Resident and four were Mixed. Only one of the 12 groups containing residents was seen in CB; the remainder occurred in SLP or the GOM. In contrast, of the 29 groups seen in the warm season, the majority were Resident ($N=15$), while six were Gulf, and four were Mixed. Four had an unknown composition; however, if at least one resident was identified, the group could be used to examine seasonal and habitat use trends for residents. Of the four unknown groups, three included at least one resident. Therefore, of the 22 groups with residents

present, eight were seen in the GOM, four in SLP, and 10 in CB/ICW (Fig 4 and 5).

Area use significantly varied by season ($p=0.001$), as did the group type predominantly seen in each season ($p=0.046$).

Overall mean group size was 7.9, but varied significantly between group types ($p=0.001$). The mean for Resident groups was 10.0 (± 6.25), while Mixed groups had a slightly larger mean of 12.0 (± 7.86) and Gulf groups were significantly smaller than Resident groups, with a mean of 3.4 (± 2.69 , $p=0.002$). Generally, group size did not vary by study area ($p=0.065$); however, it was significantly different between CB/ICW ($x=11.3\pm 6.44$) and SC ($x=4.3\pm 2.34$). Dolphins encountered in SC were generally alone, or in small groups of two or three, while rarely was a group in CB/ICW smaller than 10 (Fig. 6).

Home Range

Resident dolphins occurred further to the northwest in CB than previously surveyed, well into Chocolate Bay near the point at which the Bayou begins. Residents occurred in both the NG and SG areas, extending almost as far south as Surfside. However, Resident groups alone were almost always seen close to shore and relatively near SLP, while Mixed groups were seen further north and south in the GOM, and further offshore than Residents alone. Only one Mixed group was seen in CB, and that group had only one non-resident. Otherwise, all Mixed groups were seen in the GOM. Gulf dolphin groups were also only seen in the GOM, and extended both further

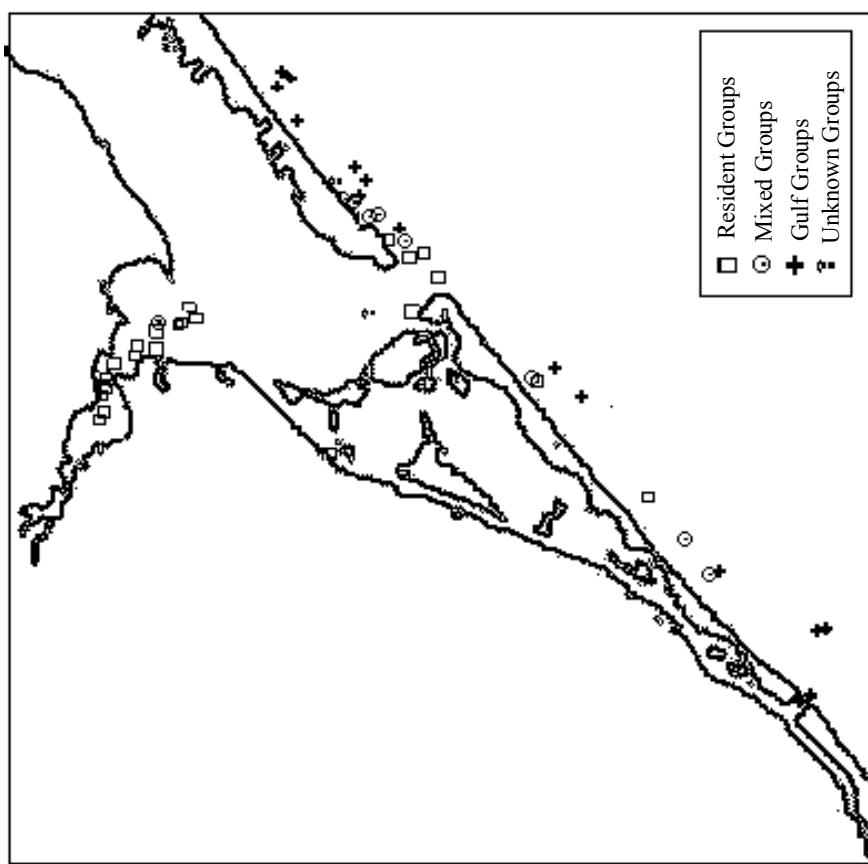


Figure 3. Initial sighting locations of all groups. Surveys from September 2002 through December 2003.

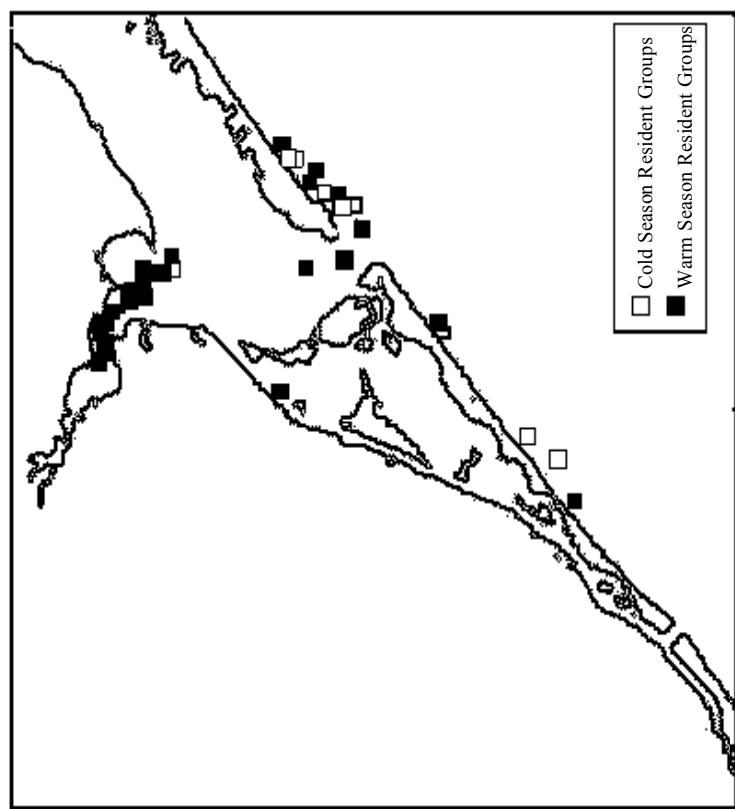


Figure 4. Seasonal sightings for all groups with residents. Surveys from September 2002 through December 2003.

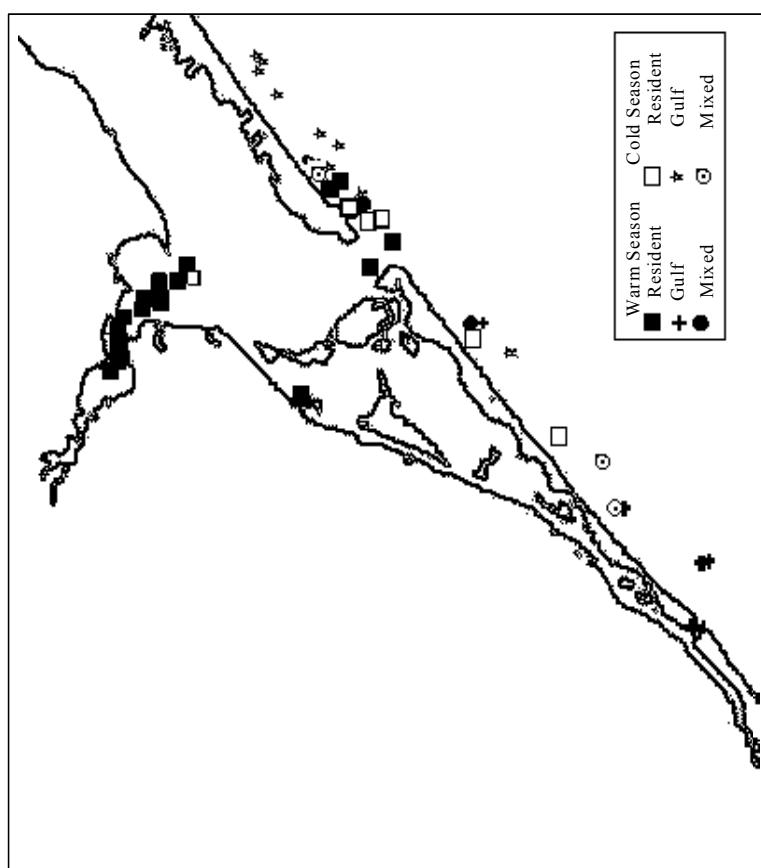


Figure 5. Seasonal sightings for all group categories. Surveys from September 2002 through December 2003.

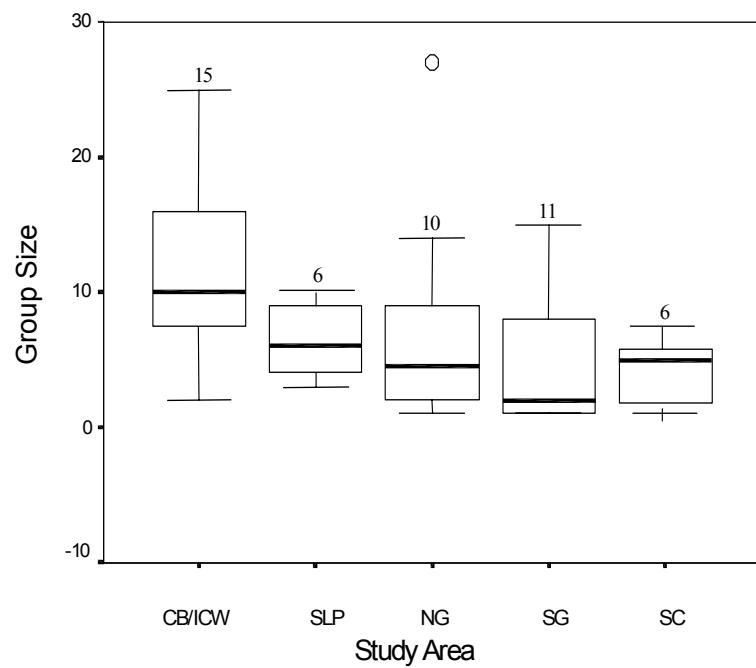


Figure 6. Boxplots of median size of all groups in all study areas. Numbers above boxes indicates sample size for each area.

northeast and southwest along the coast than Resident or Mixed groups. Gulf groups also occurred in SC (Fig. 3).

No dolphins were ever seen in WB, although residents had to traverse WB to move from SLP to CB. Since tracklines were not used, and WB had previously been established as an area not commonly used by dolphins (Irwin and Würsig in press), it was not surveyed extensively. It is likely that dolphins were present occasionally in this area, and not observed. Likewise, although BB is very shallow, it is possible that dolphins use it either to move from SLP to CB or as a potential nursery area. No dolphins were ever observed in this area; however, due to extremely shallow waters and tidal fluctuations, this area was infrequently surveyed and dolphins utilizing this area could easily have been missed.

Fish Data

NMFS fish catch data were examined for the four most commonly consumed prey species found by Barros and Odell (1990), as well as two species of mullet (Gunter 1942). These six species were Atlantic croaker, silver perch, sand seatrout, spot, striped mullet (*Mugil cephalus*) and white mullet (*Mugil curema*). Significant differences were found between the warm and cold seasons for all six species ($p < 0.05$), with a higher abundance of all species in the bay in the warm season. Resident dolphins were never observed following shrimp trawl vessels in either the CB/IWW channels or in the GOM, even when these

vessels were present and actively trawling. In the GOM, dolphins were observed behind trawlers; it is unknown but presumed that those were gulf dolphins.

Discussion

The trends observed are comparable to previous findings in this area (Maze-Foley and Würsig 1999; Irwin and Würsig in press), as well as to similar studies with dolphins moving between deeper coastal waters and protected bays (Irvine *et al.* 1981; Wilson *et al.* 1997). Naturally, environmental factors such as swell, Beaufort, salinity and depth vary with seasonal and tidal changes. During colder months, when there are more storms and therefore more precipitation, swell and Beaufort are likely to increase while salinity decreases with the influx of freshwater, particularly in bays. Daily and seasonal tidal movements will also affect salinity and depth. Therefore, factors such as salinity, depth, and prey availability have a seasonal component that is reflected in the seasonal habitat shift by resident dolphins.

The seasonal differences observed were similar to those of Sarasota Bay (Scott *et al.* 1990). In warm months, dolphins utilize the bays more often, following prey species that go into the estuaries to spawn. All six most common fish prey were found in the bays more in warm months than cold months, as were dolphins. However, while these species were the most common prey for bottlenose dolphins, they were also the most abundant of the 105 species caught in the area by NMFS. It is likely that they are the most frequently consumed species because of their high abundance, rather than being preferentially selected for some nutritive quality. Nevertheless, this assertion needs to

be explored further before firm conclusions can be drawn. Regardless of the reason for their selection of prey, dolphins appeared to be following the fish as they moved in and out of bays on a seasonal basis. The decrease in salinity and temperature in the winter may force fish into the open waters of the gulf. In the summer, fish return to the bays to spawn, and the dolphins follow. Dolphins did not appear to occur preferentially in any given area at a specific ToD, and therefore probably use all areas for all activity; however, behaviors observed in each area need to be examined to confirm this.

Additionally, at this time of year, dolphin groups had larger numbers of calves. In Sarasota, another cause of the influx of dolphins into the bay in the summer is protection for mothers and calves (Scott *et al.* 1990), which may also be a factor here. However, while gulf dolphin groups had fewer calves than resident groups, there were still calves present in the gulf groups that never utilized the SLP or bay areas. Resident and Mixed groups were also seen with calves in the GOM both in the warm and cold seasons. Therefore, protection for calves may not be a major influence on the seasonal use of the bays.

This brings up the question of disuse of the bays by the gulf dolphins. Only one non-resident dolphin was seen in CB during the course of this study, in a group that was otherwise all residents. In addition, at all times during the last eight years of intensive research in this area, the resident population size has remained fairly constant at around 35 animals. Do these factors indicate a carrying capacity within the bay of 35 animals, as suggested by Maze-Foley and Würsig (1999)? The population appears to be thriving, with six new calves this year, as well as calves seen in every other year this group has

been studied. Of the 14 animals originally identified in 1990, 11 are still present. After 1996, the only new dolphins added to the Resident population were calves or juveniles, up until this survey, when two new adults were added. One of these new adults was seen throughout the study year, and was most likely a young adult whose fin had only recently become well marked (between the first and second sightings of this individual, a very large notch was added to the fin, making it more recognizable). The second new adult was not seen until the summer, but was then sighted in two additional seasons, each time with Resident groups and at least once in the bay; therefore, it followed the criteria to be designated a resident. Since 1996, all or almost all new animals were young, presumably born to resident females. From 1997 through 2001, nine adults disappeared, while ten new young animals were added. This year, two new adults and six new calves were added, while seven of the old residents were never encountered. Of those 16 missing, seven had been added as juveniles since 1995. Why is it that the original adults have remained so consistent, while almost no new adults have immigrated, and so many of the juveniles seem to emigrate? It is possible that young males are ranging wider, as has been discovered for several other populations (Wells 1991; Lynn and Würsig 2001) and as discussed below.

Other studies note that females have shown higher degrees of residency, or have smaller home ranges than males (Smolker *et al.* 1992; Simões-Lopes and Fabian 1999). Maze-Foley and Würsig (1999) were able to identify three animals as males and three as females; of those, two males are still present, and all three females are present. Dolphins are presumed female if seen with a calf seven or more times (Maze-Foley and Würsig

2002), and an additional four dolphins were designated as females this year. Of the initial 11 dolphins identified in 1990, one of those is a confirmed male, while five of them are female. It may be the case that the resident population is a family group, perhaps even matrilineal, with the females, young, and a few older males remaining in the area while most males disperse upon maturity, similar to what is seen with killer whales (*Orcinus orca*) and long-finned pilot whales (*Globicephala melas*) (Hoelzel 1993; Ottensmeyer and Whitehead 2003). Genetic work needs to be carried out to determine sex and relatedness of all the animals in this population to further explore this hypothesis.

The trend of smaller group sizes within the bay and larger groups offshore, as seen in Sarasota (Shane *et al.* 1986) and California (Defran and Weller 1999), was not seen here. In fact, the opposite proved to be true; residents formed larger groups, particularly in the bay, while gulf dolphins were found in very small groups unless mixed together with the residents. These trends, the exclusive use of the bay by the residents, the large group sizes for the residents and even larger sizes for mixed groups, and the transient nature of the gulf dolphins, should be investigated from a behavioral perspective. The behaviors of the animals and the relationship of those behaviors to interactions between resident and gulf dolphins and habitat use may shed more light upon the observed seasonal and group patterns.

Finally, the small resight rate of the gulf dolphins indicates that their range is on a much larger scale than that of the residents. However, the two resights that occurred were several months to a year apart for both dolphins, and were either in or near SC.

This area should be surveyed more extensively to determine if gulf dolphins use it more frequently, perhaps as a resting point along the migration route, similar to the bays on the coast of Virginia (Barco *et al.* 1999).

CHAPTER III

BEHAVIOR

Introduction

This chapter will examine social structure through behavioral observation, and Chapter IV will look at the strength of associations within a population over time. These two methods will give insight into the social structure of bottlenose dolphins in San Luis Pass and how it compares to other populations. By creating time budgets of behavior, researchers are able to determine how an animal's time is allotted for self-sustenance and sociality. Behavior time budgets also provide information about daily and seasonal habitat use and movement patterns. Observing and categorizing behavior not only offers an account of the animal's physical activity, but also allows insight into possible causes of the behavior. Behaviors may be classified as activities (events), such as the aerial behavior of breaching and tail-slapping, or behavioral states such as traveling (Würsig *et al.* 2003; Ballance 1992). They may also be categorized as subsets of a more general behavior, such as components of the mating ritual for common loons (*Gavia immer*) (Gostomski and Evers 1998). Typically, a variety of events in combination lead to the categorization of a behavioral state (Shane 1990; Ballance 1992). These categories may attempt to cover the full repertoire of behaviors for a given population, compare certain behaviors by season, or simply compare components of a larger behavioral state (Hanson and Defran 1993; Hoelzel 1993; Gostomski and Evers 1998).

The most commonly explored behaviors in cetacean research are foraging/feeding, traveling, socializing/mating, and milling/resting, or subsets of these general categories (Baker and Herman 1984; Würsig 1986; Bräger 1993; Richardson *et al.* 1995; Geise *et al.* 1999; Acevedo-Gutierrez and Parker 2000). Foraging and feeding are often used interchangeably; however, foraging refers to the hunt for food while feeding refers to actual consumption. Feeding behavior of bottlenose dolphins (*Tursiops truncatus*) off California's coast included high fluke dives of long duration. This behavior is consistent with their preferred benthic prey (Hanson and Defran 1993). For bowhead whales (*Balaena mysticetes*) that winter in the Bering Sea and migrate in spring to the Beaufort Sea, the proportions of time observed feeding, traveling and socializing vary based on time of year and location along migration routes. When actively migrating, traveling is the predominant behavior, while on summer grounds, feeding predominates and socializing tapers off as summer draws to a close (Würsig *et al.* 1989; Würsig *et al.* 2003). Similarly, mating and social strategies, or socio-sexual behavior, vary by species, sex and age class, and social interactions are often an outgrowth of a species' mating strategy. Bottlenose dolphins exist in a tactile fission-fusion society where groups constantly fluctuate in size and composition, and sexual behavior may act as a means of recognition and communication, and occurs between all age classes and sexes (Connor *et al.* 2000). In contrast, humpback whales (*Megaptera novaeangliae*) migrate from summer feeding to winter mating grounds, where mating behavior ranges from large aggressive groups to lone adult male singers (Baker and Herman, 1984; Silber 1986).

Behavior often has a daily or seasonal component as well. Hawaiian spinner dolphins (*Stenella longirostris*) remain in protected bays during the day, and then move out into deeper oceanic water in late afternoon to feed on the rising deep scattering layer (DSL) (Norris *et al.* 1985; Benoit-Bird and Au 2001, 2003). Dusky dolphins (*Lagenorhynchus obscurus*) in Argentina travel in small groups in the morning and evening, while in mid-morning these groups come together after one group locates a school of fish and all the dolphins cooperatively feed. These foraging bouts are followed by a period of socializing in the afternoon within these larger aggregations, which then split up again into small groups in the evening (Würsig and Würsig 1980; Würsig 1986). Similarly, bottlenose dolphins in California have higher rates of feeding in the morning and afternoon, and decreased feeding but increased traveling at mid-day (Hanson and Defran 1993).

While bottlenose dolphins in San Luis Pass, Texas, have been studied for almost ten years, their behavior has not been systematically observed and categorized. This is an important step in answering the question of disparate habitat use by resident and gulf dolphins. Despite the fact that residents exhibit a seasonal movement pattern, it is unknown whether their day-to-day activity has a corresponding seasonal pattern. Similarly, while the gulf dolphins are seen in the coastal area year-round, their specific use of the habitat has not been examined.

The first objective of this chapter is to determine if and how behavioral states differ between resident and gulf dolphins, and what changes occur when these dolphins interact. The second objective is to identify factors that influence behavior, and the third

objective is to determine if those influences create a daily or seasonal component to behavior. I hypothesize that there is a difference in behavior between resident and gulf dolphins, and that there is also a difference in behavior when these groups join. I further hypothesize that there will be a daily and seasonal trend for residents, but not for gulf dolphins, as they use the area in a similar manner year round.

Methods

Behavioral Sampling

Surveys were completed as presented in Chapter II. A start time was taken upon joining a group, and behavior samples were recorded using the instantaneous sampling method (Mann 1999; Rose 2000). Behavioral categories were defined as follows: foraging/feeding, traveling, socializing, milling or other, with the majority of the group performing the same behavior (Shane 1990; Ballance 1992; Hanson and Defran 1993). See Table 2 for descriptions of behavior. Since it was difficult to actually observe dolphins feeding, the category of feeding/foraging will only be referred to as foraging. Behavior categories could also be combined if more than half of the group was engaged in more than one activity, such as foraging/traveling, traveling/socializing, or socializing/foraging. However, milling was never combined with any other behavior; it was assumed that if the dolphins were performing one behavior and remained in one location, then that behavior would be counted solely, while milling and traveling were mutually exclusive.

These behavior samples were taken every three minutes, or upon the first surfacing after the three-minute interval mark. If no dolphins were observed during the entire three- minute interval, then that sample was counted as not applicable (NA).

Table 2. Definitions of behavior categories as assigned every three minutes using instantaneous sampling method.

Foraging	<ul style="list-style-type: none"> ▪ Variable direction of movement ▪ Generally remaining in the same area ▪ High arching dives ▪ Fish chasing or tossing ▪ Little apparent interaction between individuals
Traveling	<ul style="list-style-type: none"> ▪ Moving in the same direction ▪ Moving steadily or rapidly ▪ Often synchronous and frequent surfacings
Socializing	<ul style="list-style-type: none"> ▪ Variable direction of movement ▪ Individuals in close proximity or touching ▪ Often interacting ▪ Frequent surface active behavior (<i>i.e.</i> tail slaps, leaps)
Milling	<ul style="list-style-type: none"> ▪ Variable direction of movement ▪ Remaining in one area in close proximity ▪ Slow swimming speeds ▪ No physical contact, surface active behavior, or long, deep dives
Other	<ul style="list-style-type: none"> ▪ Any behavior that could not be confidently or rapidly described as one of the other categories

Behavioral sampling continued until photographs were taken of all the animals, or after three consecutive recordings of NA when the dolphins were presumed lost. A behavior index was then calculated of the number of times a given behavior was observed divided by the total number of samples taken per group sighting (Karczmarski, personal

communication³). This behavior index was calculated for all possible behavior categories, so a value of zero (no instances of that behavior during that sighting) was possible.

Additionally, the mixed categories of behavior were split and calculated as one-half towards each of the three possible behaviors of traveling, foraging or socializing, in order to make the behavioral trends more apparent and robust (Hanson and Defran 1993; Würsig *et al.* 2003). This behavior index also controls for pseudoreplication due to uneven sampling durations with each group encounter. Finally, time budgets of all behaviors were calculated for each group category (Resident, Gulf, and Mixed) in each study area (CB/ICW, SLP, NG, SG, and SC, see Chapter II, Fig.1).

Environmental and seasonal factors were compared with behaviors to determine if behaviors differed seasonally, by ToD, or by depth, salinity, or bottom topography. Depth ranged from 0.6 – 15.6 m, and salinity from 0-36 ppt. Bottom topographies were categorized as follows: deep sandy bottom (NG and SG), shallow muddy bottom with oyster reefs (CB) deep channels (ICW and SC) and shallow sandy bottom with sand bars (SLP).

Analysis

Due to non-normal distributions, behavior indices were examined using Kruskal-Wallis nonparametric ANOVA's and Dunnett's T3 post hoc tests to determine if

³ Karczmarski, L. Texas A&M University at Galveston.

frequency of behaviors varied between resident or gulf dolphins, and if behaviors varied by habitat type. Behaviors were also examined for daily and seasonal trends using MANOVA and Mann-Whitney U tests, and were compared to environmental factors that could influence those trends using MANOVA. All behavior samples of NA in which dolphins were not seen were discarded and not used in analysis. Additionally, all group encounters in which behavioral sampling occurred for five minutes or less were discarded, leaving 44 groups for analysis. All statistical analyses were carried out with SPSS for Windows Version 11.0 (SPSS 2001).

Results

General resident behavior was fairly well distributed between the four main behavior categories, while gulf dolphins spent the majority of their time traveling and foraging, and mixed groups spent most of their time socializing and traveling (Fig. 7). Foraging ($p=0.045$) and socializing ($p=0.009$) varied significantly between group categories. Foraging was seen more in gulf groups than mixed groups ($p=0.007$), while socializing was seen more in resident and mixed groups than in gulf groups ($p=0.018$ and 0.029 respectively). Residents were the only group observed milling, and the proportion of “other” behavior was highest with mixed groups.

When calculated by overall study area and no splitting by group category, the proportions of foraging ($p=0.020$) and traveling ($p=0.009$) varied significantly between areas; foraging showed no distinct difference for any specific area, while travel was higher in CB/ICW than SLP ($p=0.005$), and also higher in NG than SLP ($p=0.001$).

However, when a MANOVA was run with study area and group category, and with the intercept excluded from the model, all behaviors except milling (which was only seen twice, both times with residents) varied significantly ($p<0.015$). Figures 8-10 illustrate the time budgets of behavior for each group category in each study area. The behavior category “other” included all behaviors that were not readily identifiable and is likely a combination of all behavior categories. Therefore, it is not considered in any further analysis so as not to bias the recognizable behavioral categories.

The only environmental factors that appeared to have an influence on behavior were depth and bottom topography. Foraging varied significantly for all groups between depth categories of 0-2 m and 2-4 m ($p=0.026$), with most foraging in the shallowest and deepest categories (Figure 11a). Socializing was never seen in depths deeper than eight m (Figure 11b), while traveling occurred in all depths, but slightly more in shallower depths (Figure 11c). Traveling varied significantly by bottom topography type for all groups ($p=0.016$), with more traveling in the shallow muddy and deep sandy areas than shallow sandy bottomed area ($p=0.004$ and <0.0001 , Figure 12c), while the opposite bottom topographies (shallow sandy and deep channels) had the most foraging (Figure 12a). When the interaction between depth and bottom topography was examined (excluding intercept in the model), the difference was significant for foraging ($p<0.0001$) and traveling (<0.0001), but was not significant for socializing ($p=0.143$). Socializing was seen in all bottom topographies, but was seen most with shallow muddy and shallow sandy bottoms (Figure 12b).

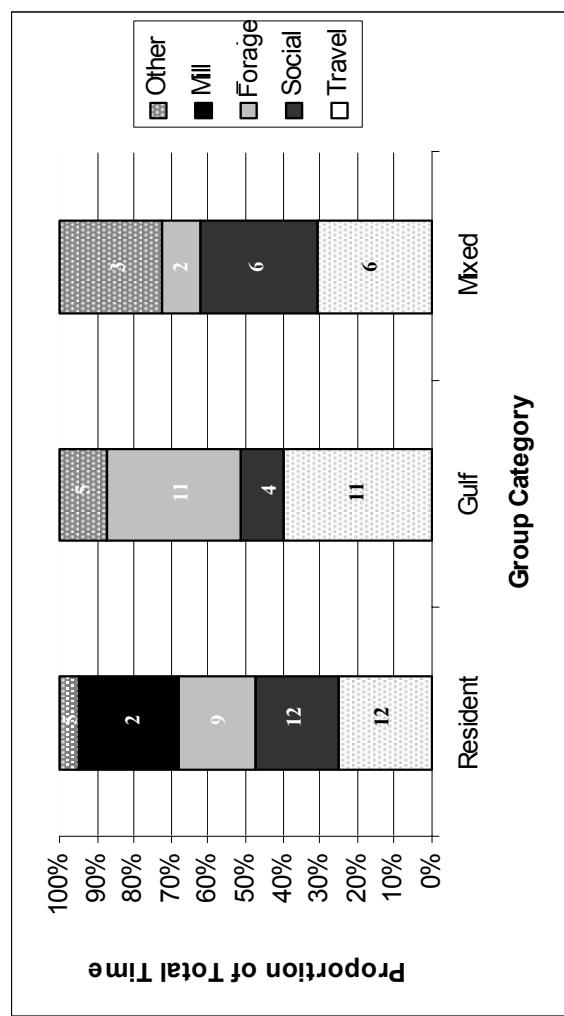


Figure 7. Overall proportion of time of all behaviors for each group category.
The numbers indicate the group sample size for each behavior.

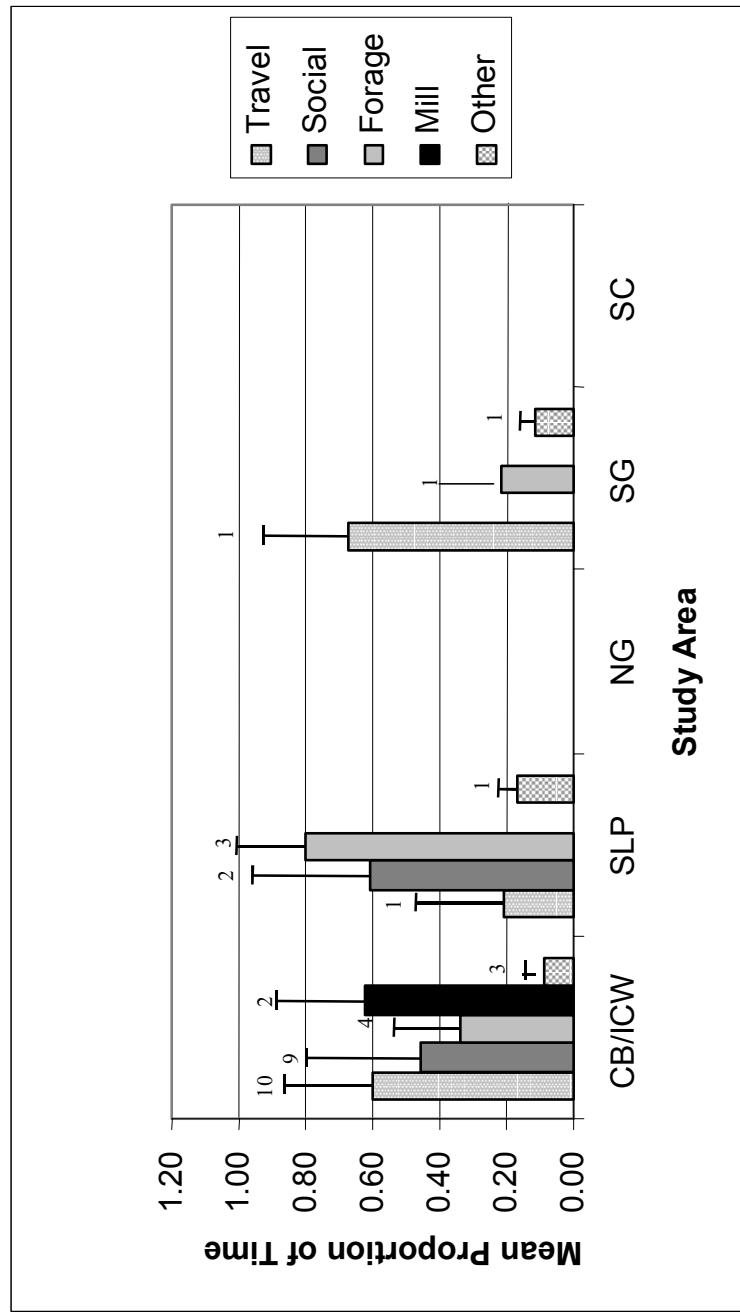


Figure 8. Mean proportion of time for behavior of resident groups in each study area. The numbers above each column indicate the group sample size for each behavior.

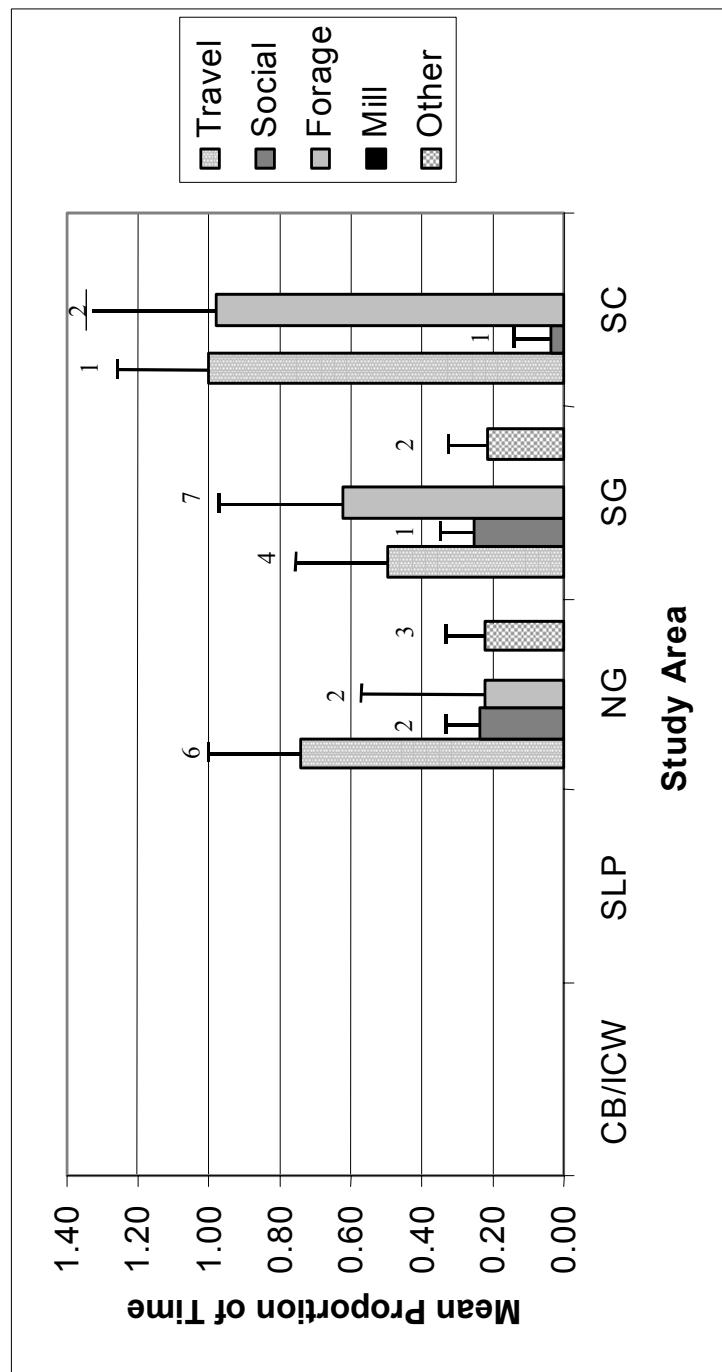


Figure 9. Mean proportion of time for behavior of gulf groups in each study area.
Numbers above each column indicate group sample size for each behavior.

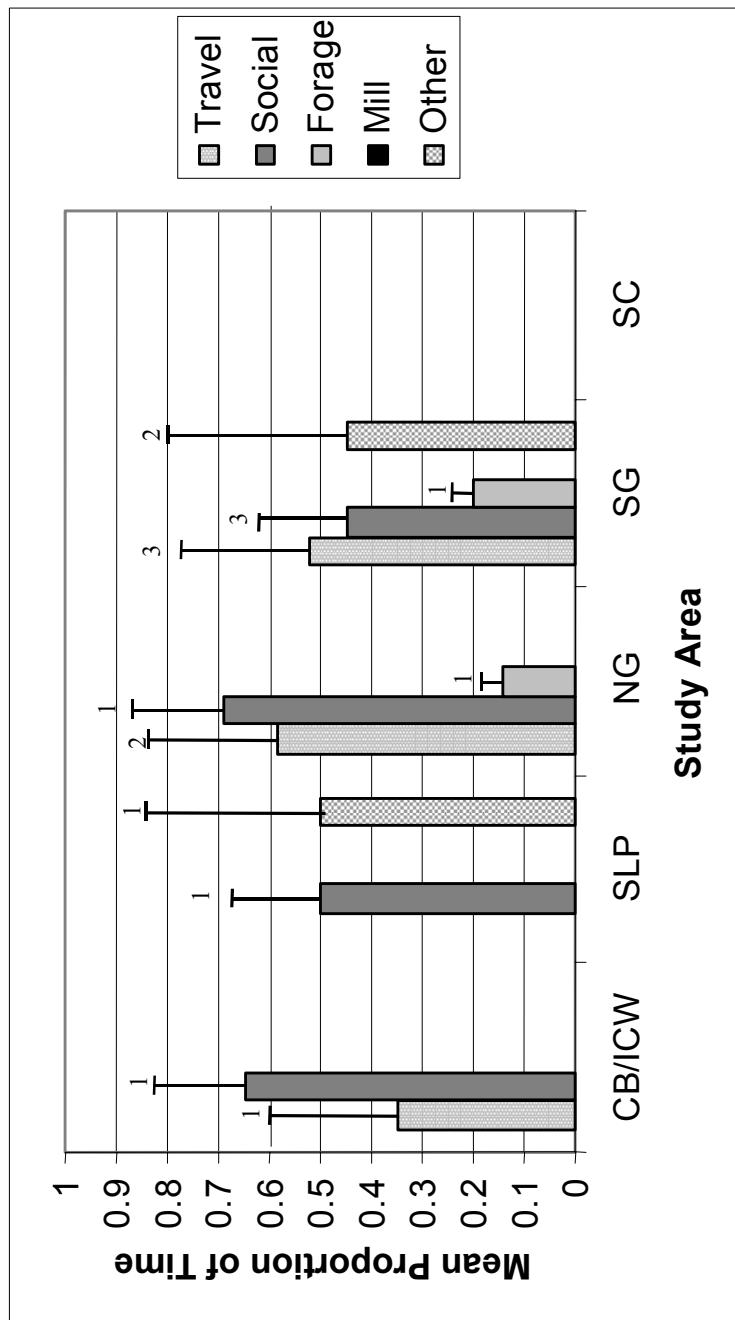


Figure 10. Mean proportion of time for behavior of mixed groups in each study area.
Numbers above each column indicate group sample size for each behavior.

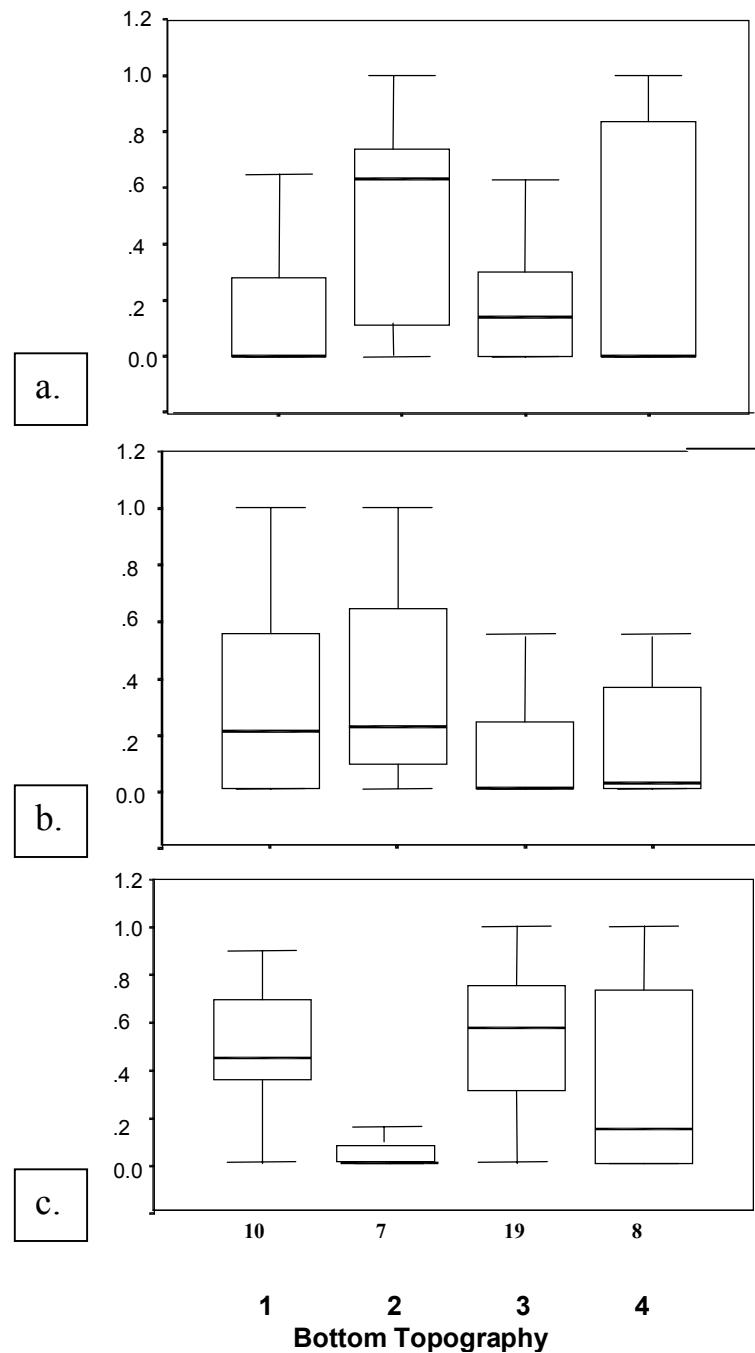


Figure 11. Boxplots of frequencies of behavior as they varied by bottom topography. (a) Foraging, (b) Socializing, and (c) Traveling. The bottom topography categories are as follows: 1=Shallow muddy bottom type, 2=Shallow sandy bottom type, 3=Deep sandy bottom type, and 4=Deep channel type. Numbers below the boxplots indicate group sample size for each bottom type, and are the same for all three behaviors.

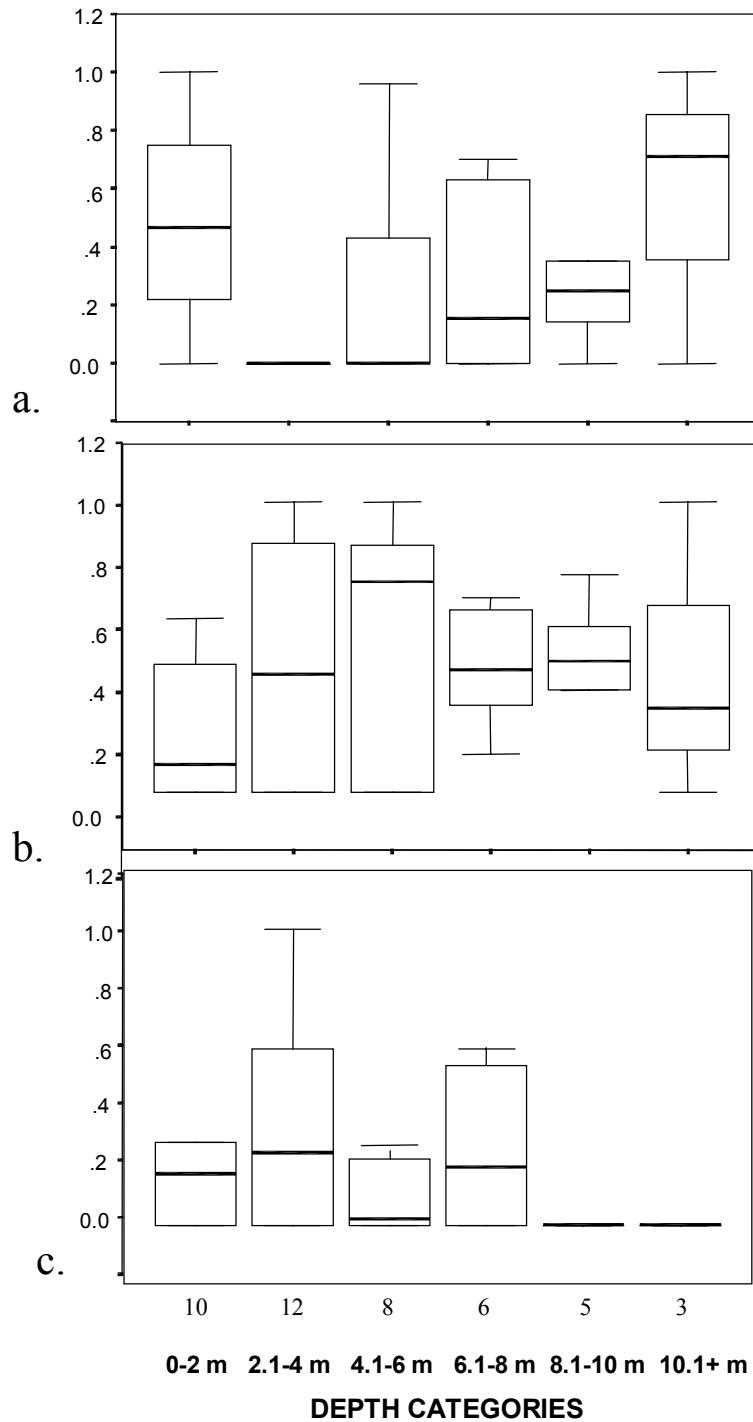


Figure 12. Boxplots of frequencies of behavior as they varied by depth categories. (a) Foraging, (b) Socializing, and (c) Traveling. Numbers below the boxplots indicate group sample size for each depth category, and are the same for all behaviors.

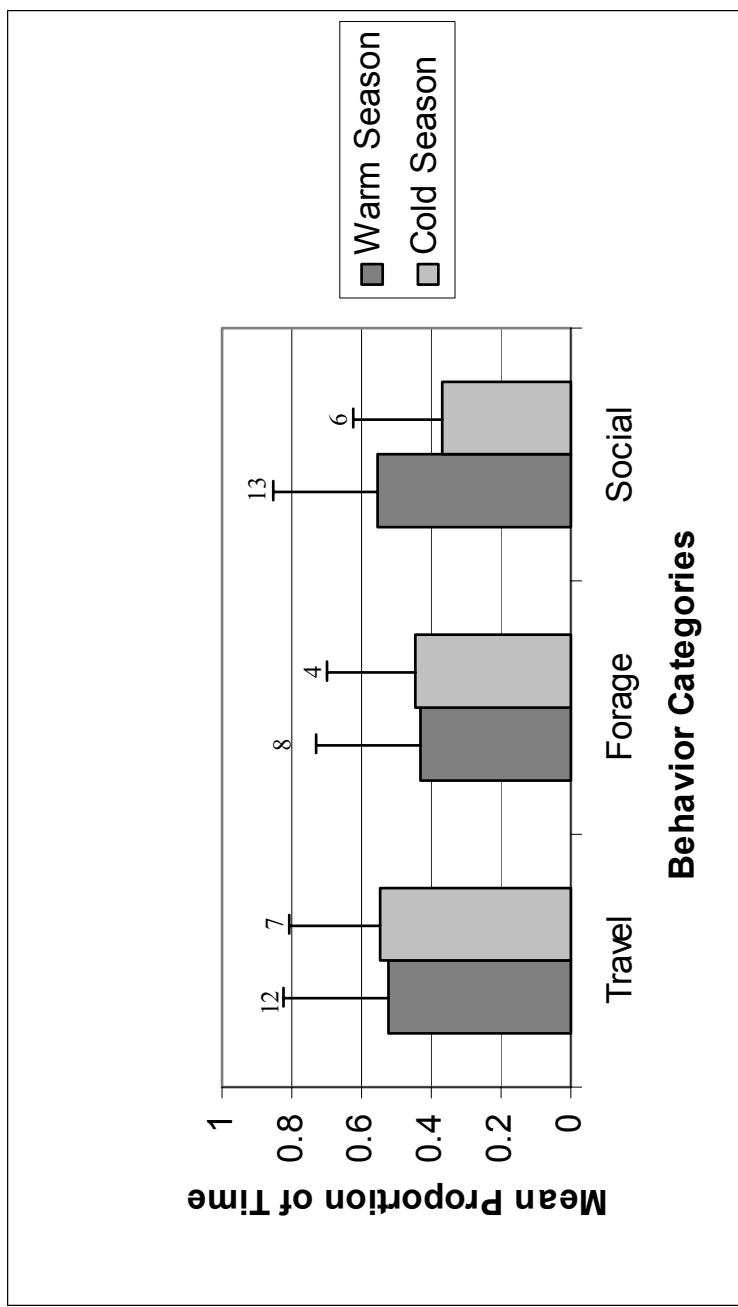


Figure 13. Mean proportion of time for the behaviors of all groups with residents for both warm and cold seasons. Includes both resident and mixed groups. Numbers above each column indicate group sample size for each behavior.

The group type encountered varied significantly by season ($p=0.046$), as well as the study area in which the dolphins were found ($p=0.001$). Behavior of residents varied significantly by ToD in both warm and cold seasons ($p=0.047$ and 0.022 , Figure 13), while behavior of mixed groups varied only in the cold season ($p=0.034$), and gulf group behavior was consistent year-round. In the warm season, socializing varied significantly between midday and late afternoon ($p=0.028$), with more seen in late afternoon. For resident groups, both foraging and socializing varied by ToD ($p=0.012$ and 0.029), with foraging seen predominantly in the morning, and socializing seen predominantly in the afternoon. Traveling was seen mostly at mid-day; however, this trend was not significant. No other seasonal or ToD trends were statistically detectable due to small sample size, but traveling appeared to peak in the morning and late afternoon for gulf dolphins, while foraging peaked midday. Also, more socializing and traveling were seen in the morning for Mixed groups than at midday, and no Mixed groups were seen in the afternoon (Figures 14-16).

The effects of group size and presence of calves were also examined against frequencies of behavior. The frequency of social behavior ($p=0.011$) varied significantly with group size, with larger groups socializing more than smaller ones. The frequency of foraging approached significance ($p=0.060$); lone individuals were observed foraging more than larger groups of 10-14 dolphins ($p=0.048$). The presence of calves in a group also had an impact on observed behavior. Foraging, traveling and socializing varied in proportion with the presence or absence of calves ($p=0.001$, 0.037 , and 0.020), while

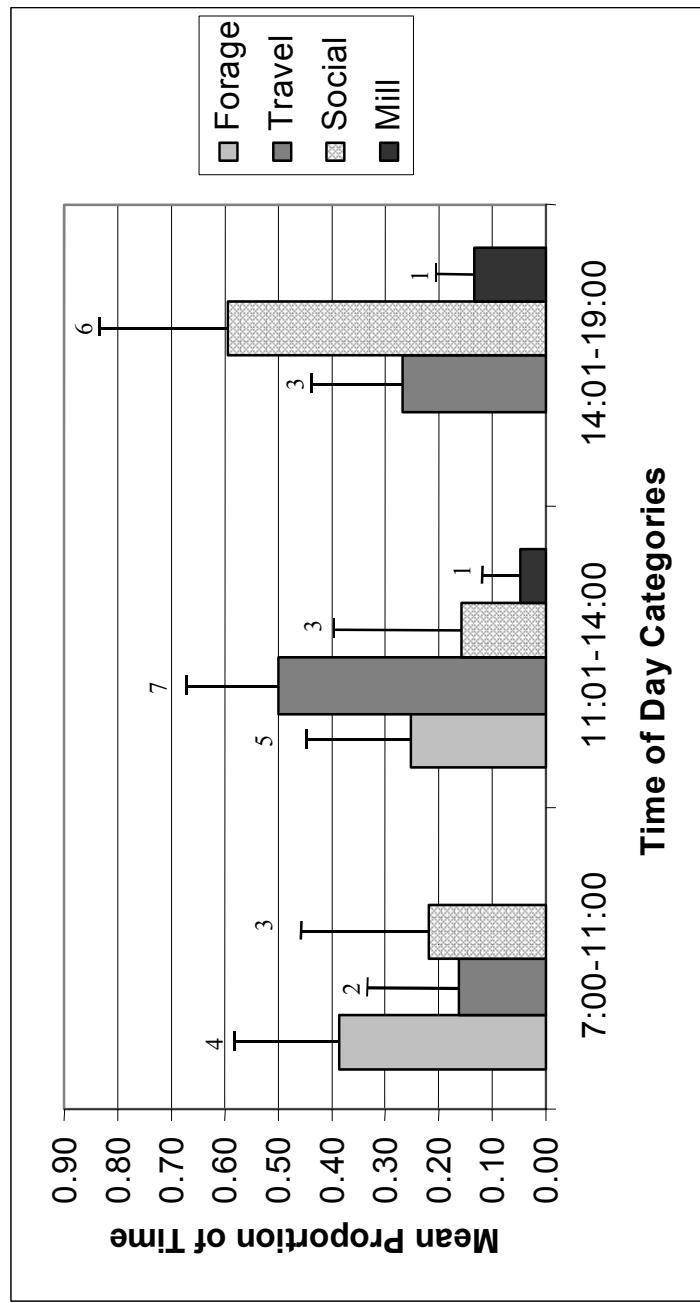


Figure 14. Mean proportion of time for each behavior by ToD for resident groups. Numbers above each column indicate group sample size for each behavior.

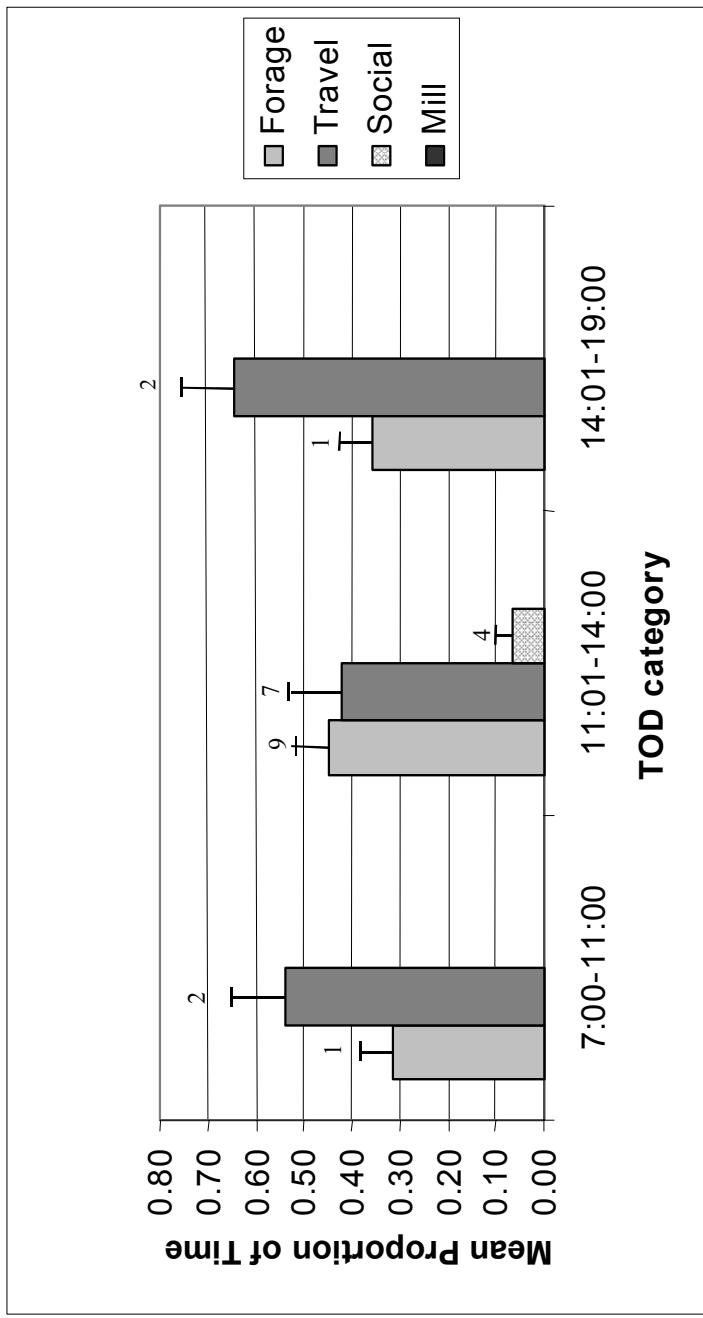


Figure 15. Mean proportion of time for each behavior by Tod for gulf groups. Numbers above each column indicate group sample size for each behavior. No statistics were run for these values due to the small sample size.

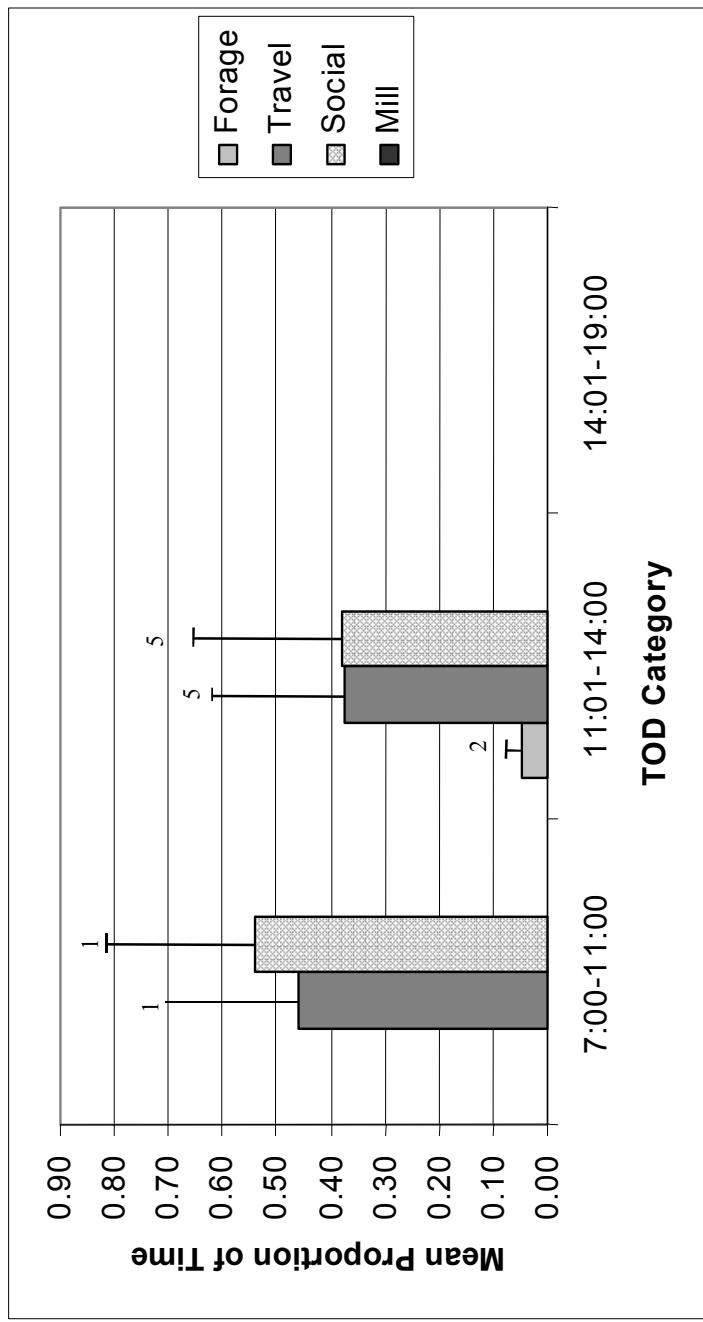


Figure 16. Mean proportion of time for each behavior by ToD for mixed groups. Numbers above each column indicate group sample size for each behavior. No statistics were run for these values due to the small sample size.

foraging and socializing varied with the number of calves in the group ($P=0.026$ and 0.027).

Discussion

Frequencies of behavior differed between residents and gulf dolphins. Gulf dolphins were generally only sighted one time during the study year, and seemed to be passing through this area as a portion of a greater migration. This theory is upheld by their behavioral patterns. Gulf dolphins were seen alone or in small groups, and spent most of their time traveling and foraging. In contrast, the resident dolphins utilize this area year round. When alone, they generally do not leave the CB or SLP areas, and their overall behavior is fairly well distributed between all four general behavioral categories. However, when resident and gulf dolphins join together in mixed groups, their behaviors change. Residents venture further into the gulf than they do alone, although never further than 5-10 km NE or SW along the coast (Beier 2001; Chapter II, Fig. 3), and group size and the rate of socializing increase. In summer, the time of year when most neonates are observed, the number of mixed groups also increases.

The resident population is quite small with only 35 animals, and has remained this size for the last ten years. This population is somewhat geographically isolated, with their exclusive use of CB; however, they are not so isolated that their only reproductive option is incestual mating. Therefore it is highly probable that the observed increase in social behavior in mixed groups represents mating between resident and gulf animals. In addition, since many resident juveniles seem to disperse from their natal

group, these large social groups may be a means of long-term contact between family members. Behavioral evidence supports these theories, but genetic sampling of resident and gulf dolphins needs to be carried out to determine what relationships, if any, exist.

The larger proportion of traveling observed in gulf dolphins may indicate that these animals are passing through the area while on a longer migration. Two gulf dolphins were resighted, either in or near SC, with both sighted approximately one year apart. This trend was observed in previous studies of the area as well (Irwin; Beier, personal communication^{4,5}). The migration may be of such duration up and down the Texas gulf coast that dolphins only pass through the same area twice a year. Shane (1977, 1990) recorded traveling as the predominant behavior of dolphins in Port Aransas, Texas. In addition, Lynn and Würsig (2001), Weller (1998), and Gruber (1981) all noted increased encounter rates at various times of year along the Texas coast, ranging from Aransas Pass and Matagorda Bay to Galveston Bay, a distance of approximately 281 km. Long distance movements have also been recorded for specific dolphins along this coastline, with distances of 517 and 622 km traveled (Jones 1991). Additionally, the Würsigs reported a migration distance of 900 km within a nine month time period for a group of five bottlenose dolphins in Argentina (Würsig and Würsig 1979; Würsig 1984), and along the southern California Bight, dolphins have a range of 732 km (Defran *et al.* 1999). Therefore, it may be that the fluctuation in numbers of dolphins represents a seasonal migration along the Texas coast. However, all catalogs of

⁴ Irwin, L.J. Independent Researcher, Volcano, HI. 2003.

⁵ Beier, A. DolphinWatch Marlborough, Nelson, New Zealand. 2003.

photographs for this area, as well as those from other coastal Texas bottlenose dolphin studies (*e.g.* Shane 1977; Henningsen and Würsig 1991; Lynn 1995) need to be compared to determine the spatial extent and duration of this apparent migration. Another possibility is that these dolphins may be moving inshore during winter months, following prey or temperature fluctuations in deeper gulf waters.

Feeding/foraging behavior differed between shallow bay and deeper gulf waters. In the gulf, foraging was similar to that observed in California, with high peduncle or fluke up dives that lasted for three to four minutes (Hanson and Defran 1993). Also, this behavior was observed mainly in individuals or small spread out groups, with little apparent interaction or cooperation among dolphins. In contrast, foraging in the bay consisted of short, shallow dives, fast chasing of fish, and dolphins often in close proximity with potential herding and cooperation. This difference in foraging behavior may be representative of differing foraging strategies between residents and gulf dolphins. It may also be an indication of prey available in each location, as well as a result of bottom topography. Most foraging was observed in SLP for residents, but was also recorded in CB. In the warm season, preferred prey species are found in the bays and near the pass. Residents may take advantage of the shallow waters of CB and SLP to chase fish and use sand bars or other dolphins as barriers. Since residents were rarely seen in CB in the cold season, they must feed in the gulf during those months; however, gulf foraging by residents was rarely observed, and always in mixed groups. Conversely, gulf dolphins were seen along the coast and in SC year-round, and were

often observed foraging. In these areas, the water is much deeper, particularly in the channel, where dolphins may use the sides of the channel to herd and capture fish.

There also may be reciprocal altruism among the residents, since they spend all their time together and may be able to count on assistance in foraging both in the present and the future. This has been seen in other dolphin populations; in Florida some bottlenose dolphins will drive prey towards other waiting dolphins (Reynolds *et al.* 2000), while in Argentina, dusky dolphins herd prey into fish balls and then feed cooperatively (Würsig and Würsig 1980). Association patterns among residents will be explored in the next chapter for evidence of long-term close associations to determine if cooperation may be occurring. Since gulf dolphins are only observed once each, it is unknown but unlikely that their associations last for any length of time. They were seen foraging alone, and must rely on their own means to catch prey. They may also have been foraging on different species than residents, and therefore utilizing different strategies. Residents were never observed following shrimp trawlers, but in the gulf, some trawl boats were observed with dolphins following, presumably feeding on discarded bycatch and benthic fauna stirred up by the nets (Corkeron *et al.* 1990). Foraging behavior needs to be examined more closely for both resident and gulf dolphins to determine what is causing the divergence of strategies.

Resident dolphins appeared to be habituated to small boat traffic, never moving away from the research vessel and often approaching and bowriding. Gulf dolphins, on the other hand, showed some amount of avoidance by angling away from the boat when traveling, and had long dive times when foraging. We often curtailed gulf group

encounters so as not to potentially harass the animals, and occasionally lost small foraging groups or had to observe from a distance. Therefore, it was often difficult to confidently describe all behavior observed in gulf dolphins, while more time was spent in close proximity with residents, and therefore behaviors were easier to categorize for residents. Thus, the proportion of the “other” category is much higher for gulf and mixed groups than for residents. However, I believe that the overall proportions of behaviors recorded reflects the true overall rate of behavior for all groups; enough time was spent with all groups and enough clear behaviors were observed to confidently attribute different proportions of behaviors to resident and gulf dolphins.

A daily pattern was observed among residents. Unlike spinner dolphins in Hawaii that feed at night on the rising DSL (Norris and Dohl 1980, Bird-Benoit and Au 2001, 2003), near-shore bottlenose dolphins generally feed in morning and evening. This population showed diurnal variation in proportions of behavior; however, its patterns differed from those seen in dusky dolphins in Argentina or bottlenose dolphins in California (Würsig and Würsig 1980; Hanson and Defran 1993, respectively). In California, dolphins feed both in the morning and evening, while traveling peaks during mid-day. In the CB/SLP population, foraging occurred mostly in the morning and some at mid-day while none was observed later in the day, and most traveling occurring mid-day followed foraging but was also seen throughout the day. In Argentina, dusky dolphins also feed in the morning, followed by a period of socializing. In the present bottlenose dolphin population, most socializing occurred in the afternoon or evening but was seen throughout the day. More milling occurred in the evening as well. Since no

observations were made at night, it is unknown what behavior occurs at that time, but it is likely a time of rest. Further behavioral observations in the evening and at night need to be carried out since the sample size of milling behavior was too small to draw strong conclusions. Still, the low proportion of milling during the day and the increase observed towards the evening lend weight to the idea that these dolphins are inactive at night. This trend occurred in radio-tagged bottlenose dolphins in Matagorda Bay, Texas, whose movement decreased and became more confined at night and were presumed to be resting (Lynn and Würsig 2001), therefore it is likely to be the case here as well.

No seasonal trend was observed for behaviors, save the increase in socializing in the warm season. This increase is likely due to a corresponding increase in mating at this time; the gestation period for bottlenose dolphins is approximately 12 months, and the summer was the peak sighting time for calves, particularly neonates, although calves were seen year round. A seasonal trend was not expected for gulf dolphins; they appear to utilize the entire area in much the same manner year round. However, it is a surprise that more of a seasonal trend was not observed for resident dolphins, since they have a strong seasonal movement pattern from bay to gulf. Perhaps their daily activities do not change regardless of area, other than their method of foraging. Again, this needs to be examined more closely; this study may not have spent enough time in each season and with each group to discover potential small changes in behavior.

Further observations of behavior, particularly foraging and socializing, need to be carried out with both resident and gulf dolphins to better identify the strategies behind observed differences. Since actual feeding was difficult to see from the surface and so

recorded occurrences of foraging behavior could be skewed, and vocalizations were not recorded, which are an important component of social behavior, these results could be biased. Further work with additional recording techniques, such as video cameras and underwater acoustic monitoring, would be recommended. Additionally, comparisons with other photo-ID catalogs should be carried out to determine the extent of the migratory range of gulf dolphins, as well as possible sightings of dispersed males from this population. Finally, behaviors should be closely monitored for any seasonal changes that may exist but were not observed in this study.

CHAPTER IV

ASSOCIATION PATTERNS

Introduction

This chapter will examine social structure by looking at associations within a population. Two individuals may be presumed in association simply by being in the same area during a given time period; therefore, the basis for and duration of associations needs to be explored to give insight into social organization and, by extension, population biology (Whitehead 1997, 1999b). Both kinship and dominance hierarchies can influence affiliations (Freeman *et al.* 1992; Kapsalis and Berman 1996; Möller *et al.* 2001), and in some species of primates and cetaceans, reciprocal altruism may play a role as well (Packer 1977; Mitani *et al.* 2000; Möller *et al.* 2001). The duration of association among individuals within a group or population can range from the matrilineal pods of killer whales (*Orcinus orca*) and long-finned pilot whales (*Globicephala melas*) which can last for a lifetime (Baird 2000; Ottensmeyer and Whitehead 2003), to the highly transient interactions observed in humpback whale (*Megaptera novaeangliae*) groups on mating grounds that only last for hours (Mobley Jr. and Herman 1985). At the group level, many species of animals exist in fission-fusion states, where group membership and size fluctuate at rates of minutes to days (Connor *et al.* 2000). This constant oscillation in group composition occurs in ungulates, primates, and cetaceans, as well as some bird and fish species (Whitehead and Dufault 1999). It is important to determine if all members in these groups are changing, or if there are some

long-term associations among individuals, and what the basis may be for associations or avoidances in order to better understand the population social structure.

In rhesus monkeys (*Macaca mulatta*), group composition is similar to that of sperm whales (*Physeter macrocephalus*), where females remain in natal groups for life while males leave as they mature. In rhesus monkeys, the amount of affiliative behavior displayed between females is determined primarily by kinship, and secondarily by attractiveness of rank to subordinates (Kapsalis and Berman 1996). In contrast, female and juvenile sperm whale associations are highest within a close social group in which members tend to be matrilineally related, and dominance appears to play no strong part (Christal and Whitehead 2001). In red deer (*Cervus elaphus*), dominance hierarchy regulates interactions. The probability of fighting between males was determined to be highest among individuals two ranks different in this hierarchy, where the risk of winning or losing and the potential resources to gain or lose were most closely balanced, while kinship did not appear to play any role (Freeman *et al.* 1992).

Photo identification has been extensively used as a method of determining durations of associations. In one of the first photo-ID studies, in Golfo San José, Argentina, a group of 53 bottlenose dolphins (*Tursiops truncatus*) was studied from 1974 through 1976. Five dolphins were always present, while six others were there until 1975, then disappeared and five new dolphins took their place in the population. In 1976, four of the original six returned to the area, and in 1984-1986, ten of these same dolphins were resighted in two different surveys of the area (Würsig and Würsig 1979; Würsig and Harris 1990). This gives an indication that these animals may have long-

term site fidelity and associations; however, it gives no quantifiable information about those associations. An association index (AI) can be created to measure how frequently two animals co-occur (Cairns and Schwager 1987; Ginsberg and Young 1992), yet this may still be inflated due to simultaneous use of an area for a period of time by those animals without true association (Whitehead 1999b). Bejder *et al.* (1998) solved this problem by replicating the AI repeatedly with random permutations of data, then evaluating resulting p-values to determine if the true p-value is low enough to be valid. Therefore, a robust AI is created from observed and replicated permutations that is distinguishable from random noise which, when combined with behavioral observation and genetic sampling, can determine the quality and duration of social structure for a population.

Such permutation studies have been carried out with several populations of bottlenose dolphins, and association patterns appear to be a reflection of mating strategy for males, based on both kinship and reciprocal altruism, and prey/predation pressures for females (Lusseau *et al.* 2003). In Shark Bay, Australia, associations are strongest among males and increase in strength as males age, while females are more sociable with lower consistent associations. Few lone males are seen as most males are found in dyads or triads, which then also form super-alliance groups as two or three of these bonded pairs join together (Smolker *et al.* 1992). Genetic studies of these male alliances show that among primary alliances with the strongest AI's, individuals are more likely to be related than not, but in super-alliances the strength of association was not correlated with relatedness (Krützen *et al.* 2003). Primary alliances then are based on kinship, and

the behavior of male alliances herding females to mate is likely an inclusive fitness mating strategy. In contrast, male alliances in Port Stephens, Australia, were not related and males were not likely to form alliances with related dolphins, although a similar herding behavior occurred. Alliance bonds typically form among juveniles and persist into adulthood, with interbirth intervals for females lasting two to four years for bottlenose dolphins, which prevents maternal siblings from associating as cohorts. Therefore, it may be that some alliances are formed with cohort members rather than kin. In this case, the mating strategy is representational of reciprocal altruism rather than inclusive fitness (Möller *et al.* 2001). In Doubtful Sound, New Zealand, an entirely different social structure is seen. This population is a geographically isolated and therefore closed population of 65 dolphins in which all AI's are moderately strong. No strong male-male alliances were seen, nor were strong female-female alliances; most groups were of mixed sex, and strong associations were seen both within and between sexes. Most affiliations between males and females lasted for the duration of the breeding season, although some lasted much longer (Lusseau *et al.* 2003). The geographic isolation of this community allows for the long-term bonding of all members of the population, and the closed gene pool seems to preclude a need for males to herd females; therefore male alliances are not formed.

The objectives of this chapter are to examine AI's for SLP resident dolphins, as well as the duration of these AI's through lagged association rates. The resulting social structure will then be compared to social structure of other populations to determine the type of social organization for this population. Behavioral evidence suggests that this

population may be a matrilineal family group where many males disperse while the females and juveniles remain in the area with the natal group, as demonstrated in Chapter III. As expressed by Christal and Whitehead (2001), competition for resources and aggression among males may not be persistent in a family group with a lack of mating activity; therefore, male alliances based on herding should not exist in this population. Male-male bonds may form among cohorts, however, and female-female bonds could exist, as females may be the core of this population.

Methods

Photographs were taken of each individual in every group encounter from December 2002 through December 2003, and then compared to catalogs to determine group composition. Association indexes (AI) were then calculated for animals seen three or more times using the simple ratio (Cairns and Schwager 1987; Ginsberg and Young 1992). This index was chosen for its accuracy, as it does not double count or average sightings, and is best for small data sets (Ginsberg and Young 1992). This index calculated the proportion of time two individuals spent together, using the formula:

$$AI = J/(A+B-J) \quad (1)$$

Where J = number of joint sightings of dolphins A and B, A = total number of sightings for dolphin A, and B = total number of sightings for dolphin B (Cairns and Schwager 1987; Karczmarski 1999). AI's fall between zero and one, zero meaning they were never observed together and one indicating they were always observed together. Strong associations were considered higher than 0.5, or seen together more than half the time.

The computer program SocProg was developed by Whitehead (1997; 1999a) to facilitate the calculation of AI's, and to run random permutations using the Monte Carlo method as described by Bejder *et al.* (1998). These random permutations were run using the same number of animals and number of sightings as the real data set. These were run in increasing numbers, until the p-value stabilized at 10,000 permutations. The p-value for the standard deviation (SD) was used for analysis, and was considered significant >0.95 (Whitehead 1999a). A Mantel test was also run to determine if association patterns differed between adults and juveniles (Mantel 1967; Whitehead 1997). Principal coordinate and cluster analyses were created to visually examine the rates and strengths of associations among all individuals, both including and excluding calves.

A temporal analysis was run to determine the lagged association rate, or the likelihood that two animals seen at time t would be seen together again at some other time d . This equation was:

$$\hat{g}(d) = \frac{\sum_A \sum_i (A, j, d)}{\sum_A \sum_i N(A, t_{A,j,d})} \quad (2)$$

where $\hat{g}(d)$ was the lagged association rate, the numerator represented the total number of repeat associations after time lag d , and the denominator represented the expected number of repeat associations after time lag d (Whitehead 1997, 1999a). If this lagged association rate lay above the null rate, then the rate of association was significantly more than random. This rate was also fit to a model that best described the type of social structure represented by the association patterns observed for this population.

A lagged identification rate was also calculated, which was the probability that an animal identified at time t would be identified again at some time lag d (Whitehead 1999a). This was also fit to a model that would best describe the rate of identification of this particular population.

Results

The simple ratio association index was calculated for dolphins seen three or more times, both including and excluding calves. Since no gulf dolphins were seen more than twice, by default this analysis was performed only on residents. In both cases, after 10,000 random permutations were run and compared to the real data, the p value of the SD was 0.999, indicating that the real data were significantly different from random. However, the number of dyads was less than expected, meaning there were fewer strongly associated dyads than would be expected for the high association rate of this population. The Mantel test for differing patterns of interaction between adults and juveniles had a t value of 0.322 with a p value of 0.626, or no significant difference in associations.

A cluster analysis was created of associations among residents, first including (Fig. 17) then excluding (Fig. 18) calves in order to examine relationships of females both with their calves and with all other dolphins without bias from the calves' presence.

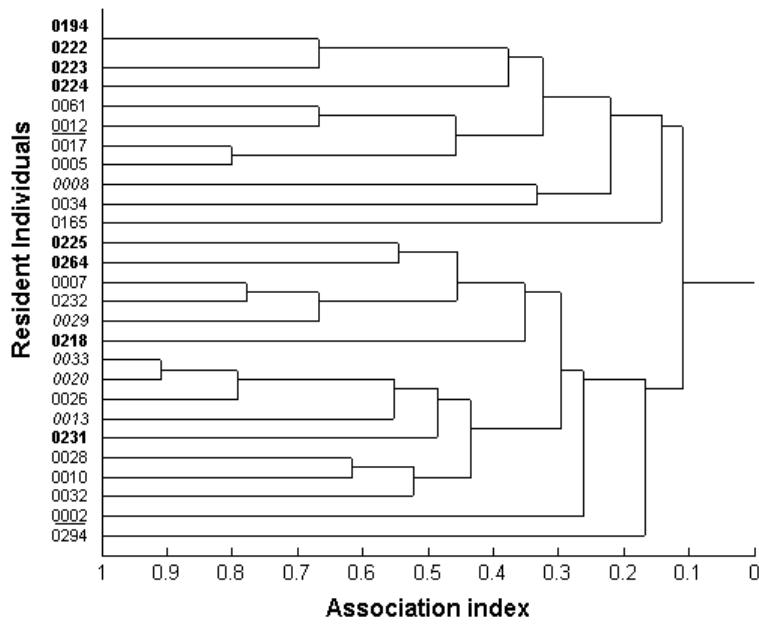


Figure 17. Cluster analysis for resident dolphins excluding calves. Calculated for dolphins observed 3 or more times. Males are underlined, females are in italics, and juveniles are in bold.

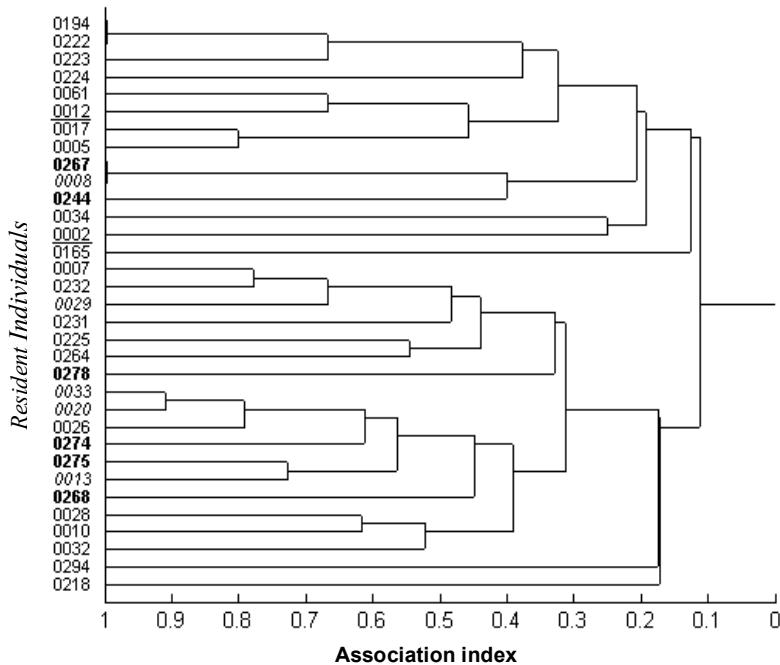


Figure 18. Cluster analysis for resident dolphins including calves. Calculated for animals observed three or more times. Males are underlined, females are in italics, and calves are in bold.

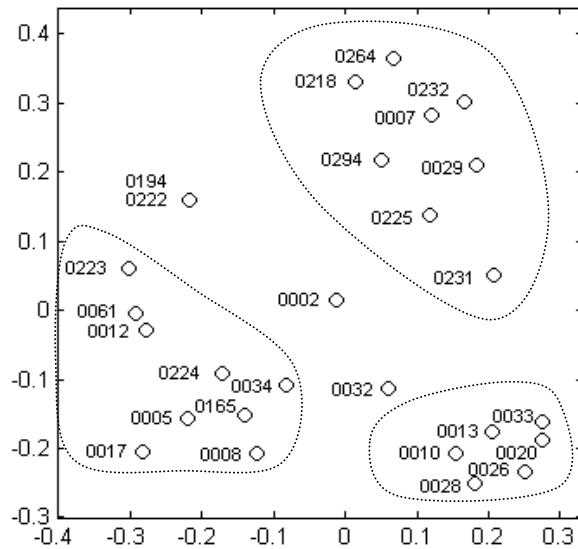


Figure 19. Principal coordinates analysis excluding calves. The clusters indicate subgroups of dolphins. The axes represent the eigenvector scores of two dimensions of the principal coordinates analysis, and the proximity of each individual is inversely proportional to the square root of their association (Whitehead 1999a).

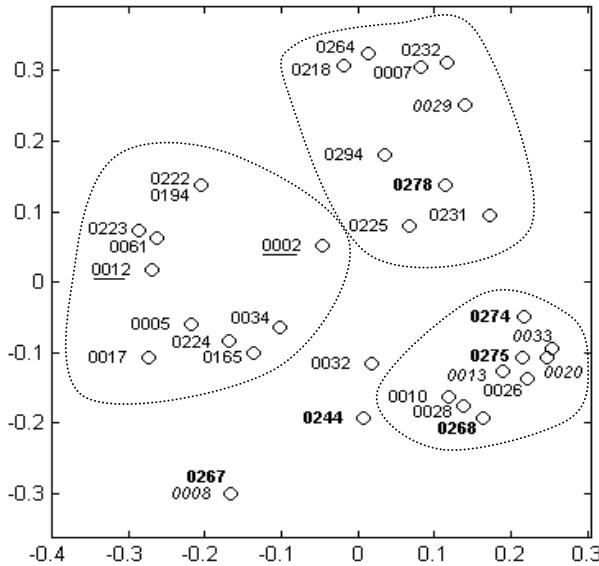


Figure 20. Principal coordinates analysis including calves. The clusters indicate subgroups of dolphins. The axes represent the eigenvalues of two dimensions of the principal coordinates analysis, and the proximity of each individual is inversely proportional to the square root of their association (Whitehead 1999a). Males are underlined, females are in italics, calves are in bold.

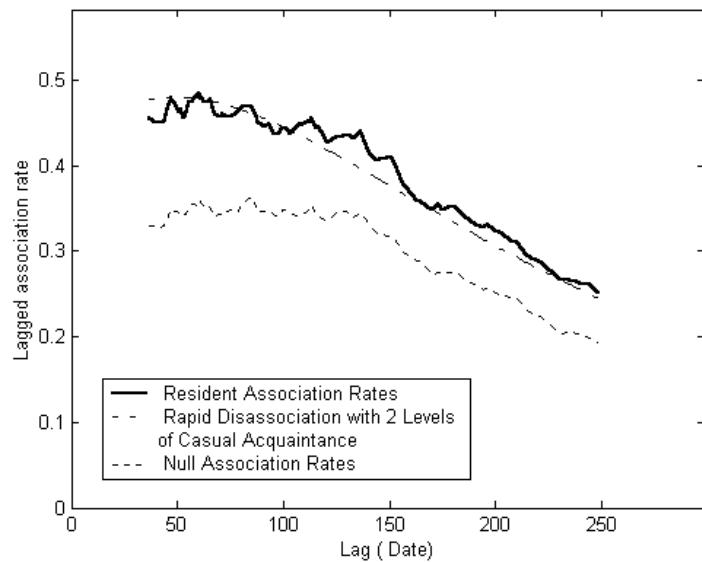


Figure 21. Lagged association rates. Calculated for residents observed three or more times, fit to a model of rapid disassociation with two levels of casual acquaintance (Whitehead 1999a).

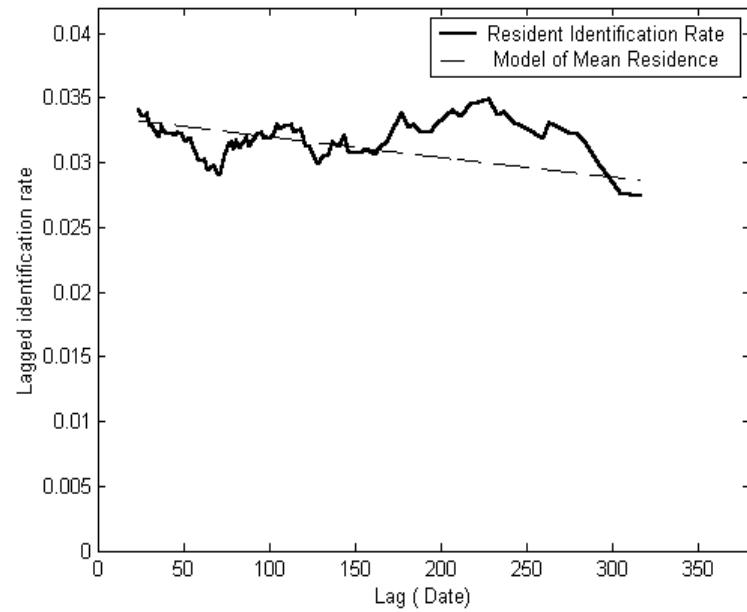


Figure 22. Lagged identification rates. Calculated for residents observed three or more times, and fit to a model of mean residence (Whitehead 1999a).

The mean AI was 0.22 ± 0.06 and the median was 0.12. The strongest associations were between dolphins 0194 and 0222 (AI=1.00), 0017 and 0005 (AI=0.80), 0007 and 0232 (0.78), and 0033 and 0020 (0.92) along with 0026 (0.79). Three sub-groups appeared to exist, one with several juveniles and known or suspected males, the second with a mix of animals, and the third with several known or suspected females. These subgroups were also seen in the principal coordinates analysis when calves were excluded, with the female band appearing separate in the lower right corner (Fig. 19). When calves were included, the female band remained distinct while the two subgroups became a bit closer in association, and 0008 and her calf separated from the other animals (Fig. 20).

The best-fit model for lagged association rates among animals seen three or more times including calves was two levels of casual acquaintance plus rapid disassociation, and lay above the null lagged rate (Fig. 21). This model can be mathematically described as: $a3 * \exp(-a1 * td) + a4 * \exp(-a2 * td)$ (Whitehead 1999a). This model indicated that there were some long-term associations, some moderate associations, and some individuals that may have been found in larger groups together but would disassociate upon group dispersal. The best-fit model for lagged identification rates was mean residence duration, or a high likelihood of re-identification as long as individuals remained resident to a given area (Fig. 22). This model can be mathematically described as: $(1/a1) * \exp(-td/a2)$ (Whitehead 1999a).

Discussion

AI's were not calculated for gulf dolphins, as all but two dolphins were only encountered once, and so any AI would be highly biased and inflated. However, AI's have been calculated for dolphins at the northeastern end of Galveston Island, both in Galveston Bay (GB) and coastal gulf areas, representing a similar population to gulf dolphins in this study, with perhaps some of the same animals. For those animals seen four or more times ($n=35$), the median AI was 0.154 in 1990 and 0.125 in 1991, with very few strong and several weak associations (Bräger *et al.* 1994). Only 35 animals out of over 1,000 were seen frequently enough to calculate AI's, indicating that only a small percentage of dolphins utilizing this area display some amount of site fidelity. Therefore, there may be some animals resident to that portion of the bay as well, and in similar numbers to the SLP population, but the majority of animals are transient. While the median AI for SLP residents was similar to that for GB, there were many more strong associations observed in SLP than GB.

These strong AI's among the entire resident population, as well as the best-fit model for lagged association rates, indicate a fission-fusion system in which all residents associate with each other, but with only average to moderately strong associations between most individuals. However, there are some high associations among a few dyads and one triad that warrant closer inspection. Two juveniles (0194 and 0222) were always seen together, and were closely associated with a third juvenile (0223, AI=0.67); each of these animals was seen nine times. Based on sighting history, these animals were probably recently weaned and only three to four years old, and due to their strong

bond and low association rates with any females are likely males. The next strongest bond, however, was between two known females (0033 and 0020, seen 10 and 11 times respectively) who were also closely associated with a third animal (0026, seen 11 times) of unknown sex but very likely a female due to membership in a band of mostly known females. These are three of the original animals, as are 0017 and 0005 (seen six and four times), another strongly bonded pair that were both grouped with the known males in 1995-96. The last of the highly associated pairs is 0007 and 0232, seen seven and nine times. The dolphin 0007 is also one of the original animals, while 0232 is a very young adult. In 1995-1996, 0007 was highly affiliated with 0004 ($AI=0.84$), a known female, and in 1990 was seen five times with 0020 and 0008, also known females (Henningsen and Würsig 1991; Maze-Foley and Würsig 2002). Additionally, dolphin 0007 was presumed to be the mother of dolphin 0218 (Irwin, personal communication⁶). Therefore, it is likely that 0007 is a female, and 0232 may be an offspring that has remained in close affiliation.

Also in 1995-96, three known males (0001, 0002, and 0012) had strong AI's ranging from .75-.82, while three known females (0004, 0006, and 0020) had moderately high AI's ranging from .50-.65. In addition, in 1990, 0029 and 0020, both female, were seen together six times, while 0013 and 0020 had a high AI of 0.78 in 1995-96 (Henningsen and Würsig 1991; Maze-Foley and Würsig 2002).

Animal 0001 is now missing, while 0002 was observed with all other dolphins and has no strong AI with any individuals and 0012 is closely associated with 0061

⁶ Irwin, LJ. Independent researcher, Volcano, Hawaii. 2004.

(AI=0.67, seen six and four times), a young animal of unknown sex. Therefore no long-term associations seem to exist among males; however, 0017 and 0005 are highly associated and were associated with known males in previous studies, and therefore they may represent a male-male bond of longer duration. Furthermore, future observations may demonstrate that current juvenile associations will persist. Similarly, all the female-female associations from 1990 and 1995-96 have weakened, and new associations between females have developed.

Dolphins are presumed female when observed with calves seven or more times; in 1995-96, dolphins 0004, 0006 and 0020 were identified as females based on this criterion (Maze-Foley and Würsig 2002), as were 0008, 0013, 0033 and 0029 during this study. It may be that some females closely associate with others in similar reproductive cycles, as seems to be the case with 0033, 0020, and 0026, and these high AI's represent a nursery group. In fact, the calves of dolphins 0033, 0020 and 0026 all were first identified on the same day in June, while 0008's calf 0267 was seen April, and 0029's calf 0278 was not seen until July. These females seem to form a separate band, while dolphin 0008 appears to be relatively solitary. Dolphin 0029 is closely affiliated with 0007 and 0232, which may represent a second female band. These strategies are shown clearly in Figures 19 and 20, where the female band that exists without calves remains close when calves are included, while dolphin 0008 disassociates from her subgroup. Calf 0244 does not have a clear pattern of association with any female; however, it was seen originally with 0008, and in every group sighting was seen with either 0008 and her new calf or 0225, a juvenile offspring of 0008. It may be that 0008 has a high

reproductive rate with a new calf every other year, and 0244 had recently been weaned just before 0008 gave birth to 0267. The frequent sightings of 0244 with 0225 may indicate babysitting by an older female sibling.

This behavioral difference among females seems to be indicative of varying maternal strategies as has been observed for females in Shark Bay, Australia and Cedar Keys, Florida, where some mother-calf pairs are highly gregarious with other females, while others are more solitary (Mann *et al.* 2000; Quintana-Rizzo and Wells 2001, respectively). This pattern may represent the cost/benefit trade-off of increased protection versus increased competition for resources in larger groups, or it may indicate a social learning strategy. In Shark Bay, some solitary females have different foraging strategies than other females found in bands, and so learning by calves may be directly from solitary mothers and socially from banded mothers (Mann *et al.* 2000; Connor 2001). A close examination of mother-calf pairs, inter-birth intervals, and association patterns for all research years should be carried out to determine if female-female associations are related to calving, specifically by time of year, and if females consistently choose the same strategy or if it varies with each offspring.

The overall social organization of this population seems to resemble that of the geographically isolated population of Doubtful Sound, New Zealand, in which all dolphins associate with each other but there are some stronger affiliations. Male behavior was much different than that observed in Sarasota, Florida or Shark Bay, Australia, with no apparent alliances or female herding behavior, but female behavior seems similar to females in those areas, with some females forming a band (Scott *et al.*

1990; Krützen *et al.* 2002). Juvenile behavior needs to be monitored and sexes obtained to determine which animals remain with the natal group and which disperse, and if any cohort associations persist among males as was observed in Port Stephens, Australia (Möller *et al.* 2001). If the SLP population were indeed a related group, males would not need to form alliances since male alliances seem to represent a mating strategy in other populations. The sample size was too small to examine association patterns of residents in mixed groups, which may indicate that male alliances as a mating strategy exist when encountering gulf dolphins that does not exist when residents are alone. Further examination of behavior and affiliations in mixed groups needs to be conducted to determine if a change in association status does in fact occur. Finally, genetic sampling of this population should be carried out to determine relatedness and sexes for all individuals, to further investigate the hypothesis that this population is a closely related matrilineal group.

CHAPTER V

SUMMARY AND CONCLUSIONS

The resident bottlenose dolphin population of Chocolate Bay/San Luis Pass is a consistently small group of around 35 animals that has demonstrated site fidelity to this area for at least 13 years (Henningsen and Würsig 1991; Maze-Foley and Würsig 2002). This population appears to consist of many adult females, few older adult males, and several young juveniles and calves. They utilize the bay system, but are also seen in the Gulf of Mexico in mixed groups of both resident and gulf dolphins. When in mixed groups, the proportion of social behavior increases, possibly indicating mating activity between resident and gulf dolphins. Low to moderate level associations exist among the community, but are highest between members of a female band and their calves. In contrast, no strong bonds exist among known adult males, although they may be developing among juveniles and subadults. It seems likely that as most males in this population mature, they disperse from the natal group, while the females remain with the group.

Differing strategies between males and females within a population is common among many species. Similar to what is observed in CB/SLP, female bands form in bottlenose dolphin populations of both Sarasota and Cedar Keys, Florida, that share smaller home ranges while the males have larger ranges and are less gregarious with all other age classes (Wells 1991; Quintana- Rizzo and Wells 2001). Males may either be solitary, as seems to be the case with the CB/SLP males and is observed in Cedar Keys,

or as in Sarasota are found in closely bonded pairs or trios. Upon reaching sexual maturity, females appear to return to natal groups; therefore female bands are at least partially based on relatedness (Wells 1991). These bands may also function as nursery groups since band membership typically includes recurring combinations of mother-calf pairs (Wells 1991). However, some females adopt a different strategy with calves, and remain solitary rather than join a group, as occurs in Shark Bay, Australia and Cedar Keys (Mann *et al.* 2000; Quintana-Rizzo and Wells 2001, respectively), and as observed by me for dolphin 0008 and her calf. Calves remain with their mothers three to six years; this is consistent with the duration recorded for mother-calf pairs in Shark Bay, Australia, where calves are also weaned around age four (Wells 1991; Mann *et al.* 2000). Mixed sex subadult groups then occur, and it is at this time that bonds may form between males, as is the case in Port Stephens, Australia (Krützen *et al.* 2003). Females then typically return to their natal group or form their own band among cohorts, while males, either solitary or in bonded groups, begin to disperse into a larger home range. Male sperm whales and rhesus monkeys also disperse upon sexual maturity, while females remain with natal groups (Kapsalis and Berman 1996; Christal and Whitehead 2001). Upon maturity, males in this case have two strategies; they may remain with one group in a smaller area or rove between several groups. The cost between the two strategies seems to lie in the distance males must travel between groups of females (Whitehead 1990). If the distance is considerable, then males will stay with one group, as is seen in the geographically isolated group of bottlenose dolphins in Doubtful Sound, New Zealand (Lusseau *et al.* 2003). However, if the distance is relatively short, then

males are more likely to travel between groups, thereby increasing the number of females with which they could potentially mate. Both of these strategies exist in Sarasota, Florida, where most males rove beyond their own community, probably as the means of genetic exchange between communities in this area, while some remain near one or two groups of females (Wells 1991). Both of these strategies also appear to exist in the CB/SLP community, where some older, solitary males remain with the resident group, although not closely associated with any other males. Other males, particularly juveniles, seem to disperse from the resident group upon sexual maturity.

There are thousands of bottlenose dolphins in the near-shore Gulf of Mexico; over a thousand were identified in Galveston Bay and adjacent gulf waters in one study alone, with only a few hundred of these observed more than once (Bräger *et al.* 1994). Additionally, no resights of gulf dolphins occurred between this study and previous studies in this area (Irwin and Würsig in press; Maze-Foley and Würsig 1999). In fact, gulf dolphins may migrate hundreds of kilometers along the Texas coastline, as bottlenose dolphins do on both the Atlantic and Pacific coasts of the U.S. (Barco *et al.* 1999; Defran and Weller 1999, respectively). Gulf dolphins in this study, as well as those in Aransas Pass, spend much of their time traveling (Shane 1990). Studies along the Texas coast have seen influxes in numbers of dolphins at varying times of year (Gruber 1981; Jones 1991; Weller 1998), supporting the idea of a long coastal migration, or possibly a seasonal movement in- and off-shore of the continental shelf.

With this multitude of dolphins constantly found along the coast, males dispersing from the resident CB/SLP population would have many females in close

proximity year-round. In addition, males could join the migration and potentially mix with multiple small resident communities found in other bays along the coastline (Lynn and Würsig 2002). Therefore, the roving male strategy is a sound explanation for the disappearance of many resident juveniles as they mature, and would also explain the small and consistent population size of the CB/SLP community.

Genetic sampling work needs to be the next step in the investigation of this population. Based on behavioral evidence and association patterns, and comparing these to trends observed for other bottlenose dolphin populations (*i.e.* Wells 1991; Möller *et al.* 2001), it is likely that this population is closely related. The band of females, while changing membership based on females with calves during a given year, is consistently made up of the same assemblage of females, and is similar to what is observed in Sarasota and Cedar Keys, Florida (Wells 1991, Quintana-Rizo and Wells 2001), as well as Shark Bay, Australia (Mann *et al.* 2000). In these areas, female band members are related females whose female offspring also return to the natal group. This is likely the case for the CB/SLP population as well, and may even make this population a close matrilineal society. However, genetic microsatellite loci from every resident dolphin need to be gathered to determine maternal relatedness. Sexes also need to be verified to determine if sex is consistent with behavioral evidence; that is, if those animals that are dispersing are indeed males. Genetic sampling from the gulf population would be useful as well to determine how closely related the two populations are, and to determine if paternity from the gulf population can be identified for resident offspring.

Perhaps a more important reason for genetic sampling is that this resident community is located in a highly industrialized and contaminated area. Galveston Bay is the 3rd largest seaport in the US, and is heavily industrialized with chemical and petroleum plants that produce 30-50% of US chemical and oil products. In addition, this area receives runoff from both the Houston area as well as river drainage from the Dallas-Ft Worth area (Morse *et al.* 1993). Chocolate Bay is a relatively pristine extension of Galveston Bay, but it is also bordered by a petrochemical plant, as well as agricultural land to the northeast, and heavy barge traffic passes through the bay and along the ICW. Bottlenose dolphins are top trophic predators, and therefore bioaccumulate toxins and organochlorides in their tissue and blubber, which can lead to immunosuppression (Salata *et al.* 1995; Aguilar *et al.* 2002). This depression of the immune system, coupled with excessive parasite loads, toxins, viral or bacterial infections can lead to mass mortality events in marine mammals, as occurred in 1987-88 on the Atlantic coast of the U.S. (Harwood and Hall 1990; Salata *et al.* 1995). A mass mortality event can remove 50% or more of a population and generate a 15-30% higher than average mortality rate, which, coupled with the slow reproductive rates and high degree of socialization among marine mammals leading to rapid transfer, can be devastating to a population (Harwood and Hall 1990). Immunosuppression can also lead to reproductive impairment. For example, female rhesus monkeys exposed to PCB's (polychlorinated biphenyls) had a difficult time carrying fetuses to full term, and those born were small and had an increase in early mortality (Rogan *et al.* 1986; Aguilar *et al.* 2002). In addition, organochlorides such as PCBs and DDE (dichlorodiphenyl

dichloroethene) and trace heavy metals such as lead and mercury, normally stored in the blubber, tissue, and bones of the mother, are released during lactation and passed on to offspring (Rogan *et al.* 1986; Frodello *et al.* 2002). The first calf typically receives the highest level of contaminants during this lactational transfer (Rogan *et al.* 1986). Genetic sampling would determine the level of relatedness within this population and by extension the level of genetic isolation, which would assist in constructing appropriate management plans for the area. Additionally, the biopsy sample obtained for genetic sampling could be examined for those contaminants that amass in blubber to determine levels of accumulation within this population in order to assess their susceptibility to immunosuppression. If this population is relatively genetically isolated, and a mass mortality event was to occur, this population could be wiped out due to its small size. However, if genetic flow does occur between resident and gulf dolphins, it is likely that the population would recover from such an event. Finally, a close examination of mother-calf sighting history should be carried out to establish age at first birth, calving rates, and interbirth intervals for all females in order to determine reproductive success and likely contaminant levels for future offspring.

This information would not only be useful for assessing management options, but would provide valuable information about human consumption risks as well. Recreational fishermen use Chocolate Bay and the adjacent Gulf of Mexico waters, as do private and commercial shrimp trawlers. Humans bioaccumulate organochlorides and toxins in their fat cells as well, and in a study on organochlorine accumulation in mothers and their children, higher levels of DDE were found in women who consumed

sport fish (Rogan *et al.* 1986). The health of bottlenose dolphins that ingest the same species of fish and crustaceans as humans can be valuable bioindicators of the contaminant levels in a given area. The exclusive and continuous use of Chocolate Bay and San Luis Pass by resident dolphins allows us an excellent opportunity to determine the health of this microenvironment, and effects that chemical plants and agricultural runoff are having on fish that we consume.

The differences in behavior and association patterns between this population and other resident bottlenose dolphin populations should be explored further in an attempt to describe influences that may be responsible for the differences. Such information is likely to advance our understanding of the functional mechanisms behind dolphin behaviors, and may also help in devising management protocols for this and other cetacean species.

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EDUCATION

MS, Wildlife and Fisheries Sciences, Texas A&M University, TX
 BA, Psychobiology, Drew University, NJ

RESEARCH EXPERIENCE

September 2001-December 2003

Investigator, Texas A&M University

Recently completed a research project to determine the home range, behaviors and association patterns of a resident community of bottlenose dolphins (*Tursiops truncatus*). Ran surveys to locate groups of dolphins, then used the techniques of photo-identification and behavioral observation to establish habitat use and behavioral patterns. Trained interns in the design and implementation of a research project. Analyzed data and prepared manuscripts for publication.

March-April 2002

Researcher with Oceanic Society Expeditions

Spent fourteen days in the Pacaya-Samiria Reserve in Peru monitoring two species of river dolphins (*Inia geoffrensis* and *Sotalia fluviatilis*) as a preliminary study for future research on interactions between dolphin populations and local fishermen in this area. Recorded abundance, distribution, and group size of dolphins. Worked with volunteers, educating them about the behavior and occurrence patterns of both species of river dolphin.

December 1999-June 2000

Research Assistant, Kewalo Basin Marine Mammal Laboratory

Actively assisted an ongoing humpback whale (*Megaptera novaeangliae*) behavior research program. Worked on both land and water research platforms; drove the research vessel, gathered photographic identifications of individual whales and behaviors, and also worked with a theodolite at the shore station to observe large-scale behavior. Helped organize, train and support a team of rotating volunteers. Worked with PhotoShop to prepare the fluke identification photographs, as well as with Word, Excel, FilemakerPro and the Internet to compile and examine the gathered data.