

Abstract

Bottlenose dolphins use a variety of foraging specializations to detect and pursue prey. Like other mammals, individual dolphins may use specialized foraging techniques that are shaped in response to habitat or particular prey resources. The long duration of the mother-calf bond presents an opportunity for mothers to transmit such specializations to their calves, and cases of observational learning by dolphins are well known from captive colonies. This study explored how specializations may influence choices of habitat use and on how such specializations may spread within a community.

A focal follow technique was used to document the foraging behavior of five resident females and their calves from June-August 2003 in Sarasota, FL. Females significantly differed in their selection of foraging habitats. Three of the five focal females used known foraging specializations, kerplunking and barrier feeding, and exhibited a preference for only one type. Females also increased the use of foraging habitats associated with their preferred foraging specializations. Limited observations, as well as anecdotal evidence from past studies, suggest that maternal transmission may play a role in the spread of kerplunking and barrier feeding within a community.

Findings suggest that the use of foraging specializations is associated with foraging habitat preferences in Sarasota Bay as well as support the importance of incorporating knowledge of social behavior into the management structure for bottlenose dolphins. Many questions still remain concerning the prey specificity, stability, and sex-specific nature of foraging specializations and future studies should concentrate on these areas of research.

Table of Contents

<i>Section</i>	<i>Page Number</i>
Introduction.....	1
Objectives.....	8
Methods.....	10
Results.....	15
Discussion.....	21
Management Implications.....	28
Conclusions.....	32
Acknowledgements.....	32
References.....	34
Appendices.....	38

Introduction

Foraging specializations allow animals to adapt to environmental variation, thus working to promote their survival. Specialized foraging behaviors provide an efficient means of detecting and pursuing prey (Partridge and Green 1985). Many foraging specializations are strongly associated with particular feeding areas, and flexibility in the use of particular foraging techniques may reduce intra-specific competition for prey resources. Foraging specializations may evolve in response to physical differences in habitat, such as topography (Hoelzel et al. 1989), or a variation in food supply (Partridge and Green 1985). Individual preference also plays an important role in the choice of a foraging specialization (Nowacek 1999).

Associations between Foraging Behaviors and Habitat Characteristics

Several types of foraging specializations are associated with particular habitat characteristics. Different specializations may be chosen based upon their usefulness in a particular habitat. Minke whales in the San Juan Islands specialize in either lunge feeding or bird-association feeding (Hoelzel et al. 1989). Specialists in either behavior target the same prey species, but, lunge feeding and bird-association feeding occur in areas that differ in bottom topography (Hoelzel et al. 1989). Tiger sharks (*Galeocerdo cuvier*) in Shark Bay use a stealth tactic to pursue potential prey items (Heithaus 2002). This type of tactic, in which the shark stalks and attacks unwary prey, is useful in the shallow seagrass areas inhabited by dugongs and sea turtles.

A variety of specializations displayed specifically by bottlenose dolphins are habitat-specific as well. Mud-plume feeding is a bottlenose dolphin foraging specialization that has been documented in the lower Florida Keys (Lewis and Schroeder

2003). This behavior was observed over seagrass flats, primarily during the flood tide. Lewis and Schroeder (2003) suggested a correlation between mud-plume feeding and seagrass flats, due to the suspended sediment that is necessary in the plume to concentrate the prey. Kerplunking is a foraging specialization that has been observed in Sarasota Bay and Tampa Bay, Florida as well as Shark Bay, Western Australia. This behavior occurs frequently either over seagrass beds or at the edge of seagrass beds where prey may be concealed (Connor 2000; Nowacek 1999). Strand feeding, a specialization in which dolphins herd fish against mud banks and then strand themselves in order to feed on the trapped fish, is dependent upon particular characteristics of mud banks (Hoese 1971). Strand feeding may also be described as a variation of barrier feeding; dolphins use the mud banks as barriers against which they herd fish. Sloping mud banks at low tide are optimal for strand feeding. At low tide, the mud bank is adequately exposed and fish are concentrated (Hoese 1971). Furthermore, dolphins are unable to strand feed on mud banks if oysters or other obstructions are prevalent, due to risk of injury.

Seagrasses are important habitats for foraging dolphins since many important prey species are found in these areas (Barros and Wells 1998). Allen et al (2001) proposed an indirect relationship between seagrasses and foraging dolphins, but both studies suggest a strong association between the distributions of foraging bottlenose dolphins and seagrasses communities. The association between the use of foraging specializations and habitat may influence the importance of different habitats, such as seagrasses, to foraging dolphins.

Associations between Foraging Specializations and Prey Resources

Foraging specializations may also be associated with variation in prey resources. The distribution of prey items may influence the choice of a specialization. For example, California sea otters (*Enhydra lutris*) are presented with a wide variety of potential prey items within their habitat range. Each item requires different hunting tactics and handling skills (Estes et al. 2003). Humpback whales in southern New England use a foraging specialization known as lobtail feeding, in which whales tail slap and create a bubble cloud to aid in prey capture. When the availability of sand lance in the area decreases, the frequency of use of lobtail feeding decreases as well (Weinrich et al. 1992). Furthermore, variations in prey size may result in variations of lobtail feeding within a population (Weinrich et al. 1992).

Foraging specializations of bottlenose dolphins may be correlated with prey resources as well. Prey distribution may affect the choice of different foraging specializations. Clumped or concentrated prey distributions are necessary for specializations such as strand feeding (Hoese 1971) and mud plume feeding (Lewis and Schroeder 2003), while the use of kerplunking and a behavior known as fishwhacking can be efficient in the capture of individual fish.

Bottlenose dolphins may use passive listening as a foraging tactic in response to the soniferous nature of several types of prey. Passive listening aids in the detection of prey through the interception of prey sounds (Barros 1993). Common prey of bottlenose dolphins in Sarasota Bay, FL includes pinfish (*Lagodon rhomboides*), pigfish (*Orthopristis chrysoptera*), sheepshead (*Archosargus probatocephalus*), spot (*Leiostomus xanthurus*), and mullet (*Mugil cephalus*), all of which are well-known sound-producers

(Barros and Wells 1998), and may influence dolphins to use passive listening to increase their foraging efficiency.

Variations in prey resources affect the choice of a specialization by an individual. The types of prey consumed by bottlenose dolphins vary by individuals (Barros and Wells 1998) and, like foraging specializations, are also subject to individual preference.

Plasticity of Foraging Strategies in Dolphins

Bottlenose dolphins are extremely varied in their use of foraging specializations (Nowacek 1999), and such behavioral plasticity is illustrated by the many types of specializations that have been observed in different communities (Connor et al. 2000; Fertl and Wilson 1997; Hoese 1971; Leatherwood 1975; Lewis and Schroeder 2003; Nowacek 1999; Rossbach and Herzing 1997; Wells et al. 1987; Wursig 1986).

In barrier feeding, dolphins use barriers to facilitate prey capture. In some cases, individuals use air bubbles to corral a school of fish into a ball during feeding events (Fertl and Wilson 1997; Wursig 1986). The use of bubbles may serve to restrict movements of the school and create a tightly contained ball of fish (Fertl and Wilson 1997). Dolphins may also use the water surface, shorelines, or seawalls as barriers against which they restrict the movement of fish (Wursig 1986). In Sarasota Bay, Florida, dolphins may herd fish against sea walls, bridge pilings, or even stationary boats.

Kerplunking is a foraging specialization that has been observed in Sarasota Bay and Tampa Bay, FL (Nowacek 1999; Wells 2001) as well as Shark Bay, Western Australia (Connor et al. 2000). This behavior occurs when an individual raises its tail flukes out of the water, forcefully brings them down on the water surface, and pushes them through the water column (Figure 1; Nowacek, 1999). This action produces a 1-2m

splash, bubble cloud, and low frequency sound (Nowacek, 1999). The function of kerplunking serves to evoke a startle response in fish, which may allow for their detection by the dolphins (Connor et al. 2000).

Figure 1: Kerplunking

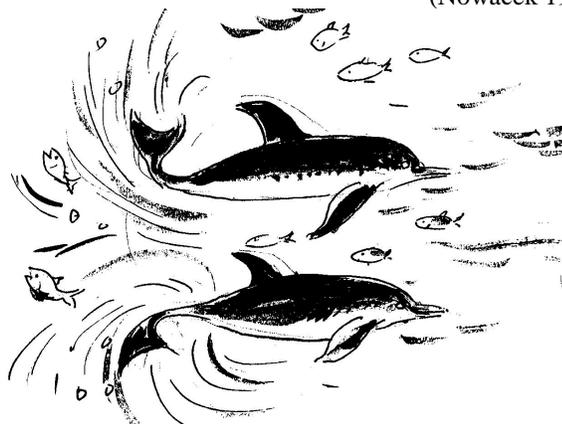
(Nowacek 1999)



Fish whacking is a strategy in which a dolphin uses its tail flukes to knock an individual fish into the air (Figure 2; Nowacek 1999). The dolphin then feeds on the stunned/injured fish once it lands back in the water (Shane 1990). Fish whacking differs visibly and functionally from kerplunking. Fish whackers swing their flukes underwater sideways and upwards, while kerplunkers bring their flukes high and drive them into the water column (R. Connor personal communication 2002). Furthermore, fish whacking is used in the terminal phase of prey capture, while kerplunking is used to assist in the detection of cryptic prey.

Figure 2: Fish Whacking

(Nowacek 1999)



Vertical Transmission of Foraging Specializations

The use of complex foraging behaviors is influenced by environmental variation and, in many cases, seems to lack a genetic basis. Therefore, it is possible that an individual's choice of using a foraging specialization may be influenced by cultural transmission. Foraging specializations that differ at the individual level may be transferred from mother to offspring through vertical transmission, a social learning process (Rendell and Whitehead 2000).

There is expected to be a high degree of maternal investment in animal societies in which individuals practice complex foraging behaviors (Johnston 1982). For example, many dependent humpback whale calves have been observed practicing elementary forms of lobtail feeding (Weinrich et al. 1992). The importance of the role that mothers play in the early lives of these calves may contribute to the spread of this behavior within the population. Guinet and Bouvier (1995) suggest that teaching behavior may be related to the practice of complex foraging behaviors, since a great deal of maternal investment is required. Observations of a killer whale mother pushing her calf towards a seal in assistance to strand feed may provide evidence of active teaching in cetaceans.

Specialized foraging behaviors may be products of cultural transmission due to their independence from life history changes and the high degree of behavioral plasticity in bottlenose dolphins (Wells 2001). Bottlenose dolphins live in a fission-fusion society (Wells 2001), in which there is a strong maternal investment in calves. Mothers and calves form long-term associations (Wursig 1986) that last until the birth of the next calf (Wells et al. 1987). The long duration of this bond indicates a high investment in the

offspring and presents an opportunity for calves to learn specialized foraging behaviors from their mothers.

Several types of specialized foraging behaviors may spread vertically, between generations, in many animal communities (Estes et al. 2003; Rendell and Whitehead 2001; Smolker et al. 1997), and the individual variation in foraging behavior and dietary patterns has been documented in many mammalian and avian species. For example, oystercatchers (*Haematopus ostralegus*) specialize in diet as well as foraging technique (Goss-Custard and Sutherland 1983). Norton-Griffiths (1968) found that young birds learn specialized foraging strategies, such as those used for opening mussels, from their parents.

In mammals, individual foraging preferences and specializations of California sea otters (*E. lutris*) are transmitted through matriline (Estes et al. 2003). Sea otter pups learn to forage during the 6-month period they spend with their mothers before weaning. The dietary patterns of the pups mirror those of their mothers', and it is likely that sea otter females actively teach the pups to forage (Estes et al. 2003).

The foraging specializations of bottlenose dolphins may spread maternally as well. Smolker et al. (1997) observed female dolphins (*Tursiops aduncus*) in Shark Bay, Western Australia using sponges as tools to aid in foraging. Only a small group of female dolphins within the Shark Bay community regularly sponge feed. The daughter of a regular sponge feeder acquired the sponging behavior, even when she foraged independently of her mother (Smolker et al. 1997). Provisioning by humans is a foraging specialization also practiced by dolphins in Shark Bay, Australia (Shane, 1990; Smolker et al. 1997). The observations of the offspring of provisioned female dolphins accepting

food from tourists suggest that provisioning may be another foraging specialization that is transmitted through matrilineal lines.

Objectives

The objectives of the present work are to:

- 1) Investigate how the choice of foraging specializations of bottlenose dolphins influences habitat use
- 2) Speculate as to how foraging specializations spread within a community

Female bottlenose dolphins in Sarasota Bay share overlapping home ranges, yet exhibit different preferred habitats (Wells et al. 1987). If foraging specializations are habitat specific, it is possible that individuals target the foraging habitat in which their preferred specialization is most useful.

Longitudinal studies provide insight into the process by which foraging behaviors may spread within a wild population (Estes et al. 2003; Sargeant and Mann 2003; Wells 2001). Anecdotal evidence (Nowacek 1999; Wells 2001) has suggested the vertical transmission of barrier feeding, kerplunking, and fish whacking in Sarasota Bay, FL. Barrier feeding, kerplunking, and fish whacking are complex foraging behaviors that are readily observable at the surface. Surface observations of such foraging behaviors allow patterns to be easily documented. Behaviors such as kerplunking and fishwhacking are also confirmed links of the foraging process and may be used to indicate a foraging state (Nowacek 1999; Nowacek 2002). Foraging is particularly difficult to observe in wild dolphins since most of the process takes place underwater. However, the many cases of observational learning by captive dolphins suggest that wild dolphins are also capable of transmitting novel complex behaviors.

If the use of foraging specializations is habitat-specific and transmitted from mother to calf, such behavioral and habitat preferences may persist through generations. The continuation of the knowledge of foraging specializations in a community is important for animals to adapt to changes in their environment.

Study Area

Surveys and behavioral observations took place in Sarasota Bay, Florida, and focused on a well-studied resident community of bottlenose dolphins. Since 1970, a longitudinal study has focused on the distribution and behavioral ecology of the resident Sarasota Bay bottlenose dolphin community (Wells 1987). Approximately 150 resident individuals occur (S. Hoffman personal communication 2004) within the study area. Photo-identification, genetic studies, and behavioral observations have yielded a considerable body of information on genetic lineages as well as individual foraging behaviors (Nowacek 1999; Wells 1991; Wells 2001).

The Sarasota Bay study area ranges from Terra Ceia Bay and the southern edge of Tampa Bay south to Siesta Key (Figure 3). The home range of the Sarasota Bay community spans 40 km of coastline, and encompasses a system of bays, protected by a series of barrier islands, as well as the Gulf of Mexico waters up to approximately 1 km offshore (Scott et al. 1990). Resident individuals extensively use shallow bays and seagrass meadows during the summer months (Barros and Wells 1998), and field effort for this study was concentrated in these areas.

Figure 3: Sarasota Bay Study Area



Methods

One season of fieldwork was conducted from June-August 2003. Field effort consisted of approximately 280 hours with 40 hours devoted to focal follows. Non-random transect surveys were conducted each day throughout the study area to search for focal animals. Once a group of dolphins was found, a sighting sheet was completed (Appendix A), containing information about group size, time of sighting, location, activity state, identity of individuals, and environmental variables, and the dolphins were approached for photographs. A Nikon-8008 camera system with a zoom-telephoto lens was used to conduct photoidentification. A hand-held GPS was used to record latitudinal

and longitudinal location of the group. The recorded activity states are shown in Table 1 (Urian and Wells 1996; Waples 1996). For the purposes of this study, individuals were assumed to be foraging when observed in a probable feed or feed behavioral activity state (Table 1). A foraging bout lasted from the onset to the end of a probable feed or feed activity state. A foraging event refers to all foraging bouts within a focal follow on a given day.

Table 1: Activity States of Dolphins

Activity State	Description
Mill	Non-directional movement
Feed	Dolphin is observed with fish in mouth
Probable Feed	Pinwheel, fish chase, multiple fast surfacings, tail out dives/peduncle out dives
Social	Active interactions with other individuals
Rest	Slow activity, absence of other activity

Five resident females and their calves were chosen as focal animals. A description of focal females and their calves, as well as effort, is provided by Table 2. The five focal females and calves may also be described as four separate maternal lineages, as F175 is a calf of FB75 (Appendix G).

Females with one-year old calves, with the exception of F157, were selected as focal animals. Weaning age of bottlenose dolphin calves occurs between the ages of 6-12 months (Essapian 1953), so one-year old calves would be at an ideal age to learn foraging specializations since they were beginning to feed on fish. F157 had a three-year old calf, yet had been observed by Sarasota Bay researchers to use known foraging specializations, and was chosen as a focal as well.

Table 2: Focal Females and Calves

Female	Age of Female	Calf	Age of Calf	Follow Time (min)	Foraging Time (min)
FB09	20 years	C094	1 year	419	117
FB75	30 years	F757	1 year	411	105
F119	13 years	CRP2	1 year	613	123
F157	>16 years	F137	3 years	408	86
F175	13 years	1751	1 year	429	153

If a focal pair was present within the group, a follow began, using the focal animal sampling method as described in Altmann (1974). A point-sampling method (Altmann 1974) with three-minute intervals was used to record the activity state, location, depth, tidal cycle, and habitat type of focals throughout the entire follow (Appendix B). A distance of approximately 20 meters was maintained from the focal pair when recording location. Habitat types included non-seagrass shallows, channel, bay, pass, gulf (Waples 1995), and seagrass shallows (Appendices D and E). In order to verify habitat, GPS coordinates were later overlaid onto a GIS seagrass map (FMRI 2002) of the study area using the ArcView 3.2 program (ESRI 1995). Group size and, when possible, group member identifications, were also recorded at three-minute timepoints.

Once focal animals entered a probable feed/feed activity state, a continuous sampling method was used to record the time and specific behaviors of the mother and time and corresponding behaviors of the calf. Recorded behaviors included dive types, foraging specializations, and surfacings (Appendix C). Distance between mother and calf in dolphin lengths was recorded continuously at the time each behavior occurred. One dolphin length was estimated to be 2.5 meters, the average length of an adult female bottlenose dolphin (Reynolds et al. 2000). Real-time narration was used to record observations during all focal follows. An Olympus PearlCorder S711 microcassette recorder and omnidirectional electret condenser microphone was also used to record

continuous data, and then used to double-check the continuous datasheet at the end of each day.

To determine the habitats in which each foraging specialization occurred, the time of occurrence of behavior was later matched to the location of the focal animal at that time. An ARCGIS program was used to overlay the specializations as points on a map of Sarasota Bay (Appendix F). For each point, a 25-meter buffer zone was created to account for the distance of the boat from the dolphins at any point in time. The percentage of each type of habitat within each buffer zone was calculated, and the habitat composing the majority of the buffer zone was selected as the habitat in which the specialization took place. The possibility that the behavior may have occurred in the minority habitat of the buffer zone is discussed in a later section.

To account for the possibility of horizontal transmission of foraging specializations, data was collected on group membership during foraging events. The proportion of time was calculated for when the focal female or calf practiced a foraging specialization in the presence of other group members, and compared to the proportion of time when the focal female or calf practiced a foraging specialization with no other group members present.

Data Analysis

To determine how females differentiated between foraging habitats, the total time spent foraging in each habitat for each female was compared to time spent in the habitat while not foraging. The habitats used by each female while not foraging may represent the habitats included within each female's home range. A chi-square test was conducted to compare habitat use among females, with the expected use of each habitat to be equal for all females. Habitats were then grouped into shallows and non-shallows areas, and a

2x2 chi-square analysis was conducted for each female to determine if habitat use differs for individuals between foraging and non-foraging states. A null model predicted that there would not be a significant difference between each female's habitat use of shallows and non-shallows areas for foraging. A Bonferroni correction was applied to account for multiple tests on individuals. This technique allowed the determination of whether each female was selecting between shallows and non-shallows areas for foraging.

Due to the suggested importance of seagrass habitats for foraging dolphins (Allen et al. 2001; Barros and Wells 1998), habitats were re-organized into seagrass and non-seagrass habitats to determine whether females prefer seagrasses for foraging. A chi-square analysis was conducted for each focal animal with a null prediction that the foraging habitat use of each female does not differ between seagrass and non-seagrass areas. A Bonferroni correction was applied to account for multiple tests on individuals.

To determine an association between foraging specializations and habitats, percentages were calculated for the amount of time kerplunking (n=55) and barrier feeding (n=33) were observed in different habitats, based upon GIS majority habitats. Comparisons were noted between each female's use of a foraging specialization and foraging habitat preference, and the association between foraging specializations and habitat.

Limited data was collected to investigate the maternal transmission of foraging specializations. Barrier feeding was used by one calf on only one occasion, yet kerplunking was observed by another calf on multiple occasions (n=4). Multiple observations of mother and calf kerplunking events allowed an investigation of the distances between the mother and calf while using this specialization.

At the observation of each kerplunk, the distance between mother and calf was estimated in number of dolphin lengths. In order to estimate the calf's proximity to the mother during kerplunking events, the distance between mother and calf in number of dolphin lengths was calculated for three types of situations: The mother kerplunks alone, the mother and calf kerplunk together, and the calf kerplunks alone. The counts for each type of situation were divided into distance categories, such as <1, 1, 2, 3, 6-10, and greater than 10 dolphin lengths. The proportion of counts in each category for each situation was calculated to determine if the calf was closer in proximity to the mother while the mother or the mother and calf kerplunked.

Results

Female Preference of Foraging Habitat

All females spent roughly similar proportions of time foraging (Table 3), and field effort was relatively equal for each female (Table 2).

Table 3: Female Foraging Activity

Females	Proportion Time Foraging
FB09	27.9%
FB75	20.54%
F119	19.87%
F157	20.77%
F175	36.36%

*All proportions normalized for effort

Each female used at least three of the available habitat types within Sarasota Bay while not foraging. The figures below illustrate the frequency of use of each habitat type with foraging state excluded (Figure 4) and while foraging (Figure 5). Figure 4 also illustrates the habitats included within each female's home range during the sampling period. Individual females exhibited different preferences for habitats while foraging

($\chi^2=462.64$; $p<0.001$), indicating that the difference among females in selection of foraging habitats was significant.

Figure 4: Habitat Use with Foraging Excluded

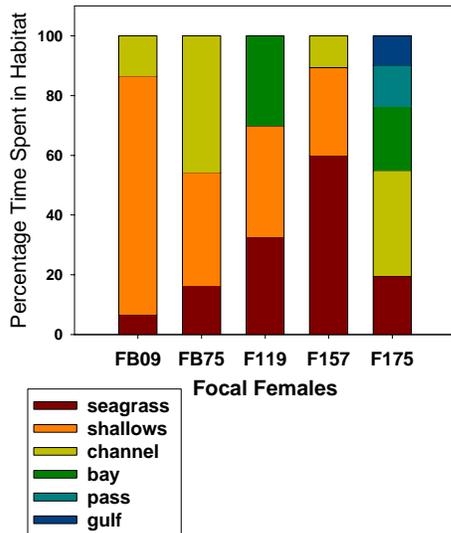
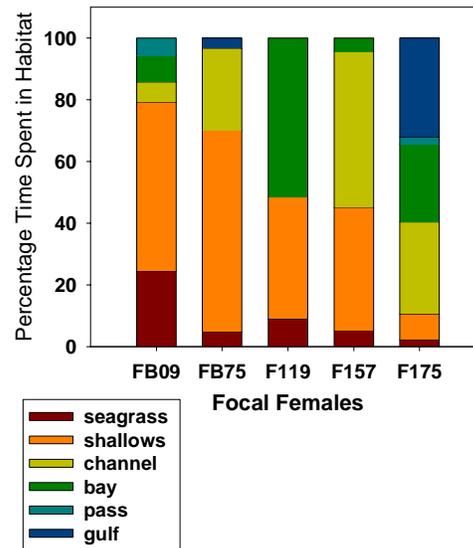


Figure 5: Habitat Use During Foraging



Three of the females (F119, F157, and F175) differentiated between shallows and non-shallows areas when selecting foraging habitats (F119 $\chi^2=15.94$, $p<0.001$; F157 $\chi^2=66.42$, $p<0.001$; F175 $\chi^2=14.70$, $p<0.001$; Bonferonni correction, $\alpha=0.005$). For each of these females, the use of shallows increases while foraging. Shallows composed a majority (>50%) of foraging habitat for F119 (69.8%) and F157 (89.3%).

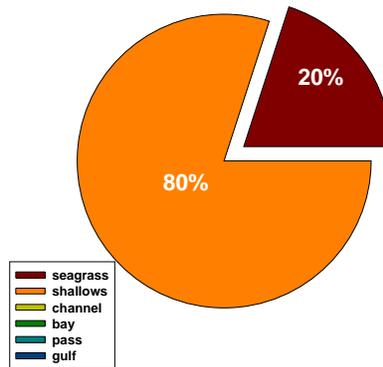
Seagrass shallows appeared to be important foraging habitats because an increase in the use of seagrass areas was noted for all but one female while foraging (Figure 5). Further tests were conducted to quantify the relative importance of seagrasses to non-seagrass shallows for each female while foraging. Each female differentiated between seagrass and non-seagrass shallows while foraging as compared to not foraging (FB09 $\chi^2=15.42$, $p<0.001$; FB75 $\chi^2=26.79$, $p<0.001$; F119 $\chi^2=16.47$, $p<0.001$; F157 $\chi^2=61.01$, $p<0.001$; F175 $\chi^2=127.29$, $p<0.001$;

Bonferonni correction, $\alpha=0.005$). Seagrasses appeared to be important foraging areas for all focal females.

Foraging Specializations in Reference to Habitat

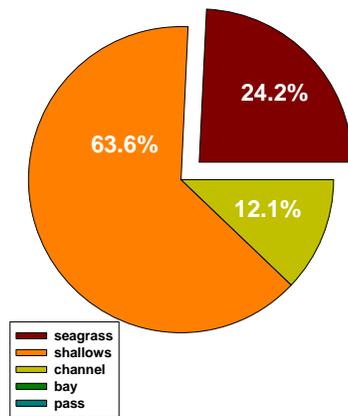
Associations were determined between foraging specializations and habitat. Kerplunking (Figure 6) was observed 80% of the time in seagrass and 20% of the time in non-seagrass shallows (n=55). When habitats were grouped into shallows and non-shallows habitats, kerplunking took place 100% of the time in shallows.

Figure 6: Habitat Use During Kerplunking



Barrier feeding (Figure 7) was observed 63.6% of the time in shallows, 24.2% of the time in seagrass, and 12.1% of the time in channel (n=33). Grouping habitats into shallows and non-shallows habitats, barrier feeding took place 87.8% of the time in shallows. The shallows habitat of Sarasota Bay appeared to be important to both kerplunking and barrier feeding.

Figure 7: Habitat Use During Barrier Feeding

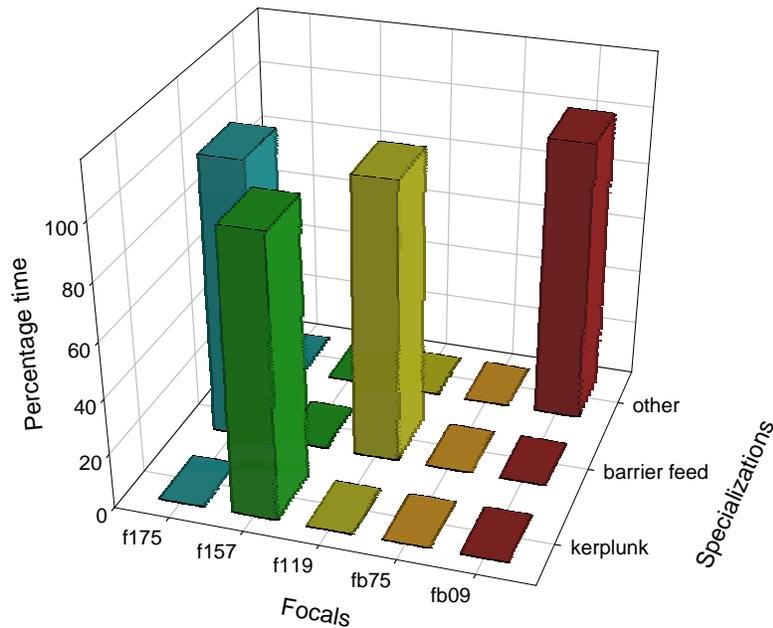


Female Preference of Foraging Specializations

Three females used known foraging specializations, and each female preferred the use of only one type (Figure 8). One female (F157) was observed kerplunking (n=25), and was the only female to use her specialization during every observed foraging event. Two females were observed barrier feeding, yet differed in their use of structures as barriers. One female (F119) used a seawall as a barrier (n=20), while the other female (F175) used bridge pilings (n=2) and a marker (n=11). Despite previous anecdotal accounts of FB09's preference for fish whacking (S. Hoffman personal communication 2003), this behavior was not observed during the study period. Instead, this female appeared to prefer foraging behaviors that were subsequently classified in an "other" category. FB09 did not use any known foraging specializations, but, her foraging behaviors were varied and not displayed by other focals. She was observed chasing fish near the surface of the water while up-side down (n=3) and sharking (n=2) in shallow water. These behaviors are not documented links in the foraging process and no captures were observed in coordination with the use of these behaviors. However, FB09 used these behaviors on multiple

occasions during probable feed states. One female (FB75) was not observed to use any distinct or recognizable foraging specializations.

Figure 8: Female Foraging Specialization Preferences



Relationship between Foraging Habitat and Use of Specialization

The three females that differentiated between shallows and non-shallows habitats for foraging were the same females that exhibited the use of known foraging specializations. These females increased their use of foraging habitats associated with their preferred specializations. F157, a kerplunker, increased her time spent in seagrass/shallows habitat from 45% of the time while not foraging to 89% of the time while foraging. In comparison, F119 and F175, both barrier feeders, increased their time spent in shallows or channel habitats while feeding. F119 increased her time in seagrass/shallows habitat from 48.6% while not foraging to 69.8% of the time while foraging. F175 was observed foraging in seagrass and channel. She increased her time spent in these habitats from 40.5% of the time while not foraging to 54.9% of the time while

foraging. These patterns suggest an association between the use of foraging specializations and foraging habitat preferences in Sarasota Bay.

Vertical Transmission of Foraging Specializations

Two of the five dependent calves used known foraging specializations (Appendix G). Each calf that used a foraging specialization only used the same behavior as its mother. For example, F119 preferred barrier feeding and F157 preferred kerplunking. When using a foraging specialization, the calf of F119 was only observed barrier feeding (n=1) while the calf of F157 was only observed kerplunking (n=30). Differences in the usage times of specializations of the calves will be discussed in a later section. In comparison, dependent calves whose mothers did not specialize also did not use foraging specializations. FB75 did not use a recognizable foraging specialization and neither did her calf. Similarly, the calf of FB09 used the same varied foraging behaviors as the mother, upside-down fish chase (n=2) and sharking (n=1).

For all the foraging events in which kerplunking was observed, there were 7 instances in which the mom kerplunked and the calf's next behavior was a kerplunk. In these instances, the distance between the mother and calf was less than or equal to 2.5 meters (one dolphin length) 85.7% of the time. In contrast, when only the mother kerplunked, the distance between the mother and calf was always greater than 2.5 meters. When the only the calf kerplunked, the distance was 2.5 meters or less only 33.3% of the time.

These results indicate that when the calf was kerplunking, she was in close proximity to the mother, especially when the mother was kerplunking as well. If a calf learns a foraging specialization from its mother, it would appear to be useful to remain close while practicing the behavior. The observed close proximity between the mother and calf during kerplunks would have presented an ideal opportunity for F137 to practice kerplunking with her mother.

Group members were present 73.3% of the time while focal mothers and calves were foraging. This high percentage of time is not surprising, since many mothers and calves spend much time in nursery groups composed of other females of similar home ranges and reproductive cycles and their calves (Reynolds et al. 2000). Of this time, group members were present 57.1% of the time when the mother calf pair used foraging specializations. There was only one occasion where another group member was observed using the same specialization, kerplunking, as that of the mother and calf. In contrast, when foraging specializations were not observed, other group members were present 87.5% of the time. The greater frequency of group member presence when the focals did not specialize may suggest that such foraging specializations are not horizontally transmitted to calves.

Discussion

Targeting Habitats for Foraging

This study suggests that the use of foraging specializations in Sarasota Bay is associated with an individual's preferred foraging habitat. However, it is still unknown whether animals base their choice of a specialization upon preferred foraging habitat characteristics or whether a preference for a foraging specialization influences the chosen foraging habitat. Nevertheless, due to such an association, it may be possible to predict the distributions of the animals that specialize, as well as their critical foraging habitats. For example, animals that specialize in kerplunking would be expected to forage in seagrass and shallows habitats.

Hastie et al. (2004) linked bottlenose dolphin distributions and preferences of habitat to foraging activity. Evidence from this study confirm the link between foraging dolphins distributions and foraging habitat preferences as well as support a direct importance of seagrass areas to foraging dolphins. Seagrasses were used by kerplunkers and barrier feeders (20% and

24% of the time, respectively). All but one of the females increased their time spent in seagrasses while foraging, regardless of specializing or not.

The patchiness of seagrasses in Sarasota Bay (Appendices D and E) may have led to an underestimate of the amount of time that seagrasses were used in the present analysis. During focal observations, habitat data was recorded in three-minute intervals. It may therefore have been possible for focals to spend time in other habitats not recorded by point-samples. Seagrass use in particular may have been underestimated since many of the seagrass areas were patchy and interspersed with non-seagrass shallows.

Previous studies have linked kerplunking to seagrass areas and suggested the behavior to be a flushing technique to drive prey out of the seagrasses (Connor et al. 2000; Nowacek 1999). Evidence from this study suggests a lesser importance of seagrasses to kerplunking than would be expected, based upon previous knowledge of the behavior. However, previous studies have also emphasized the importance of edge habitat to kerplunking (Connor et al. 2000; Nowacek 1999), and this may account for the lack of recorded use of seagrasses for kerplunking dolphins. The present study did not attempt to define edge habitat, but more refined analytical methods may provide insight into the importance of the edge effect to this behavior. Thirty-one percent of the buffer zones that were created around each kerplunk location contained both seagrass and non-seagrass shallows habitat. Ninety-one percent of the seagrass kerplunks contained non-seagrass shallows habitat, and sixteen percent of the non-seagrass shallows kerplunks contained seagrass habitat. It is therefore possible that the importance of seagrass areas to kerplunkers is greater than emphasized by the results of this study.

Individual Preference of Foraging Specializations

Each female that used a foraging specialization exhibited a preference for only one method. Nowacek (2002) noted a similar trend in Sarasota Bay, but he found that although individuals may favor particular foraging specializations, behavioral repertoires may overlap. Female preferences of foraging specializations in this study suggest that certain complex behaviors, such as kerplunking, may be favored exclusively by individuals. For example, F157 and her calf only specialized in kerplunking and used this behavior during every observed foraging event.

However, evidence also suggests that the individuals may exhibit variations of a particular specialization. F119 and F175 both used barrier feeding, yet F119 herded prey against a seawall while F175 was observed herding prey around bridge pilings and a marker. Variations of such behaviors may be a reflection of different home range characteristics, yet also illustrates the ability of bottlenose dolphins to adapt to different environments as well as the behavioral plasticity of this species. It is important to note, however, that this dataset is very limited, and further observations of foraging events within this community would provide a more complete picture of the behavioral repertoire for each animal.

The use of foraging specializations may also vary between bottlenose dolphin communities. Evidence from this study suggests that females in Sarasota Bay prefer a specialization to others. However, Mann and Sargeant (2003) observed individual dolphins in Shark Bay using multiple types of specializations. Although dolphins in the study did not use kerplunking, they did use a variation of barrier feeding by herding fish against a shoreline (Mann and Sargeant 2003). It is questionable as to why dolphins in Sarasota Bay exhibit different types of preferences for foraging specializations than dolphins in Shark Bay. Such differences may be

attributed to the relatively small sample sizes for this study, yet, differing characteristics of the study areas or the types of specializations used may influence such patterns as well.

The Role of Maternal Transmission in the Spread of Foraging Specializations

One purpose of this study was to investigate the role that the mother-calf bond may play in the spread of foraging specializations within a community. However, the present study did not aim to determine the mechanisms of this transmission, such as types of learning (Whiten and Ham 1992). Anecdotal evidence from the longitudinal Sarasota study may provide insight into how foraging specializations are spread within the community (Appendix G). Kerplunking, first observed in Tampa Bay, was not observed in Sarasota Bay until F157, originally a Tampa Bay resident, began to include Sarasota in her home range (Wells 2001). F157 has been observed kerplunking with two of her three calves in Sarasota Bay (Nowacek 2002). Besides her calves, F157 is the only individual in Sarasota Bay to use this behavior regularly.

F119 has also been observed practicing a specialization, seawall feeding, with a previous calf, F125 (J. Weiss personal observations). At the time of the observations, F125 was a dependent calf and accompanied her mother in herding fish against a seawall on numerous occasions. This calf was older than F119's calf in the present study, and this may provide an explanation for why the present younger calf was not observed seawall feeding. Since becoming independent of her mother, F125 is still occasionally observed foraging against the seawall (S. Hoffman personal communication 2003). It is unknown whether F157's now independent calves still kerplunk, as they have not been sighted recently in the study area. However, this evidence does suggest the maternal transmission of kerplunking and barrier feeding within these two lineages.

Evidence from the present study also supports support the hypothesis that foraging specializations are spread by maternal transmission. The close proximity of the calf to the mother while practicing a foraging specialization would allow the calf to learn specialized behaviors from the mother. It is expected that, due to the lack of water clarity in Sarasota Bay, it would be necessary for the calf to be close to the mother if learning a behavior.

The greater frequency of presence of group members when foraging specializations were not used by the mother or calf may indicate that the females preferred to use foraging specializations when others were not in the area. Although this evidence is merely suggestive, foraging without others may present an opportunity for the mother to transmit foraging specializations to her calf. The lack of other group members using the specializations may negate the possibility that behaviors are spread horizontally, or within generations.

All calves that used a foraging specialization displayed the strategy employed by its mother. Furthermore, the calf of the female who did not specialize also did not use a foraging specialization. These observations further support maternal transmission as a mechanism for the spread of foraging specializations. Mann and Sargeant (2003) also found calves to almost exclusively use the mother's preferred foraging strategy in Shark Bay, Western Australia.

Evidence suggests that the age of the calf may play a role in the development of the calf's use of a foraging specialization. Since weaning of bottlenose dolphin calves occurs between the ages of 6-12 months (Essapian 1953), older calves are expected to be more adept at catching prey. F157's calf, F137, was a three-year old as compared to the other focal calves who were one-year olds. F137 used her mother's specialization, kerplunking, more often than other calves used their mother's specializations. During the observed foraging events, F137 kerplunked 30 times. In contrast, CRP2, calf of F119, practiced her mother's foraging specialization, seawall

feeding, only once. The calf of F175, 1751, was not observed practicing her mother's specialization on any occasion. Although such patterns may also be explained by differing complexities of foraging specializations, varying frequencies of the mothers' use of the specializations, or the possibility of the mother and calf foraging for different types or sizes of prey, evidence suggests a learning curve likely exists for calves that learn their mother's specializations.

Maternal transmission of communication patterns has been observed within other cetacean communities. The development of male and female bottlenose dolphin signature whistles is dependent upon the mother's whistle type (Sayigh et al. 1990). The strong association of matriline, female lineages, is expected to cause female offspring to modify their whistles, in order to become distinctive from their mother's whistle. Furthermore, vocal dialects of killer whales are transmitted through matrilineal pods. These dialects are stable over generations, as well (Whitehead 1998). These examples show how the associations of related females strongly influence the development of communication patterns within a community. This evidence supports the possibility such maternal associations with offspring may influence the spread of other types of behaviors and further supports the hypothesis of maternal transmission of foraging specializations in bottlenose dolphins.

Future Research

This study provides evidence that individual choice of foraging habitat in Sarasota Bay is associated with preference of foraging specializations. Variation in prey resources also affects the use of foraging specializations, and this study raises questions about whether such behaviors are prey type specific. If animals exhibit preferences for different foraging specializations, they may be feeding on different prey. Such a scenario has been noted in California sea otters in

which individuals use different foraging specializations to feed upon different prey (Estes et al. 2003). If bottlenose dolphins use foraging specializations to feed on different prey, this may result in different caloric intakes and have implications for reproductive success.

This study provides suggestive, but not conclusive, evidence that foraging specializations may be transmitted from mother to calf. The long-term study of the Sarasota community has been essential to determine these trends. A longitudinal study that focuses on the use of kerplunking and barrier feeding as well as follows females and their calves throughout time would allow a quantitative test of whether or not these behaviors are transmitted between generations. Such a study would also provide further insight into the functions and habitat specificity of these specializations.

A longitudinal study would also address questions about the stability of the use of foraging specializations that have been raised by this study. Anecdotal evidence from the Sarasota Bay study site suggests that individuals may continue to practice specializations once independent from their mothers (S. Hoffman personal communication 2004; J. Weiss personal observations). Evidence also shows the use of foraging specializations by three generations in two lineages (Appendix G) and supports the possibility that individuals who learn complex foraging behaviors may continue to practice them over time. As another example, strand feeding of bottlenose dolphins in Georgia has been observed since 1965. Based upon the observations of a mother and calf strand feeding, Hoese (1971) suggested that this may be a learned behavior that passes through generations. Avital and Jablonka (1994) found that if a behavior is passed through one generation, there is a better chance that it will be passed on to the next, since it is possible for the actual teaching behavior to be transmitted along with the behavior. Due to the suggested association between foraging specializations and habitats, the persistence of

specialized behavior through time may also indicate the continuing importance of particular foraging habitats, as well.

The sex-specific nature of the transmission of foraging specializations in Sarasota Bay remains questionable. Mann and Sargeant (2003) suggest that females in Shark Bay, Western Australia may be more likely to acquire foraging specializations than males, as a result of the later weaning age of female calves and the increased opportunity for mothers to invest in female offspring. Females in Shark Bay have also been observed practicing their mother's specializations post-weaning, while males have not (Mann and Sargeant 2003; Smolker et al. 1997). Females within the Sarasota community form female bands. These groups of females share overlapping home ranges and tend to associate with each other more than with other individuals (Wells 1991). Once independent, juvenile females remain in close contact with their mother and younger siblings (Wells 2001), and after attaining sexual maturity, they return to their mother's band (Wells 1991). Although there is no evidence of later female weaning age in Sarasota as in Shark Bay, the increased duration of time that daughters spend with their mothers after returning to the bands provides the mother a greater chance of investing behaviorally in her female offspring (Avital and Jablonka 1994). A greater investment in females behaviorally might indicate the importance of matriline in the passage of behavioral knowledge within a community. This study has provided a baseline to the determination of the role of matriline in the transmission of foraging specializations in that it provides evidence to suggest that information may be passed from mother to calf.

Management Implications

The suggested transmission of foraging specializations as well as the link between habitat use and such behaviors indicates the need to incorporate knowledge of social behavior

into the management structure for bottlenose dolphin communities. Evidence from this study allows the Sarasota Bay community to serve as a case study in this respect. If maternal transmission is a mechanism for the spread of foraging specializations, this reinforces the importance of the mother-calf bond and suggests that there may be a critical time period for calves to learn adaptations to their environment. The vulnerability of this bond to disturbance may result in the interference of the passage of important information. Current management approaches suggest conservation in numbers; however, evidence from the present study emphasizes the importance of individual variation in behavior to the community and the need to conserve behaviors that allow adaptation to the environment.

The Sarasota community is included within the Gulf of Mexico Bay and Sound bottlenose dolphin stocks, which occupy the geographic range of the bays, sounds, and estuaries of the Gulf of Mexico (NOAA 2000). These stocks are currently managed at the community level. Results from the present study underscore the need to understand patterns and variations in social behavior within communities as well as more traditional demographic boundaries among communities. Furthermore, the link between foraging specializations and habitats, as well as the individual preference of specializations, indicates the importance of different foraging habitats to individuals.

Based upon evidence for the association between foraging specializations and habitat, if foraging specializations are stable over time, foraging habitat preferences may persist through generations, as well. One of the potential anthropogenic impacts to Sarasota Bay is habitat alteration (Wells 1993), which may change the distribution of dolphin prey. Due to the demonstrated importance of seagrass habitats to foraging dolphins (Figure 5), the knowledge of specialized behaviors may aid in foraging when seagrass coverage changes from year to year.

Suggestive evidence for the transmission of foraging behaviors from mother to calf may support the importance of the role of matriline in the passage of such knowledge and the need to manage the community at a matrilineal level.

If the mother-calf bond has a significant role in the transmission of foraging specializations within the community, particular anthropogenic actions may not threaten at the community level, but at the maternal level, by posing a significant threat to the stability of this bond. Disturbance is another potential anthropogenic impact to the Sarasota Bay community (Wells 1993). Mother-calf pairs are particularly susceptible to human-induced disturbances, especially the threat of boat strikes (Wells and Scott 1997). On average, dolphins are approached every six minutes by recreational vessels in Sarasota Bay (Nowacek et al. 2001). The mother's ability to maneuver around boats is compromised by the dependency of the calf. This potentially interferes with the mother's ability to successfully transfer learned behaviors to the calf and jeopardizes the calf's chances of foraging success. This study emphasizes the need to consider measures to reduce disturbances to mother-calf pairs as well.

The disturbance of the mother-calf bond and interruption of the potential for the transmission of foraging behaviors may cause serious implications in other dolphin populations. Spotted and spinner dolphin females and dependent calves are particularly vulnerable to the chase and encirclement procedures of tuna purse-seiners in the Eastern Tropical Pacific Ocean (Archer et al. 2001). As in Sarasota Bay, mothers and calves experience difficulty in maneuvering around boats and nets. One possible explanation for a lack of expected recovery of the depleted dolphin stocks in the ETP may be the cryptic mortality of calves in tuna purse-seining operations (Archer et al. 2001). If the mother is killed in the net and her dependent calf is released, the calf's survival chances are low, especially since its ability to learn critical

foraging behaviors from the mother is compromised. Further insight into the importance of the role of the mother-calf bond in the transmission of foraging behaviors may provide insight into trends of other dolphin populations as well as indicate a need for increased measures to prevent disturbances to this relationship.

African elephants (*Loxodonta cyclotis*) represent an example of a complex animal society that is managed at the matrilineal level due to the importance of matrilineal units in their social structure, and may serve as an example of for the management of bottlenose dolphin communities. In comparison to bottlenose dolphins, female African elephants also live in fission-fusion societies (McComb et al. 2001). The structure of female African elephants groups resembles the female bands observed in Sarasota bottlenose dolphins, and the matrilineal units are lead by the oldest female. The oldest matriarch within a group serves as a storage of social knowledge and passes this information down to group members (McComb et al. 2001). The age of the oldest matriarch is linked to the reproductive and fitness benefits of the group. Families led by older matriarchs exert dominance over those families led by younger matriarchs. This dominance increases the older matriarchal family's fitness (McComb et al. 2001). In addition to social knowledge, matriarchs also serve an ecological function to the group. For example, the survival of Namibian desert elephant groups is dependent upon the matriarch's knowledge of how water sources are distributed within the desert (Payne 2003).

Management of African elephants is based upon the importance of the oldest matriarchs for transmitting social knowledge within the groups and acknowledges that the removal of these females may have significant effects on the entire population (McComb et al. 2001). In comparison, the removal of female bottlenose dolphins that use specialized foraging behaviors in which they pass onto their calves may result in erasing the beneficial use of foraging

specializations from the community. Future generations would be at a disadvantage for adapting to the environment without the knowledge of foraging specializations.

Conclusions

Bottlenose dolphins in Sarasota Bay exhibit individual preferences for foraging specializations and increase their use of foraging habitats that are associated with their preferred behaviors. Evidence suggests that foraging specializations may be transmitted vertically within the community, from mother to calf. Similar to other complex animal societies (McComb et al. 2001), the passage of such knowledge may be critical to the survival of future generations.

The study of specialized foraging behaviors may provide the greatest insight into the evidence of culture in cetaceans. This study is limited in that it only describes the detailed behaviors of a few individuals and provides merely a snapshot into the dolphins' daily lives. However, the presence of foraging specialization and foraging habitat preferences in the focal animals indicates a need to explore such trends in the rest of the community. Further study is necessary to conclusively determine the presence of maternal transmission in Sarasota Bay as well as address the questions raised by this study. Comparisons of foraging specializations and foraging habitat preferences between communities may provide further insight into the behavioral plasticity of the species and the effects of different environmental influences.

Acknowledgements

I would like to thank the Duke Marine Lab and the Sarasota Dolphin Research Program for field and logistical support, as well as the SDRP's wealth of information on the Sarasota Bay dolphin community; Andy Read and Randy Wells for their helpful comments, advice, support, and dedication to this project; Teresa Gisburne, Hillary Farrah, and Susan Newson for assistance in the field; Ester Quintana for many hours of thoughtful insight, discussion, and valuable field training; Doug Nowacek for information about the foraging behaviors, insight for field sampling design, and drawings of foraging behaviors; Sue Hoffman and Jason Allen for field training and assistance with photoidentification; Stephanie Nowacek for the assistance with GIS seagrass coverages; Kim Bassos-Hull for advice about field sampling design and field training; Kim Urian for GIS assistance and information about the Sarasota dolphin community structure;

Danielle Waples for ArcView assistance, essential field equipment, and thoughtful discussion about this project; Cherie Jenkins and Amy Whitt for insight and suggestions; Valerie Chan for GIS assistance; Jon Cohen for statistical assistance and advice; all my friends for their continuous support and encouragement; my family (and Naia), especially my mom, for always encouraging me, supporting me, and for providing me with inspiration; and last but not least, FB09, C094, FB75, F757, F119, CRP2, F157, F137, F175, and 1751 for allowing us to follow them and for the special glimpse into their lives.

References

- Allen, M.C., Read, A.J., Gaudet, J., and Sayigh, L.S. 2001. Fine-scale Habitat Selection of Foraging Bottlenose Dolphins *Tursiops truncatus* near Clearwater, Florida. *Marine Ecology Progress Series*. 222: 253-264.
- Altmann, J. 1974. Observational Study of Behavior: Sampling Methods. *Behaviour*. 49: 227-267.
- Archer, F., Gerrodette, T., Dizon, A., Abella, K., and Southern, S. 2001. Unobserved Kill of Nursing Dolphin Calves in a Tuna Purse-Seine Fishery. *Marine Mammal Science*. 17(3): 540-554.
- Avital, E. and Jablonka, E. 1994. Social Learning and the Evolution of Behavior. *Animal Behaviour*. 48(5): 1195-1199.
- Barros, N.B. 1993. Feeding Ecology and Foraging Strategies of Bottlenose Dolphins on the Central East Coast of Florida. Ph.D. dissertation. University of Miami, Coral Gables, Florida, 328 pp.
- Barros, N.B. and Wells, R.S. 1998. Prey and Feeding Patterns of Resident Bottlenose Dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. *Journal of Mammalogy*. 79(3): 1045-1059.
- Connor, R.C. Personal communication. September 2002.
- Connor, R.C., Heithaus, M.R., Berggren, P., and Miksis, J.L. 2000. "Kerplunking": Surface Fluke-Splashes During Shallow-Water Bottom Foraging by Bottlenose Dolphins. *Marine Mammal Science*. 16(3): 646-653.
- Essapian, F.S. 1953. The Birth and Growth of a Porpoise. *Natural History*. 62(9): 392-399.
- Environmental Systems Research Institute. 1995. ArcView 3.2. Redlands, CA.
- Estes, J.A., Riedman, M.L., Staedler, M.M., Tinker, M.T., and Lyon, B.E. 2003. Individual Variation in Prey Selection by Sea Otters: Patterns, Causes, and Implications. *Journal of Animal Ecology*. 72: 144-155.
- Fertl, D. and Wilson, B. 1997. Bubble Use During Prey Capture by a Lone Bottlenose Dolphin (*Tursiops truncatus*). *Aquatic Mammals*. 23(2): 113-114.
- Florida Marine Research Institute. 2002. Florida Atlas of Marine Resources.
- Goss-Custard, J.D. and Sutherland, W.J. 1984. Feeding Specializations in Oystercatchers, *Haematopus ostralegus*. *Animal Behaviour*. 32(1): 299-300.

- Guinet, C. and Bouvier, J. 1995. Development of Intentional Stranding Hunting Technique in Killer Whale (*Orcinus orca*) Calves at Crozet Archipelago. *Canadian Journal of Zoology*. 73: 27-33.
- Hastie, G.D., Wilson, B., Wilson, L.J., Parsons, K.M., and Thompson, P.M. 2004. Functional Mechanisms Underlying Cetacean Distribution Patterns: Hotspots for Bottlenose Dolphins are Linked to Foraging. *Marine Biology*. 144: 397-403.
- Hoelzel, A.R., Dorsey, E.M., and Stern, S.J. 1989. The Foraging Specializations of Individual Minke Whales. *Animal Behaviour*. 38: 786-794.
- Hoese, H.D. 1971. Dolphin Feeding Out of Water in a Salt Marsh. *Journal of Mammalogy*. 52: 222-223.
- Hoffman, S. Personal communication. June 2003.
- Hoffman, S. Personal communication. March 2004.
- Johnston, T.D. 1982. Selective Costs and Benefits in the Evolution of Learning. *Advances in the Study of Behavior*. 12: 65-106.
- Leatherwood, S. 1975. Some Observations of Feeding Behavior of Bottle-nosed Dolphins (*Tursiops truncatus*) in the Northern Gulf of Mexico and (*Tursiops cf T. gilli*) off Southern California, Baja California, and Nayarit, Mexico. *Marine Fisheries Review*. 37(9): 10-16.
- Lewis, J.S., and Schroeder, W.W. 2003. Mud Plume Feeding, A Unique Foraging Behavior of the Bottlenose Dolphin in the Florida Keys. *Gulf of Mexico Science*. 21(1): 92-97.
- Mann, J. and Smuts, B.B. 1998. Natal attraction: Allomaternal Care and Mother-Infant Separations in Wild Bottlenose Dolphins. *Animal Behavior*. 55: 1097-1113.
- Mann, J. and Sargeant, B. 2003. Like Mother, Like Calf: The Ontogeny of Foraging Traditions in Wild Indian Ocean Bottlenose Dolphins (*Tursiops* spp.). In "The Biology of Traditions: Models and Evidence" (ed. D.M. Fragaszy and S. Perry), Cambridge University Press, New York. Pp. 236-266.
- McComb, K., Moss, C., Durant, S.M., Baker, L., and Sayialel, S. 2001. Matriarchs as Repositories of Social Knowledge in African Elephants. *Science*. 292: 491-494.
- Norton-Griffiths, M. 1968. The Feeding Behavior of the Oystercatcher *Haematopus ostralegus*. Ph.D. thesis, University of Oxford.
- Nowacek, D. P. 1999. Sound Use, Sequential Behavior and Ecology of Foraging Bottlenose Dolphins, *Tursiops truncatus*. Doctoral dissertation, Massachusetts Institute of Technology/Woods Hole Oceanographic Institution 99-16. 196 pp.

- Nowacek, D.P. 2002. Sequential Foraging Behaviour of Bottlenose Dolphins, *Tursiops truncatus*, in Sarasota Bay, Florida. *Behaviour*. 139: 1125-1145.
- Nowacek, S.M., Wells, R.S., and Solow, A.R. 2001. Short-term Effects of Boat Traffic on Bottlenose Dolphins, *Tursiops truncatus*, in Sarasota Bay, Florida. *Marine Mammal Science*. 17(4): 673-688.
- Partridge, L. and Green, P. 1985. Intraspecific Feeding Specializations and Population Dynamics. In "Behavioural Ecology (eds. R.M. Sibly and R.H. Smith) Blackwell, Oxford Pp. 207-226.
- Payne, K. 2003. Sources of Social Complexity in the Three Elephant Species. In "Animal Social Complexity: Intelligence, Culture, and Individualized Societies." (eds. F.B.M. de Waal and P.L. Tyack) Harvard University Press, Cambridge, Massachusetts. Pp.57-85.
- Rendell L. and Whitehead, H. 2001. Culture in Whales and Dolphins. *Behavioral and Brain Sciences*. 24(2): 309-324.
- Reynolds, J.E., Wells, R.S., and Eide, S.D. 2000. Life History Strategies. In: "The Bottlenose Dolphin: Biology and Conservation." University Press of Florida, Gainesville, FL. Pp. 85-104.
- Rossbach, K.A. and Herzing, D.L. 1997. Underwater Observations of Benthic-Feeding Bottlenose Dolphins (*Tursiops truncatus*) Near Grand Bahama Island, Bahamas. *Marine Mammal Science*. 13(3): 498-504.
- Sayigh, L.S., Tyack, P.L., Wells, R.S., and M.D. Scott. 1990. Signature Whistles of Free-Ranging Bottlenose Dolphins *Tursiops truncatus*: Stability and Mother-Offspring Comparisons. *Behavioral Ecology and Sociobiology*. 26: 247-260.
- Scott, M.D., Wells, R.S., and Irvine, A.B. 1990. A Long-Term Study of Bottlenose Dolphins on the West Coast of Florida. In: "The Bottlenose Dolphin." (eds. Stephen Leatherwood and Randall R. Reeves). Academic Press, San Diego, CA. Pp.235-244.
- Shane, S.H. 1990. Behavior and Ecology of the Bottlenose Dolphin at Sanibel Island, Florida. In: "The Bottlenose Dolphin" (eds. S. Leatherwood and R.R. Reeves). Academic Press, San Diego, CA. Pp. 245-266.
- Smolker, R., Richards, A., Connor, R., Mann, J., and Berggren, P. 1997. Sponge Carrying by Dolphins (Delphinidae, *Tursiops* sp.): A Foraging Specialization Involving Tool Use? *Ethology*. 103: 454-465.
- Urian, K.W. and Wells, R.S. 1996. Bottlenose Dolphin Photo-Identification Workshop. In National Marine Fisheries Service, Southeast Fisheries Science Center, Charleston, S.C. p.92.
- United States National Oceanic and Atmospheric Administration. 2000. Gulf of Mexico Bay Bottlenose Dolphin Stock Assessment.

Waples, D.M. 1995. Activity Budgets of Free-Ranging Bottlenose Dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. M.S. Thesis, University of California, Santa Cruz, 61 pp.

Weinrich, M.T., Schilling, M.R., and Belt, C.R. 1992. Evidence for Acquisition of a Novel Feeding Behavior: Lobtail feeding in humpback whales, *Megaptera novaeangliae*. *Animal Behaviour*. 44: 1059-1072.

Wells, R., Scott M.D., and A.B. Irvine. 1987. The Social Structure of Free-Ranging Bottlenose Dolphins. In "Current Mammalogy, volume 1" (ed. H.H. Genoways), Plenum Press, New York. Pp. 247-305.

Wells, R. S. 1991. The Role of Long-Term Study in Understanding the Social Structure of a Bottlenose Dolphin Community. In "Dolphin Societies: Discoveries and Puzzles" (eds. K. Pryor and K.S. Norris) University of California Press, Berkeley, California. Pp. 199-225.

Wells, R.S. 1993. The Marine Mammals of Sarasota Bay. In: "Sarasota Bay: 1992 Framework for Action." Sarasota, FL.: Sarasota Bay National Estuary Program.

Wells, R.S. and Scott, M.D. 1997. Seasonal Incidence of Boat Strikes on Bottlenose Dolphins near Sarasota, Florida. *Marine Mammal Science*. 13: 475-480.

Wells, R.S. 2001. Dolphin Social Complexity: Lessons from a Long-Term Study and Life History. In "Animal Social Complexity: Intelligence, Culture, and Individualized Societies" (eds. F.B.M. de Waal and P.L. Tyack) Harvard University Press, Cambridge, Massachusetts. Pp. 32-56.

Whitehead, H. 1998. Cultural Selection and Genetic Diversity in Matrilineal Whales. *Science*. 282: 1708-1711.

Whiten, A. and Ham R. 1992. On the Nature and Evolution of Imitation in the Animal Kingdom: Reappraisal of a Century of Research. In: "Advances in the Study of Behavior." (eds. P.J.B. Slater, J.S. Rosenblatt, C. Beer, and M. Milinski) Academic Press, New York, Pp. 239-283.

Wursig, B. 1986. Delphinid Foraging Strategies. In "Dolphin Cognition and Behavior: A Comparative Approach" (eds. R.J. Schusterman, J.A. Thomas, and F.G. Woods) Lawrence Erlbaum Assoc., Hillsdale, New Jersey. pp. 347-359.

Appendices

Appendix A. Sarasota Dolphin Research Program Sighting Sheet

Appendix B. Point-Sampling Datasheet

Appendix C. Continuous Sampling Datasheet

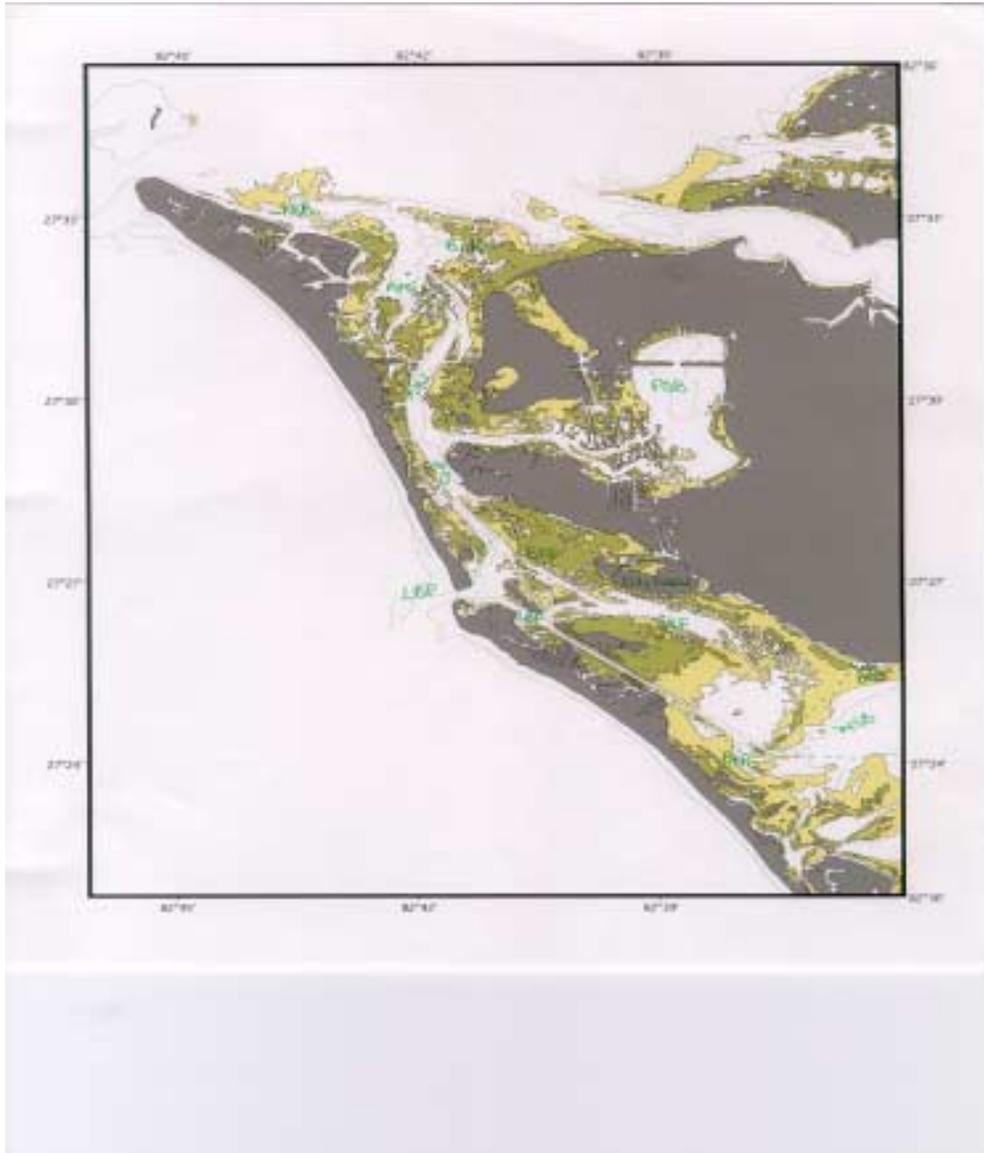
Appendix D. Northern Sarasota Bay Area Seagrass Map

Appendix E. Southern Sarasota Bay Area Seagrass Map

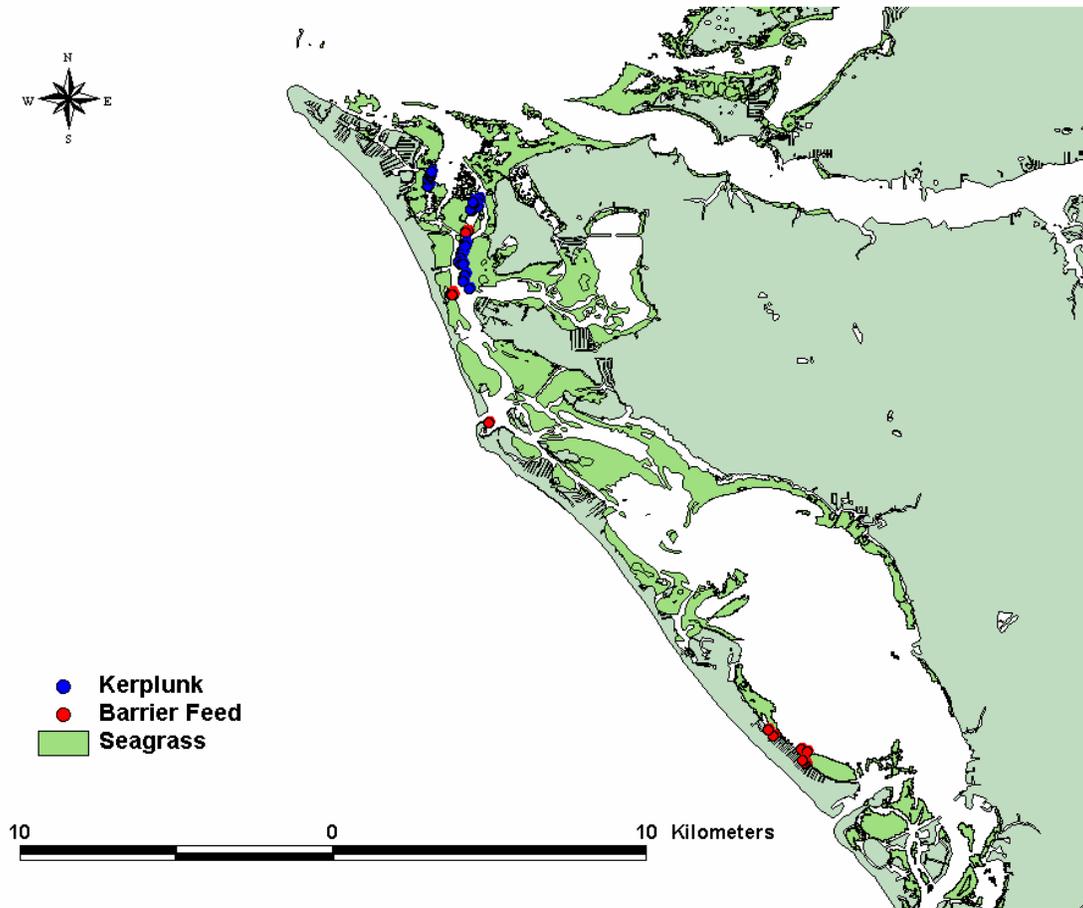
Appendix F. Foraging Specializations Habitat Map

Appendix G. Focal Female Lineages

Appendix D.
North Sarasota Bay Area Seagrass Map



Appendix F.
Foraging Specializations Habitat Map



Appendix G.
Focal Female Lineages

