Aquatic Mammals 2006, *32*(1), 10-19, DOI 10.1578/AM.32.1.2006.10

Foraging Habitats and Associated Preferential Foraging Specializations of Bottlenose Dolphin (*Tursiops truncatus*) Mother-Calf Pairs

Jessica Weiss[1]

[1]*Duke University Marine Laboratory, 135 Duke Marine Lab Road, Beaufort, NC 28516, USA*
Current Address: Geo-Marine, Inc., 2713 Magruder Boulevard, Suite D, Hampton, VA 23666, USA

Abstract

Bottlenose dolphins (*Tursiops truncatus*) 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 type or prey resources. The long duration of the mother-calf bond presents an opportunity for mothers to transmit such specializations to their calves. This study explored how the use of foraging specializations may influence selection of foraging habitats and how such specializations may spread within a dolphin community. Focal animal follows were used to document the foraging behavior of five resident females and their calves from June to August 2003 in Sarasota Bay, Florida. Sarasota Bay was classified into six habitat types based upon bathymetry and bottom topography. Individual females differed in their selection of foraging habitats. Three of the five focal females used one of two foraging specializations—kerplunking and barrier-feeding—and exhibited a preference for only one type of behavior. A significant difference in the frequency of observations of foraging specific behaviors was found between different habitat types. Limited observations, as well as anecdotal evidence from past studies, suggest that maternal transmission may play a role in the spread of foraging techniques, such as kerplunking and barrier-feeding, within the community. My findings suggest that the use of foraging specializations is associated with foraging habitat preferences in Sarasota Bay. The importance of seagrass areas to foraging dolphins and the significance of the mother-calf bond to the development of the use of foraging specializations is emphasized.

Key Words: bottlenose dolphin, *Tursiops truncatus*, foraging ecology, habitat use, vertical transmission, kerplunking, barrier-feeding, Sarasota Bay, Florida

Introduction

Foraging specializations allow animals to adapt to environmental variations and, thus, promote their survival. Specialized foraging behaviors provide an efficient means of detecting and pursuing prey (Partridge & Green, 1985), as well as reducing intraspecific competition for prey resources. The use of foraging specializations may evolve in response to physical differences in habitat, such as topography (Hoelzel et al., 1989), or variation in food supply (Partridge & Green, 1985). In addition to ecological factors, an individual's preference also plays a role in the selection of a foraging specialization (Nowacek, 1999). In this study, I examined the relationship between the use of different habitat types and foraging specializations by bottlenose dolphins (*Tursiops truncatus*) and the possibility of such preferences being passed on to future generations through cultural transmission.

Plastic Nature of Dolphin Foraging Behavior

Bottlenose dolphins are a cosmopolitan species found in many regions of the world. Their behavioral plasticity is illustrated by the many types of foraging specializations that have been observed in different communities such as kerplunking, fish-whacking, barrier-feeding, mud-plume feeding, and strand-feeding (Würsig, 1986; Wells et al., 1987; Fertl & Wilson, 1997; Nowacek, 1999; Connor et al., 2000; Gubbins, 2002; Lewis & Schroeder, 2003). Kerplunking is a foraging specialization in which an individual raises its tail flukes out of the water, forcefully slaps the water surface, and sweeps its prey under water (Nowacek, 1999). This action produces a 1- to 2-m splash; a bubble cloud; and a high amplitude, low frequency sound. The function of kerplunking appears to be to evoke a startle response in fish, which may allow dolphins to detect them better (Connor et al., 2000). Kerplunking is a behavior that is associated with foraging in that the presence of kerplunking may be used to indicate a foraging state (Nowacek, 1999, 2002). During fish-whacking behavior, a dolphin uses its tail flukes to knock fish into the air, then feeds on the stunned and injured prey once it lands in the water (Wells et al., 1987). In another type of foraging specialization, barrier-feeding, dolphins use the water surface or shorelines as barriers against which they herd fish for easy capture (Würsig, 1986). Dolphins may also herd fish against sea walls, bridge pilings, and stationary boats as has been observed in Sarasota Bay, Florida (J. Weiss, pers. obs.).

Habitat-Specific Foraging Specializations

The ecology of localized habitat types appears to determine the types of foraging specializations that dolphins use. Bottlenose dolphins display a variety of foraging specializations that are habitat-specific. For example, mud-plume feeding, a foraging specialization documented in the Florida Keys, is associated with seagrass flats due to the suspended sediment that is necessary in the plume to concentrate the prey (Lewis & Schroeder, 2003). In other areas, such as South Carolina, dolphins strand-feed by propelling their bodies onto a sloping mud bank at low tide to chase and capture beached fish along the bank, partially stranding themselves in the process (Gubbins, 2002). Strand-feeding is habitat-specific as well because the sloping mud bank must be adequately exposed to concentrate the fish and be free of dangerous obstructions (such as oyster shells) so the dolphins avoid injury while stranded (Hoese, 1971; Gubbins, 2002). The dependency of dolphins on habitats that are conducive to their foraging technique(s) and the influence of habitat characteristics on foraging efficiency (Hastie et al., 2004) indicate a need to further understand the relationship between feeding areas and foraging specializations.

Foraging Specializations and Prey Resources

The characteristics of prey resources also affect the types of foraging specializations used by bottlenose dolphins. The distribution of prey has a considerable influence; clumped or concentrated prey are necessary for specializations such as strand-feeding (Gubbins, 2002) and mud-plume feeding (Lewis & Schroeder, 2003) to be effective; however, the use of fish-whacking is more efficient in the capture of individual fish (Wells et al., 1987). Passive listening is another foraging tactic in which dolphins take advantage of prey characteristics by exploiting the soniferous nature of their prey. Passive listening aids in the detection of prey through the interception of prey sounds (Barros, 1993). Bottlenose dolphin prey includes well-known sound-producing fish such as croaker (*Micropogonias undulatus*) and spot (*Leiostomus xanthurus*) (Barros & Wells, 1998); this characteristic may allow dolphins to use passive listening to increase their foraging efficiency.

In addition, the types of prey consumed by individual bottlenose dolphins vary (Barros & Wells, 1998) and, like the use of foraging specializations, are also subject to individual preference. Similar associations between the use of foraging specializations and prey resources can be noted in other marine mammals, such as North Atlantic humpback whales (*Megaptera novaeangliae*) whose use of lobtail-feeding is directly correlated with the presence of sand lance (Weinrich et al., 1992).

Evidence for Vertical Transmission of Foraging Specializations

The use of complex foraging behaviors may be influenced by environmental variation. Foraging may also be dependent on individual preferences, which may be passed within a community by cultural transmission. A well-known example of such transmission within a group is the opening of milk bottle caps by members of the bird family Paridae (as shown, for example, by individuals of a captive group of black-capped chickadees [*Parus atricapillus*], Sherry & Galef, 1984). Birds that did not exhibit the behavior began to open milk bottles after they had interacted with milk-bottle-opening individuals.

Foraging specialization preferences may be transferred from mother to offspring through a social learning process known as vertical transmission (Rendell & Whitehead, 2001). In animal societies in which individuals practice complex foraging behaviors (Johnston, 1982), there should be a high degree of maternal investment. The foraging specializations of California sea otters (*Enhydra lutris*) are transmitted vertically through matrilineal lines, and it is likely that sea otter females actively teach their pups to forage during the 6 mo before the weaning period (Estes et al., 2003). A significant exception to the fission-fusion nature of bottlenose dolphin societies is the strong maternal investment in calves (Wells, 2003). Mothers and calves form long-term associations (Würsig, 1986; Grellier et al., 2003) that usually last until the birth of the next calf (Wells et al., 1987). The long duration and intensity of the bond provides an ideal opportunity for a calf to learn specialized behaviors from its mother, if the mother exhibits such behaviors. Indeed, the matrilineal transmission of a foraging specialization known as sponging among Indian Ocean bottlenose dolphins (*T. aduncus*) in Shark Bay, Australia, was observed through a long-term study (Smolker et al., 1997), as well as by genetic analyses (Krützen et al., 2005). This indicates that other foraging specializations within communities may be transmitted maternally as well.

Foraging Specializations in Sarasota Bay

Longitudinal studies provide insight into the nature of foraging behaviors and the process by which they may spread within a wild population (Estes et al., 2003; Mann & Sargeant, 2003; Wells, 2003). Sarasota Bay, Florida, is the site of a long-term resident community of bottlenose dolphins whose distribution and behavioral ecology has been studied extensively since 1970 (Wells et al., 1987; Wells, 1991). Barrier-feeding and kerplunking are complex foraging behaviors practiced by individuals in Sarasota Bay; the behaviors are observable at the surface and easily documented. Females 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 specialization is most useful. Anecdotal evidence (Nowacek, 1999; Wells, 2003) suggested a vertical transmission of foraging specializations within the resident community of bottlenose dolphins in Sarasota Bay. 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 individuals to adapt to changes in the environment.

Objectives

The objectives of this study were to investigate the relationship between bottlenose dolphins' foraging specialization preferences and habitat as well as to consider how foraging specializations are spread within the Sarasota Bay community.

Materials and Methods

Study Area

The home range of the Sarasota Bay community spans 40 km of the central western Florida coastline and encompasses a system of channels and bays, protected by a series of barrier islands, as well as Gulf of Mexico waters, out to approximately 1 km offshore (Scott et al., 1990). Areas within the bay study area ranged in depth from < 1 m in seagrass flats to approximately 10 m in passes connecting the bay to the Gulf of Mexico (Buckstaff, 2004). For the purposes of this study, Sarasota Bay was classified into five main habitat types, distinguished mainly by bathymetry (Table 1): (1) channel, (2) bay, (3) pass, (4) gulf, and (5) shallows (Waples, 1995). Shallows were further classified by bottom topography as seagrass shallows or non-seagrass shallows based upon the presence of seagrass at a particular location.

Table 1. Sarasota Bay, Florida habitat classification descriptions (Waples, 1995)

Habitat	Habitat description
Channel	Area of heavy boat use and a 3:1 depth ratio to surrounding water
Bay	Inshore area of depth greater than 2 m up to 6 m
Pass	Area characterized by deep water, strong currents, and bordered by sand bars
Gulf	Offshore area of depth greater than 2 m
Shallows	Area of 2 m depth at mean low tide; characterized by seagrass and sand patches

Subjects

Photo-identification, genetic studies, and behavioral observations have yielded a considerable body of information on the genetic lineages and individual foraging behaviors of Sarasota Bay residents (Wells, 1991, 2003; Nowacek, 1999). Five resident females and their calves, of four separate maternal lines, were chosen as focal animals (Table 2). Each female, with the exception of Female F157, had a dependent 1-y-old calf. Weaning of bottlenose dolphin calves occurs between the ages of 6 to 12 mo (Essapian, 1953), so 1-y-old calves would be at an ideal age to begin using foraging specializations. Female F157 and her dependent 3-y-old calf were chosen as focal animals based upon evidence that the mother frequently used a foraging specialization (Nowacek, 1999; Wells, 2003).

Data Collection Protocol

Daily, nonrandom transect surveys were conducted from a 6-m outboard motorboat from June to August 2003. Resident dolphins make extensive use of shallow bays and seagrass meadows during the summer months (Barros & Wells, 1998), and field efforts were concentrated in such areas. Once a group of dolphins was found, a sighting sheet was completed (Urian & Wells, 1996), and dolphins were approached for photographs. Standard photo-identification techniques (Würsig & Würsig, 1977) were used to identify individuals.

Once the presence of a focal female and calf pair was determined, a focal animal follow began. During the follow, behavioral data were recorded for the mother and calf at 3-min time points (a method described in Altmann, 1974), including activity state (feeding, traveling, socializing, and milling; Urian & Wells, 1996), GPS location (latitude and longitude), and habitat type (Table 1). Data were recorded for each focal individual at the first surfacing after the time interval began. A distance of approximately 20 m between the boat and

Table 2. Details of focal calf ages as well as follow and foraging times of focal females and calves studied in Sarasota Bay, Florida, in summer 2003

Female	Calf	Age of calf (y)	Follow time (min)	Foraging time (min)	Foraging time (%)
FB09	C094	1	419	117	27.90
FB75	F757	1	411	105	20.54
F119	CRP2	1	613	123	19.87
F157	F137	3	408	86	20.77
F175	1751	1	429	153	36.36

the dolphins was maintained when recording GPS location. To verify habitat, GPS-generated latitude and longitude coordinates were later overlaid onto a GIS seagrass map (Flamm et al., 2002) of the study area using the *Arc View 3.2* (Environmental Systems Research Institute, 1995) software program.

When focal females began to forage, a continuous sampling method (Altmann, 1974) was used to record the time and type of the mother's foraging behaviors. A foraging state was determined by the combination of multiple fast surfacings, tail-out/peduncle-out dives, fish chases, or a fish in the dolphin's mouth. Recorded foraging behaviors included fish chase, pinwheel (Leatherwood, 1975), fish toss, fish in mouth, sharking, kerplunk (Connor et al., 2000), fish whack (Wells et al., 1987), barrier-feed (Würsig, 1986), surface lunge, fluke-out dive, and peduncle-out dive. The corresponding time and type of the calf's behaviors were recorded as well. The recorded foraging behaviors were visible at the surface in all habitat types, with the exception of sharking, a shallow-water behavior. During a foraging state, the presence of additional group members was recorded, as well as their use of foraging specializations. Individual identifications of additional group members were recorded when possible. Real-time narration recorded observations during all focal follows. A focal follow lasted until visual contact with the focal animal was lost and not regained within three consecutive 3-min intervals.

Differentiation Among Potential Foraging Habitats

To determine how females differentiated among foraging habitats, a chi-square analysis was used to compare the amount of time each female spent foraging in a given habitat to the amount of time spent engaged in other activities within that habitat. A null model predicted the foraging habitat use to be equal for all females in each habitat and a lack of individual preference for particular habitats while foraging. Calves were excluded from this analysis because of their dependency on their mothers' habitat choices.

Habitats were regrouped into shallows and non-shallows to increase sample sizes and to allow for an analysis of female preferences for particular habitats while foraging. Shallows areas were composed of seagrass shallows and non-seagrass shallows habitats. Non-shallows were composed of channel, bay, pass, and gulf habitats (Waples, 1995). Based upon these new habitat classifications, a 2 x 2 chi-square analysis was used to compare observational data collected from each female to determine how habitat use differed for individuals between foraging and nonforaging states. A Yates correction for continuity was applied to increase the conservativeness of the tests. This technique allowed the determination of whether each female was selecting between shallows and non-shallows for foraging. All tests were conducted using *SigmaStat 2.0* at a significance level of $\alpha = 0.05$.

Habitat Locations of Foraging Specializations

To verify the habitats in which foraging specializations occurred, the time of each observed behavior was matched to the GPS location of the focal animal at the time the behavior was recorded. These points were overlaid onto a bathymetric map of Sarasota Bay with seagrass coverage using *ArcGIS* software. A 25-m buffer zone was created around each behavior point to account for the distance from the boat to the focal animal at this time. The percentage of each habitat type within the buffer zone was calculated, and the habitat composing the majority of the buffer zone was chosen to represent the habitat type of the behavior location. Percentages were calculated for the number of times kerplunking ($n = 33$) and barrier-feeding ($n = 55$) events were observed in each habitat. Comparisons were noted between the habitats in which each foraging specialization took place and each female's preferred specialization to examine associations.

Maternal Transmission of Foraging Specializations

To investigate whether foraging specializations spread by maternal transmission in Sarasota Bay, observations of focal females and their offspring using foraging specializations were compiled from previous Sarasota Bay studies (Nowacek, 1999;

S. Hoffman, pers. comm., 2003; Wells, 2003) as well as from the present study to create visual displays of focal maternal lineage foraging behavior. Displays were based on genetic lines and the observations of lineage members using foraging specializations. The use of a foraging specialization and individual preferences for specializations were noted for each family tree. Comparisons of foraging specializations were made within and across maternal lineages.

The potential for horizontal transmission of the observed foraging specializations was explored by calculating percentages of time for which focal females and calves foraged and used foraging specializations in the vicinity of other group members. Observations of foraging specialization use by other group members from the present study were compiled to quantify how often foraging calves were exposed to other individuals using foraging specializations.

Results

Field effort consisted of approximately 280 h, with 38 h devoted to focal follows (Table 2). Follow times among females were relatively similar (Table 2) and, when normalized for effort, each female spent roughly similar percentages of time foraging (Table 2).

Each female used at least three of the available habitat types while foraging in Sarasota Bay (Figures 1a & 1b). Foraging activity was habitat dependent ($\chi^2 = 462.64$, $p < 0.001$) and most commonly observed in seagrass habitats. An increase in the use of seagrass habitats while foraging, compared to habitat use while not foraging, was noted in the habitat selection of all but one female (Figure 1a). Further tests were conducted to investigate the significance of shallows habitats to foraging females. Based upon the reclassification of habitats as shallows versus non-shallows, three females differentiated between shallows and non-shallows while foraging (F119: $\chi^2 = 15.94$, $p < 0.001$; F157: $\chi^2 = 66.42$, $p < 0.001$; F175: $\chi^2 = 14.7$, $p < 0.001$; Bonferonni correction, $\alpha = 0.005$). For each female, the use of shallows increased while in a foraging state as compared to a nonforaging state (Figure 1a).

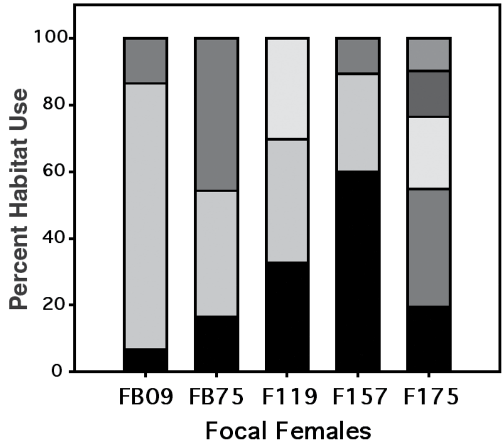

Figure 1a. Foraging state habitat use of focal females in Sarasota Bay, Florida, during summer 2003

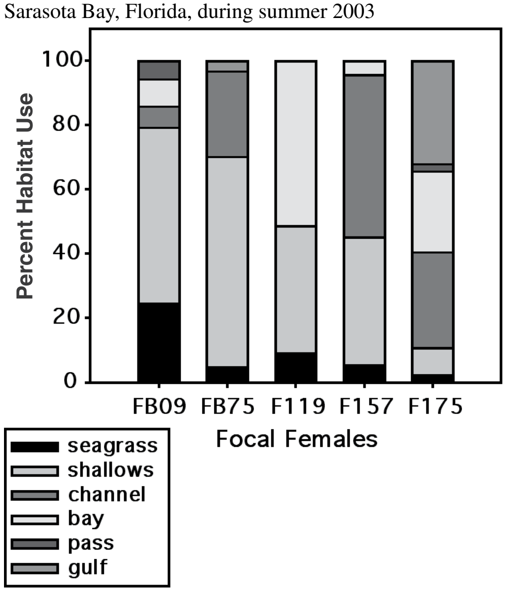

Figure 1b. Nonforaging state habitat use of focal females in Sarasota Bay, Florida, during summer 2003

Foraging Specialization and Habitat Associations

Associations between kerplunking events and habitat indicated that kerplunking occurred only in shallows habitats (Table 1, Figure 2a), although this behavior is observable from the surface and potentially could have been observed in any of the available habitat types. When shallows were reclassified as seagrass shallows versus non-seagrass shallows, a majority of the kerplunking events took place in seagrass shallows. Barrier-feeding was also documented in shallows for a majority of the time (Table 1, Figure 2b), although this behavior was also observed in channel areas (Table 1) within the bay (Figure 2b). Of the available habitats in Sarasota Bay (Table 1), kerplunking and barrier-feeding were observed more frequently in shallows.

Individual Foraging Specialization

Three focal females used known foraging specializations, and each female preferred to use only one type of behavior (Figure 3). Female F157 was observed kerplunking ($n = 25$), and females F119 and F175

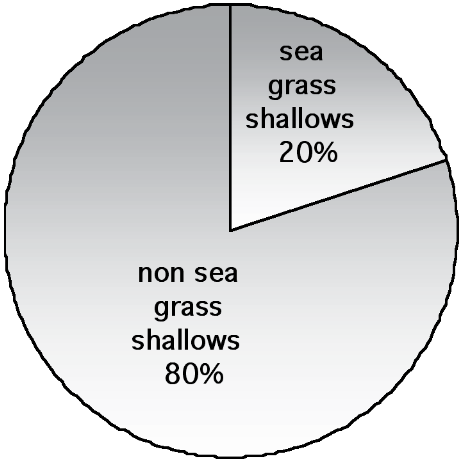

Figure 2a. Habitat use by focal female bottlenose dolphins while kerplunking in Sarasota Bay, Florida, during summer 2003

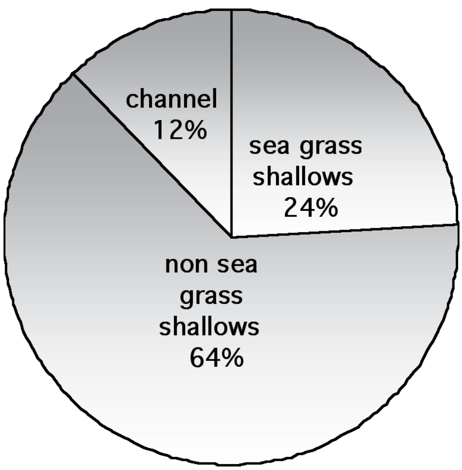

Figure 2b. Habitat use by focal female bottlenose dolphins while barrier-feeding in Sarasota Bay, Florida, during summer 2003

were observed barrier-feeding, yet they differed in their use of structures as barriers. While female F119 consistently used a seawall as a barrier (*n* = 20), female F175 herded fish around bridge pilings and channel markers (*n* = 13). The three females that used known foraging specializations were the same three females to differentiate between shallows and non-shallows habitats when foraging. A shallows habitat was associated with their preferred foraging specializations (Figures 2a & 2b), and they were observed foraging more frequently when in a shallows habitat (Figure 1a). Female F157, a kerplunker, spent 45.0% of her time in a shallows habitat while not foraging, yet spent 89.0% of her time in a shallows habitat while foraging (Figures 1a & 1b). Barrier-feeders, F119 and F175, also spent a greater amount of time in a shallows habitat while foraging compared to not foraging (Figures 1a & 1b). Female F119 was observed foraging more frequently in a shallows habitat (69.8% of foraging time) than in other areas (48.6% of foraging time). Female F175 was also observed foraging more frequently in shallows and channel habitats (54.9% of foraging time) than in other areas (40.5%) (Figures 1a & 1b).

Of the five calves, only two calves (CRP2 and F137) used foraging specializations. Each calf used only the preferred foraging behavior of its mother (F119 and F157, respectively; Figure 3). Calf CRP2 (mother F119) was only observed barrier-feeding (*n* = 1). Calf F137 (mother F157) was only observed kerplunking (*n* = 30) and used this behavior consistently when foraging.

Additional group members were present 73.3% of the time while focal females and calves were engaged in a foraging state. Of this time, group members were present 57.1% of the time when either the focal female or calf used a foraging specialization. There was only one occasion in which another group member was observed using the same specialization, kerplunking, as that of the mother and calf.

Discussion

Focal females showed an association between the use of foraging specializations and foraging habitat preferences in Sarasota Bay. The shallows habitat, composed of seagrass and non-seagrass shallows areas, was an important habitat for kerplunking and barrier-feeding. Foraging specializations occurred more often in this habitat type than in other available habitat types of Sarasota Bay. Due to such associations, it may be possible to predict the distributions of individuals that specialize, as well as their critical foraging habitats. For example, individuals that specialize in kerplunking would be expected to forage in a shallows habitat.

Hastie et al. (2004) linked bottlenose dolphin distributions and habitat preferences to foraging activity. The associations derived from this study confirm the link between foraging dolphin distributions and foraging habitat preferences, as well as support the direct importance of seagrass areas to foraging dolphins. Barros & Wells (1998) found seagrasses to be important habitats for foraging dolphins due to the presence of many important prey species in such areas. Allen et al. (2001) also proposed a significant, although indirect, relationship between seagrasses and foraging dolphins. Both studies suggested the existence of a strong association between foraging dolphins and seagrass

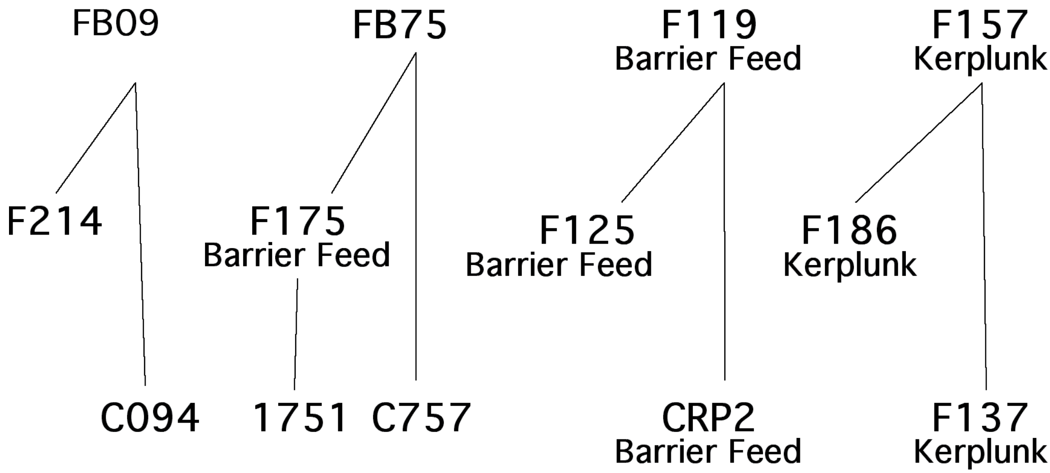

Figure 3. Focal female lineages and individual use of foraging specializations in Sarasota Bay, Florida

communities. The link between particular foraging specializations and seagrass habitats strengthens the importance of such areas to foraging dolphins, as well as identifies seagrasses as a target habitat for dolphins that use these behaviors.

Variations in the use of barrier-feeding observed in this study coincided with the demonstrated natural plasticity of dolphin foraging behavior. The use of different structures as barriers in Sarasota Bay illustrated how the behavioral repertoire of individuals may overlap. Although such variations may have been influenced by different home range characteristics, they also emphasize the ability of dolphins to adapt to different environments. It is necessary to understand such a capability of dolphins to adapt in cases where habitat degradation threatens their environment. Variations in the use of foraging behaviors may be useful for dolphins in Sarasota Bay, where anthropogenic habitat degradation (Wells, 1992) may result in a change in the availability of suitable habitat and the distribution of prey.

Observations of foraging specializations in the present study differ from the use of similar types of behaviors observed in Shark Bay, Western Australia. Although females that specialized in Sarasota Bay preferred one type of behavior, an individual in Shark Bay may use multiple types of specializations (Mann & Sargeant, 2003). It is not yet known why dolphins in Sarasota Bay exhibit different preferences for foraging specializations than dolphins in Shark Bay. Differences may potentially be attributed to characteristics of the study areas, which might require individuals to be more flexible in their use of foraging specializations or in the types of specializations used in each area. Possibly, the use of different foraging specializations by Sarasota Bay dolphins is seasonally dependent since observations were only conducted during the summer months.

When observations from the present study were compared to observations from previous studies in Sarasota Bay (Nowacek, 1999; S. Hoffman, pers. comm., 2003; Wells, 2003), similar patterns emerged in the use of foraging specializations among mothers and calves. Three of the five focal females (FB09, F119, and F157) have independent offspring, of which two have been observed in other studies using foraging specializations. Two maternal lineages in Sarasota Bay show the exclusive use of a particular foraging specialization. The existence of this pattern suggests a maternal transmission of these behaviors. The presence of other individuals in the group while focal females and calves foraged and the lack of these group members using foraging specializations may also support the potential for maternal transfer of these behaviors. Such observations suggest against the possibility of horizontal transmission, or the spread of behaviors within a generation (Rendell & Whitehead, 2001).

Although only two focal mother-calf pairs were observed practicing foraging specializations, the observations of young dependent calves using only the preferred behaviors of their mothers provided valuable insights into the role that the mother-calf bond plays in the spread of foraging specializations within a community. Mann & Sargeant (2003) also found calves to use the preferred specializations of their mothers almost exclusively in Shark Bay, Australia. 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. A critical age for calves to learn foraging specializations is also suggested by observations of the 3-y-old calf (F137) that used her specialization more consistently than any other observed calf in this study. Although weaning occurs between the ages of 6 to 12 mo (Essapian, 1953), older calves are expected to be more adept at catching prey. Furthermore, Miles & Herzing (2003) found that a greater synchrony of feeding behavior exists between mothers with 2-y-old calves than between mothers and very young (1-y-old) calves or older (4-y-old) calves, suggesting the development of a calf foraging strategy during the time of calf dependency. Grellier et al. (2003) also suggested a decrease of association between mothers and calves after 3 y of age. Although variables such as different complexities of foraging specializations and types and sizes of targeted prey may influence this pattern, it is possible that a learning curve exists for calves to master specialized behaviors.

This study provides evidence that individual choice of foraging habitat in Sarasota Bay is associated with the preference of foraging specializations. Yet, this study did not investigate the effects of prey resources and raises questions about whether such behaviors are prey-type specific. If individuals exhibit preferences for different foraging specializations, they may be feeding on different prey. Estes et al. (2003) found that California sea otters (*Enhydra lutris*), using different foraging specializations, fed on specific types of prey. If bottlenose dolphins use different foraging specializations to target different prey, individuals may experience different caloric intakes, resulting in impacts to individual fitness and implications for reproductive success.

The present study also raises questions concerning the uncertainty of the sex-specific nature of foraging specializations and their stability over time. Mann & Sargeant (2003) suggested that females in Shark Bay may be more likely to acquire foraging specializations than males, based on the later weaning age of female calves; an increased opportunity for mothers to invest in female offspring; and observations of females, but not males, practicing their mother's foraging specializations post-weaning. There is no evidence for a sex-biased weaning age in Sarasota Bay, yet daughters spend an increased amount of time with their mothers in female bands (Wells, 1991), post-weaning, providing the mother a greater chance of investing behaviorally in her female offspring. A greater investment in female offspring behavior may indicate the importance of matrilineal passage of behavioral knowledge within a community.

The stability of the use of foraging specializations in Sarasota Bay is not known once an offspring becomes independent. The long-term study of the bottlenose dolphin community in Sarasota Bay (Wells et al., 1987; Wells, 1991) has provided information of genetic lineages, as well as support for the possibility that the individuals who learn complex foraging behaviors may continue to practice them over time. Anecdotal evidence from Sarasota Bay suggests that individuals may continue to practice specializations once independent (S. Hoffman, pers. comm., 2004), although continuation of the long-term study is necessary to confirm such trends. If a behavior is retained within 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 (Avital & Jablonka, 1994). Furthermore, the combination of foraging specialization-habitat associations and the persistence of specialized behaviors through time may indicate the continuing importance of a particular foraging habitat to an individual. Foraging behaviors have an adaptive value to an individual in terms of survival and reproduction. Therefore, the passage of foraging knowledge should take precedence over other less adaptive behaviors.

The links between habitat use and foraging specializations, as well as the suggested maternal transmission of such behaviors, indicates the need to incorporate knowledge of social behavior into the management structure for bottlenose dolphin communities. Current management approaches focus on conservation of numbers of individuals, yet the conclusions of this study place an emphasis on the importance of individual variation to the community and the need to conserve behaviors that allow adaptation to the environment.

Acknowledgments

I thank Andy Read and Randy Wells for their support and guidance in conducting this study. Ester Quintana-Rizzo and Danielle Waples gave helpful comments on earlier drafts of this manuscript. Jon Cohen provided invaluable statistical advice. The field assistance of Teresa Gisburne, Hillary Farrah, and Susan Newson was greatly appreciated and integral to this study. Ester Quintana-Rizzo, Doug Nowacek, and Kim Bassos-Hull provided insight and information about field sampling design. Sue Hoffman and Jason Allen provided valuable field training and assistance with photo-identification. Stephanie Nowacek, Kim Urian, Danielle Waples, and Valerie Chan provided assistance with GIS coverages and the use of *ArcGIS* and *ArcView* programs. This manuscript also benefited considerably from comments by two anonymous reviewers. Funding and logistical support for this study was provided by the Duke Marine Laboratory and the Sarasota Dolphin Research Program. Field research was conducted under permit #522-1569-01, issued by the National Marine Fisheries Service. This paper formed part of a thesis by J.W. submitted in partial fulfillment for the degree of

Master's of Environmental Management at Duke University, North Carolina.

Literature Cited

Allen, M. C., Read, A. J., Gaudet, J., & 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.

Avital, E., & 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., & 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.

Buckstaff, K. C. (2004). Effects of watercraft noise on the acoustic behavior of bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, Florida. *Marine Mammal Science*, *20*(4), 709-725.

Connor, R. C., Heithaus, M. R., Berggren, P., & Miksis, J. L. (2000). "Kerplunking": Surface fluke-splashes during shallow-water bottom foraging by bottlenose dolphins. *Marine Mammal Science*, *16*(3), 646-653.

Environmental Systems Research Institute. (1995). *ArcView 3.2*. (380 New York Street, Redlands, CA 92373-8100).

Essapian, F. S. (1953). The birth and growth of a porpoise. *Natural History*, *62*(9), 392-399.

Estes, J. A., Riedman, M. L., Staedler, M. M., Tinker, M. T., & 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., & Wilson, B. (1997). Bubble use during prey capture by a lone bottlenose dolphin (*Tursiops truncatus*). *Aquatic Mammals, 23*(2), 113-114.

Flamm, R. O., Ward, L. I., & White, M. (Eds.). (2002). *Atlas of marine resources* (Version 1.3). Tallahassee: Florida Fish and Wildlife Conservation Commission, Florida Marine Research Institute.

Grellier, K., Hammond, P. S., Wilson, B., Sanders-Reed, C. A., & Thompson, P. M. (2003). Use of photo-identification data to quantify mother-calf association patterns in bottlenose dolphins. *Canadian Journal of Zoology*, *81*, 1421-1427.

Gubbins, C. M. (2002). *The dolphins of Hilton Head: Their natural history.* Columbia: University of South Carolina Press.

Hastie, G. D., Wilson, B., Wilson, L. J., Parsons, K. M., & 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., & 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*(1), 222-223.

Johnston, T. D. (1982). Selective costs and benefits in the evolution of learning. *Advances in the Study of Behavior*, *12*, 65-106.

Krützen, M., Mann, J., Heithaus, M. R., Connor, R. C., Bejder, L. B., & Sherwin, W. B. (2005). Cultural transmission of tool use in bottlenose dolphins. *Proceedings of the National Academy of Sciences*, *102*(25), 8939-8943.

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., & 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., & Sargeant, B. (2003). Like mother, like calf: The ontogeny of foraging traditions in wild Indian Ocean bottlenose dolphins (*Tursiops* spp.). In D. M. Fragaszy & S. Perry (Eds.), *The biology of traditions: Models and evidence* (pp. 236-266). New York: Cambridge University Press.

Miles, J. A., & Herzing, D. L. (2003). Underwater analysis of the behavioural development of free-ranging Atlantic spotted dolphin (*Stenella frontalis*) calves (birth to 4 years of age). *Aquatic Mammals*, *29*(3), 363-377.

Nowacek, D. P. (1999). *Sound use, sequential behavior and ecology of foraging bottlenose dolphins*, Tursiops truncatus. Ph.D. thesis, Massachusetts Institute of Technology/ Woods Hole Oceanographic Institution. 196 pp.

Nowacek, D. P. (2002). Sequential foraging behaviour of bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, Florida. *Behaviour*, *139*, 1125-1145.

Partridge, L., & Green, P. (1985). Intraspecific feeding specializations and population dynamics. In R. M. Sibly & R. H. Smith (Eds.), *Behavioural ecology* (pp. 207-226). Oxford: Blackwell.

Rendell, L., & Whitehead, H. (2001). Culture in whales and dolphins. *Behavioral and Brain Sciences*, *24*(2), 309-324.

Rossbach, K. A., & 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.

Scott, M. D., Wells, R. S., & Irvine, A. B. (1990). Long-term study of bottlenose dolphins on the west coast of Florida. In S. Leatherwood & R. R. Reeves (Eds.), *The bottlenose dolphin* (pp. 235-244). San Diego: Academic Press.

Sherry, D., & Galef, B. G., Jr. (1984). Cultural transmission without imitation: Milk bottle opening by birds. *Animal Behaviour*, *32*(3), 937-938.

Smolker, R., Richards, A., Connor, R., Mann, J., & Berggren, P. (1997). Sponge carrying by dolphins (Delphinidae, *Tursiops* sp.): A foraging specialization involving tool use? *Ethology*, *103*, 454-465.

Urian, K. W., & Wells, R. S. (1996). *Bottlenose dolphin photo-identification workshop* (NOAA Technical Memorandum NMFS-SEFSC-393). Final Report to the Southeast Fisheries Science Center, National Marine Fisheries Service, Charleston Laboratories, Charleston, SC. 92 pp.

Waples, D. M. (1995). *Activity budgets of free-ranging bottlenose dolphins* (Tursiops truncatus) *in Sarasota Bay, Florida.* Master's of Science thesis, University of California at Santa Cruz. 61 pp.

Weinrich, M. T., Schilling, M. R., & 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. S. (1991). The role of long-term study in understanding the social structure of a bottlenose dolphin community. In K. Pryor & K. S. Norris (Eds.), *Dolphin societies: Discoveries and puzzles* (pp. 199-225). Berkeley: University of California Press.

Wells, R. S. (1992). The marine mammals of Sarasota Bay. In *Sarasota Bay National Estuary Program*: *1992 framework for action* (pp. 9.1-9.23). Sarasota Bay, FL: Sarasota Bay National Estuary Program.

Wells, R. S. (2003). Dolphin social complexity: Lessons from a long-term study and life history. In F. B. M. de Waal & P. L. Tyack (Eds.), *Animal social complexity: Intelligence, culture, and individualized societies* (pp. 32-56). Cambridge, MA: Harvard University Press.

Wells, R. S., Scott M. D., & Irvine, A. B. (1987). The social structure of free-ranging bottlenose dolphins. In H. H. Genoways (Ed.), *Current mammalogy, Vol. 1* (pp. 247-305). New York: Plenum Press.

Würsig, B. (1986). Delphinid foraging strategies. In R. J. Schusterman, J. A. Thomas, & F. G. Woods (Eds.), *Dolphin cognition and behavior: A comparative approach* (pp. 347-359). Hillsdale, NJ: Lawrence Erlbaum.

Würsig, B., & Würsig, M. (1977). The photographic determination of group size, composition, and stability of coastal porpoises (*Tursiops truncatus*). *Science*, *198*, 399-412.