Abstract—A description of the foraging habitat of a cetacean species is critical for conservation and effective management. We used a fine-scale microhabitat approach to examine patterns in bottlenose dolphin (*Tursiops truncatus*) foraging distribution in relation to dissolved oxygen, turbidity, salinity, water depth, water temperature, and distance from shore measurements in a highly turbid estuary on the northern Gulf of Mexico. In general, environmental variation in the Barataria Basin marine environment comprises three primary axes of variability (i.e., factors: temperature and dissolved oxygen, salinity and turbidity, and distance and depth) that represent seasonal, spatial-seasonal, and spatial scales, respectively. Foraging sites were differentiated from nonforaging sites by significant differences among group size, temperature, turbidity, and season. Habitat selection analysis on individual variables indicated that foraging was more frequently observed in waters 4–6 m deep, 200–500 m from shore, and at salinity values of around 20 psu. This fine-scale and multivariate approach represents a useful method of exploring the complexity, gradation, and detail of the relationships between environmental variables and the foraging distribution patterns of bottlenose dolphin.

Environmental characterization of seasonal trends and foraging habitat of bottlenose dolphins (*Tursiops truncatus*) in northern Gulf of Mexico bays

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Identifying bottlenose dolphin (*Tursiops truncatus*) foraging habitat is critical for effective species conservation. However, simply describing foraging habitat as a geographic location or habitat type may be inadequate and incomplete given the heterogenous and variable nature of marine environments (Miller and Cribb, 2009). Therefore, measuring and quantifying the environmental variables that characterize bottlenose dolphin foraging habitat provides a more powerful and flexible tool for implementing management strategies.

For the well-studied bottlenose dolphin (*Tursiops* spp.), investigations into foraging habitat have been undertaken with a range of approaches in a wide variety of locations. In some instances, general habitat type and oceanographic features have been related to congregations of bottlenose dolphin prey by observations of increased rates of feeding, notably in estuarine areas (Ballance, 1992) and at interfaces between open ocean and protected estuaries, seagrass beds, and mangrove shorelines (Grigg and Markowitz, 1997; Harzen, 1998). Gregory and Rowden (2001) have observed feeding activity in association with tidal movement. Hastie et al. (2004) correlated surface feeding behavior with submarine habitat characteristics, and Bailey and Thompson (2006) used modeling techniques to further quantify and investigate these

relationships. Others have investigated the frequency of feeding behavior in relation to group size (Shane et al., 1986; Gregory and Rowden, 2001) and Campbell et al. (2002) suggested that larger groups are more effective and efficient in searching for food by using cooperative feeding tactics. Numerous other studies have noted similar relationships between seasonal environmental patterns and the frequency of bottlenose dolphin sightings (Wilson et al., 1997; Stockin et al., 2006), but environmental variables relating to this seasonality have not always been quantified.

The objective of our research was to investigate the differences in environmental habitat between foraging and nonforaging locations of bottlenose dolphins within an inshore bay of the Northern Gulf of Mexico (Waring et al., 2007). In addition, the marine environment of the study site was characterized on a seasonal basis. The fine-scale approach we employed measured a suite of environmental variables and allowed us to discern more spatially explicit patterns of habitat use by bottlenose dolphins.

Methods

Study area

This study was conducted in Barataria Basin, an estuary along the northern

Gulf of Mexico on the Louisiana coast directly west of the Mississippi River. The region is both humid and subtropical and is dominated by saltmarsh vegetation (Day et al., 1989). Barataria and Caminada bays lie in the lower saline portion of Barataria Basin,; they are turbid bays of less than 2 m in depth (on average), have limited tidal amplitude (less than 0.32 m), and are separated from the Gulf of Mexico by a series of barrier islands (Baltz et al., 1993).

Survey method

Monthly surveys were initiated in Barataria Basin in June 1999 and continued until May 2002. Two or more independent observers used a small 3.5-m (17-ft) motorboat to survey six designated strata in random order and sequence (Miller, 2003). When a bottlenose dolphin group was sighted, standard photo-identification techniques were used to document individuals (Würsig and Würsig, 1977). Microhabitat data were also collected. More specifically, an onboard Hydrolab (Environmental Data Systems, model CR2-SU, Austin, TX) was used to record sea-surface temperature (°C), salinity (psu), and dissolved oxygen (mg/L). Furthermore, a weighted line measured shallow depths (m), and nautical charts and mapping software were used for deeper water measurements and to determine distance to the nearest shore (m). Lastly, water samples were collected for laboratory assessment of turbidity (nephelometric turbidity units [NTU]) using a Hach 2100N Turbidimeter (Loveland, CO). Bottlenose dolphin group size and composition were recorded, as well as the presence of juveniles and calves (Miller, 2003). Behaviors were categorized as foraging, social, rest, and travel behaviors (Allen and Read, 2000). However, for this article only foraging activity defined by one or more of the following behaviors was used: fish in mouth, numerous steep dives in rapid succession, quick circling behavior at the water surface, or direct pursuit of a prey item (Allen et al., 2001). All sightings were made during daylight hours in Beaufort Sea state conditions of 3 or less.

Statistical methods

Environmental variables were assessed for univariate and bivariate normality and when necessary were transformed to meet normality requirements. Seasonal (Fall: September–November, Winter: December–February, Spring: March–May, and Summer: June–August) differences among dissolved oxygen, turbidity, salinity, water depth, water temperature, and distance from shore were assessed by using a multivariate analysis of variance (MANOVA) approach and pair-wise comparisons. Least-square means with Tukey's adjustment were performed on variables and produced a significant Shapiro-Wilks result.

A factor analysis (FA) of dissolved oxygen, turbidity, salinity, water depth, water temperature, and distance from shore was employed to examine the pattern of habitat use by bottlenose dolphins and also to highlight relationships among individual variables. The number of orthogonal components retained for interpretation was chosen after examining the scree plot for Eigen values >1, and interpretation was aided by a varimax rotation.

A logistic regression and habitat suitability curves (Saucier and Baltz, 1993) were used to investigate whether particular environmental variables were useful in describing foraging activity. The forward stepwise logistic regression with maximum likelihood estimation (with a Wald chi-square statistic) was used to select variables that were most strongly related to the observed activity. Variables investigated in this analysis were dissolved oxygen, turbidity, salinity, water depth, water temperature, distance from shore, time of day, season, and the minimum number of individuals present in a group. Variable multicollinearity was checked before the analysis by using variance inflation factor (VIF) values and the final model was evaluated by a Hosmer and Lemeshow test. Least-square means (with associated standard errors) of foraging and nonforaging observations were computed for all significant variables. To describe seasonal foraging activity, seasons in which the highest proportion of foraging and nonforaging observations took place were used for modeling.

Habitat suitability curves (Baltz et al., 1993) were constructed to characterize the patterns of dissolved oxygen, turbidity, salinity, water depth, water temperature, distance from shore, and group size at sites where foraging was observed. For this approach, we considered the proportional frequency of foraging and nonforaging activity at defined intervals for each environmental variable along its range. Specifically, a foraging habitat suitability value was calculated by dividing the probability of observing foraging in each interval by the total number of observations in each. Habitat suitability values were normalized to a scale of 0 (nonforaging) to 1 (high probability of foraging) by dividing each habitat suitability interval value by the highest habitat suitability interval value of each environmental variable.

Results

Number of survey days and frequency of bottlenose dolphin groups sighted were relatively even across seasons as was the proportion of observations during which foraging activity was observed. Nevertheless there was some variability in the number of individuals seen throughout the year (Table 1). Variability in the environmental characteristics of the study area was also evident. Significant seasonal differences in dissolved oxygen, turbidity, salinity, and water temperature were detected by a MANOVA. Posterior pair-wise comparisons were used on significant variables (Table 2). Water temperatures were significantly different across all four seasons and, as expected, were lowest in winter and highest in summer. Minimum observed dissolved oxygen levels were found

Table 1

Seasonal frequency of number of sightings, number of individuals seen (based on minimum group size), and number of sightings during which foraging behavior was observed for bottlenose dolphins (*Tursiops truncatus*) in northern Gulf of Mexico bays from June 1999 until May 2002.

	Winter	Spring	Summer	Fall	Total
Number of observations	68	60	71	70	269
Minimum number of individuals	327	422	595	550	1894
Number of foraging observations	18	24	21	25	88

Table 2

Overall and seasonal means for environmental conditions used by bottlenose dolphins (*Tursiops truncatus*) in the Barataria Bay study area measured from June 1999 to May 2002. Significant seasonal differences ($P<0.025$) in least-square means (±1 standard error [SE]) are indicated by different superscripted letters reading across each row.

Variable	Winter	Spring	Summer	Fall	Overall mean
Temperature (°C)	13.96 ±0.45[a]	23.00 ±0.47[b]	30.12 ±0.44[c]	25.99 ±0.44[d]	23.37 ±0.43
Dissolved oxygen (mg/L)	11.58 ±0.28[a]	9.07 ±0.27[b]	6.99 ±0.30[c]	7.90 ±0.29[c]	8.98 ±0.19
Salinity (psu)	24.15 ±0.51[a]	21.99 ±0.54[b]	20.84 ±0.50[b]	24.06 ±0.50[a]	22.77 ±0.27
Turbidity (NTU)	14.15 ±0.87[a]	13.50 ±0.92[a]	11.19 ±0.85[ab]	9.76 ±0.85[b]	12.08 ±0.45
Distance from shore (m)	69.04 ±12.78	111.42 ±13.61	91.73 ±12.51	70.14 ±12.60	84.77 ±6.47
Depth (m)	2.82 ±0.23	2.54 ±0.25	2.33 ±0.23	2.72 ±0.23	2.60 ±0.12

in summer and fall and increased significantly in spring and again in winter. Mean salinity values fell into two general groupings; fall-winter salinities were higher than those for summer-spring. Turbidity levels were less distinct seasonally. Although the highest turbidity levels seen in winter and spring were significantly different from those seen in fall, levels seen in summer were not significantly different from either. The MANOVA did not reveal any seasonal differences in distance from shore or water depth.

Spatial and seasonal environmental variation in the study area was considerable, and many of the variables were strongly correlated. The FA included all survey observations and resolved the six environmental variables into three orthogonal factors that explained 71% of the variation in the data (Table 3). Each of the six environmental variables loaded heavily on at least one factor. Factor 1 accounted for 30% of the variation and loaded heavily on temperature and dissolved oxygen. The signs of these loadings were opposite and represented an inverse seasonal relationship. Factors 2 and 3 each accounted for an approximate additional 20% of the variation. Factor 2 loaded strongly and positively on both salinity and turbidity and did not reflect the negative relationship expected over larger salinity gradients. Strong positive loadings for the two spatial variables of distance from shore and depth were evident

Table 3

Rotated factor loadings of environmental variables measured at observation sites of bottlenose dolphins (*Tursiops truncatus*) in lower Barataria and Caminada bays, Louisiana, from June 1999 until May 2002. Magnitude and signs of factor loadings indicate strength and direction of the influence of each variable on a factor. Figures in bold indicate the most important variable for the given factor. The variances explained by the Eigen value for each factor are expressed as absolute, proportional, and cumulative values.

	Factors		
Environmental variable	1	2	3
Temperature (°C)	**−0.88**	−0.36	−0.01
Dissolved oxygen (mg/L)	**0.94**	−0.16	−0.04
Salinity (psu)	0.02	**0.82**	0.16
Turbidity (NTU)	0.06	**0.67**	−0.19
Distance from shore (m)	−0.23	−0.05	**0.70**
Depth (m)	0.21	0.01	**0.81**
Variance explained	1.85	1.20	1.18
Proportion	0.31	0.20	0.20
Cumulative proportion	0.31	0.51	0.71

Table 4

A forward stepwise logistic regression characterizing variables important in describing bottlenose dolphin (*Tursiops truncatus*) foraging sites in Barataria Basin, Louisiana, during from June 1999 to May 2002. Individual variables were entered and kept in the model with an α-level of 0.20. Variables are listed below from highest to lowest Wald χ^2 statistic. Order of variable entry into the model is also indicated. Foraging and nonforaging least-square means (±1 standard error [SE]) were calculated for significant continuous variables, and highest and lowest proportions of foraging activity were given for season.

Order	Effect	Wald χ^2	Pr > χ^2	Foraging (Mean ±1 SE)	Nonforaging (Mean ±1 SE)
3	Temperature	6.78	<0.01	24.28 ±0.75	22.82 ±0.54
1	Minimum group size	5.54	0.02	9.27 ±0.72	5.92 ±0.52
2	Turbidity	4.79	0.03	13.22 ±0.78	11.65 ±0.56
4	Season	2.30	0.13	Spring (39.3%)	Winter (73.5%)

in factor 3. Distance from shore was greatest in open waters areas north of barrier islands where wetland areas were more sparsely distributed and also in some of the channels and passes opening into the Gulf of Mexico. These channels and passes were also typically the deepest parts of the study area.

Minimum group size followed by turbidity, temperature, and season were found to be the most important variables describing foraging sites according to a forward stepwise logistic regression (Table 4). The selected model was a reasonable fit (Hosmer and Lemeshow criterion, $\chi^2_8 = 5.79$, $P = 0.67$). Minimum group size, turbidity and temperature were all higher during foraging observations, and the incidence of foraging was highest in spring (39.3%) and lowest in winter (26.5%). Overall, foraging behavior was observed during 88 of the 269 sightings.

Specific ranges and levels of turbidity, water depth, water temperature, distance from shore, and minimum group size were found to have higher probabilities of foraging activity according to habitat suitability curves. Foraging suitability was calculated to be greatest between temperatures of 20° and 24°C (Fig. 1). Foraging was more commonly observed when dissolved oxygen content was around 6 mg/L and declined as values increased (Fig. 1). Foraging was also more often observed in salinity values around 20 psu, turbidity values between 20 and 28 NTU, distances between 200 and 500 m from shore, and water depths between 4 and 6 m (Figs. 1 and 2). A positive relationship between increased number of foraging observations and minimum group size was also evident (Fig. 2).
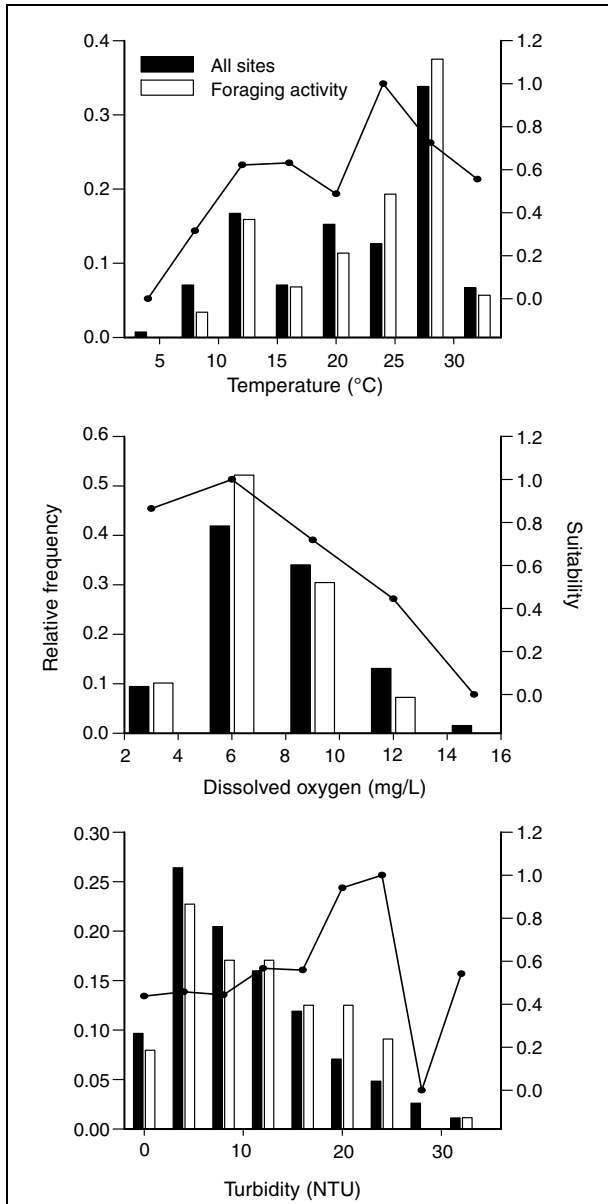
Discussion

Variables related to foraging

Our research into bottlenose dolphin foraging habitat in the northern Gulf of Mexico revealed that water temperature may be a more informative indicator of distribution and foraging activity than season. This asser-
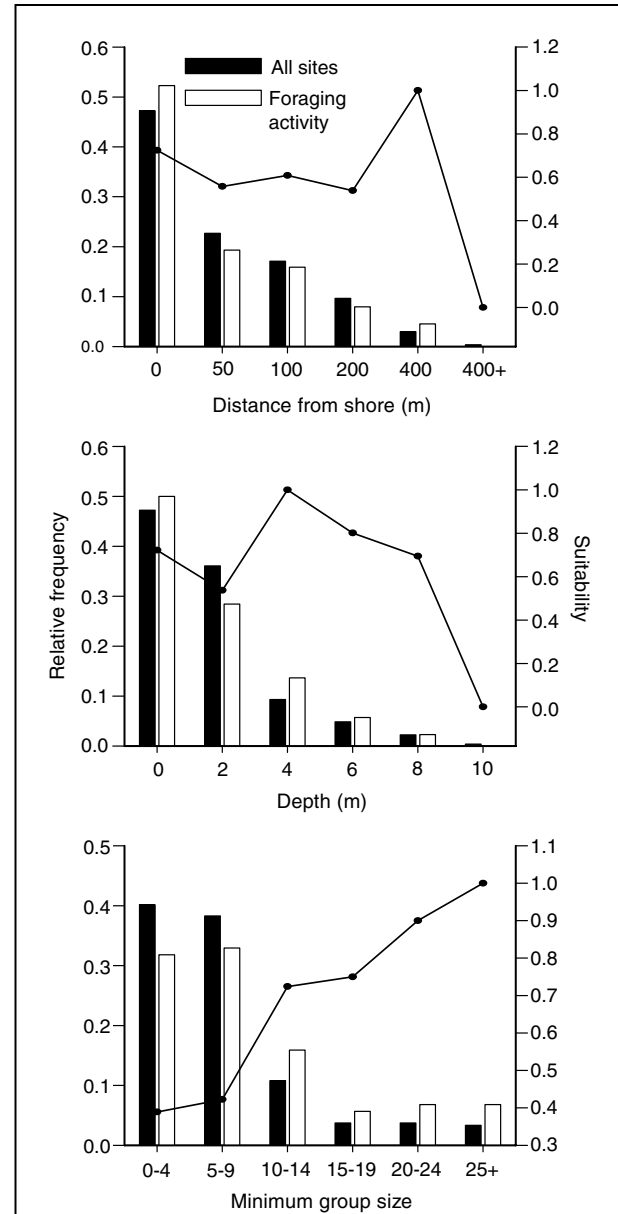
tion is consistent with documented correlations between water temperature fluctuations (associated with La Niña events) and short-beaked common dolphin (*Delphinus delphis*) distribution (Neumann, 2001) and distributional range limits for some Delphinidae species determined by water temperature (Gaskin, 1968). Furthermore, Tershy et al. (1990) found seasonal patterns that correlated with the presence of fin (*Balaenoptera physalus*) and Bryde's (*Balaenoptera edeni*) whales within the Gulf of California and that were negatively correlated with increasing water temperature.

However, the importance of other variables (i.e., dissolved oxygen, turbidity, and salinity) is noteworthy. These variables also showed significant seasonal differences (Table 2). Salinity and temperature are known to be major determinants of coastal and estuarine community structure, in part because of salt tolerances and adaptations of associated flora and fauna (Day et al., 1989). Estuaries are often considered nurseries for juvenile fish and invertebrate species and it is likely that increased prey densities are related to the noted associations between cetaceans and estuarine areas (Ballance, 1992; Grigg and Markowitz, 1997; Harzen, 1998). Selzer and Payne (1988) also documented a seasonal correlation between sea surface temperatures and salinities with Atlantic white-sided (*Lagenorhynchus acutus*) and short-beaked common dolphin (*Delphinus delphis*) distributions and hypothesized that the interactions of salinity and temperature with sea floor topography and associated upwelling may be related to prey aggregations. Studies documenting turbidity and dissolved oxygen have been less common. Brager et al. (2003) assessed Hector's dolphin (*Cephalorhynchus hectori*) habitat in relation to sea surface temperature, water depth, and water clarity and, although relationships varied by region and season, they found significant relationships between all three variables, for both individual variables and variables in combination. We also demonstrated that proportionally more foraging occurred in turbid waters, possibly indicating that higher levels of suspended sediments allow bottlenose dolphins to forage more effectively on prey that rely on visual

Figure 1

Foraging suitability curves for bottlenose dolphins (*Tursiops truncatus*) observed in northern Gulf of Mexico bays from June 1999 to May 2002 for temperature, dissolved oxygen, and turbidity (in nephelometric turbidity units [NTU]). Vertical bars indicate frequency of overall observations (black) and foraging activity (white) for each given interval. Black lines indicate the relative suitability of variable values for foraging activity.

Figure 2

Foraging suitability curves for bottlenose dolphins (*Tursiops truncatus*) observed in northern Gulf of Mexico bays from June 1999 to May 2002 for distance to shore, depth, and minimum group size. Vertical bars indicate frequency of overall observations (black) and foraging activity (white) for each given interval. Black lines indicate the relative suitability of variable values for foraging activity.

detection of predators. However, it should be noted that on an overall basis most of the foraging occurred in less turbid waters.

It is logical that the movement and distribution of prey are important features for characterizing dolphin foraging habitat. Larger group sizes were identified as an important factor in differentiating sightings based on foraging activity (Table 4, Fig. 2). Nevertheless, it is difficult to know whether increased group sizes are formed in response to favorable environmental conditions for prey congregation or whether individuals gather together as part of a strategy to increase

foraging success and efficiency. Group sizes of pan-tropical spotted (*Stenella attenuata*), spinner (*Stenella longirostris*), and short-beaked common dolphins in the eastern Pacific Ocean have been observed to mirror the diurnal group-size fluctuations of yellowfin tuna (*Thunnus albacares*), one of their common prey (Scott and Cattanach, 1998). Cockroft and Peddemors (1990) noted the synchrony of pilchard (*Sardinops ocellatus*) movements with the migration of common dolphins during winter months up the eastern coast of South Africa. Both Corkeron (1990) and Grigg and Markowitz (1997) identified food patchiness and interspecific interactions as important influences on Tursiops spp. group size.

Applications of a microhabitat approach

The ability to describe cetacean habitat hinges on the capacity to measure the suite of important and appropriate environmental variables at the correct scale for which they exert influence (Ingram and Rogan, 2002; Redfern et al., 2006). This task is not trivial and noted issues with describing and researching cetacean habitat include the following: it is often unknown which variables (and how many) are the most pertinent to study; it is difficult to obtain measurements for some variables (even when they might be considered important); the scale at which the variable may influence cetacean distribution may be masked or uncertain; and the relationship between cetacean distribution and the given environmental variable may be correlated with and confounded by additional variables or factors. Our investigations into dolphin foraging habitat addressed some of these difficulties. Specifically, foraging habitat was measured on the same scale and with variables similar to those that have been used for habitat characterization studies of potential prey items in the same study area (Baltz et al., 1993; Baltz et al., 1998). Such a basis created a strong premise for asserting that foraging habitat could be characterized in the same manner. In addition, the collection of a suite of variables was instructive for investigating variables that might be synergistic or correlated.

A description of the characteristics of cetacean foraging habitat is also contingent on accurately assessing and identifying feeding behavior and possibly accounting for variations in feeding strategies, both of which are particularly pertinent for bottlenose dolphins given that they are both flexible and opportunistic in their feeding activity (Shane et al., 1986). Observations of feeding in association with shrimp boats have been documented in Texas waters (Brager, 1993) and feeding on mudbanks by partial beaching has been observed in some salt-marsh areas (Hoese, 1971). In Shark Bay, Western Australia, a number of individuals have been observed carrying sponges on their rostra in what is hypothesized to be a foraging aid (Smolker et al., 1997). Furthermore, in different habitats bottlenose dolphins have been observed to forage on different prey items (Gannon and Waples, 2004), while individuals of some cetacean species have been documented using distinctive foraging patterns while in close proximity to one another (Hoelzel et al., 1989). These considerations emphasize the need to understand the complexity of foraging behavior for a given species and may also support the need to analyze different foraging techniques separately.

Our findings provide a useful approach to identifying variables that are important in describing bottlenose dolphin foraging habitat; however, other unquantified variables such as boat activity (Lusseau, 2005), presence of competitors and predators such as sharks (Heithaus and Dill, 2006), El Niño events (Bearzi, 2005), seabed gradients (Ingram and Rogan, 2002), and weather and climate front patterns (Mendes et al., 2002) may have confounded these observations.

Conclusions

Long-term site fidelity and residency of many bottlenose dolphin populations indicate that individual populations likely have unique relationships with the given bay, estuary, or coastline that they inhabit. Characterizing foraging habitat for the bottlenose dolphin population in Barataria Basin is therefore a useful exercise because this small population (Miller, 2003) is presently managed as a distinct estuarine stock within the northern Gulf of Mexico (Waring et al., 2007).

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