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Abundance trends and environmental habitat usage patterns of bottlenose dolphins (Tursiops truncatus) in lower Barataria and Caminada Bays, Louisiana

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ABUNDANCE TRENDS AND ENVIRONMENTAL HABITAT USAGE PATTERNS OF BOTTLENOSE DOLPHINS (*Tursiops truncatus*) IN LOWER BARATARIA AND CAMINADA BAYS, LOUISIANA

A Dissertation

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by
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ABSTRACT

The paucity of research into the environmental requirements, stock membership, abundance and residency patterns of bottlenose dolphins (*Tursiops truncatus*) in coastal Louisiana creates difficulty in understanding how local ecosystems and threats (such as fishery interactions, habitat degradation and pollution) affect populations. This study combined fine-scale environmental measurements and photo-identification techniques to describe patterns of habitat usage and abundance of bottlenose dolphins in lower Barataria Basin from June 1999 to May 2002. In addition I investigated the validity and limitations of using mark-recapture models to estimate abundance from cetacean photo-identification data.

Bottlenose dolphins were present year-round in a wide range of water temperature (10.9 – 33.9 ºC), dissolved oxygen levels (3.7 – 16.6 mg/L), salinities (11.7 – 31.5 psu), turbidity levels (1.4 – 34.0 NTU), distances from shore (3 – 800 m), and water depths (0.4 - 12.5 m). However, feeding activity was concentrated in a narrower range of conditions, 20 – 24 ºC water temperature, 6 – 9 mg/L of dissolved oxygen, turbidity values between 20 – 28 NTU, 200 – 500 m from shore, and depths of 4 – 6 m. Spatial mapping showed differences in the seasonal distribution of individuals and a tendency for feeding activity and larger group sizes to be concentrated in passes. Using distinctive natural markings present on dorsal fins, I identified 133 individual dolphins. Closed-population models were improved by inclusion of temporal and individual heterogeneity as sources of sighting variability and produced estimates of between 138 and 238 (95% CL range = 128 – 297) bottlenose dolphins for the study area. Analysis of Jolly-Seber model assumptions demonstrated the importance of ensuring cetacean surveys accurately represent temporal, geographic and demographic properties of a study population. In addition such factors as non-preferential image acquisition, group size, gender, behavior,

stability and distinctiveness of natural markings, weather conditions and boat traffic must be considered. Evidence of a relatively closed Barataria Basin population agrees with current assumptions that bay bottlenose dolphin stocks are distinct from those found in deeper, offshore waters. Furthermore, the characterization of environmental usage patterns for this bay population strengthens adequate description and management of this relatively discrete Gulf of Mexico bottlenose dolphin stock.

CHAPTER I

INTRODUCTION: ASSESSING ABUNDANCE AND ENVIRONMENTAL HABITAT USAGE PATTERNS OF BOTTLENOSE DOLPHINS IN COASTAL LOUISIANA

The Order Cetacea includes all species of whales, dolphins and porpoises. Members of this order display a wide variety of distributional ranges, social structures, foraging styles and life-history strategies (Reeves et al. 2002). The bottlenose dolphin (*Tursiops truncatus*) is one of the most commonly studied cetacean's worldwide (Leatherwood and Reeves 1990). Bottlenose dolphins inhabit both coastal and offshore waters within tropical to temperate latitudes, as evidenced by research studies conducted in such locations as Scotland (Wilson et al. 1999), the Gulf of Mexico (Shane 1980, Wells and Scott 1990), Mexico (Ballance 1992), Portugal (Harzen 1998), Belize (Grigg and Markowitz 1997), Australia (Connor and Smolker 1985), New Zealand (Williams et al. 1993), South Africa (Cockroft et al. 1990), and Argentina (Wursig and Wursig 1977). The variability in observed behavior and demographic parameters for these studies indicates the flexibility and adaptability of bottlenose dolphins in different marine environments. Individual bottlenose dolphins have relatively robust bodies with a medium sized beak and moderately tall, falcate dorsal fins (Reeves et al. 2002). Males attain a slightly larger size than females. Body color may be any tone of gray, with darker colors occurring dorsally while the belly is typically off-white or pinkish in color. Calves are usually born during the warmer months and remain associated with their mother for at least 18 months, though more commonly about three years. Group sizes may vary anywhere from 2-15 in inshore areas, up to more than 100 individuals in offshore schools. Threats to bottlenose dolphins include sharks, habitat degradation, fishery interactions and pollution. Depressed immune systems believed to be a result of viral infections have been linked to major die-offs along the U.S. Atlantic and Gulf of Mexico coasts (Reeves et al. 2002).

The paucity of research into bottlenose dolphin populations in coastal Louisiana creates doubt as to present-day population size, habitat requirements, and spatial and temporal movement patterns within the region. This dissertation focuses on characterizing abundance trends and environmental habitat usage patterns of bottlenose dolphins in a Louisiana coastal bay system. These objectives were achieved by conducting monthly habitat utilization and photo-identification surveys in lower Barataria and Caminada bays (Chapter II and IV). In addition I critically reviewed the assumptions and validity of the Jolly-Seber (J-S) model as it is commonly used to estimate population size from cetacean photo-identification data (Chapter III).

The Gulf of Mexico covers approximately 1,500,000 km^2 with an average depth of 1,700 m (Gore 1992). The principal oceanographic features for the northern Gulf of Mexico (nGOM) region include wind stress, the Loop Current, and discharge from the Mississippi and Atchafalaya rivers. The most distinctive circulation feature in the nGOM is the Loop Current (Gore 1992). Warm waters from the Caribbean enter the gulf through the Yucatan Channel and continue north along the west coast of Florida. These waters then turn clockwise and head south until eventually exiting through the Straits of Florida. On an annual to semi-annual basis eddies separate from the Loop Current and move west. These warm-core eddies rotate clockwise as they transverse the Gulf waters in anywhere from a few months to a year when they reach the shallower depths of the continental shelf and disintegrate. The Louisiana coast has undergone significant changes in the last half century due to factors such as continued leveeing of the Mississippi and Atchafalaya rivers, eustatic sea level rise (Day et al. 1995), canal dredging (Turner 1997), and both natural and anthropogenic subsidence. In fact, coastal wetland losses from 1955 to 1978 are estimated to be as high as 12,700 ha per annum (Baumann and Turner 1990). The low-lying inland wetlands include marsh grasses, submerged aquatic vegetation and estuarine ponds (Chesney et al. 2000). These estuarine areas are known to provide important habitat to juvenile fishes and crustaceans (Baltz et al. 1998) and have high primary productivity rates (Day et al. 1989, Garrison 1999). Repercussions of wetland loss and ecosystem alterations on coastal Louisiana marine mammal populations are unknown.

A variety of cetaceans have been observed in offshore regions of the Gulf of Mexico (Waring et al. 2002). Whales in deep Gulf of Mexico waters (greater than 200 m) include sperm (*Physeter macrocephalus*), Bryde's (*Balaenopotera edeni*), Cuvier's beaked (*Ziphius cavirostris*), Blaineville's beaked (*Mesopolodon densirostris*), Gervais' beaked (*Mesoplodon europaeus*), dwarf and pygmy sperm (*Kogia sima* and *Kogia breviceps*), melon-headed (*Peponocephala electra*) and short-finned pilot (*Globicephala macrorhynchus*). Oceanic dolphins in these same deep waters include Atlantic spotted (*Stenella frontalis*), bottlenose (*Tursiops truncatus*), pantropical spotted (*Stenella attenuata*), striped (*Stenella coeruleoabla*), spinner (*Stenella longirostris*), rough-toothed (*Steno bredanensis*), clymene (*Stenella clymene*), frasier's (*Lagenodelphis hosei*), and risso's (*Grampius griseus*). Included in this same category are the killer whale (*Orcinus orca*), as well as the false (*Pseudorca crassidens*) and pygmy (*Feresa attenuata*) killer whale species.

Bottlenose and Atlantic spotted dolphins are the only cetaceans that have been reported for inshore (depths less than 20 m) regions of the Gulf of Mexico. Inshore and offshore bottlenose dolphin populations in the Gulf of Mexico waters are believed to be distinctive (Waring et al. 2002). This assertion is based on the detection of hematological differences between coastal and offshore *Tursiops* individuals (Duffield et al. 1983, Duffield and Wells 1986) and the assumption that movement between relatively dissimilar marine ecosystems is limited. The 2002 U. S. Atlantic and Gulf of Mexico marine mammal stock assessments

(Waring et al. 2002) recognize inshore bottlenose dolphin stocks in the outer continental shelf, coastal regions (west, north and east), as well as numerous bays, sounds and estuaries. Population estimates are available for only three of the six inshore estuarine bottlenose dolphin stocks in Louisiana waters (Waring et al. 2002), i.e., Bay Boudreau/Mississippi Sound region (n = 1401), Terrebonne/Timbalier Bay complex (n = 100), and Barataria Bay (n = 219). These estimates were based on aerial line-transect data collected in September and October of 1993 (Blaylock and Hoggard 1994). Other research into the coastal bottlenose dolphin populations of Louisiana has been infrequent and irregular.

Habitat usage patterns (Chapter II) were examined using a fine-scale microhabitat approach (Saucier and Baltz 1993, Baltz et al. 1998). A microhabitat is a three-dimensional description of physical and chemical parameters at a point in space-time where a particular organism exists. Obviously these attributes are transitory, yet compilation of a large number of intensive microhabitat observations allows the environmental fluctuation, range and selection of a focal species to be characterized. This approach has been used to define spawning site selection (Saucier and Baltz 1993) as well as growth and recruitment factors (Baltz et al. 1998) for coastal Louisiana fishes. For my study, environmental variables used to characterize patterns of bottlenose dolphin habitat utilization were water temperature, dissolved oxygen, salinity, turbidity, distance to shore and water depth. Additionally, temporal variables including time of day, month, season and year were considered. Bottlenose dolphins were observed in Barataria Basin every month throughout the duration of the study despite significant seasonal variation in temperature, dissolved oxygen, salinity and turbidity. Variability in overall distribution of dolphin sighting locations were examined using a principal components analysis. Patterns of variability could be primarily attributed to season (i.e., negative correlation of temperature and dissolved oxygen), space-time (evident via a positive relationship between salinity and turbidity values) and a three-dimensional spatial component (evident with a connection between depth and distance to shore). Important factors in feeding sites were investigated using a logistic regression analysis. Minimum group size, temperature, turbidity and season were all determined to be significant in describing feeding versus non-feeding locations. In a related suitability analysis, specific ranges of all environmental variables were examined with regard to feeding. When overall spatial distribution was examined it was apparent that areas around Caminada Pass showed proportionately higher foraging activity. Seasonal and minimum group size distribution patterns were not tested due to variable weather conditions.

An important approach to mark-recapture methods in wildlife research is the Jolly-Seber open-population model (Jolly 1965, Seber 1965, Seber 1982). There have been embellishments and additions to the original model; however, the specific ideas and concepts presented have proven to be long lasting and valuable to the field of population estimation theory. I examined the validity of the five Jolly-Seber assumptions with regard to cetacean photo-identification data (Chapter III). The most obvious and recurrent factor was the premise that all samples and surveys are a representative subset of the entire population. Additional requirements include being aware of the temporal and geographic range of the species and adhering to randomness stipulations. Larger scale random survey design also needs to be complemented by smaller scale survey considerations. For example, image acquisition should be non-preferential, and factors that may alter an individual's probability of detection (i.e., group size, behavior or social status) must be taken into account. Natural markings used for individual identification should be reliable and recognizable. Finally, population parameter estimates need to be correctly associated with an appropriate date or time period so that the population can be accurately defined.

For bottlenose dolphins nicks and notches evident on the dorsal fin are suitable markings for photo-identification (Wursig and Wursig 1977) and were used in this study of Barataria Basin bottlenose dolphins (Chapter IV) to identify and document the behavior and movements of individual animals. The study population appeared to be relatively closed based on a discovery curve that approached zero (Williams et al. 1993). This curve suggested that only a few previously unsighted marked individuals were being captured as survey effort increased. Individual sighting histories were then used to estimate population size with Otis et al. (1978) closed-population unequal-catchability models. The probability of sighting a given individual varied on both a temporal scale as well as by individual. Population estimates for variously configured models produced fairly similar population estimates (138 - 238) with an associated 95% confidence limit range of 128 - 297.

Analysis of any population needs to incorporate the specific context of the individual under study. In marine mammal studies the context refers to the environment and ecosystem that the individual or group inhabits (Chapter II). The limitations and requirements for any statistical analysis need to be correctly understood to allow appropriate inferences to be made. Examination of the Jolly-Seber model with regard to cetacean photo-identification data gave an objective and thorough analysis of mark-recapture assumptions for a common marine mammal research strategy (Chapter III). Analysis of individual sighting histories with respect to sources of variability and knowledge of field methodology allowed the estimation of both defensible and biologically realistic population estimates for bottlenose dolphins present in the Barataria Basin (Chapter IV). Considering environmental variables that directly effect observed patterns of distribution and behavior can only enhance understanding of cetacean populations. In addition, ensuring that analyses are objective and relevant gives greater credibility and importance to associated findings.

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CHAPTER II

ENVIRONMENTAL HABITAT USAGE PATTERNS OF BOTTLENOSE DOLPHINS, *Tursiops truncatus*, IN LOWER BARATARIA AND CAMINADA BAYS, LOUISIANA

INTRODUCTION

The heterogeneous oceanic environment makes the characterization of habitat for any marine mammal species a challenging task. Marine mammals are highly mobile, often variable in their spatial and temporal distribution patterns, and interact with their immediate physical, chemical and biotic environment in ways that are difficult to directly observe and quantify. It is unclear at what resolution temporal and spatial oceanic attributes need to be examined to determine their relationship to marine mammal distribution patterns. However, definition and understanding of how cetaceans interact with and rely on their immediate environments allows the possibility for insightful and informed conservation and management of individual populations and species.

The Louisiana coastal environment has undergone significant changes in the last half century due to factors such as continued leveeing of the Mississippi and Atchafalaya rivers, eustatic sea level rise (Day et al. 1995), canal dredging (Turner 1997), and both natural and anthropogenic subsidence. Coastal wetland losses from 1955 to 1978 are estimated to be as high as 12,700 ha per annum (Baumann and Turner 1990). Estuarine areas are known to provide important habitat to juvenile fishes and crustaceans (Baltz et al. 1998) and have high primary productivity rates (Day et al. 1989, Garrison 1999). Repercussions of wetland loss and ecosystem alterations on coastal Louisiana bottlenose dolphin (*Tursiops truncatus*) populations are unknown. Inshore and offshore bottlenose dolphin populations in Louisiana waters are believed to be distinctive stocks (Waring et al. 2002). This assertion is based on the detection of hematological differences between coastal and offshore *Tursiops* individuals (Duffield et al.

1983, Duffield and Wells 1986), and the assumption that movement between relatively dissimilar marine ecosystems is limited. Six inshore coastal bottlenose dolphin stocks are recognized in Louisiana waters (Waring et al. 2002). However, population estimates from almost a decade ago (Blaylock and Hoggard 1994) were reported only for the Bay Boudreau/Mississippi Sound region (n = 1401), Terrebonne/Timbalier Bay complex (n = 100), and Barataria Bay (n = 219). Other research into the coastal bottlenose dolphin populations in Louisiana has been infrequent and irregular. The paucity of recent research leaves doubt as to how well these dated abundance trends and distributional limits relate to the present day population size, habitat requirements, and spatial and temporal movement patterns within the region.

Environmental conditions at spawning and nursery sites of coastal Louisiana fish species have been investigated using a fine-scale microhabitat approach (Saucier and Baltz 1993, Baltz et al. 1998). A microhabitat is a three-dimensional description of physical and chemical conditions at an occupied site. Obviously these attributes are transitory, yet collection of a large number of intensive microhabitat observations allows the environmental fluctuation, range and selection of the focal species to be characterized. From this point it is possible to initiate how an ecosystem's qualities connect and interact with the record of activities and abundance trends of a population.

The objective of this study was to investigate whether the distribution patterns, behavior or observed group sizes of bottlenose dolphins present in a coastal Louisiana bay system could be characterized by a suite of selected fine-scale environmental and temporal variables including temperature, dissolved oxygen, salinity, turbidity, distance from shore, depth, hour of the day, month, and year.

METHODS

Site Description

Barataria and Caminada bays represent the seaward interface of the Barataria Basin with the Gulf of Mexico (Figure 2.1). Approximately 145,000 ha of salt marsh are contained within the roughly 110 km long and 50 km wide basin (Conner and Day 1987). This relatively large estuarine system is near to the activities of several commercially important fisheries (e.g., Gulf menhaden purse seine, inshore shrimp trawl, and blue crab pot) and contains one of the largest populations of bottlenose dolphins in coastal Louisiana (Waring et al. 2002). The Barataria Basin is located along the humid, subtropical Louisiana coast directly west of the Mississippi River (Conner and Day 1987). The climatic region is characterized by hot, humid summers with relatively mild winters. Barataria and Caminada bays lie in the lower saline portion of the basin and are separated from the Gulf of Mexico by a series of barrier islands (Reed 1995). The bays average 1.6 m of precipitation per year, and salinity typically ranges between 6 and 22 practical salinity units (psu). Bay waters are both shallow (mean depth is 1.5 m) and turbid, with the diurnal tide range averaging around 30 cm (Connor and Day 1987). Bottom sediments are composed primarily of silt, clay and organic detritus, but sand, shell and shell fragments are also present. Common marsh vegetation types in this region include *Spartina alterniflora* (smooth cord grass), *Juncus roemerianus* (black rush), *Distichilis spicata* (saltgrass), *Batis maritima* (saltwort), and *Salicornia virginica* (glasswort) (Day et al. 1989).

Survey Methodology

Monthly surveys began in June 1999 and continued until May 2002. General physical and geographical characteristics, such as connectivity to the Gulf of Mexico and proximity to industrial areas, were used to divide the study area into six strata. Random sequence and order

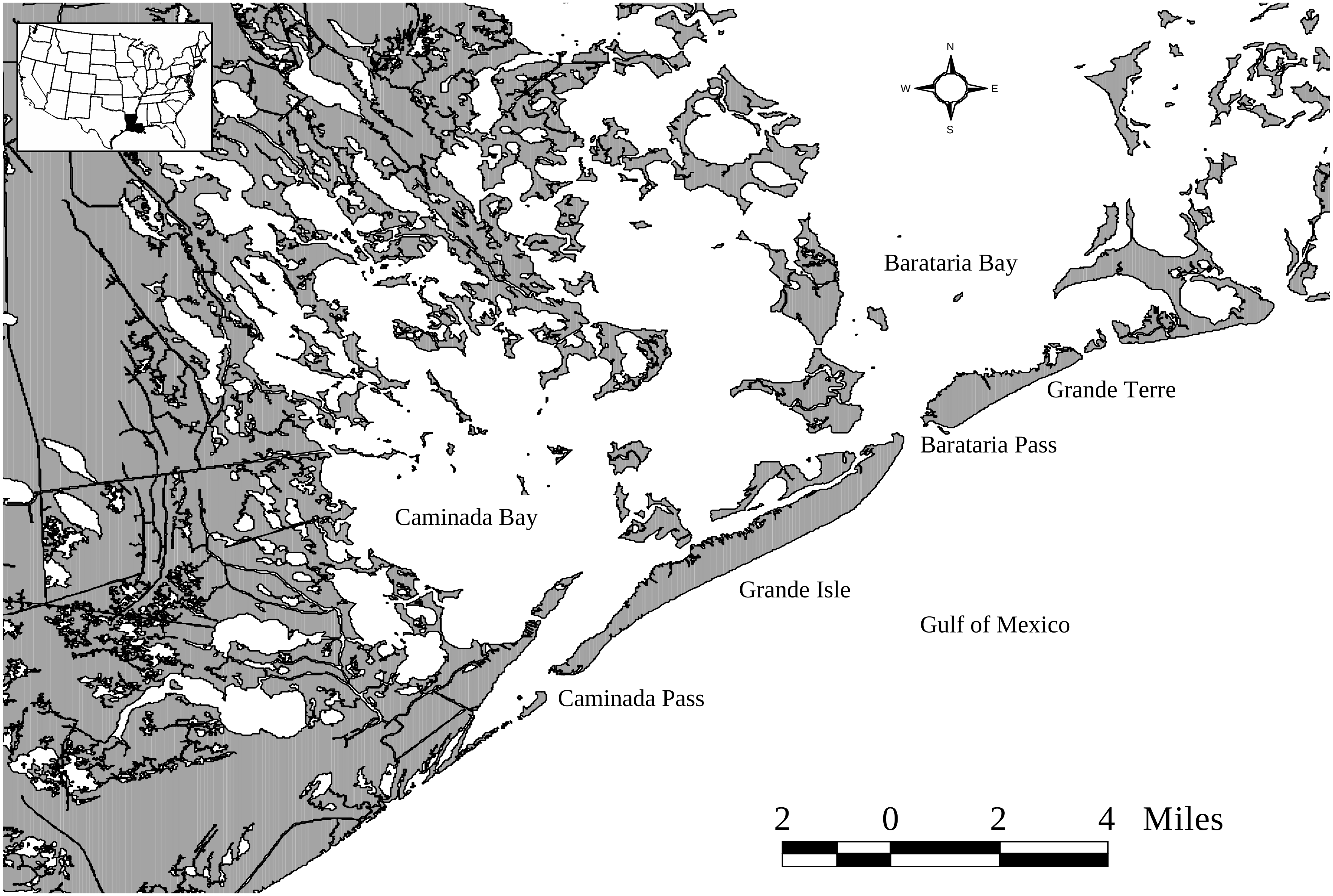

Figure 2.1. Study site location in lower Barataria and Caminada Bays, Louisiana.

of entrance into each of these strata created a stratified random sampling design. Two or more independent observers used a small motorboat during each month to survey all six strata. Once an individual or group was sighted, the boat was slowed and the individual or group was approached. The latitude and longitude of the initial observation site was marked with a hand-held geographic positioning system (GPS). Standard photo-identification techniques (Wursig and Wursig 1977) were used to photograph as many dorsal fin profiles as possible to be used in a complementary photo-identification population assessment of bottlenose dolphins in the area. This technique allows identification of individual dolphins by documenting natural markings present on the dorsal fin (see Chapters III and IV). After voluntary departure from the initial observation site, the boat was moved to the site to collect microhabitat data. The ultimate microhabitat of an individual is the site it occupies at a given point in time (Hurlbert 1981). Direct measurements made at observation sites were conducted to describe trends in microhabitat selection of individuals and groups of bottlenose dolphins. Environmental variables used to characterize microhabitat were water temperature, dissolved oxygen, salinity, turbidity, distance to shore and water depth. Additionally, temporal variables including time of day, month, season and year were considered in this study. Sea-surface temperature (°C), salinity (psu) and dissolved oxygen (mg/L) were measured with a Hydrolab Environmental Data Systems model SCR2-SU Sonde unit or the combination of a YSI model 33 S-C-T meter and a YSI model 57 oxygen meter. Water depth was determined with a weighted line marked at 10 cm intervals. A superficial substrate sample from the bay floor was obtained from a small scoop attached to a 4 m push-pole. When depths exceeded the line or push-pole length, nautical charts were referenced for depth and substrate type. Distance from shore was estimated by measuring the distance between the initial observation site and the nearest land point from detailed maps of the area. Water samples were collected for laboratory assessment of Nephloid Turbidity Units (NTU) using a Moniteck nephelometer or Hach 2100N Turbidimeter. Bottlenose dolphin group size and composition was recorded, including estimates of minimum, best, and maximum group size (Urian and Wells 1996) and the presence of juveniles and calves were noted. An individual was identified as juvenile if it was less than 80% of adult size. Individuals identified as calves exhibited two or more of the following, approximately 50% of adult size, dark coloration, limp dorsal fin, calf "head-out" surfacing pattern, neonatal vertical stripes, and consistently surfacing in "calf position" (Urian and Wells 1996). Behaviors were categorized using the following descriptors (Urian and Wells 1996, Allen and Read 2000): (1) Foraging – Fish in mouth, rapid and deep diving, quick circling behavior at the water surface, or direct pursuit of a prey item, (2) Social – Play, sexual encounters, leaping, tail-chuffing, and all other general interactive activities, (3) Rest – Slow bobbing and lack of relative motion, and (4) Travel – Directed movement, zig-zag swimming and milling. All sightings were made during daylight hours (0750 – 1850 hrs). Sighting conditions were characterized by recording Beaufort sea state, sea state, general weather conditions (such as sun, clouds or rain) and presence of glare. After all details were recorded, effort was continued at or near the point on the survey line from where the individual or group was initially sighted.

Statistical Methods

Monthly observations were pooled into seasons defined as Fall – (September, October and November), Winter (December, January and February), Spring – (March, April and May), and Summer – (June, July and August). Statistical analyses were conducted using SAS software Version 8.02 (SAS Institute 1996) unless otherwise noted. Environmental variables were assessed for univariate and bivariate normality. Power transformations were invoked to improve normality where necessary (Freund and Wilson 1997). Seasonal differences between the environmental variables, including temperature, dissolved oxygen, salinity, turbidity, distance from shore and depth, were assessed using a multivariate analysis of variance (MANOVA). Pairwise comparisons were performed on variables that produced a significant Shapiro-Wilks result (p value ≤ 0.05). Least-square means methods with Tukey's adjustment were used to indicate the character of significant seasonal differences. Overall and seasonal means and standard errors of each environmental variable were also computed. To establish whether sighting conditions differed between seasons, Beaufort Sea state values were assessed in an identical manner to the environmental variables.

A principal components analysis (PCA) of six environmental variables (temperature, dissolved oxygen, salinity, turbidity, distance from shore, and depth) was employed to examine the pattern of variability in habitat use by bottlenose dolphins. Only principal components with eigen values greater than one were chosen for further analysis as they accounted for more variation than an original variable. Inspection of the scree plot was used to confirm that the selected eigen values described a relatively large proportion of total data variability. To aid in interpretation a varimax rotation was used on selected orthogonal components.

Foraging observations were compared to all other observations to determine whether environmental conditions where feeding occurred were distinct. All behaviors associated with foraging, including direct contact, rapid and deep diving, quick circling behavior at the water's surface, and direct pursuit of a prey item, were scored as feeding activity. Non-feeding behaviors included social interactions, rest and travel. In cases where prominent behavior was indeterminable, activity was conservatively categorized as non-feeding. A logistic regression and habitat suitability curves (Saucier and Baltz 1993) were developed to investigate whether particular environmental variables were useful in describing feeding activity. A logistic regression uses maximum likelihood estimation to select variables that are most likely to predict the observed results. Residuals follow a binomial distribution so neither homoscedasticity nor normality of individual variables are required; however, multicollinearity between independent variables should be minimal (Allison 1991) and was assessed by variance inflation factors (VIF). Variables that are primarily independent should produce VIF values close to 1, with no individual value greater than 10. Specific independent variables investigated were temperature, dissolved oxygen, salinity, turbidity, distance from shore, depth, time of day, season and minimum number of individuals present in a group. Variables included in the logistic regression were considered one at a time using a forward stepwise approach. Entry and exit p-values of 0.2 were chosen to identify a suite of variables that may be important even if not significant. The variable with the greatest Chi-square score (also with an associated p-value ≤ 0.2) is the one that most reduces the log likelihood of the overall model. The next variable is chosen in the same manner; however, after each addition all variables in the model were examined via a Wald Chi-square test to ensure that they remained significant (i.e., Pr > Chi-square is less than or equal to 0.2). If the variable was no longer significant, it was eliminated from the model. The goodness-of-fit of the final model was evaluated via a Hosmer and Lemeshow test (Allison 1991) in which a non-significant Chi-square value indicates a good fit. Least-square means with associated standard deviations of feeding and non-feeding observations were computed for all significant variables. To describe seasonal feeding activity, seasons in which the highest proportion of feeding and non-feeding observations took place were calculated.

Habitat suitability curves were constructed to characterize habitat selection at feeding sites (Baltz 1990). This approach considers the proportional frequency of feeding activity across individual environmental gradients in relation to the proportional availability of an environmental variable at intervals along its observed range. Both the entire data set (i.e., resource availability) as well as the subset of observations where feeding occurred (i.e., resource use) were used to construct univariate frequency distributions and suitability curves. In addition, habitat selection for group size was assessed also. Specifically, feeding habitat suitability (S) for each defined interval of a given variable's range was calculated using the following formula:

$$S = P(E|F) / P(E)$$

where $P(E|F)$ is the probability of a feeding observation, and $P(E)$ is the total number of observations (Baltz 1990). Habitat suitability values were normalized to a scale of 0 (non-feeding) to 1 (high probability of feeding) by dividing through by the highest calculated raw suitability value for the given environmental variable. In addition, each of the univariate frequency distributions of the temporal and environmental variables was examined on an individual basis.

A Geographic Information System (GIS) was created to visualize the spatial distribution patterns of individual bottlenose dolphin sightings within the study area. Maps were prepared with ArcGIS 3.2 software (Breslin et al. 1999, Longley et al. 2001, Ormsby et al. 2001). Season, behavior and minimum group size were differentiated on projections of the study area to examine patterns of distribution. To examine areas of proportionally higher feeding activity the entire study area was divided into 16 equally sized quadrats for which the overall number of observations as well as the frequency of feeding activity was tabulated. Additional analyses on minimum group size and season were not undertaken due to variability in the ability to detect individuals between seasons, as well as the higher probability of seeing larger group sizes. Anomalous behavior of an oxygen probe required division of the data set. All multivariate statistical methods used the subset of observations where the Hydrolab Environmental Data Systems model SCR2-SU Sonde unit was used to measure dissolved oxygen content. This subset constituted the first 194 observations taken (June 1999 – May 2001). Univariate analyses on all other environmental variables used the entire dataset (n = 269).

RESULTS

On 44 survey days between June 1999 and May 2002, a total of 269 bottlenose dolphin individuals or groups were observed in the lower reaches of Caminada and Barataria bays. Number of groups, total number of individuals, incidence of feeding, and survey effort were tabulated on a seasonal basis (Table 2.1). Observations and survey effort were distributed relatively evenly across seasons. A MANOVA detected significant seasonal differences in temperature, dissolved oxygen, salinity and turbidity. Posterior pairwise comparisons using least-square means with a Tukey adjustment indicated seasonal differences for 4 of 6 environmental variables (Table 2.2). No seasonal differences in distance from shore or water depth were detected so these variables were not examined further. Temperature was significantly different between all four seasons. Lowest temperatures were measured in winter, and then progressively increased through spring, fall and lastly summer. The lowest dissolved oxygen levels were found at similar levels in summer and fall. Dissolved oxygen content climbed significantly in fall and again in winter. Mean salinity values fell into two general groupings: fall-winter salinities were higher than summer-spring. These groupings are not readily visible because listed results do not show that the p-value for differences between spring and fall was 0.028. Fall turbidity levels were significantly lower than winter and spring; however, differences in turbidity were not evident between summer, spring and winter. Beaufort sea state values were significantly different between seasons ($p < 0.0002$). Summer sea state was

Table 2.1. Seasonal frequency of groups, effort (hours), number of individuals seen and proportion of observations where feeding was observed for bottlenose dolphin groups in lower Caminada and Barataria bays, Louisiana.

	Winter	Spring	Summer	Fall	Total
No. of observations	68	60	71	70	269
Min. no. of individuals	327	422	595	550	1894
Survey effort (hours)	46.5	54	53.5	53	207
Feeding observations	18	24	21	25	88

Table 2.2. Annual and seasonal patterns of environmental conditions measured in Barataria and Caminada bays, Louisiana. Significant seasonal differences ($p \leq 0.025$) were identified using least-square means (± 1 SE) and are indicated by different letters across each row. Seasonal ranges are reported below the mean for each variable.

Variable	Winter	Spring	Summer	Fall	Overall mean (± 1 SE)
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
	(10.89 - 18.00)	(19.55 - 30.40)	(29.53 - 33.90)	(17.52 - 30.33)	
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
	(8.38 - 16.63)	(4.79 - 14.55)	(3.67 - 11.10)	(5.70 - 10.55)	
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
	(19.6 - 31.5)	(12.60 - 28.6)	(11.7 - 28.5)	(23.0 - 28.3)	
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
	(4.1 - 34.0)	(1.56 - 28.1)	(4.40 - 27)	(1.4 - 29.00)	
Distance (m)	69.04 ± 12.78	111.42 ± 13.61	91.73 ± 12.51	70.14 ± 12.60	84.77 ± 6.47
	(10 - 300)	(5 - 500)	(3 - 600)	(10 - 800)	
Depth (m)	2.82 ± 0.23	2.54 ± 0.25	2.33 ± 0.23	2.72 ± 0.23	2.60 ± 0.12
	(0.40 - 12.5)	(0.45 - 7.0)	(0.46 - 8.0)	(0.60 - 9.50)	

found to be significantly lower than both winter and fall. In addition to summer, winter sea state was close to being significantly greater than those observed in spring surveys ($p < 0.03$).

The PCA resolved the six environmental variables into three orthogonal factors that explained 71 % of the variability of the data set (Table 2.3). The first three components had eigen values greater than one. Each of the six environmental variables loaded heavily on at least one factor. Factor 1 accounted for 30 % of the variability. Heavy loadings were apparent for temperature and dissolved oxygen yet signs were opposite and reflect the seasonal patterns of temperature and dissolved oxygen evident in the study area. Factors 2 and 3 each accounted for an additional 20 % of the variability. Factor 2 loaded strongly on both salinity and turbidity. Salinity decreases as distance from Gulf waters increases, which in this case represents progressively more northern areas. However, there is also semi-annual variability in salinity values. Higher turbidity rates occur in water close to the shore and in more frequently or recently disturbed waters. Strong positive loadings for distance from shore and depth were evident in Factor 3. Distance from shore was greatest in open waters areas north of Grande Isle and Grande Terre where wetland areas were absent. Though depth was relatively homogenous throughout the study area, channels and passes were deeper. Distance from shore and water depth described a spatial three-dimensional component of the coastal landscape.

Foraging behavior was evident in 88 of the 269 sightings during this study. A forward stepwise logistic regression selected four environmental variables to describe feeding sites in the following order: minimum group size, turbidity, temperature, and season (Table 2.4). Multicollinearity was not a problem as evidenced by a mean VIF value of 1.74, with no individual VIF value exceeding 5. None of the selected variables were later discarded as a result of the stepwise procedure. The Hosmer and Lemeshow criterion found the selected model to be

Table 2.3. Rotated factor loadings of environmental variables at bottlenose dolphins sighting locations in lower Barataria and Caminada bays, Louisiana. Magnitude and signs of factor loadings indicate strength and direction of each variable's influence on a factor. The variance explained by each factors's eigenvalue are expressed as absolute, proportional, and cumulative values.

Environmental Variable	Principal Component		
	1	2	3
Temperature	-0.88	-0.36	-0.01
Dissolved Oxygen	0.94	-0.16	-0.04
Salinity	0.02	0.82	0.16
Turbidity	0.06	0.67	-0.19
Distance	-0.23	-0.05	0.70
Depth	0.21	0.01	0.81
Variance explained	1.85	1.20	1.18
Proportion	0.31	0.20	0.20
Cumulative	0.31	0.51	0.71

Table 2.4. A forward stepwise logistic regression characterizing variables important in describing bottlenose dolphin feeding locations in lower Barataria and Caminada bays, Louisiana. Individual variables were both entered and kept in the model with a α-level of 0.20. Feeding and non-feeding least-square means (± 1 SE) were calculated for significant continuous variables, while highest and lowest proportions of feeding activity were given for season.

Order	Effect	Wald χ^2	Pr > χ^2	Feeding (Mean ± 1 SE)	Non-feeding (Mean ± 1 SE)
3	Temperature	6.78	< 0.01	24.28 ± 0.75	22.82 ± 0.54
1	Min. 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 %)

a reasonable fit to the data ($\chi_8^2 = 5.79$, $p = 0.67$). Minimum group size, turbidity and temperature were all higher in feeding versus non-feeding observations. The incidence of feeding was highest in spring (39.3 %) and lowest in winter (26.5 %).

Feeding habitat suitability curves indicated selection patterns for temperature, turbidity, distance from shore, depth and minimum group size. Selected temperatures for feeding were between 20 and 24 °C (Figure 2.2). Dissolved oxygen content selection peaked around 6 mg/L and declined as values increased (Figure 2.2). Salinity selection results were somewhat ambiguous due to a small number of observations for the lowest interval of salinity values that acted to inflate the associated S value. However, there was a small peak around 20 psu. Feeding selection was pronounced for turbidity values between 20 and 28 NTU (Figure 2.2). Though a majority of observations were made in waters less than 50 m from shore, a selection for waters between 200 and 500 m from shore was apparent (Figure 2.3). Selection for feeding was highest in water depths between 4 – 6 m of water (Figure 2.3). There was a steady climb in proportion of feeding observations as minimum group size increased (Figure 2.3). There appeared to be no obvious pattern relating time of day with feeding activity. Environmental variables that were identified as important descriptors of feeding activity in the logistic regression analysis (i.e., minimum group size, temperature, turbidity and season) showed selection for feeding activity in extreme values of the resource availability, rather than mid-range values. For example, temperature and turbidity showed pronounced selection values for higher values (Figure 2.2) and as minimum group size increased so did relative feeding suitability (Figure 2.3). However, depth (Figure 2.3) and dissolved oxygen (Figure 2.2) showed relatively strong suitability in mid-range values yet were not selected in the logistic regression analysis.

GIS maps of feeding versus non-feeding sites identified areas (Figure 2.4) where feeding

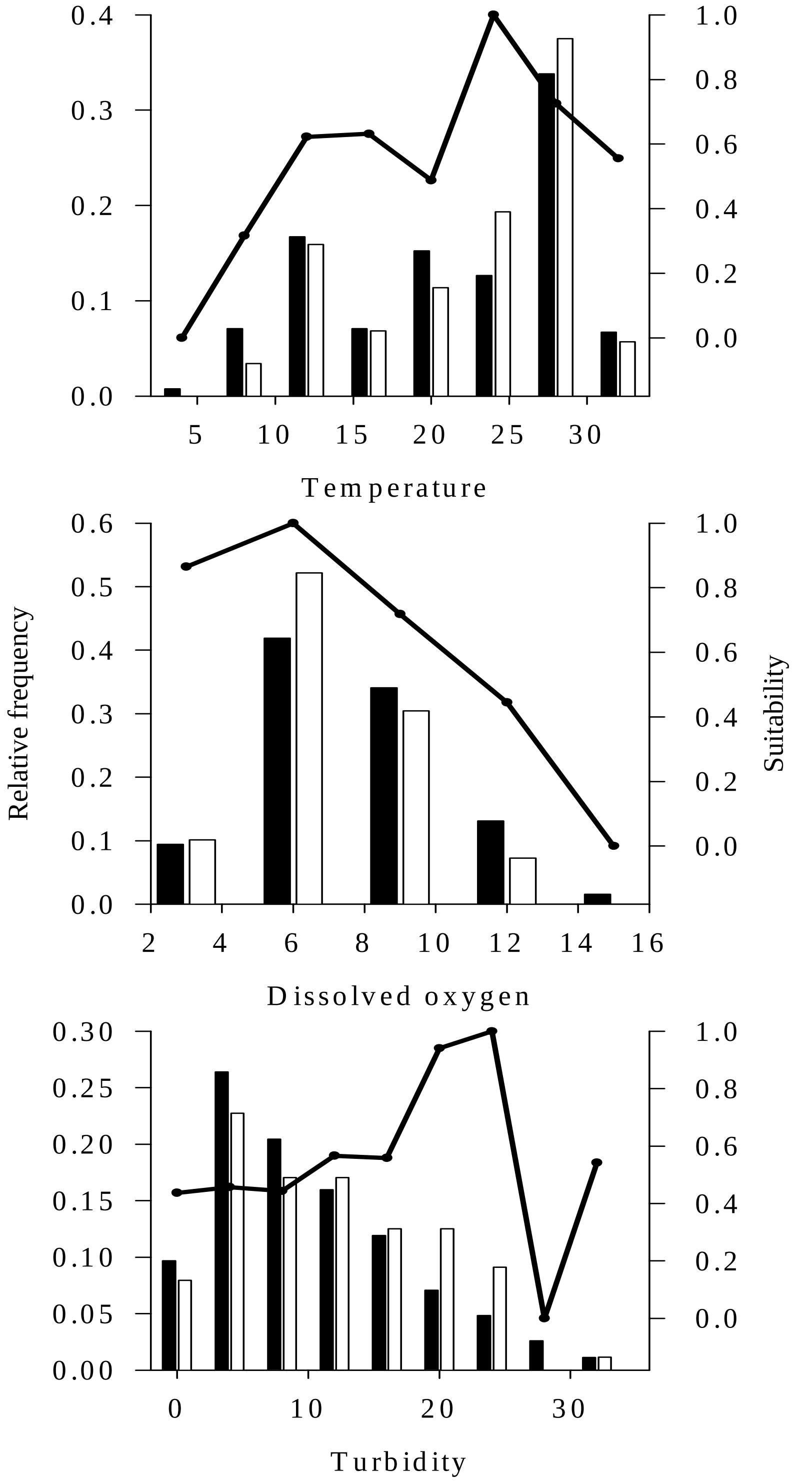

Figure 2.2. Feeding suitability curves for temperature, dissolved oxygen, and turbidity. Vertical bars indicate frequency of overall observations (black) and feeding activity (white) for each given interval. Black lines indicate the relative suitability of variable values for feeding activity.

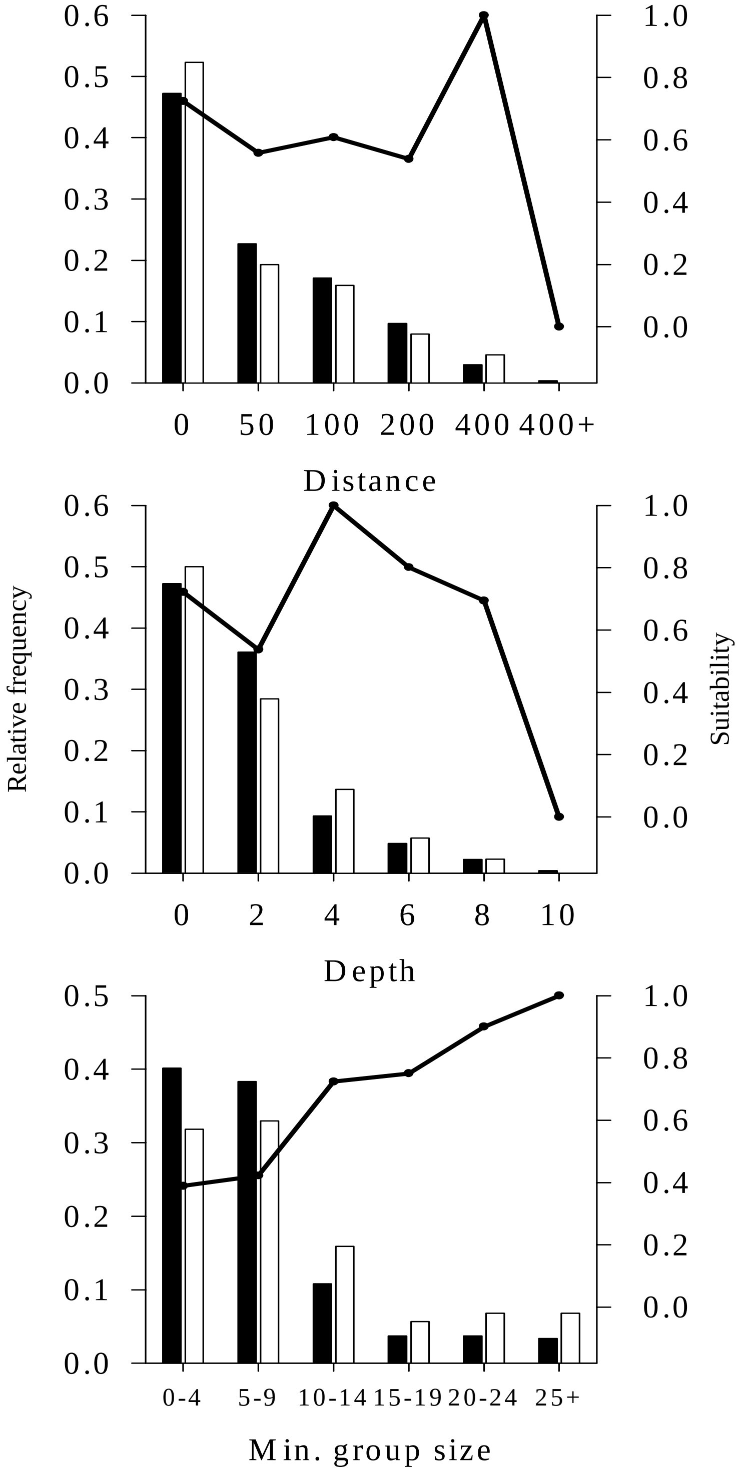

Figure 2.3. Feeding suitability curves for distance, depth and minimum group size. Vertical bars indicate frequency of overall observations (black) and feeding activity (white) for each given interval. Black lines indicate the relative suitability of variable values for feeding activity.

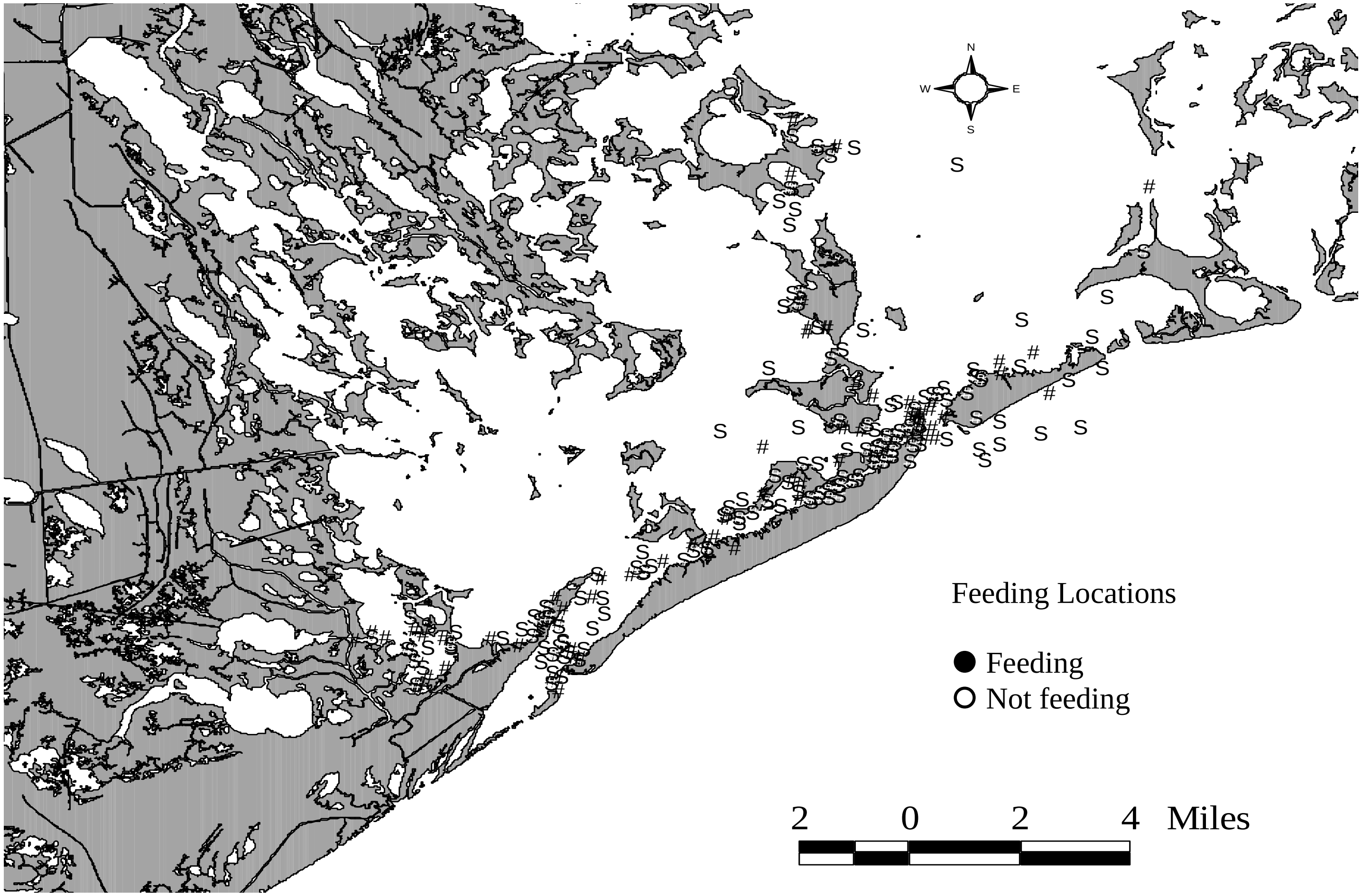

Figure 2.4. Spatial distribution of feeding and non-feeding locations of bottlenose dolphins in lower Barataria and Caminada bays, Louisiana.

activity was relatively high. More than 50% of the observations in waters directly around the Caminada Pass area involved feeding activity. The northeastern ends of both Grande Isle and Grande Terre had relatively high rates of feeding also, but only a small number of observations were made in these areas. Projections of minimum group size estimates and seasonal distribution of sighting locations showed a general pattern of larger group sizes in the passes (Figure 2.5). Distribution range in summer was more expansive, yet these findings are heavily confounded by weather conditions that prohibited surveys in some regions during colder months (Figure 2.6).

DISCUSSION

This study utilized a fine-scale approach to examine patterns in bottlenose dolphin distribution, habitat use and feeding activity. Even though four of six measured environmental variables were significantly different on a seasonal basis bottlenose dolphins were present during all surveys conducted in the study area. Overall variability in environmental conditions were driven by three sets of environmental variables (Table 2.3). Relationships between temperature and dissolved oxygen, salinity and turbidity, and distance and depth represent variability on seasonal, spatial-seasonal and spatial, scales respectively. Spatial distribution patterns within the Barataria Basin showed general aggregation and feeding activity in the channels and passes, as well as differences in the range of seasonal observations. Feeding sites were differentiated from non-feeding sites by group size, temperature, turbidity and season in the logistic regression (Table 2.4). Habitat selection analysis indicated that feeding was most common in waters 4 – 6 m deep, 200 – 500 m from shore with salinity values of around 20 psu (Figures 2.2 and 2.3).

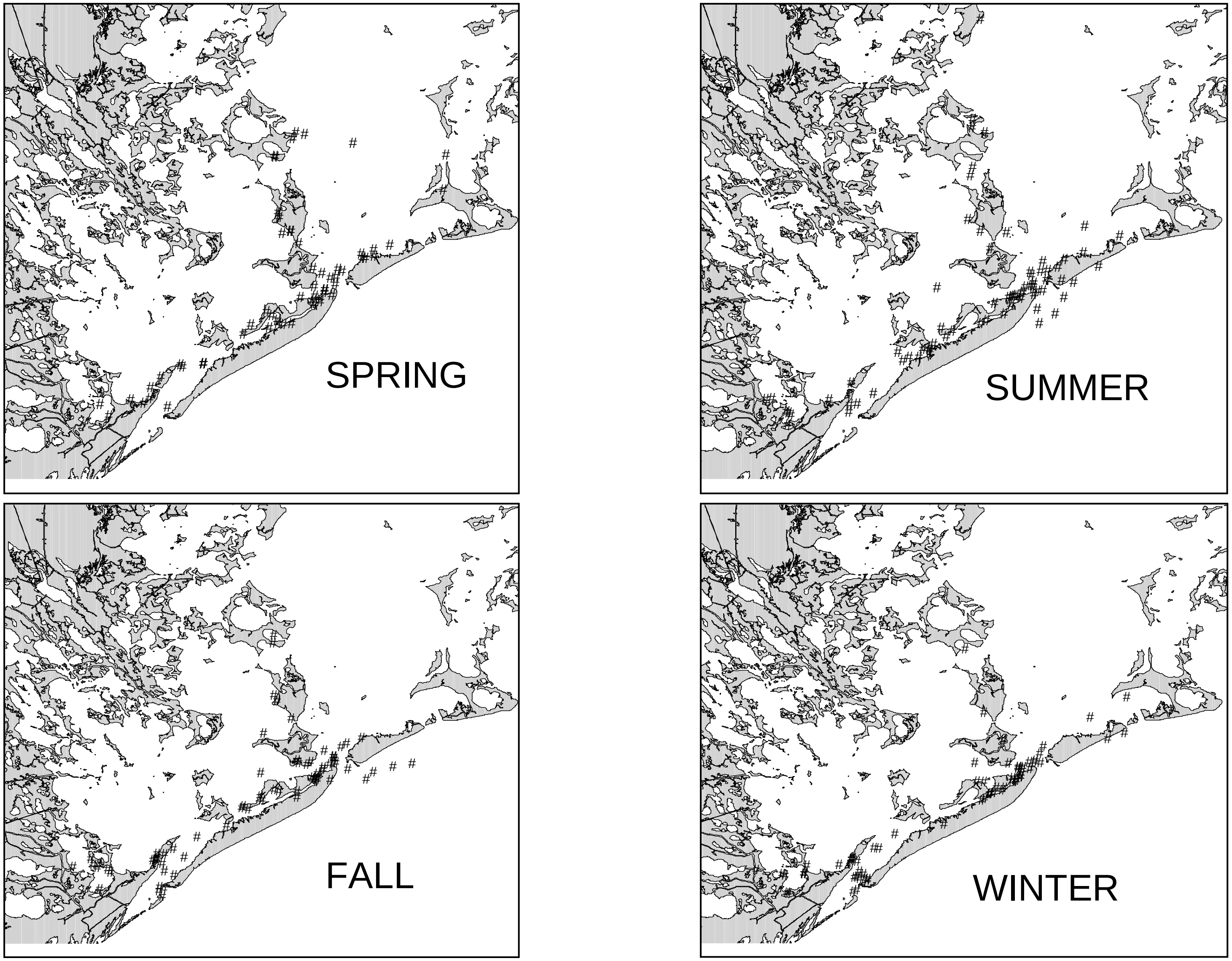

Figure 2.5. Spatial distribution of bottlenose dolphin sightings by season in the lower Barataria bay system, Louisiana.

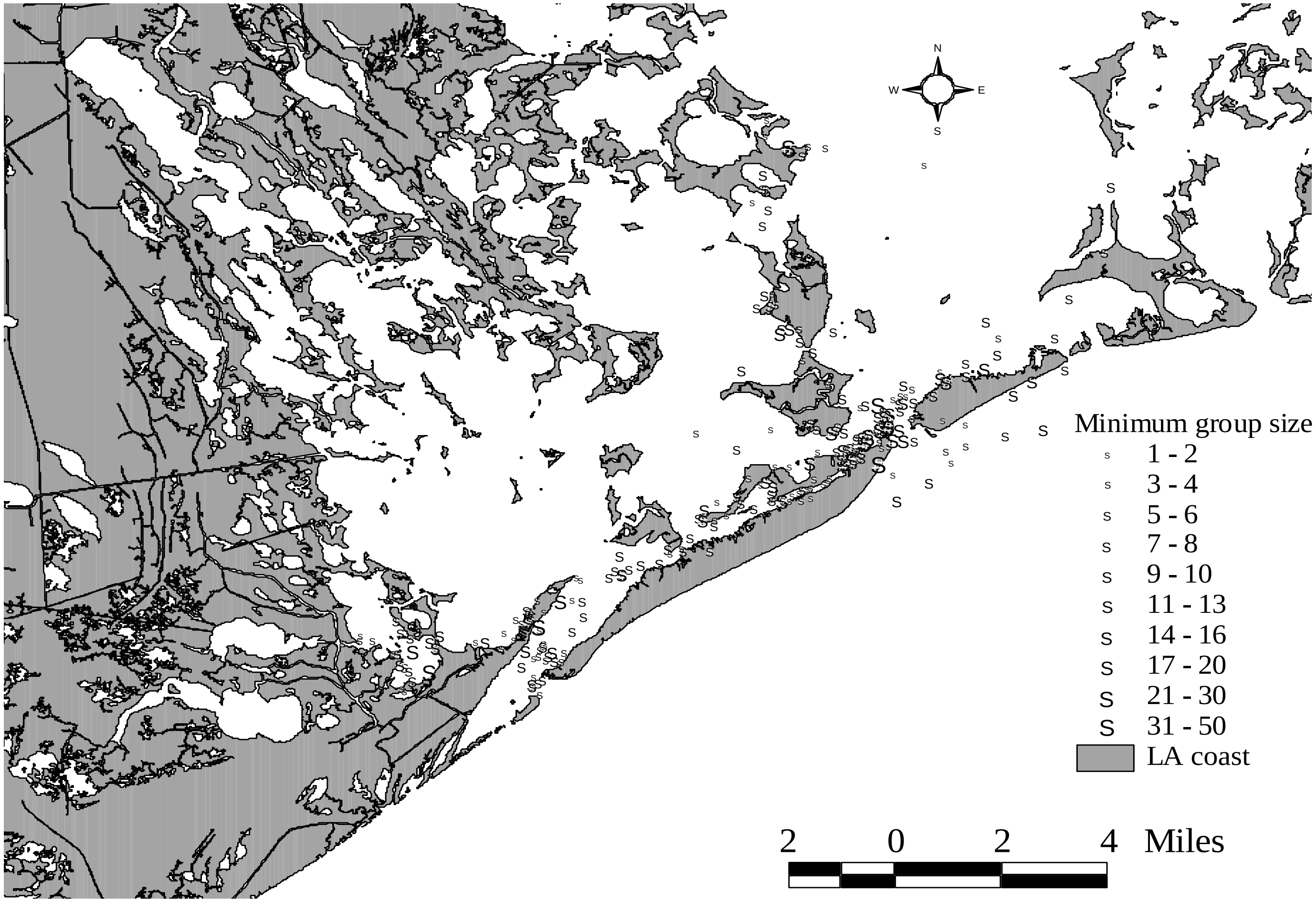

Figure 2.6. Spatial distribution of minimum group sizes of bottlenose dolphin groups in Barataria and Caminada bays, Louisiana.

Environmental Correlates with Marine Mammal Distribution

Environmental variables showed significant seasonal differences for temperature, dissolved oxygen, salinity and turbidity (Table 2.2). The inverse correlation between temperature and dissolved oxygen (Table 2.3) further indicated that seasonal differences play an important role in describing the distribution and behavior patterns of bottlenose dolphins in the Barataria basin. In addition, a logistic regression analysis noted that both season and temperature were important in describing feeding locations (Table 2.4). Numerous relationships between marine mammal distribution and seasonal trends have been detected. Commonly, the driving force in these associations is temperature fluctuations. Short-beaked common dolphins (*Delphinus delphis*) were found to move to inshore New Zealand waters during summer and spring (Neumann 2001). The occurrence of pronounced inshore movement during La Niña emphasized the correlation between warmer waters and inshore spatial distribution. In proximal waters, sea surface temperature was found to be a decisive factor in distribution limits of four species of Delphinidae (Gaskin, 1968). Similarily, Au and Perryman (1985) reported that spotted (*Stenella attenuata*) and spinner dolphins (*Stenella longirostris*) were abundant in tropical surface waters of relatively stable temperatures whereas common and striped dolphins showed preference for more variable equatorial and subtropical waters. However, these winter observations differed slightly from Reilly's (1990) findings for the same region during summer months. The two sub-groupings remained, though striped (*Stenella coerulealba*) and common (*Delphinus delphis*) dolphins became spatially separated in warmer months. In some studies, density differences in abundance have been observed on a seasonal basis. Tershy et al. (1990) found seasonal patterns to the presence of Fin (*Balaenoptera physalus*) and Bryde's (*Balaenoptera edeni*) whales within the Gulf of California, Mexico. The frequency of both species was negatively correlated with temperature. Hector's dolphins (*Cephalorhynchus hectori*) showed seasonal offshore movement (Dawson and Slooten 1988) though smaller scale diurnal observations have been inconsistent (Stone 1995, Bejder and Dawson 2001). In southern Texas there was a peak in winter abundance estimates of bottlenose dolphins (Shane 1980). However, no apparent relationship exists between season and the frequency distribution of births for the same species in the Gulf of Mexico (Urian et al. 1996).

It is a common contention that environmental variables associated with feeding activities may be proxies for the abundance or availability of important prey species (Kenney and Winn 1985, Selzer and Payne 1988). Specifically, either the distribution pattern or the preferred habitat of common prey species may be the determining factor. Salinity and turbidity were important in describing environmental variability in my study (Table 2.3) and also play important roles in distributing and providing refugia for bottlenose dolphin prey from most other predators. The former is a major determinant of community structure in estuaries and the latter reduces detection from visual nekton predators. The observed relationship between salinity and turbidity indicate the importance of both spatial and temporal components. The importance of additional spatial variables (i.e., depth and distance from shore) may be due to benefits related to prey capture or congregation. A logistic regression analysis (Table 2.4) determined that minimum group size, temperature, turibidity and season were all significant in describing feeding versus non-feeding locations. In addition habitat suitability curves (Figures 2.2 and 2.3) were able to define ranges of each specific environmental variable where feeding activity appeared to be most likely. These findings are unique in that most often a higher or lower scale of selection is presented. Several other marine mammal research findings indicate that particular environmental variables may be important indicators of prey species' distribution patterns.

One of the distinctions between the resident and transient killer whales (*Orcinus orca*) of the Pacific Northwest (Olesiuk et al. 1990, Hoezel 1993, Saulitis et al. 2000) is their primary prey choice of fish and marine mammals, respectively. These two prey choices utilize different features of bottom topography, and consequently the distribution patterns of resident and transient killer whale pods parallel these features. In Sarasota Bay, western Florida, Barros and Wells (1998) found that stomach contents of bottlenose dolphins suggest an expected correlation between prey habitat and dolphin foraging areas. Group sizes of spotted, spinner and common dolphins in the eastern Pacific Ocean were observed to mirror the diurnal group size fluctuations of yellowfin tuna, one of their common prey items (Scott and Cattanach 1998). Au and Perryman (1985) had documented, but not directly quantified, these associations over a decade earlier. In an extension to this work, Au and Pitman (1986) found positive statistical relationships between bird flocks and spinner and spotted dolphin schools. Pilchard movements up the eastern coast of South African coast have been accompanied by migration of common dolphins during winter months (Cockroft and Peddemors 1990). Sperm whale (*Physeter macrocephalus*) frequency is significantly greater on the eastern boundary of a Gulf Stream warm-core ring off Georges Bank (Griffin 1999). Entrainment of shelf waters within the warm-core ring is believed to provide suitable habitat for common prey items of sperm whales. Selzer and Payne (1988) found seasonal variation in sea surface temperatures and salinities for white-sided and common dolphins, and hypothesized that the interactions of these factors with sea floor topography and associated upwelling may be responsible for aggregating prey. In Belize, dolphins were most consistently observed at the interface between the open ocean and more protected sea-grass beds and mangrove shorelines of the Turneffe Atoll (Grigg and Markowitz 1997). This interface is often recognized as a highly productive region that may also act as a nursery for juvenile fishes. Interestingly, protected central lagoon sites and creek mouths were frequented least. Quiescent waters may not be conducive to prey capture, as tidal movement has been associated with feeding in several studies (Shane 1980, Gregory and Rowden 2001). In the Gulf of California, Ballance (1992) found sighting rates and feeding activities of bottlenose dolphins to be significantly greater in areas less than 5.5 km from productive estuarine areas. Within the Sado Estuary, Portugal, Harzen (1998) noted that specific sub-areas of the estuary appeared to be used for certain activities. Foraging was observed throughout the entire study area, although it was most prominent in areas close to openings from the estuary to open waters. Katona and Beard (1990) identified larger scale distinctions in feeding locations for humpback whale populations of the North Atlantic. Five specific feeding locations and one major winter breeding aggregation region were identified. Feeding behavior has sometimes been correlated with increased group size (Shane et al. 1986). Campbell et al. (2002) suggested that larger groups were more effective in searching for food and efficient in cooperative feeding strategy. The logistic regression performed in my study concurred with this assertion (Table 2.4). Both Corkeron (1990) and (Grigg and Markowitz 1997) identified both food patchiness and inter-specific interactions as important influences on *Tursiops* group size. Alternatively, for the same species in Cardigan Bay, West Wales, group size was unrelated to foraging activity (Gregory and Rowden 2001).

However, not all cetacean feeding behavior is predictable. Hoezel et al. (1989) found that individual minke (*Balaenoptera acutorostrata*) whales adopted specialized foraging strategies in similar oceanographic regimes. Individual foraging techniques were believed to be a product of learned behaviors. Bottlenose dolphins are both flexible and opportunistic in their feeding activity (Shane et al. 1986). In Shark Bay, Western Australia, a small number of individuals have been observed carrying sponges on their rostra as what is believed to be a foraging tool (Smolker et al. 1997). Observations of feeding in association with shrimp boats have been documented in Texas waters (Leatherwood 1975, Brager 1993) and feeding on mud-banks by partial beaching has been observed in some salt-marsh areas (Hoese 1971).

Innovative approaches to establishing habitat usage patterns, behavior budgets and movement patterns of marine mammals have been achieved by such methods as outfitting adult male seals with video cameras (Parrish et al. 2000), attaching satellite-monitored radio tags to large whales (Lagerquist et al. 2000), and using GIS to establish spatio-temporal prediction models (Hamazaki 2002). Besides the limited time for data collection, video and satellite-tags require direct implementation and proximity to individuals that often results in small sample sizes. Prediction models attempt to assess habitat suitability of areas where current survey data is not available. However, the usefulness of these models is dependent on the quality, range and resolution of data available for analysis. Recently Brager et al. (2003) was able to assess preferences of Hector’s dolphin by measuring sea-surface temperature, water depth and water clarity at both used and unused sites. This study found significant relationships between all three variables both individually and when combined, though preferences varied by region and season. Measurements on additional environmental variables would undoubtedly provide added insight into the ecology of this species.

Survey Design

The seasonal pattern of spatial distribution in bottlenose dolphin sighting locations is strongly influenced by environmental conditions that may limit survey efforts. DeMaster et al. (2001) found that Beaufort Sea state 1 conditions increased the probability of sighting beluga whales. Therefore, observed seasonal differences in density may be due to inclement weather conditions rather than movement of individuals out of a given area. In this study, I found that Beaufort Sea state conditions were lower in summer and spring. Due to the variability in seasonal weather conditions it was difficult to quantify differences in spatial patterns of feeding, seasonal observations and minimum group size (Figures 2.4, 2.5 and 2.6). Forney et al. (1991) were able to address this issue by incorporating environmental conditions as a covariate into their modeling efforts of harbor porpoises. Another issue when conducting survey work is the ability to detect groups with equal probability. It is likely that a positive bias results from the higher probability of sighting larger groups exhibiting more acrobatic activities. If there is inaccessibility of regions due to poor conditions that cause a non-representative sample of the environment or behavior to occur, the reported results may also be biased.

Conservation

Two bottlenose dolphin stocks meet at the interface of Barataria Bay and the Gulf of Mexico (Waring et al. 2002). The distribution limits of the western Gulf of Mexico (wGOM) bottlenose dolphin stock extend from presumed bay boundaries to the 18.3 m isobath all the way from the Texas border to the Mississippi River mouth. Approximately 3500 individuals are estimated to constitute the wGOM stock. The Barataria Bay "community" (see Wells et al. 1987, Waring et al. 2002) is believed to be about 219 individuals though recent work indicates that this may be an overestimate (C. Miller, Chapter IV). Distinctions between these two stocks are based in part on the assumption that movements between stock regions are limited by dissimilar climates and oceanographic conditions. In accordance with these assumed population boundaries and different marine environments the Barataria bay stock is managed separately from the wGOM under the Marine Mammal Protection Act.

CONCLUSIONS

Though many researchers have investigated environmental correlates in relation to marine mammal distribution or activities, the assessment of a synchronous suite of environmental forcing factors of bottlenose dolphin populations has been limited. Furthermore, the observed relationships between bottlenose dolphin distribution and behavior represent selection of environmental conditions, but should not be interpreted to indicate actual preferences (Baltz 1990). In an effort to provide a representative sample I used a randomly stratified survey design. The amount of effort I was able to devote to this project was limited by factors such as weather conditions, time constraints and size of the research vessel. Regardless I feel that the observations made during this study constitute a satisfactory and meaningful dataset describing environmental usage patterns of bottlenose dolphins in the area. A spatially and temporally explicit fine-scale characterization of the area would allow more definitive conclusions regarding bottlenose dolphin preference of environmental variables in this area. In addition there are many more variables that could be included in a habitat characterization. These factors may include but are not limited to tidal stage, chlorophyll *a* concentration, movement of prey, presence of predators or competitors, water velocity and age composition of groups. Despite these considerations, my findings with regard to habitat usage findings were able to effectively determine both the range and variance of important environmental variables and highlight strong variable selection for bottlenose dolphins in this region. Though the exact reasons for observed habitat selection are elusive, the development and quantification of an environmental context for population activity, movement, behavior, and residency patterns is an interesting step towards protecting individual populations and predicting future patterns of habitat use in the event of environmental change.

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CHAPTER III

ASSESSMENT OF JOLLY-SEBER ASSUMPTIONS FOR NATURALLY MARKED CETACEAN PHOTO-IDENTIFICATION DATA

INTRODUCTION

Field research on cetaceans is often hampered by highly mobile subjects, limited number of opportunities for visible contact, and heterogeneity of both oceanographic and climatic conditions. In response to these difficulties, survey design and thorough analysis has sometimes been ignored in lieu of capitalizing on scant opportunities to directly observe study animals. Consequently, general and simplified models may be employed to estimate demographic parameters. This may be necessary when assumptions of more complicated models cannot be assessed or met. However, these circumstances may result in highly variable estimates with intractable bias.

Photo-identification (photo-ID) techniques (Wursig and Wursig 1977, Olesiuk et al. 1990, Wursig and Jefferson 1990, Wells 1991) are frequently used to estimate demographic parameters of marine mammals. An appropriate photo-ID survey design is determined by a combination of factors including randomness requirements, weather conditions, behavior, and vessel restrictions. Independent observers scan the water for individuals or groups once underway. If sighted, the subjects are approached within a distance suitable for taking photographs given existing weather conditions. Markings suitable for photo-ID are then photographed for as many individuals as possible. Natural markings used in marine mammal studies include nicks and notches on the dorsal fins (Wursig and Wursig 1977, Wells 1991), saddle patch patterns (Baird and Stacey 1988, Olesiuk et al. 1990), pigmentation and markings on tail flukes (Whitehead and Waters 1990) and callosity patterns on the rostrum (Bannister 1990, Payne et al. 1990). These distinctive features are assumed to be sufficiently long lasting, slow in changing and unique enough to be recognized in subsequent sightings. Survey effort is resumed once photo-ID efforts are complete or individuals vacate the area. After completion of fieldwork, clear and complete images of the natural markings are examined for photographic quality and relative distinctiveness. Records are then analyzed to describe patterns on the appearance of new individuals, re-sighting frequencies, association patterns and distribution. Application of mark-recapture statistical theory and models can be used on individual-sighting histories to estimate population parameters. Mark-recapture model selection is dependent on the population under study, the survey methodology employed, and several other associated limitations or restrictions. Life history characteristics investigated have included population dynamics (Best and Underhill 1990, Calambokidis et al. 1990b, Karczmarski et al. 1999), social organization (Bigg et al. 1990, Whitehead 1990b), rates of survival (Buckland 1990) and reproduction (Barlow 1990), sex and age ratios (Glockner-Ferrari and Ferrari 1990), site fidelity (Wells and Scott 1990), movement patterns (Perkins et al. 1984, Calambokidis et al. 1990a) and mortality (Wells and Scott 1990).

Many excellent reviews of the history, theory and development of mark-recapture techniques, variously termed mark-and-recapture, capture-recapture, tag-recapture or band-recovery, have been published (Seber 1992, International Working Group for Disease Monitoring and Forecasting 1995, Schwarz and Seber 1999, Pollock 2000, Buckland et al. 2000). Specific to wildlife studies, important summaries of both closed- (Otis et al. 1978, Chao 2001) and open-population models (Pollock et al. 1990) have been prepared. Additionally, useful books by Caughley (1977), Begon (1979) and Thompson et al. (1998) as well as two highly influential editions of George Seber's "The Estimation of Animal Abundance and Related Parameters" (1973, 1982) are valuable contributors to the mark-recapture literature.

The starting point for mark-recapture methodology is commonly attributed to the Lincoln-Petersen (L-P) estimator (Petersen 1896, Lincoln 1930). The L-P estimator assumes there are no additions or deletions throughout the study duration, each individual has an equal probability of being captured, and identifying marks are correctly documented and permanent. For photo-ID studies, the terms capture and recapture can be used interchangeably with sighting and re-sighting, respectively. The validity of the assumption of equal capture of individuals was questioned and examined in an important monograph by Otis et al. (1978). Sources of variation in individual capture can be attributed to capture response, temporal factors and inherent individuality, that Otis et al. (1978) identified as possible sources of bias related to behavior, time and heterogeneity, respectively. Behavior refers to a directional change in probability of sighting after initial capture (i.e., either increased or decreased). Time accounts for temporally dependent variables such as survey conditions, season and time of day. Heterogeneity suggests that the uniqueness of any given individual will produce differences in probability of capture. All possible combinations of these three sources of variation have been proposed. Models describing individual heterogeneity have been the most difficult to characterize, though some effectual solutions include jackknife estimators (Burnham and Overton 1978), mixture distributions (Norris and Pollock 1996, Pledger 2000), explanatory covariates (Huggins 1989, Alho 1990) and log-linear models (Cormack 1989). Chao (2001) reviewed and summarized alternative solutions to the suite of Otis et al. (1978) models. The Otis et al. (1978) approach was important for assessing closed population models, but populations that are geographically or demographically open do not meet assumptions and require a different methodology.

In 1965, independent yet parallel descriptions of stochastic open-population model notation, assumptions and methodology were published by G. M. Jolly and G. A. F. Seber (Jolly

1965, Seber 1965). More than two capture periods are required to estimate the size, survival or recruitment rates of a population that may fluctuate due to birth, death, emigration or migration. Marked individuals are linked to a specific survey date, though time between survey dates does not need to be constant. Assumptions of the Jolly-Seber (J-S) model are that (1) every individual in the population has the same probability of being captured in any given sample, (2) every individual in the population has the same probability of survival, (3) the process of capture places similar risks and fates on all individuals, (4) marks are recognized and accurately identified on each sighting occasion, and (5) samples are instantaneous and all individuals are released immediately after capture. Special cases of the J-S model include deaths only (Darroch 1959, Jolly 1965, Seber 1982), births only (Darroch 1959, Jolly 1965, Seber 1982), constant survival and/or capture (Jolly 1982), age-dependent (Pollock 1981, Stokes 1984), cohort (Buckland 1982, Seber 1982), and temporary trap response (Robson 1969, Pollock 1975, Brownie and Robson 1983). Lebreton et al. (1992) continued the ideas of Pollock et al.'s (1990) monograph by including strata such as sex, age, size and location. Seber (1982) suggests that a minimum of ten re-sightings need to be seen on each capture occasion to avoid bias due to sparse data.

Hammond (1986) initiated serious investigations into topics of mark-recapture analysis of marine mammal photo-ID surveys. He stressed the need for proper implementation and understanding of modeling strategies. This influential work resulted in the compilation of a Special Issue of the International Report of the Whaling Commission (Hammond et al. 1990) dedicated to matters relating to mark-recapture techniques for naturally marked marine mammals. Individual contributions demonstrated the variety of applications and developments that were underway in marine mammal investigations and also acknowledged the necessity of assessing the appropriateness of model assumptions. The pivotal role of the J-S model in mark-recapture theory for open-populations makes it a worthy candidate for investigating defensibility of assumptions in regard to marine mammal photo-ID surveys. The objectives of this paper are to interpret J-S model assumptions in the context of cetacean photo-ID studies and understand the repercussions of possible violations of these assumptions.

BASIC MODEL ASSUMPTIONS

Each of the five J-S model assumptions were reviewed to discern the relevance of each assumption within the context of cetacean photo-ID research. Crucial aspects for each assumption were delineated to highlight the complexity and fine-scale obstacles that may arise when determining the degree and direction of bias when a given assumption is violated. Specifically, questions in regard to the validity of each assumption were examined to determine whether it is a factor which may hamper the use of a traditional J-S model parameter estimate for a given study population (Table 3.1).

(1) Every individual in the population has the same probability of being captured in any given sample

For capture probabilities to be approximately equal, the sighting rate for each individual must be similar. Detection of any given individual requires a number of particular events to be satisfied in sequence. In photo-ID work the individual must be detected, the group or individual must be approached within a distance suitable for image capture given the prevailing conditions, and the identifying mark must be available for image capture. A necessary step to ensure equal sighting rates is to randomize the survey protocol. Although the initial capture of animals may be deliberate, subsequent recaptures (re-sightings) may not. However, as most photo-ID research studies perform capture and recapture simultaneously, each survey must be random.

Table 3.1. Questions arising from consideration of Jolly-Seber model assumptions in regard to cetacean photo-identification research

Jolly-Seber Model Assumption	Questions to consider
(1) Every individual in the population has the same probability of being captured in any given sample	Are there differences in the chance that any given individual will be detected? Can each individual be approached within an appropriate distance for a satisfactory image to be taken?
(2) Every individual in the population has the same probability of survival	How does age, maturity or gender affect survival? Is the behavior that is causing individuals to be naturally marked related to survival?
(3) The process of capture places similar risks and fates on all individuals	Does the process of capture disproportionately affect behavior or survival of individuals?
(4) Marks are recognized and accurately identified on each sighting occasion	Are marks permanent? Are marks significantly distinct to be consistently recognized?
(5) Samples are instantaneous and all individuals are released immediately after capture	What is the temporal interval over which samples are taken during a given survey?

The random survey design must also ensure that neither location nor time of day is confounded. Specifically, certain locations should not consistently be surveyed during similar times or in predictable sequence. Another obvious, yet important consideration is that each population member must be within the limits of the study area during surveys. If the population is demographically open, the geographic range of the population must be known. The behavior and size of the group at the time of sighting may affect the ability of researchers to see individuals. For example, a large, acrobatic group is more easily visible than a few individuals quietly milling. Particular behaviors may also be linked to such covariates as group size, time of day, oceanographic features (such as tidal ebb or flow) and weather conditions. Although individuals may be detected during one or more surveys, they might not ever be captured. Once an individual is visible, it may simply ignore the vessel or react in manner that reduces the probability of image capture. If an individual consistently avoids researchers, it may never be captured. Avoidance behavior may be due to a previous experience or wariness. Alternatively, individuals may intentionally approach the research vessel. Behavior may also be correlated with distinctiveness of natural markings. For example, a positive response to boat traffic may also result in more frequent interactions and greater probability of acquiring natural markings as a result of interactions with vessels and gear. Additionally the age and experience of a calf may directly affect its response to capture efforts. Given detection and appropriate proximity, it is still not a certainty that an adequate image will be obtained. Surfacing behavior must allow the naturally marked feature to be completely visible and presented at a satisfactory aspect for photography. Covariates that are related to presentation, such as gender, age or size, may be another source of heterogeneity in capture probability.

(2) Every individual in the population has the same probability of survival.

Survival estimates are calculated from marked individuals only. Therefore survival rates for the entire population can be estimated only if survival rates for marked and unmarked individuals are similar. However, if survey techniques are biased toward a particular gender or age group resulting survival estimates may not be extended to the population without bias. These skewed estimates may be a result of differential behavioral responses to surveys, unequal probability of capture or relative distinctiveness of natural markings (see Assumptions 1 and 4). Alternatively, survival estimates may be biased downwards if the capture process caused a decline in fitness (see Assumption 3).

(3) The process of capture places similar risks and fates on all individuals

It is generally important to consider whether a capture episode may cause harm to an individual by affecting behavior, health or social status. However, the non-invasive methods of photo-ID do not pose serious risks to “captured” cetaceans. However, the proximity of research vessels and plausible disruption to individuals’ activities requires consideration. This is particularly true where researchers disrupt feeding, social, or reproductive activities. Behavioral responses to the research vessel or changes in social affiliations as a result of photo-ID work may cause heterogeneity in capture.

(4) Marks are recognized and accurately identified on each sighting occasion

Natural marking used for identification must persist throughout the duration of the study, and must also be consistently recognizable on subsequent survey dates. When an individual is incorrectly identified, the record of sighting histories obviously becomes inaccurate. The frequency and trend in re-sightings is crucial in calculating demographic parameters and also making determinations as to whether the population is closed or open. Population size estimates will be biased if an individual is not consistently or accurately re-sighted during surveys. For example, a distinctive mark that is only observable from one side reduces sighting probability by one half.

(5) Samples are instantaneous and all individuals are released immediately after capture

This final assumption pertains to both total survey time as well as each individual observation. Changes to a given population that occur while a single capture effort is being performed will confound parameter estimates. If surveys are conducted over a relatively short period this should not be a problem. However, over longer periods it may be unreasonable that there are no demographic changes to the population. In photo-ID research individuals are immediately returned to the population. Individual observation events are relatively brief in nature. The underlying and general reason for Assumption 5 is to accurately define the study population.

DISCUSSION

Close inspection of J-S assumptions in relation to photo-ID studies of naturally marked cetaceans gave rise to several important themes crucial to ensuring the valid application of models to cetacean populations. The most obvious and recurrent factor was the premise that all samples and surveys are a representative subset of the entire population. Requirements include being aware of the temporal and geographic range of the species and adhering to randomness requirements. Larger scale random survey design also needs to be complemented by smaller scale survey considerations. For example, image acquisition should be non-preferential, and factors that may alter an individual’s probability of detection (i.e., group size, behavior or social structure) must be taken into account. Natural markings used for individual identification need to be reliable and recognizable. Finally, population parameter estimates need to be correctly associated with an appropriate date or time period so that the population can be accurately defined.

Open versus Closed Populations

An overwhelmingly crucial consideration in employing any type of mark-recapture model is the initial evaluation of whether the population is open or closed. For representative samples of the entire population, the first step is knowledge of the temporal and geographical limits of the study population. There is no definitive test to determine whether a population is open or closed, and so several researchers (e.g., Otis et al. 1978, Begon 1979) suggest that prior experience and knowledge are the best guides for this determination. However, in a new initiative or research into a rare species this premise may be dependent on the very research about to be conducted. *A priori* information often aids in assessing a general core area of usage by confirming consistent re-sightings of individuals within a survey region. A closed population is assumed to have neither additions nor deletions within the temporal and spatial scale of the study. This requires both biological (births and deaths) and geographical (immigration and emigration) closure (Thompson et al. 1998). An open population allows movement into and out of the study area, as well as births and deaths. Williams et al. (1993) analyzed the number of new individuals sighted with accumulating effort to gauge whether they were encountering new individuals or consistently seeing the same individuals (i.e., “Discovery Curve”). A steady and asymptotic decrease in the number of new individuals discovered is often considered to represent a closed population. Alternatively, a consistent increase in the number of sightings of marked individuals may indicate an open population. In instances where the geographic range of the population is not adequately covered the terminal slope of the Discovery Curve may be misleading (Williams et al. 1993). This problem is particularly pronounced if the portion of the population failing to be surveyed is a specific, non-random group. Implementation of an overall random survey scheme is only assured when the complete geographic range of a population have been assessed. Therefore, determination of whether a population is open or closed is crucial for ensuring that: individual probabilities of capture are similar (Assumption 1), survival rates can be approximately extended to unmarked individuals (Assumption 2), and that estimated demographic parameters apply to a well-defined study population (Assumption 5).

Without a tremendously synchronous field effort it is rare that all samples for a given survey will be conducted simultaneously. Often researchers violate J-S Assumption 5 as logistics and capabilities of a field project do not permit a sufficient level of effort. Coordinated research efforts were able to produce a North Atlantic ocean-basin-wide population estimate for humpback whales (Smith et al. 1999). This multi-year study used standardized sampling and analysis protocols over numerous study areas. Hammond and Thompson (1991) were able to conduct a synchronous count of bottlenose dolphins present in Moray Firth, Scotland, though mark-recapture techniques were not involved.

When the closure status of a population (i.e., open or closed) cannot be determined it may be more appropriate to use an alternative method of abundance assessment. Indices denoting relative trends in abundance have been developed with varying degrees of success for several marine mammal species. Seasonal aerial surveys of endangered Florida manatee at warm-water refugia were used as an index for total population size by application of a multiple regression analysis with temporal components (Garrott et al. 1994), and later critically re-assessed with independent life-history parameter estimates and non-linear modeling (Eberhardt et al. 1999). However, beach counts of Hawaiian monk seals were an unreliable index for population size (Eberhardt et al. 1999). Udevitz (1999) developed a parametric model to account for temporal variability in index counts of Pacific Walrus. An alternative strategy to assessing abundance is quantification of cetacean occupancy patterns within a specified geographic region (Durban et al. 2000).

A population may have periods of relative demographic stability punctuated by mortality, breeding, immigration or emigration events. However, movement patterns of cetacean populations are flexible. Emigration and immigration may occur with a fairly regular and predictable temporal pattern (e.g., Humpback whales winter migration to Hawaii) involving essentially all members of the population, though less predictable temporary emigration by only a subset of individuals occurs also (e.g., Bottlenose dolphin males and transients in the Gulf of Mexico). If a population's movement patterns are relatively synchronous as in the former case, it may be possible to conduct abundance estimates during times (and locations) of peak abundance when minimal fluctuations in population occur. Less predictable temporary emigration by only a selection of individuals occurs also. This second type of emigration has recently received some specialized attention (Pradel et al. 1997). Disparate site-fidelity has been observed in some estuarine bays adjoining the Gulf of Mexico (Wells et al. 1987, Maze and Wursig 1999). So-called "residents" are individuals whose home range is consistently within a bay region whereas "transients" exhibit more extensive ranging patterns and typically intermingle and breed with nearby populations. Pollock et al. (1990) cited temporary emigration as a serious source of bias. Likewise, Hammond (1990a) noted inconsistencies in blue whale population estimates that he primarily attributed to movement patterns. Burnham (1993) has shown how to account for random emigration. However, when emigration is permanent it is not distinguishable from mortality. Whitehead (1990a) used a sperm whale example to demonstrate that likelihood-ratio tests could be used to distinguish re-immigration, emigration and mortality.

However, sample size limitations of this technique may be problematic. Transients and residents were separated in models designed by Pradel et al. (1997). These models assume resident individuals behave similarly and that movement out of a region by transients is relatively synchronous and for a known period of time.

Group and Individual Features That Effect Representative Samples

Even when geographic and temporal constraints of a given population are understood, the finer-scale details of a sample need to be considered further. Differences in probability of capture may be a result of individual characteristics and group associations or the immediate environment. Factors such as age, gender, group size and activity may influence detectability. The selection of only a sub-set of individuals for parameter estimates causes heterogeneity and bias in capture probabilities (Assumption 1) and difficulties in determining how demographic estimates can be extended to the entire population (Assumption 2). Some studies (e.g., Wells and Scott 1990) have chosen to include only adults in population size estimates to lessen possible age-related bias. Some models can assess age-related (Pollock 1981, Stokes 1984) or cohort-specific survivorship (Seber 1982). However, it is not always possible to age or sex individuals in the field. The well-documented social structure of many cetacean species (Bigg et al. 1990, Weinrich 1991, Wells 1991) indicates that the probability of seeing one individual may be highly related to the observance of other individuals. However, associations may be transitory (Connor and Smolker 1995) or related to behavior, for e.g. feeding (Smith et al. 1981, Fertl and Wursig 1995, Rossbach 1999). Consequently sightings and missed observations may be clustered (Cowan and Malec 1986). It is possible that either entire groups or individuals within a group may be missed. Wilson et al. (1999) notes that more precise estimates may be produced when non-independence of individuals in a population is taken into account. Whitehead (2001) found both evidence and lack of support for heterogeneity when investigating within-group probability of sightings for sperm whales. Behavior of the entire group may also affect sightability. Wade and Gerrodettte (1993) noted that dolphins exhibiting more "showy" behaviors could be seen from greater distances. Consistency in the presentation of features bearing natural markings should also be considered. For example, Perkins et al. (1985) noted differences in fluke presentation of discrete age classes. Whitehead (2001) found that younger sperm whales had lower identification rates despite similar levels of natural markings. Stern et al. (1990) investigated the efficiency with which individually identifiable minke whales could be photographed. Surfacings were rated as "catchable" if both angle and distance from boat were appropriate for image acquisition. Both the frequency and sequence of "catchable" surfacing was quantified. Regions where minke whales were surveyed was found to be important in describing these relationships as when behavior was more readily predictable, photographs were attained more efficiently.

Surveys are often conducted in regions where recreational and commercial boats are common. Frequent interaction with boats and proximity to human activities may cause modifications to behavior (Assumption 1), increased risk of injury (Assumptions 2 and 3) and anthropogenic pollution (Assumptions 2 and 3). A consistent response by all individuals to the initial capture process is the behavioral response defined and accounted for in the Otis et al. (1978) closed population models. However, it is unlikely that all individuals will behave in a consistent manner. Both positive and negative responses to vessels have been documented for various cetacean populations. Lesage et al. (1999) found that the vocal behavior of belugas in the St. Lawrence River estuary are modified in response to ferries and small boats even though these vessels regularly traverse the area. Collisions between large (> 80 m) ships traveling at speeds greater than 14 knots is a serious (and often fatal) problem for large whales, including fin, right, humpback, sperm and gray whales (Laist et al. 2001). In Sarasota, Florida the short-term effect of boat traffic on bottlenose dolphins (Nowacek et al. 2001) results in significant changes in swimming speed and direction, length of diving time and tightness of groups when a vessel approaches. *Tursiops* spp. in New Zealand waters respond negatively to tour boats, though interestingly males and females have different avoidance strategies (Lusseau 2003). Behavioral responses to whale-watching vessels of humpback whale pods with calves are distinct from pods without calves in Hervey Bay, Australia (Corkeron 1995). Behavioral modification was evident for all pods when vessels are within 300 m, but pods with calves also demonstrated a significant increase in diving when vessels are close. Killer whales in Johnstone Strait commonly increase swimming speed and sometimes vacate an area in the presence of boats (Kruse 1991). In the Eastern tropical Pacific small dolphins actively avoid the path of boats (Au and Perryman 1982). Alternatively, small delphinids in the Gulf of Mexico often approach research vessels to bow-ride (Wursig et al. 1998). Likewise, bottlenose dolphins in West Wales respond positively to tourist boats (Gregory and Rowden 2001). Aircraft presence may represent a more unusual occurrence in a study region. When helicopter and fixed-wing aircraft traffic are relatively close (altitude less than 185 m and lateral distance less than 250 m) behavioral responses including breaching and immediate dives are elicited from bowhead and beluga whales (Patenaude et al. 2002). *Kogia* spp. and beaked whales modify their behavior (usually by diving) in the presence of aircrafts (Wursig et al. 1998). In some cases, the effects due to the photo-ID capture process may not be immediately evident. Presence of boats introduces additional pollution into the environment through various chemical discharges from the motor. Sub-lethal stress strictly attributable to the research vessel is unlikely. Furthermore, the disadvantages of living in areas with boat traffic is most likely balanced to some extent by significant benefits such as abundance of prey and shelter.

Natural Markings

Wursig and Wursig (1977) recognized that nicks and notches present on the trailing edge of bottlenose dolphin dorsal fins are appropriate natural markers of individuals. These features were stable and recognizable throughout their two-year study. However, they noted that pigment spots and bite marks did not remain visible for this same duration. This concurred with Lockyer and Morris' (1990) assessment of the usefulness of certain wound types for re-identification purposes in the same species. Superficial scratches, deeper scratches and minor wounds are likely to heal in less than two years and often considerably shorter. The persistence of more serious wounds due to shark attacks and bullet-holes are longer lasting, yet again not always adequate markers. Specific regions of damage are found to have a bearing on long-term marking. Head, back, dorsal fin and tail flukes are more vulnerable to permanent damage. The ventral surface of humpback whale flukes is the region where most distinctive patterns occur (Carlson, Mayo and Whitehead 1990). However, the stability of patterns is not always consistent. Darker flukes show the greatest amount of change. The most dramatic pigmentation pattern changes occur during the first year of life, with generally very little change evident after the third year of life. Blackmer et al. (2000) found that morphological features of humpback whales tended to be more stable than superficial scars, scratches and pigment patterns. Specifically, dorsal fin shape and edges, the trailing edge of the fluke and the raised bumps on the caudal peduncle are relatively persistent. Additionally some evidence for persistence of markings was correlated with sexual maturity of males. The presence and size of lip patches, as well as the occurrence and shape of rostral islands has been useful in identifying individual

Southern right whales (Bannister 1990). Gowans and Whitehead (2001) examined a catalog of northern bottlenose whale (*Hyperoodon ampullatus*) photographs to detect features that may be relatively ephemeral and therefore inappropriate for mark-recapture studies. Using this approach they found that only two-thirds of the northern bottlenose whale population has reliable natural markings. A double-marking experiment using both natural markings and microsatellite genetic markers confirms the reliability of natural markings in humpback whale populations (Stevick et al. 2001). This study also indicates that errors are more likely to be made in identifying a single individual as multiple individuals, rather than correctly confirming these photographs as positive re-sightings. Individual characteristics of cetacean populations may also influence natural markings. Older individuals have a longer period to accrue scars and other markings. So regardless of whether they were randomly seen, they may be more likely to end up in a final catalog of unique individuals. Likewise, the behavior of particular age classes or genders may influence their susceptibility to accruement of marks. For example, younger bottlenose dolphins are more susceptible to predation by sharks (Mann and Barnett 1999). An important point noted by Hammond (1986) is that evidence for stability and persistence of a natural marking in one individual does not always guarantee identical results for all other members of the population.

The second part of Assumption 4 is that the mark is correctly identified. For photo-ID studies photo-quality and relative distinctiveness of the natural markings becomes very important. The quality of photograph must be satisfactory to identify a given individual with certainty from subsequent images. However, it is important to distinguish quality of image from relative distinctiveness of the given fin, fluke or other marking pattern. The inclusion of lower quality yet highly distinctive individuals would allow differential probabilities of capture based on mark type. It is also necessary that the distinguishing features used for capture be adequately conspicuous to be relatively easily recognized in subsequent photographs. Friday et al. (2000) found inconsistent levels of agreement between several judges regarding photographic quality and distinctiveness of humpback whales flukes. Similarly, some researchers (Gowans and Whitehead 2001, Stevick et al. 2001) note that the number of marks present on an individual was correlated with increased photographic quality.

The efficiency of comparing individuals has greatly benefited from computer imaging and matching programs. Many programs are species-specific and have been developed to assist in cataloguing as well as determining the relative similarity of two images. These software packages improve consistency and objectivity in matching efforts. As effort and scope of studies expand, the number of photographs and images being reviewed rapidly increases. This is important in light of Carlson et al.'s (1990) observations that experience and length of analysis time contribute to increased matching success. Mizroch et al. (1990) developed a program with a front-end data entry procedure to describe pigment pattern, notch shape, and marked regions of humpback whale flukes. A matching algorithm based on fluke descriptions assesses the plausibility of a match between two individuals. Images with highest levels of similarity are displayed together for visual inspection. Whitehead (1990b) used the relative location and type of mark present along the trailing edge of sperm whale flukes to classify individuals. This process has proved to be relatively efficient and reliable. The dorsal fin ratio method (Defran et al. 1990) measures relative distance between significant nicks and notches to the tip of a bottlenose dolphin dorsal fin. This standardized assessment method was developed into a computerized version, Finscan (Kreho et al. 1999). A silhouetted outline of the dorsal fin is developed using an interactive drawing program. From this profile the dorsal fin ratio is extracted and then used to compare individuals. Dolphins with notches on the leading edge or top of dorsal fin cannot be included in Finscan. Finally, identically marked individuals may be improbable, yet remains a possibility. Karczmarkski and Cockcroft (1998) suggest using as many nicks and notches as are available rather than just the two most prominent as per Defran et al.'s (1990) dorsal ratio method. These more distinct fins contain more information and therefore the possibility for random duplication decreases. Payne et al. (1983) calculated the possibility of identical Southern Right whale callosity patterns and found the likelihood to be acceptably small. If identical natural marking patterns were present, the size of the population would be underestimated since similar individuals may be regarded as a single individual.

Different Approaches and Alternative Solutions

Pollock (1982) presents a hybrid approach to the traditionally disparate methods of categorizing given populations as either open or closed. This so-called robust design recognizes that over an extended survey period of an open population, there are short durations when the population adheres to assumptions of closed population models. Thus, less complicated closed-population models can be used to assess capture heterogeneity over relatively short time spans. Estimates from these periods are then fed into open population models that can make more precise and accurate estimates of demographic processes including birth, death, immigration and emigration. This approach successfully combines some of the advantages for using each type of population model. Schwarz and Seber (1999) strongly recommend the implementation of this approach in wildlife study.

Adaptive sampling has been suggested as a good strategy for improving the precision of spatially clumped data (Thompson and Seber 1996, Seber 1999). By increasing sampling effort in areas where more individuals are present allows more non-zero samples to be recorded. However, when based on simple random starting points this adaptive sampling may inadequately cover the study area. Pollard and Buckland (1997) incorporated adaptive sampling into line-transect survey methods. When a specified level of density was exceeded, effort along the track-line was increased by zig-zagging back and forth along the survey route. If density then falls below the specified density criteria, effort on the regular track-line is resumed. Palka and Pollard (1999) tested the efficiency of adaptive versus traditional line-transect sampling in shipboard surveys of harbor porpoises (*Phocoena phocoena*). Adaptive sampling provides more precise estimates, which may produce lower density estimates than traditional line-transect sampling. Drummer (1999) discusses solutions to distribution of effort between intensive small area searches for cryptic animals as opposed to surveys covering larger areas but with lower detection rates of study animals. Using the variance of the abundance estimator, he concludes that a larger area should be covered at the expense of lower probabilities of sighting. However, these results assume that search intensity is linearly related to detectability.

Population dynamics have been included in log-linear models developed by Cormack (1989). These models are able to incorporate biological realism and can easily overcome the problems of negative birth and death rates sometimes encountered in the J-S model. Model fit and estimators may be investigated by omitting any specific group of individuals exhibiting particular behaviors or sighting patterns. Hammond (1990b) suggests the possibility of eliminating specific sighting histories from a dataset to improve J-S model fit for humpback whales in the Gulf of Maine. This approach was designed to reduce heterogeneity and investigate the robustness of population estimates. It was also noted that increased sample coverage might also act to alleviate both of these factors.

Despite advancements and improvements in population estimation theory and methodology there are still many problems to be resolved. Often these difficulties are dealt with on a case-by-case basis, as they have not been resolved in a more general manner. Heterogeneity of capture is a serious and complicating factor for population assessment. Carothers (1973) suggested that the greatest bias would be introduced in situations where a relatively high level of heterogeneity in capture probabilities was present. For closed population models many have built on the framework of the Otis et al. (1978) structure, yet problems still persist. Identification and inclusion of covariates such as weather conditions or sampling effort may act to partially alleviate these difficulties (Forney et al. 1991, Schwarz and Arnason 1996). In line-transect analyses, group size and weather conditions can be adjusted using regression methods (Buckland et al. 1993). Under certain assumptions, the direction and degree of bias due to heterogeneity can be determined (Pledger and Efford 1998). However, it remains an important avenue of research. Schwarz and Seber (1999) also discuss the difficulty of accounting for unmarked individuals in parameter estimation (Assumption 2). Likewise, changes in demographic parameters with age or maturity of individuals that cannot be directly aged in the field remains an obstacle. Sparse data sets can also be problematic (Gilbert 1973). Chao (1989) described a closed-population model that was able to account for poor data coverage, but the J-S model becomes unreliable in such situations (Seber 1982). Finally, uncertainty in selection between competitive models (Burnham et al. 1995, Buckland et al. 2000) and estimation of appropriate confidence intervals (Manly 1984, Cormack 1992, Cormack 1993) for some methods of population estimation are topics needing further research.

CONCLUSIONS

For wildlife populations the purpose of capture-recapture models is typically to estimate demographic parameters such as survival, recruitment, emigration, immigration and abundance (Pollock 2000). Mark-recapture methodology, bias and problems have been apparent to marine mammal scientists for the last 15 years. However, it is important that the bridge between analysis and research be clear and easily overcome. Accurate and precise population size estimation enables confidence in management and conservation efforts for marine mammals. Basic questions of modeling processes must be critically validated. Research efforts have to be matched with the temporal and spatial scales of the real system to maximize resources and utility (Baltensweiler and Fischlin 1987). In mark-recapture analyses, a model must reflect the type (open or closed) of population that accurately and realistically represents capture probabilities of individuals in the population. Otis et al. (1978) suggest using the most general model structure possible for a given analysis. General models may reduce bias, yet are relatively imprecise. Alternatively, more complex models may increase precision but introduce inaccuracy into parameter estimates. However, what ultimately drives the applicability and utility of any population model is the quality and quantity of data used.

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CHAPTER IV

MARK-RECAPTURE POPULATION ESTIMATION OF BOTTLENOSE DOLPHINS (*Tursiops truncatus*) IN COASTAL LOUISIANA (1999 – 2002)

INTRODUCTION

Population size estimation is a crucial stepping-stone for investigation of related demographic parameters such as fecundity, mortality, emigration and immigration. Furthermore, insight into population dynamics allows more complex ecological topics such as social structure, environmental usage patterns, or predator-prey theory to be examined. However, there are several obstacles to producing accurate and precise baseline population estimates: application of advances in animal abundance modeling theory, constraints of fieldwork unknown to statisticians, and ambiguous data analysis strategies. Abundance estimates for marine mammal populations are often achieved by applying mark-recapture statistical theory to photo-identification efforts (Cerchio 1998, Cerchio et al. 1998, Wilson et al. 1999). Specifically, identifying and documenting the occurrence of marked individuals allows sighting histories to be developed. Natural markings used in marine mammal studies include nicks and notches on the dorsal fins (Wursig and Wursig 1977, Wells 1991), saddle patch patterns (Baird and Stacey 1988, Olesiuk et al. 1990), pigmentation and markings on tail flukes (Whitehead and Waters 1990) and callosity patterns on the rostrum of southern right whales (Bannister 1990, Payne et al. 1990). Photographs of these natural markings are used to document and monitor individual animals. Occasionally, non-natural marks such as freeze-branding and radio-tagging are used also (Scott et al. 1990, Wursig et al. 1991). To ensure that the correct and appropriate mark-recapture analyses are being implemented in marine mammal field surveys, it is important to critically review their application in this discipline.

Mark-Recapture

The starting point for closed mark-recapture models is the Lincoln-Petersen estimator (Petersen 1896, Lincoln 1930). This restrictive model assumes there are no additions or deletions to the population during the study, each individual has an equal probability of being captured, and that identifying marks are both correctly documented and permanent. In this context, the terminology capture and recapture refer to sighting and re-sighting, respectively. The equal probability of capture assumption was questioned and examined in an important monograph by Otis et al. (1978). Causes for unequal rates of catchability were identified as behavioral (b) reaction to the capture process, temporal (t) factors and inherent individuality (h). Reaction to the capture process (behavior) refers to a change in probability of sighting as a result of initial capture. Temporal factors (time) imply that temporally dependent variables such as survey conditions, season and time of day should be taken into account. Inherent individuality (heterogeneity) suggests that the uniqueness of each given subject will produce differences in probability of capture. Most difficulty has been found in describing models inclusive of individual heterogeneity. When a constant catchability model was included, a total of eight models can be described (i.e., constant (no variability), behavior, time, heterogeneity, behavior-time, behavior-heterogeneity, time-heterogeneity and time-behavior-heterogeneity). In a recent review Chao (2001) summarized alternative solutions and approaches to all eight models.

Bottlenose Dolphin Abundance Estimates in Louisiana Waters

The 2002 U. S. Atlantic and Gulf of Mexico marine mammal stock assessments (Waring et al. 2002) recognize six possible Gulf of Mexico bay, sound, and estuarine bottlenose dolphin (*Tursiops truncatus*) stocks in Louisiana waters. However, population estimates were reported only for the Bay Boudreau/Mississippi Sound region (n = 1401), Terrebonne/Timbalier Bay complex (n = 100), and Barataria Bay (n = 219). These estimates were based on aerial line-transect data collected in September and October of 1993 (Blaylock and Hoggard 1994). Other research into the coastal bottlenose dolphin populations in Louisiana has been infrequent and irregular. Aerial surveys of coastal regions in the Gulf of Mexico made inshore and offshore estimates during 1987 (Mullin 1988, Mullin et al. 1990). Barataria, Timbalier and Terrebonne bays were included in inshore population size estimates of 500, 1232, and 2869 made in April, June and October, respectively. These aerial abundance estimates were notably greater than previous studies (Fritts et al. 1983, Scott et al. 1989). Jefferson (1996) conducted vessel-based surveys for bottlenose dolphins in offshore waters of the northwestern Gulf of Mexico in 1992 and 1993. From line-transect surveys, the estimate for Louisiana continental slope waters was 451 individuals, whereas the estimate for continental shelf waters was 520 individuals. In 1989 and 1990 aerial surveys over similar regions (Gulf of Mexico waters directly south of Louisiana greater than 200 m) counted 463 bottlenose dolphins (Mullin et al. 1994). All of these offshore studies covered large areas and have not been replicated on a regular basis. Therefore, there is doubt as to how the abundance trends noted in these various research studies relate to the present day population size in this vicinity. My research applies the closed-population unequal-catchability models (Otis et al. 1978) to describe and assess the bottlenose dolphin abundance within two adjoining bays in the lower Barataria Basin of coastal Louisiana.

METHODS

Site Description

Barataria and Caminada bays represent the seaward interface of the Barataria Basin with the Gulf of Mexico (Figure 4.1). This relatively large estuarine system is proximal to the activities of several commercially important fisheries (e.g., Gulf menhaden purse seine, inshore shrimp trawl, and blue crab pot) and contains one of the largest populations of bottlenose dolphins in coastal Louisiana (Waring et al. 2002). The Barataria Basin is located along the humid, subtropical Louisiana coast directly west of the Mississippi River (Connor and Day 1987). The climatic region is characterized by hot, humid summers with relatively mild winters. Barataria and Caminada bays lie in the lower saline portion of the basin and are separated from the Gulf of Mexico by a series of barrier islands (Reed 1995). Precipitation in the bays average 1.6 m per year and salinity typically ranges between 6 and 22 practical salinity units (psu). Bay waters are both shallow (mean depth is 1.5 m) and turbid, with the diurnal tidal-range range averaging around 30 cm (Connor and Day 1987). Bottom sediments are composed primarily of silt, clay and organic detritus, but sand, shell and shell fragments are also present.

Survey Methodology

Surveys began in June 1999 and continued until May 2002 on approximately a monthly basis. General physical and geographical characteristics such as connectivity to the Gulf of Mexico and proximity to industrial areas were used to divide the study area into six regions. Random sequence and order of entrance into each of these regions created a stratified random sampling design. One or more independent observers accompanied myself aboard a 17-foot outboard motor boat during each survey. Once an individual dolphin or group was sighted, the boat was slowed and the individual(s) were slowly approached. The latitude and longitude of the initial sighting location was marked on a hand held Garman 45 GPS unit. Standard photo-identification techniques (Wursig and Wursig 1977) were used to photograph as many dorsal fin profiles as possible. To ensure that all animals within a given group had equal probability of being sighted, individuals were not preferentially photographed based on relative distinction of their fins. Kodak 35 mm slide film was used in a Nikon N-70 camera with a 90-300 mm zoom

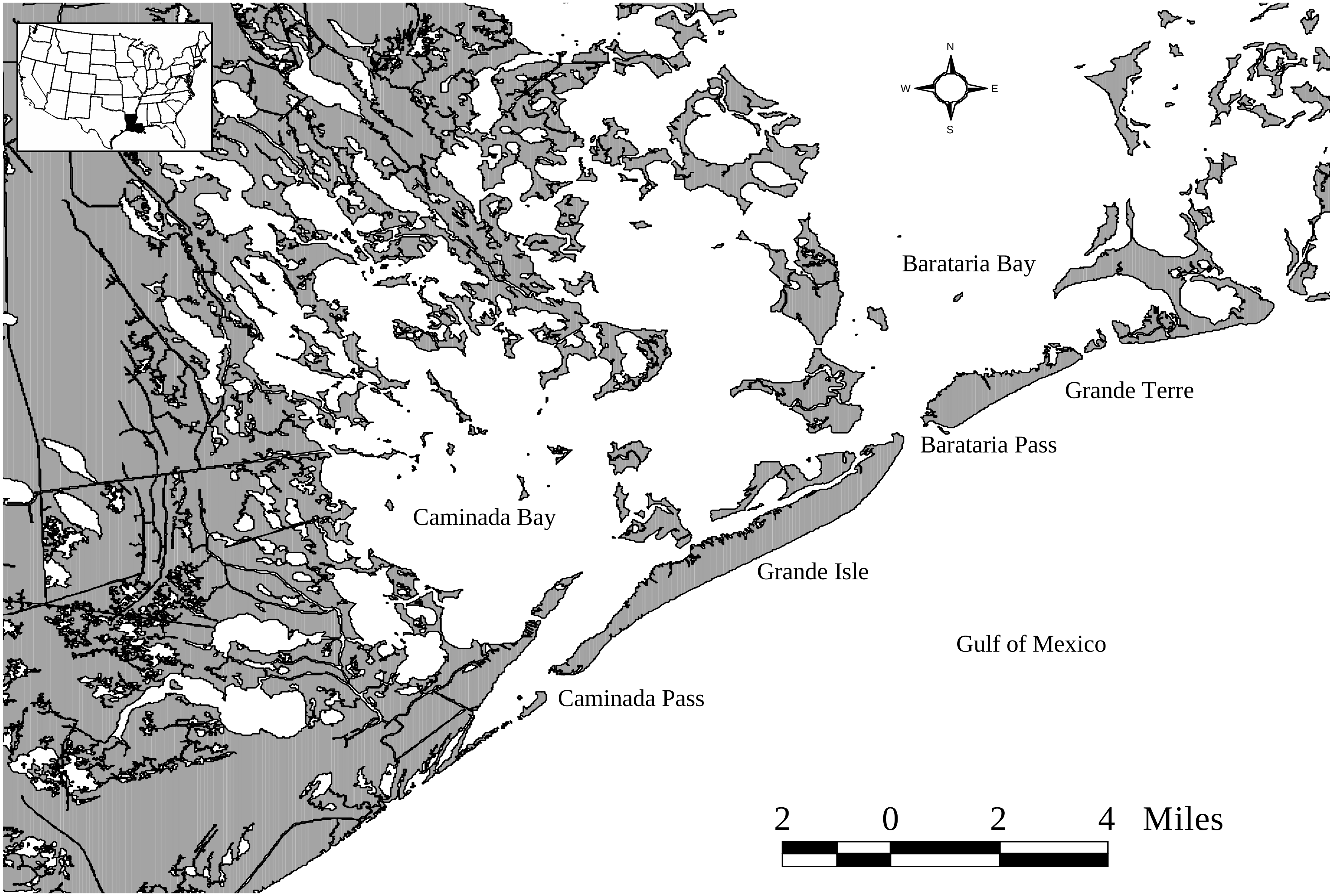

Figure 4.1. Study site location in lower Barataria and Caminada Bays, Louisiana.

lens for all pictures. Estimates of minimum, best, and maximum group size were made. The presence of juveniles and calves were noted. An individual was identified as juvenile if less than 80% of adult size. Individuals identified as calves exhibited one or more of the following: approximately 50% of adult size, dark coloration, limp dorsal fin, calf "head-out" surfacing pattern, neonatal vertical stripes, and consistently surfacing in "calf position" (Urian and Wells 1996). Behaviors were classified using the following descriptors (Urian and Wells 1996, Allen and Read 2000): (1) Foraging – Fish in mouth, rapid and deep diving, quick circling behavior at the water surface, or direct pursuit of a prey item, (2) Social – Play, sexual encounters, leaping, tail-chuffing, and all other general interactive activities, (3) Rest – Slow bobbing and lack of relative motion, and (4) Travel – Directed movement, zig-zag swimming and milling. Beaufort state, sea state, general weather conditions (such as sun, clouds or rain) and presence of glare were also noted. After the individual or group voluntarily vacated the initial site of observation, I moved back to this site and collected environmental data, including salinity, temperature, dissolved oxygen, substrate type, turbidity, distance to shore, and water depth, to be used in a related environmental habitat usage study.

Image Selection and Analysis

Based on clarity and quality, slide images were graded as excellent, medium, or poor. For population assessment purposes, only excellent images were used. All of the following elements were evident in excellent images: (1) the dorsal fin was clearly visible and large enough to detect any irregularities present on either the leading or trailing edge of the fin, (2) the given individual was surfacing on approximately a normal plane to the projection of the camera lens, and (3) the fin was not obstructed by objects such as water droplets, sections of the boat, glare or other individuals. From the selection of excellent quality images, fins with features of sufficient distinction to be recognized in subsequent surveys were identified and cataloged. To aid in comparison, fins were then categorized according to prominent fin features. Matching of dorsal fins was performed by visual inspection (using a light table and magnifying monocle) and digital analysis using the fin matching software, Finscan (Kreho et al. 1999). Finscan uses digitized images to compute dorsal fin ratios (Defran et al. 1990) and then presents groups of similar fins for initial comparison. Every image in the catalog was checked manually to confirm final decisions of fin identification and matching. Procedures implemented for treatment of images were put in place to avoid any introduction of bias through this aspect of the project. The use of computer software as well as an independent manual calculation of the dorsal fin ratio provided objective measures for both identifying individuals as unique and assessing similarity between fins. Furthermore, the use of only high quality images ensured mark recognition. Natural markings of fins in excellent quality slides were evaluated as to whether they could be easily recognized in subsequent pictures. These measures avoided the occurrence of false positives (incorrect matching of two unique slides) and false negatives (incorrect identification of two slides that are in fact a single individual).

Population Estimation

The sighting history of each individual was determined on both monthly and seasonal scales. Seasons were defined as: Fall - September, October and November, Winter - December, January and February, Spring - March, April and May, and, Summer - June, July and August. As levels of effort for eight consecutive seasons, Spring 2000 through Winter 2001/2002, were comparable, they were used exclusively for population modeling purposes. A sighting history was developed for each individual by noting their presence or absence during each of eight time intervals. Effort in hours was corrected for the time spent off-effort, i.e., while collecting photographic and environmental data or transiting between survey blocks. The number of new uniquely identified individuals was plotted against both corrected effort and total number of individuals seen at sea to produce discovery curves (Williams et al. 1993). The terminal rate of discovery (Wilson et al. 1999) described by these graphs was used to assist in decisions regarding population closure. Specifically, slopes that show asymptotic trends would suggest a relatively closed population. The terminal slope of discovery was calculated using only the last 10 % of the data to determine the ratio of previously unseen marked individuals to the cumulative number of individuals seen at sea. Program CAPTURE (Otis et al. 1978, Rexstad and Burnham 1991) and Program MARK (White and Burnham 1999) were used for population modeling purposes.

CAPTURE is specifically designed to test the eight closed-population unequal-catchability models discussed in the monograph by Otis et al. (1978). Models are identified by the parenthesizing the appropriate sources of variation (i.e., none (o), behavior (b), time (t), and heterogeneity (h)). The suite of eight Otis models can be listed as: M(o), M(t), M(b), M(h), M(tb), M(bh), M(th), and M(tbh). An overall model selection procedure was performed using a multivariate discriminant function to estimate fit on a scale of 0 (poor fit) to 1 (good fit). Seven Chi-square goodness-of-fit tests are included in CAPTURE output to examine the relative fit of two given models (e.g., M(o) versus M(t) (test 3), and M(h) versus M(hb) (test 7)). The four other models that did not include behavioral variation were explored separately in this analysis. The non-invasive photo-identification techniques used in this study were not likely to create a change in behavior as a result of "capture." Response-to-capture alterations may also be attributed to the presence of researchers; however, our small research vessel was not an unusual occurrence in the region and dolphins did appear to be habituated to the presence of similar vessels. Therefore, realistic and more appropriate models that investigated time and individual heterogeneity were the primary focus. CAPTURE also produces estimates based on similar algorithms developed by other authors that also evaluate some of the eight Otis models and give relatively similar results. Specifically, alternative estimators for Model M(t) (Chao 1989), Model M(h) (Pollock and Otto 1983, Chao 1988), and Model M(tb) (Burnham unpublished) are presented.

MARK is an interactive modeling program that provides estimates of specific demographic parameters based on the sighting histories of marked animals. Data from live animal recaptures, band or ring recoveries, known fate (e.g., radio-tracking) or a combination of these data types may be input into the various models offered by this program.   In this study I used the unequal-catchability closed-population models again based on the Otis et al. (1978) models. MARK differs from CAPTURE in that the user is able to experiment with numerous configurations of temporal or behavioral variation. For example, temporal variation can be adjusted to vary by each sighting occasion (the only setting in CAPTURE), by each year, by season or by any other relevant time scale. To aid in model selection, both Aikaike's Information Criterion corrected for small sample sizes (AICc) and deviance are computed. AICc is a transformation of the maximized log-likelihood that has been adjusted for the relatively small ratio of estimated parameters to sample size (Aikaike 1973, Hurvick and Tsai 1989). The goodness-of-fit of a given model is measured by deviance, which is the difference between the log-likelihood value of the fully saturated model versus the present model. Minimum AICc and deviance values were used to choose the best fitting models, and likelihood ratio tests determined whether reduced models could describe the given data as adequately as more saturated models.

RESULTS

From June 1999 to May 2002 over 1800 bottlenose dolphins were seen during 269 sightings (Figure 4.2). Fin matching was able to identify 133 uniquely distinguished individuals during 207 hours of active effort. One individual was sighted six times, but most (58%) were seen only once (Figure 4.3). On a seasonal scale, there was discernible variation in both the number of uniquely identified individuals as well as the minimum number of dolphins seen (Figures 4.2 and 4.4). The seasonality of sightings of individuals that were seen only once was highest in three consecutive seasons in 2000 (Figure 4.4). On-effort hours were plotted against the cumulative number of previously unseen marked dolphins to provide an approximate rate of addition of new individuals into the photo-identification catalog (not shown). Another way of investigating this trend is to create a discovery curve of new individuals versus the total number of individuals seen during surveys (Figure 4.5). The two values (t1 and t2) closest to the point at which the last 10% of cumulative individuals were seen were used to approximate the terminal rate of discovery. Terminal rates of discovery were therefore between 0.001 and 0.030 new individuals per cumulative number of individuals seen during surveys for the final 8.1 % and 12.4 % of cumulative data, respectively.

Based on seasonal sighting histories of individual dolphins, I used CAPTURE to investigate the relative fit of the eight Otis models. A multivariate discriminant function calculated a measure of relative model fit (Table 4.1). As it is unlikely that any behavior modification occurred as a result of photo-identification surveys, these models were ranked in decreasing order of fit, with and without behavioral variation included. Population estimates (N), standard errors (SE) and 95% confidence intervals (95% CI) were calculated for all models (Table 4.2). The decreasing order of model fit for the four models without behavioral variation

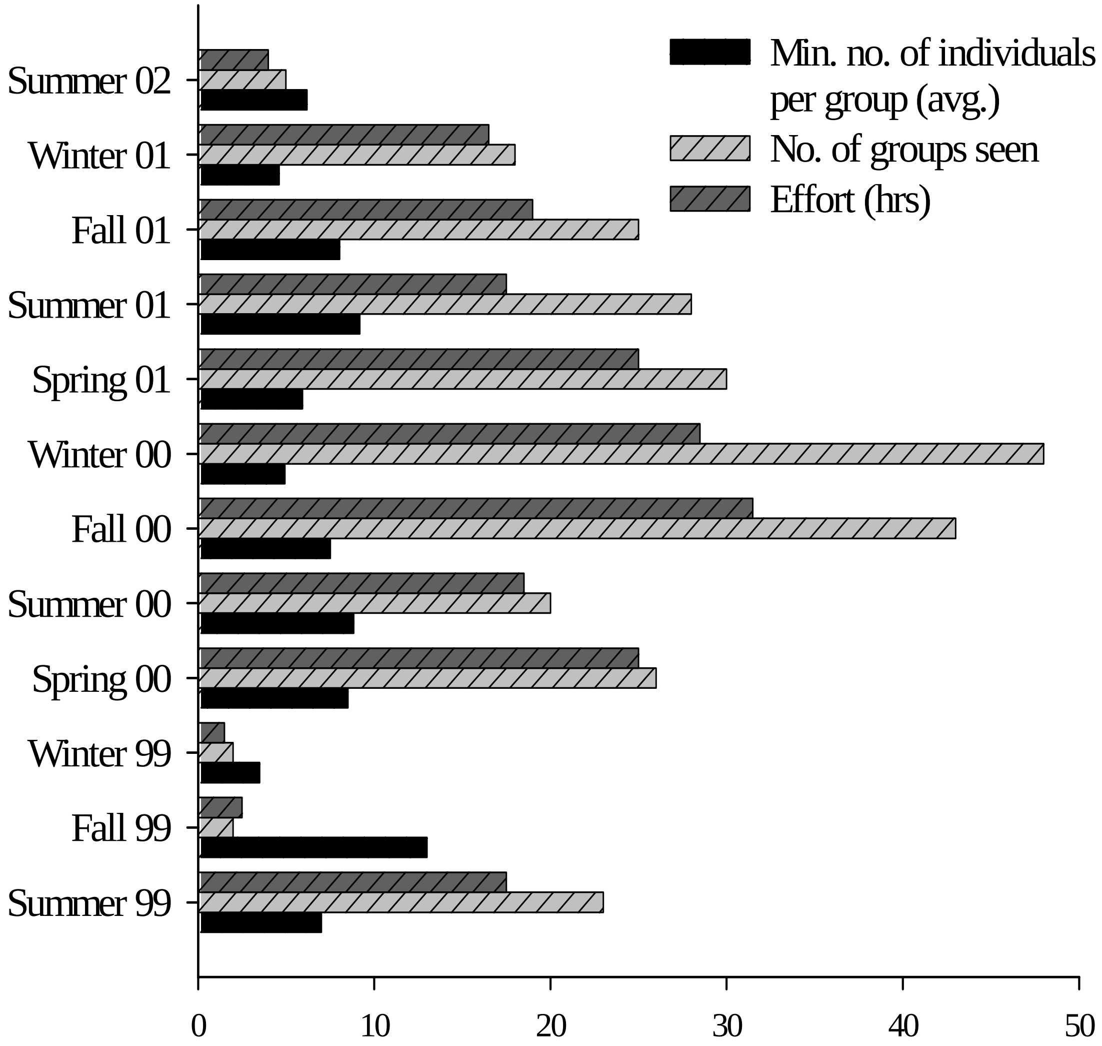

Figure 4.2. Seasonal summary of bottlenose dolphin (Tursiops truncatus) group size (average minimum number of individuals per group), group sighting frequency, and hours of survey effort in Barataria and Caminada Bays, Louisiana, from June 1999 – May 2002.

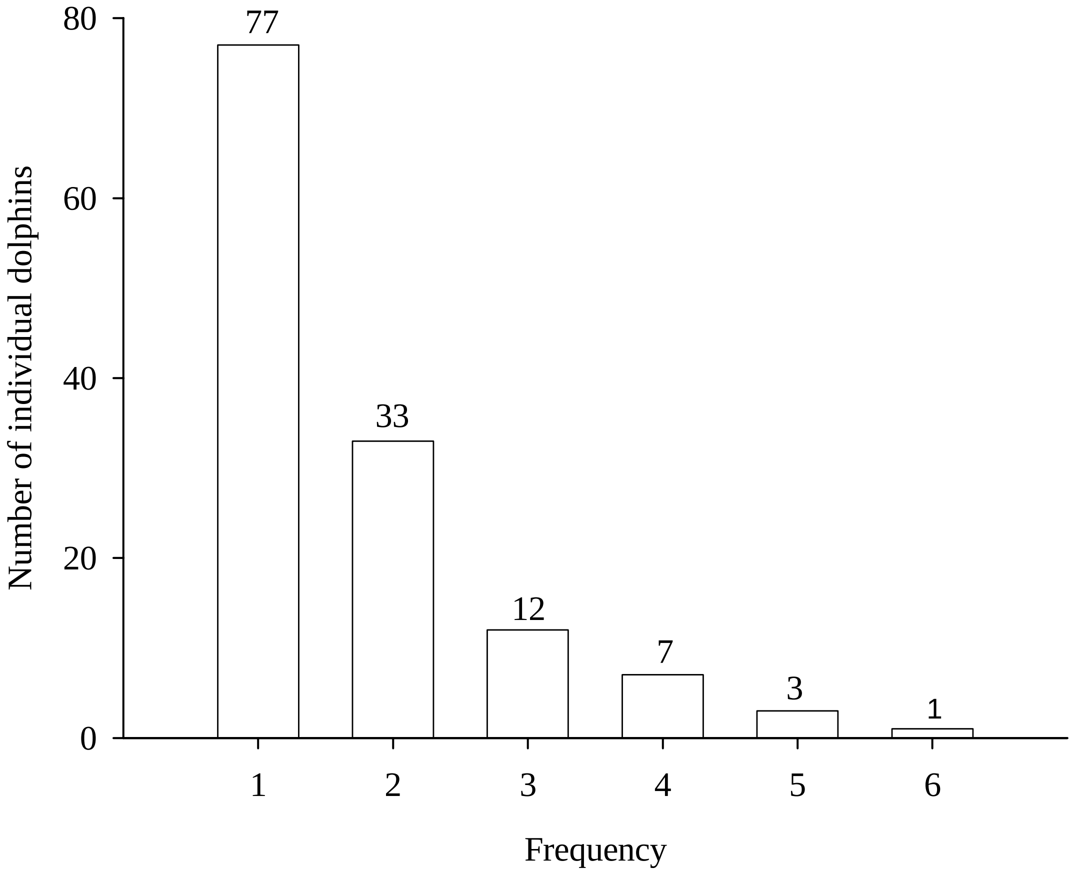

Figure 4.3. Number of sightings for each naturally marked dolphin that was identified in the Barataria and Caminada Bay study area from June 1999 – May 2002.

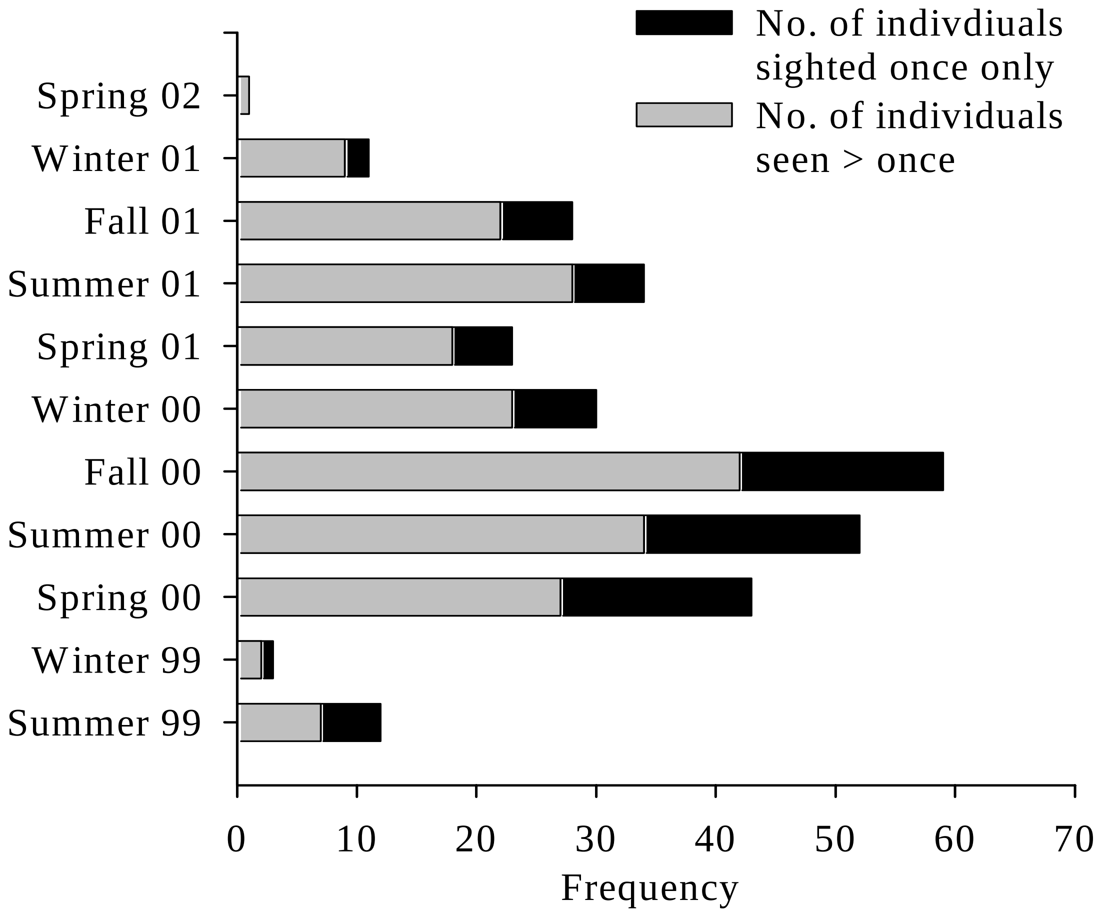

Figure 4.4. Seasonal tabulation of the total number of naturally marked dolphins identified in the Barataria and Caminada Bay study area from June 1999 – May 2002. The number of dolphins seen only once is indicated in black, whereas the entire bar represents the total number of dolphins seen during a given season.

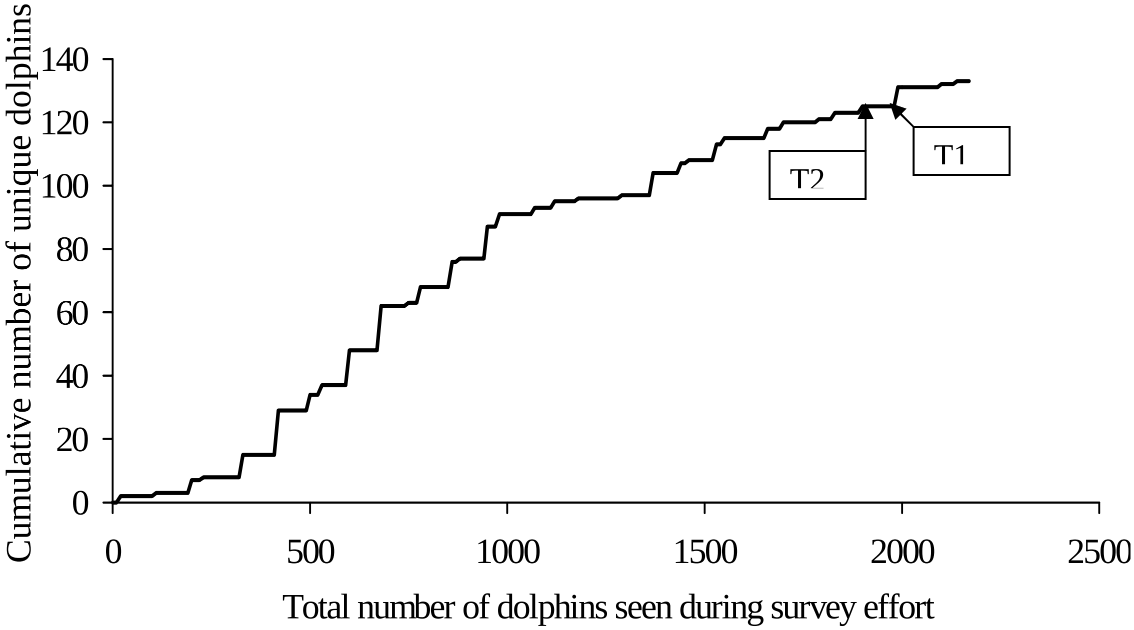

Figure 4.5. ‘Discovery curve’ (Williams et al. 1993) plotting the trend between newly identified naturally marked dolphins (y-axis) versus the cumulative number of dolphins observed during survey effort (x-axis) in Barataria and Caminada Bays from June 1999 – May 2002. The terminal slope (Wilson et al. 1999) was determined by looking at the slope of the last 8 (T1) and 12 (T2) % of cumulative number of individuals seen during surveys.

Table 4.1. Ranking of the eight closed-population unequal-catchability models (Otis et al. 1978) as assessed by the multivariate discriminant model selection criteria in Program CAPTURE. Rankings are based on maximum values and are presented with and without behavioral variation included in the model.

Model	Source of variation	Criteria value	Rank (with behavior)	Rank (without behavior)
M(o)	None	0.51	3	1
M(h)	Heterogeneity	0.43	6	3
M(b)	Behavior	0.30	7	-
M(bh)	Behavior, Heterogeneity	0.67	2	-
M(t)	Time	0.00	8	4
M(th)	Time, Heterogeneity	0.44	5	2
M(tb)	Time, Behavior	0.49	4	-
M(tbh)	Time, Behavior, Heterogeneity	1.00	1	-

Table 4.2. Barataria Bay system bottlenose dolphin population size estimates (Spring 2000 – Winter 2001/02) using closed-population unequal catchability models in Program CAPTURE

Model	Population Estimate	Standard Error	95% Confidence Limits
M(o)	180	13.70	159 - 213
M(t)	177	13.07	157 - 209
M(t) Chao (1989)	198	23.06	166 - 258
M(b)	137	6.73	130 - 157
M(h)	238	24.64	199 - 297
M(h) Chao (1988)	217	28.40	176 - 290
M(h) Pollock & Otto (1983)	138	10.58	128 - 176
M(th) Chao et al. (1992)	220	28.93	178 - 294
M(tb) Burnham	139	11.86	127 - 182
M(bh)	136	11.31	127 - 180

was: M(o), M(th), M(h) and M(t). Model selection criteria for all four models were below the suggested cut-off score of 0.75; however, since these models are a subset of all eight models this may be a moot point. Chi-square goodness-of-fit tests found that models including time and heterogeneity fit the data significantly better ($\alpha < 0.001$) than the more general model M(o). Hence, the variability in sighting probabilities is difficult to conclusively explain. All four models produced fairly similar population estimates; 138 – 238 with an associated 95% CL range of 128 – 297. The only two models whose 95% CLs did not overlap with each other were the Pollock and Otto estimator for M(h) (95% CL = 128-176) and the Chao estimator for M(th) (95% CL = 178-294).

MARK was used to model sighting rates on a yearly, seasonal (with data combined across years), and seasonal (with data separated between years) scales. In addition a constant rate of sighting was also investigated (Tables 4.3 – 4.7). Likelihood-ratio tests showed that seasonal (data not combined across years) variability described the data significantly better than any other configuration of temporal variance (Table 4.3). It should also be apparent that Models A and D (Table 4.3) are identical to CAPTURE models M(t) and M(o), respectively (Table 4.2). When temporal variability was broken down further into monthly time intervals, the resulting models became over-parameterized and produced singular estimates.

DISCUSSION

The first photo-identification research effort for a bottlenose dolphin population in Louisiana’s Barataria Basin system offered several important conclusions and findings. First, with regard to population size, this recent and year-round survey effort of bottlenose dolphins in Barataria and Caminada bays has produced an abundance estimate of between 138 and 238 individuals for this region. The population appears to be relatively closed with some evidence of

Table 4.3. Program MARK closed-population models with year-specific seasonal (A), yearly (B), non-year-specific seasonal (C) and constant (D) capture probabilities ranked by minimal Aikaike's Information Criterion corrected for small sample sizes (AICc) and lowest deviance values. Likelihood ratio test (LRT) statistics were used to compare Models B, C and D with top-ranking model A and included relevant chi-square values, degrees of freedom (DF) and p-values (p).

	Variation in capture probability	AICc	Deviance	LRT with Model A - Chi-square, DF (p)
A	Season (year-specific)	- 45.46	124.19	
B	Year	-38.08	143.73	19.54, 6 (0.0033)
C	Season (non-year-specific)	-36.05	141.72	17.53, 4 (0.0015)
D	Constant	-25.70	158.12	33.93, 7 (< 0.0001)

Table 4.4. Parameter estimates from a Program MARK closed-population model with seasonal (year-specific) probabilities of capture (Model A) where, p = sighting probability during specified time interval. The estimated population size for Model A was 176.78 (95% CL = 156.50 – 209.71).

Sighting Probability - Time Interval	Estimate	Standard Error	95% Confidence Limits
p - Spring 2000	0.14	0.03	0.09 - 0.21
p - Summer 2000	0.19	0.03	0.13 - 0.26
p - Fall 2000	0.24	0.04	0.17 - 0.32
p - Winter 2000/01	0.12	0.03	0.08 – 0.19
p - Spring 2001	0.10	0.02	0.06 – 0.15
p - Summer 2001	0.15	0.03	0.10 – 0.21
p - Fall 2001	0.12	0.03	0.08 – 0.18
p - Winter 2001/02	0.05	0.02	0.03 – 0.10

Table 4.5. Parameter estimates from a Program MARK closed-population model with yearly probabilities of capture (Model B) where, p = sighting probability during specified time interval, and N = population size estimate. Time intervals used for 2000 and 2001 were Spring 2000 – Winter 2000/2001, and Spring 2001 – Winter 2001/2002, respectively. The estimated population size for Model B was 178.34 (95% CL = 157.59 – 211.89).

Sighting Probability – Time interval	Estimate	Standard Error	95% Confidence Limits
p - 2000	0.17	0.02	0.14 - 0.21
p - 2001	0.10	0.01	0.08 - 0.13

Table 4.6. Parameter estimates from a Program MARK closed-population model with seasonal probabilities of capture (Model C) where, p = sighting probability during specified time interval, and N = population size estimate. The estimated population size for Model C was 178.21 (95% CL = 157.51 – 211.72).

Sighting Probability – Time Interval	Estimate	Standard Error	95% Confidence Limits
p - Spring	0.12	0.02	0.09 - 0.16
p - Summer	0.17	0.02	0.12 - 0.22
p – Fall	0.18	0.02	0.13 - 0.23
p - Winter	0.09	0.02	0.06 - 0.12

Table 4.7. Parameter estimates from a Program MARK closed-population model with constant probability of capture (Model D) where, p = probability of sighting throughout the study period, and N = population size estimate. The estimated population size for Model D was 179.51 (95% CL = 158.42 – 213.52).

Sighting Probability – Time Interval	Estimate	Standard Error	95% Confidence Limits
p - constant	0.14	0.01	0.11 - 0.17

site fidelity. Furthermore, the documentation and identification of individual dolphins allows the possibility of comparisons with future studies both in the study area and with those catalogued in other areas of the Gulf of Mexico. Secondly, with regard to variability in sighting probability both programs CAPTURE and MARK strongly indicated that sighting histories of bottlenose dolphins present in the Barataria Basin were variable over time and between individuals. However, determination of whether this variation in sighting probability was specifically attributable to temporal factors (such as season), differences in probability of capture for individuals, or a combination of these factors could not be resolved definitively.

Population Size

Barataria Bay has been recognized as a distinct stock by the U.S. Atlantic and Gulf of Mexico marine mammal stock assessments (Waring et al. 2002). Directly seaward of this purported stock is the western Gulf of Mexico (wGOM) coastal bottlenose dolphin stock. The wGOM stock is characterized as inhabiting the near-shore coastal waters (i.e., from the coastline or presumed bay boundary to 9.3 km seaward of the 18.3 m isobath) from the Texas border to the Mississippi River mouth. Separation of Barataria Bay and wGOM coastal stocks is based on evidence of genetic differentiation between offshore and inshore stocks in other regions (Duffield and Wells 1986) as well as the assumption that the unique oceanographic regimes of inshore and offshore waters would limit movement. The proximity of the Barataria Bay and wGOM stocks makes these distinctions difficult to confirm. However, the meaning of a management stock in this context is not synonymous with the traditional biological definition of a population (Pollock et al. 1990). The term is based on the description of a “community” (after Wells et al. 1987) in which dolphins have a high site-fidelity to the given area (so-called “residents”), possess similar genetic profiles, and interact primarily with each other. This definition permits the possibility of interbreeding with outside members as well as movement into and out of the stock management area. Although a majority of the designated estuarine stocks within the Gulf of Mexico may not strictly fall within the definition of a biological population, they can be described as functioning units of their ecosystem and so are correctly considered discrete under the Marine Mammal Protection Act. The 2002 U.S. Atlantic and Gulf of Mexico Marine Mammal Stock Assessments (Waring et al. 2002) suggests that "biologically-based" criteria, such as movement patterns, genetic profiling and contaminant loads, be combined with traditional field observations to define stock memberships.

High site fidelity has been noted in some coastal estuarine areas of the Gulf of Mexico (Scott et al. 1990, Wells 1991) but not all (Hubard 1998, Maze and Wursig 1999). All population models used in my results were closed-population models. My preliminary surveys of the region ascertained the geographic extent of this population. However, it is unlikely that the closure assumption was strictly met, as evidenced by the high number of individuals sighted only once and the low incidence of re-sightings. Alternatively, the discovery curve indicated a steady decrease in the number of new individuals seen as effort accumulated. The terminal rate of discovery suggests that the Barataria Basin population was relatively closed (Figure 4.5). The range of terminal slopes for this study (0.001 – 0.01) is comparable to Wilson et al.'s (1999) rate of 0.012 for sub-adults and 0.011 for adults in a closed bottlenose dolphin population in Moray Firth, Scotland. However, as noted in Figure 4.3, a majority (77 out of 133 = 58%) of individuals were seen in Barataria Basin on only one occasion. Additionally, my findings are weakened by the fact that this project was a new initiative and survey effort was limited. Furthermore, the detection of significant variability in both temporal and individual sighting rates makes my assumption of population closure provisional.

Extending the duration and geographical extent of the present study is required to strengthen my findings. Proximity to the Western Gulf of Mexico coastal stock as well as the estuarine stock of the Terrebonne and Timbalier bay complex makes interchange with each of these purported populations a plausible occurrence. However, whether these possible interactions are in accord with the flexible Wells et al. (1987) population definition and therefore mirror the social structure of western Florida estuarine stocks, or suggest that the Barataria bay stock is in fact part of a larger northern Gulf of Mexico meta-population requires further investigation.

Variability in Sighting Probability

There are many reasons why individuals have unique probabilities of being sighted during observation periods (Hammond 1990). Individual attributes such as age, gender, social status, and stock association are possible factors influencing both distribution and behavior patterns. Environmental conditions such as movement of potential prey, proximity to fishing vessels, and oceanographic features may also influence sighting probability on a given survey. It is also important to consider possible bias introduced by such avenues as data acquisition, verification of image matching and distinction, and modeling strategy.

Survey strategy can also cause some additional heterogeneity in capture. Non-random mixing of individuals may allow some animals to be seen more often. Moreover, surveys that are not randomized or comprehensive in their coverage of a population's range will also introduce heterogeneity. In these surveys I attempted to minimize heterogeneity by introducing a stratified survey design to ensure that no regions of the study area were preferentially covered or confounded with time of day. Results from model outputs indicated that temporal variability was significant. The occurrence and relative frequency of individuals sighted appeared to be different between 2000 and 2001 (Figures 4.2 and 4.4), yet this configuration (i.e., yearly variation in capture only) was not the best fit for the data according to MARK (Table 4.3). A closer look at the data revealed that these differences appeared to be driven by the small numbers of recaptures in Spring 2001 and Winter 2001/2002. Effort during both of these seasons was comparable to other months, though number of groups seen in Winter 2001/2002 did appear to be slightly lower (Figure 4.2). Logbook entries made during Winter 2001/2002 also indicated that climatic conditions were not ideal for taking photographs. However, survey routes during both seasons were random, covered the study area well, and had experienced observers aboard at all times. It may be possible that unknown behavioral processes, a unique age structuring of the population, or activities in the area may have been the cause of these anomalies in number of re-sightings.

Sources of variability in capture may mask each other to produce ambiguity in interpretation of model results (Otis et al. 1978). Although some of the tests in CAPTURE lack power, null hypotheses were being rejected and so the conclusions are most likely accurate. Relative effort and number of re-sightings can also affect model results. Precision is positively correlated with increasing capture probability (Cormack 1968). In my Program MARK results (Tables 4.4 – 4.7) capture probabilities ranged from 0.05 to 0.24 with a mean of approximately 0.14, and fell between the medium (mean ≈ 0.20) to poor (mean ≈ 0.05) classifications of data. Using simulated data, Otis et al. (1978) found medium quality data to correctly select the models M(o), M(th), M(h) and M(t) with the following percentages: 68.0, 25.5, 66.5 and 57.5. For poor data these percentages changed to 79.0, 5.0, 18.5 and 83.5, respectively. It should be noted that selection of the incorrect model for the simulated data did not always results in estimates that were significantly different from the true population size.

In addition to the assumptions of population closure and equal catchability, the population models used in this study also require that marks are not lost and that marks are correctly identified. Therefore, the natural marking used on individuals must be permanent and sufficiently distinct for the duration of the study, and the images used for each individual must be of sufficient quality to allow consistent identification. Lockyer and Morris (1990) found superficial and deeper scratches, as well as minor wounds to be inadequate natural markings on bottlenose dolphins. They also found that the head, back, dorsal fin and tail flukes were the most likely areas for permanent markings. Wursig and Wursig (1977) noted that both pigment spots and bite marks did not remain visible throughout their study of bottlenose dolphins in Argentina. I found dorsal fin nicks and notches to be suitable and effective natural markings for my study. However, as Hammond (1986) cautions it is important to note that evidence of persistence of a given type of mark does not guarantee identical results from similar wounds. The loss of natural markings would cause population estimates to be inflated.

Treatment of processed images is the next step in ensuring that bias does not enter an abundance assessment. It is imperative that the quality of images used is consistently excellent. Image quality classification must be made independently of the presence or extent of natural markings present on the individual (Friday et al. 2000). This independence ensures that the most distinctive individuals will not be preferentially included or matched. For accurate population estimates it is also important that non-preferential picture acquisition is practiced. Finally, matching efficiency of bottlenose dolphin natural fin markings has greatly benefited by the description of the dorsal fin ratio methods by Defran et al. (1990), as well as the Finscan software developed by Kreho et al. (1999), to assist and speed up a related process.

CONCLUSIONS

Both similarities and differences in residency patterns of individual bottlenose dolphins present in Barataria and Caminada bays, as compared with other regions of the Gulf of Mexico contribute to the understanding of population dynamics for this region. Valuable insight into the life history patterns of bottlenose dolphin populations can also be achieved by investigating population models that are able to account for differences in sighting rates. Significant variability in probability of sighting was found on both temporal and individual scales. However, several other confounding sources affecting the behavior and distribution patterns of wild bottlenose dolphin populations require consideration also (Hammond et al. 1990). Social stability and associations have been well established in cetacean populations (Bigg et al. 1990, Wells 1991). The inherent lack of independence between social affiliates violates assumptions of many basic closed-population models. Although this matter requires further investigation, it potentially affects precision but not necessarily the accuracy of estimators (Wilson et al. 1999). Another factor worthy of consideration is the role that type of activity and group size play in the ability to detect a given individual or group. For example, it seems logical that larger groups or highly acrobatic behaviors would be more visible during surveys. Likewise, one or two individuals engaged in activities with relatively long dive times would be correspondingly more difficult to detect. Some detectability models have been developed (Steinhorst and Samuel 1989) but are not widely incorporated in marine mammal research currently. Additional concerns such as the presence of boat traffic, fishing vessels, and recreational activities in the area all figure into the ability to detect and sample individual dolphins. The use of unequal-catchability models is a starting point for assessing some of these factors, yet it is far from a comprehensive solution. An appropriate future direction is to investigate models that are able to include some of the above-mentioned covariates, such as Forney et al. (1991) was able to do with sea-state in a model for harbor porpoise. Furthermore, the delineation of behavioral or demographic strata of the population with specific sighting rates should also act to increase the relative precision of resulting estimates. In short, any quantitative or qualitative variable that is able to help identify patterns of cetacean distribution is a useful tool for better understanding marine mammal populations and improving the precision and accuracy of population assessments.

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CHAPTER V

DISCUSSION

The bottlenose dolphin (*Tursiops truncatus*) is a well-studied member of the Order Cetacea (Shane et al. 1986, Leatherwood and Reeves 1990) and has been observed in a wide variety of habitats worldwide (Connor and Smolker 1985, Cockroft et al. 1990, Ballance 1992, Williams et al. 1993, Grigg and Markowitz 1997, Harzen 1998, Wilson et al. 1999). Although several projects have focused on bottlenose dolphin populations and "communities" (see Wells et al. 1987) within the northern Gulf of Mexico (Shane 1980, Wells et al. 1987, Mullin 1988, Scott et al. 1990, Wells and Scott 1990, Wells 1991, Brager 1993, Hubard 1998, Maze and Wursig 1999), there has been limited research effort along the Louisiana coast (Hubard and Swartz 2002, Waring et al. 2002). This study focused on the ecology of bottlenose dolphins in lower Barataria and Caminada bays, Louisiana, by combining fine-scale measurements of habitat use and individual identification techniques to describe environmental requirements (Chapter II) and estimate population size (Chapter IV). The latter portion of the field research was further investigated by examining assumptions of the Jolly-Seber model when used to estimate population size of cetaceans from photo-identification data (Chapter III). This research is important because dynamic changes in the Louisiana coastal zone place unknown stressors on the poorly studied bottlenose dolphins in this area. However, trends in abundance can only be determined when satisfactory survey methodology and analyses are used to estimate population size from recent survey effort.

There are several factors that make the Barataria Bay system an interesting location for small cetacean research. Barataria and Caminada bays represent the seaward interface of the Barataria Basin with the northern Gulf of Mexico (Reed 1995). The low-lying inland wetlands include marsh grasses, submerged aquatic vegetation and estuarine ponds (Chesney et al. 2000). Estuarine areas are known to provide important nursery habitat to fishes and crustaceans (Baltz et al. 1998) and have high primary productivity rates (Day et al. 1989, Garrison 1999). However, the Louisiana coastline has undergone significant changes in recent years (Day et al. 1995, Turner 1997). In fact, coastal wetland losses from 1955 to 1978 are estimated to have been as high as 12,700 ha per annum (Baumann and Turner 1990). The continued modification of habitat may have serious repercussions for numerous species in coastal Louisiana ecosystems (Chesney et al. 2000), including bottlenose dolphins.

The description of bottlenose dolphin environmental usage patterns of the Barataria Basin system developed by this study strengthens the database for appropriate management of this relatively discrete Gulf of Mexico stock. Firstly, the unique and changing environment makes it especially important to develop a defendable baseline study of present bottlenose dolphin population size so that any trends associated with habitat loss may be detected. Secondly, the characterization of environmental requirements is valuable because dissimilar oceanographic conditions are cited as one reason for the existence of distinctive inshore and offshore bottlenose dolphin stocks in coastal Louisiana and elsewhere in the northern Gulf of Mexico (Duffield et al. 1983, Duffield and Wells 1986, Waring et al. 2002). Therefore, the careful description of the habitat use by an inshore stock may allow specific differences with the environment of offshore stocks to be detected. It should be noted that environmental habitat usage patterns described in this study characterized habitat selection of measured variables at sites where individuals were observed, but not where they were absent. The basic advantage of this approach is that it uses the bottlenose dolphin's behavior to describe its distribution and abundance in the system and creates a description of environmental requirements from a dolphin's point-of-view (Baltz 1990, Chesney et al. 2000). Future research that is able to accurately characterize the entire study area could provide insights into habitat usage for general and specific activities. I addressed this in a limited fashion using suitability analyses (Chapter II) to compare general habitat use and feeding site selection, but a better characterization of resource availability would greatly increase our understanding of bottlenose dolphin ecology in the Barataria Basin. Likewise, the inclusion of additional environmental variables (such as water velocity, density of boat traffic and presence of prey) as related to patterns of habitat use would clearly enhance insights into possible interactions within the Barataria Basin ecosystem.

Using closed-population unequal-catchability models (Otis et al. 1978) I estimated that 138 – 238 (with associate range of 95% Confidence Limits = 128 – 297) (Chapter IV) bottlenose dolphins were present in my study area. While this is an important contribution to knowledge of bottlenose dolphins in this area, continued year-round monitoring of this population is necessary to detect possible declines and seasonal fluctuations in abundance levels. A methodology for assessing the status of U.S. marine mammal stocks was developed by Wade and Angliss (1997) with limits of mortality being determined by calculation of the potential biological removal (PBR) for the given population (Wade 1997). The PBR is a fisher-related mortality limit which is derived from the product of the minimum population size (i.e., the lower 20th percentile of the distribution of the abundance estimate), maximum population growth rate of the population, and a "recovery factor" based on relative status of the population relative to optimum sustainable population (OSP) (Waring et al. 2002). The current PBR of 1.4 individuals for the Barataria Bay stock (Waring et al. 2002) is based on a population size of 219 individuals as estimated by aerial surveys conducted over a decade ago (Blaylock and Hoggard 1994). This population estimate falls well within the range of estimates produced from my dissertation research. However, if the lower end of my estimates accurately reflects current population levels, the management strategy is misjudging the influence that fishery-related mortalities place on this population and PBR levels should be lowered.

The determination of population closure for the Barataria system was based on decreasing numbers of previously unseen marked individuals as survey effort accumulated, as well as evidence of some degree of site-fidelity for numerous individuals. However, clarification of this tentative characterization as a closed population would obviously benefit from continued research efforts in and adjacent to the study area. As noted in my examination of Jolly-Seber model assumptions (Chapter III) it is imperative that any samples taken be representative of the true population in order for accurate and precise estimates to be made. Extending the duration, intensity and coverage of this initial photo-identification study is an obvious and necessary first step toward satisfying this requirement. Specifically, the geographic range, temporal variation in abundance, and site-fidelity of uniquely identified individuals could be confirmed and more definitively understood. For example, performing similar surveys in regions overlapping the southern end of my study area and extending out onto the central Louisiana coast would be one way to address pertinent stock structure questions.

Findings from this research provide an innovative approach to describing environmental habitat use for dolphins, highlight the necessity to assess statistical methodology when estimating population size from cetacean photo-identification data, and aid in filling important gaps in the understanding of northern Gulf of Mexico bottlenose dolphin stock structure and population dynamics (Hubard and Swartz 2002).

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APPENDIX

CATALOG OF INDIVIDUALS AND ADDITIONAL SIGHTING MAPS

Catalog of Individuals

Titles refer to the number and location of identifying marks present on an individual's dorsal fin. Individual refers to the catalogue number assigned to the dolphin, and observation is the sequential group number the individual was observed with.

One notch on trailing edge

Individual	Observation	Date	Season-yr	Lat	Long
1	80	23-Sep-00	Fall_00	29.27155	-89.967
1	93	5-Oct-00	Fall_00	29.19798	-90.0482
2	53	28-May-00	Spr_00	29.27005	-89.9574
3	144	14-Jan-01	Win_0/1	29.30162	-89.9785
3	151	10-Feb-01	Win_0/1	29.20502	-90.042
3	227	15-Sep-01	Fall_01	29.20872	-90.0746
4	77	22-Sep-00	Fall_00	29.22245	-90.0404
4	117	14-Dec-00	Win_0/1	29.26417	-89.9591
5	61	9-Jul-00	Sum_00	29.23688	-90.0074
5	198	20-Jun-01	Sum_01	29.275	-89.937
6	69	20-Aug-00	Sum_00	29.20288	-90.0828
6	224	15-Sep-01	Fall_01	29.20952	-90.0451
6	243	11-Nov-01	Fall_01	29.19912	-90.0806
7	84	23-Sep-00	Fall_00	29.28728	-89.9372
7	209	8-Aug-01	Sum_01	29.27967	-89.954
7	259	21-Dec-01	Win_1/2	29.20743	-90.0428
8	205	21-Jun-01	Sum_01	29.21028	-90.0611
9	47	30-Mar-00	Spr_00	29.28162	-89.9639
10	77	22-Sep-00	Fall_00	29.22245	-90.0404
10	152	10-Feb-01	Win_0/1	29.21497	-90.0463
11	87	24-Sep-00	Fall_00	29.2458	-89.999
12	94	5-Oct-00	Fall_00	29.26652	-89.9926
12	152	10-Feb-01	Win_0/1	29.21497	-90.0463
12	157	10-Feb-01	Win_0/1	29.26385	-89.959
12	198	20-Jun-01	Sum_01	29.275	-89.937
12	207	21-Jun-01	Sum_01	29.21948	-90.0496
12	227	15-Sep-01	Fall_01	29.20872	-90.0746
13	152	10-Feb-01	Win_0/1	29.21497	-90.0463
14	67	19-Aug-00	Sum_00	29.35502	-89.9783
15	94	5-Oct-00	Fall_00	29.26652	-89.9926
15	211	8-Aug-01	Sum_01	29.2778	-89.9531
16	188	16-May-01	Spr_01	29.34312	-89.8912
16	195	20-Jun-01	Sum_01	29.26647	-89.9628

17	64	19-Aug-00	Sum_00	29.24438	-89.9988
17	141	13-Jan-01	Win_0/1	29.2692	-89.9603
18	172	24-Mar-01	Spr_01	29.28703	-89.9351
18	212	8-Aug-01	Sum_01	29.2805	-89.9447
19	48	30-Mar-00	Spr_00	29.30048	-89.9809
20	41	29-Mar-00	Spr_00	29.26372	-89.9601
20	79	23-Sep-00	Fall_00	29.256	-89.9825
20	246	11-Nov-01	Fall_01	29.23607	-90.011
20	258	21-Dec-01	Win_1/2	29.23112	-90.026
20	264	3-Feb-02	Win_1/2	29.23687	-90
21	153	10-Feb-01	Win_0/1	29.21233	-90.0732
22	1	10-Jun-99	Sum_99	29.2675	-89.9517
22	37	29-Mar-00	Spr_00	29.2076	-90.0806
22	62	9-Jul-00	Sum_00	29.24905	-90.0015
22	152	10-Feb-01	Win_0/1	29.21497	-90.0463
22	220	9-Aug-01	Sum_01	29.20192	-90.0817
22	230	15-Sep-01	Fall_01	29.26387	-89.9642
23	78	23-Sep-00	Fall_00	29.24643	-90.003
24	62	9-Jul-00	Sum_00	29.24905	-90.0015
24	77	22-Sep-00	Fall_00	29.22245	-90.0404
24	151	10-Feb-01	Win_0/1	29.20502	-90.042
24	197	20-Jun-01	Sum_01	29.27368	-89.9521
25	184	16-May-01	Spr_01	29.30162	-89.9758
25	204	20-Jun-01	Sum_01	29.23347	-90.0134
25	212	8-Aug-01	Sum_01	29.2805	-89.9447
26	61	9-Jul-00	Sum_00	29.23688	-90.0074
27	181	16-May-01	Spr_01	29.25817	-89.9896
27	226	15-Sep-01	Fall_01	29.21653	-90.0492
28	44	30-Mar-00	Spr_00	29.20173	-90.0759
29	44	30-Mar-00	Spr_00	29.20173	-90.0759
30	60	9-Jul-00	Sum_00	29.23585	-90.0244
31	212	8-Aug-01	Sum_01	29.2805	-89.9447
32	67	19-Aug-00	Sum_00	29.35502	-89.9783
33	231	16-Sep-01	Fall_01	29.273	-89.9652
34	232	16-Sep-01	Fall_01	29.2982	-89.9755
34	259	21-Dec-01	Win_1/2	29.20743	-90.0428
35	232	16-Sep-01	Fall_01	29.2982	-89.9755
35	259	21-Dec-01	Win_1/2	29.20743	-90.0428
36	233	16-Sep-01	Fall_01	29.30873	-89.9833

Two notches on trailing edge

Individual	Observation	Date	Season-yr	Lat	Long
37	157	10-Feb-01	Win_0/1	29.26385	-89.959
38	60	9-Jul-00	Sum_00	29.23585	-90.0244
38	61	9-Jul-00	Sum_00	29.23688	-90.0074
38	117	14-Dec-00	Win_0/1	29.26417	-89.9591
39	37	29-Mar-00	Spr_00	29.2076	-90.0806
39	114	11-Nov-00	Fall_00	29.21315	-90.084
39	152	10-Feb-01	Win_0/1	29.21497	-90.0463
40	129	15-Dec-00	Win_0/1	29.208	-90.0746
40	153	10-Feb-01	Win_0/1	29.21233	-90.0732
41	33	29-Mar-00	Spr_00	29.29168	-89.9308
41	103	10-Nov-00	Fall_00	29.2625	-89.9542
41	109	11-Nov-00	Fall_00	29.25095	-89.9917
41	152	10-Feb-01	Win_0/1	29.21497	-90.0463
42	57	24-Jun-00	Sum_00	29.30798	-89.9872
43	48	30-Mar-00	Spr_00	29.30048	-89.9809
44	47	30-Mar-00	Spr_00	29.28162	-89.9639
45	53	28-May-00	Spr_00	29.27005	-89.9574
45	58	24-Jun-00	Sum_00	29.33182	-89.9857
45	65	19-Aug-00	Sum_00	29.26877	-89.9581
45	264	3-Feb-02	Win_1/2	29.23687	-90
46	157	10-Feb-01	Win_0/1	29.26385	-89.959
47	62	9-Jul-00	Sum_00	29.24905	-90.0015
48	44	30-Mar-00	Spr_00	29.20173	-90.0759
49	47	30-Mar-00	Spr_00	29.28162	-89.9639
50	37	29-Mar-00	Spr_00	29.2076	-90.0806
50	152	10-Feb-01	Win_0/1	29.21497	-90.0463
50	205	21-Jun-01	Sum_01	29.21028	-90.0611
50	219	9-Aug-01	Sum_01	29.20372	-90.0839
51	65	19-Aug-00	Sum_00	29.26877	-89.9581
52	77	22-Sep-00	Fall_00	29.22245	-90.0404
52	214	8-Aug-01	Sum_01	29.28643	-89.9357
53	101	10-Nov-00	Fall_00	29.2725	-89.9713
54	64	19-Aug-00	Sum_00	29.24438	-89.9988
54	77	22-Sep-00	Fall_00	29.22245	-90.0404
55	95	5-Oct-00	Fall_00	29.26845	-89.9586
55	99	6-Oct-00	Fall_00	29.27008	-89.9583
55	180	16-May-01	Spr_01	29.24597	-90.0021
55	191	17-May-01	Spr_01	29.22945	-90.0243
55	193	17-May-01	Spr_01	29.2301	-90.0239
56	79	23-Sep-00	Fall_00	29.256	-89.9825
56	153	10-Feb-01	Win_0/1	29.21233	-90.0732
57	18	23-Aug-99	Sum_99	29.2722	-89.9536
58	205	21-Jun-01	Sum_01	29.21028	-90.0611

59	18	23-Aug-99	Sum_99	29.2722	-89.9536
60	77	22-Sep-00	Fall_00	29.22245	-90.0404
60	93	5-Oct-00	Fall_00	29.19798	-90.0482
62	53	28-May-00	Spr_00	29.27005	-89.9574
63	234	16-Sep-01	Fall_01	29.31172	-89.9852
64	232	16-Sep-01	Fall_01	29.2982	-89.9755
65	219	9-Aug-01	Sum_01	29.20372	-90.0839
65	220	9-Aug-01	Sum_01	29.20192	-90.0817

Three notches on trailing edge

Individual	Observation	Date	Season-yr	Lat	Long
67	77	22-Sep-00	Fall_00	29.22245	-90.0404
68	17	23-Aug-99	Sum_99	29.2671	-89.9619
69	64	19-Aug-00	Sum_00	29.24438	-89.9988
69	112	11-Nov-00	Fall_00	29.21932	-90.0492
69	172	24-Mar-01	Spr_01	29.28703	-89.9351
69	202	20-Jun-01	Sum_01	29.26262	-89.9728
70	110	11-Nov-00	Fall_00	29.25267	-89.9929
70	203	20-Jun-01	Sum_01	29.2406	-90.0055
71	99	6-Oct-00	Fall_00	29.27008	-89.9583
71	203	20-Jun-01	Sum_01	29.2406	-90.0055
71	208	8-Aug-01	Sum_01	29.26543	-89.9587
72	48	30-Mar-00	Spr_00	29.30048	-89.9809
73	55	24-Jun-00	Sum_00	29.2332	-90.0187
74	224	15-Sep-01	Fall_01	29.20952	-90.0451
75	260	2-Feb-02	Win_1/2	29.26222	-89.961
76	95	5-Oct-00	Fall_00	29.26845	-89.9586
76	232	16-Sep-01	Fall_01	29.2982	-89.9755

Four or more notches on trailing edge

Individual	Observation	Date	Season-yr	Lat	Long
77	44	30-Mar-00	Spr_00	29.20173	-90.0759
78	39	29-Mar-00	Spr_00	29.2535	-89.9834
78	62	9-Jul-00	Sum_00	29.24905	-90.0015
78	77	22-Sep-00	Fall_00	29.22245	-90.0404
78	205	21-Jun-01	Sum_01	29.21028	-90.0611
79	48	30-Mar-00	Spr_00	29.30048	-89.9809
79	64	19-Aug-00	Sum_00	29.24438	-89.9988
79	73	20-Aug-00	Sum_00	29.25158	-89.9802
80	65	19-Aug-00	Sum_00	29.26877	-89.9581
81	172	15-May-01	Spr_01	29.28703	-89.9351
81	206	21-Jun-01	Sum_01	29.21062	-90.0951
81	226	15-Sep-01	Fall_01	29.21653	-90.0492
82	84	23-Sep-00	Fall_00	29.28728	-89.9372
83	9	16-Jul-99	Sum_99	29.2825	-89.9175
83	44	30-Mar-00	Spr_00	29.20173	-90.0759
84	41	29-Mar-00	Spr_00	29.26372	-89.9601
85	64	19-Aug-00	Sum_00	29.24438	-89.9988
85	67	19-Aug-00	Sum_00	29.35502	-89.9783
85	90	5-Oct-00	Fall_00	29.27178	-89.9549
85	203	20-Jun-01	Sum_01	29.2406	-90.0055
85	208	8-Aug-01	Sum_01	29.26543	-89.9587
85	230	15-Sep-01	Fall_01	29.26387	-89.9642
86	226	15-Sep-01	Fall_01	29.21653	-90.0492
87	165	24-Mar-01	Spr_01	29.27168	-89.9633
87	224	15-Sep-01	Fall_01	29.20952	-90.0451
89	37	29-Mar-00	Spr_00	29.2076	-90.0806
89	60	9-Jul-00	Sum_00	29.23585	-90.0244
90	60	9-Jul-00	Sum_00	29.23585	-90.0244
90	229	15-Sep-01	Fall_01	29.2556	-89.9725
91	191	17-May-01	Spr_01	29.22945	-90.0243
92	47	30-Mar-00	Spr_00	29.28162	-89.9639
93	89	5-Oct-00	Fall_00	29.26613	-89.9615
94	93	5-Oct-00	Fall_00	29.19798	-90.0482
95	193	17-May-01	Spr_01	29.2301	-90.0239
96	180	16-May-01	Spr_01	29.24597	-90.0021
97	196	20-Jun-01	Sum_01	29.26948	-89.9474
97	207	21-Jun-01	Sum_01	29.21948	-90.0496
98	61	9-Jul-00	Sum_00	29.23688	-90.0074
99	60	9-Jul-00	Sum_00	29.23585	-90.0244
100	84	23-Sep-00	Fall_00	29.28728	-89.9372
101	180	16-May-01	Spr_01	29.24597	-90.0021
102	98	6-Oct-00	Fall_00	29.26355	-89.9625
102	258	21-Dec-01	Win_1/2	29.23112	-90.026

103	64	19-Aug-00	Sum_00	29.24438 -89.9988
104	64	19-Aug-00	Sum_00	29.24438 -89.9988
105	64	19-Aug-00	Sum_00	29.24438 -89.9988
106	98	6-Oct-00	Fall_00	29.26355 -89.9625

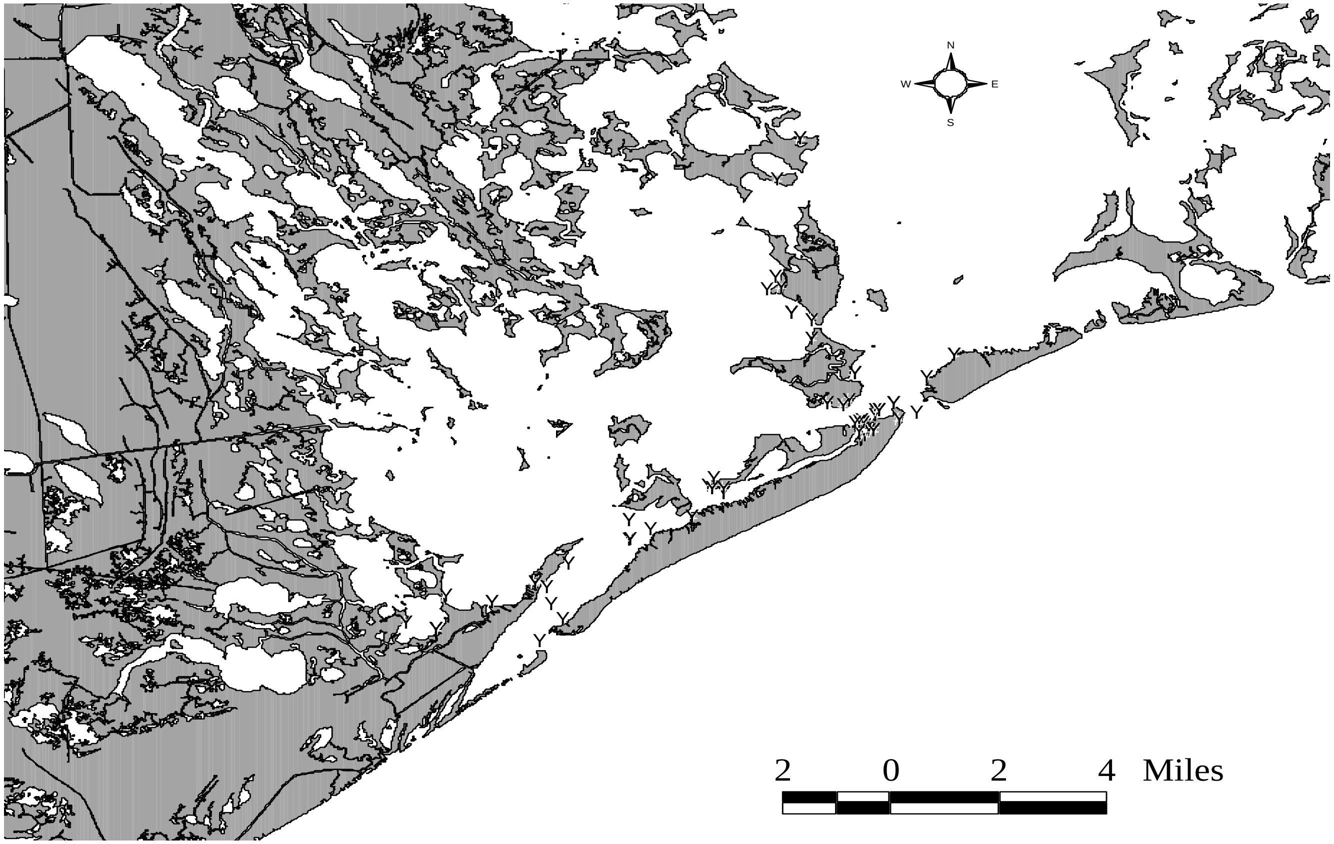
Notches present at tip of fin

Individual	Observation	Date	Season-yr	Lat	Long
107	9	05-Oct-00	Fall_00	29.27178	-89.9549
107	117	14-Dec-00	Win_0/1	29.26417	-89.9591
107	178	15-May-01	Spr_01	29.26842	-89.9575
107	203	20-Jun-01	Sum_01	29.2406	-90.0055
107	208	8-Aug-01	Sum_01	29.26543	-89.9587
108	84	23-Sep-00	Fall_00	29.28728	-89.9372
108	90	5-Oct-00	Fall_00	29.27178	-89.9549
109	89	5-Oct-00	Fall_00	29.26613	-89.9615
109	182	16-May-01	Spr_01	29.29512	-89.972
109	209	8-Aug-01	Sum_01	29.27967	-89.954
110	61	9-Jul-00	Sum_00	29.23688	-90.0074
110	73	20-Aug-00	Sum_00	29.25158	-89.9802
110	93	5-Oct-00	Fall_00	29.19798	-90.0482
111	157	10-Feb-01	Win_0/1	29.26385	-89.959
112	158	10-Feb-01	Win_0/1	29.2679	-89.9582
112	165	24-Mar-01	Spr_01	29.27168	-89.9633
112	167	24-Mar-01	Spr_01	29.30178	-89.9763
112	270	3-May-02	Spr_02	29.26647	-89.9628
113	66	19-Aug-00	Sum_00	29.29245	-89.9752
114	53	28-May-00	Spr_00	29.27005	-89.9574
115	101	10-Nov-00	Fall_00	29.2725	-89.9713
115	116	11-Nov-00	Fall_00	29.19923	-90.0454
116	80	23-Sep-00	Fall_00	29.27155	-89.967
117	99	6-Oct-00	Fall_00	29.27008	-89.9583
118	95	5-Oct-00	Fall_00	29.26845	-89.9586
119	64	19-Aug-00	Sum_00	29.24438	-89.9988
120	219	9-Aug-01	Sum_01	29.20372	-90.0839
120	232	16-Sep-01	Fall_01	29.2982	-89.9755

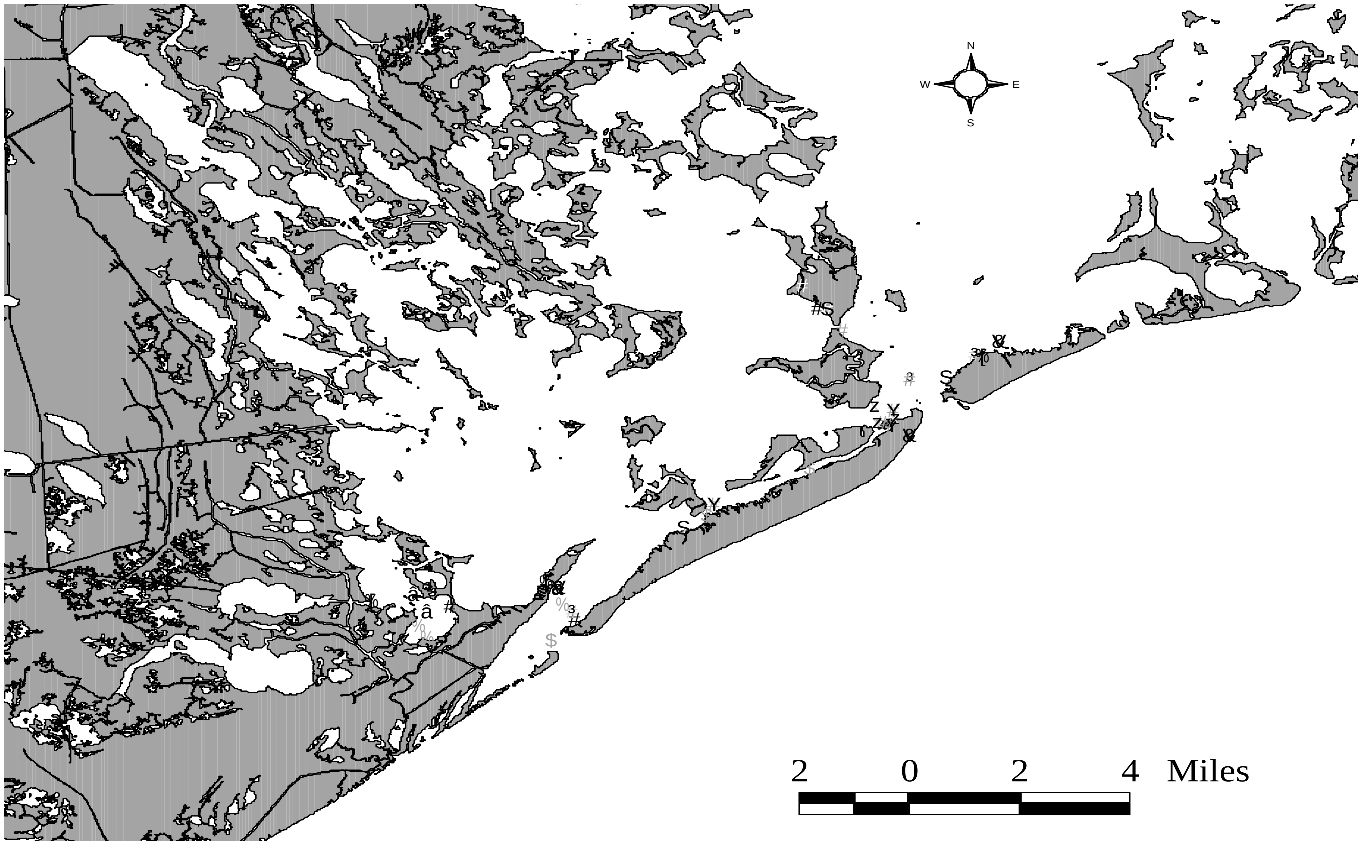
Notches present on leading edge

Individual	Observation	Date	Season-yr	Lat	Long
121	55	24-Jun-00	Sum_00	29.2332	-90.0187
121	154	10-Feb-01	Win_0/1	29.1968	-90.0837
121	194	17-May-01	Spr_01	29.24932	-89.988
121	226	15-Sep-01	Fall_01	29.21653	-90.0492
121	251	20-Dec-01	Win_1/2	29.21628	-90.0493
122	204	20-Jun-01	Sum_01	29.23347	-90.0134
122	219	9-Aug-01	Sum_01	29.20372	-90.0839
123	251	20-Dec-01	Win_1/2	29.21628	-90.0493
124	151	10-Feb-01	Win_0/1	29.20502	-90.042
125	44	30-Mar-00	Spr_00	29.20173	-90.0759
126	169	24-Mar-01	Spr_01	29.34215	-89.9847
126	170	24-Mar-01	Spr_01	29.3543	-89.9687
127	1	10-Jun-99	Sum_99	29.2675	-89.9517
128	195	20-Jun-01	Sum_01	29.26647	-89.9628
129	53	28-May-00	Spr_00	29.27005	-89.9574
130	18	23-Aug-99	Sum_99	29.2722	-89.9536
131	63	9-Jul-00	Sum_00	29.26613	-89.9639
132	25	10-Dec-99	Win_9/0	29.2726	-89.9513
132	185	16-May-01	Spr_01	29.30913	-89.9822
132	197	20-Jun-01	Sum_01	29.27368	-89.9521
133	64	19-Aug-00	Sum_00	29.24438	-89.9988
134	93	5-Oct-00	Fall_00	29.19798	-90.0482
134	101	10-Nov-00	Fall_00	29.2725	-89.9713
135	112	11-Nov-00	Fall_00	29.21932	-90.0492
135	150	10-Feb-01	Win_0/1	29.20493	-90.0446

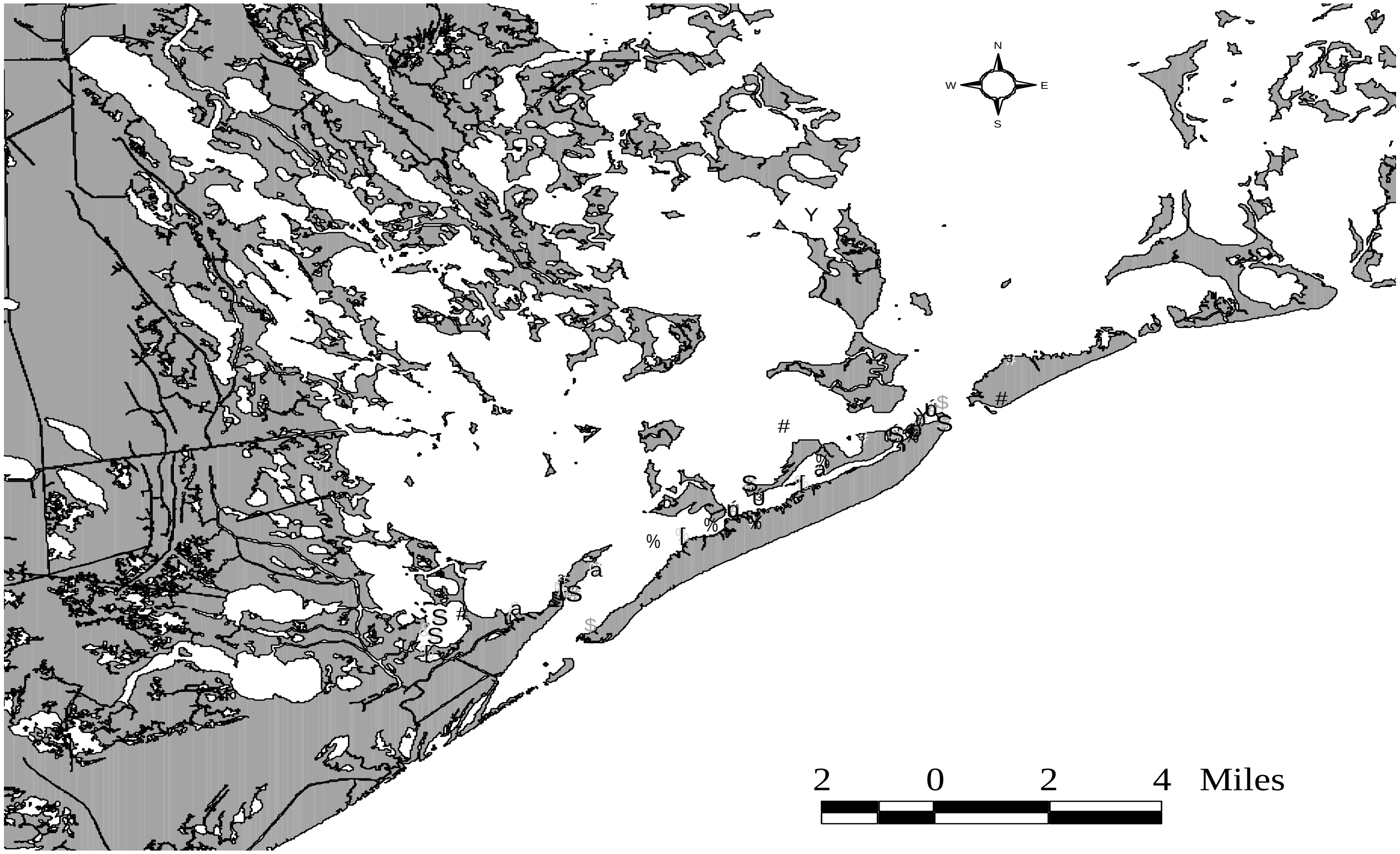
Additional Sighting Maps



Sighting locations of individual bottlenose dolphins seen only once during surveys of Barataria and Caminada Bays, Louisiana, from June 1999 to May 2002.



Sighting locations of individual bottlenose dolphins seen three times during surveys of Barataria and Caminada Bays, Louisiana, from June 1999 to May 2002.



Sighting locations of individual bottlenose dolphins seen three times during surveys of Barataria and Caminada Bays, Louisiana, from June 1999 to May 2002.

VITA

Cara Miller was born in Stirling, South Australia, on July 8th 1975. She is the daughter of Robert Miller and Donna Gavin and the younger sister of Robin Tuan. She attended Heathfield High School in the Adelaide Hills, finishing in 1992. The following year Cara accepted a tennis scholarship to Lewis-Clark State College in Idaho. At the start of her junior year she transferred to the University of Portland, Oregon, where she received a Bachelor of Science degree in life science in May 1997. After graduation Cara moved to Alaska and worked as a fisheries biologist for the National Marine Fisheries Service. This experience confirmed her interest in pursuing a graduate degree in the marine sciences. She entered the Department of Oceanography and Coastal Sciences at Louisiana State University in the fall of 1998 with a Board of Regents fellowship. While pursuing her doctoral degree, she completed a master's degree in applied statistics in May 2002 with advisor Dr. E. Barry Moser. She will earn her doctoral degree in oceanography and coastal sciences in December 2003 under the supervision of Donald M. Baltz.