A Dissertation

by

JOHN T. FROESCHKE

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DEFINING ESSENTIAL FISH HABITAT: THE INFLUENCE OF LIFE HISTORY, BIOTIC, AND ABIOTIC FACTORS

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This dissertation meets the standards for scope and quality of
Texas A&M University--Corpus Christi and is hereby approved.

Gregory W. Stunz, Ph.D., Chair

Mark Wildhaber, Ph.D., Co-chair

David McKee, Ph.D., Committee Member

Paul Montagna, Ph.D., Committee Member

Blair Sterba-Boatwright Ph.D., Graduate Faculty Representative

Harvey Knull, Ph.D.
Associate Vice President for Research and Scholarly Activity and
Dean of Graduate Studies

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Major Subject: Coastal and Marine System Science

ABSTRACT

Defining Essential Fish Habitat: The Influence of Life History,
Biotic, and Abiotic Factors

(January, 2010)

John T. Froeschke, B.S., Arizona State University
M.S. California State University, Northridge
Chair of Advisory Committee: Dr. G. Stunz

ABSTRACT

The world's fisheries have been the subject of much recent concern due to dramatic declines in their abundance, and have continued despite increased single-species management of many harvested species. As a result, management of marine ecosystems is shifting toward an ecosystem-based approach, where the importance of interactions among physical, biological, and human components of the system is recognized. However, ecosystem-based approaches rely on our ability to efficiently and effectively assess critical habitat necessary for ecosystem sustainability; for fisheries, this is known as Essential Fish Habitat (EFH). Currently, few marine systems have adequate information about EFH to implement ecosystem-based approaches to resource management, despite federal mandates to delineate and characterize these areas. The paucity of data is particularly absent beyond typical habitat-density assessments. Undoubtedly, what makes a habitat essential is a variety of abiotic and biotic interactions, but these types of information for even the most important fisheries have seldom if ever been evaluated. This dissertation research seeks to combine several aspects of Essential

Fish Habitat, specifically, the influences of abiotic, biotic, and life history on habitat use of estuarine and coastal fishes. Research was carried out using a multi-disciplinary approach integrating biological and physical sciences to improve our understanding of habitat requirements for ecologically and economically important species.

The primary goal of this dissertation was to assess environmental and biological factors that influence the quality of fish habitat. However, applying general habitat requirements for marine fishes that exhibit widely diverse and complex life history strategies can be particularly problematic. Thus, representative species from highly migratory species (sharks) and both estuarine dependent and estuarine-resident teleosts were assessed to make predictions concerning EFH across a broad spectrum of life history strategies.

Using a long-term fisheries independent dataset, I conducted the first experimental test of the 'shark nursery area concept' and identified areas along Texas' central coast as shark nursery habitat. This concept was further investigated by developing spatially-explicit estuarine habitat use models based on environmental conditions for three coastal shark species: bull (*Carcharhinus leucas*), blacktip (*Carcharhinus limbatus*), and bonnethead (*Sphyrna tiburo*) to delineate within-bay patterns of habitat usage and to determine relationships between environmental predictors and shark distribution. Status and trends of shark species in the nearshore Gulf of Mexico were also assessed using historical and current fishery-dependent data. From 1973 to 1986 and 2008 to 2009, I examined shark capture logs from recreational shark anglers on the Texas coast to characterize catch patterns, species composition, and

temporal patterns of coastal shark abundance in this region as no data currently exist and the population status for sharks in this region is uncertain.

Habitat selection and movement patterns were also investigated for representative species exhibiting a more typical estuarine-dependent life cycle using experimental mesocosms and otolith stable isotope analyses. Mesocosm experiments examined the relative influence of dissolved oxygen concentration, food abundance, habitat complexity, and predator density on habitat selection patterns of juvenile pinfish (*Lagodon rhomboides*) and Atlantic croaker (*Micropogonias undulatus*). Results from experimental mesocosoms indicate that for young (or small) fishes, the influence of predator density may be the primary determinant of fish habitat use. However other factors including dissolved oxygen or habitat type also influence habitat selection, often in complex or interactive patterns.

Connectivity among essential areas is also recognized as a critical factor influencing population dynamics of aquatic organisms. Spotted seatrout (*Cynoscion nebulosus*) is an economically and ecologically important species in the Gulf of Mexico and supports large recreational fisheries throughout its range. However, regional declines of spotted seatrout stocks on the south Texas coast have prompted concerns about the connectivity of fish among management regions in this area and the effectiveness of recently implemented regional management for this species, but essential habitat and connectivity among populations hinders proper management To examine connectivity of trout populations over a large scale, stable carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) isotopes in otoliths were used to assess the degree of exchange of adult spotted seatrout from five regions on the south Texas coast. Cross-validated classification success to five regions of

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Lastly, I thank my wife Bridgette for providing love, assistance, and encouragement. I will try to be as gracious as you have been in returning the favor. My parents Joe and Wilma have provided continued encouragement since my college career began in 1996. Words cannot convey my appreciation to them; I can only hope that following through on my promise to finish college will suffice.

DEDICATION

In dedication to my parents Joe and Wilma Froeschke.

INTRODUCTION

The world’s fisheries have been the subject of much recent concern due to dramatic declines in their abundance (Pauly et al. 2002, Christensen et al. 2003, Myers & Worm 2003; Baum & Myers 2004, Baum et al. 2005, Myers et al. 2007). Overfishing has clearly been a driving factor (Jackson et al. 2001), but other human activities have also been important in their decline (Hilborn et al. 2003, Heuter et al. 2005). This may have cascading ecological impacts, as ecosystems rely on critical trophic links for stability, resilience, and persistence (Steele & Schumacher 2000, Jackson et al. 2001, Worm et al. 2002, Myers & Worm 2003). This trend is most apparent when large portions or entire trophic levels (i.e., large predators) are removed from ecosystems (Pauly et al. 2002, Myers et al. 2007) disrupting a variety of complex ecological relationships. Moreover, overfishing combined with rapidly expanding coastal degradation (e.g., hypoxia) may severely impact fisheries population dynamics and habitat quality in coastal ecosystems (Diaz & Rosenburg 1995).

To address these problems in a more holistic approach, management of marine ecosystems is shifting towards an ecosystem-based approach where the importance of interactions among physical, biological, and human components of the system are recognized (Pikitch et al. 2004, Marasco et al. 2007). Management from an ecosystem perspective is focused on sustaining critical habitats and maintaining critical trophic linkages. This may mitigate anthropogenic influences and promote sustainable use of marine resources (Pikitch et al. 2004). However, ecosystem-based management relies on our ability to efficiently and effectively assess critical habitat necessary for ecosystem sustainability (Levin & Stunz 2005); for fisheries, also known as Essential Fish Habitat

(EFH). Essential fish habitat means those waters and substrate necessary to fish for spawning, breeding, feeding, or growth to maturity (Magnuson-Stevens Act, 16 U.S.C. 1801 et seq). Implementation of this management strategy has been problematic because of significant knowledge gaps regarding critical habitat use, population dynamics, and habitat degradation in marine habitats.

Traditionally, assessments of EFH have focused on density patterns within habitat types (Gallaway & Cole 1999). This information is obviously important, but EFH extends well beyond simple habitat-density relationships to include interactions among the biotic and abiotic characteristics of the habitat and how migration can influence defining these critical areas. This is especially true for species that use habitat in non-traditional ways (e.g., coastal migratory sharks) and even for estuarine resident species such as spotted seatrout (*Cynoscion nebulosus*) that may have relatively large ranges within the estuary and even in nearshore areas. Thus, these species make ideal models for comparative purposes while taking the concept of EFH characterization to the next level.

While one solution is to declare entire estuaries or regions as essential habitat , it is also apparent that we do not have adequate resources to conserve, protect, or restore these areas over such large spatial scales (Levin & Stunz 2005). Thus, the fist logical step is to prioritize critical areas for conservation and management which requires identification of sensitive life stages (Levin & Stunz 2005, Kinney & Simpfendorfer 2009), determination of what habitats (if any) are important to these stages, and identification of areas where high densities of organisms in critical life stages occur (Levin & Stunz 2005). For fish, survival rates of juveniles often exert the greatest influence on subsequent adult population size (Caley et al. 1996). Areas supporting high densities of juveniles with characteristics amenable to growth and survivorship have been deemed “nursery habitats” and constitute an important component of EFH (Beck et al. 2001, Heupel et al. 2007). The value of nursery habitats has been described for estuarine and coastal migratory fishes (Beck et al. 2001, Heupel et al. 2007). However in practice, the designation of nursery habitat has been slow, especially for species that use habitats in non-traditional ways (such as sharks), and this has impeded the management at the marine ecosystem level.

The goal of this dissertation research was to compare and contrast EFH parameters for marine fishes that exhibit estuarine-dependent and migratory life history strategies. Using sharks as model species, I identified and mapped nursery areas for three coastal shark species while examining the relative influence of several environmental factors on their distribution patterns to provide much needed information for ecosystem level management. My dissertation work also examined habitat use and movement patterns of estuarine fishes. I used manipulative laboratory mesocosm choice experiments to examine hierarchical and interactive relationships influencing habitat selection of juvenile estuarine fishes.

Increasingly, rates of connectivity among important habitats is recognized as an important factor regulating population dynamics (Able et al. 2005, Gillanders 2005, Rooker et al. *In press*) and a greater understanding these patterns is imperative for ecosystem level management. Habitat use affects population level responses to environmental change and fishing pressure (Kerr et al. 2007), and information on movement and mixing patterns is essential for the management of estuarine-associated fishes (Levin and Stunz 2005). To address this, I examined connectivity patterns among estuaries for spotted seatrout as there are significant gaps in our understanding of the movement and migration patterns of this important species. Moreover, spotted seatrout exhibits an estuarine life-cycle common to many other estuarine teleost species, therefore providing insight into the movement and connectivity patterns of similar estuarine species.

Collectively, it is my goal that this body of work will contribute to better management of sustainable fisheries in marine ecosystems and refinement of EFH characterization. This study identified nursery habitat for coastal and estuarine fishes in the Gulf of Mexico and evaluate the effects of migration patterns, and the interactive effect of abiotic habitat degradation (e.g., hypoxia) on these critical habitat functions. This project will aid in the prioritization of habitat for management and improve our understanding of the species-habitat requirements that is essential for effective management of marine resources.

CHAPTER 1

TESTING THE SHARK NURSERY AREA CONCEPT IN TEXAS BAYS USING A LONG-TERM FISHERIES-INDEPENDENT DATASET

ABSTRACT

Using a long-term fisheries independent dataset, the “shark nursery area concept” recently proposed by Heupel et al. (2007) was tested using the working assumptions that juvenile shark nursery habitat would: 1) have an abundance of juveniles greater than the mean abundance across all habitats where they occur; 2) use same areas repeatedly through time (years); and 3) remain within the habitat for extended periods of time. I tested this concept using young-of-the-year (Age 0) and juvenile (Age 1+) bull sharks (*Carcharhinus leucas*) from gill-net surveys conducted in Texas estuaries from 1976-2006 to determine the nursery function of nine coastal estuaries. Of the nine bay systems considered for primary bull shark nursery habitat, only Matagorda Bay satisfied all three criteria for both cohorts. Both San Antonio and Matagorda Bays satisfied the criteria as nursery habitat for juveniles. Through these analyses I identified the utility of this approaching for characterizing nursery areas, and also note some practical considerations, such as of the influence temporal or spatial scales of the study when applying the nursery role concept to shark populations.

INTRODUCTION

The shark nursery concept has existed for nearly a century but has rarely been empirically tested (Heupel et al. 2007). However, precipitous declines in global shark populations have prompted concerns among fisheries scientists about the long-term sustainability of sharks (Stevens et al. 2000), and has prompted increased focus on delineating important areas for their persistence to avoid potential ecosystem level responses associated with declines of apex predators (Heithaus et al. 2008). Management and conservation of sharks now incorporates Essential Fish Habitat (EFH) into Fishery Management Plans (NOAA 1996) which recognizes that all stages in a life cycle are important; including juvenile habitat. For many marine species there is a strong link between adult population size and juvenile recruitment patterns (Smith et al. 1998, Beck et al. 2001, Levin and Stunz 2005, Kraus and Secor 2005, Fodrie and Levin 2008); thus, delineating important juvenile habitats (nurseries) should improve shark conservation and management (NMFS 2006). However until recently, shark nursery areas were inconsistently defined and their migratory nature makes empirical demonstration of nursery habitats difficult or in some cases impossible (Heupel et al. 2007).

Meek (1916) first described shallow coastal areas as nursery habitat for *Galeorhinus sp*. and *Mustelus sp*. as general shark nursery habitat. Springer (1967) described typical shark nursery habitat use where young are born in spring or summer in shallow waters and remain there for feeding and growth; noting, however, that sharks may move from the area if forced by seasonal or temperature changes. Bass (1978) described both primary nursery areas (where females give birth or lay eggs) and secondary nurseries where older juveniles (Age 1+) remain for several years growing to maturity. Based on these observations, a number of studies have attempted to improve the nursery concept either by identifying and mapping shark nurseries (Grubbs and Musick 2007, Neer et al. 2007) or with ecological investigation of habitats where sharks occur (Simfendorfer et al. 2005, Hight and Lowe 2007, Heithaus et al. 2009, Papastamatiou et al. 2009, Ubeda et al. 2009). Both have improved our understanding of shark nursery use. However, Beck et al. (2001) suggest that other important parameters such as growth rate, survivorship, and connectivity to adult habitats be considered. However, determining these metrics is particularly problematic for highly mobile species such as sharks.

Unfortunately, the use of the term "shark nursery" habitat has varied widely in the literature, with some putative nurseries having been identified based only on the presence of a few juvenile sharks (Heupel et al. 2007). Thus, the general occurrence approach potentially identifies all coastal habitats as essential, restricting our ability to prioritize areas for conservation and management (Levin and Stunz 2005). Because not all habitats occupied by juveniles should be considered nursery habitat (Driggers III et al. 2008), more information is needed to assess nursery function and prioritize habitat for management (Beck et al. 2001, Heupel et al. 2007). To address this problem, Heupel et al. (2007) outlined a more tractable concept for the identification of shark nursery habitat by obtaining information on abundance, residency, and temporal patterns of sharks within potential nursery habitats. To identify shark nursery habitat several criteria must be met: 1) the abundance of juvenile sharks in a specific habitat is greater than the mean abundance in all habitats where juveniles occur; 2) juvenile sharks must use the habitats repeatedly through time (years); and 3) juvenile sharks must remain within the habitat for extended periods of time.

Coastal estuaries have been recognized as important nursery habitats for many aquatic species, including sharks. The shallow waters of the Gulf of Mexico support a diverse and abundant shark assemblage, including the Texas Coast (Hueter and Tyminski

2007, McCandless et al. 2007, Froeschke Chapter 2). The north-central Gulf of Mexico provides nursery habitat for several shark species including bull shark (Parsons and Hoffmayer 2007, Neer et al. 2007, Heuter and Tyminski 2007). Bull shark (*Carcharhinus leucas*) is the most abundant coastal shark in Texas estuaries (Chapter 2), and this species is known to use nurseries (Simpfendorfer et al. 2005, Neer et al. 2007, Heupel and Simpfendorfer 2008, Ortega et al. 2009). O'Connell et al. (2007) reported long-term declines of bull sharks in the Northern Gulf of Mexico, which is especially problematic because nursery habitats and long-term population trends for this species have not been investigated in Texas waters. Hueter and Tyminski (2007) examined temporal and distributional patterns of juvenile sharks off Florida and Texas. In this study, juveniles from at least 12 shark species were identified in Texas, and results suggested that several species use coastal habitats within the Gulf of Mexico as primary and/or secondary nurseries. Currently, the estuaries along the entire Texas coast are considered nursery habitat for bull sharks based only on the presence of juveniles within these (or similar) areas (McCandless et al. 2002, Hueter and Tyminski 2007, McCandless et al. 2007). However, Froeschke Chapter 2) developed a long-term fisheries independent shark catch data set to examine coastal shark habitat value in Texas estuaries based on environmental conditions for bull (*Carcharhinus leucas*), blacktip (*Carcharhinus limbatus*), and bonnethead (*Sphyrna tiburo*) sharks. In this study they found that habitat value varies greatly among estuaries in this region and that shark distribution patterns were closely linked to salinity, temperature, and proximity to inlets to the Gulf of Mexico. Bull shark was the most abundant shark species and most individuals captured were juveniles (based on length) suggesting that portions, but unlikely all of the Texas coast represents nursery habitat for this species.

In this study I evaluated bull shark temporal and spatial distribution patterns within nine major estuaries along the entire Texas coast from 1976 to 2006 to test the shark nursery hypothesis concept outlined by Heupel et al. 2007. I describe nursery habitat for an important apex predator and discuss some practical limitations of empirically applying the nursery hypothesis concept to help improve management and delineation of Essential Fish Habitat (EFH) for sharks.

MATERIALS AND METHODS

Study Area

This study was conducted in nine major bay systems along the Texas coast in northwestern Gulf of Mexico from 1975 to 2006 (Figure 1.1). Barrier islands separate estuaries from the Gulf of Mexico along the majority of the coast and saltwater exchange occurs via six major tidal inlets. Texas bays are shallow subtropical estuaries that are physically dynamic and most are proximally located near several large human population centers. This region supports a variety of habitat types and provides nursery habitat for many teleost and invertebrate species (Reese et al. 2008).

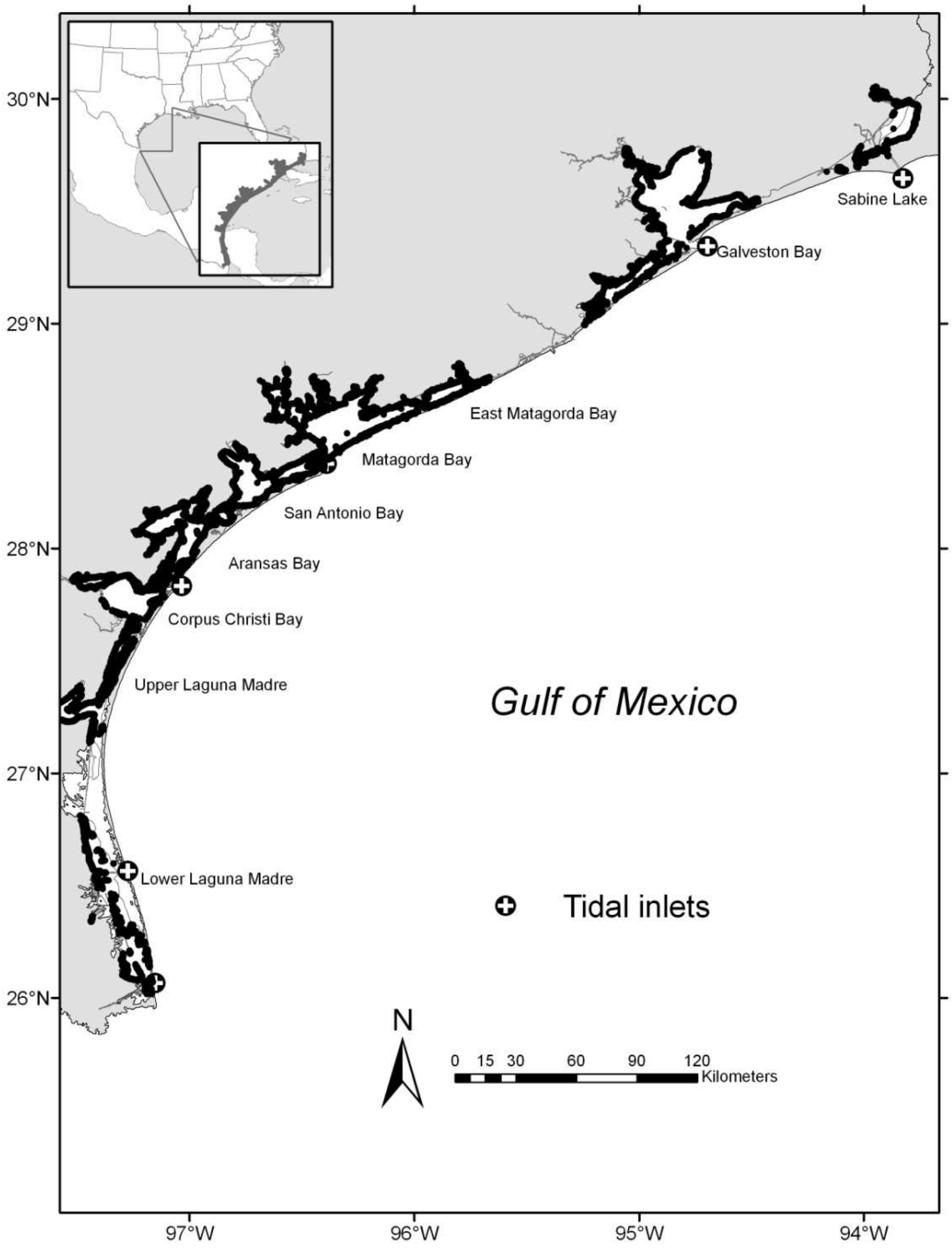


Figure 1.1. Coastal shark gill-net survey locations (n = 19709) from 1976-2006 along Texas, USA in the northwestern Gulf of Mexico. Dark shaded areas indicate where a gill net was set during the study period.

Field Collections

Bull shark catch data were obtained from Texas Parks and Wildlife Department coast wide fisheries gill-net monitoring program that was established in nine Texas bay systems in 1975 and continued through 2006. Coastal Fisheries resource monitoring data were collected as a stratified cluster sampling design; each bay system serves as non-overlapping strata with a fixed number of samples (n = 45/bay/season). Gill-nets were deployed each spring (April, May, June) and fall (September, October, November; Martinez-Andrade et al. 2009). Sample locations were drawn independently and without replacement for each season (Martinez-Andrade et al. 2009). Bull sharks were sampled using standardized 183-m gill-nets perpendicular to shore. Nets were constructed of four panels with mesh size of 76 mm, 102 mm, 127 mm, and 152 mm, respectively. Gill nets were deployed one hour before sunset, fished overnight, and retrieved within four hours of sunrise the following day, and a total set time was calculated for each sample. Each captured shark was identified to species, measured, and released. Abundance data were converted to catch-per-unit-effort (CPUE) by dividing "soak-time" of each net by the number of bull sharks captured in the sample.

This study focused on identification of both primary (i.e., young-of-the-year) and secondary (i.e., juveniles) nursery habitat. Age class of sharks was estimated from total length using published length-at-age estimates (Branstetter and Stiles, 1987, Neer et al. 2005). Bull sharks have wide ranges in size at birth (Neer et al. 2005), between 633-839 mm TL (Clark and von Schmidt 1965), and growth rates of 150-200 mm yr^{-1} (Branstetter and Stiles 1987). For this study, bull sharks < 900 mm TL were considered young-of-the-year (YOY) and used to identify primary nursery habitat. Sharks between 900 and

1600 mm TL were considered immature juveniles (hear after referred to as “juvenile(s)”) and used to identify secondary nursery habitat.

Delineation of nursery areas was based on the criteria of Heupel et al. (2007) and was tested using weighted least squares regression to simultaneously determine spatial and temporal patterns of shark abundance within each bay system. Prior to analyses, shark CPUE data from the 45 nets per season per bay were aggregated into a single mean value per season per bay. Seasonal data were subsequently aggregated into an annual mean value per bay system to stabilize variance and to remove excess zeros from the matrix (Pondella et al. 2008). Upper Laguna Madre was excluded from the analysis as no bull sharks were captured in this estuary during the 30-y study. Young-of-the-year and juvenile bull shark catch data were analyzed separately to assess ontogenetic shifts in nursery use patterns. Preliminary analyses of bull shark CPUE indicated that despite improvement from transformation, model residuals were not normally distributed, variance differed among estuaries, and residuals were temporally auto-correlated.

Weighted least squares with restricted maximum likelihood estimation (REML) was used with the following model:

$$y_{ij} = a_i + b_j + ab_{ij} + \varepsilon_{ij}$$

where

- y_{ij} is log10CPUE for bay i in year j
- a_i is the effect of bay i, $i = 1, \ldots 8$
- b_j is the effect of year j, $j = 1976 \ldots 2006$
- ab_{ij} is the interaction effect of bay with year

- ε_{ij} is the residual for bay i in year j

In addition, because of autocorrelation effects from year to year, the residuals were given a first-order autoregressive (AR1) structure; that is,

$$\varepsilon_{ij}\,(j+1) = \rho\varepsilon_{ij} + \eta_{ij}$$

$$\eta_{ij} \sim \boldsymbol{N}(0,\sigma^2_{\eta i})$$

That is, the time series for each bay has the same autocorrelation ρ, and the residuals from the AR1 process are normal with mean 0 and different variances permitted for each bay *i*. I used Akaike's information criterion (AIC) and log-likelihood ratio test to determine whether the more complex variance and/or error structures were warranted. Non-parametric bootstrapping with replacement (n = 1000) was used to estimate confidence intervals of model parameters without making assumptions about the population distribution (Efron and Tibshirani 1993). I considered all analyses significant at $\alpha = 0.05$. Analyses were carried out in R 2.71 (R Development Core Team 2008) with functions from the "mgcv" (Wood 2008), "nlme" (Pinheiro et al. 2008), and “sm” packages (Bowman and Azzalini 1997).

A central assumption of shark nurseries is that sharks are significantly more abundant in nurseries than other areas. On the Texas coast, the nine major bay systems (Figure 1.1) are considered the primary units relevant for management and encompass potential shark nursery habitat. I tested the nursery area concept criterion that juvenile bull shark abundance is significantly higher in nurseries than surrounding areas by extending the weighted least squares model with non-parametric bootstrapping. The aggregated data were resampled using bootstrapping with replacement (n = 1000). For each bootstrap iteration, annual mean bull shark CPUE was determined for each bay and areas with CPUE above the population mean for the entire study period (i.e., satisfying criterion 1) were coded as “1”, otherwise it was coded as “0.” Using this approach, I was able to test criterion 1 using the probability that mean CPUE of an individual bay is not significantly different from the population mean. This analysis was completed separately for both young-of-the-year and juvenile bull sharks.

A second requirement of shark nurseries is that young sharks must use the estuaries repeatedly through time (i.e., temporal stability). This criterion was also tested using the generalized least squares model testing that the overall slope (temporal effect) was not significantly less than zero (i.e., $\log_{10}$ CPUE was stable or increasing throughout study period). Temporal stability was examined both for the entire study population (all bays) and individually for bays satisfying criteria 1. Catch-per-unit-effort slopes and 95% confidence intervals were estimated using bootstrapping. Slope estimates for individual bays that were positive or contained 0 within their confidence intervals were considered to have satisfied criterion 2. The final assumption of shark nursery habitat is that juvenile sharks must remain within the habitat for extended periods of time. I could not examine movement patterns of individual within study sites, but it was possible to infer residency patterns of YOY bull shark "cohorts." For example, bull sharks are typically born in spring or early summer at ~ 650 mm TL (Neer et al. 2005) and grow 100-200 mm yr^{-1}. For primary nursery areas, examination of size frequency distributions of YOY sharks in putative nursery areas between spring and fall sampling should reflect a positive shift in mean size due to growth of the cohorts if individual are remaining within the study area between spring and fall. I developed length frequency histograms by season for the entire population (all bays pooled), and for bays that satisfied criteria 1 and 2 to test the hypothesis that total length of individuals is significantly longer in fall as compared to spring sampling with non-parametric bootstrap test for equality (n = 1000, Bowman and Azzalini 1997).

For juveniles (i.e. > 900 mm TL) I assessed residency patterns by examining length-frequency distributions and autocorrelation of catch patterns between consecutive years. The juvenile age class was comprised of fishes from age 1 to at least 10 based on length at age estimates; therefore, it was not possible to discern individual cohorts. As a result, I expected similar size distribution patterns between seasons as well as repeated use of years. I tested the hypothesis that total length is not significantly different between seasons with non-parametric bootstrapping (as described above). I evaluated repeated use through time by determining autocorrelation of catch-per-unit-effort patterns between years and testing the significance of including the first-order autoregressive function in the error term of the weighted least squares model using the log-likelihood test.

RESULTS

Bull sharks were sampled in nine estuaries along the entire Texas coast from 1976 to 2006, and 5666 juveniles were captured. Mean total length of captured individuals was 1024 mm TL and ranged from 324 to 2071 mm TL indicating that the shark assemblage was dominated by juveniles (Figure 1.2). Abundance of bull sharks varied widely among the nine estuaries. CPUE for both YOY and OJ bull sharks were highest along

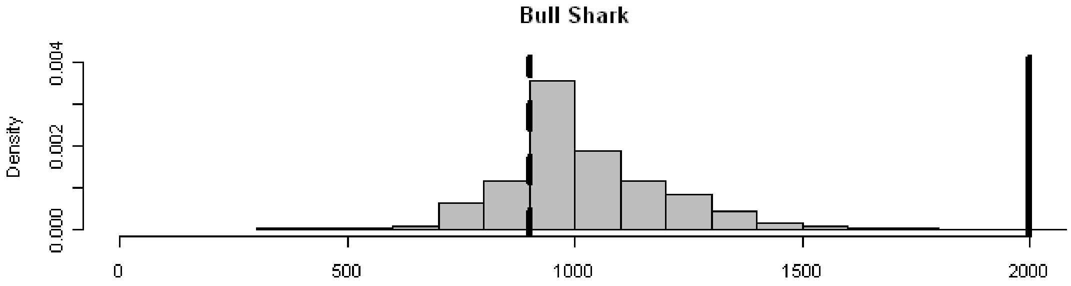


Figure 1.2. Histogram of bull shark lengths at capture during 1976-2006 along the northwestern Gulf of Mexico. Solid line indicates size at maturity and dashed line indicates estimated upper size limit of age 0 (young-of-the-year) sharks based on previous length at age studies (n = 5639).

the central Texas coast (i.e., Matagorda and San Antonio Bays), were moderate in northern bays, and low in southern lagoon systems (Figure 1.3 A-B).

Young- of-the-Year Spatial Patterns

A central assumption of shark nursery habitat is that the abundance of juvenile bull sharks in a specific bay is greater than the mean abundance in all Texas estuaries where juveniles occur. Spatial patterns were examined using weighted least squares regression where each bay was included as a covariate in the model (Table 1.1A). For all eight bays where sharks were captured, the mean population CPUE was 0.102 (Figure 1.4). Only Matagorda and San Antonio Bays had mean CPUE above the population mean for the entire study period (Figure 1.4). However, only Matagorda Bay CPUE was significantly above the population mean ($P < 0.001$, Table 1.2A).

Young-of-the-Year (YOY) Temporal Patterns

The criterion that juvenile sharks use Texas estuaries repeatedly through time (temporal stability) was also tested. For the entire population, mean CPUE increased slightly throughout the study period although a significant trend was not detected ($P = 0.12$; Table 1.1A) indicating stability of the population (Figure 1.5). Temporal patterns were also investigated individually for Matagorda Bay as this bay met criterion 1 and was considered a potential nursery area. Rate of temporal change was determined by estimating the slope of CPUE trends over time coupled with bootstrapping to obtain confidence intervals for the slope. For Matagorda Bay slope ranged between -0.00859 and 0.00545 (95% confidence intervals), and indicating temporal population stability within Matagorda Bay (Table 1.3A).

Table 1.1. A) Parameter estimates from weighted least squares model for young-of-the-year (A) and juvenile bull sharks (B). Young-of-the-year (YOY; n = 1053) and juvenile (n = 4586) bull sharks were sampled in nine estuaries along the entire Texas coast from 1976 to 2006.

A

Coefficients	Young-of-the-year Bull Shark			
	Value	Std. Error	t	P
Year	0.006445	0.004165	1.547496	0.1232
Sabine	-12.8002	8.312455	-1.53989	0.125
Galveston	-13.2326	4.694028	-2.81902	0.0053
East Matagorda	0.160321	4.694028	0.034154	0.9728
Matagorda	3.440967	4.694028	0.733052	0.4643
San Antonio	-5.97436	4.694028	-1.27276	0.2044
Aransas	-2.94231	4.694028	-0.62682	0.5314
Corpus Christi	-1.36481	4.694028	-0.29075	0.7715
Lower Laguna Madre	1.129332	4.694028	0.240589	0.8101
Year x Galveston	0.00024	0.004786	0.050135	0.9601
Year x East Matagorda	-0.00652	0.004786	-1.36302	0.1743
Year x Matagorda	-0.008	0.004786	-1.67237	0.0959
Year x San Antonio	-0.00336	0.004786	-0.70273	0.483
Year x Aransas	-0.00491	0.004786	-1.02669	0.3057
Year x Corpus Christi	-0.00574	0.004786	-1.1996	0.2316
Year x Lower Laguna Madre	-0.007	0.004786	-1.46291	0.1449

B

Coefficients	Juvenile Bull Shark			
	Value	Std. Error	t	P
Year	0.02583	0.007769	3.32426	0.001
Sabine	-51.3086	15.50692	-3.30876	0.0011
Galveston	-41.2202	9.040312	-4.5596	<0.001
East Matagorda	-0.97691	9.040312	-0.10806	0.914
Matagorda	-19.4015	9.040312	-2.14611	0.0328
San Antonio	-22.198	9.040312	-2.45545	0.0147
Aransas	-14.1505	9.040312	-1.56527	0.1188
Corpus Christi	-13.6765	9.040312	-1.51283	0.1316
Lower Laguna Madre	-0.5375	9.040312	-0.05946	0.9526
Year x Galveston	-0.00494	0.008999	-0.54949	0.5832
Year x East Matagorda	-0.02533	0.008999	-2.81498	0.0053
Year x Matagorda	-0.0157	0.008999	-1.74475	0.0823
Year x San Antonio	-0.01435	0.008999	-1.59472	0.112
Year x Aransas	-0.01852	0.008999	-2.05845	0.0406
Year x Corpus Christi	-0.01888	0.008999	-2.09761	0.0369
Year x Lower Laguna Madre	-0.02556	0.008999	-2.83993	0.0049

Table 1.2. Results from non-parametric bootstrap with resampling to test the hypothesis that CPUE is not significantly greater than the population mean for young-of-the-year (A) and juvenile bull sharks (B). For each bootstrap iteration annual mean bull shark CPUE was determined for each bay, and bays with CPUE above the population mean for the entire study period (i.e., satisfying criteria 1) were coded as “1”, otherwise it was coded as “0.” For YOY bull sharks, only Matagorda had mean CPUE significantly above the population mean for the entire study period. For juveniles, San Antonio and Matagorda Bays were CPUE significantly above the population mean for the entire study period.

A

Bay	**P**
Sabine	1.00
Galveston	1.00
East Matagorda	1.00
Matagorda	0.00
San Antonio	0.34
Aransas	0.86
Corpus Christi	1.00
Lower Laguna Madre	1.00

B

Bay	**P**
Sabine	1.00
Galveston	1.00
East Matagorda	1.00
Matagorda	0.00
San Antonio	0.02
Aransas	0.80
Corpus Christi	1.00
Lower Laguna Madre	1.00

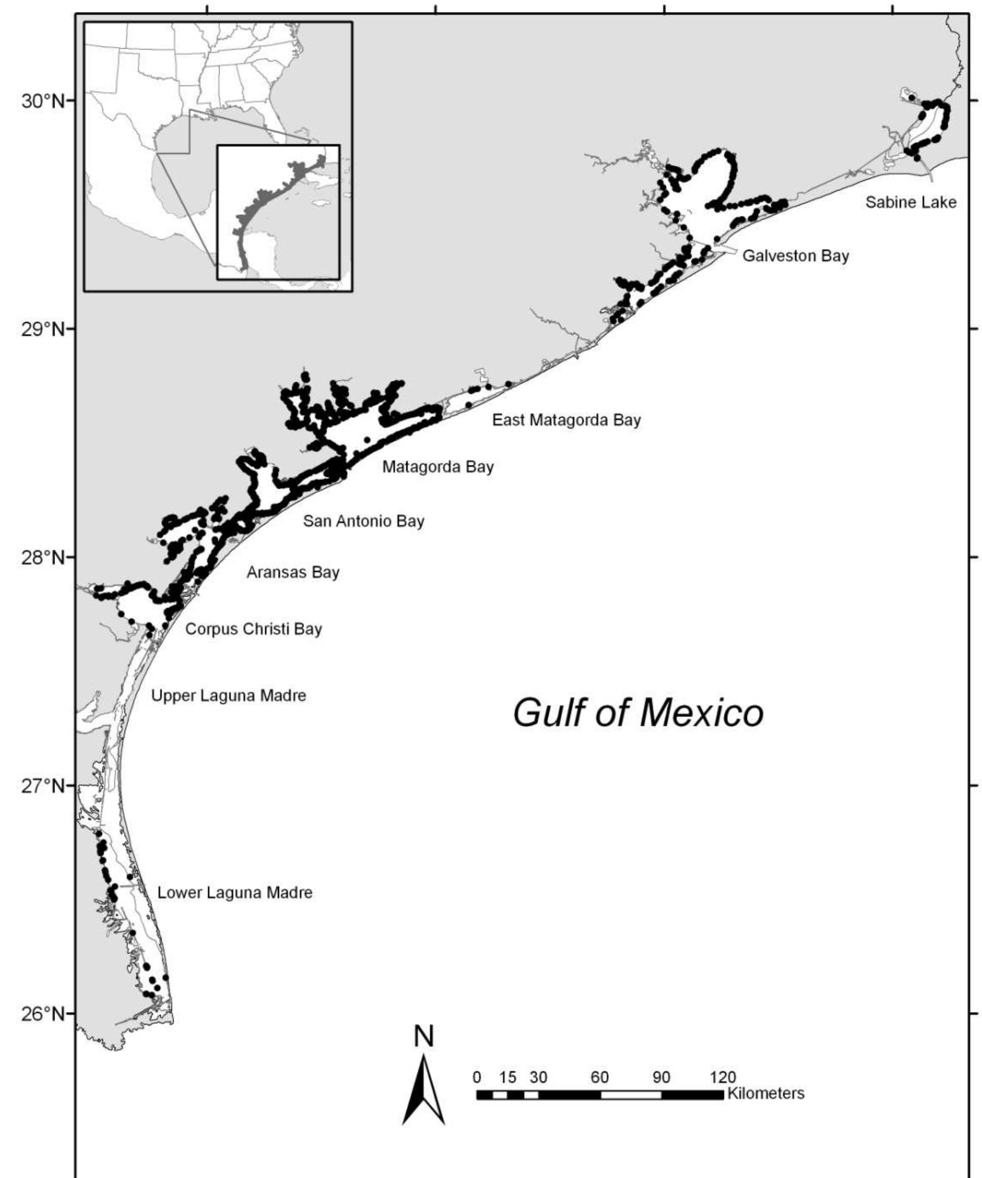
Table 1.3. Estimates of CPUE slope over time for each bay system. Results from non-parametric bootstrap with resampling to test the hypothesis that CPUE is not significantly less than zero. Bays systems with confidence intervals containing or above 0 indicate temporal stability or population increases during the study period (1976-2006) for young-of-the-year (A) and juvenile bull sharks (B).

A

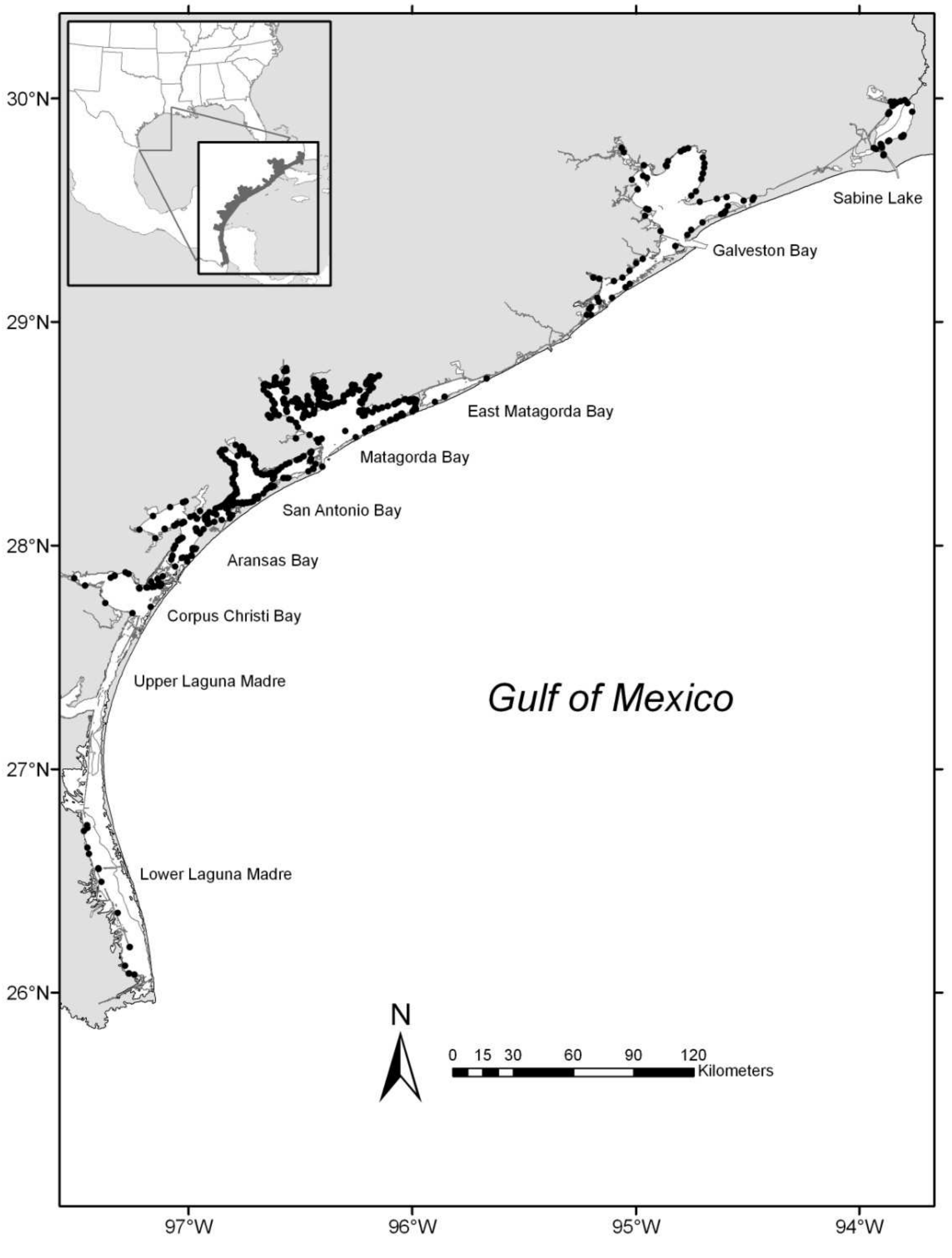
Bay	**2.5% CI**	**97.5% CI**
Sabine	0.0023	0.0115
Galveston	0.0044	0.0090
East Matagorda	-0.0008	0.0006
Matagorda	-0.0086	0.0055
San Antonio	-0.0004	0.0068
Aransas	-0.0021	0.0048
Corpus Christi	-0.0015	0.0030
Lower Laguna Madre	-0.0028	0.0016

B

Bay	**2.5% CI**	**97.5% CI**
Sabine	0.0156	0.0357
Galveston	0.0173	0.0248
East Matagorda	-0.0003	0.0012
Matagorda	0.0016	0.0018
San Antonio	0.0052	0.0178
Aransas	0.0005	0.0138
Corpus Christi	0.0035	0.0105
Lower Laguna Madre	-0.0044	0.0027


30°N
29°N
28°N
27°N
26°N
97°W
96°W
95°W
94°W
Sabine Lake
Galveston Bay
East Matagorda Bay
Matagorda Bay
San Antonio Bay
Aransas Bay
Corpus Christi Bay
Upper Laguna Madre
Lower Laguna Madre
Gulf of Mexico
N
0 15 30 60 90 120
Kilometers

(A)



B)

Figure 1.3. Capture locations for young-of-the-year (A) and juvenile (B) bull sharks along the Texas coast from 1976 to 2006.

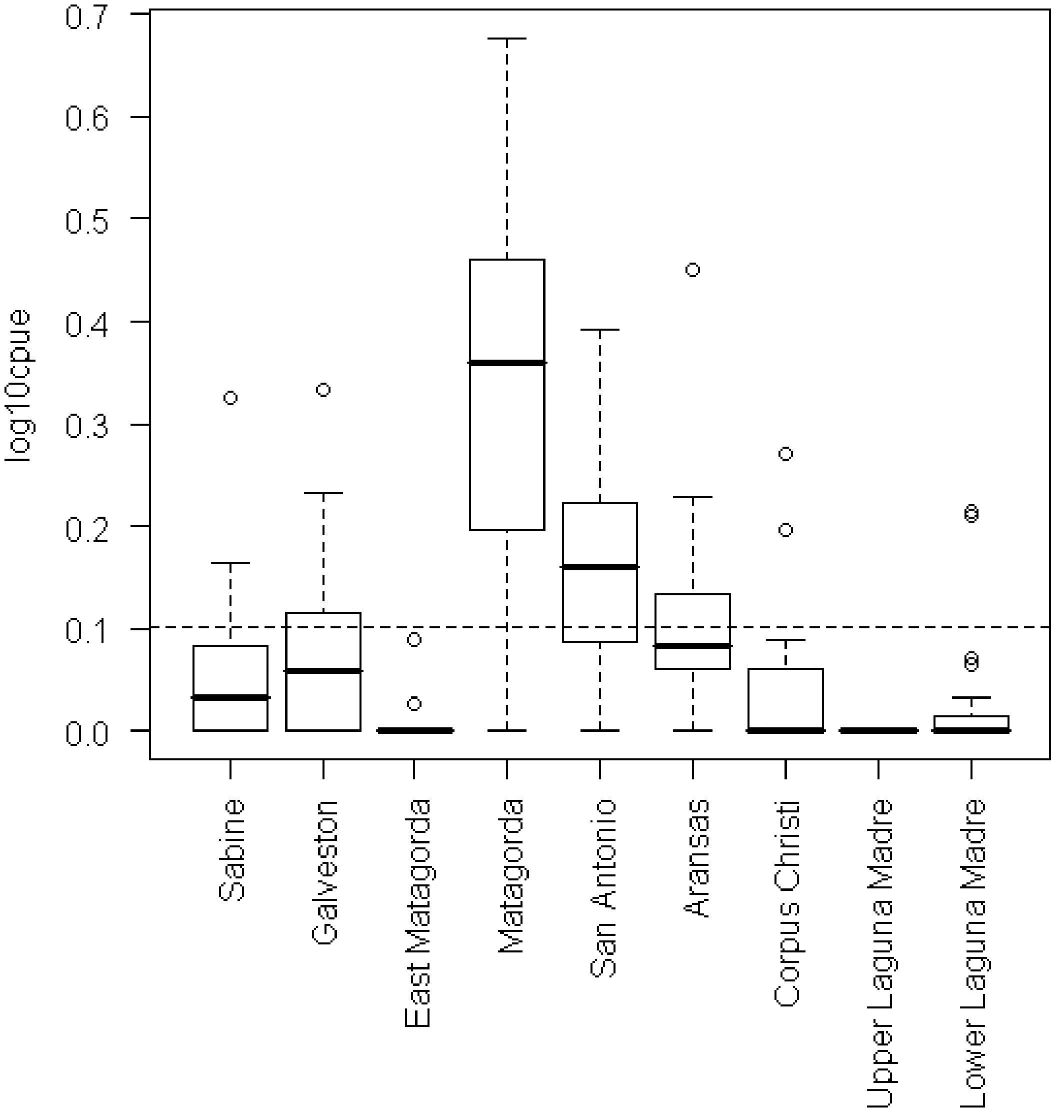


Figure 1.4. Box-and-whisker plot of young-of-the year Log_{10} CPUE. The horizontal line within each box is the median, and the boundaries of the boxes indicated 25th and 75th percentiles. Whiskers above and below the boxes indicate the 5th and 95th percentiles.

Filled circles identify outlying points. The horizontal dashed line indicates the mean population CPUE over the entire study period.

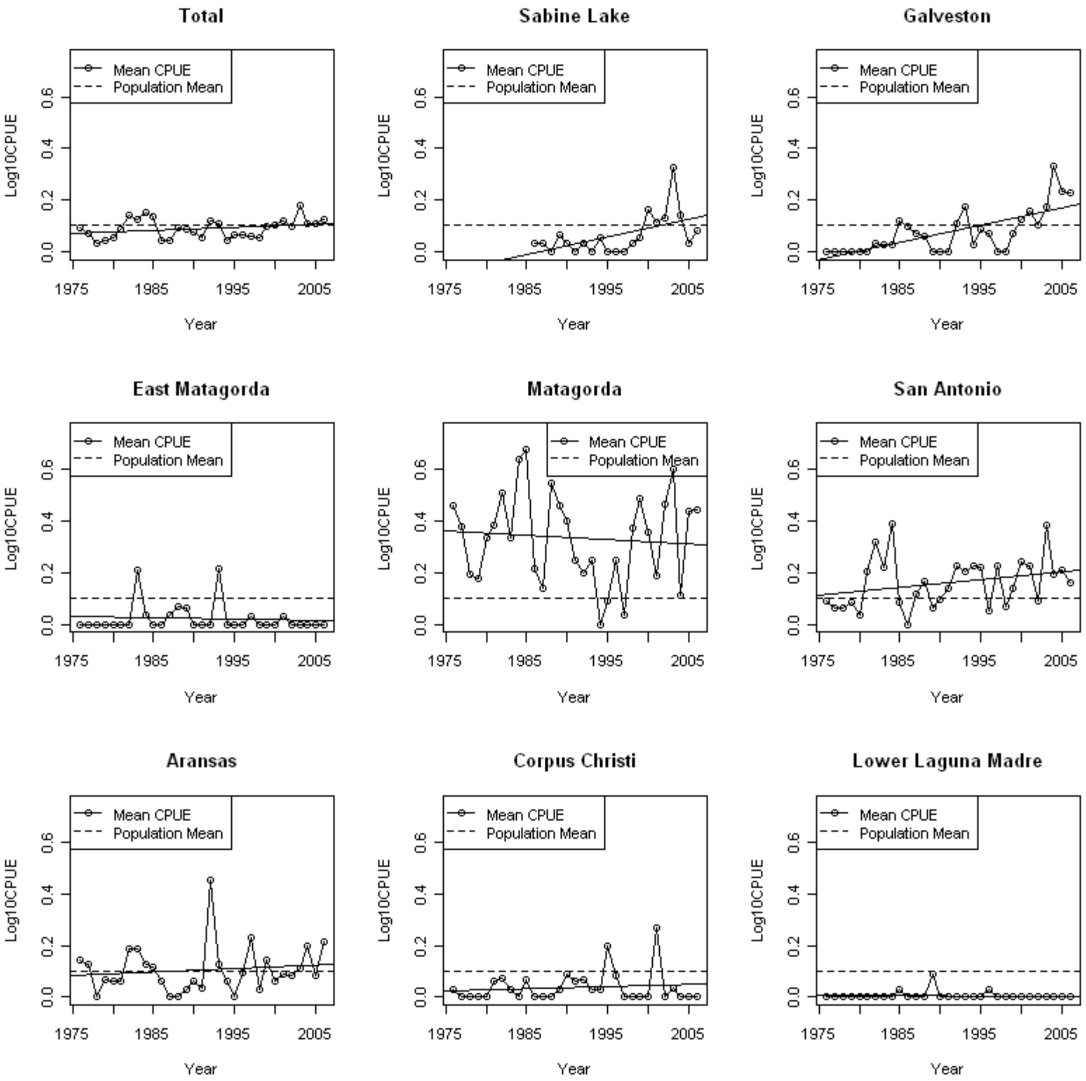


Figure 1.5. Mean annual Catch-per-unit-effort (CPUE) over time for all bays pooled, and each individual bay. Solid line indicates least-squares regression line, dashed line indicates population mean CPUE over the entire study period.

Age 0 Residency

To assess residency patterns of cohorts of YOY bull sharks I compared size-frequency distributions between spring and fall samples to test the hypothesis that total lengths of individuals were significantly longer in fall as compared to spring. Mean length of individuals captured in spring (n = 550) samples was 791± 67 mm TL (mean ± standard deviation). Mean length of fall samples (n = 503) was 844 ± 59. In Matagorda Bay, mean length in spring samples (n = 233) was 794 ± 86 mm TL. Mean length of fall samples (n = 304) was 844 ± 59 mm TL. Size frequency distributions were similar between sampling periods, although significantly larger in fall samples. This pattern was observed for the entire sample population (all bays pooled, bootstrap test of equality, P < 0.001) and for Matagorda Bay individually (P < 0.001; Figure 1.6). Moreover, the presence of autocorrelation between sampling years also indicates repeated usage of a nursery habitat. Incorporation of autocorrelation in the error structure significantly improved model performance (log likelihood test, P < 0.01).

Older Juvenile Spatial Patterns

Abundance patterns of older juvenile sharks > 900 mm TL were also examined to test the hypothesis that abundance of juvenile bull sharks in a specific estuary is greater than the mean abundance in all Texas estuaries where juveniles occur. Similar to age 0 sharks, age 1+ bull sharks were captured in all major bays except Upper Laguna Madre (Figure 1.3 B). Spatial patterns were tested using least squares regression for all 8 bays where sharks were captured (Table 1.1). For all bays, CPUE was 0.328 (Figure 1.7). Only Matagorda and San Antonio Bays had mean CPUE significantly above the population mean for the entire study period (bootstrap results, P < 0.001, Table 1.2B, Figure 1.7) satisfying criteria 1.

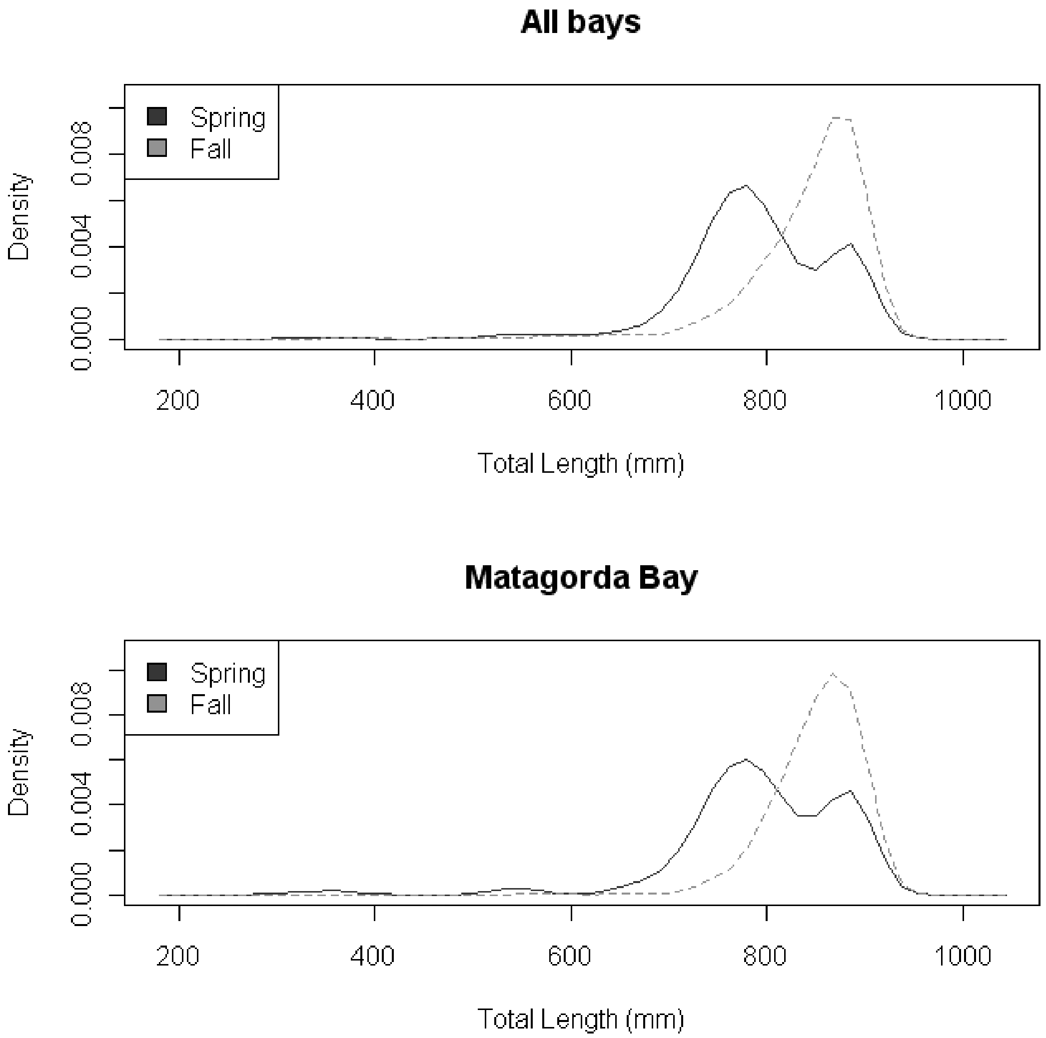


Figure 1.6. A) Length-frequency distributions of young-of-the-year bull sharks captured in Texas bays during spring and fall sampling periods between 1976-2006 (n = 550 spring, 503 fall). B) Length-frequency distributions of young-of-the-year bull sharks from Matagorda Bay during spring and fall sampling periods between 1976-2006 (n = 233 spring, 304 fall).

Older Juvenile Temporal Patterns

The criterion that juvenile sharks use Texas estuaries repeatedly through time (temporal stability) was also tested for age 1+ bull sharks. For the entire population, mean CPUE increased significantly throughout the study period ($P < 0.01$; Figure 1.8). Temporal patterns were also investigated individually for Matagorda and San Antonio

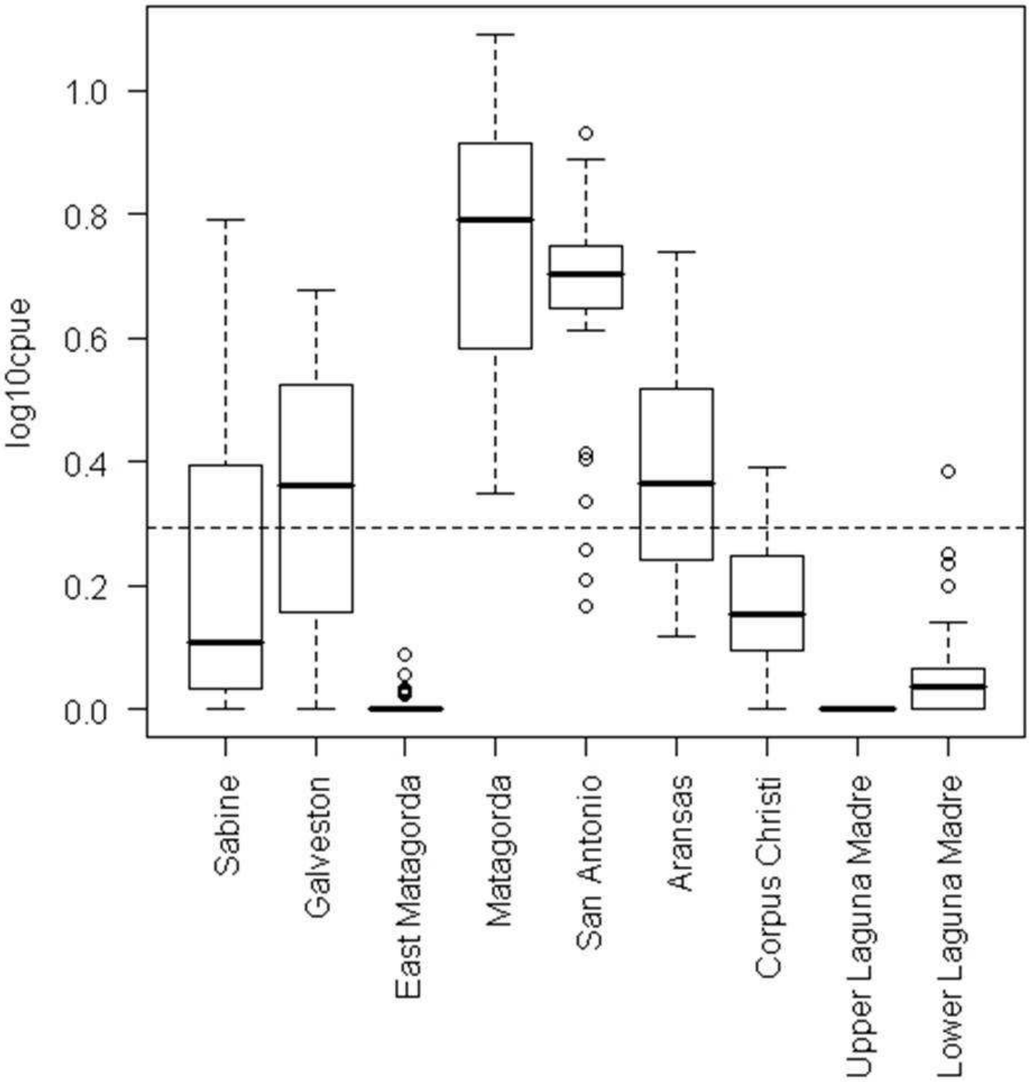


Figure 1.7. Box-and-whisker plot of Age 1+ bull sharks Log_{10}CPUE. The horizontal line within each box is the median, and the boundaries of the boxes indicated 25th and 75th percentiles. Whiskers above and below the boxes indicate the 5th and 95th percentiles. Filled circles identify outlying points. The horizontal dashed lines indicates the mean population CPUE over the entire study period.

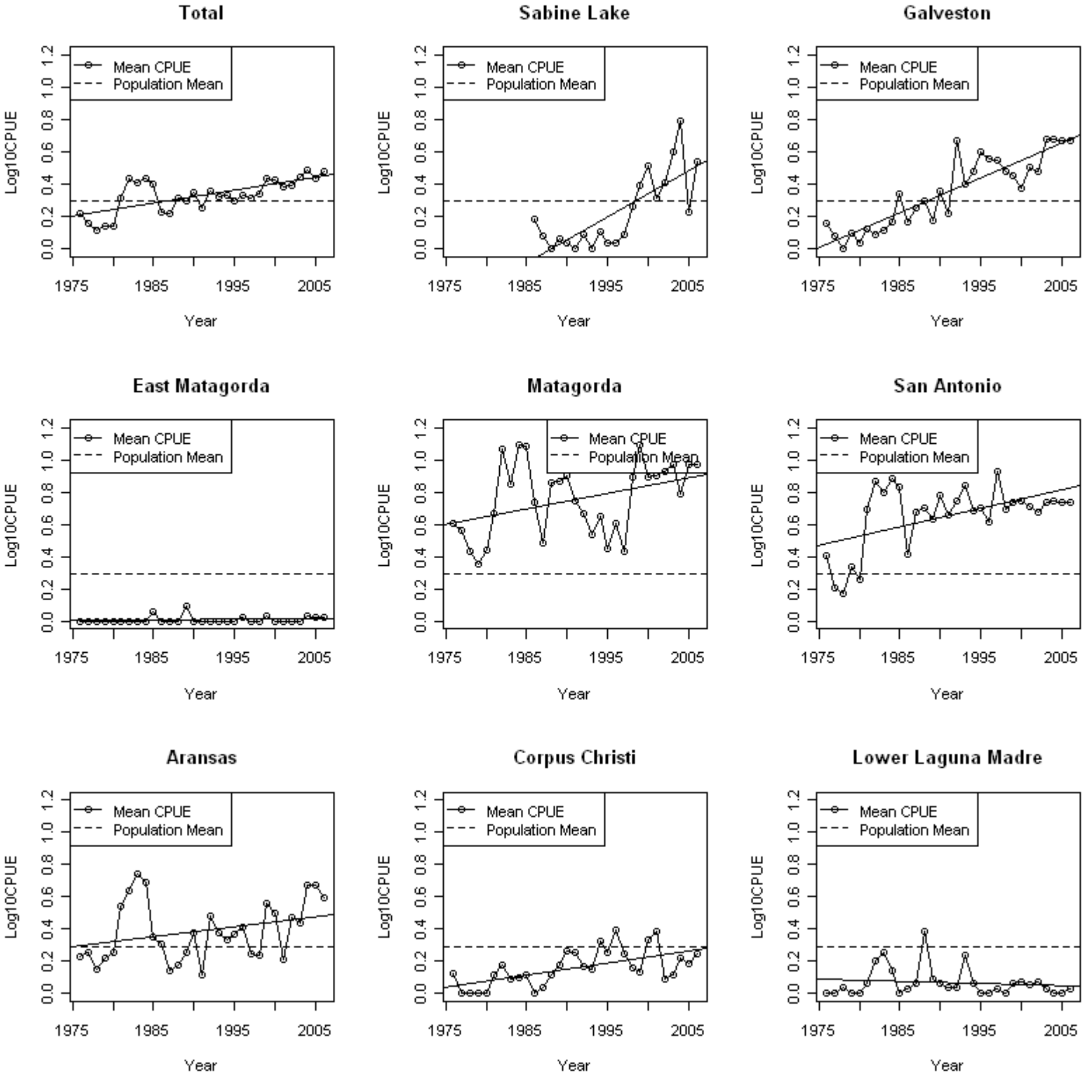


Figure 1.8. Mean annual Catch-per-unit-effort (CPUE) over time for all bays pooled, and each individual bay. Solid line indicates least-squares regression line, dashed line indicates the population mean CPUE over the entire study period.

Bays that met criteria 1. Rate of temporal change was determined by estimating the slope of CPUE trends over time coupled with bootstrapping to obtain confidence intervals for the parameter. For Matagorda and San Antonio Bays, CPUE increased significantly over time (Matagorda 0.0016 - 0.0018; San Antonio 0.0052 - 0.0178) (Table 1.3A).

Older Juvenile Residency (Criteria 3)

As our size range of older juveniles included multiple age classes (Age 1 – 10+) it was not possible to detect individual cohorts beyond age 0. To assess residency patterns of cohorts of older juvenile bull sharks we compared size-frequency distributions between spring and fall samples as well as autocorrelation of CPUE patterns among years to examine residency patterns of juvenile bull sharks. I expected to find similar size patterns between season and similar catch rates between adjacent years (significant autocorrelation). Mean length of individuals captured between seasons were similar between seasons both overall, and within Matagorda and San Antonio Bays individually (Figure 1.9). Overall, mean length of individuals captured in spring sampling was 1075 ± 137 mm TL (n = 2637). Mean length of fall samples was 1058 ± 140 mm TL (n = 1949). In Matagorda Bay, mean length in spring samples was 1048 ± 137 mm TL (n =970). Mean length of fall samples (n = 697) was 1053 ± 137 mm TL. In San Antonio Bay, mean length in spring samples was 1089 ± 146 mm TL (n =724). Mean length of fall samples (n = 681) was 1072 ± 149 mm TL. Size frequency distributions were similar between sampling periods, but significantly larger in spring samples. This pattern was observed for the entire sample population (all bays pooled, bootstrap test of equality, $P < 0.001$) and Matagorda and San Antonio Bays ($P < 0.001$; Figure 1.6). Significant autocorrelation was also detected in CPUE patterns between adjacent years, as

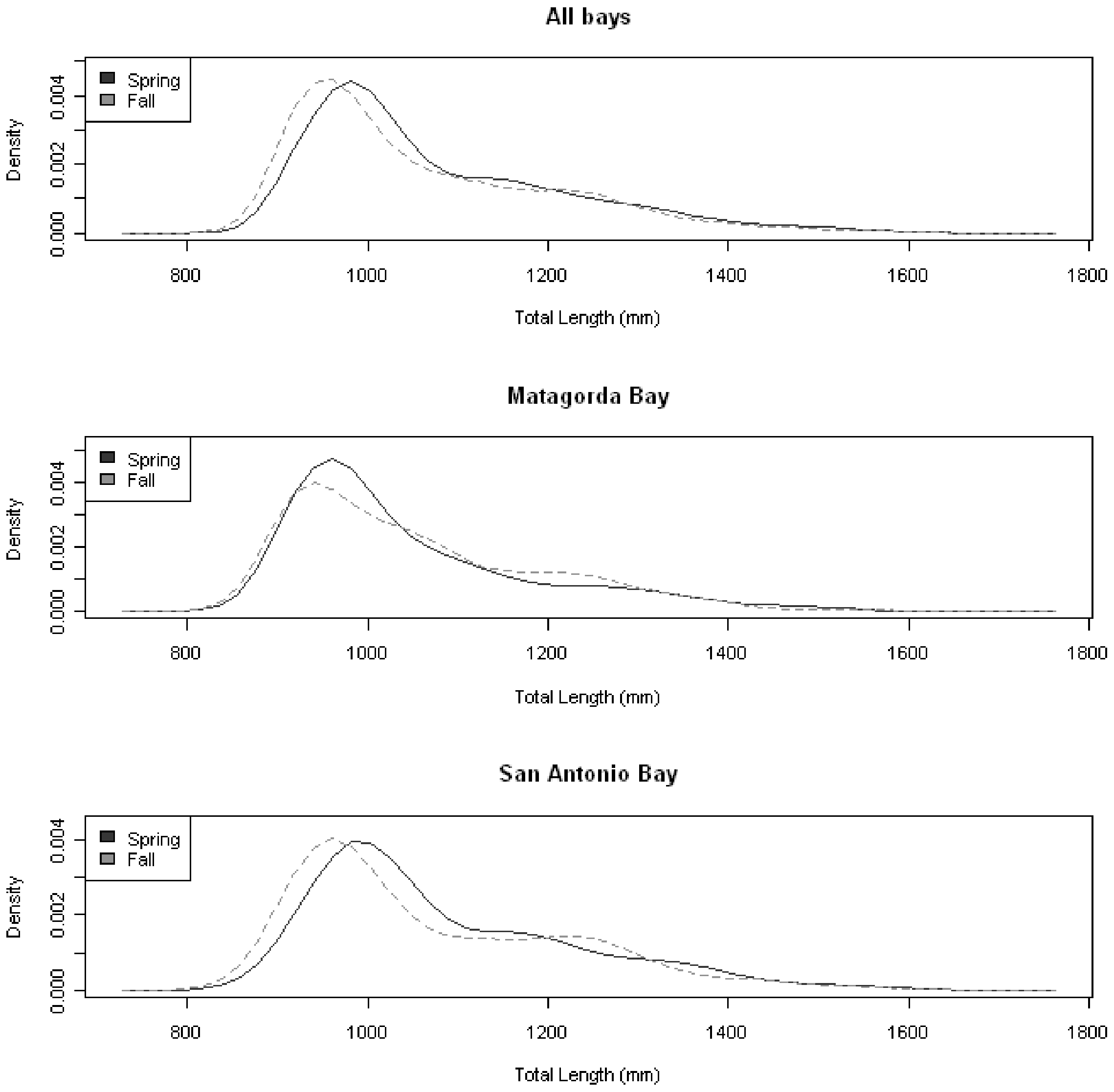


Figure 1.9. A) Length-frequency distributions of juvenile bull sharks captured in Texas bays during spring and fall sampling periods between 1976-2006 (n = 2637 spring; n = 1949 fall). B) Length-frequency distributions of juvenile bull sharks from Matagorda Bay during spring (n = 970) and fall (n = 697) sampling periods between1976-2006. C) Length-frequency distributions of juvenile bull sharks from San Antonio Bay during spring (n = 697) and fall (n = 681) sampling periods between 1976-2006.

incorporation of autocorrelation (AR-1) in the error structure significantly improved model performance (log likelihood test, $P < 0.01$).

DISCUSSION

Identification of nursery habitat remains a vital component of marine fisheries management (Bonfil 1997, Beck et al. 2001, Dahlgren et al. 2006, Heupel et al. 2007, McCandless et al. 2007). This study used criteria proposed by Heupel et al. (2007) including information on abundance, temporal stability, and residency patterns of sharks to identify nursery habitat for bull shark in Texas' coastal estuaries. This study provides the first empirical evidence of bull shark estuarine nursery use on the Texas coast, discusses ontogenetic shifts in habitat use patterns, and highlights some limitations in the implementation of nursery habitat delineation using the nursery area concept.

Of the nine bay systems considered for young-of-the-year nursery habitat, only Matagorda Bay satisfied all three criteria. Bull shark abundance in all other bays systems considered was not significantly greater than the mean population abundance (criterion 1). Abundance in San Antonio and Aransas Bays were similar to the long-term population mean while abundance in all other bays was typically low. Significant temporal trends were not detected for age 0 bull sharks at the population level (all bays considered) or within Matagorda Bay (only bay to satisfy criterion 1). Abundance levels in most bays increased during the study period (e.g., Galveston Bay and Sabine Lake). While these bays may not have traditionally served as nursery habitat, these data suggest that they may currently provide nursery functions.

I also tested the nursery hypothesis on older juvenile bull sharks to identify potential secondary nursery habitats as a recent review suggests that larger/older juveniles may be most important in sustaining adult shark populations (Kinney & Simpfendorfer 2009). For older juveniles, Matagorda and San Antonio Bays met all three nursery habitat criteria. Bull shark abundance in the other bays considered was not significantly greater than mean abundance of all bays. However, temporal patterns were stable or increasing in all bays, and size at captures estimates were similar between sampling seasons suggesting that individual cohorts may stay within the bays for extended periods.

Despite considerable interest in sustaining shark populations, the availability of sampling data with adequate temporal and spatial coverage necessary to characterize nursery habitat using these criteria are rare. Sharks typically occur in low densities and with high temporal and spatial variability in catch records, making quantitative comparisons difficult for short periods or small spatial scales (Froeschke Chapter 2). Few studies simultaneously compare nine systems over 30 y, and this study provides a unique perspective on shark nursery use. Currently, the estuarine waters along the entire coast are considered bull shark nursery area including Upper Laguna Madre (McCandless et al. 2002, Hueter and Tyminski 2007, McCandless et al. 2007), although no sharks were caught in this lagoon. Few sharks were caught in Lower Laguna Madre and East Matagorda Bay that are also considered nursery habitat. My results refine the nursery habitat concept along the Texas coast and suggest that only San Antonio and Matagorda bays may be providing nursery function for juvenile sharks.

Few studies are able to consider all potential nursery habitats in a species' range in a single study, ours is no exception (Barry et al. 2008, DeAngelis et al. 2008). Using this criteria proposed by Heupel et al. (2007), the number of sites (or habitats) considered and the temporal extent of the study affects nursery designation because it may influence the population mean and potentially nursery designation. For example, consideration of additional study areas with low bull shark abundance would have depressed the population mean potentially leading to nursery habitat designation for Aransas Bay. Juvenile bull sharks also occur on the open coast in Texas' waters and this may also constitute nursery habitat (Heuter and Tyminski 2007). Unfortunately, data necessary to test this hypothesis are currently lacking and abundance estimates between open coast and bay systems are difficult as few gear types are equally effective in both environments.

This study presents the first quantitative description of shark nursery habitat in Texas' waters and one the first tests of the shark nursery area concept in the Gulf of Mexico. I identified nursery habitat for both young-of-the-year and older juvenile bull sharks that may be most important in sustaining adult shark populations (Kinney & Simpfendorfer 2009). Moreover, CPUE increased significantly for older juveniles during the study period. Galveston Bay and Sabine Lake may now provide nursery function as abundance has been above the population mean for the last 10-15 y in each bay system. These findings suggest that nursery use may not be temporally stable and that changes in habitat (Froeschke Chapter 2) or adult stocks may influence nursery use patterns. Continued long-term monitoring may be necessary to detect these changes and evaluate changes in management practices.

Development or maintenance of sustainable shark populations has proven a difficult task despite considerable interest from fisheries scientists. Life history traits including slow growth, large size, late maturity, and low fecundity leave them susceptible to overfishing and/or habitat loss (Musick et al. 2000) and dramatic declines have been reported worldwide (Worm et al. 2002, Baum et al. 2004, Heithaus et al. 2008). Additionally, apex predators such as bull sharks provide important ecological roles influencing community structure in systems they inhabit (Heithaus et al. 2008, 2009). Development of testable hypotheses leading to more effective ways of prioritizing areas for conservation and management improves our ability to protect critical habitats, but requires detailed information on habitat usage patterns and requirements (Levin and Stunz 2005). Until recently, shark nurseries were primarily defined based on presence of juveniles and led to the inclusion of most coastal areas as nursery habitats which precluded efficient management of the most important habitats (Heupel et al 2007, Kinney & Simpfendorfer 2009). All nine bays considered in the current study were previously considered bull shark nurseries based on presence information (McCandless et al. 2002, Heuter and Tyminski 2007) which does little to prioritize areas for conservation or management. Our study considers only one of the bays as a primary nursery and two bays as secondary providing increased focus for allocation of conservation or management priorities.

While a greater understanding of nursery habitat is imperative, management strategies must include protection of all important age classes and the relative contribution of juveniles from particular nurseries to adult populations should be considered (Beck et al. 2001, Kraus and Secor 2005). Protection of young-of-the-year sharks is primarily based on teleost fisheries management practice although that may not be the most effective way to manage sharks due to their unique life history traits. Bull sharks mature late (15 y) and may use the same nursery areas repeatedly over years

(Hueter et al. 2005). My results support this pattern based on spatial and temporal catch patterns coupled with strong temporal autocorrelation of catch rates between sampling years. However, tracking of individuals is necessary to demonstrate residence or philopatry (Heupel and Simpfendorfer. 2008, Ortega et al. 2009) and would provide additional insight into movement patterns and habitat use patterns between oceanic and estuarine systems. Long-term tagging programs could also provide greater insight into the productivity rates of nursery areas and contributions of juveniles to adults stock necessary to sustain populations (Beck et al. 2001).

Bull shark distribution patterns are strongly affected by environmental conditions in their nursery habitat (Heupel and Simpfendorfer 2008, Ortega et al. 2009, Froeschke Chapter 2). In Texas estuaries, distribution patterns of bull sharks are influenced primarily by salinity, temperature, and proximity to tidal inlets (Froeschke Chapter 2). Highest catch rates were predicted in areas characterized by warm temperatures and moderate salinities (10-20), and proximate to tidal inlets. On the Texas coast, oceanic salinities are buffered with freshwater runoff from major tributaries. Sabine Lake and Galveston Bay typically receive the largest volumes of inflow and consequently have lower salinities (< 10 psu) than the southerly Texas bays. However, increased urban demands for freshwater may be altering salinity regimes in the northern bay systems resulting in higher salinities within the bays and providing more desirable habitat for age 0 bull sharks. Heupel and Simpfendorfer (2008) suggests that salinity preferences of juvenile bull sharks limit distribution patterns perhaps as a method to reduce energetic costs of osmoregulation (Marais 1978); permitting more energy for growth. Texas bays are proximally located to several large urban centers. Management practices affecting environmental conditions including salinity regimes or access to the Gulf of Mexico through tidal inlets may have dramatic impacts on bull shark populations in the Gulf of Mexico.

This test of nursery value among putative bull shark nurseries demonstrates both the utility and some potential shortcomings of the shark nursery concept. This method provides a mechanism to compare nursery values to identify the most valuable habitats but may be influenced by different spatial and temporal scales examined. Careful interpretation must be given to ensure that important areas that do not qualify as nurseries yet still provide important juvenile habitat are incorporated into the management process. For example, Aransas, Galveston, and Sabine Lake support a large number of sharks and significant increases in bull shark CPUE were detected in both Galveston Bay and Sabine Lake implying that their importance as nursery habitat may be increasing. Unfortunately, using the current criteria, there is no framework for incorporating this into nursery habitat designation suggesting that other/additional nursery delineation procedures should be considered. Recent studies on teleosts have used temporal stability of high density regions to classify nurseries (Fodrie and Levin 2008). Collaca et al. (2009) identified European hake (*Merluccius merluccius*) using spatio-temporal persistence of abundance data over a nine-year time period. This study found that areas of high density exhibited temporal stability and the most persistent nursery areas (5% of total area) included 39% of total recruitment in the study area. This approach could be extended to other species (Early et al. 2008, Collaca et al. 2009) and may be an efficient method of characterizing shark nurseries where adequate data are available. Moreover, this approach would provide a mechanism for inclusion of areas supporting persistent populations such as

Aransas and Galveston Bays in the current study. Finally, this approach incorporates habitat components and could provide insights into natural or anthropogenic induced changes to shark habitats (Early et al. 2008) and could be extended in systems such as Texas estuaries where environmental influences on habitat distribution are known (Froeschke Chapter 2). Despite these limitations, the shark nursery area concept provides a much needed refinement necessary to promote sustainable shark management.

ACKNOWLEDGMENTS

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CHAPTER 2

ENVIRONMENTAL INFLUENCES ON THE OCCURRENCE OF COASTAL SHARKS IN ESTUARINE WATERS

ABSTRACT

Long-term fisheries independent gill net surveys conducted in Texas estuaries from 1975-2006 were used to develop spatially explicit estuarine habitat use models for three coastal shark species: bull (*Carcharhinus leucas*), blacktip (*Carcharhinus limbatus*), and bonnethead (*Sphyrna tiburo*). Relationships between environmental predictors and shark distribution were investigated using boosted regression trees (BRT). Bull shark was the most abundant species (n = 5800), followed by blacktip (n = 2094) and bonnethead sharks (n = 1793). Environmental conditions influenced distribution patterns of all species and relationships were nonlinear, multivariate, and interactive. Results showed very good model performance and suggested shark distribution is most closely linked to salinity, temperature, and proximity to tidal inlets. By interpolating BRT, maps of the probability of capture were produced using ordinary kriging and showed that the central region along the Texas coast contains the most important estuarine shark habitat. This area was characterized by warm temperatures, moderate salinities, and abundant inlets. Bull sharks also extended into low salinity estuaries, while blacktip and bonnethead sharks were restricted to areas near tidal passes with moderate salinities. Juvenile sharks were frequently captured, suggesting the Texas coast may constitute important nursery areas for all three species. The development of these spatially explicit models allows for prioritization and conservation of areas in a region

that has great potential for human disturbance and climate change impacts. These results provide new insight into the habitat requirements of coastal sharks in the northwestern Gulf of Mexico and practical information for managing this resource.

INTRODUCTION

Sharks are common inhabitants of coastal seas and may exert strong influences on the structure and function of ecosystems they inhabit (Worm et al. 2005, Carlisle & Starr 2009, Papastamatiou et al. 2009). Critical coastal shark habitat including many potential nursery habitats have been degraded by human activity and disturbances such as climate change may further impair shark habitat necessary to sustain populations (Lotze et al. 2006). Alteration of habitats is of particular concern for elasmobranchs (Carlisle & Starr 2009), because Essential Fish Habitat (EFH) has not been identified for many species and environmental conditions that influence habitat selection patterns are not well understood (Parsons & Hoffmayer 2005), particularly for young sharks. Many shark species are slow growing and long-lived (Musick et al. 2000), use a variety of habitats over broad spatial scales, and often occur in low densities throughout their range. These life history characteristics typically leave them vulnerable to exploitation and make identification of important habitat problematic.

Identification of critical habitat is a well-recognized and essential component of sustainable resource management (Stoner et al. 2001, Stoner 2003). Marine species are often associated with specific physical or biological habitats. There is growing interest in developing spatially explicit habitat maps for management purposes as animal abundance or productivity is directly linked to the amount of suitable habitat available (Stoner 2003, Valavanis et al. 2008). Despite this recognition, identification of EFH has been slow for many species in part because necessary data are often unavailable or analytical techniques have been unable to reliably identify critical habitat from available data. Moreover, predicting distributions of large, rare animals based on habitat characteristics can be difficult (Rooper & Martin 2009). Sampling requires adequate spatial and temporal coverage and must account for a large number of "zero observations" in the assessment of species such as sharks.

A suite of environmental variables have been hypothesized to influence elasmobranch distributions including temperature (Morrissey & Gruber 1993, Matern et al. 2000, Ortega et al. 2009), oxygen concentration (Parsons & Carlson 1998, Heithaus et al. 2009), salinity (Heupel & Simpfendorfer 2008, Ubeda et al. 2009), and proximity to inlets in estuaries (Grubbs & Musick 2007). Short-term movement and distribution patterns has been investigated for many shark species using acoustic telemetry or tagging methods and linking distributions to physical or biological patterns at the study sites (Hight & Lowe 2007, Heupel & Simpfendorfer 2008, Ortega et al. 2009, Papstamatiou et al. 2009). However, it is difficult to definitively link variations in habitat quality to habitat selection patterns over short time scales (Ortega et al. 2009). For example, temperature and salinity influence distribution patterns of euryhaline bull sharks that may not be evident in short term studies that do not encompass the full range of environmental variation experienced by animals that influences large-scale habitat selection patterns (Heupel & Simpfendorfer 2008). Moreover, increasing rates of disturbance in aquatic habitats (Lotze et al. 2006) require improved abilities to predict changes in habitat quality for sensitive species *a priori* in order to mitigate habitat loss or population declines. To this end, fish-habitat relationships on larger scales are often investigated by associating environmental conditions with catch records using multivariate statistical techniques (Leathwick et al. 2006, Grubbs & Musick 2007, Valavanis et. al. 2008).

Coastal habitats in the Gulf of Mexico support a diverse and abundant shark assemblage (Parsons & Hoffmayer 2005). At least 16 species of coastal sharks use Gulf of Mexico waters off Florida and Texas as juvenile habitat (Hueter & Tyminski 2007, McCandless et al. 2007). However, coastal shark distribution patterns in the northwestern Gulf of Mexico including the entire Texas coast are not well understood, and there is currently no appropriate baseline with which to measure future management actions or predict the impact of natural or anthropogenic disturbances.

The goal of this study was to develop species distribution models for three coastal shark species in northwestern Gulf of Mexico to promote sustainable management of these important predators. I developed a long-term fisheries independent data set to link shark distribution and environmental conditions and develop species specific distribution models. Specifically, the goal of this study was to characterize environmental influences on shark distributions patterns of northern Gulf of Mexico.

MATERIALS AND METHODS

Study area

This study was conducted in nine major bay systems along the Texas coast in northwestern Gulf of Mexico from 1975-2006 (Figure 2.1). Barrier islands separate coastal estuaries from the Gulf of Mexico along the majority of the coast and saltwater exchange occurs via six major tidal inlets. Texas bays are shallow, subtropical estuaries that are physically dynamic, support a variety of habitat types, and provides nursery habitat for many nektonic species of recreational, commercial, or ecological importance (Reese et al. 2008).

Field Collections

Shark catch data were obtained from the Texas Parks and Wildlife Department coast wide fisheries gill-net monitoring program that was established in all Texas bay systems in 1975 and continued through 2006. Coastal Fisheries resource monitoring data were collected as a stratified cluster sampling design; each bay system serves as non-overlapping strata with a fixed number of samples per season (n = 45/bay/season). Gill-nets were deployed each spring (April - June) and fall (September - November; Martinez-Andrade et al. 2009). Sample locations were drawn independently and without replacement for each season (Martinez-Andrade et al. 2009). For this study, gill-net collection data from 9 bay systems (1975-2006, n = 19757; Table 2.1) were used to identify shark-habitat relationships and develop shark distribution within Texas' major bay systems. Sharks were sampled using standardized gill nets (183 m) set perpendicular to shore. Nets were constructed of four panels with mesh size of 76 mm, 102 mm, 127 mm, and 152 mm, respectively. Gill nets were deployed one hour before sunset, fished overnight, and retrieved within four hours of sunrise the following day (set time was noted for each sample). Captured sharks were identified to species, measured, and released. Gill nets employed in this study were inefficient at capturing sharks > 2 m, thus large sharks were rare in this study although they are present in the bay at times (Fisher, M. personal communication).

Patterns of 11 variables relevant to sharks were examined coast-wide to investigate relationships between environmental conditions and shark distributions (Table

2.1). Data including salinity, temperature, turbidity, and dissolved oxygen (DO) were collected in the surface waters (0-15 cm) at the offshore end of the gill-net during net retrieval (Martinez-Andrade et al. 2009). Turbidity readings were processed in the laboratory within 24 h using a calibrated turbidimeter. Depth at the offshore end of each gill-net set was also noted. All variables were measured during each sampling (i.e., all years and bays) although a few observations (< 1% had missing values for a single variable). Observations missing only a single variable were retained for the analysis as the modeling techniques employed accommodate missing values through the use of surrogates (Elith et al. 2008).

Freshwater inflow into the major estuarine systems was determined from USGS (1976-2006; no missing years) stream gauges (http://midgewater.twdb.state.tx.us/bays_estuaries/hydrologypage.html) to estimate the relative importance of freshwater inflow on shark habitat quality. Mean monthly surface inflow and freshwater balance were determined for each bay system (except East Matagorda Bay, data unavailable) during the study using the following equations from http://midgewater.twdb.state.tx.us/bays_estuaries/hydrologypage.html:

(1) Surface Inflow = Gauged Flow + Modeled Flow - Diverted Flow + Returned Flow

(2) Freshwater Balance = Surface Inflow - Evaporation from estuary surface + Precipitation on estuary surface.

Texas Bays are separated from the Gulf of Mexico via barrier islands that extend the entire length of the Texas coast. Saltwater exchange between bays and the Gulf of Mexico occurs via six tidal inlets (Figure 2.1). To examine potential relationships between estuarine shark distribution and the connection to the Gulf of Mexico, I calculated the distance from each sampling location to the nearest tidal connection to the Gulf of Mexico using the cost-distance function in the ArcGIS software package with the spatial analyst extension (ESRI), using the shoreline as a barrier (Whaley et al. 2007). Cost-distance functions calculate the shortest distance between two points but was constrained within geographic boundaries (e.g., water) to provide more accurate relative distance estimates than euclidian (straight-line) techniques.

Modeling approach

Boosted regression trees (BRTs) were used to examine relationships between shark distribution and environmental variables and to predict probability of capture at sites withheld from the model building for bull, blacktip, and bonnethead sharks. Prior to model fitting the entire data set was randomly partitioned into training and testing data sets (n = 9879 training; n = 9878 testing). After model fitting, probability of capture was predicted for 9878 testing samples covering the entire coast. Coast wide species distribution models were then developed by interpolating catch probabilities from the 9878 independent testing samples using ordinary kriging, a flexible spatial interpolation algorithm. In addition, suites of environmental conditions were determined for "spring" and "fall" conditions based on environmental parameters measured at each sampling location during each season. The BRT model output was then used to predict probability of capture coastwide during specific seasonal conditions. The general approach is outlined in a flowchart (Figure 2.2).

Boosted regression Trees

Boosted regression trees use a model-averaging (ensemble) method that allows for both explanation and prediction (Elith et al. 2008). Despite this utility BRTs have only recently been applied to ecological questions (Friedman 2001, Leathwick et al. 2006, Elith et al. 2008). This technique is analogous to an additive regression model that fits a large number of simple models whose predictions are then combined to give more robust estimates of the response. Each individual model consists of a simple regression tree based on a series of binary splits constructed from the predictor variables (Hastie et al. 2001). This method also incorporates a boosting algorithm that uses an iterative method to fit a forward stage-wise model that progressively adds trees while re-weighting these data to emphasize observations poorly modeled by previous trees. This technique accommodates continuous or categorical predictors, missing values, and is not affected by transformation or outliers. This technique can also fit complex non-linear relationships and often has superior predictive performance to other techniques such as generalized linear and additive models that are often used to model species-habitat relationships (Elith 2006, Leathwick et al. 2006, Elith et al. 2008, Leathwick et al. 2008, Parisen & Moritz 2009). Another strength of this technique is the ability to estimate the contribution of predictor variables to the response variable and the ability to model complex interactions. The relative importance of variables can be determined by averaging the number of times a variable is selected for splitting and the squared improvement resulting from these splits (Friedman 2001, Friedman & Meulman 2003). Values are scaled to 100 and higher numbers indicate a stronger influence on the response variable. The ability to model interactions is controlled by a tree complexity (*tc*) parameter where the value specifies the number of nodes on each tree and subsequently the ability to model interactions (Leathwick et al. 2006).

Analyses were carried out in R (version 2.7.1, R Development Core Team, 2004) using the "gbm" library supplemented with functions from Sing et al. (2005) and Elith et al. (2008). All models were fit to allow interactions using a tree complexity of 5 with a learning rate 0.01 or 0.005 to minimize predictive deviance and maximize predictive performance. During preliminary analyses, a range of tree complexities (*tc*) and learning rates were examined. Complex trees (i.e., *tc* =5) improved predictive performance and learning rates (*lr*) > 0.05 overfit training data, while rates slower than 0.005 did not improve model performance. Ten-fold cross validation of training data was used to determine the optimal number of trees for each model (i.e., number of trees giving best predictive performance) and ranged between 2400 and 3750 trees.

Despite careful model fitting, BRT models typically over-fit training data sets (Elith et al. 2008, Leathwick et al. 2008); therefore, model performance was assessed on predictions to the testing set that were with-held during cross validation. For each model, two performance metrics were determined: 1) predictive deviance and 2) the area under the receiver operator characteristic curve (ROC). Predictive deviance provides an estimate of the fit between predicted and raw values when predicting to independent data and was reported as a percentage of the total deviance for each model. Values for ROC estimate the degree to which fitted values discriminate between observed presences and absences and can be interpreted as the probability that a presence for a species drawn at random will have a higher fitted probability than an absence drawn at random (Parisen & Moritz 2009). Values of ROC range from 0.5 to 1 where a 1 indicates perfect discrimination of probabilities between presence and absence samples and a value of 0.5 indicates that model performance is no better than random. While models with ROC values > 0.6 are considered useful (Parisien & Moritz 2009), values > 0.8 are considered very good, and above > 0.9 excellent (Lane et al. 2009).

In addition to identifying important environmental variants contributing to shark distribution patterns, I also wanted to generate spatially explicit predictions of catch probability at locations withheld during model training. I predicted the probability of capture at each site in the testing data set (n = 9856) using a form of logistic regression (Elith et al. 2008) where the probability that a species occurs ($y = 1$), at a location with covariates X, $P(y = 1|X)$ using the logit: $\text{logit}(P(y = 1 \mid X) = f(X)$.

Habitat Suitability Models

Kriging is a spatial interpolation algorithm that was used to predict values at unsampled sites in the study area (Saveliev et al. 2007). This method uses the variogram to express the spatial variation, and it minimizes the error of predicted values which are estimated by spatial distribution of the predicted values. I used ordinary kriging with a spherical semiovariogram with the predicted probabilities of capture at each location (from the BRT model) as input into the kriging model. As this technique assumes normality, values were transformed prior to analysis using the natural logarithm (ln) and met this assumption. To evaluate seasonal differences in distribution patterns, environmental conditions during each season were estimated coast wide from the sampling data using kriging. Therefore, environmental conditions for "spring" and "fall

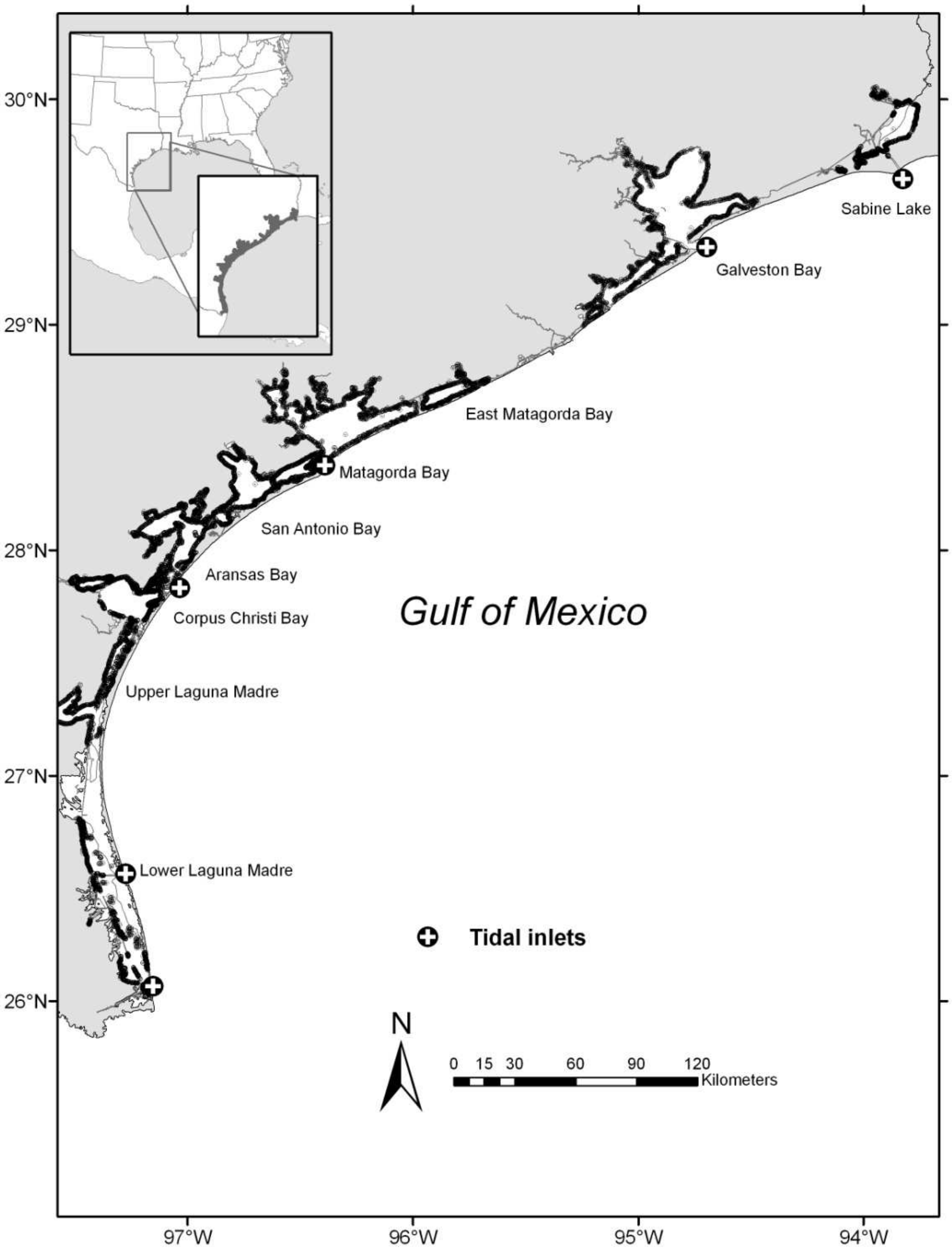

Figure 2.1. Coastal shark gill-net survey locations (n = 19757) from 1975-2006 in Texas, USA.

Table 2.1 Predictors used in the analyses.

Variable	**Description**	**Mean (range)**
Salinity (psu)	Surface salinity at offshore end of the gill net	22.8 (0-69)
Temperature℃	Surface temperature at offshore end o f gill net	26.2 (4.8-38.0)
Depth (m)	Depth at the offshore end of gill net set	1.1 (0.1-8.5)
Distance (cost-distance units)	Distance to nearest tidal inlet	12.6 (1-32)
Turbidity (NTU)	Turbidity of surface water at offshore end of gill net	28.2 (0-999)
DO (mg O_2-l^{-1})	Surface dissolved oxygen concentration at offshore end of gill net	7.9 (0.6-28.5)
Surface Inflow (acre-feet)	Mean monthly surface inflow per bay system	398594 (24-4355617)
Freshwater Balance (acre-feet)	Surface Inflow - evaporation from estuary surface	369569 (-269000-4370924)
Time (h)	Number of hours gill-net was deployed	13.7 (9.4-21.1)
Month	Month sample occurred	NA
Year	Year sample occurred	NA

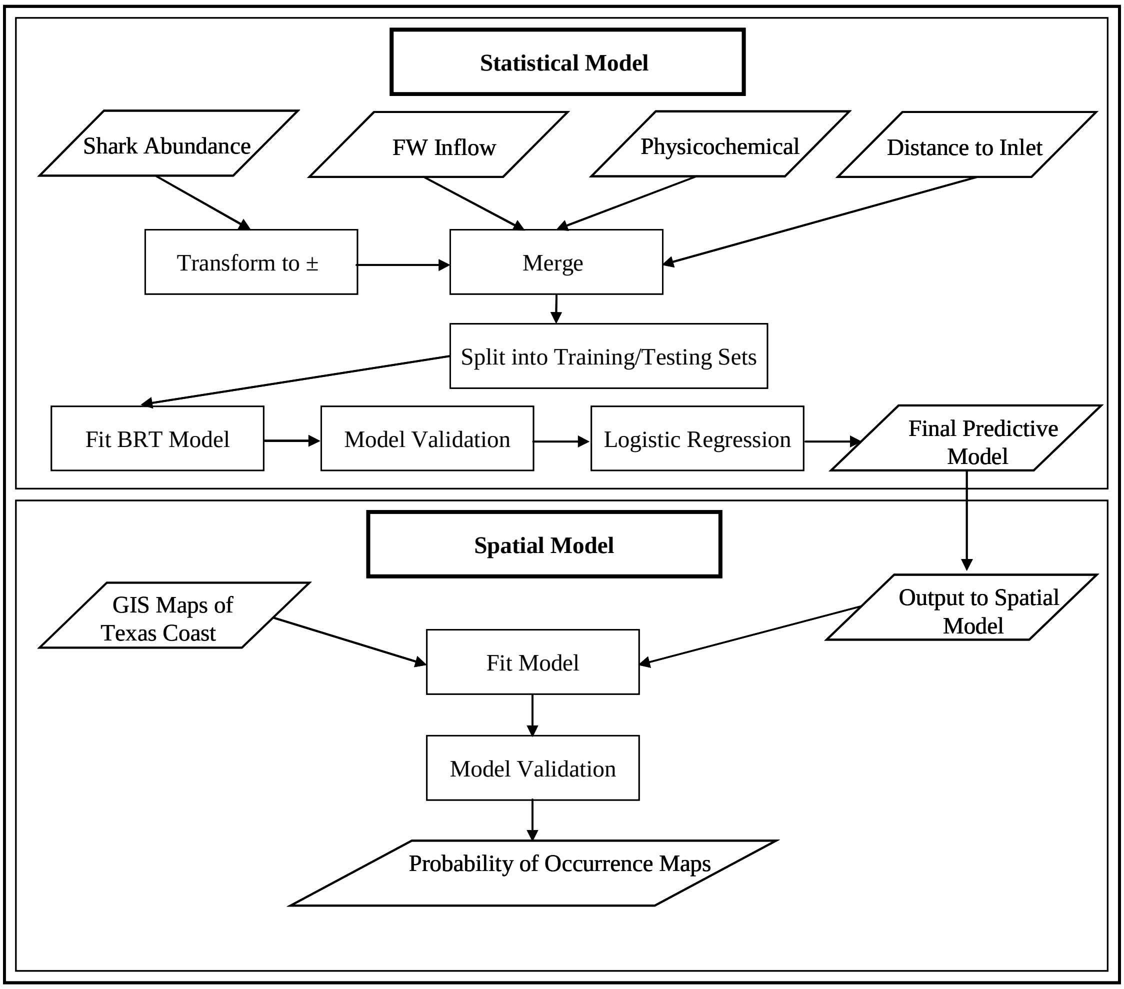

Figure 2.2. Modeling and spatial distribution of bull, blacktip, and bonnethead sharks on the Texas coast. Rectangles indicate a process and parallelograms indicate a data input or output. BRT = Boosted regression tree, GIS = Geographic information system.

were determined for the entire study area and the boosted regression tree model was used to predict probability of capture during spring and fall conditions. Predictive performance of spatial models were validated using cross-validation.

RESULTS

Physicochemical

Patterns of 11 predictor variables were examined to investigate relationships between environmental conditions and shark distributions (Table 2.1). On the Texas coast, physical conditions vary widely among bay systems. Salinity increases with decreasing latitude from hyposaline positive (Sabine Lake and Galveston Bay) to moderate (15-35 psu) along the central coast and hypersaline negative estuaries (> 35 psu) in the southernmost Upper and Lower Laguna Madre (Figure 2.3A). Mean sea surface temperature also increases slightly from north to south along the coast (Figure 2.3B). Dissolved oxygen concentration, turbidity, and sampling depths were similar among bay systems and a complete description of the environmental variables and ranges are described in Table 2.2. Freshwater inflow and balance, which affect salinity, varied dramatically along the coast with highest inflow rates in the northern bays (Sabine Lake and Galveston Bay), intermediate along the central coast and, low in the Laguna Madre (Table 2.2).

Shark Distribution and Habitat Modeling

The shark assemblage in this study was numerically dominated by three species, bull shark, blacktip, and bonnethead sharks; a total of 9,687 sharks was included in the study. Length-frequency histograms were developed for each species and suggest that the blacktip and bull shark catch was dominated by juveniles while bonnethead were collected throughout their ontogeny (Figure 2.4). With the exception of bull sharks, length distributions were bimodal, suggesting that multiple age classes may be using coastal bays.

Bull shark

Bull shark was the most abundant species sampled (frequency of occurrence = 12.0 %), and model evaluation suggested very good predictive performance to independent data (ROC = 0.84; Table 2.3). Bull shark distributions were most strongly influenced by salinity and temperature (Figure 2.5). Fitted functions from the BRT model indicate that bull sharks occur in salinities from 0-40 psu but were most common in moderate salinities (15-30 psu) and rarely occurred in areas above 35 psu (Figure 2.6). With respect to temperature, bull sharks were rare in waters below 20°C, while probability of capture increases rapidly up to 33°C and then declines precipitously. However, other variables including freshwater inflow, turbidity, and proximity to tidal inlets also influenced distribution patterns (Figure 2.5).

Spatially explicit model predictions for spring, fall, and mean overall conditions revealed that the highest probability of capturing bull sharks occurred along the central coast in Matagorda and San Antonio bays (Figure 2.7). Moderate catch rates are predicted along most of the coast including the hyposaline Galveston Bay and Sabine Lake. Low probabilities of capture were predicted in East Matagorda and Upper and Lower Laguna Madre due to combination of shallow waters and high salinities (Upper and Lower Laguna Madre). Few seasonal differences were noted between spring and fall probability of capture estimates and was supported by the relatively low importance of month in the boosted regression tree model (Figure 2.5).

Blacktip shark

Blacktip sharks were the second most abundant species sampled (frequency of occurrence = 3.4%), and model evaluation suggested good predictive performance to independent data (ROC = 0.86; Table 2.3). Similar to bull shark, fitted functions of the most influential predictors were non-linear and complex (Figure 2.6B). Fitted functions were most strongly influenced by salinity, temperature, depth, and distance to inlets suggesting a preference for warm waters near tidal inlets of moderate salinities that are proximate to deeper waters.

Spatial predictions for blacktip sharks suggest highest probability of capture along the central coast in Matagorda and San Antonio bays (Figure 2.8) and predicted distribution patterns were very similar between seasons. High probability areas were restricted near tidal inlets along the coast. Probability of capture was very low in all areas of the Sabine Lake (hyposaline) and the Upper Laguna Madre (hypersaline).

Bonnethead shark

Bonnethead sharks were captured in 3.1% of all samples. Model evaluation for this species also suggested good predictive performance of the BRT to independent data (ROC = 0.86; Table 2.3). Similar to blacktip sharks, fitted functions for bonnethead were highest at sites > 1 m depth and proximal to tidal inlets. Salinity also influenced distribution patterns, as bonnethead demonstrated a distinct preference for salinities between 20-40 psu.

Probability of capture of bonnethead were similar to blacktip sharks in that areas near tidal inlets with access to deeper waters were most important. Highest probabilities of capture were predicted near the inlets on the central coast and this was consistent between seasons, and for overall estimates (Figure 2.9). Probability of capture was low in both northern bay systems (Galveston Bay and Sabine Lake), however was higher in Lower Laguna Madre than for either bull or blacktip sharks.

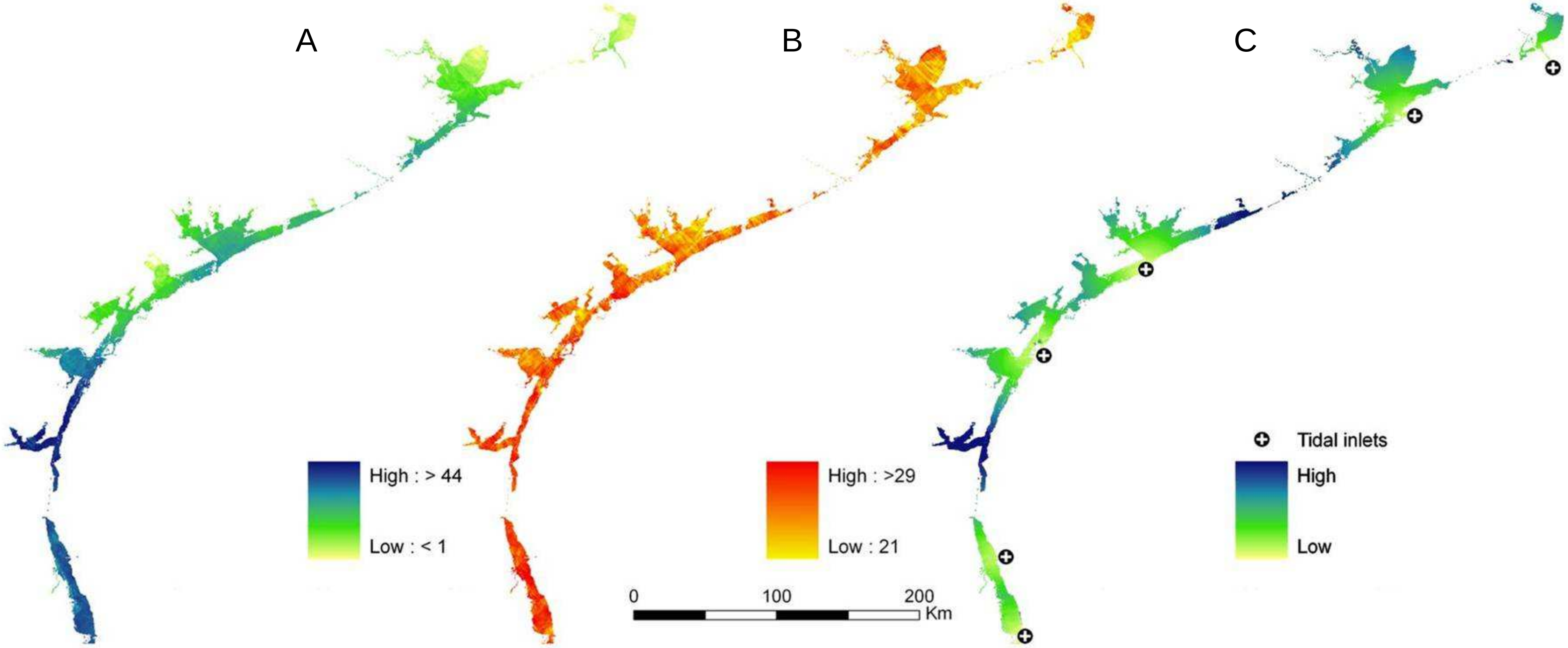

Figure 2.3. (A) Mean salinity (0 - 44 psu), (B) temperature (21 - 29 °C), (C) and distance to inlets (cost-distance units) of sample locations in Texas Bays from 1975-2006. Distance to tidal inlet was estimated using the cost-distance function in ArcGIS. Maps of mean salinity and temperature were created by kriging measured values (n = 17757) during gill-net sampling from 1976 to 2006.

Table 2.2. Summary of physicochemical predictors used in the analysis.

	Sabine Lake	Galveston Bay	East Matagorda Bay	Matagorda Bay	San Antonio Bay	Aransas Bay	Corpus Christi Bay	Upper Laguna Madre	Lower Laguna Madre
Salinity (psu)	7.9 ± 6.1	16.9 ± 8.5	20.8 ± 8.3	19.3 ± 9.0	18.7 ± 10.8	18.3 ± 9.4	29.0 ± 7.4	37.5 ± 10.1	32.2 ± 7.3
Temperature (˚C)	25.6 ± 4.1	25.5 ± 3.9	26.2 ± 4.2	25.8 ± 3.9	26.1 ± 3.7	26.2 ± 3.7	26.2 ± 3.7	26.8 ± 3.7	27.1 ± 3.5
Depth (m)	1.1 ± 0.5	1.2 ± 0.5	0.9 ± 0.3	1.1 ± 0.4	1.1 ± 0.4	1.1 ± 0.4	1.3 ± 0.6	1.1 ± 0.4	1.0 ± 0.5
Turbidity	19.6 ± 28.5	27.5 ± 31.0	33.4 ± 39.9	36.9 ± 47.7	25.4 ± 33.2	27.1 ± 33.6	24.1 ± 33.4	27.6 ± 44.7	33.4 ± 56.9
DO (mg 0_2 l^{-1})	7.7 ± 1.6	7.9 ± 2.0	7.8 ± 1.9	7.7 ± 1.7	8.1 ± 2.0	8.4 ± 2.1	7.7 ± 1.8	7. 5 ± 1.9	7.9 ± 2.1

Table 2.3. Predictive performance of BRT models evaluated on three data sets, training (n = 9879), cross-validation (n = 9879), independent (n = 9878) for 5 coastal shark species. **lr* = learning rate, **nt* = number of trees fitted.

			Percentage Deviance Explained				Area under the receiver operating characteristic curve (ROC)			
Species	*lr**	*nt**	Independent	Cross-validation	Training	Total deviance	Independent	Cross-validation (SE)	Train	Frequency of occurrence
Bull shark	0.01	3500	24.3%	20.3%	40.0%	0.752	0.84	0.823 (0.005)	0.928	12%
Blacktip shark	0.005	3750	18.6%	18.3%	45.7%	0.308	0.87	0.848 (0.006)	0.962	3%
Bonnethead shark	0.005	2400	18.6%	18.3%	45.7%	0.277	0.86	0.881 (0.009)	0.963	3%

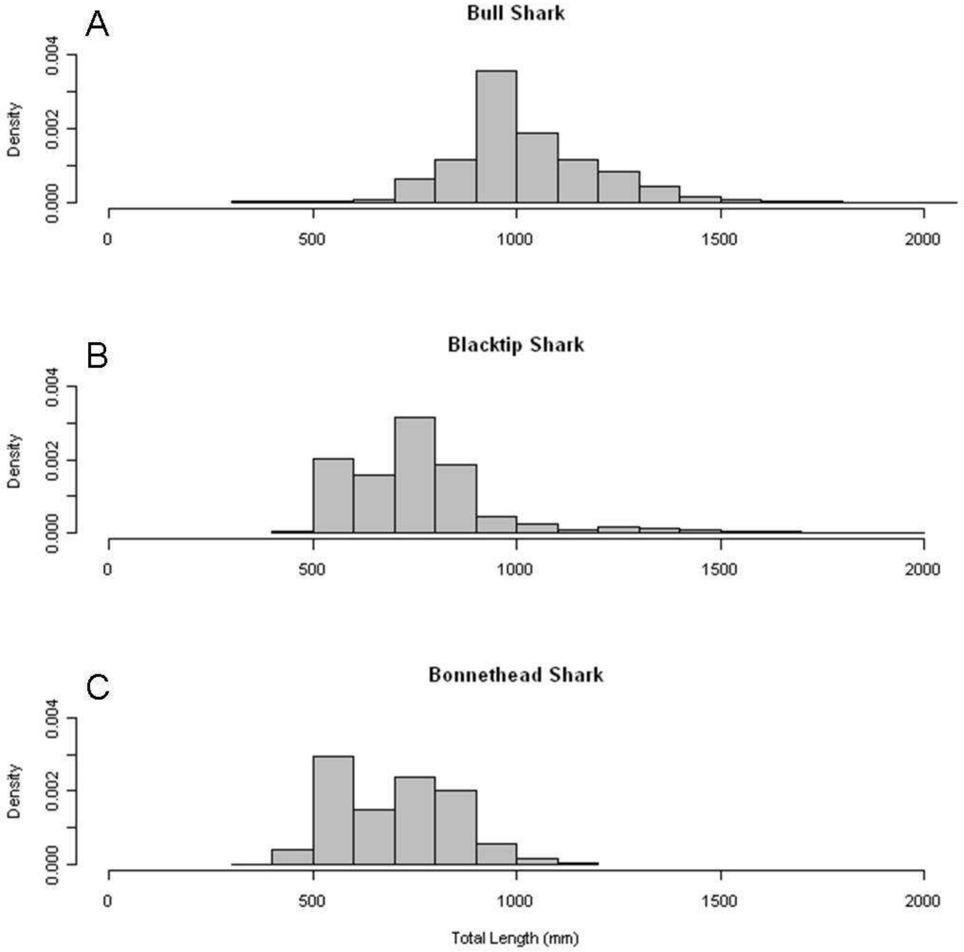

Figure 2.4**.** Size frequency and probability density histogram of (A) bull shark (*Carcharhinus leucas*), (B) blacktip shark (*Carcharhinus limbatus*), and (C) bonnethead shark (*Sphyrna tiburo*).

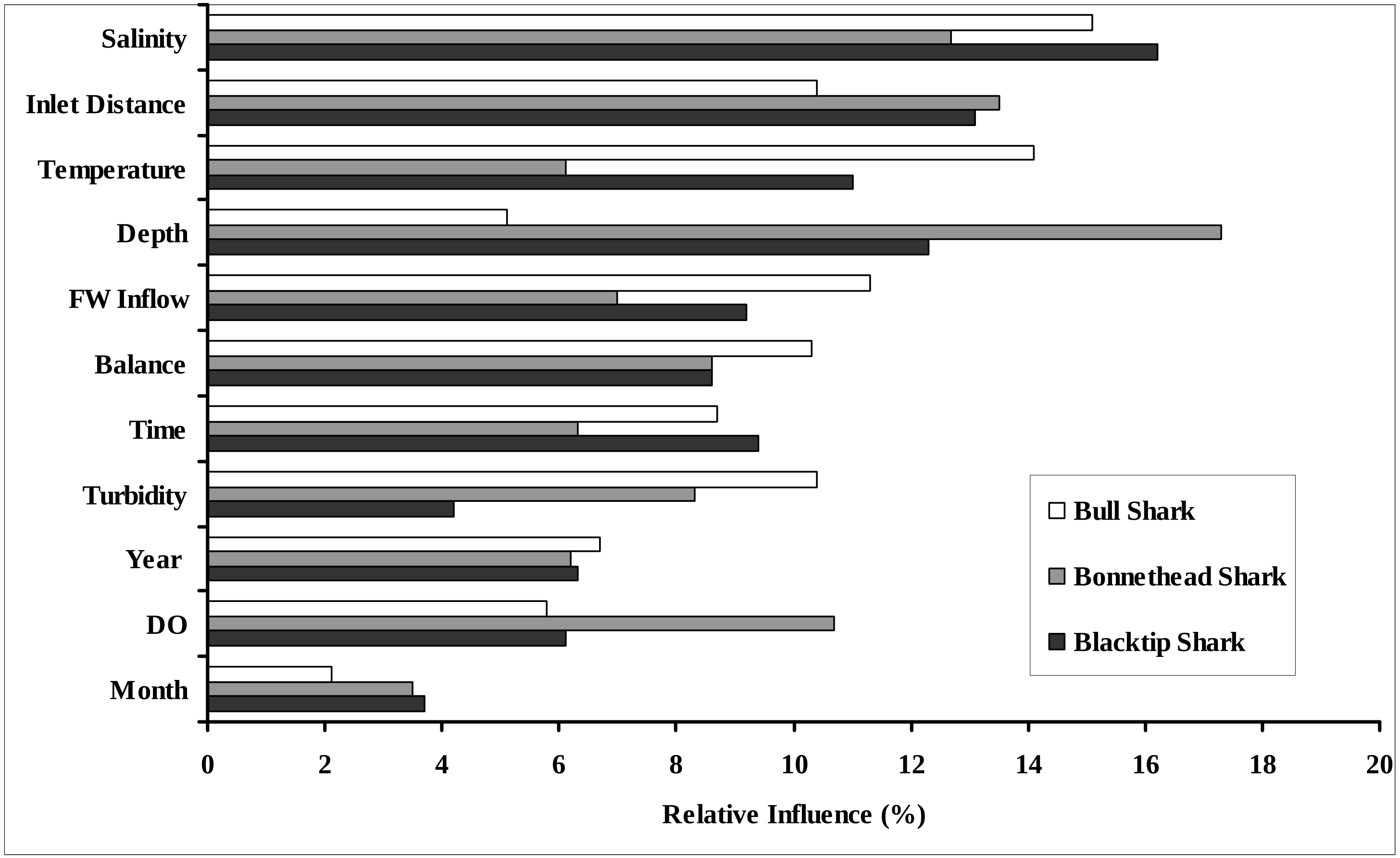

Figure 2.5. Average contributions (%) of environmental variables predicting presence or absence of three coastal shark species. Variables are ranked in decreasing order based on average overall contribution.

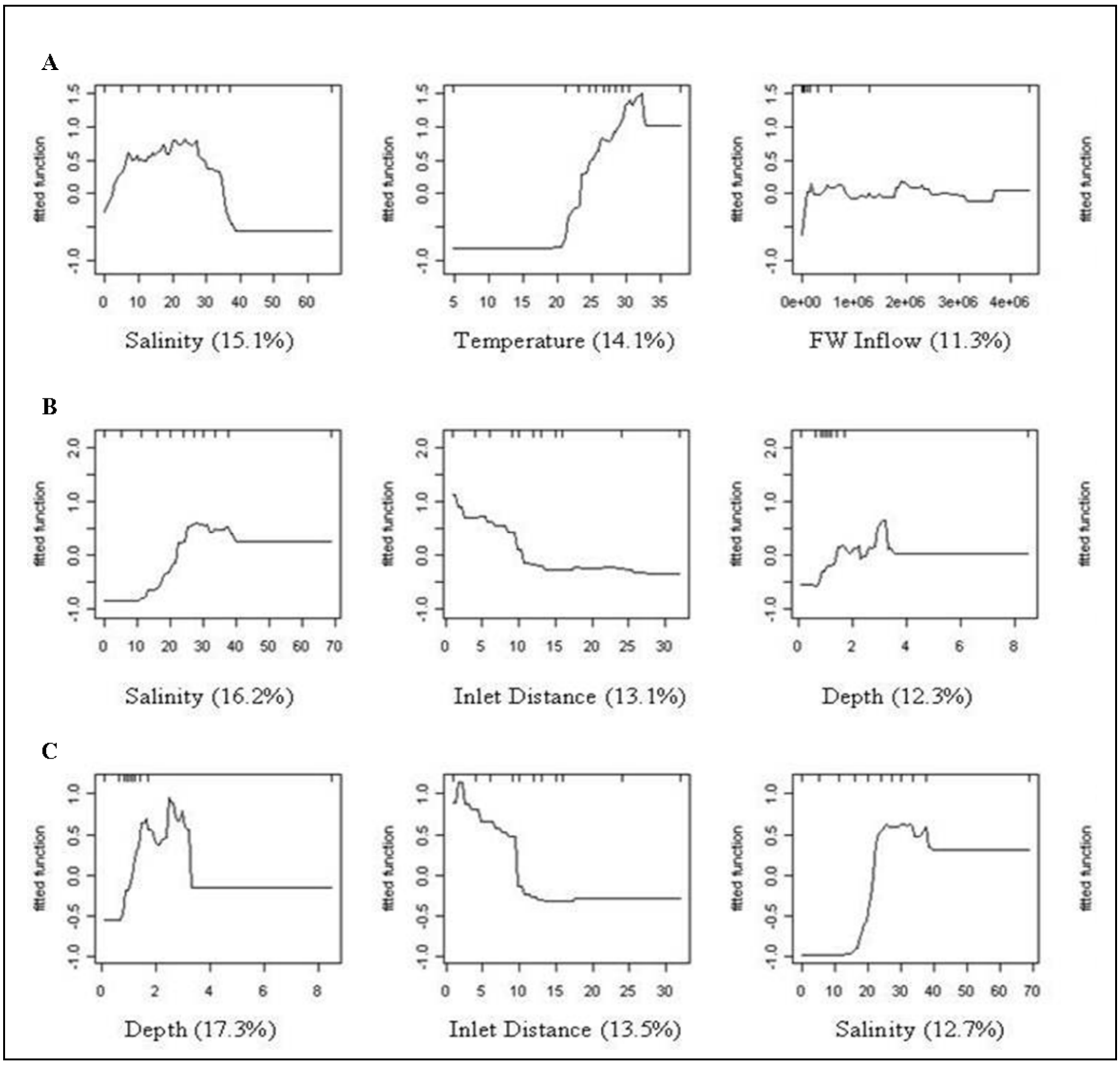

Figure 2.6. Functions fitted for the three most important predictor variables by a boosted regression trees (BRT) model relating the probability of occurrence of sharks to the environment. (A) bull shark(*Carcharhinus leucas*), (B) blacktip shark (*Carcharhinus limbatus*), and (C) bonnethead shark (*Sphyrna tiburo*). Y axes are on the logit scale with mean zero.

Table 2.4. Cross-validation results of ordinary kriging model for each species.

	Bull Shark	**Blacktip Shark**	**Bonnethead Shark**
Mean	< 0.01	< 0.01	0.01
Root-Mean-Square	0.12	0.05	0.05
Average Standard Error	0.40	0.06	0.11
Mean Standardized	-0.01	0.00	0.12
Root-Mean-Square Standardized	0.37	0.83	0.53
n	7856	7856	7856

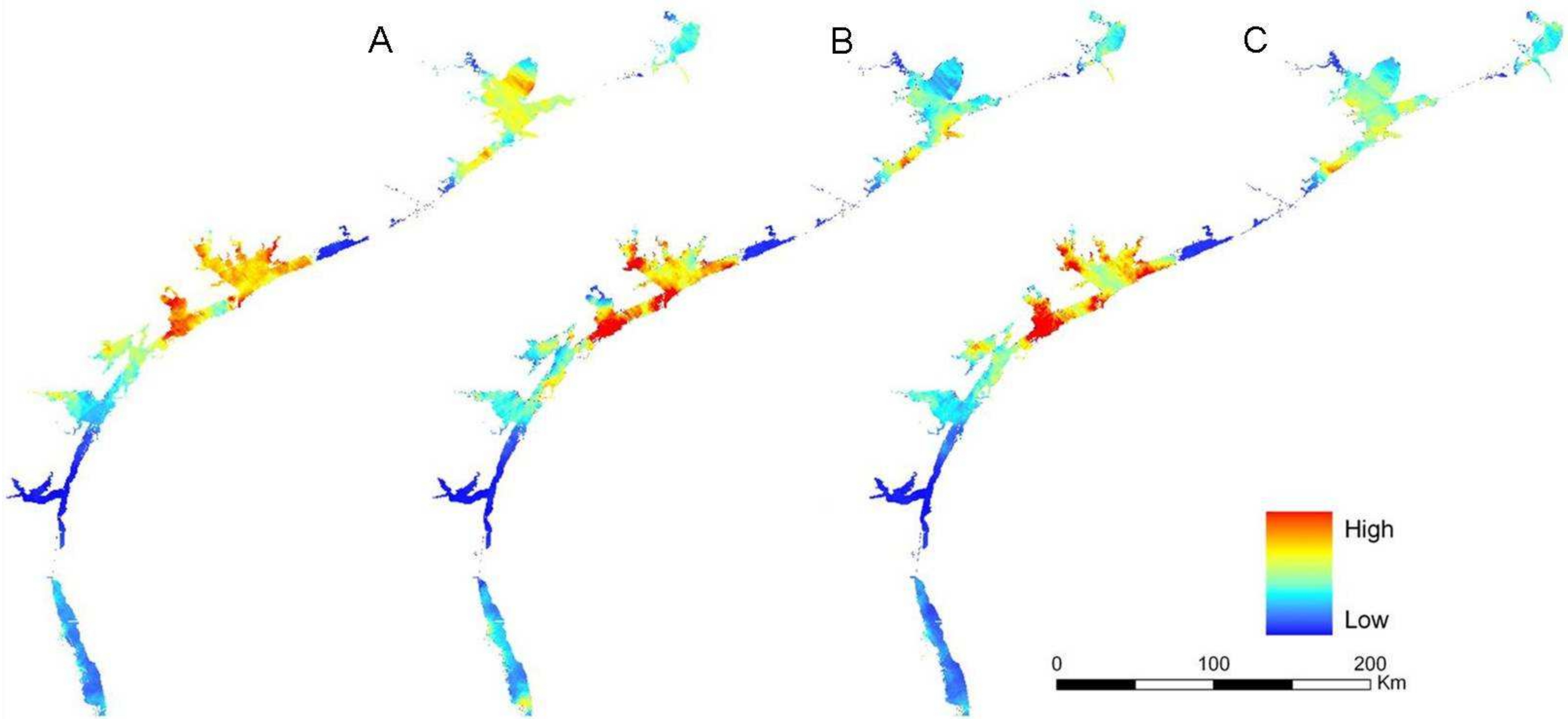

Figure 2.7. Probability of capture maps of bull shark (*Carcharhinus leucas*) along the Texas coast as predicted by a boosted regression tree model for (A) spring, (B) fall, and (C) mean overall conditions. Predictions were restricted to areas within 1-km of the shoreline.

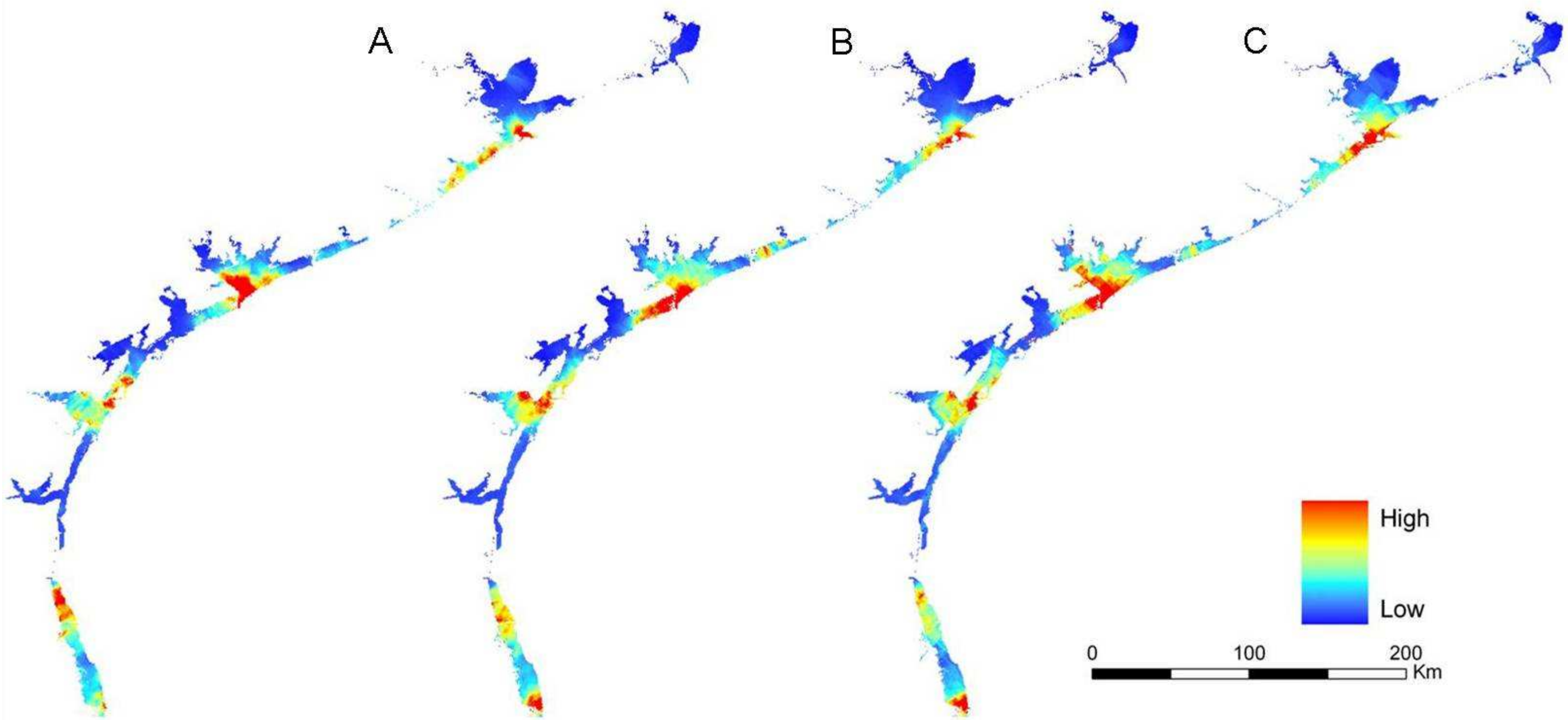

Figure 2.8. Probability of capture maps of blacktip shark (*Carcharhinus limbatus*) along the Texas coast as predicted by a boosted regression tree model (A) spring, (B) fall, and (C) mean overall conditions. Predictions were restricted to areas within 1-km of the shoreline.

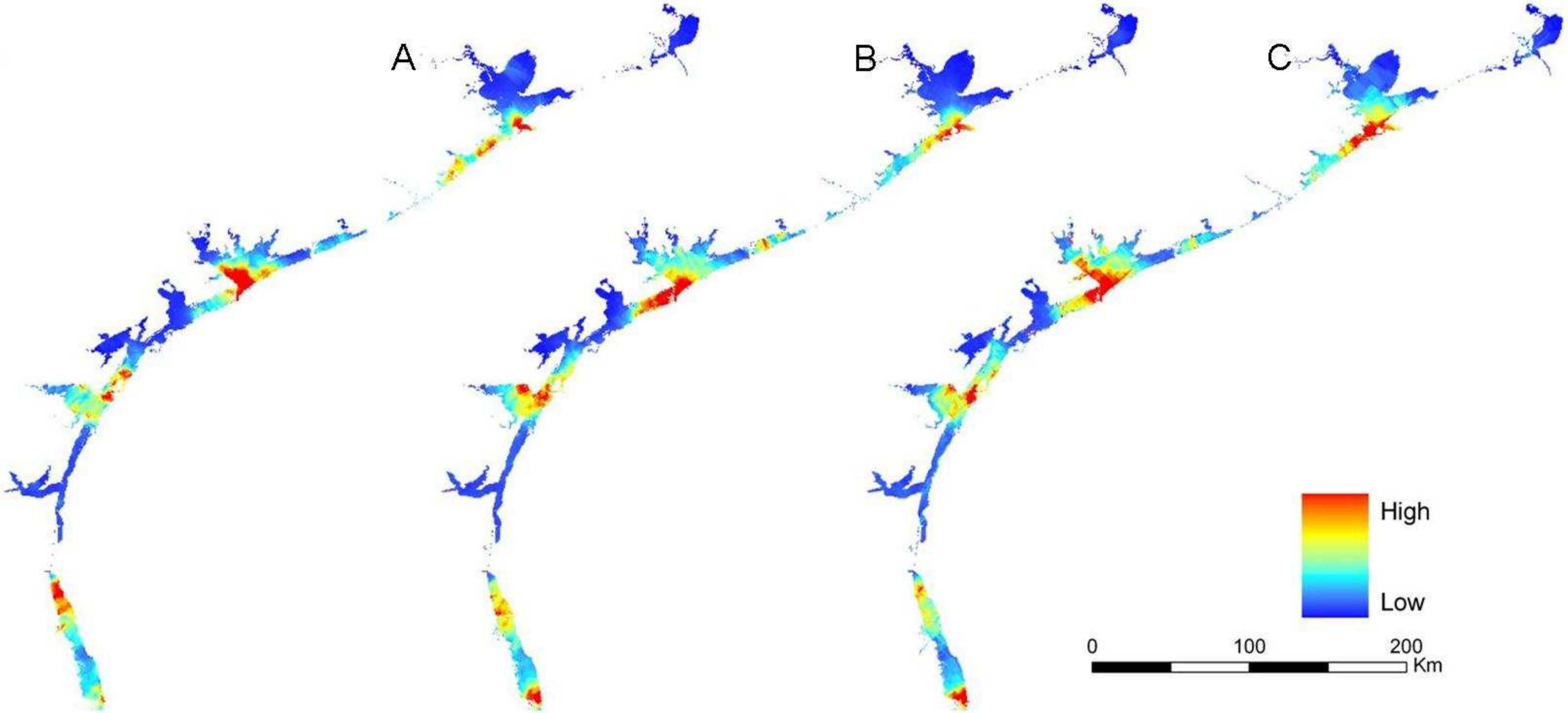

Figure 2.9. Probability of capture maps of bonnethead shark (*Sphyrna tiburo*) along the Texas coast as predicted by a boosted regression tree model (A) spring, (B) fall, and (C) mean overall conditions. Predictions were restricted to areas within 1-km of the shoreline.

DISCUSSION

Distribution patterns of sharks were influenced by several environmental variables. Overall, both general and species specific patterns were observed. All three species displayed distinct salinity preferences and this variable was the most important factor in the BRT model for blacktip and bull sharks, and the third most influential variable for bonnethead. These species were most common in moderate salinities (bull shark 10-30 psu; blacktip 20-35 psu; bonnethead 20-40 psu) and avoided hypersaline waters. Capture rates of blacktip and bonnethead were low in low salinity waters (i.e., < 10 psu) while bull sharks were common in these areas. Bull sharks are unique in their ability to osmoregulate long-term in low salinity waters. Thorson et al. (1973) hypothesized that salinity would not influence coastal bull shark distribution patterns. However our data, as well as other recent studies (Simpfendorfer et al. 2005, Heupel and Simpfendorfer 2008), indicate that bull shark captures occurred within a distinct range of moderate salinities. However, blacktip sharks were uncommon in low salinities and were largely restricted to areas between 20-35 psu. This salinity preference is similar to results from Florida, USA estuaries were blacktips were found between 20-36 psu; however, juveniles were restricted to a much narrower range (31-36 psu; Bethea et al. 2006). Movement of bonnethead in a Florida, USA estuary was also influenced by salinity and were found between 11 and 36 psu over a two year period (Ubeda et al. 2009), similar to the results of this long-term study.

Distribution patterns of sharks in relation to salinity may be a mechanism to reduce the energetic costs associated with osmoregulation permitting increased growth rates and reducing times in size classes where mortality rates are highest. Avoidance of hypersaline areas such as Upper Laguna Madre may reflect their inability or physiological costs of osmoregulation in hypersaline conditions. Based on length-at-age estimations, the majority of sharks captured in this study were juveniles (except bonnethead) and evidence suggests that energetic costs of osmoregulation are highest for young sharks when surface to volume ratio is lowest (Heupel & Simpfendorfer 2008). Juvenile blacktip sharks were captured in a narrow range of salinities in Florida, USA (31-36 psu) while adults occurred in a much broader range (21-36 psu; Bethea et al. 2006). Studies of juvenile bull sharks in Florida estuaries found similar patterns (Simpfendorfer et al. 2005, Heupel & Simpfendorfer 2008). Selection of habitats based on salinity has been demonstrated in teleost fishes as a mechanism to reduce energetic costs of osmoregulation (Marais 1978); therefore, permitting more energy for growth or reproduction. Laboratory experiments on euryhaline killifish (*Fundulus heterclitus*) indicate that osmoregulation typically requires 6 - 10 % of the total energy budget and fish select areas closest to their own osmolarity (Kidder 2006). Previous studies have hypothesized that use of low salinity waters is based on prey access or predator avoidance (Pillans & Franklin 2004, Pillans et al. 2005). However, Heupel and Simpfendorfer (2008) suggest that salinity preferences limit distribution patterns of juvenile bull sharks between 7 and 20 psu. Our study expands these findings over a wider range of salinities (0-60 psu) for three shark species, and supports the hypothesis that sharks are using behavior to reduce metabolic demands of osmoregulation.

Temperature also strongly influenced distribution patterns of sharks. Few sharks were captured below 20°C; however, catch rates increased rapidly with increasing temperature between 20-33°C before declining again. Selection for warm temperatures is also consistent with habitat use to maximize physiological performance as mean temperatures were warmer in samples where were sharks were present and this pattern was consistent across all months sampled. Like most other coastal species, juvenile blacktip sharks use estuaries as nursery habitat to reduce mortality rates (Beck et al. 2001), and the preference for increased temperatures may increase growth rates and boost metabolic rates (Beck et al. 2001, Heupel et al. 2007). In a study of blacktip sharks, Heupel and Simpfendorfer (2002) reported highest mortality rates during the first 15 weeks of life when animals are smallest and susceptible to the widest range of predators. Size of captured blacktip sharks in the current study indicate that most animals captured are juveniles and habitat usage could reflect areas permitting some combination of rapid growth or lower mortality rates. Increasing catch rates of juvenile bull sharks with temperature was also reported by Simpfendorfer et al. (2005) while temperature was only moderately important for bonnethead (Ubeda et al. 2009). Similarly, in this study, temperature was not an important predictor of catch rates for bonnethead as depth and distance to inlets most strongly influenced distribution patterns for this species.

Temperature influences metabolic rate and determines rates of biochemical reactions and in this case blacktip and bull sharks may be using behavioral thermoregulation as a means to increase growth rates. However, at extremely high temperatures (i.e., > 33°C) catch rates of sharks were low, suggesting an upper thermal limit on habitats sharks can occupy.

Realized spatial distribution patterns integrate biological and environmental influences that ultimately determine habitat usage patterns. Fry (1947) stated that the environment influences activities (i.e., movement) of an organism through metabolic effects and various environmental attributes interact in their effects on metabolism (Neill et al. 1994). Along the Texas coast, salinity and temperature were the greatest determinants of habitat usage patterns and were moderated by climate patterns, river inflow, and water exchange with the Gulf of Mexico via tidal inlets. Although distribution patterns of bull sharks were not restricted to areas near tidal inlets, they are likely important components of habitat both as access corridors and as a source of oceanic type waters. The brackish estuarine waters along the central Texas coast may represent the best integration of these factors contributing to higher probability of capture estimates in these areas. Probability of blacktip and bonnethead shark captures were highest in areas proximate to tidal inlets where waters are typically warm, near oceanic salinities, with access to deeper waters. Observed distribution patterns could also result from phenomenon correlated with environmental patterns, such as prey or predator density which was not included in this study. However, Heupel and Hueter (2002) found no correlation between habitat selection and prey abundance of blacktip sharks in a Florida nursery suggesting other factors are the primary determinants of habitat use patterns. Blacktip sharks were most abundant near the Matagorda Bay inlet where abundance of other sharks (their primary predators) are also highest suggesting that predation risk alone may not be driving the observed patterns.

Despite the utility of our modeling approach, there are some limitations to this methodology. Model evaluation indicated very good performance of the BRT at predicting independent testing data although the inference value may be limited due to high residual deviance in the models. However, data mining techniques can only find patterns that actually exist (Brodley et al. 1999) and the high residual deviance in the

BRT models for all three species may suggest that some variables important in the habitat usage of these species may not have been included in the study. Biotic components, including prey availability, movement patterns (Papastamatiou et al. 2009) or philopatry (Heuter et al. 2005) of individuals were not available in this area and thus, not considered in this study. Additionally, distributional models are correlational, thus do not elucidate the mechanisms for species-habitat associations. Experimental approaches examining factors that influence habitat quality including growth rates or survivorship of individuals are necessary to determine causation (Valavanis et al. 2008). However, using our approach, we were able to simultaneously examine parameters and ranges of parameters related to habitat suitability laying the ground-work for future hypothesis driven studies. Spatially explicit models permit applications that are not feasible with other approaches (Stoner et al. 2001) including 1) prediction of distribution patterns related to dynamic environmental patterns (i.e., temperature, salinity etc.), 2) identification of habitats needed for conservation of species, and 3) predictions of effects of habitat disturbance or alteration from either natural or anthropogenic causes.

Spatially explicit maps permit rapid identification and delineation of important habitats. For the shark species in the current study, areas along the central coast near tidal inlets provide highest probability of capture. Bull sharks extend considerable distances into estuaries where low or moderate salinity waters are available. All species were rare in hypersaline habitats (i.e., Upper Laguna Madre) and areas distant from access points to the Gulf of Mexico. Realized distribution patterns of these species may integrate both the spatial arrangement of habitats and the environmental conditions to determine habitat quality. In July 2005, the US Army Corps of Engineers dredged and reopened Packery Channel creating a new tidal connection to the Gulf of Mexico near Upper Laguna Madre and Corpus Christi Bay to increase water exchange, moderate salinities, and provide an additional ingress point for estuarine nekton (Reese et al. 2008). This management action may also improve habitat quality for sharks in this area by moderating salinities and providing additional access to these areas. Continued monitoring will be necessary to evaluate this impact.

Despite considerable interest, progress in identification of critical habitats for large mobile species (i.e., sharks) has been slow. This is due in part to the paucity of data over adequate spatial and temporal scales to characterize distribution patterns and empirical difficulties modeling species habitat distributions of rare animals (Rooper and Martin 2009). This long-term (32-year), statewide assessment of nine estuaries provides a first attempt at delineating critical habitat and identification of important environmental influences on shark habitat value in northwestern Gulf of Mexico. In addition, I provide a framework in which to consider potential impacts of habitat alteration on shark habitat quality *a priori*, an important consideration in light of continued human expansion and alteration of coastal habitats (Lotze et al. 2006). In Texas estuaries increasing temperatures and declining dissolved oxygen concentrations have been reported (Applebaum et al. 2005) and reduced freshwater inflow to the Texas Coast is predicted due to global climate change (Ward 2009). Improving our ability to manage coastal shark stocks is imperative as shark populations have declined in the Gulf of Mexico (Baum & Myers 2004). Also, blacktip shark is an important component of the U.S. commercial shark fishery (NMFS 2008) and are also heavily targeted in Mexican fisheries (Hueter et al. 2007). While blacktip shark is not currently overfished in the Gulf of Mexico (NMFS 2008); increasing fishing pressure or alteration of critical coastal habitats lends the potential for overexploitation of this species as well.

Long-term conservation requires identification and protection of critical ecosystems and the myriad of processes that influence habitat value (Levin and Stunz 2005). Our results provide new insight into the habitat requirements of coastal sharks in the northwestern Gulf of Mexico and should provide practical information for conserving shark habitat and managing coastal resources. The development of spatially explicit models from boosted regression tree analyses allows for prioritization of areas for conservation and provides insight into critical ecosystem attributes (i.e., salinity regimes) that merit protection. Areas with high probabilities of capture typically had warm temperatures and moderate salinities, highlighting the importance of both freshwater inflow and access to the Gulf of Mexico via tidal inlets for shark habitat suitability.

AKNOWLEDGMENTS

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CHAPTER 3

IS PADRE ISLAND NATIONAL SEASHORE ESSENTIAL SHARK HABITAT? EXAMINATION OF AN IMPORTANT RECREATIONAL SHARK FISHERY

ABSTRACT

Currently, there are limited data representing Essential Fish Habitat (EFH) or nursery habitat for coastal sharks in the Gulf of Mexico from Louisiana to Mexico. However, based on preliminary catch data and the similar habitat characteristics of the Texas coast to other reported shark habitats it is probable that the coastal waters of Texas may be EFH and/or nursery habitat for some species of sharks. Currently, knowledge about the population status and trends of the shark resource in this area are limited leading to uncertainty in the appropriate management strategies, ultimately leading to more restrictive harvest regulations in the region. To address this problem, fisheries dependent catch records of shark species in the nearshore Gulf of Mexico were described using historical and current data. From 1973 to 1986 and 2008 to 2009, I analyzed shark capture logs from recreational shark anglers on the Texas coast. In this study, juveniles from at least 16 shark species were identified. Results suggested that several species use coastal habitats within the Gulf of Mexico as primary and/or secondary nurseries. Most sharks were captured within Padre Island National Seashore and this area supports a growing recreational shark fishery and suggests that this resource should be managed cautiously to encourage economic and ecological sustainability.

INTRODUCTION

Ecological impacts of apex predators can be dramatic (O'Connell et al. 2007). In oceanic ecosystems, large sharks function as top predators, and their abundance and distribution patterns may have cascading effects on the ecosystems they inhabit (Terborgh et al. 2001, Daskalov et al. 2007, Myers et al. 2007, Heithaus et al. 2008). Sharks are typically slow growing, long lived species (Musick et al. 2000) that use a variety of habitats over broad spatial scales. Their life history characteristics leave them vulnerable to exploitation and many shark populations worldwide are in decline (Myers & Worm 2003, Baum & Myers 2004, Brierley 2007, Myers et al. 2007, Whitney and Crow 2007).

In the Gulf of Mexico, declines of both oceanic and coastal shark populations have been reported (Baum & Myers 2004, O'Connell et al. 2007, Powers et al. *In review*). Two formerly abundant pelagic species, oceanic whitetip and silky sharks have declined over 99 and 90%, respectively since the 1950’s (Baum & Myers 2004) while dramatic declines of bull shark (a coastal species) were reported in Lake Ponchatrain, Louisiana (O'Connell et al. 2007). Using fishery-dependent data, Powers et al. (*In review*) reported declines of large sharks in the northern Gulf of Mexico. This trend has continued despite the incorporation of most shark populations and their Essential Fish Habitat (EFH) needs into all Fishery Management Plans (NOAA 1996).

Population trends and basic biological information on shark populations in the Gulf of Mexico are limited, particularly in the Northwest region. Currently, there are very limited data representing EFH or nursery habitat for coastal sharks in the Gulf of Mexico from Louisiana to Mexico. However, based on preliminary catch data and the similar habitat characteristics of the Texas coast to other reported shark habitats (Hueter and Tyminski 2007), it is possible the coastal waters of Texas may be EFH for some species of sharks. Hueter and Tyminski (2007) examined temporal and distributional patterns of juvenile sharks primarily off Florida but included some data for Texas. In this study, juveniles from at least 16 shark species were identified, and results suggested that several species use coastal habitats within the Gulf of Mexico as primary and/or secondary nurseries. Parsons and Hoffmayer (2007) characterized the north-central Gulf of Mexico as nursery habitat for several shark species. This study reported species-specific habitat preferences based in part on salinity preferences, noting that Atlantic sharpnose (*Rhizoprionodon terraenovae*) were restricted to higher salinity coastal areas as opposed to hyposaline estuaries. Coastal waters off Louisiana were also reported as important juvenile habitats based as both pupping and nursery areas were reported in this region (Neer et al. 2007). However, differences in relative value between estuarine and coastal habitat use for sharks along the Northwestern Gulf of Mexico coast are unknown. Froeschke (Chapter 2) related estuarine shark distribution patterns in Texas to environmental factors and found that salinity, temperature, and proximity to tidal inlets were primary determinants of habitat use. Bull shark nursery use of Texas bays was also investigated in Texas' estuaries and found that at least some bays provide shark nursery functions (Froeschke Chapter 2); however, the relative habitat value of the 500-km open coast along Texas is relatively unknown. Moreover, there are no quantitative data for this region to make ecological assessments of this important shark resource.

The Texas coast encompasses approximately 500 km of shallow soft-bottom habitat that supports a growing recreational shark fishery, especially at Padre Island National Seashore (PINS). For example, the annual Sharkathon angling tournament based at PINS began at 2004 and now constitutes the largest land-based fishing tournament in the world (http://www.sharkathon.com). While this tournament is catch-and-release only and has a strong emphasis on conservation, the rapidly rising participation may serve as a proxy of fishery effort on coastal sharks in Texas. Other angling tournaments targeting sharks in the Gulf of Mexico have shown similar increases in angler participation in recent years (Powers et al. *In review*). However, the population status or trends of the shark fishery are poorly known, and there is no ecological baseline to estimate past or future impacts. Currently, there are no fisheries independent data for the assessment of coastal sharks in this region. Absence of data coupled with anecdotal declines of this fishery has created uncertainty in the status of the shark resource. In response, Texas fishing regulations have been altered for sharks (effective 1 September 2009; Texas Parks and Wildlife (TPWD) http://www.tpwd.state.tx.us/newsmedia/releases/?req=20090603a). Texas Parks and Wildlife established regulations that increased minimum total length for most shark species from 61 to 162.5 cm total length.

The purpose of this study was to use current and historical fishery-dependent sampling data collected in cooperation with recreational anglers to assess species composition and abundance patterns of coastal sharks on the Texas coast with particular emphasis on PINS. These data will provide the first assessment of the shark resource in terms or relative abundance, species composition, and temporal trends in catch patterns for sharks along the Texas coast.

MATERIALS AND METHODS

Shark Collection

From 1973 to 1986 and 2008 to 2009, sharks were collected at sites along the nearshore coast of Texas with particular effort along PINS (Figure 3.1). Samples were collected via hook-and-line from recreational anglers as part of the Corpus Christi Shark Club (1973 – 1986) that kept extensive catch records including species identification, and length, however, record keeping was discontinued after 1986. During 2008 and 2009, catch logs were obtained from a shark angling tournament (http://www.sharkathon.com) and recreational anglers targeting sharks. All sharks included in the analyses were identified to species and measured (mm TL).

Length-Frequency Analysis

Length-frequency distributions were calculated for the eight most abundant species captured from 1973 to 1986 where enough data was available to assess length (age)-specific catch patterns. Kernel smoothing was used to estimate length-frequencies (Venables and Ripley 2002). Length of maturity was estimated for each species from published life-history literature (Branstetter and Stiles, 1987, Kohler 1996, Joung et al. 2005).

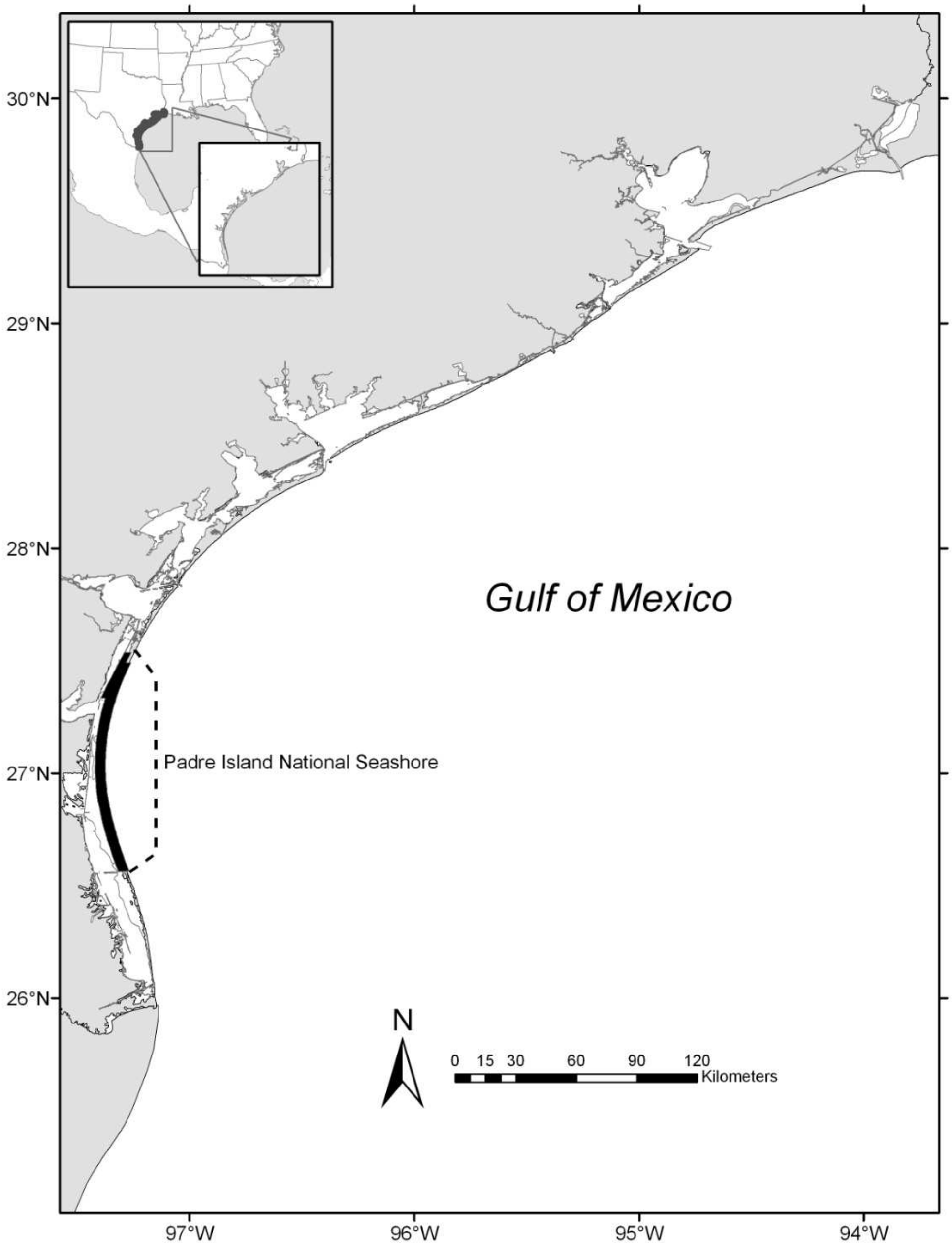


Figure 3.1. Study area of fisheries-dependent shark sampling on the Texas coast from 1973 to 1986 and 2008 to 2009.

Length-time series

Reductions in size (length) of individuals may be indicative of population decline or over-fishing (Powers et al. *In review*). Fisheries-dependent sampling are often biased toward the largest animals of a particular species (Powers et al. *In Review*). However, this bias was incorporated to examine temporal patterns in maximum sizes of the four most common shark species at PINS to test the hypothesis that maximum length of captured individuals is stable over time at PINS. Data management, calculations, length-frequency, and regression analyses were implemented in R (R Development Core Team 2008).

Community Analysis

Seasonal patterns of shark species composition were analyzed by mulitvariate methods. Ordination of samples was performed using the non-metric multidimensional scaling (MDS) and implemented in Primer software (Clarke and Gorley, 2001). The total number of each shark species was determined for each season (winter, spring, summer, fall) from 1973 to 1986. Catch data were transformed using dispersion weighting (Clarke et al. 2006) prior to analysis, and a Bray-Curtis resemblance matrix was used. A non-parametric multivariate plot of the spatial relationship of the shark catch patterns among seasons was created. Community structure of shark species was also analyzed with MDS and hierarchical cluster analysis to assess similarity in catch patterns among species and the similarities of community structures was ranked. Bray-Curtis cluster analysis results were subsequently superimposed using 50% similarity on the MDS plot of the spatial relationship among species.

RESULTS

Historical Data

From 1973 to 1986 anglers captured 802 sharks representing at least 17 species on the Texas coast (Table 1). Bull shark (*Carcharhinus leucas*) was the most abundant species (n = 321) and comprised 40% of the total catch. Tiger shark (*Galeocerdo cuvier*), blacktip shark (*Carcharhinus limbatus*), sandbar (*Carcharhinus plumbeus*), and scalloped hammerhead (*Sphyrna lewini*) ranked second through fifth, respectively, in abundance (Figure 3.2). The top eight species comprised 90% of the total catch (Table 3.1). During 2008-2009 sampling 79 sharks were captured from six species (Table 3.2). Blacktip was the most abundant species, followed by bull, and Atlantic sharpnose sharks (Figure 3.3).

Distinct seasonal patterns were observed in shark catch patterns. Few sharks were caught in the winter months of December to February, and the number of sharks captured each month increased peaking during the summer months May to August. Seven of the eight most abundant species in the catch clearly demonstrated this strong seasonal pattern (Figure 3.4). Sandbar shark was most abundant during the spring season (March - May) and captured very infrequently in the remaining months of the year.

Length-frequency analyses were conducted for the eight most abundant species to examine habitat use patterns necessary to determine important habitat for all important life stages. Length at maturity was estimated for each species to determine both juvenile and adult habitat use. Overall, coastal habitats supported both juvenile and adult age classes for most species. Bull sharks were primarily captured as adults while tiger, and blacktip sharks were frequently captured at both juvenile and adult age classes (Figure

3.5A). In contrast, captured sandbar sharks were collected almost exclusively as adults (Figure 3.5B).

Table 3.1. Collection information of sharks captured on the Texas coast from hook-and-line sampling from 1973 to 1986.

Species	**Common name**	**Abundance**	**Mean total length in cm (range)**	**Mean Temperature (range)**
Carcharhinus brevipinna	Spinner	29	159 (79 - 231)	26 (22 - 30)
Carcharhinus falciformis	Silky	2	262 (188 - 335))	20 (NA)
Carcharhinus isodon	Fine Tooth	5	94 (69 - 152)	29 (NA)
Carcharhinus leucas	Bull	321	242 (76 - 470)	27 (18 - 30)
Carcharhinus limbatus	Blacktip	71	129 (36 - 203)	26 (18 - 30)
Carcharhinus obscurus	Dusky	5	200 (76 - 328)	21 (18 - 27)
Carcharhinus plumbeus	Sandbar	73	215 (183 - 236)	21 (12 - 29)
Carcharias taurus	Sand Tiger	5	278 (264 - 300)	22 (16 - 29)
Galeocerdo cuvier	Tiger	106	287 (89 - 386)	28 (18 - 31)
Isurus oxyrinchus	Shortfin Mako	1	264 (NA)	16 (NA)
Negaprion brevirostris	Lemon	40	254 (66 - 302)	26 (22 - 31)
Rhizoprionodon terraenovae	Atlantic Sharpnose	22	70 (58 - 100)	26 (22 - 29)
Sphyrna lewini	Scalloped Hammerhead	61	221 (183 -290	26 (21 - 31)
Sphyrna mokarran	Great Hammerhead	21	303 (208 - 439)	26 (22 - 30)
Sphyrna sp.	Hammerhead sp.	23	235 (185 - 300)	27 (23 - 30)
Sphyrna tiburo	Bonnethead	16	67 (53 - 117)	24 (18 - 26)
Sphyrna zygaena	Smooth Hammerhead	1	201 (NA)	28 (NA)

Table 3.2. Collection information of sharks captured on the Texas coast from hook-and-line sampling from 2008 to 2009.

Species	**Common name**	**Number Captured**	**% Abundance**	**Mean total length in cm (range)**
Carcharhinus limbatus	Blacktip	48	60.8%	140 (53 - 198)
Carcharhinus leucas	Bull	20	25.3%	170 (91 - 198)
Sphyrna tiburo	Bonnethead	6	7.6%	61 (57 - 71)
Rhizoprionodon terraenovae	Atlantic Sharpnose	3	3.8%	56 (37 - 66)
Carcharhinus acronotus	Blacknose	1	1.3%	119 (NA)
Carcharhinus brevipinna	Spinner	1	1.3%	193 (NA)

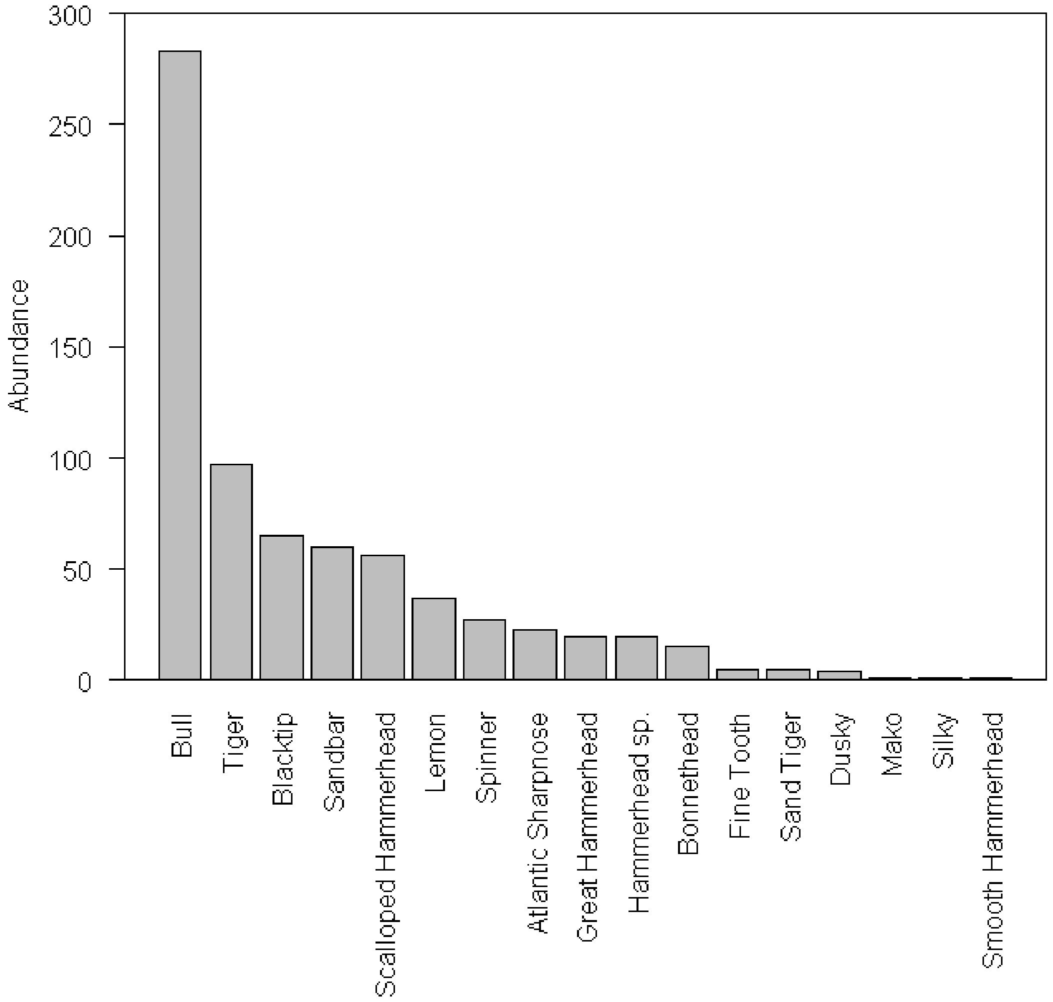


Figure 3.2. Total abundance of each shark species captured between 1973 - 1986 on the Texas coast. Most samples were collected within Padre Island National Seashore.

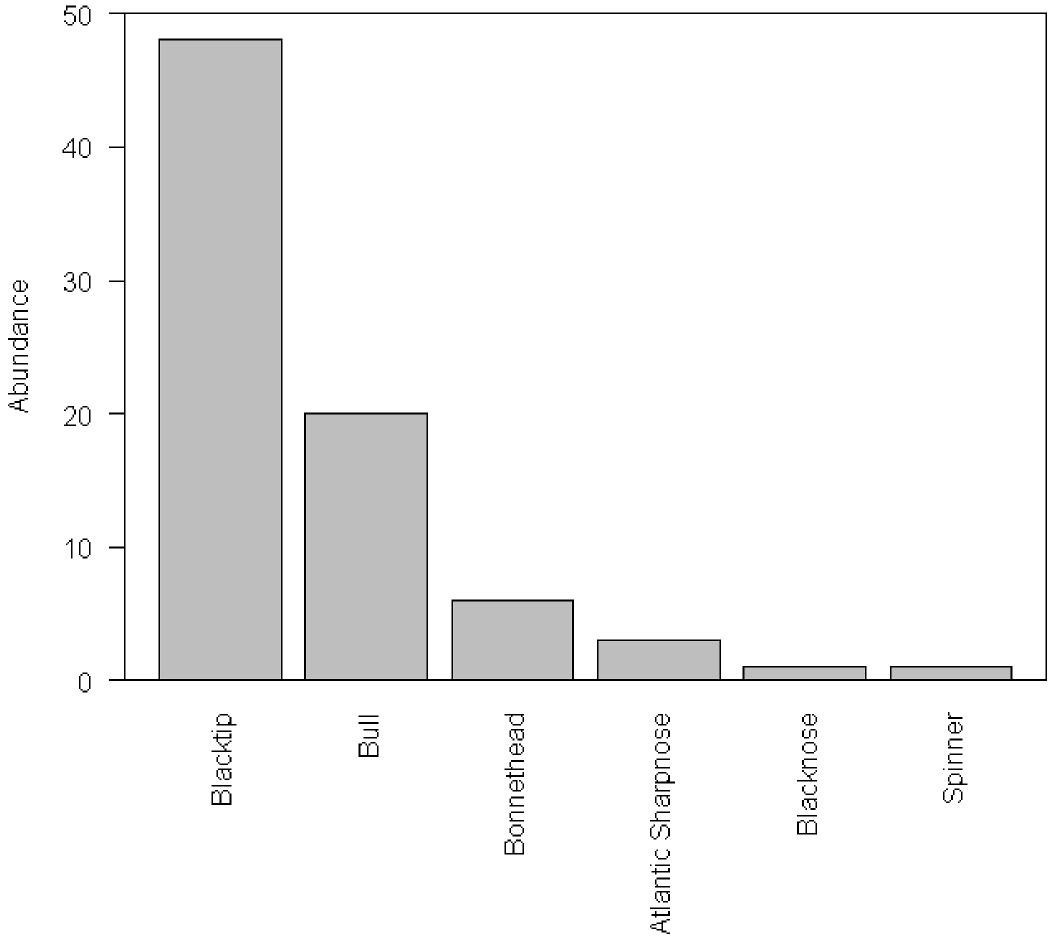


Figure 3.3. Total abundance of each shark species captured between 2008 - 2009 on the Texas coast. Most samples were collected within Padre Island National Seashore.

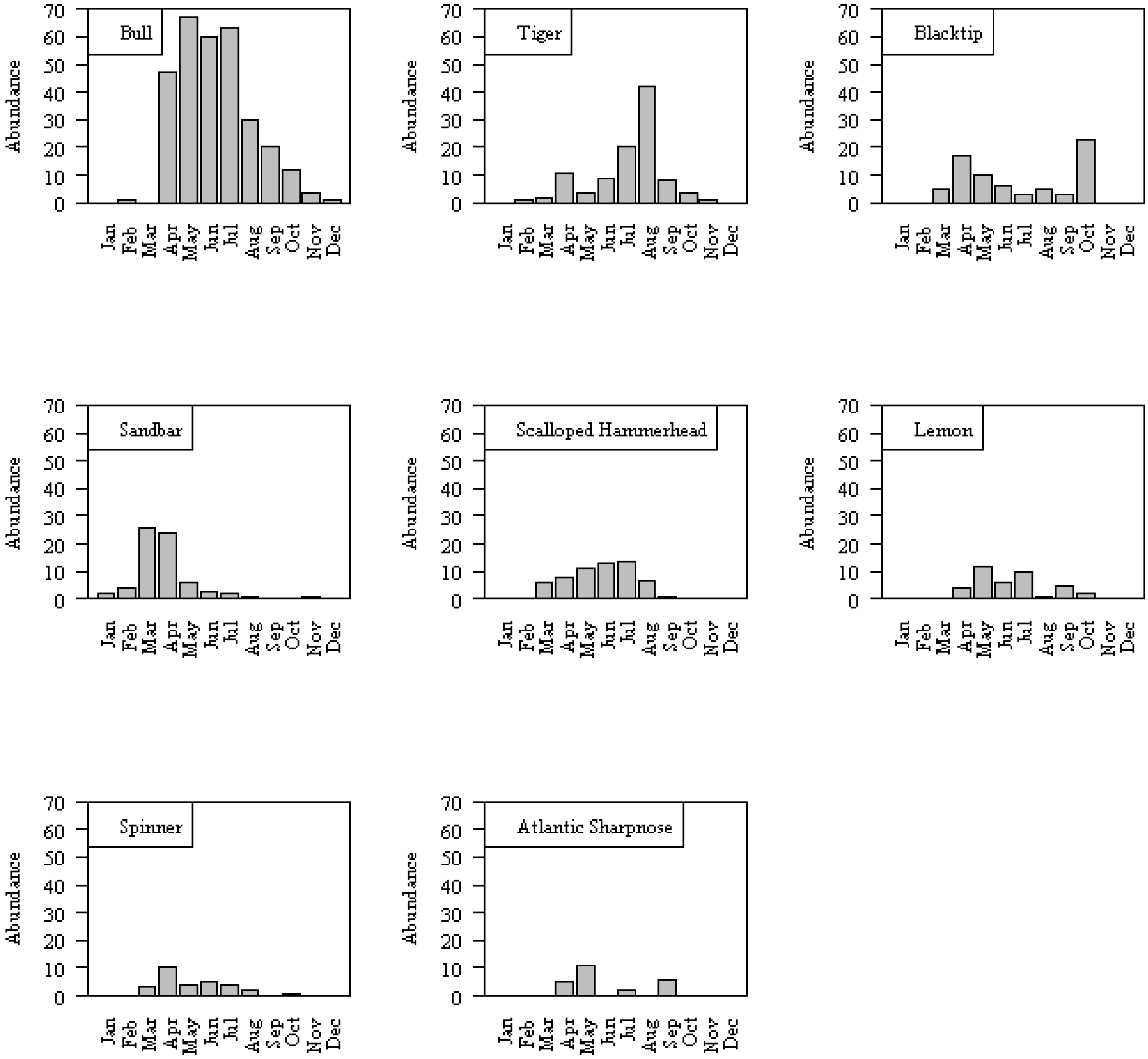
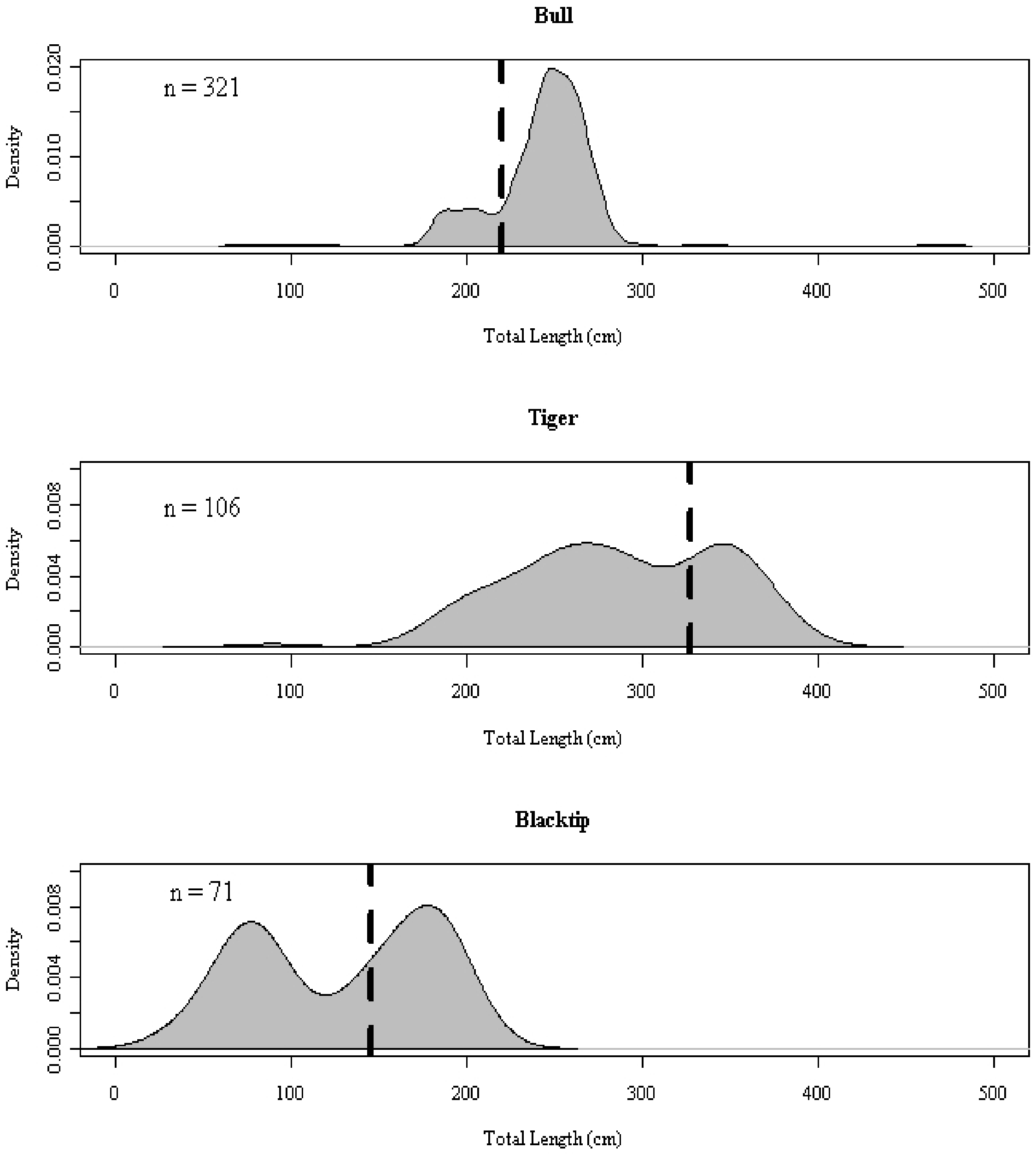
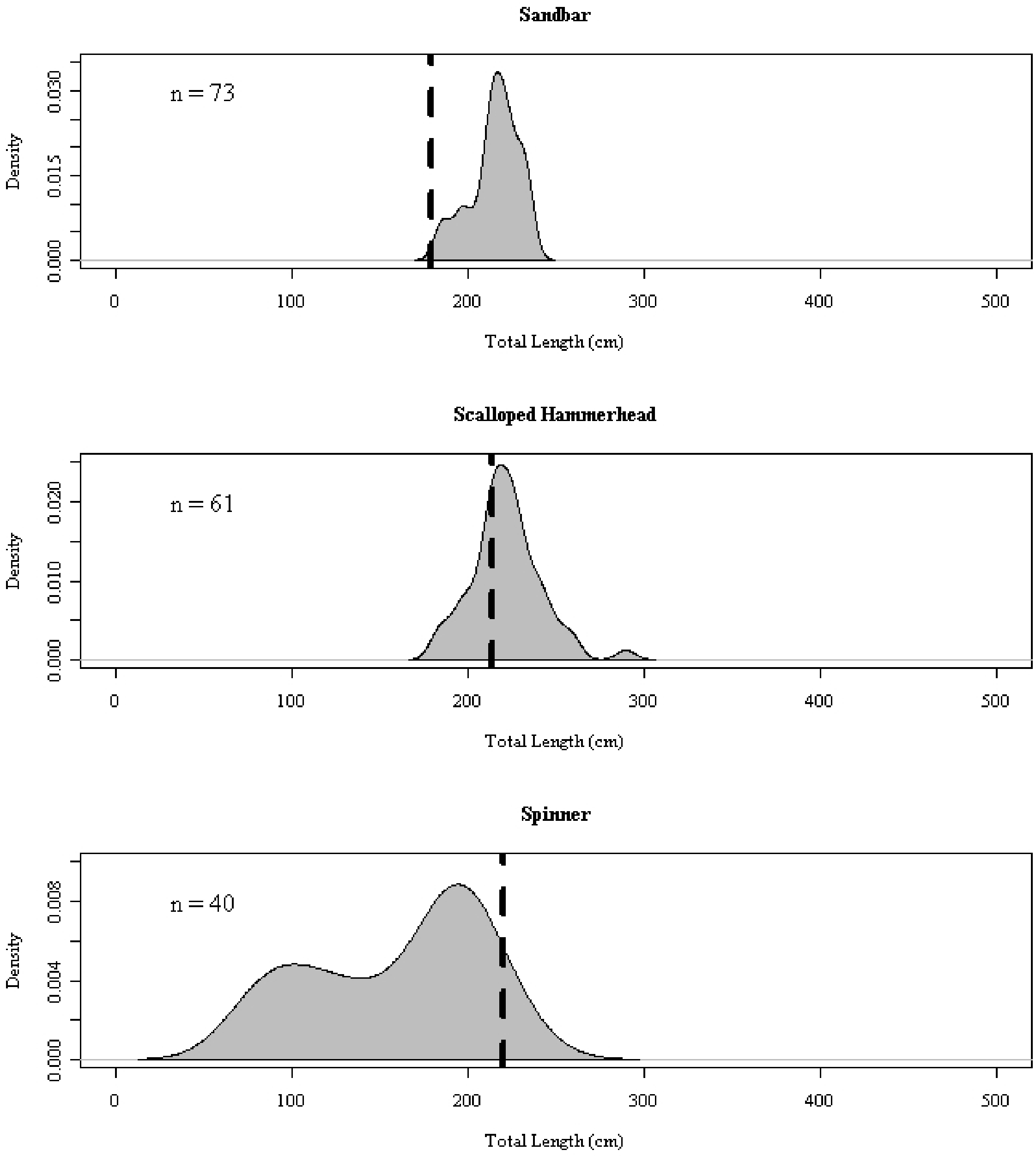


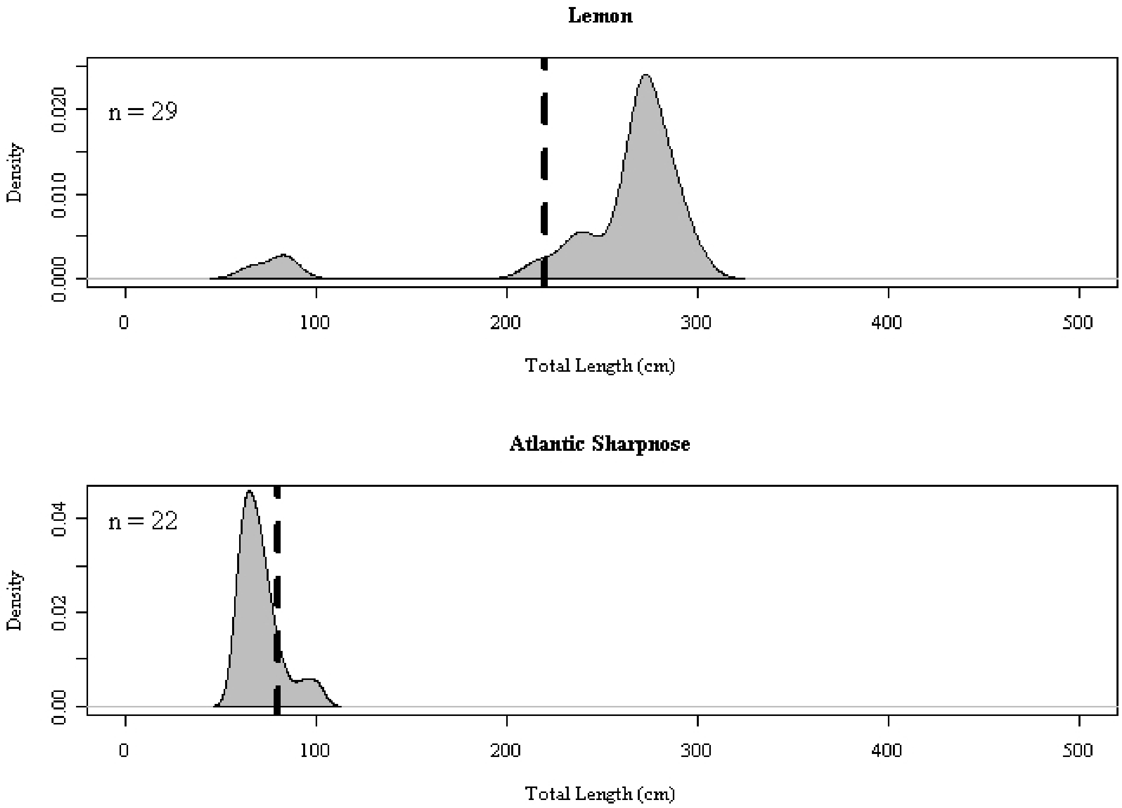
Figure 3.4. Abundance by month of top nine species captured from 1973 to 1986.


Bull
n = 321
Density
0.000
0.010
0.020
0
100
200
300
400
500
Total Length (cm)
Tiger
n = 106
Density
0.000
0.004
0.008
0
100
200
300
400
500
Total Length (cm)
Blacktip
n = 71
Density
0.000
0.004
0.008
0
100
200
300
400
500
Total Length (cm)

A)


Sandbar
n = 73
Density
0.000
0.015
0.030
0
100
200
300
400
500
Total Length (cm)
Scalloped Hammerhead
n = 61
Density
0.000
0.010
0.020
0
100
200
300
400
500
Total Length (cm)
Spinner
n = 40
Density
0.000
0.004
0.008
0
100
200
300
400
500
Total Length (cm)

B)



C)

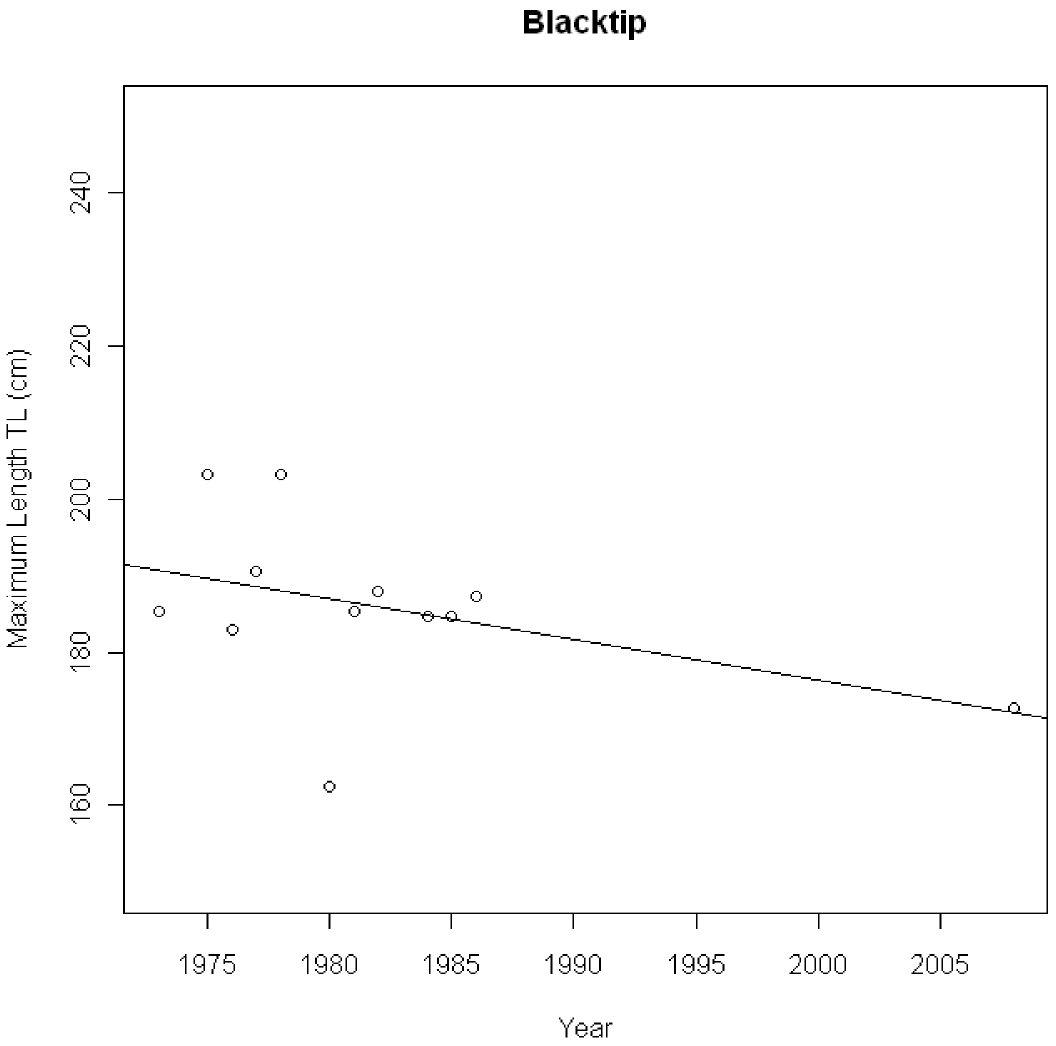
Figure 3.5. (A) Size frequency distribution of bull (*Carcharhinus leucas*), tiger (*Galeocerdo cuvier*), and blacktip sharks (*Carcharhinus limbatus*). (B) Size frequency distribution of sandbar (*Carcharhinus plumbeus*), scalloped hammerhead (*Sphyrna lewini*), and spinner sharks (*Carcharhinus brevipinna*). (C) Size frequency distribution of lemon (*Negaprion brevirostris*), and Atlantic sharpnose (*Rhizoprionodon terraenovae*) sharks. Dashed line indicates length at maturity.

Scalloped hammerhead and blacktip sharks were collected in both juvenile and adult age classes (Figure 3.5B). Lemon and Atlantic sharpnose sharks were uncommon, however most lemon sharks were estimated to be sexually mature, while the Atlantic sharpnose catch was dominated by juveniles (Figure 3.5C).

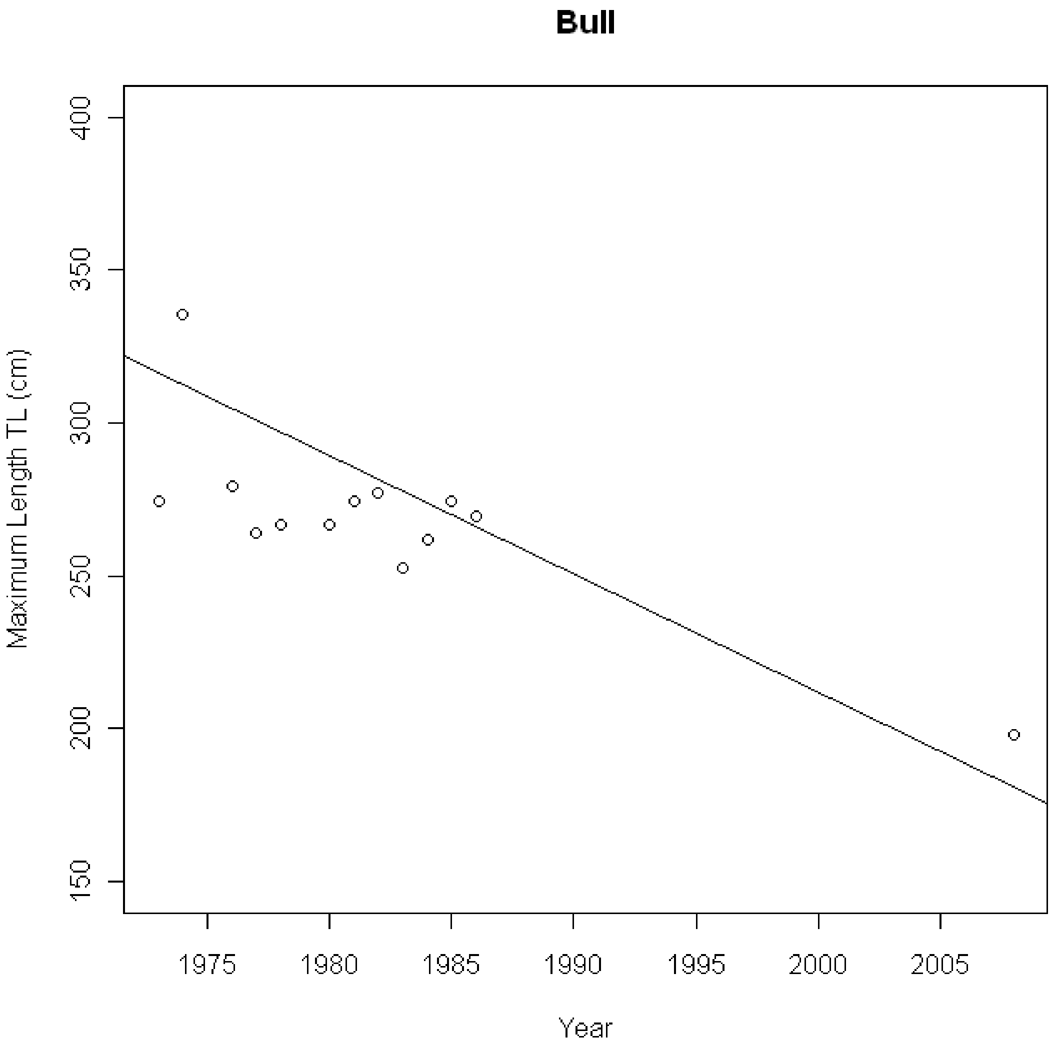
Using both historical and recent collections, temporal patterns of maximum length of captured individuals was examined. Temporal patterns were examined for the most abundant species: blacktip, bull, sandbar, tiger sharks. Overall, trends of maximum length at capture appear stable for most species (Figure 3.6A-D). Only maximum length of bull sharks declined significantly over time (linear regression, $F_{1,12} = 5.3$, $p = 0.04$, $R^2 = 0.31$).

Community patterns

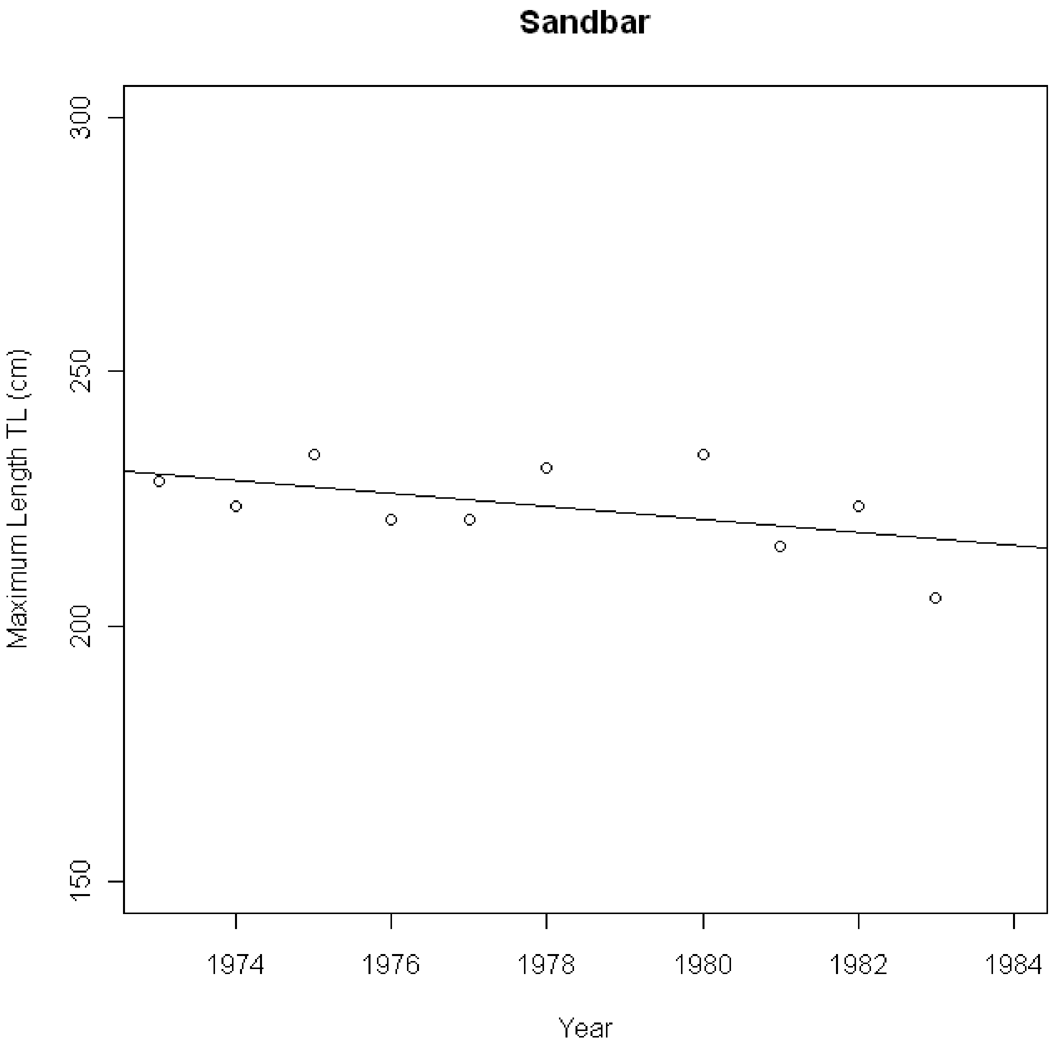
Analysis of seasonal community structure using MDS showed little intra-annual variability in shark species composition with the exception of winter. During winter the assemblage was discernable in the MDS plots (Figure 3.7) due to the presence of sandbar sharks and the absence of most other species during this period. Species composition patterns were assessed using Bray-Curtis cluster analysis and MDS ordination. Results of cluster analysis indicate that the shark assemblage is comprised of a core group of eight species (> 50% similarity, Figure 3.8A). Non-metric multidimensional scaling was also used with Bray-Curtis analysis superimposed using 50% similarity and suggested a similar pattern of a core shark assemblage with similar catch patterns along with rare species that are rare in the Gulf of Mexico (i.e., sand tiger shark) by year from 1973-1986. or in coastal areas (i.e., shortfin mako shark) were occasionally encountered and are depicted as outliers in the MDS plot (Figure 3.8B).


Blacktip
Maximum Length TL (cm)
160
180
200
220
240
1975
1980
1985
1990
1995
2000
2005
Year

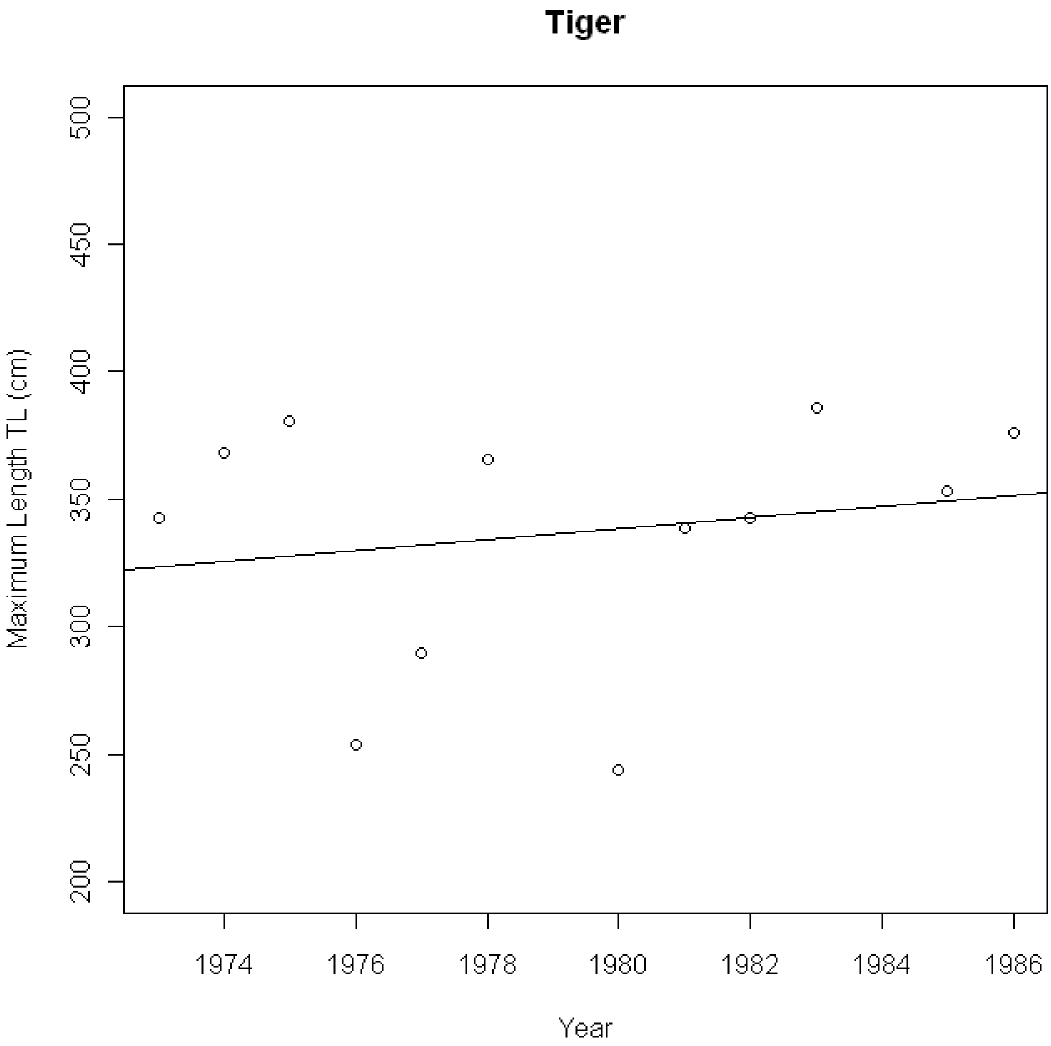
A)


Bull
Maximum Length TL (cm)
150
200
250
300
350
400
1975
1980
1985
1990
1995
2000
2005
Year

B)


Sandbar
Maximum Length TL (cm)
150
200
250
300
1974
1976
1978
1980
1982
1984
Year

C)



D)

Figure 3.6. (A) Maximum length of blacktip shark captured each year. No significant change in maximum size over time (linear regression, $F_{1,10}$ =2.3, p = 0.15, R^2 = 0.19). Excluding data from 2007 did not alter affect results (linear regression, $F_{1,9}$ =0.6, p = 0.47, R^2 = 0.06). (B) Maximum length of bull shark captured each year. Maximum size of bull shark decreased significantly over time (linear regression, $F_{1,12}$ = 5.3, p = 0.04, R^2 = 0.31). Excluding data from 2007 did not alter affect results (linear regression, $F_{1,11}$

=0.6, $p = 0.47$, $R^2 = 0.06$). (C) Maximum length of sandbar shark captured each year. No significant change in max size over time (linear regression, $F_{1,8} = 2.9$, $p = 0.13$, $R^2 = 0.26$). (D) Maximum length of tiger shark captured each year. No significant change in max size over time (linear regression, $F_{1,10} = 0.4$, $p = 0.55$, $R^2 = 0.04$)

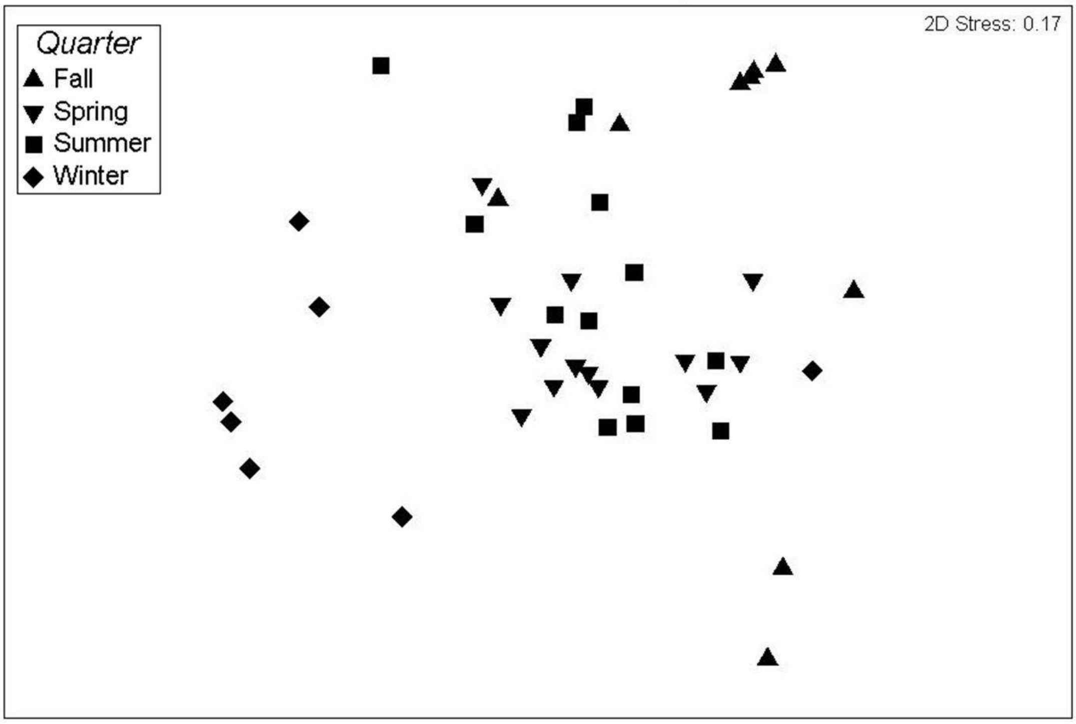


Figure 3.7. Non-Metric Multidimensional scaling ordination of Bray-Curtis similarities among season of shark species composition on the Texas coast from 1973-1986.

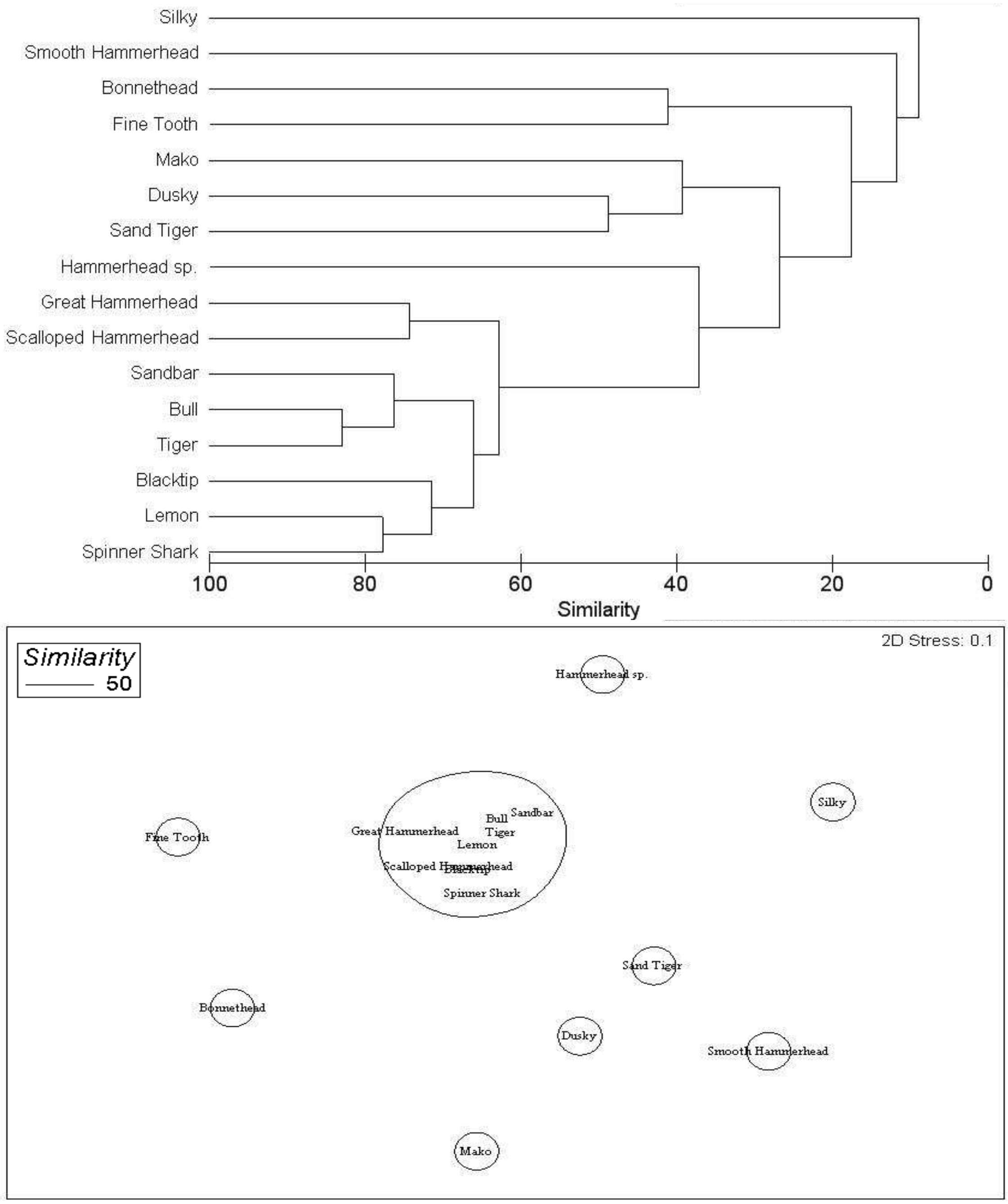


Figure 3.8. Bray-Curtis cluster analysis (a) and MDS ordination with Bray-Curtis analysis superimposed using 50% similarity of shark species composition by year from 1973-1986.

DISCUSSION

Coastal ecosystems are susceptible to human or natural impacts and many regions are undergoing rapid change (Jackson 2001, Lotze et al. 2006) such as reductions of species at high trophic levels (Pauly et al. 1998, Heithaus et al. 2008). Removal of these apex predators can have consequences in maintaining the stability, diversity, or productivity of ecosystems (Jackson 2001, Heithaus et al. 2008). However, natural or historical abundance estimates for the species are often unavailable or inadequate to assess historical patterns in species composition or abundance (Pauly 1995, Baum et al. 2005, Heithaus et al. 2008, Powers et al. *In review*). This lack of data have often been referred to as the "shifting baselines" problem as many areas have no appropriate baseline from which to assess potential ecosystem impacts (Pauly 1995, Jackson 2001), and this is the case for nearshore shark population along the Northwestern Gulf of Mexico. Fisheries-independent data were unavailable for this region and assessment of the nearshore shark resource in the Gulf of Mexico has only recently begun in 2008. Unfortunately, understanding distribution patterns of wide ranging or rare species often requires long-term data sets to detect trends in population status (Trenkel and Rochet 2009). Therefore, we used fishery-dependent data, the only available data in this region to characterize the coastal shark resource in the Northwestern Gulf of Mexico as considerable uncertainty exists about the population status and long-term trends of this resource that has prompted more restrictive harvest regulations from Texas Parks and Wildlife.

From 1973 to 1986, bull shark was the most commonly reported species in this study, while tiger shark ranked second, blacktip third, and sandbar shark fourth. In contrast, blacktip was the most abundant shark captured in 2008-2009, bull shark were second, and no tiger or sandbar sharks were recorded in angler logs during this period. Fewer species were also reported during recent sampling, however, this may likely be due to dramatically reduced sampling effort. These changes in abundance may reflect population level effects in the Gulf of Mexico (Baum et al. 2004, Powers et al. *In revision*) or simply reflect an artifact of sampling bias using such data. In this case it was not possible to compare indices of abundance as effort was not controlled or known. This problem is typical with fisheries dependent data and novel approaches are being employed to evaluate population trends from fishery dependent data. Change in size (or weight) of capture can be indicative in demographic changes or perhaps population declines (Powers et al. *In revision*). Based on available data, the size structure of most shark species was temporally stable suggesting population stability. Only bull shark declined in maximum size through time and this pattern should be further investigated to verify this effect. Thus, temporal patterns examining the maximum length captured per year of the most abundant shark species were examined. Powers et al (*In revision*) reported significant declines in maximum size of sharks captured in off-shore angling tournaments over an eight-decade study period in the Gulf of Mexico highlighting the importance of establishing ecological baselines wherever possible.

Seasonality of shark habitat usage was poorly described in this area. Based on historical catch data, I found distinct seasonal patterns. Sharks were captured most frequently from spring to fall with only sandbar shark being common in winter catch records. While this pattern could result from reduced effort alone during winter months, median sea surface temperatures of coastal waters in this region were below 16°C between December and February (NOAA/National Weather Service Cooperative Weather Observer Station #1071, Port Aransas, TX, USA). Most shark species captured in this study are subtropical/tropical species and are rare during these temperate conditions (Musick et al. 2000). Froeschke (Chapter 2) reported similar patterns in a study of blacktip, bonnethead, and bull sharks in Texas' estuaries, as sharks were rarely captured below 20°C also suggesting that sharks may migrate to warmer waters during winter months. However, further migration studies are warranted and necessary to document this pattern. A shark tagging program initiated in 2007 by Texas A&M University-Corpus Christi in collaboration with the U.S. Geological survey in Columbia, Missouri may provide greater insight into migration or movement patterns of sharks in this region. Long-distance seasonal migrations of sandbar from the western Atlantic into the Gulf of Mexico have been reported during winter (Springer 1960, Grubbs et al. 2007). Moreover, for juvenile sandbar sharks, emigration from temperate estuaries was correlated with declining temperatures and recapture data from tagging studies suggests that these animals are moving south to warmer wintering areas (Grubbs et al. 2007). Data from the current study suggests that the Gulf of Mexico coastal waters may serve as a winter area for sandbar sharks while the other species may emigrate from coastal waters during winter months.

In an effort to prevent depletion of exploited fish stocks, NOAA mandated incorporation of Essential Fish Habitat (EFH) into fishery management plans in effort to protect habitat important in all life-stages of important species (NOAA 1996) as there is likely a strong relationship between adult stock size and recruitment (Smith et al. 1998). Thus, delineating areas or habitats supporting juveniles that will ultimately contribute to adult stocks was a major focus of this study. My analyses of length-at-capture suggest that most species occur on the Texas coast throughout their ontogeny, and this area has the potential to serve as nursery area for some exploited species. However, the presence of juveniles alone is inadequate to characterize nursery function (Beck et al. 2002, Heupel et al. 2007, Kinney & Simpfendorfer 2009), and further quantitative study is needed to test the nursery potential for this area. The estuarine or coastal areas of the Texas coast are thought to serve as nurseries for at least 11 shark species (McCandless et al. 2002, 2007) although this has only been tested and confirmed for bull shark. Using the nursery criteria developed by Heupel et al. (2007), bull shark nursery use was demonstrated in San Antonio and Matagorda Bays along the central Texas coast (Froeschke Chapter 2), but due to data availability, this study only assessed estuarine and not nearshore coastal areas. Although tiger sharks do not use discrete nursery habitat, they do occur as juveniles along the Texas coast (Driggers III et al. 2008), and were observed in this study. The abundance patterns suggest that this species was at least seasonally abundant although more work is necessary to estimate temporal trends in abundance in this region. Moreover, tiger sharks have low fecundity and resilience to fishing pressure (Whitney and Crow 2008), suggesting a conservative approach to management for this ecologically important species.

Sharks typically function as apex predators and may have an important role in maintaining ecological integrity and also serve as ‘indicators’ of ecosystem change (Heithaus et al. 2008). However, status and trends of shark populations on this coast are poorly known although precipitous declines of several shark species have been reported in the Gulf of Mexico (Baum and Myers 2004, O'Connell et al. 2007, Powers et al. *In revision*) prompting concerns of the sustainability of Texas' coastal shark resource. These data suggest that the Texas' coastal waters support a diverse and abundant shark assemblage that likely provides both adult and juvenile EFH for several exploited shark species. Future studies emphasizing quantitative estimates of abundance, habitat use, and movement patterns may provide valuable information to manage this resource. In absence of this critical information, a cautious approach is recommended for the management of these species.

ACKNOWLEDGMENTS

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CHAPTER 4

HIERARCHICAL AND INTERACTIVE HABITAT SELECTION IN RESPONSE TO ABIOTIC AND BIOTIC FACTORS: THE EFFECT OF HYPOXIA ON HABITAT SELECTION OF JUVENILE ESTUARINE FISHES

ABSTRACT

Habitat selection is a shared process among animals where individuals choose areas that differ in biotic and abiotic characteristics to maximize individual fitness. We used manipulative laboratory mesocosm choice experiments to examine hierarchical and interactive relationships influencing habitat selection of estuarine fishes. We assessed selection among substrate, dissolved oxygen (DO) concentration, food availability, and predation risk using two common juvenile estuarine fish species. For two species, pinfish (*Lagodon rhomboides*) and Atlantic croaker (*Micropogonias undulatus*), oxygen concentration greatly influenced selection patterns; fishes strongly avoided DO, and at higher levels factors such as substrate or food showed interactive relationships between an abiotic stressor and biotic habitat components. However, both species strongly avoided predators even when alternative habitat was severely oxygen limited. These results show that predation risk may be the greatest determinant of habitat selection. Expansion of low DO areas in the world's oceans is a major anthropogenic disturbance and is rapidly increasing. Assessing impacts of hypoxia on habitat usage of mobile organisms is critical as changes in environmental metrics including predator distribution and DO levels may alter habitat selection patterns disrupting critical ecosystem processes and trophic interactions. Our results indicate that juvenile fishes forgo emigration from hypoxia due to

predation risk. If similar patterns occur for juvenile fishes in estuaries they may potentially suffer from reduced growth, reproductive output, and survivorship.

INTRODUCTION

Habitat selection is a nearly universal process among animals where individuals must choose among habitats that differ in biotic and abiotic characteristics (Johnson 1980; Huey 1991). The hierarchy of habitat selection for an individual should reflect factors potentially limiting an individual's fitness. For example, ideal habitats would provide high net energetic return rate (to maximize growth and reproduction) and low mortality (Gilliam and Fraser 1987). These conditions rarely exist in nature and individuals must choose between sub-optimal environments to balance physiological performance with predation risk.

Habitat selection patterns of fishes have been well-described and offer a good model to test the relative roles of abiotic versus biotic habitat characteristics. For example, estuaries are recognized as high quality habitat types as they are food-rich, structurally complex, and provide refuge from predation (Beck et al. 2001). However, human activities have dramatically altered both abiotic and biotic properties of coastal ecosystems at an alarming rate (Altieri 2008; Halpern et al. 2008). For example, in many coastal estuaries, predator densities have been dramatically reduced (Lotze et al. 2006), important habitats such as seagrass meadows and oyster reefs have declined (Levin and Stunz 2005), and dissolved oxygen (DO) concentrations are falling (e.g., hypoxia) worldwide (Rabalais et al. 2007, Diaz and Rosenburg 2008). These habitat alterations may influence habitat selection of ecologically important species and could precipitate large-scale community changes in marine ecosystems.

A critical abiotic attribute often compromised in marine ecosystems is dissolved oxygen (DO). Oxygen levels are a widespread problem (Diaz and Rosenburg 2008), not limited to particular marine areas, and interact with biotic habitat characteristics in very complex ways (Breitburg 2002, Rabalais et al. 2002, Altieri 2008), ultimately altering the distribution of individuals (Lenihan et al. 2001, Bell and Eggleston 2005). Successful avoidance of hypoxia (DO concentration < 2 mg O_2 l^{-1}) is dependent upon movement responses and physiological tolerances which are typically species specific (Pihl et al. 1991). In aquatic ecosystems, low levels of oxygen have been associated with reduced abundance, biomass, diversity, growth, and have also been attributed to population declines of some estuarine fishes (Eby et al. 2005, Powers et al. 2005, Montagna and Ritter 2006, Vaquer-Sunyer and Duarte 2008, Long and Seitz 2009, Montagna and Froeschke 2009). Mitigation of human impacts to ecosystems requires an improved understanding of attributes animals use for habitat selection, particularly as it relates to importance of abiotic and biotic factors on habitat choice.

Hypoxia is becoming a more common phenomenon in estuaries and is thought to be increasing in occurrence worldwide including in the Gulf of Mexico (Diaz and Rozenberg, 2008). The Gulf of Mexico supports a variety of economically and ecologically important species that may be impacted by declining DO levels. The seasonal presence of a large dead zone in the Gulf of Mexico at the mouth of the Mississippi river is well documented and also occurs within estuarine waters along the Texas coast (Montagna and Ritter 2005). The presence of a hypoxic zone has been documented annually in Corpus Christi Bay, Texas since 1988 and there is a long-term trend of decreasing dissolved oxygen levels in these waters (Applebaum et al. 2005). This hypoxic zone also had reduced diversity of both benthic and mobile organisms (including fishes) and lower abundance and biomass of epifauna (Montagna and Froeschke 2009).

Pinfish (*Lagodon rhomboides*) and Atlantic croaker (*Micropogonias undulatus*) are two of the most abundant estuarine fishes in the Gulf of Mexico and shallow coastal estuaries comprise important nursery habitat for these species (Reese et al. 2008). Both can be found in a variety of habitats including seagrass meadows and sand bottom and are sensitive to hypoxia (Wannamaker and Rice 2000). Thus, these species provide excellent models for testing hypotheses about factors influencing habitat selection patterns of estuarine fishes.

The goal of this study was to assess the relative importance of biotic and abiotic factors on habitat selection. Specifically, I compared the relative importance of predator density, substrate, and food availability in comparison with varying levels DO concentration to assess ecological impacts of declining oxygen concentrations on habitat selection patterns. I used a series of replicated laboratory mesocosm choice experiments with two ecologically important estuarine fishes as models.

METHODS

Collection of study organisms

Juvenile Atlantic croaker ("croaker") and pinfish were collected from shallow estuarine habitats in Aransas and Corpus Christi Bays, Texas USA using bag seines. Mean standard length (SL) of croaker and pinfish was: (mean ± standard error) 38 ± 4.5 mm SL and 35 ± 2.5mm SL respectively. Animals were held at wet laboratory facilities in aerated and filtered 38-l aquaria. Fish were maintained in holding tanks at 23-25 °C and 30-35 psu; DO concentrations were maintained between 6.0-6.5 mg O_2 l^{-1}. Fish were acclimated to aquaria for at least 3 d prior to experimental procedures and fed frozen mysid shrimp daily to satiation and kept on a 12-h light/dark photoperiod.

Experimental design

I used a sequential series of replicated experimental mesocosm trials to test for habitat selection patterns for both species at varying levels of predator density, substrate type, DO concentration, and food. Replicated two-way choice trials were completed in a 225-cm x 60-cm x 75-cm mesocosm filled to 25 cm with filtered seawater (Figure 4.1). Washed sand was used to simulate sand habitat (Stunz et al. 2001) while shoal grass (*Halodule wrightii*) was simulated using an artificial seagrass unit (ASU). Artificial seagrass units are replicate seagrass habitat and are created from polyethylene ribbon attached to a mesh base placed under a sand substrate. ASU's were used as a proxy for seagrass because preliminary trials on selection patterns of juvenile pinfish and croaker showed no significant selection patterns between shoal grass and the ASU's (one sample t-test, pinfish $t = 1.88$, $df = 7$, $p = 0.10$, croaker $t = 0.95$, $df = 9$, $p = 0.36$).

A DO gradient was established using a Plexiglass divider, and releasing nitrogen and oxygen gas into each chamber of the mesocosm. During experimental trials, the divider was raised 60 mm to permit fish movement (Wannamaker and Rice 2000). Dissolved oxygen concentrations were measured at the center and at each end of the mesocosm prior to introduction of experimental fish and at the conclusion of each experiment using a Thermo Scientific Orion 3-Star DO meter (Thermo Electron Corporation Beverly, MA USA). Trials were not run if DO levels deviated more than ± 0.40 mg O_2^{-1} from target levels. Wannamaker and Rice (2000) demonstrated that pinfish and croaker could detect and avoid the hypoxia in a laboratory mesocosm and our preliminary experiments showed significant avoidance of the oxygen depleted chamber (one sample t-test, pinfish, $p = 0.01$; croaker, $p = 0.02$).

Experimental procedure

To determine the relative importance of substrate and DO concentrations on habitat selection patterns, I established a range of substrate-DO combinations. First, I conducted a substrate control experiment to determine selection patterns based on the habitat type (seagrass vs. sand) without a DO treatment (both chambers 6.0 mg O_2^{-l}). I then conducted a series of experiments, each testing fish habitat selection patterns between two substrate-DO combinations (Figure 4.1). Experiments were conducted at DO levels from 1 to 6 mg O_2^{-l} to identify potential graded, threshold or interactive responses. Trials were first set up with the low DO treatment within the seagrass substrate and high DO treatment within the sand substrate. Reciprocal experiments were completed by establishing low oxygen treatment in sand bottom substrate and high oxygen concentration in seagrass.

For all experiments, three fish (approximating natural densities; Stunz et al. 2002) were randomly selected from holding aquaria for each trial. Fish were released in the center of the mesocosm as close as possible to the divider near the bottom, acclimated for 10 min and then fish habitat selection patterns were noted every min for 30 min. The acclimation period occurred after the divider was raised to permit movement and exploration of all treatments. For every trial the locations of all three fish were averaged into a single response as individual fish within a trial were not independent and the mean percent occurrence in each habitat was calculated following a 10-min acclimation. The low and high oxygen sides of the chamber were re-assigned for each replicate to eliminate bias toward any particular end. Observations were made by a single observer > 2 m away from the tank with the observer peering over an opaque barrier to prevent observer interference to fish behavior. During preliminary trials, this method of observation did not elicit a startle or other behavior responses from the fish. Since, these experiment were relatively short-term, I was able to make live direct observations during the entirety of the experiment.

To assess the relative importance of food availability relative to hypoxia for both species, the experimental mesocosm was modified by placing a food enriched treatment (mysid shrimp) on one side, while food was absent in the other. Fish were fasted for 24 h and three fish were placed in the mesocosm with DO concentration at 4.0 mg O_2^{-1}. One chamber was enriched with 6.07 ± 0.07 g (mean ± standard error) of frozen mysid shrimp per trial and habitat choice was monitored every 20 seconds for 10 min after acclimation (n = 6). Excess food was removed after every trial. A second experiment (n = 6) was repeated, but mysid shrimp were placed in a low oxygen treatment (1.0 mg O_2 l^{-1}), while the other chamber remained at 4.0 mg O_2 l^{-1} but without the mysid shrimp food treatment.

The relative influence of predator-presence and DO concentration on habitat selection patterns was also examined by introducing predatory fish. Three sub-adult red drum (*Sciaenops ocellatus*) (mean ± standard error) 190 ± 8 mm SL were used for the predation trials. Predators were acclimated for 48 h. The Plexiglass partition separating sides of the mesocosm was modified by cutting eight 4-cm round holes near the bottom of the divider to permit movement of juvenile fishes throughout the entire mesocosm but restricted the movement of the red drum predators to one chamber. I performed preliminary trials that showed that juvenile fish would readily pass through holes in the partition. For the initial experiment (n = 6) both sections of the mesocosm were set to 4.0 mg O_2 l^{-1}. A second experiment (n = 6) was conducted in which the predatory red drum were placed in the 4.0 mg O_2 l^{-1} DO treatment and the side without predators set to 1.0 mg O_2 l^{-1}.

Statistical analyses

The response variable for all habitat selection trials was the mean proportion of time the three fish spent in each chamber in the mesocosm. Data were arc-sin square root transformed and tested against the null hypothesis of 50% of the time spent in each side of the mesocosm using a two-tailed, one-sample, student's t-test ($\alpha = 0.05$). All data management and analyses were conducted using SAS 9.1.3 software (SAS Institute, Inc., 2000).

RESULTS

Habitat selection experiments

In normoxic conditions (both chambers 6 mg O_2 l^{-1}), both pinfish and croaker displayed significant habitat preferences. Pinfish selected the seagrass treatment ($p = 0.02$) (Figure 4.2A), while croaker selected sand bottom ($p = 0.007$) (Figure 4.2C). Based on significant habitat selection preference patterns in the previous trials, I designed experiments to test the importance of habitat type (e.g., seagrass and sand bottom) and oxygen concentration on habitat selection patterns. For pinfish both habitat type and DO levels influenced selection patterns. Dissolved oxygen exerted greater influence on selection patterns during hypoxic conditions (i.e., DO $\leq$ 2.0 mg O_2 l^{-1}), while habitat type was more important during moderate hypoxia or normoxic conditions (i.e., DO $\geq$ 2.0 mg O_2 l^{-1}; Figure 4.2A).

Despite the preference for vegetated habitat in the control experiment, pinfish avoided the low oxygen-seagrass treatment when DO levels were decreased to 1.0 mg O_2 l^{-1} and selected the alternative 4.0 mg O_2 l^{-1} sand bottom treatment ($p = 0.01$) (Table 4.1). A similar pattern was observed during 1.0 mg O_2 l^{-1} seagrass vs. 2.0 mg O_2 l^{-1} sand bottom experiment as pinfish displayed significant selection for increased oxygen treatment despite a relatively small difference in DO concentrations between treatments. However, this pattern was not observed when oxygen levels were increased, simulating moderate levels of hypoxia. During the 2.0 mg

O_2 l^{-1} seagrass vs. 4.0 mg O_2 l^{-1} sand substrate experiment, pinfish selection patterns were more variable, although fish spent more time in the lower oxygen seagrass chamber. Overall, no significant selection patterns were detected for this experiment ($p = 0.33$). In the 4.0 mg O_2 l^{-1} seagrass vs. 6.0 mg O_2 l^{-1} sand bottom experiment, a similar pattern was observed as fish selected the lower oxygen seagrass chamber, but the response was variable and a significant selection pattern was not detected ($p = 0.12$). Habitat selection patterns of pinfish were also determined when DO concentrations were reduced in the sand bottom treatment relative to their preferred seagrass habitat. In this situation, pinfish displayed significant selection patterns for the increased DO-seagrass treatment, as this treatment contained both the favored abiotic and biotic conditions within one chamber of the mesocosm (Figure 4.2B).

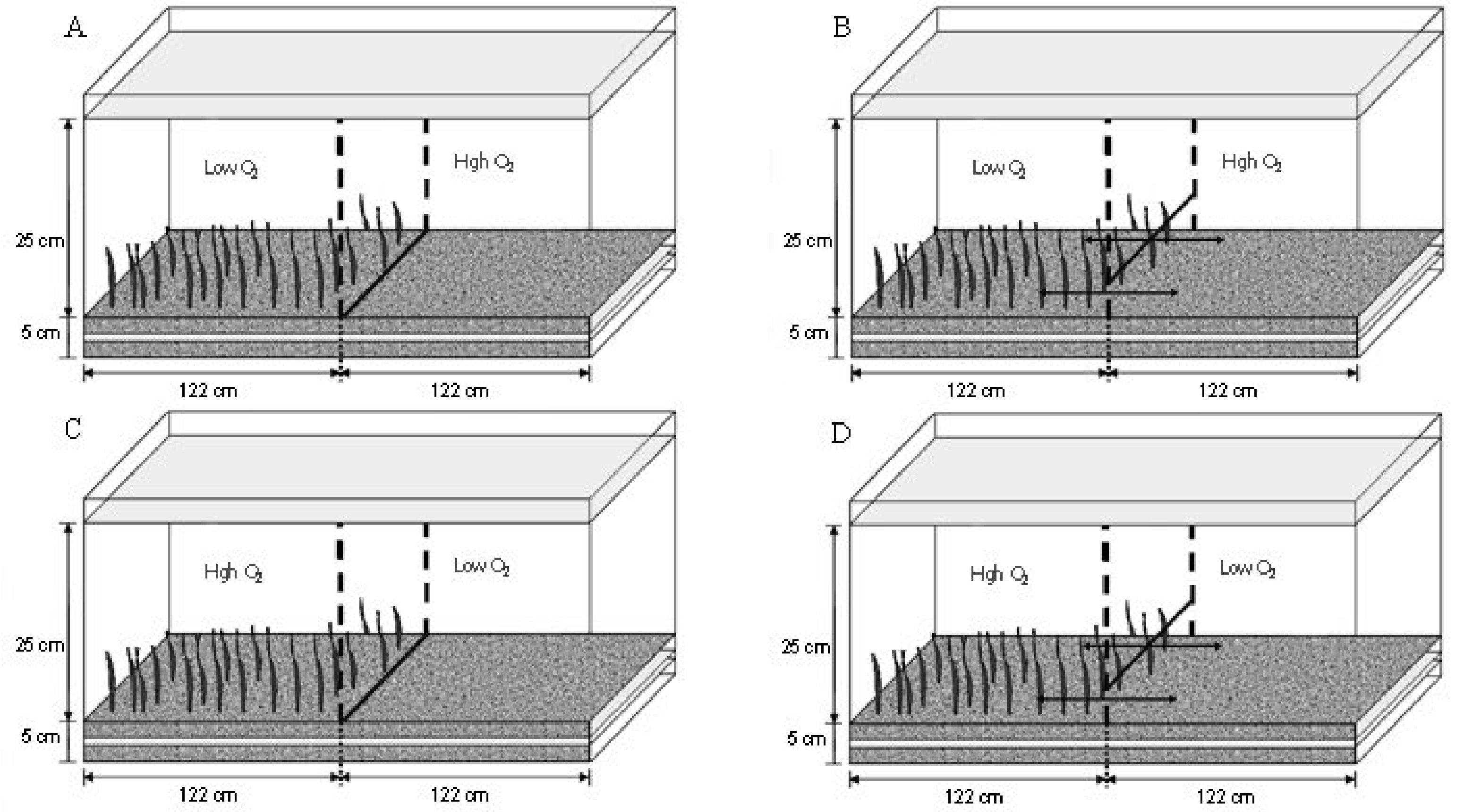


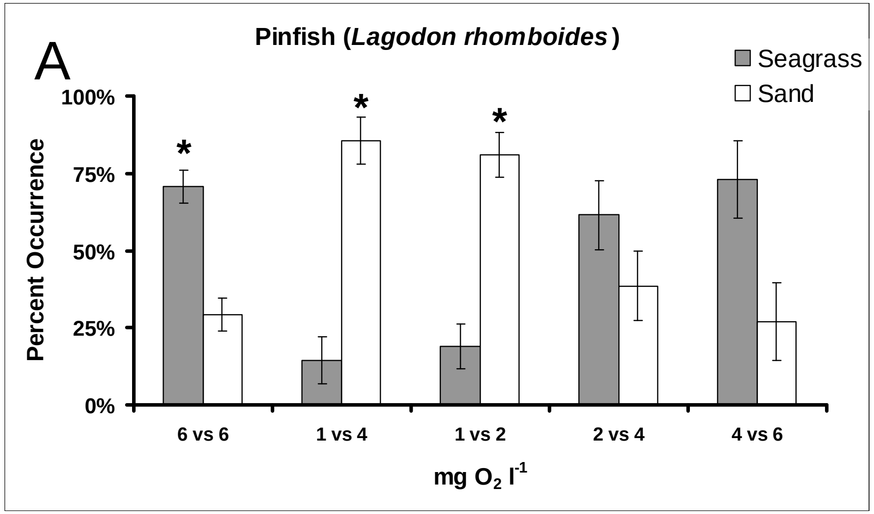
Figure 4.1. Diagram of experimental mesocosm set up. (A) describes the experimental set-up prior to fish introduction where the seagrass treatment is placed in the low DO treatment. (B) describes the set-up after the fish are introduced. (C) describes the experimental set-up prior to fish introduction where the sand treatment is placed in the low DO treatment. (D) describes the set-up after the fish are introduced.

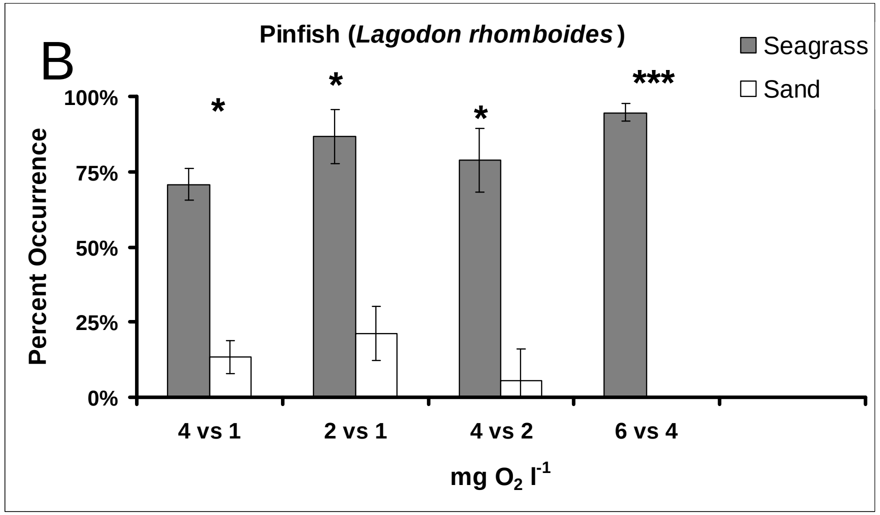
Table 4.1. Summary of substrate-DO concentration mesocsom experiments. Preference indicated significant selection for one chamber of the substrate-DO combination. P-values are indicated from one-sample t-tests against the null expectation of 50% selection for each chamber. Six replicates (n = 6) were conducted for each substrate-DO combination for pinfish (*Lagodon rhomboids*) and croaker (*Micropogonias undulatus*).

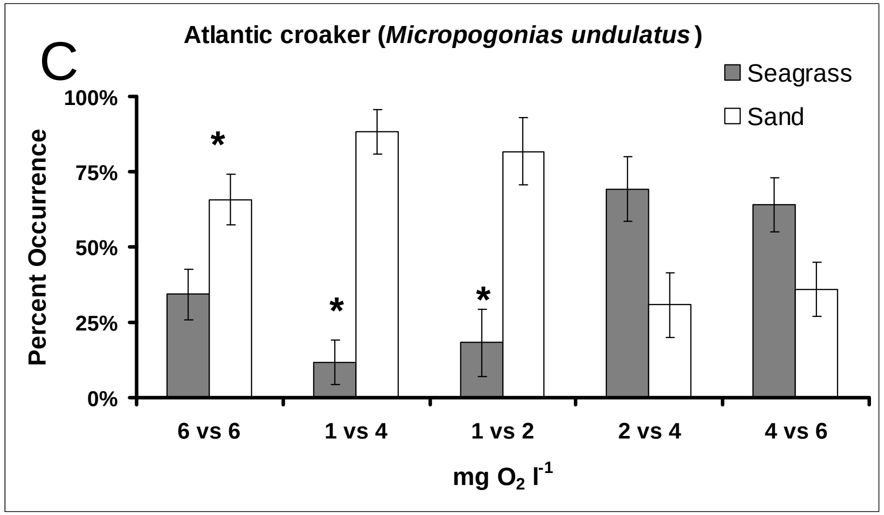
Species	**Substrate-DO Treatment combination**	**Preference**	**df**	**t**	**p**
Lagodon rhomboides	6.0 mg O_2 l^{-1} Seagrass and vs. 6.0 mg O_2 l^{-1} Non-vegetated	6.0 mg O_2 l^{-1} Seagrass	5	3.6	0.016
Lagodon rhomboides	1.0 mg O_2 l^{-1} Seagrass and vs. 4.0 mg O_2 l^{-1} Non-vegetated	4.0 mg O_2 l^{-1} Non-vegetated	5	3.8	0.011
Lagodon rhomboides	1.0 mg O_2 l^{-1} Seagrass and vs. 2.0 mg O_2 l^{-1} Non-vegetated	2.0 mg O_2 l^{-1} Non-vegetated	5	3.6	0.016
Lagodon rhomboides	2.0 mg O_2 l^{-1} Seagrass and vs. 4.0 mg O_2 l^{-1} Non-vegetated	none	5	1.1	0.33
Lagodon rhomboides	4.0 mg O_2 l^{-1} Seagrass and vs. 6.0 mg O_2 l^{-1} Non-vegetated	none	5	1.9	0.121
Lagodon rhomboides	4.0 mg O_2 l^{-1} Seagrass and vs. 1.0 mg O_2 l^{-1} Non-vegetated	4.0 mg O_2 l^{-1} Seagrass	5	3.8	0.012
Lagodon rhomboides	2.0 mg O_2 l^{-1} Seagrass and vs. 1.0 mg O_2 l^{-1} Non-vegetated	2.0 mg O_2 l^{-1} Seagrass and	5	2.6	0.048
Lagodon rhomboides	4.0 mg O_2 l^{-1} Seagrass and vs. 2.0 mg O_2 l^{-1} Non-vegetated	4.0 mg O_2 l^{-1} Seagrass	5	8.7	< 0.001
Lagodon rhomboides	6.0 mg O_2 l^{-1} Seagrass and vs. 4.0 mg O_2 l^{-1} Non-vegetated	6.0 mg O_2 l^{-1} Seagrass	5	3.8	0.014
Micropogonias undulatus	6.0 mg O_2 l^{-1} Seagrass and vs. 6.0 mg O_2 l^{-1} Non-vegetated	6.0 mg O_2 l^{-1} Non-vegetated	5	4.5	0.007
Micropogonias undulatus	1.0 mg O_2 l^{-1} Seagrass and vs. 4.0 mg O_2 l^{-1} Non-vegetated	4.0 mg O_2 l^{-1} Non-vegetated	5	4.3	0.008
Micropogonias undulatus	1.0 mg O_2 l^{-1} Seagrass and vs. 2.0 mg O_2 l^{-1} Non-vegetated	2.0 mg O_2 l^{-1} Non-vegetated	5	2.9	0.034
Micropogonias undulatus	2.0 mg O_2 l^{-1} Seagrass and vs. 4.0 mg O_2 l^{-1} Non-vegetated	4.0 mg O_2 l^{-1} Non-vegetated	5	1.7	0.14
Micropogonias undulatus	4.0 mg O_2 l^{-1} Seagrass and vs. 6.0 mg O_2 l^{-1} Non-vegetated	6.0 mg O_2 l^{-1} Non-vegetated	5	1.4	0.209
Micropogonias undulatus	4.0 mg O_2 l^{-1} Seagrass and vs. 1.0 mg O_2 l^{-1} Non-vegetated	4.0 mg O_2 l^{-1} Seagrass	5	6.0	0.002
Micropogonias undulatus	2.0 mg O_2 l^{-1} Seagrass and vs. 1.0 mg O_2 l^{-1} Non-vegetated	2.0 mg O_2 l^{-1} Seagrass	5	30.5	< 0.001
Micropogonias undulatus	4.0 mg O_2 l^{-1} Seagrass and vs. 2.0 mg O_2 l^{-1} Non-vegetated	none	5	2.5	0.056
Micropogonias undulatus	6.0 mg O_2 l^{-1} Seagrass and vs. 4.0 mg O_2 l^{-1} Non-vegetated	none	5	1.7	0.151

Habitat selection patterns were also determined for croaker. In contrast to pinfish, croaker is a habitat generalist (Petrick et al. 1999). However, the influence of habitat type and DO concentration was similar between both species. Dissolved oxygen exerted greater influence on selection patterns during hypoxic conditions (e.g. DO ≤ 2.0 mg O_2 l^{-1}), while habitat type was more important during moderate hypoxia or normoxic conditions. Habitat selection experiments with croaker were investigated by placing favored substrate (sand bottom as determined from preliminary trials) and high oxygen treatment in separate chambers. Similar to pinfish, croaker avoided their preferred habitat type when DO levels were 1.0 mg O_2 l^{-1}. This was observed for both the 4.0 mg O_2 l^{-1} seagrass vs. 1.0 mg O_2 l^{-1} sand bottom ($p = 0.002$) and 2.0 mg O_2 l^{-1} seagrass vs. 1.0 mg O_2 l^{-1} sand bottom experiments ($p < 0.001$) (Table 4.1, Figure 4.2C). When minimum DO levels were increased in the sand bottom chamber to 2.0 and 4.0 mg O_2 l^{-1}, respectively, selection patterns were more variable. Overall, croaker selection patterns were similar to pinfish, as the mean proportion of time spent in elevated DO-seagrass chamber was higher; although, significant patterns were not detected for either the 4.0 mg O_2 l^{-1} seagrass vs. 2.0 mg O_2 l^{-1} sand bottom ($p = 0.06$) or 6.0 mg O_2 l^{-1} seagrass vs. 4.0 mg O_2 l^{-1} sand bottom ($p = 0.15$) experiments.

Habitat selection patterns of croaker were also determined during a reciprocal set of experiments where oxygen levels were reduced in the seagrass substrate relative to sand bottom substrate. Croaker demonstrated significant avoidance of seagrass when DO levels were reduced to 1.0 mg O_2 l^{-1} within this treatment. This pattern was observed during both the 1.0 mg O_2 l^{-1} seagrass vs. 2.0 mg O_2 l^{-1} sand bottom ($p = 0.034$) and the 1.0 mg O_2 l^{-1} seagrass vs. 4.0 mg O_2 l^{-1} sand bottom ($p = 0.008$) experiments (Fig 4.2D). However, when oxygen levels were increased


A
Pinfish (*Lagodon rhomboides*)
Seagrass
Sand
Percent Occurrence
100%
75%
50%
25%
0%
*
*
*
6 vs 6
1 vs 4
1 vs 2
2 vs 4
4 vs 6
mg O_2 l^{-1}


B
Pinfish (*Lagodon rhomboides*)
Seagrass
Sand
Percent Occurrence
100%
75%
50%
25%
0%
*
*
*
***
4 vs 1
2 vs 1
4 vs 2
6 vs 4
mg O_2 l^{-1}


C
Atlantic croaker (*Micropogonias undulatus*)
Seagrass
Sand
Percent Occurrence
100%
75%
50%
25%
0%
*
*
*
6 vs 6
1 vs 4
1 vs 2
2 vs 4
4 vs 6
mg O_2 l^{-1}

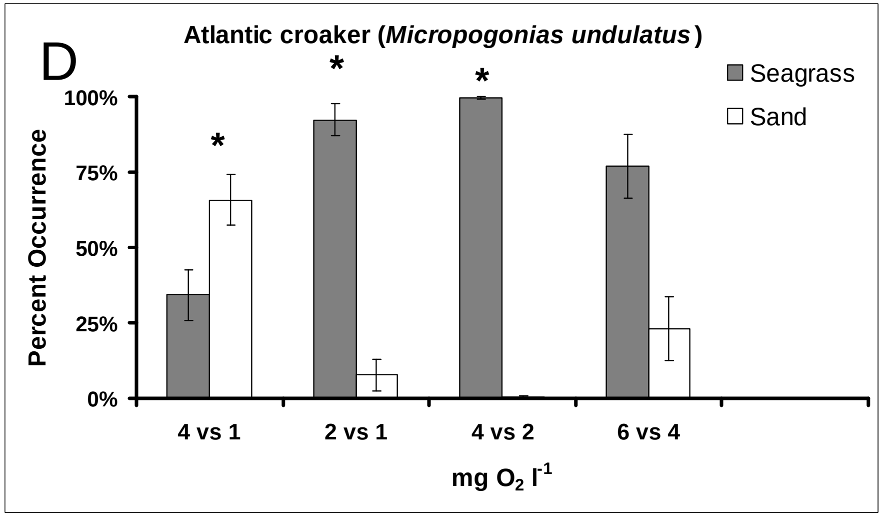

D
Atlantic croaker (*Micropogonias undulatus*)
Seagrass
Sand
Percent Occurrence
100%
75%
50%
25%
0%
*
*
*
4 vs 1
2 vs 1
4 vs 2
6 vs 4
mg O_2 l^{-1}

Figure 4.2. Mean ± SE percentage occurrence of pinfish and croaker in each habitat*DO treatment combination. Each solid-open bar pair represents six replicate 30 minute mesocosm trials with the following treatments: 1A) high DO-sand, low DO-seagrass; 1B) low DO-sand, high DO-seagrass; 1C) high DO-sand, low DO-seagrass; 1D) low DO-sand, high DO-seagrass. Significant results from one-sample Student’s t-tests are indicated by * = $p < 0.05$ and *** = $p < 0.001$.

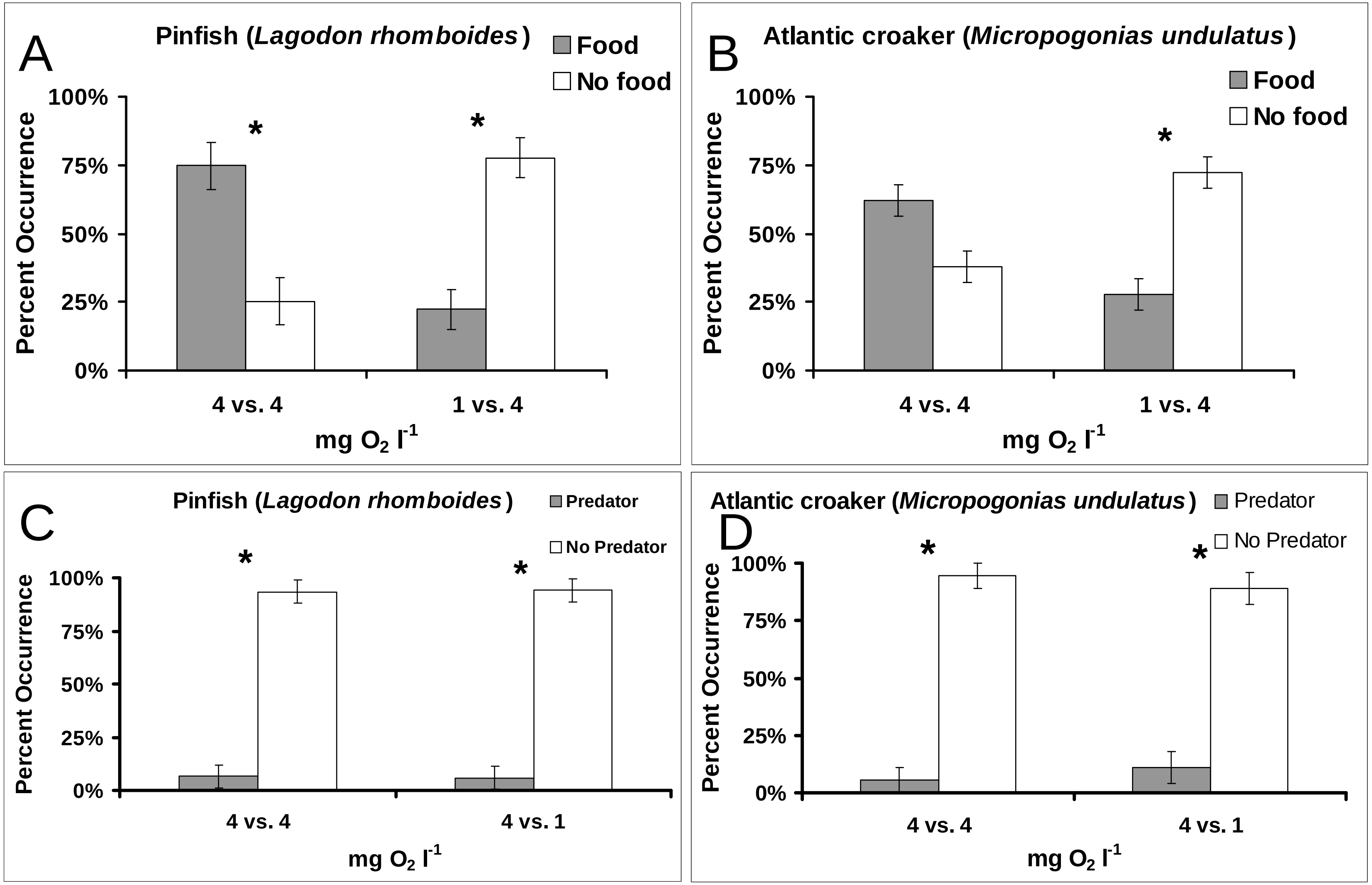

A
Pinfish (*Lagodon rhomboides*)
Food
No food
Percent Occurrence
100%
75%
50%
25%
0%
4 vs. 4
1 vs. 4
mg O_2 l^{-1}
B
Atlantic croaker (*Micropogonias undulatus*)
Food
No food
Percent Occurrence
100%
75%
50%
25%
0%
4 vs. 4
1 vs. 4
mg O_2 l^{-1}
C
Pinfish (*Lagodon rhomboides*)
Predator
No Predator
Percent Occurrence
100%
75%
50%
25%
0%
4 vs. 4
4 vs. 1
mg O_2 l^{-1}
D
Atlantic croaker (*Micropogonias undulatus*)
Predator
No Predator
Percent Occurrence
100%
75%
50%
25%
0%
4 vs. 4
4 vs. 1
mg O_2 l^{-1}

Figure 4.3. Mean ±SE percentage of time pinfish (2A) and croaker (2B) spent in each food enhanced*DO treatment combination. Each solid-open bar pair represents six replicate 10 min. mesocosm trials with the following treatments: 1) 4.0 mg O_2 l^{-1} and mysid shrimp food supplement vs. 4.0 mg O_2 l^{-1} without food supplement treatment; 2) 1.0 mg O_2 l^{-1} and mysid shrimp food supplement vs. 4.0 mg O_2 l^{-1} without food supplement treatment. 2C-D) Mean percentage of time pinfish (2C) and croaker (2D) spent in each chamber of the mesocosm in the presence of a three red drum predators with two different DO*predator combinations. Significant results from one-sample Student's t-tests are indicated by * = $p < 0.05$.

to 2.0 mg O_2 l^{-1} in the seagrass and to 4.0 mg O_2 l^{-1} in the sand bottom chambers, selection patterns deviated from prior experiments. In both the 2.0 mg O_2 l^{-1} seagrass vs. 4.0 mg O_2 l^{-1} sand bottom and the 4.0 mg O_2 l^{-1} seagrass vs. 6.0 mg O_2 l^{-1} no significant selection patterns were detected ($p = 0.14$; $p = 0.21$, respectively).

Food vs. DO selection experiments

The addition of food resources influenced selection patterns of pinfish during moderate hypoxia (4.0 mg O_2 l^{-1}) but did not influence selection patterns at 1.0 mg O_2 l^{-1}. Both chambers of the mesocosm were initially set to 4.0 mg O_2 l^{-1} and a mysid shrimp food supplement was added to one side . Pinfish showed a significant preference for food ($p = 0.05$) (Figure 4.3A). During a second experiment food treatment was placed in a reduced oxygen treatment (1.0 mg O_2 l^{-1}), while the other chamber remained at 4.0 mg O_2 l^{-1} without a food supplement. Pinfish avoided the food enriched chamber and exhibited a significant selection for the 4.0 mg O_2 l^{-1} treatment despite the lack of food ($p = 0.02$). Both experiments were repeated for croaker. During moderate hypoxia (4.0 mg O_2 l^{-1}) food enrichment did not influence selection patterns ($p = 0.09$), and croaker avoided the food supplemented treatment when placed in the low oxygen treatment ($p = 0.01$) (Figure 4.3B).

Predator presence vs. DO selection experiments

The presence of predators exerted a strong influence on selection patterns for both species at all levels of DO concentration tested. An initial experiment was conducted to determine the effect of predator presence on the habitat selection patterns in absence of a DO difference (both chambers set to 4 mg O_2 l^{-1}). Both species strongly avoided predators in the control experiment (no DO concentration difference, pinfish, $p = 0.001$; croaker, $p = 0.001$) (Figure 4.3C-D). In a second experiment fish had a choice between predators with 4.0 mg O_2 l^{-1}

and no predators with 1.0 mg O_2 l^{-1}. Both species chose chambers without predators, despite the low oxygen concentration (pinfish, $p = 0.001$; croaker, $p = 0.007$).

Overall, habitat selection patterns in response to biotic and abiotic factors were similar between species. Dissolved oxygen concentration was an important determinant of habitat selection patterns during hypoxic conditions. However, the importance decreased dramatically during normoxic conditions while the presence of preferred habitat type (substrate) became increasingly important. The addition of mysid shrimp as a food source influenced selection patterns of pinfish at DO 4.0 mg O_2 l^{-1}; however, the influence of food presence was not important when placed in a low oxygen treatment. The response of habitat selection patterns to DO, substrate, and food was strongly interactive. During hypoxic conditions, DO concentration was an important determinant of habitat selection patterns. However, as oxygen levels increased, the relative importance on fish habitat selection decreased and substrate preference became more important. As with substrate, food availability influenced selection patterns of pinfish at 4.0 mg O_2 l^{-1}, however, food availability was unimportant at 1.0 mg O_2 l^{-1}, again suggesting an interactive response to overall habitat selection patterns. The presence of predators exerted the greatest influence on habitat selection. Both species strongly avoided predators even when the alternative habitat was severely hypoxic (1.0 mg O_2 l^{-1}) suggesting a hierarchical response to habitat selection with respect to predator abundance as described by Wildhaber and Lamberson (2004) (Figure 4.4).

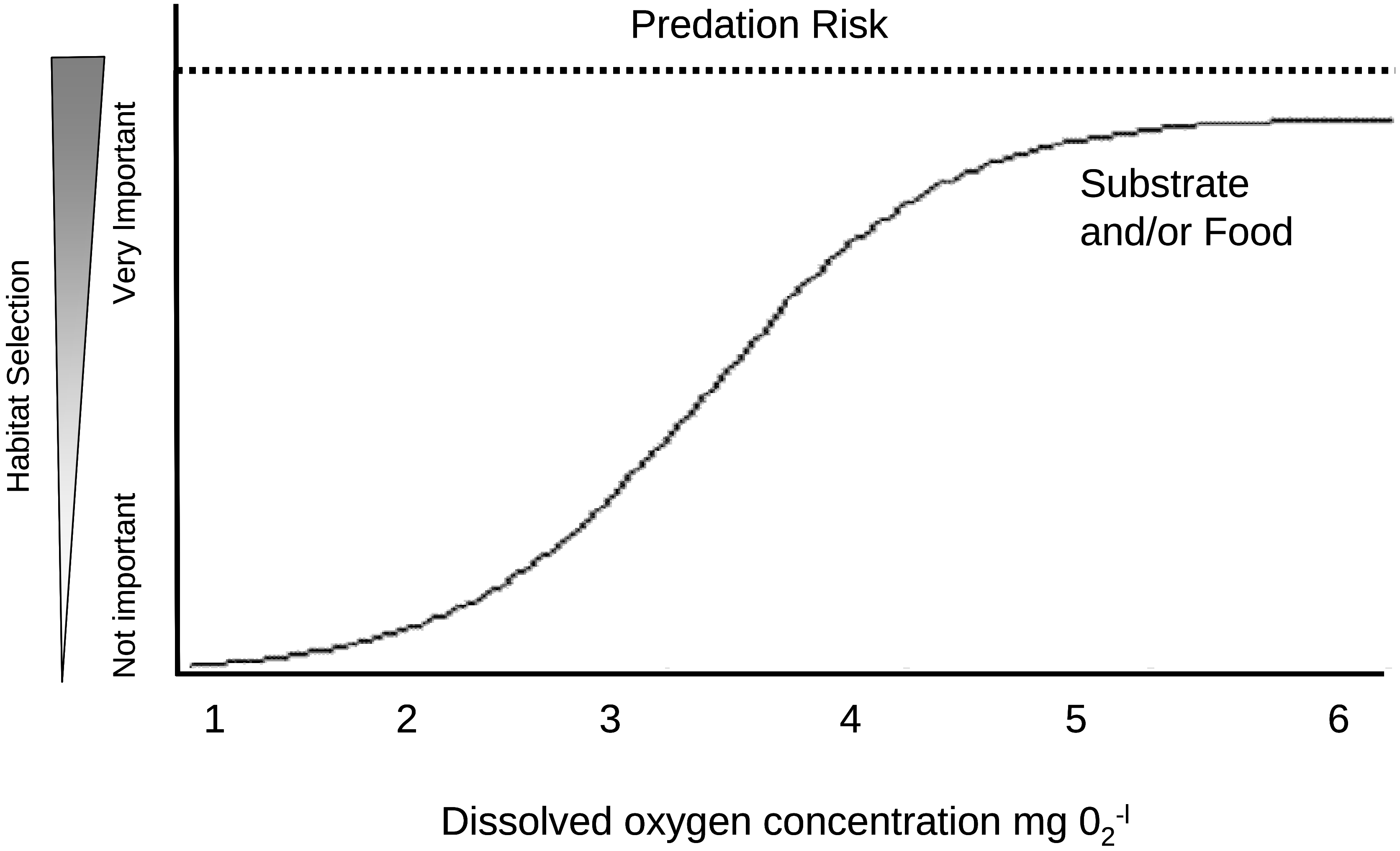

Predation Risk
Substrate and/or Food
Habitat Selection
Very Important
Not important
1
2
3
4
5
6
Dissolved oxygen concentration mg 0_2^{-l}

Figure 4.4. A general mechanistic hypothesis of habitat selection of juvenile estuarine fishes based on our experimental observation. Dissolved oxygen concentration was an important determinant of habitat selection patterns when concentrations were below 2 mg O_2 l^{-1}. The presence of preferred habitat type (substrate) and food availability became increasingly important with increasing oxygen concentration. During low oxygen conditions food availability or substrate type did not influence habitat selection however the relative importance increased with DO concentration. Patterns of habitat selection in response to predation risk and the DO concentrations were similar between species. Predation risk (dashed line), at least in the case of high predator density in this study, exerted the greatest influence on habitat selection patterns of juvenile estuarine fishes (of the factors examined in the current study) across all levels of DO concentration considered.

DISCUSSION

Habitat selection influences distribution, abundance, and population dynamics of mobile organisms (Johnson 1980, Bell et al. 1987, Levin et al. 1997, Stunz et al. 2001, Morris 2003). Preferential selection for high quality habitats may increase growth rates or survivorship, ultimately contributing disproportionately to adult populations (Beck et al. 2001). However, habitat quality may be influenced by a myriad of abiotic and biotic factors and improved management of marine resources requires a detailed understanding of the mechanism used by fishes to select the highest quality habitat available (Morris 2003). Our results describe the relative importance of some abiotic (oxygen) and biotic factors (predator density, vegetation, food) involved in habitat selection for two model estuarine species and provide further insight to the overall process.

In this study, predation risk exerted the greatest influence on habitat selection patterns of juvenile fishes, while selection patterns between DO, habitat type, and food were interactive (Fig. 4.4), and selection patterns were similar between species. In absence of a predator treatment, DO concentrations strongly influenced selection patterns. At low DO concentrations (1 mg O_2 l^{-1}) negative effects were observed as fishes avoided low oxygen treatments while at higher levels, adequate DO levels allowed other factors such as “preferred” substrate or prey availability to influence habitat usage patterns. In contrast to DO, the presence of the "preferred" substrate or food did not affect selection patterns during hypoxic conditions but became increasingly important as DO concentrations increased. To identify potential graded or threshold effects, experiments were also conducted in intermediate hypoxia (DO 2-6 mg O_2 l^{-1}). In experiments with moderate hypoxia where the "preferred" habitat type (as determined from previous experiments) and DO levels were placed in separate chambers few significant selection patterns were observed as fishes were compromising selection patterns between "preferred" habitat type and DO availability.

Abundance of estuarine organisms is typically higher in structurally complex habitats such as seagrass meadows (Jordan et al. 1997, Levin et al. 1997). Seagrass meadows are particularly important habitats for newly recruited juvenile fishes (Burfeind and Stunz 2006). In experiments without DO treatments, pinfish showed significant selection preference for seagrass habitat although croaker, a habitat ‘generalist’ preferred non-vegetated habitat. This is consistent with previous laboratory experiments (Petrik et al. 1999) and field observations (Jordan et al. 1997) for these species. Despite significant substrate preferences, both species avoided their “preferred” substrate when placed in low DO concentrations while at higher levels, adequate DO levels allowed other factors such as “preferred” substrate or prey availability to influence habitat usage patterns. In a Galveston TX estuary, both recruitment and growth rates of pinfish were higher in seagrass as compared to sand habitats (Levin et al. 1997). Juvenile red drum also grew significantly faster in vegetated as compared to sand substrates in experimental field enclosures (Stunz et al. 2002). Similar to the substrate treatment, the addition of food only influenced selection patterns of pinfish in absence of hypoxic conditions. Pinfish avoided the food enriched treatment when placed in the low oxygen treatment, suggesting that food availability is not a strong driver of habitat selection in estuarine ecosystems where food is typically abundant (Heck et al. 2003).

The ability of estuarine organisms to detect and avoid hypoxia in laboratory mesocosms was previously reported (Wannamaker and Rice 2000, Stierhoff et al. 2009).

As with the current study, avoidance patterns were greatest when DO treatments were below 2 mg O_2 l^{-1}. This coincides with the level at which fish emigrate from hypoxic areas and is associated with significant reductions in abundance (Breitburg 2002), and diversity (Vaquer-Sunyer 2008, Montagna and Froeschke 2009). Habitat selection patterns of flatfishes in the Gulf of Mexico were altered by low DO levels with reduced habitat suitability in regions with hypoxia and increased suitability in nearby refuges (Switzer et al. 2009). This study suggests wide-scale alteration of habitat selection pattern due to hypoxia and suggests that this factor alone may induce emigration or avoidance of otherwise suitable habitats. In estuaries, hypoxia may reduce quality of nursery habitat even if preferred habitat types and food resources are abundant.

Hypoxia impacts may be most severe for juveniles as the dispersal potential may be limited due to their small size and increased risk of predation during movement away from hypoxic zones. In this study, predation risk exerted the greatest influence on habitat selection patterns of juvenile fishes. In a study of intermittent hypoxia in Chesapeake Bay, juvenile fishes were less able to escape than adults and mortality rates of juveniles was extremely high (Breitburg 1992). Increased mortality rates of small fish due to hypoxia may be associated with increased oxygen demands of juveniles, reduced swimming speeds (Breitburg 1992), or increased predation risk associated with emigration**.** Results from the current study provide further evidence for predator-mediated habitat selection (Jordan et al. 1997), and the critical role that predators play in ecosystem regulation (Heck and Valentine 2007). Long and Seitz (2008) reported increased susceptibility of benthic prey to predators from hypoxia in Chesapeake Bay. However, Altieri (2008) suggests that responses to hypoxia may reduce predation and hypoxia tolerant species such as quahog clam (*Mercenaria mercenaria*) may benefit from non-lethal hypoxia events. However reductions in abundance and diversity of species sensitive to hypoxia have been observed (Altieri 2008, Montagna and Froeschke 2009). If juvenile fishes forgo emigration from hypoxia due to predation risk, they are subject to the physiological effects of hypoxia and long-term impacts on fish populations may be observed. Landry et al (2007) reported reduced reproductive output and Eby (2005) predicted long-term population declines of croaker resulting from exposure to hypoxic conditions. However, species specific responses to hypoxia is typical and has been reported in both laboratory and field studies (Wannamaker and Rice 2000, Froeschke and Montagna 2009, Switzer et al. 2009). These results suggest that environmental stressors such as hypoxia can be important determinants on community structure (Menge and Sutherland 1987, Lenihan 2001), where some species may benefit but net declines in diversity and resilience may be expected from ecosystem stressors.

Hypoxia may exert direct or indirect effects on population dynamics of juvenile fishes. Populations may be affected directly from hypoxia either through increased mortality or decreased recruitment due to avoidance of hypoxic areas. Indirect effects including reduced growth rate, increased density dependent competition in normoxic refuges and greater predation risk have been hypothesized previously. While indirect effects are more difficult to empirically demonstrate (Heck and Valentine 2007), they may exert greater long-term effects on the population dynamics and community structure of estuarine systems. For example, the rate of juvenile survival is often cited as the best predictor of subsequent adult population size (Caley et al. 1996, Levin and Stunz 2005) and hypoxia induced exposure has been shown to reduce growth rates of some fishes

(Chabot and Dutil 1999, Eby et al. 2005, Stierhoff et al. 2006) and increase their duration in critical life stages where predation risk is high (Levin et al. 1997, Levin and Stunz 2005). Moreover, reduced growth rate may delay sexual maturity and reduce total reproductive output leading to long-term reductions in population size. Growth rates of croaker were reduced significantly inside a hypoxic estuary and subsequent reductions of demographic rates were predicted to result in long-term population declines in the estuary (Eby et al. 2005). Stierhoff et al. (2006) reported reduced feeding and growth rates of *Paralichthys dentatus* and *Pseudopleuronectes americanus* due to moderate hypoxia while similar results were also reported for *Gadus morhua* (Chabot and Dutil 1999). Reduced growth rates may ultimately lead to substantial reductions in fisheries productivity, predator densities, and ultimately a disruption of vital ecosystem links and trophic interactions to the detriment of ecosystem based management goals.

Expansion of low oxygen areas is currently considered among the most damaging environmental problems (Diaz and Rosenburg 2008). This problem will intensify as low oxygen zones increase both temporally and spatially throughout coastal and estuarine regions from enhanced nutrient deposition and warming seas (Diaz and Rosenburg 2008, Vaquer-Sunyer and Duarte 2008). Assessing impacts of these changes on habitat usage of mobile organisms is critical as changes in environmental metrics including predator distribution and DO levels may alter habitat selection patterns and reduce fitness levels of individuals and potentially disrupting vital ecosystem links and trophic interactions to the detriment of ecosystem-based management goals.

CHAPTER 5

POPULATION CONNECTIVITY OF SPOTTED SEATROUT ON THE SOUTH TEXAS COAST

ABSTRACT

Regional declines of spotted seatrout stocks (*Cynoscion nebulosus*) along the south Texas coast have prompted concerns about the connectivity of their populations among management regions. The effectiveness of a recently implemented regional management strategy to protect the largest recreational fishery on the Texas coast requires information on mixing rates and movement patterns of adult spotted seatrout. Stable carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) isotopes in otoliths were used to assess the degree of connectivity of adult spotted seatrout from five regions on the south Texas coast. Spotted seatrout were collected during 2007 from multiple locations within each region. Otolith $\delta^{13}C$ and $\delta^{18}O$ values were quantified to determine if region specific tags could be indentified and to assess the degree of mixing among regions. Significant differences of $\delta^{13}C$ and $\delta^{18}O$ were detected among regions and used for classification with linear discriminant function analysis. Cross-validated classification success of spotted seatrout to five regions of the coast was 64%. Classification patterns indicated that mixing was most likely between adjacent regions although some long-term migrations likely occur and indicate that mixing rates among regions should be incorporated into management activities.

INTRODUCTION

Identification of critical habitat requirements for important life stages of exploited fish populations remains a critical component to their management (Levin and Stunz

2005, Kerr et al. 2007). Increasingly, rates of connectivity among important habitats is recognized as an important factor regulating population dynamics (Able et al. 2005, Gillanders 2005, Rooker et al. *In press*). Habitat use affects population level responses to environmental change and fishing pressure (Kerr et al. 2007), and information on movement and mixing patterns is essential for the management of estuarine-associated fishes (Levin and Stunz 2005). Using chemical signatures as natural tags in fish otoliths is becoming an increasingly common tool to investigate fish movement, mixing patterns (Gillanders 2002, Rooker et al. 2004, Fodrie and Herzka 2008) and the appropriate spatial scale of management (Anderson and Karel 2009, Rooker et al *In press*).

Chemical signatures in otoliths can be used to develop habitat-specific markers in fish and has been used to discriminate origins or connectivity of fishes from estuarine, coastal, or marine environments ultimately identifying origins of important fish stocks (Thorrold et al. 2001, Kraus and Secor 2005, Dorval et al. 2007, Rooker et al. 2008a). Otolith material is accreted chronologically; therefore material from particular regions of the otolith can be used to assess age-specific movement patterns. Often stable isotopes and trace elements have been used in conjunction to identify habitats or assess connectivity. However, trace elements are often subject to strong inter-annual variability (Rooker et al. *In press*). Stable isotope ratios in otoliths also discriminate among habitats, potentially with less temporal variability and, recent studies have employed this method to address natal origins and mixing patterns of marine and estuarine fishes including sciaenids (Rooker et al 2008a, Rooker et al. 2008b). Moreover, otolith elemental chemistry was used to accurately distinguish spotted seatrout nursery habitat over small spatial scales (Dorval et al. 2007, Comyns et al. 2008)

Spotted seatrout (*Cynosicon nebulosus*) support a substantial recreational fishery throughout the Gulf of Mexico (Van Voorhees and Pritchard 2004, Stunz and McKee 2006), including Texas where more than 1,000,000 individuals are harvested annually (Green and Campbell 2005). Economic value of this fishery in Texas exceeded two billion dollars in 2006 (NOAA 2008). However, recent declines in this resource, especially in south Texas, have prompted management action including a limit of one "trophy-size" fish (> 635 mm TL) person^{-1} day^{-1} and a bag limit reduction from ten fish to five fish per person per day in the Lower Laguna Madre, TX USA. This region has historically been among the most productive regions for spotted seatrout and declines have prompted concern about the future status of this fishery (McKinney 2007). However, the degree of mixing of spotted seatrout among estuaries or between marine and estuarine environments in this region is poorly known, potentially hampering conservation efforts for this species (Beck et al. 2001, Lowe et al. 2003, Kraus and Secor 2005).

Genetic (Gold et al. 2003, Anderson and Karel 2009) and tagging studies (Baker and Matlock 1993) have also provided important information about movement and mixing rates of spotted seatrout. However, the degree of connectivity among many local populations remains poorly understood (Secor and Rooker 2005), potentially impairing effective management strategies for this species (Pulliam 1988, Metcalfe and Arnold 1997, Beck et al. 2001). Tagging studies suggest movement of spotted seatrout are limited among Texas Bays (Baker and Matlock 1993). However, long-standing anecdotal information from fishers suggest extensive wide-ranging movements of adult spotted seatrout on the southern Texas coast including exchange between nearshore coastal and estuarine environments. Obviously, if large-scale movement patterns exits, these migrations would have important implications for fisheries management, as spotted seatrout is currently managed regionally in Texas.   For example, anecdotal evidence suggests that Baffin Bay and its adjacent Laguna Madre waters support high abundances of "trophy" spotted seatrout due to connectivity with coastal nearshore populations of spotted seatrout. This hypothesized population of migrating trout "tide-runners" move in through inlets from the Gulf of Mexico during spring and populate the region. However, maintaining connectivity to these areas with the Gulf of Mexico requires frequent dredging of a nearby tidal inlet (East Cut Inlet, Port Mansfield TX, USA) at considerable expense, but also prompts concerns over potential closure and detrimental impacts to valuable spotted seatrout populations.

More information on movement patterns and connectivity of adult spotted seatrout movements are needed to assess mixing rates or evaluate source/sink dynamics among regions on the Texas coast (Pulliam 1988). The purpose of this study was to evaluate whether otolith $\delta^{13}C$ and $\delta^{18}O$ could be used to estimate recent movement patterns of adult spotted seatrout collected in estuarine and coastal environments and make predictions about exchange rate between estuarine and near-shore waters

MATERIALS AND METHODS

Adults spotted seatrout (n = 96) were collected during spring and summer 2007 from three bays, the Landcut, connectivity corridor region between Upper and Lower Laguna Madre, and a nearshore open coast region (i.e., surf zone) on the Gulf of Mexico (Figure 5.1). Regions were chosen *a priori* to estimate mixing rates of spotted seatrout among coastal ocean and nearby estuaries; at least three sites were sampled within each region. The collection of fish from the Landcut (i.e., "tide-runners") occurred during the purported seasonal spring migration of surf fish into the Laguna Madre. I employed experienced guides to collect samples that have seasonally targeted the tide-runner spotted seatrout over the past two decades. According to their anecdotal claims, these fish could be easily recognized based on morphological characteristics and their guiding ability to track and follow migrating schools from the surf through the Landcut and into Upper Laguna Madre (including Baffin Bay).

Sagittal otoliths of adult spotted seatrout were removed, and rinsed with deionized water (DIH_2O). Otoliths were embedded in Stuers epoxy resin and sectioned using a low-speed ISOMET saw. Transverse sections were cut through the core at 2.0 mm width, attached to a sample plate on a New Wave MicroMill System, and the outer edge of the otolith corresponding to the region accreted immediately prior to capture was removed. The drill path was determined from a standard template developed from sectioned spotted seatrout otoliths.

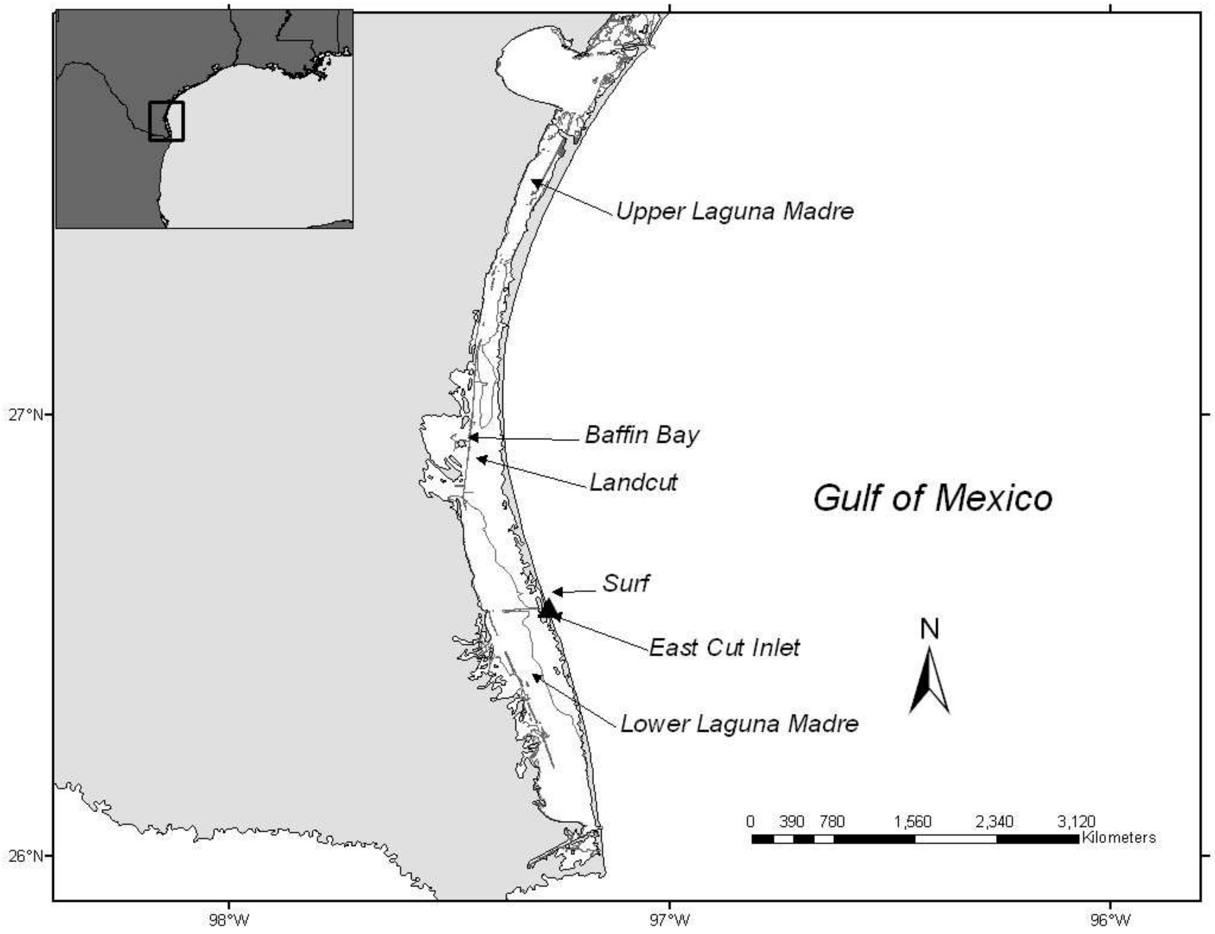


Figure 5.1. Map of study area of the Texas coast in the northern Gulf of Mexico with labels of the five sampling regions.

On each otolith, 11 passes were made to a depth of 50µm. Surface profiling of each otolith was used to correct for imperfect surfaces on the otolith section and ensured consistent milling depth.

Carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) isotopes were measured on a stable isotope mass spectrometer at the Environmental Isotope Laboratory, Department of Geosciences, University of Arizona. Stable $\delta^{13}C$ and $\delta^{18}O$ isotope ratios reported here are based on isotopic ratios of $^{13/12}C$ and $^{18/16}O$ relative to an in-house standard calibrated to Pee Dee Belemnite (PDB).

Statistical Analysis

To examine potential size effects on otolith elemental composition, otolith weights among were first compared among regions using one-way ANOVA with region as a fixed factor. Weights were transformed $\log_{10}(x+1)$ prior to analysis due to heterogeneity of variances among sample regions. As significant differences were found in mean $\log_{10}$ otolith weight among regions, $\delta^{13}C$ and $\delta^{18}O$ values were regressed against $\log_{10}(x+1)$ otolith weights to investigate potential ontogenetic shifts is isotopic composition that could otherwise confound regional differences (Comyns et al. 2008). Standardized residuals were extracted from the linear regression analyses and used in subsequent multivariate analysis of variance (MANOVA) and linear discriminant analysis. A MANOVA was performed to determine if standardized $\delta^{13}C$ and $\delta^{18}O$ values differed among the five regions. Linear discriminant analysis was used to develop regional classification signatures for each region considered. The performance was evaluated using cross-validation with the jack-knife leave one out classification system.

Linear discriminant analysis assumes similar among group covariance matrices and this assumption was tested and met ($\chi 2$ df = 12, p = 0.16) using the "test" option in the DISCRIM Procedure in SAS 9.1.3 software (SAS Institute, Inc., 2000).

RESULTS

A total of 96 adult spotted seatrout were collected from five regions on the south Texas coast to examine spatial differences in otolith $\delta^{13}C$ and $\delta^{18}O$ values (Table 5.1). Stable isotope values of carbon and oxygen were significantly different among regions (MANOVA, $p < 0.001$). Univariate contrasts of isotope values indicated significant differences among regions for both carbon and oxygen ($\delta^{13}C$ ANOVA $F_{4,91} = 4.7$, p = 0.002; $\delta^{18}O$ ANOVA $F_{4,91} = 31.8$, $p < 0.001$). Values of $\delta^{13}C$ were similar among surf, landcut, and Lower Laguna Madre regions (Figure 5.2). Upper Laguna Madre was $\delta^{13}C$ enriched while Baffin Bay was $\delta^{13}C$ depleted. Mean (SD) $\delta^{13}C$ otolith values by region were Upper Laguna Madre = -2.8‰ (1.7), Baffin Bay = -6.1‰ (2.4), landcut = -4.2‰ (1.7), Lower Laguna Madre = -4.0‰ (2.7), surf = -4.4‰ (2.1). Overall, $\delta^{18}O$ values declined from north to south. Mean (SD) $\delta^{18}O$ otolith values by region were Upper Laguna Madre = 0.2‰ (0.4), Baffin Bay = 0.3‰ (0.7), landcut = -0.3‰ (0.4), Lower Laguna Madre = -1.5‰ (2.7), surf = -0.9‰ (0.5).

Linear discriminant analysis with cross-validated classification was used to test the ability to discriminate regions with stable isotope values. Overall classification success among the five regions was 64% and accurate classification region varied among regions (Figure 5.3). Baffin Bay had the highest classification success rate (85%) and misclassified individuals (3) were assigned to the adjacent Upper Laguna Madre. Classification rates for Lower Laguna Madre were also high (75%) and all misclassified individuals were assigned to the Surf. Accuracy of classification of the remaining three regions was variable, Upper Laguna Madre (42%), landcut (60%), and surf (59%) and misclassified individuals were assigned to two or more regions.

Table 5.1. Collection information for adult spotted seatrout (*Cynoscion nebulosus*) collected in five regions on the south Texas coast.

Region	**Sample size**	**Mean total length in cm (range)**
Upper Laguna Madre	20	394 (250 - 550)
Baffin Bay	20	408.5 (280 - 630)
Landcut	20	431 (328 - 550)
Lower Laguna Madre	19	372 (300 - 530)
Surf	17	352 (290 - 410)

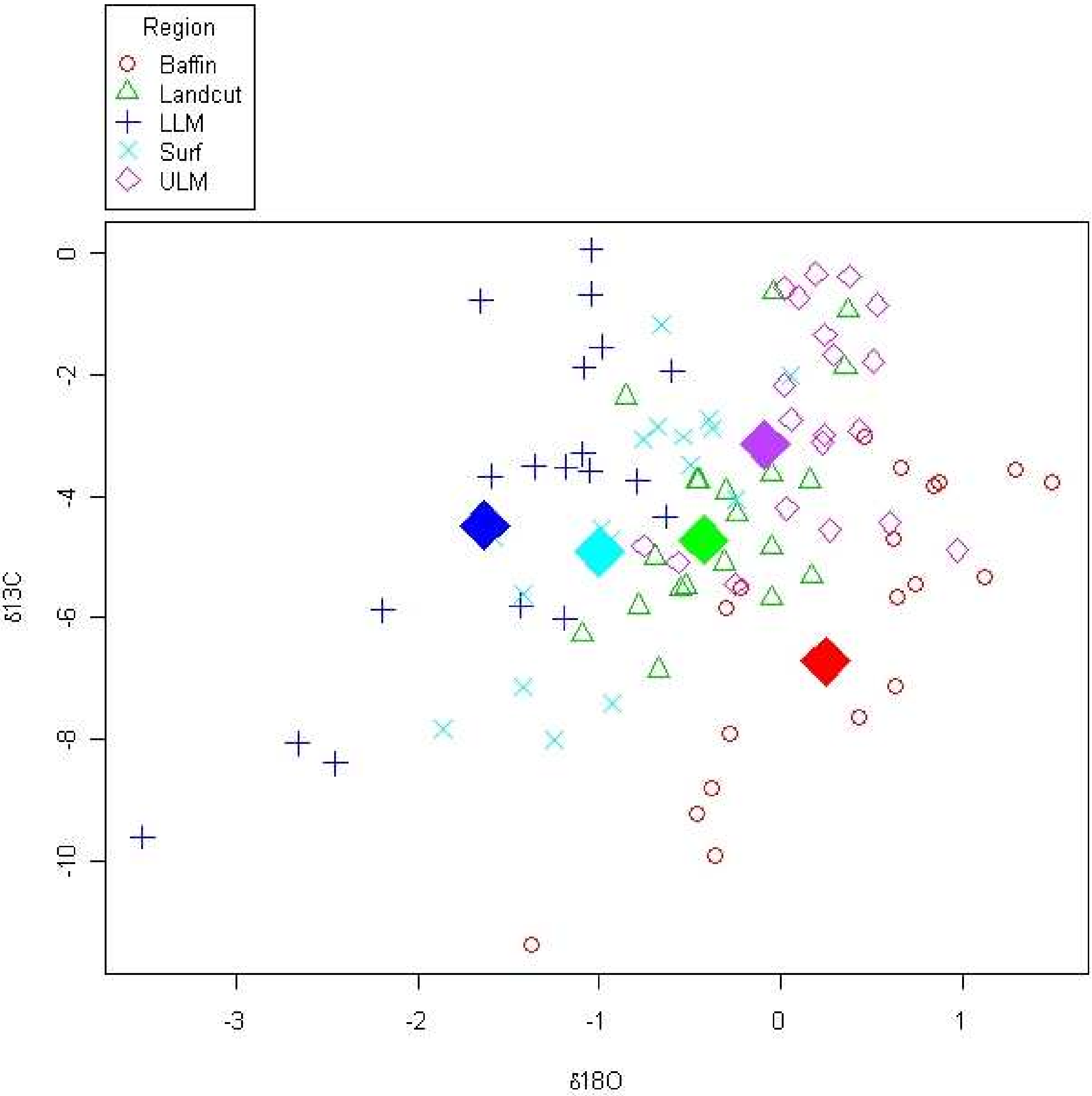


Figure 5.2. Otolith δ^{13}C and δ^{18}O values for adult spotted seatrout (*Cynoscion nebulosus*). Group means by region are indicated by filled diamond symbols.

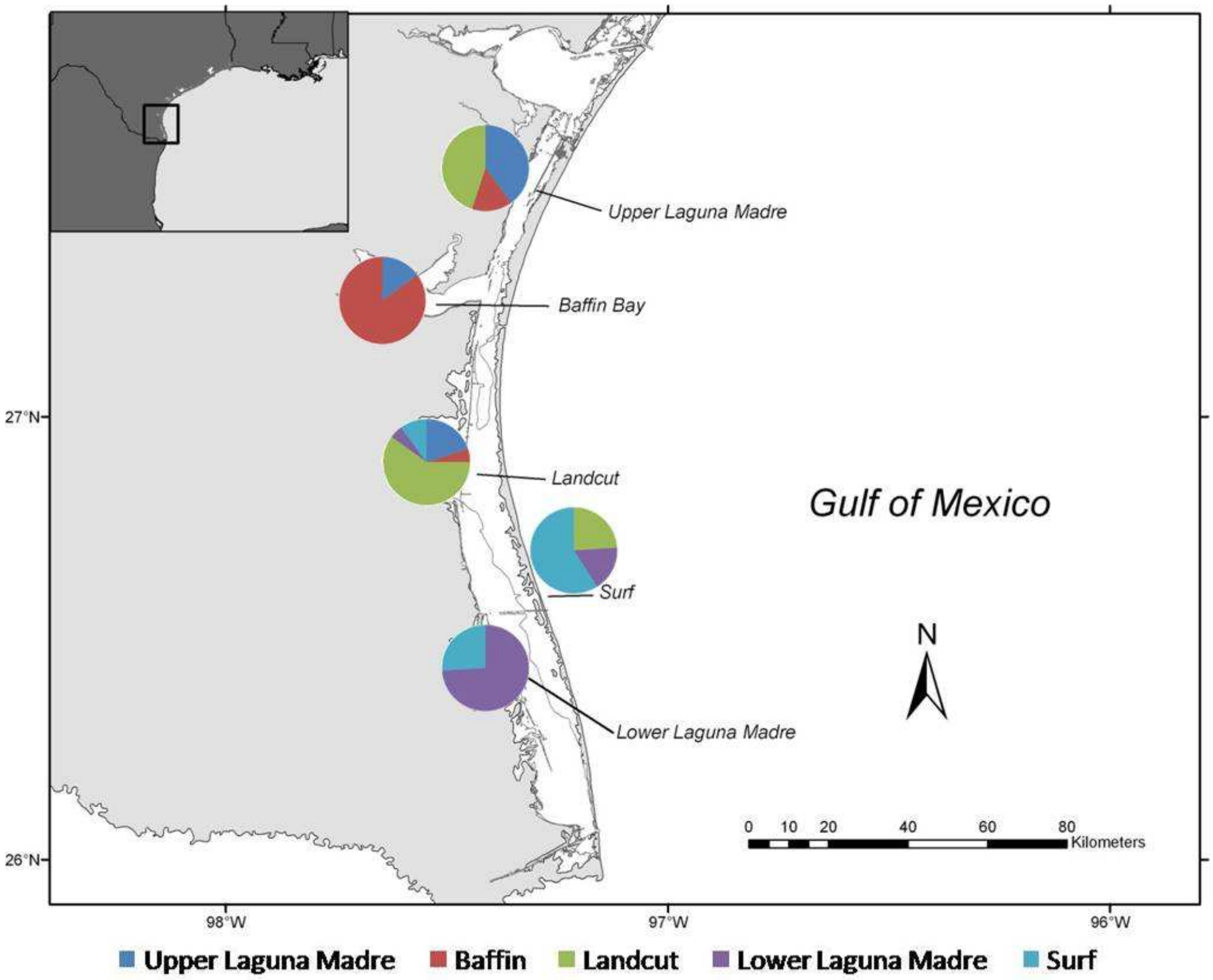


Figure 5.3. Map of classification accuracy by region. Overall rate of correct classification was 64%. Reassignment accuracy varied by region, Upper Laguna Madre (42%), Baffin Bay (85%), Landcut (60%), Lower Laguna Madre (74%), Surf (59%).

DISCUSSION

Significant spatial variation was detected for both δ^{13}C and δ^{18}O isotopes in adult spotted seatrout otoliths. Otolith δ^{13}C was highest for spotted seatrout in Upper Laguna Madre, intermediate in the landcut, surf, and Lower Laguna Madre regions. Baffin Bay had the lowest mean $\delta^{13}C$ values. There is often a positive relationship between salinity and $\delta^{13}C$ values (Harrod et al. 2005, Kerr et al. 2007, Rooker et al. *In Press*) and with exception of Baffin Bay, this broad pattern was observed in this study as well. Baffin Bay had the lowest $\delta^{13}C$ values of the five regions considered, although this region is typically among the most saline areas along the Texas coast due to low freshwater input and isolation from the Gulf of Mexico (Chapter 2). The relatively low $\delta^{13}C$ values for Baffin Bay in this study may have resulted from unusually low salinity values for this region just prior to collection. Dietary influences in $\delta^{13}C$ values have also been reported (Thorrold et al. 1997, Høie et al. 2004), and may have been partly responsible for the unexpectedly low $\delta^{13}C$ values from animals collected in this region. Despite differences in habitat, and likely basal carbon sources between coastal and estuarine systems $\delta^{13}C$ values were similar among surf, Lower Laguna Madre, and landcut samples. Overall, it is likely that both salinity and diet are responsible for the observed variability in otolith $\delta^{13}C$ patterns observed among study sites.

A north to south latitudinal gradient was observed for otolith $\delta^{18}O$ values in this study. The two northern most study sites (Upper Laguna Madre and Baffin Bay) had the highest $\delta^{18}O$ values while the other sites showed a gradient of decreasing $\delta^{18}O$ values with decreasing latitude. This pattern is also consistent with increasing $\delta^{18}O$ values with increasing salinities (Dufour et al. 1998, Bastow et al. 2002). Rooker et al. (*In Press*) reported a similar trend in a study of otolith $\delta^{18}O$ in red drum (*Sciaenops occellatus*) on the Texas coast.

Results presented in this study indicate considerable promise for estimating rates of movement among regions and suggest potential for future identification of natal habitats with examination of the core otolith regions corresponding to the first year of life (Rooker et al. 2008b). However, considerable intrannual variability often occurs and typically requires matching to a known otolith library (Kerr et al. 2007, Comyns et al. 2008, Rooker et al. *In press*). Unfortunately, this was beyond the scope of this study, although future efforts will examine this question. Rooker et al. (*In Press*) was able to successfully indentify natal origins of adult red drum on the Texas coast using stable isotopes and matching with previously collected juveniles of the same year class. Patterns of classification success in this study suggest that mixing likely also occurs among adjacent estuaries and the Gulf of Mexico. Genetic studies of spotted seatrout in Texas support this finding as genetic divergence among regions was low, but significant isolation by distance was reported (Anderson and Karel 2009). However, individuals collected in Baffin Bay were accurately classified (85%) and misclassified individuals were placed in the adjacent Upper Laguna Madre region. This suggests that this population may have less mixing or dispersal than other regions. Baffin Bay is well known as a “trophy trout” location (> 635 mm TL; Stunz and McKee 2006) and supports a unique, but important fishery targeting these large individuals. Our results suggest limited exchange of individuals from this region and suggest this population should be managed conservatively.

Spotted seatrout is the most popular recreational marine fish in the Gulf of Mexico (Stunz and McKee 2006, James et al. 2007, Comyns et al. 2008) and is intensively managed by Texas Parks and Wildlife Department to maintain this resource (Anderson and Karel 2009). Enhancement through stocking efforts has occurred since 1991, additional length restrictions were added in 2004, creating a slot limit to protect trophy-size trout (Stunz and McKee 2006), and in 2007 the bag-limit was reduced in Lower Laguna Madre from 10 to five fish per person per day (TPWD 2007). Despite these efforts, concerns remain for the overall health of this fishery, and this problem is exacerbated due to uncertainty as to the proper spatial scale of management for this species (Anderson and Karel 2009). For example, stocking efforts have estuarine specific broodstocks, and fingerlings are only stocked in regions from which broodstock were taken as there is evidence of adaptive differences to salinity or temperature gradients along the Texas coast (King and Zimmerman 1993, Anderson and Karel 2009).

Results of this study in conjunction with tagging and genetic studies on the Texas coasts suggest that management of estuarine specific regions is likely appropriate for spotted seatrout. However, in light of regional declines, mixing among adjacent estuaries and the Gulf of Mexico should be considered when evaluating population level trends. Moreover, our results suggests that current harvest limits in Lower Laguna Madre could be expanded to nearby regions including the Gulf of Mexico, as its likely that exchange of individuals regularly occur among these regions. However, the implementation of regional management plans remains controversial. Uncertainty in mixing rates, population connectivity, and concerns of adverse economic impacts in more restrictive areas ensure that this issue will remain and continued efforts documenting population dynamics, habitat use, and connectivity patterns are necessary to provide sound advice for the sustainable management of this fishery.

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SUMMARY AND CONCLUSIONS

Estuarine and coastal environments provide essential habitat for many recreationally or commercially important species. However, overexploitation and habitat degradation have reduced fisheries resources worldwide (Lotze et al. 2006, Worm et al. 2006). Moreover, the uncertainty in the effects of changing environmental conditions (i.e., climate change) on aquatic ecosystems has caused concern about the viability of fisheries resources, and the economic, ecological, and recreational opportunities they support. Moreover, these changes have occurred despite considerable effort to manage fisheries resources (NOAA 1996, 2002, 2006). In response to this paradigm, management is shifting towards ecosystem based approaches (Pikitch et al. 2004); however, this requires specific information about habitat use and population dynamics of critical species. This includes identification of Essential Fish Habitat (EFH) and sensitive life stages for critical species (Levin and Stunz 2005, Kinney & Simpfendorfer 2009). In many cases, current data are inadequate for ecosystem approaches. This dissertation research examined several aspects of EFH, specifically, abiotic, biotic, and life history influences of habitat use for estuarine and coastal fishes.

Representative species with different life histories including highly migratory species (sharks) as well as estuarine-resident teleosts (red drum, spotted seatrout, pinfish) were studied to determine environmental attributes influencing habitat use. Species examined varied widely in size, home ranges, and habitat usage. To study these fishes hypothesis driven and statistical modeling approaches were applied. Research was carried out using a multi-disciplinary approach integrating biological and physical sciences to improve understanding of habitat requirements for ecologically and economically important species.

As survival rates of juveniles is often among the best predictors of future adult populations, substantial interest has been placed on understanding habitat requirements of juvenile fishes and mapping these areas determining environmental determinants of habitat use (Stoner et al. 2001, 2003). In this dissertation research, I identified and mapped nursery areas for three coastal shark species while examining the relative influence of several environmental factors on their distribution patterns. My research indicates that the central Texas coast constitutes essential nursery habitat for bull sharks (Figure 6.1) and likely other shark species. This region is characterized by moderate salinities, warm temperatures, and access to the Gulf of Mexico through tidal connections. Habitat usage patterns were similar over the 32-y study period and these results offer novel insight into habit requirements of coastal sharks.

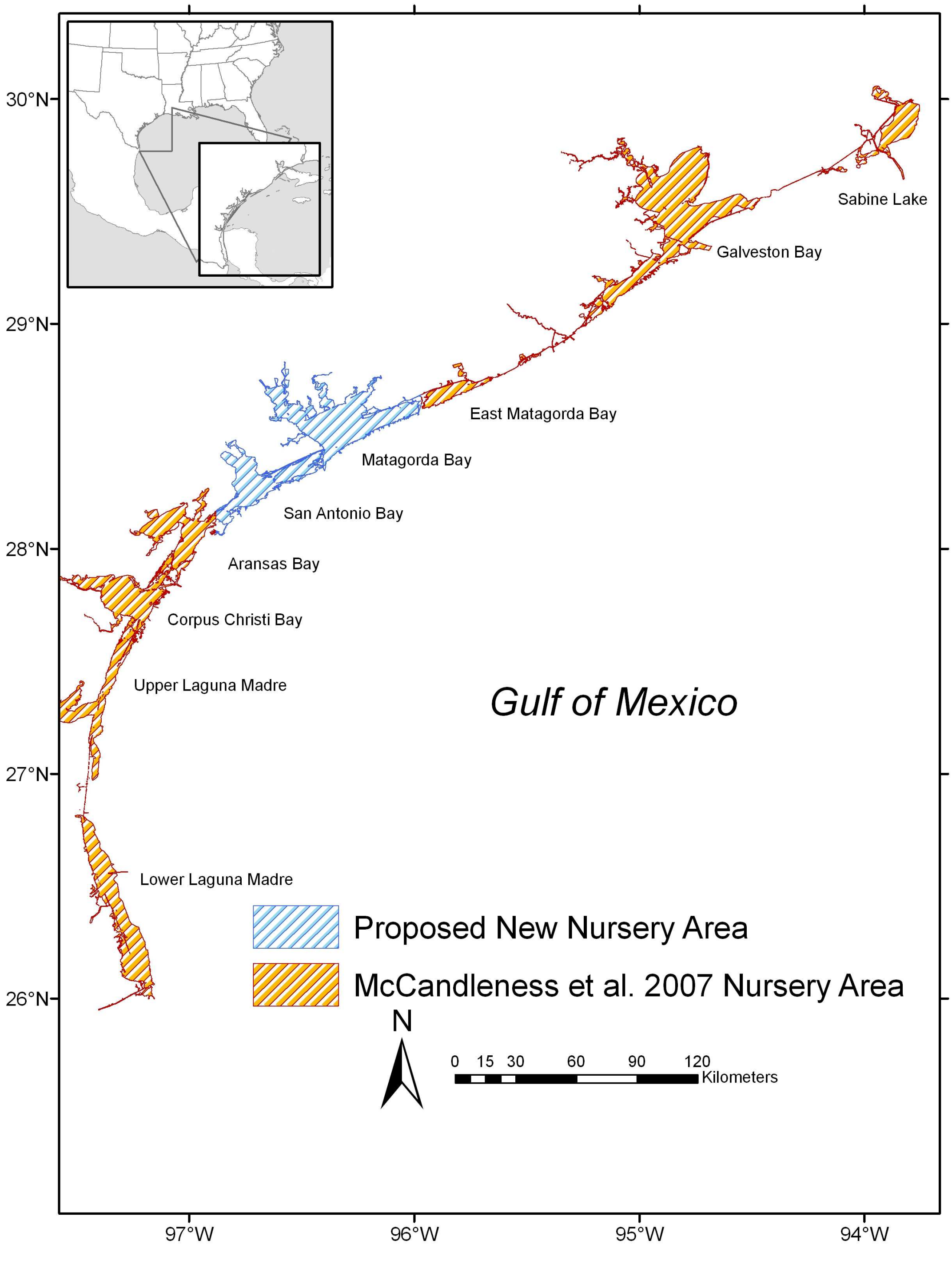

Figure 6.1. Current and proposed areas designated as nursery habitat for bull shark in Texas coastal estuaries. Historically, the entire coastal estuarine system was considered

nursery habitat. Using the criteria of Huepel et al. (2007) in the current study, only San Antonio and Matagorda bays provide nursery habitat.

In contrast to estuarine waters, species composition and habitat requirements of coastal sharks in the Gulf of Mexico are poorly understood. However, sharks are intensively fished in the Gulf of Mexico (Baum et al. 2004), especially on Padre Island National Seashore, and there are concerns about the sustainability of this resource. I examined species composition, seasonal patterns, and temporal trends of coastal sharks in this region using historical, fisheries-dependent data. This region supports a diverse and abundant shark population, although at least one species (bull shark) has declined in size at capture over time. This is often an indication of overfishing (Powers et al. *In revision*) and suggests that this resource should be managed cautiously.

My research also examined habitat use and movement patterns of estuarine fishes. I used manipulative laboratory mesocosm choice experiments to examine hierarchical and interactive relationships influencing habitat selection of juvenile estuarine fishes. I assessed selection among substrate, dissolved oxygen concentration, food availability, and predation risk using two common juvenile estuarine fish species (pinfish and Atlantic croaker). Fish habitat selection was affected by both abiotic and biotic factors. Overall, predation risk may be the greatest determinant of habitat selection for small juvenile fishes, although impacts such as declining oxygen levels in coastal regions may significantly alter the structure and function of these areas.

Increasingly, rates of connectivity among important habitats is recognized as an important factor regulating population dynamics (Able et al. 2005, Gillanders 2005, Rooker et al. *In press*). Habitat use affects population level responses to environmental change and fishing pressure (Kerr et al. 2007) and information on movement and mixing patterns is essential for the management of estuarine-associated fishes (Levin & Stunz 2005). However, the degree of connectivity among local populations remains poorly understood (Secor & Rooker 2005) potentially impairing effective management strategies for some species (Pulliam 1988, Metcalfe & Arnold 1997, Beck et al. 2001).

Spotted seatrout (*Cynosicon nebulosus*) supports the largest recreational fishery throughout the Gulf of Mexico (Van Voorhees & Pritchard 2004, Stunz & McKee 2006). Economic value of this fishery in Texas exceeded two billion dollars in 2006 (NOAA 2008). This species is intensively managed to sustain the resource, however, regional declines of this species on the south Texas coast have prompted increased regulatory action. Unfortunately, little is known about movement patterns or exchange rates among estuaries or between estuaries and the Gulf of Mexico creating uncertainty in the appropriate scale of management for this species. I used otolith $\delta^{13}C$ and $\delta^{18}O$ values to determine if region specific tags could be indentified to assess the degree of mixing among regions for spotted seatrout. Results indicated that mixing was most likely between adjacent regions, although some long-term migration is likely to occur.

Increasingly, the interrelatedness of biological, physical, and spatial processes necessary to ecosystem maintenance is being recognized (Pikitch et al. 2004, de Ruiter et al. 2005). Research focus is rapidly shifting toward integrative, multi-disciplinary approaches incorporating experimental research, quantitative modeling, and the impacts of human activities on ecosystems processes. Indeed, the results of my research indicate both broad-scale (e.g., salinity regime) and fine-scale (e.g., predator abundance) impacts to habitat quality for marine and estuarine fishes. My dissertation research also provides insight into impacts of habitat loss, changes in freshwater inflow into coastal estuaries (i.e., salinity regime), or declining dissolved oxygen concentrations of aquatic resources. Overall, my dissertation research has provided new insight into habitat requirements of representative species in northwestern Gulf of Mexico. I conducted research using novel techniques and identified areas warranting further research to improve resource management in the Gulf of Mexico.

This dissertation research also proposes many new avenues for future examination. For example, the distributional modeling of sharks within Texas estuaries raises the question of individual responses to changing environmental conditions as well as residency patterns and connectivity among adjacent systems (e.g., Gulf of Mexico). These results also demonstrate the need for hypothesis driven studies to further the correlational based distribution models proposed here. Similarly, my results with spotted seatrout suggests considerable movement among estuaries, potential exchange with coastal environments, and the need to refine our understanding of movement and connectivity patterns of this and similar species. Again, further hypothesis driven studies, assessing movement patterns of individuals may further our understanding of these ecosystems and could be extended to incorporate large numbers of individuals or species in complex ways through statistical or simulation (e.g., agent based models) to investigate individual to ecosystem levels impacts of connectivity of habitat quality questions. My laboratory work examining responses of juvenile estuarine fishes to abiotic and biotic factors suggested that fish select habitat in interactive and complex ways. While this research effectively answered questions and proposed a simplistic decision tree type model of habitat selection, this work would benefit from larger-scale modeling and field based approaches to validate the patterns found in my experiments.

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BIOGRAPHICAL SKETCH

John Thomas Froeschke received a Bachelor of Science in Biology (Summa Cum Laude) from Arizona State University in 2000. Upon graduation he entered the Master's in Biology program at California State University, Northridge in 2001 working under Dr. Larry G. Allen. John completed his M.S. Biology in 2004 and worked as a research biologist for the Vantuna Research Group at Occidental College from 2004 to 2006. John is also a member of the American Society of Ichthyologists and Herpetologists and the American Fisheries society and has presented his work at conferences throughout the United States as well as in Brazil (2004) and Canada (2008). John is also an avid research diver and has logged more than 500 dives investigating fisheries ecology issues in the United States, Mexico, and Honduras. To date, John has authored, or co-authored five peer reviewed manuscripts on a variety of fishery-related topics. John now resides in Tampa, Florida and is employed as a Fisheries Biologist for the Gulf of Mexico Fishery Management Council where he continues his efforts toward contributing knowledge necessary for sustainable use of marine resources.