FACTORS INFLUENCING THE NURSERY DYNAMICS OF JUVENILE BULL SHARKS IN TWO ESTUARIES ALONG THE TEXAS COAST

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by

Amanda J. Lofthus

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APPROVED:

Jeffrey R. Wozniak, PhD
Thesis Co-Director

Philip Matich, PhD
Thesis Co-Director

Diane L. Neudorf, PhD
Committee Member

Amber J. Ulseth, PhD
Committee Member

John B. Pascarella, PhD
Dean, College of Science and Engineering Technology

DEDICATION

I dedicate this thesis document to my parents, Allison and Eric, and my little brother, Connor. Thank you all for always pushing me to accomplish my dreams, no matter how crazy they might seem, and for always believing in me and providing invaluable support along this journey. I would not have been able to get through this degree without all of your love and encouragement.

ABSTRACT

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Nursery habitats provide refuge for juvenile organisms to grow and develop, and are utilized by several shark species, including bull sharks (*Carcharhinus leucas*). Bull sharks utilize estuaries adjoining the Gulf of Mexico as nursery habitat, and are the most abundant shark species found along the Texas coast. However, little is known about their nursery dynamics in this region, especially for the young-of-the-year (YOY) age class. This study investigated how predation risk and abiotic factors influenced the occurrence and densities of YOY bull sharks in two Texas estuaries: San Antonio Bay and Sabine Lake using *in-situ* drumline sampling and historical long-term gillnet monitoring (1985-2018). In San Antonio Bay, the densities of larger sharks posing a threat to YOY bull sharks was highest in the months of May and June, and significantly influenced by location within the estuary. No predatory sharks were sampled in Sabine Lake, suggesting that this entire estuary may serve as important nursery habitat. In both systems, densities of YOY bull sharks were highest in low salinity waters near river mouths, and in San Antonio Bay, lower predation risk was a significant factor predicting densities of YOY bull sharks. YOY bull shark densities were also influenced by temperature, dissolved oxygen, and location within the estuary. Understanding the effects of changing environmental conditions on predation risk and YOY bull shark habitat use allows us to better understand shark nursery dynamics along the Texas coast, and identify important nursery habitats for this estuarine predator.

KEY WORDS: Marine fish ecology, Nursery habitat, Coastal ecology, Population dynamics, Elasmobranchs

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CHAPTER I

General Introduction & Literature Review

Fish Nursery Habitats

Nursery habitats are utilized by marine, estuarine, and freshwater fish, and provide refuge for juvenile organisms to grow and develop (Beck *et al.* 2001, Dahlgren *et al.* 2006, Sheaves *et al.* 2006). Juvenile fish, especially during their first year of life, experience the greatest survival challenges of any age class due to predation risk, competition, and the learning curve of finding habitats that provide food and safety (Beck *et al.* 2001, Heupel *et al.* 2011, Metcalfe *et al.* 1987). Nursery habitats are typically characterized by lower predation risk than surrounding habitats, high densities of juvenile individuals, and fast growth rates of juveniles. As such, these nurseries often provide a greater contribution to the adult population of a species than other habitats (Beck *et al.* 2001). The definition of a nursery habitat has not always been clear in the literature, and has undergone several changes and clarifications since researchers first began investigating habitats that seemed to support high numbers of juvenile organisms.

History of the Nursery Habitat Concept

Nurseries are defined as habitat "that fosters, develops, or promotes…a place where animals are cared for" (Babcock 1993). This definition led to the labeling of any habitat that contained juvenile organisms, regardless of abundance or residence times, as nursery habitat. From a management perspective, this was problematic as it is impossible to conserve every habitat that may contain juvenile fish, and conservation effort focused on protecting habitats critical for juvenile survival would be more beneficial (Beck *et al.* 2001, Dahlgren *et al.* 2006). The first ecologically robust definition of a nursery habitat came in 2001, where it was suggested that the value of different nursery habitats could be measured by their per area contribution to the adult population (Beck *et al.* 2001). This approach was widely accepted by the fisheries community, and several consecutive studies used this framework as a tool for the identification of nursery habitats for a variety of fish species (Sheridan & Hays 2003, Kraus & Secor 2005). However, in 2006, it was suggested that certain habitat areas, though their per unit area contribution to the adult population may be less, are still critically important for sustaining adult populations (Dahlgren *et al.* 2006). Larger areas of a single habitat type may have an inherently lower per unit area contribution to the adult population due to their large size, but may still be important for sustaining fish populations and providing nursery habitat (Dahlgren *et al.* 2006). It was suggested that the nursery habitat definition be refined to 'Effective Juvenile Habitat' (EJH): "a habitat for a particular species that contributes a greater proportion of individuals to the adult population than the mean level contributed by all habitats used by juveniles, regardless of area coverage" (Dahlgren *et al*. 2006). Although recognized for making some beneficial clarifications and looking beyond the actual size of a habitat, this approach was still criticized for not considering processes that underlie the functionality of nursery habitats, since many juveniles use a mosaic of habitats during their growth and development (Nagelkerken *et al.* 2015). It was argued that migration corridors between habitats, which had previously been overlooked in nursery area definitions, are critically important, and protecting these corridors should be a conservation aim along with protecting areas for juvenile growth and development (Nagelkerken *et al.* 2015). While protecting migration corridors is an interesting conservation strategy to consider, it brings up issues with delineating boundaries between aquatic habitats, especially marine ones. Including migration corridors within the nursery habitat definition could potentially lead to the classification of a majority of the ocean as nursery habitat, since many species have pelagic larvae and ocean currents connect a wide range of habitats. This challenge is unique to marine and aquatic environments, as boundaries between ecosystems are often more discrete in terrestrial systems (Cadenasso *et al.* 2003).

Another publication from 2015 focused on incorporating ideas of ecosystem complexity and dynamics into the definition of EJH, arguing that only measuring the output of juveniles from a given habitat location ignores the critical processes and ecosystem dynamics that allow a specific area to produce such a high output of juveniles and function as a nursery habitat (Sheaves *et al.* 2015). Factors such as habitat connectivity and population dynamics, ecological and ecophysiological factors, and resource dynamics play key roles in the functionality of nursery habitats, and the ability of these habitats to output individuals into adult populations (Sheaves *et al.* 2015). Moving forward, there is a need for both broad and fine scale investigations into nursery habitats to determine the factors and interactions underpinning ecosystem function, as examining ecosystems on a large scale can reveal important migration corridors and connectivity between habitat types, but can also hide key processes that are essential for nursery habitat function.

Elasmobranch Nurseries – a Review of Significant Research

A group of fish of recent conservation concern that are known to utilize nursery habitats are the elasmobranchs, specifically sharks. Threats from overfishing, habitat loss, and other anthropogenic influences have caused declines in shark populations around the globe (Baum *et al.* 2005). In turn, identifying critical nursery habitats utilized by sharks has become increasingly important. Although nursery habitat use is common in this group, not all sharks utilize nursery habitats, with the young of some species being born in open ocean habitats offering little refuge from predation (Springer 1976, Parsons & Hoffmayer 2005, Heupel *et al.* 2007). Species such as the tiger shark (*Galeocerdo cuvier*) may experience less risk in these open ocean habitats as juveniles due to their larger sizes at birth, although sharks with small size-at-birth including atlantic sharpnose (*Rhizoprionidon terraenovae*) and blacknose sharks (*Carcharhinus acronotus*) are also born off-shore in areas characterized by higher predation risk (Carlson 2002, Parsons & Hoffmayer 2005, Heupel *et al.* 2007). However, both *R. terraenovae* and *C. acronotus* have high reproductive rates and large litter sizes, so juvenile mortality is likely not as detrimental to the population as it would be for species with lower reproductive rates, and may explain why these species don't utilize nursery habitats. Shark species with lower reproductive rates, small litter sizes, slower growth rates, and larger size at maturity tend to utilize nursery habitats more frequently, including species such as the bull (*Carcharhinus lecuas*), thresher (*Alopias vulpinas*), blacktip (*Carcharhinus limbatus*), and scalloped hammerhead shark (*Sphyrna lewini*) (Duncan & Holland 2006, DeAngelis *et al.* 2008, Cartamil *et al.* 2010, Heupel & Simpfendorfer 2011). There is likely a complex interaction of factors including size-at-birth, life history strategy, availability of nursery habitat, growth rates, and size at maturity that influence whether or not a species utilizes nursery habitats. A majority of current knowledge on shark nursery habitat use is concentrated on a few tropical shark species that utilize accessible coastal nursery areas, and many critical nursery areas have yet to be identified through quantitative measures (Heupel *et al.* 2018).

The use of nursery habitats by sharks was first observed by Springer, when he described that coastal shark species often come into shallow, nearshore areas to give birth. He noted that these nursery areas were often, but not always, separate from adult shark populations, and the juvenile sharks remained in them until sexual maturity (Springer 1967). After this paper, shark nursery habitats were not the focus of much research again until 1996, when NOAA issued a mandate requiring the identification of essential fish habitat in U.S. fishery management plans, which included the identification of nursery habitats (Bonfil 1997, Grubbs 2001, Merson & Pratt 2001, Heuter & Tyminski 2007, McCandless *et al.* 2007, Parsons & Hoffmayer 2007, Steiner *et al.* 2007). Due to the lack of substantive information on shark nurseries when this mandate first appeared, it led to the broad-scale application and utilization of teleost management strategies for elasmobranchs, including the often-used strategy of protecting younger age classes (Kinney & Simpfendorfer 2008). Sharks have different life history traits than teleosts: many teleost populations have a steep stock-recruitment curve, meaning that populations have high recruitment from nursery areas even when the breeding population is small, whereas sharks tend to have a much shallower stock-recruitment curve where recruitment is high only if the breeding population has sufficient numbers (Kinney & Simpfendorfer 2008). While solely protecting nursery habitats can be a beneficial strategy for managing populations of shorter-lived species with higher reproductive outputs, which does include some sharks such as the dusky smoothhound (*Mustelus canis*), if used in isolation the strategy of protecting younger age classes is not always effective in the management of slow-growing species with lower reproductive outputs, such as some larger sharks (Kinney & Simpfendorfer 2009). Protecting shark nursery habitats and juvenile age classes should still be a conservation priority, but needs to be paired with effective management of adults, as well as juveniles on the verge of reproductive maturity, to ensure recruitment of juvenile sharks into adult populations (Simpfendorfer 1999, Kinney & Simpfendorfer 2009).

Even with increasing interest in the study of shark nurseries, prior to 2007, many habitats were labeled as shark nurseries based solely on the presence or record of juvenile sharks inhabiting an area, without investigations into their densities, habitat use, or whether these patterns stayed consistent through time (Heupel *et al.* 2007). The three criteria now commonly used to identify shark nurseries are 1) juvenile sharks are more commonly encountered in a habitat than other nearby areas, 2) juvenile sharks remain in a habitat or return to that habitat for extended periods of time, and 3) the habitat is repeatedly used by juvenile sharks across years (Heupel *et al.* 2018).

Shark Nursery Characteristics and Geographic Locations

Shark nurseries are typically found in shallow, energy-rich coastal areas (Bass 1978). Shallow depths characteristic of these nursery habitats can exclude larger sharks, which are the main predators of juvenile elasmobranchs, likely decreasing predation risk in these nurseries (Castro 1993, Heithaus 2004, Guttridge *et al.* 2012). It is generally accepted that nurseries both provide a refuge from spatially dependent predation risk and provide abundant food resources for juvenile organisms, and this has been shown in several cases (Brantsetter 1990, Heupel & Heuter 2002). However, some research has found that this is not always the case in elasmobranch nurseries. In Kanahoue Bay, Hawaii, a habitat known to provide nursery habitat for juvenile scalloped hammerheads (*Sphyrna lewini*), it was found that attrition of neonate sharks was higher than expected during their first year of life, and the hypothesized primary cause was low body condition due to starvation (Duncan & Holland 2006). Prey abundance estimates in the same bay also found that prey populations had crashed in recent years, so it is possible that these habitat areas historically provided abundant food resources, but can no longer provide sufficient resources due to overfishing and habitat degradation depleting potential prey populations. Due to natal philopatry, *S. lewini* continues to use these habitats as nurseries even though they have been degraded and no longer provide sufficient food resources (Duncan & Holland 2006).

Globally, estuaries are recognized as important nurseries for several shark species, including Spinner (*Carcharhinus brevipinna*), Blacktip (*Carcharhinus limbatus*), Bull (*Carcharhinus leucas*), Lemon (*Negaprion brevirostris*), Scalloped Hammerhead (*Sphyrna lewini),* and Sandbar (*Carcharhinus plumbeus*) sharks (Heuter & Tyminski 2007, Steiner *et al.* 2007, Froeschke *et al.* 2010a). Estuaries are the mixing zones between riverine and marine ecosystems, and due to this complexity, contain a variety of habitats characterized by differing environmental conditions (McLusky & Elliott 2004). Most juvenile sharks are restricted to marine habitats within estuaries, but around the world, bull sharks (*Carcharhinus leucas*) utilize rivers adjoining estuaries as nursery habitats (Heupel *et al.* 2010, Matich *et al.* in press, Thorson 1971, Tillett *et al.* 2012). Spatially, the environmental conditions (e.g., salinity, dissolved oxygen, and water temperature) in these heterogeneous ecosystems are dictated by many factors, including the magnitude of freshwater inflow, local precipitation, bathymetry, latitude, tidal cycles, and the degree of hydrological connectivity to the adjoining ocean (Hughes *et al.* 1998). Temporally, these conditions can be highly variable, as seasonal pulsing events of freshwater inflows and large-scale storm events can dramatically influence water quality throughout an estuary (Lotze *et al.* 2006, Wetz & Yoskowitz 2013). For example, after Hurricane Fran hit North Carolina in 1996, significant amounts of freshwater and organic matter were deposited in the estuary, causing drastic reductions in salinity and anoxic conditions linked to the increased nutrient availability which persisted for almost a month (Mallin *et al.* 1999). This unique hydrology of estuarine systems, coupled with high levels of productivity, results in estuaries providing important habitat that can support a diversity of fish and aquatic invertebrate species which are often important food resources for shark populations (Beck *et al.* 2001).

Shark Nursery Habitat in Texas

The Texas coast is characterized by a series of brackish bays limited in connectivity to each other, and separated from the Gulf of Mexico by barrier islands. These bays are known to support juveniles of several shark species, with bull sharks as the most abundant species across the coastline (Heuter & Taminski 2007, Plumlee *et al.* 2018). Bull sharks are unique among shark species in their ability to tolerate freshwater for extended periods of time by physiologically-mediated osmoregulation (Pillans *et al.* 2005). These sharks still maintain plasma urea levels above those of the environment while in freshwater, although overall urea, Na^+ and Cl^- concentrations are decreased resulting in lower osmotic pressures than those of sharks living in higher salinities (Pillans *et al.* 2004, Larsen *et al.* 2011). Salt absorption occurs through mitochondrial-rich cells in the gills, and salt is also reabsorbed in the kidneys and rectal gland, with excess water excreted as urine (Larsen *et al.* 2011, Reilly *et al.* 2011). This physiological ability provides access to additional habitats not available to other shark species, including rivers and brackish backwaters of estuaries, enabling bull sharks to reach abundant levels in the Gulf of Mexico (Heupel & Simpfendorfer 2008). However, little is known about freshwater habitat use in juvenile bull sharks along the Texas coast (Matich *et al.* 2017).

In Texas, San Antonio Bay and Matagorda Bay have each been identified as bull shark nurseries at an ecosystem level, and Sabine Lake and Galveston Bay are hypothesized to serve this function more recently in the early 2000's (Figure 1) (Heupel *et al.* 2007, Froeschke *et al.* 2010). However, ecosystems are rarely homogenous, and particular areas within these systems may play a more critical role in providing the refuge habitat characteristic of nurseries than others, as suggested by the higher than expected densities of young-of-the-year (YOY) bull sharks found near river mouths in Sabine Lake, Matagorda Bay, and Galveston Bay (Matich *et al.* in review).

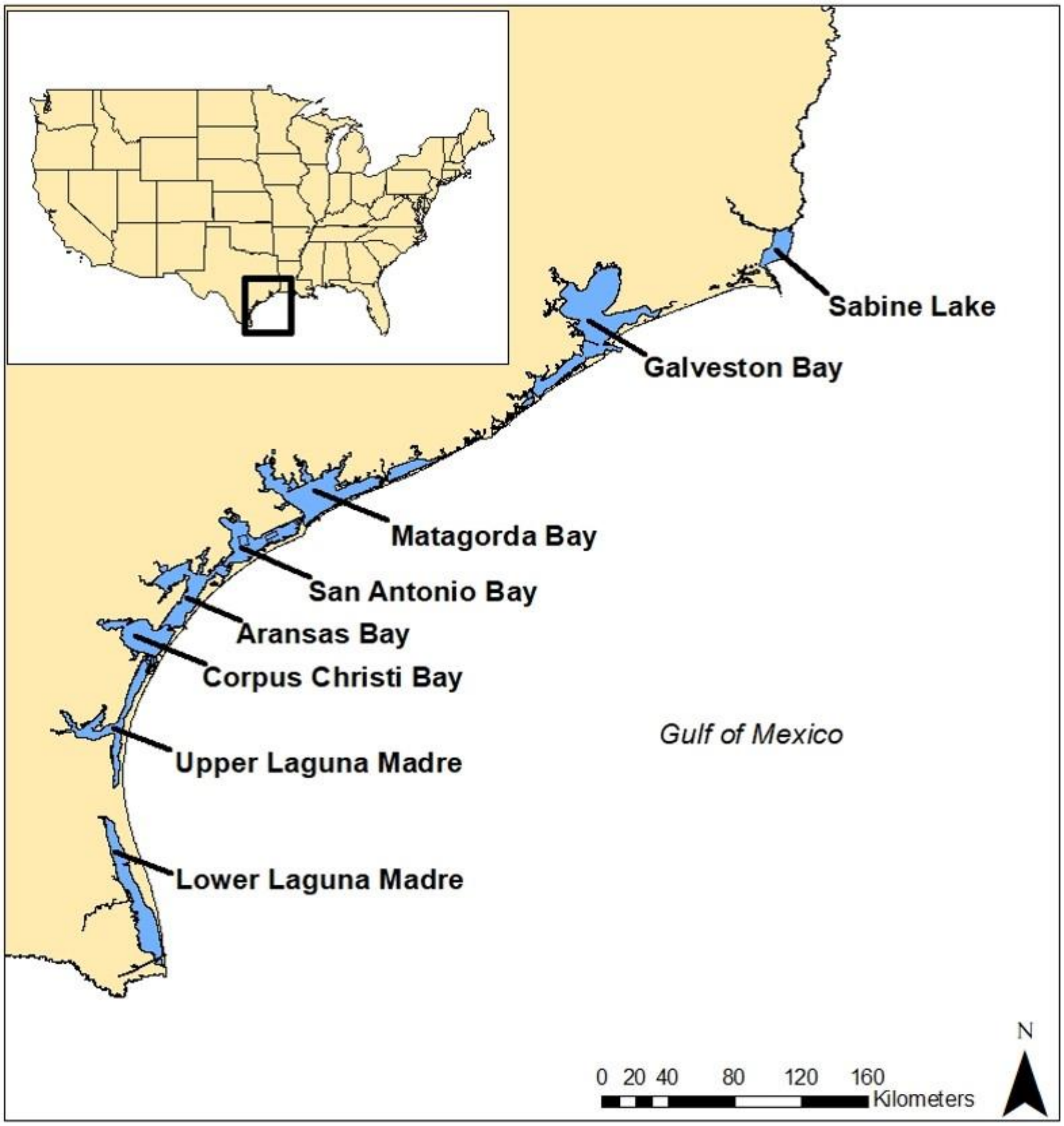

Figure 1. The Texas coast consists of a series of bays, limited in connectivity to each other and separated from the Gulf of Mexico by large barrier islands.

Young-of-the-year (YOY) bull sharks are less than one year of age, and are generally less than ninety centimeters in total length (Brantsetter & Stiles 1987, Froeschke *et al.* 2010). They are the most vulnerable age class due to their small size, lack of experience finding and capturing prey, and lack of experience evading predators (Grubb 2010, Heithaus 2007). Along the Texas coast, little is known about YOY bull sharks, as catch rates of these individuals are lower than expected in several bays (Matich *et al.* in review). This presents an important knowledge gap necessary for understanding the factors driving the behavior and life history of this abundant shark species within native nurseries.

Predation risk is known to influence habitat use patterns of organisms, including juvenile sharks (Heithaus 2007, Valeix *et al.* 2009, Guttridge *et al.* 2012). Shark nursery habitats are typically characterized by lower predation risk, allowing juvenile sharks to grow and develop with lower risk of mortality (Heithaus 2007). Based on bite width-total length relationships, large sharks greater than 1.5 meters in total length including bull sharks, spinner sharks (*Carcharhinus brevipinna*), and blacktip sharks (*Carcharhinus limbatus*) pose the greatest threat to YOY bull sharks in Texas estuaries (Plumlee *et al.* 2018), as intraguild and intraspecific predation are known to occur among shark species (Clua *et al.* 2014, Lowry *et al.* 2009, Matich *et al.* 2015). However, this risk is unlikely spatially homogenous, leading to some habitats providing more refuge than others for YOY bull sharks. It's likely that most predatory sharks, excluding bull sharks, are physiologically restricted to marine microhabitats within estuaries typically found adjacent to the Gulf of Mexico (Hammerschlag 2006). Salinities in Texas estuaries are directly linked to freshwater inflows and tidal inputs (Powell 1976, Powell *et al.* 2002). Therefore, it is likely that predation risk in these systems is correlated with proximity to saltwater tidal inlets; however, data are currently unavailable to test this hypothesis. YOY bull sharks disproportionately use river mouths in some estuaries; but is unclear if reduced predation risk is the driving factor, as opposed to food availability or favorable environmental conditions (Matich *et al.* in review).

Along the Texas coast, individual bays have been labeled as bull shark nursery habitat, but it has not been examined whether certain habitats within each bay, such as rivers and river mouths, support higher densities of YOY bull sharks, and if so, why certain habitats are used more frequently than others.

Study Sites

The two estuaries I conducted research in are San Antonio Bay and Sabine Lake (Figure 1). Sabine Lake is the northernmost bay along the Texas coast and is characterized by brackish, low-salinity waters (Powell 1976, Powell *et al.* 2002).This system is mid-sized (364.2 km^2) and typically has cooler water temperatures and lower dissolved oxygen concentrations than bays found at lower latitudes (Froeshke et al. 2010b). Sabine Lake is connected to the Gulf of Mexico through Sabine Pass, an 8km tidal pass in the south of the estuary. San Antonio Bay is a large (531 km^2), mid-latitude bay along the Texas coast characterized by moderate salinities. Temperature in this system is generally warmer, and dissolved oxygen concentrations are higher than in Sabine Lake (Froeshke *et al.* 2010b). The main connection to the Gulf of Mexico for San Antonio Bay is through Pass Cavallo at the southern end of Matagorda Bay, or through Cedar Bayou between San Antonio Bay and Aransas Bay.

Across both systems, bull sharks are the most abundant shark species captured, but San Antonio Bay has a higher catch per unit effort (CPUE) of bull sharks (Plumlee *et al.* 2018). Sharks of other species occur in Sabine Lake at very low frequencies, while San Antonio Bay supports higher numbers other species, including Blacktip sharks

(*Carcharhinus limbatus*), Spinner sharks (*Carcharhinus brevipinna*), Finetooth sharks (*Carcharhinus isodon),* Atlantic sharpnose sharks (Rhizoprionodon terraenovae), and Bonnetheads (*Sphyrna tiburo*) (Plumlee *et al.* 2018). YOY bull shark capture frequencies within rivers mouths occur at expected frequencies in San Antonio Bay, but are higher than expected in Sabine Lake (Matich *et al.* in review).

Herein, I present a project examining the extrinsic factors influencing YOY bull shark densities along the Texas Gulf Coast in San Antonio Bay and Sabine Lake. Below are the research questions used to guide my data collection:

Research Questions

Question #1: What environmental conditions (e.g., salinity, temperature, depth, dissolved oxygen) influence the densities of large, predatory sharks within two Texas estuaries, Sabine Lake and San Antonio Bay?

Question #2: What are the effects of predation risk and environmental conditions (salinity, temperature, depth, dissolved oxygen) on densities of YOY bull sharks within these two Texas estuaries?

Objectives and Hypotheses

My thesis was split into two research components: 1) a combination of field sampling and the use of a historical dataset to determine the distribution and densities of predatory sharks within San Antonio Bay and Sabine Lake, and the environmental conditions influencing occurrence patterns of these larger sharks; and 2) use of a historical gillnet dataset to examine how predation risk and abiotic factors, such as salinity, influence the densities of YOY bull sharks in these same estuaries.

Environmental conditions influencing the distribution of large, predatory sharks

The main objective of this project component was to understand the gradients of predatory shark occurrence throughout San Antonio Bay and Sabine Lake to generate estimates of predation risk. Little is known about large, predatory sharks along the Texas coast, as most sampling has targeted juvenile individuals with equipment that is inefficient at capturing larger sharks. In my research, I examined whether salinity, depth, dissolved oxygen, temperature, and location within the bay directly affected the distribution of large, predatory sharks that could pose a threat to young-of-the-year bull sharks.

I hypothesized that:

1) Predation risk will be positively correlated with salinity and depth; as larger sharks are limited to areas of greater depth, and can only enter a bay through access points leading to the Gulf of Mexico. Shark species other than bull sharks also have less of a range of salinity tolerances, and will likely be found in areas with higher salinities near access points to the Gulf of Mexico.

Abiotic and biotic factors influencing the occurrence and density of YOY bull sharks

The main objectives of this project component was to examine how predation risk and environmental conditions influenced densities of young-of-the-year bull sharks. I examined abiotic factors, including salinity, dissolved oxygen, depth, and water temperature, and also predation risk.

I hypothesized that:

1) YOY bull sharks will use lower salinity habitats to escape higher predator occurrence in the bays. Freshwater will exclude potential

predatory sharks besides bull sharks, and rivers in each bay are distant from the Gulf of Mexico.

2) YOY bull sharks will be caught at higher densities in habitat areas with lower predicted predation risk, as juvenile sharks will preferentially select habitats to decrease their encounter rates with predatory sharks.

CHAPTER II

Influence of Predation Risk and Environmental Conditions on Densities of Young-of-the-Year (YOY) Bull Sharks in Two Texas Estuaries

Introduction

Juvenile organisms, especially during their first year of life, experience the greatest survival challenges of any age class due to the risk of predation, competition with other species and conspecifics, and the challenge of finding habitats that provide food and safety (Metcalfe *et al.* 1987, Beck *et al.* 2001, Grubb 2010, Heupel *et al.* 2011). Typically, nursery habitats are characterized by lower predation risk than surrounding habitats, high densities of juvenile individuals, and fast growth rates of juvenile animals (Beck *et al.* 2001, Heithaus 2007). As such, nursery areas often provide a greater contribution to the adult population of a species than other habitats on a per area basis, which was proposed as the first widely accepted fish nursery habitat criteria (Beck *et al.* 2001). Globally, coastal areas and estuaries are recognized for providing critical nursery habitat for many marine fish species due to their protective functions and high productivity, with juveniles migrating to estuaries, growing and accumulating biomass, and transitioning back to utilizing marine habitats as adults (Beck *et al.* 2001).

Estuaries are known to provide nursery habitat for elasmobranchs worldwide, but many critical habitat areas have yet to be identified (Conrath & Musick 2010, Heupel & Simpfendorfer 2011, Heupel *et al.* 2018, Martins *et al.* 2018). Threats from overfishing, habitat loss, and other anthropogenic influences have caused declines in shark populations around the globe, and identifying critical nursery habitats has become increasingly important, as protecting shark populations requires conserving habitats that are critical for the recruitment of juveniles into adult populations (Dulvy *et al.* 2017, Roff *et al.* 2018). Prior to 2007, many habitats were labeled as shark nurseries based solely on the presence or record of juvenile sharks inhabiting an area, without investigations into their densities, habitat use, or whether these patterns stayed consistent through time (Heupel *et al.* 2007).

In recent years, knowledge on shark nursery habitats has greatly increased, and we now have a greater understanding of how environmental conditions and large-scale ecosystem changes can impact juvenile sharks within these habitats. Rising estuarine temperatures in Pamlico Sound, North Carolina have been correlated with increasing use of the estuary as nursery habitat by juvenile bull sharks. This represents a range expansion for the species in the Atlantic, as bull sharks were previously not found in this system, and provides evidence that these sharks might be able to adjust to rising sea surface temperatures by shifting to habitats found at higher latitudes (Bangley *et al.* 2018). Increasing coastal development near shark nurseries in Bimini, Bahamas, is correlated with a decrease in the survival rate of juvenile lemon sharks (*Negaprion brevirostris*) compared to juveniles of the same species in areas with little to no anthropogenic impacts (Jennings et al. 2008).

Shark nurseries are typically found in shallow, energy-rich coastal areas, such as estuaries and mangrove forests (Bass 1978). Shallow depths characteristic of these nursery habitats can exclude larger predatory sharks, which are the main predators of juvenile elasmobranchs, likely decreasing predation risk in shark nurseries (Stump *et al.* 2017, Hollensead *et al.* 2018). In Bimini, Bahamas, juvenile lemon sharks (*Negaprion brevirostris*) preferentially use mangrove lined habitats to decrease exposure to larger conspecifics (Guttridge *et al.* 2012, Stump *et al.* 2017). Dorso-ventrally flattened smalltooth sawfish (*Pristis pectinata*) in the Everglades also showed risk-averse behavior, and selected shallow habitats close to shore, likely to escape the occurrence of larger predators within deeper areas (Hollensead *et al.* 2018).

Most juvenile shark species are restricted to marine microhabitats within estuaries, but around the world, bull sharks (*Carcharhinus leucas*) utilize rivers adjoining estuaries as nursery habitats (Heupel *et al.* 2010, Matich *et al*. in review, Thorson 1971, Tillett *et al.* 2012). Bull sharks are unique among shark species in their ability to tolerate freshwater for extended periods of time through physiologically-mediated osmoregulation (Pillans *et al.* 2005). These sharks still maintain plasma urea levels above those of the environment while in freshwater, although overall urea, Na^+ and Cl^- concentrations are decreased resulting in lower osmotic pressures than those of sharks living in higher salinities (Pillans *et al.* 2004, Larsen *et al.* 2011). Salt absorption occurs through mitochondrial-rich cells in the gills, and salt is also reabsorbed in the kidneys and rectal gland, with excess water excreted as urine (Larsen *et al.* 2011, Reilly *et al.* 2011). This provides access to additional habitats not available to other shark species, including rivers and brackish backwaters of estuaries, enabling bull sharks to reach abundant levels in estuaries adjoining the Gulf of Mexico (Heupel & Simpfendorfer 2008, Froeschke *et al.* 2010a, Plumlee *et al.* 2018). Estuaries provide a low mortality environment for bull sharks, with as many as 77% of individuals in a Florida nursery surviving past 18 months of age (Heupel & Simpfendorfer 2011). Other juvenile shark species that are restricted to marine microhabitats within nurseries, such as lemon sharks (*N. brevirostris*), have lower annual survival estimates of between 38% and 65% of individuals (Gruber et al. 2001).

Within estuaries, bull sharks undergo ontogenetic habitat shifts, with YOY and juvenile sharks utilizing brackish and freshwater habitats that provide refuge and adequate food resources, and switching to more productive marine microhabitats within estuaries, and eventually completely marine habitats, as they age and increase in size. Although they are known to use freshwater and brackish habitats as juveniles, little is known about riverine habitat use by juvenile bull sharks along the Texas coast (Matich *et al.* 2017).

The Texas coast is characterized by a series of bays limited in connectivity to each other, and separated from the Gulf of Mexico by barrier islands (Figure 2). These bays are known to support juveniles of several shark species, with bull sharks as the most abundant species across the coastline (Heuter & Taminski 2007, Plumlee *et al.* 2018). In Texas, San Antonio Bay and Matagorda Bay have each been identified as bull shark nurseries at the bay-ecosystem level, and Sabine Lake and Galveston Bay are hypothesized to serve this function more recently in the early 2000's (Froeschke *et al.* 2010a). However, ecosystems are rarely homogenous, and particular areas within these systems may play a more critical role in providing the refuge habitat characteristic of nurseries than others.

Young-of-the-year (YOY) bull sharks are less than one year of age, and are generally less than ninety centimeters in total length (Brantsetter & Stiles 1987, Froeschke *et al.* 2010a). Along the Texas coast, little is known about YOY bull sharks, as catch rates of these individuals are much lower than other juvenile size classes. This presents an important knowledge gap necessary for understanding the factors driving the behavior and life history of this abundant top predator within its native nurseries along the Texas coast, which supports some of the highest densities of bull sharks in the western Atlantic and Gulf of Mexico (Matich *et al.* 2017).

Predation risk is known to influence habitat use patterns of organisms, including juvenile sharks (Heithaus 2007, Valeix *et al.* 2009). Based on bite width-total length relationships, large sharks greater than 1.5 meters in total length including bull sharks, spinner sharks (*Carcharhinus brevipinna*), and blacktip sharks (*Carcharhinus limbatus*) pose the greatest threat to juvenile bull sharks in Texas estuaries, as intraguild and intraspecific predation are known to occur among shark species (Clua *et al.* 2014, Lowry *et al.* 2009, Matich *et al.* 2015, Plumlee *et al.* 2018). Other species besides bull sharks are restricted to higher salinity areas typically found adjacent to the Gulf of Mexico, and larger bull sharks tend to utilize marine microhabitats within estuaries (Froeschke *et al.* 2010b, Matich *et al.* 2015). Salinities in Texas estuaries are directly linked to freshwater inflows and tidal inputs (Powell 1976, Powell *et al.* 2002). Therefore, it is likely that predation risk in these systems is correlated with salinity, with the highest risk found in close proximity to saltwater tidal inlets; however, no studies have confirmed this. YOY bull sharks disproportionately use river mouths in some estuaries; but is unclear if reduced predation risk is the driving factor, as opposed to food availability or favorable environmental conditions (Matich *et al.* in review)

Along the Texas coast, individual bays have been labeled as bull shark nursery habitat, but it has not been examined whether habitats characterized by certain environmental conditions, such as low salinity river mouths, support higher densities of YOY bull sharks, and if so, why these habitats are used more frequently than others. The goal of this study was to examine the influence of predation risk and environmental conditions on YOY bull shark densities along the Texas Gulf Coast in San Antonio Bay and Sabine Lake.

Methods

Study sites

Data collection for this study occurred in San Antonio Bay (28.3540° N, 96.7601° W; Figure 2) and Sabine Lake (29.8951° N, 93.8452° W; Figure 2) along the Texas coast. Sabine Lake is the northernmost bay along the Texas coast and is characterized by brackish, low-salinity waters (Froeschke *et al.* 2010b). This system is mid-sized (364.2 km^2) and typically has cooler water temperatures and lower dissolved oxygen concentrations than bays found at lower latitudes (Froeschke *et al.* 2010b). Sabine Lake is connected to the Gulf of Mexico through Sabine Pass, an 8km tidal pass in the south of the estuary. San Antonio Bay is a large (531 km^2), mid-latitude bay along the Texas coast characterized by moderate salinities. Temperature in this system is generally warmer, and dissolved oxygen concentrations are higher than in Sabine Lake (Froeschke *et al.* 2010b). The main connection to the Gulf of Mexico for San Antonio Bay is through Pass Cavallo at the southern end of Matagorda Bay, or through Cedar Bayou between San Antonio Bay and Aransas Bay.

Across both systems, bull sharks are the most abundant shark species captured, but San Antonio Bay has higher catch per unit effort (CPUE) of bull sharks (Plumlee *et al.* 2018). Sharks of other species occur in Sabine Lake at very low frequencies, while San Antonio Bay supports higher numbers other species, including Blacktip sharks (*Carcharhinus limbatus*), Spinner sharks (*Carcharhinus brevipinna*), Finetooth sharks (*Carcharhinus isodon),* Atlantic sharpnose sharks (Rhizoprionodon terraenovae), and

Bonnetheads (*Sphyrna tiburo*) (Plumlee *et al.* 2018). YOY bull shark capture frequencies within rivers mouths occur at expected frequencies in San Antonio Bay, but are higher than expected in Sabine Lake (Matich *et al.* in review).

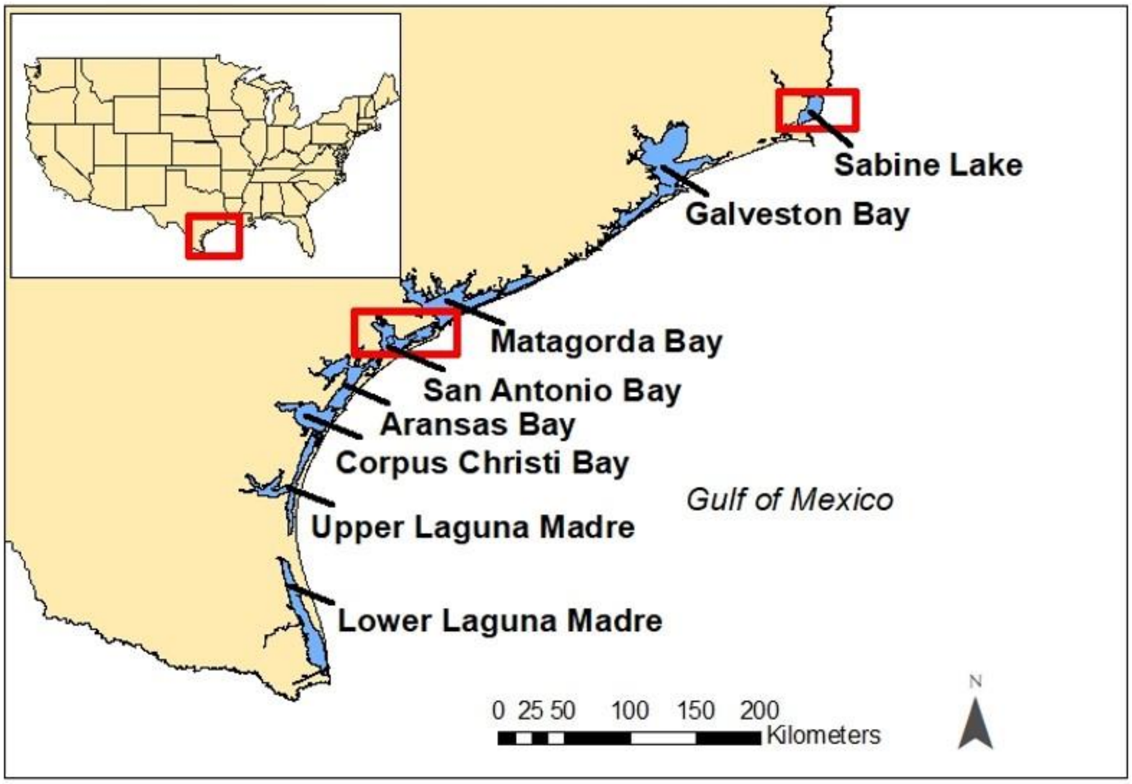

Figure 2. Map of the bays along the Texas coast. Sabine Lake and San Antonio Bay were the focus of this study, and are denoted by red boxes.

Data collection

To evaluate the densities of YOY bull sharks in San Antonio Bay and Sabine Lake, and examine how predation risk and environmental conditions influence these densities, the following approaches were used: 1) In-situ drumline sampling was conducted across each estuary to sample for larger, predatory sharks; 2) Select years of Texas Parks and Wildlife (TPWD) fisheries-independent gill net data, which began in

1985 and continued sampling through September 2018, were used to determine densities of YOY sharks; and 3) TPWD gill-net data was also used to look at historical patterns of predation risk based on the rare catches of large, predatory sharks during the same 34-year period.

Drumline Sampling

To evaluate relative risk present across salinity, depth, and environmental gradients presented by larger, predatory sharks (>150 cm total length) in each ecosystem, baited drumlines were used (Figure 3). Four 2.5 km x 2.5 km sites were selected in both San Antonio Bay and Sabine Lake (Figure 4).

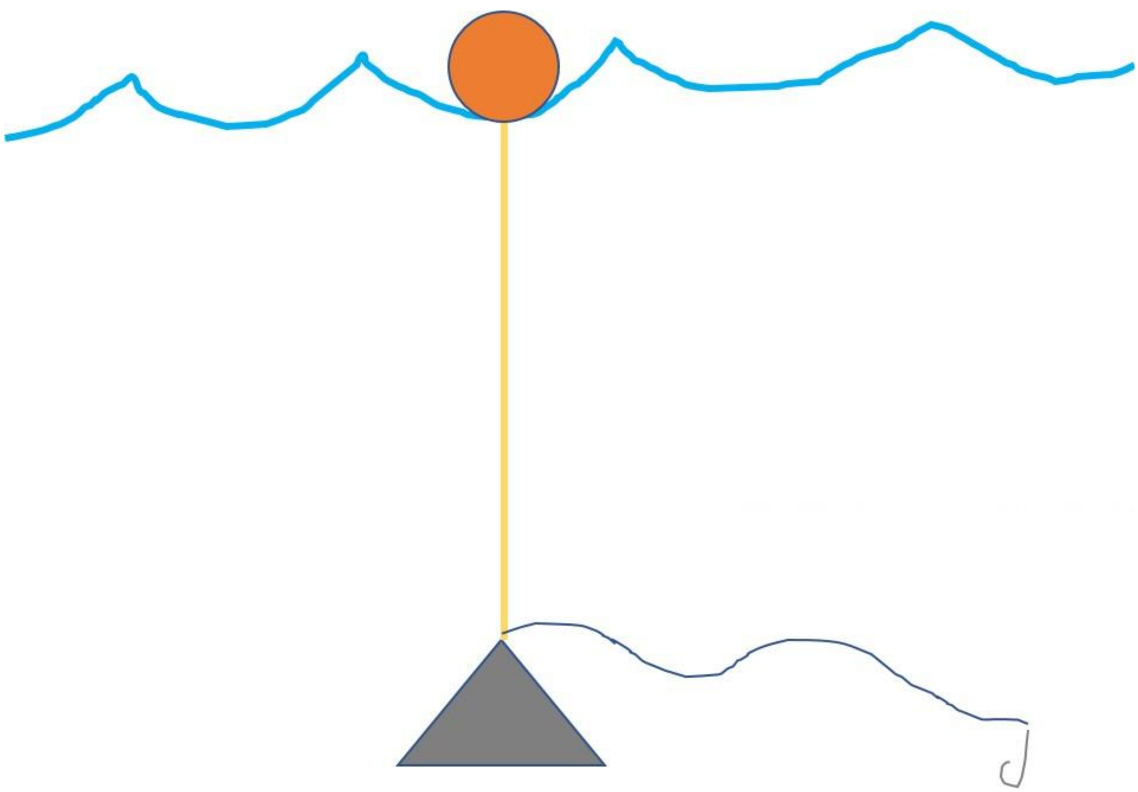

Figure 3. Drumlines were anchored to a cement weight, with an attached 10-15m of 400 kg monofilament line ending in a baited hook.

Drumlines were anchored to a cement weight, with an attached 10-15m of 400 kg monofilament line ending in either a 15/0 or 16/0 circle hook (Figure 3). Hooks were baited with either mullet (*Mugil cephalus*), bonito (*Sarda sarda*), red drum (*Sciaenops ocellatus*), trevally jack (*Caranx hippos*), spotted seatrout (*Cynoscion nebulosus*), atlantic croaker (*Micropogonias undulatus*), or ladyfish (*Elops saurus*). This sampling method targets larger sharks greater than 150 cm total length known to prey upon smaller elasmobranchs (Matich *et al.* 2015). Within each sampling site, six drumlines were set 400 m apart to minimize interference between bait at separate drumlines, and each drumline was considered an independent sampling event (Figure 4). Sampling occurred from May-September and each sampling day focused on a single site, with the goal of spending one full day of sampling per month at each site. Hooks were allowed to soak for one hour in between drumline checks, and bait was replaced after each round of checks. A full day of sampling consisted of 6-8 hook hours per drumline. When sharks were captured, they were brought alongside the sampling boat, identified to the species level, tagged with number ID tags for identification, and precaudal, fork, total, and stretch total length along with gape width and girth were measured. Bull sharks were assigned to size/age classes based on total length measurements (YOY <90 cm total length (TL), Juvenile 90-150 cm TL, Predatory >150 cm TL). Sharks were then released back into the bay and the drumlines were re-baited, and returned to the water to continue sampling. Drumlines without sharks were also rebaited and replaced for further sampling. Environmental conditions (salinity - ppt, temperature - °C, depth - m, dissolved oxygen - mg/L) were recorded at each drumline deployment using a YSI Pro 2030 and a Garmin GPS. Catch per unit effort (CPUE) of predatory (>150 cm) sharks in each region served as an estimate of predator encounter rate, following a similar protocol as Matich & Heithaus (2015).

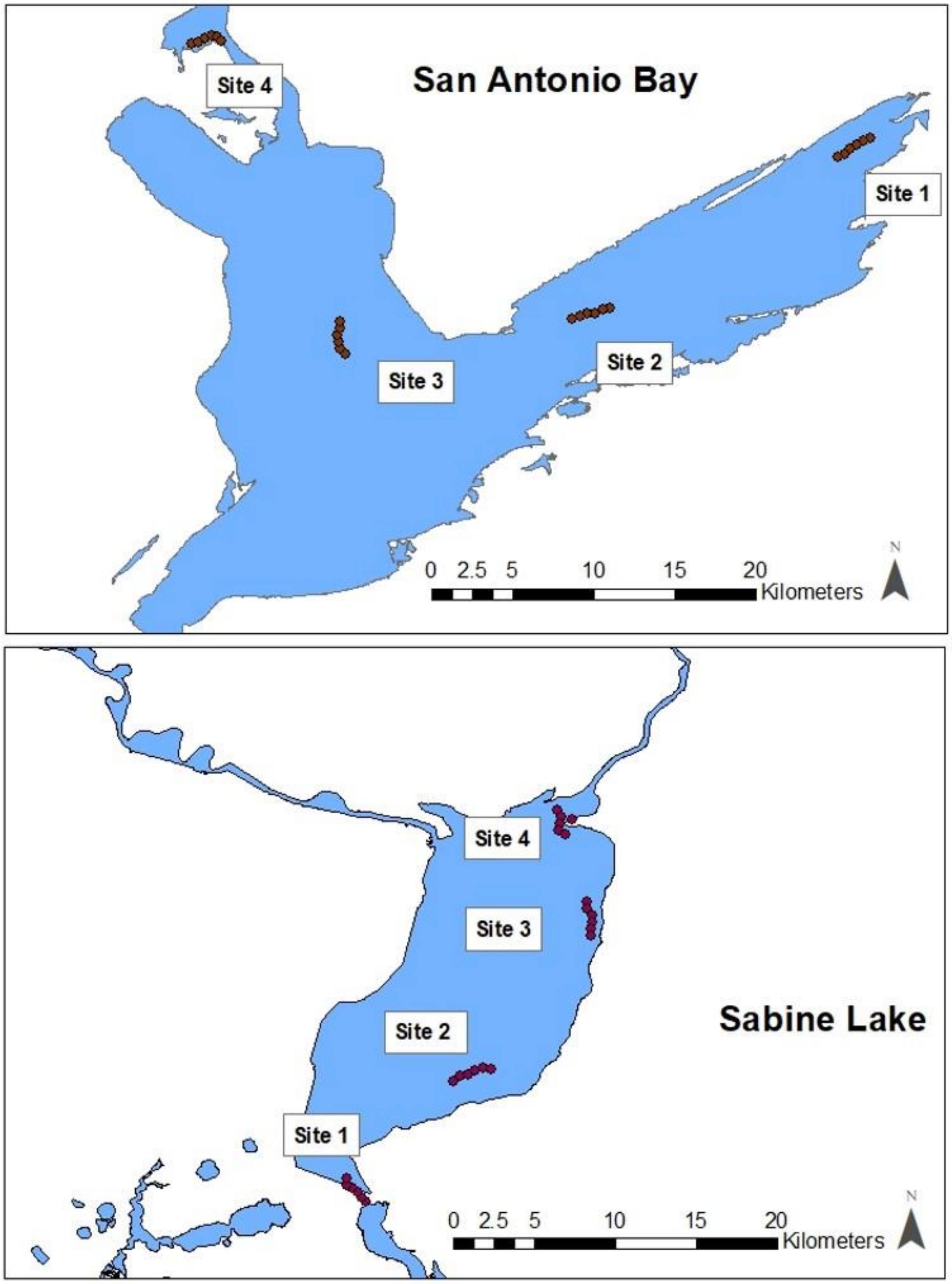

Figure 4. Map of sampling sites within San Antonio Bay and Sabine Lake. Four sampling locations were chosen per bay, and six drumlines, denoted by red circles, were set 400 meters apart within each sampling site.

Historical TPWD Gillnet Sampling

To evaluate densities of YOY bull sharks in these two bays, catch data from long-term, fisheries independent gillnet surveys conducted by Texas Parks and Wildlife Department was used. TPWD has been conducting gillnet surveys in both Sabine Lake and San Antonio Bay since 1985 to monitor fishes in nearshore habitats, and regulate recreational fisheries. This sampling followed a stratified cluster sampling design (Martinez-Andrade *et al.* 2009), with 45 gillnets set in the spring (April-June) and 45 set in the fall (August-November) in random locations. Gillnets were set around an hour before sunset and allowed to soak overnight, and were collected within 4 hours of sunrise (Mean sampling time ± SD = 13.1 ± 1.3 hours). Gillnets consisted of monofilament net (183 m long, 1.2 m deep, with 45.7 m sections of 7.6, 10.2, 12.7, and 15.2 stretched mesh tied together in ascending order) set perpendicular to the shoreline with the smallest mesh size closest to the shore. Data were obtained from gillnets set in San Antonio Bay and Sabine Lake in May, June, and September to align with the months of our 2018 *in-situ* drumline sampling, and only years where the gillnet sampling distribution aligned with the 2018 TPWD gillnet sampling distribution were included in analyses. Any sharks captured were identified to the species level, counted, and total length (from tip of snout to tip of tail in mm) was measured. Data on environmental conditions were recorded at the beginning and end of each sampling event (salinity – psu, depth – m, temperature – °C, and dissolved oxygen – mg/L), along with the date, time, and location of capture. Data on environmental conditions used in any analyses was collected at the offshore end of the gillnets during net retrieval.

The 34-year fisheries independent gillnet dataset from TPWD was also used to look at historical patterns of predation risk in these two bays, and compare them with predation risk estimates generated from our *in-situ* drumline surveys. One caveat to this is that gillnets are inefficient at capturing large sharks >1.5 m TL (Froeschke et al. 2010b). For the purposes of our study, we assumed that gillnets were equally ineffective in all locations at capturing sharks >1.5m, and used the CPUE of large sharks in the gillnets as density estimates for predatory sharks in the area, with the understanding that these are likely underestimates. Only data from predatory sharks caught in May, June, and September were used in order to align with the months of our *in-situ* drumline sampling conducted in 2018, and only years where the gillnet sampling distribution aligned with the 2018 TPWD gillnet sampling distribution were used in analyses.

Data Analysis

Drumline Sampling for Predatory Sharks

Risk was quantified across each estuary using CPUE of predatory sharks (>150 cm TL) as an estimate of predation risk. Since several species of bait fish were utilized during drumline sampling, a chi-square analysis was conducted to make sure bait type was not influencing capture rates of predatory sharks. To account for zero-inflated data, all data were transformed into occurrence (whether or not a shark was captured), concentration (how many sharks were captured if sharks did occur), and catch per unit effort (number of sharks sampled per hook hour). Predation risk estimates were calculated for each ecosystem using ordinary kriging in ArcGIS for spatial interpolation of risk values from known sampling locations to unstudied areas of the bays (Saveleiv et al. 2007, Froeschke et al. 2010b). Since no predatory sharks were sampled on drumlines in Sabine Lake, this was only done for San Antonio Bay. Station codes were determined for each drumline sampling location based on the codes TPWD uses during gillnet sampling, in order to determine whether location within the estuary was important and whether predatory shark captures rates were comparable between gear types (drumline and gillnet). Generalized linear models were conducted in SPSS using ecosystem, month, and station code as fixed factors and salinity, temperature, dissolved oxygen, and depth as random factors. Salinity was chosen as a factor for analyses rather than distance to the Gulf of Mexico because 1) salinity and distance were highly collinear, and 2) this study focused on the environmental conditions driving the distributions of larger sharks within these systems; geographic distance remained static throughout the sampling period, whereas salinity was constantly fluctuating.

Historical TPWD Gillnet Sampling – Predatory Sharks

Generalized linear models were also used to analyze the gillnet dataset from TPWD to examine historical patterns of predation risk across both San Antonio Bay and Sabine Lake. From the full 34 year dataset, years were selected for analysis where the sampling distribution closely matched the TPWD gillnet sampling distribution of 2018, when drumline sampling was also occurring in the bays. A total of 20 years of gillnet data were used for San Antonio Bay, and 24 years of gillnet data were used in analyses for Sabine Lake. Ecosystem, station code, salinity, temperature, dissolved oxygen, and depth were included as factors in the analysis. A spearman rho correlation was performed on predation risk values from the drumline predation risk interpolation risk raster and the TPWD gillnet predation risk raster to determine the correlation between the two maps, and box statistics were also calculated in ArcGIS to determine the correlation matrix between the two raster files. Since no large sharks were sampled on drumlines in Sabine Lake, this was only done for San Antonio Bay.

Historical TPWD Gillnet Sampling - YOY Bull Sharks

To visualize patterns in occurrence, and determine the relationship between YOY bull shark density and predation risk, historical YOY bull shark densities from the TPWD gillnet data were overlaid on the maps of predicted predation risk created for both San Antonio Bay and Sabine Lake in ArcGIS. CPUE (# sharks/hook hour) of YOY bull sharks was calculated for each TPWD gillnet sampling event, and generalized linear models were again used in SPSS to examine the correlation between environmental, spatial, and biotic factors and the CPUE of YOY bull sharks. Predation risk was included as a factor in the analysis, using the extract values to points feature in ArcGIS to extract predation risk raster values to discrete gillnet sampling locations. The predation risk raster which was used to generate these point values was created by giving equal weight to predation risk values from *in-situ* drumline sampling and the historical TPWD gillnet sampling. Temperature, salinity, dissolved oxygen, depth, and station code were also included as factors in the analysis. Only sampling conducted in May, June and September was included to align with the months of *in-situ* drumline sampling, and only data from years where sampling closely aligned with the TPWD gillnet sampling distribution in the summer of 2018 were used.

Results

Drumline Sampling – Predatory Sharks

Drumline sampling during the summer of 2018 resulted in a total of 775 hook hours and 18 sharks captured. Bait type did not have a significant influence on CPUE of predatory sharks based upon results of the chi-square analysis ($\chi^{14}_{1050} = 10.818$, $p = .700$). Bull sharks made up the majority of captures in both bay systems, with one neonate blacktip as the only other species sampled. Most bull sharks captured were in the juvenile age class (90-150cm TL), but 2 of the bull sharks were YOY (<90cm TL), and 4 bull sharks were classified as predatory sharks (>150 cm TL). There was an overall catch per unit effort (CPUE) of predatory sharks across both ecosystems of .0052 sharks/hook hour. In just San Antonio Bay, CPUE of predatory sharks was .0120 sharks/hook hour. Comparatively, the total number of hours of gillnet sampling conducted by TPWD was 20,287 hours with only 11 predatory sharks sampled during that time, which is a CPUE of .0005 sharks/net hour. In just San Antonio Bay, CPUE of predatory sharks in gillnets was .0010 sharks/net hour. Across both gear types, drumline sampling was ten times more effective at sampling predatory sharks than gillnet sampling.

During drumline sampling, all four predatory sharks were sampled in San Antonio Bay, and no predatory sharks were sampled in Sabine Lake. CPUE of predatory sharks was highest at Sites 1 (.0118 sharks/hook hour) and 2 (.0365 sharks/hook hour) in San Antonio Bay (Figure 5). No large sharks were captured at Sites 3 and 4 in San Antonio Bay. Predicted predation risk gradients for San Antonio Bay show that predation risk (CPUE of predatory sharks) is higher near tidal inlets leading to the Gulf of Mexico, and decreases as you move towards freshwater inflows into the system (Figure 5).

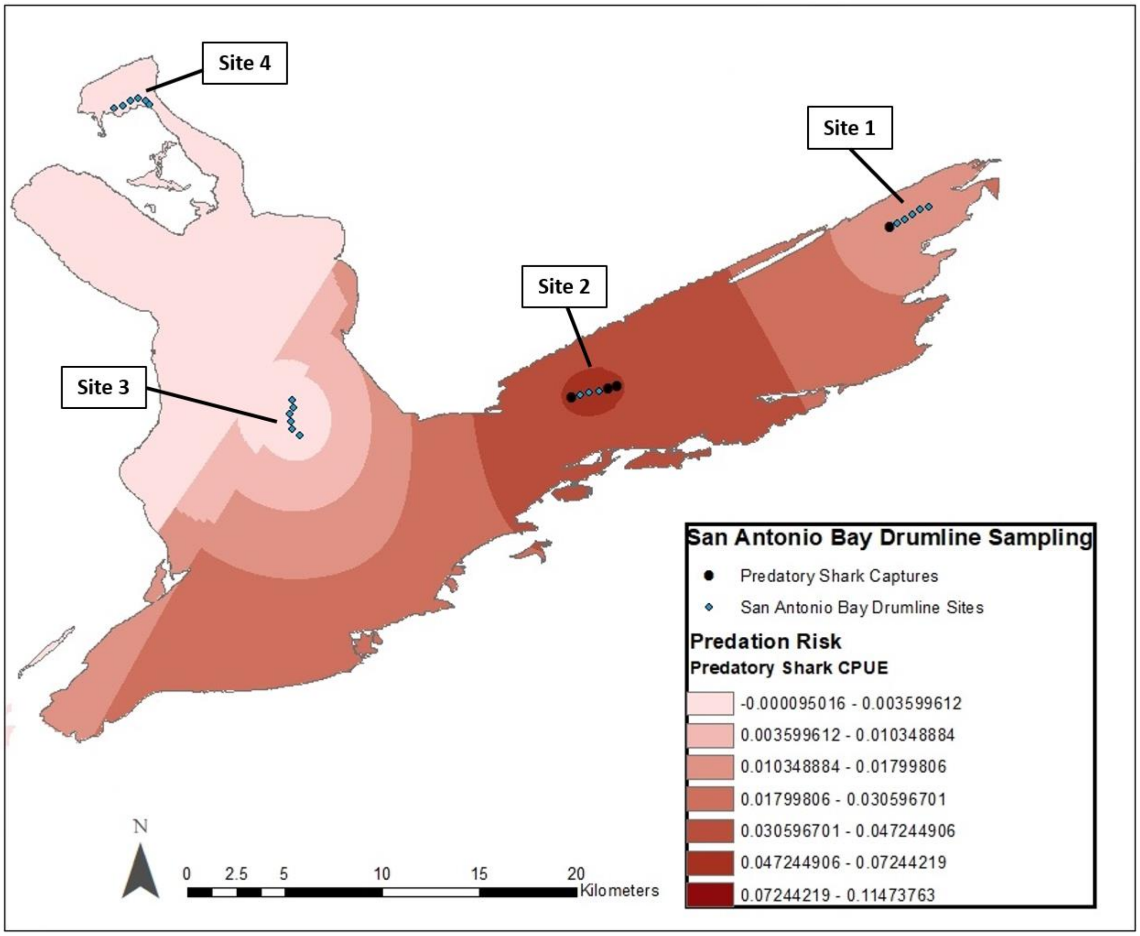

Figure 5. Predicted predation risk gradient generated for San Antonio Bay using ordinary kriging in ArcGIS using data from *in-situ* drumline sampling. Drumline locations are denoted by blue circles, and predatory shark captures are denoted by black circles. Sampling sites 1 and 2 had the highest predicted predation risk.

Station code significantly predicted the occurrence of predatory sharks based on the generalized linear model performed on the drumline data from both ecosystems (χ^{18}_{202} = 29.540, p = .030, η^2=.114; Table 1, Figure 6). Captures of predatory sharks in San Antonio Bay all occurred at Sites 1 and 2 (Figure 4).

Table 1

Environmental Conditions Influencing Predatory Shark Densities

	Temperature	Salinity	Dissolved Oxygen	Depth	Station Code	Month
San Antonio Bay Drumlines	.890 (.000)	.815 (.001)	.638 (.000)	.732 (.000)	**.042*** (.114)	.386 (.016)
San Antonio Bay Gillnets	.538 (.001)	.399 (.002)	.100 (.001)	.064 (.008)	**$1.1x10^{-16}$*** (.663)	**.006*** (.085)
Sabine Lake Gillnets	**.015*** (.005)	.156 (.002)	**.002*** (.012)	.856 (.000)	.898 (.047)	.143 (.001)

P-values for the generalized linear models run on the drumline sampling data and TPWD's gillnet datasets examining the occurrence of predatory sharks in San Antonio Bay and Sabine Lake. Bold numbers with asterisks indicated significant p-values<.05. Effect size measures (partial eta-squared, η^2) for each factor are shown in parentheses.

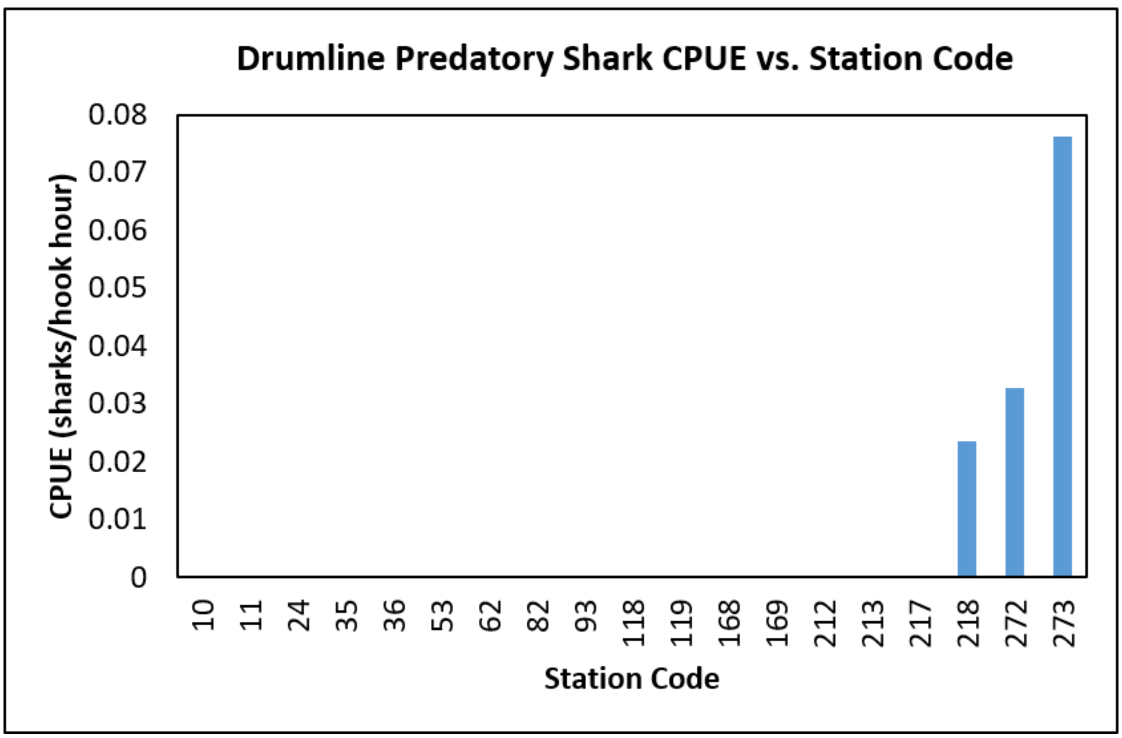

Figure 6. Catch per unit effort (CPUE) of predatory sharks versus station code in San Antonio Bay from *in-situ* drumline sampling.

TPWD Gillnet Sampling – Predatory Sharks

A total of 674 gill-nets were deployed in the years selected for analysis in San Antonio Bay, which were 1985-1986, 1988, 1991, 1995, 1999-2000, 2002-2005, 2007-2008, 2010, 2012-2013, and 2015-2018. Nine predatory sharks were sampled across the ecosystem during this time period. Seven sites had captures of one predatory shark, and 118 sites had no captures of predatory sharks (Figure 7). All predatory sharks sampled in this system were captured at sites nearer to the Gulf of Mexico (Sites 1 and 2, Figure 4), and no large sharks were captured near freshwater inputs (Sites 3 and 4, Figure 4). Predation risk values at gillnet sampling locations from the *in-situ* drumline and TPWD gillnet predation risk gradients in San Antonio Bay were positively correlated (r(99)= .609, p= 2.22 x 10^{-11}), indicating that capture locations of predatory sharks from the gillnet data aligned well with locations where predatory sharks were sampled from *in-situ* drumline sampling. Box statistics on the two predation risk rasters in GIS also indicated a positive correlation (correlation matrix= .6356).

Station Code (χ^{117}_{674}= 289.95, p< .001, η^2=.663) and month (χ^{2}_{674}= 10.148, p=.006, η^2=.085) significantly predicted the occurrence of predatory sharks in San Antonio Bay based upon results from the generalized linear model run on data in this system (Table 1). May had the highest CPUE of large sharks, whereas June had the lowest CPUE of large sharks (Figure 8). Station codes with significant CPUE of large sharks all occurred in the southern region of San Antonio Bay (Figure 7, Figure 8).

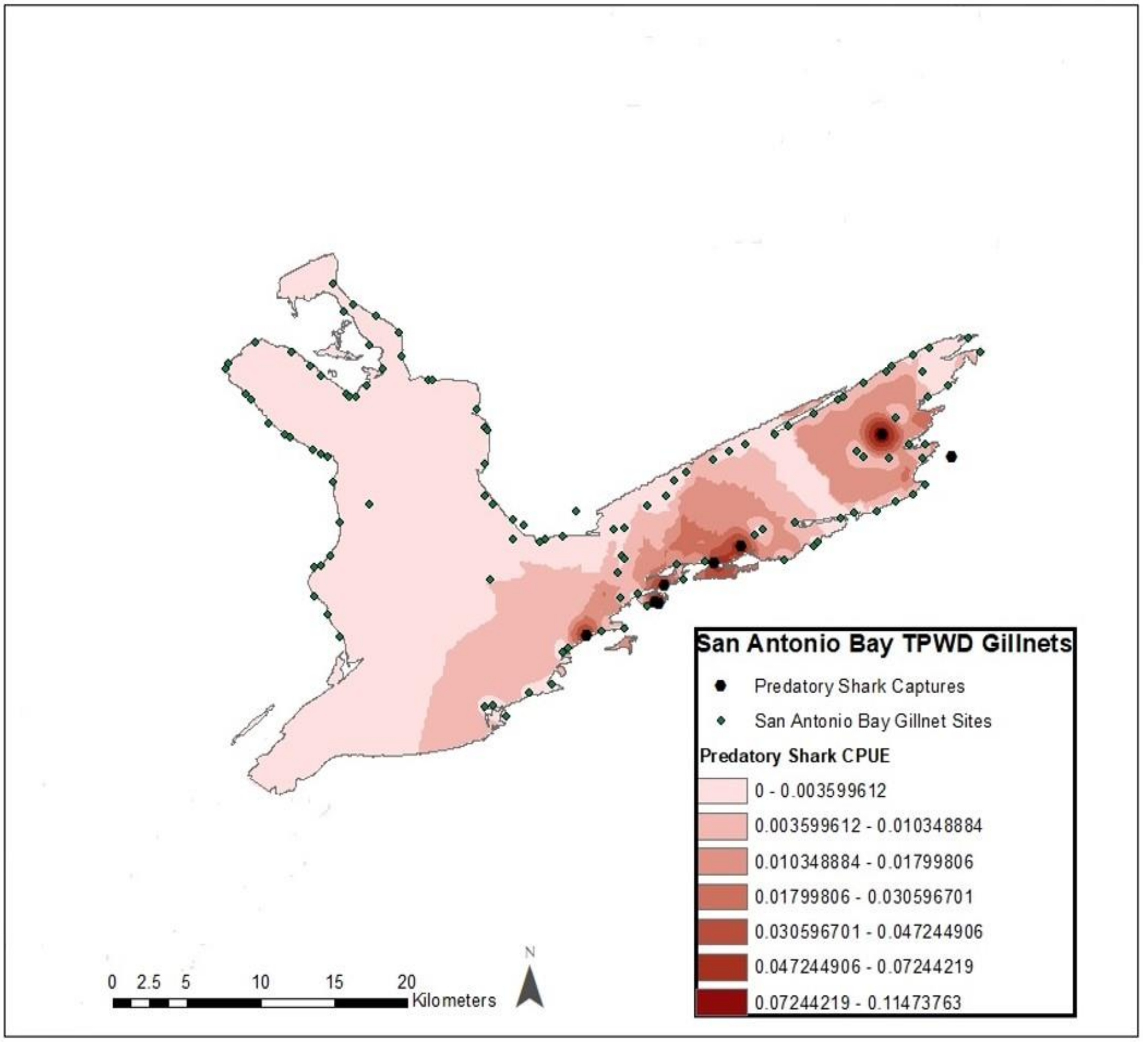

Figure 7. Predicted predation risk gradient generated for San Antonio Bay using ordinary kriging in ArcGIS using data from TPWD's historical gillnet sampling. Captures of predatory sharks are denoted by black circles, and gillnet sampling locations are denoted by green circles. Predation risk was highest in the southern region of San Antonio Bay.

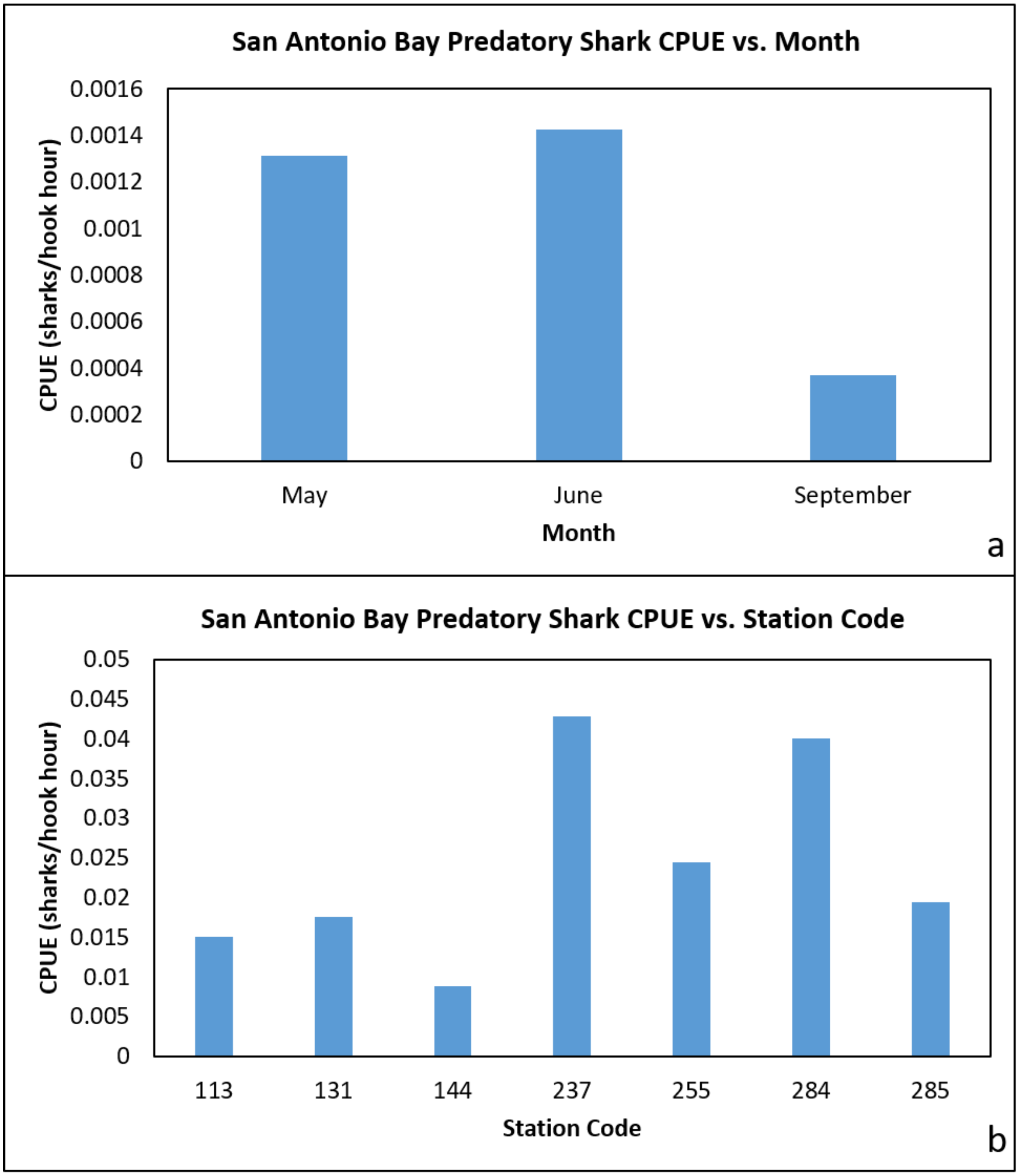

Figure 8. Catch per unit effort (CPUE) of predatory sharks versus a) month and b) station code in San Antonio Bay from TPWD gillnet sampling. May and June had a higher CPUE of predatory sharks than September.

In Sabine Lake, a total of 879 gill-nets were deployed in the years selected for analysis, which were 1989-1990, 1992, 1994-1998, 2000-2004, 2006-2008, 2010, 2012-2018. Only 2 predatory sharks were sampled in the bay, and both captures occurred in the northern reaches of Sabine Lake, one in 2006 and one in 2018. Predation risk estimates for this system show highest risk in the northern reaches of the bay near freshwater inputs, with risk decreasing as you move towards the Gulf of Mexico (Figure 9).

Dissolved oxygen (χ^1_{1879}= 9.271, p=.002, η^2=.012) and temperature (χ^1_{1879}= 5.868, p=.015, η^2=.005) significantly predicted the capture of predatory sharks within Sabine Lake based upon the results of the generalized linear model run on data from this system (Table 1). Larger sharks were captured at temperatures above 31°C, and dissolved oxygen concentrations above 8 mg/L (Figure 10). However, the Sabine Lake model had a non-significant overall omnibus fit score (p=.648), suggesting that it is a poorer overall model at predicting occurrence of large sharks in this system than the San Antonio Bay model.

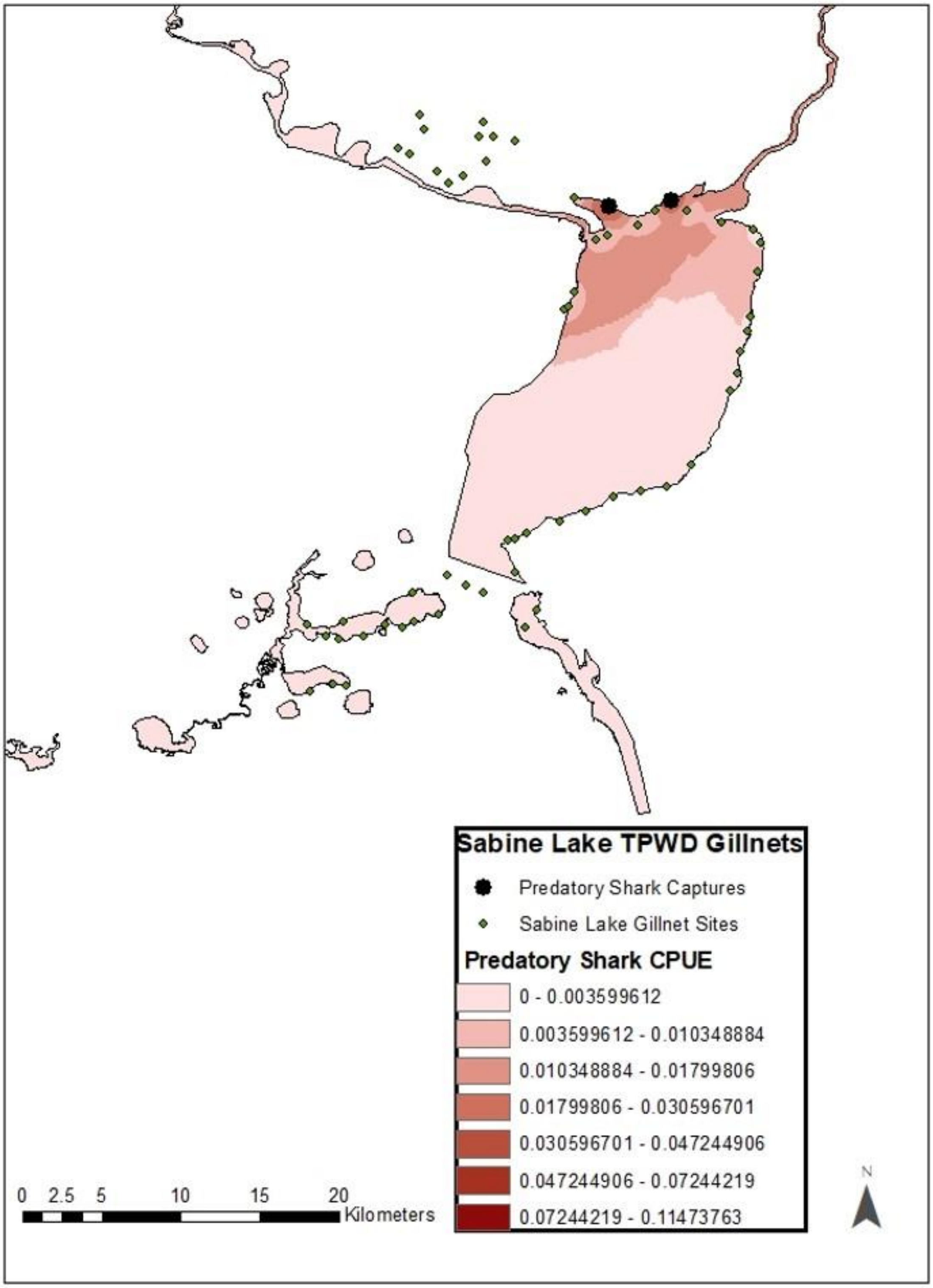

Figure 9. Predicted predation risk gradient generated for Sabine Lake using ordinary kriging in ArcGIS using data from TPWD's historical gillnet sampling. Captures of predatory sharks are denoted by black circles, and gillnet sampling locations are denoted by green circles. Predation risk was highest in the north of the bay.

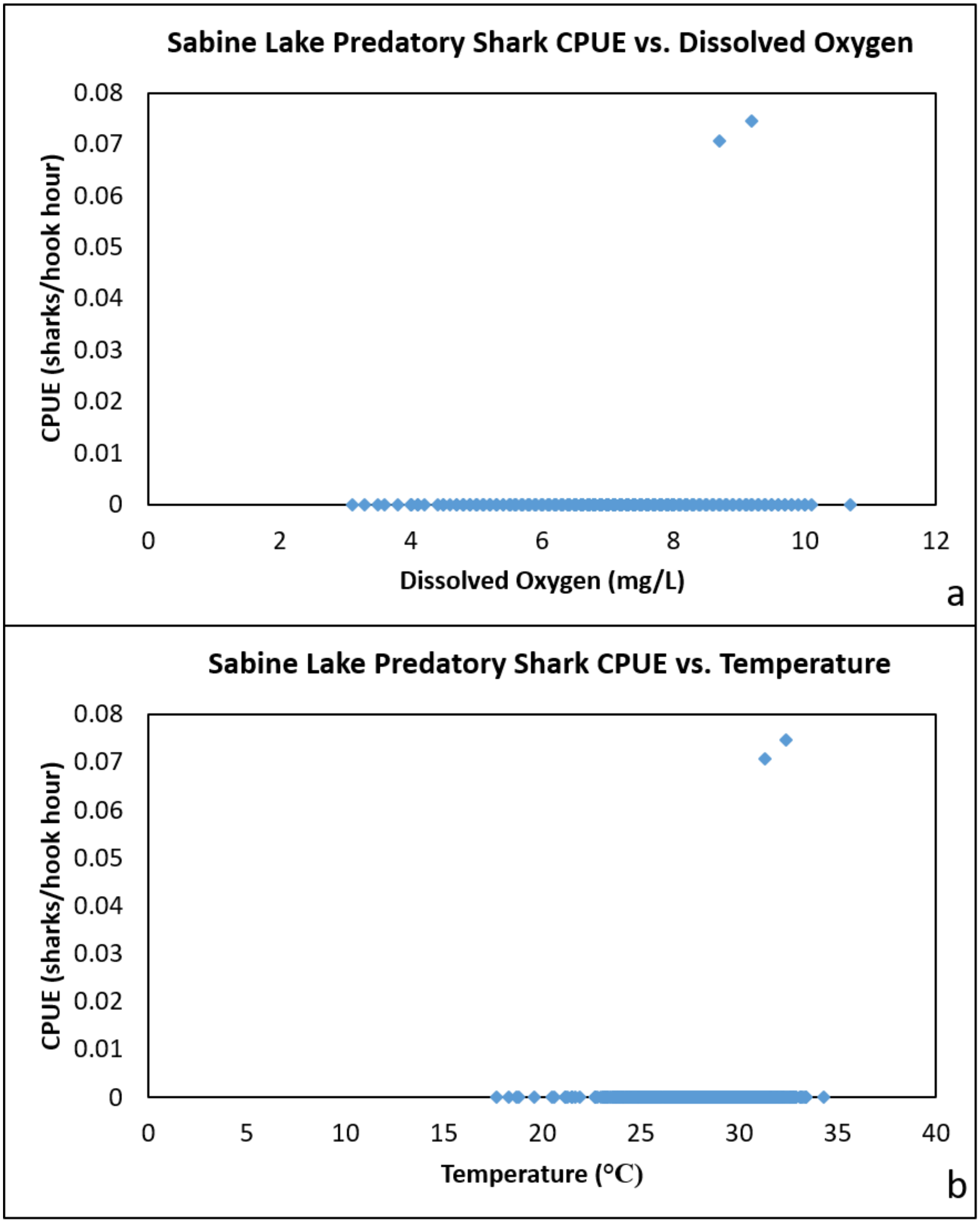

Figure 10. Catch per unit effort (CPUE) of predatory sharks versus environmental conditions of a) dissolved oxygen and b) temperature in Sabine Lake from TPWD gillnet sampling. Predatory sharks were captured at dissolved oxygen concentrations above 8 mg/L, and temperatures above 31°C.

TPWD Gillnet Sampling – YOY Bull Sharks

A total of 200 YOY sharks were sampled throughout the years used for analysis, with 108 caught in San Antonio Bay and 92 caught in Sabine Lake. In San Antonio Bay, temperature (χ^{1}_{676} = 5.002, p= .025, η^2=.006), salinity (χ^{1}_{676} = 5.906, p= .015, η^2=.011), predation risk (χ^{1}_{676} = 6.893, p= .009, η^2=.014), station code (χ^{117}_{676} = 162.458, p= .003, η^2=.336), and month (χ^{3}_{676} = 29.468, p< .001, η^2=.006) were significant predictors of YOY bull shark densities (Table 2, Figure 11). YOY bull sharks in San Antonio Bay were caught at most often in the month of June at moderate-high temperatures, low-moderate salinities, higher dissolved oxygen concentrations, and in areas of low predation risk (Figure 11). In Sabine Lake, temperature (χ^{1}_{880} = 12.547, p< .001, η^2=.012), salinity (χ^{1}_{880} = 7.919, p= .005, η^2=.009), dissolved oxygen (χ^{1}_{880} = 4.591, p= .032, η^2=.006), and station code (χ^{60}_{880} = 94.632, p= .003, η^2=.070) were significant predictors of YOY bull shark densities (Table 2). Overall, YOY bull sharks were caught at temperatures above 29°C and not exceeding 33°C, salinities below 20 ppt, dissolved oxygen concentrations above 6 mg/L, and at stations in the upper reaches of Sabine Lake (Figure 12).

Table 1

Factors Influencing YOY Bull Shark Densities

	Temperature	Salinity	Dissolved Oxygen	Depth	Station Code	Month	Predation Risk
San Antonio Bay	**.025*** (.006)	**.015*** (.011)	.211 (.004)	.768 (.000)	**.003*** (.336)	**.000001*** (.006)	**.009*** (.014)
Sabine Lake	**.0004*** (.012)	**.005*** (.009)	**.032*** (.006)	.108 (.002)	**.003*** (.070)	.123 (.010)	.057 (.004)

Note:.P-values for the generalized linear models run on TPWD's gillnet datasets examining the factors influencing YOY bull shark CPUE in San Antonio Bay and Sabine Lake. Significant p-values are denoted in bold with an asterisk. Effect size measures (partial eta-squared, η^2*) for each factor are shown in parentheses.*

Plots of YOY densities from selected TPWD gillnet sampling years overlaid on predicted predation risk maps generated in ArcGIS revealed different patterns in each system (Figure 13, Figure 14). In Sabine Lake, densities of YOY sharks were highest where predation risk was predicted to be the highest, with up to 8 YOY sharks caught in a single sampling event with high predicted CPUE of predatory sharks (Figure 14). In San Antonio Bay, densities of YOY sharks were highest in the upper reaches where predicted predation risk was lowest, with up to 8 YOY sharks sampled in a single sampling event in areas of no predicted predation risk (Figure 13).

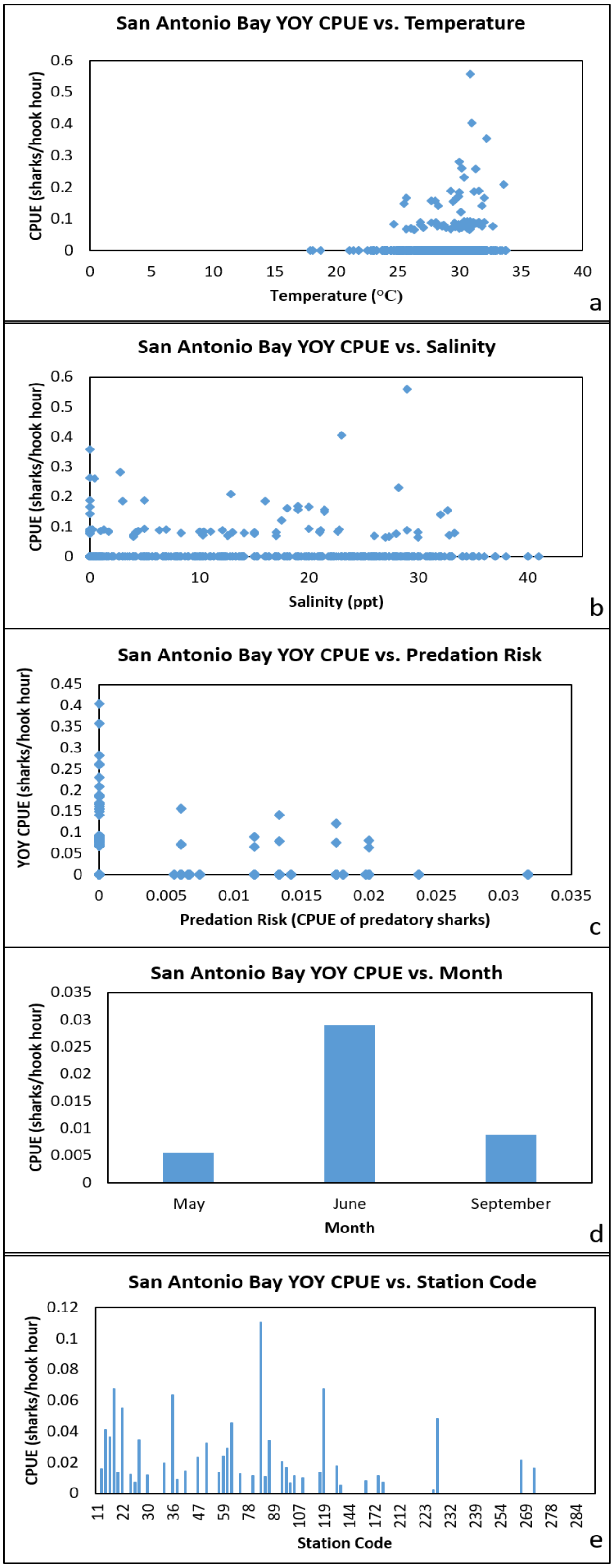

Figure 11. Catch per unit effort (CPUE) of young-of-the-year (YOY) bull sharks versus environmental conditions of a) temperature and b) salinity, c) predation risk, d) month, and e) station code in San Antonio Bay from TPWD gillnet sampling.

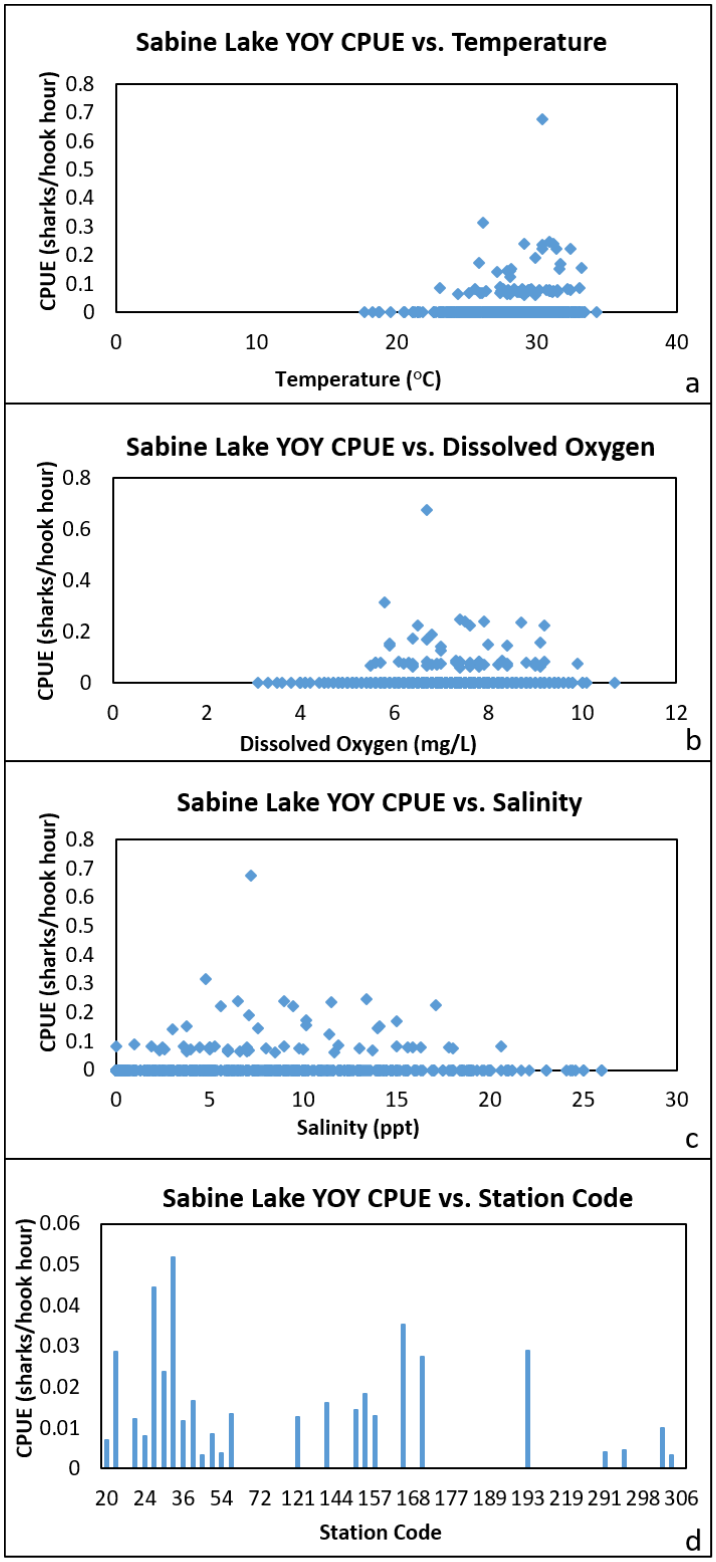

Figure 12. Catch per unit effort (CPUE) of young-of-the-year (YOY) bull sharks versus environmental conditions of a) temperature, b) dissolved oxygen, and c) temperature, and d) predation risk in Sabine Lake from TPWD gillnet sampling.

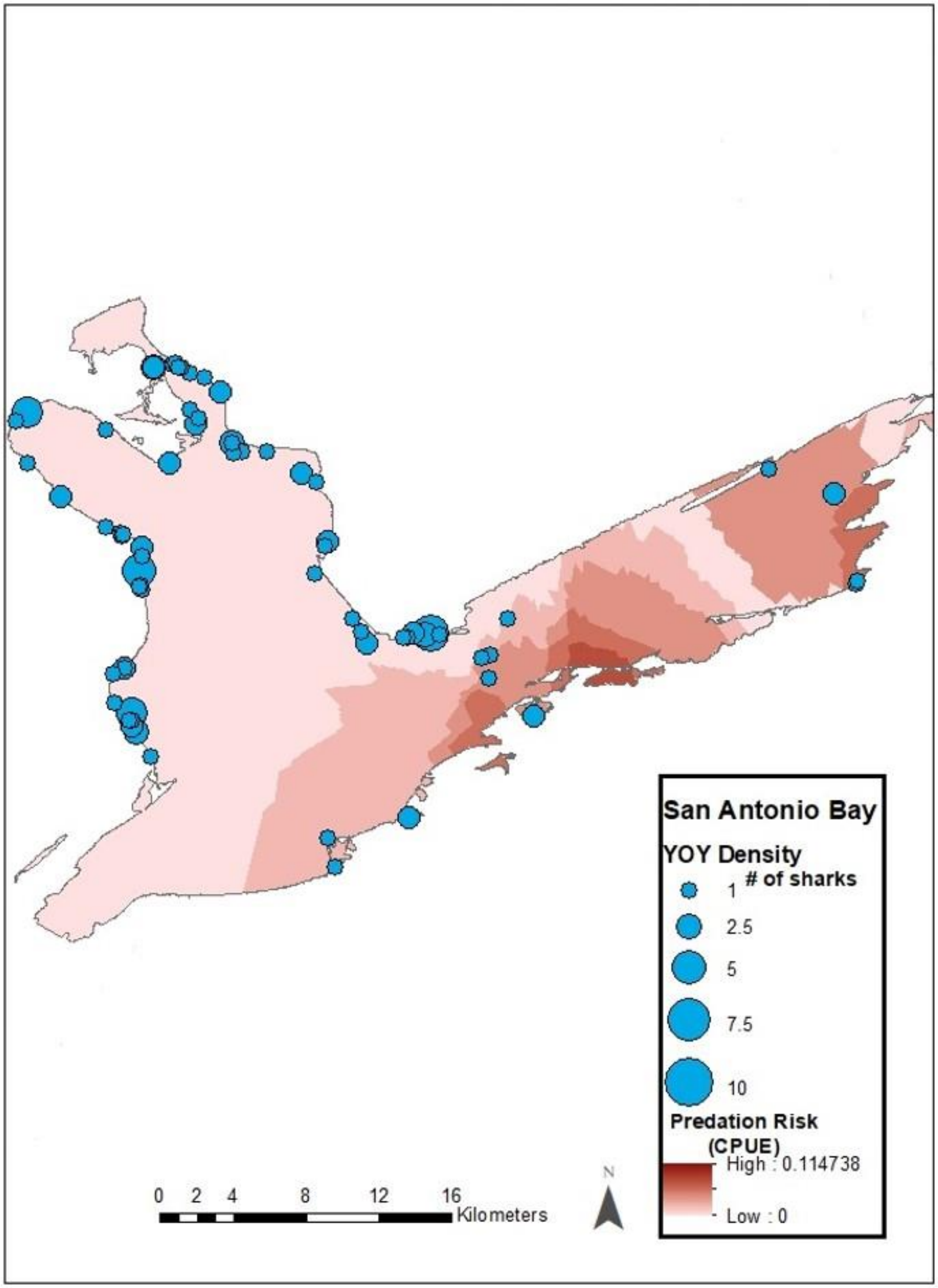

Figure 13. YOY bull shark densities overlaid on the predation risk gradient generated for San Antonio Bay giving equal weight to predation risk from the TPWD gillnet data and data from *in-situ* drumline sampling. The size of the blue circles corresponds with the density of YOY bull sharks captured per sampling event.

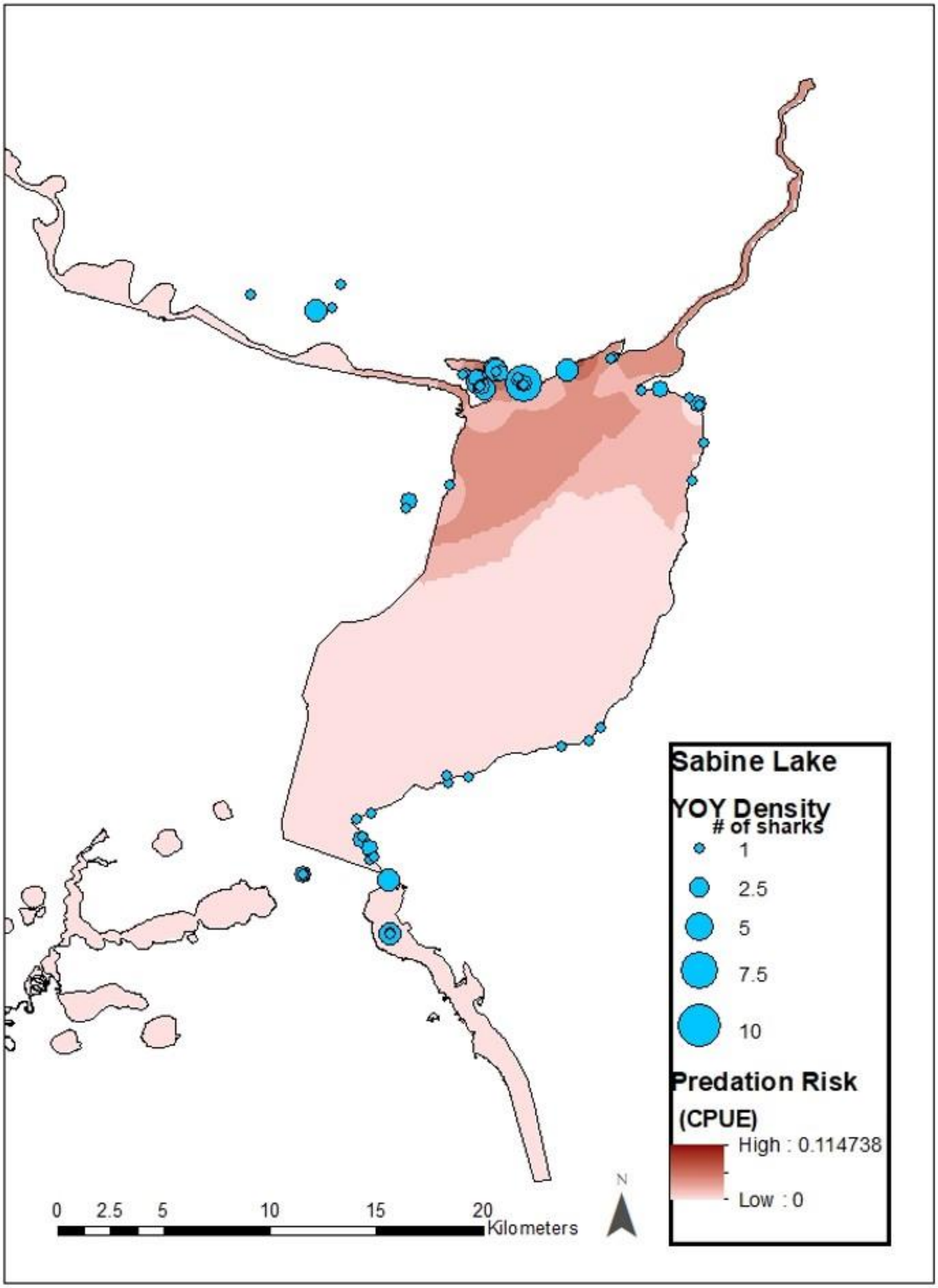

Figure 14. YOY bull shark densities overlaid on the predation risk gradient generated for Sabine Lake from the TPWD gillnet data. The size of the blue circles corresponds with the density of YOY bull sharks captured per sampling event.

Discussion

In San Antonio Bay, predatory shark density was influenced by month and station code and in Sabine Lake, densities of predatory sharks were influenced by temperature and dissolved oxygen. Fewer predatory sharks were captured in Sabine Lake than in San Antonio Bay across both sampling gear types. YOY bull sharks were caught at lower densities in areas characterized by higher predation risk in San Antonio Bay, and were also caught at higher densities when temperatures were warmer, salinities were moderate, and during the month of June. In Sabine Lake, YOY bull sharks were caught at warmer temperatures, lower salinities, and moderate dissolved oxygen concentrations, and predation risk did not significantly influence these densities. Across analyses for both YOY and predatory sharks, station code was the most important factor influencing shark CPUE (Table 1, Table 2), suggesting that location within each estuary is important in driving the observed densities of both YOY and predatory sharks.

This study is one of the first to selectively target larger sharks within Texas bays using drumline sampling, and to compare the efficacy of different sampling mechanisms for targeting these larger sharks. Previous research in these systems has only relied on gillnets, which are considered ineffective at sampling sharks >150 cm in total length (Froeschke *et al.* 2010b). A combination of drumline and historical gillnet sampling was used to evaluate the environmental conditions influencing the occurrence of predatory sharks in San Antonio Bay and Sabine Lake, and predation risk gradients generated from these two methods were then utilized in analyses examining factors predicting YOY bull shark densities in these same two systems.

Based on the CPUE from the different gear types, drumlines (CPUE of .005) were ten times more effective at sampling larger sharks in these systems than gillnets (CPUE of .001), which was expected as gillnets are not often able to sample large sharks >1.5 m (Froeschke *et al.* 2010a). This allowed for the analyses of variations in the density of predatory sharks across these two systems. Results from *in-situ* drumline sampling support the TPWD gillnet data showing that larger sharks do exist within these bays, and are potentially influencing habitat use decisions of YOY bull sharks.

Predation Risk – Drumline Sampling & Historical TPWD Data

In San Antonio Bay, 4 large sharks were captured on drumlines and 9 large sharks were sampled via gillnets over 20 years of TPWD gillnet monitoring. The predation risk gradient from drumline sampling in 2018 (Figure 5) matches up with the historical predation risk gradient based upon TPWD's gillnet sampling for San Antonio Bay (Figure 7). Although there is a positive correlation between the two maps (Figure 5, Figure 7), this value would likely be higher if drumline sampling had occurred closer to shore, as drumlines were often set offshore in deeper areas (2-7m) which were unsuitable for gillnet sampling. Based upon both the *in-situ* drumline data and the TPWD gillnet data, it appears that the capture rates of large sharks in San Antonio Bay is influenced by time of year, with most captures occurring in May and June, and location within the bay (station code), with the lower reaches of the bay (Sites 1 and 2, Figure 4) having higher densities of large sharks. For Sabine Lake, larger sharks were captured in areas of high dissolved oxygen concentration and high temperature based upon the gillnet data. No large sharks were captured in Sabine Lake during drumline sampling, and only two were captured across 24 years of TPWD gillnet monitoring. These differences in densities of large sharks between San Antonio Bay and Sabine Lake suggest inherent differences between these two ecosystems, and possible differences in their roles as nursery habitat for bull sharks.

Predictions that salinity and depth would influence the occurrence of large sharks within the two bays were not supported, as station code and month were the most significant factors in San Antonio Bay (Figure 6, Figure 8), and temperature and dissolved oxygen were the most significant factors predicting the occurrence of large sharks in Sabine Lake (Figure 10). Station code indicates location within the estuary, and the station codes with significant captures of large sharks in San Antonio Bay were all in the lower reaches of the ecosystem (Sites 1 and 2, Figure 4). Overall CPUE of predatory sharks (.005) across San Antonio Bay and Sabine Lake is less than comparable studies in other locations within the Gulf of Mexico (.019 in Florida's Shark River Estuary), suggesting that bays along the Texas coast are lower in overall predation risk than other nursery locations in the region (Matich *et al.* 2015).

YOY Bull Shark Densities

Based on the CPUE of predatory sharks from a combination of historical gillnet sampling and *in-situ* drumline sampling, predicted predation risk gradients were generated for both Sabine Lake and San Antonio Bay to determine potential areas of refuge habitat for YOY bull sharks (Figure 5, Figure 7, Figure 9). YOY bull sharks are the most vulnerable age class due to their small size and lack of experience evading predators and finding habitats that offer food resources, and not much is known about this age class along the Texas coast. By including biotic factors such as predation risk along with environmental conditions, these analyses allowed us to gain a broader understanding of shark habitat use patterns along the Texas coast. In San Antonio Bay, YOY shark densities were significantly influenced by predation risk, temperature, salinity, month, and location within the bay (station code) (Figure 11). In Sabine Lake, densities of YOY bull sharks were significantly influenced by dissolved oxygen concentrations, salinity, temperature, and location within the bay (station code) (Figure 12).

Many of these factors were expected to predict the occurrence of YOY sharks based on studies in Texas and in other systems, especially temperature and salinity (Simpfendorfer et al. 2005, Froeschke et al. 2010a). Previous research along the Texas coast has found that distributions of juvenile bull sharks were most strongly influenced by salinity and temperature, and in the Caloosahatchee River in south Florida, temperature and salinity were again the important factors determining CPUE of immature bull sharks (Froeschke *et al.* 2010b, Simpfendorfer *et al.* 2005).

Risk was a significant predictor of YOY bull shark CPUE in San Antonio Bay, with YOY sharks caught at lower densities in areas of higher predicted predation risk. This aligns with nursery habitat theory and previous studies investigating response to predation risk in elasmobranchs (Guttridge *et al.* 2012). In Bimini, Bahamas, juvenile lemon sharks utilized a mangrove lined inlet more frequently and for longer periods of time when the tide was high and depth was deeper, which coincided with an increase in the presence of potential intraspecific predators (Guttridge *et al.* 2012). Consequential experimental manipulations of predation risk in the same system revealed that the presence of a large predator initiated a flight response in juvenile lemon sharks, with a negative relationship between body size and refuge habitat use, suggesting that younger and smaller sharks are more likely to make habitat use decisions based upon potential or perceived predation risk (Stump *et al.* 2017).

The same pattern was not seen in Sabine Lake, where three YOY bull sharks were caught in the same gillnet as a predatory shark in September 2018. Young-of-the-year bull sharks and predatory sharks may be co-occurring in this system due to the infrequent occurrences of predatory sharks within Sabine Lake (Figure 14). Only two predatory sharks were caught in the twenty-four years of TPWD gillnet data analyzed, and no predatory sharks were captured during drumline sampling in this ecosystem, suggesting that encounters with predatory sharks within Sabine Lake are rare (Figure 14). The infrequent occurrence of larger sharks in Sabine Lake suggests that this entire ecosystem may function as a refuge from predators, and potentially serve as important nursery habitat.

Inherent differences between the two ecosystems may explain the different patterns seen in catches of larger sharks and in locations of high densities of YOY bull sharks in San Antonio Bay and Sabine Lake. In San Antonio Bay, which has higher overall average salinities, warmer temperatures, and higher estimates of predation risk, the highest densities of YOY bull sharks are occurring in the northern reaches of the bay (Sites 1 and 1, Figure 4), away from areas with high predicted predation risk (Figure 13). Density maps of YOY sharks suggest that areas near freshwater inputs in the bay may serve as more critical nursery habitat, with higher densities of YOY sharks in these regions than in areas closer to the Gulf of Mexico which are characterized by higher occurrences of predatory sharks (Figure 13). Sabine Lake, with its characteristic lower salinities, lower temperatures, low occurrence of predatory sharks, and lower overall shark densities may serve as a nursery habitat throughout its entirety, instead of having areas more likely to function as nursery habitats than others (Froeschke *et al.* 2010a).

The overall importance of location within an estuary (station code) as an explanatory factor suggests that a variable besides the environmental conditions and predation risk is important in driving the observed shark density patterns of this study. Factors such as current, freshwater inflows, in-water habitat type, prey availability, or current flow could be influencing these patterns, and further investigations on these potential factors are needed to determine which are important in driving both YOY bull shark and predatory shark densities. Investigations into the fine-scale movement patterns of both YOY and larger sharks throughout both of these estuaries can also help to elucidate some of the potential factors, and would allow us to gain a better understanding of fine-scale habitat use patterns. Acoustic tracking can further reveal fine scale patterns in habitat use that may not be apparent from single point sampling, which was used in our study, and may provide information on movement of these sharks as well.

Understanding the factors driving the densities of both YOY bull sharks and predatory sharks is important moving forward, as coastal areas and estuaries around the world are experiencing a variety of threats, both from anthropogenic and natural influences. An important issue that has prominent impacts on estuaries in Texas is freshwater extraction, where water from rivers is extracted to provide drinking water for large urban centers. Freshwater inflows are important to Texas estuaries and have the potential to cause large scale changes in salinity, dissolved oxygen concentrations, and nutrient input into these systems (Montagna et al. 2011). Increased freshwater extraction leading to decreased freshwater inflows into these systems will likely increase salinities across the coastline. Based on our study, salinity is an important factor driving the density of YOY bull sharks in both San Antonio Bay and Sabine Lake, with YOY bull sharks caught at the highest densities in low-moderate salinities in both systems. Increasing salinity may make these currently utilized habitats unsuitable in the future, and may potentially drive an increased use of riverine habitats adjoining estuaries as nurseries by YOY bull sharks, or a northward shift in YOY bull shark densities, with rising densities seen in systems with lower overall salinities such as Galveston Bay and Sabine Lake.

As coastal development and anthropogenic impacts to estuarine areas across the world increase in upcoming years, research investigating how these systems function, and what drives the densities and movement patterns of species within these systems, especially important predators, are critical in light of this sometimes rapid change. Understanding the effects of changing environmental conditions on predation risk and YOY bull shark habitat use in San Antonio Bay and Sabine Lake allows us to better understand bull shark nursery dynamics along the Texas coast, and identify important nursery habitats for this estuarine predator.

CHAPTER III

Conclusion

Nursery habitats are utilized by several shark species, and are often located in coastal regions around the world. Although knowledge on shark nursery dynamics, characteristics, and locations has greatly increased in the last two decades, many critical habitats have yet to be identified, and in many systems, knowledge of the mechanisms underlying nursery habitat function are not fully known (Froeschke *et al.* 2010a, Heupel & Simpfendorfer 2011, Bangley *et al.* 2018, Matich *et al.* 2017, Marie *et al.* 2017, Heupel *et al.* 2019). Protecting nursery habitats is critical to the protection of shark populations, which are facing global threats from overfishing, habitat loss, and anthropogenically-mediated climate change.

Shark nursery habitats are commonly located in coastal regions around the world, and there are several known nursery habitats in the Gulf of Mexico. In Texas, the series of bays along the coast supports juveniles of several shark species, with bull sharks as the most abundant species across the coastline. Individual bays within Texas have been labeled as nursery habitat, but these systems are heterogeneous, and it has not been examined whether certain areas within the bays, such as areas characterized by lower predation risk, support higher densities of YOY bull sharks. Little is known about the presence of predatory sharks in bays along the Texas coast and the environmental conditions influencing their occurrence, and no studies have looked at predation risk as a factor influencing YOY bull shark densities in these systems. The goal of this study was to examine the extrinsic factors, including predation risk, salinity, temperature, dissolved oxygen, depth, and month, that influence YOY bull shark habitat use patterns in two bays along the Texas Gulf Coast: San Antonio Bay and Sabine Lake.

To answer this question, field work was split into two key components: 1) determining the densities of large, predatory sharks within these two bays, and the environmental conditions influencing their occurrence, and 2) examining how predation risk and environmental conditions influence the densities of YOY bull sharks within these same two estuaries. It was hypothesized that salinity and depth would influence the occurrence of predatory sharks within these two systems, and that YOY bull sharks would avoid areas characterized by higher predation risk.

This study provides novel insights into the presence of predatory sharks in bays along the Texas coast, and compares the efficacy of different types of sampling gear for sampling these larger sharks. Predation risk estimates generated from sampling efforts were then used in analyses examining the factors influencing densities of YOY bull sharks in the same estuaries.

Predation Risk within San Antonio Bay and Sabine Lake – In-situ Drumline Sampling and Historical TPWD Gillnet Data

Previous research in both San Antonio Bay and Sabine Lake has used gillnets, which are generally ineffective at sampling predatory sharks greater than 150 cm in total length, although some large sharks are occasionally caught. This study used *in-situ* drumline sampling, a method designed to target larger sharks, which allowed the estimation of areas characterized by high predation risk in both San Antonio Bay and Sabine Lake, and the comparison of this with historical estimates of predation risk from TPWD's gillnet sampling.

Results from drumline sampling indicated that the density of predatory sharks and the corresponding estimated predation risk is higher in San Antonio Bay than in Sabine Lake. San Antonio Bay had 4 predatory sharks captured over a total of 775 hook hours, for an overall predatory shark CPUE of .005 sharks/hook hour, and Sabine Lake had no captures of predatory sharks.

Although sharks greater than 150 cm in total length were rarely captured in TPWD's gillnet sampling, catches of predatory sharks did sometimes occur, and these infrequent occurrences were used in analyses. Over the years selected for analysis, 9 predatory sharks were sampled in San Antonio Bay, and 2 predatory sharks were sampled in Sabine Lake. The overall CPUE of predatory sharks from gillnet sampling was .001 sharks/hook hour, which was lower than corresponding CPUE of predatory sharks from drumline sampling (.005 sharks/hook hour), supporting previous knowledge that gillnets are less effective at sampling larger sharks.

Based on these encounter rates of predatory sharks, predation risk may be lower in these two Texas bays than in other estuarine systems adjoining the Gulf of Mexico. A study investigating predation risk using drumlines in the Shark River Estuary in the Florida Everglades had an overall CPUE for predatory sharks of .019 sharks/hook hour, indicating higher occurrences of predatory sharks within this Florida estuary than within either San Antonio Bay or Sabine Lake (Matich *et al.* 2015). This may indicate that these two bays along the Texas coast provide more refuge habitat characteristic of nurseries than other bull shark nursery locations in the Gulf of Mexico (Beck *et al.* 2001, Heithaus 2007, Matich *et al.* 2015). The bays along the Texas coast are separated from the Gulf of Mexico by barrier islands, and only a few discrete tidal canals connect these systems to the Gulf of Mexico. The difficulty and distance required to enter these systems may play a role in the low numbers of predatory shark catches seen across both systems, especially in Sabine Lake, as it is connected to the Gulf of Mexico through an 8 km long tidal canal.

Generalized linear models performed on the predatory shark drumline CPUE revealed station code as the only significant factor predicting the occurrence of predatory sharks, which did not align with my original hypotheses that salinity and depth would be correlated with predation risk. Station code shows the geographic location of captures within the bay system, and all predatory shark drumline captures in San Antonio bay occurred in just 3 station codes, all of which were located in the southeast region of the bay (Sites 1 and 2, Figure 5). The overall importance and explanatory power of location within the bay (station code) suggests that there is a factor I did not measure in this study, such as in-water habitat type, prey abundance, or current flow that is important in driving the densities of these predatory sharks. Field sampling for this study also only occurred during five months of 2018, and so further patterns and relationships between environmental conditions and predatory shark occurrence may be elucidated through increased sampling effort, and sampling that occurs at more locations within each bay. Drumline sampling only occurred at 4 sites, none of which were located on the western side of the bay, and so increasing the number of sampling locations within San Antonio Bay will give us higher spatial resolution of predatory shark densities in this system.

Based upon TPWD's gillnet data, station code and month were significant factors predicting the occurrence of predatory sharks in San Antonio Bay, with predatory sharks captured at stations in lower reaches of the bay (Sites 1 and 2, Figure 5), and most frequently sampled during the month of June (Figure 8). In Sabine Lake, higher dissolved oxygen concentrations and higher temperature were significant factors predicting the occurrence of predatory sharks (Figure 9). Although it was again expected that salinity and depth would be significant predictors of predatory shark occurrence, results aligned with other studies from the Gulf of Mexico, where temperature has been shown to be an important factor driving the distribution of bull sharks in estuaries along the Texas coast (Froeschke *et al.* 2010b). Research investigating predation risk in other estuarine systems has found that bull sharks are often size-segregated in nurseries, with the largest sharks found outside of the nursery in marine habitats in the Gulf of Mexico (Simpfendorfer *et al.* 2005). Since other shark species besides bull sharks are restricted to areas of higher salinity or marine microhabitats within estuaries, and larger bull sharks are also commonly found at higher salinities or within marine microhabitats, it makes sense that the region of San Antonio Bay near freshwater inflows and the entirety of Sabine Lake had no captures of predatory sharks during my drumline sampling. The area of San Antonio Bay near freshwater inputs commonly had salinities between 2-14 ppt, and the entirety of Sabine Lake is characterized by brackish, low-salinity waters, oftentimes not exceeding 17-20 ppt (Powell *et al.* 2002, Froeschke *et al.* 2010b). These low salinities would exclude most large sharks from entering the northern reaches of San Antonio Bay and the entirety of Sabine Lake, which may indicate that Sabine Lake serves as refuge from predation risk throughout the whole estuary, a common characteristic of nursery habitats (Beck *et al.* 2001, Heithaus 2007).

The predation risk gradients generated from both *in-situ* drumline sampling and the TPWD historical gillnet sampling correlated well with each other in San Antonio Bay, with a concentration of predation risk occurring within the lower reaches of the bay

(Sites 1 & 2 from drumline sampling). Some of the discrepancies in the correlation between these two maps may be due to the location of drumline sampling in relation to TPWD's gillnet sampling: drumline sampling often took place offshore in deeper areas that were unsuitable for TPWD's gillnet sampling, whereas gillnet sampling always started from shore and ended at shallower depths.

YOY Bull Shark Densities within San Antonio Bay and Sabine Lake – TPWD Historical Gillnet Data

YOY bull sharks are a vulnerable age class due to their small size and lack of experience evading predators and finding habitats that provide resources, and not much is known about this age class along the Texas coast. This study was the first to specifically investigate habitat use patterns of this age class in Texas, and to include predation risk as a potential biological factor influencing distributions and densities of these YOY sharks. In San Antonio Bay, predation risk was a significant factor driving the observed density patterns of YOY bull sharks, along with temperature, salinity, month, and station code (Figure 8). Temperature and salinity were previously found to influence distributions of bull sharks along the Texas coast, and results from this study fit into this, with the added dimension of predation risk. (Froeschke *et al.* 2010b). The greatest densities and highest number of catches of YOY bull sharks occurred near the inflow of the Guadalupe River in San Antonio Bay, and this was also where predation risk was estimated to be the lowest (Figure 11).

In Sabine Lake, the highest densities and largest number of catches of YOY bull sharks also occurred near river mouths in the system, primarily near the mouth of the Neches River in the northwest corner of the bay. However, in Sabine Lake, predation risk was not a significant factor predicting the occurrence of YOY bull sharks, and the highest densities of YOY sharks were actually found in areas with the highest predicted predation risk. This may be due to the infrequent encounters with predatory sharks in this system, as only two predatory sharks were sampled in Sabine Lake over the twenty-four years included in analyses. The low abundance and temporally unpredictable occurrence of predatory sharks within this system likely wouldn't be enough to influence habitat use patterns of YOY bull sharks, which would explain why YOY bull shark CPUE was highest in the areas of highest predicted predation risk. As discussed earlier, Sabine Lake in its entirety may provide the refuge habitat characteristic of nurseries due to its low salinity waters and low occurrence of predatory sharks.

Conclusion

Environmental conditions influencing the densities of YOY bull sharks in this study (temperature, dissolved oxygen, and salinity) aligned with results from other studies conducted on bull sharks in the Gulf of Mexico (Froeschke et al. 2010b). However, the most important factor in all of my analyses across both estuaries was station code, which is a measure of location within an estuary. The overwhelming importance of station code as an explanatory variable (Table 1, Table 2) suggests that a variable that was not specifically examined in this study (such as in-water habitat type, current, prey availability, freshwater inflows, shoreline characteristics, etc.) that is related to location is strongly influencing the densities of both YOY and predatory sharks within San Antonio Bay and Sabine Lake. Future research focused on identifying and examining other potential factors that may be influencing habitat use patterns and densities of sharks along the Texas coast will aid in determining exactly what about certain locations within these estuaries is driving the observed density patterns of bull sharks.

Knowledge of shark nursery habitats, including their locations, functions, and general characteristics, has increased in the past two decades (Froeschke *et al.* 2010a, Heupel & Simpfendorfer 2011, Bangley *et al*. 2018, Matich *et al.* 2017, Marie *et al.* 2017, Heupel *et al.* 2019). Due to the spatial heterogeneity of nurseries and the complex interactions that regulate nursery habitat function, there is a growing need for both small large scale studies with the goal of elucidating the factors important to ecosystem function, and how these factors drive behavior and habitat use of juvenile sharks within native nurseries. This study provides a fine scale investigation into how predation risk and environmental conditions influence densities of YOY bull sharks within two Texas estuaries, and also provides new information about predation risk within these systems. Understanding how nursery habitats function, and gaining a better understanding of important habitat areas that may offer a refuge from predation for juvenile and YOY bull sharks within larger bays is important, especially in the light of the threats currently facing coastal ecosystems.

Coastal areas and estuaries across the world are experiencing increasing anthropogenic impacts due to population growth, large-scale climate change, and destruction and disruption of essential ecosystem components (Doney *et al.* 2012). Research investigating how these systems function and what drives the densities and movement patterns of species within these systems, especially important predators, are critical in light of this often rapid change. Understanding the effects of changing environmental conditions on predation risk and YOY bull shark habitat use in San

Antonio Bay and Sabine Lake allows us to better understand shark nursery dynamics along the Texas coast, and helps to identify discrete areas of important nursery habitat for this estuarine predator.

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Wetz, M. S., & Yoskowitz, D. W. (2013). An 'extreme' future for estuaries? Effects of extreme climatic events on estuarine water quality and ecology. *Marine Pollution Bulletin*, *69*(1- 2), 7-18.

VITA

Amanda J. Lofthus

EDUCATION

M.S. – Biology, Sam Houston State University, Huntsville, Texas, 2017 – present
Thesis: "Factors influencing the nursery dynamics of juvenile bull sharks (*Carcharhinus leucas*) in two estuaries along the Texas coast"
Advisors: Dr. Philip Matich and Dr. Jeffrey Wozniak

- Drumline sampling was used to estimate predation risk gradients across two Texas estuaries: San Antonio Bay and Sabine Lake
- Utilized a historical TPWD dataset to determine how predation risk and environmental conditions influenced occurrence patterns and densities of juvenile bull sharks in these same systems

B.S. (Honors) - Biology (ecology emphasis), Boise State University, Boise, Idaho, 2013 - 2017
Honors Senior Project: "How noise affects foraging in pallid bats (*Antrozous pallidus*)"
Advisor: Dr. Jesse Barber

- Utilized laboratory experiments and noise playback while bats were foraging, all interactions were recorded with high-speed cameras
- Behaviorally coded all videos, and determined the effect of noise on foraging time and capture success in pallid bats

AWARDS/FELLOWSHIPS

SHSU Graduate Travel Award	2019
Joey Harrison Biological Sciences Student Research Award	2018
Boise State University Top 10 Scholar	2017
Idaho EPSCoR MURI Fellowship	2016
Boise Cascade Environmental Research Fellowship	2016
BSU Dean's List High-Highest Honors	2013-2017

SCHOLARSHIPS

Sam Houston State COSET Graduate Achievement Scholarship	2018 - 2019
Sam Houston State General Graduate Scholarship	2018 -2019
Sam Houston State COAS Special Graduate Scholarship	2018
Boise State Honors College Browns Scholarship	2013-2017
Boise State Biology Department Scholarship	2015-2017
Boise State Presidential Scholarship	2013-2015

PRESENTATIONS

Lofthus AJ, Wozniak JR, Matich P. Talk: *Environmental conditions influencing spatial variability in predation risk for juvenile bull sharks in two Texas estuaries.* Texas A&M Ecological Integration Symposium, College Station, Texas, April 5th, 2019.

Lofthus AJ, Wozniak JR, Matich P. Talk: *Influence of environmental factors on predation risk gradients for juvenile bull sharks across two Texas estuaries*. Gulf Estuarine Research Society Annual Meeting, Galveston, Texas, November 8th, 2018.

Lofthus AJ, Matich P. Poster Presentation: *Factors influencing the nursery dynamics of juvenile bull sharks (Carcharhinus leucas) along the Texas coast*. 65th Southwestern Association of Naturalists Meeting, San Marcos, Texas, April 13th, 2018.

Lofthus AJ, Matich P. Talk: *Effects of changing salinities on the estuarine nursery dynamics of a coastal predator, (Carcharhinus leucas)*. Texas A&M Ecological Integration Symposium, College Station, Texas, April 6th, 2018.

Lofthus AJ, Matich P. Talk: *Do rivers serve as important nursery habitat for juvenile bull sharks (Carcharhinus leucas) along the Texas coast?* MSGOS 7th Annual Research Forum, Corpus Christi, Texas, December 2, 2017.

Rubin JJ, Chadwell BA, McClure CJW, Miner KA, **Lofthus AJ**, Kawahara AY, Barber JR. Talk: *The bat-moth arms race: Evolution of an anti-predator sensory illusion.* 54th Animal Behavior Society Meeting, Ontario, Canada, June 16, 2017.

Lofthus AJ, Miner KA, Rubin JJ, Barber JR. Poster Presentation: *Does Noise Mask Foraging Cues Used by Pallid Bats (Antrozous pallidus)?* Boise State University Undergraduate Research Conference, Boise, Idaho, April 17, 2017.

Lofthus AJ, Barber JR. Poster Presentation: *How Noise Affects Foraging in Pallid Bats (Antrozous pallidus)*. Idaho Conference on Undergraduate Research, Boise, Idaho, July 28, 2016.

PUBLICATIONS

Bauer, A. M., Beach-Mehrotra, M., Bermudez, Y., Clark, G. E., Daza, J. D., Glynne, E., ...& **Lofthus, A. J.** (2018). The Tiny Skull of the Peruvian Gecko Pseudogonatodes barbouri (Gekkota: Sphaerodactylidae) Obtained via a Divide-And-Conquer Approach to Morphological Data Acquisition. *South American Journal of Herpetology*, *13*(1), 102-116.

TEACHING EXPERIENCE

BIO 1436 Foundations of Science – Sam Houston State University Fall 2017 – present

- Teaching Assistant, 4 lab sections per semester

RESEARCH EXPERIENCE

Reef Ecology Lecturer/Scientific Divemaster, Operation Wallacea, Vanua Levu, Fiji (June-August 2019)

- Gave a series of lectures and in-water practicals focused on coral reef ecology, conservation, and fish, invertebrate, and coral ID to high-school aged students
- Led reef surveys using stereovideo cameras, 3-D modeling, and benthic transects, and taught students how to successfully operate all three survey methods and cameras
- Supervised and guided groups of up to six divers

Research Assistant, TRIES Coastal Marine Ecology Program, Sam Houston State University (April 2018-September 2018)

- Organized and led shark and gar tagging trips on the Texas coast
- Set longlines and drumlines, and took measurements, fin clips, and tissue samples from all fish captured including bull sharks, spinner sharks, blacktip sharks, alligator gar, red drum, and other estuarine species
- Dissected and extracted stomach contents from a variety of estuarine fish including alligator gar, red drum, bull sharks, atlantic croaker, and others
- Prepared blood, liver, muscle, and plasma samples for stable isotope analysis

Field Team Assistant, Earthwatch Whooping Crane Expeditions, Sam Houston State University (December 2017-March 2019)

- Assisted with Earthwatch expeditions focused on protecting Whooping Cranes and coastal habitat in Texas, supervising up to 12 volunteers
- Conducted behavioral surveys on whooping cranes in both urban and marsh environments, and assessed abundance of blue crabs and carolina wolfberries using habitat transects

Lab Technician, Barber Sensory Ecology Lab, Boise State University (January 2015-July 2017)

- Responsible for daily care and husbandry of bats kept in the lab
- Assisted with data collection and analysis for a project examining tail length in Saturniid moths as an anti-bat strategy
- Backpacked in and measured noise levels at different locations in the Pioneer Mountains to aid in site selection for a landscape level noise study
- Performed acoustic analysis and video digitization on bat-moth interactions and moth flight trajectories

- Conducted two independent projects: one describing aerial hunting behavior in pallid bats and the other examining the mechanism of how noise affects foraging in pallid bats

Volunteer Diver, Conservation Cambodia, Koh Rong, Cambodia (May-June 2015)
- Constructed and placed artificial reef pods to provide new habitat and increase fish diversity in heavily trawled areas of the Gulf of Thailand
- Conducted reef clean up dives and daily diving surveys of fish species at artificial reef sites
- Completed my PADI Advanced Open Water Diver certification.

Research Assistant, Fort Worth Zoo Conservation Expedition, British Virgin Islands (July 2014)
- Research focused on the endangered Anegada Rock Iguana
- Constructed, baited, and monitored camera traps in locations frequented by iguanas and their feral cat predators
- Analyzed plant transects in various locations to determine the iguana's impact on seed dispersal

CO-CURRICULAR ACTIVITIES

Scuba Diving Involvement
- PADI Divemaster (Active Status - Certification received July 2017)
- Scientific Divemaster for Operation Wallacea in Fiji from June-August 2019
- Divemaster Intern at Rich Coast Diving in Costa Rica from June-August 2017
- 146 logged open water dives

Secretary, SHSU Biological Sciences Graduate Student Organization (2017-2019)
- Recorded meeting minutes and organized social and volunteer events for the organization
- Participated in ongoing seminar program with local high school introducing AP Biology students to a variety of research of research topics and potential STEM career paths

Lead Ambassador, Girls in Ocean Science (2019-present)
- Organized campus-wide events promoting the involvement of girls in the fields of ocean science, including beach clean-ups and
- Networked with women involved in marine science careers around the globe, and discussed strategies to increase involvement and discussion of the topic

Aquarist Volunteer, Aquarium of Boise (2015-2017)
- Responsible for guiding tours and educating the public about the different fish, invertebrates, and reptiles on exhibit, and about the importance of oceans and marine conservation

- Assisted with daily tank maintenance, cleaning of exhibits, and animal care and husbandry
  Helped with special Aquarium events (Marine Biologist For a Day, Autism Night)