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Identifying Suitable Habitat for Three Highly Migratory Sharks (Great Hammerhead, Tiger, and Bull) and Assessing Their Spatial Vulnerability to Commercial Longline Fishing in the Southwest Atlantic Ocean and Gulf of Mexico

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UNIVERSITY OF MIAMI

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By

Hannah J. Calich

A THESIS

Submitted to the Faculty
of the University of Miami
in partial fulfillment of the requirements for
the degree of Master of Science

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Identifying Suitable Habitat for Three
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Tiger, and Bull) and Assessing Their Spatial
Vulnerability to Commercial Longline
Fishing in the Southwest Atlantic Ocean
and Gulf of Mexico

Abstract of a thesis at the University of Miami.

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Aquatic highly migratory species (HMS) are economically and ecologically important, however, their highly migratory nature makes them difficult to study and thus there are knowledge gaps relating to their movement and habitat use patterns. Highly migratory sharks are likely to interact with commercial longline fishing gear and be caught as target or bycatch, which can threaten their populations. Understanding the environmental factors that influence and drive the movements of highly migratory sharks may help researchers better predict their presence and subsequently identify areas where they are vulnerability to fisheries. Here I evaluated the overlap between habitat suitability and gear restricted zones for three co-occurring apex predatory sharks in the Southwest Atlantic Ocean and Gulf of Mexico (great hammerhead *Sphyrna mokarran*, tiger *Galeocerdo cuvier*, and bull sharks *Carcharhinus leucas*) to identify areas in this region where these species are vulnerable to and protected from commercial longline fishing. This research was accomplished in three integrated steps. First, I reviewed and summarized what is known about the environmental drivers of great hammerhead, tiger, and bull shark habitat use and movement patterns. Second, I used the results of this

review to parameterize and subsequently generate habitat suitability models for these three species. Third, I used these models to spatially compare where each species' highly suitable habitat overlaps with longline gear restricted areas within the Southwest Atlantic Ocean and Gulf of Mexico, to identify regions where these species were both vulnerable to and protected from longline fishing gear. The results of this thesis have implications to the management of these species as well as for the conservation of other highly migratory aquatic species.

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Chapter 1 - Introduction

Aquatic highly migratory species (HMS) such as sharks, billfish, tuna, and swordfish are ecologically and economically important species (Clarke *et al.*, 2006; Estes *et al.*, 2011; Heithaus *et al.*, 2008; Meltzer, 1994; Pons *et al.*, 2016; Shiffman & Hammerschlag, 2014). As large predators, these HMS may impact ecosystem structure and function through top-down effects, which can have important socio-economic, conservation, and management implications (Baum & Worm, 2009; Collette *et al.*, 2011; Ruppert *et al.*, 2013). Many HMS are also economically valuable and thus there is a strong incentive to capture them in commercial fisheries (Collette *et al.*, 2011; Dent & Clarke, 2015; Lynch, Graves & Latour, 2011). However, due to overexploitation from both targeted and incidental capture, many HMS have undergone significant population declines over the last 50 years (Meltzer, 1994; Myers & Worm, 2005; Neubauer *et al.*, 2013). Accordingly, implementing effective conservation strategies for HMS has become a management priority in recent years (Myers & Worm, 2005; Pons *et al.*, 2016; Sibert & Hampton, 2003).

Complicating conservation efforts, however, is that HMS require unique monitoring and management strategies in comparison to less mobile or sedentary species (Lascelles *et al.*, 2014; Meltzer, 1994). Specifically, HMS can be difficult to locate, study, and manage due to their relative rarity and the concealing nature of the marine environment combined with their wide-ranging movements, often across domestic and international boundaries (Meltzer, 1994). Additionally, the habitat use patterns of these species can vary regionally so trends observed in one location may not be applicable elsewhere (Lascelles *et al.*, 2014; Schlaff, Heupel & Simpfendorfer, 2014). Tagging and fisheries capture data are both commonly used to learn about the movements of these animals (Evans *et al.*, 2011; Gallagher *et al.*, 2014b; Hammerschlag, Gallagher & Lazarre, 2011a; Sibert & Hampton, 2003; Worm *et al.*, 2005). However, these techniques only provide spatial and temporal snapshots of a species' distribution, which may not be sufficient to summarize the diverse habitat use patterns of a HMS. Furthermore, these types of data often lack sufficient information to permit predictive capabilities and thus managers are often faced with policy decisions in data poor situations (Hammerschlag *et al.*, 2011a).

Highly migratory sharks are some of the most threatened aquatic vertebrates, particularly those that are accessible to fisheries (Dulvy *et al.*, 2014). This is primarily due to the high demand for shark fin soup, which can sell for hundreds of dollars per bowl (Clarke *et al.*, 2006) as well as the fact that these species can be caught as bycatch (the accidental capture of non-target species or sizes) in commercial fisheries (Oliver *et al.*, 2015). Within the Southeast region (SER) of the USA's exclusive economic zone (EEZ), which extends from the Virginia-North Carolina border to the Texas-Mexico border, many highly migratory shark species are caught as target or bycatch in the pelagic longline (PLL) and bottom longline (BLL) fisheries (Carlson *et al.*, 2012; Karp, Desfosse & Brooke, 2011). While the targeted capture of sharks within the SER is restricted and regulated (Carlson *et al.*, 2012), many species remain vulnerable to being caught as bycatch in both the BLL and PLL fisheries. While many of the sharks caught as bycatch in these fisheries will be released (Karp *et al.*, 2011), recent studies have shown that certain species are vulnerable to both at-vessel or post-release mortality, or sublethal losses in fitness (Gallagher *et al.*, 2014c; Morgan & Burgess, 2007). Thus, it has been argued that perhaps the most effective way to conserve sharks and/or reduce bycatch mortality or fitness loss is to prevent sharks from interacting with fishing gear in their essential habitat through gear modifications or spatial closures, such as marine protected areas (MPAs; Gallagher *et al.*, 2014b; Godin, Carlson & Burgener, 2012; Gulak, Santiago & Carlson, 2015; Myers & Worm, 2005).

To effectively implement protected areas, managers must be able to identify suitable habitats and have an understanding of species-specific habitat use patterns (Mora *et al.*, 2003; Norse, 2010). However, this is a difficult task for highly migratory species, such as large sharks that may routinely cross domestic or international boundaries (Myers & Worm, 2005). Moreover, individuals from the same species often exhibit different habitat use patterns, possibly due to differences in physiology or life history stage (Escalle *et al.*, 2015; Speed *et al.*, 2010). Thus, making generalizations as to the effectiveness of MPAs for migratory sharks may be species and life-stage specific (Graham *et al.*, 2016). Despite this, some highly mobile marine predators, such as sharks, can spend disproportionately large amounts of time in relatively focused areas due to favorable environmental conditions, such as optimal water temperatures that support high food availability (Queiroz *et al.*, 2016). These areas of high suitability are strong candidates for place-based management, such as MPAs or time-area closures. Identifying these highly suitable habitats often requires detailed knowledge about a species environmental preferences and related movement patterns, which is lacking for many marine predators (Hays *et al.*, 2016).

In tropical and temperate waters, three co-occurring marine predators of high economic and ecological importance are great hammerhead (*Sphyrna mokarran*), tiger (*Galeocerdo cuvier*), and bull sharks (*Carcharhinus leucas*). While co-occurring, these species are known to differ in their ecology and biology, and their varying habitat use patterns can cause them to have different levels of exposure to commercial longline gear, both as target and bycatch species (Compagno, 1984; IUCN, 2014). Despite their differences, great hammerhead, tiger, and bull sharks are all species of conservation concern in the subtropical Atlantic Ocean and Gulf of Mexico. Great hammerheads are experiencing significant population declines (Miller *et al.*, 2014) while tiger and bull shark populations have declined over the past several decades (Baum *et al.*, 2003; Myers *et al.*, 2007), though presently their populations may be stabilizing (Carlson *et al.*, 2012). Globally, these species are experiencing varying levels of population decline as a result of interactions with fishing gear (IUCN, 2014). All three species have relatively slow growth rates and low fecundity, which leaves their populations vulnerable to overexploitation (Froeschke, Froeschke & Stinson, 2013; IUCN, 2014; Worm *et al.*, 2013), and may result in ecosystem-wide impacts with long-term ecological and economic consequences (Heithaus *et al.*, 2008).

To identify where these species are vulnerable to interacting with longline fishing gear, this thesis begins with a comprehensive literature review that will be used to summarize the habitat use patterns of the focal species and identify environmental drivers of their movements. Once relevant variables have been identified, this information will be used to parameterize generation of habitat suitability models. Satellite tag data from the focal species and remotely sensed environmental data of the relevant variables will be used to create habitat suitability models to identify regions of high and moderately suitable habitat within the SER. Once identified, these high and moderately suitable regions will be compared to existing longline gear restricted areas to determine locations where the habitats of the focal species are protected from and vulnerable to longline fisheries in the SER at both species-specific and seasonal levels.

The results of this thesis will be used to address two primary research aims. First, this thesis will summarize the habitat use patterns and the environmental drivers of the movements of great hammerhead, tiger, and bull sharks. Second, this thesis will identify highly suitable habitats for these species, quantify how much their highly suitable habitat is protected from longline gears, and determine how this protection varies seasonally. In turn, I will also identify whether there are any areas of highly suitable habitat shared by the study species where they are currently unprotected, which may serve as priorities to focus future management strategies. Understanding when and where these species are vulnerable to longline gear has conservation and management implications that may help reduce the impacts of longline fisheries on these species. Additionally, the protocols developed here can be applied to other economically and ecologically important migratory species such as other sharks, tunas, marine mammals, turtles, and billfish to better understand their movement ecology and aid in the evaluation of current conservation and management strategies.

The chapters that comprise my thesis are:

1. Introduction
2. A review of movements and associated environmental influencers on the habitat use patterns of great hammerhead, tiger, and bull sharks
3. Overlap between habitat suitability and gear restricted zones reveals areas of vulnerability and protection for highly migratory sharks
4. Discussion

Chapter 2 - A review of the movements and associated environmental influencers on the habitat use patterns of great hammerhead, tiger, and bull sharks

Background

Understanding the habitat use patterns of top predators and the biophysical drivers of their movements is important for understanding their movement ecology, predicting their potential ecosystem impacts, and for implementing effective conservation management (Estes *et al.*, 2011; McCauley *et al.*, 2012; Nathan *et al.*, 2008). Such an understanding is also needed for predicting responses of predators to environmental change (Hoegh-Guldberg & Bruno, 2010; Schlaff *et al.*, 2014). For example, changing water temperatures may benefit some species by allowing them to colonize habitats that were once unavailable to them, but may hinder others by forcing migratory species to relocate to more desirable locations, or stressing sedentary species that cannot avoid the changing conditions (Heath *et al.*, 2012).

Many marine fish are directly or indirectly threatened by anthropogenic impacts including overfishing, habitat modification, and climate change (Dulvy *et al.*, 2014; Heath *et al.*, 2012; Kaiser *et al.*, 2002; Myers & Worm, 2003; Worm *et al.*, 2009). For example, recent tracking studies from the North Atlantic Ocean have revealed that pelagic sharks actively select and aggregate in space-use "hotspots" characterized by thermal fronts of high productivity (Queiroz *et al.*, 2016). However, shark longline fishing vessels also target these same areas, leading to an 80% spatial overlap, driving population declines of highly targeted species, thus demonstrating the need for conservation management (Queiroz *et al.*, 2016). Conservation plans to mitigate these types of stressors on marine fishes commonly include implementing MPAs and/or time-area closures (Gaines *et al.*, 2010; Meester *et al.*, 2004; Norse, 2010; Worm *et al.*, 2009).

To effectively implement protected areas, managers must be able to identify critical habitats and have an understanding of species-specific habitat use patterns (Mora *et al.*, 2003; Norse, 2010). For example, while great hammerhead (*Sphyrna mokarran*), tiger (*Galeocerdo cuvier*) and bull sharks (*Carcharhinus leucas*) are all co-occurring species, they are also known to differ in their ecology and biology (Compagno, 1984). Over the last 30+ years, technological advances in tracking and satellite technology have enabled researchers to greatly expand their knowledge of the movement ecology of these highly migratory species (Hammerschlag *et al.*, 2011a). While co-occurring, these species vary in their threat status (IUCN, 2014). Additionally, their habitat use patterns, environmental preferences and associated suitable habitat also likely differ, thus these species may require different conservation management approaches.

Accordingly, in the present study I conducted a comprehensive literature review related to the movement ecology of great hammerhead, tiger, and bull sharks. Specifically, I synthesized previously published data on the movements, habitat use patterns, and environmental conditions these animals have been recorded occupying to answer the following three primary questions: (1) what is the scale and scope of studies that have assessed the movements and habitat use patterns of great hammerhead, tiger, and bull sharks and do any disparities exists in the species, sex, or life-stages surveyed, or locations studied? (2) What is the movement scale and activity space of these species, and how do they differ inter- or intra-specifically? And (3) what are the environmental preferences of these species that appear to influence habitat use patterns, and do they differ by sex or life-stage? Taken together, I discuss the movement ecology and environmental drivers of these three economically and ecologically important predators as well as identify gaps in this knowledge and subsequently provide topics for future research.

Methods

To conduct this literature review, I used the Web of Science online database (https://webofknowledge.com). Search terms included the scientific names of each species in combination with each of the following search terms: 'habitat', 'movement', 'migration', 'environment', and 'behavior' for a total of 15 search combinations. The search was restricted to peer-reviewed publications that appeared in scientific journals (i.e., excluding book chapters, conference abstracts, student theses, government reports, etc.). The search generated papers that fell between the earliest records within Web of Science through until March 2015, when the literature search was completed.

All search results were scrutinized to determine relevance for further analysis. Specifically, a publication was retained if it utilized original data and met at least one of the following three other criteria: (1) investigated the movement or habitat use patterns of one of the study species, (2) examined movement or habitat use patterns in relation to an environmental variable; and (3) evaluated occurrence and/or abundance patterns in relation to an environmental variable or habitat type.

The following data were then extracted from each retained publication if the data were available in the source: (1) species studied, (2) sample size, (3) total length, (4) sex, (5) maturity status, (6) study location (including latitude and longitude), (7) habitat type occupied (reef, estuary etc.), (8) distance shark travelled, (9) home range size or activity space, (10) distance from shore, (11) depth range occupied, (12) vertical movement range, (13) water temperature inhabited, (14) salinity level inhabited, and (15) chlorophyll A concentration inhabited. Water temperature, salinity level, and chlorophyll A concentration were chosen to be the environmental variables analyzed in this study because a preliminary review of the literature indicated that these variables were evaluated frequently and appeared correlated with the other variables identified.

Since the goal of this review was to summarize what is known about each species' movement and habitat use patterns in relation to environmental variables, if a given study provided habitat use data for multiple study species the applicable data for each study species was recorded separately (e.g., if a study found great hammerhead sharks at 25 °C and tiger sharks at 28 °C, both observations were recorded separately).

To standardize the temperature data recorded in this review the quantitative data (e.g., the mean water temperatures and the temperature ranges) were binned into 4.9 °C bins while qualitative data (e.g., data on “warm” or “cool” waters) were omitted from analysis. For example, if a study reported a temperature range of 20 - 27 °C, that study was recorded in the 20 - 24.9 °C, and 25 - 29.9 °C bins. If a study only provided a mean temperature value e.g., 27 °C, that study was recorded in the 25 - 29.9 °C bin.

Chi-square analysis was completed to determine if the number of publications that discussed the movements and potential environmental preferences of the study species were evenly distributed throughout the literature (note that if a publication included data on multiple study species the paper was counted once for each species in order to determine how many times each species had been studied, not how many papers exist in general). Additionally, chi-square analysis was also completed to determine if male and female sharks have been equally studied. For both tests a p-value of < 0.05 was considered statistically significant.

Geographic coordinates for each study were recorded during the literature review to determine if there are any spatial biases in the data and if the results recorded here represent a worldwide analysis or if they are regionally restricted. For tracking studies, I recorded the location of tag deployment even if the tagged animals dispersed from the general study location over time because I was specifically interested in where studies were occurring. If coordinates were not explicitly stated in the text and could not be determined from an included figure, Google Earth was used to determine study coordinates (when possible). One representative location was recorded per study. Studies that occurred in two or more distinct locations (e.g., two countries) were excluded from spatial analysis to avoid biasing the results towards a particular study. ArcGIS 10.3.3 was used to identify geographic trends in research locations. Location data was imported into ArcGIS to determine where researchers have studied the habitat use of the study species. Kernel density estimates (KDEs) were created to illustrate the global research trends observed in this review. Kernel density maps were created for each of the study species and were classified using natural breaks (Jenks).

Results

Here I conducted a comprehensive literature review on the movements, habitat use, and associated environmental preferences or influencing factors for great hammerhead, tiger, and bull sharks. This literature review search identified 691 studies, of which 102 unique studies met the criteria and were subsequently chosen for detailed analysis to answer the three primary study questions below.

(1) What is the scale and scope of studies that have assessed the movements and habitat use patterns of great hammerhead, tiger, and bull sharks and do any disparities exists in the species, sex, or life-stages surveyed, or locations studied?

From the 102 studies chosen for review, 120 unique records of great hammerhead, tiger, and bull shark movement and/or habitat use patterns were identified (a subset of the 102 unique studies analyzed in this review presented data on multiple study species; see Appendices A-C for summarized data). Chi-square analysis revealed that investigations of this kind for the three focal species have not been equal ($\chi^2 = 27.45$, df = 2, $p < 0.001$), with only 13 studies including investigations on the movement and environmental drivers of great hammerheads, while tiger and bull sharks have been more thoroughly studied (55 and 52 studies, respectively). The maximum number of individual sharks included in a single study was 1,334 for great hammerheads, 4,757 for tiger sharks, and 6,970 for bull sharks.

Within these studies, 60% of the great hammerhead studies that reported maturity state focused on mature individuals (n = 3 of 5 studies), while 76% of the tiger shark studies included a combination of maturity states (n = 16 of 21 studies), and 46% of the bull shark studies focused on immature sharks while 41% included both mature and immature animals (n = 34 of 39 studies, combined). Lastly, 46% of great hammerhead studies, 65% of tiger shark studies, and 67% of bull shark studies reported the sex(es) of the animals (n = 6 of 13 studies, 36 of 55 studies, and 35 of 52 studies, respectively).

Of the studies that reported sex, the vast majority of the studies included both sexes (n = 5 of 6 studies for great hammerheads, n = 28 of 36 studies for tiger sharks, and n = 32 of 35 studies for bull sharks). Within the studies that included animals from both sexes, more females were studied than males (n = 18 of the 22 tiger shark studies, $\chi^2 = 8.909$, df = 1, p = 0.003, and 12 of the 18 of bull shark studies, $\chi^2 = 2$, df = 1, p = 0.157, included more females than males). Note that this analysis could not be run on all studies that included both sexes because sex specific sample sizes were not always provided.

Great hammerhead, tiger, and bull sharks have been studied in a wide variety of tropical and subtropical habitats (Figure 2.1). Great hammerhead and tiger shark habitat use is very diverse and many studies occurred in a combination of habitats (great hammerhead = 4 of 13 and tiger = 24 of 55 studies). In comparison, half of the bull shark studies were focused on hyposaline habitats (e.g., estuaries, rivers, lagoons and/or mangroves; 26 of 52 studies).

Geographic coordinates were determined for 76 of the studies included in this review. The spatial distribution of the studies included in this review varied globally (Figure 2.2). During this review, great hammerhead shark habitat use was studied in the waters surrounding all continents except Europe and Antarctica (n = 8). Similarly, tiger and bull shark habitat use has been studied in waters from all continents except Europe, Asia, and Antarctica (n = 32 for tiger and 36 for bull).

While the geographic distribution of the studies was similar among species, study density varied (Figure 2.2). Great hammerheads were primarily studied off North America in the Gulf of Mexico and Caribbean Sea, as well as off Northwestern Australia in the Eastern Indian and Western Pacific Oceans. Tiger sharks were primarily studied in the Pacific Ocean near the Hawaiian Archipelago and off Western Australia in the Eastern Indian Ocean. Bull sharks were primarily studied off North America in the Gulf of Mexico, Caribbean Sea, and the Western Atlantic Ocean as well as off of Eastern Australia in the South Pacific Ocean.

(2) What is the movement scale and activity space of these species, and how do they differ inter- or intra-specifically?

Great Hammerhead Sharks

Relatively little is known about the movements of great hammerhead sharks. The only study reviewed here that reported a travel distance for this species was Hammerschlag *et al.* (2011b), who tracked a great hammerhead from the Florida Keys to New Jersey as it followed the Gulf Stream for ~1,200 km over 62 days. While this study extended the known range of great hammerheads it also emphasized how little is known about this species' movements. None of the papers reviewed during this study reported a home range size [e.g., a kernel density estimate (KDE)] for great hammerheads (however, after this review was completed, Graham *et al.* (2016) reported a 50% core habitat use area of 85,061 km^2 for great hammerhead sharks). A small subset of studies (n = 5, 38%) reported sighting great hammerheads 0.2 - 1 km from shore, and all 5 studies reported sightings 400 - 500 m from shore. While the vertical movements of great hammerheads have not been studied in detail, great hammerheads have been repeatedly caught in shallow water (< 60 m; e.g., Cliff, 1995; Dudley & Cliff, 2010; Heithaus *et al.*, 2007a; Sadowsky, 1971; Stevens & Lyle, 1989; Taniuchi, 1974) and have been sighted in waters as shallow as 1 - 3 m (Vaudo & Heithaus, 2009). While there are likely intraspecific variations between individual great hammerheads, there has not been enough research conducted on the movements of these species to analyze this topic.

Tiger Sharks

In comparison to great hammerheads, tiger shark movements have been relatively well documented. Multiple studies have documented long-distance movements of tiger sharks. The longest documented tiger shark migration recorded in this review involved a 362 cm female travelling at least 8,000 km from Shark Bay, Australia to Southeast Africa over 99 days (Heithaus *et al.*, 2007b). Additional long-distance migrations of 3,500 km and over 4,000 km have also been documented by Hammerschlag *et al.* (2012a) and Ferreira *et al.* (2015), respectively.

In addition to long distance migrations, multiple studies have reported that tiger sharks have “large” or “sizable” home ranges that can vary in scale from 100’s to 1000’s of kilometers (Heithaus *et al.*, 2002; Holland *et al.*, 1999; Papastamatiou *et al.*, 2011). However, only a few studies have reported specific home range sizes. Hammerschlag *et al.* (2012a) reported an activity space size up to 8,549 km^2, while Meyer *et al.* (2009a) and Tricas, Taylor and Naftel (1981) both reported values of ~100 km^2. Werry *et al.* (2014) reported a three-dimensional 50% KDE range of 949 - 3,770 km^3. Variations in these (limited) values may be due to varying study durations, the presence of resource distribution “hotspots” (e.g., Papastamatiou *et al.*, 2011), intraspecific variations between animals, or a combination of any of these factors.

Intraspecific variations in tiger shark residency have been documented by Hammerschlag *et al.* (2012a), Papastamatiou *et al.* (2013), and Ferreira *et al.* (2015), who all documented individual tiger sharks following different residency patterns despite being tagged in the same general location. For example, Hammerschlag *et al.* (2012a), documented tiger shark residency times in Florida and the Bahamas varying from < 5 to ≥ 60 days while Papastamatiou *et al.* (2013) documented some tiger sharks utilizing a core area while others demonstrated inter-island movements. Similarly, Ferreira *et al.* (2015) reported 50% KDEs ranging from 1,167 - 634,944 km^2. Ferreira *et al.* (2015) also demonstrated that tagging duration is not necessarily proportionate to home range size (one of the sharks in their study was tagged for 191 days yet had a smaller home range than a shark tagged for 70 days).

The vertical movements of tiger sharks were examined in 10 of the studies included in this review. Overall, most tiger sharks spent the majority of their time in < 100 m of water (which frequently corresponds to the mixed layer above the thermocline), with periodic dives below 300 m (Hazin *et al.*, 2013; Holland *et al.*, 1999; Meyer, Papastamatiou & Holland, 2010; Nakamura *et al.*, 2011). While dives below 300 m are common, few tiger sharks have been recorded below 1,000 m. The deepest dives recorded in this review both came from adult female sharks (270 cm and 370 cm total lengths) that dove to 1,112 m and 1,136 m, respectively (Afonso & Hazin, 2015; Werry *et al.*, 2014). After undergoing rapid vertical descents, tiger sharks have been documented performing gradual ascents. Combined, these movements are referred to as “yo-yo” diving (Ferreira *et al.*, 2015; Holmes *et al.*, 2014; Nakamura *et al.*, 2011; Werry *et al.*, 2014). Lastly, if tiger sharks are in shallow habitats, and therefore are unable to dive, they have a tendency to spend more time near the bottom (Holland *et al.*, 1999).

Tiger shark’s diving and habitat use patterns appear to be mediated by developmental stage and time of day. For example, ontogenetic shifts in diving behaviour have been documented by Afonso and Hazin (2015). These authors observed young of the year and juvenile tiger sharks inhabiting shallow habitats while larger sharks (150 - 300 cm) moved to oceanic habitats and engaged in deeper dives. In addition to ontogenetic shifts in vertical diving behaviour, tiger shark habitat use can follow diel patterns, though these patterns are not always consistent. For example, while Afonso and Hazin (2015) documented tiger sharks staying in slightly shallower waters (0 - 10 m) at night, and moving slightly deeper during the day (10 - 60 m with a mode between 20 - 40 m), Tricas *et al.* (1981) tracked a tiger shark moving to oceanic waters near sunset and returning to shallow reefs before dawn.

Bull Sharks

In comparison to great hammerhead and tiger sharks, the movement patterns of bull sharks have been moderately studied. Overall, bull sharks tend to remain in the same location over long periods of time with limited horizontal movements, though occasionally individual bull sharks will undergo longer distance migrations (Brunnschweiler & Baensch, 2011; Brunnschweiler & Barnett, 2013; Carlson *et al.*, 2010). For example, the vast majority of bull sharks documented in Carlson *et al.* (2010) and Hammerschlag *et al.* (2012b) only travelled short distances (< 200 km) and remained in shallow inshore areas near where they were tagged. However, both studies also documented a single bull shark travelling over 1,000 km (1,506 km over 85 days, and 1,200 km over 68 days, respectively), which indicates at least a low level of intraspecific variation in the horizontal movements of bull sharks.

Consistent with their small-scale movements, bull sharks exhibit high site fidelity and have small home ranges. Hammerschlag *et al.* (2012b) documented 16 bull sharks inhabiting a home range of 2,260 km^2 over an 11-month period. Additionally, Curtis, Parkyn and Burgess (2013) identified a 50% utilization distribution of < 0.001 - 0.593 km^2 for bull sharks that were tracked with a hydrophone for 2 - 26 hours. Similarly, Ortega *et al.* (2009) actively tracked eight bull sharks over 1.2 - 4.3 km^2 for 6 - 24 hours (though short study duration is an important factor to consider when evaluating the results of the previous two studies).

Bull shark's movement and home range patterns appear to vary with sex and life stage, particularly when hyposaline habitats are involved. While many bull sharks have been documented staying close to river mouths or moving around river mouths seasonally (Drymon, Ajemian & Powers, 2014; Heupel *et al.*, 2010), this patterns appears to vary by sex and life stage. For example, multiple studies have reported that female bull sharks are found closer to shore and/or near estuary mouths, while male bull sharks are generally found further offshore (McCord & Lamberth, 2009; Werry *et al.*, 2011; Werry & Clua, 2013). In comparison to adults, immature bull sharks are generally reported near river mouths and can spend much of their time in estuary habitats, presumably to benefit from the reduced predation risk (Heupel & Simpfendorfer, 2008; Werry *et al.*, 2011). As such, estuaries are recognized as nursery grounds for bull sharks (Froeschke, Stunz & Wildhaber, 2010a; Snelson & Williams, 1981; Snelson, Mulligan & Williams, 1984; Thorburn & Rowland, 2008; Werry *et al.*, 2012). This is also supported by the fact that pregnant female bull sharks have been reported in river and estuary habitats (Snelson & Williams, 1981; Snelson *et al.*, 1984; Werry *et al.*, 2011; Werry *et al.*, 2012).

(3) What are the environmental factors that appear to influence the habitat use patterns of these species and do they differ by sex or life-stage?

The three primary environmental variables that were analyzed in this study were temperature, salinity, and chlorophyll A concentration. However, only two of the studies included in this review quantitatively evaluated chlorophyll A concentrations with respect to habitat use or movement (Meyer *et al.*, 2010; Papastamatiou *et al.*, 2013). Since both studies focused on tiger sharks, comparisons for this metric between species could not be completed (tiger sharks were reported in waters with chlorophyll A values of ~0.1 - 0.15 mg/m3; Meyer *et al.*, 2010; Papastamatiou *et al.*, 2013). However, species-specific comparisons were conducted for water temperature and salinity.

Water Temperature

Overall, temperature data were obtained from 5 great hammerhead, 18 tiger, and 25 bull shark studies, respectively (Figure 2.3). Great hammerhead sharks were primarily recorded in waters ranging from 25 - 29.9 °C, but have been recorded in waters from 17 - 31 °C (Hammerschlag *et al.*, 2011b; Vaudo & Heithaus, 2009). Heithaus *et al.* (2007a) determined that in the Florida Keys, the predicted probability of catching great hammerheads decreases as water temperature increases (from ~17.5 °C to ~ 32.5 °C). While this does not necessarily mean great hammerheads avoid waters outside of this temperature range (i.e., it is possible that great hammerheads are less interested in feeding outside of this range and thus are more difficult to sample), the overall thermal range recorded in the present study suggests that > 31 °C may be too hot for many great hammerheads. Lastly, sexual segregation has been proposed in two studies, which when combined suggest that males are more commonly found in cooler, offshore waters while females can be found closer to shore, particularly pregnant females as they may give birth in coastal bays (Cliff, 1995; Gallagher *et al.*, 2014a).

Tiger sharks have been primarily recorded in waters from 20 - 24.9 °C, but they have been documented in temperatures ranging from 4 - 33 °C (Afonso & Hazin, 2015; Fitzpatrick *et al.*, 2012). This large temperature range is due to tiger shark's well documented vertical "yo-yo" diving (e.g., Nakamura *et al.*, 2011). Overall, horizontal tiger shark migrations have been repeatedly attributed to increases in water temperature and alterations in prey abundance, but the degree to which each of these variables influences habitat use, and the exact temperatures that influence these movements remains unclear (Heithaus, 2001; Heithaus & Dill, 2002; Holmes *et al.*, 2012; Lowe, Wetherbee & Meyer, 2006; Meyer *et al.*, 2009a; Meyer *et al.*, 2010).

Bull sharks have been primarily recorded from 25 – 29.9 °C, with an overall range of ~14 - 40 °C (Heupel *et al.*, 2010; Shipley, 2005). Three studies reviewed in this analysis recorded dead bull sharks at temperatures < 10 °C (Curtis, Adams & Burgess, 2011; Matich & Heithaus, 2012; Snelson & Williams, 1981), while Snelson *et al.* (1984) reported bull sharks gathering around the heated outflow of power plants when the water temperature was 10 - 15 °C, suggesting that bull sharks cannot tolerate water temperatures below 10 °C.

Salinity

While salinity can be an important driver of elasmobranch habitat use (Schlaff *et al.*, 2014), few studies have reported *in situ* salinity values for great hammerhead or tiger sharks. For example, Parker and Bailey (1979) documented great hammerhead and tiger sharks in 33 - 34 ppt and Rezzolla, Boldrocchi and Storai (2014) documented tiger sharks in 38 – 41 ppt. While tiger sharks have been reported in above average ocean salinity levels, Heithaus *et al.* (2002) reported that the tiger sharks observed in their study avoided a specific area, potentially due to hypersaline waters (> 60 ppt).

In comparison, the salinity range of bull sharks has been studied in depth because bull sharks are euryhaline and can tolerate a wide range of salinities (reviewed in Hammerschlag, 2006). Overall, bull sharks have been observed in waters from 0 - 42 ppt (Snelson & Williams, 1981; Thorburn & Rowland, 2008) though specific sex and life-stage specific trends can influence habitat choice within this range.

Neonate and young juvenile bull sharks have been repeatedly documented in low salinity rivers and lagoons, suggesting these habitats may act as nurseries for young bull sharks (Froeschke *et al.*, 2010a; Snelson & Williams, 1981; Snelson *et al.*, 1984; Thorburn & Rowland, 2008; Werry *et al.*, 2012). For example, Thorburn and Rowland (2008) reported that 86% of immature bull sharks were caught in < 5 ppt (and 32% of those animals were caught in 0 ppt). Werry *et al.* (2012) hypothesized that inhabiting low salinity habitats may increase survivorship of young bull sharks through reduced competition and predation, though specific drivers of size-based segregation may differ regionally. Similarly, Heupel and Simpfendorfer (2011) also reported that juvenile neonate bull sharks can survive in lower salinity waters compared to other similar species (such as lemon, tiger, or blacktip sharks), which also supports the theory that low salinity environments may encourage survivorship through reduced competition and predation. Though not examined in detail in this study, dissolved oxygen may also be an important driver in bull shark habitat use, particularly for early life history stages in estuary habitats (Heithaus *et al.*, 2009; Shipley, 2005). Once bull sharks start to mature they begin to move offshore into higher salinity habitats. For example, Froeschke *et al.* (2010a) reported that while immature bull sharks prefer between 7 - 20 psu, adult bull sharks were most commonly found in salinities from 15 - 30 psu. Similarly, Snelson and Williams (1981) reported that while bull sharks can be found in lagoons year round, adult bull sharks spend most of their time outside lagoons.

Adult male and female bull sharks have been documented using different habitats, with males being found further offshore and females being found closer to shore and occasionally in estuarine habitats (Werry *et al.*, 2012; Werry & Clua, 2013). However, since most studies examined in this review simply reported adult bull sharks in ~0 - 35 ppt, it was not possible to examine sex specific trends in detail.

Conclusions

Overall there is an obvious disparity in the amount of research that has been undertaken on the movements of the study species and the environmental factors that may influence their habitat use patterns. While the three focal species overlap in some parts of their range, they each have unique movement patterns that may render them susceptible to different anthropogenic impacts. For example, from the little movement data available, great hammerheads appear to primarily occupy coastal areas of the continental shelf with occasional long-distance migrations up to ~1,200 km into pelagic waters (e.g., Espinoza *et al.*, 2014; Hammerschlag *et al.*, 2011b; Heithaus *et al.*, 2007a). These movement patterns suggest that these animals may be primarily susceptible to commercial fisheries within countries' territorial waters (for example, within the USA's EEZ), but may also be vulnerable to offshore pelagic fisheries in international waters as well. To help reduce these anthropogenic impacts, management efforts could be concentrated in coastal areas of the continental shelf and be focused on reducing great hammerhead shark interactions with commercial fisheries.

In comparison, tiger shark movements have been well documented and the results of this review suggest that individual differences in movement patterns are common. For example, while some tiger sharks have large home ranges (e.g., up to 8,549 km^2; Hammerschlag *et al.*, 2012a) or undergo long distance migrations (e.g., up to 8,000 km; Heithaus *et al.*, 2007b), others show high site fidelity and have small home ranges (e.g., up to 109 km^2; Meyer *et al.*, 2009a). The reasons behind this diversity are not well understood, but may be related to prey accessibility, age-class, and/or sex (e.g., Afonso & Hazin, 2015; Hammerschlag *et al.*, 2012a). Understanding the drivers behind these movement patterns could have important implications for marine spatial planning as they may help managers identify biologically important locations. The high diversity of movement patterns tiger sharks can demonstrate means that these animals could be vulnerable to a range of anthropogenic impacts from commercial fisheries to urban pollution. Thus, multiple management strategies may be required to help mitigate these impacts. For example, tiger sharks that show high site fidelity are likely to benefit from marine protected areas or shark sanctuaries (Graham *et al.*, 2016), while highly migratory sharks are more likely to benefit from management measures designed to reduce capture in commercial fisheries (e.g., gear restrictions and retention limits).

Lastly, bull sharks are a coastal species that have small home ranges and generally do not undertake long distance movements (though occasional migrations have been documented; Carlson *et al.*, 2010; Hammerschlag *et al.*, 2012b). As a coastal species, bull sharks are likely to interact with both highly urbanized habitats as well as commercial fisheries within territorial waters (Curtis *et al.*, 2013; Werry *et al.*, 2012). Living in somewhat spatially restricted coastal environments means that bull sharks may be more vulnerable to anthropogenic impacts in specific locations, but also that they are likely to benefit from marine protected areas, because they are unlikely to migrate far outside of them (Graham *et al.*, 2016). This protection may be particularly effective if protected areas are implemented coastally and potentially near estuary mouths, if pregnant female or juvenile bull sharks have been observed using these areas (e.g., Snelson & Williams, 1981; Werry *et al*., 2012).

Great hammerhead, tiger, and bull sharks occupy a wide variety of habitats throughout tropical and subtropical waters. However, a relatively unexplored environment for all three species has been highly urbanized habitats. Given that in comparison to more offshore environments, urbanized environments can be disproportionately vulnerable to anthropogenic stressors such as urban run-off and it's associated pollutants, anti-fouling paint from boats, or recreational fishing (Islam & Tanaka, 2004; Werry *et al.*, 2012), understanding if and how the focal species utilize urbanized environments may have conservation and management implications. For example, while limited research has investigated the impacts of urbanization on great hammerhead or tiger sharks, some studies have investigated how bull sharks utilize near-shore or urban environments. For example, Werry *et al.* (2012) suggested that because of increased destruction to natural habitats, urbanized environments might be an increasingly important habitat for bull sharks. In particular, since pregnant female bull sharks appear to give birth in near-shore river or estuary environments (Snelson &

Williams, 1981; Snelson *et al.*, 1984; Werry *et al.*, 2012), understanding how urban environments may impact these animals could help improve current management plans.

This review identified clear species-specific differences in the environmental conditions occupied by the study species. While great hammerheads have been found in tropical and subtropical habitats, they have not been documented in waters > 31 ºC. Moreover, this species may also avoid hypo- and hyper- saline waters as they have only been recorded in waters of 33 - 34 ppt salinity. Additionally, as was discussed with their movement patterns, great hammerheads may also sexually segregate, with males being found further offshore in cooler waters and females staying closer to shore in warmer waters (Cliff, 1995; Gallagher *et al.*, 2014a), though more research is necessary to confirm this theory.

Tiger sharks have been found in a wide range of temperatures, which is consistent with their diverse movement patterns. In particular, they are known to "yo-yo" dive throughout the water column, presumably as a predatory strategy (Afonso & Hazin, 2015; Nakamura *et al.*, 2011). Thus, it is possible that these animals are resilient to changing water temperatures and prioritize prey capture over maintaining a consistent body temperature. Overall, the degree to which prey and/or water temperature influence the movement ecology of tiger sharks remains unknown. Similarly to great hammerheads, tiger sharks have been recorded in average ocean salinities. However, tiger sharks have also be documented being absent from a habitat with > 60 ppt and Heithaus *et al.* (2002) suggested this may be due to tiger sharks avoiding hypersaline environments, which again would be consistent with their offshore, migratory habitat use patterns.

In comparison to great hammerhead and tiger sharks, the environmental tolerances of bull sharks have been very well studied because bull sharks are euryhaline and are able to survive in a wide range of salinities (Hammerschlag, 2006). Their ability to withstand a wide salinity range means that bull sharks can move into environments that are either hyper- or hyposaline to the open ocean, including estuary and mangrove habitats (e.g., Werry *et al.*, 2012). Additionally, bull sharks can be found in warmer waters than great hammerhead or tiger sharks (e.g., up to 40 ºC; Shipley, 2005). Combined, the salinity and temperature trends of bull sharks are consistent with the fact that these animals are normally found in near-shore, coastal, relatively shallow environments.

While this study was a comprehensive review of current literature, it was limited to English, peer-reviewed studies that were available via Web of Science as of March, 2015. While these limitations restricted the number of articles that were included in this review, the search terms used during the review process resulted in 691 studies, which was determined to be sufficient to proceed with analysis. This study was not intended to be a complete review of all habitat use studies ever completed on these animals, rather it is a summary of the general habitat use and movement patterns of the study species. This study demonstrated that while the movements of highly migratory species can be complex, there are trends in their movement patterns that can be used to better understand and manage these animals. The results from this study can be used to develop habitat suitability models and to identify biologically important habitats, which can aid in the development or modification of current management and conservation strategies.

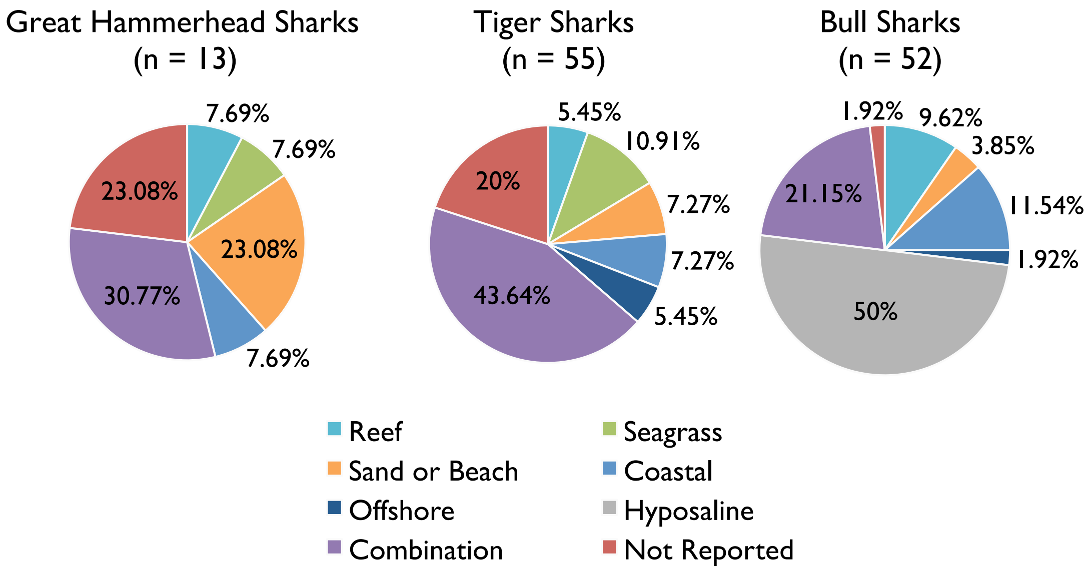

Figure 2.1. Habitats great hammerhead, tiger, and bull sharks have been studied in.

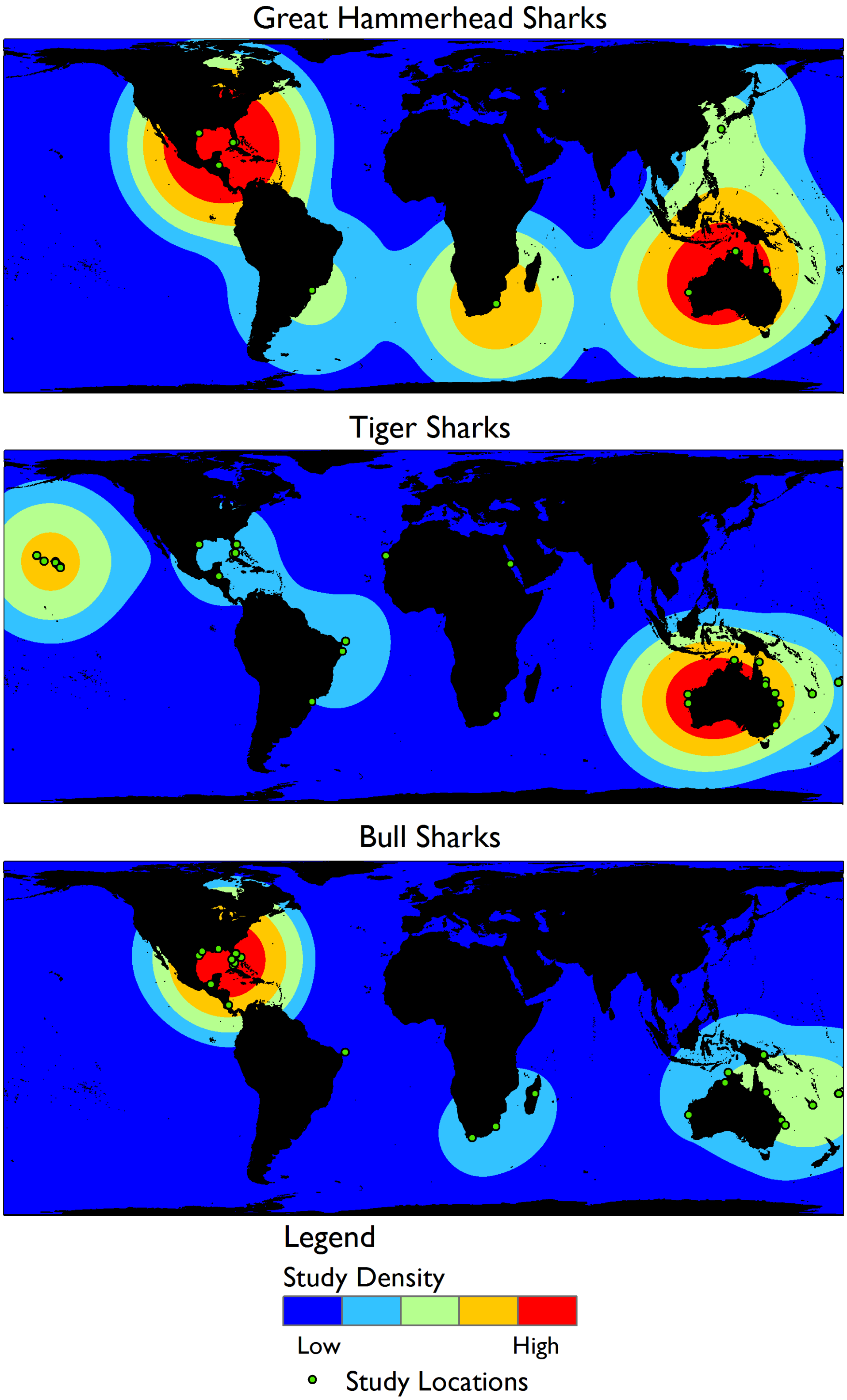

Figure 2.2. The spatial distribution and relative kernel density of the studies included in this review.

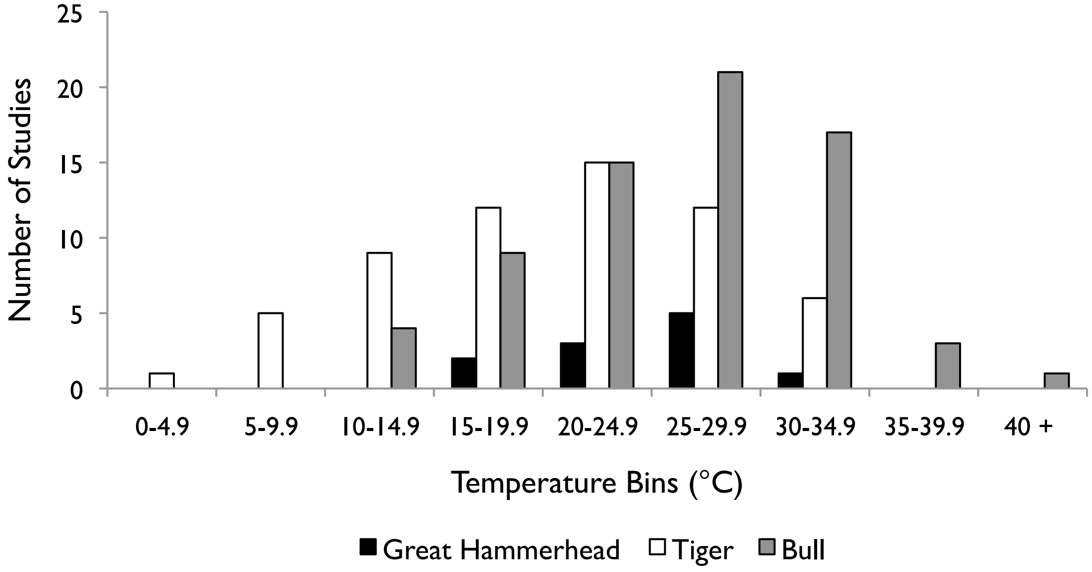

Figure 2.3. Temperature ranges great hammerhead, tiger, and bull sharks have been recorded in.

Chapter 3 - Overlap between habitat suitability and gear restricted zones reveals areas of vulnerability and protection for highly migratory sharks

Background

Within the Southeast region (SER) of the USA's exclusive economic zone (EEZ), which extends from the Virginia-North Carolina border to the Texas-Mexico border, many shark species are caught as target or bycatch in the pelagic longline (PLL) and bottom longline (BLL) fisheries (BLL and PLL, respectively; Carlson *et al.*, 2012; Karp *et al.*, 2011). While the targeted capture of sharks within the SER is restricted and regulated (Carlson *et al.*, 2012), it remains poorly known if the most suitable habitats for these species are being protected, thus supporting sustainable fisheries. Moreover, many species remain vulnerable to being caught as bycatch in both the BLL and PLL fisheries if the fisheries overlap with high suitable shark habitats. While many of the sharks caught as bycatch in these fisheries will be released (Karp *et al.*, 2011), recent studies have emphasized that certain species are vulnerable to both at-vessel or post-release mortality or sublethal losses in fitness (Gallagher *et al.*, 2014c; Morgan & Burgess, 2007). Thus, it has been argued that perhaps the most effective way to conserve sharks and reduce bycatch mortality or fitness loss is to prevent sharks from interacting with fishing gear in their essential habitat through spatial closures or gear modifications (Gallagher *et al.*, 2014b; Godin *et al.*, 2012; Gulak *et al.*, 2015; Myers & Worm, 2005).

Several gear restricted areas have been implemented in the SER to reduce fisheries interactions with a variety of aquatic species including (but not limited to): bluefin tuna (*Thunnus thynnus*), pilot whales (genus *Globicephala*), as well as sandbar (*Carcharhinus* *plumbeus*) and dusky sharks (*Carcharhinus obscurus*). However, it is unclear if these gear restricted areas could be beneficial for other highly migratory species of economic and ecological importance. Focusing on three sympatric migratory sharks (great hammerhead, tiger, and bull sharks), this study seeks to fill these knowledge gaps by (1) identifying suitable habitat for these species within the SER, (2) determining what proportion of their suitable habitat is protected from longline gears, and (3) assessing the magnitude of this suitable habitat protection at both species-specific and seasonal levels. Taken together, I discuss whether current gear restricted zones, established for other species, provide effective protection of highly suitable habitat for great hammerhead, tiger and bull sharks. In turn, I identify whether there are any areas of highly suitable habitat shared by the study species where they are currently unprotected, which may serve as priorities to focus future management strategies.

Methods

Study Species

This study focused on great hammerhead, tiger, and bull sharks because they are all apex predators of conservation concern that co-occur in the subtropical Atlantic Ocean, yet exhibit different habitat use patterns and thus have different levels of exposure to longline gear, both as target and bycatch species (Compagno, 1984; IUCN, 2014). Great hammerhead sharks are experiencing significant population declines (Miller *et al.*, 2014) while tiger and bull sharks have declined over the past several decades (Baum *et al.*, 2003; Myers *et al.*, 2007) but presently their populations may be stabilizing (Carlson *et al.*, 2012). Globally, these species are experiencing varying levels of population decline as a result of interactions with fishing gear (IUCN, 2014). All three species have relatively slow growth rates and low fecundity, which leaves their populations vulnerable to overexploitation (Froeschke *et al.*, 2013; IUCN, 2014; Worm *et al.*, 2013). Population changes (increase or decrease) may have ecosystem-wide impacts with long-term ecological and economic consequences (Heithaus *et al.*, 2008).

Study Area

This study was restricted to the SER for three reasons: first, all of the satellite tagged sharks included in this study were present within the SER; second, there are three active US commercial longline fisheries in the SER that may impact these species (the bottom longline shark fishery, the bottom longline reef fish fishery, and the pelagic longline tuna and swordfish fishery); and third, the SER is a distinct management zone that provided a natural cut-off point between subtropical and temperate zones, which restricted analysis to habitats where these species are regularly observed.

Data Collection

Capturing and handling

Sharks were captured using baited circle-hook drumlines following Gallagher *et al.* (2014c), which allowed captured sharks to maintain ram ventilation while hooked, thus promoting shark survivorship. After a 1-hour soak period, the gear was retrieved. If captured sharks showed a significant amount of stress (e.g., lack of vigorous movements) the shark was released without tagging to promote survivorship. Sharks showing low to minimal signs of stress were secured on a platform or alongside the stern of the boat. A saltwater hose and pump was inserted into the shark's mouth to ensure the shark was receiving highly oxygenated water while it was immobilized for tagging.

Tagging

Each shark was measured, sexed, and tagged with a Smart Position and Temperature Transmitting tag (SPOT5, Wildlife Computers; http://www.wildlifecomputers.com). Since great hammerhead sharks are sensitive to capture and handling stress (Gallagher *et al.*, 2014c), this species was tagged with a towed SPOT tag that could be quickly attached via a tether and titanium dart anchored into the musculature at the base of the first dorsal fin. In comparison, tiger and bull sharks were tagged by affixing the tag to the first dorsal fin using titanium bolts, neoprene and steel washers, and high carbon steel nuts. This gear combination helps protect the shark's fin from metal corrosion while ensuring the tag eventually detaches from the shark (Hammerschlag *et al.*, 2011b). To minimize biofouling, tags were coated in Propspeed, a non-toxic, non-metallic anti-fouling agent.

The geographic location of each tagged shark was determined via Doppler-shift calculation made by the Argos Data Collection and Location Service (www.argos-system.org) whenever the shark's dorsal fin (and thus the SPOT5 tag) broke the surface of the water and was received by a passing Argos satellite. The accuracy of the location depended on the number of transmission received by Argos satellites.

Data Analysis

Satellite data was downloaded from Argos and filtered for location accuracy. Argos provides location accuracy using location classes (LC) 3, 2, 1, 0, A, B, and Z (in decreasing accuracy). These classes are associated with the following error estimates LC 3 < 250 m, 250 m < LC2 < 500 m, 500 m < LC1 < 1500 m (Hammerschlag *et al.*, 2011a). While Argos does not report error estimates for LC 0, A, or B, Tougaard, Teilmann and Tougaard (2008) have estimated the error estimates associated with LC A and B to be > 1 km and > 5 km, respectively. LC Z estimates are highly unreliable and as such were removed from the data set.

Following Graham *et al.* (2016), filtered points were then interpolated and regularized to minimize any spatial biases that may exist as a result of the irregular sampling intervals at which SPOT-derived data are acquired. Geopositions were interpolated and regularized to 12-hour frequency up to a three day interval using the piecewise cubic hermite interpolating polynomial (MatLab, The Mathworks, Natick, MA, USA), which has been shown to be highly accurate under similar circumstances (Tremblay *et al.*, 2006). To investigate for potential differences in seasonal patterns, geopositional data were then evaluated with respect to one of three temporal periods: (1) year-round, representing the entire dataset; (2) warm season, representing May through October, and (3) cool season, representing November through April.

Environmental Variables

To identify suitable habitat for the three focal species, habitat suitability models were developed based on five environmental variables: bathymetry, bathymetric slope, chlorophyll A concentration, sea surface temperature, and surface current magnitude (Table 3.1). These variables were selected because the results of Chapter 2, as well as an additional review of previous studies that have created habitat suitability models for sharks, indicated that these variables might help predict the habitat use patterns of the study species (e.g., McKinney *et al.*, 2012; Sousa, 2009). Geospatial rasters for all environmental variables were downloaded using the MGET toolbox for ArcGIS (Roberts *et al.*, 2010) except for multibeam bathymetry, which was download directly from

NOAA (2016), and bathymetric slope which was derived using the surface slope tool in ArcGIS.

Since sea surface temperature, chlorophyll A concentration, and current magnitude all vary seasonally, these rasters were averaged for each temporal period under analysis (year-round, warm and cool seasons) using the cell statistics tool in ArcGIS.

All rasters were then projected to NAD 1983 UTM Zone 17N and clipped to the USA's EEZ to restrict analysis to US territorial waters. Lastly, all of the rasters were resampled to 1 km resolution for consistency in spatial extent and resolution.

Habitat Suitability Models

This study used a maximum entropy (MaxEnt) approach to develop habitat suitability models for each of the study species. A MaxEnt approach was chosen because it is appropriate for presence only data and uses a set of environmental variables to fit a probability distribution of species occurrence over the study area (Phillips, Anderson & Schapire, 2006). MaxEnt has been previously used to create habitat suitability models for blue sharks (*Prionace glauca*; Sousa, 2009), basking sharks (*Cetorhinus maximus*; Siders *et al.*, 2013) and whale sharks (*Rhincodon typus*; Hacohen-Domene *et al.*, 2015; McKinney *et al.*, 2012) based on location data (from surveys and/or satellite tags) and remotely sensed environmental data.

Prior to creating each model, preliminary analyses were run to ensure that each of the models created in this study only included relevant variables that significantly improved model performance. To accomplish this, correlation analysis was first run in ArcGIS to ensure no highly correlated variables were included in any of the models (following a recommendation by Merow, Smith & Silander, 2013). Next, the models were evaluated following a step-wise procedure developed by Yost *et al.* (2008). Briefly, each model was initially created with the five explanatory environmental variables listed in Table 3.1. Models were then run in replicate (n =10) using randomly chosen, non-repeating (cross validated) background samples to allow for statistical comparisons between model variations. Once the five-variable models were completed, the variable that contributed the least to the overall training gain of each model was eliminated and the model was re-run with the four remaining variables. This procedure was repeated five times until only one variable remained. Once all of the model variations were complete, the models were evaluated based on their 'area under receiver operating characteristic curve' (AUC) values, which is an index of model performance that provides a single measure of model accuracy (Yost *et al.*, 2008). Multiple Mann-Whitney U tests were then used to determine the combination of variables that resulted in the highest AUC score with the least number of variables, to avoid overfitting the model.

Once the most influential variables were identified, final habitat suitability models were developed for each species (great hammerhead, tiger, and bull sharks) and for each temporal period (year-round, warm and cool season) to account for species and seasonal variations. Lastly, each model (n = 9) was reclassified based on natural breaks to identify areas that were predicted to have a high, moderate, and low probability of species presence.

Gear Prohibited Zones

Areas where PLL and/or BLL are restricted throughout the SER were identified using two sources: the HMS Commercial Compliance Guide (NOAA, 2014), and the US Code of Federal Regulations (Titles 15 and 50). Shapefiles of the areas identified in these guides were either downloaded from federal websites or constructed in ArcGIS using coordinates provided in one of the sources listed above. In total, 85 areas that restrict BLL and/or PLL were identified (Figure 3.1).

Gear prohibited areas were categorized as year-round, warm, or cool depending on when longline gear is restricted within each area. Restricted areas that overlap with both the warm and cool seasons were placed into the year-round category, even if they did not restrict longline gear all year (i.e., the mid-Atlantic shark closure, which runs from Jan 1-July 31, is included in the year-round model because it overlaps with both the warm and cool seasons).

Identifying Protected Suitable Habitat

The habitat suitability models that had been reclassified to identify areas with a high, moderate, or low probability of species presence were intersected with the gear prohibited zones in ArcGIS to identify where habitats with a high or moderate probability of species presence are protected from longline gear (note that the moderately suitable areas include areas with a high and moderate probability of species presence). Analysis of warm and cool seasonal trends included both the locations where longing gear was prohibited during a specific season as well as the year-round closures. Locations with a high or moderate probability of species presence that overlap with gear restricted areas were identified as protected zones because BLL and PLL gear cannot be used in these habitats and thus the animals are protected from these gears when occupying these areas.

To determine how much of each species' suitable habitat is protected from longline fishing gear, the area of the protected zones (in km^2) was divided by the total modeled habitat area with a high or moderate probability of species presence (in km^2). This result was then converted to a percentage to indicate the percentage of a species' habitat with a high (or moderate) probability of presence that is protected from longline fishing gear, which is hereafter referred to as percent suitable habitat protected.

Results

In total, 23 great hammerhead, 65 tiger, and 29 bull sharks were captured and tagged between March 2010 and December 2015. Following filtering and interpolation, 4,663 data points from 96 animals were used to create habitat suitability models (Table 3.2).

MaxEnt models were created for each of the study species during each temporal period, for a total of 9 individual models (Figures 3.2 - 3.4). All models performed better than random and would be classified as "good" (≤ 0.9 AUC > 0.7) or "very good" (AUC ≥ 0.9), which means they are useful and informative (See Table 3.3 for AUC scores; Baldwin, 2009; Swets, 1988). While the combination of variables that were incorporated into each model varied, the most commonly included environmental variable was bathymetry, which was included in each of the models, while bathymetric slope, which did not significantly improve any of the models, was not included in any model (Table 3.3).

Habitats with a high or moderate probability of great hammerhead, tiger, or bull shark presence varied by species and season (Figures 3.2 – 3.4; Table 3.4). In all three temporal periods, tiger sharks had the largest high, and moderately suitable habitat area followed by great hammerhead, then bull sharks. Seasonally, there is more high, and moderately suitable habitat for great hammerhead sharks in the cool season, while tiger and bull sharks have more high, and moderately suitable habitat in the warm season.

Highly suitable habitats where great hammerhead, tiger, and bull sharks are protected from longline fishing gear also vary by species and season (Figures 3.5 – 3.7). For example, while 78% of highly suitable great hammerhead habitat is protected in the warm season, only 36% is protected in the cool season. In comparison, only 2% of highly suitable bull shark habitat is protected in the warm season while 100% is protected in the cool season. Lastly, highly suitable tiger shark habitat is protected relatively consistently in the warm and cool seasons (48% and 66%, respectively).

Conclusions

In the present study, I used MaxEnt modeling to identify and characterize habitat suitability for three sympatric highly migratory sharks found within the SER and subsequently determine what proportion of their highly suitable habitat is protected from longline gear.

While great hammerhead, tiger, and bull sharks co-occupy the SER, they also exhibit interspecific differences in habitat suitability (Figures 3.2 – 3.4). Despite these differences, there were trends in the environmental variables that helped predict the presence of these species. For example, bathymetry was identified as an environmental variable that significantly improved all habitat suitability models across species and seasons (Table 3.3). This is likely due to relationships that exist between bathymetry and various other important factors for sharks, such as prey fish abundance and diversity (e.g., Collins *et al.*, 2012), and predictable environmental gradients (e.g., frontal or convergence zones; Queiroz *et al.*, 2016). The second most commonly included variable across models was sea surface temperature, which is well established to play an important role in driving distributional patterns of various pelagic fishes such as tuna and billfish (Worm *et al.*, 2005). In contrast, the least relevant variable for all habitat suitability models was bathymetric slope. Bathymetric slope was included in this study because it had been previously incorporated into MaxEnt models for satellite tagged whale sharks (McKinney *et al.*, 2012). However, whale sharks are a filter feeding species and it is plausible that while the upwelling associated with bathymetric slope influences whale shark habitat use, it does not influence the habitat use of the predatory species evaluated here.

The environmental variables that were included in each of the seasonal habitat suitability models can be compared to previously published literature to help indentify variables that may motivate the study species to undergo seasonal migrations to different habitats. For example, current magnitude significantly improved model performance for great hammerheads in the warm season, but not in the cool season, suggesting current magnitude is most important to great hammerheads during the warm season. This finding supports a theory presented by Hammerschlag *et al.* (2011b) that great hammerhead sharks may move into the Gulf Stream to follow prey species as they migrate North during the warm season. Additionally, while sea surface temperature helped predict great hammerhead habitat use in both the warm and cool seasons, great hammerheads are found in shallower waters during the warm season than in the cool season, which may make these species more vulnerable to nearshore threats in the warm season.

In comparison, the tiger shark habitat suitability models were significantly improved by incorporating chlorophyll A in the warm season, but this factor was replaced by current magnitude in the cool season. The range of chlorophyll A values that helped predict tiger shark presence was quite low in the warm season, suggesting that tiger sharks are more likely to be present in offshore waters (where chlorophyll A values are generally lower, in comparison to coastal areas). During the cool season, surface current magnitude can help predict tiger shark presence, suggesting tiger sharks may be found closer to the Gulf Stream in the cool season than the warm season. Since both chlorophyll A and current magnitude are related to ocean productivity, these results are consistent with the fact that multiple studies have associated tiger sharks movements with variations in prey abundance (Heithaus, 2001; Heithaus & Dill, 2002; Holmes *et al.*, 2012; Lowe *et al.*, 2006; Meyer *et al.*, 2009a; Meyer *et al.*, 2010).

Lastly, incorporating sea surface temperature into the bull shark model during the cool season significantly improved model performance, but this was not the case in the warm season, suggesting bull sharks may be more strongly impacted by a temperature minimum, than a temperature maximum. This theory is consistent with the fact that within the SER bull sharks have been documented in waters up to 40 °C (Shipley, 2005), which is higher than great hammerhead or tiger sharks (see Chapter 2) but have been reported dead in waters < 10 °C (Matich & Heithaus, 2012) and have been reported gathering around the heated outflow of power plants when the water temperature was 10 - 15 °C (Snelson *et al.*, 1984).

Year-round, the amount of highly suitable habitat protected from longline gears within the SER differed by species (Figure 3.5). Overall, highly suitable great hammerhead and tiger shark habitat was relatively well protected (41.18% and 50.23%, respectively). This protection was primarily due to the East Florida Coast Closed Area, which is closed to vessels with PLL gear onboard year-round. As both great hammerhead and tiger sharks are caught in the PLL fishery (Gallagher *et al.*, 2014b), and great hammerhead sharks are extremely sensitive to capture stress (Gallagher *et al.*, 2014c), this protected area is likely providing a significant benefit to these species. In comparison, suitable habitats for bull sharks are relatively poorly protected within the SER year-round. However, when interpreting this result, it is worth considering that within the SER the area of suitable habitat for bull sharks is comparatively smaller than for great hammerhead or tiger sharks (highly suitable bull shark habitat is less than 10% of the size of highly suitable great hammerhead habitat and less than 2% of the size of highly suitable tiger shark habitat). When the habitat suitability models created here (Figures 3.2 – 3.4) are compared to previous work by Graham *et al.* (2016), who determined core habitat use areas for bull sharks, it is clear these core home ranges and the modeled highly suitable habitat areas for bull sharks are primarily within state waters, which were outside the scope of this study. While bull shark populations in the study region appear to be stable at this time (Carlson *et al.*, 2012), the relatively small size of the highly suitable coastal areas identified for bull sharks in this study may make these locations easy targets for designation of future gear restricted zones or MPAs should managers identify the need to implement protective measures for this species.

The percentage of highly suitable habitat protection within the SER for great hammerhead, tiger, and bull sharks varied seasonally. Highly suitable great hammerhead habitats are well protected in the warm season (78.48%), but there is a large area of vulnerable highly suitable habitat during the cool season, west of southern Florida and Everglades National Park (ENP; Figures 3.6 – 3.7). In comparison, highly suitable tiger shark habitats are relatively well protected during the warm season (48.33%), though some highly suitable habitats both north and east of the East Florida Coast Closed Area are vulnerable to longline gears. In the cool season, highly suitable habitats for tiger sharks are also relatively well protected (66.05%), except for west of southern Florida and ENP, in relatively the same area where highly suitable great hammerhead habitats are also vulnerable to longlines (Figure 3.7 – 3.8). Thus, extending restrictions on longline gear to this area of federally managed waters east of southern Florida and ENP may have positive outcomes for both great hammerhead and tiger sharks (Figure 3.8).

In contrast, only 2.39% of highly suitable bull shark habitat is protected in the SER during the warm season, while 100% is protected in the cool season (Figures 3.6 – 3.7). When these results are compared to the year-round model (Figure 3.5) it is clear that the vulnerable areas identified in the year-round model are very similar to those identified in the warm season model. Since the seasonal models indicate that highly suitable bull shark habitat is protected in the cool season, and only truly vulnerable in the warm season, a seasonal closure to longlines in these highly suitable habitats during the warm season would likely provide sufficient protection for bull sharks if further management becomes necessary.

The primary limitation of this study is that the results are based on modeled habitat. While MaxEnt modeling has been used in a wide variety of studies (Baldwin, 2009; Jones & Cheung, 2015), it still results in a model. Thus, these results should be validated with fisheries capture data to confirm the habitats identified here are truly locations where these species are vulnerable to longing gear. Additional study limitations may include, small sample sizes and spatial errors, which are commonly discussed limitations of satellite tag data. However, MaxEnt is resilient to both of these limitations. Maxent models can be developed with anywhere from 5 - 50 presence locations, and little benefit is seen by adding additional locations above 50 (Baldwin, 2009). Given that in this study a minimum of 272 and a maximum of 3310 locations were included, sample size is not likely a limitation of this study. Additionally, MaxEnt is relatively resilient to spatial errors in location data up to 5 km (Baldwin, 2009). While it's possible some locations may have originally had spatial errors above 5 km (the spatial error associated with location class B has been estimated to be > 5km; Tougaard *et al.*, 2008), all of the location data used in this study was filtered and interpolated to minimize any impact unreliable locations may have had on the results.

It is important to also consider that all of the great hammerhead, tiger, and bull sharks included in this study were tagged in the same general region within the tropical and temperate Atlantic Ocean (with most being tagged between Miami and Islamorada Florida, and some being tagged in the Bahamas). Within this region population and sub-population ranges are not fully known. As such, it is possible the results presented here may be biased towards animals that spend the majority of their time in the subtropical Atlantic and it would be valuable to incorporate data from other tagging studies, particularly those originating in the Gulf of Mexico. Additionally, further research is required to determine if the environmental preferences of the animals examined here can be applied to other populations, or if there are regional differences in the environmental preferences and habitat use patterns of the study species. Lastly, while subadult and adult individuals of both sexes were tagged in this study, future studies should investigate if size or sex impacts the habitat use of these species.

In summary, this study demonstrated that despite being highly migratory, it is possible to identify highly suitable habitat for great hammerhead, tiger, and bull sharks. Despite the fact that these species are co-occurring apex predators, there are interspecific differences in the environmental variables that influence suitable habitat and these differences can directly impact each species' vulnerability to longline gear. Additionally, while the gear restricted areas discussed in this study were not necessarily implemented to protect great hammerhead, tiger, or bull sharks, they are providing a substantial amount of protection for these animals. The protocol developed here can be applied to other economically and ecologically important migratory species such as other sharks, tunas, marine mammals, turtles and billfish, and may be used in conjunction with predictions of sea surface temperature to determine how habitats and relative levels of protection will vary under future climate change scenarios.

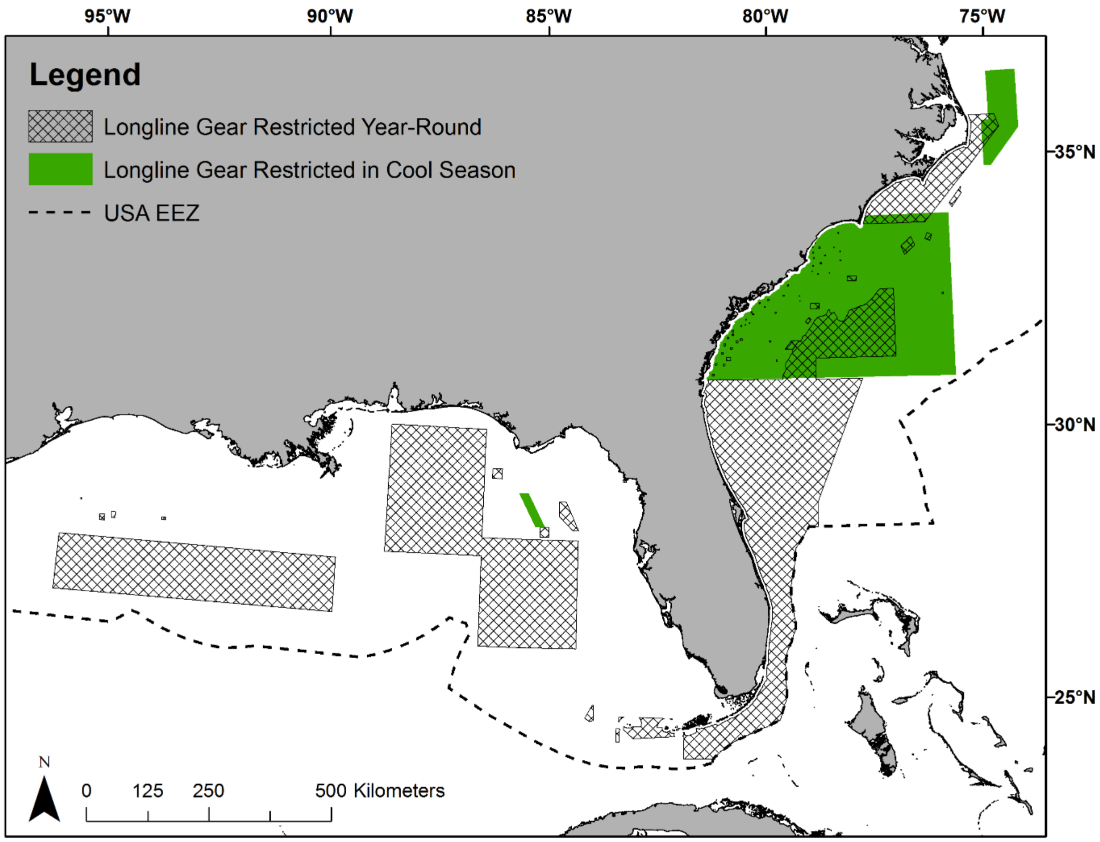

Figure 3.1. Regions where bottom and/or pelagic longline gear is prohibited in the southeast region of the USA's EEZ year-round, which is the same as during the warm season (May - October), and exclusively in the cool season (November - April). Note that in the cool season the year-round closures still apply.

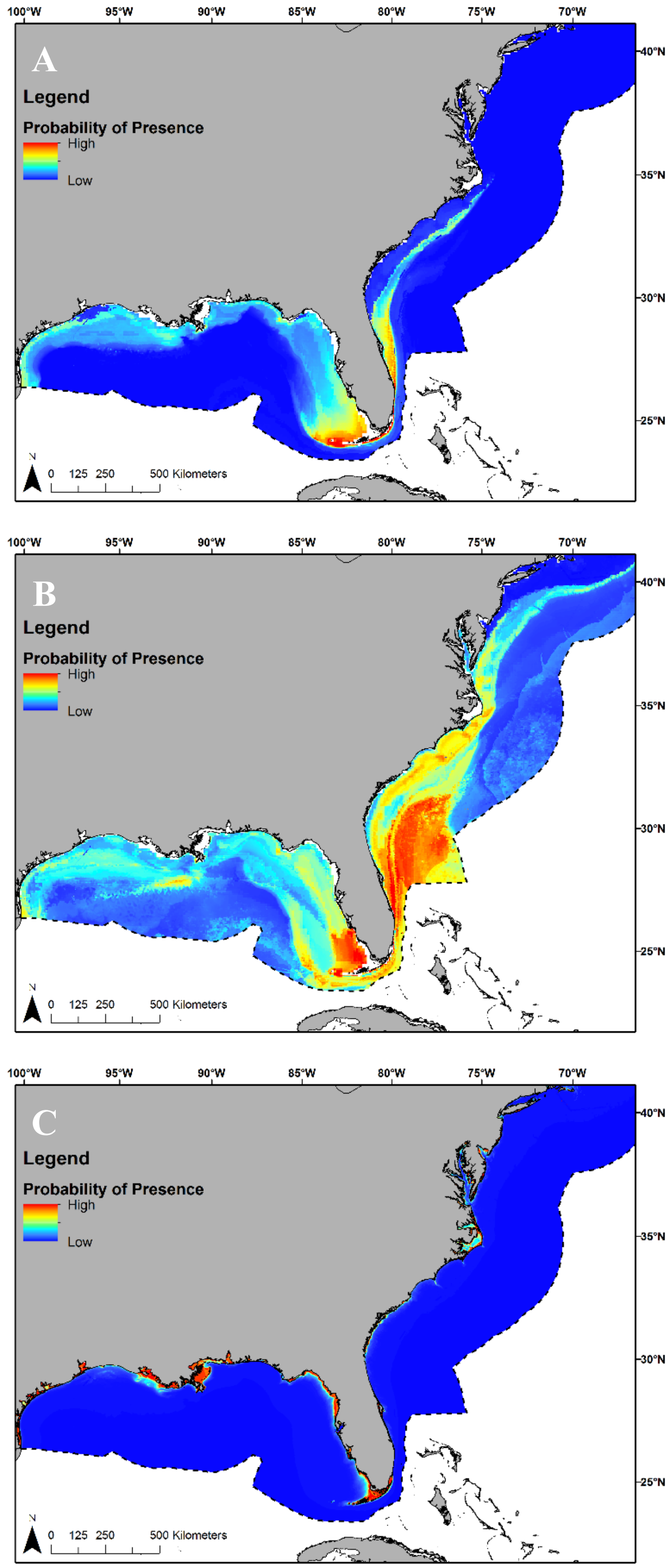

Figure 3.2. Probability of great hammerhead (A), tiger (B), and bull shark (C) presence within the southeast region of the USA's EEZ year-round.

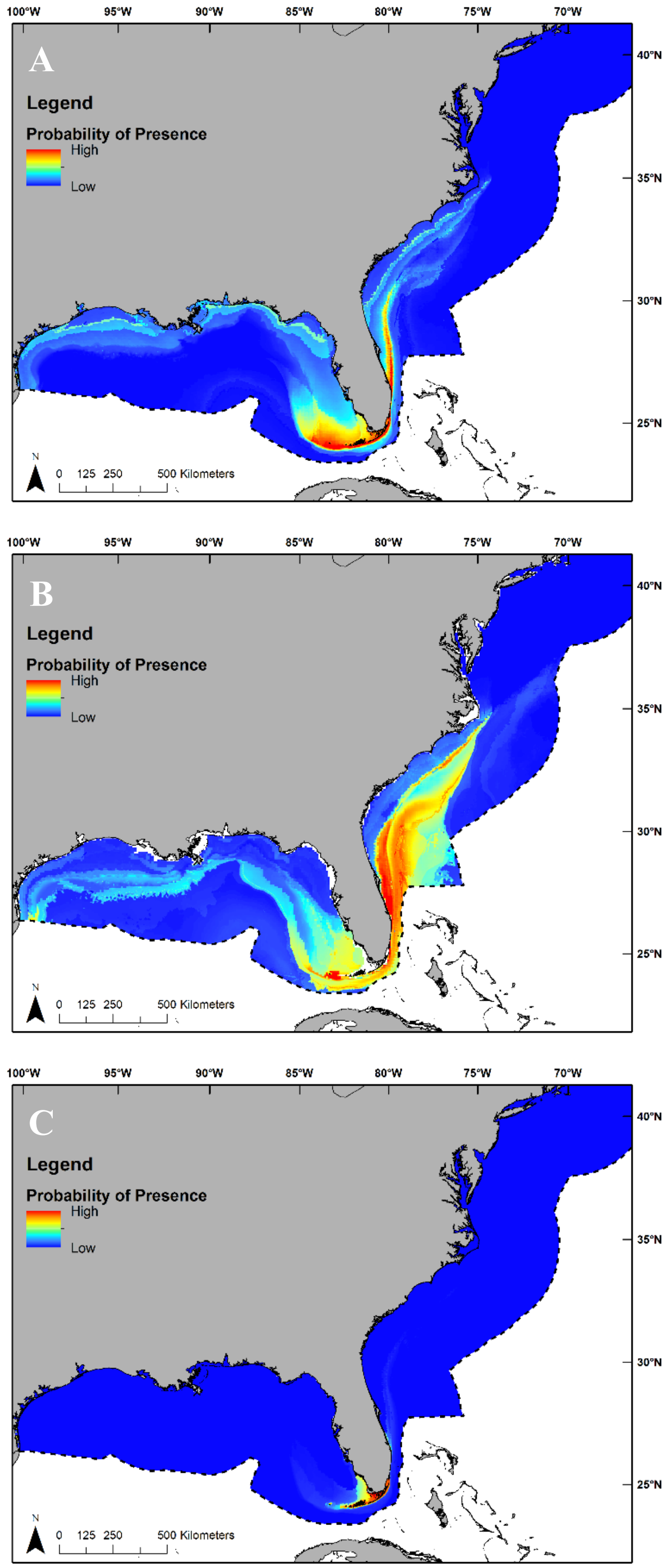

Figure 3.3. Probability of great hammerhead (A), tiger (B), and bull shark (C) presence within the southeast region of the USA’s EEZ in the cool season (November - April).

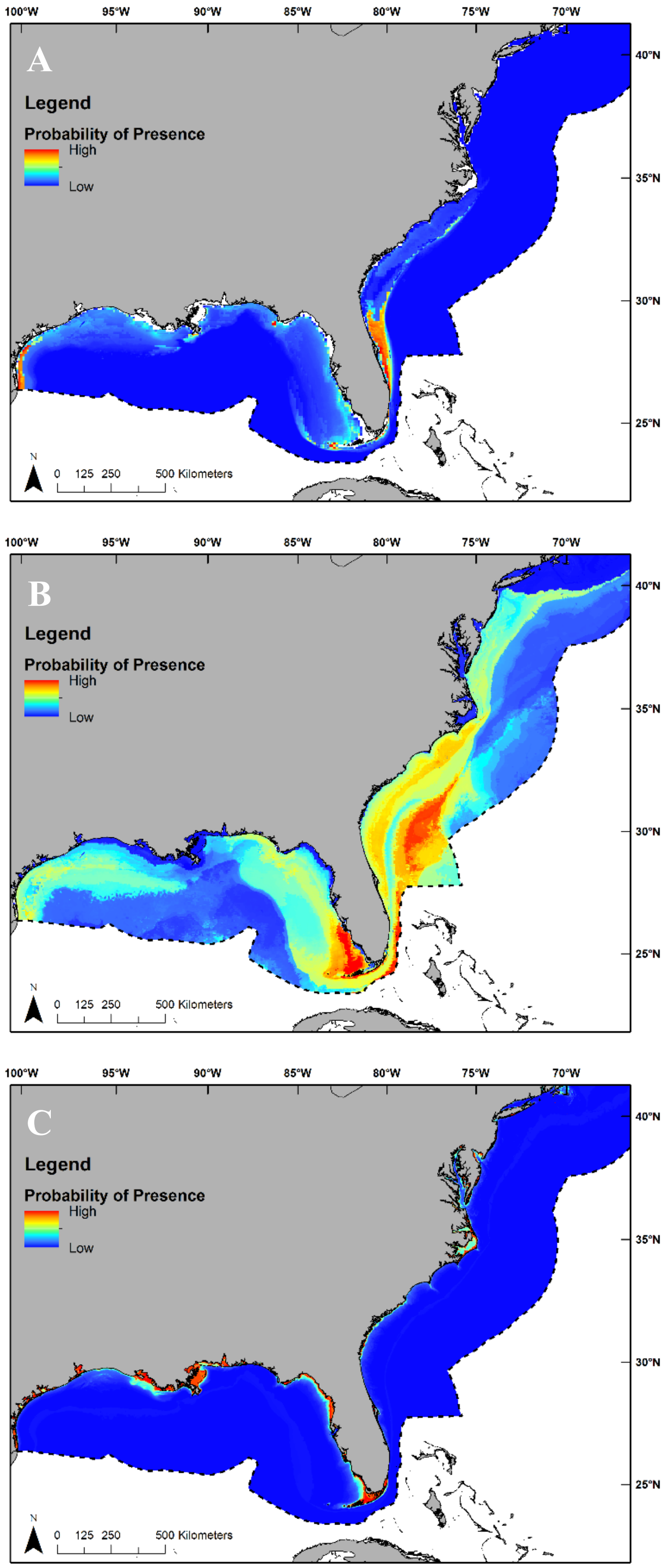

Figure 3.4. Probability of great hammerhead (A), tiger (B), and bull shark (C) presence within the southeast region of the USA's EEZ in the warm season (May - October).

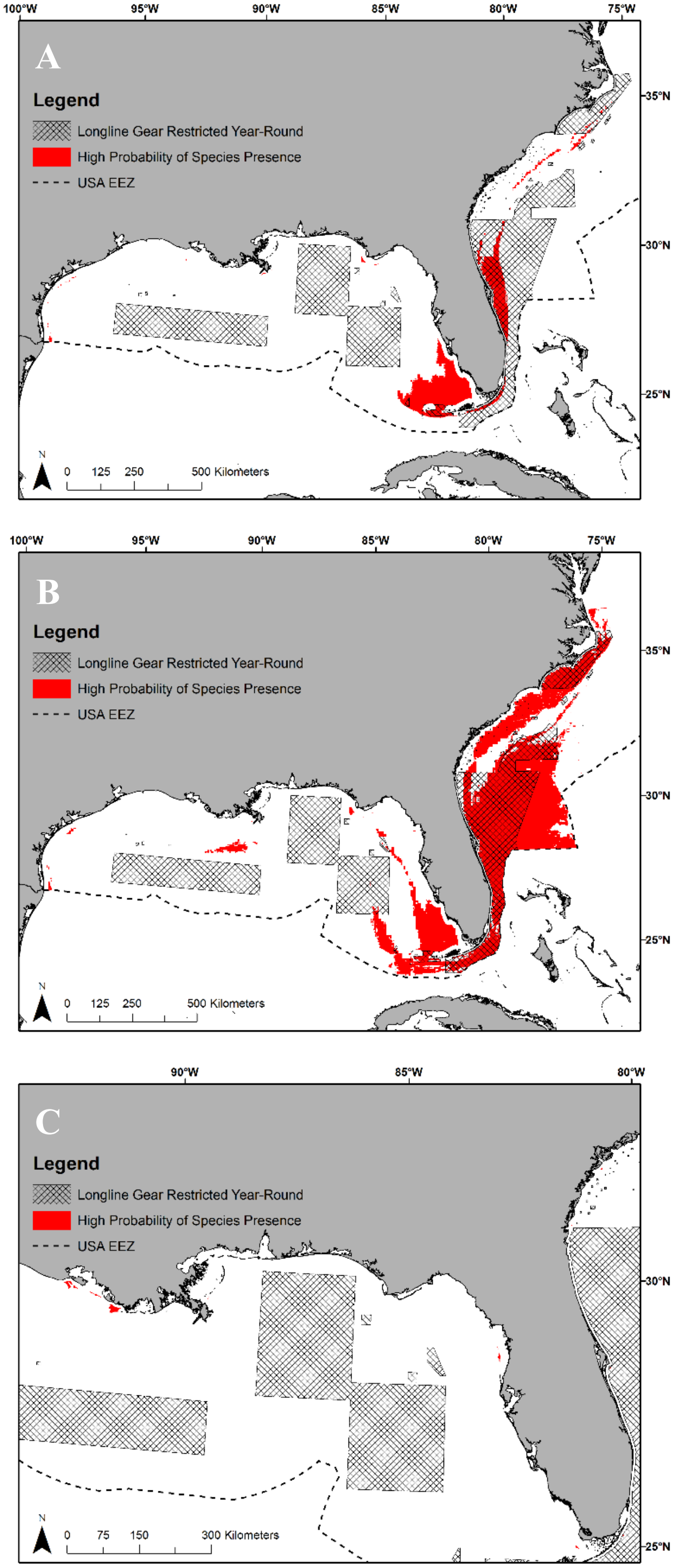

Figure 3.5. Locations where highly suitable great hammerhead (A), tiger (B), and bull shark (C) habitats are protected from longline fishing gear in the SER year-round.

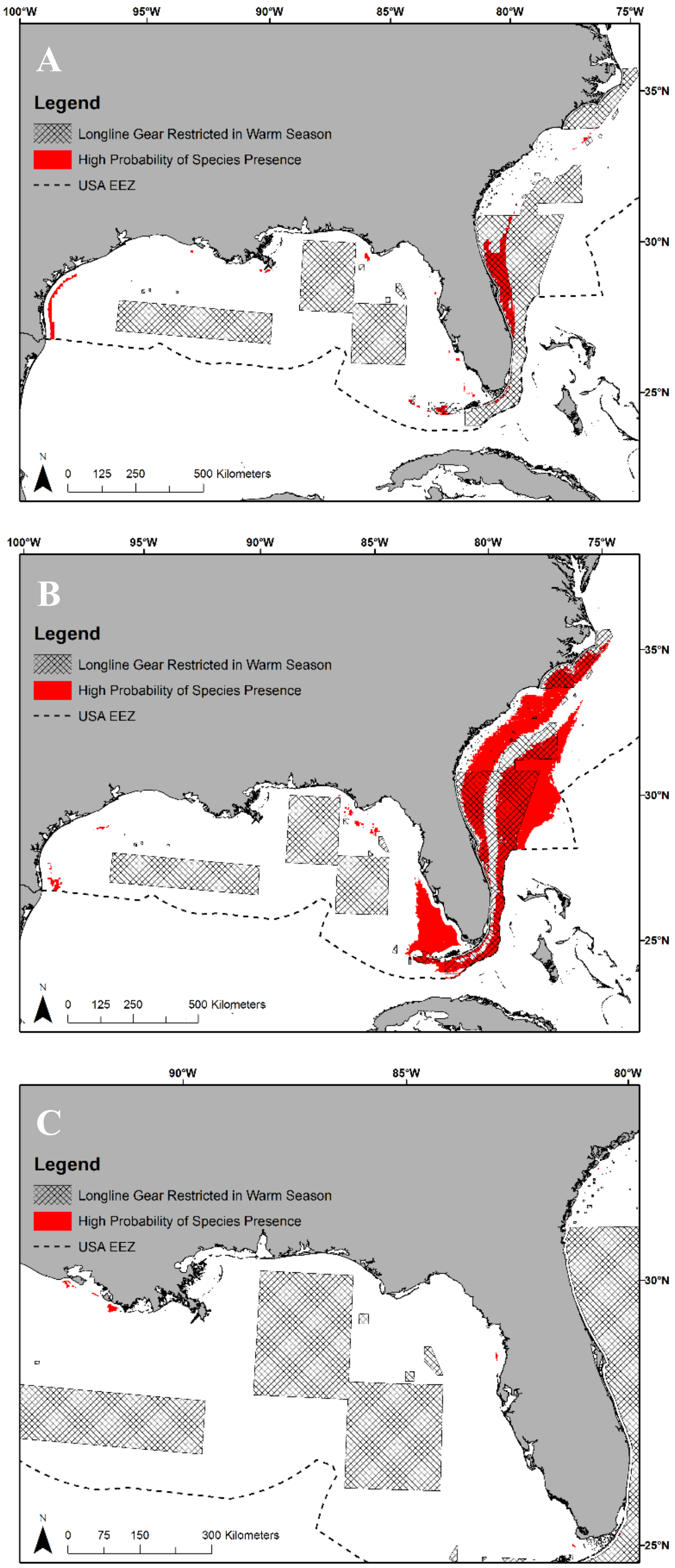

Figure 3.6. Locations where highly suitable great hammerhead (A), tiger (B), and bull shark (C) habitats are protected from longline fishing gear in the SER in the warm season (May - October).

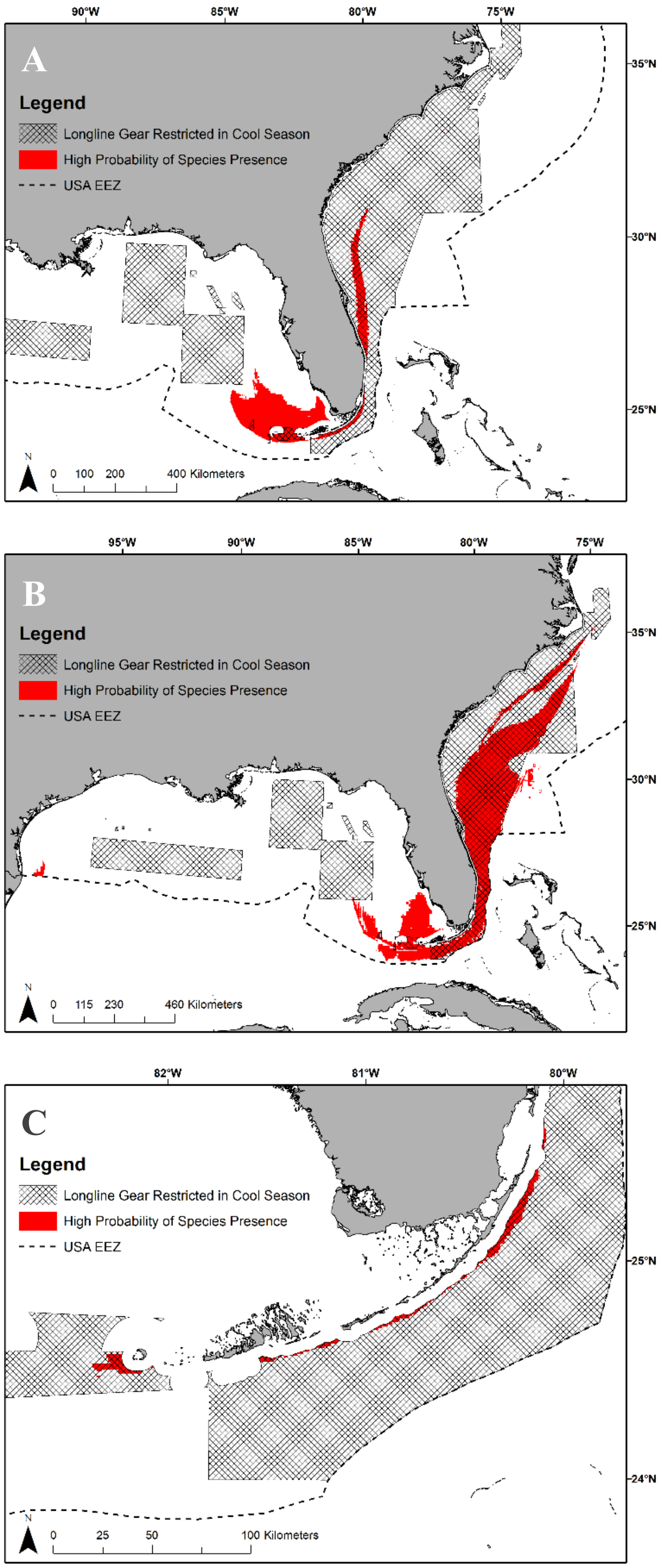

Figure 3.7. Locations where highly suitable great hammerhead (A), tiger (B), and bull shark (C) habitats are protected from longline fishing gear in the SER in the cool season (April - November).

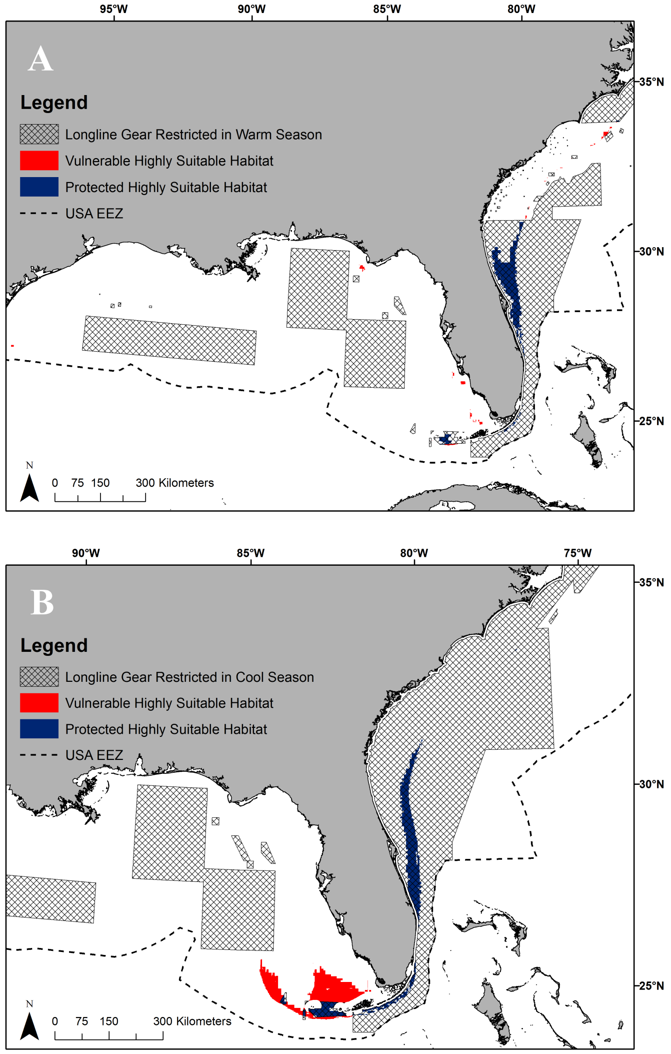

Figure 3.8. Locations where highly suitable great hammerhead and tiger shark habitats are vulnerable to and protected from longline fishing gear in the SER in the warm season (A; May - October) and cool season (B; November - April).

Table 3.1 The environmental variables used to create preliminary MaxEnt habitat suitability models in this study.

Variable	**Unit**	**Resolution**	**Temporal Range**	**Source**
Sea Surface Temperature	°C	4 km	Monthly Mar. 1, 2010–May 31, 2015*	NASA MODIS-Aqua
Chlorophyll A Concentration	mg/m^3	4 km	Monthly Mar. 1, 2009–May 31, 2015	NASA OceanColor
Surface Current Magnitude	m/s	1/12 °	Daily Mar. 1, 2009–May 31, 2015	HYCOM
Multibeam Bathymetry	m	~ 500 m**	N/A	NOAA
Bathymetric Slope	% Rise	1 km	N/A	ArcGIS Derived

* Data from Mar. 1, 2009 – Mar. 1, 2010 was unavailable.

** The multibeam bathymetry raster was filled with ETOPO1 data with 1 arc minute resolution in locations where multibeam data was unavailable.

Table 3.2 Summary statistics of the sharks included in this study. Note that some sharks were present in both seasons.

	Year-Round	**Warm**	**Cool**		
Species	Number of sharks (Number of interpolated locations)			**Sex (F:M)**	**STL (cm)**
Great Hammerhead	25 (557)	16 (272)	14 (285)	10:15	124-450
Tiger	45 (3310)	35 (2321)	28 (989)	37:8	175-403
Bull	26 (796)	12 (326)	23 (467)	18:8	170-269

Table 3.3. The environmental variables used to create each of the final MaxEnt habitat suitability models in this study.

Species	**Mean**	**SD**	**95% CI**	**Range**
Year-Round				
Great Hammerhead (Test AUC = 0.94)				
Bathymetry (m)	75.43	336.51	46.94 - 103.93	1 - 3939
Current Magnitude (m/s)	0.258	0.171	0.242 - 0.274	0.061 - 1.441
SST (°C)	25.69	1.35	25.58 - 25.80	21.42 - 28.42
Tiger (Test AUC = 0.786)				
Bathymetry (m)	549.42	834.1	520.87 - 577.97	1 - 5280
Chlorophyll A (mg/m^3)	0.713	1.366	0.666 - 0.76	0.077 - 13.614
Current Magnitude (m/s)	0.476	0.346	0.464 - 0.488	0.047 - 1.566
SST (°C)	25.17	2.35	25.09 - 25.25	13.59 - 28.09
Bull (Test AUC = 0.954)				
Bathymetry (m)	29.52	120.77	19.47 - 39.57	1 - 929
Warm Season				
Great Hammerhead (Test AUC = 0.962)				
Bathymetry (m)	31.23	65.63	23.18 - 39.27	1 - 870
Current Magnitude (m/s)	0.313	0.205	0.284 - 0.343	0.1 - 1.51
SST (°C)	28.41	0.81	28.31 - 28.51	27.02 – 29.61
Tiger (Test AUC = 0.812)				
Bathymetry (m)	579.55	889.97	543.3 - 615.8	1 - 5280
Chlorophyll A (mg/m^3)	0.656	1.23	0.606 - 0.706	0.048 - 15.89
SST (°C)	27.73	2	27.65 - 27.81	19.15 - 30.7
Bull (Test AUC = 0.958)				
Bathymetry (m)	23.55	103.13	10.32 - 36.77	1 - 929
Cool Season				
Great Hammerhead (Test AUC = 0.927)				
Bathymetry (m)	116.17	458.82	62.19 - 170.14	1 - 3939
SST (°C)	22.76	2.22	22.5 - 23.02	18.53 - 26.22
Tiger (Test AUC = 0.879)				
Bathymetry (m)	476.91	676.02	434.16 - 519.66	1 - 4742
Current Magnitude (m/s)	0.542	0.366	0.518 - 0.565	0.081 - 1.5
SST (°C)	23.73	1.55	23.63 - 23.83	17.36 - 26.02
Bull (Test AUC = 0.98)				
Bathymetry (m)	33.92	132.23	19.4 - 48.44	1 - 787
SST (°C)	24.48	0.92	24.39 - 24.56	18.57 - 27.02

Table 3.4. Area (in km^2) of highly and moderately suitable habitat, as well as area of protected habitat in the SER for great hammerhead (GH), tiger (T), and bull sharks (B) year-round, as well as in the warm, and cool seasons (May - October and November - April, respectively).

	Highly Suitable Habitat	**Moderately Suitable Habitat**	**Protected Highly Suitable Habitat**	**Protected Moderately Suitable Habitat**	**Percent Highly Suitable Protected**	**Percent Moderately Suitable Protected**
			Year-Round			
GH	55012.40	280798.08	22654.28	52818.29	41.18%	18.81%
T	257563.52	617440.99	129373.47	198315.17	50.23%	32.12%
B	500.82	9229.89	11.98	309.98	2.39%	3.36%
			Warm Season			
GH	23272.02	201122.95	18262.93	41185.18	78.48%	20.48%
T	207757.95	648663.73	100407.89	204754.99	48.33%	31.57%
B	500.82	9229.89	11.98	309.98	2.39%	3.36%
			Cool Season			
GH	46609.67	322281.10	16809.88	98928.33	36.07%	30.70%
T	165435.72	395608.20	109264.70	164774.74	66.05%	41.65%
B	418.10	3623.15	418.09	1351.14	100.00%	37.29%

Chapter 4 - Discussion

While great hammerhead, tiger, and bull sharks are all co-occurring apex predators within the SER, their movement and habitat use patterns vary, which can impact their vulnerability to longline fisheries. This thesis used a combination of techniques (a literature review and habitat suitability models) to address two primary research aims: (1) to summarize the habitat use patterns and the environmental drivers of the movements of great hammerhead, tiger, and bull sharks, and (2) to identify highly suitable habitats for these species, quantify how much their highly suitable habitat is protected from longline gears, and determine how this protection varies seasonally.

While there is still a lot that is unknown about the movements and environmental ranges of great hammerheads, this thesis summarized what is known about these animals within the SER. Great hammerhead sharks are most commonly found in coastal tropical and subtropical marine habitats in water temperatures of approximately 25 °C. While their habitats are on average 75 m deep and they can dive to at least 60 m (e.g., Vaudo & Heithaus, 2009), these animals can also be found in pelagic habitats (e.g., Table 3.3 and Hammerschlag *et al.*, 2011b). Great hammerheads are found in productive waters and current magnitude (which can be related to ocean productivity) can be used to predict their presence. While great hammerheads appear to primarily occupy coastal areas of the continental shelf they can also undergo occasional long-distance migrations of at least ~1,200 km into pelagic waters (e.g., Espinoza *et al.*, 2014; Hammerschlag *et al.*, 2011b; Heithaus *et al.*, 2007a). Taken together, these movement and habitat use patterns suggest that great hammerhead sharks may be primarily susceptible to commercial fisheries within countries' territorial waters (for example, within the US exclusive economic zone), but may occasionally be vulnerable to offshore pelagic fisheries in international waters as well.

In comparison, tiger sharks are found in a wide range of coastal and pelagic tropical and subtropical marine habitats. The temperatures tiger sharks have been recorded in range from 4 - 33 °C. This large range is due to their well-documented vertical "yo-yo" diving through the water column (see Chapter 2). Consistently, the sea surface temperature range predicted by the habitat suitability models was from 14 - 28 °C, with a mean at 25.17 °C, which is consistent with sea surface temperatures observed in tropical and subtropical habitats. Tiger sharks can dive to 1136 m and their mean habitat depth is 549 m, which is consistent with movements into pelagic waters. Similarly to great hammerhead sharks, tiger sharks have been documented in productive waters and chlorophyll A and current magnitude (which can both be proxies for productivity) can help predict their presence. Consistent with the high diversity of habitats these animals can be found in, tiger sharks can follow a wide range of movement patterns, from long distance migrations, to establishing small home ranges in spatially restricted areas. Combined, these patterns suggest that tiger sharks are likely to be vulnerable to offshore commercial fishing in international waters, but may occasionally be susceptible to anthropogenic threats in coastal waters as well (such as pollution or fisheries in coastal waters).

Lastly, bull sharks are most commonly found in coastal tropical and subtropical waters. However, unlike great hammerhead and tiger sharks, bull sharks are not restricted to marine environments. In fact, bull sharks have been documented in salinity ranges from 0 - 42 ppt (see Chapter 2). Bull sharks are generally found in slightly warmer waters than great hammerhead or tiger sharks. While there is overlap between the three species temperature preferences, bull sharks have been recorded in waters from ~14 - 40 °C, and appear to prefer waters from 25 - 29.9 °C. This slightly higher temperature range (in comparison to great hammerhead or tiger sharks) can be explained by the fact that bull sharks use shallower habitats compared to the other study species. For example, the mean habitat depth recorded in the bull sharks' year-round habitat suitability model was 29 m, compared to 75 m for great hammerhead and 549 m for tiger sharks. Similarly to great hammerhead and tiger sharks, bull sharks prefer productive areas with abundant prey (e.g., Drymon *et al.*, 2014; Parker & Bailey, 1979). However, unlike the other two study species, bull sharks are a coastal species that have small home ranges and generally do not undertake long distance movements. Thus, bull sharks are likely to interact with commercial fisheries within territorial waters as well as highly urbanized habitats.

This study demonstrated that despite being highly migratory, it is possible to identify highly suitable habitat for great hammerhead, tiger, and bull sharks. Additionally, these models can be used to address the second aim of this thesis, which was to identify highly suitable habitat for the study species, quantify how much of their highly suitable habitat is protected from longline gears, and determine how this protection varies seasonally.

Within the SER, there were clear species-specific and seasonal patterns in habitat suitability (Figures 3.2 – 3.4), which were generally consistent with the findings from the literature review. In terms of how effectively current gear restricted areas protect highly suitable shark habitat, this protection also varies by species and season (Figures 3.5 – 3.7). Despite the fact that the gear restricted areas included in this thesis may not have been specifically designated to protect the habitats of the study species, some of the gear restricted areas are protecting a substantial amount of highly suitable shark habitat, particularly for great hammerhead and tiger sharks. However, there are also locations where highly suitable habitats are vulnerably to longline fishing gear, which could serve as locations for future management areas, should they be warranted (e.g., Figure 3.8).

Year-round, highly suitable great hammerhead and tiger shark habitat was relatively well protected (41.18% and 50.23%, respectively). This protection was primarily due to the East Florida Coast Closed Area, which is closed to vessels with PLL gear onboard year-round. In comparison, suitable habitats for bull sharks are relatively poorly protected within the SER year-round. This was because most of the modeled highly suitable bull shark habitat was within state waters, which was outside the scope of this study. However, the relatively small size of the highly suitable bull shark habitat outside of state waters may be an easy target for future gear restricted zones or MPAs should managers identify the need to implement protective measures for this species.

While the percentage of protected highly suitable great hammerhead, tiger, and bull shark habitat within the SER varied seasonally, the East Florida Coast Closed Area protected substantial areas of highly suitable great hammerhead and tiger shark habitat in both seasons as well as highly suitable bull shark habitat in the cool season. Thus, despite not necessarily being implemented to specifically protect great hammerhead, tiger, or bull shark habitat, this area is likely providing substantial protection for these species.

In contrast, there is a region west of South Florida and ENP where highly suitable great hammerhead and tiger shark habitats are vulnerable to longline gears (Figure 3.8). Thus, extending restrictions on longline gear to this area of federally managed waters

East of Southern Florida and ENP may have positive outcomes for both great hammerhead and tiger sharks.

In addition to modeling current species distributions, habitat models can be important tools for exploring how climate change may impact biodiversity over time (Jones & Cheung, 2015). For example, Jones and Cheung (2015) constructed species distribution models for 802 exploited marine and invertebrate species world wide using three habitat modeling programs (one of which was MaxEnt), and concluded that on average the models predicted a poleward shift in species habitat following both low and high emissions scenarios. The authors also predicted that regional hotspots would change and that there may be localized extinctions, particularly near the equator. Additionally, previous research on bluefin tuna (*Thunnus thynnus*) in the Gulf of Mexico has reported that increases in water temperature will cause changes in the habitat suitability of both adult and larval individuals (Muhling *et al.*, 2011). While the habitat models generated here may provide insights as to how the study species will respond to various climate change scenarios in the oceans (e.g., increasing temperatures), future research is required to develop true predictive models. Lastly, it is worth considering that if the study species change their distribution as a result of climate change induced increases in water temperature, which consequently shifts their highly suitable habitat, the effectiveness of the current longline gear restricted areas for the protection of great hammerhead, tiger and bull sharks in the SER will also change and may need to be modified to maintain effective protection (if necessary).

Being able to identify the habitats and environmental ranges that these species prefer can help focus conservation efforts through targeted spatial planning. While only great hammerheads are currently considered Endangered by the IUCN (2014), tiger and bull sharks are both considered Near Threatened so their populations should also be closely monitored. Despite being co-occurring, the variation in each species' movement ecology means that it may not be appropriate to group these species together into the same management plan (except for in very unique cases, such as in The Bahamas, where all shark fishing has been banned and all three species inhabit the same areas; Graham *et al.*, 2016). The results of this present study may help managers identify where spatial management plans are likely to be successful, should conservation measures be deemed necessary.

Despite being co-occurring apex predators, there are interspecific differences in the habitat use patterns of great hammerhead, tiger, and bull sharks, as well as differences in the environmental variables that can predict their presence, and these differences can directly impact each species' vulnerability to longline gear. Additionally, while the gear restricted areas discussed in this study may not have been specifically implemented to protect this study's focal species, they are providing a substantial amount of protection for these animals. The protocol developed here can be applied to other economically and ecologically important migratory species such as other sharks, tunas, marine mammals, turtles and billfish, and may be used in conjunction with predictions of sea surface temperature to determine how habitats and relative levels of protection will vary under future climate change scenarios.

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APPENDIX A

SUMMARIZED GREAT HAMMERHEAD SHARK LITERATURE REVIEW TABLE

Appendix A. Summary of great hammerhead shark studies included in Chapter 2 of this thesis. Table codes - Dist. Travel: distance a shark travelled; Home Range: home range size; Location: general study location; GPS: was a GPS location recorded? (Yes or No); Habitat type: general habitat type the study occurred in; Temp/Salinity/Chloro: temperature, salinity, or chlorophyll A range sharks were documented in; Distance from shore: how far the sharks were documented from shore; Max. Depth: the maximum depth documented in a study; Mat: Maturity status (Mature, Immature, Subadult); Sex: sex of animal(s) included in a study (Male, Female, Both sexes). An “x” indicates a category was not specifically addressed in a study, though it may have been briefly discussed.

Reference	**Dist. Travel (km)**	**Home Range**	**Location**	**GPS**	**Habitat Type**	**Temp (°C)**	**Salinity (ppt)**	**Chloro. (mg/m^3)**	**Distance from shore (km)**	**Max. Depth (m)**	**Mat.**	**Sex**
Cliff (1995)	x	x	KwaZulu-Natal, South Africa	Y	x	18.5-26.1	x	x	300-500	14	M & I	Both
Dudley and Cliff (2010)	x	x	KwaZulu-Natal, South Africa	Y	Sand/Beach	x	x	x	400	14	x	x
Espinoza *et al.* (2014)	x	x	Great Barrier Reef, Australia	Y	Combination	x	x	x	x	x	M & I	Both
Hammerschlag *et al.* (2011b)	1200	x	Florida Keys, Florida, USA	Y	Reef	17-27.9	x	x	500	x	x	M
Heithaus *et al.* (2007a)	x	x	Florida Keys, Florida, USA	Y	Combination	x	x	x	x	13	M	Both
Heithaus *et al.* (2013)	x	x	Shark Bay, Australia	N	Seagrass	x	x	x	x	x	x	x
Lyle (1984)	x	x	Northern Territory, Australia	N	Coastal	x	x	x	x	x	x	x

Reference	Dist. Travel (km)	Home Range	Location	GPS	Habitat Type	Temp (°C)	Salinity (ppt)	Chloro. (mg/m^3)	Distance from shore (km)	Max. Depth (m)	Mat.	Sex
Parker and Bailey (1979)	x	x	Mustang and Padre Islands, Texas, USA	Y	Sand/Beach	26-27	33-34	Abundant prey	200-400	x	x	x
Pikitch *et al.* (2005)	x	x	Glover's reef atoll, Belize	N	Combination	x	x	x	x	x	I	x
Sadowsky (1971)	x	x	Bom Abrigo, Cananéia	N	Sand/Beach	26.2	x	x	x	28	M	x
Stevens and Lyle (1989)	x	x	Northern Australia	N	x	x	x	x	x	3	x	Both
Taniuchi (1974)	x	x	Southwest Japan	Y	x	x	x	Abundant prey	x	60	x	Both
Vaudo and Heithaus (2009)	x	x	Shark Bay, Australia	Y	Combination	20-31	x	x	500-1,000	3	x	x

APPENDIX B

SUMMARIZED TIGER SHARK LITERATURE REVIEW TABLE

Appendix B. Summary of tiger shark studies included in Chapter 2 of this thesis. See Appendix A for table codes.

Reference	**Dist. Travel (km)**	**Home Range**	**Location**	**GPS**	**Habitat Type**	**Temp (°C)**	**Salinity (ppt)**	**Chloro. (mg/m^3)**	**Distance from shore (km)**	**Max. Depth (m)**	**Mat.**	**Sex**
Afonso and Hazin (2014)	33-1,193	x	Northeastern Brazil	Y	Combination	x	x	x	1-25	264	I	Both
Afonso and Hazin (2015)	x	x	Recife, Brazil	Y	x	4-31.2	x	x	x	1,112	x	Both
Afonso *et al.* (2011)	x	x	Natal and Recife, Brazil	Y	Offshore	x	x	x	1-3	14	x	x
Brunnschweiler (2009)	x	x	Shark Reef Marine Reserve, Fiji	N	Reef	x	x	x	x	38	x	F
Brunnschweiler, Abrantes and Barnett (2014)	x	x	Shark Reef Marine Reserve, Fiji,	N	Reef	x	x	x	x	30	x	F
Carlson, Grace and Laco (2002)	x	x	Florida & South Carolina, USA	Y	Combination	x	x	x	16.7-92.6	42	I	x
Clua *et al.* (2013)	x	x	New Caledonia, France	Y	x	x	x	x	x	x	M & I	Both
Crow and Hewitt (1988)	x	x	Florida Keys, Florida, USA	Y	x	x	x	x	x	5.5	x	F

Reference	Dist. Travel (km)	Home Range	Location	GPS	Habitat Type	Temp (°C)	Salinity (ppt)	Chloro. (mg/m^3)	Distance from shore (km)	Max. Depth (m)	Mat.	Sex
Dale *et al.* (2011),	x	x	French Frigate Shoals, Hawaii	Y	Combination	x	x	x	x	60	M & I	Both
Dicken and Hosking (2009)	x	x	Aliwal Shoal MPA, South Africa	N	Reef	x	x	x	5	27	M & I	Both
Driggers *et al.* (2008)	x	x	Southeastern USA	Y	Combination	x	x	x	x	366	I	x
Dudley (1997)	x	x	Queensland & South Africa	N	Sand/Beach	x	x	x	200-500	15	x	x
Dudley and Cliff (2010)	x	x	. KwaZulu-Natal, South Africa	N	Sand/Beach	x	x	x	400	14	x	x
Espinoza *et al.* (2014)	x	x	Great Barrier Reef Marine Park, Australia	Y	Combination	x	x	x	x	> 80	M & I	Both
Ferreira *et al.* (2015)	> 4,000	1,167 - 634,944 km^2	Ningaloo Reef, Western Australia	N	Coastal	6-33	x	x	x	400	Most SA	Both

Reference	**Dist. Travel (km)**	**Home Range**	**Location**	**GPS**	**Habitat Type**	**Temp (°C)**	**Salinity (ppt)**	**Chloro. (mg/m^3)**	**Distance from shore (km)**	**Max. Depth (m)**	**Mat.**	**Sex**
Fitzpatrick *et al.* (2012)	x	x	Raine Island, Australia	Y	Combination	< 12-33	x	x	68±71 (nesting) & 115±131 (non-nesting)	600	x	Both
Hammerschlag *et al.* (2012a)	1,000-3,500	1,945-8,549 km^2	Florida Keys, Florida, USA & West End Bahamas	N	Combination	x	x	x	x	x	x	Both
Hazin *et al.* (2013)	209	x	Recife, Brazil	Y	Coastal	13-29	x	x	2-209	304	I	Both
Heithaus (2001)	x	x	Shark Bay, W. Australia	Y	Combination	14-24	x	x	x	15	M & I	Both
Heithaus (2005)	x	x	Shark Bay, W. Australia	Y	Seagrass	14-23	x	x	x	15	x	x
Heithaus and Dill (2002)	x	x	Shark Bay, W. Australia	Y	Seagrass	14-> 20	x	x	x	12	x	x
Heithaus *et al.* (2007a)	x	x	Florida Keys, Florida, USA	Y	Combination	x	x	x	x	13	x	x

Reference	Dist. Travel (km)	Home Range	Location	GPS	Habitat Type	Temp (°C)	Salinity (ppt)	Chloro. (mg/m^3)	Distance from shore (km)	Max. Depth (m)	Mat.	Sex
Heithaus *et al.* (2002)	x	x	Shark Bay, W. Australia	Y	Seagrass	x	May avoid >60	x	x	15	x	Both
Heithaus *et al.* (2006)	x	x	Shark Bay, W. Australia	Y	Seagrass	x	x	x	x	15	x	Both
Heithaus *et al.* (2001)	x	x	Shark Bay, W. Australia	Y	Combination	x	x	x	x	15	x	x
Heithaus *et al.* (2013)	x	x	Shark Bay, W. Australia	N	Seagrass	x	x	x	x	x	x	x
Heithaus *et al.* (2007b)	136-8,000	x	Shark Bay, W. Australia	N	Seagrass	x	x	x	x	> 800	x	Both
Holland *et al.* (1999)	35	"Large"	Oahu, Hawaii	N	Combination	x	x	x	3.5	335	x	Both
Holmes *et al.* (2014)	80-1,800	x	SE Australia	Y	Combination	5.9-29.5	x	x	x	920	I & Sa	Both
Holmes *et al.* (2012)	x	x	Queensland, Australia	N	x	x	x	x	0.5-1	12	M & I	Both

Reference	Dist. Travel (km)	Home Range	Location	GPS	Habitat Type	Temp (°C)	Salinity (ppt)	Chloro. (mg/m^3)	Distance from shore (km)	Max. Depth (m)	Mat.	Sex
Krogh (1994)	x	x	New South Wales, Australia	Y	Combination	x	x	x	< 0.5- > 1	36	M & I	Both
Lowe *et al.* (1996)	x	x	Main Hawaiian Islands	N	x	x	x	x	x	118	x	x
Lowe *et al.* (2006)	x	x	French Frigate Shoals, Hawaii	Y	x	x	x	x	x	x	M & I	F
Lowry, Williams and Metti (2007)	x	x	New South Wales, Australia	N	Offshore	x	x	x	x	x	x	x
Meyer *et al.* (2009a)	x	"Large"	Hawaii	N	Combination	x	x	x	x	x	M & I	Both
Meyer *et al.* (2009b)	x	x	Oahu, Hawaii	N	Offshore	x	x	x	4.8	140	x	x
Meyer *et al.* (2014)	x	x	Hawaii	N	x	x	x	x	x	100	x	Both

Reference	Dist. Travel (km)	Home Range	Location	GPS	Habitat Type	Temp (°C)	Salinity (ppt)	Chloro. (mg/m^3)	Distance from shore (km)	Max. Depth (m)	Mat.	Sex
Meyer *et al.* (2010)	1,200	x	French Frigate Shoals, Hawaii	Y	Combination	7- > 24	x	~0.1-0.15	1,200	~600	x	F
Nakamura *et al.* (2011)	x	x	Hawaii	Y	x	14.6-27.6	x	x	x	> 100	x	Both
Papastamatiou *et al.* (2010)	x	x	Oahu, Hawaii	Y	x	x	x	x	1	60	x	x
Papastamatiou *et al.* (2013)	x	x	Hawaiian Archipelago	N	Coastal	23-26	x	Avg 0.12; (F peak > 0.11, M peak > 0.14)	x	100	M & I	Both
Parker and Bailey (1979)	x	x	Mustang and Padre Islands, Texas, USA	Y	Sand/Beach	26-27	33-34	Abundant prey	0.2-0.4	x	x	x
Pikitch *et al.* (2005)	x	x	Glover's reef atoll, Belize	Y	Combination	x	x	x	x	x	I	F

Reference	Dist. Travel (km)	Home Range	Location	GPS	Habitat Type	Temp (°C)	Salinity (ppt)	Chloro. (mg/m^3)	Distance from shore (km)	Max. Depth (m)	Mat.	Sex
Rezzolla *et al.* (2014)	x	x	Angarosh reef, Sudan	Y	Combination	25	38-41	x	x	43	x	F
Sadowsky (1971)	x	x	Bom Abrigo, Cananéia	N	Sand/Beach	26.2	x	x	x	28	x	Both
Simpfendorfer (1992)	x	x	Townsville, Australia	Y	Combination	x	x	x	x	x	M & I	Both
Stevens and McLoughlin (1991)	x	x	Northern Australia	N	x	x	x	x	x	180	M & I	Both
Tricas *et al.* (1981)	~ 82 km/day	~ 100 km^2	French Frigate Shoals, Hawaii	N	Combination	x	x	x	900	> 140	x	F
Vaudo and Heithaus (2009)	x	x	Shark Bay, W. Australia	Y	Combination	20-31	x	x	0.5-1	3	x	x
Vaudo and Heithaus (2013)	x	x	Shark Bay, W. Australia	Y	Combination	x	x	x	x	3	x	x

Reference	Dist. Travel (km)	Home Range	Location	GPS	Habitat Type	Temp (°C)	Salinity (ppt)	Chloro. (mg/m^3)	Distance from shore (km)	Max. Depth (m)	Mat.	Sex
Vaudo *et al.* (2014)	24-1,147	x	USVI & Bermuda	N	Combination	8.9-30	x	x	x	828	M & I	Both
Werry *et al.* (2014)	1,114	109 km (3D KDE avg. 2,360 km^3)	Australia	N	Combination	5.6-32.2	x	x	x	1,136	M & I	Both
Wirsing, Heithaus and Dill (2006)	x	x	Shark Bay, Australia	Y	Coastal	> 20	x	x	x	12	x	Both
Wirsing, Heithaus and Dill (2007)	x	x	Shark Bay, Australia	Y	x	x	x	x	x	x	x	x
Witzell (1987)	x	x	Atlantic, Pacific, and Indian Oceans	N	Combination	x	x	x	x	x	x	x

APPENDIX C

SUMMARIZED BULL SHARK LITERATURE REVIEW TABLE

Appendix C. Summary of bull shark studies included in Chapter 2 of this thesis. See Appendix A for table codes.

Reference	**Dist. Travel (km)**	**Home Range**	**Location**	**GPS**	**Habitat Type**	**Temp (°C)**	**Salinity (ppt)**	**Chloro. (mg/m^3)**	**Distance from shore (km)**	**Max. Depth (m)**	**Mat.**	**Sex**
Afonso *et al.* (2011)	x	x	Natal and Recife, Brazil	Y	Offshore	x	x	x	1-3	14	x	x
Blackburn, Neer and Thompson (2007)	x	x	Louisiana, USA	N	Hyposaline	15-37	0-37.3	x	x	11	I	Both
Brunnschweiler (2009)	x	x	Shark Reef Marine Reserve, Fiji	N	Reef	x	x	x	x	30	x	F
Brunnschweiler and Baensch (2011)	x	x	Shark Reef Marine Reserve, Fiji	N	x	x	x	x	x	x	M & I	Both
Brunnschweiler and Barnett (2013)	x	x	Shark Reef Marine Reserve, Fiji	N	Reef	x	x	x	x	30	M	Both
Brunnschweiler and Van Buskirk (2006)	210	x	Walker's Cay, Bahamas	N	Combination	20-32	x	x	x	140	M	Both
Brunnschweiler *et al.* (2014)	x	x	Shark Reef Marine Reserve, Fiji	N	Reef	x	x	x	x	30	x	Both

Reference	Dist. Travel (km)	Home Range)	Location	GPS	Habitat Type	Temp (°C)	Salinity (ppt)	Chloro. (mg/m^3)	Distance from shore (km)	Max. Depth (m)	Mat.	Sex
Brunnschweiler, Queiroz and Sims (2010)	x	x	Walker's Cay, Bahamas & Shark Reef Marine Reserve, Viti Levu, Fiji	N	Reef	25- > 26	x	x	x	mean = 68	x	Both
Carlson *et al.* (2010)	2-1,506	x	Coastal SE USA and Gulf of Mexico	Y	Coastal	16-32	x	x	“Coastal”	96	Sa	Both
Cliff and Dudley (1991)	x	x	Natal, South Africa	Y	Coastal	17.4-26.5	x	x	x	x	M & I	Both
Curtis and Macesic (2011)	x	x	Indian River, Florida, USA	Y	Hyposaline	30.1-32	12.5-30.9	x	x	4	I	x
Curtis *et al.* (2011)	x	x	Indian River, Florida, USA	Y	Hyposaline	20-37	1.1-42	x	x	6	M & I	Both

Reference	Dist. Travel (km)	Home Range	Location	GPS	Habitat Type	Temp (°C)	Salinity (ppt)	Chloro. (mg/m^3)	Distance from shore (km)	Max. Depth (m)	Mat.	Sex
Curtis *et al.* (2013)	0.31-14.52	< 0.001-0.593 km^2	Indian River, Florida, USA	Y	Hyposaline	18.5-34.2	1.2-31.9	x	x	3.9	x	Both
Daly *et al.* (2014)	433-709	x	Pinnacle Reef, Mozambique	Y	Reef	x	x	x	3.7	x	M	Both
Driggers *et al.* (2012)	x	x	Western North Atlantic Ocean	Y	Coastal	x	x	x	x	x	x	x
Drymon *et al.* (2014)	x	x	Mobile Bay, Alabama, USA	Y	Hyposaline	29-32	10-11	“Highly productive area”	x	mean = 3	I	x
Dudley (1997)	x	x	Queensland, Australia & KwaZulu-Natal, South Africa	Y	Sand/Beach	x	x	x	500	15	x	x

Reference	Dist. Travel (km)	Home Range	Location	GPS	Habitat Type	Temp (°C)	Salinity (ppt)	Chloro. (mg/m^3)	Distance from shore (km)	Max. Depth (m)	Mat.	Sex
Espinoza *et al.* (2014)	x	x	Great Barrier Reef Marine Park, Australia	Y	Combination	x	x	x	x	x	M & I	Both
Froeschke *et al.* (2013)	x	x	Texas, USA	N	Hyposaline	5.5-37.8	0-49	x	x	x	x	x
Froeschke *et al.* (2010a)	x	x	Texas, USA	N	Combination	20-33	0-40	x	x	x	I	x
Froeschke *et al.* (2010b)	x	x	Texas, USA	Y	Hyposaline	x	x	x	x	x	I	x
Hammerschlag *et al.* (2012b)	1,200	2,260 km^2	Florida, USA	N	Combination	x	x	x	“Inshore”	x	M	x
Heithaus *et al.* (2007a)	x	x	Florida Keys, Florida, USA	Y	Combination	x	x	x	x	13	M & I	Both

Reference	Dist. Travel (km)	Home Range	Location	GPS	Habitat Type	Temp (°C)	Salinity (ppt)	Chloro. (mg/m^3)	Distance from shore (km)	Max. Depth (m)	Mat.	Sex
Heithaus *et al.* (2009)	x	x	Everglades, Florida, USA	Y	Hyposaline	17.3-31.3	0.2-33.4	x	x	3	I	Both
Heupel and Simpfendorfer (2008)	x	11 km of river mouth	Florida, USA	N	Hyposaline	14.4-32.4	0.1-34.0	x	x	x	I	Both
Heupel and Simpfendorfer (2011)	x	x	Florida, USA	Y	Hyposaline	x	x	x	x	x	I	Both
Heupel *et al.* (2010)	27	x	Florida, USA	Y	Hyposaline	14.4-34.1	0.1-34.7	x	x	6.1	I	Both
Kan and Taniuchi (1991)	x	x	Sepik River, Papua New Guinea	Y	Hyposaline	x	x	x	x	x	I	M
Matich and Heithaus (2012)	x	x	Everglades, Florida, USA	Y	Hyposaline	9.1-33.1	0.2-39	x	x	7	I	Both
Matich and Heithaus (2014)	x	x	Everglades, Florida, USA	Y	Hyposaline	x	x	x	x	x	I	x

Reference	**Dist. Travel (km)**	**Home Range**	**Location**	**GPS**	**Habitat Type**	**Temp (°C)**	**Salinity (ppt)**	**Chloro. (mg/m^3)**	**Distance from shore (km)**	**Max. Depth (m)**	**Mat.**	**Sex**
McCord and Lamberth (2009)	22	x	Breede Estuary, South Africa	N	Hyposaline	20-24	15-35	x	2 out to sea; 20 upstream	4.6	M	F
Ortega *et al.* (2009)	9.7-20.6	1.2-4.3 km^2	Caloosahatchee River, FL, USA	Y	Hyposaline	x	6.5-12.5	x	x	x	I	Both
Parker and Bailey (1979)	x	x	Mustang and Padre Islands, Texas, USA	Y	Sand/Beach	26-27	33-34	"Abundant prey"	200-400	"Surface"	x	x
Pillans and Franklin (2004)	x	x	Brisbane river and Moreton Bay, Australia	Y	Hyposaline	x	0-33	x	x	x	I & Sa	x
Shipley (2005)	x	x	Sabine Pass, Gulf of Mexico	Y	Coastal	20-40	12.3-34.8	x	300-800	3	M & I	Both
Simpfendorfer *et al.* (2005)	x	x	SW Florida	Y	Coastal	14.6-32.1	0.2-35.6	x	x	6.2	I	x
Snelson and Williams (1981)	x	x	Indian River, Florida, USA	Y	Hyposaline	20-32	18-42	x	x	4	M & I	Both

Reference	Dist. Travel (km)	Home Range	Location	GPS	Habitat Type	Temp (°C)	Salinity (ppt)	Chloro. (mg/m^3)	Distance from shore (km)	Max. Depth (m)	Mat.	Sex
Snelson *et al.* (1984)	x	x	Indian River, Florida, USA	Y	Hyposaline	x	29-30	x	x	3.7	M & I	Both
Sosa-Nishizaki *et al.* (1998)	x	x	Usumacinta River, Tabasco, Mexico	Y	Hyposaline	x	~2-3	x	x	x	M & I	Both
Stener and Michel (2007)	x	x	Ten-thousand Islands, Florida, USA	N	Hyposaline	26.7-32.6	16-38.1	x	x	3	I	Both
Taniuchi *et al.* (2003)	x	x	Betsiboka River, Madagascar	Y	Hyposaline	26.5	2.96	x	x	4	x	Both
Thorburn and Rowland (2008)	x	x	Northern Territory and Kimberley, W. Australia	Y	Hyposaline	20.8-32.5	0-41.1 (86% caught in < 5)	x	"Several 100 kms"	21	I	Both
Thorson (1971)	175 in 1 day	x	Barra del Colorado, Costa Rica	Y	Hyposaline	x	x	x	x	x	x	x
Thorson and Lacy (1982)	x	x	Nicaragua & Costa Rica	N	Combination	x	x	x	x	x	M & I	Both

Reference	Dist. Travel (km)	Home Range	Location	GPS	Habitat Type	Temp (°C)	Salinity (ppt)	Chloro. (mg/m^3)	Distance from shore (km)	Max. Depth (m)	Mat.	Sex
Thorson, Cowan and Watson (1973)	x	x	Costa Rica & Florida, USA	Y	Combination	x	0 & 34	x	x	x	M & I	x
Tillett *et al.* (2011)	x	x	Northern Australia	Y	Combination	x	x	x	x	x	M & I	x
Tremain, Harnden and Adams (2004)	x	x	Indian River, Florida, USA	Y	Combination	x	x	x	x	x	x	x
Werry and Clua (2013)	x	x	New Caledonia	Y	Combination	x	x	x	0.02-30	< 1,500	x	Both
Werry *et al.* (2011)	x	x	Queensland, Australia	Y	Hyposaline	21-23.5	< 5-36	x	x	x	M & I	Both
Werry *et al.* (2012)	x	x	Nerang River, Australia	Y	Hyposaline	x	6-32	x	x	10	M & I	Both
Wiley and Simpfendorfer (2007)	Up to 160	x	Everglades, Florida, USA	Y	Coastal	50% bw 25-31	50% bw 15-29	x	x	50% bw 1.2-2.4	I	Both
Yeiser, Heupel and Simpfendorfer (2008)	x	40 km^2 weekly	Pine Island, Florida, USA	N	Combination	x	x	x	x	7	M & I	Both