Factors Influencing Long Distance Movements of Tiger Sharks, Galeocerdo cuvier

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FACTORS INFLUENCING LONG DISTANCE MOVEMENTS OF TIGER SHARKS,
*Galeocerdo cuvier*

By

Stacy A. Assael

A THESIS

Submitted to the Faculty
of the University of Miami
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Sharks are top predators in most marine habitats and may impact ecosystem structure and function through trophic cascades. Therefore, studies of large shark movements are ecologically important, particularly given current global population declines of many large shark species as a result of overfishing. The purpose of this project was to identify the effects of various environmental factors (sea surface temperature, salinity, sea surface currents, and Earth’s magnetic field intensity) on tiger shark (*Galeocerdo cuvier*) movements in the Atlantic Ocean, with a primary focus of the influence of Earth’s magnetic field. Previous studies have concluded that several species of shark are capable of detecting small electromagnetic pulses under controlled experimental conditions; however, evidence is lacking regarding whether sharks utilize the Earth’s magnetic field to navigate the open ocean. To investigate this, four mature female tiger sharks were satellite tagged and tracked for a minimum of 6 months and a maximum of 10 months. Geographic Information Systems (GIS) were used to analyze how the aforementioned environmental factors influenced the sharks’ onshore and open water movements, and, in the case of two sharks, their eastward and westward movements. Sea surface temperature and salinity appear to play a minor role in shark distribution patterns. All four sharks occupied a similar range of
sea surface temperature (25-29°C) and salinity (36-37psu) regardless of their onshore and open water movements. Sea surface currents were a poor indicator for the eastward and westward movements of the two sharks that were examined for these effects. Neither shark had a high percentage of occurrence in easterly moving water when moving east, and vice versa. Furthermore, one of the sharks was identified most frequently in water moving in the easterly direction during west-oriented movements. A relationship was found between shark movements and the Earth’s total field intensity. While onshore, the four sharks were distributed in a limited range of total field intensities. This greatly differed from when the sharks traveled in the open ocean where they had fewer occurrences over a broad range of total field intensities. Such a pattern may suggest that these sharks are able to detect the changing values of Earth’s magnetic field, and may be using these cues to navigate during migration.
Dedication

In loving memory of my unforgettable father, Aaron Assael. Thank you for always believing in me.
Acknowledgments

This project would not have been made possible without the endless amounts of patience, support and guidance from my Master’s Thesis committee members Dr. Neil Hammerschlag, Maria Estevanez, and Dr. Jill Richardson. A special thank you to Dr. Chris Harrison for his time spent working with me on this project. Initial interpolation of raw shark data was from Hammerschlag et al. (2012), generated by Dr. Jiangang Luo. Data for this project were collected with help from the many hardworking members of University of Miami’s Shark Research Program.
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Chapter 1: Introduction

1.1 Background/ Literature Review

Imagine traveling half way around the world with no map, no street signs, and no compass. The odds that one would reach a desired destination are improbable; and the odds that one would make it back to the original starting place are even less so. So, how is it that a wide variety of organisms are capable of making thousand mile long migrations and returning to exactly where they began?

Many animals have adapted to address this challenge in a variety of ways. While only a few species have exemplified what can be characterized as “true navigation”, the concept of knowing where you are and how to reach your desired destination (Boles and Lohmann, 2003), several species have demonstrated the ability to move with intention. It is theorized that these truly navigating species are capable of identifying where they are, as well as accurately selecting their intended direction of travel, by interpreting environmental characteristics such as Earth’s magnetic field and/or celestial cues. One such animal that has been definitively classified as a true navigator is the Caribbean spiny lobster, *Panulirus argus*. In an experiment by Boles and Lohmann (2003), *P. argus* were placed in an experimental pool and exposed to a spectrum of magnetic intensities commonly encountered in their home range. Upon exposure to these fields, the lobsters were able to orient themselves in a direction that would lead them back to their original capture site.

Similar studies using hatchling loggerhead sea turtles, *Caretta caretta*, produced comparable results (Fuxjager *et al.*, 2011). Young loggerhead turtles are known to spend much of their early life history in the North Atlantic Gyre. Fuxjager *et al.* (2011) illustrated
that when the hatchling turtles were exposed to varying magnetic field intensities encountered along their pelagic travels, the turtles would orient themselves in a direction that would maintain their position in the advantageous waters of the gyre (Fuxjager et al., 2011; Merrill, 2010). For example, when exposed to a field intensity of 46,200 nT, which is generally located at the northeastern portion of the gyre, the hatchlings would orient themselves south so as to remain within the gyre. Similarly, when exposed to a field intensity of 44,000 nT, in the general vicinity of south Portugal, the hatchlings would orient themselves southwest. However, when the turtles were presented with a magnetic field intensity outside of their known range, the turtles were unable to position themselves in a direction that would bring them back to their desired location (Lohmann et al., 2008 and Fuxjager et al., 2011).

1.1.1 Sharks Magnetic Sense

Many studies have indicated that sharks possess a powerful magnetic sense. One recent study evaluated the responses of juvenile scalloped hammerheads, *Sphyrna lewini*, and sandbar sharks, *Carcharhinus plumbeus*, to an electromagnetic stimulus (Kajiura and Holland, 2002). One shark per trial was introduced to a 10m x 20m pen that contained four equally spaced electrodes. In the center of the pen, and equidistant to the center of each electrode was a syringe that released a squid rinse. For each trial, the squid rinse was released in order to engage the shark. After this release, one of the four electrodes was activated, and the number of tail beats per minute, as well as the shark’s orientation towards the active dipole, was recorded. Although the hammerhead and sandbar sharks behaved differently from one another in the presence of an electric stimulus, it was evident that both species were capable of electroreception (Kajiura and Holland, 2002).
A more recent study by Meyer *et al.*, (2004), provided similar findings also utilizing juvenile sandbar sharks and a scalloped hammerhead shark. During the trials, sharks were conditioned to associate an increase in magnetic field intensity emitted from a coil with food. When the manipulated field was activated the sharks were presented with food. The magnetic fields used for this study ranged from 25,000 nT at the coil’s center to 100,000 nT at the coil’s outer edge (Meyer *et al.*, 2004). During each trial, they counted the number of times a shark passed over the designated food source both when the field was active and inactive. Analysis of the data showed a much greater number of passes over the food source in the presence of a magnetic stimulus, further supporting the hypothesis that sharks are able to detect the geomagnetic field (Meyer *et al.*, 2004).

Past studies have provided observational data on how sharks may use a magnetic sense in the wild. Klimley (1993) observed that scalloped hammerhead sharks were able to swim in a relatively straight line for a period of approximately 32 minutes at night. Such directionality could not be attributed to ocean currents due to the fact that there were times where the animal’s route was opposite or perpendicular to the currents. It was theorized that this “highly directional swimming” was due to environmental characteristics such as the geomagnetic field (Klimley 1993).

In addition to directional swimming, scalloped hammerheads are known to congregate around seamounts where geomagnetic abnormalities are particularly prevalent (Klimley 1993). In his study, Klimley (1993) compared the movements of four scalloped hammerheads to and from the Espiritu Santo Seamount, located in the lower Gulf of California, Mexico, with the geomagnetic gradients surrounding the seamount. According to his data, the hammerheads consistently swam over “fixed geographic paths” at a depth
of 175m where the magnetic intensity gradient is three times steeper than that of the ocean’s surface and even more so than within deeper waters (Klimley 1993).

1.1.2 Earth as a Magnet

The idea of Earth possessing magnetic properties has existed for thousands of years. However, it was not until the late 16th or early 17th century that William Gilbert (1544-1603) concluded that Earth not only has magnetic properties but is essentially one giant magnet (Merrill, 2010). Further knowledge of seismology has led to a more nuanced understanding of the Earth’s internal composition. Because seismic waves travel at different speeds upon entering various mediums, geologists were able to conclude that the earth can be broken down into three primary layers: the crust, mantle, and core (Merrill, 2010). Closer analysis of both seismic data and internal temperature has led geologists to believe that the core is comprised of both a solid inner layer and a fluid outer layer.

The inner working of Earth represents a constant battle between temperature and pressure. Within Earth’s center, pressure dominates, resulting in a solid ball of iron. However, Earth’s outer core is dictated by temperature, resulting in what is a “fluid” layer (Merrill, 2010). Despite the physical state of the inner core, it is still exceptionally hot (achieving temperatures similar to those of the surface of our Sun). Therefore, the heat from the inner core is transferred to the bottommost layer of the outer core causing it rise. This causes the uppermost layer of the outer core to sink, due to displacement and to variation in density; we refer to this “cycle” as a convection current (Merrill, 2010). Because Earth’s internal makeup is composed of metallic materials, the “cycling” of
these materials produces a magnetic field. In other words, whenever there are electrons moving along a current a magnetic field arises.

In addition to Earth’s primary planet-wide magnetic field, there are also secondary localized magnetic fields known as anomalies. Magnetic anomalies are defined as areas where the total field deviates from the primary magnetic field (Merrill, 2010). The areas located near oceanic ridges where seafloor spreading is known to occur have stronger magnetic anomalies, because their source, the oceanic crust, is closer due to the relatively shallow topography of the ridge crest. Magma from the Earth’s mantle surfaces in areas where tectonic plates diverge and cools, forming rocks such as basalt and gabbro (Merrill, 2010). Due to their magnetic properties, the ferromagnetic minerals within these rocks are able to orient their magnetization with the magnetic field, essentially recording the location of the North Pole. As one moves perpendicular to the source (in either direction) the strength of the anomaly decreases; conversely the age of the rock increases.

1.1.3. Environmental Influences

Past studies have examined how sharks move relative to environmental factors. The migration patterns of basking sharks (Cetorhinus maximus), salmon sharks (Lamna ditropis), and great hammerhead sharks (Sphyrna mokarran) have all been studied in relation to sea surface temperature, sea surface currents/sea surface height, as well as ocean productivity. A study by Weng et at. (2008) determined the movement patterns of L. ditropis were best explained by the primary production of an area, whereas sea surface height had little influence. Similarly, C. maximus movements were directly related to food availability (Sims, 2003). Furthermore, Hammerschlag et al. (2011b) suggested that
long distance movements of great hammerhead sharks can be predicted by warm water movement such as the Gulf Stream.

1.2. Statement of Problem

Tiger sharks had previously been thought to spend most of their lives in coastal waters. However, recent advances in telemetry technology have indicated that *G. cuvier* exhibits extensive movements out into the Atlantic Ocean (Hammerschlag *et al*., 2012). The goal of this study was to identify cues sharks may be utilizing while navigating in pelagic environments that provide few visual or terrestrial landmarks. The primary focus was on the role of magnetic fields during these lengthy and complex movement patterns, in an effort to investigate whether the magnetic sense could be a primary navigational tool for sharks in the open ocean. In other words, this project aimed to determine how tiger sharks are able to orient themselves for open sea migrations, thus providing critical information for future studies to explain the purpose of such offshore activities (Hammerschlag *et al*., 2011a).

1.3. Hypothesis of the Proposed Study

The main objective of this study was to determine which physical factors in the marine environment may influence tiger shark movements. The movement of four tiger sharks were compared to five potentially influential environmental characteristics: Earth’s magnetic field, sea surface temperature (SST), surface currents, salinity, and bathymetry. These sharks, TS 68488, TS 68494, TS 68495, and TS 68496, nicknamed “Linda”, “Mary Kent”, “Miko”, and “Wells Fargo II”, respectively, were selected due to their extensive movements into the offshore Atlantic Ocean. It was hypothesized that sharks were using the magnetic field as their primary navigational tool, with information from the other
aforementioned factors utilized supplementally. This may explain how these sharks are capable of returning to their place of origin after venturing out into the open ocean.
Chapter 2: Description of Proposed Research Activities/Methodology

2.1. Description of the Study Area

The four tracks used in this study were chosen due to their extensive movements into the pelagic waters of the Atlantic Ocean. The greatest movement was that of TS 68488, whose furthest point extended almost 4000 km from the coast of south Florida; about equal to the width of the United States. Relative to key oceanic features, the furthest point of TS 68488’s path was about 451 km northwest of the Mid-Atlantic Ridge. The smallest track was that of TS 68496, whose most westerly point was about 674 km from Norfolk, Virginia, and whose most northerly point was 1,500 km from its original starting point. Overall, the area from 85°N, 20°E to 30°N, 50°E encompassed the entire spatial extent of all four tracks (Figure 1).

2.2. Data Description, Data Format, and Data Source

For this project, four pre-recorded tiger shark tracks were used. These four sharks were selected due to their long distance movements out into the Atlantic Ocean. All sharks were caught in the Western Bahamas and equipped with a smart position or temperature transmitting (SPOT) tag. The animals used in the study were all female and ranged in length from 280 cm to 365 cm. Satellite transmission began on either February 19 or 20 of 2011 (depending on when the shark was caught) and continued on through fall 2011. One track lost its signal in August, while the others communicated up until mid-September/early October and even early December.

Shark positions were determined by Doppler Shift calculations made by Argos Data Collection and Location Services (www.argos-system.org) whenever an orbiting satellite received a signal from a tag once it broke the surface of the water. Since surfacing was
irregular, the sharks’ paths were then interpolated from location data and regularized to a frequency of 1 minute (following Hammerschlag et al., 2012, interpolation of data by Jiangang Luo). The 1 minute data tracks were then sampled and one point for every 12 hrs was extracted, such that two positions per day per shark were produced. The 12 hr data set is what was used for this project and what is referenced for the remainder of the paper.

Using Geographic Information Systems (GIS), these tracks were then compared to a map of earth’s total magnetic field intensity (downloaded from www.ngdc.noaa.gov). In addition to the geomagnetic field, other variables including SST, salinity, sea surface currents (the easterly surface water movement, u (m/s)), and bathymetry were input to the map. The Marine Geospatial Ecology Tools 0.8a39 was used to download data for SST, salinity, and surface currents from the Hybrid Coordinate Ocean Model (HYCOM) data accessed through ArcMap. This information is located in the Global 1/12° global analysis (GLBa0.08) folder found within MGET. The mean value for each of the aforementioned variables was calculated from a specified 10 month time frame (February 2011 through December 2011) and provided values for the spatial extent mentioned in Section 2.1. Bathymetric values were downloaded from the General Bathymetric Chart of the Oceans website (www.gebco.net, GEBCO_08 Grid). Measurements for the desired study area were extracted using GridViewer and then input to ArcMap.

2.3. Using GIS for Data Analysis

Each of the four sharks’ regularized tracks were input into Geographic Information Systems using ArcMap 10. Using GIS, the value of each environmental factor at every point along the sharks’ path was extracted. Furthermore, onshore and open water movements were compared by selecting those points that occurred on the continental shelf
in a depth range of <200 m (Weaver, 1950), and those that occurred off the continental shelf in deeper waters. The data set of TS 68488 included a total sample size of n=495, such that 126 were onshore and 369 were in the open ocean; the track for TS 68495 included a total sample size of n=379 data points, such that 212 onshore and 167 open ocean; the track for TS 68494 included a total sample size of n= 374, such that 11 points located onshore and 363 in the open ocean; the track of TS 68496 included a total sample size of n=382, such that 144 were onshore and 238 were in the open ocean. Two of the four sharks used in this study, TS 68488 and TS 68495, returned to their original tagging location. Points from TS 68488 and TS 68495’s “open ocean” data set were extracted based on date to identify when they moved in a distinct easterly and westerly direction. Those points classified as “easterly movements” illustrated when the shark swam in an easterly movement from the tagging location out into the Atlantic Ocean, while the points classified as “westerly movements” indicated when the shark swam in a westerly movement back towards the initial tagging location. The easterly track of TS 68488 was composed of 130 data points and her westerly track was composed of 70 data points, whereas the easterly track of TS 68495 was composed of 167 data points, and her westerly track was composed of 11 data points. Once the four shark tracks were separated into their specific categories (i.e. onshore, open ocean, eastward, and westward), the value of each environmental factor at every data point was identified. Relative frequencies, expressed as proportions, were then used to illustrate the number of shark occurrences in a given range of environmental values.
An additional application of GIS for this project was to measure the area encompassed by each shark along their journey. Using the “Minimum Bounding Geometry” tool in GIS, the smallest polygon (minimum convex polygon, MCP), which contained all the points for each shark was determined. Then the area of each individual polygon as well as the area of overlap for all four sharks based on the MCP values was measured.
Chapter 3: Data Limitations and Study Relevance

3.1. Data Limitations

The scope of this study was limited by several factors. The most important limitation was that of the Argos satellite tags. These tags only provide a geographic location when the shark’s dorsal fin breaks the surface, which required that the data be interpolated. A result of this shortcoming is that the exact location of the animal in the water column is unknown when not at the surface. Therefore, it is possible that alternate navigational cues may be used while swimming at deeper depths. For instance, the magnetic strength of deep water anomalies is strongest at the source and gradually decreases with decreasing depth as the sensor moves away from the bottom (Merrill, 2010). Furthermore, the tags used are only known to transmit for an average of up to one year. As a result, it is unknown whether or not these long distance movements are “annual migrations.” Longer transmission time frames could allow for the identification of other possible explanatory factors, including the pursuit of desired prey species or knowledge of areas of high seasonal productivity.

Another significant limitation of this project relates to satellite positioning. The Argos satellite only makes (approximately) four complete rotations around Earth per day. Data from the individual tag can only transmit to the Argos satellite when the satellite is in the proper position to receive the information. As a result it is probable that there were times when each shark did surface, but this information went unrecorded. Furthermore, four consecutive transmissions are required to generate one geographic point; less time lapse between multiple successive points produces a more accurate location (Hammerschlag et al., 2012).
The results of this study were also affected by the limited sample size. Although a significant number of sharks have been equipped with a working satellite tag, a large portion of the tags malfunction or suffer from technical issues and stop transmitting. Therefore, many sharks will only produce tracks that are very short lived. Additionally, there is evidence that, in a few cases, these tags have been removed from the animal; in this event, the tags will continue to transmit from a stationary position.

3.2 Benefits of the Study

Telemetry studies are capable of providing in depth information about a shark’s life history. In the case of large marine predators these data are critical to understanding ocean ecology and trophic webs, as well as the status of many vulnerable shark populations. Information from this study can be used to identify essential habitats of *G. cuvier*, and a similar approach could be used in future studies to evaluate habitat use and the factors driving movements of highly mobile marine species. Knowing where sharks are, where they are going, and how they are getting there can potentially lead to improved management of shark populations. For example, such information would allow for seasonal closures in nursery areas so that large females can give birth without being subjected to fishing pressure. These data can also potentially be useful in creating maximally efficient marine protected areas (MPAs), promoting the recovery of overfished and threatened shark species.
Chapter 4: Results and Analyses

4.1 Sea Surface Temperature

The range of values for SST was compared for each shark’s onshore (depth ≤ 200 m) and open water movements. While onshore all sharks primarily occurred in warmer water temperatures and spent most of their time in 25-29°C water. During their open water movements, sharks TS 68495 and TS 68496 continued to occur in a surface temperature range of 25-29°C (Figures 9 through 12). Sharks TS 68488 and TS 68494, however, occurred in a much broader range of SST values moving into water as cool as 20°C. Throughout her open water movements, TS 68488 spent majority of her time in water of 25-29°C, whereas TS 68494 was predominantly identified in 21-25°C water.

![Relative Proportion of Shark Occurrences Within Specific Sea Surface Temperature Ranges (Onshore and Offshore)](image)

Figure 1. Relative proportion of shark occurrences with specific sea surface temperature ranges for all four shark’s onshore and offshore data points.

The proportion of the sharks’ occurrences within a specific temperature range during their eastward and westward movements was then assessed (Figures 13 & 14). Two sharks, TS 68488 and TS 68495, swam a route that allowed them to return to their original
starting point. During her easterly movements, TS 68488 spent 80% of her time in water temperatures ranging from 21-25°C, while during her westerly movements she spent 20%, 35%, and 25% in water temperatures of 0-21°C, 21-25°C, and 25-29°C respectively. TS 68495 also split her easterly movements almost evenly with 45% of her occurrences identified in 21-25°C water, and 55% of her occurrences identified in 25-29°C water. When swimming back toward shore, TS 68495 spent 90% of her recorded distribution in water ranging from 21-25°C.

4.2 Salinity

All sharks occurred in a similar range of salinity regardless of their onshore or open water location (Figures 15 through 18). All of TS 68495 and TS 68494’s track points located on shore fell between 36 and 37 psu. TS 68488 and TS 68496 also had a high percentage of points occurring in that specific salinity range (84% and 59%). This trend was observed offshore, as well, in that all four sharks continued to stay within a salinity
range of 36-37 psu. TS 68494, TS 68495, TS 68488 and TS 68496 were all identified within this range for at least 87% of their track points.

The easterly and westerly movements of TS 68488 and TS 68495 followed the same pattern (Figures 19 & 20). During TS 68488’s eastward movements 87% of her occurrences occurred within 36-37 psu, and 97% of her westward movements occurred within 36-37 psu. Similarly, 100% of TS 68495’s eastward movements, and 80% of her westward movements were recorded within the same salinity range.
4.3 Sea Surface Currents

The sea surface currents were measured in m/s in the eastward direction (negative values indicated a westward motion), and this parameter was only relevant to TS 68488 and TS 68495 (Figures 21 & 22). When swimming east in the open ocean, 48% of TS 68488’s occurrences were in water moving greater than 0.05m/s. During her movement in the westward direction, only 10% of her occurrences were in water moving west at a rate of greater than 0.05m/s. TS 68495 had the greatest number of her easterly occurrences (28%) in water moving at a rate between 0.02 and 0.05m/s. Similarly, the majority of her westward occurrences (50%) were in water moving east at a rate of greater than 0.05m/s. Only 20% of TS 68495’s westward track points were in water moving westward at a speed greater than 0.07m/s.
4.4 Total Field Intensity

While on the Continental Shelf all four sharks occurred in a very narrow range of total field intensity values. The majority of the shark’s onshore points were recorded in a field intensity between 44,000 and 46,000 nT. This may be a result of the study subjects having the same onshore starting location, but as they swam throughout the continental shelf, there was no evident pattern indicating a greater number of occurrences along a specific intensity within the data set. For instance, TS 68494 spent 100% of her onshore movements in a field intensity range of 44,000-46,000 nT (Figure 23). However, TS 68488 spent about 55% of her onshore time in a field intensity range of 44,000-46,000 nT and 45% of it in a range of 46,000-48,000 nT (Figure 24). TS 68496 and TS 68495 also spent a fair amount of time (25% and 40% respectively) in field intensities between 48,000 and 50,000 nT (Figures 25 & 26).
Throughout their open water movements, each shark swam through a much broader range of total field intensities. For instance, TS 68488 experienced field values between 38,000 nT and 50,000 nT, a range of 12,000 nT. Even TS 68494, who had 100% of her onshore occurrences in a narrow range of total field intensities, experienced a field intensity ranging from 44,000-50,000 nT, a span of 6,000 nT. TS 68495 occurred in a field intensity which varied from 40,000-50,000 nT, a 10,000 nT range, and in the case of TS 68496, she experienced a range of 8,000 nT distributed from 42,000-50,000 nT.

The easterly and westerly occurrences for TS 68488 followed a pattern similar to their complete open water movement (Figure 27). While moving out toward the open ocean (headed east), TS 68488 occurred within a total field intensity range of 42,000-50,000 nT and no more than 45% of her eastward occurrences were within a given bracket of values (44,000-46,000 nT). When moving back toward shore (headed west), she occurred in the range of 38,000-50,000 nT. During this movement, no more than 25% of her occurrences were within one specific range of values (38,000-40,000 nT).
TS 68495’s easterly and westerly movements differed dramatically from her overall open water track (Figure 28). When headed east, 90% of her track points were documented in the field intensity range of 44,000-46,000 nT. However, when TS 68495 swam westward back toward shore, her track points occurred in a much broader range of values: 42,000-50,000 nT. Also, during her westerly movement, no more than 25% of her track points occurred in a given range of field values.

4.5 Minimum Convex Polygon

Using the “Minimum Bounding Geometry” tool, the smallest polygon which contained all the points for each shark was determined. TS 68496, swam over the smallest expanse of ocean, encompassing an area of 649,000 km². TS 68495, followed by TS 68494, swam through an increasingly larger extent of space; TS 68495’s track extended throughout an area of 1,900,000 km², while TS 68494’s track extended throughout an area of 1,800,000 km². All sharks roamed through an enormous area; however, it was TS 68488 whose track was most impressive. Encompassing an area of 60,000,000 km², TS 68488...
swam throughout an area equivalent to almost 3 billion football fields. The area of overlap for all four of the sharks’ paths extended across 307,000 km² (Figure 29).
Chapter 5: Discussion and Conclusions

5.1 Discussion

The purpose of this paper was to identify which environment factors, if any, were utilized by tiger sharks during their long distance movements. Although TS 68488 and TS 68495’s routes differed from one another, both sharks were able to swim thousands of miles out into the Atlantic Ocean and return to the exact region in which they started given the distances over which they traveled. It is highly unlikely that such routes occurred by chance as opposed the sharks’ ability to follow an environmentally-cued highway.

Based on this study’s qualitative results, a clear pattern of increased occupancy as a result of SST was observed. A study by Sequeira et al. (2012) aimed at identifying which environmental factors could be used to predict the spatial distribution of whale sharks. Seventeen years of observational data (i.e. whale shark sightings) were used to identify known spatial and temporal locations of whale sharks. When broken down by season, SST appeared to be a strong explanatory factor for whale shark location. The seasonal clockwise rotation of SST strongly correlated with the presence of *R. typus* (Sequeira et al., 2012). This study was able to identify a range of SST preferred by the whale sharks within the Indian Ocean. Similar to the tiger sharks used in this study which preferred a temperature range of 25-29°C, the whale shark sightings most commonly occurred in a temperature range of 26.5- 30 °C (Sequeira et al., 2012). The seasonal sightings of whale sharks off the coast of South Africa in the summer, India and Thailand in the autumn, and the Seychelles in winter and spring, supported by predictive models (Sequeira et al., 2012), further highlighting the relationship between shark distribution and SST. Although the temporal
scale of the whale shark project far exceeded that of this specific project, both identified shark movement patterns influenced by SST.

Additional studies have also identified SST as a good indicator for the presence of large marine fish such as tuna and billfish (Hammerschlag et al., 2011b; Hammschlag et al., 2012). It has been suggested that marine predators, including tiger sharks, remain in warm productive waters, such as that of the Gulf Stream, to pursue prey (Hammerschlag et al., 2012). This may also be true in the case of great hammerhead sharks, *Sphyrna mokarran*, which have been documented swimming up the eastern coast of the United States, an area of high prey abundance (Rountree, 1990; Hammschlag et al., 2011b). It is possible that the tiger sharks tagged in this study may be following a particular temperature range to increase their chance of encountering desired prey species. In a study by Fuxgaer et al. (2011), it was suggested that sea turtles, a primary source of food for tiger sharks, migrate annually to the North Atlantic Gyre, as such, it is possible that tiger sharks, such as TS 68488, are following an abundance of prey out into the Atlantic Ocean.

A study by Mansfield et al. (2014), further supports the theory that tiger sharks may be following sea turtles as they move offshore into the eastern Atlantic Ocean. Seventeen neonate loggerhead sea turtles were satellite tagged along the southeast coast of Florida. Data collected from the turtles revealed that these turtles’ paths were generally directed in the north-northeast direction, similar to that of these sharks within this study. Additionally, the turtles’ routes were environmentally constrained, remaining within waters averaging a SST of $21.4 \pm 3.4 \, ^\circ C$ (based on daily temperature derived from HYCOM). This is consistent with the temperature range of the each shark’s offshore movements.
Sea surface currents did not appear to influence the long distance movements of the tiger sharks used in this study. The speed of the currents where most of the shark points occurred was extremely slow. Although it is energetically cost effective to swim in water moving in the same direction, perhaps the rate of current flow (max speed=0.05m/s) was relatively low in general, such that it was not a major factor influencing the sharks’ movements. Furthermore, in the case of TS 68495, there was a large portion of time during which she was swimming against the current; 50% of her westward occurrences were in water moving at a rate of 0.05m/s in the eastward direction. These results are consistent with a study by Sleeman et al. (2010) where they considered sea surface currents and their effects on whale shark migrations off the coast of Australia. It was concluded that surface currents had little to no influence on these animals’ movements. Some of the animals swam faster than the surface currents in which they occurred and in some cases, were recorded swimming against the current (Sleeman et al., 2010).

The tiger sharks movements relative to salinity illustrated a pattern similar to that of SST. All four sharks had the greatest number of occurrences within a salinity value between 36 and 37 psu. It is likely that these animals are not actively seeking this particular range of salinity, but rather that these values correlate with water temperature. In other words, these animals may be seeking out a particular water temperature, and as a result occur in a narrow range of salinity values.

The primary focus of this study was to determine how tiger sharks navigate throughout World’s open oceans. Of the several environmental factors considered for this study, total magnetic field intensity displayed the most pronounced trends. All of the sharks’ onshore occurrences (where depth is <200 m) were identified in a very limited
range of total field intensity. This may be attributed to the fact that onshore waters are easier to navigate. It may also be that there is no real need for “navigation” when onshore, where there may be distinguishing bathymetric and benthic features across relatively small distances. However, for those points where the sharks were offshore (water depth >200 m), all four sharks occurred in a much broader range of field values. The four sharks in this study all swam headed north/north east from their original tagging location. Coincidentally, Earth’s total magnetic field intensity increases in a northerly direction. Over the course of their travels the sharks encountered a broad range of total field values that increased as they swam north away from their tagging location, and decreased as they headed back south. This may suggest that tiger sharks are able to recognize the total field intensity value of their starting location, and that they may follow a path of increasing or decreasing intensities toward and away from their desired location.

The ability to use Earth’s magnetic field as a means for navigation has been positively identified in the Pacific sockeye salmon (*Oncorhynchus nerka*) (Putman *et al.*, 2013). Putman *et al.* (2013) suggested that salmon are able to return to their original reproductive area by knowing and heading towards the total field intensity value of their destinations. Fifty-six years’ worth of fisheries data from the Fraser River in Vancouver, British Columbia, was used to identify the route used by adult salmon when reentering their original geographic area, the Fraser River, as it relates to Earth’s magnetic field. Shifts in the magnetic field such that the northern entrance to the river was most similar to the river mouth resulted in an increased proportion of salmon entering along the northern route. Similar results were found when the magnetic field intensity of the southern entrance was most similar to the river mouth. Such results may explain a similar role in tiger shark
navigation, using Earth’s magnetic field as a navigational tool guiding their movements towards the desired location.

Sharks’ magnetic reception is just one of their many highly evolved senses. The course of their journey may be influenced by using just one sense or combination of senses at a given time. For example, the linear distance traveled by TS 68495 in both an easterly and westerly direction were approximately 1,800 km in length. Although the easterly and westerly distances were almost equal, her eastward movements occurred over the span of 1 month and generated 60 recorded data points. In comparison, her westward movements occurred over the span of 4 days and generated 10 data points. It could be that TS 68495 was pursuing prey or a mate when traveling east, and using a navigational tool, such as total field intensity, on her way back west. The Minimum Bounding Geometry tool helped to further this project in that it identified an area in the ocean where the four sharks occurred. All four sharks passed through an area of 307,000 km²; equivalent to about 15 million football fields. This is a huge area however, future studies with a larger sample size will mostly likely result in a smaller area of overlap. This information can be used in conjunction with core areas of use (e.g. kernel density values as in Hammerschlag et al., 2012) to identify a smaller, more valuable area for conservation. Such results and should be used when considering future marine protected areas (MPAs).

5.2 Conclusions

It is without question that global shark populations are on the decline (Musick et al., 1993; Baum et al., 2003; Ferretti et al., 2003 Valudo et al., 2014). Understanding where these animals are, as well as the means by which they travel, are extremely important to the development of conservation and fisheries management policies. Temperature and
salinity may be good indicators for predicting the presence of sharks however, it is unclear if sharks are using these factors synergistically or as their sole means of navigation. It may be possible that the limited temperature and salinity ranges encountered by each shark are a result of following prey that prefer specific environmental characteristics, such as those of the Gulf Stream. Furthermore, sea surface currents had very little impact on where the sharks occurred. In most cases, individuals were swimming faster than the surface currents, or even swam against the current. It has been suggested that tiger sharks, and perhaps other shark species, are using Earth’s magnetic field to navigate. When traveling in the open ocean these animals occurred over a wide range of magnetic field values. This may indicate that they are following a gradient of changing field values as they move in any given direction.

One other factor to consider is that no two animals followed a similar pattern. Although all four tracks used in this study were from adult female tiger sharks, the high variation amongst individuals suggests there may be intraspecific variation. In other words, individuals of the same species may exploit different environmental factors when navigating. Likewise, it is also possible that each individual is using different cues during different legs of their movement, or even more than one factor at a time. This may be the case for TS 68495: the results of her westward movement showed no evidence of her moving along changing field intensities. However, her eastward movement was much more direct and did exist over a wide range of values. Both paths are equal in distance but occurred over very different lengths of time; her westerly route may have been induced by following prey, whereas her easterly route may have been a result of actively swimming along a gradient.
In addition to evaluating the navigational tools used by *G. cuvier*, this study was able to quantify their spatial distribution. The results of this study identified individuals that swam several thousand miles offshore thus providing additional evidence that tiger sharks are more pelagic than previously thought for this species. This study also illustrated the spatial expanse that tiger sharks are able to cover over the course of 7 to 10 month time frame. Learning that tiger sharks are swimming through the open ocean over a tremendous area, specifically one that encompassed 3 billion football fields, will lead to an improved understanding of *G. cuvier* life history. Telemetry studies such as this have the potential to provide information as to where these large predators are breeding and pupping.
Figures

Figure 8. All four tiger shark tracks mapped with bathymetry. The highlighted area along the coast indicates the continental shelf (depth is 0-200m); darker blue indicates deeper water.
Figure 9. Continental shelf and open ocean data points for Linda mapped with sea surface temperature (°C).
Continental Shelf and Open Ocean Locations for TS 68496 ("Wells Fargo II") with Sea Surface Temperature

Legend
- Open Ocean
- Continental Shelf

Sea Surface Temperature
Celsius
- High: 29.1665
- Low: 3.5344

Figure 12. Continental shelf and open ocean data points for Wells Fargo II mapped with sea surface temperature (°C).
Figure 13. Eastward and westward movements for Linda mapped with sea surface temperature (°C).
Figure 14. Eastward and westward data points for Miko mapped with sea surface temperature (°C).
Figure 15. Continental shelf and open ocean data points for Linda mapped with salinity (psu).
Continental Shelf and Open Ocean Locations for TS 68495 ("Miko") with Sea Surface Salinity

Legend
- Continental Shelf
- Open Ocean

Salinity
- psu
  - High: 37.4426
  - Low: 13.4824

Figure 16. Continental shelf and open ocean data points for Miko mapped with salinity (psu).
Figure 17. Continental shelf and open ocean data points for Mary Kent mapped with salinity (psu).
Figure 21. Eastward and westward locations for TS 68488 ("Linda") with Sea Surface Currents.
Continental Shelf and Open Ocean Locations for TS 68488 ("Linda") with Total Field Intensity

Figure 23. Continental shelf and open ocean data points for Linda mapped with total field intensity (nT).
Continental Shelf and Open Ocean Locations for TS 68494 ("Mary Kent") with Total Field Intensity

Legend
- Continental Shelf
- Open Ocean
- USA

Total Field Intensity (nT)
- High: 59335.2
- Low: 22512.5

Figure 15. Continental shelf and open ocean data points for Mary Kent mapped with total field intensity (nT).
Eastward and Westward Locations for TS 68488 ("Linda") with Total Field Intensity

Figure 27. Eastward and westward data points for Linda mapped with total field intensity (nT).
Eastward and Westward Locations for TS 68495 ("Miko") with Total Field Intensity

Legend
- East
- West
- USA

Total Field Intensity (nT)
- High: 59335.2
- Low: 22512.5

Figure 23. Eastward and westward data points for Miko mapped with total field intensity (nT).
Figure 29. Total area in which all four sharks occurred such that the green polygon is that of Linda, the purple is that of Mary Kent, the pink is that of Miko, and the yellow is that of Wells Fargo II. The black grid polygon is the area of overlap from all four sharks.
Literature Cited


