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Halmos College of Natural Sciences and Oceanography

Using Knowledge of Shark Biology and Behavior to Inform Management and Conservation Efforts for the Globally Distributed and Fishery Exploited Shortfin mako (*Isurus oxyrinchus*)

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Table of Contents

1. Abstract

The shortfin mako (*Isurus oxyrinchus*) is a regionally endothermic lamnid shark with a circumglobal distribution in temperate and tropical waters. This species has special adaptations for a highly migratory, apex predator lifestyle, including specialized anatomical structures, the retia mirabilia, that allows maintenance of a higher than ambient internal body temperature, a higher percentage of red muscle fibers located closer to its body core compared to ectothermic sharks, and specialized dermal denticles to help achieve the remarkable swimming speeds for efficient predation. However, many parts of the life history of the shortfin mako are still unknown, and difficult to study due to the highly migratory nature and large size of these sharks.

Shortfin mako populations have declined in many areas of the world's oceans as a result of a combination of exploitation pressures, including both directed fisheries and bycatch in teleost fisheries. Given these declines and conservation concerns, the shortfin mako is currently categorized as Vulnerable to extinction on the International Union for Conservation of Nature (IUCN) Red List. Although international agreements to protect the shortfin mako exist in the Atlantic, they lack the strength of punitive measures if signatory countries fail to comply with their responsibilities. Additionally, insufficient catch data from many nations prevent accurate population assessments, and in many areas the stock status of the shortfin mako is incompletely known or unknown.

Current national and international management efforts are insufficient to halt or reverse this declining population trend, in part due to a lack of knowledge about the sharks' behaviors. Little is definitively known about feeding, movement, mating, or habitat use behaviors of these sharks. The relatively new scientific discipline of conservation behavior can inform fisheries management and conservation planning for this species. Increased research is needed to better understand the movement ecology of shortfin makos, including how they interact with each other, with other species, with the physical environment, and spatial fishing effort. This information, along with more accurate population assessments, will form the basis for future ecosystem-based management plans to conserve the shortfin mako throughout its range.

This capstone reviews the existing literature on the biology and behavior of the shortfin mako shark, and makes recommendations about how research on conservation behavior can potentially improve the population and conservation status of this key, marine apex predator.

Keywords: shortfin mako, conservation behavior, fisheries management

2. Introduction

Conservation behavior is a relatively new scientific field which holds promise for the conservation of endangered or threatened species. Specifically, conservation behavior is the discipline that applies known animal behaviors, including habitat selection, foraging preferences, anti-predator behaviors, sexual selection, social interactions, and other behaviors to aid in conservation planning (Blumstein and Fernandez-Juricic, 2010). In the marine realm, conservation behavior research can help fisheries managers and conservationists by informing the modification of fishery practices to reduce their impact on bycatch species, especially sharks. Using knowledge of animal behaviors to determine best fishery practices could help halt or even reverse the decline of some overexploited species.

Overfishing and other anthropogenic effects, such as habitat destruction, pollution, and climate change have caused a large decrease in populations of many marine species (Duffy et al., 2014). Unfortunately, conservation and fisheries management advocates are often at odds about the best methods to preserve populations of sharks (Techera and Klein, 2011). Most shark fisheries around the world have developed with no management plans, leading to rapid population decreases, with slow recovery of populations once fishing pressure has eased (Musick et al., 2000). It is estimated that approximately 21% of the world's chondrichthyans are in danger of extinction, particularly in the Atlantic and Indian Oceans, including 52% of oceanic pelagic species (Dulvy et al., 2008). Detailed life histories are only known for a fraction of the approximately 1196 species of chondrichthyans, knowledge of which is important when studying population dynamics (Calliet, 2015). Information on the behavior of many pelagic shark species, in particular, is lacking due to the difficulties of observing these large animals in their natural environment and keeping them alive in captivity (Nelson, 1977). Many of these sharks show seasonal movements between habitats, are difficult to handle or sample, and of little commercial value, so research on their life histories has been lacking (Calliet, 2015). Tracking the sharks *in* situ can be difficult due to large home ranges, and often requires large vessels, thus becoming cost-prohibitive (Lowe and Goldman, 2001).

Most often, the types of shark behaviors that are well-studied are based on studies conducted on smaller species held in captivity, and relate to prey detection and capture, or how sharks react to different chemical, physical, or electrical stimuli. However, since most studies of behavior have not been done *in situ*, it is not well-understood how shark behavior may differ in natural conditions. Furthermore, such captive studies are not practical for the larger shark species which are fishery exploited. Little is currently known about how many species of sharks interact with conspecifics and heterospecifics, or how their behaviors may change in different spatial or temporal scales. Due to their position near the top of trophic food webs of many marine ecosystems, sharks often influence how these communities are structured (Speed et al., 2010). Sharks not only directly affect prey species through predation, but also indirectly by effecting prey behavior through their avoidance of risk of predation. When the removal of sharks no longer maintains the balance between prey populations, this can lead to mesopredator release, an increase in competition between prey species, and a reduction in the number of species present in an ecosystem. Since sharks have such a vital role in ocean habitats, their removal could have serious consequences for global oceanic biodiversity (Dulvy et al., 2008; 2014).

Biological characteristics of sharks, such as slow growth, late age at maturity, and small number of offspring, make them more susceptible to overexploitation than other fishes (Bustamante and Bennet, 2013; Gallagher et al., 2014). As a result, since the late 1990’s some pelagic shark species have seen a reduction of up to 80% of their population (Mucientes et al., 2009). What is known of shark behaviors is often overlooked when management and conservation plans are created for sharks or their prey items. Many sharks with circumglobal distributions are managed similarly over broad ranges, or not at all in some areas. There are often significant differences in behaviors between populations due to a variety of habitats, prey items, and demographics, which can affect the abundance and distribution of sharks in different areas.

Tag and recapture-based and satellite-tracking studies can provide data on the movements and growth of individual sharks, but offer little information on their interactions with other sharks and prey items. Recently, new technologies have improved understanding of shark movement ecology, and begun revealing a complex array of behavioral patterns in many shark species. However, without a true understanding of how sharks move from one habitat to another, how they use those habitats, and how they segregate by size, sex, or species, formulating successful management or conservation plans for shark species will be difficult (Speed et al., 2010).

One pelagic shark species whose importance has grown in the past few decades, both as a species with a directed commercial fishery in some areas, and as bycatch in fisheries worldwide, is the shortfin mako. Due to its speed, power, and agility, the shortfin mako is also prized by recreational fishers. Biological characteristics of the shortfin mako, such as slow growth, late age at maturity, and low fecundity makes them particularly susceptible to overexploitation (Levesque, 2008; Tsai et al., 2014). Shortfin makos are currently listed as Vulnerable globally by the IUCN Red List (http://www.iucnredlist.org/details/39341/0), critically endangered in the Mediterranean Sea, and near-threatened in the northeast Pacific (Dulvy et al., 2008). With few natural predators, other than white sharks (Maia et al., 2006), shortfin makos are an example of an oceanic species whose populations have been directly affected by anthropogenic activities.

The shortfin mako is one of the few shark species targeted with their own fishery, where they are captured for their meat and fins. They comprise about 10% of total annual North American shark landings, and as high as 7% of the bycatch in the Atlantic swordfish longline fisheries (Dulvy et al., 2008). Pressures from fisheries and environmental changes have begun negatively affecting populations of the shortfin mako in many areas. In the North Atlantic, an almost 70% decrease in the population has occurred. However, research on how shortfin mako behavior has influenced these population impacts has lagged. More needs to be done to study their behaviors in multiple life history stages, and in different environments, to develop conservation and management plans that ensure the continuation of the species throughout its range.

Shortfin makos inhabit different areas of the water column at different life stages, possibly making juveniles near the surface more susceptible to direct fishing pressure or as bycatch in longline fisheries (Bustamante and Bennett, 2013). A trait common in many shark species is segregation of individuals based on size or sex (Speed et al., 2010). Sexual segregation in mako populations may lead to increased ratios of one sex over the other in different areas due to differential fishing pressures (Mucientes et al., 2009). Fisheries, through their targeting of stocks in certain areas, could show selectivity for one sex over the other which can lead to sex-specific fishery mortality (Tsai et al., 2014). For example, if more female sharks are caught by certain fisheries, this could reduce the fecundity of the population in that area and may result in local extirpation of the species. These are just two behaviors that should be considered by fisheries policymakers when developing new fisheries management plans. Understanding behaviors such as these will help also inform managers when developing conservation plans to protect this species from overexploitation in shark fisheries, and can alter practices in the fisheries where they are often caught as bycatch.

3. Biology

Shortfin makos are pelagic sharks in the family Lamnidae, with a circumglobal distribution in tropical and temperate oceans (Semba, 2011; Duffy and Francis, 2001; Velez-Marin and Maquez-Farias, 2009). They have even been found in subpolar waters off Atlantic Canada, usually associated with the Gulf Stream, but as far north as the Gulf of Saint Lawrence (Campana et al., 2005). In many areas, their diet consists of 98% teleost fish, but they also prey on cephalopods, crustaceans, marine mammals, sea turtles, and other sharks (Campana et al., 2005; Wood et al., 2009). They are a highly migratory species of shark that show movements related to differences in water temperature (Semba et al., 2011; Vaudo et al., 2016) and seasonal prey abundance (Wood et al., 2009).

As an evolutionary group, all sharks are carnivorous. However, their prey choices range from microscopic zooplankton to large marine mammals and other sharks (Motta and Wilga, 2001). This has led to the emergence of a multitude of feeding mechanisms and behaviors among extant shark species. These include suction feeding, ram feeding, bite feeding, bite and gouge feeding, and filter feeding. All modern sharks have a ventral, sub-terminal mouth, short jaws, and highly mobile cartilaginous connections that allow the jaws on the non-filter feeding sharks to saw and shred prey. The shortfin mako is a ram feeder, like other lamnoids, and thus has a wider gape than suction-feeding shark species. Ram feeders swim over their usually slower swimming prey and then swallow it whole or take large chunks of flesh out of it. However, some ram feeders like white sharks (*Carcharodon carcharias*) and shortfin makos may approach their prey at great speeds. This can create a large movement of displaced water in front of the mouth, which then pushes the prey away. To compensate for this, they have developed hydraulic suction abilities to force the water back toward the mouth, and the food items into the mouth and down the esophagus.

Shortfin makos are obligate ram ventilators that swim with their mouths open to force water over the gills (Carlson et al., 2004). Reduced branchiostegal systems in the gills do not allow active pumping of water over the gills, so the sharks must move their bodies forward to force water over their gills and continue oxygen exchange. They also keep moving in order to provide lift, as they lack swim bladders with associated buoyancy control mechanisms found in teleosts. In order to maintain their active, regionally endothermic metabolism, shortfin makos have developed highly specialized gills that increase oxygen consumption, and are constructed to withstand the pressure associated with ram ventilation at high speeds (Wegner et al., 2010). The gills of the shortfin mako have 2-3 times the surface area, with a much thinner water-blood barrier, than in non-endothermic shark species. Blood flows diagonally through the lamellae, which is unusual among shark species, but is thought to increase the efficacy with which hemoglobin in the blood becomes saturated with oxygen. This design forces the blood through the gills more quickly and recirculates it sooner.

Shortfin makos also have larger hearts than other shark species, which increases the volume of oxygenated blood pumped to their aerobic muscles, as well as the speed at which it is moved through their body. With hearts that more closely resemble mammal or bird hearts than hearts found in other sharks, shortfin makos can increase their heart rate to compensate for greater metabolic demands. This differs from other shark species that increase stroke volume to compensate for greater activity (Carlson et al., 2004). Shortfin mako blood contains high hemoglobin concentrations to increase the amount of oxygen that can be transported through the body, while their muscle fibers show elevated myoglobin that increases the amount of oxygen available to the aerobic muscles (Wegner et al., 2010). These adaptations are important not only for maintaining an internal body temperature greater than the ambient water temperature, but also allow the shortfin makos to swim at speeds of up to 70 km/hr (Diez et al., 2015). They are able to achieve these speeds because of biological adaptations, such as their use of retia mirabilia, their large percentage of red muscle tissue in relation to other shark species, and special adaptations of their dermal denticles.

3.1 Retia mirabilia

As in some other lamnid species, shortfin makos are partial regional endotherms that have evolved a closely-packed network of small veins and arteries (the retia mirabilia) that serves as a counter-current, heat exchange mechanism to maintain the internal temperature of certain areas of their bodies above ambient water temperature (Bernal et al., 2011). Parts of their bodies have been measured at temperatures of up to 8° C above the surrounding waters (Carlson et al. 2004). Retia mirabilia use counter-current heat exchange to distribute heat produced by the red locomotor muscles to other muscles, the eyes, brains, and viscera (Bernal et al., 2011; Lowe and Goldman, 2001). The amount of heat produced by the red muscles is regulated by the sharks through changes in depth or swim speed (Bernal et al., 2011). Red muscle and white muscle fibers display similar patterns of heating and cooling, but white muscles take longer to warm than the heat-producing red muscles.

Increased internal temperatures cause a corresponding increase in heart rate, as well as in the volume and speed of the blood being pumped through the body (Bernal et al., 2011). This causes warmer blood to spread throughout the body more quickly, helping to maintain a higher internal temperature in important areas of the body. For example, the stomach temperature of shortfin makos has been measured from 1.7-8°C above the ambient water temperature, with the magnitude of the temperature difference related to the size of the individual shark (Sepulveda et al., 2004). A decrease in stomach temperature of 0.12 °C/ min has been observed when makos ingest prey and begin the digestion process. However, stomach temperatures appear to be relatively constant in larger, adult sharks, but may vary greatly and be more directly affected by ambient temperature in smaller, juvenile sharks (Bernal et al., 2011).

The ability to regulate internal temperatures shows ontogenetic changes as the shortfin mako matures and increases in size (Bernal et al., 2011). Larger sharks appear to better able to regulate and maintain higher internal temperatures than smaller juveniles, but all shortfin makos have been observed with a visceral and locomotor muscle temperature greater than the ambient temperature in their environment. The retia give the sharks a predatory advantage, providing them with greater visual acuity and muscle control in colder waters, and helping with prey capture when they dive below the thermocline. Since they are able to maintain their internal temperature above the ambient temperature, they can inhabit a wider range of habitats than many other shark species, display an increased metabolism, and are able to utilize energy more efficiently in locomotion and digestion than ectothermic shark species.

3.2 Red muscle fibers

The location of the red, locomotor muscles in shortfin makos is not only important in helping maintain the sharks' high body temperature, but also allows them to continue swimming at higher aerobic levels than non-lamnid sharks (Carlson et al., 2004). This allows the shortfin mako to swim aerobically and with increased swimming efficiency for longer periods of time than other shark species and prey. The combination of location and concentration of these red muscle fibers allows for conductive heat transfer between the red muscle fibers and the white muscle fibers surrounding them (Bernal et al., 2005). The higher temperature of the red and white muscle fibers allows the shortfin mako to relax and contract its muscles at a faster rate, creating more power when the muscles are used (Carlson et al., 2004). This adaptation gives them the capability to increase their swim speed faster than ectothermic fish species. The shortfin makos display impressive burst swimming speeds when in pursuit of prey because the muscles near their core never completely lose their heat.

Their specialized muscle fibers are also adaptive because shortfin makos often dive below the thermocline in pursuit of prey (Bernal et al., 2011). At temperatures below 15° C, red muscles would not allow for efficient swimming (Bernal et al., 2005). Unlike mammals which have thermogenic tissues not associated with locomotion, shortfin makos must continuously swim in order to maintain their red muscle and internal temperature above that of the ambient environment. If the sharks ceased to swim and their red muscle fibers were allowed to cool, the muscles would no longer function effectively, and could be permanently damaged.

3.3 Dermal denticles

The shortfin mako has dermal denticles that are loosely anchored in the skin and can be manipulated to decrease drag when swimming (Motta et al., 2012; Diez et al., 2015). The denticles disrupt the boundary layer between the skin and water, thus decreasing turbulence and drag (Diez et al., 2015). These denticles are smaller than in other shark species and have three longitudinal riblets with shallow grooves (Motta et al., 2012). They range in size from 99.7-263.7 µm long and 73.9-229 µm wide (Diez et al., 2015). The denticle density in shortfin makos, measured at 44.6-75 denticles/mm^2, is higher than in 35 other species of more sedentary and benthic shark species. Density is not uniform over the entire body of these fishes, however, with the greatest number of denticles on the anterior and posterior surfaces of the body, with lessening of denticle density mid-body. Denticles on the dorsal surface of the pectoral fins are less dense on the leading edge of the fin, and increase in density as they move toward the posterior edge. Conversely, on the anterior side of the pectoral fins, the denticles are thickest on the leading edge, gradually decreasing in abundance toward the trailing edge. The denticles on the caudal fins have lower densities on the trailing edge than the leading edge, and show the greatest density on the lateral surfaces of both the dorsal and ventral lobes. The density, size and shape of the denticles differ depending on where on the body they are located (Diez et al., 2015).

The smallest denticles are located on the caudal keel and posterior edge of the pectoral and caudal fins, while the largest are found in the mouth and along leading edges of the pectoral and dorsal fins (Diez et al. 2015). Denticles found along the leading edge of the fins are flattened, less erectile, and more rounded than in other areas of the body. Along the flanks, the denticles are highly mobile and can be erected as much as 50° off of the plane of the body (Motta et al., 2012). The change in angle of the denticles in relation to the body is a passive mechanism caused by the flow of water over the skin. As the denticles increase in height off of the body, they decrease flow velocity of water over the body (Diez et al., 2015). When erect, the denticles produce multiple tiny vortices along the skin (Motta et al., 2012; Diez et al., 2015). These vortices reduce friction along the skin, lessen drag, and facilitate flow over the body of the shark (Diez et al., 2015). In this way, they help increase swimming efficiency and decrease metabolic costs of fast swimming through the water.

3.4 Metabolic Rates

Standard metabolic rates (SMR) have not been observed for shortfin makos because this measurement requires the specimen to be completely at rest, which is not possible for ram ventilators. However, extrapolating to 0 velocity, Carlson et al. (2004) determined that the SMR for shortfin makos is 240 mg O_2/kg/hr. This SMR is not significantly higher than in other shark species (Sepulveda et al., 2007). Maximum metabolic rates (MMR) of shortfin makos are higher than most other pelagic shark species, with a routine metabolic rate (RMR) up to 3.4 times that of ectothermic species at different temperatures. These rates were derived using swim tunnel respirometers in the lab, which may not accurately reflect actual metabolic rates *in situ*. However, the MMR and RMR determined for the shortfin makos is most likely higher than other species, even under natural conditions, due to the specialized cardiovascular and complex muscular systems of these sharks. They have higher red muscle densities than other shark species, which may provide them with enhanced aerobic muscular performance, leading to higher metabolic rates overall.

Differences in experimental design, difficulties with stimulating the sharks to swim, and stresses associated with capture and confinement, may skew results in metabolic experiments done on sharks (Sepulveda et al., 2007). Furthermore, the inability to perform these experiments on individuals of larger size classes may not accurately reflect the actual metabolic rate of larger specimens, who tend to have higher metabolic rates than the juveniles most often studied in this manner. Future *in situ* studies of shortfin makos from many size and age classes will help scientists to better understand how shortfin mako metabolism affects behaviors related to feeding, reproduction, and habitat use.

3.5 Reproductive biology

Male shortfin makos have paired radial testes. Their spermatophores are small, tightly packed, and do not dissolve easily in seawater like those of other lamnid sharks.

Females have a single right ovary suspended from the dorsal abdominal wall by a mesovarium. There is a large surface area in this ovary which produces many yolked oocytes, in contrast to the planar ovaries found in other elasmobranch species. Fertilization occurs in the anterior oviduct near the ostium, located in the area where the two lobes of the liver and two oviducts meet (Gilmore, 1993). The fertilized ova are then encapsulated, and the egg capsules move to the uterus. Within these egg capsules, there may be only one or multiple fertilized ova and many unfertilized ova. The uterus has a highly vascularized epithelium, which is important for oxygenation for the fetuses.

Shortfin makos are aplacental viviparous sharks that display intrauterine oophagy (Gilmore, 1993; Bustamante and Bennett, 2013; Joung and Hsu, 2005), where the young eat unfertilized eggs contained within the same egg capsule. They develop a “yolk stomach,” in which they store large amounts of yolk for future energy needs (Joung and Hsu, 2005). Intrauterine cannibalism is not thought to occur with the shortfin mako, as is common in the sand tiger shark (*Carcharias taurus*) (Gilmore, 1993).

There are five stages of embryonic development in the shortfin mako (Joung and Hsu, 2005). In stage 0, the largest ova are fertilized and encapsulated in an egg case. During this stage, the females continues to produce smaller ova that are subsequently added to the egg capsule to be consumed by the embryo after hatching. Embryos in stage 1 consume uterine milk until they reach a size of 1-14cm total length (TL). While in stage 1, they also begin consuming the unfertilized ova in the egg case with them. Because they have no teeth, they crush the small ova between their jaws. These embryos are still unpigmented, are developing external gill filaments, and the beginning of their “yolk stomach” can be seen. Stage 2, which lasts while embryos are 26-42 cm TL, sees the development of peg-like fangs in both the upper and lower jaws, vascularization of the abdomen, and the beginning of pigment on the tip of the caudal fin. By the end this stage, the females stop producing additional small ova to be consumed by the embryos, and the “yolk stomach” reaches its largest size. In stage 3, the embryos “yolk stomachs” begin to shrink, as the female has stopped producing additional nutritive ova, to replenish the embryo’s reserves. Their gill filaments begin to recede and their bodies become pigmented. However, the skin during this stage is still smooth because the dermal denticles have not begun forming. When they reach about 40 cm TL, the embryos shed their teeth from the upper jaw first, then the lower, starting in the center of the mouth and moving toward the angle of the jaw. The fourth stage encompasses a TL of 62 cm until parturition. At this stage of development, the embryos are fully pigmented, have resorbed their external gills, and have developed the lunate caudal fin and teeth seen in adults. The liver increases in size rapidly, and excess yolk stored in the liver can be used by the neonates after parturition to increase their probability of survival.

Little is definitively known about parturition of shortfin makos, with only 35 litters of this species having been studied worldwide by 2001 (Duffy and Francis, 2001). However, it is thought that pelagic shark species tend to produce smaller embryos in larger litters than nearshore species because of lower physiological stress from predators and changing environmental conditions, which are more common for sharks in shallow waters (Gilmore, 1993). Shortfin makos may produce 12-18 pups per litter after either a 9-13 month gestation (Semba et al., 2011), 15-18 month gestation (Bustamante and Bennett, 2013), or 23-25 month gestation (Joung and Hsu, 2005). However, 20-21 month gestation appears to be most likely in litters in both the south Pacific and north Atlantic (Duffy and Francis, 2001). The uncertainty of gestation length is due to the growth models used by different researchers, and possible differences in pup size at parturition in different areas. Pups studied in one New Zealand litter each had stomachs full of yolk, but there was less yolk present than in other litters that had been studied previously, which could signify that these pups were closer to parturition (Duffy and Francis, 2001). The lack of knowledge about parturition for shortfin makos creates uncertainty when developing the best conservation processes for this species.

4. Life History

At parturition, it is believed that the shortfin mako pups are 61-80 cm TL (Semba et al., 2011; Bishop et al., 2006; Bustamante and Bennett, 2013), and grow rapidly during their first year, with both sexes increasing at about 3.2 cm TL each month during that time (Bishop et al., 2006). This is followed by a rapid decrease in growth rate for the next few years, and then a slow steady growth rate until reaching maturity. As is common in species that display sexual dimorphism with larger females, males grow more slowly than females after the first year, and reach their maximum size earlier in life.

Sexual dimorphism is common in many species, and according to the fecundity advantage hypothesis, females continue to grow and do not reach sexual maturity until after males in order to attain a larger size before reproducing, thus increasing their fecundity (Semba et al. 2011). The larger their body, the more eggs they can produce and the larger their offspring. The larger the offspring are, the better their survivability after parturition. The shortfin mako is a sexually dimorphic species in which females are larger than males and continue to grow even after reaching sexual maturity. Male shortfin makos reach sexual maturity at around 5-9 years (Bustamante and Bennett, 2013; Semba et al. 2011; Bishop et al., 2006) and between 195cm TL (Bustamante and Bennett, 2013) and 250cm TL (Bishop et al., 2006). Males are mature when their claspers are elongated and the terminal ends have calcified (Bustamante and Bennett, 2013). Females are sexually mature at 16-21 years (Bustamante and Bennett, 2013; Semba et al., 2011; Bishop et al., 2006) and between 265 cm TL (Bustamante and Bennet, 2013) and 362 cm TL (Bishop et al., 2006). Females are considered mature if they have pups *in utero*, large vitellogenic ova, or an oviducal gland that is differentiated from the uterus (Bustamante and Bennett, 2013). The variations observed in size at maturity could be the result of differences in environmental factors experienced in different areas of the shortfin mako's range, or a result of the quality of prey items available to individual sharks.

The bioenergetics demands of shortfin makos are higher than those of any other shark species that has been observed (Wood et al., 2009). The amount of energy consumed increases as the sharks grow until the onset of maturity, and then begins decreasing as less energy is required for growth. At that time, females began allotting more energy to reproduction. Unlike males, females continue to grow in size after reaching sexual maturity (Semba et al., 2011), but devote, on average, 86,299 KJ/yr for reproductive purposes (Wood et al, 2009). As a result, adult shortfin makos must ingest approximately 4.5% of their body weight per day in order to satisfy their energetic demands. It is believed that they reach maturity at the around the same age worldwide (Bishop et al., 2006), but differences in how ages are calculated for individual specimens by different researchers has led to a range of possible ages at maturity.

Accurately estimating ages is imperative for proper stock assessment and management because it provides information about population demographics, growth rates, age at maturity, and longevity (Bishop et al., 2006). There are inherent difficulties when aging sharks due to lack of calcified structures in the body, so vertebrae are usually used (Calliet, 2015). In some deep sea species, there is a lack of any calcified vertebrae, so fin spines, caudal thorns, or neural arches can also be used to age. Tagging and injection of oxytetracycline, both commonly used with many teleost species are difficult to do on sharks because of the expense and broad range many sharks inhabit which reduces the likelihood of recapture. Currently, the method most used to age sharks is to remove the calcified vertebrae or fin spines, and count the deposition bands. Usually, the vertebrae are thinly sectioned and then stained so that the bands can be clearly seen. X-rays and x-ray spectrometry have also been used in some studies to see growth bands more clearly based on calcium or phosphorous deposited within them. In order to produce a size at age growth curve, enough individuals of each size class must be analyzed to show a clear pattern.

When aging sharks, the most important determination is deciding which band is the birthmark that developed when the individual began growing after parturition (Calliet, 2015), and the translucent or opaque bands after that are then counted. Verification is important, so either one reader counts the same section several times, or multiple readers each count the same section of vertebrae. Another method used for verification is to compare the count to the vertebral bands and growth of a tagged individual that has been recaptured, or by using length-frequency analysis. When validating vertebrae, readers determine how often new vertebral bands are laid (Calliet, 2015). This process is complete for a species when every age class has been validated and the birthmark band has been determined, which allows absolute ages to be determined.

In the past, it was thought that shortfin makos deposited one vertebral band every two years, so aging estimates were lower (Bishop et al., 2016). However, recent studies in the north Atlantic, and the use of bomb radiocarbon isotope deposition in the south Pacific (Bishop et al., 2016; Calliet, 2015), have shown that makos actually deposit one vertebral band for each year of growth. Differences found in band formation among specimens of shortfin makos could be the result of where studies are conducted, how they are conducted, and what age classes are being studied (Calliet, 2015). Due to different ontogenetic habitat use, certain age classes may be more represented at some sites than others. When studies are conducted, it is important to consider that there may also be differences in how vertebral bands are laid based on size and age of the shark. Therefore, determining longevity and absolute age of shortfin makos can be difficult. However, counting one vertebral band per year, the maximum age observed for females was 29 years and for males was 28 years (Bishop et al., 2016). Therefore, shortfin makos are believed to live for longer than 29 years. The difficulties with validating vertebral bands of every age class of a pelagic shark with a circumglobal distribution, and the low probability of catching the oldest, largest individuals in such a species, make more accurate longevity estimates for these sharks unrealistic.

Shortfin mako populations display a 1:1 sex ratio at smaller individual sizes (Casey and Kohler, 1992). As makos increase in size, especially after 240cm, the population shows a shift toward female dominance. Natural mortality rates of 0.09-0.16 for female shortfin makos are important to know because female total lifetime fecundity and mortality are useful in determining a fished population’s ability to increase in number (Bishop et al., 2006). The overall estimate of natural mortality for the species is 0.10-0.15, which shows low natural mortality and productivity levels for the shortfin mako.

5. Behavior

Studying “natural” shark behavior is almost impossible due to the inherent difficulties associated with observing sharks *in situ* (Nelson, 1977). Behaviors that may be considered natural, such as feeding preferences, social interactions, and habitat use observed in the wild, could actually be abnormal if the presence of the researchers affects those behaviors. Therefore, new techniques should be developed to try to reduce the presence of researchers, and thus allow observations of more natural behaviors. When divers directly observe sharks, they usually do so in either baited or unbaited situations. Baited situations have allowed scientists to study the mechanisms of feeding used by shark species, but fail to provide the ability to observe natural feeding behaviors. Unbaited studies may produce few results because the large ranges exhibited by many shark species like the shortfin mako, may make encountering individuals less likely without bait to lure the sharks near the divers. As early as the 1970’s, researchers began experimenting with technologies such as remote monitoring using acoustic telemetry. In the four decades since, new technologies have allowed researchers to continue to study more complex and varied behaviors between and within shark species.

Acoustic telemetry can be used to study habitat use for shark species that do not range far, but is less effective for pelagic species with large ranges (Heithaus et al., 2001). It is difficult to get precise locations for tagged animals, and they provide no information about the behavior of the sharks as they interact with their habitat and other animals that share that environment. Acoustic tags are less useful in areas with patchy habitats as well, since it is difficult to determine what type of habitat the animals are in at any given time. One solution to this issue could be the use of shark-mounted cameras (Crittercam). This method has been successfully used to study the ecology and behavior of pinnipeds, and may be useful in shark research as well.

Crittercam, attached to the shark's dorsal fin, is a small camera and recording device that can be programmed to record continuously or at specified intervals for up to 6 hours (Heithaus et al., 2001). They are also able to record environmental data, and will detach from the animal after a predetermined time frame. After release, they float to the surface and emit a VHF signal to be retrieved by researchers. Unlike other, more bulky tag methods previously used in tracking studies, Crittercam is attached close to the midline and near the center of mass, so it does not appear to affect the swimming behavior of the sharks. If the shark is unable to be captured to have the Crittercam attached directly to the dorsal fin, it can be tethered to the body, however, this will reduce the turning speed of the camera, so some shark behaviors may not be captured. Crittercam has been successfully used in the study of white sharks, another lamnid shark, and could be used to study shortfin makos in the future.

The behaviors of shortfin makos are complex and just beginning to be understood. As with many predators, an important driver of changes in habitat use and movement of these sharks is likely the abundance and distribution of prey items. Understanding habitat use and movement behavior of shark species is important to understand their ecology and inform conservation and management plans for these species (Heithaus et al., 2001). Sex-specific behaviors, such as sex-biased dispersal, resource use, and habitat use, may make shortfin makos particularly susceptible to overexploitation in some areas (Bustamante and Bennett, 2013). Many species of sharks show behavioral changes in different spatial distributions, or at different times of the year (Mucientes et al., 2009). These factors should be considered in the implementation of any new policies or regulations that affect shortfin makos.

5.1 Movement Behavior

Having a better understanding of how shortfin makos are distributed within their habitats, and their vertical and horizontal movements through these habitats, can provide policy makers with additional information regarding the efficacy of management and conservation plans (Vaudo et al., 2017).The movements of shortfin makos have been found to vary depending on the part of their range being studied. In the southeast Pacific, makos were observed traveling approximately 37 km per day, with a general onshore movement during the winter months (Abascal et al., 2011). They prefer waters between 13.4° and 24.1° C, with their vertical movements changing depending on sea surface temperature and time of day. They spend most of their time in the mixed layer, but display foraging behavior during the day with rapid descents below the thermocline, followed by slow ascents. This behavior could be used for prey detection, as olfactory cues for prey tend to travel horizontally in the oceans. These dives are short and followed by long periods of time in the surface waters when sea surface temperatures are lower. At night they prefer surface waters, rarely descending more than 150 m. This difference in depth between day and night could be a result of diel prey distribution or attempts to stay within the mixed layer.

Vertical movements of shortfin makos in the southeast Pacific appear to depend on the dissolved oxygen (DO) levels in the water column (Abascal et al., 2011). The oxygen minimum zone in this area of the Pacific is well-developed because of high primary production. Due to high metabolic demands, these sharks prefer waters with a DO concentration greater than 3 mL/L. However, during dives below the mixed layer, they have been recorded spending short amounts of time in anoxic waters with DO levels of 0.5mL/L or lower.

In the northeast Pacific, shortfin makos have been well documented off the southern California coast, where they are popular with sports fishers, commercial fishers, and also caught as bycatch in driftnet fisheries targeting swordfish (*Xiphias gladius*) and thresher sharks (*Alopias vulpinus*) (Holts and Bedford, 1993). The catch is most abundant June-August and usually consists of juvenile individuals less than two years of age. Tagged sharks there showed variations in speed, depth, and direction. Immediately after release, they dove below the thermocline, possibly to rid themselves of excess body heat acquired during the struggle against capture, or to replenish oxygen supplies in more oxygen-rich waters. This is similar to behaviors observed in other studies of shortfin makos (Holts and Bedford, 1993; Klimley et al., 2002). They then swam at relatively constant speeds closer to the surface. They tended to be more active at night, and least active mid-morning. The sharks stayed at shallow depths, or made short dives, usually staying above the thermocline. Unlike in other shark species studied in this area, juvenile shortfin makos in the southern California bight do not appear to demonstrate movements that are topographically-oriented. However, their movements do appear to be influenced by local currents and eddies that were spawned by the California Current.

Another study done on shortfin mako movement off of the southern California coast near the La Jolla submarine canyon showed that they are more active than co-occurring ectothermic species (Klimley et al., 2002). Unlike the juvenile shortfin makos studied in the southern California bight, these three makos were adults (one female, two males). All three animals dove immediately after release, and then slowly ascended into the mixed layer. The female shark preferred to stay in the mixed layer or within the thermocline, while the males spent more time below the thermocline. Furthermore, all three sharks displayed oscillating dive patterns, known as "yo-yo" diving, with 30 minutes to an hour and a half between successive dives, which is common in many marine vertebrates (Klimley et al., 2002). This behavior is thought to help raise the fish's body temperature after diving below the thermocline. Although shortfin makos prefer staying in waters >14°C, they lose body heat when diving into deeper water. Since shortfin makos maintain their body temperature well above ambient water temperatures, rising toward the warmer waters near the surface may help reduce metabolic costs associated with maintaining their temperatures after these dives. It could also be used by individual animals as a behavior to assist with gathering information from different layers of the water column, such as olfactory or magnetic cues. Lastly, it may reduce the metabolic costs associated with swimming by using energy to rise through the water column, and then slowly drift downwards. In this manner, the animals use less energy to maintain their place in the water column as they move horizontally through the ocean.

The three sharks were active at night, but one of the males and the female showed more activity at night than the other male, who showed no difference between day and night activity (Klimley et al., 2002). The average water temperature that all three shortfin makos inhabited was 19-19.9°C. However, one of the males preferred waters between 13-13.9°C, while the other male tended to remain in water between 17-17.9°C.

These three individuals moved in a general offshore direction after release (Klimley et al., 2002). They displayed heading persistence, with one male and the female moving in a southwesterly direction almost continuously after release. The other male displayed more variable directional swimming than the others, but he also tended to continue in one direction for long periods of time. These sharks may be able to maintain consistent headings while swimming long distances using irradiance, chemical gradients, or geomagnetic fields, but the exact mechanism has not yet been determined. They may also use magnetic fields related to submarine topographical features as indicators to change their swimming behaviors. One of the males and the female swam along the axis of the La Jolla submarine canyon, while the other male changed direction once reaching the pinnacle of a seamount. This observation raises the question of whether bathymetric topography influences adult mako swimming behavior more than it does for juveniles.

The apparent preference for deeper, colder water in adult males, regular diving behavior below the thermocline, the female staying above the thermocline, and the use of bottom topography to elicit behavioral changes, demonstrate why it is imperative that more needs to need to be studied regarding the movement behaviors of large pelagic sharks. Different fishing gear and techniques may cause an increase in bycatch of one sex over the other, as females, like the juveniles studied in the southern California Bight, appear to spend most of their time in the surface layers of the water, while males spend more time at greater depth. Not understanding how these sharks use topographical features or magnetic fields to determine where they will swim, or how their movements change in different areas and at multiple life history stages, could cause the accidental extirpation of the shortfin mako in some areas of the Pacific Ocean due to fishing pressure.

Knowledge of how shortfin makos are distributed in the water column, and how they move vertically through it, can help managers and policy makers when determining the risks to the sharks from certain fisheries activities (Vaudo et al., 2016). Knowing where the sharks are most likely to be located in the water column could inform best practices by fisheries to reduce the amount of interaction between the sharks and fishing gear, and ultimately reduce the amount of mako bycatch. Most movement studies done in the western North Atlantic have only provided information on horizontal movement of individuals, and show a strong correlation between Sea Surface Temperature (SST) and shark movement patterns. However, using satellite tags to study vertical movement in the water column as shown that their behaviors are more complex than previously thought.

Shortfin makos in the Northwestern Atlantic exhibit bounce diving, where they descend rapidly, and then slowly rise repeatedly throughout the day (Vaudo et al., 2016). Just as in the Northeastern Pacific, makos in the Northwest Atlantic are more active and dive deeper during the day than at night. This pattern could have developed in conjunction with the diurnal vertical migration of their prey items. It is also thought that makos are visual hunters, so they dive deeper during the day when their prey is more visible at depth. However, temperature is also a factor in how the sharks use the water column. In areas of the Northwest Atlantic, where water temperatures decrease more rapidly with depth, shortfin makos do not dive as deeply as they do in the Gulf of Mexico, where the thermocline is less pronounced and the sharks spend more time at deeper depths, presumably to stay out of higher surface water temperatures (Vaudo et al., 2016). These different regional behaviors demonstrate how makos use the water column to stay within their optimal temperature range, between 10-15°C and 28°C. In the Atlantic Ocean, shark tagging has occurred since 1962 as part of the Cooperative Shark Tagging Program (CSTP) administered by the National Marine Fisheries Service (Kohler et al., 2002). This program is important in determining population parameters, stock structures, distribution of different age classes, exploitation rates in international fisheries, and movements of species across international borders. Researchers use fin tags inserted through the first dorsal fin, or dart tags shot into the musculature along the back near the first dorsal fin, with return instructions in multiple languages. In order to increase fisher participation in this program, rewards have been used as incentives should a tag be returned with accurate catch information. From 1964-2000, most of the information received was from recreational fishers, who accounted for 53% of the total number of tags returned. The remainder came from commercial fishers representing 14 countries. The results of this tagging program showed that most makos moved less than 500 nm from their original tagging location. However, one individual traveled from the northeast US coast to the coast of Western Sahara, Africa in 1.4 years, a total distance of 2,867 nm. Three fourths of the recaptured sharks were at liberty for less than 2 years, although one male was recaptured almost 13 years later approximately 250 nm from where he was first tagged.

However, conventional tagging programs are limited because they can only provide vector distances of how far the makos have moved away from their original capture sight when they are recaptured. These vector distances can severely underestimate the actual distances travelled. Vaudo et al. (2017), using satellite tags, found that individual sharks in the Northwest Atlantic travelled long distances to southern parts of their range, and then swam back close to their tagging regions typically within a year. Although it is unknown what causes these sharks to undertake such long journeys, as typical biological drivers such as feeding and reproduction do not seem to play a part, traditional tag-recapture studies would fail to provide data regarding how far these sharks have actually moved.

Information inferred from traditional tagging studies resulted in the ‘Sargasso Sea’ hypothesis (Casey and Kohler, 1992), where it was proposed that shortfin makos in the northwestern Atlantic follow a predictable migration pattern each year as water temperatures change. This hypothesis posits that until April, shortfin makos are found south of Cape Hatteras. As the Gulf Stream moves more northward in the late spring and early summer, the sharks follow the warming waters up to the Grand Banks. Between June and October, anglers catch shortfin makos all the way up to the Gulf of Maine. It is believed that the entire area over the continental shelf south of Cape Cod may be an important feeding ground for both juvenile and subadult populations of makos in the northwest Atlantic. In November and December, the sharks move back offshore and more southward into the Sargasso Sea following the receding Gulf Stream waters.

Recently, however, by employing satellite telemetry, Vaudo et al., (2017) found that shortfin mako movements in the Northwest Atlantic is not as easily explained as the ‘Sargasso Sea’ hypothesis would imply. Individual shark movement is more variable than the hypothesis suggests. There is no coordinated movement of the entire population in the Northwestern Atlantic as the seasons change. The satellite telemetry showed that the sharks do not stay in the Sargasso Sea, perhaps because of the low primary productivity there, after retreating from cooler waters in the north, as was once believed. Instead, individuals traverse through the Sargasso Sea to the south or to the US Mid-Atlantic Bight, where some sharks stay all year. Therefore, creating conservation or management plans based on the ‘Sargasso Sea’ hypothesis could prevent adequate protection for less-mobile groups in this population.

After almost forty years of tagging programs, it has been found that very few makos move between the eastern and western North Atlantic, and that the populations in the northern and southern Atlantic show enough genetic differences that there also appears to be little exchange between these populations (Kohler et al., 2002). Even in the Western Atlantic basin, there is little mixing between the populations of the Northwest Atlantic and the Gulf of Mexico (Vaudo et al., 2017).This demonstrates the problems with treating this circumglobally distributed species as one population for conservation and management purposes. Localized overexploitation in any area of the shortfin mako’s range may lead to extirpation of that population with little chance of recovery from new recruitment or immigration from other populations.

5.2 Feeding behavior

As with most shark species, shortfin makos appear to be opportunistic predators that will switch to different prey items depending on the availability of that item at different times of the year. Teleosts were the most important prey group for shortfin makos in the northeast Atlantic, found in 93.7% of the stomachs that contained prey (Maia et al., 2006). There appears to be a preference for fast-swimming prey items such as swordfish and lancetfish. This implies that makos may use a similar feeding strategy to white sharks, and attack their prey vertically from below. Cephalopods in 40.4% of stomachs, and crustaceans in 36.4%, were also important food groups, which occur at much higher frequencies than those observed in the South Pacific during other studies. There are seasonal differences within each group, with a switch to Clupeiformes species and garfish (*Belone belone*) during the spring, similar to what has been observed in other studies showing a switch to bluefish during the summer in the northwest Atlantic. Juvenile and Young-of-Year (YOY) sharks consumed less crustaceans in the winter and spring, and seemed to show a preference for other elasmobranchs. However, overall, less elasmobranchs were observed as prey in the northeast Atlantic than other areas due to the less complex open water habitats inhabited by the makos there.

Most shark species eat 3-14% of their total body weight each week (Motta and Wilga, 2001). All size classes of shortfin makos caught by the Spanish and Portuguese longline fleets consume small prey, but the average size of prey is 22.6% of the shark's body size (Maia et al., 2006). The largest prey item retrieved in this area was 87% of the shark's size. They also show overlap between meals, so prey items were found at varying stages of digestion, which could indicate that prey capture relies more on opportunistic encounters with prey rather than digestion being completed before another prey item is captured. This may be an important behavior for endothermic sharks that require high caloric intake to maintain their internal body temperatures.

The prey items contained in the shortfin mako stomachs do not differ significantly between adult individuals of both sexes (Maia et al., 2006), as has been found in scalloped hammerheads (*S. lewini*). In adult scalloped hammerheads, females move offshore and eat larger pelagic prey, thus attaining greater size than males that stay closer to shore (Motta and Wilga, 2001). There were also no significant differences between YOY and juvenile prey items, unlike in other elasmobranch species (Maia et al., 2006). In many shark species, changes in dentition occur with changes in life history stages, leading to corresponding changes in prey preference (Motta and Wilga, 2001). This could explain why there are significant dietary trophic level differences between adults and juveniles, and adults and YOY individuals, in shortfin makos (Maia et al., 2006). For larger prey items, bite analysis shows that the sharks use a successive biting technique to ingest more and more of the body, or bite off large chunks of flesh at a time. Makos show a preference for Atlantic mackerel over squid, so the switching of bait used in the swordfish fishery to more squid or exclusively squid, could be used to help reduce bycatch of the shortfin mako in the northeast Atlantic.

In the California current off the western coast of the United States, shortfin makos exist alongside other shark species, but due to their opportunistic diet preferences, they are not greatly affected by competition with other shark species. Shortfin makos show a more diverse selection of prey items than thresher sharks (*Alopias vulpinus*), which are another regionally endothermic species, and ectotherms such as the blue shark (*Prionace glauca*) (Preti et al., 2012). Differences in vertical movements within the water column separate these three shark species and have allowed the creation of separate feeding niches in the same area. The diet of shortfin makos consists of both cephalopods and teleosts. Blue sharks also pursue a wide variety of prey items, but show a preference for cephalopods, while thresher sharks feed mainly on coastal teleosts. The most important prey items in this area for the shortfin mako is jumbo squid (*Dosidicus gigas*), followed by Pacific Saury (*Cololabis saira*). Other species found in the stomachs of shortfin makos in the California Current include several teleost species, blue sharks, and a short-beaked common dolphin (*Delphinus delphis*). The differences seen between the prey choices of individuals varies not only by season, but is affected by class size and location as well. Where the populations in the northwest Atlantic feeds mainly on teleosts, those in the northeast Pacific feed primarily on squid. Therefore, fisheries plans to reduce bycatch by switching from teleosts to cephalopod bait, or vice versa, on one coast of the US will not work the same on the other coast.

Top-down trophic models of marine ecosystems often show sharks as the apex predators (Wood et al., 2009). They affect prey communities through predation, and help control prey populations. Management and conservation plans for large, pelagic sharks are often based on ecosystem models that emphasize the importance of top-down control on that ecosystem, and how removal of top predators affect the functioning of the ecosystem as a whole (Harford, 2013). The removal of the sharks actually benefits other species, such as marine mammals and turtles, more than their main teleost prey species. This is because teleost species face predation from so many sources that they have high fecundity and fast growth rates. These traits reduce the effects of predation on their population numbers. It is believed that sharks affect teleost prey populations less than other predators due to low feeding rates in comparison to those predators.

However, shark populations may be adversely affected by the removal of prey fish through anthropogenic fishing effort (Harford, 2013). For example, in the eastern North Pacific, after prey fish were removed by fisheries, salmon shark (*Lamna ditropis*) populations increased after a reduction in blue shark numbers in that area. The reduction in blue sharks could be a result of increased competition with the salmon sharks for prey, after prey availability was decreased due to fishing pressures. However, the trophic relationships between different shark species, as well as with their prey items, has not been well studied in many areas.

Understanding how shark behaviors change depending on the prey being captured at different life stages or different times of the year is important when trying to develop fishing practices that will lower the bycatch of these animals. In some species, feeding behavior changes based on the size of prey items that they are pursuing (Motta and Wilga, 2001). Others show differences in pre- or post-capture behaviors depending on the type of prey that they are capturing. Vigorous head and body shaking may occur as sharks attempt to tear off smaller pieces of larger prey. If done with bait on a longline J-hook, the shark could become foul hooked through another part of the head or the gills, thus causing increased mortality in a population.

The trophic interactions of shortfin makos and bluefish (*Pomatomus saltatrix*) in the western North Atlantic is an example of a predator/prey relationship recently studied (Harford, 2013). In the spring and summer, shortfin makos migrate from deeper waters to inshore waters from North Carolina to Maine. Bluefish also migrate at this time to the same areas. This corresponds with a diet change for the shortfin makos from mainly squid to mostly bluefish. During this period, bluefish comprise more than 86-92% of the sharks' diet, indicating that makos may exert predation pressure on bluefish populations. However, shortfin makos are affected by fishing pressures, and their numbers have declined in the past few decades. It was believed that the reduction in the number of sharks would release the bluefish from predation pressure, thus helping bluefish population numbers. However, bluefish are heavily fished, both recreationally and commercially, so their abundance has also declined during the same period. Since many other teleost prey species that were once common in the western North Atlantic were overexploited in the past, or are currently overexploited, the decrease in bluefish populations may explain the corresponding decrease in the shortfin mako population in this region. The shrinking shortfin mako population could be the result of a lack of alternative prey items available to the sharks. One exception is Atlantic herring (*Clupea harengus*), which increased in abundance in the northern Atlantic Ocean, from the Gulf of Maine to Georges Bank, during the period of 1983 to 2008. The increase in availability of this prey item for the sharks is reflected in a corresponding increase of herring as a percentage of the sharks' diet. It is possible that in the future, if bluefish biomass continues to decrease, herring will play a larger role than bluefish in the diet of shortfin makos off of the coast of New England (Harford, 2013).

Overall, it was found that predators at lower trophic levels had a much greater effect on trophic structure than predators at the higher levels occupied by the shortfin mako or bluefish (Harford, 2013). When determining what factors most affect shortfin mako populations, the strongest relationships are shown between the decrease in bluefish biomass and shortfin mako biomass, and fishing mortality and decreased shark abundance. Using modeling that was able to test the effect of different factors on shortfin makos, environmental change and other trophic interactions had less of an effect on the shark population of the western North Atlantic (Harford, 2013). Competition between the bluefish fishery and shortfin makos is apparent. In the models, the closure of the bluefish fishery would result in a 40% increase in shortfin mako biomass, and a decrease in fishing pressure on bluefish allowed an increase of 20% biomass for both bluefish and shortfin makos. However, a shutdown of shortfin mako fishery effort created a fourfold increase in shark biomass but did not affect bluefish populations, signaling that the shortfin mako does not exert a strong top-down control of the ecosystem in this region.

Changes in effort in bluefish fisheries can have dramatic effects on the shortfin mako fishery in the western North Atlantic (Harford, 2013). Slight increases in fishing effort for bluefish negatively affect shortfin mako catch rates. Conversely, if bluefish fishing effort is decreased to 0, this would lead to an increase of 1.4 times current catch levels for the sharks. It is thought that bluefish catch rates are slightly below Maximum Sustainable Yield (MSY). If they were to be increased to MSY, this would cause a 15%

reduction in shortfin mako catch. The models used to study the interaction of bluefish and shortfin makos does have limitations. More research should be done on accurately measuring mako densities, rates of consumption of the makos, and to understand the foraging behavior of these sharks. This knowledge will help scientists create better models that can be used to forecast how changes in fishing effort will affect both prey fish and the sharks themselves.

5.3 Mating Behavior

Little is known about mating behaviors among shortfin makos, but it is believed that mating tends to occur in late summer (Semba et al., 2011). Therefore, growth models are used to estimate the gestation period, using size measurements of pups *in utero* and the smallest free-swimming individuals captured. Females are thought to travel to between 20° and 30° N and S latitude to pup (Corrigan et al., 2015; Gilmore, 1993). An important nursery area in the North Pacific is in the Southern California Bight (Sepulveda et al., 2004). Parturition usually occurs in spring or summer, although winter parturition has also been noted in some areas (Semba et al., 2011; Gilmore, 1993). In the southern ocean, around New Zealand, parturition begins in late winter and continues into mid-summer (Duffy and Francis, 2001). It is possible that shortfin makos may be capable of breeding all year round, but a smaller GSI in males after July makes mating throughout the year unlikely (Joung and Hus, 2005). The entire reproductive cycle is estimated to take as long as three years (Corrigan et al., 2015; Semba et al., 2011; Tsai et al., 2014; Joung and Hsu, 2005; Duffy and Francis, 2001), although some researchers believe a two year cycle is also possible (Tsai et al., 2014). Currently, there is a lack of definitive information regarding the mating behaviors of these sharks.

Genetic investigation in one case so far so has revealed polyandry in shortfin makos (Corrigan et al., 2015), potentially contradicting the hypothesis (Gilmore 1993) that polyandry is expected to be infrequent as a result of the scarcity of chance encounters with potential mates in the open ocean. Despite the difficulties in finding mates, sperm storage has not been found in shortfin makos (Corrigan et al., 2015). Both females and males are thought to have multiple mates because of results of genetic analysis of offspring (Hueter et al., 2005)). These types of genetic analyses are important for pelagic species that are difficult to study due to their broad ranges. Corrigan et al. (2015) used microsatellite allele counts to demonstrate that the single shortfin mako litter examined showed at least two, possibly three, different males that contributed paternal DNA. However, due to skewed results, the actual number of males involved could have been greater than three. It is thought that this is accomplished through the use of specific mating grounds, although this is speculation based on the sex ratio of populations in certain areas becoming more even during the mating season.

Genetic evidence shows that several shark species show philopatry, or the returning of individual animals to the same areas in the oceans during different life stages or activities (Hueter et al., 2005; Chapman et al. 2015). Philopatry can be related to natal areas or sex-specific, where one sex shows this tendency more than the other, such as the sexual segregation seen in many shark species. Understanding philopatric behavior and the distribution and movement patterns of shortfin makos is important when assessing the stock strength and population ecology of the sharks in different parts of their ranges (Holts and Bedford, 1993). In highly migratory species, philopatry to certain areas, whether natal, feeding, or mating locations, means that even these species that have been thought to move throughout a large range and replenish depleted stocks through recruitment and immigration could be overfished in certain areas, leading to localized stock depletion (Hueter et al., 2005).

The study of philopatry in sharks is just beginning, with tracking and genetics studies used to find evidence of individuals returning to the same areas again and again (Hueter et al., 2005; Chapman et al. 2015; Lea et al. 2015). In many cases, when using a genetic approach, the greater the genetic divergence of animals of one species that come together for seasonal migrations, the more evidence there is for philopatric behavior by these individuals. Nuclear DNA markers are inherited from both males and females, while mitochondrial DNA markers are passed down from females to their offspring. Therefore, when using mitochondrial DNA markers, females are often found to show more philopatry to certain areas than males. Again, there are downsides to this method of studying philopatry. The variances in allele frequencies used to determine if there are distinct natal or post-natal groups from different areas may be difficult to determine if these areas fail to contribute sufficient individuals to recruitment to be measured as unique groups. Also, small errors in the measurements of the variation in allele frequency may lead to large errors in the estimation of migrants from different areas (Hueter et al., 2005).

Management and conservation of stocks of highly migratory pelagic sharks can be difficult, as they may display philopatry for certain areas at different life history stages, but these areas may cross state, national, or regional fisheries management council borders, thus complicating attempts to consistently manage and protect populations there (Hueter et al., 2005; Vaudo et al. 2017). For example, female shortfin makos in the Atlantic give birth in the Gulf Stream, so newborns use the current to disperse widely throughout the northern Atlantic (Casey and Kohler, 1992). It is believed that this prevents predation on newborn shortfin makos, both from large pelagic predators and other mako sharks. The largest specimens of makos in the north Atlantic are found in the Gulf of Mexico and off the southeastern United States, while the smallest individuals are often observed off of the Grand Banks. Not only pupping locations, but also important mating and feeding areas for the shortfin mako, span the entire northern Atlantic for this species, and management plans should reflect this complexity of different habitats in state, national, and regional management policies that encompass this area (Hueter et al., 2005).

If shark populations aggregate at different times of the year for feeding or mating, fishing pressure in that location may cause a more rapid decline in population numbers. Habitat preference is often based on different factors, including water temperatures and local productivity that provide suitable prey for each life stage of these sharks (Bustamante and Bennett. 2013). However, shortfin mako populations show clear regional segregation of size classes and sexes, which does not clearly coincide with changes in prey availability, temperature, or productivity. It is thought that sexual segregation observed in these sharks in the South Pacific may be due to social factors to help reduce sexual harassment of females, leading to increased ratios of one sex over the other in different areas. In the South Pacific, males are predominant in longline fishing areas. However, in other areas, females are caught more by fisheries, which could reduce the fecundity of the population of makos in that area and may result in local extirpation of the species (Bustamante and Bennett, 2013).

5.4 Habitat use

Habitat use during different life stages can affect population dynamics, intra- and inter-specific interactions, and ecosystem structure. Juvenile shortfin makos prefer warmer sea surface temperatures (Bustamante and Bennett, 2013). During the summer months, the waters off of Chile warm to between 17°C and 22°C, which correlates with an increase in production and prey items in the area (Bustamante and Bennett, 2013). These factors have also been shown to be important aspects of nursery grounds off the southern California coast. Young-of-year sharks in the Southern California Bight show greater movements both horizontally and vertically during the day, and a positive correlation between the length of the individual and how deeply they dive (Sepulveda et al., 2004). On average, YOY spend more than 80% of their time at depths less than 12m. They rely on visual cues to capture prey, which may explain why they dive to greater depths during the day when light penetrates deeper into the water column. They may move between depths to search the water column for prey, to increase their body temperatures after short dives below the thermocline, to use different water masses or bottom topography for navigation, or to surprise attack prey from below. Whatever the explanation, YOY shortfin makos show the same oscillating dive behavior seen in other age classes of shortfin makos and other species of pelagic sharks. Their location near the surface may make YOY individuals more susceptible to surface fisheries than other age classes, and small changes in fisheries practices, like the deeper setting of gill nest in the Southern California Bight have already decreased the number of YOY shortfin makos caught as bycatch in those fisheries.

In Mexico, shortfin makos are usually caught off of the northwest Pacific coast along the western shoreline of the Baja California peninsula (Velez-Marin and Marquez-Farias, 2009). Catches in this areas are highest around Cabo San Lucas and Islas Marías. Between 1986 and 2003, there were no shortfin makos caught along the central Mexican coast. The sharks are found past the continental shelf in deep waters off of the western Baja California coast all year round. However, from January through March, they are found in other areas closer to the coast and the Gulf of California. Then, from April to September, shortfin makos are widely distributed, and found all the way down to the southern Gulf of Tehuantepec. They are common throughout the northwestern Mexican Pacific waters from October to December. The high number of small shortfin makos captured along the western Baja California coast, the Gulf of California and Islas Marías could indicate that this area serves as part of the shortfin mako nursery found in the Southern California Bight.

It is well-documented that many shark species use nursery areas to increase the survivability of their offspring (Heupel et al., 2007). Identifying and protecting shark nursery areas is imperative for the conservation of endangered and vulnerable shark species. The more philopatric a species is for their natal habitat, the more essential protection of their specific nursery areas is for conservation of its abundance (Hueter et al., 2005). However, one issue that has prevented proper identification of nursery areas is a lack of a consistent definition to describe such areas (Heupel et al., 2007). The accepted definition for a nursery area, most often used by teleost and invertebrate ecologists, is an area where there are high densities of juveniles that are protected from excessive predation, provide environmental conditions that allow maximum growth, and make a significant contribution to adult recruitment. However, for sharks, this definition is often not employed, and many areas are considered nursery areas because a few juveniles have been observed there, without any studies done to determine if the conditions in these areas actually do increase the pups' chances of survival. This has created problems with scientifically justifying measures that are proposed to protect such areas. For example, observations of coastal shark species show that parturition occurs in shallower water than that in which adults tend to reside. As a result, many ecologists traditionally made broad proclamations regarding the importance of coastal areas as nurseries. This outlook fails to identify specific areas that serve as important nursery grounds, which may prevent the proper levels of protections for those areas.

This point of view regarding sharks began to change in the 1970's when scientists began to differentiate primary and secondary nursery sites for different shark species (Heupel et al., 2007). Primary nurseries were the locations where parturition and the youngest juveniles dwelt, while secondary nurseries were where larger juveniles and subadults reside before they join the adult population. The separation of the different nursery areas is difficult to determine, but it is often based on environmental or biological conditions, such as water temperature, prey availability, and predation risks.

One difficulty in determining what constitutes a nursery area for sharks is the high mobility of these fishes (Heupel et al., 2007). Pelagic species may have less well-defined nursery areas or no nursery areas at all. Instead, they may simply have pupping grounds that the young quickly disperse from after parturition. Also, different species of sharks may use nursery grounds for different amounts of time or for different reasons, such as increased access to prey or decreased exposure to predators.

The definition of what constitutes a nursery or pupping area for different species has continued to evolve. The best definition to date is that a nursery is an area where YOY are more often observed in comparison to other areas, sharks tend to stay in these areas for long periods of time, and year after year there is a new YOY class in the same area (Heupel et al., 2007). This definition clearly defines an area as important for conservation, whether it is a well-delineated, protected nursery like those found for many coastal species, or broader pupping grounds for pelagic species, based on scientifically valid observations of the continued occurrence of YOY there. Using this definition, the southern California Bight could be an important nursery ground for shortfin makos in the Pacific because individuals less than 2 years of age are caught there regularly (Holts and Bedford, 1993). Identifying these areas is an important step toward protecting species such as shortfin makos whose entire distributional life history is not well known at the present time.

Because of the number of individuals between 70 and 100 cm TL caught in Chilean waters, it is believed that this may be an important southeastern Pacific pupping ground or nursery for the shortfin mako during the spring and summer (Bustamante and Bennett, 2013). However, between 2005 and 2010, the number of young of the month (YOM) individuals decreased from 25% of the total catch to just 9% of the total catch. At the same time, there was also a decrease in young of year individuals caught. This may because of a decrease in the number of mature females returning to these pupping grounds by 2010. Juvenile makos spend up to 90% of their time in the upper mixed layer down to approximately 20m, which makes them more susceptible to fishing efforts. Thus the decrease in captured YOM and YOY individuals is a significant indicator of the health of this population. Management changes, such as minimum size limits, catch quotas, and restricted fishing areas should be implemented to prevent the catching of immature shortfin makos off the Chilean coast in order to ensure that this population persists.

6. Fisheries and shortfin makos

Fishing is by far the biggest threat to pelagic shark species (Dulvy et al., 2008). Shortfin makos are highly prized in recreational fisheries in many developed nations (French et al., 2015). In Australia they are only able to be captured and released by recreational anglers, as they are a protected species there. There is a correlation in fight time between shark size and sea surface temperature, with larger sharks fighting anglers for longer in warmer waters, up to 513 minutes, making them more desirable catches. Longer fight times lead to higher physiological stress, which in many species results in post-release mortality. However, out of 30 sharks tagged after being caught by recreational anglers (French et al., 2015), only 3 died within the 30 days that they were monitored post-release. This equates to a 90% post-release survival rate which is much higher than in many ectothermic species that are caught recreationally. This could be due to the higher metabolism and aerobic abilities displayed by the shortfin mako that result from its endothermy. These traits aid shortfin makos in recovering from the stresses related to being landed by anglers.

The three shortfin makos that did die post-release had short fight times, so it is believed that their mortality was the result of physical damage arising from the gear used by the fishers rather than any physiological stress (French et al., 2015). Two of the sharks were foul-hooked using J-hooks. One of these was hooked through the gills with a large amount of bleeding, and the other was deep-hooked possibly causing internal injuries. The third was caught using a circle hook through the jaw, so the cause of death was not apparent. These examples show that the type of gear used to catch these sharks has direct impacts on post-release survival, so it is important to enact regulations that prevent foul-hooking by recreational anglers though the use of circle hooks.

Sharks are also caught as bycatch in many global fisheries. Bycatch can refer to incidental catch, secondary catch, and unwanted individuals (Dulvy et al., 2014).

Incidental or secondary bycatch are animals that are caught and used in similar ways as the primary catch species or that have an economic benefit for the fisher to retain them. Unwanted bycatch are species which fishers try to avoid because they are not useful or profitable, they cause damage to gear, or they are caught while hunting the target species, thus reducing primary catch.

Bycatch can affect biodiversity through the removal of prey items and top predators such as sharks (Gilman et al., 2008). It can change foraging behaviors of predators as they begin to associate fishing gear with prey items. Depredation, the removal by predators of part, or all, of a target species from fishing gear, is a cause of significant economic loss to fisheries. Due to the economic consequences of depredation, predators perceived to be responsible, such as whales or sharks, may face increased injury or mortality at the hands of the fishers who are trying to prevent these losses.

Few studies have been done to determine the survivability of sharks caught as bycatch and released. There is most likely a combination of biological, environmental, and operational variables that together cause post-release mortality of sharks caught as bycatch (Gallagher et al., 2014). Different target species are caught in different ways, which may increase or decrease the interaction of sharks with the fishery. The strength of bycatch regulations for sharks varies from nation to nation.

The US and Australia have strict regulations on shark landings (Dulvy et al., 2014). However, a large percentage of shark landings come from nations without comprehensive fisheries plans for sharks. Many nations have banned shark finning, but still, 26-73 million sharks are caught each year in the finning industry (Clarke et al. 2006), with an estimated value of $400-550 million. More than 9,500 mt of shark fins are exported to Hong Kong annually. About 70% of the shark species identified in the Hong Kong fin market are pelagic shark species, including the shortfin mako (Dulvy et al., 2008). There is also a growing global market for shark meat, liver oil, and gill rakers (Dulvy et al., 2014). In many developing nations, such as Brazil, shark meat can serve as an important protein source for the population (Bornatowski et al., 2014). However, sharks are not included in the fisheries statistics of many nations, and mislabeling of the type of shark meat being sold in local markets can hinder efforts to manage artisanal fisheries that take different shark species. In Brazil alone, there are over one million artisanal fishermen. Worldwide, only about 15% of sharks caught by fishers are identified at the species level (Lack and Sant, 2006).

Shortfin makos in the Atlantic Ocean are caught in longline fisheries of many nations, including Cuba, Denmark, Venezuela, Korea, and Taiwan (Casey and Kohler, 1992). The four nations that catch the largest percentage of shortfin makos each year are the United States, Canada, Japan, and Spain. In the western north Atlantic, shortfin makos can represent 2-9% of the bycatch in the swordfish longline fisheries. The abundance of shortfin makos caught as bycatch is affected by the seasonality of the specific fishery, the fishing gear used, and the biological factors associated with the target species of the fishery.

Shortfin makos are found seasonally in Canadian waters (Campana et al., 2005). Canada instituted a complete ban on finning in 1994, and implemented restrictions on recreational fishing for makos to hook and release only. Since 1995, commercial fisheries directed at shortfin makos can catch the sharks using longlines, landlines, or rod and reel, with an annual catch limit of 250 mt. However, they do not have any restrictions on makos caught as bycatch by commercial pelagic fisheries. None of these catch limits or policies that have been implemented were based on accurate estimations of the shortfin mako populations in this area. Between 1994 and 2003, landings of shortfin makos in Atlantic Canadian waters decreased from 160mt to just 60 mt, which is about 4% of the reported North Atlantic catch.

There is currently no directed Canadian fishery for shortfin makos, but they are often caught as bycatch in longline fisheries for swordfish in the Scotia-Fundy region, or caught in gillnet fisheries for groundfish (Campana et al., 2005). In the longline fisheries, most of the shortfin mako bycatch has occurred in the late spring and summer in deep waters off the continental shelf. This mako bycatch is mostly retained due to the high value of the meat and fins of this shark. Since Canadian waters are the northern edge of the shortfin makos range, the sharks only comprise 2-3% of the total catch in these fisheries. Using CPUE equations, it was determined that the population in the northern Atlantic appears to have stabilized since 1988. However, using the average size of the shortfin makos that were landed to determine population health instead, a decrease in size in this area since 1998 could indicate a decline in the adult population of these sharks.

The US swordfish fishery currently covers the entire western Atlantic from Georges Bank to off equatorial South America (Casey and Kohler,1992).The swordfish longline fishery has used monofilament line with a few deep-set hooks and artificial light sticks since 1978. In the US longline fisheries in the western North Atlantic and Gulf of Mexico, swordfish, yellowfin tuna (*Thunnus albacares*), and bigeye tuna (*Thunnus obesus*) are all targeted. Since 2004, the fisheries are only able to use circle hooks after the US National Marine Fisheries Service (NMFS) banned the use of J-hooks. This has helped reduce foul-hooking of sharks, but they are still caught frequently in these fisheries.

The shortfin mako is one of the shark species most vulnerable to longline mortality when caught in the US Atlantic fisheries, along with the night shark (*Carcharhinus signatus*), scalloped hammerhead shark (*Sphyrna lewini*), dusky shark (*Carcharhinus obscurus*), bigeye thresher shark (*Alopias superciliosus*), and longfin mako (*Isurus paucus*) (Gallagher et al., 2014). This vulnerability stems from a combination of biological factors of these species, such as slow growth, late age at maturity and relatively low fecundity. Therefore, mortality due to interactions with longlines may affect these species disproportionately. Changes should be made to how the longline fisheries operate in order to help decrease bycatch of these vulnerable sharks. These changes could include altering the depths and times that hooks are set at, setting time-area closures to decrease overlap with shark distribution, and developing deterrents to repel sharks that approach the hooks.

The Japanese longline fishery, which targets tuna, and often captures shortfin makos as bycatch, covers the entire Atlantic basin (Campana et al., 2005). Shortfin makos are also caught as bycatch in the Atlantic by the Portuguese and Spanish swordfish fisheries (Maia et al., 2006). These fisheries employ monofilament longlines at depths to 18m to capture the swordfish, with Atlantic mackerel (*Scomber scombrus*) and squid the baits most often used (Campana et al., 2005). Their surface longline fleet catches swordfish off of the coast of Africa and in the northern Atlantic between 35° and 45°N. Since 1998, in the entire North Atlantic, the reported average catch of makos is approximately 2300mt. However, a significant portion of shortfin makos caught in international waters are most likely unreported.

In the Mediterranean Sea, there are no pelagic shark-directed fisheries (Megalofonou et al., 2005). However, sharks are caught as bycatch in the swordfish and tuna fisheries. As restrictions on catch of swordfish have increased for the Spanish swordfish fleet in the Atlantic, and the international market for sharks has grown, the fleet has also begun to actively target pelagic sharks. Studies of how many sharks are caught as bycatch in the Mediterranean has been done for small areas, but not in a coordinated way among the Spanish, Italian, and Greek fleets that fish there. The data collected on the specimens that are caught is often not species specific.

Due to the many nations that fish using multiple fishing techniques and gear around the Mediterranean Sea, the amount of bycatch can vary greatly in different areas of the Mediterranean. The main gear type employed by the different fisheries is the swordfish longline (Megalofonou et al., 2005). However, "American type" swordfish longline, albacore longline, bluefin longline, and driftnets are also used. All of these gear types use J-hooks of different sizes on branch lines. The number of hooks varies between 350-4000 hooks per line depending on which fishing gear is being used. Two species of mackerel (*Scomber scombrus* and *Scomber japonicus*) and 2 genera of squid (*Illex* spp. and *Loligo* spp.*)* are used as bait for the swordfish and Bluefin tuna fisheries, while sardines (*Sardina pilchardus* and *Sardinella* spp.) are used in the albacore fishery. The methods most used to study the bycatch rates of these fisheries is by adding fishery observers to the fleet or by interviewing the fishers upon their return to port. Very few sharks are discarded, as there is a growing market for sharks in the Mediterranean.

Between 1998 and 1999, 8733 sharks were caught as bycatch in the Mediterranean fisheries, with the highest shark catch rates in the swordfish fisheries (Megalofonou et al., 2005). There was also a marked seasonality in the rate of sharks caught, with the highest rates being in late spring and summer for the longline fishery, and in June for the driftnet fishery. The highest shark catch rates were found in the Alboran Sea, with the lowest rates in the Straits of Sicily and the Catalonian Sea. Of these sharks, 8295 were blue sharks caught as bycatch. Shortfin makos comprise the second most often caught shark species with a total of 321 individuals, most often caught in the Alboran Sea or Levantine basin. Almost all shortfin mako individuals caught were juveniles, with a close to 1:1 sex ratio of the individuals for which sex was determined.

Shark catch rates were lower in 1998-1999 than those observed in past years, which could be an indication of a decrease in population of these sharks. Catch rates are consistently lower in the Mediterranean than in the adjacent Atlantic, which may be an indication of either lower productivity in the Mediterranean Sea or more depleted shark populations than in the Atlantic. Either way, shortfin makos appear to be one of the most overexploited species of shark in the Mediterranean.

In the southeast Pacific, shortfin makos are often caught in longline and gillnet fisheries off the coast of South America, and there is an artisanal shortfin mako fishery in Peru and Chile (Bustamante and Bennett, 2013). As more valuable teleost species have declined in these waters, the number of sharks that are landed has increased in Chile. In 1978, when records began on shark landings in Chilean fisheries, 33 tons of shortfin makos were caught annually. By the early 1990's, that amount had increased dramatically. Between 1999 and 2009, the landings of shortfin makos by commercial fisheries increased four-fold in this area from 237 tons to 950 tons, largely due to lack of regulation in the shark fishery. In Peru, the shark fisheries have minimum body sizes required for sharks that are landed. However, in Chile, the only regulations are on the types of gear that are used to catch them. Shortfin makos appear to be declining in Chilean waters due to poor annual recruitment, likely a result of heavy exploitation with little regulation.

Since complete information about the life history of the shortfin mako is currently lacking, and populations within different areas of a species' range may display different life-history traits and demographics (Calliet, 2015), it is important to understand exactly how exploitation in certain areas will affect the shortfin mako. Size limit restrictions for caught sharks should be implemented for the shortfin mako throughout its range due to poor population growth estimates. Until more accurate survival rates and fecundity for this species are known, implementing worldwide size limits on catch may help protect vulnerable populations of shortfin makos from overexploitation.

It is important that policy makers understand not only the interaction of sharks with longline fisheries, but also, the attitude of fishers toward sharks, how sharks are currently handled by these fishers, identify new methods to reduce interactions with sharks, and determine areas where new research should be focused (Gilman et al., 2008).

Some longline fishery fleets are small, consisting of 17 boats in South Africa, while others are composed of up to 1500 ships in Japan and Peru. They also range from distant water fleets that make trips that can be up to 3 months long, and inshore fleets that may only be at sea for a couple of days. The amount of interaction with sharks for each fleet is dependent on how and when fishing gear is deployed, and if sharks are actively sought during certain times of the year, as in Peruvian and Chilean artisanal longline fisheries. Gear used may even vary between different ports in the same fisheries. It is believed that gear such as wire ladders, squid bait, light sticks, and setting hooks at shallow depths all lead to increased shark interactions with longlines.

Sharks account for differing levels of the total catch in fisheries around the world, and shortfin makos generally comprise the second most caught species of pelagic shark in these fisheries, after blue sharks. Sharks account for 27% of the total catch in Australian fisheries (Gilman et al., 2008). In 1999 less than 25% of the total catch in Fiji longline fisheries was sharks, and fell to only 5.5% annually between 2002 and 2005. In Italy sharks make up 18% of the catch, while in Peru they account for less than 1% during the mahi mahi season. Data from South Africa indicates that sharks account for 16.2% of the total catch. In 2001, sharks comprised half of the total catch in the swordfish longlines and 16% of the tuna longlines in Hawaii. After 2004, the swordfish longline fishery in Hawaii was required by NMFS to stop using J-hooks with squid and switch to circle hooks with fish as bait, which reduced the percentage of sharks caught to 14% in that fishery. In the US Atlantic longline fisheries, sharks accounted for 15% of the total catch. In the southeastern Pacific, CPUE for individual sets ranged from 0 to 230 sharks/1000 hooks for shortfin mako sharks (Bustamante and Bennett, 2013). The percentage of sharks caught in the longline fisheries will continue to increase, especially in the Pacific, where shark-directed longline fisheries are now growing in size.

In the Atlantic Ocean, shortfin makos account for 2-9% of the total sharks caught in longline fisheries (Casey and Kohler 1992), and in the Mediterranean they comprise approximately 4% of the total sharks caught in these fisheries (Megalofonou et al., 2005). Data from Pacific longline fisheries is not reported uniformly between the many nations that harvest there, but it is reasonable to infer that shortfin mako catch rates are on par with those in the better monitored Atlantic and Mediterranean basins. Shark bycatch rates per 1000 hooks in fisheries from 8 countries that are active in the Pacific Ocean, southern Atlantic Ocean, or Mediterranean Sea are shown in **Figure 1**. This table uses catch data from 2008 (Gilman et al., 2008). The catch rates listed for Australia are based on a subset of fleet data, for Chile they are rough estimates based on weights landed instead of number of individuals. Rates for the Japanese fleets are calculated using logbook entries. This lack of consistent and accurate recordkeeping creates issues when researchers attempt to compare different fisheries based in different nations. This table also illustrates the insufficient data collection on shark bycatch in many nations. Catch rates shown below between 0.7 and 17 sharks per 1000 hooks signifies a high confidence in the accuracy of shark catch rates for those fisheries, which excludes the data from both Chile and Japan.

Table 1: Shark catch rates per 1000 hooks for 12 national pelagic longline fisheries (taken from Gilman et al., 2008).

a Rough estimate based on Australian Commonwealth Scientific and Research Organization, unpublished data from a subset of the fleet and time period, possibly not representative.

b Rough estimate based on interview responses.

c Based on number of sharks recorded in vessel logbooks [27].

Pelagic Longline Fishery	Shark Catch Rate (number /1000 hooks)
Australia tuna and billfish longline fishery	5.5 (*a*)
Chile artisanal mahi mahi and shark longline fishery	24 (*b*)
Chile longline swordfish fishery	8 (*b*)
Fiji longline tuna fishery	1.1
Italy Mediterranean industrial longline swordfish fishery	0.74
Japan distant water longline	0.021 (*c*)

tuna fishery	
Japan offshore longline fishery	0.175 (*c*)
Japan nearshore longline fishery	0.020 (*c*)
Peru artisanal longline mahi mahi and shark fishery	0.99
South Africa longline tuna and swordfish fishery	4
USA-Hawaii tuna	2.2
USA-Hawaii swordfish	16.7

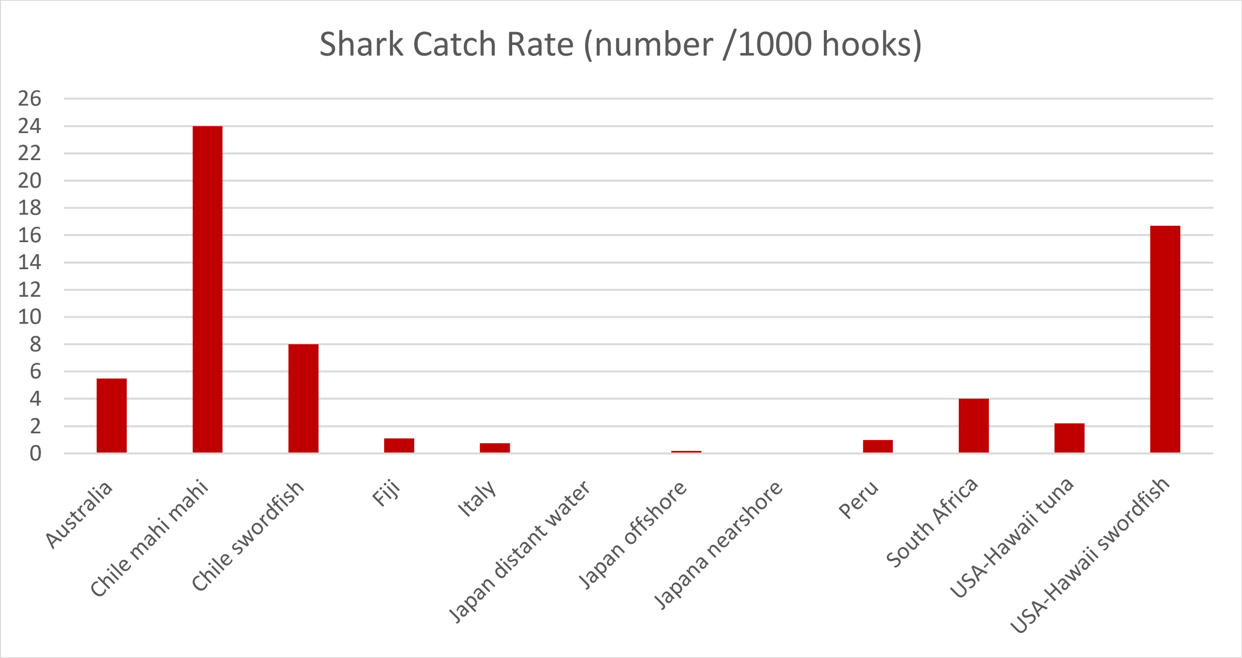

Figure 2: Shark catch rates by nation, per 1000 hooks set in longline fisheries, based on data from Gilman et al., 2008.

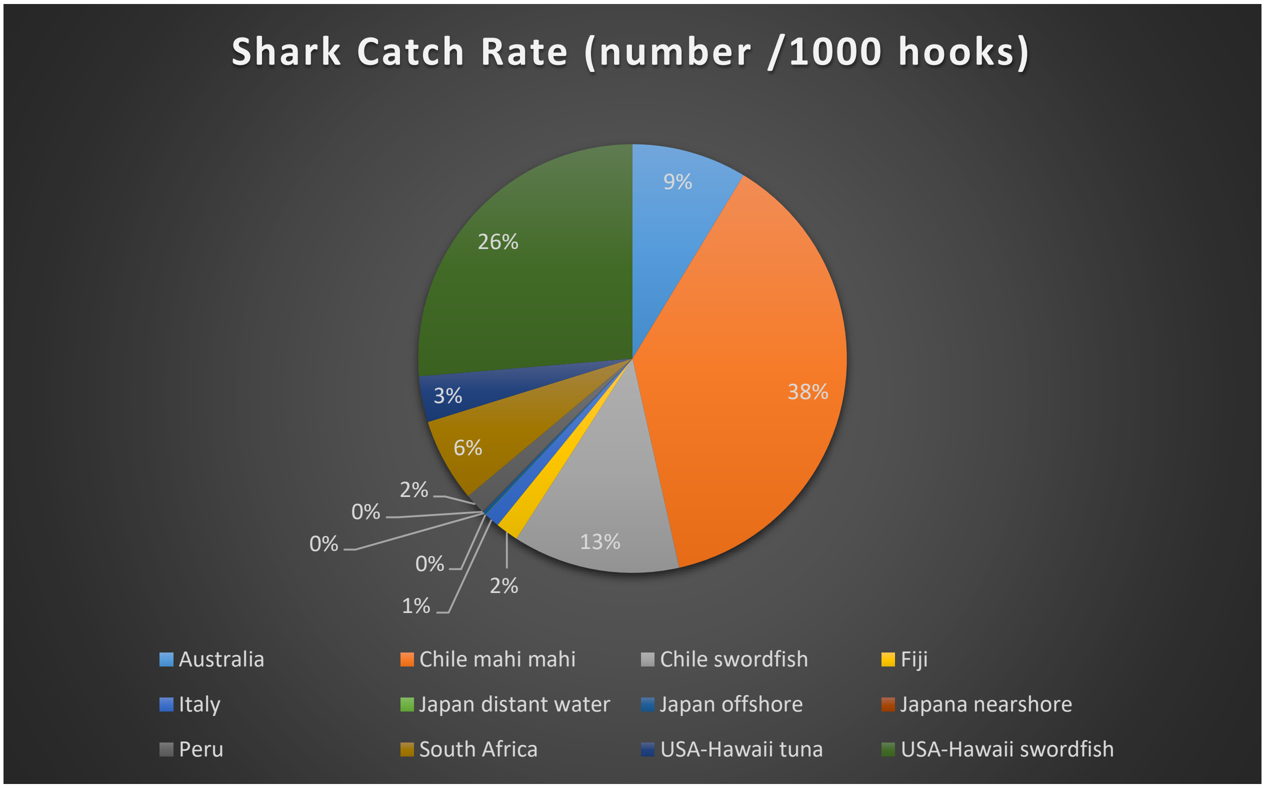

Figure 3: Pie graph of shark catch rates per 1000 hooks set in pelagic longline fisheries, using data from Gilman et al., 2008

Statistical analysis shows that the mean bycatch rate of shortfin makos in longline fisheries around the world is 5.29 individuals per 1000 hooks set. However, as can be seen by **Figure 2** and **Figure 3**, the actual catch rate of different shark species varies widely between locations. The Chilean Mahi-Mahi fleet and Hawaiian swordfish fleet alone account for more than half of the individual sharks caught in 2008. However, the graphs are only as accurate as the data collected, so if the Japanese logbooks are not accurate, or the estimates of the Chilean bycatch done by weight instead of number of individuals are incorrect, the total number of individuals caught as bycatch each year could be higher, and the percentage of that total that each nation is responsible for may be higher as well.

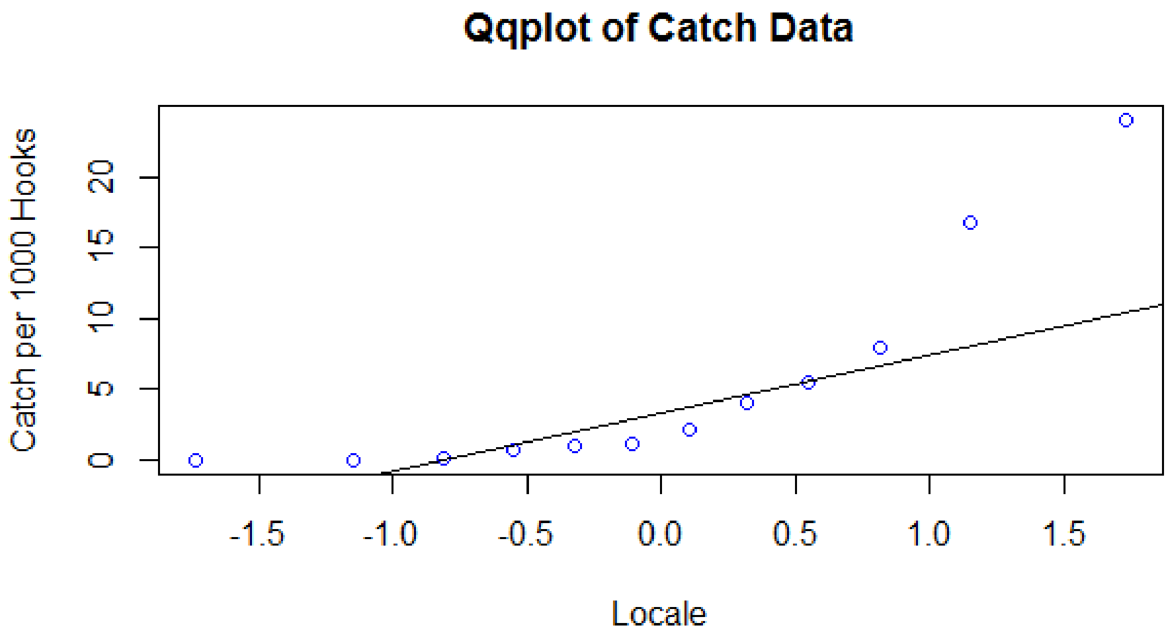

Figure 4: Qqplot of sharks caught per 1000 hooks created with R, using data from Gilman et al., 2008

A Shapiro-Wilk normality test (p=0.001688) and qqplot of sharks caught per 1000 hooks (**Figure 4**) show that the data presented by Gilman et al. (2008) is from a non-normally distributed data set. A one sample t-test results in t = -0.0012895, df = 11, and p-value = 0.999, so bycatch of shark species, and thus shortfin makos, differs significantly between nations. Therefore, any international management and conservation plans for shortfin mako must use the data from each nation to formulate a comprehensive global conservation plan for the shortfin mako, instead of making broad global or even ocean basin decrees that fail to address more localized threats to the sharks. Data collection must be standardized between nations to ensure that any conservation and management plans accurately reflect each nation's bycatch numbers.

Certain types of fisheries gear present a greater danger than others to shortfin makos. One gear of particular concern is driftnets. The United Nations recognized the negative effect driftnets had on many bycatch species, especially sharks, and passed resolutions 44/225 and 46/215 in 1989 and 1991 which called for a moratorium on driftnet fishing by June 30, 1992 (Tudela et al., 2005). This was followed by additional restrictions in many regions, including the Mediterranean Sea. The EU fleet banned driftnet fishing outright in 2002, followed by ICCAT adopting a similar resolution in 2003. In the rest of the Mediterranean, driftnet fishing has continued, but the General Fisheries Commission for the Mediterranean adopted a binding resolution in 1997 that mandated all driftnets had to be less than 2.5km in length. Unfortunately, enforcement of these regulations has been lax in many areas, and illegal driftnet fishing still results in the capture and death of many different bycatch species, from cetaceans and turtles to sharks.

One nation where enforcement of driftnet regulations is lax is Morocco. The total number of shortfin mako individuals estimated as bycatch in Southwest Mediterranean Moroccan driftnet fisheries in 2003 was between 7,000 and 8,000 individuals, and was comparable to the bycatch rates of blue sharks and thresher sharks (Tudela et al., 2005). Shortfin makos were caught in 58.8% of the fisheries operations studied, which indicates that they are more likely to come into contact with the drift net gear than either blue sharks (54.4%) or thresher sharks (49.3%). The gear used in these fisheries is not selective, and shows a ratio of 1.9:1 of swordfish/sharks caught. When swordfish catch is low due to the migratory patterns of the fish, the Moroccan fleet in the Southwest Mediterranean shifts fishing efforts to capture sharks directly. When this occurs, shortfin makos are three times more likely to be caught than either blue sharks or thresher sharks. Targeted capture of sharks by the Spanish fleet in the Alboran Sea located in the southwest Mediterranean caused the populations of both shortfin makos and thresher sharks to decline precipitously between 1984 and 1994. Enforcement of the drift net ban must be ensured by the Moroccan government or the shark populations fished there face similar collapse.

Longline fisheries for billfish are of particular concern for international conservation efforts because of the high number of species that are caught as bycatch by this gear. How longlines are set varies based on what type of fish is being targeted (Ward et al., 2008). This may create the opportunity for other species to come in to contact with the gear, increasing the chance that they will become bycatch in these fisheries. In order to decrease this possibility, several gear modifications have been introduced to protect bycatch species. For example, "tori" lines are used to scare seabirds away from longlines when they dive to steal the bait from hooks near the surface, and large round hooks and deeper set longlines protects endangered sea turtle species. For sharks that are caught as bycatch, new regulations have been enacted that ban finning or restrict landing of sharks entirely. This should lead to sharks simply being cut loose from the longline which would allow them to escape alive. However, sharks are still sometimes killed at sea to retrieve longline hooks, and finning is still rampant in many areas, with up to 52,000,000 sharks being killed per year, a majority of them caught on longlines (Ward et al., 2008).

One change to longline gear that was instituted to reduce the unintentional bycatch of sharks was the replacement of wire leaders with nylon or other synthetic materials (Ward et al., 2008). Wire leaders were first introduced in the 1920s to prevent the loss of gear and hooked animals on longlines. These leaders also prevent sharks from escaping when they are accidentally caught on longlines. Replacing the wire leaders with nylon leaders allows the sharks to bite through the line and free themselves.

However, the efficacy of this gear to reduce bycatch is also dependent on what type of hook is used on the line (Ward et al., 2008). Since circle hooks are often snagged through the corner of the mouth, this keeps the line from falling between the teeth, thus preventing the shark from biting through it. If J-hooks are used, they usually become lodged in the esophagus or stomach, so the shark is able to sever the line between their teeth. The use of J-hooks also increases the chances for sharks to be snagged in their gills or another body part as they swim past the line, and as previously mentioned, may increase sea turtle bycatch. Another issue with nylon leaders is that they may increase the likelihood of target species freeing themselves from longlines, which could be too great of an economic cost for fishers to choose that gear. Wire leaders have been found to reduce the catch of some species that rely on visual acuity to capture prey, as they are more visible than nylon leaders. Increased swallowing of hooks bitten off nylon leaders may also create long term health issues that manifest in reduced fitness of individuals after consuming multiple hooks. However, no studies have been done yet to determine what the long term effects may be for sharks that have escaped multiple longlines.

Overall, nylon leaders actually increase the profitability of longline fisheries because of the increased capture of visual hunters such as bigeye tuna (Ward et al., 2008). Nylon leaders cost approximately $12,000 a year to replace lost gear, however, even after deducting that cost, longlines that exclusively use nylon leaders realize a profit of about $8,000 more a year for fishers than wire leaders. The actual amount may be less once labor costs are included, but it proves that nylon leaders are an economically feasible alternative to wire leaders in longline fisheries. Further studies should be done on these gear types to develop the most cost-effective plan to help reduce shark bycatch and either increase or not affect fisher profits.

Shortfin makos may become distressed and injured as a result of becoming entangled in fishing gear, or by encountering abandoned gear and other anthropogenic waste objects that cause serious injuries (Wegner and Cartamil, 2012). Organisms such as barnacles that encrust on the surface of objects floating through the water column may create a stronger adhesion between the shark and the object that prevents the shark from freeing itself. On one rope found wrapped around a male shortfin mako, 52 individual barnacles from four species were found fouling it everywhere except where the rope had cut into the shark's musculature. It is believed that the immune response caused by injury from the rope probably prevented the barnacles from attaching there. Without an external substrate like the rope, the only barnacles ever found directly attached to a shortfin mako were small *C. virgatum* individuals that had settled on the teeth. The rope, and barnacles attached to the rope, caused the shark to develop scoliosis due to the increased drag and altered hydrostatic equilibrium from the large number of barnacles on the ventral body surface of its body. Any management plans to help protect shortfin makos should not only regulate fishing activity, but also require periodic sweeps of areas with persistent shark presence to ensure that there are not excessive amounts of debris endangering these animals. Understanding how the shortfin mako moves through the water column will help determine how deeply and in what areas these debris sweeps should be completed.

7. Data issues

In order to develop better management and conservation plans for shark populations in different areas, more precise studies should be done by individual nations to determine accurate catch and bycatch rates, as well as the species most exploited by these countries (Dulvy et al., 2014). In some areas of the world's oceans, such as the northern Indian Ocean and parts of the Pacific, the local marine species are not well known. In surveys of Indonesian fish markets, 20 new species of sharks have been discovered (Dulvy et al., 2014). There could be many more species yet to be discovered. This lack of knowledge about unknown shark species, and imprecise information about sharks that are caught, makes realistic stock assessments difficult. Currently, it is believed that shark catches are underreported by many fishers, and only about 15% (Dulvy et al., 2008) to 33.3% (Dulvy et al., 2014) of the catches that are reported internationally are identified down to the species level.

7.1 Demographic Considerations

In an effort to develop fisheries and conservation plans that more accurately reflect the health of populations of data poor species, like the shortfin mako, researchers use demographic modeling (Tsai et al., 2014). The issue with this type of modeling is that it treats both sexes as though they have identical life histories, or that population health is more directly affected by females. Shortfin makos are a sexually dimorphic species so the life histories of females and males differ. Most importantly for demographic modeling, the sex ratio of the population varies with size of the individuals. Therefore, it is imperative that modeling done on mako populations reflect both male and female life histories. These models should also factor in reproductive behaviors, as different behaviors rely on the abundance of both males and females, and the presence or absence of these behaviors can affect population dynamics.

Demographic modeling shows that alternate reproductive behaviors and sex of the shark cause shortfin mako populations to respond differently to mortality caused by fishing (Tsai et al., 2014). Without considering fisheries-related mortality in the models, the finite rate of population increase was 1.047 per year if only considering females, 1.051 per year for monogamous behavior in both sexes, 1.010 for polyandrous behavior, and 1.082 for polygynous behavior scenarios. Once current fishing mortality was added into the model, the rate of increase was < 1.0 in all cases, indicating that whatever reproductive behavior shortfin makos deploy, their populations may be unable to cope with current fisheries pressure. Both the female only and the polygynous models indicated that protection of females and neonates will help the population recover. Other demographic models show that under current fishing pressure, the population is likely to continue to decline, although protecting females and neonates can increase the probability that the population may recover. However, if the shortfin makos display polyandrous mating behaviors (as suggested by Corrigan et al., 2015), even the protection of females and neonates does not prevent the decline of the population. There is little doubt that unless current fishing practices are altered, shortfin mako populations could be half of their current numbers within 40 years. Protecting females and neonates may slow that decline, but management plans that only protect adults and subadult females do not significantly decrease this possibility. These different results demonstrate why it is important to understand the reproductive behaviors of the shortfin mako before attempting to develop conservation and management plans for the species.

Demographic models that are based exclusively on females may greatly underestimate the effect of fisheries on shortfin mako populations, but even two-sex models may not accurately predict population dynamics if they reflect inaccurate reproductive behaviors (Tsai et al., 2014). Due to a lack of data, it is usually assumed in these models that the population displays only one reproductive behavioral strategy and that individuals only mate once a year. More studies need to be completed to better understand shortfin mako reproductive behaviors because population growth parameters will vary based on if the sharks are monogamous or polygamous.

Each sex also faces different mortality rates due to a myriad of environmental or biological factors, so these should be included in any models. Due to the sexual dimorphism in shortfin makos, males, who are often smaller than females, could have higher mortality rates (Tsai et al., 2014). If this is true, then conservation measures should be enacted to protect males more, since females already have a higher survival rate. However, mating behavior needs to be clearly understood to ensure that demographic models correctly portray population dynamics for the shortfin mako, as different mating strategies increase the importance of one sex over another. Females that are unable to locate a mate in polyandrous breeding populations do not reproduce, thus negatively affecting the population. In a polygynous population, population decline rates would be lower, even with less reproductive males present, because a smaller number of males mate with a greater number of females. Regardless of the mating behavior found in shortfin mako populations, it is apparent that in order for their populations to recover, most fisheries mortality must be eliminated, especially of immature individuals. However, the high economic benefits enjoyed by fishers who catch these sharks will make any size limitation restrictions difficult to enforce.

Another common type of modeling used by researchers when accurate data is lacking for a species is an Ecological Risk Assessment (ERA), which can determine the susceptibility of a population to overexploitation (Cortes et al., 2010). This is an important tool when dealing with species where more research needs to be conducted, such as with the shortfin mako. It is useful with these species because it can be conducted at three different levels depending on the information available for each species. The first level is qualitative, so it relies more on anecdotal evidence and observations, instead of hard data. The second is semi-quantitative for those species where some research may have been done. The third level is completely quantitative, for populations on which there are multiple data sets from extensive research. These ERAs are currently used by organizations around the world, including the United States National Oceanographic and Atmospheric Administration (NOAA), the International Commission for the Conservation of Atlantic Tunas (ICCAT) in their Ecosystems Working Group, and the Australian Fisheries Management Authority.

An ERA was conducted on several pelagic shark species in the Atlantic by ICCAT to determine how susceptible they are to negative effects from the longline fisheries there (Cortes et al., 2010). Data was used from 6 fleets for the susceptibility analysis, the US, Brazil, Venezuela, Uruguay, Portugal, and Namibia, separately at first, and then on all fleets combined. After determining that enough data was available from bycatch information collected from these fisheries, a fully quantitative approach was used to estimate a direct measure of productivity (*r*) for the shark species, as well as an estimate of susceptibility employing Walker’s approach (Cortes et al., 2010). Walker’s approach determines susceptibility of overexploitation as a product of the probabilities of availability, encounterability, selectivity, and post-capture mortality. Using estimates of life history information based on existing literature, and statistical analysis to determine the median of 10,000 iterations for each factor, *r* was calculated for each species. Walker’s approach was then used to determine the probability of each species being caught. Both the number of times that fishing fleets overlap with the spatial distribution of the stock being studied, and fishing gear overlaps with depth distribution of the sharks, were estimated. Also, selectivity of that fishing gear to actually catch sharks, and the number of individuals that were captured and discarded dead, was calculated.

In the early 2000s, shortfin makos were the second most commonly caught shark species as bycatch in Atlantic longline pelagic fisheries, with annual catches of 6,000-8,000 tons (Simpfendorfer et al., 2008). Although catch data is less accurate for other species, it is thought that thresher sharks, silky sharks (*Carcharhinus falciformis*), and oceanic whitetips (*Carcharhinus longimanus*) are probably caught at similar rates as the shortfin mako. By 2004, the population of shortfin makos in the North Atlantic had declined to levels below those required to maintain MSY (Simpfendorfer et al., 2008). However, in 2012, when ICCAT met to discuss a more recent stock assessment of populations of shortfin makos in both the North and South Atlantic, it was found that these populations had rebounded and were no longer being overfished (ICCAT, 2012 .p.10). When a quantitative approach is applied to pelagic shark species, productivity is determined using population modeling, while susceptibility is calculated by determining the product of four characteristics of those populations. These characteristics are availability of the species where fisheries operate, encounterability at different depths that the species exists at concurrently with fishing gear, selectivity of the species to capture by fishing gear, and post-capture mortality.

Shortfin makos showed a post-capture mortality of as high as 92% (Cortes et al., 2010). The results indicate that the shortfin mako is highly susceptible to being overexploited based on Walker's approach and has a low *r* value. It is included with the silky shark and bigeye thresher sharks, as one of the most vulnerable shark species in the Atlantic, although shortfin mako susceptibility varies in different areas of their range as can be seen in (**Figure 5**).

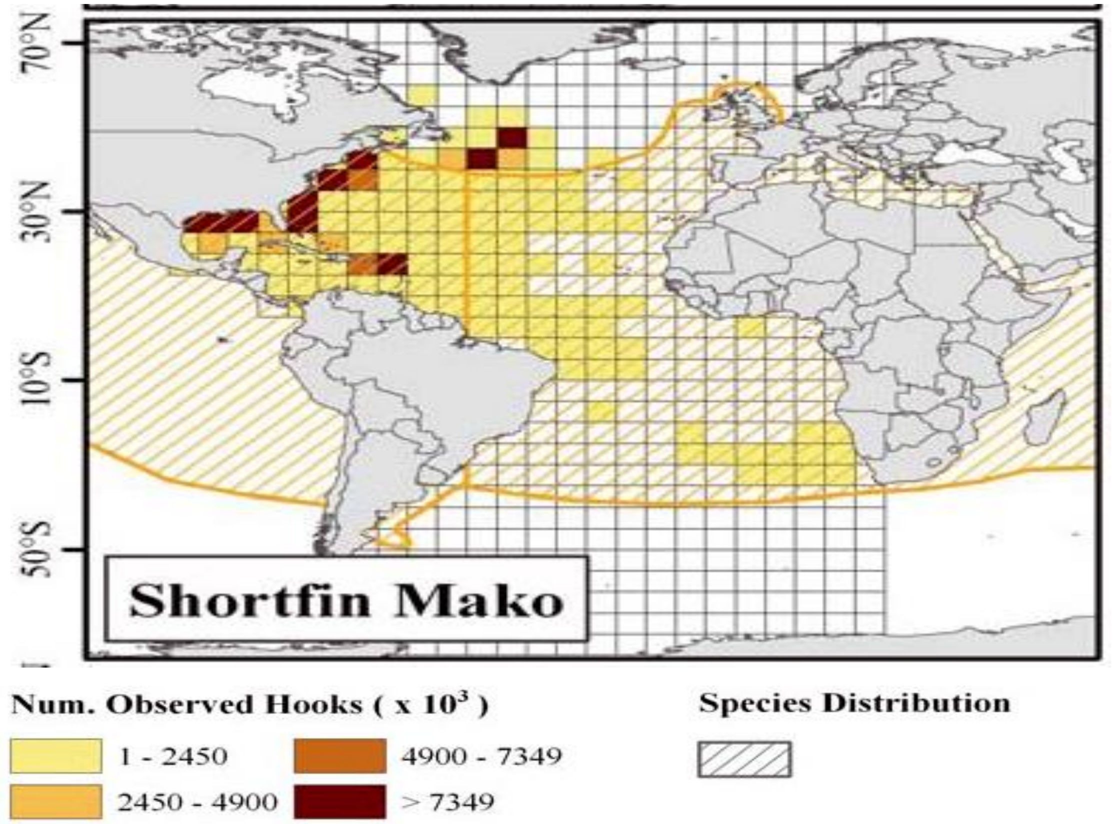

Figure 5: Map showing susceptibility of shortfin makos to fishing pressure throughout the Atlantic, from Cortes et al, 2010. The darker the color, the more susceptible the shortfin mako is to being overexploited in that area.

Of the 11 species of pelagic sharks studied, shortfin makos were ranked the second most vulnerable species after silky sharks (Cortes et al., 2010). Their *r* value was calculated at 0.018 annually. The four probabilities used in Walker's approach were 0.95 for availability, 1 for encounterability, 0.85 for selectivity, and 0.92 for post-capture mortality, giving them a susceptibility of 0.74. Actual effects of the longline fisheries in the Atlantic on the shortfin mako may be greater than what was determined, because shortfin makos also display low intrinsic rates of population increase, second only to bigeye threshers among pelagic shark species. The combination of these factors could make the shortfin mako the most threatened pelagic shark species in the Atlantic basin, and serve as precautionary evidence that the shortfin mako may be just as endangered in other areas within its range where there is less data on current shark populations.

Another factor that has become more important in modeling in recent years is anthropogenic climate change. Further modeling should be done to determine how climate change may affect shortfin mako populations through its effects on prey fishes. In the Pacific, tuna species, which are prey for the sharks, display different recruitment strengths based on environmental conditions (Lehodey et al., 2003). A combination of sea surface temperature, food availability, currents, and risks of predation affect tuna recruitment. Lower tuna recruitment may then lead to lower prey availability for the sharks, which can conceivably affect shortfin mako recruitment. Skipjack and yellowfin tuna show higher recruitment during El Niño, while albacore tuna recruitment strengthens during La Niña. It is believed that anthropogenic climate change will cause the development of El Niño to occur more often and at much stronger levels than in the past. Understanding how these dramatic shifts in oceanic currents and temperatures will affect important prey species may help scientists understand how climate change will also affect the survival of the sharks themselves.

8. Current conservation/management plans

Currently, conservation and management of shark species are multi-layered, including state, national, regional, and international plans (Techera and Klein, 2011). However, inconsistency in enforcement of these plans has led to regulatory loopholes that continue to endanger particularly vulnerable shark species. In addition, the numerous methods used to manage shark populations provide different levels of protection throughout their range. Moving forward, new plans for the management and conservation of shark species should synchronize these different methods into a coherent strategy that provides adequate protection and management at different life stages and in different parts of the sharks’ ranges.

Due to the highly migratory nature of pelagic sharks such as the shortfin mako, any management plans for fisheries that take the sharks as bycatch, as well as any conservation plans for the sharks, must include state, federal, and international regulations in order to truly be effective (Musick et al., 2000). Management plans should err on the side of caution (i.e. use the precautionary principle), as any plans created with the small amount of data available on pelagic sharks may lack reliable population estimates, and many of the ways that anthropogenic actions affect these populations are just now beginning to come to light. Additionally, it is imperative that managers use different population models when developing new management plans for sharks, as they have different life histories than teleosts, which often have higher fecundity and faster growth rates.

Developing conservative quotas and size restrictions on shark catches may help maintain populations of certain shark species, even if they are often caught as bycatch within other fisheries (Musick et al, 2000). Since female shortfin makos mature later and at larger sizes than males, it is important to protect the size classes that are necessary for adequate recruitment to maintain their populations. In an effort to decrease the large number of sharks that are discarded dead at sea, more nations should outlaw the practice of finning. If shark fins are desired, regulations should be enacted by all fishing nations that require that the entire shark carcass is landed and brought back to port with fins attached. Any undesired sharks that are landed live should be released immediately after they are freed from fishing gear to reduce fishing mortality. Lastly, new fisheries management plans must be developed along both the United States Atlantic and Pacific coasts, to protect highly migratory species such as the shortfin mako. These plans will ensure that the shortfin makos will have adequate protection throughout their range, both across state boundaries, as well as international borders.

When developing fisheries plans, it is important to understand the population dynamics of a species. The shortfin mako is a highly migratory species with the entire northern Atlantic believed to be one population (Campana et al., 2005). Analysis of microsatellite DNA of makos across the North Atlantic shows little differentiation. Shortfin makos in the north Atlantic have been recorded swimming 35.7 nautical miles per day and traveling more than 1200 nautical miles in 37 days (Casey and Kohler, 1992). However, when shortfin makos in the western North Atlantic were observed making long trips to the south, they quickly returned to the areas that they started their journey from originally (Vaudo et al., 2017). Despite the lack of genetic differentiation between populations of shortfin makos in the North Atlantic, there was little interaction recorded between this population in the Northwestern Atlantic and another population in the Gulf of Mexico.

The maximum distance that has been recorded for one individual was 2452 nautical miles which traveled between the United States and Spain (Casey and Kohler, 1992). However, most recaptured individuals appear to stay within 300 nautical miles of where they are first tagged, usually staying in surface water between 17° and 22°C. Individual shortfin makos in the Northwestern Atlantic have been tracked moving through the territorial waters of 17 different nations and the open ocean (Vaudo et al., 2017). A comprehensive management plan that reflects the complex movement behavior of these sharks needs to be formulated on the international level, in order to ensure that the makos are protected both regionally, and throughout their range.

8.1 International management

The conservation of marine species in the open ocean is difficult due to the uncertainty of how changes to the ocean from anthropogenic activities affect the 21 chondrichthyan species that inhabit the open water far from land (Dulvy et al., 2008). These species also often move between the Economic Exclusion Zone (EEZ) of more than one country, or outside of the EEZ of any country, thus making stock assessment and regulation enforcement unbalanced throughout the species' ranges. Vaudo et al., (2017) for example, showed that makos in the western North Atlantic crossed the management jurisdictional zones of at least 17 nations. However, some international and national regulations have been instated to try to conserve these species. Twenty-two nations and the European Union have enacted catch limits of sharks, although the species protected differs from country to country, and the levels of protection afforded by these catch limits vary. Finning has also been banned in 19 countries, the European Union, and nine Regional Fisheries Management Organizations (RFMOs). However, lack of enforcement and ambiguity of how to determine the fin-to-carcass weight ratio currently in use to enforce these bans has allowed the practice to continue. In the USA, Australia and Central America, regulations require the whole shark be landed (fins attached) which helps enforcement efforts and data collection on the species of sharks being landed. Regulation of Mexican shark fisheries began in May 2007 with gear restrictions and area closures (Velez-Marin and Marquez-Farias, 2009). These national and regional efforts can only be so effective without robust international management and conservation plans that continue to protect the shortfin mako as it moves from the waters of one nation to another and outside of the Economic Exclusion Zones (EEZs) of any nation.

At the international level, conservation of shark species is most often managed through the listing of shark species on conservation status-associated Appendices of The Convention on International Trade in Endangered Species (CITES) or the Convention on Conservation of Migratory Species of Wild Animals (CMS) (Techera and Klein, 2011). Species listed under CITES are managed through restrictions on international trade based on a species current population status. Under CITES, the highest level of protection is given to species listed under Appendix I, which outlaws all trade in individuals of that species or their body parts. Appendix II requires that trade of the listed species should be controlled through permitting, but few species of shark are currently listed under Appendix II. The species included are the porbeagle shark (*Lamna nasus*), the scalloped hammerhead (*Sphyrna lewini*), the great hammerhead (*Sphyrna mokarran*), the smooth hammerhead (*Sphyrna zygaena*), the oceanic whitetip shark (*Carcharhinus longimanus*) the whale shark (*Rhincodon typus*), basking shark (*Cetorhinus maximus*), and white shark. There are also two other groups of sharks that have been approved to be added to Appendix II, but that action was delayed until October 4, 2017. These groups are thresher sharks and silky sharks (https://cites.org/sites/default/files/notif/E-Notif-2016-068-A.pdf). The third level of protection provided by CITES is under Appendix III, where individual member states can list species without the agreement of other signatories. Member states will often use Appendix III to increase awareness in the international community of species that may be threatened or in danger of being threatened if trade is not regulated. The issue with CITES, as with many international treaties, is that member states can circumvent the restrictions put in place. For example, for species on CITES Appendix I or II, signatories can opt out of restrictive trade policies by filing reservations, which allow them to trade in the species using the Appendix below where the species is actually listed. For the shark species listed in Appendix II, this means that member states that submit a reservation in relation to the import and export of these sharks are not bound by the same permitting restrictions as the rest of the signatories.

Under the CMS, species of concern are also listed, like with CITES (Techera and Klein, 2010). However, CMS has more specific guidelines within a Memorandum of Understanding (MoU) passed by signatories in 2010. The MoU calls for international cooperation for the development of both conservation and management plans that follow an ecosystem-based model with a precautionary approach. Unlike CITES, CMS also details specific measures to manage and conserve highly migratory shark species. These measures are non-binding but assist member states with the development of plans that help protect and properly manage these shark species.

The Convention on Biodiversity (CBD) calls for the creation of conservation plans that are ecosystem-based, which include marine protected areas (MPAs), and adaptive management schemes based on scientific, not economic considerations (Techera and Klein, 2010). However, the language of the CBD is weak, and does not specifically state what the member states must do when developing their plans. Philopatry of shark species can be used to designate specific areas that are important for conservation. However, since many species of shark like shortfin makos are highly migratory, the creation of MPAs within one member state may not provide enough protection for the conservation of the species if neighboring states do not create similar areas. Therefore, additional international cooperation will be required so that any MPAs created by member states encompass enough area to ensure that threatened populations are protected throughout their range.

Fisheries regulations made under the UN Convention on the Law of the Sea (UNCLOS) delineated each nation’s Exclusive Economic Zone (EEZ), which extends out to 200 nautical miles from their shores, and their sovereign waters that exist within 12 miles of their coastline (Techera and Klein, 2010). Member states are instructed to cooperate on highly migratory species that move from one nation’s waters to another’s, and to uphold international fisheries regulations on any ships sailing the high seas under their flag. However, there are few specific fisheries regulations laid out in UNCLOS, other than setting catch limits and MSY for their waters. The 1995 Fish Stocks Agreement attempted to provide more guidance for member states on what they are specifically required to do for highly migratory species, and advocated for the use of Regional Fisheries Management Organizations (RFMOs) to develop comprehensive management plans. However, there are no RFMOs that have been created for the management of sharks. Other organizations, such as regional tuna organizations, have become important in shark conservation due to the high interaction between these fisheries and shark species. However, despite regulating the intentional catch of sharks, they have not addressed bycatch of shark species in tuna fisheries nor finning of sharks that are caught, and the regulations that are passed are often weak and non-binding.

The International Plan of Action for the Conservation and Management of Sharks (IPOA- Sharks) was adopted in 1999 (Techera and Klein, 2010).Signatory states are required to develop plans of action for managing sharks caught in their waters and conserving shark species. The IPOA-Sharks is a more comprehensive management and conservation strategy than those found in CITES, CMS, CBD, UNLCOS, or the 1995 Fish Stocks Agreement. However, because it is not a treaty, it requires voluntary participation by signatories, so it can only make non-enforceable recommendations for member states. As a result, many member states have been slow to create national regulations. By 2011, only 14 states had developed their plans more than 10 years after signing the IPOA-Sharks. Due to low political will among the signatories to enact the recommendations of the IPOA, and the voluntary nature of the plan, implementation has not been uniform (Dulvy et al., 2008) Some progress has occurred on the regional level, but this inability to enforce national regulations is another example of how international management and conservation of shark species needs to be reimagined in a way that creates a more unified plan throughout the sharks' range. These unified plans should incorporate what is known about shark behavior to ensure that what is developed will be optimal for the continuation of these species.

There are currently few international regulations that deal with the management of highly migratory pelagic shark species such as the shortfin mako which occur in relationship with, and are caught as bycatch in, fisheries that target Highly Migratory Species (HMS) of fish. In the Atlantic, shortfin makos can comprise up to 10% of the total catch in longline fisheries (Megalofonou et al., 2005). The International Commission for the Conservation of Atlantic Tunas (ICCAT) is an organization that was established at the Conference of Plenipotentiaries in 1966 (Levesque, 2008). Today 43 nations have signed the treaty, and it overseas the management of fisheries for tunas and closely-related species in the Atlantic Ocean. It also holds the signatories responsible for collecting data on other species that are caught as bycatch in the tuna fisheries. However, only five recommendations have been made for management of shark bycatch populations, possibly because ICCAT was determining the importance of studying populations of bycatch species based on their economic importance.

The first resolution related to shark species caught as bycatch did not occur until 1995, almost 30 years after the ICCAT agreement was first signed (Levesque, 2008). This resolution required ICCAT members to provide shark bycatch data to ICCAT and the Food and Agriculture Organization (FAO) of the United Nations. In 2002, a resolution passed directing signatories to create and implement their nation's International Plan of Action for the Conservation and Management of Sharks (IPOA). It also arranged a follow-up meeting in 2003 to discuss blue sharks and shortfin makos, and a population assessment to be completed in 2004 for these species. There was a lack of compliance among member nations in regards to completing their IPOA's, so in 2003, another resolution was passed that all signatories had to submit their IPOA's within 6 months. By 2005, ICCAT required all member nations to submit annual shark catch data, curbed the practice of finning by requiring a minimum 5% fin to shark carcass weight ratio, recommended further shark research, and advocated for additional population assessments for blue sharks and shortfin makos in 2005 and 2007.

After their initial stock assessment for shortfin makos in 2004, the ICCAT determined that shortfin mako populations could be depleted by as much as 50% in the North Atlantic (Levesque, 2008). They found population depletion in the South Atlantic as well, but not to the same degree as that observed in the North Atlantic. In December of 2005, ICCAT passed resolution 05-05, which addressed shortfin mako bycatch reduction. This resolution originally required all party members to implement the resolution and report their results to the Commission. However, later the wording of the resolution was altered to state that the Standing Committee on Research Statistics should conduct stock assessments of the shortfin mako and blue sharks and recommend management alternatives to member states by 2008. They were to use data collected from signatories regarding biological parameters, catch effort, and discards, and compile that information to make their recommendations to the Commission. This change in verbiage is an example of one of the many problems faced by international bodies tasked with the conservation and management of HMS like shortfin makos. Due to differences in reporting standards between nations, a lack of compliance of member states with resolution requirements, weak enforcement of those requirements, and a lack of consequences for non-compliant members, ICCAT has not been able to make lasting positive changes in shark management. ICCAT members must make management of pelagic shark species a priority if the population reductions that have been observed are to be slowed or reversed in the Atlantic.

9. Issues with current conservation/management plans

Successful conservation and management plans using conservation behavior as a basis are only as effective as the policies and laws in place to protect and conserve species at risk of excess exploitation and possible extinction. The extent and strength of these policies and laws varies widely in different areas of the shortfin mako’s range. In developing nations, poor enforcement of policies and lack of education about the role sharks play in ecosystem health, along with a fear of shark attacks on people, can lead to overexploitation of certain shark species or senseless killings of sharks out of fear (Bornatowski et al., 2014). Conservation plans should be dynamic, so that as conditions change, and shark species face different threats to their survival, governments can move quickly to regulate these new interactions with mankind.

For example, in recent years, shark-based ecotourism has become an important source of revenue for some nations. It has been estimated that one shark can add up to $178,000 to the local diving industry if alive, but only $200 to the economy if it is caught in a fishery (Bornatowski et al., 2014). Without proper regulation of this tourism industry, however, local shark populations could face behavioral changes that affect their ability to interact or reproduce with individuals from other populations, leading to a reduction in the number of sharks in that area. This, combined with increased pressures from fisheries, has led to 83% of the shark species that are important for tourism being listed on the IUCN Red List with various levels of threat status. Increased public education of the benefits of sharks to local economies can lead to greater pressure on lawmakers to create and pass strong conservation laws to protect sharks. However, education will only really change society if the prevailing image of sharks as mindless man-eating machines is also addressed.

Shark attacks have been on the increase in many areas, including around Brazil, due to a higher number of people living in coastal areas and entering sharks' habitats (Bornatowski et al., 2014). Despite warnings posted on beaches where shark activity has been observed, many people ignore these signs and enter the water. When shark attacks occur, governments are forced to take some action to assuage public concerns. This can often lead to excessive killing of sharks, such as the shark culls of "aggressive" animals instituted by the Australian government after a spate of recent shark attacks. Public opinion of sharks remains largely negative due to a lack of education in non-scientific arenas and the desire for revenge after shark attacks. Shark control programs using gill nets which are currently in place in South Africa and Australia that were developed to decrease the number of "dangerous" shark species that come into contact with humans are often ineffective and negatively affect other species of sharks, sea turtles, mammals, and teleosts. A Brazilian program developed by the State Committee for the Prevention of Shark Attacks, which is 97% effective in reducing shark attacks, uses drumlines and longlines to capture sharks moving toward the beaches. The sharks are taken to the edge of the continental shelf and released, where they continue their migration northward. These sharks have never been recaptured near beaches, which proves the effectiveness of this strategy.

10. Current conservation solutions

Understanding how shark species interact with each other, with prey, and with the physical environment, will help the formation of new ecosystem-based management plans for fisheries in the area (Preti et al., 2012), and creation of MPAs for sharks. It is necessary to ensure that prey species biomass is maintained at a sufficient level to not only support fisheries activities, but also to allow predators to continue to forage at optimal levels that allow for the continuation of natural feeding ecology. One of the issues for developing area closures for conservation of shark species is the link between species distribution and oceanic features such as currents, which makes defining spatial borders of protected areas more difficult (Watson et al., 2008). Another is that spatial closures should not only decrease bycatch of shark species, but also must maximize the capture of target species. Essential fish habitat must be protected to allow prey fish to support populations through successful spawning and recruitment. (Preti et al., 2012).

Currently, Marine Protected Areas (MPAs), do not cover enough area to help prevent local and regional shark extinctions. Less than 10% of critical habitat for more than 97% of marine species is currently protected by MPAs (Davidson and Dulvy, 2017). However, shark conservationists have had some success, with 29% of the areas in the ocean that are currently protected, designated as conservation areas specifically for sharks. Although it is not realistic to cover the entire range of a species like the shortfin mako with MPAs, it is imperative that current MPAs are expanded to include more critical hotspots in the oceans. These hotspots are important areas for a multitude of endangered marine organisms, and will help protect large pelagic predators like the shortfin mako as they travel through, as well as their prey.

Unfortunately, not all nations have the political will or funding to undertake large conservation projects and policing of MPAs. Just 12 countries in the world are home to more than half of the endangered chondrichthyan species (Davidson and Dulvy, 2017). These nations are Colombia, Brazil, Uruguay, Argentina, China, Taiwan, Japan, South Africa, Mozambique, Australia, Indonesia, and the Philippines. Out of these nations, South Africa and Australia have the highest likelihood of creating meaningful conservation areas, and being able to fund adequate staffing to police them. Japan, Taiwan, and China could fund new MPAs, but lack the political will and conservation management policies seen in other developed nations. Other nations like Mozambique and Indonesia lack the ability to fund the creation of or the policing of MPAs. They will require significant investment in MPAs and fisheries management that is given along with other types of developmental aid by the international community.

Fishing practices need to be modified to reduce the interactions of sharks with fishing gear (Preti et al., 2012). Shark species, such as the shortfin mako, will face new challenges as the environment that they exist in changes due to anthropogenic climate change. Climate change will intensify in the future, so changes to trophic webs will need to be monitored so that fishing plans can be modified to reflect new realities. This type of dynamic fisheries management plan is currently uncommon but will become more necessary as changes to the natural world progress.

Several different techniques have been used in an attempt to decrease bycatch of shark species in longline fisheries. Using the electrosensory abilities of sharks to deter interactions with longlines is one method being explored in Canada (Godin et al., 2013). Certain metals that are electropositive oxidize in seawater and create electrical fields that can be sensed by the sharks. These electrical fields are thought to create avoidance behaviors in some shark species. Researchers studied the effects of these metals on a swordfish fishery in the north Pacific to see if these metals could be used to prevent sharks from approaching longlines. What they found was that there was no significant decrease in bycatch rates of sharks between standard hooks and those treated with electropositive metals. The use of small tuna clips to attach the deterrents to the hooks, was both time consuming for the fishers, and created a larger object attached to the longline. This then lowered the catch of swordfish because they are highly visual hunters and the increased size of the hooks, with the metal deterrents attached, prevented the swordfish from approaching those hooks.

In laboratory experiments, the avoidance of interactions with fishing gear treated with electropositive metals showed much higher results than in this field test. It is believed that this could be because pelagic species have lower electrosensory abilities in comparison to nearshore sharks which are easier to maintain in laboratory conditions, and thus are more often experimented on by researchers. Other environmental factors, such as shark abundance, hunger, and competition, could also have limited the effectiveness of the deterrent in the field. This example shows the intricacies of trying to develop new gear that both prevents excessive bycatch, but does not impact overall catch of the target species in a fishery.

11. Conclusion

Using behavior as a basis for conservation and management plans of shortfin makos could be a useful addition to management efforts to halt or reverse the decline in their populations around the world. The highly migratory nature and difficulties associated with studying the behavior of shortfin makos reduce the effectiveness of current fisheries management and conservation plans for this species. In order to better protect this declining species, more must be done in order to understand the behaviors of these sharks. Governments on every level need to invest in studies that allow researchers to better comprehend how shortfin makos behave throughout their range, and how they interact with fisheries and the physical environment. It is apparent that the lack of verifiable information regarding shortfin mako behavior decreases the effectiveness of management plans that are currently in place, and makes formulation of new regulations difficult and ineffective. International treaties and regulatory bodies must become stronger so that there are real consequences when member states do not comply with agreements that they have signed.

Better knowledge of how shortfin makos move through the world's oceans can be used to regulate fisheries practices to decrease the encounter rates of the sharks with fishing equipment. Protecting important migration routes with area closures for fisheries during important times of year when the sharks are moving from winter to summer habitats would help decrease the bycatch of individuals, especially in gill net and longline fisheries. Monitoring of important movement routes and identification of temporal regions of concentrations of the shortfin makos will allow targeted removal of discarded fishing gear and other anthropogenic items, which could decrease the number of animals whose behavior is affected due to entanglement. How shortfin makos move vertically through the water column, and how they interact with their physical habitat are also important behaviors for adult sharks.

Since shortfin makos display sexual segregation, and males and females utilize depths differently and at different times, these sex-based factors need to be taken into consideration whenever new management policies are enacted. If new fisheries plans fail to consider how the sharks are distributed within their range, they may disproportionally affect one sex over the other. This could decrease the reproductive potential of the population, leading to local extirpations of shortfin mako populations.

Mating behavior of shortfin makos should be studied to develop better predictive population trend models that more closely reflect the shark's actual demographic composition and reproductive behaviors. Understanding parturition in shortfin makos and their use of specific nursery or pupping grounds will help managers create regulations that protect the shortfin mako during these crucial times. In specific areas, such as the Southern California Bight and off the coast of Chile, commercial fisheries should either be completely banned, or they should follow fishing practices that reduce the chances of YOY and juveniles encountering the gear.

Realistic measures that will stabilize or increase shortfin mako populations worldwide should be enacted, with inclusion of conservation behavior knowledge as a part of management plans at the state, regional, and international levels. More research should be done on shark feeding behavior, movement, and habitat use, in order to develop fisheries techniques that reduce shark bycatch (Dulvy et al., 2008). Furthermore, when new fisheries management plans are enacted for important shortfin mako prey items, they should be approached in an ecosystem-based manner, to ensure that the biomass of prey remains high enough to support the local population of shortfin makos. Without considering shortfin mako behavior when management policies are created, the new policies will be no more effective than existing fisheries management plans, and shortfin mako populations will continue to decline, eventually to a point where recovery is no longer an option. If this occurs, the consequences could be disastrous for many economically important food fishes as well, because of the cascading ecosystem effects of large declines in shortfin mako sharks as functional major apex predators.

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