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Assessing the Dynamics of the Southeast Florida Shark Community from 2013-2019 Via Catch per Unit Effort and Stable Isotope Analysis

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Thesis of Alexandra Barth

Submitted in Partial Fulfillment of the Requirements for the Degree of

Master of Science Marine Science

Nova Southeastern University
Halmos College of Arts and Sciences

April 2023

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NOVA SOUTHEASTERN UNIVERSITY
HALMOS COLLEGE OF ARTS AND SCIENCES

ASSESSING THE DYNAMICS OF THE SOUTHEAST FLORIDA SHARK COMMUNITY
FROM 2013-2019 VIA CATCH PER UNIT EFFORT AND STABLE ISOTOPE ANALYSIS

By:
Alexandra Barth

Submitted to the Faculty of
Halmos College of Arts and Sciences
in partial fulfillment of the requirements for
the degree of Master of Science with a specialty in

Marine Science

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April 2023

ABSTRACT

Sharks, as well as other top predators, are in drastic decline worldwide. As apex and near-apex predators, species such as nurse, lemon, and tiger sharks maintain balanced marine ecosystems by enacting top-down trophic control. However, this cascading effect is diminished with exploitation via commercial and recreational fishing. Sharks are generally long-lived, mature late, have long reproductive cycles, and produce few offspring. Much remains to be learned about the community structure, population trends and conservation statuses of shark populations worldwide. Comprehensive studies on the composition of the shark community in Southeast Florida north of Miami have been limited. This study assessed the species composition and seasonal changes of the Southeast Florida shark community through a combination of drumline surveys and observation of seasonal intraspecific trophic changes via stable isotope analysis. The most common shark species encountered near coastal Southeast Florida included nurse sharks, sandbar sharks, lemon sharks, tiger sharks, and great hammerhead sharks. Catch per unit effort (CPUE) was greater during most rainy seasons (June through November) compared to most dry seasons (December through May), though not significantly. Most of the study species displayed overlap in trophic niches, and some exhibited significant seasonal differences in carbon, but not nitrogen, stable isotope ratios as well. While CPUE did not change significantly between seasons, the effects of seasonality and water depth significantly influenced the total number of sharks captured throughout the study.

Keywords: Shark tagging; catch per unit effort; stable isotopes; *Ginglymostoma cirratum*; *Carcharhinus plumbeus*; *Negaprion brevirostris*

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INTRODUCTION

Preface

Overfishing is the main cause of population decline in marine life on a global scale. Since 1970, the global abundance of sharks and rays that occupy pelagic ecosystems, such as great hammerhead sharks (*Sphyrna mokarran*), dusky sharks (*Carcharhinus obscurus*), and giant oceanic manta rays (*Mobula birostris*) has declined by 71% due to a significant increase in fishing pressure (Pacoureaux et al., 2021). Most shark species have life histories that involve slow growth rates, late maturity, and greater investment into growth and survival as juveniles that results in low fecundity as adults. This biological predisposition, combined with exploitation via overfishing, could cause slow recovery rates for many shark species (Cortés, 2002; Frisk et al., 2001; Musick et al., 2000). From an ecological standpoint this would be detrimental to marine ecosystems worldwide. Decreasing numbers of large predatory sharks, for example, have been shown to alter the abundance, distribution and behaviors of smaller elasmobranchs, marine mammals, and sea turtles at lower trophic levels. Elevated numbers of mesopredators and other lower-level heterotrophs would result in greater predation pressure on autotrophs, which provide the greatest concentration of energy to marine food webs (Ferretti et al., 2010). As predators in their respective ecosystems, sharks exert top-down trophic control, keep marine food webs balanced by helping to ensure sustainable numbers of species at lower trophic levels, and therefore play a crucial role in maintaining the health of the world's oceans (Baum et al., 2003; Ferretti et al., 2010).

The combination of shark mortality via targeted commercial and recreational exploitation and incidental bycatch, typical life history strategies of most shark species and a lack of knowledge about the conservation statuses and population trends of many species in different geographic regions, warrant sustainable conservation and fisheries management efforts (Hussey et al., 2012). To effectively conserve sharks, it is important to know which species they prey upon, as well as which geographic regions they utilize throughout the year. This would allow for the identification of essential habitats, or areas where sharks hunt and reproduce, and regions through which they migrate, as well as the development of effective management strategies for each species (Cáceres, 2022).

Conservation Issues

Shark ecology is a relatively new field of study and did not begin in earnest until the mid-1900s. Ecological research on sharks has been conducted almost exclusively on wild individuals, as many species are difficult to maintain in captivity (FAO, 2012; Worm et al., 2013). Unfortunately, much remains to be learned about the seasonal changes in abundance, population trends, and conservation statuses of many shark species worldwide (Heithaus et al., 2007). According to the International Union for the Conservation of Nature (IUCN) Red List database, approximately 25% of all known shark species are considered Threatened, an umbrella term that includes all species with a Vulnerable, Endangered, or Critically Endangered conservation status, and about 45% of all existing shark species are considered Data Deficient on a global scale (Dulvy et al., 2004; Ferretti et al., 2010; IUCN, 2011).

Major threats to pelagic and benthic shark species, and the percentage of annual mortality for which these threats are responsible, include fishing pressure (96.1%), which can be further divided into directed commercial fishing (37.1%), fisheries bycatch (57.9%), recreational fishing (0.7%), and artisanal/subsistence fishing (5.8%); habitat destruction (2.9%), and pollution (0.4%) (<http://www.red-list.org>). In the 1980s, designated shark fisheries were established to harvest a variety of products from these organisms, such as their fins, of which 4,406 tons of dried product are sold annually, as well as their meat, gill plates, and liver oil (Clarke et al., 2006; McClenachan et al., 2016; Rose, 1996; Simpfendorfer & Dulvy, 2017). Some of the first indicators of the overexploitation of sharks by fisheries on a global scale were the “boom and bust” patterns of consecutively increasing and decreasing capture rates, as well as an increase in the international trade of shark fins (Brander, 1981; Manire & Gruber, 1990). Some of the species most commonly targeted in the shark fin market include sandbar (*Carcharhinus plumbeus*), tiger (*Galeocerdo cuvier*), great hammerhead (*Sphyrna mokarran*), and bull sharks (*Carcharhinus leucas*) (Clarke et al., 2006). Catch rates rose to a range from 63 to 273 million sharks annually in the early 2000s, before declining due to overfishing (Davidson et al., 2016). Increasing numbers of sharks, rays, and chimeras have been captured accidentally and purposefully in every ocean since researchers began to record capture data in 1950. According to the Fisheries and Aquaculture Organization (FAO, 2017) fishers captured the following biomass (in tons) of elasmobranchs from 1950 to 2017: 92,142 tons African waters, 176,679 tons in the Americas, 235,034 tons in Asia, 7,313,073 tons in Europe, and 27,266 tons in Oceania.

In the Atlantic Ocean, shark populations decreased significantly from 1970 to 2000, after which point their abundance stabilized at low levels. Overall, Atlantic shark species have experienced a decline in abundance of 46.1% (Pacoureau et al., 2021). Sharks have had a long history of exploitation in both the Northeast Atlantic Ocean and Mediterranean Sea (Lotze et al., 2006). The Eastern tropical Atlantic in particular is considered a hotspot for multiple shark species, as well as for longline fisheries. Many of these longline fishing vessels are based in Spain, which is home to the world's largest shark fisheries (Kroodsma et al., 2018; Queiroz et al., 2016, 2019; Vedor et al., 2021). Numbers of shark landings have fluctuated over the years throughout the Atlantic. Recently, however, there have been downward trends in these numbers and relatively low catch per unit effort rates, which could be indicators of decreasing populations of some shark species (Ferretti et al., 2008). In fact, certain large coastal species such as hammerhead sharks within the family *Sphyrnidae* are rarely encountered, or entirely absent, in the Gulf of Mexico, as well as the Caribbean and Mediterranean Seas (Ferretti et al., 2008; Shepherd & Myers, 2005; Ward-Paige, 2010).

Many shark species are generalist predators that help sustain highly interconnected food webs across different geographic regions through their migratory behaviors (Bascompte et al., 2015), so declining shark populations can have cascading effects on the ecosystems they inhabit (Roff et al., 2018).

Catch Per Unit Effort

Catch per unit effort (CPUE) is method used to analyze population trends of shark species throughout this study and refers to the number of fish caught per amount of effort expended, such as the total number of fish caught per total number of fishing trips undertaken (Maunder et al., 2006). In this study, “effort” refers to the total number of sharks caught, for the total amount of soak time in minutes of each drumline deployed. “Soak time” refers to the amount of time drumlines remained submerged in water. Analyzing catch rates of shark species over time can provide useful information, such as insight into the health of regional shark populations, as well as how certain populations respond to exploitation. For example, lower catch rates in certain regions over time, as well as less frequent encounters with larger, mature individuals and more frequent encounters with smaller, immature individuals, can signal regional declines in populations of certain shark species. Decreases in total CPUE for all species encountered in a certain region,

and CPUE values for individual shark species, can indicate decreasing populations as well (Roff et al., 2018).

Changing environmental conditions, such as sea surface temperature which can fluctuate throughout the year, can significantly affect CPUE. The abundance of certain prey species may also change at intra-annual timescales (Mitchell et al., 2014). In the context of shark research, the CPUE values calculated could provide further insight into the time of year at which sharks are most abundant in certain areas, when certain species are encountered most often, and/or when sharks are most likely to take bait from hooks because of energetic needs. Additionally, calculating CPUE of various species over long time periods can improve knowledge of these species' seasonal variations in abundance versus population changes when anthropogenic exploitation occurs (Tinari & Hammerschlag, 2021).

Using CPUE is not without its limitations, however. It is difficult to obtain an accurate measure of species abundance in a certain region unless sampling is conducted consistently, for a long period of time and in the same area(s) of interest (Kessel et al., 2016). For CPUE to provide an accurate indicator of abundance, the region where sampling occurs, and an organism's preferred habitat, must be one and the same. Although CPUE does not indicate a perfectly accurate measure of species abundance, it does provide a useful estimate (Harley et al., 2001).

Stable Isotopes

Isotopes of different elements also provide useful ecological information in the context of population ecology. All elements exist in both stable and unstable (or radioactive) forms, and these various forms are known as isotopes. Most elements used in biological research have at least two stable isotopes, with one of the two existing in greater abundance in nature (Ehleringer & Rundel, 1989). Stable isotopes are non-radioactive forms of an element that possess the same number of protons and electrons that are characteristic of that element but have a different number of neutrons (Michener & Lajtha, 2008). The stable isotopes of carbon and nitrogen are useful in the field of ecology, especially when studying ecophysiology, as well as trophic relationships, and the directions in which energy and organic matter travel through food webs (McCutchan & Lewis, 2001; Tykout, 2004). Stable isotopes of carbon include ^{12}C and ^{13}C , with ^{12}C being more abundant in nature, and stable isotopes of nitrogen include ^{14}N and ^{15}N , with ^{14}N being more abundant in natural settings (Ehleringer & Rundel, 1989).

Stable isotope standards utilized internationally for carbon and nitrogen include Pee Dee Belemnite (PDB) and atmospheric nitrogen, respectively. Pee Dee Belemnite is Cretaceous-era fossilized limestone from the squid-like marine organism *Belemnitella americana*, located in the Pee Dee Formation in South Carolina (Estrada et al., 2003). The lowercase form of the Greek letter delta (δ), pronounced “del” when discussing stable isotope content, is used to indicate the concentration, in parts per thousand (ppt), of the heavier to lighter isotope of the element (i.e. carbon and nitrogen) relative to the internationally accepted standards. Analyzing the concentrations of stable isotopes within an organism’s tissues may be used to help answer a variety of ecological questions. For example, the stable isotopes of carbon and nitrogen, which are $^{13}\text{C}:^{12}\text{C}$ (or $\delta^{13}\text{C}$) and $^{15}\text{N}:^{14}\text{N}$ (or $\delta^{15}\text{N}$), respectively, can be used to reconstruct an organism’s dietary history based on the carbon and nitrogen content of the prey consumed, and thus its trophic niche (Post, 2002; Tykocinski, 2004; Wada et al., 1991).

Stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope concentrations within an organism’s bodily tissues are influenced by that organism’s diet, metabolism, and habitat, and changing concentrations of these assimilated isotopes can be indicators of habitat change, seasonal migration, and/or availability of different prey species from different trophic levels at certain times of the year (Katzenberg, 2007).

Stable Isotopes of Carbon

Marine environments are generally more enriched in $\delta^{13}\text{C}$ than freshwater and estuarine ecosystems (Matich et al., 2011), and each group of primary producers in every type of aquatic biome worldwide (freshwater, brackish, and saltwater) has its own unique baseline concentration of $\delta^{13}\text{C}$ (Ehleringer & Rundel, 1989). Concentrations of $\delta^{13}\text{C}$ in primary producers like phytoplankton, seagrass, and seaweed, which form the base of most photosynthetic marine food webs, represent the flow of basal nutrients from this origin point to higher trophic levels (France, 1997; Vander Zanden & Vadeboncoeur, 2002).

Nearshore ecosystems are an important source of carbon in marine food webs, and this high $\delta^{13}\text{C}$ content is caused by a greater concentration of phytoplankton, algae, seagrasses, and other marine plant species that inhabit these coastal areas (Carlisle et al., 2012; Dunton, 1989; France, 1995; Hobson et al., 1994; Thomas & Cahoon, 1993). Coastal ecosystems in the epipelagic zone are interconnected with mesopelagic and bathypelagic food webs. The majority of carbon that supports mesopelagic and bathypelagic species comes from sources of primary productivity

in the epipelagic zone, or fast-sinking particulate organic matter (POM) at depth with similar isotopic signatures (Richards et al., 2018). The $\delta^{13}\text{C}$ concentrations of organisms at higher trophic levels reflect the $\delta^{13}\text{C}$ content of primary producers and POM at the base of the food web (Katzenberg, 2007).

The $\delta^{13}\text{C}$ content within an organism's tissues provides an estimate of that organism's dietary sources, as $\delta^{13}\text{C}$ is enriched $\sim 0.5\text{-}1\text{‰}$ relative to the prey consumed by an organism (Hobson, 1999). Isotopic relationships between $\delta^{13}\text{C}$ for whole bodies of organisms and their diets are similar for different species on the same diet, as well as the same species on different diets (DeNiro & Epstein, 1978). In other words, the $\delta^{13}\text{C}$ content of organisms at all trophic levels reflects the $\delta^{13}\text{C}$ of the primary producers at the base of each food web, and indicates the type of ecosystem, such as terrestrial, freshwater, or marine, in which these organisms live (Kelly, 2000).

The accuracy of $\delta^{13}\text{C}$ determination in an organism's tissues is limited by certain factors. First, seasonal variations may occur in the carbon isotope composition of an organism's diet. For example, in certain subtropical estuarine ecosystems such as Bundaberg in Queensland, Australia, mangroves contributed more primary productivity during the dry season, while saltmarsh grasses contributed more primary productivity during the rainy season (Jinks et al., 2020). Second, the assumption exists that herbivores will consume any available plant species randomly; however, most herbivorous species are usually selective about their diet. There is evidence that herbivores prefer C_3 plants and tend to avoid consuming C_4 plants, and the $\delta^{13}\text{C}$ values of plants eaten may differ from the average $\delta^{13}\text{C}$ value of all available plants in a certain region (Caswell et al., 1973; Jinks et al., 2020).

Stable Isotopes of Nitrogen

In contrast to stable carbon isotope ratios, stable nitrogen isotope ratios can be used to estimate an organism's trophic position. The $\delta^{15}\text{N}$ value of an organism's whole body is more positive than that of their diet, and the nitrogen content of an organism's tissues is enriched $\sim 3\text{-}4\text{‰}$ relative to that of the prey items it consumes (DeNiro & Epstein, 1981; Hobson, 1999; Hobson & Clark, 1992a; Hobson et al., 1996; Mizutani et al., 1991, 1992). Animals incorporate dietary ^{15}N preferentially over ^{14}N , as the latter is much lighter and more easily excreted from the body (DeNiro & Epstein, 1981). However, organisms such as juvenile sharks assimilate $\delta^{15}\text{N}$ into their tissues and excrete it at a much faster rate than adults because their bodies require more nitrogen to maintain sufficient metabolic and growth rates. Therefore, sharks with longer stretched total

lengths (STL) are more likely to hunt prey that occupy higher trophic positions, which results in a greater $\delta^{15}\text{N}$ within the sharks' tissues (Ponsard & Averbuch, 1999). Overall, the $\delta^{15}\text{N}$ within an organism's tissues indicates the trophic level of that organism's prey and allows for estimation of the predatory organism's trophic position (Hobson, 1999).

Stable Isotope Analysis in Ecological Research Settings

Stable isotope analysis (SIA) is minimally invasive and requires only a small tissue sample from the organism in question. This method is interpretive in nature and does not allow researchers to determine which specific prey items a shark has consumed yet provides long-term trophic position estimates as isotopes are integrated into bodily tissues (e.g., muscle, cartilage, blood) (Harrison, 2015; Shiffman et al., 2012). Different tissue types in all organisms, including elasmobranchs, assimilate stable isotopes at varying rates (Bearhop et al., 2004; Hobson & Clark, 1992). For example, blood and plasma are highly metabolically active and assimilate stable isotopes in a matter of days or weeks (Marcus et al., 2019). By comparison, muscle and cartilaginous fin tissue have much longer assimilation rates. For example, stable isotopes in elasmobranchs fully assimilate into muscle in 390-540 days, and into dermal fin tissue in 576 days (Matich et al., 2010). Cartilage, which is one of the least metabolically active types of tissue in elasmobranchs, requires months to years to fully integrate stable isotopes from prey (Marcus et al., 2019). Most of these rates were calculated for relatively small elasmobranchs in captive settings, such as the ocellate river stingray (*Potamotrygon motoro*) and sandbar shark (*Carcharhinus plumbeus*). However, field studies, including a study on whale shark foraging behavior, suggest that these laboratory estimates are similar to isotopic assimilation rates occurring in wild elasmobranchs, and that relative assimilation time based on tissue type is expected to be the same (Marcus et al., 2019; Matich et al., 2010).

Concentrations of stable isotopes such as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ can be determined by analyzing samples of dermal fin tissue from sharks, which in turn provides data about each species' trophic ecology and possible migratory behaviors (Carlisle et al., 2012). The diets of most temperate and tropical shark species are dependent on seasonality and life stage (Wetherbee & Cortés, 2004). Large long-lived shark species exhibit isotopic concentrations that may represent their trophic positions over the course of successive life stages as they grow from neonates to sexually mature adults. Most juvenile sharks prey on smaller organisms that are closer to the base of the food web and, therefore, maintain lower $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ within their tissues during this life stage. Conversely,

as sharks grow, they tend to prey on organisms that occupy higher trophic positions, thereby causing increased $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. The $\delta^{15}\text{N}$ bioaccumulates from the bottom of the food web up to the highest trophic levels (Post, 2002; Wetherbee & Cortés, 2004). Long-term, general dietary trends can help researchers understand a shark's life history, and stable isotope analysis provides baseline information about the feeding habits and relative trophic positions of these species. Any significant deviations from this baseline could indicate an individual in the process of adapting to ecological disturbances, especially in unprotected coastal areas.

The Study Area and Goals of the Project

Coastal Southeast Florida is home to an abundance of marine life and provides important habitats for many shark species, including those whose populations face overexploitation (Tinari & Hammerschlag, 2021). The subtropical climate in Southeast Florida means that this region, and the state overall, experience dry and rainy seasons as opposed to a four-season year. The dry season typically lasts from December to May while the rainy season occurs from June through November (Lascody, 2002).

The overall goal of this study was to analyze dietary patterns (using stable isotope analysis), and temporal patterns in CPUE of the species that comprise the Southeast Florida shark community, using data from shark tagging surveys conducted by NSU's Guy Harvey Research Institute between 2013 and 2019. The surveys were conducted to document and describe the composition of the shark community in this region.

The subsequent data analyses aimed to identify changes in CPUE between the dry or rainy seasons. Stable isotope analysis was used to determine species-specific differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ content and assess whether these variables changed based on seasonality.

Ecology of Common Southeast Florida Shark Species

The shark species encountered most frequently during the course of this study included nurse sharks (*Ginglymostoma cirratum*), sandbar sharks (*Carcharhinus plumbeus*), lemon sharks (*Negaprion brevirostris*), tiger sharks (*Galeocerdo cuvier*), and great hammerhead sharks (*Sphyrna lewini*). Other species caught less frequently included bull sharks (*Carcharhinus leucas*), Caribbean reef sharks (*Carcharhinus perezi*), blacknose sharks (*Carcharhinus acronotus*), Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*), blacktip sharks (*Carcharhinus limbatus*), and dusky sharks (*Carcharhinus obscurus*). Each of these species makes up part of the shark community of Southeast Florida.

Nurse Sharks

Nurse sharks (*Ginglymostoma cirratum*) occupy subtropical and tropical reefs, are opportunistic predators and, due to their generalist diet, are likely to prey upon whichever benthic organisms are most common in their habitat, based on a seasonal and/or depth-related shift in that abundance (Compagno, 2001; Rosa et al., 2006; Tilley et al., 2013). These sharks consume diverse benthic organisms, such as small teleosts, cephalopods, gastropods, bivalves, sea urchins, and crustaceans. This species exhibits high site fidelity and may inhabit depths from 1 to 130 m (Compagno, 2001; Rosa et al., 2006). Due to relatively small home ranges and a lack of large-scale migrations, they are especially susceptible to exploitation by coastal fishing activities, such as gill netting, longlining, spear fishing, and recreational fishing competitions. Aside from fishing, anthropogenic factors that negatively impact nurse sharks may include water pollution, deforestation (which increases terrestrial runoff), and boat damage, both to the reefs they inhabit and to individual sharks themselves. Overall, nurse sharks are identified by the IUCN Red List as Data Deficient globally, and Near Threatened in the Western Atlantic Ocean (Rosa et al., 2006).

Sandbar Sharks

The sandbar shark (*Carcharhinus plumbeus*) is a highly migratory coastal to pelagic species that is usually encountered in the higher latitudes of the Northwest Atlantic Ocean, specifically near the northeastern coast of the United States, from June through October. A combination of photoperiod and water temperature are thought to initiate migratory behaviors in sandbar sharks. This migration results in movement from summer nursery grounds such as the Delaware Bay and Chesapeake Bay toward the Atlantic and Gulf coasts of South Florida. Individuals older than seven years of age venture into deeper waters during this time. Conversely, longer days beginning in June influence movement into the summer nursery areas and nearshore waters located in more northern latitudes (Grubbs et al., 2007).

Sandbar shark populations in South Carolina exhibit dietary changes as individuals develop from neonates into juveniles. For example, although young-of-year (individuals born during the given year) and juveniles both have generalist diets, young-of-year are more particular, preying almost exclusively upon small benthic crustaceans. By contrast, juveniles incorporate pelagic fish species like the Atlantic menhaden (*Brevoortia tyrannus*) into their diet (Shiffman et al., 2014). Seasonal migrations of sandbar sharks toward the southern portion of their range in mid-October

and toward the northern portion of their range in June could cause them to target different prey species dependent upon latitude (Grubbs et al., 2007).

This species is both targeted intentionally and caught as bycatch in commercial longline fisheries that harvest tuna and swordfish. Recreational fishers tend to target sandbar sharks as well. These exploitative activities, in addition to this species' 20–26-year lifespan and females' 8-16-year age-at-maturity, make it especially vulnerable to overfishing (Casey et al., 1985). The IUCN Red List identifies the sandbar shark as an Endangered species based on data collected from populations worldwide (Musick et al., 2009). However, this species is recovering, especially in regions like the United States that have fisheries management regulations in place. The rate of sandbar shark mortality is now lower than its maximum sustainable yield (MSY), which refers to the maximum number of organisms that can be caught without causing population declines in a particular species (Simpfendorfer & Dulvy, 2017).

Lemon Sharks

The lemon shark (*Negaprion brevirostris*) is a subtropical/tropical coastal species that mainly occurs over sandy or muddy-bottomed substrata where it can forage for bony fishes, stingrays, and crustaceans (Florida Museum of Natural History, 2018). Neonates and juveniles are site-limited, remaining in shallow nursery areas such as mangrove estuaries. Young lemon sharks prefer these sheltered habitats for protection from larger predators, as well as metabolic regulation via warmer water temperatures (Speed et al., 2010). Adults typically migrate farther offshore to deeper waters during winter months. Although lemon sharks undergo seasonal offshore migrations, they prefer to travel close to the boundaries of continental shelves (Sundström, 2015). Major threats to this species worldwide include commercial longlining in the US, Mexico, and Belize to support the consumption of meat and fins. The IUCN Red List identifies lemon sharks as Near Threatened globally (Rose, 1996).

Tiger Sharks

Tiger sharks (*Galeocerdo cuvier*) inhabit a mix of coastal and pelagic waters from warm-temperate to tropical latitudes worldwide (Simpfendorfer, 2009). Like the nurse shark, this species is an opportunistic feeder, though the tiger shark occupies a higher trophic position and consumes different prey items, including sea birds, sea turtles, carcasses of marine mammals, and even garbage. This species exhibits top-down trophic control on organisms such as green sea turtles (*Chelonia mydas*). The threat of predation by tiger sharks tends to intimidate herbivorous prey

species, resulting in them limiting their grazing activities to the outer edges of seagrass beds in case they need to quickly flee from an approaching predator. This, in turn, increases the abundance and density of seagrass beds by preventing overgrazing (Burkholder & Heithaus, 2001).

Tiger sharks undergo seasonal migrations, moving to higher latitudes during spring and summer months, and returning to lower latitudes in winter. Several tiger sharks that were tagged with dorsally mounted satellite tags in Bermuda inhabited coastal Bahamian waters during the winter and traveled north into pelagic waters of the Western North Atlantic Ocean during the summer (Wetherbee et al., 2011). Additional individuals that were tagged in this region and monitored from 2009-2012 exhibited similar movement patterns. Most adult tiger sharks involved in this study occupied the coastal, reef-bound waters of the Bahamas, Turks and Caicos, and Anguilla/Saint Martin during winter months. These individuals spent summer months in more temperate, pelagic waters to the north/northeast of Bermuda (Lea et al., 2015).

Because this species can grow to lengths of over 550 cm, it is a popular target among recreational fishers, in addition to being commercially targeted for economically valuable meat, fins, liver oil, and cartilage. These anthropogenic threats have led to the tiger shark's Near Threatened classification by the IUCN (Simpfendorfer, 2009). The Florida Fish and Wildlife Conservation Commission (FWC) categorizes the tiger shark as a Group 3 species, meaning that harvesting this species in Florida state waters is illegal (FWC, 2018).

Great Hammerhead Sharks

Great hammerhead sharks (*Sphyrna mokarran*) inhabit the continental shelf in tropical latitudes, and are considered coastal and occasionally pelagic sharks, as they may be encountered at depths of up to 300 m (Denham et al., 2007). Great hammerhead sharks consume a variety of prey items, from crustaceans, cephalopods, and bony fishes to other elasmobranchs (Hammerschlag et al., 2011). Like many of Florida's other shark species, great hammerheads migrate to higher, northern latitudes during the summer months. During a pilot study on the habitat use of the great hammerhead, an individual that was affixed with a satellite tag in the Florida Keys in February 2010 traveled toward the coast of New Jersey as spring approached. Researchers hypothesized that this shark migrated in the same direction in which the Gulf Stream current flows (Hammerschlag et al., 2011). There is a greater abundance of great hammerhead sharks in South Florida during winter months, as their southward, or low latitude, seasonal migration from the Northwest Atlantic Ocean and northern Gulf of Mexico coincides with decreasing air and water

temperatures. Individuals occupying coastal waters likely benefit from the higher oxygen concentrations present within South Florida waters during winter, as opposed to the warmer summer months during which these waters are less enriched in oxygen (Heithaus et al., 2007).

The great hammerhead becomes stressed easily when caught with fishing gear. This likely occurs because this species is an obligate ram ventilator, which requires it to swim constantly to obtain oxygen (Denham et al., 2007). They also utilize burst swimming techniques while hunting, which, when they are caught by fishers, is thought to contribute to a disruption in blood chemistry, increased physiological stress, and more frequent post-release mortality relative to other elasmobranchs (Gallagher et al., 2014). Great hammerhead sharks also experience high rates of mortality when they are caught as bycatch in pelagic/bottom longlines and gill nets. Additionally, they are targeted by recreational and commercial fishers for their fins, all of which contribute to their Critically Endangered conservation status and trend of decreasing abundance assigned by the IUCN Red List (Denham et al., 2007).

Other Shark Species Encountered in Southeast Florida

Several other shark species that were found off the coast of Southeast Florida, but recorded in comparatively lower numbers, included bull sharks (*Carcharhinus leucas*), Caribbean reef sharks (*Carcharhinus perezii*), blacknose sharks (*Carcharhinus acronotus*), Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*), blacktip sharks (*Carcharhinus limbatus*), and dusky sharks (*Carcharhinus obscurus*).

Bull sharks (*Carcharhinus leucas*) occupy subtropical and tropical waters and establish nurseries in low-salinity rivers and estuaries, such as the Caloosahatchee River and Indian River Lagoon (Heupel et al., 2010). During spring and summer months, bull sharks migrate northward along the US Atlantic coast, returning to more southern waters such as those of Florida in fall and winter months. However, it is not known exactly where off the coast of Florida their preferred wintering habitat is located (Castro, 1983).

Caribbean reef shark (*Carcharhinus perezii*) populations are concentrated mainly within the Caribbean Sea. Although it is possible to encounter this species in Southeast Florida, especially in and around the Gulf Stream current, they rarely travel north of the Florida Keys (Rosa et al., 2006). Blacknose sharks (*Carcharhinus acronotus*) are native to Florida and prefer to inhabit tropical to warm-temperate waters, sandy substrate, and coral reefs, specifically at insular and continental shelves. However, they are found more often near Florida's Gulf Coast where the

continental shelf is wider than that of Florida's Atlantic Coast (Compagno et al., 2005). The Atlantic sharpnose shark (*Rhizoprionodon terraenovae*) is a coastal species that may be encountered from the Yucatán Peninsula to Montreal, Canada, and undergoes seasonal migrations from inshore habitats in the summer to deeper offshore waters of up to 280 m in the winter (Compagno, 1984).

Blacktip sharks (*Carcharhinus limbatus*) maintain nursery areas along the Gulf Coast of Florida and return to these sites for at least the first three years of life from May through July, migrating toward South Florida and the Florida Keys during winter months (Hueter et al., 2004). This species occurs throughout the year in locations such as Melbourne, Florida, and the Florida Keys, but is scarcer from May through early September. Specifically, they are present in greatest concentrations off the coasts of both Daytona Beach, Florida from September through November, and Melbourne Beach, Florida from November to December (Castro, 1996; Dodrill, 1977). The northernmost region of the blacktip sharks' migratory range is in Delaware Bay, but they generally spend summer months in the more temperate waters off the coasts of North Carolina and Georgia before returning to Florida waters in September (Castro, 2011; Kohler et al., 1998).

Dusky sharks (*Carcharhinus obscurus*) occupy coastal and pelagic marine ecosystems and are highly migratory (Compagno, 1984; Kohler, 1996). They migrate along the East Coast of the United States primarily from New Jersey to South Carolina, occasionally migrating to Southeast Florida. Adults travel to temperate latitudes during the summer months (Castro, 1993; Dudley et al., 2005; Musick & Colvocoresses, 1986).

MATERIALS AND METHODS

Shark Tagging Surveys and Sample Processing

During this study, the shark community in nearshore waters off the coast of Broward County in Southeast Florida was assessed via shark tagging surveys conducted by NSU's Guy Harvey Research Institute (Figure 1). Research expeditions with NSU/GHRI were conducted on 193 individual days, year-round, from 2013 to 2019, and involved the use of drumlines. A buoy marked with the GHRI's permit number floated on the surface to mark the location of the drumline, a rope connected the buoy at the surface with a 22.7-kg cement-filled weight on the seafloor, and approximately 9.3 m of 900-lb (408.2-kg) test monofilament fishing line was attached to the weight with a shackle. Finally, two lengths of monofilament line were attached to a baited Mustad

16/0 triple strength circle hook as a leader (Figure 2). Ten such drumlines, placed in depths ranging from 7.62 to 30.48 meters of water, were each baited with one-third of an Atlantic bonito (*Sarda sarda*), and allowed to remain in the water for 1.5 to 2 hours. When sharks were caught, they were brought to the swim platform mounted at the stern of the research vessel with their caudal fin secured by a tail rope.

The following data were recorded during each capture event: latitude and longitude, shark species, sex, pre-caudal length (PCL), fork length (FL), and stretched total length (STL). Morphometric measurements, specifically PCL, FL, and STL, were recorded once the shark was secured (Figure 3). Next, two tissue samples were collected by clipping 2 to 4-cm pieces of dermal tissue from the distal end of the first dorsal fin. A uniquely numbered roto-tag, which is similar in appearance to a cattle ear tag, was inserted into the first dorsal fin for identification purposes. The hook was removed, and the shark released when all data were collected. One of the two fin samples collected was placed in 100% ethanol for genetic analysis, and the other was placed in an empty Eppendorf tube, stored in a cooler on ice in the field, and immediately placed in a standard freezer at -18 °C when returned to Nova Southeastern University's Oceanographic Center in preparation for stable isotope analysis.

To prepare the dorsal fin samples, which included dermal tissue and cartilage, for stable isotope analysis, the tissue was oven-dried at 60 °C for at least 48 hours to remove all moisture. A mortar and pestle were used to homogenize each of the dried samples. One microgram (μg) of each tissue sample was measured out and weighed with a microbalance. The processed samples were sent to the Stable Isotope Facility at UC Davis where they were analyzed using continuous-flow Isotope-Ratio Mass Spectrometry (IRMS) to determine the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ concentrations present within each tissue sample (Frisch et al., 2016).

Bovine liver standard was used for IRMS at UC Davis. Overall, 61 samples of bovine liver standard were used, and were distributed amongst shark fin samples so that each bovine liver standard sample was subjected to IRMS after every 9 shark fin samples. Following 9 shark fin samples and 1 bovine liver standard sample (10 samples total), 2 duplicate samples of previously analyzed shark fin tissue were subjected to IRMS to ensure reproducibility of the IRMS procedure. This also allowed us to compare the stable isotope content of a shark fin sample to that of its duplicate.

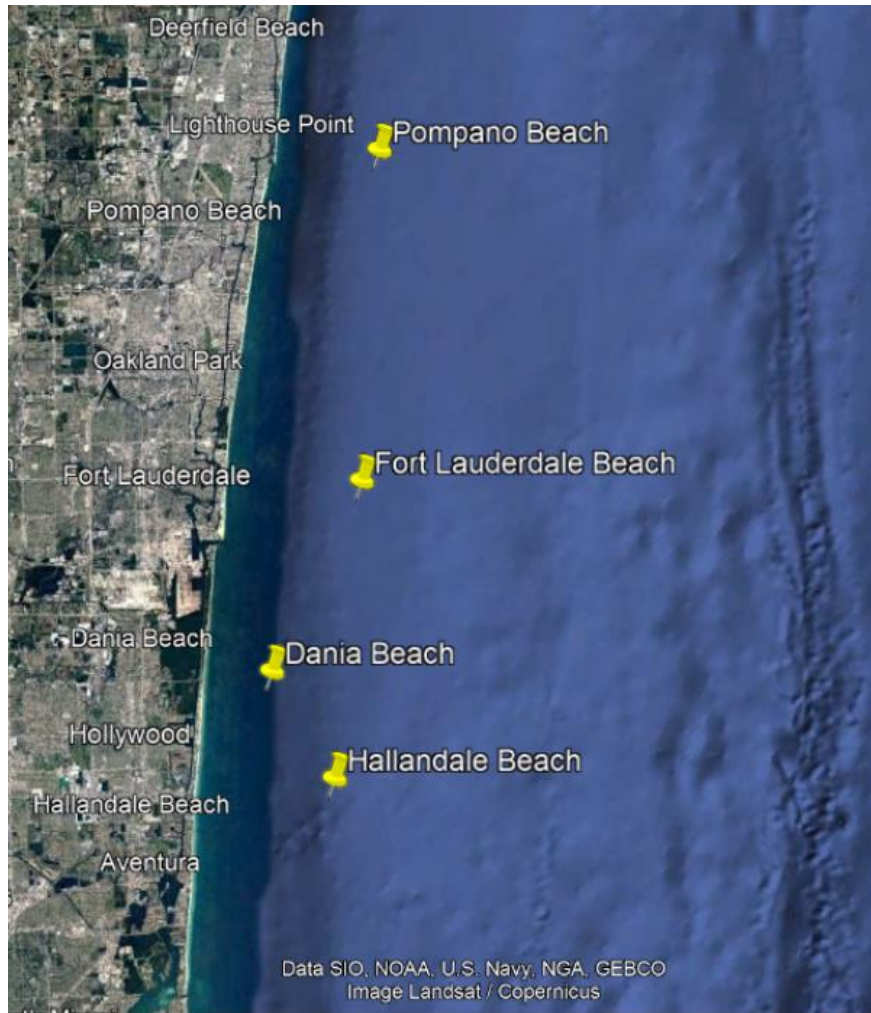


Figure 1.- Locations near coastal Southeast Florida where NSU/GHRI shark tagging surveys took place (Source: Google Earth).

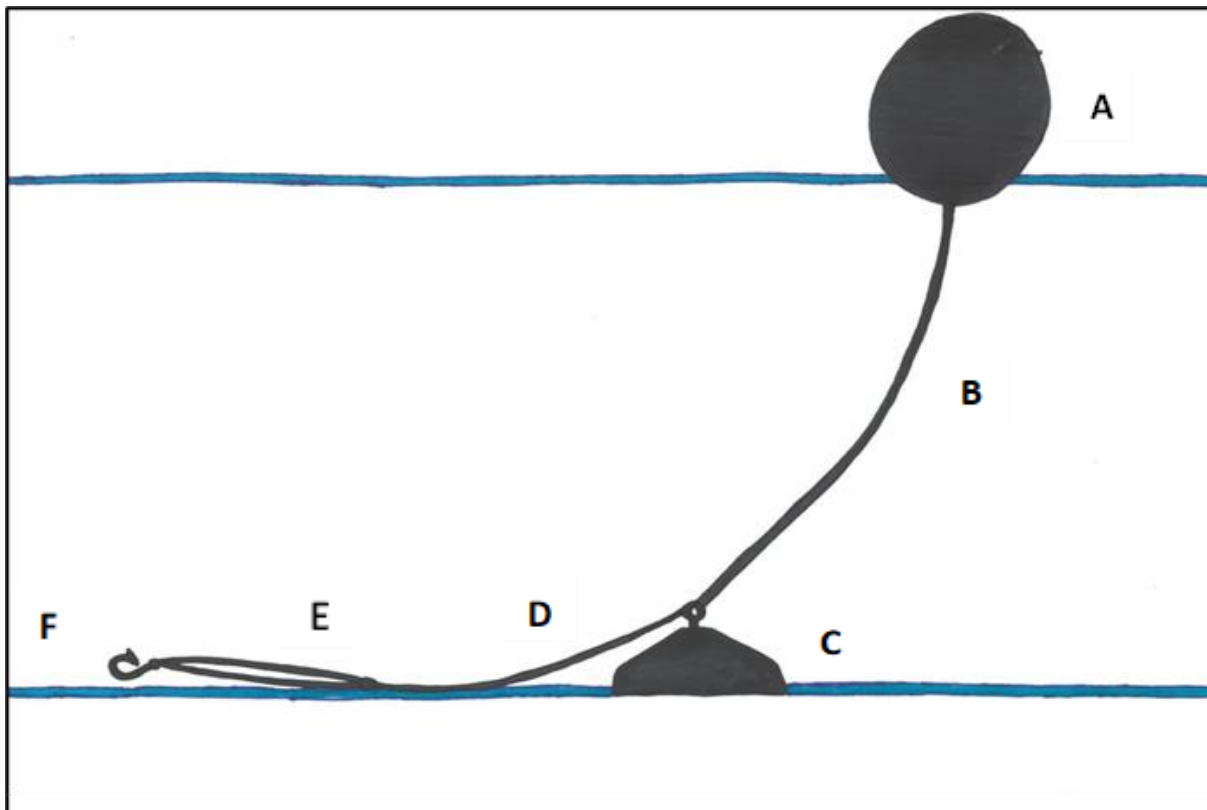


Figure 2.- Diagram of drumlines used in this study: (A) buoy; (B) rope attaching buoys to cement weight on the seafloor; (C) 22.7-kg cement weight; (D) 900-lb (408.2-kg) test monofilament main line; (E) double-stranded 900-lb (408.2-kg) test monofilament; (F) Mustad 16/0 triple strength circle hook.

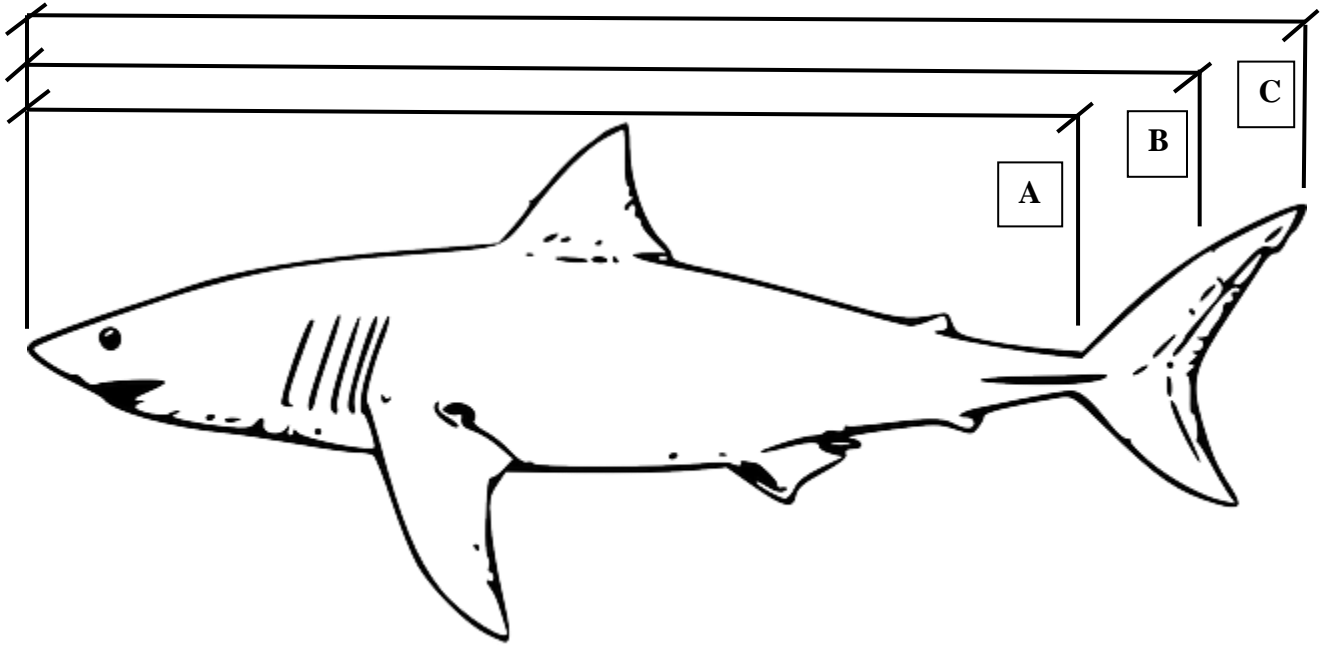


Figure 3.- Morphometric measurements of a shark: (A) precaudal length (PCL); (B) fork length (FL); and (C) stretched total length (STL).

CPUE and Species Abundance Analyses

To better understand seasonal patterns, as well as which species were encountered most often within the South Florida shark community, CPUE was calculated. Catch per unit effort (CPUE) was calculated for the entire study period, and additional CPUE calculations were completed for dry seasons, rainy seasons, individual years, and individual shark species. The time during which the study occurred was divided into years (2013-2019), and each year was further divided into dry and rainy seasons, after which the number of each shark species captured was determined for each season (Table 1).

To calculate soak times and subsequent CPUE values, the following equations were used:

$$\text{Soak Time (Bait Remaining)} = \text{Total Minutes Submerged}$$

$$\text{Soak Time (Shark on the Line or No Bait Remaining)} = \frac{\text{Total Minutes Submerged}}{2}$$

$$\text{CPUE} = \frac{\text{Total Sharks Caught}}{\text{Total Soak Time}}$$

Bar graphs were then constructed to visually display the CPUE of each shark species captured throughout the period during which the study took place (Figure 4). An additional bar graph was constructed to display the total CPUE for each of the 5 most commonly captured shark species, as well as their CPUE during all dry and rainy seasons (Figure 5). Two time series plots were created to display the mean annual CPUE and variances for each year from 2013-2019, and the mean CPUE and variances for each season from 2013-2019, respectively (Figures 6,7). Additionally, a Shapiro-Wilk test was conducted to assess the normality of the CPUE data, after which a Kruskal-Wallis test was conducted to determine whether CPUE was significantly different between dry and rainy seasons during each year from 2013-2019.

The relationship between total numbers of sharks captured during each season from 2013-2019, and the specific depths at which drumlines were deployed (7.62 m, 12.19 m, 18.28 m, 24.38 m, and 30.48 m), was assessed for normality with a Jarque-Bera test, which is typically used in larger data sets with more than 50 data points. Following the Jarque-Bera test, a two-way ANOVA

without replication was conducted to examine whether significantly different numbers of sharks were captured at certain depths from one season to the next throughout the study.

Stable Isotope Analysis

When calculating $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ content within tissue samples, the concentration of each stable isotope within body tissue can be calculated as:

$$\delta X = [(R_{\text{SAMPLE}}/R_{\text{STANDARD}}) - 1] * 1000 \text{ ‰}$$

where X represents the stable isotope of interest (i.e., ^{13}C or ^{15}N) and R represents the ratio of $^{13}\text{C}:^{12}\text{C}$ or $^{15}\text{N}:^{14}\text{N}$ for the sample and a known standard (either PDB for $\delta^{13}\text{C}$ or atmospheric N_2 for $\delta^{15}\text{N}$), respectively.

An x-y scatterplot was constructed to display the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for each shark species (Figure 8). A hull plot overlaid with minimum convex polygons, which help provide estimates of trophic niche width, provided a visual estimate for similarities in each species' $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, and therefore potential similarities in preferred prey and/or habitat usage (Figure 9). Relationships between $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and STL were explored for nurse, sandbar, lemon, tiger, and great hammerhead sharks, and displayed as scatterplots with trendlines and R^2 values (Figures 10, 11, 12, 13, 14). Finally, two-sample t-tests were conducted to examine the means of seasonal $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for the 5 most common shark species and determine whether these means differed significantly between dry and rainy seasons from 2013-2019 (Table 2).

RESULTS

Survey Capture and CPUE Results

This study included 193 days, or 331,054 minutes (approximately 5,518 hours), of fishing time, with a combined total of 541 sharks captured during these research expeditions (Table 1). The sample set includes tissue samples collected in the field from 228 nurse sharks, 122 sandbar sharks, 64 lemon sharks, 43 tiger sharks, 29 great hammerhead sharks, 15 bull sharks, 14 Caribbean reef sharks, 11 blacknose sharks, 12 Atlantic sharpnose sharks, and 2 blacktip sharks, all of which make up part of the shark community of coastal Southeast Florida. We were unfortunately unable to collect a tissue sample from the single dusky shark encountered during one of our surveys.

Overall, average CPUE was similar between rainy seasons (0.0031 sharks/min) and dry seasons (0.0028 sharks/min) from 2013-2019. In terms of individual years and seasons, the greatest average year-round CPUE value existed during 2016 (0.0103 sharks/min) and the highest seasonal

CPUE value occurred during the 2016 rainy season (0.0617 sharks/min). The lowest year-round CPUE value occurred in 2019 (0.0019 sharks/min), and the lowest seasonal CPUE value occurred during the 2019 dry season (0.0017 sharks/min) (Figures 6, 7). A Shapiro-Wilk test indicated that the CPUE data was not normally distributed ($p < 0.05$). Since this CPUE data was not normally distributed, a Kruskal-Wallis test was conducted to determine whether CPUE was significantly different between dry and rainy seasons from 2013-2019. Results showed that, although total counts and CPUE of captured sharks varied slightly between seasons from 2013-2019, CPUE was not significantly different at intra-annual timescales from 2013-2019 ($p > 0.05$).

Even though CPUE did not vary significantly with seasonality, season and water depth had a significant impact on total number of sharks captured throughout the study. Since there were more than 50 data points in this data set ($n=70$), a Jarque-Bera test was used to confirm that this data was normally distributed ($p > 0.05$). This data was subjected to a two-way ANOVA without replication, and corresponding p -values indicated that the total number of sharks caught during dry and rainy seasons from 2013-2019, and at depths of 7.62 m, 12.19 m, 18.28 m, 24.38 m, and 30.48 m, were significantly different (seasons: $df=13$, $F=9.70$, $p\text{-value}=8.13 \times 10^{-10}$; depths: $df=4$, $F=3.94$, $p\text{-value}=0.0072$).

Table 1.- Total numbers of all shark species captured from 2013-2019, as well as total numbers of each species captured during dry vs. rainy seasons; numbers of males, females, and individuals whose sex was unknown; STL ranges in cm, and total CPUE for each species (# sharks caught per minute of fishing time).

Shark Species	Total	Dry Season	Rainy Season	Females	Males	Sex Unknown	Min STL	Max STL	CPUE
<i>G. cirratum</i>	228	93	135	98	107	23	67	274	0.0012
<i>C. plumbeus</i>	122	70	52	100	15	7	140	250	0.00067
<i>N. brevirostris</i>	64	18	46	20	38	6	219	290	0.00035
<i>G. cuvier</i>	43	19	24	29	13	1	104	392	0.00024
<i>S. mokarran</i>	29	14	15	17	11	1	233	337	0.00016
<i>C. leucas</i>	15	5	10	5	7	3	199	255	0.000082
<i>C. perezii</i>	14	1	13	6	8	0	145	210	0.000077
<i>C. acronotus</i>	11	1	10	2	8	1	96	132	0.000066
<i>R. terraenovae</i>	12	5	7	5	3	4	84	102	0.000060
<i>C. limbatus</i>	2	0	2	2	0	0	159	175	0.000011
<i>C. obscurus</i>	1	0	1	1	0	0	N/A	330	0.0000055

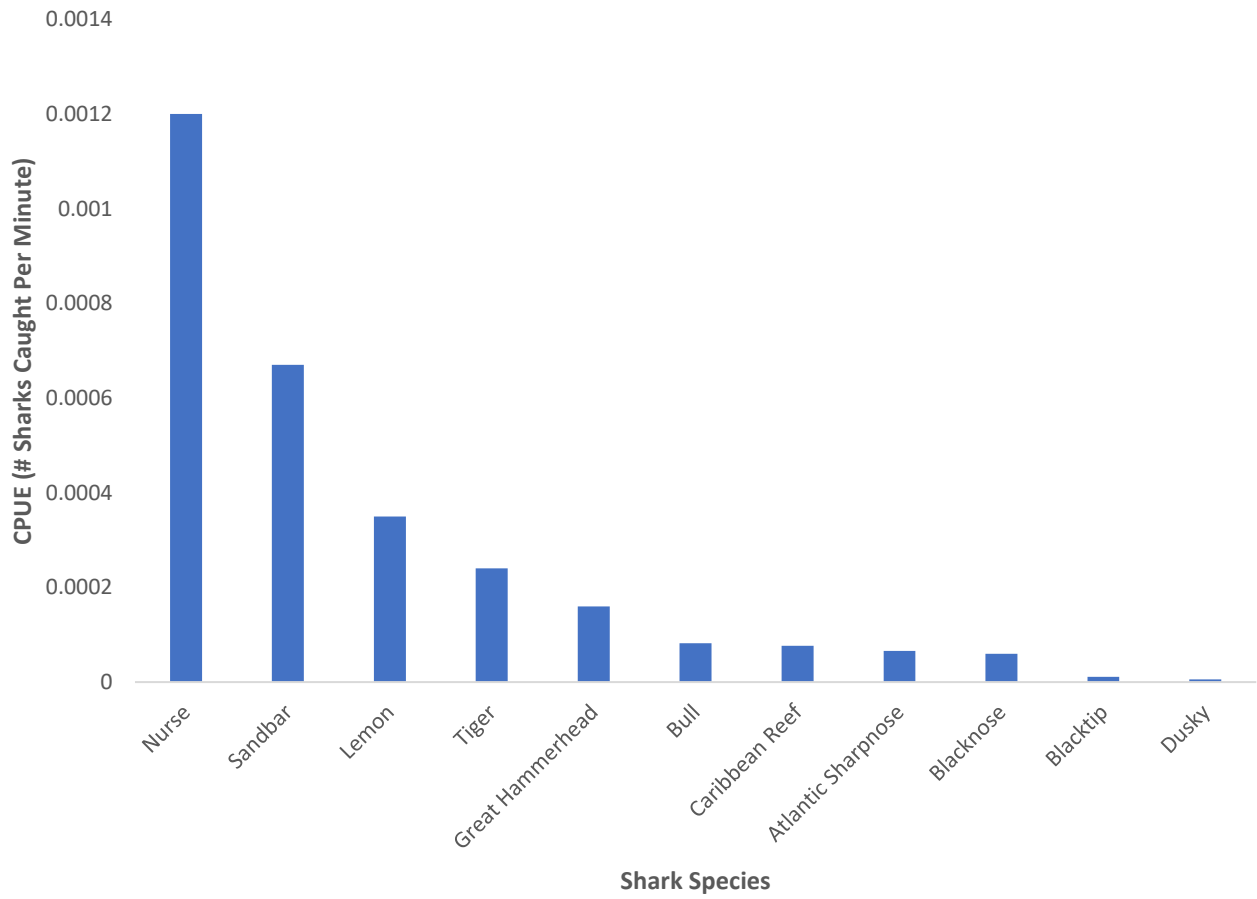


Figure 4.- Total CPUE for each shark species captured from 2013-2019.

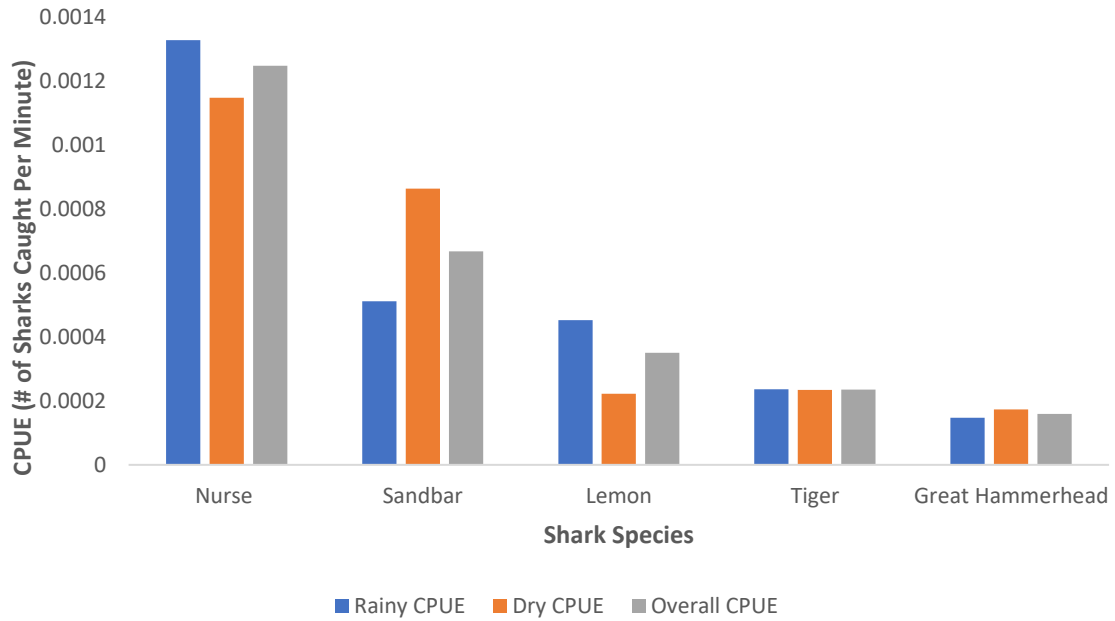


Figure 5.- Total CPUE for the five most common shark species in this study, and for each species during rainy and dry seasons.

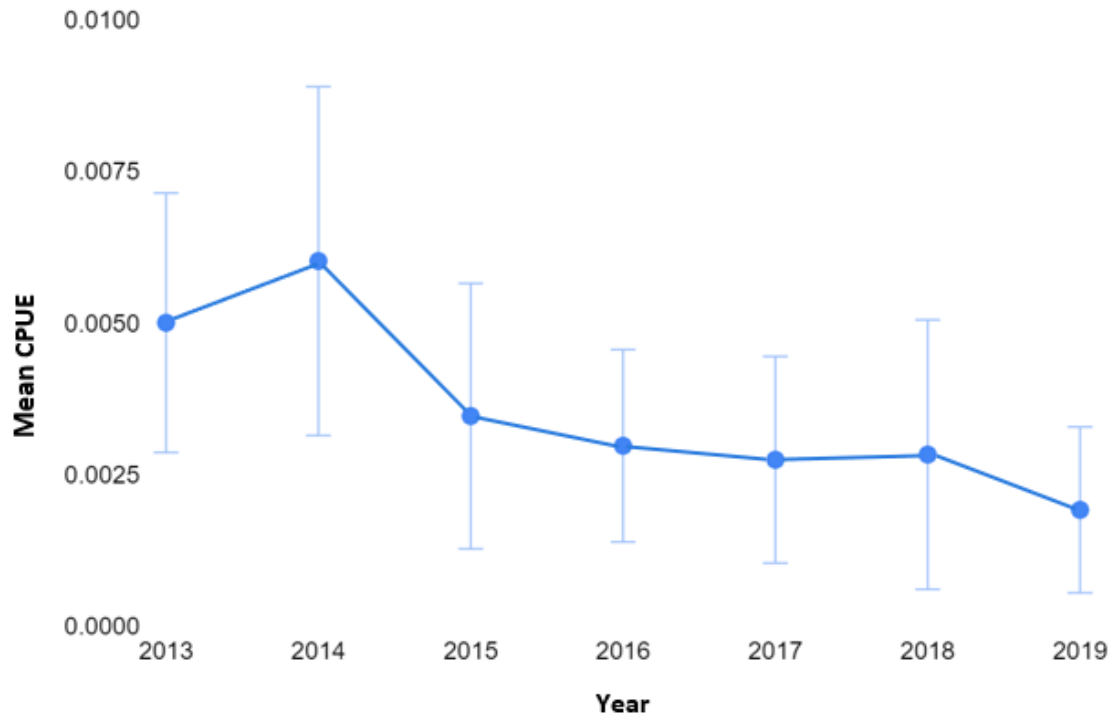


Figure 6.- Mean annual CPUE and standard deviations (displayed by error bars) from shark tagging surveys conducted between 2013-2019.

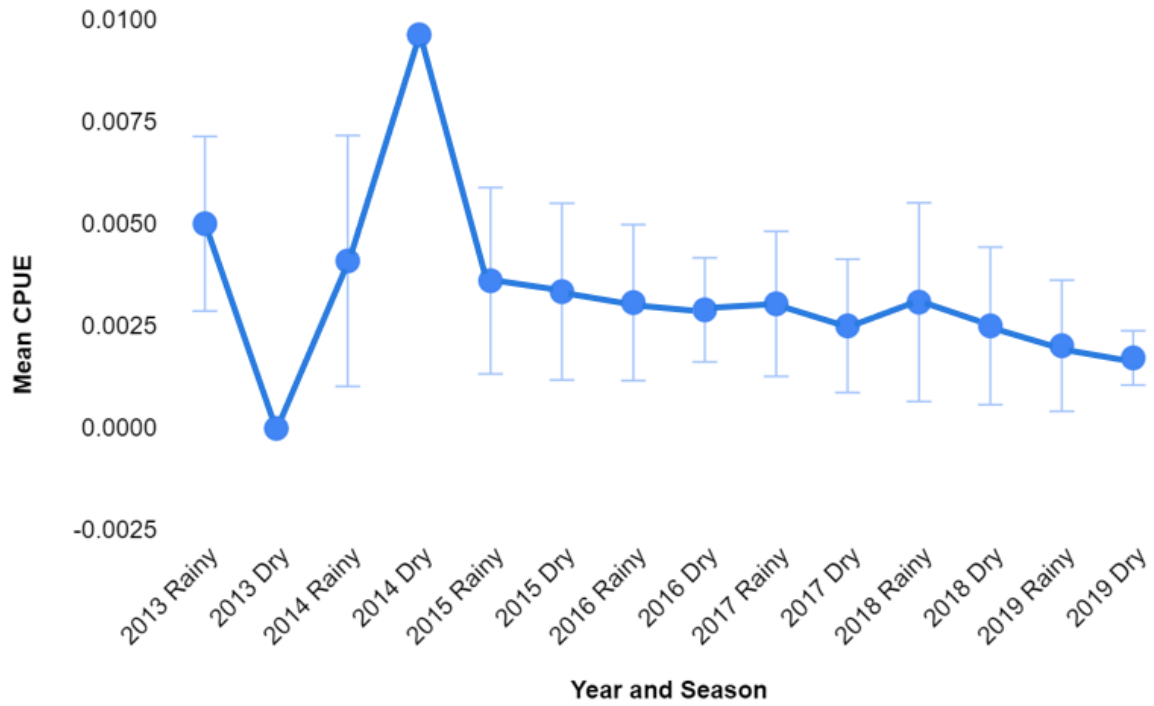


Figure 7.- Mean CPUE and standard deviations (displayed by error bars) from shark tagging surveys conducted during rainy and dry seasons from 2013-2019.

Stable Isotope Analysis Results

There was a noticeable amount of overlap in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of all species, as well as a small number of outlying data points, which can be observed in both the x-y scatterplot and the hull plot with minimum convex polygons constructed to compare stable isotope data among shark species (Figures 8, 9).

Two-sample t-tests determined whether $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively, were significantly different between dry and rainy seasons for each species. Nurse shark $\delta^{13}\text{C}$ (t statistic=-2.103, t critical two-tail=1.971, p-value=0.0367), sandbar shark $\delta^{13}\text{C}$ (t statistic=3.231, t critical two-tail=2.002, p-value=0.002), as well as tiger shark $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ($\delta^{13}\text{C}$: t statistic=-2.765, t critical two-tail=2.023, p-value=0.009; $\delta^{15}\text{N}$: t statistic=2.024, t critical two-tail=2.020, p-value=0.049) were significantly different between dry and rainy seasons (Table 2).

The possible relationship between STL, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively, in nurse, sandbar, lemon, tiger, and great hammerhead sharks was modeled using scatterplots. Based on the low R^2 values ($R^2 < 1$) in all cases, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were partially, but not strongly correlated with STL in any of these 5 species (Figures 10, 11, 12, 13, 14).

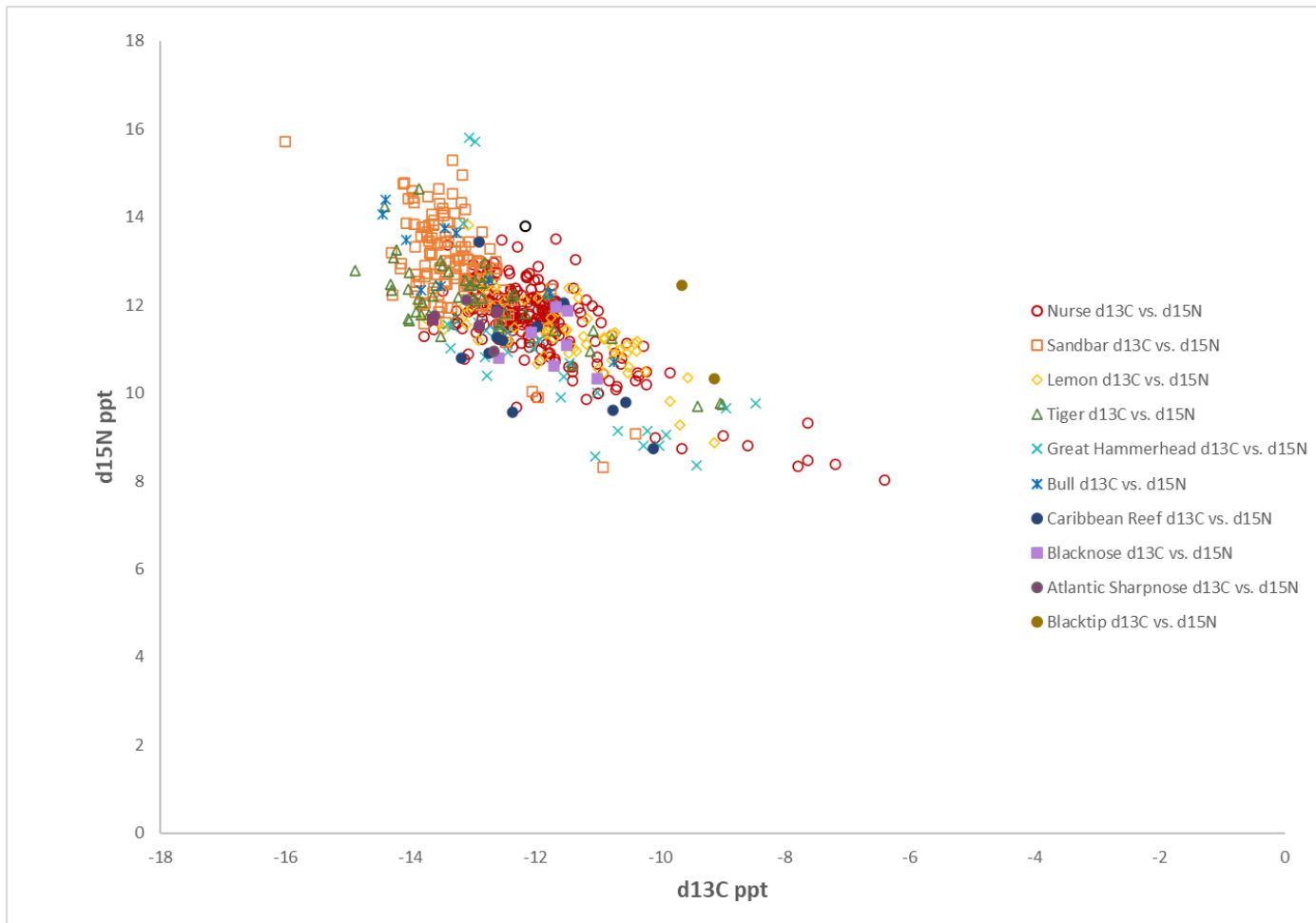


Figure 8.- The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of nurse, sandbar, lemon, tiger, great hammerhead, bull, Caribbean reef, blacknose, Atlantic sharpnose, and blacktip sharks caught from 2013-2019.

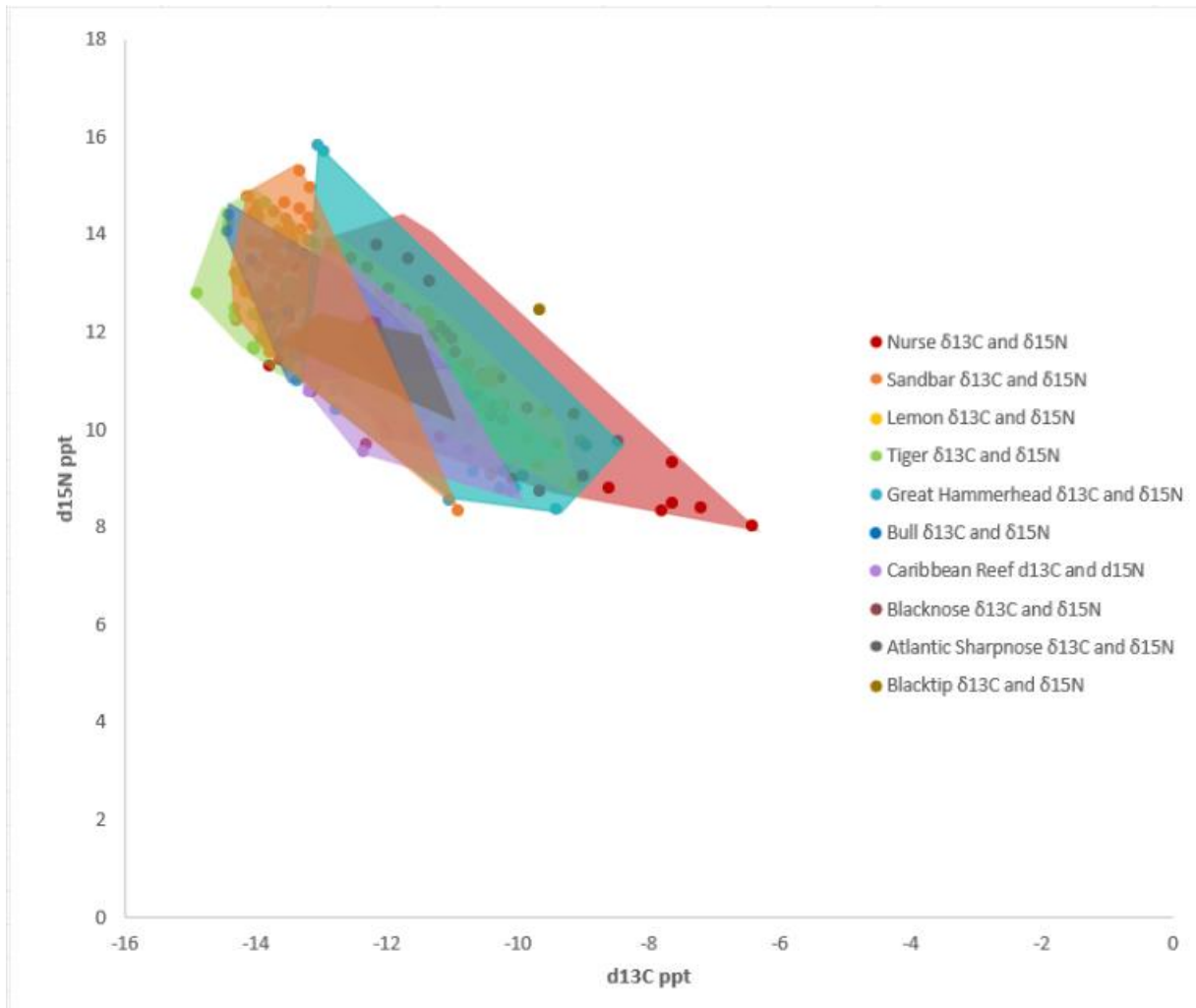


Figure 9.- Hull plot utilizing the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of each individual shark from each species. Every minimum convex polygon represents the trophic niche width of a different shark species.

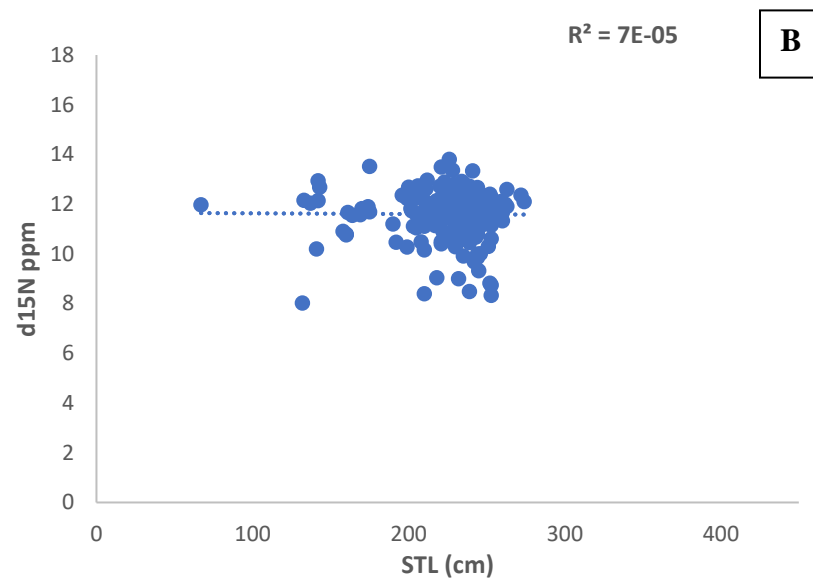
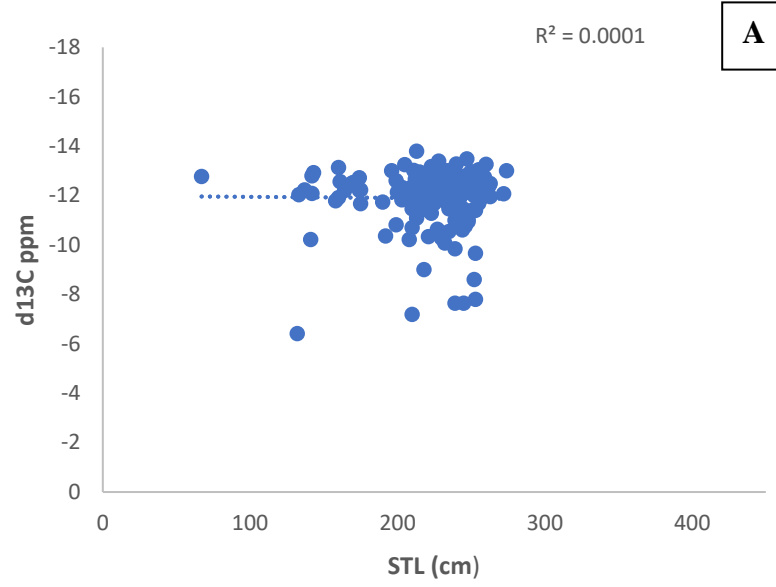


Figure 10.- Nurse shark STL (cm) compared with (A) $\delta^{13}\text{C}$ and (B) $\delta^{15}\text{N}$ in dermal/cartilaginous tissue.

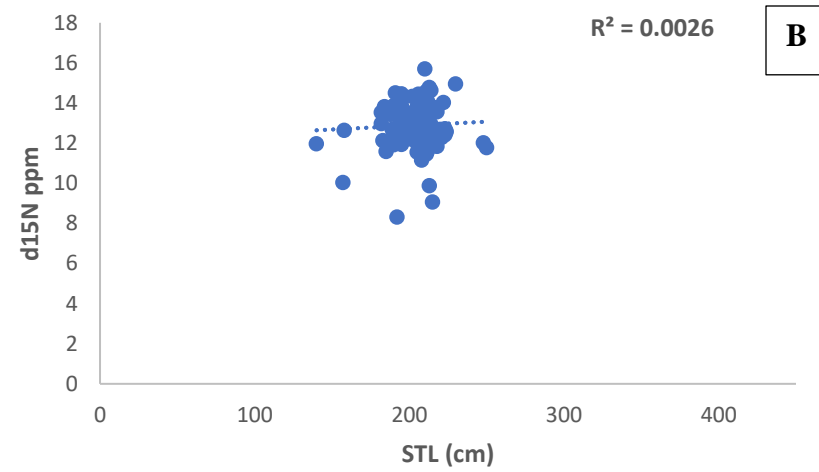
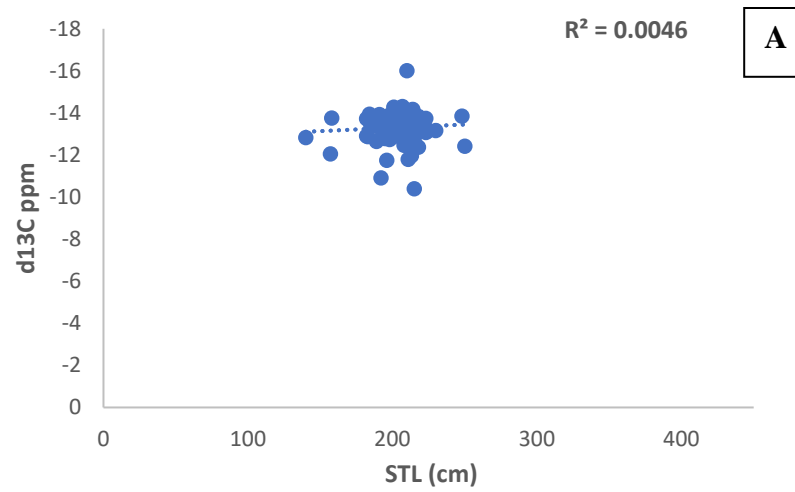


Figure 11.- Sandbar shark STL (cm) compared with (A) $\delta^{13}\text{C}$ and (B) $\delta^{15}\text{N}$ in dermal/cartilaginous tissue.

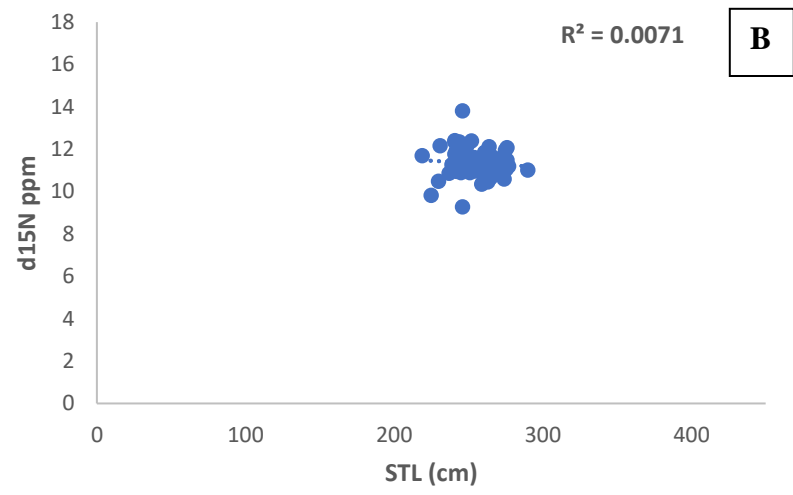
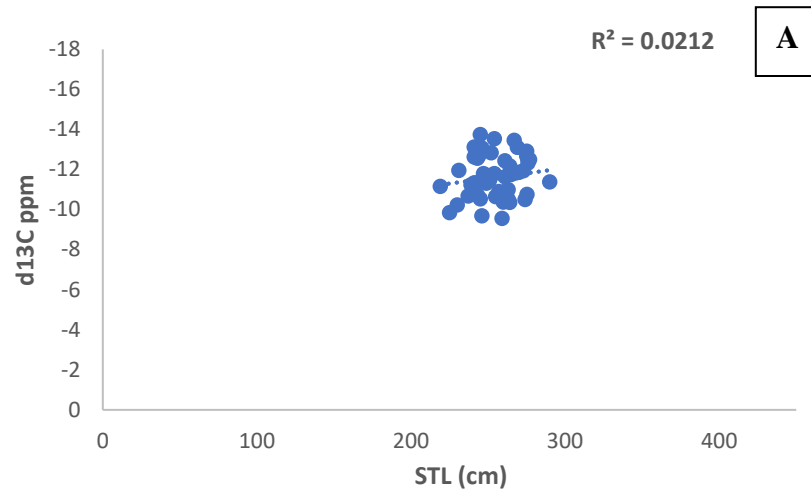


Figure 12.- Lemon shark STL (cm) compared with (A) $\delta^{13}\text{C}$ and (B) $\delta^{15}\text{N}$ in dermal/cartilaginous tissue.

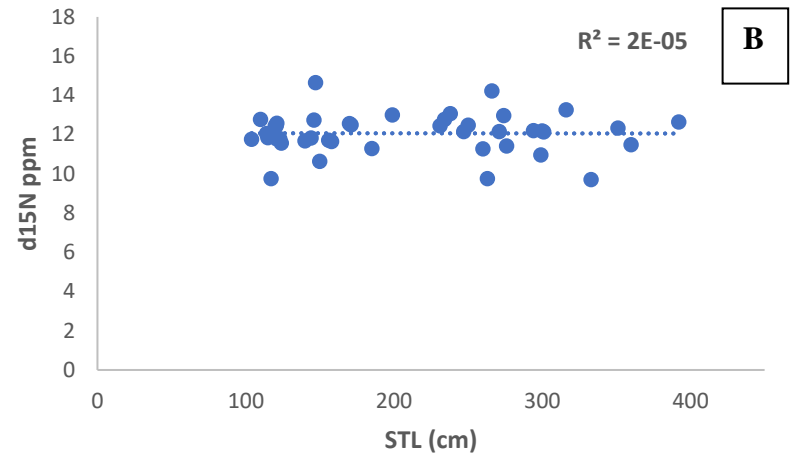
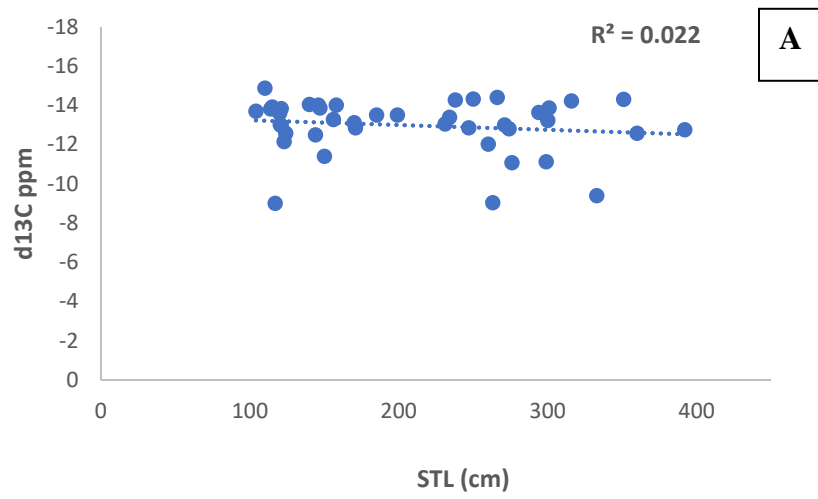


Figure 13.- Tiger shark STL (cm) compared with (A) $\delta^{13}\text{C}$ and (B) $\delta^{15}\text{N}$ in dermal/cartilaginous tissue.

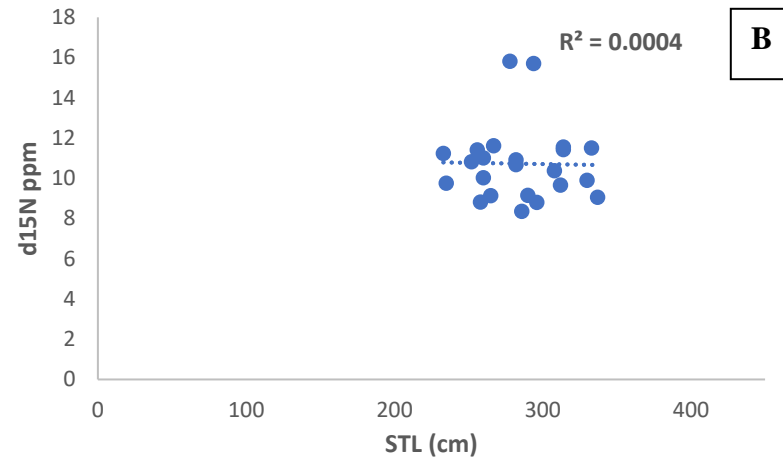
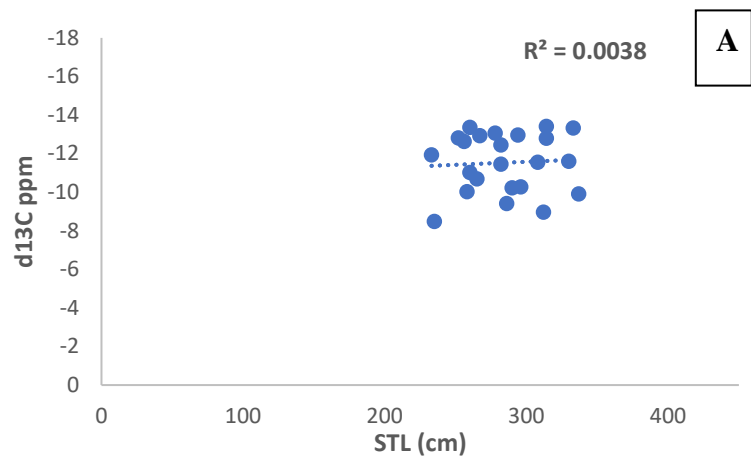


Figure 14.- Great hammerhead shark STL (cm) compared with (A) $\delta^{13}\text{C}$ and (B) $\delta^{15}\text{N}$ in dermal/cartilaginous tissue.

Table 2.- Results of two-sample t-tests for nurse, sandbar, lemon, tiger, and great hammerhead sharks. Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, respectively, were analyzed during rainy vs. dry seasons.

	$\delta^{13}\text{C}$	$\delta^{13}\text{C}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{15}\text{N}$	$\delta^{15}\text{N}$
	T Statistic	T Critical	P-Value	T Statistic	T Critical	P-Value
		Two-Tail			Two-Tail	
Nurse	-2.103	1.971	0.0367	1.830	1.974	0.069
Sandbar	3.231	2.002	0.002	-1.540	2.002	0.129
Lemon	1.065	2.015	0.293	-0.541	2.026	0.592
Tiger	-2.765	2.023	0.009	2.024	2.020	0.049
Great Hammerhead	-1.221	2.069	0.234	-0.009	2.069	0.993

DISCUSSION

The aim of this study was to enhance knowledge of the Southeast Florida shark community near Broward County, as well as to discover how seasonality affects CPUE, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$, for each individual study species and for the Southeast Florida shark community as a whole.

CPUE Interpretations

Although CPUE did not vary significantly between seasons, CPUE values were generally greater during most rainy seasons than during most dry seasons (Figures 6, 7). Some species also exhibited seasonal differences in CPUE. Nurse and lemon sharks had greater CPUE values during rainy seasons, sandbar and great hammerhead sharks had greater CPUE during dry seasons, and CPUE for tiger sharks was approximately equal between rainy and dry seasons (Figure 5). Nurse sharks exhibited the greatest total CPUE throughout the study period, which could have been caused by their preference for shallow reef habitats and site-limited life history strategies (Compagno, 2001; Rosa et al., 2006; Tilley et al., 2013). By contrast, of the 5 most commonly encountered shark species, great hammerhead sharks had the lowest total CPUE for the entire study period (Figure 5). This may be due to a combination of ecological factors, such as this species' seasonal migratory behaviors, the possibility that they prefer deeper water than that in which surveys took place, as well as their critically endangered conservation status and decreasing population trends worldwide (Denham et al., 2007; Hammerschlag et al., 2011).

SIA Interpretations

Stable isotope analysis was used to further explore the seasonal population trends displayed by Southeast Florida shark species. Some species, such as nurse sharks and sandbar sharks, both displayed significant seasonal differences in $\delta^{13}\text{C}$ (Table 2). Although nurse sharks are site-limited, they may experience significant seasonal changes in primary productivity within their habitats (Compagno, 2001; Rosa et al., 2006; Tilley et al., 2013). By contrast, sandbar sharks undergo seasonal migrations and partake in both temperate and sub-tropical food webs throughout the year, based on seasonality (Grubbs et al., 2007). Tiger sharks experienced significant seasonal differences in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, which could be influenced by their migratory behaviors and indicate seasonal diet changes (Lea et al., 2015; Wetherbee et al., 2011).

When comparing $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios among the shark species involved in this study, the resulting scatterplot, as well as the hull plot with minimum convex polygons, displayed overlap among the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of nurse, sandbar, lemon, tiger, great hammerhead, bull, Caribbean reef,

blacknose, Atlantic sharpnose, and blacktip sharks (Figure 9). Overlapping data points could be the result of individuals of each species targeting some of the same prey species, and/or prey species at similar trophic levels (Carlisle et al., 2012; Wetherbee & Cortés, 2004). Conversely, outlying data points may be caused by migration and incorporating stable isotopes from food webs at different geographic locations (Grubbs et al., 2007). Interestingly, based on observations of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ compared with STL, body size was partly, but not strongly, correlated with stable isotope content in the tissues of the 5 most frequently encountered species (Figures 10, 11, 12, 13, 14). These weak correlations could be caused by the indiscriminate diets of generalist species, such as nurse and tiger sharks, as well as the seasonal migrations undertaken by sandbar, lemon, tiger, and great hammerhead sharks, and their exposure to different food webs, and different potential prey items, throughout the year (Burkholder & Heithaus, 2001; Denham et al., 2007; Grubbs et al., 2007; Lea et al., 2015; Rosa et al., 2006; Sundström, 2015; Wetherbee et al., 2011).

Similar Studies and Unexpected Findings

A study conducted in the Lower Florida Keys, in which shark populations were surveyed using longlines and benthic drumlines, resulted in similar findings regarding abundance of different shark species based on seasonality. The most commonly encountered shark species throughout this study, on both types of fishing gear, was the nurse shark. The great hammerhead shark was encountered far less often on both longlines and drumlines (Heithaus et al., 2007). Nurse sharks may have been more common in the Florida Keys, in part, because of their ability to live and hunt in structurally complex environments (Moffa, 2004). Dominance of nurse sharks in both our study, and the study conducted in the Florida Keys, may have also occurred because of historical declines of populations of other species. For example, gillnet fisheries were once common in the Florida Keys, and may have caused a decline in shark species aside from nurse sharks (Viele, 1996). Since this species is abundant year-round and site-limited, it was surprising to see a significant change in $\delta^{13}\text{C}$ in Southeast Florida nurse sharks between dry and rainy seasons.

During fall and winter months, many pelagic and partially pelagic shark species migrate southward along the east coast of the United States, as well as the west coast of Florida (Hueter et al., 2005; Kohler et al., 1998). In the Florida Keys, capture probabilities generally increased as water temperatures increased, which occurs during Florida's rainy season. Species such as nurse and lemon sharks experienced the most noticeable increase in capture probability as water

temperatures increased in the Florida Keys (Heithaus et al., 2005). Likewise, these two species were captured more often during the rainy season in Southeast Florida, as well (Figure 5). By contrast, species such as the great hammerhead shark experienced the greatest probability of capture in the Florida Keys when water temperatures were coldest (Heithaus et al., 2007). This observation coincides with the great hammerhead's seasonal southward migration from the Northern Gulf of Mexico and the Northwestern Atlantic Ocean (Heithaus et al., 2007). Despite the great hammerhead shark's prevalence in the Florida Keys during the dry season, in our survey areas in Southeast Florida, there was not a noticeable difference in the numbers of great hammerhead sharks captured during the dry vs. rainy seasons from 2013-2019 (dry season: n=14; rainy season: n=15).

Significance of the Study

The makeup of the Southeast Florida shark community north of Miami has not been studied extensively. Therefore, this study provides a baseline assessment of this community, including the most commonly encountered shark species in this region, as well as their relative abundance and stable isotope concentrations based on seasonality. We have provided data that future researchers can build upon and, in doing so, create a more complete assessment of shark communities, seasonal species abundances, and important habitats utilized by sharks throughout Florida state waters. This sort of data, and collaboration amongst researchers, is crucial for the ongoing success of shark conservation efforts.

Future Directions

There are several directions that can be pursued to expand upon the data collected in this study. For example, the same research strategies and protocol can be implemented elsewhere in Florida, to obtain a more accurate assessment of shark community dynamics statewide, as well as how communities from different regions of the state overlap and interact with one another. Additionally, further field research could be conducted in the same geographic region to assess how populations of the species featured in this study continue to change over time. Other types of tags such as acoustic tags and satellite tags could be used to determine habitats used by these species year-round (especially highly migratory species), including potential migratory routes, breeding grounds, and hunting grounds. Long-term tagging studies, CPUE data, and stable isotope

data have the potential to improve upon existing knowledge on population trends, as well as the regional and global conservation statuses, of a multitude of shark species.

REFERENCES

- Bascompte, J., Melián, C.J., & Sala, E. (2005). Interaction strength combinations and the overfishing of a marine food web. *Proceedings of the National Academy of Sciences U.S.A.*, 102, 5443-5447. <https://doi.org/10.1073/pnas.0501562102>
- Baum, J.K., Myers, R.A., Kehler, D.G., Worm, B., Harley, S.J. & Doherty, P.A. (2003). Collapse and conservation of shark populations in the Northwest Atlantic. *Science*, 299(5605), 389-392.
- Bearhop, S., Adams, C.E., Waldron, S., Fuller, R.A. & Macleod, H. (2004). Determining trophic niche width: a novel approach using stable isotope analysis. *Journal of Animal Ecology*, 73(5), 1007-1012.
- Bizzarro, J.J., Carlisle, A.B., Smith, W.D. & Cortés, E. (2017). Diet composition and trophic ecology of Northeast Pacific Ocean sharks. *Advances in Marine Biology*, 111-148. <https://doi.org/10.1016/bs.amb.2017.06.001>
- Bonfil, R. (1994). *Overview of World Elasmobranch Fisheries*. Food and Agriculture Organization of the United Nations Rome.
- Brander, K. (1981). Disappearance of common skate *Raia batis* from Irish Sea. *Nature*, 290, 48-49.
- Brena, P.F., Mourier, J., Planes, S. & Clua, E. (2015). Shark and ray provisioning: functional insights into behavioral, ecological and physiological responses across multiple scales. *Marine Ecology Progress Series*, 538, 273–283. <https://doi.org/10.3354/meps11492>
- Burns, R.C. & Hardy, R.W.F. (1975). Description and Classification of Diazotrophs. In: Nitrogen Fixation in Bacteria and Higher Plants. *Molecular Biology, Biochemistry and Biophysics*, 21. Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-642-80926-2_2
- Cáceres, C., Kiszka, J. J., Luna-Acosta, A., Herrera, H., Zarza, E., & Heithaus, M. R. (2022). Predatory fish exploitation and relative abundance in a data-poor region from the Caribbean coast of Colombia, inferred from artisanal fishery interview surveys and baited remote underwater video systems. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 32(9), 1401-1415.
- Carlisle, A.B., Kim, S.L., Semmens, B.X., Madigan, D.J., Jorgensen, S.J., Perle, C.R., Anderson, S.D., Chapple, T.K., Kanive, P.E. & Block, B.A. (2012). Using stable isotope analysis to understand the migration and trophic ecology of the Northeastern Pacific white shark (*Carcharodon carcharias*). *PLoS One*, 7(2), 1-15.

- Carlson, J., Charvet, P., Avalos, C., Blanco-Parra, MP, Briones Bell-lloch, A., Cardenosa, D., Espinoza, E., Morales-Saldaña, J.M., Naranjo-Elizondo, B., Pérez Jiménez, J.C., Schneider, E.V.C., Simpson, N.J., Talwar, B.S., Crysler, Z., Derrick, D., Kyne, P.M. & Pacoureau, N. (2021). *Carcharhinus acronotus*. The IUCN Red List of Threatened Species 2021. <https://dx.doi.org/10.2305/IUCN.UK.2021-1.RLTS.T161378A887542.en>.
- Carlson, J., Charvet, P., Blanco-Parra, MP, Briones Bell-lloch, A., Cardenosa, D., Derrick, D., Espinoza, E., Morales-Saldaña, J.M., Naranjo-Elizondo, B., Pérez Jiménez, J.C., Schneider, E.V.C., Simpson, N.J., Talwar, B.S., Crysler, Z., Pacoureau, N. & Kyne, P.M. (2021). *Carcharhinus perezii*. The IUCN Red List of Threatened Species 2021. <https://dx.doi.org/10.2305/IUCN.UK.2021-1.RLTS.T60217A3093780.en>.
- Carlson, J., Charvet, P., Blanco-Parra, MP, Briones Bell-lloch, A., Cardenosa, D., Derrick, D., Espinoza, E., Morales-Saldaña, J.M., Naranjo-Elizondo, B., Pacoureau, N., Pérez Jiménez, J.C., Schneider, E.V.C., Simpson, N.J. & Talwar, B.S. 2021. *Rhizoprionodon terraenovae*. The IUCN Red List of Threatened Species 2021. <https://dx.doi.org/10.2305/IUCN.UK.2021-1.RLTS.T39382A124408927.en>.
- Casey, J.G., Pratt, H.L., & Stillwell, C.E. (1985). Age and growth of the sandbar shark (*Carcharhinus plumbeus*) from the western north Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences* 42, 963-975.
- Castro, J.I. (1996). Biology of the blacktip shark, *Carcharhinus limbatus*, off the Southeastern United States. *Bulletin of Marine Science*, 59(3), 508-522.
- Castro, J.I. (1993). The shark nursery of Bulls Bay, South Carolina, with a review of shark nurseries of the southeastern coast of the United States. *Environmental Biology of Fishes*, 38, 37–48.
- Castro, J.I. (2011). *The Sharks of North America*. Oxford University Press, New York.
- Castro, J.I. (1983). *The Sharks of North American Waters*. Texas A&M University Press, College Station, Texas (USA).
- Caswell, H., Reed, F., Stephenson, S.N. & Werner, P.A. (1973). Photosynthetic pathways and selective herbivory: a hypothesis. *The American Naturalist*, 107, 465-480.
- Chaudhary, C., Saeedi, H., Costello, M.J. (2016). Bimodality of latitudinal gradients in marine species richness. *Trends in Ecology and Evolution*, 31, 670–676. <https://doi.org/10.1016/j.tree.2016.06.001>
- Clarke, S.C., Magnussen, J.E., Abercrombie, D.L., McAllister, M.K., Shivji, M.S. (2006). Identification of Shark Species Composition and Proportion in the Hong Kong Shark Fin Market Based on Molecular Genetics and Trade Records. *Conservation Biology*, 20(1), 201-211.

- Clarke, S.C., McAllister, M.K., Milner-Gulland, E.J., Kirkwood, G.P., Michielsens, C.G.J., Agnew, D.J., Pikitch, E.K., Nakano, H. & Shivji, M.S. (2006). Global estimates of shark catches using trade records from commercial markets. *Ecology Letters*, 9, 1115-1126.
- Compagno, L.J.V. (1984). *FAO species catalogue. Vol.4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 1. Hexanchiformes to Lamniformes*. FAO, Rome, Italy.
<https://policycommons.net/artifacts/1422268/fao-species-catalogue/2036355/>
- Compagno, L.J.V. (1984). *FAO species catalogue. Sharks of the World. An Annotated and Illustrated Catalogue of Shark Species to Date. Part II (Carcharhiniformes)*. FAO, Rome, Italy.
- Compagno, L. J. V. (2001). *Sharks of the World: An Annotated and Illustrated Catalogue of Shark Species Known to Date*. Italy: Food and Agriculture Organization of the United Nations.
- Compagno, L. J. V., Dando, M. & Fowler, S. (2005). *A Field Guide to the Sharks of the World*. Harper-Collins.
- Cortés, E. (2002). Incorporating uncertainty into demographic modeling: application to shark populations and their conservation. *Conservation Biology*, 16, 1048-1062.
- Craig, H. (1953). The geochemistry of the stable carbon isotopes. *Geochimica et Cosmochimica Acta*, 3, 53-92.
- Davidson, L.N., Krawchuk, M.A. & Dulvy, N.K. (2016). Why have global shark and ray landings declined: improved management or overfishing? *Fishes*, 17, 438-458.
- Davis, S., & Ogden, J.C. (1994). *Everglades: The Ecosystem and Its Restoration (1st ed.)*. CRC Press. <https://doi.org/10.1201/9781466571754>
- Degens, E.T., Behrendt, M., Gotthardt, B. & Reppmann, E. (1968). Metabolic fractionation of carbon isotopes in marine plankton 11. Data on samples collected off the coasts of Peru and Ecuador. *Deep Sea Research*, 15, 11-20.
- Delwiche, C.C. & Steyn, P.L. (1970). Nitrogen isotope fractionation in soils and microbial reactions. *Environmental Science & Technology*, 4, 929-935.
- Delwiche, C.C., Zinke, P.J., Johnson, C.M. & Virginia, R.A. (1979). Nitrogen isotope distribution as a presumptive indicator of nitrogen fixation. *Botanical Gazette*, 140, S65-S69.

- Denham, J., Stevens, J.D., Simpfendorfer, C., Heupel, M.R., Cliff, G., Morgan, A., Graham, R., Ducrocq, M., Dulvy, N.K., Seisay, M., Asber, M., Valenti, S.V., Litvinov, F., Martins, P., Lemine Ould Sidi, M., Tous, P. & Bucal, D. (2007). *Sphyrna mokarran*. The IUCN Red List of Threatened Species 2007.
<http://dx.doi.org/10.2305/IUCN.UK.2007.RLTS.T39386A10191938.en>
- DeNiro, M.J. & Epstein, S. (1978). Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta*, 42, 495-506.
- DeNiro, M.J. & Epstein, S. (1981). Influence of diet on the distribution of nitrogen isotopes in animals. *Geochimica et Cosmochimica Acta*, 45, 341–351.
- Dodrill, J.W. (1977). A hook and line survey of the sharks found within five hundred meters of shore along Melbourne Beach, Brevard County, Florida. M.S. Thesis, Florida Institute of Technology.
- Dudley, S.F. & Simpfendorfer, C.A. (2006). Population status of 14 shark species caught in the protective gillnets off KwaZulu-Natal beaches, South Africa, 1978-2003. *Marine and Freshwater Research*, 57, 225-240.
- Dulvy, N.K., Baum, J.K., Clarke, S., Compagno, L.J.V., Cortés, E., Domingo, A., Fordham, S., Fowler, S., Francis, M.P., Gibson, C., Martínez, J., Musick, J.A., Soldo, A., Stevens, J.D., Valenti, S. (2008). You can swim but you can't hide: the global status and conservation of oceanic pelagic sharks and rays. *Aquatic Conservation*, 18, 459-482.
- Dulvy, N.K., Fowler, S.L., Musick, J.A., Cavanagh, R.D., Kyne, P.M., Harrison, L.R., Carlson, J.K., Davidson, L.N.K., Fordham, S., Francis, M.P., et al. (2014). Extinction risk and conservation of the world's sharks and rays. *eLife* 3, e00590.
- Dulvy, N.K. & Reynolds, J.D. (2002). Predicting extinction vulnerability in skates. *Conservation Biology*, 16, 440-450.
- Dunton, K.H., Saupe, S.M., Golikov, N., Schell, D.M. & Schonberg, S.V. (1989). Trophic relationships and isotopic gradients among Arctic and Subarctic marine fauna. *Marine Ecology Progress Series*, 56, 89-97.
- Edmunds, P.J., Leichter, J.J. & Adjeroud, M. (2010). Landscape-scale variation in coral recruitment in Moorea, French Polynesia. *Marine Ecology Progress Series*, 414, 75–89.
- Ehleringer, J.R. and Rundel, P.W. (1989). Stable Isotopes: History, Units, and Instrumentation. *Ecological Studies*, 68.
- Estrada, J.A., Rice, A.N., Lutcavage, M.E. & Skomal, G.B. (2003). Predicting trophic position in sharks of the north-west Atlantic Ocean using stable isotope analysis. *Journal of the Marine Biological Association of the UK*, 83, 1347-1350.

- Estrada, J.A., Rice A.N., Natanson, L.J. & Skomal, G.B. (2006). Use of isotopic analysis of vertebrae in reconstructing ontogenetic feeding ecology in white sharks. *Ecology*, 87, 829–834.
- Fabinyi, M. (2011). Historical, cultural and social perspectives on luxury seafood consumption in China. *Environmental Conservation*, 39(1), 83-92.
- Ferretti, F., Myers, R.A., Serena, F. & Lotze, H.K. (2008). Loss of large predatory sharks from the Mediterranean Sea. *Conservation Biology*, 22, 952-964.
- Ferretti, F., Worm, B., Britten, G.L., Heithaus, M.R. & Lotze, H.K. (2010). Patterns and ecosystem consequences of shark declines in the ocean. *Ecology Letters*, 13, 1055-1071. <https://doi.org/10.1111/j.1461-0248.2010.01489.x>
- Fisheries and Aquaculture Organization (2019). Effort and Catch Per Unit Effort. <http://www.fao.org/3/x5685e/x5685e04.htm#4.2%20the%20mathematical%20formulation>
- Fisheries and Aquaculture Organization (2012). FishStatJ—software for fishery statistical time series. <http://www.fao.org/fishery/statistics/software/fishstatj/enS>
- Fisheries and Aquaculture Organization (2016). The State of World Fisheries and Aquaculture 2016. Contributing to food security and nutrition for all. Rome.
- Fisheries and Aquaculture Organization Information and Statistics Branch (2017). Global Capture Production 1950-2017. http://www.fao.org/figis/servlet/SQServlet?file=/usr/local/tomcat/8.5.16/figis/webapps/figis/tem/hqp_6413302926577349727.xml&outtype=html
- Florida Fish and Wildlife Conservation Commission (2018). Fishing: Saltwater Fishing: Recreational Regulations: Sharks. <http://myfwc.com/fishing/saltwater/recreational/sharks/>
- Florida Museum of Natural History. Discover Fishes: *Carcharhinus plumbeus*. <https://www.floridamuseum.ufl.edu/fish/discover/species-profiles/carcharhinus-plumbeus/>
- Florida Museum of Natural History. Discover Fishes: *Galeocerdo cuvier*. <https://www.floridamuseum.ufl.edu/discover-fish/species-profiles/galeocerdo-cuvier/>
- Florida Museum of Natural History. Discover Fishes: *Negaprion brevirostris*. <https://www.floridamuseum.ufl.edu/discover-fish/species-profiles/negaprion-brevirostris/>
- France, R.L. (1995). Carbon-13 enrichment in benthic compared to planktonic algae – food web implications. *Marine Ecology Progress Series*, 124, 307–312.

- France, R.L. (1997). Stable carbon and nitrogen isotopic evidence for ecotonal coupling between boreal forests and fishes. *Ecology of Freshwater Fish*, 6, 78-83.
- Frisch, A.J., Ireland, M., Rizzari, J.R., Lönnstedt, O.M., Magnenat, K.A., Mirbach, C.E. & Hobbs, J.A. (2016). Reassessing the trophic role of reef sharks as apex predators on coral reefs. *Coral Reefs*.
- Frisk, M.G., Miller, T.J. & Fogarty, M.J. (2001). Estimation and analysis of biological parameters in elasmobranch fishes: a comparative life history study. *Canadian Journal of Fisheries and Aquatic Sciences*, 58, 969-981.
- Gallagher, A.J., Hammerschlag, N., Shiffman, D.S. & Giery, S.T. (2014). Evolved for extinction: The cost and conservation implications of specialization in hammerhead sharks. *BioScience*, 64(7): 619-624.
- Gallagher, A.J., Serafy, J.E., Cooke, S. & Hammerschlag, N. (2014). Physiological stress response, reflex impairment, and survival of five sympatric shark species following experimental capture and release. *Marine Ecology Progress Series*, 496, 207-214.
- Gaston, K.J. (1996). Biodiversity—Latitudinal gradients. *Progress in Physical Geography*, 20, 466–476. <https://doi.org/10.1177/030913339602000406>
- Gaston, K.J. & Blackburn, T.M. (1996). The spatial distribution of threatened species: Macroscales and New World birds. *Proceedings of the Royal Society of Biological Sciences, B*, 263, 235–240. <https://doi.org/10.1098/rspb.1996.0037>
- Graham, K.J., Andrew, N.L. & Hodgson, K.E. (2001). Changes in relative abundance of sharks and rays on Australian southeast fishery trawl grounds after twenty years of fishing. *Marine and Freshwater Research*, 52, 549-561.
- Grenyer, R., Orme, C.D.L., Jackson, S.F., Thomas, G.H., Davies, R.G., Davies, T.J., Jones, K.E., Olson, V.A., Ridgely, R.S., Rasmussen, P.C., Ding, T., Bennett, P.M., Blackburn, T.M., Gaston, K.J., Gittleman, J.L. & Owens, I.P.F. (2006). Global distribution and conservation of rare and threatened vertebrates. *Nature*, 444, 93–96. <https://doi.org/10.1038/nature05237>
- Grubbs, R.D., Musick, J.A., Conrath, C.L. & Romine, J.G. (2007). Long-term movements, migration, and temporal delineation of a summer nursery for juvenile sandbar sharks in the Chesapeake Bay region. *American Fisheries Society Symposium*, 50, 87-107.
- Gulland, J.A. (1969). *Manual of Methods for Fish Stock Assessment – Part 1. Fish Population Analysis*. Fish Stock Evaluation Branch Fishery Resources and Exploitation Division, Food and Agriculture Organization of the United Nations.

- Hammerschlag, N., Gallagher, A.J., Lazarre, D.M. & Slonim, C. (2011). Range extension of the endangered great hammerhead shark *Sphyrna mokarran* in the Northwest Atlantic: Preliminary data and significance for conservation. *Endangered Species Research*, 13, 111-116.
- Hammerschlag, N. & Sulikowski, J. (2011). Killing for conservation: the need for alternatives to lethal sampling of apex predatory sharks. *Endangered Species Research*, 14, 135-140.
- Harley, S.J., Myers, R.A. & Dunn, A. (2001). Is catch-per-unit-effort proportional to abundance? *Canadian Journal of Fisheries and Aquatic Sciences*, 58, 1760–1772. <https://doi.org/10.1139/cjfas-58-9-1760>
- Harrison, S. (2015). Diet shifts detected in sandbar sharks using a nonlethal technique. *Fisheries* 40(2), 52. <https://doi.org/10.1080/03632415.2015.1003276>
- Heithaus, M.R. (2005). Habitat use and group size of pied cormorants (*Phalacrocorax varius*) in a seagrass ecosystem: possible effects of food abundance and predation risk. *Marine Biology*, 147, 27–35.
- Heithaus, M.R. (2001). The biology of tiger sharks, *Galeocerdo cuvier*, in Shark Bay, Western Australia: Sex ratio, size distribution, diet, and seasonal changes in catch rates. *Environmental Biology of Fishes*, 61, 25-36.
- Heithaus, M.R. (2004). *Predator–prey interactions*. In *The biology of sharks and their relatives*. Edited by J.C. Carrier, J. Musick, and M.R Heithaus. CRC Press, Boca Raton, FL.
- Heithaus, M.R., Burkholder, D., Hueter, R.E, Heithaus, L.I., Pratt Jr., H.W. & Carrier, J.C. (2007). Spatial and temporal variation in shark communities of the lower Florida Keys and evidence for historical population declines. *Canadian Journal of Fisheries and Aquatic Sciences*, 64, 1302-1313.
- Heupel, M.R., Carlson, J.K. & Simpfendorfer, C.A. (2007). Shark nursery areas: concepts, definition, characterization and assumptions. *Marine Ecology Progress Series*, 337, 287-297.
- Heupel, M.R., Collins, A. & Simpfendorfer, C.A. (2010). Long-term presence and movement patterns of juvenile bull sharks, *Carcharhinus leucas*, in an estuarine river system. *Marine and Freshwater Research*, 61, 1-10.
- Hicks, C.C., Cohen, P.J., Graham, N.A.J., Nash, K.L., Allison, E.H., D’Lima, C., Mills, D.J., Roscher, M., Thilsted, S.H., Thorne-Lyman, A.L., MacNeil, M.A., (2019). Harnessing global fisheries to tackle micronutrient deficiencies. *Nature*, 574, 95-98.
- Hobson, K. A. (1999). Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia*, 120(3), 314-326.

- Hobson, K.A. & Clark, R.G. (1992). Assessing avian diets using stable isotopes I: Turnover of ^{13}C in tissues. *Condor*, 94, 181–188.
- Hobson, K.A., Piatt, J.F. & Pitocchelli, J. (1994). Using stable isotopes to determine seabird trophic relationships. *Journal of Animal Ecology*, 63, 786-798.
- Hobson, K.A., Schell, D.M., Renouf, D. & Noseworthy, E. (1996). Stable carbon and nitrogen isotopic fractionation between diet and tissues of captive seals: implications for dietary reconstructions involving marine mammals. *Canadian Journal of Fisheries and Aquatic Sciences*, 53, 528–533.
- Hueter, R.E., Heupel, M.R., Heist, E.J. & Keeney, D.B. (2005). Evidence of philopatry in sharks and implications for the management of shark fisheries. *Journal of Northwest Atlantic Fisheries Science*, 35, 239-247.
- Hughes, T.P., Bellwood, D.R. & Connolly, S.R. (2002). Biodiversity hotspots, centres of endemism, and the conservation of coral reefs. *Ecology Letters*, 5, 775–784.
- Hussey, N.E., MacNeil, M.A., Olin, J.A., McMeans, B.C., Kinney, M.J., Chapman, D.D. & Fisk, A.T. (2012). Stable isotopes and elasmobranchs: tissue types, methods, applications and assumptions. *Journal of Fish Biology*, 80, 1449-1484.
- International Atomic Energy Agency (2018). *Stable Isotopes*.
<https://www.iaea.org/topics/nuclear-science/isotopes/stable-isotopes>
- International Commission for the Conservation of Atlantic Tunas (ICCAT) (2019). *Report of the 2019 ICCAT Shortfin Mako Shark Stock Assessment Update Meeting*, 41.
- Isotopic Fractionation. (2016). Encyclopedia Britannica, Inc.
<https://www.britannica.com/science/isotopic-fractionation>
- Jetz, W., Thomas, G.H., Joy, J.B., Redding, D.W., Hartmann, K. & Mooers, A.O. (2014). Global distribution and conservation of evolutionary distinctness in birds. *Current Biology*, 24, 919–930. <https://doi.org/10.1016/j.cub.2014.03.011>
- Jinks, K.I., Rasheed, M.A., Brown, C.J., Olds, A.D., Schlacher, T.A., Sheaves, M., York, P.H. & Connolly, R.M. (2020). Saltmarsh grass supports fishery food webs in subtropical Australian estuaries. *Estuarine, Coastal and Shelf Science*, 238, 1-9.
- Katzenberg, M.A. (2007). Stable Isotope Analysis: A Tool for Studying Past Diet, Demography, and Life History. In *Biological Anthropology of the Human Skeleton, Second Edition*, 413-441.
- Kelly, J.F. (2000). Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. *Canadian Journal of Zoology*, 78, 1-27.

- Kohler, N. (1996). National Marine Fisheries Service Cooperative Shark Tagging Program. Shark News. *Newsletter of the IUCN SSC Shark Specialist Group*, 7, 1-2.
- Kohler, N.E., Casey, J.G. & Turner, P.A. (1998). National Marine Fisheries Service Cooperative Shark Tagging Program, 1962-1993: An atlas of shark tag and recapture data. *Marine Fisheries Review*, 60, 1-87.
- Kopp, D., Robert, M. & Pawlowski, L. (2017). Characterization of food web structure of the upper continental slope of the Celtic Sea highlighting the trophic ecology of five deep-sea fishes. *Journal of Applied Ichthyology*, 34(1), 73-80.
- Kroodsma, D.A., Mayorga, J., Hochberg, T., Miller, N.A., Boerder, K., Ferretti, F., Wilson, A., Bergman, Bjorn, White, T.D., Block, B.A., Woods, P., Sullivan, B., Costello, C. & Worm, B. (2018). Tracking the global footprint of fisheries. *Science*, 359, 904-908.
- Lea, J.S.E., Wetherbee, B.M., Queiroz, N., Burnie, N., Aming, C., Sousa, L.L., Mucientes, G.R., Humphries, N.E., Harvey, G.M., Sims, D.W. & Shivji, M.S. (2015). Repeated, long-distance migrations by a philopatric predator targeting highly contrasting ecosystems. *Scientific Reports*, 5, 11202. <https://doi.org/10.1038/srep11202>
- Leichter, J.J., Stokes, M.D., Hench, J.L., Witting, J. & Washburn, L. (2012). The island-scale internal wave climate of Moorea, French Polynesia. *Journal of Geophysical Research Oceans*, 117, C06008.
- Leu, M., Hanser, S.E. & Knick, S.T. (2008). The human footprint in the west: a large-scale analysis of anthropogenic impacts. *Ecological Applications*, 18, 1119–1139.
- Logan, J.M. & Lutcavage, M.E. (2010). Stable isotope dynamics in elasmobranch fishes. *Hydrobiologia*, 644, 231–244.
- Lotze, H.K., Lenihan, H.S., Bourque, B.J., Bradbury, R.H., Cooke, R.G., Kay, M.C., Kidwell, S.M., Kirby, M.X., Peterson, C.H. & Jackson, J.B.C. (2006). Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science*, 312, 1806-1809.
- Lowdon, J.A. & Dyck, W. (1974). Seasonal variations in the isotope ratios of maple leaves and other plants. *Canadian Journal of Earth Sciences*, 11, 79-88.
- Lucifora, L.O., García, V.B., Menni, R.C. & Worm, B. (2012). Spatial patterns in the diversity of sharks, rays, and chimaeras (Chondrichthyes) in the Southwest Atlantic. *Biodiversity and Conservation*, 21, 407–419. <https://doi.org/10.1007/s10531-011-0189-7>
- Lucifora, L.O., Garcia, V.B. & Worm, B. (2011). Global diversity hotspots and conservation priorities for sharks. *PLoS One*, 6, 1–7. <https://doi.org/10.1371/Citation>
- Mace, G.M., Gittleman, J.L. & Purvis, A. (2003). Preserving the tree of life. *Science*, 300, 1707–1709. <https://doi.org/10.1126/science.1085510>

- MacNeil, M.A., Drouillard, K.G. & Fisk, A.T. (2006). Variable uptake and elimination of stable nitrogen isotopes between tissues in fish. *Canadian Journal of Fisheries and Aquatic Sciences*, 63, 345–353.
- Manire, C.A. & Gruber, S.H. (1990). Many sharks may be headed toward extinction. *Conservation Biology*, 4, 10-11.
- Matich, P., Ault, J.S., Boucek, R.E., Bryan, D.R., Gastrich, K.R., Harvey, C.L., Heithaus, M.R., Kiszka, J.J., Paz, V., Rehage, J.S. & Rosenblatt, A.E. (2017). Ecological niche partitioning within a large predator guild in a nutrient-limited estuary. *Limnology and Oceanography*, 62, 934–953.
- Matich, P., Heithaus, M.R. & Layman, C.A. (2011). Contrasting patterns of individual specialization and trophic coupling in two marine apex predators. *Journal of Animal Ecology*, 80, 294-305.
- Matich, P., Heithaus, M.R. & Layman, C.A. (2010). Size-based variation in inter-tissue comparisons of stable carbon and nitrogen isotopic signatures of bull sharks and tiger sharks. *Canadian Journal of Fisheries and Aquatic Sciences*, 67, 877–885.
- Matich, P., Kiszka, J.J., Heithaus, M.R., Le Bourg, B. & Mourier, J. (2019). Inter-individual differences in ontogenetic trophic shifts among three marine predators. *Oecologia*, 189, 621-636. <https://doi.org/10.1007/s00442-019-04357-5>
- McClenachan, L., Cooper, A.B., & Dulvy, N.K. (2016). Rethinking trade-driven extinction risk in marine and terrestrial megafauna. *Current Biology* 26, 1640-1646.
- Maunder, M.N., Sibert, J.R., Fonteneau, A., Hampton, J., Kleiber, P. & Harley, S.J. (2006). Interpreting catch per unit effort data to assess the status of individual stocks and communities. *Journal of Marine Science*, 63, 1373-1385.
- McCutchan, J.W., Lewis, T. (2001). Seasonal variation in stable isotope ratios of stream algae. *Internationale Vereinigung für Limnologie*, 27(6), 3304-3307.
- Michener, R., & Lajtha, K. (2008). *Stable isotopes in ecology and environmental science*. John Wiley & Sons.
- Minagawa, M. & Wada, E. (1984). Stepwise enrichment of ^{15}N along food chains: Further evidence and the relation between $\delta^{15}\text{N}$ and animal age. *Geochimica et Cosmochimica Acta*, 48, 1135-1140.
- Mitchell, J.D., Collins, K.J., Miller, P.I. & Suberg, L.A. (2014). Quantifying the impact of environmental variables upon catch per unit effort of the blue shark *Prionace glauca* in the western English Channel. *Journal of Fish Biology*. <https://doi.org/10.1111/jfb.12448>

- Mizutani, H., Fukuda, M. & Kabaya, Y. (1992). ^{13}C and ^{15}N enrichment factors of feathers of 11 species of adult birds. *Ecology*, 73, 1391–1395.
- Mizutani, H., Kabaya, Y. & Wada, E. (1991). Nitrogen and carbon isotope compositions relate linearly in cormorant tissues and its diet. *Isotopenpraxis*, 27, 166–168.
- Montoya, J.P., Carpenter, E.J. & Capone, D.G. (2002). Nitrogen fixation and nitrogen isotope abundances in zooplankton of the oligotrophic North Atlantic. *Limnology and Oceanography*, 47(6), 1617-1628.
- Motta, P.J., & Huber, D.R. (2004). Prey capture behavior and feeding mechanics of elasmobranchs. *Biology of sharks and their relatives*, 1, 165-195.
- Mucientes, G., Vedor, M., Sims, D.W. & Queiroz, N. (2022). Unreported discards of internationally protected pelagic sharks in a global fishing hotspot are potentially large. *Biological Conservation*. <https://doi.org/10.1016/j.biocon.2022.109534>
- Musick, J.A., Burgess, G., Cailliet, G., Camhi, M. & Fordham, S. (2000). Management of sharks and their relatives (Elasmobranchii). *Fisheries*, 25(9), 9-13.
- Musick, J.A. & Colvocoresses, J.A. (1986). Seasonal recruitment of subtropical sharks in Chesapeake Bight, USA. In *IOC Workshop Report (IOC)*. UNESCO.
- Musick, J.A., Stevens, J.D., Baum, J.K., Bradai, M., Clò, S., Fergusson, I., Grubbs, R.D., Soldo, A., Vacchi, M. & Vooren, C.M. (2009). *Carcharhinus plumbeus*. *The IUCN Red List of Threatened Species 2009*. <http://dx.doi.org/10.2305/IUCN.UK.2009-2.RLTS.T3853A10130397.en>
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A. & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403, 853–858. <https://doi.org/10.1038/35002501>
- Myers, R.A. & Worm, B. (2005). Extinction, survival or recovery of large predatory fishes. *Philosophical Transactions of the Royal Society of London B*, 360, 13-20.
- Newsome, S.D., Etnier, M.A., Monson, D.H. & Fogel, M.L. (2009a). Retrospective characterization of ontogenetic shifts in killer whale diets via $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis of teeth. *Marine Ecology Progress Series*, 374, 229–242.
- Orme, C.D.L., Davies, R.G., Burgess, M., Eigenbrod, F., Pickup, N., Olson, V.A., Webster, A.J., Ding, T., Rasmussen, P.C., Ridgely, R.S., Stattersfield, A.J., Bennett, P.M., Blackburn, T.M., Gaston, K.J. & Owens, I.P.F. (2005). Global hotspots of species richness are not congruent with endemism or threat. *Nature*, 436, 1016–1019. <https://doi.org/10.1038/nature03850>

- Pacoureau, N., Rigby, C.L., Kyne, P.M., Sherley, R.B., Winker, H., Carlson, J.K., Fordham, S.V., Barreto, R.B., Fernando, D., Francis, M.P., Jabado, R.W., Herman, K.B., Liu, K., Marshall, A.D., Pollom, R.A., Romanov, E.V., Simpfendorfer, C.A., Yin, J.S., Kindsvater, H.K. & Dulvy, N.K. (2021). Half a century of global decline in oceanic sharks and rays. *Nature*, 589, 567-571.
- Paterson, R. (1990). Effects of long-term anti-shark measures on target and non-target species in Queensland, Australia. *Biological Conservation*, 52, 147-159.
- Pauly, D. (2006). Major trends in small-scale marine fisheries, with emphasis on developing countries, and some implications for the social sciences. *Maritime Studies*, 4(2), 7–22.
- Pauly, D. & Zeller, D. (2016). Sea Around Us Concepts, Design and Data. Sea Around Us: Fisheries, Ecosystems & Biodiversity. searoundus.org
- Peterson, B.J. & Fry, B. (1987). Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics*, 18, 293-320.
- Ponsard, S. & Averbuch, P. (1999). Should growing and adult animals fed on the same diet show different $\delta^{15}\text{N}$ values? *Rapid Communications in Mass Spectrometry*, 13, 1305-1310.
- Post, D.M. (2002). Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology*, 83(3), 703-718.
- Pressey, R.L., Cabeza, M., Watts, M.E., Cowling, R.M. & Wilson, K.A. (2007). Conservation planning in a changing world. *Trends in Ecology and Evolution*, 22, 583–592. <https://doi.org/10.1016/j.tree.2007.10.001>
- Puertas, P.E. & Bodmer, R.E. (2004). 8. Hunting Effort as a Tool for Community-Based Wildlife Management in Amazonia. In K. Silvius, R. Bodmer & J. Fragoso (Ed.), *People in Nature: Wildlife Conservation in South and Central America*, 123-136. New York Chichester, West Sussex: Columbia University Press. <https://doi.org/10.7312/silv12782-008>
- Purvis, A., Agapow, P. M., Gittleman, J. L., & Mace, G. M. (2000). Nonrandom extinction and the loss of evolutionary history. *Science*, 288(5464), 328-330.
- Queiroz, N., Humphries, N.E., Couto, A., Sims, D.W. *et al.* (2019). Global spatial risk assessment of sharks under the footprint of fisheries. *Nature*, 572: 461-466.
- Queiroz, N., Humphries, N. E., Couto, A., Vedor, M., Da Costa, I., Sequeira, A. M., ... & Sousa, L. L. (2019). Global spatial risk assessment of sharks under the footprint of fisheries. *Nature*, 572(7770), 461-466.

- Queiroz, N., Humphries, N.E., Mucientes, G., Hammerschlag, N., Lima, F.P., Seales, K.L., Miller, P.I., Sousa, L.L., Seabra, R. & Sims, D.W. (2016). Ocean-wide tracking of pelagic sharks reveals extent of overlap with longline fishing hotspots. *Proceedings of the National Academy of Sciences U.S.A.*, 113, 1582-1587.
- Richards, T.M., Gipson, E.E., Cook, A., Sutton, T.T. & Wells, R.J.D. (2018). Trophic ecology of meso- and bathypelagic predatory fishes in the Gulf of Mexico. *ICES Journal of Marine Science*, 1-11.
- Rigby, C.L., Barreto, R., Carlson, J., Fernando, D., Fordham, S., Francis, M.P., Herman, K., Jabado, R.W., Liu, K.M., Marshall, A., Pacoureau, N., Romanov, E., Sherley, R.B. & Winker, H. (2019). *Carcharhinus obscurus*. The IUCN Red List of Threatened Species 2019: <https://dx.doi.org/10.2305/IUCN.UK.2019-3.RLTS.T3852A2872747.en>.
- Rigby, C.L., Carlson, J., Chin, A., Derrick, D., Dicken, M. & Pacoureau, N. (2021). *Carcharhinus limbatus*. The IUCN Red List of Threatened Species 2021. <https://dx.doi.org/10.2305/IUCN.UK.2021-2.RLTS.T3851A2870736.en>.
- Rigby, C.L., Espinoza, M., Derrick, D., Pacoureau, N. & Dicken, M. (2021). *Carcharhinus leucas*. The IUCN Red List of Threatened Species 2021. <https://dx.doi.org/10.2305/IUCN.UK.2021-2.RLTS.T39372A2910670.en>.
- Rivest, E.B. & Gouhier, T.C. (2015). Complex environmental forcing across the biogeographical range of coral populations. *PLoS One*, 10:e0121742.
- Roff, G., Brown, C.J., Priest, M.A. & Mumby, P.J. (2018). Decline of coastal apex shark populations over the past half century. *Communications Biology*, 1(1), 223.
- Rosa, R.S., Castro, A.L.F., Furtado, M., Monzini, J. & Grubbs, R.D. (2006). *Ginglymostoma cirratum*. The IUCN Red List of Threatened Species 2006. <http://dx.doi.org/10.2305/IUCN.UK.2006.RLTS.T60223A12325895.en>
- Rosa, R.S., Mancini, P., Caldas, J.P. & Graham, R.T. (2006). *Carcharhinus perezii*. The IUCN Red List of Threatened Species. <http://dx.doi.org/10.2305/IUCN.UK.2006.RLTS.T60217A12323052.en>.
- Rosauer, D.F. & Mooers, A.O. (2013). Nurturing the use of evolutionary diversity in nature conservation. *Trends in Ecology and Evolution*, 28, 322–323. <https://doi.org/10.1016/j.tree.2013.01.014>
- Rose, D.A. (1996). An overview of world trade in sharks and other cartilaginous fishes. TRAFFIC Network, Cambridge, UK.
- Rosenblatt, A.E., Heithaus, M.R., Mather, M.E., Matich, P. & Nifong, J.C. (2013). The roles of large top predators in coastal ecosystems: new insights from Long-Term Ecological Research. *Oceanography*, 26, 156–167.

- Saporiti, F., Bearhop, S., Silva, L., Vales, D.G., Zenteno, L., Crespo, E.A., Aguilar, A. & Cardona, L. (2014). Longer and less overlapping food webs in anthropogenically disturbed marine ecosystems: confirmations from the past. *PLoS One*, 9:e103132.
- Schoeninger, M.J. & DeNiro, M.J. (1984). Nitrogen and carbon isotopic composition of bone collagen from marine and terrestrial animals. *Geochimica et Cosmochimica Acta*, 48, 625-639.
- Schwarcz, H.P., (1969). The stable isotopes of carbon. In *Handbook of Geochemistry* (editor K.H. Wedepohl), 2, 1-16. Springer.
- Shephard, S., Trueman, C., Rickaby, R. & Rogan, E. (2007). Juvenile life history of NE Atlantic orange roughy from otolith stable isotopes. *Deep-Sea Research Part I*, 54, 1221-1230.
- Shepherd, T.D. & Myers, R.A. (2005). Direct and indirect fishery effects on small coastal elasmobranchs in the northern Gulf of Mexico. *Ecological Letters*, 8, 1095-1104.
- Shiffman, D.S., Frazier, B.S., Kucklick, J.R., Abel, D., Brandes, J. & Sancho, G. (2014). Feeding ecology of the Sandbar Shark in South Carolina estuaries revealed through $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope analysis. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science*, 6 (1), 156–169.
- Shiffman, D.S., Gallagher, A.J., Boyle, M.D., Hammerschlag-Peyer, C.M. & Hammerschlag, N. (2012). Stable isotope analysis as a tool for elasmobranch conservation research: a primer for non-specialists. *Marine and Freshwater Research*, 63, 635–643.
- Simpfendorfer, C. (2009). *Galeocerdo cuvier*. The IUCN Red List of Threatened Species 2009. <http://dx.doi.org/10.2305/IUCN.UK.2009.2.RLTS.T39378A10220026.en>
- Simpfendorfer, C.A. & Dulvy, N.K. (2017). Bright spots of sustainable shark fishing. *Current Biology*, 27, R97–R98.
- Smith, B.N. & Epstein, S. (1971). Two categories of $^{13}\text{C}/^{12}\text{C}$ ratios for higher plants. *Plant Physiology*, 47, 380-384.
- Smith, S.E, Au, D.W., & Show, C. (1998). Intrinsic rebound potentials of 26 species of Pacific sharks. *Marine and Freshwater Research*, 49, 663-678.
- Southeast Data, Assessment and Review (SEDAR) (2016). Update Assessment to SEDAR 21. HMS Dusky Shark. *SEDAR*, North Charleston, SC, USA.
- Speed, C.W., Field, I.C., Meekan, M.G. & Bradshaw, C.J.A. (2010). Complexities of coastal shark movements and their implications for management. *Marine Ecology Progress Series*, 408, 275-293.

- Steele, K.W. & Daniel, R.M. (1978). Fractionation of nitrogen isotopes by animals: a further complication to the use of variations in the natural abundance of ^{15}N for tracer studies. *Journal of Agricultural Science*, 90, 7-9.
- Stevens, J.D., Bonfil, R., Dulvy, N.K. & Walker, P.A. (2000). The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. *ICES Journal of Marine Science*, 57, 476-494.
- Sundström, L.F. (2015). *Negaprion brevirostris*. The IUCN Red List of Threatened Species 2015. <http://dx.doi.org/10.2305/IUCN.UK.2015.RLTS.T39380A81769233.en>
- The International Union for the Conservation of Nature Red List of Threatened Species. (2023). The IUCN Red List of Threatened Species. <https://www.iucnredlist.org/en>
- Thomas, C.J. & Cahoon, L.B. (1993). Stable isotope analyses differentiate between different trophic pathways supporting rocky-reef fishes. *Marine Ecology Progress Series*, 95, 19–24.
- Tilley, A., López-Angarita, J., Turner, J.R. (2013). Diet reconstruction and resource partitioning of a Caribbean marine mesopredator using stable isotope Bayesian modelling. *PLoS ONE*, 8(11), e79560. <https://doi.org/10.1371/journal.pone.0079560>
- Tinari, A.M. & Hammerschlag, N. (2021). An ecological assessment of large coastal shark communities in South Florida. *Ocean & Coastal Management*, 211, 105772.
- Tittensor, D.P., Mora, C., Jetz, W., Lotze, H.K., Ricard, D., Berghe, E.V., & Worm, B. (2010). Global patterns and predictors of marine biodiversity across taxa. *Nature*, 466(7310), 10981101. <https://doi.org/10.1038/nature09329>
- Turner, T.F., Collyer, M.L. & Krabbenhoft, T.J. (2010). A general hypothesis-testing framework for stable isotope ratios in ecological studies. *Ecology*, 91(8), 2227-2233.
- Tykout, R.H. (2004). Stable isotopes and diet: You are what you eat. Proceedings of the International School of Physics “Enrico Fermi” Course, CLIV IOS Press.
- Vander Zanden, M.J. & Vadeboncoeur, Y. (2002). Fishes as integrators of benthic and pelagic food webs in lakes. *Ecology*, 83, 2152–2161.
- Vedor, M., Queiroz, N., Mucientes, G., Couto, A., da Costa, I., dos Santos, A., Vandeperre, J.F., Afonso, P., Rosa, R., Humphries, N.E. & Sims, D.W. (2021). Climate-driven deoxygenation elevates fishing vulnerability for the ocean’s widest-ranging shark. *eLife*, 10, e62508. <https://doi.org/10.7554/eLife.62508>
- Viele, J. (1996). The Florida Keys (Vol. 1). Pineapple Press Inc.

- Wada, E.M., Mizutani, H. & Minagawa, M. (1991). The use of stable isotopes for food web analysis. *Critical Reviews in Food Science & Nutrition*, 30(4), 361-371.
- Waldron, A., Mooers, A.O., Miller, D.C., Nibbelink, N., Redding, D., Kuhn, T.S., Roberts, J.T. & Gittleman, J.L. (2013). Targeting global conservation funding to limit immediate biodiversity declines. *PNAS*, 110, 1–3. <https://doi.org/10.5061/dryad.p69t1>
- Ward, E. Introduction to Bayesian Isotope Mixing Models. NOAA Northwest Fisheries Science Center. Seattle, Washington, U.S.A. <https://afsuw.files.wordpress.com/2012/05/intro-to-mixing-models.pdf>
- Ward-Paige, C.A. (2015). Monitoring elasmobranch populations using scuba divers: patterns, trends and potential biases.
- Wetherbee, B.M., Cortés, E. & Bizzarro, J.J. (2012). Food consumption and feeding habits. In Carrier, J.C., Musick, J.A., & Heithaus, M.R. (Ed.) *Biology of Sharks and Their Relatives*, Second Edition. 239-253.
- Wetherbee, B., Harvey, G., Burney, N., Aming, C., Teter, S. & Shivji, M. (2011). Are tiger sharks reef sharks or pelagic sharks? Movements of tiger sharks in the Western North Atlantic. *American Elasmobranch Society Behavior & Ecology Presentation*.
- Worm, B., Davis, B., Kettner, L., Ward-Paige, C.A., Chapman, D., Heithaus, M.R., Kessel, S.T. & Gruber, S.H. (2013). Global catches, exploitation rates, and rebuilding options for sharks. *Marine Policy*, 40, 194-204.
- Wright, A.J. & Kyhn, L.A. (2015). Practical management of cumulative anthropogenic impacts with working marine examples. *Conservation Biology*, 29, 333–340.
- Xu, W., Cheung, S.G., Zhang, Z. & Shin, P.K.S. (2017). Dual isotope assessment of trophic dynamics of an intertidal infaunal community with seasonal shifts in food sources. *Marine Biology*, 165, 21.
- Zanden, M.J.V., Clayton, M.K., Moody, E.K., Solomon, C.T. & Weidel, B.C. (2015). Stable isotope turnover and half-life in animal tissues: A Literature Synthesis. *PLoS ONE*, 10(1), e0116182. <https://doi.org/10.1371/journal.pone.0116182>