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WHO’S MINDING THE MAKOS? APPLICATIONS OF MOVEMENT PATTERNS AND HABITAT UTILIZATION FOR MANAGEMENT OF SHORTFIN MAKO SHARK AND INTERSECTION WITH OFFSHORE ENERGY EXPLORATION

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BY

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ABSTRACT

The absence of coordinated international management for shortfin mako sharks (*Isurus oxyrinchus*, hereafter: mako) in the Northwest Atlantic Ocean and the Gulf of Mexico, coupled with a lack of knowledge about large-scale mako movements and habitat use, have hampered effective mako shark management in the North Atlantic (Campana, 2016). In addition to fishing pressure, anthropogenic factors like the expansion of oil rigs into deeper pelagic waters and development of offshore wind farms in the Northwest Atlantic are likely to influence mako habitat use (Bailey, Brooks, and Thompson, 2014). Our work used a longitudinal satellite telemetry dataset to investigate the movement patterns of 60 mako sharks in relation to a suite of human interactions, including jurisdictional boundaries, management measures, and energy exploration in the western North Atlantic and Gulf of Mexico. Altogether, mako sharks visited 27 different Exclusive Economic Zones in the North Atlantic Ocean. Sharks tagged off the U.S. showed seasonal and behavioral influences in their transboundary movements, as well as potential demographic deviances. Sharks tagged off of Mexico showed less variability in their transboundary movements as a response to season and movement behavior. Current U.S. management strategies provide insufficient protection for the North Atlantic shortfin mako stock. We found, the degree of overlap between the shark's core area and existing oil rigs to be negligible, and offshore oil rigs and the Block Island Wind Farm did not significantly affect shark movement behavior. However, we show that the proposed locations of offshore wind farms are within a highly utilized area for mako sharks in the western North Atlantic. Our study emphasizes the need to implement cooperative international management

and improvement in U.S. management strategies to facilitate the recovery of the North Atlantic shortfin mako stock. In addition, we highlight the need to develop a deeper understanding of offshore wind farms' effect on mako sharks and other highly migratory species.

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PREFACE

The following thesis has been submitted in manuscript format and is composed of two separate manuscripts being prepared for publication. The first chapter of this thesis corresponds to the first manuscript, "Who's Minding the Makos? Applications of habitat use and movement patterns for management of shortfin mako shark populations in the North Atlantic Ocean", following the formatting guidelines of the journal *Fisheries Research*. The second chapter of this thesis corresponds to the second manuscript, "Intersection of offshore energy exploration and habitat of a highly migratory top level predator in the North Atlantic Ocean", following the formatting guidelines of the journal *Renewable Energy*.

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CHAPTER 1

Who's minding the makos? Applications of habitat use and movement patterns for management of shortfin mako shark populations in the North Atlantic Ocean

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Abstract

The shortfin mako shark is a highly migratory species known for highly variable movement patterns characterized by long seasonal migrations coupled with high site fidelity under certain environmental conditions (Bryne et al., 2019). Shortfin mako shark migrations cross multiple boundaries, leaving shortfin mako sharks exposed to highly variable fishing efforts (Campana et al., 2016). The absence of effective large-scale mako management coupled with overexploitation have resulted in the IUCN classifying the North Atlantic shortfin mako stock as endangered (Rigby et al., 2019). We used a large satellite tracking dataset of 60 mako sharks tagged off the coast of the U.S. and Mexico to investigate shortfin mako movement patterns relative to jurisdictional boundaries in the western North Atlantic and the Gulf of Mexico. In addition, we assessed the ability of current U.S. management strategies to provide the protection needed for the North Atlantic shortfin mako shark population to recover. Thirty-six sharks tagged off the U.S. provided 10,414 detections, and 24 sharks tagged off Mexico provided 8,407 detections. As a whole, the 60 sharks visited 27 different Exclusive Economic Zones in the North Atlantic Ocean. Sharks tagged off the U.S. showed demographic-based, behavioral and seasonal influences, in their transboundary movements. Sharks tagged off of Mexico showed less variability in their transboundary movements as a response to season and movement behavior. Current U.S. management strategies provide insufficient protection for the North Atlantic shortfin mako stock. Our study emphasizes the need to implement cooperative international management and improvement in U.S. management strategies to facilitate the recovery of the North Atlantic shortfin mako stock.

Abbreviations

EEZ – Exclusive Economic Zone

EFHs – Essential Fish Habitats

GOM – Gulf of Mexico

HMS – Highly Migratory Species

ICCAT – International Commission for Atlantic Tunas

IUCN – International Union for Conservation of Nature

MPAs – Marine Protected Areas

NMFS – National Marine Fisheries Service

NOAA – National Oceanic and Atmospheric Administration

SSM – State-space model

U.D. – Utilization Distribution

WNA – Northwest Atlantic

1. Introduction

The shortfin mako shark (*Isurus oxyrinchus*, hereafter: mako) is a member of the Lamnidae family and known for being one of the fastest and most active fish in the global oceans (Casey and Kohler, 1992; Compagno, 2001). Mako sharks are considered a single stock across the North Atlantic Ocean Basin (Natanson et al., 2020). However, recent tracking studies suggest that the Northwestern mako stock my consist of sub-stocks between the Northwest Atlantic (WNA) and Gulf of Mexico (GOM) (Gibson et al., 2021; Vaudo et al., 2017). Mako sharks are endothermic, which allows for their enhanced swimming, visual, central nervous system, and digestive functioning (Compagno, 2001). As a highly migratory species (HMS), mako sharks are characterized by high variable movement patterns and inhabiting neritic and oceanic zones of temperate and tropic waters globally (Casey and Kohler, 1992; Compagno, 2001; Rogers et al., 2015; Vaudo et al., 2017).

As a result of their highly migratory behavior, mako sharks have shown transboundary seasonal variability in their migrations (Campana, 2016). Their movement patterns are closely associated with several environmental variables including, sea surface temperature, productivity levels, and prey availability (Casey and Kohler, 1992; Rogers et al., 2015; Vaudo et al., 2017). In the WNA, mako sharks occupy waters along the continental shelf in the northern portion of the Gulf Stream between Cape Hatteras, North Carolina, and the Grand Banks, Canada, in the warmer summer months in early fall (Vaudo et al., 2017). As it gets cooler through late fall and winter, makos move off shelf waters and travel south, aggregating around Cape Hatteras (Vaudo et al., 2017).

In the Gulf of Mexico (GOM), mako sharks show general seasonal variability in their movements. Makos spend winter in the southern portion of the GOM and move North towards the U.S. EEZ in the Summer (Gibson et al., 2021; Rooker et al., 2019). However, these seasonal movements are substantially less prominent than those in the WNA, probably because of the consistency in oceanographic properties in the GOM compared to the WNA (Bryne et al., 2019; Vaudo et al., 2017).

Individual variations and a lack of understanding of demographic differences in mako shark seasonal migrations relative to jurisdictional boundaries contribute to the insecurity of global mako management efforts (Gibson et al., 2021; Natanson et al., 2020; Vaudo et al., 2017). Further, growing evidence suggests that makos display more resident behavior under certain environmental conditions (see e.g., Bryne et al., 2019; Francis et al., 2018). Therefore, an improved understanding of demographics-based seasonal mako shark occupancy and variability of movement behavior among jurisdictional boundaries would enable more effective large-scale management and assessment of mako shark stocks (Natanson et al., 2020).

Although few fishing nations have defined shark fisheries, mako sharks are a common bycatch species in pelagic fisheries due to their targeted prey species, large body size, and migratory behavior (Bryne et al., 2017; Campana, 2016; Vaudo et al.,2017). Mako sharks are retained in large numbers globally due to high fishing effort, their popularity as sportfish, and their high economic value (Bryne et al., 2017; Campana, 2016; Gallagher, 2014; Holts and Bedford, 1993). The combination of high retention rates and low-productive life-history traits leave mako sharks susceptible to severe overexploitation (Block et al., 2011; Bryne et al., 2017; Campana, 2016;

Gallagher et al., 2014). As of 2019, the International Union for Conservation of Nature (IUCN) has listed makos as endangered in their Red List for threatened species (Rigby et al., 2019).

There is growing concern regarding the North Atlantic Ocean mako shark stock in particular. Overexploitation coupled with international mismanagement has led to substantial declines in the population (Sims, Mucientes, and Queiroz, 2018). The North Atlantic mako shark stock is overfished and currently experiencing overfishing (ICCAT, 2019). In the absence of fishing pressure, stock assessments show that the mako shark spawning stock fecundity will continuously decline until 2035 (ICCAT, 2019). The most optimistic and likely unrealistic models project mako shark spawning stock fecundity to reach maximum sustainable yield in 2070 (ICCAT, 2019). These continued declines result from immature sharks enduring the highest fishing efforts (Bryne et al., 2017; ICCAT, 2019).

To mitigate the population decline in the North Atlantic mako stock the International Commission for the Conservation of Atlantic Tunas (ICCAT) recommended decreasing the quota for makos, specifically to rebuild the stock by 2040, the retention of mako sharks should be prohibited (ICCAT, 2017; Sims, Mucientes, and Queiroz). Objections to this recommendation led ICCAT to a new proposal of releasing live sharks for commercial fisheries and increased length restrictions for recreational fisheries (ICCAT, 2017; Sims, Mucientes, and Queiroz). However, these restrictions are not legally binding unless individual nations adopt the recommendations as policies, ultimately resulting in uncoordinated international management (Sellheim, 2020).

In the absence of cooperative international management, HMS that undergo frequent transboundary movements are among the most vulnerable to overexploitation (Calich, Estevanez, and Hammerschlag,2018; Pacoureau et al., 2021). Yet, the allocation of management responsibility for highly migratory sharks is lacking, challenging the ability to successfully manage HMS on a global scale (Campana, 2016). Mako sharks, in particular, have been historically overlooked by management, contributing to their overexploitation in pelagic fisheries (Baum et al., 2003; Bryne et al., 2017; Musick et al., 2000).

Despite studies showing makos visiting up to 17 different Exclusive Economic Zones (EEZs), no single governing body oversees international mako management (Game et al., 2009; Sellheim, 2020; Vaudo et al., 2017). Thus, several governing bodies including, the Convention on International Trade in Endangered Species, Regional Fisheries Management Organizations, Convention on Migratory Species, Food and Agriculture Organization, and the 1995 United Nations Fish Stock Agreement, independently contribute to the management of makos (Game et al., 2009). However, the uncoordinated activities of each body lead to asynchronous and ultimately ineffective international mako management.

There is a high degree of variability of mako shark conservation efforts in the WNA and GOM due to the lack of coordinated international shark management. Fishing nations are only required to abide by the laws set by their respective nation's government (Sellheim, 2020). However, relatively few fishing countries prioritize shark conservation and implement management strategies for mako sharks (Sellheim, 2020). Further, many countries that implement shark management lack a critical understanding of mako shark movements and habitat use to manage the species at the appropriate spatial scale (Francis et al, 2018; Sellheim, 2020).

The U.S. National Marine Fisheries Service (NMFS) has implemented several management strategies dedicated to mako shark conservation. These management strategies include gear restrictions, designating essential fish habitats, spatial area closures, and the adoption of ICCAT's recommendations. However, the difficulties that coincide with accumulating a representative sample of HMS habitat use and distributions challenges the ability to evaluate how U.S. mako management contributes to rebuilding the North Atlantic mako stock.

Essential fish habitats (EFHs), developed by the National Oceanic and Atmospheric Administration (NOAA), are species-specific boundaries designed to define biologically critical habitats, such as areas utilized for spawning, feeding, or growth (Federal Register, 2017). EFH boundaries are defined with fishery-dependent data and literature reviews to estimate species distributions (Federal Register, 2017). However, due to a lack of data, EFH for mako sharks does not consider habitat suitability models, or demographic (NFMS, 2017).

Marine protected areas (MPAs) are a second spatial management mechanism to protect the marine environment, including some shark species. MPAs have recently expanded into further offshore pelagic waters (Lubchenco and Grorud-Colvert., 2015). However, there are several concerns regarding the effectiveness of large MPAs located further offshore (Lubchenco and Grorud-Colvert., 2015; White et al., 2017). First, the fixed nature of MPAs challenges their ability to protect migratory species, especially those that follow targeted fish species (Campana, 2016). Second, management must develop MPAs in an area with adequate funding for enforcement (Game, 2009; White, 2015). Finally, the size and placement of MPAs are of critical importance. Incomplete coverage of a HMS track, especially biologically important portions, can be detrimental to the population (White et al., 2017). Detailed information about demographic-based mako shark movement behavior relative to established spatial management boundaries, such as EFHs and MPAs, in U.S. waters will provide insight for future spatial management improvements.

In March of 2019, NFMS adopted ICCAT's recommendations and passed Amendment 11 to the 2006 Consolidated Fisheries Management Plan (Federal Register, 2019). The passing of Amendment 11 bans the retention of live mako sharks in commercial fisheries and increases the size limits for legal retention of mako sharks in recreational fisheries (Natanson et al., 2020). For the first time, minimum lengths to legally retain mako sharks in recreational fisheries are differentiated by sex (Natanson et al., 2020). To legally keep a mako shark before Amendment 11, it had to be a minimum fork length of 137.2 cm (Federal Register, 2019). Under Amendment 11, mako sharks now must have a minimum fork length of 180.3 cm and 210.8 cm for males and females, respectively (Federal Register, 2019; Natanson et al., 2020). The goal of Amendment 11 is to reduce male mako landings by 47%, female landings by 78%, and total landings by 68% (Federal Register, 2019). However, considering the novelty of the amendment, the effectiveness of these new restrictions is unknown.

Recreational fishing generally occurs in nearshore habitats within state waters and can have substantial effects on fish stocks (Hartill et al., 2020). As HMS occupancy spans across multiple Regional Fishery Management Council boundaries, Atlantic HMS, like the mako shark, are managed by NMFS, and Regional Fishery Management Councils must adhere to their regulations (NMFS, 2006). However, mako sharks occupy both oceanic and nearshore habitats (Francis et al., 2018). There has been an increase in anecdotal reports of mako sharks in state waters due to the installation of the Block Island Wind Farm (ten Brink and Dalton, 2018). Yet, the magnitude of concern which Regional Fishery Management Councils and individual states must have for mako sharks is unclear.

This study uses satellite telemetry from mako sharks in the WNA and GOM from a dataset that has generated over 58,000 reported locations from 85 sharks over seven years. This dataset is indicative of the large-scale movements and habitat use of makos in the WNA and GOM. It constitutes the largest fisheries-independent database on the movements of mako sharks. Coupling our tagging data with demographic information, including sex, retainability status, and reproductive status, we can provide an in-depth understanding of makos' demographic-based spatial ecology in the North Atlantic Ocean relative to jurisdictional boundaries and current mako management strategies. Specifically, we will use the large dataset to quantify the occurrence of mako sharks among jurisdictional waters, EFHs, MPAs, regional and state waters, patterns among demographics, and predict how Amendment 11 modifies retention of legal-sized makos in recreational fisheries.

The goals of this study are to a) Quantify the importance of waters among jurisdictions in the WNA and GOM for mako sharks; b) Identify jurisdictional waters where core areas of mako shark activity occur; c) Examine seasonal variation in habitat use of mako sharks among jurisdictional boundaries; d) Identify jurisdictional waters where "resident" behavior of mako sharks occur; e) Quantify the importance of waters among U.S. states for mako sharks; f) Examine the overlap of mako shark core areas of activity and EFHs and MPAs g) Predict potential impacts of Amendment 11 on retention of mako sharks in U.S. recreational fisheries

2. Methods

2.1. Tagging and Data Collection

To investigate mako shark movements in the WNA and GOM, we caught and tagged sharks in three locations via rod and reel. Two tagging locations were along the U.S. East coast in the vicinity of Block Island, Rhode Island (~41.16°N, 71.58°W), and Ocean City Maryland (~38.10°N, 74.50°W). The third location was off the Yucatan Peninsula, around Isla Mujeres, Mexico (~21.29°N, 86.29°W). We either brought the sharks onboard or secured them along the side of the boat for tagging (Bryne et al., 2017& 2019; Vaudo et al., 2017). We covered the shark's eyes with a wet towel to reduce stress and placed a saltwater hose in their mouth to irrigate the gills of sharks brought on board (Bryne et al., 2017& 2019; Vaudo et al., 2017). We then identified the shark's sex and measured its length before releasing it (Bryne et al., 2017& 2019; Vaudo et al., 2017).

We used Smart Position Only Transmitters (SPOT; Wildlife Computers, Redmond WA) that communicate with the Argos satellite network (www.argos-system.org) and transmit the shark's location when the dorsal fin breaks the water's surface (Bryne et al., 2019; Vaudo et al., 2017). Argos locations are associated with observational (Jonsen, Flemming and Myers., 2005). There are six location class error radii 3, 2, 1, 0, A, B, that span from < 350m to >1000m, respectively (Freitas et al., 2008). Location class Z detections were omitted from the analysis as they represent invalid locations (www.argos-system.org).

2.2. Data Pre-Processing

2.2.1. State-Space Model

If not accounted for, tagging studies may be subject to tagging location biases, where the animals spatial use may be biased towards the tagging site, and differences in swimming behavior as a response to tagging (Block et al., 2011, Vaudo et al., 2017). This is especially true for tracks with shorter durations, because as time passes animals can disperse from their tagging location and show more natural movement behavior and habitat use (Harrison et al., 2018). Rooker et al. (2019) found that tracks lasting 150 days or greater show biologically representative animal movement behavior. Of the tracks used in this study, 73% exceeded 150 days, and the average tracking duration of the population was 276 days (Supplementary table 1).

Though the longevity of our dataset assists in mitigating tagging location and post-release behavior biases, we further accounted for these biases by excluding the first 5 days of each track. Previous work (Vaudo et al., 2017) suggests removing the first ten days of each track to account for post-release behavior and allow for dispersal from sampling location, we only omitted the first five days. The sharks in this study dispersed on average over 200 km from the tagging location within the first five days since being tagged (Figure S1). Further, Vaudo et al. (2016) found minimal impact of tagging on mako swimming behavior, therefore excluding the first five days of the track is sufficient to account for post-release behavior.

Sharks that are more surface-oriented are detected more frequently and may influence population-level distribution patterns as a consequence of SPOT tags only communicating with the Argos satellite system when the dorsal fin breaks the surface. Thus, potential differences in surface behavior may bias the population-level spatial distribution towards more surface-oriented sharks (Block et al., 2011; Freitas et al., 2008). To mitigate this bias, we used a state-space modeling (SSM) approach. SSMs to account for ARGOS observation error, irregular detections, and reduce autocorrelation (Gibson et al., 2021; Jonsen and Patterson., 2020). We used the 'foiegras' package in Rstudio to fit a simple random walk state-space model (SSM) to the location data (Jonsen and Patterson., 2020; R Core Team, 2019). Because sharks in this study reported on average four times per day, we used a 12-hour timestep to produce two daily location estimates.

The SSM uses a speed-distance angle filter to predict the most probable trajectory and omit obvious outliers (Jonsen and Patterson., 2020). Because the turning angle element of the SSM does not consider time between successive location estimates, it may remove valid points in data associated with long gaps. Our data was associated with long gaps; therefore, we forewent using the turning angle element of the SSM. We set the max speed for the sharks to 2.5 m/s. We developed all tracks simultaneously. We removed tracks less than 20 days in duration before fitting the SSM and filtered out fitted location estimates associated with gaps that exceeded ten days in time, as short tracks and long data gaps may lead to flawed model fits (Bailey et al., 2008; Block et al., 2011).

2.2.2. Developing Mako Core Areas

We used a bivariate normal kernel density analysis to estimate utilization distributions (U.D.) for different demographics of the population to identify demographic-based highly utilized areas for mako sharks in the WNA and GOM. We first developed individual U.D.s for each shark using the ‘adehabitatHR’ package in R (Calenge, 2006). We used “href” as the smoothing parameter (h), which uses the reference bandwidth in the calculation (Calenge, 2019). We constructed the U.D.s over a 0.05° x 0.05° grid, using the \`marmap\` package in R to set boundaries for inaccessible locations (Vaudo et al., 2017). We then averaged the U.D.s to acquire population-level U.D.s to avoid potential bias towards sharks that report more frequently (Shimada et al., 2017). Utilization distribution isopleths are percent density contour lines that contain a defined proportion of the population (Calenge, 2019). Core areas are areas that the animal spends the majority of their time (Vander Wal & Rogers, 2012). We defined the 50% U.D. isopleth as the core area, because it represents where 50% of the location data is located within a relatively small periphery (Simpfondorfer., 2012; Vander Wal & Rogers, 2012; Vaudo et al., 2017).

2.3. Quantifying the importance of waters among jurisdictions in the WNA and GOM for mako sharks

To estimate the jurisdictions with the highest proportion of mako shark location estimates, we calculated the relative proportion of location estimates per jurisdictional EEZ and high seas in the WNA and GOM in a similar fashion as Rooker et al. (2019). First, we imported mako shark location estimates derived from the SSM in ArcGIS pro, version 2.6.3 (hereafter, GIS). We then imported the EEZ shapefiles, retrieved from https://www.marineregions.org/, into GIS. Previous work identified differences in movement behavior between mako sharks in the GOM and WNA (see e.g., Vaudo et al., 2017). Therefore, we subset the population by tagging country to account for potential variability in migratory behavior. We then broke down the location estimates per EEZ by sex and reproductive status at the time of tagging.

We classified sharks as immature, subadult, or mature using the updated growth parameters derived by Natanson et al. (2020). Immature male sharks have a fork length less than 173 cm, subadult male sharks have fork lengths between 173 cm and 187 cm, and mature male sharks have a fork length greater than 187 cm (Natanson et al., 2020). Immature female sharks have fork lengths less than 263 cm, subadult females have fork lengths between 263 cm and 291 cm, and mature females have fork lengths greater than (Natanson et al., 2020).

2.4.Identifying demographic-based differences in core areas of mako shark activity among jurisdictional waters

Previous work has identified demographic-based segregation in shark habitat use (Natanson et al., 2020). However, the degree to which mako sharks display demographic-based habitat use is known. To determine if makos in this study segregate their core habitat use by demographics, we developed mako shark core areas partitioned by sex and reproductive status. We then calculated the proportion of the mako shark core areas located within each EEZ to identify demographic differences in highly utilized jurisdictional waters by makos.

To quantify the proportion of the core area within EEZs, we first uploaded the mako shark core area into GIS as a polygon shapefile. We then calculated the total area of the core area in kilometers. Next, we segregated the core area by the EEZ that it overlapped with and calculated the individual areas of each portion in square kilometers. To calculate the proportion of the core area by EEZs, we divided the area of each segment of the core area by the total area of the core area and multiplied the quotient by 100.

2.5.Identifying Jurisdictional waters where "resident" behavior of mako sharks occur

We estimated mako shark's movement behavior throughout their tracks using the move persistence model found in the 'foiegras' package in R (Jonsen and Patterson, 2020; R Core Team, 2019). The move persistence model identifies portions of the track where the animal shows more resident behavior, characterized by slower swimming speeds and frequent turning and transient behavior, characterized by faster swimming speeds and infrequent turning (Byrne et al., 2019). The model does so by identifying differences in turning angles and travel speeds to estimate behavior along a continuum between 0-1 (Jonsen et al., 2019). When move persistence approaches 0, this signifies low movement persistence, indicating more resident behavior (Jonsen et al., 2019). Conversely, when move persistence approaches 1, this signifies high movement persistence, indicating more transient behavior (Jonsen et al., 2019).

To estimate the probability of a random shark occurring within an EEZ in the WNA and GOM as a function of movement behavior, we ran a general additive model (GAM) fit with a multinomial logistic regression family, following Harrison et al. (2018) and Spaet et al. (2020b). We fit the GAMs using the 'mgcv' package in R (Wood, 2011). As a fixed effect, we included the move persistence index derived from the SSM fit with a cubic regression spline. To account for individual variation in movement behavior, we included individual I.D. as a random effect in the model

(Harrison et al., 2018). We grouped EEZs with less than 1% of the total location estimates as an "Other" category (Harrison et al., 2018).

We developed models according to tagging country to account for potential regional differences in movement behavior (see e.g., Bryne et al., 2019; Vaudo et al., 2017). We then ran models for the entire sample, in addition to models divided by sex. However, we did not run models including reproductive status for males because the substantial differences in sample size between reproductive status may influence the interpretation of the model's results (Spaet et al., 2020a). In addition, we grouped Venezuela and Honduras into the "other" category for males tagged off Mexico because there was not enough data within these countries to produce robust model predictions for them individually.

2.6. Examining seasonal variation in habitat use of mako sharks within jurisdictional waters

To estimate the probability of a random shark occurring within an EEZ in the WNA and GOM as a function of the month of the year, we used a similar approach to estimating mako movement behavior among EEZs. We used a multinomial distributed GAM from the 'mgcv' package to evaluate the effect of month of the year and the probability of occurrence within an EEZ (Wood, 2011). We included the month of the year as a fixed effect fit with a cyclic cubic regression spline to adhere to mako shark's annual migration patterns (Casey and Kohler, 1992; Harrison et al., 2018). We had individual I.D. as a random effect term to avoid differences in individual variation in migration patterns influencing results (Harrison et al., 2018). We grouped EEZs with less than 1% of the total location estimates as an "Other" category (Harrison et al., 2018). We developed models segregated by tagging country for the whole population and males and females. We used the meteorological definitions of seasons whereby Spring corresponds to March – May, Summer corresponds to June-August, Fall is represented by September-November, and Winter is represented by December-February.

2.7. Quantifying the importance of waters among U.S. states for mako sharks

To determine the U.S. state waters that mako sharks most frequently occurred in, we followed a similar procedure described in "2.3. *Quantifying the importance of waters among jurisdictions in the WNA and GOM for mako sharks."* However, to localize the analysis, only location estimates made in U.S. waters were considered. We imported the U.S. State Boundary shapefile, retrieved from https://marinecadastre.gov/data/, into GIS. We then calculated the relative proportion of location estimates within each state's jurisdictional boundary. We broke down the location estimates per boundary by sex and reproductive status at the time of tagging.

2.8. Examining the overlap of mako shark core areas and EFHs and MPAs

To assess the ability of EFHs and MPAs to protect mako sharks adequately, we used GIS to calculate the percent of the U.S. mako core areas partitioned by tagging county, sex, and reproductive status, that overlapped with the shortfin mako shark EFHs and MPAs in the WNA and GOM in GIS. First, we clipped the mako shark core area to the U.S. EEZ. We then calculated the total area (km) of the U.S. core area, and the area (km) overlapped with EFHs in the WNA and GOM. Finally, we divided the area of the overlap by the total area of the U.S. core area and multiplied the quotient by 100. We repeated these steps to calculate the percent of the U.S. core area that overlaps with MPAs capable of protecting mako sharks in the WNA and GOM. We defined MPAs as being capable of protecting mako sharks as those established to conserve natural heritage and sustainable production that enforce fishing restrictions. The EFH and MPA shapefiles were imported into GIS from https://www.habitat.noaa.gov/protection/efh/newInv/index.html and https://marineprotectedareas.noaa.gov/dataanalysis/mpainventory/ respectively.

2.9. Predict theoretical impacts of Amendment 11 on retention of mako sharks in U.S. recreational fisheries

The goal of Amendment 11 is to reduce the fishing mortality of mako sharks by increasing the amount of time they have before they are vulnerable to fishing pressure. To test the plausibility of this goal, we used a reparametrized von bertalanffy growth function to calculate the number of days that elapsed between tagging and when a shark was considered retainable by pre-and post-Amendment 11 criteria.

The von bertalanffy growth equation is a common function used to validate age at length for many fish species (Cailliet et al., 2006). Traditionally it calculates length at time by:

$$L_t = L_{inf} \left(1 - e^{-kt(t-t_0)}\right)$$

However, as suggested by Cailliet et al. (2006) and Rosa et al. (2017) we used a reparametrized Von Bertalanffy Growth equation that replaces t_0 with L_0:

$$L_t = L_{inf} - (L_{inf} - L_0)\, e^{-kt}$$

L_t represents length as a function of time (t), L_{inf} is the asymptotic length, L_0 is the size at birth, and k is the rate constant (Cailliet et al., 2006). We then rearranged the growth function to predict the day of the track as a function of length:

$$t = \left(\frac{1}{k}\right) * (LN\ (L_{inf} - L_0) / (L_{inf} - L_t))$$

We used the growth parameters derived from Rosa et al. (2017), where $L_0 = 63$ cm for males and females, $L_{inf} = 241.8$ cm and 350.3 cm, and k = 0.136 and 0.064 for males and females, respectively. First, we applied the rearranged growth function to each shark's track to calculate the day the shark reached the length corresponding to pre-Amendment 11 minimum lengths for legal retainment (137.2 cm for males and females). We then repeated the procedure using the growth function to calculate the day that the shark reached the length corresponding to post-Amendment 11 minimum lengths for retainment (180.3 cm and 210.8 cm for males and females, respectively). To mitigate the potential bias towards longer tracks, we resampled the data to ensure that a single track could not account for more than 10% of the data. We then used a Welch's t-test to test the hypothesis that the difference in the number of days makos take to grow to retainable lengths under pre-amendment 11 standards is statistically different than under post-Amendment 11 standards.

3. Results

3.1. Tagging and Data Collection

We obtained 58,574 (Females = 24,371, Males = 34,204) usable detections from eighty-five sharks (Females = 35, Males = 50) equipped with SPOT tags. We tracked the sharks from March 2013 to October 2019, with tracking duration for the sharks ranging from 4 to 754 days. Female sharks ranged from 89-252 cm in fork length, and males ranged from 117-220 cm.

All U.S. females (n = 18) were immature when tagged. The majority of males tagged in the U.S. (n = 33) were immature when tagged (n = 24), five of the males were subadults, and four were mature. Like the females tagged off the U.S., all females tagged off Mexico (n = 18) were immature. Interestingly, we tagged only one immature male off Mexico, five were subadult, and 11 were mature.

3.2. Data Pre-Processing

3.2.1. State-Space Modeling

The simple random walk SSM provided 18,821 (Females = 8,624, Males = 10,197) location estimates from 60 sharks (Females = 28, Males = 32) (Figure 1). We developed Location estimates for every 12 hours, and tracking duration ranged from 21- 746 days. Removing short tracks and omitting one track that did not converge in the SSM removed many original tracks.

All tracks estimated for females tagged in the U.S. (n = 13) and Mexico (n = 15) were immature. The SSM estimated tracks from 23 males tagged in the U.S., 17 of which were immature, four were subadults, and two were mature. All tracks estimated for males tagged off Mexico (n = 9) were either subadult (n = 4) or mature (n = 5).

3.3. Quantifying the importance of waters among jurisdictions in the WNA and GOM for mako sharks

3.3.1. Mako Sharks Tagged off of the U.S.

To determine the EEZs most frequently visited by tagged mako sharks, we calculated the relative proportion of location estimates within EEZs in the WNA. Our results show that the mako sharks tagged in U.S. waters visited 17 different EEZs (Table 1). However, 97% of the location estimates were within U.S., International, and Canadian waters. Over 50% of the location estimates made by 36 mako sharks tagged in U.S. waters remained in U.S. waters (57.4%). The majority of the location estimates within the U.S. EEZ were from immature males (56.9%), followed by immature females (27.9%), subadult males (8%), and mature males (7.18%). About 30% of the location estimates were made in high seas by 22 sharks. Of the location estimates in high seas, the majority were from immature males (40%) and immature females (37%), followed by subadult males (16.5%) and mature males (6.4%). Canadian waters contained about 10% of the location estimates from 17 sharks. Following the same pattern as the U.S. and high seas, immature males had the highest proportion of location estimates in Canadian waters (51.3%), Immature females were responsible for 39.5% of these location estimates, subadult and mature males had far fewer location estimates (7.5% and 1.7% respectively).

3.3.2. Mako Sharks Tagged off Mexico.

Our results show that mako sharks tagged off Mexico visited 20 different EEZs. Many location estimates (97.7%) were in Mexican, U.S., Cuban, Venezuelan, and Honduran waters (Table 2). The majority of the location estimates (~80%) were within the Mexican EEZ from 23 sharks. Immature females were responsible for the most significant proportion of location estimates in the Mexican EEZ (66.8%), followed by mature males (20.4%) and subadult males (12.8%). The U.S. waters contained 9.4% of the location estimates from 16 sharks. Of the U.S. location estimates, immature females were responsible for 47.5%, while 29.1% and 23.4% were from subadult and mature males, respectively. About 5% of the location estimates were within the Cuban EEZ. However, interestingly the same number of sharks were within the Cuban EEZ as the U.S. EEZ. Of the location estimates within the Cuban EEZ, the vast majority (82.3%) were from immature females, followed by mature males (9.8%) and subadult males (7.9%). Less than 2% were within the Venezuelan and Honduran EEZs made by two and six sharks, respectively. All the location estimates in Venezuelan waters were from immature females. Of the location estimates within the Honduran EEZ, 83.8% were from immature females, and 16.19% were from mature males.

3.4. Identifying demographic-based differences in core areas of mako shark activity among jurisdictional waters

3.4.1. Mako Sharks Tagged off the U.S.

3.4.1.1.Immature Females.

The immature female's core area for sharks tagged in U.S. waters was restricted to the U.S. EEZ, along the U.S. East Coast (Figure 3). The core area extends from 33.8°-42.7°N and from the U.S. East Coast to 68.3°W (Figure 2A).

3.4.1.2. Immature Males.

The core area for immature males tagged in U.S. waters extended from 35.3°-42.1°N and from the U.S. East Coast to 68.5°W (Figure 2B). Like the immature females, this core area was located entirely within the U.S. EEZ, along the U.S. East Coast (Figure 3).

3.4.1.3.Subadult Males.

Subadult males tagged off the U.S. had two distinct core areas (Figure 2C). The larger of the core areas extended from 30.3°-40.2°N and from the U.S. East Coast to 67.4°W. The smaller of the two core areas spread from 42°-45.1°N and 61.3°-57.6°W. Although the most significant proportion of the core areas are within the U.S. EEZ (65.8%), the core areas overlap with three other different jurisdictional boundaries including, high seas (23.9%), Canada (10%), and Bermuda (< 1%) (Figure 3).

3.4.1.4.Mature Males.

Like the subadult males, mature males tagged in the U.S. showed two distinct core areas in the WNA (Figure 2D). The larger core area extended along the U.S. East Coast from 35.9°-44.2°N and from the U.S. East Coast to 65.6°W. The second core area was located further offshore and extended from 41.5°-46.4°N and 49.9°-43.9°W. This core area overlapped with the U.S. EEZ (60.3%), high seas (33.5%), and the Canadian EEZ (6.2%) (Figure 3).

3.4.2. *Makos Tagged off Mexico.*

3.4.2.1.Immature Females.

Immature females tagged off Mexico had one core area off the Yucatan Peninsula extending from 18.8°-24.6°N and 88.5 – 85.3°W (Figure 5A). The majority of the core area was within the Mexican EEZ (81%), with a smaller proportion (19%) overlapping with the Cuban EEZ (Figure 5).

3.4.2.2. Subadult Males.

There were three different core areas for subadult males tagged off Mexico (Figure 4B). The larger core area was off of the Yucatan Peninsula, extending from 20.4°-24.8°N and 90.7°-85.2°W. The second core area spanned from 24.3°-25.1°N and 84.3°-83.4°W. The third core area occupied the Southwestern portion of the GOM along the Mexican East Coast, extending from the coastline to 20.2°N and 93.6°W. The subadult male core area overlaps with three different EEZs, including Mexico (87%), Cuba (9.8%), and the U.S. (3.3%) (Figure 5).

3.4.2.3. Mature Males.

There was only one core area for mature males tagged off Mexico (Figure 4C). This core area was also located off the Yucatan Peninsula, extending from 20.8°-24.5°N and 88.5°-85.8°W. The mature male core area overlapped with the Mexican (97.6%) and Cuban (2.4%) EEZs (Figure 5).

3.5. Identifying Jurisdictional waters where "resident" behavior of mako sharks occur

We used a move persistence model to estimate mako swimming behavior throughout their tracks (Figure 6). We used a multinomial distributed GAM to estimate the effect of move persistence on the probability of occurrence for a randomly selected shark among EEZs in the WNA and GOM.

3.5.1. Mako sharks tagged off the U.S.

Results of the GAM were similar for the total sample tagged off the U.S. and male sharks tagged off the U.S. (Figure 7A and C). There is a high probability of occurrence in the U.S. EEZ (>75%) for a wide range of move persistence (~0-0.77), indicating that makos display both residential and transiting behavior within the U.S. EEZ. The probability of occurrence decreases in U.S. waters, but increases in international and "other" waters as move persistence increases beyond 0.8.

Female mako sharks tagged off the U.S. had more variability in the effect of move persistence on the probability of occurrence (Figure 7B). Females had the relatively highest likelihood of occurrence within the Canadian and U.S. EEZ under low move persistence conditions. Like males, as move persistence increased, the probability of occurrence decreased in Canadian and U.S. waters and increased in International and "other" waters.

3.5.2. Makos tagged off Mexico

Results of GAM indicated that the whole population of makos tagged off Mexico, females, and males all showed similar trends in probability of occurrence among EEZs as a response to move persistence (Figure 8A, B, and C). Overall, the Mexican EEZ sustained the highest likelihood of occurrence for resident and transient behavior. Notably, the probability of occurrence increases within the Cuban EEZ and decreases within the Mexican EEZ for the total sample and females as move persistence increases. However, these variations are marginal as makos continued to have the highest likelihood of occurrence within Mexican waters (~ 80%). Males showed less variation in the probability of occurrence among EEZs relative to females.

3.6. Examining seasonal variation in habitat use of mako sharks within jurisdictional waters

We used a multinomial distributed GAM to estimate the effect of the month of the year on the probability of occurrence for a randomly selected shark within EEZs in the WNA and GOM.

3.6.1. Mako sharks tagged off the U.S.

For the entire sample of sharks tagged off the U.S., the probability of occurrence was highest in the U.S. EEZ during the spring (March-May) through summer (June-August) (Figure 9A). During the fall (September-November) probability of occurrence decreased in U.S. waters and increased in high seas. This trend continued into the winter (December - February), where the likelihood of occurrence was highest in high seas. There was a slight increase in mako shark occurrence in Canadian and "other" waters during the fall, which continued into the winter for the "other" countries. However, overall, there was minimal seasonal variation in mako shark occurrence in Canadian and other EEZs.

Females showed a higher degree of variation in seasonal movements among jurisdictional waters (Figure 9B). During the spring, probability of occurrence was relatively high in U.S. and "other" waters. Mako occurrence decreased in U.S. and "other" waters through the summer and increased Canadian waters, and to a lesser degree high seas. During the fall, the probability of occurrence remained the highest in International and Canadian waters, began increasing in "other" waters and continued to decrease in U.S. waters. Occurrence then decreased in Canadian and high seas and increased in U.S. and "other" waters through the winter.

Male sharks tagged in U.S. waters displayed similar seasonal trends as the total sample (Figure 9C). During the late winter and early spring, the probability of occurrence for males was highest in high seas, followed by a peak in occurrence in the U.S. EEZ during the Summer through early fall and early winter. Throughout the winter, the probability of occurrence increased in high seas. Like the total sample, there was little seasonal variability across jurisdictional waters in Canada, except for a slight increase in late fall, or in "other" waters, except for an increase in occurrence in the spring.

3.6.2. Mako sharks tagged off Mexico

All three models ran for sharks tagged off Mexico yielded similar results (Figure 10). Overall, there was substantially less seasonal variation in movements across EEZs for makos tagged off the Yucatan Peninsula relative to makos tagged off the U.S. The highest probability of occurrence remained within the Mexican EEZ for all seasons, with a meager chance of occurrence for all other jurisdictional waters considered in the model. There was slightly more variability in occurrence for female sharks than males (Figure 10B and C). However, this may be due to the differences in sample sizes between the two demographics.

3.7. Quantifying the importance of waters among U.S. states for mako sharks

Less than 1% of the location estimates made by tagged mako sharks in U.S. waters were within state waters (Table 3). The majority of the location estimates from the few sharks that did visit state waters were in Rhode Island and Massachusetts. Interestingly, immature sharks contributed all the location estimates within state waters, primarily immature males, except for South Carolina.

3.8. Examining the overlap of mako shark core areas and EFHs and MPAs

3.8.1. EFHs

The shortfin mako shark EFH overlapped with about half of the mako shark core areas. Over half of the core areas from the U.S. tagged immature females (51.1%), immature males (61.1%), and mature males (51.5%) overlapped with the EFHs (Table 5, Figure 11). However, the EFHs overlapped with only 33.6% of the U.S.-tagged subadult male core areas. Notably, of the core areas of subadult males tagged off Mexico that fall in U.S. waters, 60.7% overlap with the shortfin mako shark EFH (Figure 11).

3.8.2. MPAs

Only core areas from sharks tagged off the U.S. East Coast overlapped with the U.S. MPAs in the WNA. Overall, there was minimal overlap between the core areas and MPAs in the WNA.

3.8.2.1. *Immature Females*.

Only 0.5% of the U.S. tagged immature female core area overlapped with MPAs (Table 4, Figure 12A). Of the MPA sites that the core area overlap, 26.4% of them prohibit commercial fishing and restrict recreational fishing, 22.6% of them restrict both commercial and recreational fisheries or have unknown restrictions, 20.8% of them restrict recreational fishing, 18.9% prohibit commercial and recreational fishing. Less than 10% prohibit commercial fishing, and restrict recreational fishing, respectively. Additionally, most MPA sites that overlap with the immature female core area are year-round (96.2%).

3.8.2.2.Immature Males.

Only 0.4% of the U.S. tagged immature male core area overlapped with MPAs in the WNA (Table 4, Figure 11B). Of the MPA sites overlapping with the immature male core area, the majority restricted commercial and recreational fishing (26.5%). Sites that prohibit commercial fishing and restrict recreational fishing constituted 23.5%, followed by 20.6% that restrict recreational fishing, 14.7% prohibited commercial and recreational fishing, 11.8% prohibited commercial fishing, 2.9% restricted commercial fishing. The majority of the MPA sites that overlapped with the immature mako shark core area were year-round (94.2%).

3.8.2.3.Subadult Males.

About 0.4% of the total area encompassed by the U.S. tagged subadult male core areas overlapped with MPAs in the WNA (Table 4, Figure 11C). The majority of the sites that overlapped with the core area prohibited commercial fishing and restricted recreational fishing (31%). About 20.7% restricted commercial and recreational fishing, 17.2% prohibited commercial and recreational fishing, 13.8% restrict recreational fishing, 12.1% prohibit commercial fishing, and 5.2% restrict commercial fishing. Like immature sharks, most of the MPAs that the subadult male core areas overlap with are year-round (98.3%).

3.8.2.4. Mature Males.

The core areas for mature males tagged in the U.S. had the lowest percent of the core area overlapping with MPAs in the WNA (0.3%) (Table 4, Figure 11C). Prohibited commercial and restricted recreational fishing sites and restricted recreational fishing sites made up the majority of sites overlapping with the core area (26.5% each). Sites that restricted commercial and recreational fishing overlapped with 23.5% and 11.8% of the sites prohibited commercial and recreational fishing. Less than 10% respectively of the core areas prohibited commercial fishing and restricted recreational fishing. The majority of the MPAs that overlapped with the mature male core areas are year-round (94%).

3.9. Predict theoretical impacts of Amendment 11 on retention of mako sharks in U.S. recreational fisheries

We hypothesized that the number of days makos take to grow to retainable lengths under pre-Amendment 11 standards is statistically different than the mean number of days makos take to grow to retainable lengths under post-Amendment 11 standards. The mean days required to grow to retainable lengths under the criteria after Amendment 11 were greater than the mean days required to grow to retainable lengths under the criteria before Amendment 11. According to a Welch's t-test this was not a statistically significant difference ($p > 0.05$, Table 6). These results do not support our hypothesis.

4. Discussion

4.1. Quantifying the importance of waters among jurisdictions in the WNA and GOM for mako sharks

The far-reaching, multinational habitat utilization of mako sharks highlights the need to develop a more comprehensive understanding of mako's transboundary movement characteristics to allocate mako management responsibilities. We used a large longitudinal tracking dataset to provide invaluable insights into mako transboundary movement patterns. Between March 2013 and October 2019, mako sharks tagged off the U.S. and Mexico visited 27 unique EEZs (including high seas) in the WNA and GOM. These results are consistent with studies that elucidate the extent of mako shark's transboundary movements (see e.g., Bryne et al., 2017; Casey and Kohler, 1992; Gibson et al., 2021; Vaudo et al., 2017) and highlight the need for international cooperative mako management.

4.1.1. Mako sharks tagged off the U.S.

Mako sharks tagged off the U.S. visited numerous EEZs covering an extensive portion of the WNA. Their movements ranged as far north as Canada, and as far South as Venezuela. These far-reaching movements crossed multiple jurisdictional boundaries, all of which vary in their mako management strategies. Our results also imply that U.S., the high seas, and Canadian waters may hold biologically important habitats for makos. There is also high degree of commercial and recreational fishing efforts within these regions, suggesting that there is a high likelihood of mako sharks and fishing efforts to overlap (Vaudo et al., 2017). The majority of the mako sharks within these jurisdictional boundaries were immature males and females, implying that the U.S., Canadian, and high seas within the WNA may serve as a biologically critical habitat for immature sharks, which agrees with findings from Natanson et al. (2020).

4.1.2. Mako sharks Tagged off of Mexico

Though the sharks tagged off of Mexico generally remained within the GOM, they embarked on numerous transboundary movements. These makos also visited numerous EEZs, spanning from the Gulf Coast of the U.S. to Venezuela. Many fisheries in the Gulf Coast target shark species or land sharks as bycatch and are inconsistent in their management policies, exposing sharks to a high variety of fishing efforts (Pérez-Jiménes and Mendez-Loeza, 2015). Our results clearly demonstrate the importance of Mexican jurisdictional waters for makos, which is characteristic of heavy recreational and commercial fishing efforts (Pérez-Jiménes and Mendez-Loeza, 2015). Although the majority of location estimates from makos tagged off Mexico fell within the Mexican, U.S., Cuban, Venezuelan, and Honduran EEZs, in the GOM, over 80% of the location estimates occurred within the Mexican EEZ, and the marginal difference between the proportion of location estimates within the Mexican EEZ and U.S. EEZ is over 70%. Notably, we did not derive tracks from immature males off Mexico. Immature females were responsible for most of the location estimates within each EEZ, while the proportion of location estimates from subadult and mature males varied.

4.2. Identifying demographic-based differences in core areas of mako shark activity among jurisdictional waters

4.2.1. Mako sharks tagged off the U.S.

The core areas for immature males and females remained confined to the U.S. EEZ between North Carolina and Massachusetts, suggesting that the U.S. East coast is a critically important habitat for immature mako sharks. Previous work has also identified this region as a highly utilized area for immature sharks (see e.g., Natanson et al., 2020; Vaudo et al., 2017) and acknowledged it as potential essential nursery grounds for makos (Natanson et al., 2020). As such, management should be mindful of this region, as the protection of nursey grounds are essential to the rehabilitation of the North Atlantic mako stock.

Interestingly, subadult and mature shark core areas of activity were more extensive. Although the low sample size of subadult and mature makos may influence the locations of these core areas, mako sharks have previously demonstrated demographic-based differences in movement patterns (Mucientes et al., 2009; Schrey and Heist, 2003). The reasons for demographic-based differences in habitat utilization are still unspecified. However, some suggestions include food availability, environmental conditions, searching for mates, and evading fishing pressure (Block et al., 2011; Mucientes et al., 2009; Schrey and Heist, 2003; Vaudo et al., 2017).

Regardless of the reasons for their movements, as larger sharks utilize a greater variety of habitats, they inevitably expose themselves to higher variations of fishing efforts and regulations. Further, it is unknown whether these are exclusively size-based differences or if they are also sex-based dispersal, as all the females tagged off the U.S. in this study were immature. Therefore, increased tagging efforts for large females in the WNA are required to confirm if these movement patterns signify male-based dispersion (see e.g., Gibson et al., 2021; Schrey and Heist, 2003) or if larger females also demonstrate widespread habitat utilization.

4.2.2. Makos Tagged off of Mexico

The locations of the core areas for all three demographics show less demographic-based variability in habitat utilization across EEZs relative to the WNA. Core areas from immature females and subadult and mature males predominately fell within the Mexican EEZ and partially within the Cuban EEZ. Although the U.S. is the second most frequently visited EEZ, only subadults had a small portion of their core area fall within the U.S. EEZ. This contradiction is not surprising when considering that 80% of all location estimates fell within the Mexican EEZ.

Our results further highlight the importance of Mexico's waters to mako sharks. Though 80% of all the location estimates fell within the Mexican EEZ, over 80% of the core areas for each demographic overlapped with the Mexican EEZ, and almost 100% of the mature male core area fell within the Mexican EEZ. This is concerning when considering the region in which the core areas overlap off the Yucatan Peninsula have over 10 different fishing communities that target sharks (Pérez-Jiménes and Mendez-Loeza, 2015).

Our results show that larger sharks may inhabit the GOM relative to the WNA. Unlike makos tagged off the U.S., none of these location estimates were from immature males. Furthermore, though all of the females in this dataset are immature, the sharks tagged off the U.S. were generally smaller (FL = 169.7cm, 158.4cm for females and males, respectively) than those tagged off Mexico (FL = 196.1cm, 187.5 for females and males, respectively). In addition, Gibson et al. (2021) tagged mature females in the Northwestern GOM (see Gibson et al., 2021 for details). Habitat utilization of large sharks has important management implications. For instance, the presence of mature females within the GOM suggest that the GOM may serve as mating and pupping grounds (Natanson et al., 2020). The ecological characteristics of the GOM support this hypothesis, as they offer a controlled environment for pupping grounds, allowing juveniles to develop essential survivorship skills before undergoing large migrations in search of prey and mates (Tunçer and Kabasakal, 2016).

A more in-depth understanding of habitat utilization of mature females in the GOM relative to jurisdictional boundaries may indicate EEZs that serve as pupping grounds. Our results show that large females frequently visited five different EEZs and most heavily utilized two different EEZs, all of which vary in their mako management strategies, highlighting the importance of unified mako management in the GOM to mako sharks.

4.3. Identifying Jurisdictional waters where "resident" behavior of mako sharks occur

4.3.1. Mako sharks tagged off the U.S.

Core areas are a valuable method to identify general areas indicative of high site fidelity for mobile species, however, recent advancements in modeling approaches allow for a more in-depth insight into animal movement behavior. Results of the GAM investigating probability of makos occurring within an EEZ as a response to movement behavior show that mako sharks tagged off the U.S. showed the highest likelihood of displaying more residential behavior within the U.S. EEZ. The combination of the core area of immature mako activity entirely falling along the U.S. East Coast and the high likelihood of residential behavior occurring within this region clearly demonstrates the importance of the U.S. East Coast to the recovery of the North Atlantic mako shark stock.

However, U.S. waters were not constrained to residential behavior. The U.S. maintained its position as the most probable EEZ for a wide range of MOVE PERSISTANCE MODEL values as makos also displayed transiting behavior within the EEZ. The presence of both residential and transiting behavior within the U.S. EEZ may imply that these waters containing both biologically essential habitats and critical migratory pathways, most likely the Gulf Stream.

Vaudo et al. (2017) suggested an adjustment to Casey and Kohler's (1992) Sargasso Sea Hypothesis, stating that makos mainly use the Sargasso Sea for long migrations. Our findings support this modification. As move persistence reached its maximum, the probability of occurrence decreased from the U.S. EEZ and increased in high seas. The high probability of occurrence in high seas for high MOVE PERSISTANCE MODEL scores, coupled with a low likelihood of low MOVE PERSISTANCE MODEL scores, suggests that offshore high seas mainly serve as migration pathways for mako sharks in the WNA.

Makos showing a higher likelihood of resident behavior in nearshore habitats and more transient behavior as they move offshore into high seas are consistent with previous studies (see e.g., Block et al., 2011; Bryne et al., 2019; Francis et al., 2019; Rogers et al., 2015). These movement patterns may result from resident behavior's strong association with shallow shelf locations, higher productivity, and potentially cooler temperatures (Francis et al., 2019; Rogers et al., 2015). Interestingly, all of these oceanographic features are characteristic of the Mid-Atlantic cold pool, which arises along the U.S. Northeastern coast from Spring to early Fall, corresponding to when makos are most probable within the U.S. EEZ (Kohut and Brodie, 2019). The Mid-Atlantic cold pool is characteristic of attracting HMS (Kohut and Brodie, 2019), potentially drawing and inducing residential behavior in mako sharks when it arises.

The high variability in female movements relative to male movements suggests that makos display sex-based differences in regional movement behavior. The high likelihood of occurrence in Canadian waters for females showing residential behavior, and overall low likelihood for males suggests that Canadian waters are ecologically important habitats for immature females. However, the intentions behind sex-based dispersal in immature mako sharks remain undetermined (Natanson et al., 2020).

4.3.2. Makos tagged off Mexico

Bryne et al. (2019) identified differences in movement behavior for makos between the GOM and WNA, which agree with our findings. Makos in the GOM and WNA displayed apparent differences in the probability of occurrence within EEZs as a function of move persistence. There was minimal variability in the probability of occurrence among EEZs in the GOM as a response to move persistence for the whole population of makos tagged off Mexico and between females and males. The Mexican EEZ sustained its position as the EEZ with the highest probability of occurrence for resident and transiting behavior. These findings support the hypothesis that makos show higher site fidelity within the GOM (Bryne et al., 2017; Vaudo et al., 2017). These findings coupled with all three demographic core areas of activity falling mostly within Mexican waters solidify the notion that the Mexican EEZ is an ecologically important habitat for mako sharks in the GOM.

Although minor, it is noteworthy that the probability of occurrence within the Cuban EEZ increases when sharks (primarily female) show transiting behavior. This increase in the likelihood of occurrence coupled with core areas overlapping with the Cuban EEZ may suggest that sharks use Cuba as frequent migratory pathways.

4.4. Examining seasonal variation in habitat use of mako sharks within jurisdictional waters

4.4.1. Mako sharks tagged off the U.S.

There was evident seasonal variation in the probability of occurrence across EEZs as a function of the month of the year for mako sharks tagged in the WNA. Further, seasonal variations of occurrence within EEZs also appeared to differentiate by sex. Males tagged off the U.S. displayed similar trends to the population-level movements, which is most likely due to males making up most of this population. Interestingly, the likelihood of occurrence in high seas is reasonably low for most of the year, except for late winter through early spring. However, a portion of the subadult and mature male core areas are within high seas. While this discrepancy may be a consequence of omitting reproductive status in the GAM, it may also indicate a strong seasonal influence dictating the locations of core use areas, as seen in Gibson et al. (2021), Rogers et al. (2015), and Vaudo et al. (2017).

Seasonal occurrence among EEZs were much more variable for female mako sharks. Although there were some similarities in their likelihood of occurrence relative to U.S. and high seas compared to males, there was increased variability in their probability of occurrence relative to Canadian and "other" countries. The high probability of occurrence in Canadian waters in the mid-summer is exclusive to females, suggesting potential sex-based differences in habitat utilization during this time. Demographic differences in habitat use were also evident during the winter when females occupied the high seas or “other” waters and males occupied U.S. waters.

Though there was some evidence of sex-based differences in habitat utilization, most notably during the late summer and fall, both sexes had a high likelihood of occurrence in U.S. waters in early-summer. These conflicting results are consistent with existing literature. For instance, Gibson et al. (2021), Schrey and Heist (2003), and Mucientes et al. (2009) documented sex-based dispersal in makos. However, results from both Natanson et al. (2020) and Corrigan et al. (2018) neglect the idea of sex-based dispersal.

Overall, Natanson et al. (2020) saw little evidence to support the notion of sex-based dispersal. However, they did see some segregation in June and October, similar to our findings in this study, which is surprising, given that Mollet et al. (2000) estimated mating to occur summer - fall. Based on the sex-based dispersal patterns in this study, it is plausible for mating to occur in early summer when males and females are most probable in U.S. waters. However, the most dramatic sex-based dispersal occurs in late summer and early fall, conflicting with the notion that mating occurs in the fall. Thus, more in-depth research on sex-based dispersal is necessary to identify potentially biologically essential areas for reproduction in the WNA.

It is worth noting that partition is assumed to occur in late winter and early spring (Duffy and Francis, 2001; Mollet et al., 2000). During this time, the probability of females in the U.S. EEZ increases, possibly supporting the perception that the U.S. East Coast may serve as important pupping grounds.

The distinct transboundary movements of mako sharks in the WNA suggest that makos may benefit from seasonally variable management, such as time/area closures. Time/area closures have previously been utilized to mitigate by-catch and the overexploitation of vulnerable species (Bangley et al., 2020; O'Keef, Cadrin, and Stokesbury, 2014). However, proper timing of the time/area closure is dependent on a well-rounded understanding of demographic based-species distribution (Bangley et al., 2020). For instance, when considering makos in the U.S., it may be beneficial to prohibit mako landings when females are likely to inhabit the region as it may indicated potential mating or pupping grounds as males are within the U.S. EEZ for most of the year.

4.4.2. Makos Tagged off Mexico

There was little-to-no seasonal variability in mako shark's probability of occurrence among EEZs for the entire population, females, and males of makos tagged off Mexico. Furthermore, the highest likelihood of occurrence remained in the Mexican EEZ throughout the whole year. These results imply that makos within the GOM stay in the GOM (Vaudo et al., 2017) and do not frequently embark on seasonal migrations that cross jurisdictional boundaries.

Although these results support Vaudo et al. (2017), they conflict with Gibson et al. (2021), who reported long transboundary excursions through multiple EEZs by mature males. As mentioned in Gibson et al. (2021), these discrepancies may be a consequence of differences in the size of sharks in the sample. Yet, males tagged in this study were either subadult or mature and showed the least amount of variability in seasonal transboundary movements relative to females. In addition, Rooker et al.

(2019) identified general seasonal variability in mako movements relative to jurisdictional boundaries in the GOM. However, one shark was responsible for most of the large multinational excursions (Rooker et al., 2019). Individual variability in seasonal migrations and limited sample sizes may account for these discrepancies. In general, there is limited information regarding mako sharks in the GOM. As such, increased research efforts on mako sharks in the GOM are required to gain a comprehensive understanding of mako habitat use in the GOM. However, our results, when coupled with the high proportion of core areas and probability of occurrence among all behavioral states, show that the Mexican EEZ is a highly utilized, and likely a biologically important, region throughout the year.

4.5. Quantifying the importance of waters among U.S. states for mako sharks

Although makos showed high site fidelity within U.S. waters, their frequency of occurrence within state water boundaries was minimal. Less than 1% of the location estimates within U.S. waters fell within state waters. Of the sharks located in state waters, 100% were immature sharks, likely because of their high abundance within the U.S. EEZ. These results are not surprising given mako's offshore habitat and highly migratory behavior (Casey and Kohler, 1992, Compano, 2001). In addition, mako's common prey species inhabit offshore environments, such as tuna and swordfish (Campana, Marks, and Joyce, 2005; Compano, 2001). As such, makos require federal management to rebuild their population, and Regional Fishery Management Councils should continue to adhere to NMFS protocols.

4.6. Examining the overlap of mako shark core areas and EFHs and MPAs

4.6.1. EFHs

Relative to MPAs, EFHs had a higher degree of overlap with mako shark core areas in the U.S. EEZ. However, considering EFHs are developed from 95% U.D. isopleths determined from an extensive literature search, the proportion of the core areas (50% U.D. isopleth) covered by EFHs is concerning (NMFS, 2017). The core area with the most significant overlap is only a little over halfway covered by the EFH. Considering the large sample size of our dataset, our results imply that the current shortfin mako shark EFH may not accurately depict mako's distribution in the WNA.

Due to data constraints, the formulation of EFHs for makos does not consider demographic-specific data (NMFS, 2017). However, potential demographic-based differences in distribution shown in this study and others suggest that the inclusion of demographic data may benefit the placement of shortfin mako EFHs.

4.6.2. *MPAs*

As a consequence of MPA's fixed structure, it is uncertain how efficiently MPAs can protect highly migratory species (Campana, 2016; Game et al., 2009). One potential method to mitigate this uncertainty is implementing large offshore MPAs (Loheheno and Grorud-Colvert, 2015; White et al., 2017). However, the economic feasibility of properly maintaining large offshore MPAs is dubious (Game et al.,2009). Therefore, intricate planning of MPA placement is vital for them to protect biodiversity to its full potential (Game et al., 2009). MPAs have proven to be an effective conservation tool for highly mobile sharks if positioned correctly and adequately enforced. For instance, models have shown that current MPAs along the U.S. Southeastern coast can protect tiger shark populations and even catalyze increases in population size over time (Morgan et al., 2020).

However, this study shows minimal overlap between mako core areas in U.S. waters and MPAs for immature males and females and subadult and mature males. As a result, current MPAs cannot provide the protection required to recover the mako shark population in the North Atlantic Ocean. These results show that further inspection of MPA placement relative to species distribution is needed to protect makos adequately and potentially other highly migratory sharks via spatial management in the Northeast.

Although the primary purpose of MPAs is beyond single-stock management, sharks have historically been overlooked by management, resulting in suffering populations globally (Dulvy et al., 2014). The depletion of apex predators can lead to large-scale irreparable ecosystem changes, altering key ecosystem processes (Block et al., 2011). Such changes may potentially lead to detrimental events such as mass parasitism or disease (Block et al., 2011, Salomon et al., 2010). Cascading impacts due to the decline in shark populations due to fishing pressure have previously been recognized (Baum and Worm, 2009; Block et al., 2011; Myers and Worm, 2003; Ruppert et al., 2013). As such, fisheries management must prioritize vulnerable shark species that inhabit the U.S. East Coast to preserve ecosystem health.

4.7. Predict theoretical impacts of Amendment 11 on retention of mako sharks in U.S. recreational fisheries

We provided the first insight, to our knowledge, of the potential impact that Amendment 11 may have on facilitating mako population recovery in the WNA. Our results imply that the installment of Amendment 11 is not substantial enough to provide the level of protection needed for mako sharks to recover from overexploitation in the WNA. These results suggest that the mako sharks in this study grow too fast for the difference in the length requirements between pre-and post-Amendment 11 criteria to significantly increase the time that mako sharks have to swim freely.

However, due to the size increase for post-Amendment 11 standards, fewer sharks were considered unretainable, leaving a limited sample size (n = 7) for pre-Amendment 11 standards compared to post-Amendment 11 standards (n = 43). Although t-tests are robust enough to function with small sample sizes (see e.g., Winter, 2013), because of the relatively small sample of sharks, the number of days before sharks grow to retainable lengths under pre-Amendment 11 criteria may be misrepresented. In addition, this study only focused on the effect that Amendment 11 has on recreational fishing. However, Amendment 11 also prohibit commercial fisheries from retaining live mako sharks (Federal Register, 2019). Therefore, to fully capture the impact of Amendment 11, the new provisions on recreational and commercial fishing must be considered.

Despite our small sample size, it is not surprising that Amendment 11 may not have a substantial impact on mako stock recovery. Following the 2019 stock assessment, ICCAT recommended that a total ban of retention of North Atlantic shortfin mako sharks may allow the stock to recover by 2045 (ICCAT, 2019). If even limited retention of makos is permitted, makos have only a 60% of population recovery by 2070 (ICCAT, 2019). With this in mind, it is unlikely that Amendment 11 will have significant implications for population recovery.

Although the U.S. provides multiple levels of protection for mako sharks, our results indicate that these measures are inefficient to restore the mako shark population, thus calling the need to reevaluate U.S. mako management strategies. As technology for tracking and sampling environmental conditions continues to improve, one evaluation method increasing in popularity is habitat suitability modeling (Calich, Estevanez, and Hammerschlag, 2018). These models are employed to identify suitable habitats for vulnerable, highly migratory species to identify biologically essential habitats and improve spatial management planning (e.g., Birkmanis et al., 2020). Additionally, identifying areas that correspond to residential behavior, such as done here, coupled with seasonal migrations (e.g., Bangley et al., 2020; Bryne et al., 2019; Gibson et al., 2021) and environmental conditions (e.g., Bryne et al., 2019; Francis et al., 2019; Rogers et al., 2015) will assist in developing effective spatial management areas.

5. Conclusions

We identified the most highly visited EEZs by 60 mako sharks from 2013-2019. We supplied invaluable insight into their seasonal migrations and behavioral patterns relative to jurisdictional boundaries. We have also demonstrated potential demographic-based differences in mako transboundary movement behavior. In doing so, this work provided insight into EEZs that may hold biologically essential areas. The inclusion of seasonal and behavioral data when developing management strategies will reduce mako's exposure to seasonally high fishing pressure (Queiroz et al., 2019). Further, there was a considerable difference between the variation in transboundary seasonal and behavioral movement patterns and the degree of sexual segregation between mako sharks in the WNA and GOM. Therefore, mako sharks may benefit from management strategies that adhere to geographical rather than political boundaries (Vaudo et al., 2017; USCOP, 2004).

Ultimately, the mako shark's greatest threat comes from pelagic longline bycatch and unsustainable and inconsistent international fisheries management (Rooker et al., 2019; Sellheim, 2020). Though the call for international cooperative shark management has long been acknowledged, minimal action has taken place to achieve this goal (Cortez et al., 2007). For instance, as of August 2019, the Convention on International Trade in Endangered Species has listed makos as an Appendix II species (Cardeñosa et al., 2020). In doing so, all import and export trades are on record, and those involved must have a permit allowing for the transactions (Sellheim, 2020). While overall, this will increase the knowledge of mako shark landings, these new regulations do not ensure improved global conservation of makos, as they permit the international trade of mako products (Sellheim, 2020).

As a consequence of inconsistence management, HMS, such as mako sharks, are subject to a high level of variability in fishing efforts throughout their lifetime (Campana, 2016). Even among the seven EEZs makos most frequently visited in this study, there is a high degree of variability in fishing regulations, let alone the total 27 EEZs makos visited. For example, sharks tagged off the U.S. faced a range of no live landings (Canada), size, gear, and spatial regulations (U.S.), and a lack of regulations (high seas) (Federal Register, 2019; Gibson et al., 2021; Natanson et al., 2020; Whorley, n.d.). Makos tagged off Mexico faced a range from no-take (Honduras), spatial and length restrictions (Mexico, U.S., and Venezuela), gear restrictions (U.S.), and allowed landings as long as the fin remains attached (Cuba) (Gibson et al., 2021; Hacohen-Domené, 2020; Marques et al., 2019; NPOA-Sharks, 2015; Tavares, Rodriguez, and Morales, 2016). Although implementing global management strategies is a daunting task, it is crucial to preserve this endangered highly migratory species.

Although makos are not on the U.S. Endangered species list, the IUCN has classified them as endangered species (Rigby et al., 2019). As such, biologically important habitats for mako sharks must be a priority for global fisheries management. Here we identified the U.S. East coast as potentially biologically critical habitat for makos, however, it is evident that the U.S. must adjust its management strategy to support the recovery of the North Atlantic mako shark population.

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References

Aguilar, C., González-Sansón, G., Hueter, R., Rojas, E., Cabrera, Y., Bell-lloch, A. B., ... & Baker, P. (2014). Shark catches in the northwest region of Cuba. *Latin American Journal of Aquatic Research*, *42*(3), 477-487.

Bailey, H., Shillinger, G., Palacios, D., Bograd, S., Spotila, J., Paladino, F., & Block, B. (2008). Identifying and comparing phases of movement by leatherback turtles using state-space models. *Journal of Experimental Marine Biology and Ecology*, *356*(1-2), 128-135.

Bangley, C. W., Curtis, T. H., Secor, D. H., Latour, R. J., & Ogburn, M. B. (2020). Identifying important juvenile Dusky Shark habitat in the northwest Atlantic Ocean using acoustic telemetry and spatial modeling. *Marine and Coastal Fisheries*, *12*(5), 348-363.

Baum, J. K., & Worm, B. (2009). Cascading top-down effects of changing oceanic predator abundances. *Journal of Animal Ecology*, *78*(4), 699-714.

Birkmanis, C. A., Partridge, J. C., Simmons, L. W., Heupel, M. R., & Sequeira, A. M. (2020). Shark conservation hindered by lack of habitat protection. *Global Ecology and Conservation*, *21*, e00862.

Block, B. A., Jonsen, I. D., Jorgensen, S. J., Winship, A. J., Shaffer, S. A., Bograd, S. J., ... & Costa, D. P. (2011). Tracking apex marine predator movements in a dynamic ocean. *Nature*, *475*(7354), 86-90.

[dataset]Bureau of Ocean Energy Management (BOEM) and National Oceanic and Atmospheric Administration (NOAA). MarineCadastre.gov. *{Federal and State Waters}*. Retrieved *{6/21/2021}* from marinecadastre.gov/data.

Byrne ME, Cortés E, Vaudo JJ, Harvey GCMN, Sampson M, Wetherbee BM, Shivji M. (2017) Satellite telemetry reveals higher fishing mortality rates than previously estimated, suggesting overfishing of an apex marine predator. *Proc. R. Soc. B* 284: 20170658. http://dx.doi.org/10.1098/rspb.2017.0658

Byrne, M. E., Vaudo, J. J., Harvey, G. C. M., Johnston, M. W., Wetherbee, B. M., & Shivji, M. (2019). Behavioral response of a mobile marine predator to environmental variables differs across ecoregions. *Ecography*, *42*(9), 1569-1578.

Cailliet, G. M., Smith, W. D., Mollet, H. F., & Goldman, K. J. (2006). Age and growth studies of chondrichthyan fishes: the need for consistency in terminology, verification, validation, and growth function fitting. *Environmental Biology of Fishes*, *77*(3-4), 211-228.

Calenge, C. (2006) The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling*, 197, 516-519

Calenge, C. (2019). Home range estimation in R: the adehabitatHR package. *Office national de la classe et de la faune sauvage: Saint Benoist, Auffargis, France*

Calich, H., Estevanez, M., & Hammerschlag, N. (2018). Overlap between highly suitable habitats and longline gear management areas reveals vulnerable and protected regions for highly migratory sharks. *Marine Ecology Progress Series*, 602, 183-195.

Campana, S. E. (2016). Transboundary movements, unmonitored fishing mortality, and ineffective international fisheries management pose risks for pelagic sharks in the Northwest Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences*, *73*(10), 1599-1607.

Cardeñosa, D., Fields, A. T., Babcock, E. A., Shea, S. K., Feldheim, K. A., & Chapman, D. D. (2020). Species composition of the largest shark fin retail-market in mainland China. *Scientific reports*, *10*(1), 1-10.

Casey, J. G., & Kohler, N. E. (1992). Tagging studies on the shortfin mako shark (*Isurus oxyrinchus*) in the Northwest Atlantic. *Marine and Freshwater Research*, *43*(1), 45-60.

Compagno, L. J. (2001). *Sharks of the world:An Annotated and Illustrated Catalogue of Shark Species Known to Date*. *Volume 2 Bullhead, Mackerel and Carpet Sharks (Hertodontiformes, Lamniformes and Orectolobiformes).* (No. 1). Food & Agriculture Organization of the United Nations, species catalogue for fishery purposes, Rome, Italy.

Corrigan, S., Lowther, A. D., Beheregaray, L. B., Bruce, B. D., Cliff, G., Duffy, C. A., ... & Rogers, P. J. (2018). Population connectivity of the highly migratory shortfin mako (Isurus oxyrinchus Rafinesque 1810) and implications for management in the Southern Hemisphere. *Frontiers in Ecology and Evolution*, *6*, 187.

Cortés, E., Brown, C. A., & Beerhircher, L. R. (2007). Relative abundance of pelagic sharks in the Northwest Atlantic Ocean, including the Gulf of Mexico and Caribbean Sea. *Gulf and Caribbean Research*, *19*(2), 37-52.

De Winter, J. C. (2013). Using the Student's t-test with extremely small sample sizes. *Practical Assessment, Research, and Evaluation*, *18*(1), 10.

Dulvy, N. K., Fowler, S. L., Musick, J. A., Cavanagh, R. D., Kyne, P. M., Harrison, L. R., ... & White, W. T. (2014). Extinction risk and conservation of the world's sharks and rays. *elife*, *3*, e00590.

Duffy, C., & Francis, M. P. (2001). Evidence of summer parturition in shortfin mako (Isurus oxyrinchus) sharks from New Zealand waters. *New Zealand Journal of Marine and Freshwater Research.* 35(2), 319-324,

ESRI 2011. ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute.

Federal Register. (2019). National Oceanic and Atmospheric Administration Atlantic Highly Migratory Species; Shortfin Mako Shark Management Measures; Final Amendment 11. https://www.govinfo.gov/content/pkg/FR-2019-02-21/pdf/2019-02946.pdf

Federal Register. (2017). National Oceanic and Atmospheric Administration Atlantic Highly Migratory Species: Essential Fish Habitat. https://www.govinfo.gov/content/pkg/FR-2017-09-07/pdf/2017-18961.pdf

Francis, M. P., Shivji, M. S., Duffy, C. A., Rogers, P. J., Byrne, M. E., Wetherbee, B. M., ... & Meyers, M. M. (2019). Oceanic nomad or coastal resident? Behavioural switching in the shortfin mako shark (*Isurus oxyrinchus*). *Marine Biology*, *166*(1), 5.

Freitas, C., Lydersen, C., Fedak, M. A., & Kovacs, K. M. (2008). A simple new algorithm to filter marine mammal Argos locations. *Marine Mammal Science*, *24*(2), 315-325.

Gallagher, A. J., Orbesen, E. S., Hammerschlag, N., & Serafy, J. E. (2014). Vulnerability of oceanic sharks as pelagic longline bycatch. *Global Ecology and Conservation*, *1*, 50-59.

Game, E. T., Grantham, H. S., Hobday, A. J., Pressey, R. L., Lombard, A. T., Beckley, L. E., ... & Richardson, A. J. (2009). Pelagic protected areas: the missing dimension in ocean conservation. *Trends in Ecology & Evolution*, *24*(7), 360-369.

Gibson, K. J., Streich, M. K., Topping, T. S., & Stunz, G. W. (2021). New Insights Into the Seasonal Movement Patterns of Shortfin Mako Sharks in the Gulf of Mexico. *Frontiers in Marine Science*, *8*, 5.

Hacohen-Domené, A., Polanco-Vásquez, F., Estupiñan-Montaño, C., & Graham, R. T. (2020). Description and characterization of the artisanal elasmobranch fishery on Guatemala's Caribbean coast. *PloS one*, *15*(1), e0227797.

Harrison, A. L., Costa, D. P., Winship, A. J., Benson, S. R., Bograd, S. J., Antolos, M., ... & Block, B. A. (2018). The political biogeography of migratory marine predators. *Nature Ecology & Evolution*, *2*(10), 1571-1578.

Hartill, B. W., Taylor, S. M., Keller, K., & Weltersbach, M. S. (2020). Digital camera monitoring of recreational fishing effort: applications and challenges. *Fish and Fisheries*, *21*(1), 204-215.

Holts, D. B., & Bedford, D. W. (1993). Horizontal and vertical movements of the shortfin mako shark, Isurus oxyrinchus, in the Southern California Bight. *Marine and Freshwater Research*, *44*(6), 901-909.

ICCAT. (2019). Report of the 2019 ICCAT Shortfin mako assessment meeting. *International Commission for the Conservation of Atlantic Tunas, Madrid* (2017).

ICCAT. (2017). Draft Recommendation by ICCAT on the Conservation of North Atlantic Stock of Shortfin Mako Caught in Association with ICCAT Fisheries. (Doc. No. PA4-812B/2017); https://www.iccat.int/com2017/DocENG/PA4_812B_ENG.pdf

Jonsen, I. D., Flemming, J. M., & Myers, R. A. (2005). Robust state–space modeling of animal movement data. *Ecology*, *86*(11), 2874-2880.

Jonsen, I. D., McMahon, C. R., Patterson, T. A., Auger-Méthé, M., Harcourt, R., Hindell, M. A., & Bestley, S. (2019). Movement responses to environment: fast inference of variation among southern elephant seals with a mixed effects model. *Ecology*, *100*(1), e02566.

Jonsen, I.D., Patterson, T.A. (2020). foieGras: fit latent variable movement models to animal tracking data for location quality control and behavioural inference Zenodo. https://doi.org/10.5281/zenodo.3899972

Kohut, J., & Brodie, J. (2019). *Offshore Wind and the Mid-Atlantic Cold Pool*[White Paper]. Rutgers University Center of Ocean Observing Leadership. https://rucool.marine.rutgers.edu/wp-content/uploads/2020/10/PartnersWorkshop_WhitePaper_Final.pdf

Lubchenco, J., & Grorud-Colvert, K. (2015). Making waves: The science and politics of ocean protection. *Science*, 350(6259), 382-383.

Marquez, R., Tavares, R., & Ariza, L. A. (2019). Elasmobranch species in the artisanal fishery of Sucre State, Venezuela. *Ciencias Marinas*, *45*(4), 181-188.

Mollet, H. F., Cliff, G., Pratt Jr, H. L., & Stevens, J. (2000). Reproductive biology of the female shortfin mako, *Isurus oxyrinchus* Rafinesque, 1810, with comments on the embryonic development of lamnoids. *Fishery Bulletin*, (2).

Morgan, A., Calich, H., Sulikowski, J., & Hammerschlag, N. (2020). Evaluating spatial management options for tiger shark (*Galeocerdo cuvier*) conservation in US Atlantic Waters. *ICES Journal of Marine Science*, *77*(7-8), 3095-3109.

Mucientes, G. R., Queiroz, N., Sousa, L. L., Tarroso, P., & Sims, D. W. (2009). Sexual segregation of pelagic sharks and the potential threat from fisheries. *Biology letters*, *5*(2), 156-159.

Musick, J. A., Burgess, G., Cailliet, G., Camhi, M., & Fordham, S. (2000). Management of sharks and their relatives (Elasmobranchii). *Fisheries*, *25*(3), 9-13.

Myers, R. A., & Worm, B. (2003). Rapid worldwide depletion of predatory fish communities. *Nature*, *423*(6937), 280-283.

Myers, R. A., Baum, J. K., Shepherd, T. D., Powers, S. P., & Peterson, C. H. (2007). Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science*, *315*(5820), 1846-1850.

Natanson, L. J., Winton, M., Bowlby, H., Joyce, W., Deacy, B., Coelho, R., & Rosa, D. (2020). Updated reproductive parameters for the shortfin mako (*Isurus oxyrinchus*) in the North Atlantic Ocean with inferences of distribution by sex and reproductive stage. *Fishery Bulletin*, *118*(1), 21-53.

NMFS (National Marine Fisheries Service). (2017). Final Amendment 10 to the 2006 Consolidated Atlantic Highly Migratory Species Fishery Management Plan: essential fish habitat and environmental assessment. National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Office of Sustainable Fisheries, Highly Migratory Species Management Division, Silver Spring, MF, Public Document. https://www.federalregister.gov/documents/2017/09/07/2017-18961/atlantic-highly-migratory-species-essential-fish-habitat

NMFS (National Marine Fisheries Service). (2006). Final Consolidated Atlantic Highly Migratory Species Fishery Management Plan. National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Office of Sustainable Fisheries, Highly Migratory Species Management Division, Silver Spring, MF, Public Document. pp. 1600. https://media.fisheries.noaa.gov/dam-migration/atlantic-hms-consolidated-fmp.pdf

[dataset]NOAA. (n.d.) [Essential Fish Habitat GIS Data]. Retrieved December, 2020, from https://www.habitat.noaa.gov/protection/efh/newInv/index.html

[dataset]NOAA. (n.d.) [Marine Protected Areas GIS Data]. Retrieved December, 2020, from https://marineprotectedareas.noaa.gov/dataanalysis/mpainventory/

NPOA-Sharks, 2015. National Plan of Action for the Conservation and Management of Chondrichthyes in the Republic of Cuba. Ministry of the Food Industry. Havana, Cuba. 48 p.

O'Keefe, C. E., Cadrin, S. X., & Stokesbury, K. D. (2014). Evaluating effectiveness of time/area closures, quotas/caps, and fleet communications to reduce fisheries bycatch. *ICES Journal of Marine Science*, *71*(5), 1286-1297.

Pacoureau, N., Rigby, C. L., Kyne, P. M., Sherley, R. B., Winker, H., Carlson, J. K., ... & Dulvy, N. K. (2021). Half a century of global decline in oceanic sharks and rays. *Nature*, *589*(7843), 567-571.

Pérez-Jiménez, J. C., & Mendez-Loeza, I. (2015). The small-scale shark fisheries in the southern Gulf of Mexico: Understanding their heterogeneity to improve their management. *Fisheries Research*, *172*, 96-104.

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.

R Core Team (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rigby, C.L., Barreto, R., Carlson, J., Fernando, D., Fordham, S., Francis, M.P., Jabado, R.W., Liu, K.M., Marshall, A., Pacoureau, N., Romanov, E., Sherley, R.B. & Winker, H. 2019. *Isurus oxyrinchus*. *The IUCN Red List of Threatened Species* 2019: e.T39341A2903170. https://dx.doi.org/10.2305/IUCN.UK.2019-1.RLTS.T39341A2903170.en. Downloaded on 11 January 2021.

Rogers, P. J., Huveneers, C., Page, B., Goldsworthy, S. D., Coyne, M., Lowther, A. D., ... & Seuront, L. (2015). Living on the continental shelf edge: habitat use of juvenile shortfin makos *Isurus oxyrinchus* in the Great Australian Bight, southern Australia. *Fisheries Oceanography*, *24*(3), 205-218.

Rooker, J. R., Dance, M. A., Wells, R. D., Ajemian, M. J., Block, B. A., Castleton, M. R., ... & Walter, J. F. (2019). Population connectivity of pelagic megafauna in the Cuba-Mexico-United States triangle. *Scientific Reports*, *9*(1), 1-13.

Rosa, D., Mas, F., Mathers, A., Natanson, L. J., Domingo, A., Carlson, J., & Coelho, R. (2017). Age and growth of shortfin mako in the North Atlantic, with revised parameters for consideration to use in the stock assessment. International Commission for the Conservation of Atlantic Tunas. *ICCAT SCRS/2017/111, 22p.[Working paper.]*.

Ruppert, J. L., Travers, M. J., Smith, L. L., Fortin, M. J., & Meekan, M. G. (2013). Caught in the middle: combined impacts of shark removal and coral loss on the fish communities of coral reefs. *PloS One*, *8*(9), e74648.

Salomon, A. K., Gaichas, S.K., Shears, N. T., Smith, J.E., Madin, E.M., & Gaines, S. D. (2010) Key features and context-dependence of fishery-induced trophic cascades. *Conservation Biology*, 24(2), 382-394.

Schrey, A. W., & Heist, E. J. (2003). Microsatellite analysis of population structure in the shortfin mako (Isurus oxyrinchus). *Canadian Journal of Fisheries and Aquatic Sciences*, *60*(6), 670-675.

Sellheim, N. (2020). The CITES appendix II-Listing of mako sharks—Revisiting counter arguments. *Marine Policy*, *115*, 103887.

Shimada, T., Limpus, C., Jones, R., & Hamann, M. (2017). Aligning habitat use with management zoning to reduce vessel strike of sea turtles. *Ocean & Coastal Management*, *142*, 163-172.

Simpfendorfer, C. A., Olsen, E. M., Heupel, M. R., & Moland, E. (2012). Three-dimensional kernel utilization distributions improve estimates of space use in aquatic animals. *Canadian Journal of Fisheries and Aquatic Sciences*, *69*(3), 565-572.

Sims, D. W., Mucientes, G., & Queiroz, N. (2018). Shortfin mako sharks threatened by inaction. *Science*, *359*(6382), 1342-1.

Spaet, J. L., Manica, A., Brand, C. P., Gallen, C., & Butcher, P. A. (2020a). Environmental conditions are poor predictors of immature white shark Carcharodon carcharias occurrences on coastal beaches of eastern Australia. *Marine Ecology Progress Series*, *653,* 167-179.

Spaet, J. L., Patterson, T. A., Bradford, R. W., & Butcher, P. A. (2020b). Spatiotemporal distribution patterns of immature Australasian white sharks (Carcharodon carcharias). *Scientific reports*, *10*(1), 1-13.

Tavares, R., Rodriguez, J. P., & Morales, M. (2016). Nursery area and size structure of the lemon shark population, Negaprion brevirostris (Poey, 1868), in Los Roques Archipelago National Park, Venezuela. *Universitas Scientiarum*, *21*(1), 33-52.

ten Brink, T. S., & Dalton, T. (2018). Perceptions of commercial and recreational fishers on the potential ecological impacts of the Block Island Wind Farm (US). *Frontiers in Marine Science*, *5*, 439.

Tunçer, S., & Kabasakal, H. (2016). Capture of a juvenile shortfin mako shark, Isurus oxyrinchus Rafinesque, 1810 (Chondrichthyes: Lamnidae) in the Bay of Edremit, northern Aegean Sea (Turkey). In *Annales, ser. hist. nat* (Vol. 26, pp. 31-36).

USCOP (US Commission on Ocean Policy). (2004). *An ocean blueprint for the 21st century*. US Commission on Ocean Policy.

Vander Wal, E., & Rodgers, A. R. (2012). An individual-based quantitative approach for delineating core areas of animal space use. *Ecological Modelling*, 224(1), 48-53.

Vaudo, J. J., Byrne, M. E., Wetherbee, B. M., Harvey, G. M., & Shivji, M. S. (2017). Long-term satellite tracking reveals region-specific movements of a large pelagic predator, the shortfin mako shark, in the Northwest Atlantic Ocean. *Journal of Applied Ecology, 54*(6), 1765-1775.

Vaudo, J. J., Wetherbee, B. M., Wood, A. D., Weng, K., Howey-Jordan, L. A., Harvey, G. M., & Shivji, M. S. (2016). Vertical movements of shortfin mako sharks Isurus oxyrinchus in the Northwest Atlantic Ocean are strongly influenced by temperature. *Marine Ecology Progress Series*, 547, 163-175.

[dataset]VLIMAR Gazetteer & VLIZS Maritime Boundaries Geodatabase. (n.d). [Maritime Boundary GIS Data]. Accessed March, 2019, from https://www.marineregions.org/about.php

White, T. D., Carlisle, A. B., Kroodsma, D. A., Block, B. A., Casagrandi, R., De Leo, G. A., ... & McCauley, D. J. (2017). Assessing the effectiveness of a large marine protected area for reef shark conservation. *Biological Conservation*, *207*, 64-71.

White, E. R., Myers, M. C., Flemming, J. M., & Baum, J. K. (2015). Shifting elasmobranch community assemblage at Cocos Island—an isolated marine protected area. *Conservation Biology*, *29*(4), 1186-1197.

Whorley, D., n.d. *North Atlantic Shortfin Mako Management 2020-2021*. Fisheries and Oceans Canada., https://ecologyaction.ca/sites/default/files/images-documents/shortfin%20mako.pdf

Wildlife Computers. (2019). SPOT Transmitting Tags. Retrieved December 10, 2020, from https://wildlifecomputers.com/our-tags/spot-argos-satellite-tags/spot/

Wood, S.N. (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society* (B) 73(1):3-36

Figures

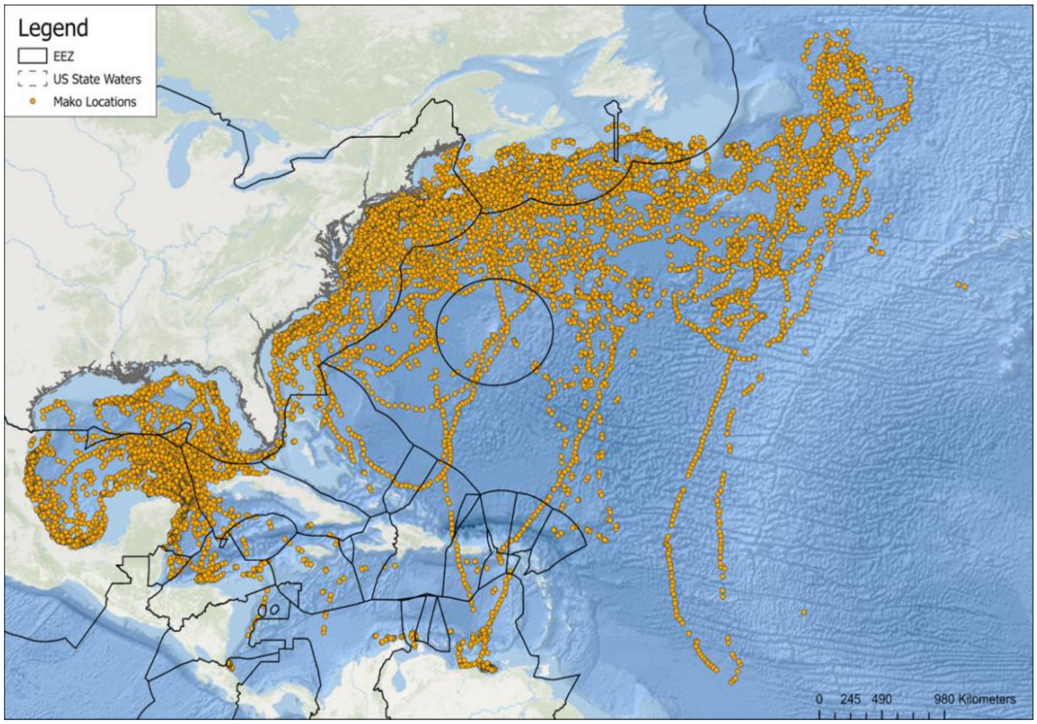

Figure 1. Estimated shortfin mako shark location estimates after the SSM. Solid black lines represent country EEZs in the WNA and GOM. Dashed grey lines represent U.S. state water jurisdictions.

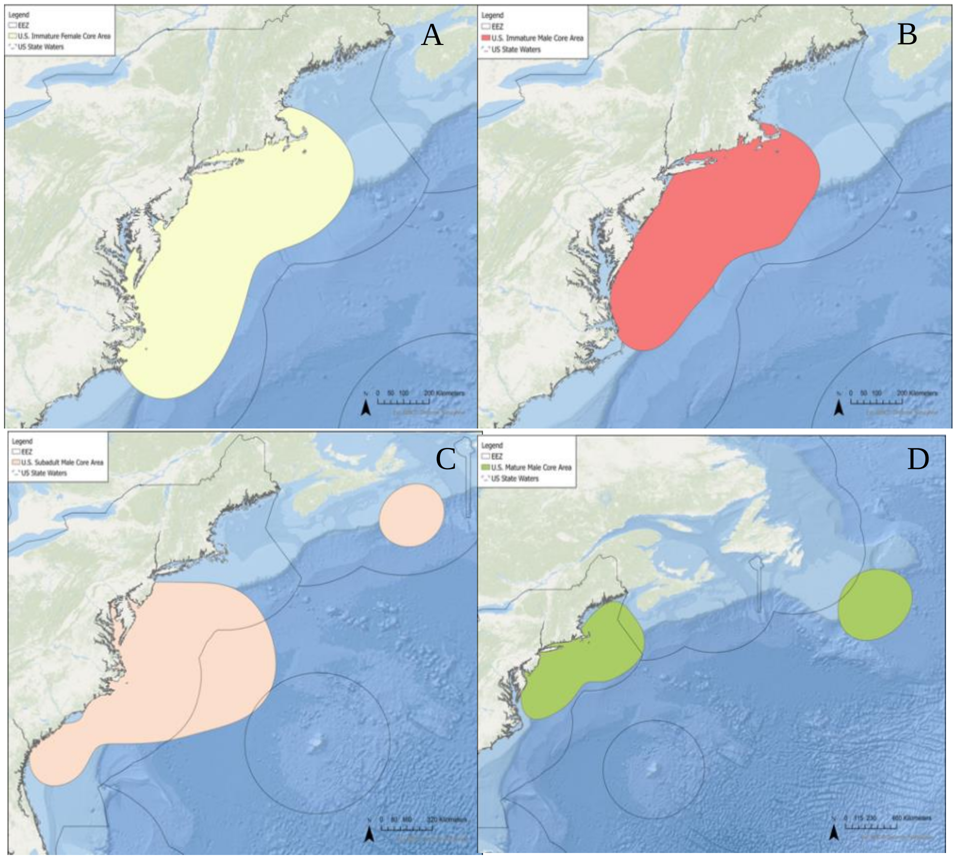

Figure 2. Core areas of immature females (A), immature males (B), subadult males (C), and mature males (D) of sharks tagged off U.S. Black solid lines represent EEZs, grey dashed lines represent U.S. State waters.

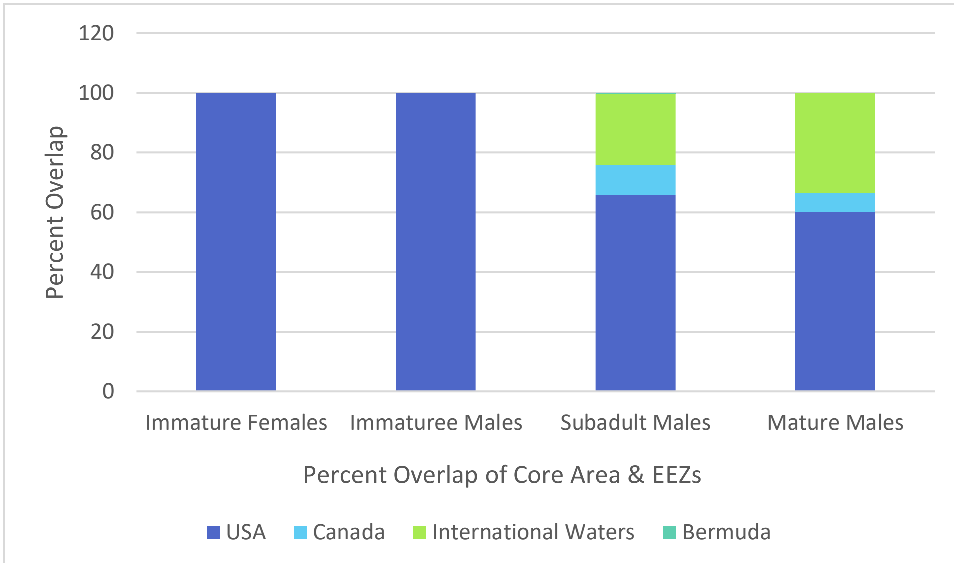

Figure 3. Percent of core areas from immature females, immature males, subadult males, and mature male sharks tagged off the U.S. in each country's EEZ.

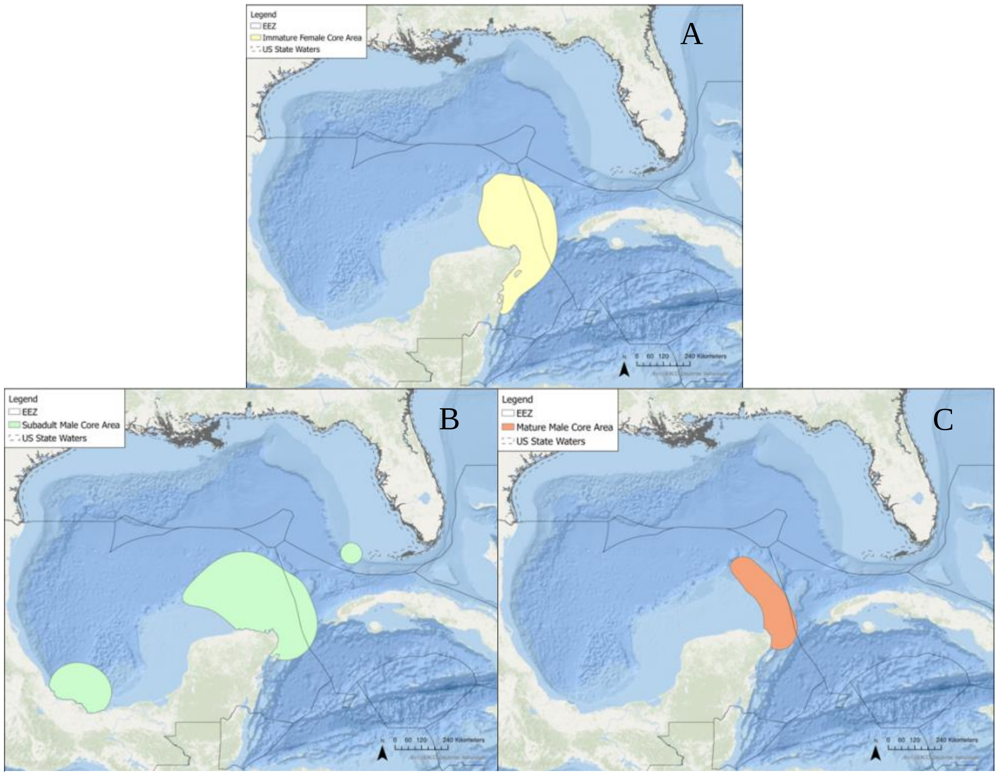

Figure 4. Core areas of immature females (A), subadult males (B), and mature males (C) of sharks tagged off Mexico. Black solid lines represent EEZs, grey dashed lines represent U.S. State waters.

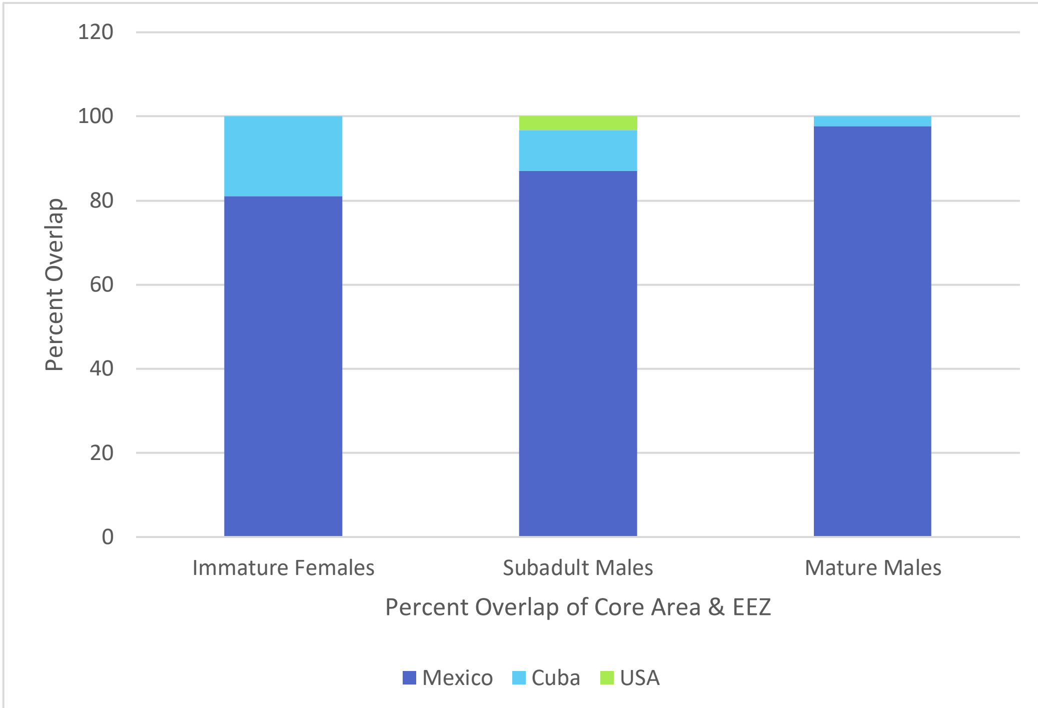

Figure 5. Percent of core areas from immature females, subadult males, and mature males of sharks tagged off Mexico in each country's EEZ.

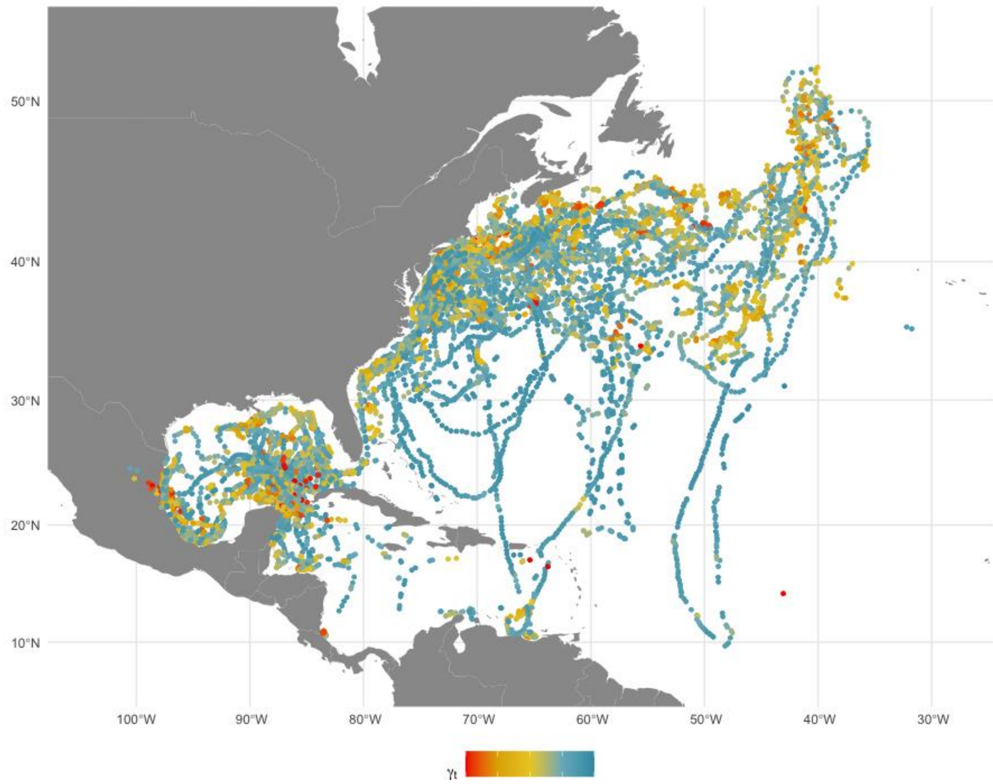

Figure 6. Estimated shortfin mako shark location estimates after the SSM with swimming behavior estimated from the MPM. (y_t) represents move persistence. As (y_t) decreases towards 0, this indicates more residential behavior. As (y_t) increases towards 1, this indicates more transiting behavior.

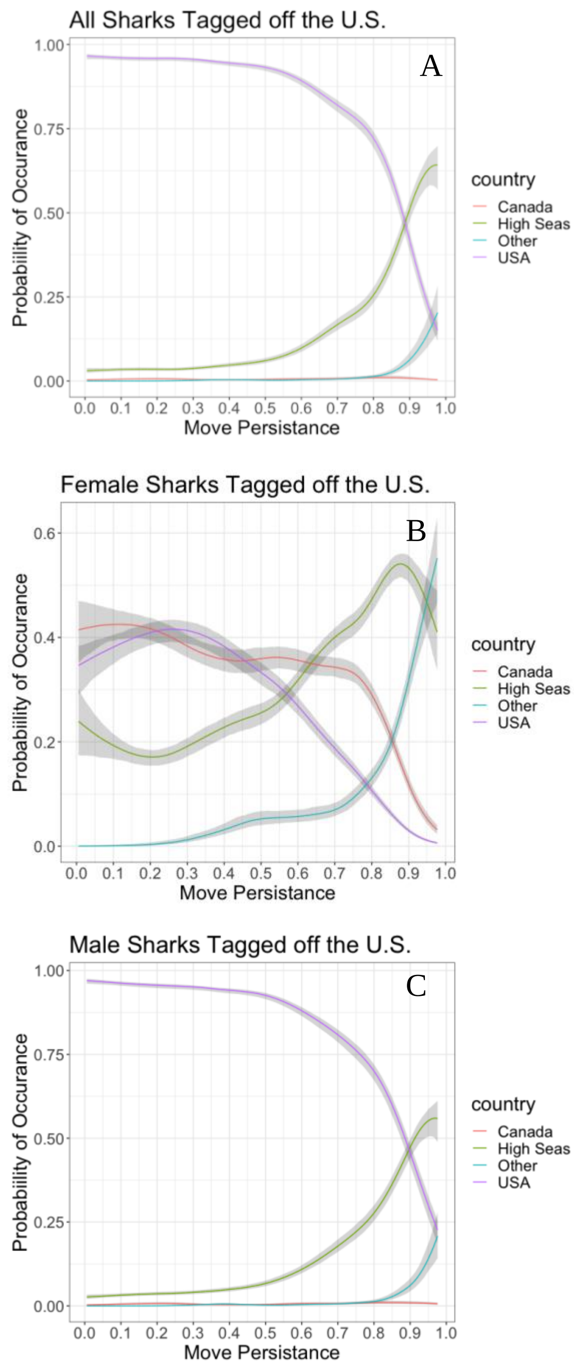

Figure 7. Probability of a random shark occurring in an EEZ as a function of movement behavior predicted by the multinomial GAM for all sharks tagged off the U.S. (A), female sharks tagged off the U.S. (B), and male sharks tagged off the U.S. (C). Lines represent the estimated effect of movement behavior on the probability of a shark occurring within an EEZ (Spaet et al., 2020b). Shading represents the interquartile range of estimates produced by a posterior distribution of model parameters (Harrison et al., 2018). The x-axis represents movement behavior from the move persistence model, where values closer to 0 indicate resident behavior and values closer to 1 indicate transient behavior.

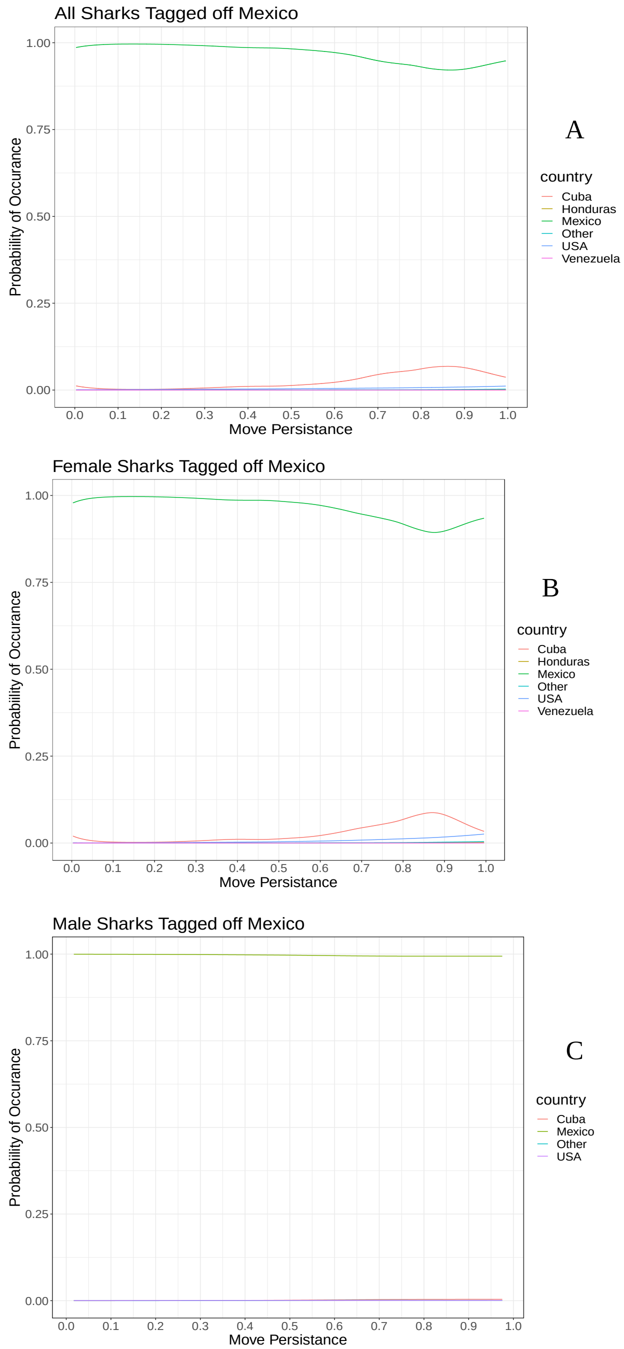

Figure 8. Probability of a random shark occurring in an EEZ as a function of movement behavior predicted by the multinomial GAM for all sharks tagged off Mexico (A), female sharks tagged off Mexico (B), and male sharks tagged off Mexico (C). Lines represent the estimated effect of movement behavior on the probability of a shark occurring within an EEZ (Spaet et al., 2020b). Shading represents the interquartile range of estimates produced by a posterior distribution of model parameters (Harrison et al., 2018). The x-axis represents movement behavior from the move persistence model, where values closer to 0 indicate resident behavior and values closer to 1 indicate transient behavior.

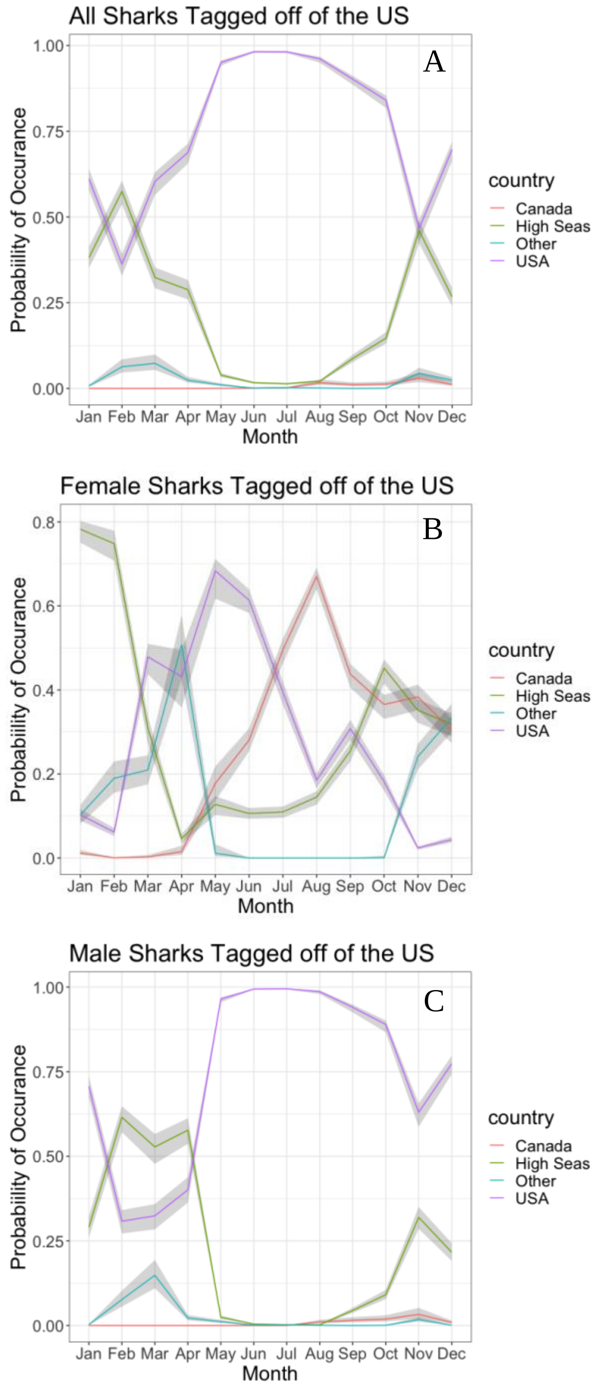

Figure 9. Seasonal probability of a random shark occurring in an EEZ boundary predicted by the multinomial GAM for all sharks tagged off the U.S. (A), female sharks tagged off the U.S. (B), and male sharks tagged off the U.S. (C). Lines represent the estimated effect of month of the year on the probability of a shark occurring within an EEZ (Spaet et al., 2020b). Shading represents the interquartile range of estimates produced by a posterior distribution of model parameters (Harrison et al., 2018).

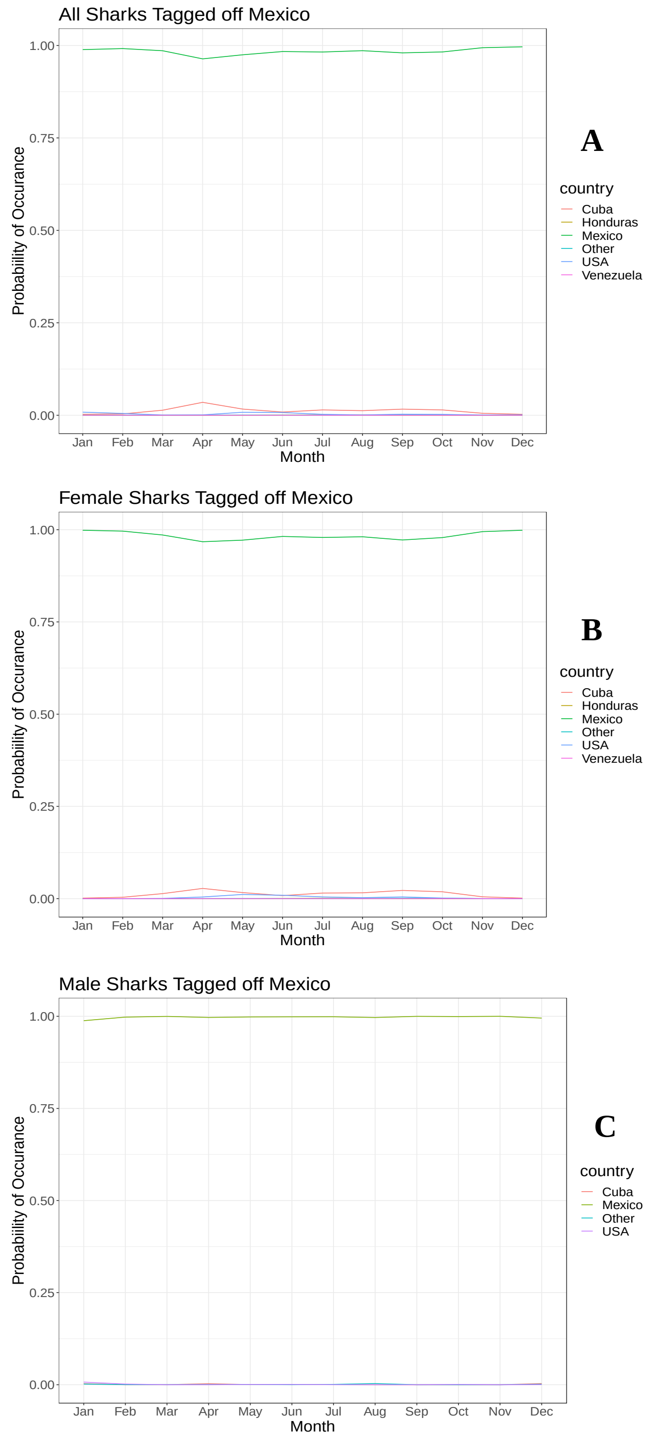

Figure 10. Seasonal probability of a random shark occurring in an EEZ boundary predicted by the multinomial GAM for all sharks tagged off Mexico (A), female sharks tagged off Mexico (B), and male sharks tagged off Mexico (C). Lines represent the estimated effect of month of the year on the probability of a shark occurring within an EEZ (Spaet et al., 2020b). Shading represents the interquartile range of estimates produced by a posterior distribution of model parameters (Harrison et al., 2018).

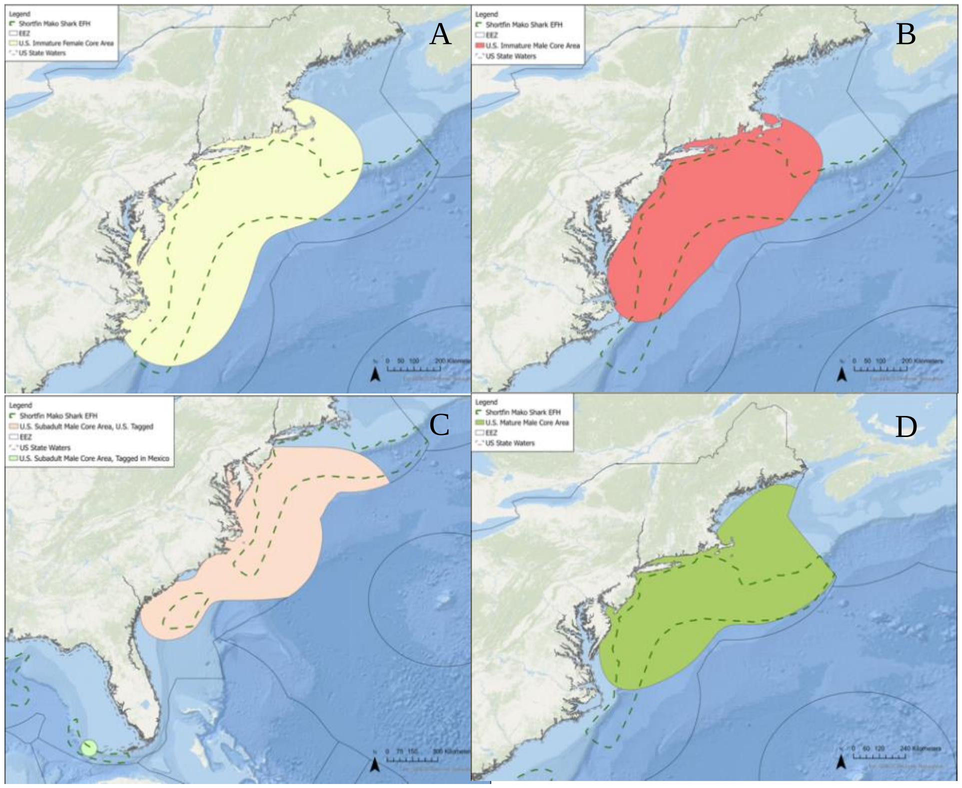

Figure 11. Core areas in U.S. waters of immature females (A), immature males (B), and mature males (D) of sharks tagged in the U.S. and NOAA's shortfin mako shark EFH (areas within the dark green dashed boundaries) in the WNA. Figure C shows core areas of subadult males in the U.S. EEZ, the pink core area is from subadult males tagged off U.S. waters, the light green core area is from subadult males tagging off Mexico. Black solid lines represent EEZs, grey dashed lines represent U.S. State waters.

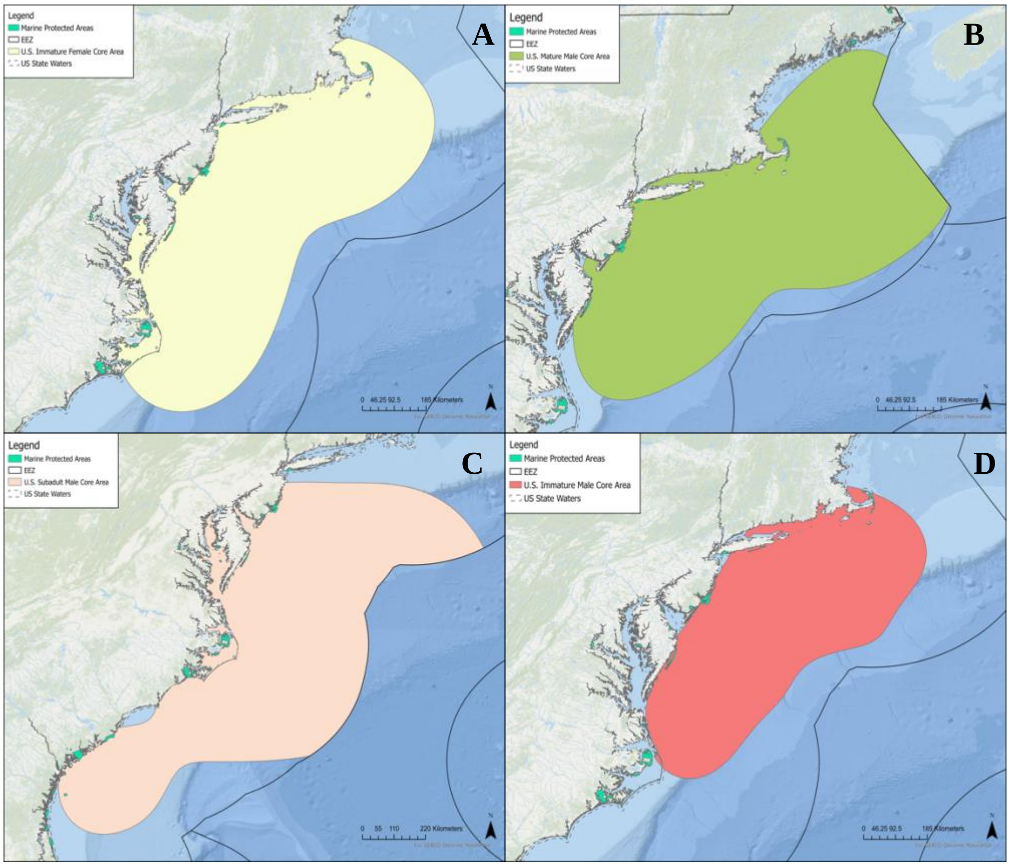

Figure 12. Core areas in U.S. waters of immature females (A), immature males (B), subadult males (C), and mature males (D) of sharks tagged off the U.S. and MPAs in the WNA. Black solid lines represent EEZs, grey dashed lines represent U.S. State waters.

Tables

Table 1: Relative proportion of location estimates from makos tagged in U.S. waters relative to EEZs in the WNA and GOM. The "Proportion per EEZ" column represents the relative proportion of the location estimates U.S. tagged population in each EEZ. The columns showing the proportion of the different demographics represent the percent of the location estimates within the respective country EEZ that are made up by each demographic.

EEZ	*Proportion per EEZ*	*Number of Location Estimates*	*Number of Unique Sharks*	*Percent Immature Female*	*Percent Immature Male*	*Percent Subadult Male*	*Percent Mature Male*
USA	57.40	5978	36	27.90	56.93	8	7.18
International	29.54	3076	22	37.06	40.05	16.48	6.40
Canada	10.07	1049	17	39.47	51.29	7.53	1.72
Bermuda	0.77	80	7	40	18.75	11.25	30
Venezuela	0.76	79	1	0	100	0	0
Bahamas	0.75	78	4	64.10	0	35.90	0
Dominican Republic	0.19	20	2	45	55	0	0
Puerto Rico	0.12	13	1	0	100	0	0
Anguilla	0.12	12	1	0	100	0	0
Antigua & Barbuda	0.06	6	1	100	0	0	0
Cuba	0.06	6	1	0	0	10	0
Turks & Caicos	0.06	6	1	100	0	0	0
US Virgin Islands	0.04	4	1	0	100	0	0
British Virgin Islands	0.03	3	1	0	100	0	0
Jamaica	0.02	2	1	0	0	100	0

Table 2: Relative proportion of location estimates from makos tagged off Mexico relative to EEZs in the WNA and GOM. The "Proportion per EEZ" column represents the relative proportion of the location estimates Mexican tagged population in each EEZ. The columns showing the proportion of the different demographics represent the percent of the location estimates within the respective country EEZ that are made up by each demographic.

EEZ	*Proportion per EEZ*	*Number of Location Estimates*	*Number of Unique Sharks*	*Percent Female*	*Percent Immature Male*	*Percent Subadult Male*	*Percent Mature Male*
Mexico	80.15	6738	23	66.80	0	12.81	20.39
USA	9.40	790	16	47.47	0	29.11	23.42
Cuba	5.11	430	16	82.33	0	7.91	9.77
Venezuela	1.78	150	2	100	0	0	0
Honduras	1.25	105	6	83.81	0	0	16.19
International	0.84	71	11	71.83	0	8.45	19.72
Costa Rica	0.36	30	1	100	0	0	0
Belize	0.27	23	2	34.78	0	0	65.22
Columbia	0.23	19	2	100	0	0	0
Jamaica	0.21	18	2	94.44	0	0	5.56
Cayman Islands	0.12	10	2	60	0	0	40
Nicaragua	0.07	6	1	100	0	0	0
Bahamas	0.05	4	1	100	0	0	0
Puerto Rico	0.05	4	1	100	0.	0	0
Aruba	0.02	2	1	100	0	0	0
Dominican Republic	0.02	2	1	100	0	0	0
Haiti	0.02	2	1	100	0	0	
Quitasueno Bank	0.01	1	1	100	0	0	0
Saba	0.01	1	1	100	0	0	0
US Virgin Islands	0.01	1	1	100	0	0.	0

Table 3: Relative proportion of location estimates from makos in U.S. waters relative to U.S. state waters in the WNA and GOM. The "Proportion per State" column represents the relative proportion of the location estimates within U.S. waters in each jurisdiction. The columns showing the proportion of the different demographics represent the percent of the location estimates within the respective state that are made up by each demographic.

State	***Proportion per State***	***Number of Location Estimates***	***Number of Unique Sharks***	***Percent Female***	***Percent Immature Male***	***Percent Subadult Male***	***Percent Mature Male***
Rhode Island	0.28	19	3	5.26	94.74	0	0
Mass	0.22	15	5	20	80	0	0
New York	0.12	8	3	25	75.00	0	0
North Carolina	0.04	3	2	66.67	0.00	33.33	0
No State	99.34	6723	52	30.27	50.01	10.52	9.13

Table 4: Proportion of U.S. tagged mako core areas in U.S. waters that overlap with MPAs in the NWA and GOM. Fishing Restrictions and Constancy are the precent of the portion of the MPA that overlaps with the core areas that must adhere to the corresponding site restrictions.

	Immature Female Core Area	*Immature Male Core Area*	*Subadult Male Core Area*	*Mature Male Core Area*
Total Overlap	0.5%	0.4%	0.4%	0.3%
Fishing Restriction				
Recreational Fishing Restricted	20.8%	20.6%	13.8%	26.5%
Commercial Fishing Restricted	3.8%	2.9%	5.2%	2.9%
Commercial and Recreational Fishing Restricted	22.6%	26.5%	20.7%	23.5%
Commercial Fishing Prohibited and Recreational Fishing Restricted	26.4%	23.5%	31%	26.5%
Commercial Fishing Prohibited	7.5%	11.8%	12.1%	8.8%
Commercial and Recreational Fishing Prohibited	18.9%	14.7%	17.2%	11.8%
Constancy				
Year-Round	96.2%	94.2%	98.3%	94%
Seasonal	3.8%	5.8%	1.7%	5.9%

Table 5: Mako core areas in U.S. waters that overlap with shortfin mako EFHs in the NWA and GOM.

	Percent of US Core Area that overlaps with EFH
Tagged in the US	
Immature Females	51.1%
Immature Males	61.1%
Subadult Males	33.7%
Mature Males	51.5%
Tagged off Mexico	
Subadult Males	60.7%

Table 6: Results from the Welch's t-test to investigate Amendment 11's impact on the time makos have before they are susceptible to fishing effort.

	Mean of pre-Amendment 11 (days)	***Mean of post-Amendment 11 (days)***	***Difference (days)***	***95% CI Lower***	***95% CI Upper***	***t***	***df***	***p***
Days Safe	119.9	155.7	35.8	-122.9	51.3	-0.9	15.2	0.4

CHAPTER 2

Intersection of offshore energy exploration and habitat of a highly migratory top level predator in the North Atlantic Ocean

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Abstract

To adhere to the ever-growing demand for consumer energy, the U.S. intends to expand offshore oil and natural gas extraction in the Gulf of Mexico and wind power in the Northwest Atlantic. Introducing anthropogenic infrastructure into the open ocean ultimately increases the interaction between these structures and highly migratory oceanic species (Bailey, Brooks, and Thompson, 2014). Though highly migratory species are among the most vulnerable to widescale population changes, there is a considerable knowledge gap regarding offshore oil rigs and wind farms' impact on highly migratory oceanic species (Bailey, Brooks, and Thompson, 2014). Our goal for this study was two-fold. First, we aimed to assess offshore rigs and windfarms' interaction with the shortfin mako shark, an endangered, highly migratory species. Second, we estimated the amount of influence that offshore rigs and wind turbines might have on large-scale shark movement behavior. We used a large satellite tracking dataset of 60 sharks to derive shark core areas and quantify the overlap between highly utilized areas and offshore oil rigs and wind farms in the Gulf of Mexico and Northwest Atlantic Ocean. In addition, we employed a step-selection function to assess the influence that offshore rigs and wind farms may have on shark movement behavior. The degree of overlap between the shark's core area and existing oil rigs was negligible. Further, offshore oil rigs and the Block Island Wind Farm did not significantly affect shark movement behavior. However, the substantial overlap between proposed offshore wind lots and shark core areas in the Northwest Atlantic exposes the need to develop a deeper understanding of offshore wind farms' effect on highly migratory species like the shortfin mako shark.

Abbreviations

BIWF – Block Island Wind Farm

GOM – Gulf of Mexico

HMS – Highly Migratory Species

IUCN - International Union for Conservation of Nature

OWFs – Offshore Wind Farms

SSM – State-space Model

SSF – Step-selection function

U.D. – Utilization Distribution

WNA – Northwest Atlantic

1. Introduction

With the global demand for consumer energy ever-growing, energy exploration is expanding to offshore resources. Offshore oil and gas rigs (hereafter: rigs) and active lease lots for oil and gas exploration are expanding into deeper pelagic waters off the Gulf of Mexico (GOM). Simultaneously, the U.S. is looking to renewable sources to meet the high demand for consumer energy while concurrently combating global climate change. Currently, the spotlight is on offshore wind energy development in the Northwest Atlantic (WNA). However, the environmental impact of expanding offshore energy exploration into deeper oceanic habitats remains unclear.

Over 3,000 active rigs and over 1,400 active leases exist in the GOM (BOEM, n.d.). The rigid substrate formed from the foundation and the stationary vertical structure set the stage for an artificial reef system to develop on and around rigs (Claisse et al., 2014). Rigs have the highest secondary production levels off the California coast than any other studied marine habitat (Claisse et al., 2014). Presently, the number of artificial reefs sustained by active and decommissioned rigs outweigh the number of natural reefs in the GOM, making it the world's most extensive artificial reef system (Ajemian et al., 2015; Franks, 2000; McKinney et al., 2012). The artificial reef network in the GOM attracts a high taxonomic diversity of species (Franks, 2000). Many well-known transient species show relatively high site fidelity close to rigs, residing in the area for days to even weeks (Edwards and Sulak, 2006; Filmalter et al., 2015; Haugen and Papastamatou, 2019; Methratta and Dardick, 2019).

Aside from their contribution to global climate change, rigs are associated with numerous detrimental ecological effects. For instance, during the exploration and installation process, there is increased boat traffic and a high degree of habitat destruction from drilling and laying pipelines (Cordes et al., 2016). Further, drilling is associated with fluid discharge that pollutes the surrounding waters (Gray et al., 1990). While operational, there is heavy boat traffic to transfer products to and from the rig, as well as the ongoing risk of catastrophic oil spills and blowouts, such as the Deepwater Horizon accident and the blowout at the Ixtoc I rig, both in the GOM (Cordes et al., 2016; Jernelöv, 2010). Expanding rigs into deeper oceanic waters inevitably introduces these risks to new environments. Therefore, it is imperative to gather baseline data of habitat use by marine organisms before expanding rigs to observe long-term environmental impacts that coincide with rig expansion.

The development of offshore wind farms (OWFs) is relatively new. Denmark installed the first operational offshore wind turbine in 1991 and the first operational OWF in 2002 (Lindeboom et al., 2015). Regardless of its modernity, the expansion of OWFs has catalyzed. Europe has over 4,000 turbines, and Asia now has over 800 turbines (Diaz and Soares, 2020). In comparison to Europe and Asia, the U.S. is currently in its infancy for offshore wind development. The U.S. has two commercially operational OWFs, the Block Island Wind Farm (BIWF), consisting of five turbines, and the Coastal Virginia Offshore Wind pilot project, consisting of two wind turbines. However, the U.S. plans for a rapid expansion of OWFs in the WNA to derive 20% of the nation's energy from OWFs by 2030 (DOE, 2008; Lindenberg, 2009).

Although it is indisputable that the expansion of OWFs will reduce anthropogenic carbon emissions, the response to the installation of OWFs in the WNA has been controversial. Relative to other renewable energy sources, wind energy is a clean energy source with readily available resources and technology for construction (Esteban et al., 2011). Additionally, the ocean provides a vast area for a widespread expansion of OWFs, and stronger, more stable wind patterns relative to onshore wind (Bergström et al., 2014). Yet, the large-scale impacts that OWFs may have on the ecosystem are undetermined (Halouani et al., 2020). There are several risks with rapidly introducing new human-made infrastructure into an environment already bearing a suite of anthropogenic disturbances (Raoux et al., 2017).

Evidence shows both positive and negative ecological impacts of offshore wind; therefore, the planning phase must consider ecosystem impacts (Punt et al., 2009). Previous work shows that the construction phase of OWFs is exclusively associated with adverse environmental effects (Bergström et al., 2014). Such negative impacts include noise from construction, most prominently from pile driving, increased vessel traffic, water pollution, and escalating the risk of vessel collisions with marine organisms (Bailey, Brooks, and Thompson, 2014; Bangley et al., 2020; Secor et al., 2020). If not adequately planned, construction activities may disrupt biologically significant habitats (Secor et al., 2020). Insight to habitat utilization patterns and seasonal timings of migrations can inform energy companies when the least intrusive time to manufacture OWFs may be (Bergström et al., 2014; Methratta and Dardick, 2019; Secor et al., 2020).

The operational phase of OWFs instills positive and negative impacts on the surrounding environment (Bergström et al., 2014). OWFs act as artificial reefs, similar to the rigs in the GOM (Baily, Brooks, and Thompson, 2014; Bangley et al., 2020;

Bray et al., 2016; Halouani et al., 2020; Snodgrass et al., 2020). In Europe, colonization of species establishing the food web base appeared within the first years of OWF installation (Bergström et al., 2016). The establishment of lower trophic species allows for an enhanced forage base that ultimately develops a highly productive and attractive environment (Halouani et al., 2019; Methratta and Dardick, 2019).

Along with introducing an artificial reef habitat, OWFs alter oceanographic variables that impact productivity levels (Friedland et al., 2021). Wind turbines produce sizable wind wakes, increasing the intensity of vertical mixing and pulling up' valuable nutrients into the euphotic zone, making them accessible to primary producers, and ultimately increasing the local ecosystem productivity (Brogström, 2008; Floeter et al., 2017). This increased productivity due to the combined artificial reef system and favorable oceanographic variables is likely to propagate up trophic levels, and attract migratory predators (Friedland et al., 2021).

The large-scale assessment of impacts of offshore energy exploration on marine organisms is unclear, as there is a lack of baseline data for many marine animals (Bray et al., 2016). There is a considerable knowledge gap concerning how rigs may impact larger pelagic species, especially highly migratory species (HMS) (Snodgrass et al., 2020). In the GOM, most of the research associated with fish habitat utilization of artificial reefs focuses on demersal and highly valued targeted species using potentially biased fishery-dependent data (Snodgrass et al., 2020). Similarly, most existing research on OWF environmental impacts focuses on local ecosystem effects from a single wind farm (Lindeboom et al., 2015). Though local ecosystem effects of OWFs are critical to investigate, excluding large-scale environmental responses to OWFs obstructs a holistic understanding of OWFs impacts (Lindeboom et al., 2015; Methratta and Dardick, 2019). Further, much of the species-specific OWF impact studies conducted have been focused on marine mammals and sea birds, leaving other ecologically important groups like highly migratory fish species and apex predators vastly understudied (Bailey, Brookes, and Thompson, 2014; Methratta and Dardick, 2019).

Though the number of environmental impact studies of offshore infrastructure is increasing, the whole-scale ecosystem impacts remain unknown (Willsteed et al., 2018). A considerable knowledge gap exists about how introducing an artificial reef system in the open ocean will alter the ecosystem in the GOM and even more so in the WNA. The introduction of anthropogenetic infrastructure in the open ocean is likely to influence marine organism habitat use through attraction or avoidance (Bailey, Brooks, and Thompson, 2014). For instance, an artificial reef system may increase resident behavior during marine migrations, thereby potentially changing local ecosystem processes, such as food web interactions (Secor et al., 2020). Predictive models of the effects of OWFs on food webs support this idea. Ecopath with Ecosim models indicate that the installation of OWFs will increase ecosystem activity and the local abundance of migratory apex predators (Raoux et al., 2017, 2019).

Sufficient baseline data of species distribution and habitat utilization relative to offshore energy exploration before construction is imperative to accurately investigate the environmental impacts over time (Bray et al., 2016). Further, at least two years of baseline data are required to truthfully encapsulate the migratory behaviors of species

(Bailey, Brookes, and Thompson, 2014; Diederichs et al., 2008). Unfortunately, marine animals' abundance, distribution, and habitat utilization concerning offshore energy exploration are poorly understood, especially for OWFs and HMS (Bailey, Brookes, and Thompson, 2014; Secor et al., 2020).

Historically, accurately assessing the effects of human activity in marine ecosystems on a large scale has been limited by considerable knowledge gaps of marine species' natural spatial distributions and migratory behaviors (Bergström et al., 2014). However, the continuous development of satellite telemetry has opened the doors to acquire large-scale, high-resolution, and long-term animal movement data (Jonsen, 2005; Vaudo et al., 2017). This study used a large long-term satellite tracking dataset on movements and habitat use of shortfin mako sharks (*Isurus oxyrinchus*, hereafter: mako) to investigate core areas of activity and movement patterns in relation to offshore energy exploration in the WNA and GOM.

Makos are a well-known HMS covering long distances in a short time and displaying residential behavior in areas of high productivity (Bryne et al., 2019l Casey and Kohler, 1992). As such, mako core areas of activity are likely a proxy or productive and ecologically important habitats along continental shelf ecosystems in the WNA and GOM. In addition, apex predators maintain healthy community structures through top-down control (Block et al., 2011). Therefore, conservation strategies periodically use top predators as indicators for biodiversity and ecosystem health (Sergio, Newton and Marchesi, 2005).

Mako sharks are a highly valued migratory apex predator caught and retained in large numbers and one of the most vulnerable populations to overexploitation

(Gallagher, 2014). The North Atlantic mako stock is presently overfished and experiencing overfishing, placing it on the International Union for Conservation of Nature's (IUCN) red list for endangered species (Bryne et al., 2017; Campana, 2016; Gallagher, 2014; Rigby et al., 2019). Makos are commonly caught as bycatch in commercial and recreational fisheries in the North Atlantic (Bryne et al., 2017). They are retained in large numbers due to their high economic value, as their whole body is marketable, and they make up a large portion of the global shark fin trade (Compano, 2001; Fields et al., 2017).

The high productive reef system supported by offshore energy infrastructure sustains attractive habitats to migratory sharks (see e.g., Ajemian e al., 2020; Filmalter et al., 2015; Haugen and Papastamatou, 2019; McKinney et al., 2012; Robinson et al., 2013). In addition, recreational fisheries heavily exploit artificial reefs (Claisse et al., 2014). Therefore, expanding reef systems into pelagic waters elevates the chance of vulnerable species like makos encountering fishing efforts and catalyzing their overexploitation (Claisse et al., 2014; Eddy, Brill, and Bernal, 2016; Franks, 2000; Snodgrass et al., 2020; Stehfest et al., 2013).

As a result of their highly migratory behavior, ecological importance, attraction to productive habitats, and endangered classification, makos serve as a suitable species to use to investigate the large-scale impacts that the expansion of offshore energy exploration may have on overlooked HMS and top predators. Additionally, baseline data of mako habitat use in the WNA and GOM before offshore energy construction exists. Therefore, we have the opportunity to identify pre-development areas of core activity and movement patterns and evaluate temporal changes in habitat use over the next few decades as offshore energy exploration and development drastically expand.

Goals

This project will use a long-term satellite tracking dataset of mako sharks to 1) determine the spatial ecology of our tagged mako sharks relative to rigs and active leases in the GOM and OWF development in the WNA, 2) Evaluate the degree of influence that active rigs and the BIWF may have on mako movement behaviors, and 3) Provide adequate baseline data of mako spatial ecology relative to the proposed OWFs in the WNA.

2. Methods

2.1. Tagging and Data Collection

We tagged sharks in three locations, two off the U.S. East coast in the vicinity of Block Island, Rhode Island (~41.16°N, 71.58°W), and Ocean City, Maryland (~38.10°N, 74.50°W), the third location was off the Yucatan Peninsula, around Isla Mujeres, Mexico (~21.29°N, 86.29°W). Sharks were caught via rod and reel and brought onboard or secured along the side of the boat (Bryne et al., 2017, 2019; Vaudo et al., 2017). Sharks brought on board had their eyes covered with a wet towel to reduce stress, and we placed a saltwater hose in their mouth to irrigate their gills (Bryne et al., 2017& 2019; Vaudo et al., 2017). Sharks were sexed, and their total and fork lengths were measured (Bryne et al., 2017& 2019; Vaudo et al., 2017).

We attached a Smart Position Only Transmitter (SPOT; Wildlife Computers, Redmond WA) to the dorsal fin of each shark. SPOT tags communicate with the Argos satellite network (www.argos-system.org) and transmit the shark's location when the dorsal fin breaks the water's surface (Bryne et al., 2019; Vaudo et al., 2017). Argos locations are associated with observational error spanning rom <350m to >1000m correlated with six location class error radii: 3, 2, 1, 0, A, B (Freitas et al., 2008). Location class Z detections were omitted from the analysis as they represent invalid locations (www.argos-system.org). The observation error associated with individual ARGOS detections results from the number of satellites the tag communicated with, the time for the detection to reach the satellites, and the time between sequential detections (Jonsen, Flemming and Myers., 2005).

2.2.Data Pre-Processing

Satellite telemetry studies are associated with a spatial bias towards sampling locations (Block et al., 2011; Harrison et al., 2018). In addition, post-release behavior can lead to animals displaying abnormal swimming behavior as a response to the tagging procedure (Talwar et al., 2017).The sharks in this study traveled over an average of 200 km within the first five days since being tagged. Therefore, to account for sampling location bias, we removed the first five days of each track. Removing the first five days of each track simultaneously accounted for post-release behavior, as previous work (Vaudo et al., 2016) found negligible differences in swimming behavior as a response to tagging.

Additionally, tagging location bias is greater for shorter tracks (Harrison et al., 2019). However, in this study the tracks used had an average duration of 276 days. Rooker et al. (2019), suggests that tracks lasting a minimum of 150 days are accurate representatives of animal habitat use. In this study 73% of our tracks exceeded 150 days, suggesting our dataset resembles biologically representative mako shark habitat use in the WNA and GOM.

2.2.1. State-Space Modeling

SPOT tags only communicate with the Argos satellite system when the dorsal fin breaks the surface. As a result, sharks that are more surface-oriented detect more frequently, thus biasing the population-level spatial distribution towards their habitat use (Block et al., 2011; Freitas et al., 2008). To account for surface behavior bias and ARGOS location error, we fit a simple random walk state-space model (SSM) to the location data using the package 'foiegras' in RStudio (Jonsen and Patterson., 2020; R Core Team, 2019). The SSM uses a maximum likelihood estimation approach (Jonsen and Patterson., 2020). It includes a speed distance angle filter to predict the most probable trajectory at pre-determined regularized time steps while simultaneously accounting for Argos observation error (Jonsen and Patterson., 2020).

We used the SSM to produce location estimates for every 12 hours, as sharks in this study reported on average four times per day. We set the max speed for the sharks to 2.5 m/s and forwent using the turning angle component of the SSM, as our data was associated with long gaps. The turning angle component of the SSM does not consider time, therefore it has a tendency to omit valid location estimates for data associated with long time intervals between successive locations. We developed all tracks simultaneously.

Prior studies show that short tracks and long gaps in data compromise the SSM's ability to accurately estimate trajectories (Bailey et al., 2008; Block et al., 2011). To account for this, we removed tacks less than 20 days in duration before fitting the SSM and filtered out fitted location estimates associated with gaps that exceeded ten days in time (Bailey et al., 2008; Block et al., 2011).

2.2.2. Developing Mako Core Areas

We identified highly utilized areas for tagged mako sharks using a bivariate normal kernel density analysis to estimate a population-level utilization distribution (U.D.) using the location estimates from the SSM. Population-level U.D. estimates are susceptible to pseudo-replicative effects, as the U.D. estimate may be biased towards sharks that detect more frequently (Shimada et al., 2017). To mitigate this bias, we followed the framework from Shimada et al. (2017). We developed individual U.D.s for each shark using the 'adehabitatHR' package in R using the reference bandwidth "href" as the smoothing parameter over a 0.05° x 0.05° grid (Calenge, 2006). We then averaged the individual estimated densities per grid cell to develop a final population-level U.D. estimate (Shimada et al., 2017). To derive mako core areas, we used the 50% U.D. isopleths (Simpfendorfer., 2012; Vaudo et al., 2017). The 50% U.D. isopleth is commonly used as an animal's core area, as it is the periphery that holds 50% of the population (Calenge, 2019). When considering the relative size of the 50% isopleth boundary, this suggests that this area is where an animal spends the majority of their time (Vander Wal & Rogers, 2012). Additionally, we set boundaries for the U.D. to exclude inaccessible locations (i.e., on land) using the 'marmap' package in R.

2.3. Oil Rigs

2.3.1. Evaluating the proportion of active rigs and active oil and gas leases in mako core areas.

We calculated the relative proportion of rigs and leases that fall within the mako core area to determine the degree of overlap between active rigs and mako core areas and active lease areas for oil and gas exploration and mako core areas. To do so, we uploaded the mako core areas into ArcGIS pro as polygon shapefiles. We then imported the rig location and lot shapefiles from https://www.data.boem.gov/Main/Mapping.aspx and selected the active rigs and lease lots. We determined the proportion of rigs within the core area by dividing the number of rigs within the core area by the total rigs in the GOM then multiplied the quotient by 100. We used the same procedure to determine the proportion of active leases within the core area.

2.3.2. Degree of influence rigs have on mako movement behavior.

To determine whether or not makos disproportionally used the habitat around the rigs relative to other available habitats, we implemented a step-selection function (SSF) using the 'amt' package in R (Signer, Fieberg, and Avgar, 2011). SSFs use step lengths to link successive locations and identify future available steps based on speeds and turning angles (Thurfiell, Ciutu, and Bouce, 2014). SSFs then use a conditional logistic regression to predict which next step the individual is most probable to take based on pre-defined predictive variables (Fieberg et al., 2021).

Our goal was to evaluate whether or not makos disproportionately used the area around rigs. Therefore, the only covariate considered was the zone of influence around the rig. While there is no empirical evidence concerning the range of influence rigs may have on mako movement, previous research suggests that rigs have a 10 km range of influence for tuna, a highly migratory species and one of the mako shark's common prey species (Girard, Benhamour, and Dagorn, 2004; Snodgrass et al., 2020). To construct the zones of influence, we created a 10 km buffer around each rig in the GOM in ArcGIS pro and imported the buffers into R in raster format.

As mentioned, the only predictor variable for the SSF was whether or not the shark is within the zone of influence. However, the model cannot accurately predict the effect that the zone of influence may have on mako's movement if they never visited the zone of influence (Fieberg et al., 2018). Therefore, the only tracks considered were those from sharks with at least one location estimate within the zone of influence.

2.4.Offshore Wind Farms

2.4.1. Evaluating the degree of overlap between OWF and mako core areas.

To quantify the overlap between proposed offshore wind lots and mako core areas, we calculated the percent of the area encompassed by active offshore wind lease lots and wind planning areas that fall within the mako core area. We did so by using ArcGIS pro using similar methods as Stenhouse et al. (2020). We downloaded the shapefiles for the leased wind development lots and the wind planning areas from https://www.boem.gov/renewable-energy/mapping-and-data/renewable-energy-gis-data and imported them into ArcGIS pro, and calculated the total area of the leased wind development lots and the wind planning areas in km^2. We then calculated the area of the leased wind development lots and the wind planning areas that fall within the mako core area. To quantify the proportion of the proposed lots within the core area, we divided the area of the leased lots that fall within the core area by the total area of the leased lots and multiplied the quotient by 100. We then repeated this procedure with the wind planning areas.

2.4.2. Degree of influence BIWF has on mako movement behavior.

Offshore wind turbines are hypothesized to support artificial reef habitats, thus potentially altering migratory pathways. One way to test this hypothesis is to use an SSF. Here we used an SSF to determine the influence that BIWF may have on mako movement behavior. Specifically, we used an SSF in a very similar way as we did for the rigs in the GOM to determine if makos disproportionately use the habitat around the wind turbines relative to all other available habitats.

Similar to rigs, there is no empirical evidence concerning offshore wind turbines' range of influence on mako movement. Therefore, we again used 10km as the zone of influence, assuming that the artificial reef habitat surrounding the turbines will have a similar zone of influence as those surrounding the rigs in the GOM. Additionally, the only predictor variable for the SSF was whether or not the shark is within the zone of influence. The only tracks considered were those from sharks with at least one location estimate within the zone of influence.

3. **Results**

3.1.Tagging and Data Collection

Eighty-five sharks provided 58,574 usable detections from March of 2013 to October of 2019. Of the sharks reported, thirty-six were females, ranging in size from 89-252cm in fork length and providing 24,371 detections, and 49 were males, ranging in size from 117-220cm in fork length and providing 34,203 detections. Tracking duration ranged from 4-754 days.

3.2.Data Pre-Processing

3.2.1. State-Space Modeling

We received a total of 18,821 location estimates from 60 sharks from the simple random walk SSM (Figure 1). Of the sharks included, 27 were females providing 8,624 location estimates, and 33 were males, providing 10,197 location estimates. The majority of the reduction in usable tracks came from removing tracks less than 20 days in time and long gaps. Additionally, the SSM did not converge for one of the tracks; therefore, we omitted it from the sample.

3.2.2. Developing mako core areas

The population-level U.D. estimates showed that the mako sharks used an extensive amount of the WNA and GOM. The mako shark home range (95% U.D. isopleth) extended from 9.95°-50.39°N and 98.27°-37.47°W (Figure 2). The U.D. estimates also showed two distinct core areas (50% U.D. isopleth). The first core area was off of the U.S. east coast, spanning from Massachusetts to North Carolina (34.49°-42.48°N and 75.11°-68.31°W). The second core area was off of the Yucatan Peninsula (19.05°-24.96°N and 89.1°-85.15°W).

3.3.Oil Rigs

3.3.1. Evaluating the proportion of active rigs and oil and gas leases in mako core areas.

There was little overlap between the mako's highly utilized area and the active rigs. The mako shark core area in the GOM was located further south of both active rigs and active lease lots. While a substantial proportion of rigs (82.4%) fell within the mako's home rage, there were no rigs within the core area (Table 1, Figure 4).

Additionally, a considerable proportion of the active leased lots for oil and gas explorations (95.5%) were within the mako's home rage (Table 1, Figure 3). However, there were no active lease lots in the core areas.

3.3.2. Degree of influence rigs have on mako movement behavior.

Three sharks had at least one location estimate within the oil rig zone of influence. Two of the sharks were mature males (FL = 178cm and 201cm), and the third shark was an immature female (FL = 252cm). Results from the SSF showed that rigs have a negligible effect on mako movement behavior, as all three coefficients were close to 0 with p-values > 0.05 (Table 2, Figure 5). While two of the three sharks showed negative selection for the habitat surrounding the rigs, the magnitude of their avoidance behavior was insignificant ($p > 0.05$). The SSF results for shark 162045 had relatively large confidence intervals. The small sample size of location estimates around the rigs ($n = 6$) results in large confidence intervals. Additionally, there does not appear to be any difference in movement behavior around the rigs by sex or size. However, this is difficult to conclude with a small sample size ($n=3$).

3.4.Offshore Wind Farms

3.4.1. Evaluating the degree of overlap between OWF and mako core areas.

BOEM has active leases for offshore wind development with 17 different energy companies. The percent overlap analysis showed that 100% of the area that active leases encompass fell within the mako core area in the WNA (Table 3, Figure 6).

In addition to the active leases, there are 11 different call areas for future offshore wind development. The percent overlap analysis showed that 5 of the 11 call areas were entirely within the mako core area, making up 43% of the total area that the call areas encompass (Table 3 Figure 5). The call areas that fell within the core area all are a subset of the New York Bight Wind Energy Area off Long Island, NY, and New Jersey (Figure 6).

3.4.2. Degree of influence BIWF had on mako movement behavior.

Like the rigs, three sharks had at least one location estimate within the BIWF zone of influence from 2016-2019. Two of the sharks were immature females (FL = 158 and 185), and one shark was an immature male (FL = 150). Results of the SSF show a negative selection for all three sharks. However, the magnitude of all three selection strengths was insignificant ($p > 0.05$), suggesting that BIWF has a negligible effect on mako movement behavior (Table 5, Figure 7). Additionally, all three individuals had large 95% confidence intervals, most likely due to the small sample size of detections within the zones of influence.

4. **Discussion**

4.1.Oil Rigs

Results from quantifying the number of rigs and active leases in the core area and the SSF imply that the tagged makos in this study do not disproportionately utilize the waters around the oil rigs. Despite many of the rigs and active leases falling within the makos' home range (82.4% and 95.5%, respectively), there was no overlap between the rigs or leases with the mako core area in the GOM. Similarly, results of the SSF suggest that rigs have negligible effects on mako movement behavior.

However, these results do not align with previous tracking studies of makos in the GOM. Gibson et al. (2021) and Rooker e al. (2019) show that the core areas of their tagged makos are located in the northwestern portion of the GOM, overlapping with the active rigs and leased lots. Additionally, while the motivation behind their aggregations is unknown, silky, tiger, porbeagle, and whale sharks have been reported aggregated around rigs (see e.g., Ajemian et al., 2020; Filmalter et al., 2015; Haugen and Papastamatou, 2019; McKinney et al., 2012; Robinson et al., 2013). Whale sharks, in particular, presented directed movements towards rigs and foraging behavior around rigs (McKinney et al., 2012; Robinson et al., 2013).

One explanation for the discrepancy between our results and the results of previous work may be the migratory behavior of mako sharks in the GOM and tagging location. Although makos are a well-known HMS, they show substantially less migratory behavior in the GOM than other regions, such as the WNA (Vaudo et al., 2017). Oceanographic properties, such as temperature, primary productivity, and turbidity, influence mako movement behavior (Birkmanis et al., 2020; Gibson et al., 2021; Vaudo et al., 2017 and 2016). However, in the GOM, there is a high degree of consistency among these oceanographic properties (Bryne et al., 2019; Vaudo et al., 2017). In this study, the Sharks reported in the GOM were tagged off the Yucatan Peninsula, around Isla Mujeres, Mexico. The Yucatan Peninsula is across the GOM from the rigs and leased lots in the North-Western Region of the GOM. The consistency in environmental conditions reduces the need for makos to make energetically costly migrations to locate ecologically favorable conditions that artificial reefs provide (Bryne et al., 2019; Vaudo et al., 2017).

Gibson et al. (2021) also found high site fidelity for makos in the GOM. Specifically, larger females in the GOM displayed strong sight fidelity, indicating potential regional and demographic differences in migratory behavior for mako sharks (Gibson et al., 2021). Most of the sharks tagged off Mexico and reported in the GOM were large females (Supplementary Table 1). If larger females are characteristic of higher site fidelity, most sharks tagged off Mexico may not deviate from the Yucatan Peninsula.

Additionally, vertical habitat utilization for makos may differ by size, in that larger makos spend more time in deeper water (Mucientes et al., 2009). Considering that most of the sharks tagged in the GOM were relatively large, they may not have reported as often. In this case, we would have filtered out their tracks during data analysis. Although previous work suggests demographic segregation for sharks (see e.g., Haulsee et al., 2018; Mucientes et al., 2009; Natanson et al., 2020), more research is needed to determine the magnitude of demographic-based differences in migratory behavior and vertical habitat use for mako sharks in the GOM.

It is noteworthy that future expansion of rigs and exploration for oil and gas may intrude on essential habitats for mako sharks. High site fidelity for mako sharks in the GOM suggests a biologically significant and preferred habitat (Vaudo et al., 2017). For instance, the GOM may serve as potential mating and pupping grounds (Casey and Kohler., 1992; Gibson et al., 2021; Kohler et al., 2002; Natanson et al., 2020). Increased intrusive human activity from noise and water pollution, vessel traffic, and habitat destruction may disturb critical habitats, increasing the hardships makos endure to rebuild their depleting population.

Even more so, recreational fisheries, which are permitted to land live makos, heavily exploit rigs (Claisse et al., 2014). If rigs exclusively serve as attracting devices for makos, or if rigs expand into mako core areas, this could increase the landings of this endangered species. Increased fishing effort in the GOM may be detrimental to the mako population as most of the sharks in the GOM in our study and those showing site fidelity close to the rigs in Gibson et al. (2021) were large females. More research is required to assess the influence that rigs, and active leased lots may have on the mako movement in the Northwestern portion of the GOM.

4.2.Offshore Wind Development

The results from the percent overlap analysis between BOEM's OWF leased lots and call areas and the mako core area in the WNA imply that the proposed lots in the New England region will have a high degree of overlap with mako shark habitat utilization. Notably, the wind planning areas were either entirely within or outside of the core area. The northernmost call areas, all of which are the New York Bight call areas, are entirely within the core area, while the southern call areas of the North and South Carolina coasts were entirely outside of the core areas.

These results are not surprising as the New England shelf region sustains a highly productive environment heavily utilized by marine organisms. Marine animals show high site fidelity and migratory behavior along the WNA continental shelf, where many OWFs are proposed (Bryne et al., 2019). HMS commonly use the current direction from Gulf Stream along the WNA shelf to save energy for long-distance seasonal migrations (Risch et al., 2014; Rulifson et al., 2020). Additionally, the Gulf Stream is characterized by many unique oceanographic features as it is the most extensive frontal system in the North Atlantic Ocean (Chambault et al., 2017). Frontal systems generate high productive ecosystems, ultimately attracting a suite of marine organisms propagating up trophic levels (Wingfield et al., 2011).

The enriched oceanographic properties generated from the Gulf Stream facilitate a vital habitat for many sharks and migratory species along the WNA shelf (Shaw et al., 2021). Makos, in particular, are known to use the Gulf Stream for migrations and have displayed resident behavior along the WNA continental shelf as a result of favorable thermal and highly productive conditions (Campana, Marks, and Joyce, 2005; Casey and Kohler 1992; Rogers et al., 2015; Vaudo et al., 2017). This region may also be potential pupping grounds for makos (Natanson et al., 2020). Placing OWFs along the NWA shelf region will inevitably lead to a high degree of interaction between OWFs and mako sharks, and other HMS that use the Gulf Stream. However, the effects that OWFs may have on HMS and elasmobranch species have been drastically overlooked (Lindeboom et al., 2015).

One valuable method to begin looking at how OWFs may influence migratory behavior is SSFs. Here the SSF showed that makos neither favor nor avoid the BIWF. However, these findings may result from the small sample size of makos with at least one location estimate within the BIWF's zone of influence since its installment in 2016. This small sample size is most likely a result of BIWF's proximity to shore. Makos tend to stay offshore, and preliminary results of this study show that less than 1% of the total tracking dataset visited state waters.

An in-depth understanding of habitat use of HMS in the WNA is critical before introducing human-made, large-scale, and long-term ecosystem changes (Shaw et al., 2021). Although the SSF in this study suggested that BIWF has negligible influence on the mako movement, this framework can be used before, during, and after future OWF construction to provide fine-scale insights into habitat use of HMS in the WNA. SSFs can also provide insight into how an ecosystem is used by incorporating movement coefficients concurrently with environmental variables (Signer, Fieberg, and Avgar, 2018). Such information can provide invaluable insight into the impacts that OWFs may have on sharks and other HMS.

While ecological advantages may arise from introducing an artificial reef habitat in previously low productive environments, many of these benefits are contingent upon fishing regulations in and around OWFs (Bray et al., 2016; Methratta and Dardick 2019). If the highly productive environment attracts makos and other HMS to OWFs, their interactions with fishing efforts could increase. Local fishers have already noticed elevated fishing efforts around the BIWF (ten Brink and Dalton, 2018). There is a common understanding among recreational fishers and charter boats that if they are not catching much, they move to the BIWF (ten Brink and Dalton, 2018). The increased fishing effort around OWFs poses an increased risk to vulnerable populations such as the mako sharks. This risk increases as OWFs further expand.

A vastly understudied impact of offshore wind is its effects on electromagnetic organisms. Our results show that the OWFs and their electromagnetic field-producing cables will likely overlap with migratory pathways and core areas of mako sharks. Additionally, the further offshore that OWFs expand, the more likely it is that the cables will intersect with numerous marine animal migratory pathways (Friedland et al., 2021; Hutchinson et al., 2020). Electromagnetic fields produced by cables may impact elasmobranch species in their movement and behavior (Hutchinson et al., 2018). Sharks are reportedly attracted to and deterred by electromagnetic fields (see e.g., Porsmoguer et al., 2015; Robbins et al., 2011; Sigenthalet et al., 2016). Yet, detailed information on the magnitude of OWF cables impacting migratory elasmobranch species is lacking (Bangley et al., 2020).

Lastly, even though most OWF projects in the WNA are in the pre-construction planning phase, we must think long-term about OWF (Friedland et al., 2021). Specifically, we must keep in mind the potential ecological impacts of decommissioning wind turbines. The effects from decommissioning are analogous to those from construction (Bergström et al., 2014). For HMS, this may imply avoidance of commonly used habitats increasing energetic costs during seasonal migrations. Further research on the impacts of decommissioning is needed to understand how the ecosystem may respond.

5. **Conclusions**

This study has provided insight into the interactions between mako shark habitat utilization and offshore energy exploration in the WNA and GOM. Further, we have showcased a method to evaluate the degree of influence human-made infrastructure may have on the movement behavior of marine organisms using SSFs and provided critical baseline data in regard to mako shark habitat utilization and offshore energy infrastructure. As the search for energy expands into deeper pelagic waters, it is vital to incorporate the ecological impacts of the activity in the planning process, including both direct and indirect effects.

Despite the absence of knowledge surrounding offshore energy infrastructure and many marine species, offshore energy exploration is rapidly and drastically expanding. Without baseline data, the long-term effects that construction, operation, and decommissioning may have on marine animals will remain unknown (Bailey, Brookes, and Thompson, 2014). Considering highly migratory species are especially difficult to manage and are vulnerable to high fishing efforts, baseline data of their habitat use relative to offshore energy exploration is critical (Pacoureau et al., 2021).

Makos, in particular, are among the most susceptible to population declines as a consequence of their high retention rate coupled with low-productive life-history traits (French, 2015). Because managers do not plan to implement fishing exclusions around the new infrastructure, expanding offshore energy structures into their habitat will likely increase fishing mortality for this already overfished species (Bergström et al., 2014; Bray et al., 2016; Methratta and Dardick, 2019). For top migratory predators, the potential for the effects of overexploitation to cascade and affect other species is a crucial consideration moving forward (Lindeboom et al., 2015). The depletion of apex predators, such as makos, can lead to large-scale and irreparable ecosystem and economic (see e.g., Myers et al., 2007) changes by altering top-down control trophic processes (Block et al., 2011). As a consequence of anthropogenic activity, the decline of sharks may lead to detrimental trophic cascades (Baum and Worm, 2009; Block et al., 2011; Myers and Worm, 2003; Ruppert et al., 2013). Further, mako core areas correlate with high productive habitats, commonly associated with high levels of biodiversity (Vaudo et al., 2017). The high degree of overlap between OWF proposed lots and rigs and core areas in previous studies (e.g., Gibson et al., 2021; Rooker et al., 2019) suggests that this new infrastructure will overlap with areas of highly utilized areas for species other than mako sharks.

It has become evident that more fine-tuned research is needed to obtain a complete understanding of mako shark and other HMS movement behavior in the WNA and GOM as it relates to established and future anthropogenic offshore energy exploration. As the energy demand continues to rise and humans increasingly exploit offshore resources, knowledge of habitat use by highly migratory and vulnerable species is imperative for effective marine management as these ecosystems undergo large-scale artificial changes.

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References

Ajemian, M. J., Drymon, J. M., Hammerschlag, N., Wells, R. D., Street, G., Falterman, B., ... & Stunz, G. W. (2020). Movement patterns and habitat use of tiger sharks (*Galeocerdo cuvier*) across ontogeny in the Gulf of Mexico. *Plos one*, *15*(7), e0234868.

Ajemian, M. J., Wetz, J. J., Shipley-Lozano, B., Shively, J. D., & Stunz, G. W. (2015). An analysis of artificial reef fish community structure along the northwestern Gulf of Mexico shelf: potential impacts of "Rigs-to-Reefs" programs. *PloS one*, *10*(5), e0126354.

Bailey, H., Brookes, K. L., & Thompson, P. M. (2014). Assessing environmental impacts of offshore wind farms: lessons learned and recommendations for the future. *Aquatic biosystems*, *10*(1), 1-13.

Bailey, H., Shillinger, G., Palacios, D., Bograd, S., Spotila, J., Paladino, F., & Block, B. (2008). Identifying and comparing phases of movement by leatherback turtles using state-space models. *Journal of Experimental Marine Biology and Ecology*, *356*(1-2), 128-135.

Bangley, C. W., Curtis, T. H., Secor, D. H., Latour, R. J., & Ogburn, M. B. (2020). Identifying important juvenile Dusky Shark habitat in the northwest Atlantic Ocean using acoustic telemetry and spatial modeling. *Marine and Coastal Fisheries*, *12*(5), 348-363.

Baum, J. K., & Worm, B. (2009). Cascading top-down effects of changing oceanic predator abundances. *Journal of Animal Ecology*, *78*(4), 699-714.

Broström, G. (2008). On the influence of large wind farms on the upper ocean circulation. *Journal of Marine Systems*, *74*(1-2), 585-591.

Bergström, L., Kautsky, L., Malm, T., Rosenberg, R., Wahlberg, M., Capetillo, N. Å., & Wilhelmsson, D. (2014). Effects of offshore wind farms on marine wildlife—a generalized impact assessment. *Environmental Research Letters*, *9*(3), 034012.

Birkmanis, C. A., Freer, J. J., Simmons, L. W., Partridge, J. C., & Sequeira, A. M. (2020). Future distribution of suitable habitat for pelagic sharks in Australia under climate change models. *Frontiers in Marine Science*, *7*, 570.

Block, B. A., Jonsen, I. D., Jorgensen, S. J., Winship, A. J., Shaffer, S. A., Bograd, S. J., ... & Costa, D. P. (2011). Tracking apex marine predator movements in a dynamic ocean. *Nature*, *475*(7354), 86-90.

BOEM. (n.d.). State Activities. https://www.boem.gov/renewable-energy/state-activities

[dataset]BOEM. (n.d.) [Renewable Energy GIS Data]. Retrieved December, 2020, from https://www.boem.gov/renewable-energy/mapping-and-data/renewable-energy-gis-data

Bray, L., Reizopoulou, S., Voukouvalas, E., Soukissian, T., Alomar, C., Vázquez-Luis, M., ... & Hall-Spencer, J. M. (2016). Expected effects of offshore wind farms on Mediterranean marine life. *Journal of Marine Science and Engineering*, *4*(1), 18.

[dataset]Bureau of Safety and Environmental Enforcement, Office of Technical Data Management, Data Administration Unit (2021) [Offshore oil rig GIS Data].

Retrieved December, 2020, from https://www.data.boem.gov/Main/Mapping.aspx

Byrne, M. E., Vaudo, J. J., Harvey, G. C. M., Johnston, M. W., Wetherbee, B. M., & Shivji, M. (2019). Behavioral response of a mobile marine predator to environmental variables differs across ecoregions. *Ecography*, *42*(9), 1569-1578.

Byrne, M. E., Cortés, E., Vaudo, J. J., Harvey, G. C. M., Sampson, M., Wetherbee, B. M., & Shivji, M. (2017). Satellite telemetry reveals higher fishing mortality rates than previously estimated, suggesting overfishing of an apex marine predator. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1860), 20170658.

Calenge, C. (2006) The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling*, 197, 516-519

Calenge, C. (2019). Home range estimation in R: the adehabitatHR package. *Office national de la classe et de la faune sauvage: Saint Benoist, Auffargis, France*

Campana, S. E. (2016). Transboundary movements, unmonitored fishing mortality, and ineffective international fisheries management pose risks for pelagic sharks in the Northwest Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences*, *73*(10), 1599-1607.

Campana, S. E., Marks, L., & Joyce, W. (2005). The biology and fishery of shortfin mako sharks (Isurus oxyrinchus) in Atlantic Canadian waters. *Fisheries Research*, *73*(3), 341-352.

Casey, J. G., & Kohler, N. E. (1992). Tagging studies on the shortfin mako shark (Isurus oxyrinchus) in the Northwest Atlantic. *Marine and Freshwater Research*, *43*(1), 45-60.

Chambault, P., Roquet, F., Benhamou, S., Baudena, A., Pauthenet, E., de Thoisy, B., ... & Chevallier, D. (2017). The Gulf Stream frontal system: A key oceanographic feature in the habitat selection of the leatherback turtle?. *Deep Sea Research Part I: Oceanographic Research Papers*, *123*, 35-47.

Claisse, J. T., Pondella, D. J., Love, M., Zahn, L. A., Williams, C. M., Williams, J. P., & Bull, A. S. (2014). Oil platforms off California are among the most productive marine fish habitats globally. *Proceedings of the National Academy of Sciences*, *111*(43), 15462-15467.

Compagno, L. J. (2001). *Sharks of the world: an annotated and illustrated catalogue of shark species known to date* (No. 1). Food & Agriculture Org..

Continental Shelf Associates, Inc. 2002. Deepwater Program: Bluewater Fishing and OCS Activity, Interactions Between the Fishing and Petroleum Industries in Deepwaters of the Gulf of Mexico. U.S. Department of the Interior, Minerals Management Service, Gulf of Mexico OCS Region, New Orleans, LA. OCS Study MMS 2002-078. 193 pp. + apps.

Cordes, E. E., Jones, D. O., Schlacher, T. A., Amon, D. J., Bernardino, A. F., Brooke, S., ... & Witte, U. (2016). Environmental impacts of the deep-water oil and gas industry: a review to guide management strategies. *Frontiers in Environmental Science*, *4*, 58.

Díaz, H., & Soares, C. G. (2020). Review of the current status, technology and future trends of offshore wind farms. *Ocean Engineering*, *209*, 107381.

Diederichs, A., Nehls, G., Dähne, M., Adler, S., Koschinski, S., & Verfuß, U. (2008). Methodologies for measuring and assessing potential changes in marine mammal behaviour, abundance or distribution arising from the construction, operation and decommissioning of offshore windfarms. *BioConsult SH report to COWRIE Ltd*.

Eddy, C., Brill, R., & Bernal, D. (2016). Rates of at-vessel mortality and post-release survival of pelagic sharks captured with tuna purse seines around drifting fish aggregating devices (FADs) in the equatorial eastern Pacific Ocean. *Fisheries Research*, *174*, 109-117.

Edwards, R. E., & Sulak, K. J. (2006). New paradigms for Yellowfin tuna movements and f distributions–implications for the Gulf and Caribbean region.

ESRI 2011. ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute.

Esteban, M. D., Diez, J. J., López, J. S., & Negro, V. (2011). Why offshore wind energy?. *Renewable Energy*, *36*(2), 444-450.

Fieberg J, Bohrer G, Davidson SC, Kays R (2018) Short course on analyzing animal tracking data. Presented at the North Carolina Museum of Natural Sciences, Raleigh, NC, USA. May 21–23, 2018. https://movebankworkshopraleighnc.netlify.com/index.html

Fieberg, J., Signer, J., Smith, B., & Avgar, T. (2021). A 'How to'guide for interpreting parameters in habitat‐selection analyses. *Journal of Animal Ecology*, 90(5), 1027-1043.

Filmalter, J., Cowley, P., Forget, F., & Dagorn, L. (2015). Fine-scale 3-dimensional movement behaviour of silky sharks Carcharhinus falciformis associated with fish aggregating devices (FADs). *Marine Ecology Progress Series*, *539*, 207-223.

Floeter, J., van Beusekom, J. E., Auch, D., Callies, U., Carpenter, J., Dudeck, T., ... & Möllmann, C. (2017). Pelagic effects of offshore wind farm foundations in the stratified North Sea. *Progress in Oceanography*, *156*, 154-173.

Franks, J. (2000, January). A review: pelagic fishes at petroleum platforms in the Northern Gulf of Mexico; diversity, interrelationships, and perspective. In *Pêche thonière et dispositifs de concentration de poissons, Caribbean-Martinique, 15-19 Oct 1999*.

French, R. P., Lyle, J., Tracey, S., Currie, S., & Semmens, J. M. (2015). High survivorship after catch-and-release fishing suggests physiological resilience in the endothermic shortfin mako shark (Isurus oxyrinchus). *Conservation Physiology*, 3(1).

Friedland, K. D., Methratta, E. T., Gill, A. B., Gaichas, S. K., Curtis, T. H., Adams, E. M., ... & Brady, D. C. (2021). Resource occurrence and productivity in existing and proposed wind energy lease areas on the northeast U.S. Shelf. *Frontiers in Marine Science*.

Freitas, C., Lydersen, C., Fedak, M. A., & Kovacs, K. M. (2008). A simple new algorithm to filter marine mammal Argos locations. *Marine Mammal Science*, *24*(2), 315-325.

Gallagher, A. J., Orbesen, E. S., Hammerschlag, N., & Serafy, J. E. (2014). Vulnerability of oceanic sharks as pelagic longline bycatch. *Global Ecology and Conservation*, *1*, 50-59.

Gibson, K. J., Streich, M. K., Topping, T. S., & Stunz, G. W. (2021). New Insights Into the Seasonal Movement Patterns of Shortfin Mako Sharks in the Gulf of Mexico. *Frontiers in Marine Science*, *8*, 5.

Girard, C., Benhamou, S., & Dagorn, L. (2004). FAD: Fish Aggregating Device or Fish Attracting Device? A new analysis of yellowfin tuna movements around floating objects. *Animal Behaviour*, *67*(2), 319-326.

Gray, J. S., Clarke, K. R., Warwick, R. M., & Hobbs, G. (1990). Detection of initial effects of pollution on marine benthos: an example from the Ekofisk and Eldfisk oilfields, North Sea. *Marine ecology progress series*, 285-299.

Halouani, G., Villanueva, C. M., Raoux, A., Dauvin, J. C., Lasram, F. B. R., Foucher, E., ... & Niquil, N. (2020). A spatial food web model to investigate potential spillover effects of a fishery closure in an offshore wind farm. *Journal of Marine Systems*, *212*, 103434.

Harrison, A. L., Costa, D. P., Winship, A. J., Benson, S. R., Bograd, S. J., Antolos, M., ... & Block, B. A. (2018). The political biogeography of migratory marine predators. *Nature ecology & evolution*, *2*(10), 1571-1578.

Haugen, J. B., & Papastamatiou, Y. (2019). Observation of a porbeagle shark Lamna nasus aggregation at a North Sea oil platform. *Journal of Fish Biology*, *95*(6), 1496-1499.

Haulsee, D. E., Breece, M. W., Brown, L. M., Wetherbee, B. M., Fox, D. A., & Oliver, M. J. (2018). Spatial ecology of Carcharias taurus in the northwestern Mid-Atlantic coastal ocean. *Marine Ecology Progress Series*, *597*, 191-206.

Hutchison, Z. L., Gill, A. B., Sigray, P., He, H., & King, J. W. (2020). Anthropogenic electromagnetic fields (EMF) influence the behaviour of bottom-dwelling marine species. *Scientific reports*, *10*(1), 1-15.

Hutchison, Z., Sigray, P., He, H., Gill, A. B., King, J., & Gibson, C. (2018). Electromagnetic Field (EMF) impacts on elasmobranch (shark, rays, and skates) and American lobster movement and migration from direct current cables. *Sterling (V.A.): U.S. Department of the Interior, Bureau of Ocean Energy Management. OCS Study BOEM*, *3*, 2018.

ICCAT. (2019). "Report of the 2019 ICCAT Shortfin mako assessment meeting." *International Commission for the Conservation of Atlantic Tunas, Madrid* (2017).

Jernelöv, A. (2010). The threats from oil spills: now, then, and in the future. *Ambio*, *39*(5), 353-366.

Jonsen, I. D., Flemming, J. M., & Myers, R. A. (2005). Robust state–space modeling of animal movement data. *Ecology*, *86*(11), 2874-2880.

Jonsen, I.D., Patterson, T.A. (2020). foieGras: fit latent variable movement models to animal tracking data for location quality control and behavioural inference Zenodo. https://doi.org/10.5281/zenodo.3899972

Jonsen, I.D., Patterson, T.A., Costa, D.P. et al. (2020) A continuous-time state-space model for rapid quality control of argos locations from animal-borne tags. *Movement Ecology* 8:31. https://doi.org/10.1186/s40462-020-00217-7

Kohler, N. E., Turner, P. A., Hoey, J. J., Natanson, L. J., & Briggs, R. (2002). Tag and recapture data for three pelagic shark species: blue shark (Prionace glauca), shortfin mako (Isurus oxyrinchus), and porbeagle (Lamna nasus) in the North Atlantic Ocean. *Col. Vol. Sci. Pap. ICCAT*, *54*(4), 1231-1260.

Lindeboom, H., Degraer, S., Dannheim, J., Gill, A. B., & Wilhelmsson, D. (2015). Offshore wind park monitoring programmes, lessons learned and recommendations for the future. *Hydrobiologia*, *756*(1), 169-180.

Lindenberg, S. (Ed.). (2009). *20% Wind Energy By 2030: Increasing Wind Energy¿ s Contribution to US Electricity Supply*. Diane Publishing.

Martin, C. J., & Lowe, C. G. (2010). Assemblage structure of fish at offshore petroleum platforms on the San Pedro Shelf of southern California. *Marine and Coastal Fisheries*, *2*(1), 180-194.

McKinney, J. A., Hoffmayer, E. R., Wu, W., Fulford, R., & Hendon, J. M. (2012). Feeding habitat of the whale shark Rhincodon typus in the northern Gulf of Mexico determined using species distribution modelling. *Marine Ecology Progress Series*, *458*, 199-211.

Methratta, E. T., & Dardick, W. R. (2019). Meta-analysis of finfish abundance at offshore wind farms. *Reviews in Fisheries Science & Aquaculture*, *27*(2), 242-260.

Mucientes, G. R., Queiroz, N., Sousa, L. L., Tarroso, P., & Sims, D. W. (2009). Sexual segregation of pelagic sharks and the potential threat from fisheries. *Biology letters*, *5*(2), 156-159.

Myers, R. A., & Worm, B. (2003). Rapid worldwide depletion of predatory fish communities. *Nature*, *423*(6937), 280-283.

Myers, R. A., Baum, J. K., Shepherd, T. D., Powers, S. P., & Peterson, C. H. (2007). Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science*, *315*(5820), 1846-1850.

Natanson, L. J., Winton, M., Bowlby, H., Joyce, W., Deacy, B., Coelho, R., & Rosa, D. (2020). Updated reproductive parameters for the shortfin mako (Isurus oxyrinchus) in the North Atlantic Ocean with inferences of distribution by sex and reproductive stage. *Fishery Bulletin*, *118*(1), 21-53.

Pacoureau, N., Rigby, C. L., Kyne, P. M., Sherley, R. B., Winker, H., Carlson, J. K., ... & Dulvy, N. K. (2021). Half a century of global decline in oceanic sharks and rays. *Nature*, *589*(7843), 567-571.

Punt, M. J., Groeneveld, R. A., Van Ierland, E. C., & Stel, J. H. (2009). Spatial planning of offshore wind farms: A windfall to marine environmental protection?. *Ecological Economics, 69*(1), 93-103.

Porsmoguer, S. B., Bănaru, D., Boudouresque, C. F., Dekeyser, I., & Almarcha, C. (2015). Hooks equipped with magnets can increase catches of blue shark (Prionace glauca) by longline fishery. *Fisheries Research*, *172*, 345-351.

R Core Team (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Raoux, A., Lassalle, G., Pezy, J. P., Tecchio, S., Safi, G., Ernande, B., ... & Niquil, N. (2019). Measuring sensitivity of two OSPAR indicators for a coastal food web model under offshore wind farm construction. *Ecological Indicators*, *96*, 728-738.

Raoux, A., Tecchio, S., Pezy, J. P., Lassalle, G., Degraer, S., Wilhelmsson, D., ... & Niquil, N. (2017). Benthic and fish aggregation inside an offshore wind farm: Which effects on the trophic web functioning?. *Ecological Indicators*, *72*, 33-46.

Rigby, C.L., Barreto, R., Carlson, J., Fernando, D., Fordham, S., Francis, M.P., Jabado, R.W., Liu, K.M., Marshall, A., Pacoureau, N., Romanov, E., Sherley, R.B. & Winker, H. 2019. *Isurus oxyrinchus*. *The IUCN Red List of Threatened Species* 2019: e.T39341A2903170. https://dx.doi.org/10.2305/IUCN.UK.2019-1.RLTS.T39341A2903170.en. Downloaded on 11 January 2021.

Risch, D., Castellote, M., Clark, C. W., Davis, G. E., Dugan, P. J., Hodge, L. E., ... & Van Parijs, S. M. (2014). Seasonal migrations of North Atlantic minke whales: novel insights from large-scale passive acoustic monitoring networks. *Movement ecology*, *2*(1), 1-17.

Robbins, W. D., Peddemors, V. M., & Kennelly, S. J. (2011). Assessment of permanent magnets and electropositive metals to reduce the line-based capture of Galapagos sharks, Carcharhinus galapagensis. *Fisheries Research*, *109*(1), 100-106.

Robinson, D. P., Jaidah, M. Y., Jabado, R. W., Lee-Brooks, K., El-Din, N. M. N., Malki, A. A. A., ... & Ormond, R. F. (2013). Whale sharks, Rhincodon typus, aggregate around offshore platforms in Qatari waters of the Arabian Gulf to feed on fish spawn. *PLoS One*, *8*(3), e58255.

Rogers, P. J., Huveneers, C., Page, B., Goldsworthy, S. D., Coyne, M., Lowther, A. D., ... & Seuront, L. (2015). Living on the continental shelf edge: habitat use of juvenile shortfin makos Isurus oxyrinchus in the Great Australian Bight, southern Australia. *Fisheries Oceanography*, *24*(3), 205-218.

Rooker, J. R., Dance, M. A., Wells, R. D., Ajemian, M. J., Block, B. A., Castleton, M. R., ... & Walter, J. F. (2019). Population connectivity of pelagic megafauna in the Cuba-Mexico-United States triangle. *Scientific reports*, *9*(1), 1-13.

Rulifson, R. A., Bangley, C. W., Cudney, J. L., Dell'Apa, A., Dunton, K. J., Frisk, M. G., ... & Post, W. C. (2020). Seasonal presence of Atlantic Sturgeon and sharks at Cape Hatteras, a large continental shelf constriction to coastal migration. *Marine and Coastal Fisheries*, *12*(5), 308-321.

Ruppert, J. L., Travers, M. J., Smith, L. L., Fortin, M. J., & Meekan, M. G. (2013). Caught in the middle: combined impacts of shark removal and coral loss on the fish communities of coral reefs. *PloS one*, *8*(9), e74648.

Secor D, O'Brien M, Rothermel E, Wiernicki C, Bailey H. 2020. Movement and habitat selection by migratory fishes within the Maryland Wind Energy Area and adjacent reference sites. Sterling (V.A.): U.S. Department of the Interior, Bureau of Ocean Energy Management, Office of Renewable Energy Programs. OCS Study BOEM 2020-030. 109 p.

Sergio, F., Newton, I., & Marchesi, L. (2005). Top predators and biodiversity. *Nature*, *436*(7048), 192-192.

Shaw, R. L., Curtis, T. H., Metzger, G., McCallister, M. P., Newton, A., Fischer, G. C., & Ajemian, M. J. (2021). Three-Dimensional Movements and Habitat Selection of Young White Sharks (Carcharodon carcharias) Across a Temperate Continental Shelf Ecosystem. *Frontiers in Marine Science*, *8*, 151.

Shimada, T., Limpus, C., Jones, R., & Hamann, M. (2017). Aligning habitat use with management zoning to reduce vessel strike of sea turtles. *Ocean & Coastal Management*, *142*, 163-172.

Siegenthaler, A., Niemantsverdriet, P. R. W., Laterveer, M., & Heitkönig, I. M. A. (2016). Aversive responses of captive sandbar sharks Carcharhinus plumbeus to strong magnetic fields. *Journal of fish biology*, *89*(3), 1603-1611.

Signer, J., Fieberg, J., & Avgar, T. (2018). Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. *Ecology and evolution*, *9*(2), 880-890.

Signer J., Fieberg J., Avgar T. (2011). Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. *Ecology and Evolution*, 2019 9, 880-890. URL https://doi.org/10.1002/ece3.4823.

Simpfendorfer, C. A., Olsen, E. M., Heupel, M. R., & Moland, E. (2012). Three-dimensional kernel utilization distributions improve estimates of space use in aquatic animals. *Canadian Journal of Fisheries and Aquatic Sciences*, *69*(3), 565-572.

Snodgrass, D. J., Orbesen, E. S., Walter, J. F., Hoolihan, J. P., & Brown, C. A. (2020). Potential impacts of oil production platforms and their function as fish aggregating devices on the biology of highly migratory fish species. *Reviews in Fish Biology and Fisheries*, *30*, 405-422.

Stehfest, K. M., Patterson, T. A., Dagorn, L., Holland, K. N., Itano, D., & Semmens, J. M. (2013). Network analysis of acoustic tracking data reveals the structure and stability of fish aggregations in the ocean. *Animal Behaviour, 85*(4), 839-848.

Stenhouse, I. J., Berlin, A. M., Gilbert, A. T., Goodale, M. W., Gray, C. E., Montevecchi, W. A., ... & Spiegel, C. S. (2020). Assessing the exposure of three diving bird species to offshore wind areas on the U.S. Atlantic Outer Continental Shelf using satellite telemetry. *Diversity and Distributions*, *26*(12), 1703-1714.

Talwar, B., Brooks, E. J., Mandelman, J. W., & Grubbs, R. D. (2017). Stress, post-release mortality, and recovery of commonly discarded deep-sea sharks caught on longlines. *Marine Ecology Progress Series*, 582, 147-161.

ten Brink, T. S., & Dalton, T. (2018). Perceptions of commercial and recreational fishers on the potential ecological impacts of the Block Island Wind Farm (U.S.). *Frontiers in Marine Science*, *5*, 439.

Thurfjell, H., Ciuti, S., & Boyce, M. S. (2014). Applications of step-selection functions in ecology and conservation. *Movement ecology*, *2*(1), 4.

U.S. Department of Energy. (2008, July). *20% Wind Energy by 2030 Increasing Wind Energy's Contribution to U.S. Electricity Supply* (DOE/GO-102008-2567). https://www.nrel.gov/docs/fy08osti/41869.pdf

Vander Wal, E., & Rodgers, A. R. (2012). An individual-based quantitative approach for delineating core areas of animal space use. *Ecological Modelling*, 224(1), 48-53.

Vaudo, J. J., Byrne, M. E., Wetherbee, B. M., Harvey, G. M., & Shivji, M. S. (2017). Long-term satellite tracking reveals region-specific movements of a large pelagic predator, the shortfin mako shark, in the Northwest Atlantic Ocean. *Journal of Applied Ecology*, *54*(6), 1765-1775.

Vaudo, J. J., Wetherbee, B. M., Wood, A. D., Weng, K., Howey-Jordan, L. A., Harvey, G. M., & Shivji, M. S. (2016). Vertical movements of shortfin mako sharks Isurus oxyrinchus in the Northwest Atlantic Ocean are strongly influenced by temperature. *Marine Ecology Progress Series*, *547*, 163-175.

Wildlife Computers. (2019, October 10). SPOT Transmitting Tags. Retrieved December 10, 2020, from https://wildlifecomputers.com/our-tags/spot-argos-satellite-tags/spot/

Willsteed, E. A., Jude, S., Gill, A. B., & Birchenough, S. N. (2018). Obligations and aspirations: a critical evaluation of offshore wind farm cumulative impact assessments. *Renewable and Sustainable Energy Reviews*, *82*, 2332-2345.

Wingfield, D. K., Peckham, S. H., Foley, D. G., Palacios, D. M., Lavaniegos, B. E., Durazo, R., ... & Bograd, S. J. (2011). The making of a productivity hotspot in the coastal ocean. *PloS one*, *6*(11), e27874.

Figures

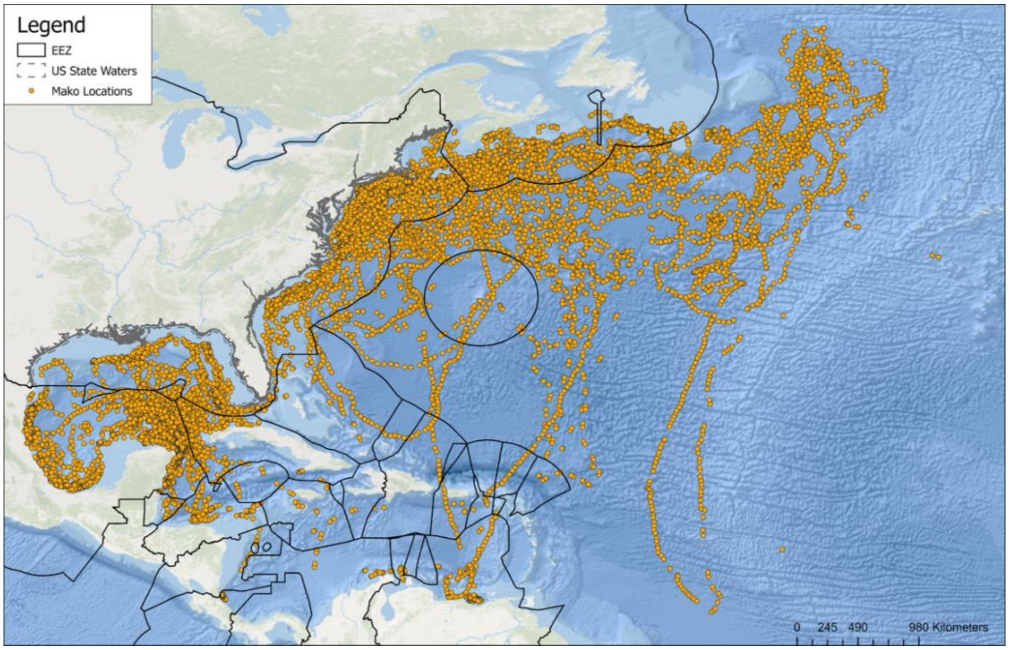


Figure 1: Location estimates for 60 mako sharks tagged off the US East Coast and Isla Mujeres, Mexico from March 2013- October 2019, using a 12-hour time step

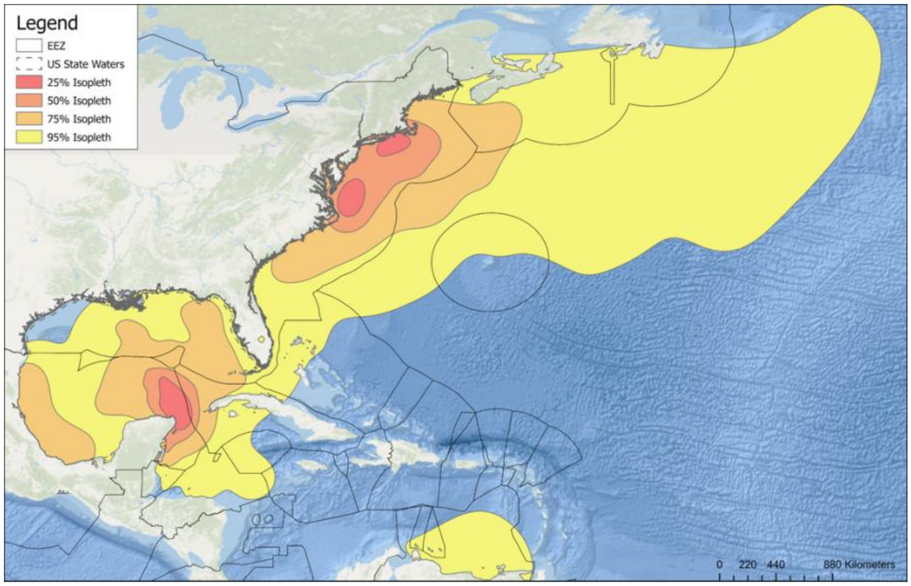


Figure 2: Population-level utilization estimates for 60 mako sharks tagged off the US East Coast and Isla Mujeres, Mexico from March 2013- October 2019, using a 12-hour time step. The U.D. includes the 95% isopleth (yellow), 75% isopleth (orange), 50% isopleth (red orange) and 25% isopleth (red). Solid black lines represent exclusive economic zones, and dashed grey lines represent US state waters.

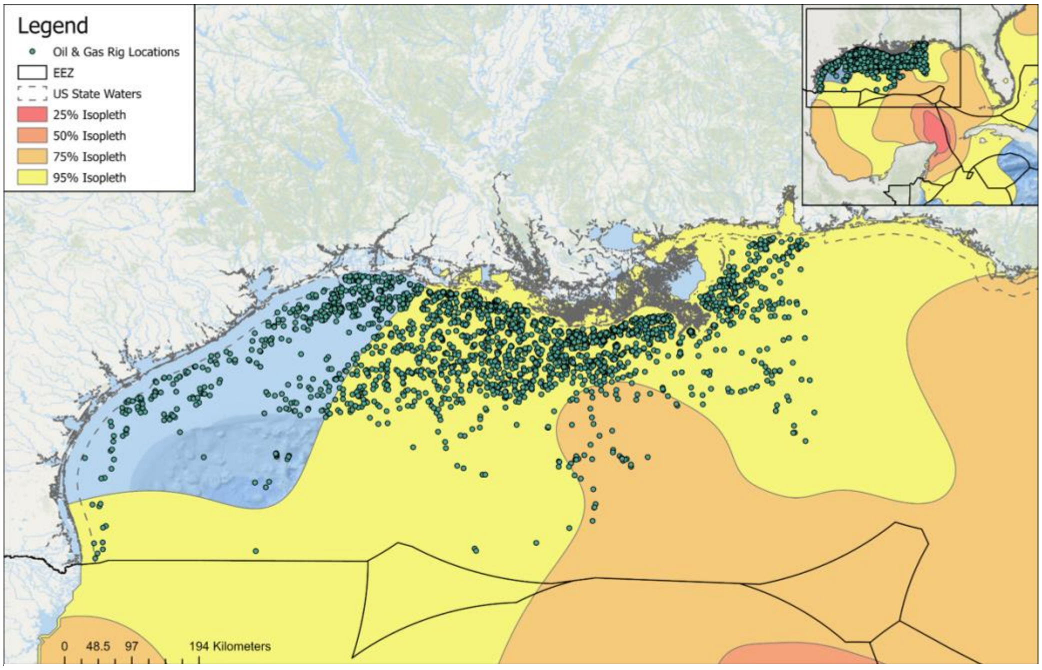


Figure 3: Active oil and gas rigs in the GOM and Population-level utilization estimates for 60 mako sharks tagged off the US East Coast and Isla Mujeres, Mexico from March 2013- October 2019, using a 12-hour time step. The UD includes the 95% isopleth (yellow), 75% isopleth (orange), 50% isopleth (red orange) and 25% isopleth (red). Solid black lines represent exclusive economic zones, and dashed grey lines represent US state waters.

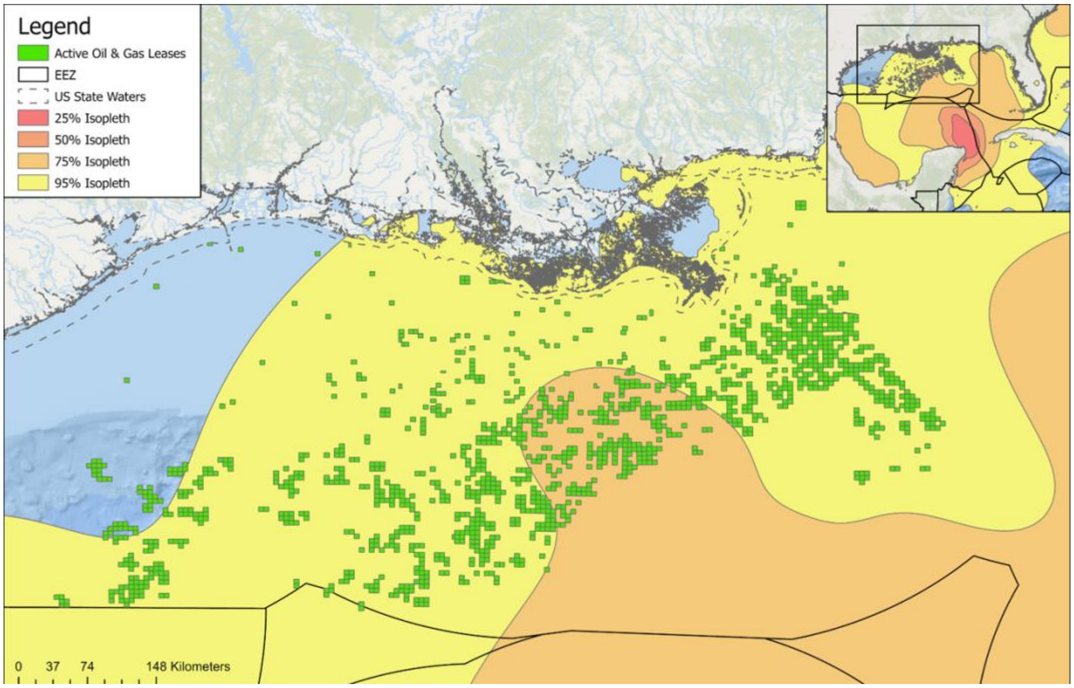


Figure 4: Active oil and gas leases in the GOM and Population-level utilization estimates for 60 mako sharks tagged off the US East Coast and Isla Mujeres, Mexico from March 2013- October 2019, using a 12-hour time step. The UD includes the 95% isopleth (yellow), 75% isopleth (orange), 50% isopleth (red orange) and 25% isopleth (red). Solid black lines represent exclusive economic zones, and dashed grey lines represent US state waters.

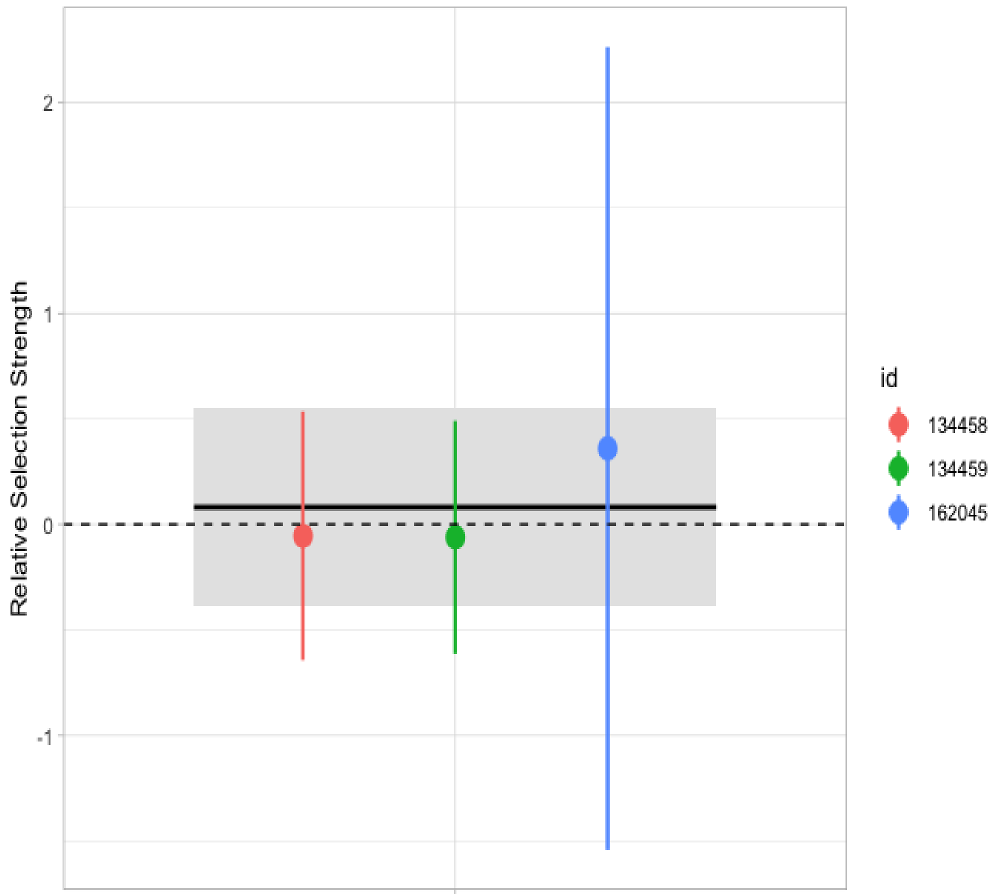


Figure 5: Point estimates for habitat selection strength regarding rigs from the SSF (Signer et al., 2018). Animal IDs are represented by the different colors, lines extending from the point estimates represent the individual 95% CIs. The population-level estimate is shown with the solid black line and the grey box shows the population-level 95% CI.

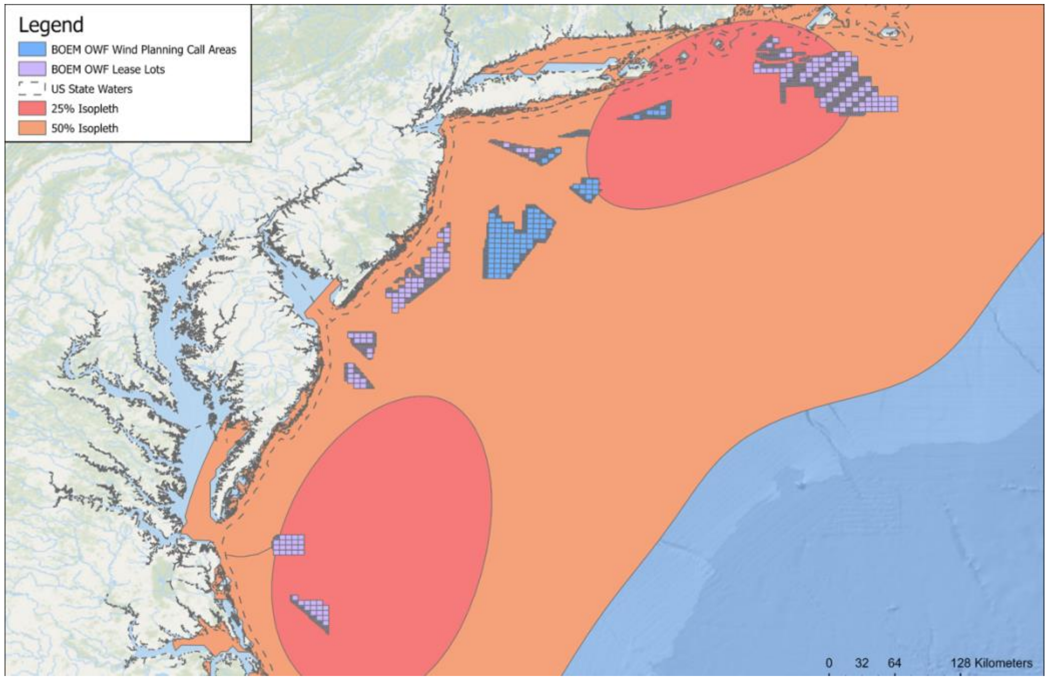


Figure 6: BOEM proposed offshore wind call areas (blue) and lease lots (purple) with mako core area in WNA from the population-level U.D. 50% isopleth (red orange) and 25% isopleth (red). Dashed grey lines represent US state waters.

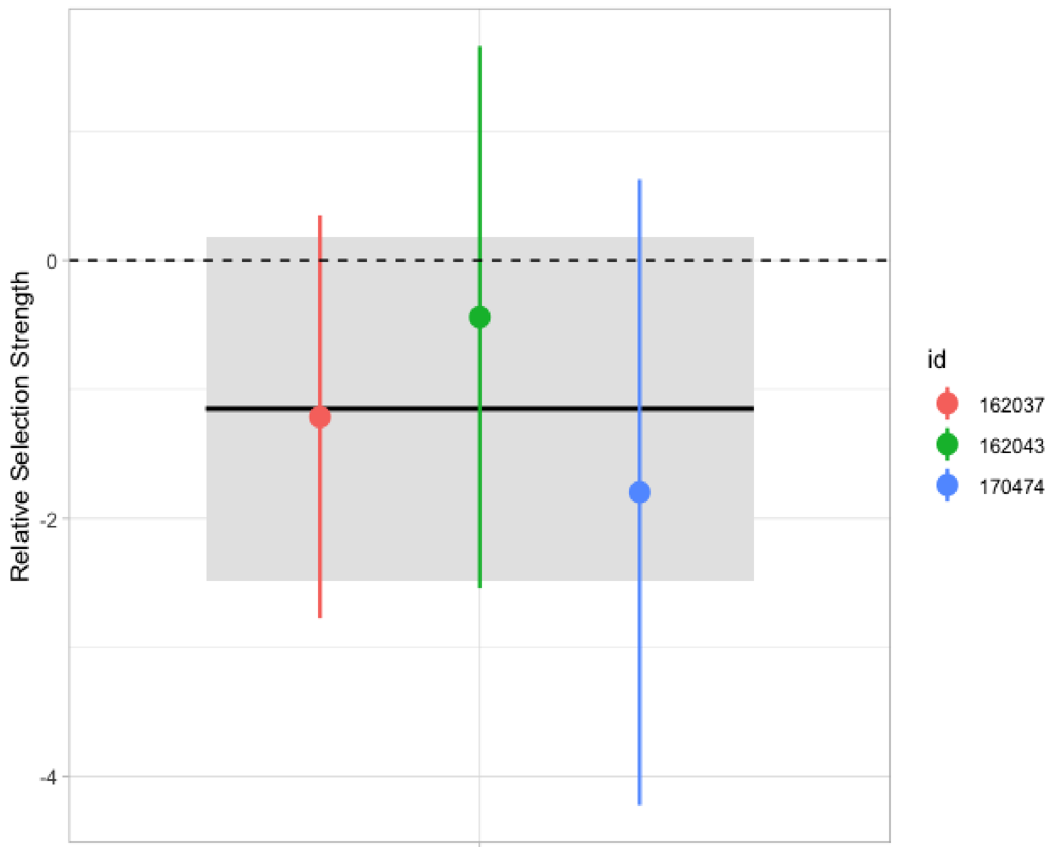


Figure 7: Point estimates for habitat selection strength regarding BIWF from the SSF (Signer et al., 2018). Animal IDs are represented by the different colors, lines extending from the point estimates represent the individual 95% CIs. The population-level estimate is shown with the solid black line and the grey box shows the population-level 95% CI.

Tables

Table 1: Proportion of active oil and gas rigs and active leased lots for oil and gas exploration in the GOM that are within the population-level mako shark UD% isopleths

Isopleth	Oil and Gas Rigs		Active Leases	
	Count	Relative Proportion	Count	Relative Proportion
95%	2,465	82.40%	1,399	95.50%
75%	68	0.02%	249	17.10%
50%	0	0%	0	0%
25%	0	0%	0	0%

Table 2: Coefficients of step-selection function (SSF) for three mako shark tracks and offshore oil and gas rigs.

I.D.	Sex	FL (cm)	Habitat	Coef	exp(coef)	se(coef)	z	Pr(>|z|)	Lower 95 CI	Upper 95 CI
134458	F	252	Oil Rig	-0.054	0.947	0.301	-0.180	0.857	-0.643	0.535
134459	M	178	Oil Rig	-0.061	0.941	0.281	-0.216	0.829	-0.612	0.491
162045	M	201	Oil Rig	0.360	1.433	0.971	0.371	0.711	-1.542	2.262

Table 3: Percent of area (km^2) of the BOEM offshore wind development lease lots that are within the population-level mako core area (50% U.D. isopleth).

Lease Owner	**Percent Overlap**
National Grid	100%
DWW Rev I	100%
Deepwater Wind South Fork	100%
Vineyard Wind (X2)	100%
Beacon Wind	100%
Mayflower Wind Energy	100%
Bay State Wind	100%
Sunrise Wind	100%
Empire Offshore Wind	100%
Atlantic Shores Offshore Wind	100%
Ocean Wind	100%
GSOE I	100%
Skipjack	100%
U.S. Wind	100%
Commonwealth of Virginia Research Lease	100%
Dominion	100%
Avangrid Renewables	100%

Table 4: Percent of area (km^2) of the BOEM offshore wind development call areas that are within the population-level mako core area (50% U.D. isopleth).

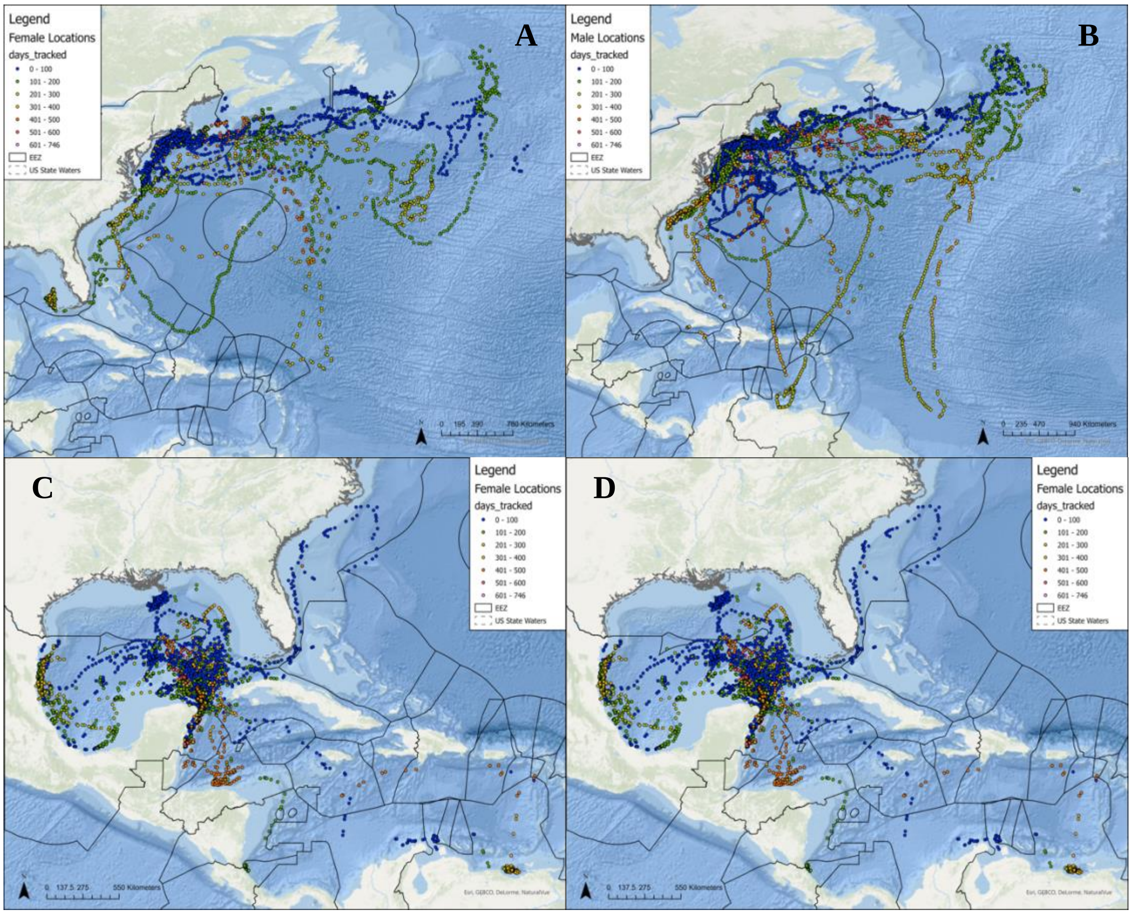
Call Area	**Percent Overlap**
New York Bight Wind Energy Area - Fairways North	100%
New York Bight Wind Energy Area - Fairways South	100%
New York Bight Wind Energy Area - Hudson North	100%
New York Bight Wind Energy Area - Central Bight	100%
New York Bight Wind Energy Area - Hudson South	100%
North Carolina Wind Energy Area - Wilmington East	0%
North Carolina Wind Energy Area - Wilmington West	0%
South Carolina Call Area - Cape Romain	0%
South Carolina Call Area - Charleston	0%
South Carolina Call Area - Grand Stand	0%
South Carolina Call Area - Winyah	0%

Table 5: Coefficients of step-selection function (SSF) for three mako shark tracks and Block Island Wind Farm (BIWF).

I.D.	Sex	FL (cm)	Habitat	Coef	exp(coef)	se(coef)	z	Pr(>|z|)	Lower 95 CI	Upper 95 CI
162037	F	158	BIWF	-1.213	0.297	0.795	-1.525	0.127	-2.772	0.346
162043	F	185	BIWF	-0.441	0.644	1.070	-0.412	0.681	-2.538	1.657
170474	M	150	BIWF	-1.797	0.166	1.236	-1.453	0.146	-4.220	0.626

Supplementary Material

Appendix A. Tagging Summary



Supplementary Figure A.1: Distribution of tracks of females tagged off the U.S. (A), males tagged off the U.S. (B), females tagged off Mexico (C), and males tagged off Mexico (D). Color or locations represent days at liberty. Grey dotted likes represent U.S. state water boundaries. Solid black lines represent national EEZs.

Supplementary Table A.1. Tagging summary for mako shark caught between March 2013 – October 2019. Shark IDs marked with * indicates they were used after the SSM

Shark ID	Tagging Location	Date Deployed	Days Tracked	Sex	Fork Length (cm)
113690*	Isla Mujeres	03/23/2013	406	F	180
113691*	Isla Mujeres	03/25/2013	274	F	175
124464*	Ocean City, MD	05/20/2014	351	M	150
126574*	Ocean City, MD	05/17/2014	354	M	153
128413	Isla Mujeres	04/08/2013	265	F	250
128414	Isla Mujeres	04/08/2013	58	M	175
128416*	Ocean City, MD	05/27/2013	97	M	168
128417*	Ocean City, MD	05/28/2013	305	F	175
128418*	Ocean City, MD	05/28/2013	251	M	172
128419*	Ocean City, MD	05/31/2013	402	M	155
128420*	Isla Mujeres	03/21/2014	120	M	186
128421	Block Island, RI	08/15/2013	11	F	89
128422*	Block Island, RI	09/11/2014	393	M	128
128429*	Ocean City, MD	05/28/2013	88	M	198
128431*	Ocean City, MD	05/20/2014	378	F	188
134451*	Isla Mujeres	03/24/2014	200	M	179
134452	Isla Mujeres	03/24/2014	137	M	195
134453	Isla Mujeres	03/22/2014	588	F	148
134454	Isla Mujeres	03/23/2014	665	F	180
134455	Isla Mujeres	03/23/2014	296	M	193
134456*	Isla Mujeres	03/25/2014	746	M	193
134457	Isla Mujeres	03/30/2014	3	M	205
134458*	Isla Mujeres	03/29/2014	196	F	252
134459*	Isla Mujeres	03/25/2014	288	M	178
134461*	Ocean City, MD	05/19/2014	514	M	155
134462*	Ocean City, MD	05/19/2014	539	F	178
134463*	Ocean City, MD	05/20/2014	437	M	179
134465	Ocean City, MD	06/14/2016	47	M	192
134467	Ocean City, MD	05/22/2014	77	M	192
134468*	Ocean City, MD	05/21/2014	97	M	180
134469*	Isla Mujeres	04/13/2015	421	F	180
147199*	Isla Mujeres	04/17/2017	404	M	177
147207*	Ocean City, MD	05/31/2015	83	M	175
147212	Isla Mujeres	03/20/2015	11	M	164

147213*	Isla Mujeres	04/06/2016	49	M	173
147215*	Ocean City, MD	05/15/2015	46	F	158
147217*	Ocean City, MD	05/19/2015	166	M	117
147218*	Ocean City, MD	05/19/2015	79	M	121
147219*	Ocean City, MD	05/19/2015	516	M	158
147220*	Ocean City, MD	05/23/2015	624	M	158
147221	Ocean City, MD	05/24/2015	550	F	122
147222	Ocean City, MD	05/25/2015	348	M	143
147223	Ocean City, MD	05/26/2015	331	M	156
147224*	Ocean City, MD	05/27/2015	244	F	167
147225*	Ocean City, MD	05/26/2015	253	M	192
147226*	Ocean City, MD	05/22/2014	94	F	147
147229*	Isla Mujeres	04/25/2016	604	F	229
150133	Isla Mujeres	04/10/2016	18	M	220
150136*	Isla Mujeres	04/12/2016	240	M	203
150138*	Isla Mujeres	04/13/2016	421	F	244
150139*	Isla Mujeres	04/20/2016	168	F	196
150140	Isla Mujeres	04/13/2016	60	M	203
150141*	Isla Mujeres	04/20/2016	188	F	246
159137*	Isla Mujeres	04/14/2016	465	F	183
162037*	Ocean City, MD	06/15/2016	65	F	158
162038*	Ocean City, MD	06/15/2016	99	M	169
162041*	Isla Mujeres	04/11/2017	585	F	175
162042*	Block Island, RI	08/10/2016	145	M	130
162043*	Block Island, RI	08/20/2016	345	F	185
162044*	Isla Mujeres	04/15/2017	184	F	168
162045*	Isla Mujeres	04/14/2017	215	M	201
162046*	Isla Mujeres	04/16/2017	447	F	176
162048*	Isla Mujeres	04/16/2017	305	F	146
162049*	Isla Mujeres	04/14/2017	347	F	170
162050*	Isla Mujeres	04/14/2017	423	F	170
162051*	Isla Mujeres	04/17/2017	93	M	193
170462*	Ocean City, MD	06/02/2017	74	M	152
170463*	Ocean City, MD	06/04/2017	78	M	155
170464*	Block Island, RI	07/19/2017	222	F	133
170465	Ocean City, MD	06/04/2017	400	M	157
170466*	Ocean City, MD	05/25/2018	260	F	155
170467*	Ocean City, MD	05/25/2018	21	M	124
170471*	Ocean City, MD	05/29/2018	209	M	168
170473*	Ocean City, MD	05/25/2018	83	F	170

170474*	Ocean City, MD	06/07/2018	190	M	150
170475*	Ocean City, MD	06/07/2018	509	F	173
170476	Ocean City, MD	05/30/2018	143	F	132
170480	Isla Mujeres	04/05/2018	266	M	212
170484	Ocean City, MD	05/25/2019	151	M	173
170485	Ocean City, MD	06/01/2019	131	M	132
170487	Block Island, RI	10/02/2018	17	M	137
170866*	Block Island, RI	08/23/2018	192	F	126
174038	Ocean City, MD	05/31/2019	67	F	137
174039	Ocean City, MD	05/31/2019	31	M	152
174040	Ocean City, MD	05/31/2019	68	F	147

Appendix B. Supplementary Results for Chapter 1

Supplementary Table B.1. Percent Deviance Explained for the multinomial GAM predicting occurrence of a mako shark among EEZs in the WNA and GOM as a function of movement persistence.

Tagged Off the U.S.	
Sample	% Deviance explained
All Data	44.20%
Females	48.90%
Males	62.80%
Tagged Off Mexico	
Sample	% Deviance explained
All Data	44.40%
Females	47.30%
Males	38.30%

Supplementary Table B.2. Percent Deviance Explained for the multinomial GAM predicting seasonal occurrence of a mako shark among EEZs in the WNA and GOM

Tagged Off the U.S.	
Sample	% Deviance explained
All Data	51.80%
Females	41.70%
Males	62.80%
Tagged Off Mexico	
Sample	% Deviance explained
All Data	46.70%
Females	47.30%
Males	55.80%