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Movement ecology of shortfin makos off Texas and the Gulf of Mexico

Prepared by:

Greg Stunz, Ph.D.

Kesley Banks, Ph.D.

Daniel Coffey, Ph.D.

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Personnel

Principal Investigator(s):
PI: Gregory W. Stunz, Ph.D., (361) 825-3254, gregory.stunz@tamucc.edu
Co-PI: Kesley G. Banks, Ph.D., (361) 825-3071, kesley.banks@tamucc.edu
Co-PI: Daniel M. Coffey, Ph.D., (361) 825-2519, daniel.coffey@tamucc.edu
Harte Research Institute for Gulf of Mexico Studies, Texas A&M University-Corpus Christi,
6300 Ocean Drive, Unit 5869, Corpus Christi, TX 78412

Consulting TPWD Project Coordinator:
Mark Fisher, Ph.D., (361) 729-2328, Mark.Fisher@tpwd.state.tx.us
Texas Parks and Wildlife Department, 702 Navigation Circle, Rockport, TX 78382

Introduction:

In the recent Pelagic Shark Working Group meeting, the Texas Parks and Wildlife (TPWD) recognized the shortfin mako shark (*Isurus oxyrinchus*; hereafter mako shark) as a high-priority species for the State of Texas and determined the status to be 'S2-Imperiled.' This designation means this species is at high risk of extirpation in the jurisdictional range, with few populations or occurrences, steep declines, and severe threats to their population status. Thus, the clear recommendation was for more research and monitoring of this species. Highly migratory species (HMS), like the mako shark, are often apex predators that serve critical ecological functions within vast marine ecosystems (Block et al. 2011). Managing entities face serious and complex challenges as HMS frequently cross multiple jurisdictional boundaries during their long-distance movements, which also expose individuals to varying natural and anthropogenic pressures (e.g., dynamic environmental conditions, prey resources, levels of fishing effort around man-made [artificial] habitat vs. open ocean, and illegal/unreported/unregulated fishing; Rooker et al. 2019). While these movements and their consequences present complex challenges to management, knowledge of these movement patterns and understanding the various sources of mortality is essential for identifying the spatial and temporal scales at which a fishery can be best managed. Failure to recognize or accurately identify the stock structure of an exploited species can lead to changes in biological attributes and productivity, loss of genetic diversity, and overfishing and depletion of less productive stocks (Stevens et al. 2000; Pinsky & Palumbi 2014). Unfortunately, the management of many HMS fisheries continues to be hindered by large data gaps regarding seasonal movement patterns, stock structure, and uncertainty regarding fisheries-related mortality.

Mako sharks are highly prized in recreational fisheries and as high-value bycatch in directed commercial pelagic longline fisheries (Campana et al. 2016; Queiroz et al. 2019). Like other shark species, mako sharks have low resilience to fishing mortality due to their inherent life history characteristics (e.g., slow growth, late age-at-maturity; Cortés et al. 2010; Natanson et al. 2020). In the Atlantic Ocean, mako sharks are assessed as North Atlantic and South Atlantic stocks by the International Commission for the Conservation of Atlantic Tunas (ICCAT). The most recent stock assessment, conducted in 2017, suggested the North Atlantic shortfin mako stock was overfished and experiencing overfishing and that annual catch levels (3,600 – 4,750 mt) would need to be reduced to 500 mt or less to end overfishing and begin rebuilding the stock (ICCAT 2017). In response to these assessment findings, the United States

(U.S.) National Marine Fisheries Service (NMFS) passed Amendment 11 to the 2006 Consolidated Atlantic Highly Migratory Species Fishery Management Plan. The Amendment, consistent with ICCAT recommendations to end overfishing, established recreational size limits of 71 in fork length (FL) for males and 83 in FL for females and required commercial longline vessels to safely release any mako sharks alive at the time of haulback (NMFS 2019). Despite these regulations, recently updated projections suggest that reducing annual catch levels to 500 mt would only result in a 52% probability of rebuilding the stock and ending overfishing by 2070 (ICCAT 2019). This bleak outlook resulted in a retention ban on mako sharks caught in the North Atlantic Ocean (NMFS 2022) and the listing of mako sharks on the Species of Greatest Conservation Need list in the Texas Conservation Action Plan (TPWD 2012, Texas Register 2019). In 2021, the NMFS announced that there was substantial scientific and commercial evidence to warrant listing mako sharks as threatened or endangered under the Endangered Species Act, initiating a status review of this species (NFMS 2021). Despite their declining status, little research has been conducted on this species regarding their movements and habitat use in the Gulf of Mexico (GOM).

Several data deficiencies highlighted in the most recent stock assessment (ICCAT 2017) continue to hinder mako shark management, including sparse information regarding the species movement ecology and uncertainty surrounding estimates of fishing mortality (comprising at-vessel and post-release mortality; Musyl et al. 2011; Musyl and Gilman 2019). Specifically, existing knowledge of mako shark distribution patterns, stock boundaries, and fishing mortality is primarily informed by fisheries landings data and conventional tag-recapture studies (Wood et al. 2007; ICCAT 2017). While these data are informative, they are limited by low recapture rates and are inherently biased by spatiotemporally variable fishing effort and the absence of information between the point of capture and recapture. These are potentially serious limitations to accurate stock assessment – especially if mako sharks are exposed to varying levels of fishing mortality during their migratory movements (Braccini et al. 2016).

Preliminary data from the nine satellite-tagged mako sharks (5 males, 4 females) tagged off the coast of Texas showed wide-reaching dispersal patterns, with two tagged individuals exiting the GOM (Gibson et al. 2021). Furthermore, while most of these sharks have displayed seasonal core distribution areas along the GOM shelf edge off Texas, these long-distance seasonal movements have only been observed for mature male mako sharks, suggesting that differences in migratory patterns between sexes may exist. Many of the females tagged off Texas had bite marks consistent with shark mating behavior, supporting the identification of gestation and parturition grounds in the northern GOM (Natanson et al. 2020). Additionally, the sample size of mature females is limited in the GOM, but a few mature females have been documented to be present in the western GOM most of the year (Natanson et al. 2020; Gibson et al. 2021). Although increased sample sizes are much needed to refine and corroborate these patterns, these findings have pronounced implications for regional management and suggest the potential for sex- and region-specific variation in fishing mortality (e.g., Mucientes et al. 2009). Accordingly, further investigation of this putative stock sub-structure is clearly warranted.

In addition to information regarding mako shark stock structure and population connectivity, finer-scale movement and habitat use data are also needed for effective fisheries management. This need stems from observations that many HMS can also exhibit extended residence (i.e., weeks to months) to certain oceanographic features characterized by high productivity (e.g., Luo et al. 2015) and man-made [artificial] structures (e.g., oil and gas infrastructure; Hoolihan et al. 2014). Even if residency to a site is relatively short (i.e., days to weeks), many HMS may also exhibit fidelity to them, returning to specific sites from year to year to exploit seasonal productivity (Block et al. 2011). Preliminary studies have shown these same patterns for mako sharks in the GOM (Gibson et al. 2021). Such behaviors can make HMS, despite their high mobility, vulnerable to spatiotemporally-explicit activities (e.g., fisheries). In fact, many species, including mako sharks, have already been demonstrated to be highly susceptible to these activities (Campana et al. 2016; Queiroz et al. 2019). Thus, knowledge of finer-scale movements and habitat use is essential to determining how, when, and where mako sharks interact with fisheries to inform conservation and spatial management planning.

For accurate stock assessments, estimates of all components of fisheries-related mortality, including at-vessel (i.e., removals; [traditionally defined as “fishing mortality”]) and post-release (i.e., discard) mortality are essential for estimating population productivity (Cortés et al. 2010; Musyl and Gilman 2019). For mako sharks, at-vessel estimates of fishing mortality have primarily been derived through landings and observer data (e.g., Campana et al. 2016), while post-release mortality estimates have been derived from observations of sharks tagged with pop-up satellite archival tags (PSATs; Musyl et al. 2011; Campana et al. 2016) or meta-analysis of these studies (Musyl and Gilman 2019). While these studies have provided valuable information, they are subject to limitations, including a reliance upon fisheries-dependent data and a focus on mako sharks captured and released in pelagic longline fisheries where handling may be a significant factor in post-release mortality (Campana et al. 2016). Discrepancies between fishing mortality estimates derived from fishery-independent versus fishery-dependent data further limit confidence in assessment projections. These discrepancies were highlighted by a recent satellite telemetry study (Byrne et al. 2017) which produced estimates of fishing mortality that were 10-fold higher than those used in the 2012 stock assessment for North Atlantic mako sharks (calculated from conventional tag-recapture data; Wood et al. 2007). Although these estimates were based solely on harvested individuals, quantifying all sources of fisheries-related mortality is essential for reducing uncertainty in stock assessment results and advancing non-retention or catch-and-release strategies (ICCAT 2019; Musyl and Gilman 2019). Accordingly, additional electronic tagging studies providing fishery-independent estimates of all sources of fishing mortality are especially relevant and timely for effectively managing this species (Byrne et al. 2017; ICCAT 2017, 2019).

Objective(s):

The objectives of this study are to 1) identify migration corridors and population connectivity of mako sharks to further our knowledge of stock structure; 2) determine the extent of spatiotemporal interactions between mako sharks and fish aggregating devices (FADs) such as oil and gas infrastructure; and 3) estimate two sources of fishing mortality for mako sharks captured in the GOM recreational fishery.

Study Site:

Mako sharks are a highly migratory species. Thus, the work occurred over an expansive area in waters important to the State of Texas, and PIs will target mako sharks in State and Federal waters. Specifically, sites near TPWD artificial reefs such as BA-A-133 (27° 50’ 6” N, 96° 0’ 46.8” W) and MU-A-85 (27° 43’ 37.2” N, 96° 11’ 27.6” W), as mako sharks are known to use these structures. Data analysis was conducted at the Harte Research Institute of Gulf of Mexico Studies, Texas A&M University-Corpus Christi (6300 Ocean Drive, Corpus Christi, TX).

Methods:

Shark handling and tagging was conducted in accordance with approved guidelines of Texas A&M University-Corpus Christi (Institutional Animal Care and Use Committee-Animal Use Protocol #08-18 and #2020-04-01), Texas Parks and Wildlife Department Scientific Research Permit #SPR-0303-279, and National Oceanic and Atmospheric Administration Letter of Acknowledgement #SHK-LOA-21-26. Mako sharks were captured via hook and line >40 nautical miles out of Port Aransas, Texas, or from shore along the Padre Island National Seashore. In these rare events, sharks were landed in the surf with their gills remaining submerged in the water. Sharks captured offshore were either secured alongside the vessel or brought onboard via a cradle with a saltwater hose placed in the mouth to irrigate the gills. All sharks were tagged at their capture location. During the tagging procedure, individuals were sexed, measured [fork length (FL); cm], and externally tagged. Each individual was tagged with a smart position or temperature tag (SPOT5 or SPOT6; Wildlife Computers, Redmond, WA, United States) for satellite tracking and a conventional dart tag (Floy©, Seattle, WA, United States), which included a phone number, email address, unique identification number, and "reward" for reporting recaptures. For SPOT tag attachment, four small holes were drilled into the distal portion of the leading edge of the dorsal fin, and stainless-steel hardware was used to secure the tag. Prior to deployment, SPOT tags were coated in antifouling paint to prevent excessive biofouling that can inhibit successful communication with satellites. SPOT tags were programmed with a maximum of 70 transmissions per day and had an estimated battery life of 2 C years. The Argos system assigned locations to one of seven accuracy classes, each with an associated error estimate. In decreasing order, the accuracy location classes (with estimated error) were: 3 (<250 m), 2 (250–500 m), 1 (500–1500 m), and 0 (>1500 m), with unbounded accuracy for location classes A, and B. Class Z locations were considered poor location estimates and, therefore, were omitted from further analyses.

Location data obtained from satellite-tagged mako sharks were used to identify migration corridors and estimate the connectivity between sub-regions of the GOM and beyond (i.e., international exchange). Prior to analysis, removed erroneous locations overlapping land. We fit a continuous-time correlated random walk state-space model (SSM) to the temporally irregular raw Argos location data using the *foieGras* package (Jonsen and Paterson 2020, Jonsen et al. 2019, 2020) in R. This approach accounted for observation errors in location data and provided location estimates at regular time steps along each track. Given that 84.9% of temporal gaps between positions in our tracks were <24 h, we used a time step of 24 h in the SSM to produce one position per day for each mako shark. To reduce spurious SSM-position estimates associated with long detection gaps (Bailey et al. 2008), tracks were segmented when gaps between raw satellite locations were >7 days (corresponding to 0.6% of gaps) and reassembled after modeling (Block et al. 2011). Tracks (or track segments) with less than 10 transmissions and 5 transmit days in duration were excluded. Erroneous SSM locations interpolated onto land were corrected using the *pathroutr* package in R (London 2020). The SSM locations were used to estimate population-level kernel utilization distributions (KUD) using the *adehabitatHR* package with the "href" bandwidth estimator in R (Calenge 2015). The resulting KUD was used to calculate core use (50% KUD) and home range (95% KUD) areas.

Remotely sensed environmental data were extracted along tagged mako shark tracks to characterize oceanographic conditions the sharks experienced. Daily mean sea surface temperature (SST; °C) was obtained from the Multi-scale Ultra-high Resolution (MUR) SST Analysis fv04.1 (0.01° resolution), and mean 8-day and monthly composite chlorophyll *a* concentration (mg m-3) was obtained from Aqua

Moderate Resolution Imaging Spectroradiometer (MODIS; 0.05° resolution) using the *rerddapXtracto* package in R. For grid cells obscured by cloud cover in the 8-day chlorophyll a concentration data, monthly mean chlorophyll *a* concentration values were used. Bathymetry (m) was extracted from the ETOPO1 Global Relief Model (0.1° resolution). The geolocation error radius from each daily SSM position was used to calculate a mean value for each environmental variable.

Locations of standing oil and gas platforms in the northern GOM were obtained from the Bureau of Ocean Energy Management (BOEM 2020), while the locations of known artificial reefs were obtained from data sets compiled by the National Oceanic and Atmospheric Administration (NOAA) Office of Coastal Management (updated Dec. 2015; NOAA 2020a), Alabama Marine Resources Division (AL MRD 2019), Mississippi Department of Marine Resources (MS DMR 2020) and Florida Fish and Wildlife Conservation Commission (FWC 2019), Louisiana Department of Wildlife and Fisheries (LDWF 2020a), TPWD Artificial Reef Program (TWPD 2020), and Horner (2013). In addition, datasets compiled by NOAA's Office of Coast Survey (NOAA 2020c) and Horner (2013) were used to identify the locations of shipwrecks and obstructions. After aggregating these data, post-processing was completed to ensure that structures were not duplicated and presumably still present at the location and collectively referred to as artificial habitat. Locations of natural hard-bottom habitat in the northern GOM were obtained from NOAA's Coral Essential Habitat (NOAA 2020b), BOEM's confirmed relic patch reefs (BOEM 2020), Shirley (2012), Horner (2013), and NOAA's southeast Fisheries Science Center side scan and multibeam and sonar data (C. Gardner, National Marine Fisheries Service, personal communication). Distance to the nearest artificial and natural hard-bottom habitat was calculated as the shortest in-water distance (km) from a sampling location using the Cost Distance tool in ArcGIS.

We fit a joint time-varying move persistence model to the regularized data to identify periods of area-restricted and transiting movement behavior along individual tracks. The model calculates a move persistence index (γ_t) between successive location estimates, which captures the autocorrelation in speed and directionality. The move persistence index objectively identifies changes in behavior along a continuum ranging from 0 (low speed and directionality indicative of area-restricted behavior) to 1 (high speed and directionality indicative of transiting behavior) rather than switching between discrete behavioral states (e.g., Bailey et al. 2008; Michelot et al. 2017). The joint move persistence model estimates a single, pooled random variance parameter jointly across the tracks, which can often better resolve subtle changes in movement behavior. One-step-ahead (prediction) residuals were calculated from the SSM fit to evaluate model performance.

To investigate which factors are associated with changes in move persistence, we modeled the response of γ_t to a suite of candidate predictor variables using generalized additive mixed models (GAMMs). We incorporated sex, FL, bathymetry, SST, log-transformed chlorophyll *a*, and distance to artificial and natural hard-bottom habitats as candidate predictor variables. Since known locations of artificial and natural hard-bottom were restricted to the northern GOM within the U.S. Exclusive Economic Zone (EEZ), only mako shark SSM locations within the GOM (boundaries defined by Felder et al. 2009) were included in GAMM analyses. Prior to model fitting, data exploration was carried out per Zuur et al. (2010). Collinearity between candidate predictor variables was assessed with Pearson correlation coefficients and variance inflation factors (VIF) using the *corvif* function in R. High VIF (>3) indicated high collinearity between shark sex and size; therefore, each variable was included separately during model selection. Move persistence was logit transformed and modeled using a Gaussian distribution with an identity link function using the *mgcv* package in R. Thin plate regression splines were estimated for each candidate predictor variable, and we included a correlation structure with an autoregressive process of order 1 (AR1) to account for serial correlation in time series data. As observations were repeated measures collected from the same individuals, we modeled individual sharks as a random effect to account for variation among individual responses to environmental variables. Models were explored using unrestricted smooths, but final models limited the basis (k) used to represent the smooth terms at 5 (Keele 2008). Model selection was based upon an information-theoretic approach through minimization of the second-order Akaike Information Criterion (AICc; Burnham and Anderson 2002) using the *MuMIn* package (Bartoń 2020). Models with substantial support were selected based on a ΔAICc < 2 from the model with the lowest AICc and included in model averaging based on Akaike weights (w; Burnham and Anderson 2002). Significant predictor variables ($p < 0.05$) with high relative importance (sum of model weights over all models including each explanatory variable) were retained in the final model used for the graphical representation of terms, calculation of deviance explained, and adherence to statistical assumptions of residuals.

We inferred post-release (i.e., discard) mortality using SPOT tag reporting rates (Gallagher et al. 2014). It is usually impossible to distinguish capture-related mortality from natural mortality several days after capture; therefore, estimates of post-release mortality were restricted to a fixed number of days after release. For mako sharks, Campana et al. (2016) showed that if post-release mortality was going to occur, it usually happened within a day or two following release; however, some post-release mortalities occurred up to a week or more (Campana et al. 2016). Therefore, we restricted the classification of post-release mortality events to the first 14 days following release (Gallagher et al. 2014; Byrne et al. 2017). Any tags that ceased to report during this 14-day period were classified as capture-related mortalities. As there is potential to classify tags that malfunction as mortalities, our estimate is conservative, minimizing the likelihood of underestimating the true post-release mortality rate. Fates were compared to fight time, which included the time when the shark was hooked through when the shark was released, using a Kruskal-Wallis test.

Fishing mortality from harvest was identified from angler recapture reports or using clues from downloaded tracks. Specifically, harvests were identified if a tag consistently reports from a fixed location on land or if a reporting tag begins a continuous track towards a fishing port, indicating the tag is onboard a fishing vessel. When possible, additional information regarding harvests was obtained, including the approximate date and location of capture and information regarding the fishery in which the shark was harvested. We classified the known fates of individual mako sharks as alive or dead during discrete time intervals after release and used known-fate models in the MARK program (White and Burnham 1999) to estimate harvest-specific survival probabilities (SF). Known-fate models are binomial generalized linear models of survival, which allow for comparisons of survival by individual covariates such as sex and size (Byrne et al. 2017). Conveniently, annual survival probabilities can be estimated by the product of the survival likelihoods of each sample interval. We used tagging data from all reporting shark tags, even those with tracking periods of less than one year. After estimating harvest-specific survival probability (SF), we estimated instantaneous fishing mortality as $F = -\ln(SF)$. To account for model uncertainty, we calculated a range of F using the 95% CI of our annual SF estimate.

Results:

From 2016 to 2021, 21 makos were tagged with SPOT tags off the coast of Texas (**Table 1**). Twelve were tagged as a part of this project, and nine were tagged prior to the beginning of this project. Twenty sharks were tagged >40 nautical miles offshore from Port Aransas, and one was tagged from shore along the Padre Island National Seashore, Texas. Based on published 50% size-at-maturity data, 14 of the 15 male makos (168 – 237 cm FL) were mature or nearing maturity (182 cm FL; Natanson et al. 2020), and five of the six tagged females (165 – 361 cm FL) were mature or nearing maturity (280 cm FL; Natanson et al. 2020). Two females had recent (i.e., fresh with no healing or scarring) bite marks anterior to the dorsal fin at capture, which could suggest mating or fighting behaviors were occurring. One female was recaptured 3 h after being released post-tagging in the same location; this individual was subsequently re-released (Gibson et al. 2021). Tracking duration varied widely from 10 to 887 days (mean = 270 days; median = 166 days), with 12 mako sharks tracked for >100 days. To allow for dispersion from the tagging site, only tracks exceeding 14 days at liberty were included in movement analyses (Vaudo et al. 2017), which excluded the only female tagged from shore and three males tagged ~50 nautical miles from shore. Two omitted males reported less than a day, with the third reporting for 10 days before ceasing reporting.

Table 1. Tagging information for shortfin mako sharks (*Isurus oxyrinchus*) tagged in the northwestern Gulf of Mexico. Release fate corresponds to survivor (S) or post-release mortality (M).

Shark	Sex	Mature	FL (cm)	Site	Tagging Location	Tagging Date	Last Detection Date	Fight + Handling Time (min)	DAL	Fate
1	M	No	168	Ranzell Rocks	27.52°N, 96.71°W	25 Feb 2016	27 Apr 2016	30	62	S
2	F	Yes	290	PINS	26.62°N, 97.30°W	26 Mar 2016	06 Apr 2016	45	11	M
3	M	Yes	210	MU-A-85ST	27.73°N, 96.20°W	08 Apr 2016	16 Mar 2018	30	707	S
4	F	Yes	353	HI-389	27.90°N, 93.58°W	21 Mar 2017	25 Aug 2019	63	887	S
5	M	Yes	196	MU-A-85ST	27.73°N, 96.19°W	13 Mar 2018	06 Aug 2020	18	877	S
6	M	Yes	218	BA-A-133BST	27.84°N, 96.19°W	18 Mar 2018	16 Oct 2018	22	212	S
7	F	Yes	361	BA-A-133BST	27.84°N, 96.19°W	18 Mar 2018	13 Apr 2018	50	26	S
8	F	Yes	282	BA-A-133BST	27.84°N, 96.19°W	19 Mar 2018	04 Apr 2018		16	S
9	M	No	189	BA-A-133BST	27.84°N, 96.01°W	28 Feb 2019	11 Apr 2020	190	408	S
10	F	No	165	BA-A-133BST	27.84°N, 96.01°W	09 Apr 2020	22 Sep 2020	30	166	S
11	F	Yes	295	MU-A-85ST	27.73°N, 96.19°W	02 Feb 2021	30 May 2021	53	117	S
12	M	Yes	208	MU-A-85ST	27.73°N, 96.19°W	23 Feb 2021	06 Apr 2022	31	407	S
13	M	Yes	203	MU-A-85ST	27.73°N, 96.19°W	24 Feb 2021		62	0	M
14	M	Yes	212	MU-A-85ST	27.73°N, 96.19°W	24 Feb 2021	03 May 2021	28	68	S
15	M	Yes	226	MU-A-85ST	27.73°N, 96.19°W	24 Feb 2021	24 Feb 2021	35	0	M
16	M	Yes	200	MU-A-85ST	27.73°N, 96.19°W	24 Feb 2021	14 Jan 2022	11	324	S
17	M	Yes	206	MU-A-85ST	27.73°N, 96.19°W	24 Feb 2021	14 Oct 2021	25	232	S
18	M	Yes	208	MU-A-85ST	27.73°N, 96.19°W	24 Feb 2021	04 May 2021	15	69	S
19	M	Yes	188	MU-A-85ST	27.73°N, 96.19°W	24 Feb 2021	06 Mar 2021	13	10	M
20	M	Yes	237	MU-A-85ST	27.73°N, 96.19°W	24 Feb 2021	27 Jun 2021	30	123	S
21	M	Yes	205	MU-A-85ST	27.73°N, 96.19°W	25 Feb 2021	02 Apr 2022	25	401	S

DAL, days at liberty

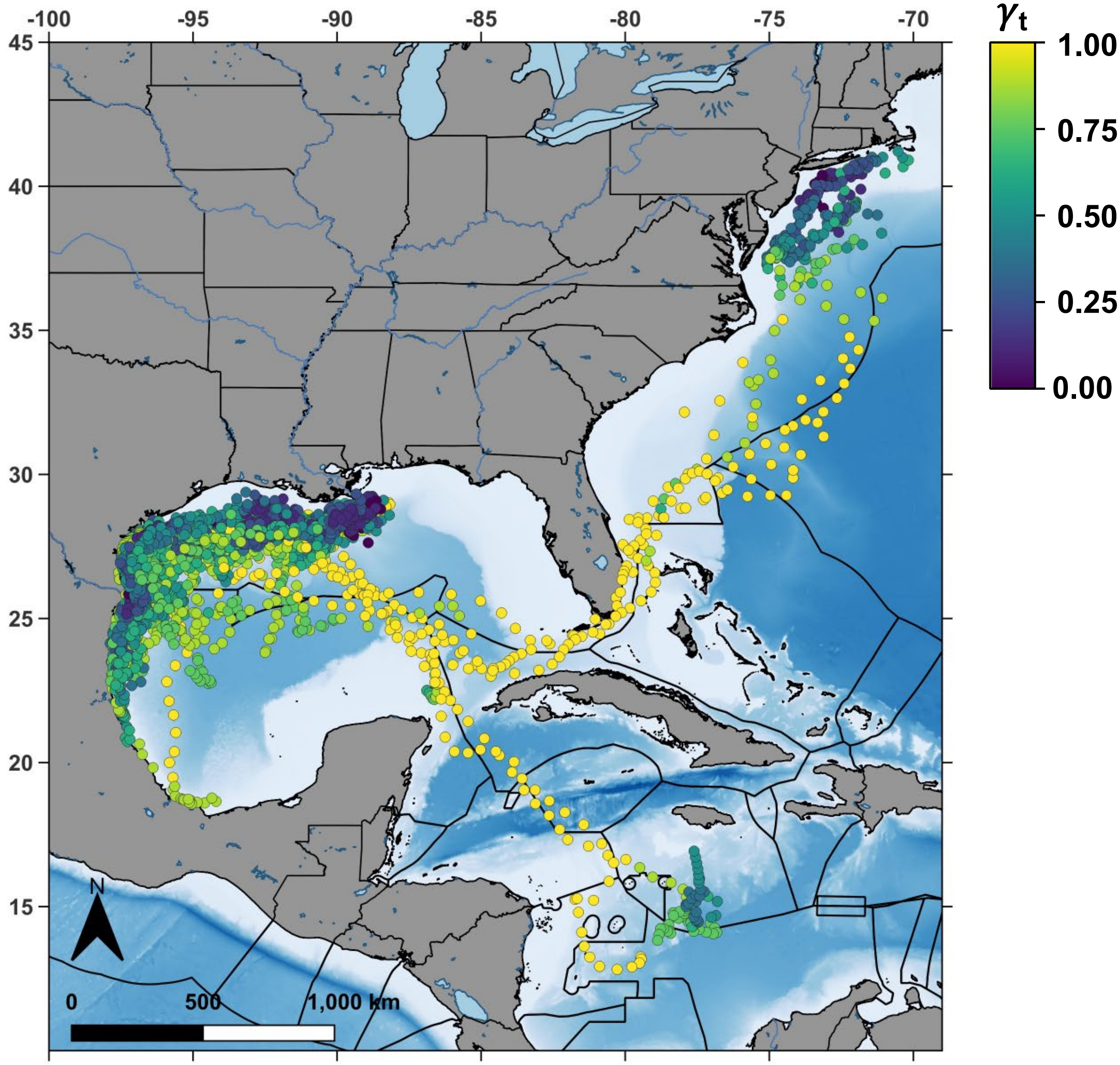

Figure 1. Daily location estimates from the continuous-time correlated random walk state-space model for all satellite-tagged shortfin mako sharks tagged off the Texas coast with tracks exceeding 14 days at liberty (n = 17). Each location is colored according to its associated move persistence (γ_t) estimated from the joint time-varying move persistence model. Black lines denote Exclusive Economic Zones for each country. The move persistence index identifies changes in behavior along a continuum ranging from 0 (low speed and directionality indicative of area-restricted behavior) to 1 (high speed and directionality indicative of transiting behavior).

Objective 1: Identify migration corridors and population connectivity of mako sharks to further our knowledge of stock structure

Building upon our existing dataset (see Gibson et al. 2021), this study further demonstrated year-round space use in the GOM, particularly in the northwestern GOM west of the central stem of the Mississippi River Delta (~89.1°W; **Figure 1**). Only two mature males that were previously tracked for multiple years exited the GOM during the summer months and returned to the northwestern GOM in the winter months (**Figure 1**). Shark 3 traveled to the Caribbean Sea in two consecutive summers and returned to the Texas coast in late fall each year. Shark 5 traveled through the Straits of Florida and up the Atlantic coast to the northeast U.S. in two consecutive summers, returning the first year during winter. For both male sharks (Sharks 3 and 5), these long excursions were characterized by directionally persistent migration followed by a long seasonal residency before returning to the GOM. The spatial and temporal persistence between years of this transiting behavior may suggest key migration corridors in the Straits of Florida and Yucatán Channel connecting the GOM to the western North Atlantic Ocean.

Conversely, several other sharks did not exit the western GOM but moved into the southwestern GOM near the Mexican shoreline before moving into deeper water and returning northward toward the continental shelf off the Texas coast. Only Shark 11 exhibited increased move persistence indicative of transiting or migratory behavior. Conversely, Sharks 10, 12, and 14 demonstrated decreased move persistence indicative of area-restricted or resident behavior when moving up and down the Mexican coast, predominantly off Tamaulipas. Mako sharks traversed a geographical area of 12.8°–41.2°N latitude and 69.8°–97.7°W longitude, which included the GOM, Atlantic Ocean, Caribbean Sea, and the management jurisdictions for at least 12 nations and international waters (see Gibson et al. 2021). Though, 15 of 17 mako sharks with tracks exceeding 14 days remained exclusively within the GOM and the EEZs of the U.S. and Mexico. Population-level core use areas (50% KUD) occurred almost exclusively within the northwestern GOM, and home range areas (95% KUD) predominantly occurred within the GOM, outside of the two males that migrated to the Caribbean Sea and northeast U.S. (**Figure 2**).

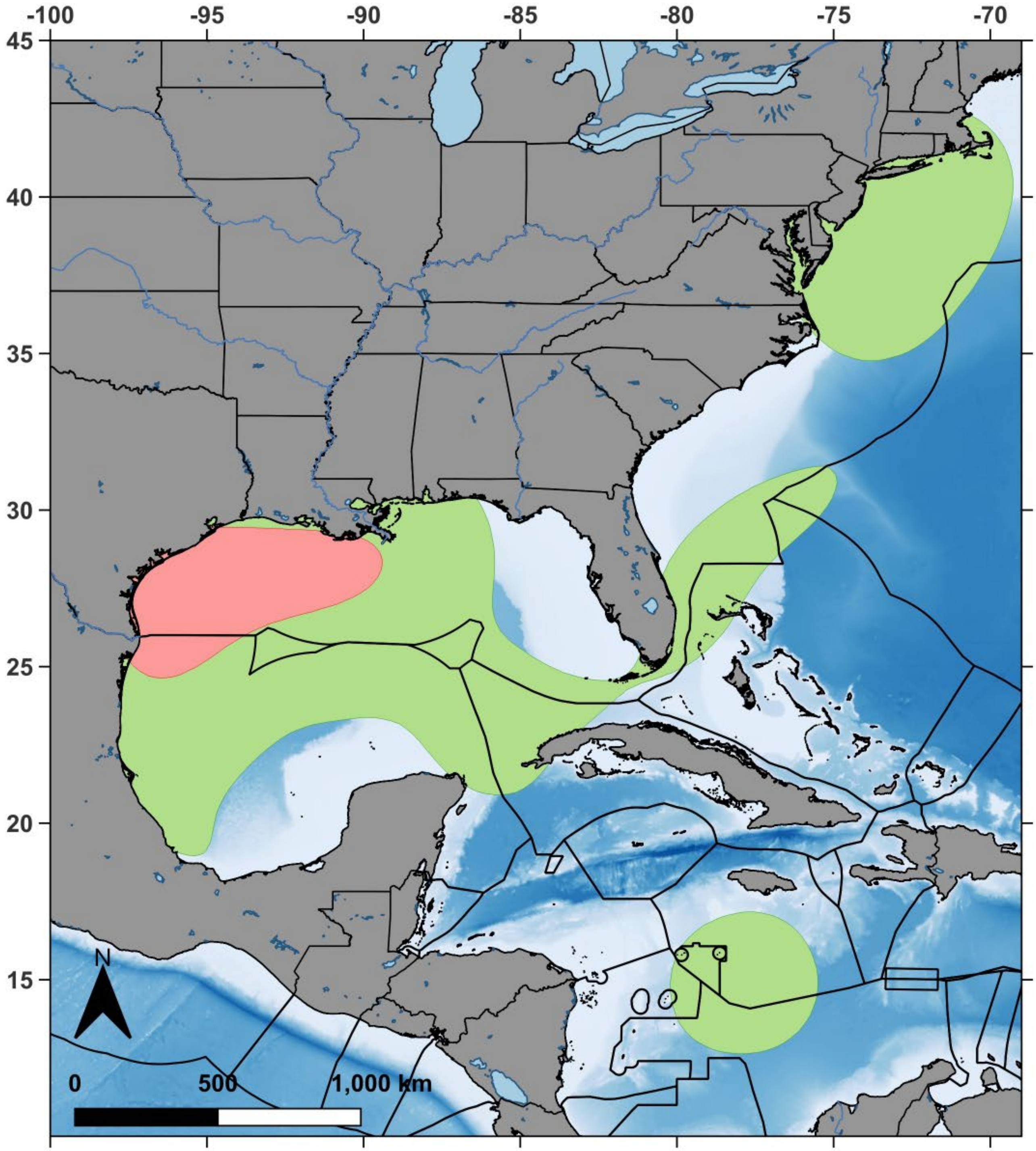

Figure 2. Population-level kernel utilization distributions (KUD) calculated from all satellite-tagged shortfin mako sharks tagged off the Texas coast with tracks exceeding 14 days at liberty (n = 17). Core use areas (50% KUD) are shaded red and home range areas (95% KUD) are shaded green. Black lines denote Exclusive Economic Zones for each country.

Objective 2: Determine the spatiotemporal extent of interactions between mako sharks and fish aggregating devices (FADs) such as oil and gas infrastructure

SST, log-transformed chlorophyll *a*, bathymetry, and distance to natural hard-bottom habitat were included in the GAMM that best fit the move persistence data. The model only explained 0.74% of deviance in move persistence by mako sharks indicating there are additional factors beyond our model explaining the majority of variation in their movement. Residual analyses indicated a satisfactory fit for low to moderately high move persistence values; however, a departure from normality was observed at high move persistence values (i.e., transiting behavior) and must be interpreted with caution. Overall, mako sharks had movements that became less persistent or directed in shelf and slope habitats shallower than 500 m and when experiencing SSTs below 26°C and chlorophyll *a* concentrations below 0.22 mg m^{-3} (**Figure 3**). While distance to artificial habitat was not included in the final best-fit model, mako sharks exhibited lower move persistence (i.e., decrease in speed and directionality) as distance increased greater than 200 km from natural hard-bottom habitats. In contrast, increases in move persistence (i.e., increases in speed and directionality) predominantly occurred in offshore pelagic habitats (>500 m depth) and when experiencing warm SSTs above 26°C (**Figure 3**). Move persistence also increased to some extent in more productive waters with chlorophyll *a* concentrations above 4.48 mg m^{-3}.

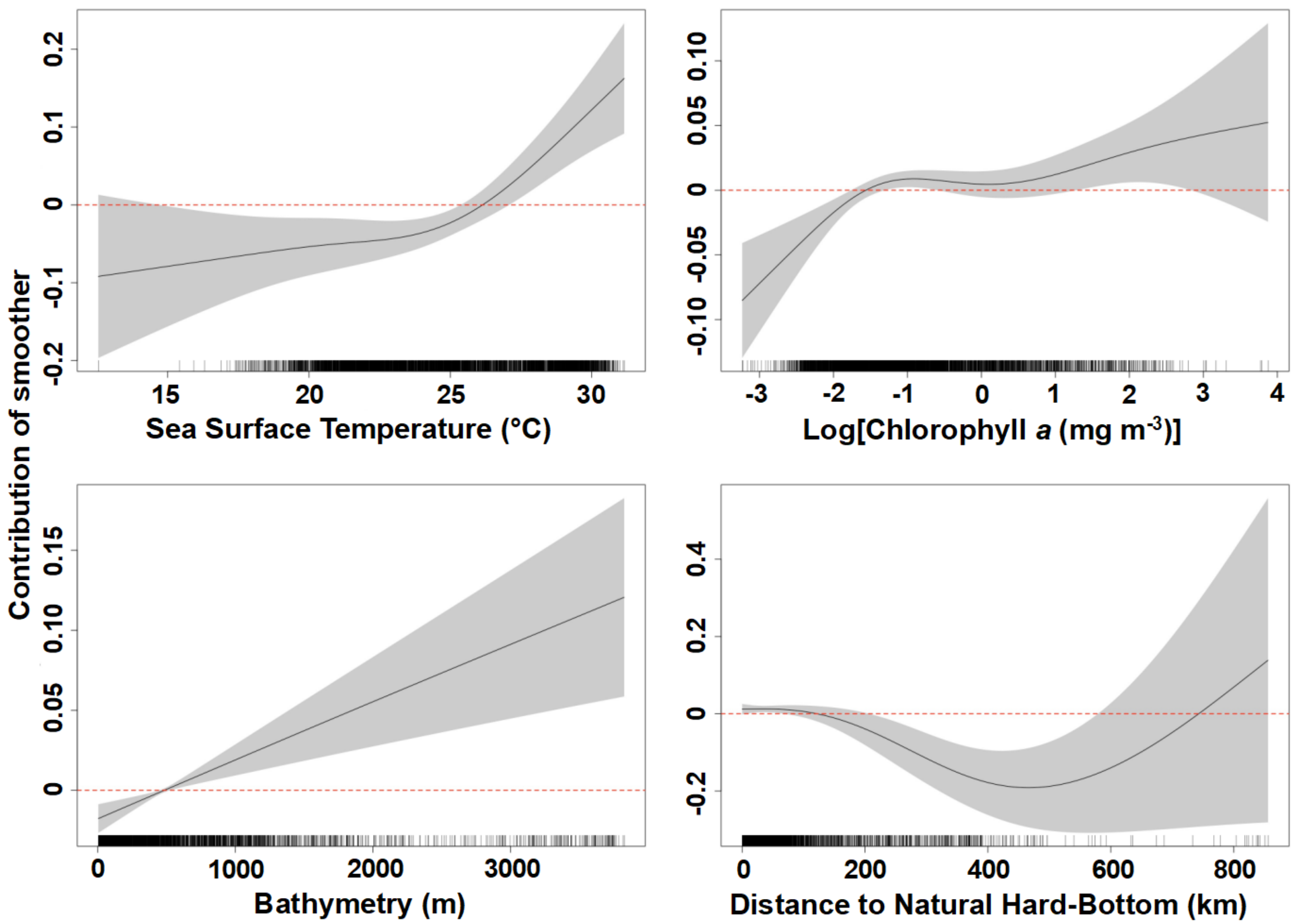

Figure 1. Estimated response curves (black solid line) of component smooth functions on daily move persistence of shortfin mako sharks from the best-fit generalized additive mixed model. Shaded areas represent 95% confidence limits of uncertainty in the centered smooth. Vertical axes are partial responses (estimated, centered smooth functions) on the scale of the linear predictor. Ticks on x-axis denote values for which there are data. Positive values on y-axis (above red dashed line) indicate increased move persistence (high speed and directionality indicative of transiting behavior) by shortfin mako sharks.

Objective 3: Estimate two sources of fishing mortality for mako sharks captured in the GOM recreational fishery

Of the 21 tagged mako sharks, three reported at least one message before ceasing communication before the 14-day period, therefore, were classified as post-release mortalities (**Table 1**). One tag did not report any messages (Shark 13) but was likely cracked during release, allowing water intrusion into the tag and causing a malfunction. The shark was observed to have swum off strong, suggesting the possibility of survival. However, due to the lack of detections from this tag, two mortality estimates were calculated. One included this shark as a mortality to be conservative, and the second estimate had the shark as a survivor. Post-release mortality including Shark 13 was 19.0%, while post-release mortality excluding this individual was 14.3%. Fight time (which includes fight and handling time) was not significantly different between fates (Kruskal-Wallis: chi-squared = 0.1136, p = 0.736). Fishing mortality was 0% for this study as no sharks were reported harvested and no track suggested harvest (i.e., a continuous track towards a fishing port, indicating the tag is onboard a fishing vessel).

Discussion:

This study comprises the most comprehensive electronic tracking dataset on mako sharks, especially adults, in the GOM to date. It has significant implications for management, especially since the degree of international exchange between the U.S. GOM and other nearby countries (e.g., Mexican waters) is relatively high. Because information regarding the stock structure and mortality estimates for mako sharks in the North Atlantic is limited and especially lacking in the GOM, this project provided much-improved data for use in stock assessments and the development of spatial management plans. Collectively, these data can aid the development of spatially-explicit stock assessment models, which commonly produce more precise estimates than models that do not consider movement (Braccini et al. 2016). This project also provided robust estimates of post-release mortality (14.3% – 19.0%) critical for effective fisheries management. Collectively, the information obtained in this study will be essential in developing future federal and international management plans promoting the sustainability of this economically and ecologically important living marine resource.

Contrary to our previous study with a more limited sample size, this study revealed both mature males and females remained in the northwestern GOM year-round. Moreover, the home range (95% KUD) of 60 makos previously tagged off the U.S. western North Atlantic and Isla Mujeres, Mexico (Vaudo et al. 2017; Byrne et al. 2019; Manz 2021) displayed minimal distributional overlap with the core use areas (50% KUD) of mako sharks tracked in this study which occurred entirely within the northwestern GOM (i.e., west of the Mississippi River Delta). While our results may be biased due to the tagging location of all mako sharks in this study occurring in the northwestern GOM, long track durations (mean 270 days) in this study revealed demographic-based differences in core use areas (50% KUD) and home ranges (95% KUD) of mako shark movements among western North Atlantic U.S. and international waters. Furthermore, only two mature males made extensive large-scale migrations that crossed multiple management jurisdictions, demonstrating the need for cooperative international management to conserve and rebuild the declining western North Atlantic stock. These individuals exited the GOM beginning in the late summer-early fall and returning in late fall-early winter each year. While the timing of these directed migrations showed a pattern, the destination of these excursions and residency time at each destination varied individually. Resident behavior of these two individuals overlapped previously reported core use areas (50% KUD) of juvenile mako sharks during summer and fall months in the western North Atlantic but never in the GOM (Vaudo et al. 2017). Observations of non-migratory individuals (i.e., partial migration; Papastamatiou et al. 2013) and disparate tracks of migratory individuals underscore the complexity of mako shark behavior and habitat use. Therefore, our results suggest the northwestern GOM may be a previously unidentified important area for mako sharks, supporting a fairly resident population and attracting transiting mako sharks from elsewhere in the western North Atlantic.

Bathymetry had the most consistent effect on move persistence, with more resident behavior primarily associated with shelf and shelf-slope waters. A similar association has been observed for mako sharks in the eastern North Pacific Ocean (Block et al. 2011), South Australian Bight (Rogers et al. 2015), and the western South Pacific Ocean (Francis et al. 2019). Shelf and shelf-slope waters may be attractive to mako sharks due to the abundance and variety of prey available compared to deep-water oceanic habitats. Mako sharks were also more likely to adopt resident behavior in cool waters below 26°C, reflecting the prevalence of resident behavior north of the warm waters of the Gulf Stream and Sargasso Sea in the western North Atlantic by Byrne et al. (2019). In contrast, mako sharks increased move persistence (increased speed and directionality) when experiencing high chlorophyll *a* concentrations, suggesting avoidance of nearshore areas with high nutrient input (e.g., Mississippi River plume). This finding was supported by Wells et al. (2018) for scalloped hammerhead sharks (*Sphyrna lewini*) satellite-tracked in the GOM.

Despite that 19 of the 21 (90.4%) mako sharks were captured and tagged near oil and gas infrastructure (**Table 1**), distance to artificial structure was not found to have a significant influence on the move persistence of mako sharks; though, move persistence decreased (decrease in speed and directionality) at distances greater than 200 km from natural hard-bottom habitats. To facilitate Objective 2, we originally planned to deploy SPOT tags equipped with Fastloc-GPS technology on mako sharks. When at the surface, Fastloc uses GPS to acquire highly accurate positions (up to 20 m resolution), which are subsequently transmitted through the Argos satellite system. Compared to Fastloc-equipped tags, conventional SPOT tags (such as those used in this study) estimate positions via Doppler-shift calculations from consecutive transmissions received in a single satellite pass by the Argos satellite system and result in accuracies as high as <250 m. While this error is not problematic for estimating migratory pathways across large spatial scales, it can hinder finer-scale analyses, such as area-restricted movements associated with mesoscale oceanographic features or artificial structures (e.g., oil and gas infrastructure). Future studies should utilize high-resolution tracking technologies, such as Fastloc-GPS, if and when they become commercially available to scientists and resource managers to further evaluate the impact of FADs on mako shark behaviors and fine-scale movements around these and other structures.

Of the 21 tagged mako sharks, three (14.3%) reported at least one message before ceasing communication before the 14-day period and were classified as post-release mortalities. These results are similar to the only other study that quantified post-release mortality (10%) for recreationally caught shortfin makos sharks in Australia (French et al. 2015). Our post-release mortality further increased to 19.0% when including another tag (Shark 13) that did not report any messages. Despite increasingly sophisticated technology, Argos-linked satellite tags can fail to transmit position estimates (Hays et al. 2007). Distinguishing these tag failures from post-release mortality events is critical, especially when examining imperiled populations such as mako sharks (Cooke 2008). It is possible that the SPOT tag was inadvertently cracked during release causing a malfunction, or this particular individual may not have spent sufficient time (>90 s) on the surface to allow the fin-mounted SPOT tag to communicate with the Argos satellite system long enough to estimate position, which double-tagged individuals of other shark species have demonstrated (e.g., Drymon and Wells 2017; Meyer et al. 2018). Fight time was not significantly different between fates, and the high aerobic scope associated with the species' endothermy may have enabled it to cope with long fight times and the associated physiological responses to capture (French et al. 2015). In this study, we also observed 0% fishing mortality, which is considerably lower than the 30% (12 of 40) satellite-tagged juvenile mako sharks tracked in the western North Atlantic that were harvested by vessels from countries bordering the GOM including the U.S., Mexico, and Cuba (Byrne et al. 2017).

Results from this study demonstrate that most mako sharks remained in the northwestern GOM year-round, yet some are capable of undertaking large-scale movements. If mature male and female mako sharks show philopatry to relatively small areas within national EEZs, such as the U.S. and Mexico, that adopt and enforce current management recommendations, these regions may have a disproportionate impact on rebuilding and emphasize the need for national management. Correspondingly, large-scale movements across multiple jurisdictional boundaries observed for two mature males in this study emphasize the need for international cooperative management to conserve this imperiled species. Intra-population variability in movement has clear importance in the context of managing HMS at the ocean basin scale, and the development of meaningful, spatially explicit models will rely heavily on rates of exchange among different regions (Sibert and Hampton 2003). Our study and others suggest migratory variations and potential sex- and size-based segregation within the North Atlantic stock that may warrant consideration in future management strategies. Thus, while our study provides new information on the movement ecology for mako sharks in the WNA, especially for mature individuals that have been underrepresented in previous scientific efforts, additional tagging efforts across the GOM focused on mature individuals are needed to identify mating and parturition grounds and better assess the patterns observed here. These studies will allow a robust evaluation of the possibility of multiple reproductive stocks, leading to more management confidence and aiding rebuilding efforts.

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Reviewed by:

________________________________ Date: ______________________

Mark Fisher, Ph.D., TPWD Project Coordinator

Approved by:

________________________________ Date: ______________________

Tammy Brooks, Federal Aid Coordinator