Estimating at-vessel mortality rates of shortfin mako sharks caught in the US pelagic longline fishery and examining environmental drivers of their depth use in the North Atlantic Ocean

A Thesis

presented to

the Faculty of the Graduate School
at the University of Missouri-Columbia

In Partial Fulfillment
of the Requirements for the Degree
Master of Science

by

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JULY 2022
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Acknowledgments

Thank you to the members of my committee for the help and support they provided me throughout my thesis work. Thank you, Dr. Michael Byrne, for supporting me over the last few years and for all the time spent working through problems and logistics related to my thesis. Especially for the thoughtful insight and knowledge base that helped broaden my thought processes. Thank you to Dr. Eric Hoffmayer for the help working through tagging logistics and encouragement throughout my time working on the mako shark project. Thank you as well to Dr. Lauren Sullivan and Dr. Craig Paukert for serving on my committee and providing guidance and support along the way.

I would also like to express my appreciation for Brooke Anderson who helped during the fieldwork and Dr. James Sulikowski for overseeing logistical parts of the project. I would like to especially thank Captain Gordy on Fishing Vessel Sarah Brent for allowing us to deploy tags on mako sharks and welcoming us kindly onto his vessel. A special thanks to Sascha Cushner, Cody Rewis, and the observers who have organized the logistics of delivering tags to the observer program and helped put out tags on mako sharks caught as bycatch in association with US pelagic longline fisheries. Furthermore, I want to thank all the captains who agreed to allow the observers to deploy tags on mako sharks caught as bycatch on their vessels. This project also would not have been possible without all the help from prior observers who collected data through the observer program. I would like to thank NOAA for funding and for observer data.

I would like to thank Dr. Joanna Whittier and Dr. Samniqueka Halsey for working on side projects with me while my assigned thesis was delayed. Thanks to all my fellow graduate students who talked through my research, helped review analysis and papers,
and provided support and friendship throughout my graduate career at the University of Missouri.

Finally, I would like to thank my friends and family who have provided support and offered a helping hand throughout the struggles of my master’s degree, especially Alli Schumacher, Chelsea Olson, Holly Jamieson, David Hicks, and my sisters and parents.
# Table of Contents

Acknowledgments............................................................................................................... ii

List of Tables ...................................................................................................................... v
  Chapter 2 ......................................................................................................................... v
  Chapter 3 ......................................................................................................................... v

List of Figures .................................................................................................................... vi
  Chapter 2 ........................................................................................................................ vi
  Chapter 3 ....................................................................................................................... vii

Abstract ............................................................................................................................... x

Chapter 1: History, biology, and conservation of the shortfin mako shark ..................... 1
  References ....................................................................................................................... 8

Chapter 2: Examining regional differences in at-vessel mortality of shortfin mako sharks caught in the U.S. Pelagic Longline Fleet. ............................................................ 16
  Introduction ................................................................................................................... 16
  Methods ......................................................................................................................... 20
  Results ........................................................................................................................... 24
  Discussion ..................................................................................................................... 26
  References ..................................................................................................................... 32
  Tables and Figures ........................................................................................................ 43

Chapter 3: Evaluating environmental drivers of shortfin mako shark vertical habitat use in the North Atlantic Ocean ............................................................................ 52
  Introduction ................................................................................................................... 52
  Methods ......................................................................................................................... 56
  Results ........................................................................................................................... 60
  Discussion ..................................................................................................................... 62
  References ..................................................................................................................... 66
  Tables and figures ......................................................................................................... 75
  Conclusions ....................................................................................................................... 85
Chapter 2

Table 2.1: Summary statistics of the fishing gear variables, hook depth (m) and soak time (hours), and sea surface temperatures (°C) used to group U.S. Atlantic pelagic longline regions described by the National Marine Fisheries Service (NMFS). SST = sea surface temperature (°C), GOM = Gulf of Mexico, NED = Northeast District, NEC = Northeast Coast, MAB = Mid-Atlantic Bight. 43

Table 2.2: Logistic regression results for examining the effect of year on at-vessel mortality (AVM) in the Gulf of Mexico (GOM) from 2000 – 2019 and Western North Atlantic (WNA) from 2000 – 2020, regions of the U.S. pelagic longline fishery described by the National Marine Fisheries Service (NMFS). Models in bold represent best fit model ranked by Akaike’s Information Criterion (AIC). 44

Table 2.3: Generalized additive model (GAM) results for the effect of environmental, biological, and fishing gear characteristics on at-vessel mortality (AVM) of the shortfin mako shark in the Western North Atlantic (WNA) and Gulf of Mexico (GOM) regions of the US pelagic longline fishery from 2000 – 2020. The predictors are smooth terms for hook depth (m), leader length (m), gangion distance (m), soak time (hours), shark size (cm), mainline length (km), and sea surface temperature (SST, °C). Edf = estimated degrees of freedom. AUC = Area under the curve. Bold values represent significant terms in the model. 45

Chapter 3

Table 3.1: Capture variables for all released shortfin mako sharks caught in the U.S. Pelagic longline fishery off the coast of North Carolina. M = Male, F = Female, U = Undetermined. PSAT = Pop-up satellite archival tag. 75
List of Figures

Chapter 2

Figure 2.1: Pelagic Observer Program statistical regions in the U.S. Atlantic defined by the National Marine Fisheries Service (NMFS). CAR = Caribbean, GOM = Gulf of Mexico, FEC = Florida East Coast, SAB = South Atlantic Bight, MAB = Mid Atlantic Bight, NEC = Northeast Coastal, NED = Northeast District, SAR = Sargasso, NCA = North Central Atlantic, TUN = Tuna North, and TUS = Tuna South…………………...46

Figure 2.2: Top panel: Probability of at-vessel mortality (AVM) output from binomial logistic regression models from 2000 – 2019 in (A) the Gulf of Mexico (GOM) and (B) Western North Atlantic (WNA) in the U.S. pelagic longline fishery (error bars represent 95% confidence intervals), and numbers observed mako shark catches in (C) the GOM and (D) WNA annually………………………………………………………………..47

Figure 2.3: Smooth function estimates and 95% confidence intervals from generalized additive models (GAMs) obtained by applying the double penalty approach with REML estimation on mako shark catch data from 2000 – 2020 in the Gulf of Mexico (GOM) region of the U.S. The covariates included are hook depth (m), leader length (m), gangion distance (m), soak time (hours), shark size (cm), mainline length (km), and sea surface temperature (SST; ºC). The y axis represents the estimated smooths and the x axis represents each covariate value. edf = estimated degrees of freedom…………………..48

Figure 2.4: Model predictions from the generalized additive models examining the influence of significant covariates influencing at-vessel mortality (AVM) in the WNA and GOM regions of the U.S. pelagic longline fishery. A) Effect of soak time on the predicted probability of AVM in the WNA, B) Effect of hook depth on the predicted probability of AVM in the GOM, C) effect of shark size on the predicted probability of
AVM in the GOM and WNA, and D) the effect of SST on the predicted probability of AVM in the GOM and WNA. GOM = Gulf of Mexico, WNA = Western North Atlantic, FL = fork length, SST = sea surface temperature………………………………………….49

**Figure 2.5**: Smooth function estimates and 95% confidence intervals from generalized additive models (GAMs) obtained by applying the double penalty approach with REML estimation on mako shark catch data from 2000 – 2020 in the Western North Atlantic (WNA) region of the U.S. pelagic longline fishery. The covariates included are hook depth (m), leader length (m), gangion distance(m), soak time (hours), shark size (cm), mainline length (km), and sea surface temperature (SST; °C). The y-axis represents the estimated smooths and the x axis represents each covariate value. edf = estimated degrees of freedom………………………………………………………………………………..50

**Figure 2.6**: Density plot of the 1000 iterations of a Monte Carlo simulation estimating the survival probability of mako sharks captured on longline gear in the GOM and WNA regions of the US pelagic longline fishery. The vertical lines represent mean values for each region. GOM = Gulf of Mexico, WNA = Western North Atlantic………………51

**Chapter 3**

**Figure 3.1**: Suspected mortality of tagged mako shark caught in pelagic longline gear off the coast of North Carolina, USA. Y-axis represents the depth of the shark in meters and x-axis represents time. The tag detached and floated to the surface after 8 hours………76

**Figure 3.2**: Example of post-release recovery behavior marked by low variance in dive depth at the beginning of the dive track. The red vertical line represents the end of the identified recovery period…………………………………………………………77
Figure 3.3: Generalized additive model smooth predicted estimates for temperature use over time of shortfin mako sharks tagged off the coast of North Carolina. The mean predicted temperatures are plotted on top of a boxplot of temperature use each day of deployment. The redline represents the daily mean predicted temperature. The blue represents the mean temperature used over the length of the deployment period. 78

Figure 3.4: The depth-temperature time series show the relationship between depth use and temperature recorded from the three tagged mako sharks in the North Atlantic. 79

Figure 3.5: Map on the left: Sea surface temperature (SST) contour chart of the US Atlantic Ocean. Data/image provided by the NOAA/NESDIS/OSPO, Maryland, USA, from their Web site at http://ospo.noaa.gov/. Map on the right: Tagging and pop-off locations of three sharks tagged off the coast of North Carolina in the North Atlantic Ocean. 80

Figure 3.6: Forest plot showing the effect of oceanographic features on the depth use of shortfin mako sharks in the North Atlantic Ocean. Variance in depth, mean depth, and maximum depth were used as proxies for depth use. All models included individual shark as a random effect. The plot shows the effect of the mixed layer depth (MLD) and sea surface temperature (SST, °C). The bars represent the 95% confidence intervals. The dotted vertical line is on zero. 81

Figure 3.7: Generalized linear mixed model results showing the effect of the mixed layer depth (MLD) on mako shark daily depth use with each individual shark included as a random effect. Daily depth variance, mean daily depth, and maximum daily depth were used as a proxy for depth use. 82
**Figure 3.8:** Generalized linear mixed model results showing the effect of SST on mako shark daily depth use with each individual shark included as a random effect. Daily depth variance, mean daily depth, and maximum daily depth were used as a proxy for depth use.

**Figure 3.9:** Population level model predictions from generalized linear models showing the effect of mixed layer depth (MLD) on depth use at different sea surface temperatures (SST).
Abstract

Shortfin mako sharks, *Isurus oxyrinchus*, have historically been a small part of recreational and commercial fisheries in the United States (U.S.). Recent stock assessments have identified declines in mako shark stocks that have caused widespread concern among researchers and managers. The National Marine Fisheries Service (NMFS), in accordance with recommendations from the International Conservation Committee for Atlantic Tunas (ICCAT), have introduced live release regulations for all commercial and recreational fishers that catch mako sharks. However, if mako sharks are caught as bycatch in commercial fisheries experience high at-vessel mortality rates (AVM) than these conservation measures may do little to help rebuild the stock. I examined AVM of mako sharks in two regions of the US Atlantic pelagic longline fishery, the Gulf of Mexico (GOM) and the Western North Atlantic (WNA), and AVM was found to be higher in the GOM (32.4%, 95% CI: 29.5 – 35.4%) and 25.7% (95% CI: 24.6% - 26.8%) in the WNA. At-vessel mortality was evaluated in relation to environmental, biological, and fishery characteristics. The variables influencing AVM in these two regions differed where sea surface temperature (SST), hook depth, and shark size were important in the GOM, whereas soak time, shark size, and SST were important in the WNA. In both regions, AVM increased in warmer waters. The relationship between shark size and AVM differed between regions where larger sharks in the GOM were more susceptible to AVM and intermediately sized sharks (~ 80 – 250 cm) had higher AVM in the WNA. Lastly, AVM decreased when hooks were set deeper in the water column in the GOM, and AVM increased with longer soak times in WNA.
Combining the estimates of AVM from this study and a PRM rate of 0.358 (sd = 0.06; Bowlby et al. 2021), the probability of survival of a shark hooked on a longline in the GOM was estimated at 42.6% (95% CI: 33.7 – 52.1%) and 47.4% (95% CI: 38.6 – 56.9%) in the WNA. Given the high AVM rates in both regions and the relatively low change of survival, the most effect management strategies to help rebuild mako shark stocks should focus on bycatch reduction.

Further, I examined the mako shark vertical habitat use patterns in relation to environmental drivers in a dynamic and diverse marine ecosystem of the North Atlantic Ocean. Overall, mako sharks’ vertical habitat use was related to temperature and mixed layer depth. Increased vertical habitat was correlated with the mixed layer depth where sharks dove to greater depths more frequently as the mixed layer deepened. Although encountering a broad range of temperatures, mako sharks tended to inhabit mean temperature ranges from 17 – 20 ºC. In this study, it appeared that mako sharks altered their vertical habitat to find waters that were within their optimal temperature range.
Chapter 1: History, biology, and conservation of the shortfin mako shark

The vulnerability of sharks to overfishing has been recognized across coastal and oceanic habitats, and overfishing has resulted in ~42.7% of shark species worldwide listed as threatened by the International Union for Conservation of Nature (IUCN, Dulvey et al. 2021; Pacoureau et al. 2021). Many shark species are apex predators, and there is concern about the consequences their removal may have on the stability and productivity of marine communities (Heithaus et al. 2008; Ferretti et al. 2010; Britten et al. 2014). Concern for high and rising shark extinction risk has resulted in calls for increased management, but measures are often hindered by data deficiency and conflicting political priorities for shark conservation (Davidson et al. 2016; Dulvy et al. 2021). Although shark fisheries around the world are common, there is little direct harvest (Bonfil 1994; Walker 1998) and most sharks are caught incidentally as bycatch (Molina and Cooke 2012). Sharks caught as bycatch are either retained or discarded at sea, and discarded sharks are often unaccounted for in fisheries management leading to an underestimate of actual fishing mortality and obscuring the role of overfishing in population declines (Dulvy et al. 2014).

Pelagic sharks live in the upper layers of the water column of the open ocean and are common bycatch species. Many species have experienced significant declines throughout their global ranges, including oceanic whitetip (Carcharhinus longimanus; Young et al. 2017; Rigby et al. 2019a), blue (Prionace glauca; Rigby et al. 2019b; Sherley et al. 2019), bigeye thresher (Alopias superciliosus; Rigby et al. 2019c), common thresher (A. vulpinus; Rigby et al. 2019d), longfin mako (Isurus paucus; Rigby et al. 2019e) and shortfin mako (I. oxyrinchus; Rigby et al. 2019f; Sherley et al. 2019) sharks.
Pelagic longline fisheries account for more shark bycatch than any other fishery (Oliver et al. 2015), and bycatch may exceed catch of target species (Molina and Cooke 2012).

Pelagic sharks have high bycatch risk in pelagic longline fisheries because their habitat use and foraging behaviors often overlap with those of commercially targeted species, such as billfish and tuna (Baum et al. 2003; Mejuto et al. 2008). Many pelagic sharks exhibit life history traits such as slow growth rates, late ages at maturity, and long gestation periods, which result in low productivity and slow population growth rates (Cortes 1998). Thus, unlike teolosts such as billfish and tunas, the biology of pelagic sharks makes them less resilient to fishing mortality and increases population recovery times (Au et al. 2008).

The shortfin mako (hereafter mako shark) is among the pelagic sharks most vulnerable to overfishing (Cortes et al. 2010). The mako shark is a large, highly migratory species in the family Lamnidae with circumglobal distribution in temperate and tropical waters (Rigby et al. 2019f, Santos et al. 2020), associated with the open ocean, continental shelf, and shelf edge habitats (Rogers et al. 2015; Vaudo et al. 2017; Francis et al. 2019; Nasby-Lucas et al. 2019; Santos et al. 2021). Individuals spend most of their time in the upper part of the water column (<300m) but can dive to depths greater than 800m (Vaudo et al. 2016; Francis et al. 2019; Nasby-Lucas et al. 2019; Santos et al. 2021). Their distribution in the water column is heavily influenced by water temperature and time of day (Vaudo et al. 2017; Nasby-Lucas et al. 2019; Santos et al. 2020). Mako sharks are apex predators that forage on a variety of prey including teleosts, chondrichthyes, crusteaceans, cephalopods, marine mammals and sea turtles (Stillwell and Kohler 1982; Maia et al. 2006). Mako sharks are particularly susceptible to over
exploitation because their slow growth rates (Natanson et al. 2006), late age of sexual maturation (7 - 9 years for males and 15 - 21 years for females; Bishop et al. 2006; Natanson et al. 2006), 15 –18 month gestation period and three-year reproductive cycle (Mollet et al. 2000) resulting in low productivity and slow population growth (Cortes et al. 2010).

There is no global abundance estimate for mako sharks, but the most recent stock assessments suggest a global decline of the species (Rigby et al. 2019f, ICCAT 2019). Mako shark populations have declined across the North Pacific Ocean (ISC 2018) and Indian Ocean (Brunel et al. 2018), but the steepest declines are documented in the North and South Atlantic Oceans (ICCAT 2019). Mako sharks are caught by numerous countries across the entire North Atlantic Ocean (Byrne et al. 2017; Vaudo et al. 2017) and are managed by the International Conservation of Atlantic Tunas (ICCAT), the inter-governmental organization responsible for management and conservation of pelagic sharks in the Atlantic. In the U.S., mako sharks are managed as a Highly Migratory Species (HMS) under the Magnuson-Stevens Act (16 U.S.C. 1801) and Atlantic Tunas Convention Act (ATCA; 16 U.S.C. 971) because they are primarily caught in fisheries targeting tuna and tuna-like species. Mako sharks have been a small, but valued part of U.S. recreational and commercial fisheries, but in 2020 the U.S. catch represented only 3% of the total catch in North Atlantic (NMFS 2022).

Mako sharks are primarily caught as bycatch by commercial fishers targeting swordfish (*Xiphias gladius*) and tuna (*Thunnus spp.*) or recreationally, on rod and reel. Makos have traditionally been retained (Campana et al. 2005), due to the high value of their meat which has been priced at $20-44/kg in U.S. markets (Dent and Clark 2015).
Mako shark fins represented at least 2.6% of the global shark fin trade between 1990 and 2001 (Clarke et al. 2006), and 2.4 – 4.2% in shark fin markets in China from 2015 – 2017 (Cardeñosa et al. 2020), and are also used for leather, while their jaws and teeth are used for decoration and souvenirs. Given the commercial value of mako sharks and their distributional overlap with commercial longline fleets (Queiroz et al. 2016), the species experiences high fishing mortality in the North Atlantic (Byrne et al. 2017).

The most recent ICCAT North Atlantic mako shark stock assessment determined the stock is overfished and overfishing is occurring (ICCAT 2019). Reported catches from 2015- 2017 in the North Atlantic equaled ~3,100 tons (t) annually, and population model predictions indicated drastic reductions in these catch levels are required to halt population decline and allow population recovery (ICCAT 2019). Based on model predictions, a total allowable catch (TAC) of zero would be required to allow the stock to rebuild without the occurrence of overfishing (ICCAT 2021). Given that zero fishing mortality is assumed unachievable, model projections predict the North Atlantic stock has a ~50% chance of recovery by 2070 if the TAC is < 500 t, including dead discards. To achieve a probability of recovery > 60%, TAC would have to be reduced to < 300 t. Unfortunately, regardless of reduction in catch, model projections predict a continued population decline until 2035 even if no fishing occurs (ICCAT 2019, 2021).

Based on vulnerable biological characteristics and stock assessment projections, mako sharks have recently been classified as Globally Endangered by the IUCN Red List (Rigby et al. 2019f) and given Appendix II listing in the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) to implement strict regulation and control of the trade of this species (CITES 2019). In response to stock
assessments, ICCAT adopted management Recommendation 17-08 (Rec. 17-08) in November 2017 as an immediate measure to end overfishing and allow the stock to begin rebuilding. Rec. 17-08 prohibits the harvest of live mako sharks caught in pelagic longline fisheries and requires the prompt release of any mako shark captured alive. The National Marine Fisheries Service (NMFS) responded to Rec. 17-08 with Amendment 11 to the Highly Migratory Species (HMS) Fishery Management Plan (NMFS 2019) which placed live release regulations into effect for US fishers. Amendment 11 requires a federal shark limited access permit to harvest commercially, and sharks may only be harvested if they are dead on haulback. All live mako sharks are required to be released in a manner that maximizes the chance of survival post-release while putting the crew aboard the fishing vessel at minimal risk (NMFS 2019). Further, in November 2021, ICCAT introduced the two-year management Recommendation 21-09, which prohibits any retention of mako sharks caught in association with ICCAT fisheries (ICCAT 2021).

The effectiveness of management measures that require a live-release regulation depends on two sources of mortality, at-vessel mortality (AVM) and post-release mortality (PRM). At-vessel mortality represents an event where an individual shark is dead when brought back to the vessel where death is directly related to capture, whereas PRM represents an event when a fish dies after being released from fishing gear where death is related to the effects of the capture and release process. At-vessel mortality for mako sharks has been estimated at 35.6% in the Portuguese longline fishery (Coelho et al. 2012), 26.2% in the Canadian longline fishery (Campana et al. 2015), and 28.6% in US Atlantic longline fishery (Gallagher et al. 2014). To date there are few published studies of mako shark PRM rates in the Atlantic Ocean. Campana et al. (2015) estimated
a 30% PRM rate in the Canadian pelagic longline fishery based on a sample size of 26 sharks monitored by satellite telemetry. The ICCAT Shark Research and Data Collection Program (SRDCP) estimated a 22.8% PRM rate from 35 satellite tagged sharks from Brazilian, Portuguese, Spanish, Uruguayan and United States vessels in the Atlantic during 2018-2019 (Miller et al. 2020). Recently, Bowlby et al. (2021) published a PRM rate of 35.8% in the North Atlantic.

In addition to documenting mortality, assessing sub-lethal behavioral changes following stress from capture on longlines may provide knowledge on how to reduce mortality to resource managers. Catch and release fishing may have sublethal population level consequences resulting from individual fitness related outcomes associated with the physical trauma and physiological imbalances of capture (Cooke et al. 2002). Sublethal effects are likely even when individuals survive capture and are released (Skomal, 2007), and may reduce individual fitness through disrupted production, reduced growth, and behavior modification leading to decreased foraging ability or predator avoidance (Cooke et al. 2002; Wilson et al. 2014). Several studies have documented that mako sharks exhibit modification in dive behavior when released (Loefer et al. 2005; Hoolihan et al. 2011; Bowlby et al. 2021). Post-release recovery periods for mako sharks have been shown to last up to five days (Hoolihan et al. 2011; Bowlby et al. 2021). Different handling procedures, water temperatures at release, and shark size may influence behavior impairments and lead to varied post-release recovery patterns. Management strategies aimed at reducing post-release recovery could ultimately aid in reducing post-release mortality.
Given the steep population declines and the vulnerable characteristics of the stock, research on mako shark bycatch and mortality needs to focus on better understanding the factors that make this species vulnerable to mortality when caught as bycatch. Fleet specific AVM rates are essential for determining management strategies that will increase the probability of mako shark survival. With the aim of better understanding AVM of mako sharks caught as bycatch my thesis will focus on assessing environmental conditions and fishing practices influencing AVM of mako sharks caught in different geographical regions of the US North Atlantic and Gulf of Mexico. The following chapters are writing as manuscripts for submission.
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Developments in Environmental Biology of Fishes Special Issue: Age and Growth of Chondrichthyan Fishes: New Methods, Techniques and Analysis


https://dx.doi.org/10.2305/IUCN.UK.2019-1.RLTS.T60225A3095898.en


https://dx.doi.org/10.2305/IUCN.UK.2019-1.RLTS.T39341A2903170.en


https://doi.org/10.1111/conl.12688


Chapter 2: Examining regional differences in at-vessel mortality of shortfin mako sharks caught in the U.S. Pelagic Longline Fleet.

Introduction

The vulnerability of sharks to overfishing has been widely recognized (Cortes et al. 2010; Worm et al. 2013; Dulvy et al. 2014; Barreto et al. 2016), with overfishing considered a primary driver of the listing of ~42.7% of shark species as threatened by the International Union for Conservation of Nature (IUCN, Dulvy et al. 2021; Pacoureu et al. 2021). Bycatch is a large contributor to overfishing and is considered one of the greatest threats to shark populations, especially pelagic sharks (Dulvy et al. 2014; Pacoureau et al. 2021). Concern for pelagic shark populations has driven research on bycatch reduction and fishing mortality (Campana et al. 2015; Eddy et al. 2016; Miller et al. 2020, Bowlby et al. 2021; O’Farrell and Babcock 2022).

The shortfin mako shark, *Isurus oxyrinchus*, is a pelagic shark highly vulnerable to overfishing (Cortes et al. 2010) which is commonly caught as bycatch in commercial fisheries targeting tuna and swordfish (Byrne et al. 2017; O’Farrell and Babcock 2022). The most recent stock assessment in the North Atlantic Ocean suggested the stock is overfished and experiencing overfishing (ICCAT 2019). This prompted the National Marine Fisheries Service (NMFS) to implemented live release regulations for all United States (U.S.) fishers, which prohibits the harvest of live mako sharks caught in pelagic longline fisheries (NMFS 2019). Further, in November 2021, ICCAT introduced a management recommendation which prohibits any retention of mako sharks caught (ICCAT 2021). The live release and retention bans implemented by ICCAT and NMFS are aimed at reducing mortality. However, retention bans do not mitigate two sources of
fishing mortality; at-vessel mortality (AVM) and post-release mortality (PRM). At-vessel mortality, also known as haulback or hooking mortality, represents the proportion of individuals that are dead when brought back to the vessel. Thus, death is directly related to interactions with fishing gear. At-vessel mortality of mako sharks has been estimated at 26.2% in the Canadian pelagic longline fishery (Campana et al. 2015), 35.6% in the Portuguese longline fishery (Coelho et al. 2012) and 28.6% in the US Atlantic longline fishery (Gallagher et al. 2014). Assuming that all live sharks are released, these results suggest AVM may make up an important source of total fishing mortality.

At-vessel mortality may be influenced by fishing practices (set durations, number of hooks, hook depth), environmental factors (dissolved oxygen, temperature) and biological factors such as fish size and ventilation morphology (Morgan and Burgess 2007; Coelho et al. 2012; Butcher et al. 2015; Ellis et al. 2017). Hooking depth was shown to be an important predictor of AVM in sandbar (Carcharhinus plumbeus) and dusky (Carcharhinus obscurus) sharks caught in demersal longlines (Butcher et al. 2015). However, the effect of hooking depth on AVM was different between species, with the probability of AVM increasing with depth for sandbar shark and decreasing with depth with dusky sharks, potentially related to species physiology. Soak time (the duration of time the longline is in the water) has been shown to increase AVM in blue sharks (Diaz and Serafy 2005). Previous studies have suggested that warmer water temperatures increase physiological stress in sharks (Hyatt et al. 2018), and increase AVM of blue, dusky, night (Carcharhinus signatus) and silky (Carcharhinus falciformis) sharks caught in commercial longline fisheries increased with temperature (Gallagher et al. 2014). Because warmer waters contain lower amounts of dissolved oxygen, the ability
to mitigate oxygen deficiencies from capture may be lower in warmer waters (Skomal and Bernal 2010). Mako sharks are ram ventilators with high oxygen requirements and can only withstand brief periods of inactivity before going hypoxic (Bernal et al. 2012), and being tethered to a longline may reduce the ability to ram ventilate, potentially leading to higher AVM rates.

U.S. pelagic longline fisheries are opportunistic, multispecies fisheries, and fishers may vary gear and fishing style to best target available species, reduce bycatch, or use new technologies. There are 11 geographical regions identified by the NMFS used in monitoring U.S. Pelagic longline fisheries (Figure 1, CAR = Caribbean, GOM = Gulf of Mexico, FEC = Florida East Coast, SAB = South Atlantic Bight, MAB = Mid Atlantic Bight, NEC = Northeast Coastal, NED = Northeast District, SAR = Sargasso, NCA = North Central Atlantic, TUN = Tuna North, and TUS = Tuna South). Target species and hook fishing depth for different regions are highly variable (Beerkircher et al. 2002). For example, in the MAB, NEC, and NED fishing depth commonly ranges from 22 – 35 m where the primary target species is tuna, and in the GOM, FEC, SAB, and TUS ranges from 35 – 67 m where the primary target species is swordfish (Beerkircher et al. 2002). Fishers may vary other operational aspects of fisheries including mainline length, soak time, and the time-of-day fishing starts.

Tagging studies have shown that the GOM and temperate western North Atlantic off the northeast coast of North America are hotpots for mako sharks (Queiroz et al. 2016, Byrne et al 2019) with limited movements between the GOM and North Atlantic Ocean (Vaudo et al. 2017). These regions have been classified as different marine ecoregions based on sea surface temperature and currents (Spalding et al. 2007;
Longhurst 2007), where the GOM is a subtropical/tropic region characterized by warmer waters compared to the temperate North Atlantic (Wilkinson et al 2009). Gallagher et al. (2014) used data from the Pelagic Observer Program (POP) to quantify AVM of mako sharks caught in the US pelagic longline fishery from 1995 – 2012, and found no evidence that operational, environmental, and biological variables influenced AVM of mako sharks. However, this study did not account for regional differences in water temperatures and fishing practices. Given that increased stress responses in warmer waters have been observed for multiple fish species (Gallagher et al. 2014; Schlenker et al. 2016; Hyatt et al. 2018) and the variation in fishing gear between regions (Beerkircher et al. 2002), estimating AVM by region may give added insight into the variables that influence mako shark AVM in the US pelagic longline fishery. Not accounting for regional variation may have masked the effects of variables that are regionally important predictors of AVM.

The goals of this study are to, 1) estimate annual AVM rates for the GOM and western North Atlantic regions of the U.S. Atlantic pelagic longline fishery, 2) determine how biological factors, environmental factors, and fishing practices influence mako shark AVM regionally, and 3) use estimated AVM rates and PRM rates from the literature to estimate survival probability of mako sharks hooked on a longline. Given that mako sharks are obligate ram ventilators with high oxygen requirements (Bernel et al. 2012), I predict that longer soak times, shallower hook sets, and shorter leaders would increase AVM of mako sharks. Given the relationship between warmer water and dissolved oxygen, I predict that mortality would increase when longlines are set in warmer water temperatures, and because larger sharks have been shown to have lower lactate
production during capture (Gallagher et al. 2014), I predict that smaller sharks would be more susceptible to AVM. Further, I predict there will be differences in AVM rates between regions due to the variability in fishing practices and water temperatures in different regions.

Methods

Data acquisition and preparation

Mako shark catch data from 2000 - 2020 were obtained from the US pelagic longline observer program (Southeast Fisheries Science Center, 2021). The Pelagic Observer Program (POP) was created in 1992 and monitors the US pelagic longline fleet ranging from Newfoundland along the Western Atlantic to Florida and throughout the GOM. The POP is used to monitor and evaluate the harvest and status of pelagic fish stocks. Observers on selected longline vessels record spatial coordinates, target species, environmental data, and gear configurations, as well as information on individual species caught, including size, sex, and whether the animal was alive or dead on haulback. Observer coverage of the total number of reported longline sets by the US pelagic longline fleet prior to 2007 was approximately 4-5%, and > 8% annually thereafter (Diaz et al. 2009). A coverage level of 8% was introduced to produce a statistically reliable sample of Highly Migratory Species (HMS), such as swordfish and yellowfin tuna (Thunnus albacares, Morrell 2019). An observer coverage rate of < 5% can provide sufficient information to support stock assessment, fish size and age structure, and selectivity (MSC 2021), whereas coverage >5% is required when estimating endangered, threatened, and protected species bycatch (Babcock et al. 2003, Brooke 2014).
Mako shark observations differed between geographical areas identified by NMFS (Figure 1). The regions with the least mako shark observations were CAR, NCA, SAR, FEC, SAB, and TUN and were removed from further analysis, because when combined they represented 8.6% of observations. Mako shark observations occurred mainly in NEC, MAB, NED and GOM and combined they represented ~91% of the data. The mean hook depth ranged from 15 – 28 m in the MAB, NED, and NEC (Table 2.1), whereas mean hook depth in the GOM was 66 m (Table 2.1). The mean SST in the MAB, NED, and NEC ranged from 17 – 22 ºC, whereas mean SST in the GOM was 26 ºC (Table 2.1). Mean soak time for all regions was ~ 8 hours (Table 2.1) Considering the differences in geographical location and fishing practices these regions were partitioned into two groups for further analyses. The NEC, NED, and MAB were grouped into one region called the Western North Atlantic (WNA), while the GOM was modeled as a separate region.

Annual variation of at-vessel mortality

To quantify annual variation in AVM, I used a logistic regression model using a logit link function:

$$\ln \left( \frac{p}{1-p} \right) = \beta_0 + \beta_1 (year_i)$$

Where $Pi$ is the probability of AVM, $\beta_0$ is the intercept, $\beta_1$ is the regression coefficient for the effect of the categorical variable year. To test the hypothesis that AVM varied annually, I used an information-theoretic approach using Akaike’s Information Criterion (AIC; Burnham and Anderson 2002) to compare the model that included an effect of year to a null model for each region. I compared models using $\Delta$AIC, which is difference in AIC values between all models and the model with the lowest AIC, providing a measure
of relative support, where ΔAIC values ≤ 2 are well supported (Burnham and Anderson 2002). At-vessel mortality was considered to vary across years if the model that included an effect of year had the lower AIC, and if the ΔAIC between the two models was > 2.

**Effects of environmental conditions and fishing practices on at-vessel mortality**

I evaluated the effects of gear, fishing practices and environmental conditions on mako shark AVM using generalized additive models (GAM; Hastie and Tibshirani 1986). Generalized additive models are nonparametric analogues to generalized linear models (GLM; McCullagh and Nelder, 1989) that allow for the incorporation of nonlinear effects of covariates on the response variable through the application of smoothing functions. I used GAMs because they are well suited to identify potential nonlinear effects of shark size, environmental conditions, and fishing practices on AVM. Models were fitted with a binomial distribution and log-link and took the general form:

\[
\log\left(\frac{p}{1-p}\right) = \beta_0 + f_1(\text{hook depth}) + f_2(\text{leader length}) \\
+ f_3(\text{gangion distance}) + f_4(\text{soak time}) + f_5(\text{shark size}) \\
+ f_6(\text{mainline length}) + f_7(\text{SST})
\]

Where \( P \) is the probability of AVM, \( \beta_0 \) is the intercept constant, and \( f_i \) ‘s are the unspecified smooth functions for each covariate used in the model. Covariates considered included soak time (h), shark size (Fork Length, FL, cm; tip of snout to fork of tail), hook depth (m), SST (ºC) recorded onboard the vessel, mainline length (km), gangion distance (a gangion is a 300-500 lb test nylon monofilament that is commonly used to attach the leader to the mainline, the gangion distance is the length in meters between gangions), soak time (hours), and leader length (a leader is a section of steel or monofilament attached to the hook and length is recorded in meters). To confirm there were no
collinearity issues, correlation among the predictor variables was assessed by calculating correlation coefficients. No collinearity issues were detected based on a correlation threshold of $|r| > 0.70$ (Dormann et al. 2013). Sex was not identified for 1649 (21%) sharks and was therefore not included as a potential covariate.

I used a double penalty approach to make inferences on which covariates had meaningful effects on AVM. The double penalty approach applies a default penalty to each smooth term to determine non-linearity and a second penalty that allows a linear term to be shrunk to null (Marra and Wood 2011). Combined all model terms can be penalized and completely removed from the model where the effective degrees of freedom (edf) tend towards zero. Marra and Wood (2011) showed that this approach was superior to stepwise/iterative procedures that are influenced by the order of steps. I considered covariates significant where edf $\geq 1$. The relationship between covariates and AVM were examined using partial dependence plots, which show the effect of a variable while holding all other variables in the model constant (Friendman, 2001). The covariates that were determined significant were used to make predictions of AVM. These predictions were used to investigate the effects of important covariates on AVM. Models were parametrized using restricted maximum likelihood and were fit using the “mgcv” package (Wood 2011) in R (R core team 2022).

To evaluate model performance, I used K-fold cross validation ($k = 10$) to calculate a receiver operating characteristic area under the curve (AUC, Greiner et al. 2000). The AUC statistic is a measure of overall model predictive accuracy and represents the probability that a model will correctly identify the positive case when presented with a randomly chosen pair of cases in which one is positive, and one is
negative (Hanley and McNeil 1982). An AUC of 1.0 represents perfect prediction, whereas value of 0.50 represents prediction equal to random chance and a value of -1.0 indicates complete failure.

**Survival probability of hooked sharks**

Under the assumption that all sharks that are alive at-vessel are released, I estimated the survival probability for mako sharks captured on a longline in either the GOM or WNA. I used Monte Carlo (mc) simulation using the mean predicted AVM for each region and a PRM estimate from the literature (Bowlby et al. 2021). For each simulation I first estimated AVM probability by pulling from a normal distribution using the mean and standard deviations of the mean predicted AVM for a region. Next, I simulated the proportion of sharks from a hypothetical population of 1000 hooked individuals to die prior to haulback by sampling 1000 times from a binomial distribution with AVM serving as the probability of success. Surviving sharks from this step were then subject to PRM. I randomly pulled a PRM probability from a normal distribution with mean = 35.8, and sd = 0.06 based on published estimates from Bowlby et al. (2021). The number of released sharks to then succumb to PRM was simulated from a binomial distribution with PRM serving as the probability of success. Survival was then calculated as the proportion of 1000 hooked sharks to ultimately survive. This process was repeated 1000 times for each region.

**Results**

**Annual variation of at-vessel mortality**

In the US pelagic longline observer data, observed mako catch included 972 observations in the GOM, and 6173 in the WNA from 2000 – 2020. Observed mako
shark catch differed by regions where annual observations in the GOM ranged from 2 sharks in 2020 to 137 sharks in 2009, and in the WNA from 65 sharks in 2020 to 794 sharks in 2017. In the GOM, captured mako sharks ranged from 71 – 330 cm with a mean FL of 164.2 cm, whereas in the WNA, mako sharks caught ranged from 71 – 360 cm, with a mean FL of 138.7 cm.

When examining annual variation of AVM, I removed 2020 due to low sample sizes because of the lack of observer coverage, leaving 970 observations in the GOM, and 6108 observations in the WNA. On average there are 257 less observations of mako sharks per year in the GOM than in the WNA (Figure 2.2). There was support for the model that allows AVM to vary across years in the WNA, but not in the GOM (Table 2.2). Mean estimated AVM in the GOM is 32.4% (95% CI: 29.5 – 35.4%) and 25.7% (95% CI: 24.6% - 26.8%) in the WNA. Annually in the GOM, AVM rate ranged from 13% in 2019 to 56% in 2001, whereas AVM in the WNA ranged from 16% in 2015 to 38% in 2006 (Figure 2.2).

Effects of environmental conditions and fishing practices on at-vessel mortality

After filtering out incomplete records, observed mako shark catch in the GOM included 829 observations and the WNA included 5852 observations from 2000 – 2020. Hook depth, shark size, and SST had significant effects on AVM in the GOM (Table 2.3) and the double penalty approach reduced the effects of gangion distance, leader length, and mainline length to 0 (Figure 2.3). The edf of SST, shark size, and hook depth were all close to one representing the small effect of these variables on AVM (Table 2.3, Figure 2.3). K-fold cross validation revealed a prediction success rate of 54% (Table 2.3). The
probability of AVM in the GOM increased as SST and shark size increased, and probability of AVM decreased as hook depth increased (Figure 2.4).

The most important variables influencing AVM in the WNA were soak time, shark size, and SST (Table 2.3), whereas hook depth, leader length, and mainline length were penalized to zero (Figure 2.5). Soak time had a high edf value representing the strong effect on AVM (Table 2.3 Figure 2.5). The edf values of shark size and SST were close to 1 representing the small effect of these variables on AVM (Table 2.3). Gangion distance was not penalized to zero but was not considered significant because of an edf < 1 (Table 2.3, Figure 2.5). K-fold cross validation revealed a prediction success rate of 56% (Table 2.3). Model predictions suggest AVM increases with soak time but levels out after ~10 hours, and although the effect is small intermediate sized sharks from ~ 100 – 250 cm are less susceptible to AVM than larger sharks (Figure 2.4). The probability of AVM in the WNA increased as SST increased (Figure 2.4).

*Survival probability of hooked sharks*

From the mc simulation, given the mako shark AVM rates from this study from the GOM (mean = 0.324, sd = 0.016) and WNA (mean = 0.257, sd = 0.006), and a PRM rate of 0.358 (sd = 0.06; Bowlby et al. 2021), the probability of survival of a shark hooked on a longline in the GOM was estimated at 42.6% (95% CI: 33.7 – 52.1%) and 47.4% (95% CI: 38.6 – 56.9%) in the WNA (Figure 2.6).

**Discussion**

Previous estimates of mako shark AVM rates in the western North Atlantic have ranged from 26.2% in the Canadian pelagic longline fishery (Campana et al. 2015) to
28.6% in the US Atlantic pelagic longline fishery (Gallagher et al. 2014). In this study, a predicted AVM rate of 25.7% in the WNA was consistent with previous AVM rates, however a predicted AVM of 32.4% in the GOM was higher than the estimates from Campana et al. (2015) and Gallagher et al. (2014). However, mako shark AVM in the GOM was consistent with AVM rates in the Portuguese longline fishery (35.6%, Coehlo et al. 2012). Using 19 years of data, the estimates of AVM reported in our study represent the most comprehensive results to date of mako shark AVM in the U.S. pelagic longline fishery.

There was evidence of annual variation of AVM in the WNA, but not in the GOM (Table 2.2). The annual variation of AVM in the WNA may be related to seasonal or spatial patterns that are inherent to the species, while the lack of evidence for annual variation in the GOM may be related to the smaller sample size overall (970 observation: Figure 2.2). The small sample sizes in the GOM likely led to higher variability in the data and wider confidence intervals which may have affected the precision of the results. It is important to consider that increased mako shark observations in some years in the GOM may be due to increased observer coverage. For example, in 2007 and 2008 the NMFS enhanced observer coverage in the GOM due to concerns of bycatch mortality of bluefin tuna during the spawning season (Beerkircher et al 2009).

Model results showed that shark size, SST, hook depth, and soak time are significant predictors of AVM (Table 2.3). It is important to note that each region had unique variables influencing AVM. For example, soak time had little effect in the GOM but had a large effect in the WNA (Table 2.3). Moreover, overall, the effect sizes in the WNA were higher than in the GOM (Table 2.3), potentially due to the smaller sample
sizes in the GOM. Contrasting our study, Gallagher et al. (2014) found no significant effects of environmental, biological, or fishing gear practices on AVM of mako sharks using observer data from 1995 – 2012. A potential explanation for the different results between this study and Gallagher et al. (2014) is the modeling of AVM across the entire US Atlantic longline fleet that covers distinct ecoregions. Modeling the GOM and WNA regions independently resulted in considerably different conclusions in how variables influence AVM of mako sharks (Table 2.3). This study documents the importance of modeling regional differences over large geographical areas and emphasizes the need for further investigation of potential regional specific management practices to reduce AVM in mako sharks.

Individual stress response to capture is a dynamic process influenced by oxygen and metabolic requirements, which are influenced by environmental variables like water temperature and dissolved oxygen, or biological factors like fish size. The relationship between elevated water temperature and stress response has been documented across a range of species (Wilkie et al. 1996; Nelson 1998; Hoffmayer et al. 2012; French et al. 2015; Hyatt et al. 2018), where higher temperatures result in increased metabolic rate, thus higher oxygen requirements (Carlson et al. 2004). Although the effect was small, warmer water temperatures in both the WNA and GOM resulted in higher AVM rates (Figure 2.4). Our results are supported by studies that found oxygen consumption rates in obligate-ram ventilating species increases with water temperature (Carlson and Parsons 2001). Further, this may be exacerbated by the fact that dissolved oxygen decreases as water temperatures increases. Combined, low dissolved oxygen, warmer waters, and increased physical exertion to ram ventilate may speed up lactate accumulation in the
blood leading to acidosis, and potentially accelerating mortality. The relationship between water temperature and oxygen consumption may also explain why model predictions show that mako shark AVM in the GOM decreases when sharks are caught on hooks sets deeper in the water (Figure 2.4). This pattern has been observed in several other shark species (Gallagher et al. 2014). The cooler temperature at deeper depths may lower oxygen consumption requirements when mako sharks struggle on the line when hooked.

Exhaustion associated with increased time on the line is known to affect the severity of acidosis in sharks, where blood lactate concentration increases as capture duration increases (Marshall et al. 2012; French et al. 2015; Bouyoucos et al. 2018), which can subsequently cause mortality (Morgan and Carlson 2010; Massey et al. 2022). While we did not measure time on the line, longer soak times can lead to longer time on the line which has been shown to increase AVM (Morgan and Carlson 2010). In the WNA the probability of AVM increases as soak time increases, but levels out when soak times were longer than 10 hours (Figure 2.4). It has been suggested that some species of sharks exposed to longer hook durations may go through physiological recovery while still hooked (Brooks et al. 2012). This may be an explanation for why after 10 hours, AVM does not continue to increase.

Previous studies have found size related differences in response to capture stress (Gallagher et al. 2017; Scarponi et al. 2021). However, there are inconsistencies with the findings where smaller sizes lead to higher stress responses and consequent mortality in some studies (Diaz and Serafy 2005; Carruthers et al. 2009; Coehlo et al. 2012; Coehlo et al. 2013; Coehlo et al. 2017), but not in others (Scarponi et al. 2021; Whitney et al. 2022).
Contrary to my prediction, larger sharks in the GOM experience higher rates of AVM than smaller sharks, and in the WNA intermediately sized (~ 80 – 250cm) sharks experience lower rates of AVM (Figure 2.4). Our results differ from many studies that indicate smaller sharks display higher AVM rates (Diaz and Serafy 2005; Carruthers et al. 2009; Coehlo et al. 2012; Coehlo et al. 2013; Coehlo et al. 2017). Further research on the stress response of large sharks would give insight as to why we found higher rates of AVM with increased shark size.

In the GOM and WNA, the predicative success rate was 54% and 56%, respectively, meaning there are likely other factors that we did not measure that predict AVM of mako sharks. It is possible that high variation in individual response to stress, and therefore AVM, may hinder the predictive accuracy of models. A limitation of this study could be that soak time was used as proxy for actual time on the line. Knowledge of time on the line may have increased the predictive accuracy the model. However, time on the line cannot be managed for because it cannot be controlled by the fisher, but soak time can be controlled in some degree by the fisher. Further, we used SST as an environmental measure and not temperature of hook depth. Temperature at hook depth may be more influential on mortality because sharks spend most of the time in that temperature while hooked.

Based on simulations, the probability of survival for a mako shark caught on a longline in GOM and WNA was 42.6% (95% CI: 33.7 – 52.1%) and 47.4% (95% CI: 38.6 – 56.9%), respectively (Figure 2.6). This estimate is similar to results from Campana et al. (2015) who used both AVM and overall PRM to estimate overall fishing-related mortality rate of 49.3% (95% CI: 23 – 72%). The results of this study highlight the issue
that AVM may make up an important source of mortality for mako sharks caught on pelagic longlines demonstrating that up to one third of mako sharks caught in U.S. Atlantic PLL fishery may die even if all sharks are released alive.

Management implications

Mortality may be fishery specific due to fishing gear configurations and water temperature; however, small changes to gear or fishing strategy may help improve AVM of mako sharks. Given the regional model results (Table 2.3, Figure 2.4), management strategies that minimize soak time in the WNA could improve at-vessel mortality rates. The knowledge that smaller sharks have lower AVM rates may be important in management, because it has been previously noted that populations of low productivity shark species are negatively impacted by high mortality in juvenile age classes (Cortes et al. 2010). However, due to the high proportion of mako sharks caught on pelagic longlines that may be subject to mortality (Figure 2.6), overall management strategies should focus on reducing overall mako shark bycatch. Bycatch mitigation strategies for mako sharks focusing on fishing gear have been inconclusive (Rey & Munoz-Chapuli 1991, Williams 1998) and temporary spatial closures have been suggested as a solution to reducing mako shark bycatch (Grantham et al. 2008; O’Farrell and Babcock 2021). Our results indicate that even if the retention ban is followed it may be possible that only approximately half of the mako shark caught on a given longline will survive. Given that model projections predict a continued population decline until 2035 even if no fishing occurs (ICCAT 2019), future studies and management initiatives focused on reducing bycatch are necessary to help stop population decline.
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Tables and Figures

Table 2.1: Summary statistics of the fishing gear variables, hook depth (m) and soak time (hours), and sea surface temperatures (°C) used to group US Atlantic pelagic longline regions described by the National Marine Fisheries Service (NMFS). SST = sea surface temperature (°C), GOM = Gulf of Mexico, NED = Northeast District, NEC = Northeast Coast, MAB = Mid-Atlantic Bight.

<table>
<thead>
<tr>
<th></th>
<th>SST</th>
<th>Hook Depth</th>
<th>Soak time</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Min</td>
<td>Mean</td>
<td>Max</td>
</tr>
<tr>
<td>GOM</td>
<td>16.0</td>
<td>26.0</td>
<td>35.0</td>
</tr>
<tr>
<td>NED</td>
<td>10.0</td>
<td>17.0</td>
<td>30.0</td>
</tr>
<tr>
<td>NEC</td>
<td>13.0</td>
<td>23.0</td>
<td>29.0</td>
</tr>
<tr>
<td>MAB</td>
<td>6.0</td>
<td>22.0</td>
<td>32.0</td>
</tr>
</tbody>
</table>
Table 2.2: Logistic regression results for examining the effect of year on shortfin mako shark, *Isurus oxyrinchus*, at-vessel mortality (AVM) in the Gulf of Mexico (GOM) from 2000 – 2019 and Western North Atlantic (WNA) from 2000 – 2020, regions of the U.S. pelagic longline fishery described by the National Marine Fisheries Service (NMFS). Models in bold represent best fit model ranked by Akaike’s Information Criterion (AIC).

<table>
<thead>
<tr>
<th>Region</th>
<th>Model</th>
<th>ΔAIC</th>
<th>AIC</th>
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<tbody>
<tr>
<td>Gulf of Mexico</td>
<td><strong>Null</strong></td>
<td>0.0</td>
<td><strong>1105.19</strong></td>
</tr>
<tr>
<td></td>
<td><em>AVM ~ year</em></td>
<td>3.4</td>
<td>1108.58</td>
</tr>
<tr>
<td>Western North Atlantic</td>
<td><strong>AVM ~ year</strong></td>
<td>0.0</td>
<td><strong>6876.03</strong></td>
</tr>
<tr>
<td></td>
<td><em>Null</em></td>
<td>57.3</td>
<td>6933.29</td>
</tr>
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</table>
Table 2.3: Generalized additive model (GAM) results for the effect of environmental, biological, and fishing gear characteristics on at-vessel mortality (AVM) of the shortfin mako shark in the Western North Atlantic (WNA) and Gulf of Mexico (GOM) regions of the US pelagic longline fishery from 2000 – 2020. The predictors are smooth terms for hook depth (m), leader length (m), gangion distance (m), soak time (hours), shark size (cm), mainline length (km), and sea surface temperature (SST, °C). Edf = estimated degrees of freedom. AUC = Area under the curve. Bold values represent significant terms in the model.

<table>
<thead>
<tr>
<th>Model</th>
<th>Coefficients</th>
<th>edf</th>
<th>P-value</th>
<th>AUC %</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gulf of Mexico</td>
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<td>0.0337</td>
<td></td>
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<tr>
<td></td>
<td>$S(\text{Leader length})$</td>
<td>0.63</td>
<td>0.0721</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$S(\text{Gangion distance})$</td>
<td>0.00</td>
<td>0.6019</td>
<td></td>
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<tr>
<td></td>
<td>$S(\text{Soak})$</td>
<td>0.24</td>
<td>0.2454</td>
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<td></td>
<td>$S(\text{Shark size})$</td>
<td>1.02</td>
<td>0.0527</td>
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<tr>
<td></td>
<td>$S(\text{Mainline length})$</td>
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<td>0.6195</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$S(\text{SST})$</td>
<td>1.23</td>
<td>0.0546</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>54%</td>
</tr>
<tr>
<td>Western North Atlantic</td>
<td>$S(\text{Hook depth})$</td>
<td>0.00</td>
<td>0.7620</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$S(\text{Leader length})$</td>
<td>0.21</td>
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<tr>
<td></td>
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<tr>
<td></td>
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<td>$S(\text{Shark size})$</td>
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</tr>
<tr>
<td></td>
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<td></td>
<td></td>
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Figure 2.1: Pelagic Observer Program statistical regions in the U.S. Atlantic defined by the National Marine Fisheries Service (NMFS). CAR = Caribbean, GOM = Gulf of Mexico, FEC = Florida East Coast, SAB = South Atlantic Bight, MAB = Mid Atlantic Bight, NEC = Northeast Coastal, NED = Northeast District, SAR = Sargasso, NCA = North Central Atlantic, TUN = Tuna North, and TUS = Tuna South.
Figure 2.2: Top panel: Probability of at-vessel mortality (AVM) output from binomial logistic regression models from 2000 – 2019 in (A) the Gulf of Mexico (GOM) and (B) Western North Atlantic (WNA) in the U.S. pelagic longline fishery (error bars represent 95% confidence intervals), and numbers observed mako shark catches in (C) the GOM and (D) WNA annually.
Figure 2.3: Smooth function estimates and 95% confidence intervals from generalized additive models (GAMs) obtained by applying the double penalty approach with REML estimation on mako shark catch data from 2000 – 2020 in the Gulf of Mexico (GOM) region of the U.S. The covariates included are hook depth (m), leader length (m), gangion distance (m), soak time (hours), shark size (cm), mainline length (km), and sea surface temperature (SST; °C). The y axis represents the estimated smooths and the x axis represents each covariate value. edf = estimated degrees of freedom
Figure 2.4: Model predictions from the generalized additive models examining the influence of significant covariates influencing at-vessel mortality (AVM) in the WNA and GOM regions of the U.S. pelagic longline fishery. A) Effect of soak time on the predicted probability of AVM in the WNA, B) Effect of hook depth on the predicted probability of AVM in the GOM, C) effect of shark size on the predicted probability of AVM in the GOM and WNA, and D) the effect of SST (°C) on the predicted probability of AVM in the GOM and WNA. GOM = Gulf of Mexico, WNA = Western North Atlantic, FL = fork length, SST = sea surface temperature.
Figure 2.5: Smooth function estimates with estimated degrees of freedom (edf) and 95% confidence intervals from generalized additive models (GAMs) obtained by applying the double penalty approach with REML estimation on mako shark catch data from 2000 – 2020 in the Western North Atlantic (WNA) region of the U.S. pelagic longline fishery. The covariates included are hook depth (m), leader length (m), gangion distance (m), soak time (hours), shark size (cm), mainline length (km), and sea surface temperature (SST; °C).
Figure 2.6: Density plot of the 1000 iterations of a Monte Carlo simulation estimating the survival probability of mako sharks captured in the U.S. pelagic longline fishery in the Gulf of Mexico (GOM) and Western North Atlantic (WNA) regions. The vertical lines represent mean values for each region.
Chapter 3: Evaluating environmental drivers of shortfin mako shark vertical habitat use in the North Atlantic Ocean

Introduction

Marine environments are characterized by vertical gradients of physical properties, such as temperature, salinity, and density. In the open ocean, the water column is characterized by three layers: an upper mixed layer, the thermocline, and a deep zone of colder water. The thermocline separates warm water near the surface of the ocean from deeper, cooler water limiting oxygen and nutrient transport, influencing the thermal structure of the water column (Fiedler 2010). The mixed layer depth is a well-mixed, homogenous region where there is little variation in temperature or density with depth (Kara et al. 2000). The characteristics of thermal stratification have been known to shape the vertical movement and distribution of pelagic fishes (Kitagawa et al. 2000; Furukawa et al. 2014; Aspillaga et al. 2017; Gaube et al. 2018; Andrzejaczek et al. 2019). The shift in temperature of the water column at the thermocline often constrains the vertical movement of fishes due to physiological limitations (Musyl et al. 2011; Furukawa et al. 2014), whereas some species can descend to deep cooler water, but may need to return to the surface to increase their body temperature (Schaefer et al. 2009; Thums et al. 2013; Nakamara et al. 2015; Tolotti et al. 2017).

The pelagic marine ecosystem off the east coast of North America is a dynamic, diverse system with distinct ecoregions from the Florida East Coast region to the Northeast Continental Shelf region (Spalding et al. 2007; Fautin et al. 2010). The Florida East Coast and South Atlantic Bight regions are dominated by the Gulf Stream (Atkinson et al. 1985) with relatively constant temperature and salinity. The continental shelf
creates multiple habitats dominated by tidal currents near the inner shelf, winds influenced by the Gulf stream in the middle shelf and dominated by the Gulf Stream in the outer shelf. The temperature and salinity fluctuate seasonally, and Gulf Stream waters are much less variable. Ocean bottom features create thermal fronts, eddies, and gyres that spin off the edge of the Gulf Stream, creating a consistent upwelling of deep nutrient waters (Fautin et al. 2010). The Northeast Continental shelf consists of very cold waters and abrupt changes in temperatures due to the Gulf Stream flowing north and the Labrador Current flowing south (Townsend et al. 2006).

The shortfin mako shark (*Isurus oxyrinchus*, hereafter; mako shark), a member of the family Lamnidae, is a highly migratory species that is distributed through temperature and tropical oceanic waters. During their migrations mako sharks have been shown to use a variety of habitats throughout the open ocean and continental shelf (Vaudo et al. 2017; Byrne et al. 2019) and travel over 2000 km from the Gulf of Mexico (GOM) to the northeastern United States (U.S.; Vaudo et al. 2017; Gibson et al. 2021). These sharks have been seen routinely traveling distances greater than 50 km per day (Nasby-Lucas et al. 2019) and up to 141 km per day (Francis et al. 2019).

Apparent depth distributions, temperature preferences, and vertical movement of mako sharks have been reported on by studies using Pop-up Satellite Archival Tags (PSATs; Vetter et al. 2008; Stevens et al. 2010, Abascal et al. 2011; Musyl et al. 2011; Vaudo et al. 2016; Nasby-Lucas et al. 2019; Santos et al. 2020). These studies have indicated mako sharks use a large range of depth, but generally suggest that these sharks occupy surface waters and make occasional deeper dives below the thermocline. The mako shark is a regionally endothermic shark that can maintain internal temperatures 6 -
8 °C warmer than ambient water temperature (Carey et al. 1981). Endothermic species, like the mako, can regulate internal body temperature using specialized circulatory mechanisms that retain heat (Dickson and Graham 2004; Bernal et al. 2012). Endothermy in fishes is hypothesized to allow expansion of the thermal niche and exploitation of cooler waters (Dickson & Graham 2004, Weng et al. 2005, 2008, Campana et al. 2010), and enhanced muscle and digestive performance potentially enabling mako sharks to exploit fast-moving prey and inhabit a broad range of environmental temperatures (Block et al. 1993; Weng et al. 2005). However, the thermal niche expansion hypothesis has recently been challenged by Harding et al. (2021) who found regionally endothermic fishes do not encounter broader temperature ranges than their ectothermic counterparts.

Studies have found that mako sharks’ distribution in the water column is heavily influenced by water temperature where their preferred range in temperature regions is 18 - 22 °C (Vetter et al. 2008; Stevens et al. 2010, Abascal et al. 2011; Musyl et al. 2011; Vaudo et al. 2016; Nasby-Lucas et al. 2019; Santos et al. 2020), whereas Vaudo et al. (2016) found mako sharks tracked in tropical and subtropical waters spent considerable time in waters ranging from 22 - 27 °C. Vaudo et al. (2016) also found that sharks crossing through warmer waters of the Gulf Stream and Loop Current spent more of their time in deeper water. These findings show that although mako sharks use a wide range of temperature, most of their time appears to be concentrated in a relatively narrow temperature range.

Satellite tagging has been increasingly used to study large pelagic fish vertical movement patterns. Advancement of these technologies has allowed researchers to study movement patterns and behavior in relation to oceanographic characteristics (Braun et al.
2019), providing a more robust understanding of habitat utilization. Pop-up satellite archival tags provide high resolution time series of depth and temperature measurements at specified time intervals. This information can be used to infer animals’ movement and habitat use. The advantage of PSAT’s is that they can be programmed to detach from the animal after a specified tracking period is over. Once detached from the animal, tags float to the surface and transmit archived data to the Advanced Research and Global Observation Satellite (Argos) network. Data received by the Argos satellites are retransmitted to a receiving station and sent to a processing center before being sent to the Argos user, thus negating the need to recover the tag to obtain the data.

However, typically the entire dataset from the tag cannot be transmitted due to battery and transmission capabilities. This may result in electronic tags that have lower temporal resolution as deployment length increases (Patterson et al. 2011). Temporal resolution of depth data has been shown to strongly influence the interpretations of vertical movement rates in billfishes (Hoolihan et al. 2009) and sailfish (Hoolihan et al. 2011). Most studies of mako shark vertical movements in the western North Atlantic have used PSATs that transmitted summarized data in 1 – 12-hour periods, or only a subset of the data was successfully transmitted (Loefer et al. 2005; Vaudo et al. 2016; Nasby-Lucas et al. 2019).

Given the diversity of the western North Atlantic Ocean and the ability for mako sharks to travel long distances in a short period of time, sharks in this region regularly traverse distinct ecoregions with unique thermal characteristics (Byrne et al. 2019). Tagging sharks in this region of the world provide an opportunity to study how mako sharks change their behaviors in response to different thermal habitats. Therefore, the
objectives of this study are to 1) evaluate how thermal stratification influences mako sharks’ depth use and 2) evaluate temperature use of mako sharks across a range of habitats using high-resolution PSAT data. Despite mako sharks being an endothermic species, I predict that they will alter their use of the water column to spend most of their time in a narrow temperature range even as they experience a broad range of temperatures.

**Methods**

*Satellite tag and deployment*

I used Lotek PSAT Life tags (Lotek Wireless, Newmarket, Ontario) which are designed specifically for short-term post-release studies. Tags were programmed to archive pressure (depth) and temperature every 5 minutes and detach after 28-days post-deployment. In the case of a mortality or a premature tag detachment, tags were programmed with a “fail-safe” method where the tag will detach from the shark if it registers a constant depth for 5-days. For example, if a tag detaches from a shark and floats to the surface, after 5 days of floating at the same depth the fail-safe will be initiated, and the tag will start transmitting data to the Argos satellite.

Nineteen mako sharks were caught off the coast of North Carolina in the North Atlantic Ocean using pelagic longline gear commonly used by commercial fishers targeting sharks. The sharks were caught using a mix of mackerel and squid bait, in sea surface temperatures (SST) ranging from 16 – 17 °C, and with a soak time of four hours. Sharks were left in the water for tagging and hooks were not removed. The leader was cut as close to the end of the hook as possible, considering the safety of the crew and regular fishing practices. All mako sharks caught were brought alongside the vessel and a tagging
pole was used to insert tags into the dorsal musculature just below the first dorsal fin. Tags were attached to each shark using a plastic-coated stainless-steel dart anchor (Hallprint, SSD, 57mmx 15 mm, Victoria Harbor, Australia). A 13-cm tether made of 250-lb test monofilament with heat shrink tubing attached the anchor to the satellite tag. The heat shrink tubing is used to minimize abrasions from the shark. The monofilament was attached to the tag and the anchor using 1.6 mm stainless steel sleeves.

Data analysis

Recovery periods following longline capture were assessed before examining vertical habitat use. Recovery periods for each shark were examined using the recorded depth (pressure) data from each tag. Previous studies have suggested that mako sharks’ recovery period from capture can persist for up to 5 days and has been characterized by slow descent, followed by little change in depth and temperature (Loefer et al. 2005; Hoolihan et al. 2011; Bowlby et al. 2021). The variance of depth records was considered as a proxy for vertical variability or movement amplitude (Tolotti et al. 2017; Bowlby et al. 2021). Bowlby et al. (2021) found variance to be a useful measure of recovery periods. I subset the depth records from each shark to the first seven days post-release because this was likely to capture any recovery period based on previous values from the literature (Hoolihan et al. 2011; Bowlby et al. 2021). Depth variance was calculated over two-hour windows using a rolling variance function in the “zoo” package (Zeileis 2005) in R (R Core Team 2021). The package computes a rolling variance by moving over a user defined window of observations over the full sampling period. When missing data points were encountered the moving variance was calculated on the next available data point in the dataset. I visually identified sharks that exhibited a recovery period as those
with variance ~ 0 or prolonged surface behavior immediately following release. Low variance values indicate the depths are close to the mean, and to each other, representing little change in depth which is indicative of post-release recovery behavior of mako sharks. The duration of recovery period was marked by an increase in depth variance representing a shark diving deeply and more regularly. Identified recovery periods were removed from subsequent analyses.

To analyze mako shark depth use in relation to thermal stratification, I used three attributes to characterize shark movement in the water column; daily depth variance, daily maximum depth (m), and daily mean depth (m). I calculated depth variance from the recorded depth time series in 24-hour intervals as a measure of daily vertical variability. High variance values represent increased depth range use whereas low variance represents decreased depth ranges. For example, variance increases when sharks dive more regularly and more deeply.

The mixed layer depth (MLD) was used as a proxy for stratification in this study. This region is a part of the upper ocean where there is little variation in temperature or salinity with depth (Kara et al. 2003). Highly stratified environments will tend to have shallower mixed layers than well mixed areas. To obtain measures of thermal stratification, I created daily average temperature at depth profiles using package “RchivalTag” (Bauer 2020) in R (R Core Team 2021). The time series recorded from the tag for each shark was binned into 10m depth intervals with interpolated mean, minimum, and maximum temperatures for each depth interval. The binning of the depth-temperature time series into 10m resolution instead of the raw time series data increased the number of records per depth to calculate average temperatures and removed excess
noise from daily temperature profiles (Bauer et al. 2015). The surface temperature (SST, °C) for each day was calculated as the temperature recorded from the tags when the shark was at the surface. Mixed layer depth was calculated from the daily temperature at depth profiles as the depth at which temperature (T) = SST – 0.8 degrees (Kara et al. 2000; Kara et al. 2003; Fielder 2010). The temperature criterium of 0.8 degrees has been shown to produce layer depths that are accurate to within 20m (Kara et al. 2003). Days that the shark did not come to the surface were not used in further analysis because there was no measure of SST or mixed layer depth.

To investigate the relationships among thermal stratification and depth use, I ran generalized linear mixed-effect models (GLMMs) using the “lme4” (Bates 2015) package in R (R Core Team 2021). I used generalized linear mixed models to include a random effect to account for individual shark variation in depth use and because the data was not normally distributed. The models included fixed effects for mixed layer depth and SST and a random effect for individual shark. Three models were run with a response variable for daily depth variance, mean dive depth, or maximum dive depth. Models were fit assuming a gamma distribution and a log-link function because the data was positive, continuous, and right skewed. Because daily depth variance had a large scale, this variable was scaled by dividing the value by 100 before analysis. Significant effects of predictor variables were assessed by examining beta coefficients and associated 95% confidence intervals.

I used the temperature time series transmitted by each tag to examine trends in mean daily temperature use during deployment periods. I evaluated mako shark temperature use over time via generalized additive model (GAM; Hastie and Tibshirani
The first day of deployment was removed to account for any post-release recovery behavior. Given that mako sharks were tagged in a dynamic region and likely traveled through many thermal habitats, if mean predicted temperature remained relatively constant, it could be inferred that mako sharks adjust their movements to seek out preferred temperatures. I used days at liberty (DAL) as the explanatory variable as a measure of time and the temperature as the response variable. The models took the form of

\[ Y \sim \beta_0 + f_1(DAL) \]

Where \( Y \) is the temperature, \( \beta_0 \) is the intercept constant, and \( f_1 \) is the unspecified smooth function for DAL. Models were parametrized using restricted maximum likelihood and were fit using the “mgcv” package (Wood 2011) in R (R core team 2022).

**Results**

I tagged nineteen sharks ranging from 122 – 198 cm, with a mean fork length of 152 cm (Table 3.1). Eighteen of the tagged sharks were healthy, with no outward injury and swam away from the boat. I tagged ten males, seven females, and could not determine the sex of two individuals. Nine tags failed to transmit, seven tags transmitted data for the 28-day deployment period, and three tags detached pre-maturely. One of the tags that detached pre-maturely was a suspected mortality, however the tag detached from the shark eight hours post-release, making it difficult to confirm (Figure 3.1). There were no other observed mortalities. I used data from the seven tags that transmitted for the 28 – day deployment period.

I determined six sharks exhibited a recovery period. Recovery periods were characterized by low depth variance immediately following release (Figure 3.2). Variance
in dive depths during the recovery periods was < 100 m and markedly increased in
variance to ranges from 500 – 2000 following the recovery periods. Recovery period
durations were constrained to the first 24-hour post-release, with a mean of 8.7 hours
(range: 2.8 -17.5 hours; Table 3.1). Recovery periods were removed from further
analysis.

After removing days to account for post-release recovery behavior, there were
163 total days of data across seven sharks. For all sharks there were 19 total days where
the sharks did not come to the surface. These days were removed from analysis, and SST
and MLD were calculated for the remaining 144 days. Mako sharks experienced a wide
range of temperatures, ranging from 27.2 ºC - 5.7 ºC. However, mean daily temperatures
for all sharks ranged from 17 – 20 ºC with an overall mean of 19 ºC (Figure 3.3). Mako
sharks spent most of their time within the top 50 m of the water column, with occasional
deeper dives (Figure 3.4). Maximum recorded depths for individual sharks ranged from
160 - 900m.

Mako sharks traversed a variety of habitats (Figure 3.5) with mixed layer depths
ranging from 0 – 353m, and SSTs ranging from 13 – 24 ºC. Mean depth, maximum
depth, and variance were positively affected by MLD (Figure 3.6). In highly stratified
waters with a shallow mixed layer, sharks tended to use shallow depths with limited
variation, and make shallower maximum dives than in waters with deeper mixed layers
(Figure 3.7). For all three metrics of depth use, coefficient estimates of SST crossed over
zero indicating the relatively small effect SST had on depth use (Figure 3.6). However,
all values were positive suggesting that sharks tended to use deeper waters in warm
habitats (Figure 3.8). Overall, mean depth, maximum depth, and variance tended to increase in warmer habitats with deep mixed layers (Figure 3.9).

**Discussion**

Water temperature preferences of mako sharks tagged off the coast of North Carolina were consistent with previous results in temperate regions (18 to 22 ºC; Nasby-Lucas et al. 2019; Santos et al. 2020), but cooler than the range reported by Vaudo et al. (2016) in tropical regions. Fine-scale depth use data from our study showed that mako sharks typically occupy surface waters but occasionally make deeper dives. This pattern has previously been reported for mako sharks (Vaudo et al. 2016; Nasby-Lucas et al. 2019; Santos et al. 2020). Despite being tagged in an ecologically diverse region and encountering a variety of thermal habitats, mako sharks spent most of their time within a narrow temperature range from 17 – 20 ºC. This result is similar to Vaudo et al. (2016) who found mako shark movements were strongly associated with temperature in the western North Atlantic Ocean and Gulf of Mexico.

For ectothermic sharks, variations in the heat content of warmer mixed layers of the ocean are expected to play a role in vertical movements (Sims 2003). However, for endothermic sharks this concept is less developed. Our results confirmed that the depth use by the endothermic mako shark varies based on thermal stratification (Figure 3.6). In our study, increased depth variance and depth use was correlated with the MLD where individuals dove to greater depths more frequently as the mixed layer deepened. Similarly, this trend has been observed in ectothermic species such as Atlantic salmon (*Salmo salar* L.; Strom et al. 2018), dolphinfish (*Coryphaena hippurus*; Furukawa et al. 2011), hammerhead sharks (*Sphyrna lewini*; Bessudo et al. 2011) and oceanic white tip sharks.
sharks that dive to deeper depths with deeper MLD (Tolotti et al. 2017). One potential
explanation that has been proposed is that thermal stratification aggregates prey
resources, which affects the depth of foraging of predatory fishes. However, given the
temperature preferences of mako sharks in this study it may be possible that the
association with the MLD and increased depth use relates to the shark’s ability to dive
deeper when more warm water is available. Braun et al. (2019) found a similar pattern
where blue sharks (Prionace glauca) were able to dive deeper into the water column
using warm water eddies to forage in the mesopelagic.

Although the effect was small, mako shark mean and max depth use increased in
warmer water temperatures (Figure 3.6). Moreover, it appears that ambient water
temperature influences vertical habitat use where mako sharks seek out their preferred
temperature ranges (Figure 3.3). There is some evidence that mako sharks dive deeper
and avoid very warm surface waters (Figure 3.4). One shark remained below 100 m for
4.5 consecutive days, and only briefly rose to 5m for 1 hour before again diving below
100m (Figure 3.4). The deeper depths during this time were at the high end of the shark’s
typical temperature range (198507; Figure 3.4). The avoidance of warm surface waters
has been observed in several pelagic species such as the bluefin tuna (Thunnus thynnus;
Teo et al. 2007), porbeagle sharks (Lamna nasus; Campana et al. 2010), and salmon
sharks (L. ditropis; Coffey et al. 2017). These results suggest that there may be
physiological challenges associated with moving through warmer water temperatures.
Further, the temperature-depth data recorded by the tags show that sharks were exploring
different depths to stay within their preferred temperature range (Figure 3.4), suggesting
that despite traveling through different habitats mako sharks sought out specific temperatures (Figure 3.3).

**Recovery period**

The results of this study suggest that mako sharks released in good condition recover quickly from capture. The estimated durations of recovery for individuals in this study (mean = 8.7 hours) were shorter than other studies evaluating recovery behavior of shortfin mako sharks (up to 5 days; Hoolihan et al. 2011; mean = 3.8 days, Bowlby et al. 2021). During the identified recovery periods in our study, depth variance was low indicating sharks exhibited reduced vertical diving following release. These results are consistent with observations of mako sharks exhibiting little change in depth immediately following release (Loefer et al. 2005; Hoolihan et al. 2011; Bowlby et al. 2021). The behavioral change observed may be related to the shark’s recovery from the physiological effects of exhaustive exercise associated with capture (Skomal and Chase 2002; Skomal, 2007).

**Limitations and Conclusion**

The low sample size of this study was due to high tag failure rates and pre-mature tag detachment. The tags used in this study had a 37% success rate, a 47% failure rates, and a 16% pre-mature detachment rate. Tag failure may be caused by tag malfunction. Further studies should consider using an increased sample size of satellite tag deployment to further investigate the effects of the mixed layer depth and temperature on mako shark depth use. The tags used in this study did not provide geo-location estimates, but the combination of high-resolution vertical movement data and geographical location would allow researchers to have direct measures of what habitats sharks were passing through in
relation to their depth use. However, given the similarities in water column use and
temperature ranges from this study to other studies these results may be representative of
mako sharks tracked in the North Atlantic Ocean off the coast of North America. The
sharks tracked in my study were only tracked for a short time (28 days) during one
season, therefore it may be important to note that vertical habitat use may change
seasonally.

Mako sharks tagged in this study did not regularly access the coldest water, which
is a pattern that has been observed for other endothermic pelagic predators (Madigan et
al. 2020). The results presented in this study and other studies indicate that although
mako sharks may have a broad thermal tolerance, their depth use is driven by their
optimal temperature range. Mako sharks used deeper depths when warm water persisted
deep into the water column, which was demonstrated when the SST was warm, and the
mixed layer was deep. Even in lamnid sharks, entering cooler waters can result in
reduced muscle performance (Bernal et al. 2005). Further, regional endotherms do not
have whole-body endothermy and much of their body remains at ambient temperature,
which likely puts limits on their performance in cold water (Shiels et al. 2011). This may
be an explanation for why mako sharks in this study used deeper depths when warmer
water temperatures persisted deeper in the water column.
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https://doi.org/10.1038/s41598-018-25565-8


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reveal niche expansion in salmon sharks. Science 310:104–106

https://doi.org/10.1126/science.1114616


Tables and figures

Table 3.1: Capture variables for all released shortfin mako sharks caught in the U.S. Pelagic longline fishery off the coast of North Carolina. M = Male, F = Female, U = Undetermined. PSAT = Pop-up satellite archival tag.

<table>
<thead>
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<th>ID</th>
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<tr>
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**Figure 3.1**: Suspected mortality of tagged mako shark caught in pelagic longline gear off the coast of North Carolina, USA. Y-axis represents the depth of the shark in meters and x-axis represents time. The tag detached and floated to the surface after 8 hours.
Figure 3.2: Example of post-release recovery behavior marked by low variance in dive depth at the beginning of the dive track. The red vertical line represents the end of the identified recovery period.
Figure 3.3: Generalized additive model smooth predicted estimates for temperature use over time of shortfin mako sharks tagged off the coast of North Carolina. The mean predicted temperatures are plotted on top of a boxplot of temperature use each day of deployment. The red line represents the daily mean predicted temperature. The blue line represents the mean temperature used over the length of the deployment period.
Figure 3.4: The depth-temperature time series show the relationship between depth use and temperature recorded from the three tagged mako sharks in the North Atlantic.
Figure 3.5: Map on the left: Sea surface temperature (SST) contour chart of the US Atlantic Ocean. Data/image provided by the NOAA/NESDIS/OSPO, Maryland, USA, from their Web site at http://ospo.noaa.gov/. Map on the right: Tagging and pop-off locations of three sharks tagged off the coast of North Carolina in the North Atlantic Ocean.
Figure 3.6: Forest plot showing the effect of oceanographic features on the depth use of shortfin mako sharks in the North Atlantic Ocean. Variance in depth, mean depth, and maximum depth were used as proxies for depth use. All models included individual shark as a random effect. The plot shows the effect of the mixed layer depth (MLD) and sea surface temperature (SST, °C). The bars represent the 95% confidence intervals. The dotted vertical line is on zero.
Figure 3.7: Generalized linear mixed model results showing the effect of the mixed layer depth (MLD) on mako shark daily depth use with each individual shark included as a random effect. Daily depth variance, mean daily depth, and maximum daily depth were used as a proxy for depth use.
Figure 3.8: Generalized linear mixed model results showing the effect of SST on mako shark daily depth use with each individual shark included as a random effect. Daily depth variance, mean daily depth, and maximum daily depth were used as a proxy for depth use.
Figure 3.9: Population level model predictions from generalized linear models showing the effect of mixed layer depth (MLD) on depth use at different sea surface temperatures (SST).
Conclusions

The primary objective of my thesis was to evaluate regional differences in AVM rates of shortfin mako sharks caught in accordance with the US pelagic longline fishery. My results provided support for previous research suggesting the AVM may make up an important source of fishing mortality and hinder management focused on the live release of sharks. My results showed the importance of considering regional effects when studying animals over a large, diverse, geographical area. Given the high AVM in this study, future research should focus on reducing overall bycatch of mako sharks to help rebuild the North Atlantic stock of shortfin makos. Contrary to my predictions, larger shortfin mako sharks in the GOM had higher AVM rates which does not line up with previous research on capture stress and mortality of sharks. Further research on large sharks’ stress response in warmer water may give insight as to why I saw this pattern in mako sharks caught in the GOM.

Further, I sought to determine how mako shark vertical habitat use was influenced by environmental drivers in a diverse, dynamic marine ecosystem of the North Atlantic Ocean off the coast of the US and Canada. High tag failure rates led to small sample size, but I was still able to provide conclusions on how thermal stratification influenced depth use. Four mako sharks tagged in my study traveled from the coast of North Carolina through the Gulf Stream. Throughout the deployment periods mako sharks altered their vertical habitat use to stay within a narrow temperature range, even as they passed through many different marine habitats. From my results, it appears that mako shark movements are driven my thermal stratification, where these sharks select specific temperatures despite having a broad thermal tolerance.