Navigating Our Changing Oceans:

An Assessment of Climate Change Impacts to Highly Migratory Species in the North Atlantic Ocean

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LIST OF ABBREVIATIONS AND ACRONYMS

AMO	Atlantic Multidecadal Oscillation
AMOC	Atlantic Meridional Overturning Circulation
ATCA	Atlantic Tuna Convention Act
CPUE	Catch Per Unit Effort
CS	Caribbean Sea
DO	Dissolved Oxygen Concentration
EBFM	Ecosystem-Based Fisheries Management
EEZ	Exclusive Economic Zone
EM	Electronic Monitoring
ER	Electronic Reporting
ESA	Endangered Species Act
FADs	Fish Aggregating Devices
FAO	Food and Agriculture Organization of the United Nations
GOM	Gulf of Mexico
HCR	Harvest Control Rule
HMS	Highly Migratory Species
ICCAT	International Commission for the Conservation of Atlantic Tunas
LC	Loop Current
MMPA	Marine Mammal Protection Act
MSA	Magnuson-Stevens Act
MSE	Management Strategy Evaluation
NMFS	National Marine Fisheries Service
OMZ	Oxygen Minimum Zone
RFMO	Regional Fishery Management Organization
SCRS	Standing Committee on Research and Statistics

SUMMARY

This report examines the effects of climate change on highly migratory species (HMS) in the North Atlantic and the implications for HMS fisheries in the United States. Key findings of this report include:

- Various HMS are projected to be affected in significantly different ways (e.g., warmer water vs. colder water species, adults vs. juveniles, etc.), and there is still significant uncertainty about many of the anticipated changes.
- Climate change will likely affect many HMS aspects (e.g., physiology, behavior, distribution, survival, and regional population level) through impacts from changing marine environmental conditions, including changes to climate variability, warmer ocean surface temperatures, lower dissolved oxygen concentration (DO) levels, and changes to ocean currents.
- Among the most immediate (e.g., one to two decades) of these impacts, surface ocean warming will contribute to changes in the range of geographic and/or depth distributions of HMS (e.g., poleward and/or deeper water shifts for colder water species), while less oxygenated (i.e., warmer) waters will likely result in a higher occurrence of post-release mortality for HMS that are commonly caught and released into the water (e.g., large pelagic sharks).
- In the long-term horizon (e.g., more than three decades), climate-induced changes in climate variability will contribute to altering the dynamics of large-scale (e.g., global and regional ocean currents) and medium-scale (e.g., frontal zones, eddies, and gyres) oceanographic processes that regulate HMS behavior and distribution and fisheries dynamics.
- While some HMS stocks are currently healthy, other populations are being fished unsustainably and/or have biomass levels below sustainable levels. Some HMS may experience positive effects (e.g., increased habitat suitability for warm water species) due to climate change. For many other HMS, climate change effects will likely create additional stressors that could threaten stock health (e.g., habitat loss and reduced growth and survival rates).
- Climate-induced impacts will affect HMS stock and fisheries dynamics, which will need to be accounted for in fisheries science, management, and governance. Building resilience will be necessary to ensure fisheries are sustainable and meet socioeconomic goals in the long term.
- A crucial part of increasing resilience is expanding our scientific understanding of how climate change will affect the marine environment in the North Atlantic, its ecosystems, and the dynamics of HMS fisheries, and incorporating that understanding into decision-making.
- The resilience attributes of management and governance systems include effectively accounting for and adapting to current and anticipated changes; focusing holistically on the ecosystem; scaling appropriately to species' climate change-impacted ranges; ensuring inclusivity, participation, and transparency; and emphasizing continual learning and experimentation.
- An analysis of social and economic factors is a critical next step for better understanding and identifying actions for building the resilience capacities of fishing communities.
- In HMS fisheries, adding a resilience-focused approach could lead to better management outcomes than those seen today, even with the expected impacts of climate change.

INTRODUCTION

Highly migratory species (HMS)—tunas, sharks, billfishes, and swordfish—are critical for a thriving ocean and for the well-being of people around the world. Many HMS are top predators that help to maintain a balanced ecosystem (Heithaus et al., 2008). HMS fisheries—mainly tuna and swordfish fisheries—also provide sustenance to millions and support livelihoods around the world. Tuna fisheries are especially valuable, contributing more than $40 billion each year to the global economy (McKinney et al., 2020). However, HMS face a multitude of threats, in particular overfishing and the effects of climate change.

HMS fisheries

Across the North Atlantic Ocean, fishing fleets from dozens of countries fish for HMS. By volume, the most-landed tuna species is skipjack, followed by yellowfin, bigeye, albacore, and Atlantic bluefin tuna. Purse seine fishing accounts for most tuna production, followed by gillnet, pole & line, longline, handline, and troll (McKinney et al., 2020). Swordfish is primarily caught in pelagic longline fisheries, and the top swordfish fishing nations include Spain, the United States, Canada, Portugal, and Japan (ICCAT, 2020). Some shark species are prohibited from being landed in domestic and international fisheries. Atlantic billfishes cannot be retained in the United States for commercial purposes but can be fished recreationally. Sharks and billfishes are often caught as bycatch in tuna and swordfish fisheries.

Atlantic HMS populations support commercial and recreational fisheries in the United States and their fishing communities along the Eastern Seaboard and in the Caribbean Sea (CS) and Gulf of Mexico (GOM). U.S. commercial fishermen use a variety of gear types to catch tunas, swordfish, and sharks, including pelagic longline, bottom longline, gillnet, handline, and green-stick. For-hire fishermen and private anglers also fish for tunas, swordfish, sharks, and billfishes, including during fishing tournaments held on the Atlantic and Gulf coasts.

Management and regulation

Management of HMS fisheries in the international context begins with the International Commission for the Conservation of Atlantic Tunas (ICCAT), a Regional Fishery Management Organization (RFMO) that includes more than 50 countries and is responsible for the management of tunas and other highly migratory stocks in the Atlantic Ocean and adjacent seas. The United States is a party to ICCAT, and the Atlantic Tuna Convention Act (ATCA) requires the Secretary of Commerce to develop domestic regulations to comply with ICCAT obligations and delegates this responsibility to the National Marine Fisheries Services (NMFS). These agreements include catch limits and country-specific allocations for various species, as well as conservation measures for HMS. In addition to ATCA, the United States manages HMS in accordance with the Magnuson-Stevens Act (MSA) and other U.S. laws including the Marine Mammal Protection Act (MMPA) and the Endangered Species Act (ESA).

Conservation status of HMS

The stock statuses of Atlantic and GOM HMS vary. North Atlantic swordfish is hailed as an international conservation success story. International and domestic measures helped the stock to recover to sustainable levels, and the stock was declared fully rebuilt in 2009 (NMFS, 2019).

Similarly, an international rebuilding plan was put in place in 2010 for Northern Atlantic albacore tuna, and the stock was declared rebuilt in 2016 (ICCAT, 2016a). West Atlantic skipjack tuna stocks are currently considered to be healthy and not experiencing overfishing (ICCAT, 2014). The Atlantic yellowfin tuna stock biomass is also considered to be healthy, although ICCAT's science committee, the Standing Committee on Research and Statistics (SCRS), has warned that catches above sustainable levels across ICCAT fisheries could threaten the stock in the future (ICCAT, 2019a). The stock status of bigeye tuna, however, is of great conservation concern. The stock is threatened by overall exceedances of ICCAT quota and the use of fish aggregating devices (FADs) by purse seine fleets targeting skipjack tuna, which also catch juvenile bigeye tuna, thus decreasing the spawning capability of the stock (ICCAT, 2018a).

The abundance of many shark species in the Atlantic has been declining, depleted by overfishing (Pacoureau et al., 2021). These declines are especially alarming given that many shark species play a key role in ecosystems as apex predators. Some species, such as North Atlantic shortfin mako sharks, are currently caught at unsustainable levels (ICCAT, 2019b). Shark bycatch remains an issue in pelagic longline and seine net fisheries. Globally, bycatch represents a significant source of fishing pressure for many shark populations (Dulvy et al., 2008; Oliver, 2015; Stevens et al., 2000).[1] The incidental catch of sharks in these fisheries is particularly concerning due to the poor status of several of these populations.

ICCAT has yet to implement conservation and management measures for many shark species, making international coordination to rebuild shark populations difficult for species that cross between Exclusive Economic Zones (EEZs) and the high seas. In addition, many of these species are "data deficient," meaning there is insufficient information to assess their status (Dulvy et al., 2014). Domestically, fishermen in federal and state commercial and recreational fisheries catch sharks, requiring management across jurisdictions. Recreational fisheries can represent a significant source of fishing mortality for sharks, especially for vulnerable coastal shark species (Kilfoil, 2017). More reliable data are urgently needed to better manage these fisheries.

Billfishes are largely caught as bycatch in tuna and swordfish fisheries. Billfish species are also popular targets in recreational HMS fisheries in more tropical locations including the Caribbean. Like other HMS, billfish species have mixed stock statuses. The blue marlin population is currently overfished and overfishing continues (ICCAT, 2018b). The results of the most recent stock assessment indicated that the Atlantic white marlin was overfished but is not currently undergoing overfishing (ICCAT, 2019c). Western Atlantic sailfish are likely not overfished or experiencing overfishing, but scientists recommended interpreting the assessment results with caution due to a large amount of uncertainty (ICCAT, 2016b).

[1] The term "bycatch" is used in different ways in fisheries literature. In this report, we adopt the Food and Agriculture Organization of the United Nations (FAO) definition of bycatch used in Roda et al. (2019): "the catch of organisms that are not targeted. This includes organisms that are outside legal-size limits, over-quotas, threatened, endangered and protected species, and discarded for whatever other reasons, as well as non-targeted organisms that are retained and then sold or consumed." Discards refer specifically to the portion of the catch that is returned to the ocean (dead and alive) due to regulatory, economic, or other reasons.

Domestic socioeconomic context

Both commercial and recreational HMS fisheries in the Atlantic and GOM contribute significantly to the U.S. economy. HMS are harvested commercially year-round, though average monthly landings revenue is typically lower for most species from February through April as compared to other months (NMFS, 2021a). Larger tunas, especially bluefin and bigeye, are typically sold to sushi and sashimi markets and can procure higher prices for quality fish. Albacore, a smaller tuna, is sold seasonally and regionally as a fresh-product market, but at lower prices than the larger tunas. High-end restaurants are the typical end-market for swordfish, domestically. HMS recreational fishing generates significant economic activity through tournaments, for-hire fishing, or fishing trips made by private anglers.

Several HMS commercial fisheries have experienced declines in profitability and in the number of participants over the past decades. For example, the U.S. pelagic longline fleet reached its largest size in the late 1980s with over 400 vessels in operation (Graves, 2013). Today, after a series of regulatory changes – including a reduction in available fishing grounds – and market forces such as rising fuel costs and competition from imported frozen products, fewer than 90 vessels continue to fish (NMFS, 2019, 2020). From 2015 to 2019, the U.S. pelagic longline fleet averaged approximately 4 percent of total Atlantic pelagic longline tuna, billfishes, and swordfish landings/discards, and less than 0.3 percent of pelagic shark (blue shark, shortfin mako, and porbeagle) landings/discards (NMFS, 2021b).

Hurricanes also represent a major threat to the resilience of coastal Atlantic and GOM fishing communities. Over the past two decades, Hurricanes Katrina, Rita, Sandy, Irma, Maria, Harvey, and others have caused significant damage to fishing communities along the Atlantic and GOM coasts and in the CS. According to climate models, global average tropical cyclones intensity is expected to increase by 2–11% by 2100, while frequency is expected to decrease by 6–34% by the late 21st century (Knutson et al., 2010). In other words, while we may experience fewer hurricanes overall, we can expect the tropical storms and hurricanes that do occur to be more intense and damaging globally, including in the Atlantic and GOM (Biasutti et al., 2012). Fishing communities located in coastal areas are particularly vulnerable to these more intense storm systems.

In addition to natural disasters, man-made shocks can affect the resilience of the fisheries and fishing communities. For example, on April 20, 2010, an explosion and subsequent fire at the Deepwater Horizon drilling rig off the coast of Louisiana caused oil to flow for 86 days into the GOM. In response to the oil spill, NMFS closed portions of the GOM EEZ to fishing, resulting in significant losses for fishermen. More than a decade later, GOM fishermen report that they are still recovering economically from the oil spill.

More recently, the COVID-19 pandemic dealt an economic blow to Atlantic and GOM HMS fisheries. In response to restaurant closures, many commercial fishermen stopped fishing in the spring of 2020 because they did not have buyers for their fresh products, resulting in significant loss of revenue for the fishery. Overall, commercial landings revenue dropped 36% from April through June 2020, with the steepest decline in April (NMFS, 2021a). The economic challenges facing HMS fisheries have spillover effects for domestic buyers and markets for HMS species, consumers of these fish, and fishing equipment supply businesses.

Climate change and resilience

Climate change poses an additional challenge to the health of HMS stocks. HMS are sensitive to ocean temperature and associated levels of dissolved oxygen (DO) (Boyce et al., 2008; Brill, 1994; Schlaff et al., 2014; Stramma et al., 2012). Scientists project that many HMS will shift their ranges poleward in response to climate-driven changes to the ocean environment (Monllor-Hurtado et al., 2017) and that some, particularly in equatorial areas, will experience changes to their abundances (decreases for swordfish (Erauskin-Extramiana et al., 2020) and increases for yellowfin and skipjack tuna, except in the Western Central Equatorial Pacific (Erauskin-Extramiana et al., 2019)). Several HMS are particularly affected by low oxygen levels, and scientists project that climate change will potentially make survival more difficult for many HMS, especially after being released alive from fishing gear (Dapp et al., 2016; Dell'Apa et al., 2018; Gallagher et al., 2014a). In some coastal and marine regions around the globe, oxygen-rich layers of water will become shallower, driving some species to the surface where they will become more vulnerable to fishing gear (Prince & Goodyear, 2006; Stramma et al., 2012; Vedor et al., 2021). In addition, climate change is expected to impact key habitat areas that are critical to certain HMS life stages. For example, the timing and location of spawning is projected to shift for bluefin tuna in the northern GOM (Muhling et al., 2011), and certain populations of sharks will likely lose important nursery habitat (Crear et al., 2020).

These and other factors raise key questions about the future geographic distribution of HMS stocks; their future population levels, productivity, and survival; and their vulnerability to fishing gear. Given how profound some of these impacts may be—especially for populations already struggling to rebuild—a key priority is developing a greater understanding of these stocks and how their ranges, productivity, and population levels will respond to climate change over time. These new realities will also require improvements to domestic and international coordination as stocks shift across jurisdictions and political boundaries and the development of innovative regulatory and fishing practices that facilitate adaptation in the face of climate change.

Fisheries management has begun to incorporate climate resilience considerations, alongside long-standing goals of sustainability. While sustainability principles will remain crucial, resilience refers to the ability of a system to resist, recover, adapt, or transform in the face of stressors, including climate-related impacts. This includes not only the natural system but also the related socioeconomic environment. Management measures that foster resilience can play a key role in helping to meet sustainability and socioeconomic goals in the face of climate change (Free et al., 2019; Gaines et al., 2018; Holsman et al., 2019; Kritzer et al., 2019; Pinsky and Mantua 2014).

In this report, we focus on key species that are important to U.S. Atlantic and GOM HMS fisheries because the United States is equipped with highly developed fishery management and scientific expertise, providing a helpful foundation for the development of resilient fishery management systems. Existing innovation in U.S. fisheries, including gear modifications, electronic technologies, and tradeable bycatch quota systems, can form the basis for new tools to build resilience. We have an opportunity in the United States to build on these efforts and test and deploy innovative approaches to foster climate resilience that can serve as a model for other fisheries—particularly for transboundary stocks—domestically and internationally.

ASSESSING THE POTENTIAL CLIMATE IMPACTS ON HIGHLY MIGRATORY SPECIES

Overview of climate impacts

The effects of climate change on the world's coastal and marine ecosystems, and their fisheries, have been studied for decades (Cheung et al., 2010; Doney et al., 2012; Fields et al., 1993; Kleisner et al., 2017; Stock et al., 2011; Walther et al., 2002). HMS are a priority for many domestic and international fishing communities and for conservationists. True to their name, most HMS expand their range of movement and habitat as they mature, with some species covering thousands of miles over a few months, potentially spanning dozens of EEZs, plus areas beyond national jurisdiction. Climate impacts on HMS are likely to exacerbate these dynamics and potentially alter the distributions of individual species in ways that make ensuring the sustainability of catches more difficult. Here we draw upon a wide body of scientific literature on HMS in the Northwest Atlantic, including the GOM and CS, across species and their life stages (i.e., eggs, larvae, juveniles, and adults) to assess potential impacts of climate-driven environmental changes to these species and resultant repercussions for fisheries and fishery management in this region.

Changes now and in the future

Some of the effects of climate change on ocean environments are happening now, though they will most likely be amplified over the next century. For example, global sea surface temperatures are warmer than in the past, and because water holds less oxygen as it heats up, some water masses are less oxygenated than they were previously. Other forecasted climate-driven changes on coastal and marine environments will be more evident in years to come, especially those related to changes in large-scale oceanographic processes (e.g., global ocean currents) (Barange et al., 2018). Therefore, some changes appear to be more urgent than others, in particular ocean warming and associated water deoxygenation, as these changes have most likely already altered HMS behavior and distribution over recent decades.

Analyses of predicted future changes in HMS distribution and abundance are based on complex climate projections, with different projection results based upon various sources of information, both for the species and the fishery. For example, some climate projections are based only on known HMS life histories and ecology, while others are based on historical fishing effort as a proxy for species abundance (Liu et al., 2015). By analyzing these factors' relationships to environmental conditions, projections explore how species may respond to future environmental changes. However, some of these projections do not account for possible changes in fishing activity due to other factors (e.g., changes in markets or fisheries management), which might be just as relevant as environmental changes.

Regardless, some climate-induced changes in ocean environments have already been reported as evidence for possible modifications of HMS behavior and distribution, with direct implications for fisheries targeting these species. For example, an increasing trend in sea surface temperature in the Atlantic Ocean over the last four decades has corresponded to an increase in the proportion of yellowfin and skipjack tuna (two species that have a higher preference for warmer waters than other tunas) in the catches of longline fisheries, with a stronger increase during the last twenty years

(Monllor-Hurtado et al., 2017). Similarly, suitable habitat for bigeye tuna (a species with a stronger preference for colder, deeper waters than most other tunas) has shifted significantly in a northwest direction in the Atlantic Ocean, likely due to changes in environmental conditions linked to climate change (Erauskin-Extramiana et al., 2019).

The major identified climate-driven environmental changes expected to affect HMS are:

- climate variability (i.e., periodic variability in ocean conditions over several decades);[2]
- warmer ocean surface temperatures;
- lower dissolved oxygen concentration (DO) levels and regional-based shoaling of oxygen-depleted waters; and
- changes in ocean currents.[3]

Global climate models project an increase of ~2°C in surface water temperature of the North Atlantic by 2100. The Atlantic Meridional Overturning Circulation (AMOC)[4] is also progressively undergoing a considerable reduction in strength, resulting in colder ocean surface temperatures in the subpolar region across the Atlantic Ocean and a warming and poleward shift of the Gulf Stream (Caesar et al., 2018; Thornalley et al., 2018). Furthermore, by the end of 2100, average DO levels between depths of 200 and 700 m (i.e., the main depth layers where most HMS live, reproduce, and forage) are projected to decrease globally throughout the mid- and high-latitudes, primarily in more coastal regions along the eastern basin (Leung et al., 2019). Climate change is expected to alter key ocean circulation processes and dynamics in the North Atlantic and GOM that influence HMS foraging, habitat, migration, and spawning (Bryden et al., 2005; Claret et al., 2018; Grose et al., 2020; Lehrter et al., 2017; Parsons & Lear, 2001; Scavia et al., 2002).

In response to projected changes in these marine environmental conditions by the end of this century, we can expect species-specific changes in HMS physiology, phenology (e.g., migration timing), behavior, distribution, survival, and reproductive success (Asch, 2015; Chen et al., 2011; Dell'Apa et al., 2018; Monllor-Hurtado et al., 2017; Poloczanska et al., 2016). In turn, these changes in HMS responses will create challenges for fisheries that have developed their operations, management, supply chains, and governance regimes around the current state of marine conditions.

Impacts of warming waters

The most visible and widest impact of climate change on HMS will be a shift in both geographical (i.e., latitudinal and longitudinal) and vertical (i.e., depth) distributions, leading to changes in species catchability in HMS fisheries. This is due to a combination of thermal preference (i.e., the range of ambient water temperatures that a given species prefers to live in) and complex predator-prey

[2] Specifically, the long-term changes associated to climate change rather than interannual or interdecadal natural climate fluctuations.
[3] Due to a lack of sufficient studies and projections focused on HMS, this literature review excludes other climate-driven environmental changes (e.g., ocean acidification and changes in storm activity) that may also be important in triggering a behavioral response in HMS. Future research is needed to enhance the understanding of these climate-based impacts to HMS and their fisheries.
[4] The AMOC is the specific component of the Meridional Overturning Circulation (MOC) (the global ocean current circulation system transporting heat, salt, carbon, and nutrients throughout the ocean) that plays a central role in redistributing heat and freshwater across the Atlantic Ocean. In turn, these heat and freshwater transports can influence the local climate (Buckley & Marshall, 2016).

interactions (e.g., climate-driven movements of prey and associated changes in predatory HMS distribution). HMS have broader thermal tolerances than many other fish species but may be limited by climate-induced changes in prey species composition and availability (Muhling et al., 2015). For example, evidence suggests that an expansion of preferred habitat and altered prey species distribution has shifted Atlantic swordfish distribution both into northern and southern latitudes, while abundance is projected to decrease in the equatorial Atlantic, including the GOM (Erauskin-Extramiana et al., 2020). In contrast, some warm-water species, such as skipjack and yellowfin tunas and oceanic whitetip sharks, may expand their habitat both in the North Atlantic and GOM. HMS with a preference for warmer waters may also expand their depth distribution as warming extends through the water column, which could make them more vulnerable to deeper longline fishing sets. For pelagic sharks, changes in species distribution and behavior will likely be more pronounced in ectothermic ("cold-blooded") than endothermic ("warm-blooded") species, and in juveniles compared to adults (Bernal et al., 2012; Dickson & Graham, 2004; Vaudo et al., 2016).

Ocean warming may also alter HMS behavior, migration timing, locations of key reproductive areas, and reproductive success. In particular, the Atlantic bluefin tuna spawning area in the GOM is predicted to shift northward and the spawning season to begin earlier in the spring by 2050 (Muhling et al., 2011). These changes, coupled with warmer waters in this basin, could reduce larval survival in this species (Muhling et al., 2015). For skipjack and yellowfin tuna, warmer surface waters may favor larval growth, leading to long-term increases in stock biomass (Dell'Apa et al., 2018; Luckhurst & Arocha, 2016; Muhling et al., 2015; Reglero et al., 2014).

Impacts of decreases in dissolved oxygen levels

Warmer waters also lead to decreased DO throughout the open ocean, which reduces HMS habitat suitability because their high-performance metabolic rates require high DO levels (Brill 1996; Idrisi et al. 2003; Bernal et al. 2009). A particular risk to HMS is a projected expansion of the oxygen minimum zone (OMZ). The OMZ, which is comprised of a thick layer of deeper (between 200 and 800 m depth, depending on the region) oxygen-depleted waters, may expand in the water column and result in a compression ("shoaling") of the vertical habitat that is sufficiently oxygenated to be suitable for HMS into a narrower surface layer (Prince & Goodyear 2006; Prince et al. 2010; Vedor et al. 2021). The most severe shoaling effects are projected in the eastern Atlantic Ocean, with greatest impacts for shallow-water species with a smaller DO range of tolerance such as skipjack tuna, Atlantic blue marlin, Atlantic sailfish, and blue sharks. Low ambient oxygen conditions reduce growth, maturation, recruitment, and survival for HMS with greater impacts on larvae and juveniles compared to adults. Juvenile pelagic sharks in shallow estuary and coastal nursery areas are particularly vulnerable to low DO conditions (Crear et al., 2019, 2020; Schlaff et al., 2014).

In addition to compressing habitat, lower DO levels create physiological stress for HMS. This may contribute to higher post-release mortality rates in bycatch species, including Atlantic blue marlin, sailfish, bluefin tuna, and sharks (Dapp et al., 2016; Dell'Apa et al., 2018; Stieglitz et al., 2016). Mortality will also be higher where warmer temperature and resulting lower DO conditions create a combined stressor, particularly in the warmer GOM, although the type of fishing gear and operations (combined with species characteristics and traits) remain the most significant factors for determining mortality (Davis, 2002; Huang et al., 2016).

Impacts of changing ocean currents

Climate change will also alter key regional ocean circulation patterns and processes, with differing impacts across HMS species and life stages. Many HMS species forage in regional frontal zones in the ocean,[5] due to the convergence of organic matter and prey species in these areas. Regional currents within spawning grounds may affect spawning cues and larval survival. A projected climate-driven weakening of the GOM Loop Current (LC) may reduce Atlantic bluefin tuna spawning success and billfish larvae survival, although impacts are complex (Liu et al., 2015; Muhling et al., 2011). Potential changes in the Gulf Stream position and strength may affect swordfish and other billfish species distributions in relation to frontal zones and key offshore areas of high productivity.

Species-specific impacts

For the potential impacts of climate change on HMS, we considered an initial list of commonly caught HMS (both target and bycatch) in the U.S. Atlantic pelagic longline fishery using logbook data (2015-2019) provided by the National Marine Fisheries Service (Alan Lowther, 2020 - personal communications). Using this logbook data, we generated a list of species and crosschecked it with the list of species managed by ICCAT to ensure key species important to both domestic and international fisheries were included. We analyzed the available scientific literature and compiled projected impacts from the literature for these species. In this section, we present the results for species-specific impacts of climate change, which are summarized in Table 1, as divided by groups of species. Importantly, though HMS fisheries interact with marine mammal, seabird, sea turtle and small/large coastal shark species, we opted to focus our attention on large pelagic fish species. Therefore, subsequent research is needed for these excluded taxa.

[5] Frontal zones in the ocean are boundary areas between water masses with distinct biological or chemical properties (e.g., temperature, salinity, nutrients, etc.).

Table 1. Summary of potential climate impacts to key HMS in the North Atlantic, including GOM and CS.

	Range and distribution	Abundance	Growth and Survival	Reproduction
North Atlantic swordfish	●Projected poleward shifts[1] ●Potential changes in regional migration patterns[2] ●Regional changes in oceanographic processes (e.g., frontal zones and eddies) may alter species distribution[3,4]	●Global decrease of ~22% by 2100, with largest decrease in the equatorial Atlantic Ocean[1]	●Regional changes in oceanographic processes (e.g., frontal zones and eddies) may alter larval transport and potential survival[5,6]	
BAYS tunas (bigeye, albacore, yellowfin, and skipjack)	●Projected poleward shifts for yellowfin tuna[7] and skipjack tuna[7,8] and albacore tuna[9] by 2100 ●Projected global poleward shift for bigeye tuna by 2100[9]	●Projected increase in abundance of yellowfin tuna in equatorial Atlantic and skipjack tuna in subtropical Atlantic (mainly in GOM[10] and CS) by 2100[9] ●Lower abundance of bigeye tuna in tropical waters projected globally by 2100[9]	●Potential higher growth rate and survival for larvae of skipjack tuna, yellowfin tuna, and albacore tuna in GOM due to warmer waters[11,12,13] ●Potential higher post-release mortality (discarded species) due to warmer, less oxygenated waters, especially in the GOM and CS[14,15,16] ●Potential (region-based and mainly in the GOM) lower survival of yellowfin tuna larvae due to reduced oxygen in the water[17]	
Atlantic bluefin tuna	●Projected poleward and deeper shifts by 2100[9]		●Reduced larvae survival due to excessive (> 29 °C) warmer waters[11] and reduced oxygen in the water[18] ●Potential higher post-release mortality of adult spawners in the GOM due to warmer, less oxygenated waters[13,19,20]	●Ocean warming in GOM projected to result in earlier spawning in the spring by 2050[21] ●Projected northward shift of suitable habitat for larvae in the GOM by 2050 due to ocean warming[21] (more studies needed due to complexity in climate model predictions on climate-driven changes in ocean temperatures in northern GOM)[22]
Istiophorid billfishes (Atlantic blue marlin, white marlin, Atlantic sailfish)	●Warming through the water column in the GOM may result in blue marlin exploring deeper waters (likely to follow their prey species)[13]	●Regional habitat compression for shallow-water species (e.g., blue marlin and sailfish) in eastern Atlantic due to reduced oxygen in surface water[23,24]	●Potential reduced growth rate and survival in sailfish larvae, especially in the GOM and CS, due to decreased oxygen levels in the water[13,25] ●Potential higher post-release mortality due to warmer, less oxygenated waters, especially in the GOM and CS[26] ●Regional changes in oceanographic processes (e.g., frontal zones and eddies) may alter larval transport and potential survival[13,27]	
Ectothermic sharks	●Suitable habitat for many warm-water species (e.g., oceanic whitetip shark) may expand due to ocean warming[28,29,30,31,32] ●Spatiotemporal mismatch of juvenile dusky shark migration patterns with current area closures (i.e., Mid-Atlantic Shark Closed Area) due to ocean warming[33]	●Regional habitat compression for blue shark in eastern Atlantic due to reduced oxygen in surface water[34]	●Potential higher post-release mortality (bycatch species) across species due to warmer, less oxygenated waters, especially in the GOM and CS, though based on species-specific sensitivities to oxygen levels in the water[35,36,37,38,39] ●Projected reduction in suitable nursery habitat in Chesapeake Bay for sandbar shark by 2100 due to climate-induced environmental changes (e.g., water temperature, salinity, and dissolved oxygen), resulting in potential reduction in population growth[40]	
Endothermic sharks	●Ocean warming may drive juvenile shortfin mako deeper, especially in the warmer GOM[41] ●Changes in ocean temperatures may be less impactful in endothermic sharks as they can actively modulate their internal body temperature and retain heat, but juveniles may experience a larger distribution change due to ocean warming[28,41,42] ●Regional changes in temperatures and frontal zones dynamics may alter porbeagle shark range and vertical distribution in pelagic waters at the U.S./Canada border[39,45]		●Most likely will experience higher post-release mortality (bycatch species) than ectothermic species due to higher oxygen needs (e.g., higher probability of asphyxiation when remaining caught in pelagic and bottom longline fisheries for longer periods)[28,39,43,44]	

[1] Erauskin-Extramiana et al., 2020; [2] Chang et al., 2013; [3] Hoey, 1983; [4] Podestá et al., 1993; [5] Govoni & Hare, 2001; [6] Govoni et al., 2003; [7] Monllor-Hurtado et al., 2017; [8] Dueri et al., 2014; [9] Erauskin-Extramiana et al., 2019; [10] Muhling et al., 2015; [11] Reglero et al., 2014; [12] Luckhurst & Arocha, 2016; [13] Dell'Apa et al., 2018; [14] Graham et al., 1989; [15] Brill, 1994; [16] Arrizabalaga et al., 2015; [17] Wexler et al., 2011; [18] Miyashita et al. 1999; [19] Orbesen et al. 2019; [20] Teo et al. 2007; [21] Muhling et al. 2011; [22] Liu et al. 2012; [23] Prince & Goodyear 2006; [24] Stramma et al. 2012; [25] Simms et al., 2010; [26] Prince et al., 2010; [27] Trenkel et al., 2014; [28] Bernal et al., 2012; [29] Musyl et al., 2011; [30] Carlson & Gulak, 2012; [31] Howey-Jordan et al., 2013; [32] Tolotti et al., 2015; [33] Bangley et al., 2020; [34] Vedor et al., 2021; [35] Schlaff et al., 2014, [36] Carlson & Parson, 2001; [37] Gallagher et al., 2014a; [38] Gallagher et al., 2014b; [39] Campana et al., 2016; [40] Crear et al., 2020; [41] Vaudo et al., 2016; [42] Dickson & Graham, 2004; [43] Skomal & Mandelman, 2012; [44] Dapp et al., 2016; [45] Campana & Joyce, 2004

North Atlantic swordfish

Based on projections of CPUE (catch per unit effort) from historical data on CPUE and habitat suitability modeling, researchers project that global swordfish populations will decrease by ~22% by the end of 2100 (Erauskin-Extramiana et al., 2020), likely due to various environmental changes linked to climate change. The largest decrease in abundance is projected for the equatorial Atlantic Ocean including the GOM and CS, while there could be relative increases at the northern and southern boundaries of the swordfish range (Erauskin-Extramiana et al., 2020). Sea surface temperature is also known to influence seasonal and regional patterns of Atlantic swordfish distribution (equatorial Atlantic Ocean), with a usual southeast summer migration (June through August) and a northwest migration thereafter (Chang et al., 2013).

Higher swordfish catches are associated with oceanic frontal systems, including eddies, ring edges, and surface thermal zones, most likely because their prey species commonly aggregate at these oceanic systems allowing swordfish to use these features to forage (Hoey, 1983; Podestá et al., 1993). Another key oceanographic area for swordfish is the Charleston Gyre region and the Charleston Bump, which are periodically influenced by the presence of eddies and rings developing from the Gulf Stream. This region is an important fishing ground for the U.S. pelagic longline fishery targeting swordfish (Cramer 1996, 2001; Sedberry & Loefer, 2001), and observations of swordfish larvae in thermal fronts created by the Charleston Bump further suggest that these waters might serve as a nursery for swordfish (Govoni & Hare, 2001; Govoni et al., 2003). Hence, it is important to study how climate-driven changes in this region could impact stock recruitment and associated fishing activities.

BAYS tuna – bigeye, albacore, yellowfin, and skipjack tunas

Owing to their preference for warmer and shallower waters (Arrizabalaga et al., 2015; Boyce et al., 2008; Graham & Dickson, 2004), yellowfin tuna and skipjack tuna will likely be able to migrate toward northern latitudes in response to rising sea surface temperatures (Monllor-Hurtado et al., 2017), and evidence suggests that these species may become more abundant across the equatorial (yellowfin tuna) and subtropical (skipjack tuna, and mainly in the GOM and CS) Atlantic Ocean by 2100 (Erauskin-Extramiana et al., 2019).[6] Additionally, modeling results project significant shifts in habitat distribution and abundance in the North Atlantic for albacore tuna (i.e., poleward shift) by 2100, with a global projection for a poleward shift in abundance and a concurrent decline in tropical waters for bigeye tuna[7] by 2100 (Erauskin-Extramiana et al., 2019). Ocean warming and changes in food availability are predicted to reduce suitable habitat for skipjack tuna in tropical waters and thus shift populations northward (Dueri et al., 2014),[8] although Erauskin-Extramiana et al. (2019)[9] predicted no significant shift for skipjack tuna in the eastern Atlantic. In the northern GOM, researchers predict that

[6] Projections on potential future distribution and relative abundance of tunas provided by Erauskin-Extramiana et al. (2019) are exclusively based on environmental change and do not account for other important processes such as population and fisheries dynamics and trophic (i.e., predator-prey) interactions. These additional aspects are relevant since they can amplify the warming signal throughout the food web.

[7] Bigeye tuna have a wider range of tolerance for ambient water temperature compared to other BAYS species, which allow this species to spend more time in deeper, colder waters than other BAYS tunas (Boyce et al. 2008; Lam et al. 2014)

[8] Importantly, and contrary to the projections by Erauskin-Extramiana et al. (2019), results of this study for skipjack tuna are based on more comprehensive modeling integration of the species population dynamic, life history, metabolic rates, and behavioral responses under the combined effects of environmental conditions and fishery exploitations.

[9] Brill et al. (2005) recommended avoiding a classification of "tropical" and "temperate" tunas because these terms usually refer to sea surface conditions, and these species do not live solely at the sea surface.

warmer temperatures will expand habitat and increase abundance of adult skipjack tuna by 2090 (Muhling et al., 2015). Warmer surface waters in the GOM may also favor survival and growth of skipjack larvae, which occur in higher abundances at temperatures above 29°C. Yellowfin tuna and albacore tuna larvae may also benefit from warmer waters in the GOM, albeit to a lesser extent compared to skipjack tuna larvae (Dell'Apa et al., 2018; Luckhurst & Arocha, 2016; Reglero et al., 2014). Mature yellowfin tuna, however, cannot inhabit waters warmer than 30°C (Blank et al., 2002).

Warm-water tunas (i.e., yellowfin tuna and skipjack tuna) and albacore tuna have a low tolerance for reduced DO levels (Arrizabalaga et al., 2015; Brill, 1994; Graham et al., 1989), so post-release mortality may increase (when released back into the water if discarded) under climate change. Specifically, skipjack tuna have a much narrower minimum oxygen range than yellowfin tuna, and albacore tuna are also very intolerant of low DO levels. In contrast, bigeye tuna have a higher tolerance for reduced DO levels than other tunas, due to specific blood-oxygen binding characteristics (Lowe et al., 2000). In the Atlantic, reduced DO levels as well as changes in food density will reduce skipjack tuna habitat suitability in shallow waters (50-150 m depth) (Dueri et al., 2014). Low DO may primarily impact juvenile and larval yellowfin tuna, delaying hatching time and reducing survival, growth rate, and development (Wexler et al., 2011).

Atlantic bluefin tuna

Due to specialized traits that confer a form of warm-bloodedness, Atlantic bluefin tuna (herein, bluefin tuna) can inhabit colder, deeper waters than most other tuna species (Boyce et al., 2008)[10] but become stressed and overheated at higher temperatures (greater than 26-28°C) (Block & Stevens, 2001; Block et al., 2005; Boyce et al., 2008; Sharp & Vlymen, 1978; Teo et al., 2007). Therefore, bluefin tuna are likely to respond to warming surface temperatures by shifting their distribution to more northern and/or deeper waters. Recent results projected a northward shift of bluefin tuna habitat distribution and abundance in the western Atlantic, and no significant shifts in the eastern Atlantic, by 2100 (Erauskin-Extramiana et al. 2019).

Bluefin tuna abundance and habitat may be further influenced by long-term cycles of climate variability in the North Atlantic, which can be affected by climate change. During warmer (positive) phases of the Atlantic Multidecadal Oscillation (AMO), bluefin populations shift toward the northeast Atlantic, whereas during colder (negative) AMO phases, populations shift more toward the southwest (Failletaz et al., 2019).

The effects of climate change on bluefin tuna spawning and larval survival are complex. The western Atlantic bluefin tuna population currently spawns in the northern GOM between March and June (Knapp et al., 2014; Mather III et al., 1995; Muhling et al., 2013; Teo & Block, 2010), triggered by a combination of optimum water temperature (bluefin tuna larvae require temperatures between ~25-28°C and usually cannot survive temperatures above ~29°C (Reglero et al., 2014)) and the presence of oceanographic features that create high biological productivity, including zooplankton prey. Researchers project that warming surface waters in the GOM will drive bluefin spawning earlier in the spring, with a 62% increase in suitable habitat for spawning in early spring (March) and a 39-61% decrease in late spring (May-June) by 2050 (Muhling et al., 2011). Furthermore, rising temperatures will likely shift suitable habitat for bluefin tuna larvae northward (Muhling et al., 2011).

[10] All species in the *Thunnus* genus are characterized by the capacity to retain metabolic heat, or "endothermy." However, Atlantic bluefin tuna are considered the most endothermic species among the *Thunnus* genus (Shiels et al. 2015).

However, climate change may also alter key oceanographic features, complicating the effects of warming. Researchers predict that the LC, which transports warm water into the northern GOM through the current and through the propagation of anticyclonic (clockwise) eddies (Dietrich & Lin, 1994; Mendoza-Alfaro & Alvarex-Torres, 2012), may decline in strength by 25% by 2050 (Liu et al., 2015; Muhling et al., 2015). These oceanographic changes may reduce surface warming in the GOM, potentially mitigating the above predicted effects on spawning grounds and larval habitat (Liu et al., 2012). Substantial weakening of the LC could actually contribute to mitigating regional warming in the northern GOM, which may benefit larval growth and survival, although more studies are needed to analyze the synergistic effect of global warming and reduced strength of the LC (Block, 2005; Lindo-Atichati et al., 2012; Rooker et al., 2012; Teo et al., 2007; Tidwell et al., 2007). Changes in eddy formation may negatively affect breeding behavior and conditions for larval transport and survival (Bakun, 2013; Dell'Apa et al., 2018, Teo et al., 2007; Teo & Block, 2010; Trenkel et al., 2014). In the long term, these climate-driven changes in circulation patterns may also reduce bluefin tuna population size and breeding success if more suitable environmental conditions no longer coincide with more favorable migration and spawning windows (Domingues et al., 2016; Dufour et al., 2010).

Less oxygenated waters will create higher stress for bluefin tuna, which have lower tolerance to reduced DO levels than most other tunas (Brill, 1994). This will increase post-release mortality for this species, which is caught as bycatch in the U.S. pelagic longline fishery (Block et al., 2005; Dell'Apa et al., 2018; Medina et al., 2002; Orbesen et al., 2019; Teo et al., 2007). In the GOM, the compounding effects of potential future northern shift of spawning grounds, warmer water, reduced DO, and extreme oxygen depletion from Mississippi River runoff may put spawning bluefin tuna at particular risk of post-release mortality (Dell'Apa et al., 2018; Medina et al., 2002; Teo et al., 2007). Lower oxygen levels also reduce survival, growth rate, and development of bluefin tuna larvae (Miyashita et al., 1999).

Istiophorid billfishes

Istiophorid billfishes (e.g., Atlantic blue marlin, white marlin, and sailfish) generally prefer shallow depths (Boyce et al., 2008; Kraus & Rooker, 2007),[11] which makes them vulnerable to vertical habitat compression due to shoaling of the OMZ (Prince & Goodyear, 2006; Stramma et al., 2012). Stramma et al. (2012)[12] found that suitable oxygen habitat in the upper surface layer of the tropical East Atlantic declined by 15% between 1960 and 2010. Tagging studies revealed that blue marlin in the eastern Atlantic, where OMZ shoaling is more likely to occur, are limited to shallower waters with higher DO levels (Prince & Goodyear, 2006; Prince et al., 2010). However, similar potential OMZ shoaling/habitat compression dynamics are most likely not present in the western Atlantic. For blue marlin in the GOM, in the absence of a vertically compressed OMZ, warmer surface temperatures may drive deeper vertical migrations of prey species, thus distributing blue marlin populations into deeper waters (Dell'Apa et al., 2018). Billfish prey species are also subject to vertical habitat compression, so billfishes in the eastern Atlantic may see higher foraging opportunities with increased predator-prey

[11] Billfishes are characterized by regional cranial endothermy, which allows them to maintain eye and brain at warmer temperatures than those of ambient water (Block, 1992) and thus help these species to occasionally withstand brief periods of colder waters. Swordfish have similar warm-blooded capabilities that allow them to inhabit cold, deeper waters (Fritsches et al., 2005), although they have a wider range for temperature tolerance than billfishes (Boyce et al., 2008).
[12] Stramma et al. (2012) constructed maps of historical changes (1960-2010) in vertical depths of DO for the 3.5 ml/l hypoxic threshold (i.e., OMZ) for billfishes in the tropical Atlantic, and also compared tagging data on vertical movements of blue marlin in both the western North Atlantic and eastern tropical Atlantic to validate mapping outcomes in regard to changes in species habitat use associated with the OMZ vertical expansion.

interactions in a compressed, shallow space (Prince & Goodyear, 2006, 2007; Stramma et al., 2012).[13] This could make both billfishes and their prey species more susceptible to interactions with surface fishing gear (e.g., pelagic longline fisheries) in this region (Prince et al., 2010; Stramma et al., 2012). Higher CPUEs may be misleading in this scenario because they reflect changes in species density, not true species abundance. Additionally, billfish post-release mortality will likely be higher under climate change because reduced DO levels, in conjunction with warmer waters, cause high metabolic stress in billfishes (Prince et al., 2010). Lower DO conditions also reduce billfish larval growth, as has been observed for sailfish (Simms et al., 2010).

Climate-driven changes in ocean circulation will likely affect billfish feeding and spawning. The LC is projected to decrease in strength by 25% by 2100, likely affecting egg and larval transport and mortality, and overall billfish reproductive success and future population size (Dell'Apa et al., 2018; Trenkel et al., 2014).

Ectothermic sharks

Ectothermic shark species[14] are "cold-blooded" animals unable to control body temperature independently of ambient water temperature. Because large pelagic sharks are generally ectotherms, water temperature is a key environmental factor controlling their movements and metabolism (Bernal et al., 2012; Carlson et al., 2004; Schlaff et al., 2014). Many of these sharks, notably blue sharks and oceanic whitetip sharks, are known to behaviorally thermoregulate through daily and seasonal migration patterns through the water column and to warmer or cooler regions. Thus, warming temperatures are likely to alter pelagic shark geographic and vertical distributions (Bernal et al., 2012; Schlaff et al., 2014). Oceanic whitetip sharks, which prefer warmer (20-26°C) (Carlson & Gulak, 2012; Howey-Jordan et al., 2013; Musyl et al., 2011; Tolotti et al., 2015) and shallower (less than 125 m) waters (Howey-Jordan et al., 2013; Musyl et al., 2011), may see geographic expansion due to warming surface waters.

The dusky shark, a species of great conservation concern in the Northwest Atlantic and GOM,[15] is commonly found in warmer (24-26°C) and shallower (20-75 m) waters and appears to not exhibit daily changes in depth or temperature ranges (Hoffmayer et al., 2014).[16] The dusky shark was also reported as a species highly likely to undergo a shift in distribution in the western North Atlantic due to climate change (Hare et al., 2016). Of particular concern is evidence that warming waters are altering juvenile dusky shark migration patterns, creating a temporal mismatch between their arrival to the Mid-Atlantic Shark Closed Area[17] and the dates when the closure goes into effect (Bangley et al., 2020).

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[13] In fact, larger average sizes for landed Atlantic sailfish were found in both the eastern tropical Atlantic and eastern tropical Pacific compared to fish caught in western, non-compression areas in these basins, which was interpreted as the result of enhanced predator-prey interactions (Prince & Goodyear, 2006; Prince et al., 2010).

[14] Within the list of commonly caught (including as bycatch) pelagic sharks in the Atlantic, ectothermic species include: blue shark, oceanic whitetip shark, dusky shark, bigeye thresher shark, night shark, silky shark, sandbar shark, tiger shark, smooth hammerhead, scalloped hammerhead, and great hammerhead.

[15] Based on the most recent stock assessment, the dusky shark population is overfished and experiencing overfishing owing to fishing pressure (i.e., bycatch and recreational fishing) and the species life history characteristics (e.g., slow growth rate, late maturity, low fecundity) (Kilfoil, 2017; Romine et al., 2009; SEDAR, 2016).

[16] Although spending most of the time at or below these shallow waters on the continental shelf, dusky sharks can occasionally dive to deeper waters outside the shelf edge (maximum recorded depth at 573 m – Hoffmayer et al., 2014).

[17] The Mid-Atlantic Shark Closed Area was established in 2005 to close a coastal area off North Carolina to bottom longline fisheries seasonally (from January 1 through July 31) to protect overwintering habitat for juvenile sharks.

The bigeye thresher shark, considered the most vulnerable species to pelagic longline fisheries in the Atlantic due to its low productivity (Cortés et al., 2015; Fernandez-Carvalho et al., 2015), exhibits atypical thermal behavior for an ectothermic shark.[18] As a result, bigeye thresher sharks may be less affected by projected ocean warming. More research is needed to determine how potential changes in bigeye thresher stock distribution, both geographically and vertically, could affect interactions with pelagic fisheries.

The scalloped hammerhead shark inhabits waters warmer than 22°C (Castro, 2011; Schulze-Haugen & Kohler, 2003) and can have a deeper distribution than other pelagic sharks: ~500 m with occasional dives to ~1000 m (Compagno, 1984; Klimley, 1993, Jorgensen et al., 2009). Juvenile scalloped hammerhead sharks migrate to significantly deeper and colder waters than adults at night (though still within the upper 50 m depth), which may make them more susceptible to interactions with pelagic longline fisheries operating at night in deeper waters within shallow sets targeting swordfish (Santos & Coelho, 2018). More studies are needed on how climate-driven changes in temperature and DO levels may affect habitat and depth distribution of juvenile and adult scalloped hammerhead sharks and how these changes will affect vulnerability to fishing.

As with tunas and billfishes, pelagic sharks are vulnerable to higher metabolic stress and thus higher post-release mortality under reduced DO conditions (Carlson & Parson, 2001; Schlaff et al., 2014). Hammerhead sharks are among the most vulnerable to capture stress and post-release mortality (Gallagher et al., 2014a), whereas blue sharks tend to have lower at-vessel mortality rates (Campana et al., 2016), particularly when caught in deeper waters (Gallagher 2014b). However, the vertical distribution of blue sharks is also affected by DO-based habitat compression (i.e., OMZ shoaling) in the tropical East Atlantic (Vedor et al. 2021), similar to the scenario described above for istiophorid billfishes (Prince et al., 2010; Stramma et al., 2012), which will make this species more susceptible to interactions with pelagic longline fishing gear at the surface in this region.

Climate-driven warming and reduced DO conditions are likely to be particularly harmful for juvenile pelagic sharks, which are most sensitive to low-oxygen conditions. The bays, estuaries, and coastal waters that function as nursery areas for many juvenile sharks are subject to more extreme warming and low-DO conditions due to shallower depths and surface runoff-driven eutrophication (Froeschke et al., 2010; Oh et al., 2017; Ward-Paige et al., 2015). In Chesapeake Bay, the most important nursery area for sandbar sharks in the western Atlantic, projected climate-driven changes in temperature, salinity, and DO levels are likely to significantly reduce suitable nursery habitat by 2100, with resultant negative impacts on population growth (Crear et al., 2020).

Endothermic sharks

Endothermic shark species[19] are "warm-blooded" animals capable of regulating their body temperature independently of ambient water temperature. This may make them less susceptible to climate-driven

[18] The bigeye thresher shark is suspected to possess regional endothermy due to the presence of what appears to be a vascular counter-current heat exchanger (i.e., *rete mirabile*) in their orbital section that could function as a mechanism to retain metabolic heat in the brain and eyes (Weng & Block, 2004). This is reflected by this species diving regularly to greater depths than any other ectothermic pelagic sharks and by exhibiting daily vertical distribution through the water column. It is therefore considered both an epipelagic and mesopelagic species in tropical and subtropical ocean waters (Fernandez-Carvalho et al., 2015).

[19] Within the list of commonly caught (including as bycatch) pelagic sharks caught in the Atlantic, endothermic species include: white shark, longfin mako shark, shortfin mako shark, porbeagle shark, and common thresher shark.

changes in ocean temperature (Bernal et al., 2012; Dickson & Graham, 2004).[20] However, juveniles are less able to regulate their body temperatures and thus may experience a larger change in habitat and depth distribution as a result of climate change.

For shortfin mako sharks, juveniles show a clear preference for warmer waters (~22-27°C) and exhibit daily shifts to maintain water temperatures (Vaudo et al., 2016). When temperatures exceed 28°C, such as within the GOM, they dive to deeper waters, suggesting that ocean warming may expand juvenile shortfin mako distribution to deeper depths.[21] As for adults, projections indicate a decrease in core shortfin mako habitat of ~25% by 2100 in the eastern North Pacific (Hazen et al., 2013). Climate impacts for the western Atlantic have not been projected.

Common thresher sharks inhabit waters between 16-21°C and migrate between shallower depths (0-200 m) at night and cooler, deeper waters during the day, likely following prey species (Cao et al., 2011; Cartamil et al., 2011). This may mean they are more susceptible to fisheries interactions occurring at night in surface waters (e.g., certain pelagic longline fisheries targeting swordfish).

Porbeagle sharks have the narrowest thermal preference range of endothermic sharks in the western Atlantic, and are primarily caught in colder waters between 5 and 10°C (Campana & Joyce, 2004),[22] although juveniles spend most of their time in waters between 6 and 20°C (Skomal et al., 2021). Porbeagle sharks forage in colder frontal zones in the spring, where they are commonly caught by Canadian pelagic longline fisheries (Campana & Joyce, 2004). Despite this preference for cold water, tagging studies show that adult females might routinely migrate to southern, warmer waters in the Gulf Stream and Sargasso Sea, suggesting that this area might be a possible pupping ground for porbeagle sharks in the North Atlantic (Campana et al., 2010), although this theory has been recently questioned due to results of tagging studies suggesting that this migratory behavior also exists in juveniles (Skomal et al., 2021). Based on known thermal preferences and climate projections, this colder-water shark may shift its distribution northward or to deeper waters in response to ocean warming, but more studies are needed to model how porbeagle populations and their prey species could be impacted by climate change.

Finally, and similarly to ectothermic sharks, endothermic sharks may also experience increased fishing mortality rates due to climate-driven reductions in DO levels and related increases in post-release mortality (Bernal et al., 2012; Campana et al., 2016; Dapp et al., 2016; Skomal & Mandelman, 2012). Due to generally higher metabolic and oxygen requirements compared to ectothermic species (Bernal et al., 2012), it is also highly likely that endothermic sharks will experience higher post-release mortality from pelagic and bottom longline fisheries due to a higher probability of asphyxiation from remaining on a line for prolonged periods (Campana et al., 2016).

[20] However, their horizontal (i.e., geographic) and vertical (i.e., depth) distributions might change in response to habitat changes in prey species (Sergeant et al., 2014).
[21] Assuming water warming would not occur exclusively at the ocean surface.
[22] This study considers sea surface temperature, as opposed to ambient water temperature at fishing depth which would be more appropriate to infer the species' thermal preference.

BUILDING RESILIENCE TO CLIMATE CHANGE IMPACTS

Key attributes of climate resilience

Over the past few decades, fisheries management and science have focused on sustainability, namely providing for today's needs while sustaining fish populations, protecting habitats, and ensuring people who depend on fishing can maintain their livelihoods. More recently, particularly as our understanding of how climate change will affect fisheries has increased, the focus is expanding to incorporate principles for building climate resilient systems that are not only sustainable but also can resist, recover from, or adapt and transform in the face of change or shocks (Holsman et al., 2019; Ojea et al., 2017; Pinsky and Mantua, 2014). Climate resilience builds on the principles of sustainable management with an increased emphasis placed on measures that help systems buffer against climate change, or otherwise respond through forms of adaptive management. Doing so requires considering the links between socioeconomic and ecological systems, prioritizing long-term strategic thinking that takes future conditions into account, and implementing measures that help systems withstand uncertain or unforeseen climate-related risks (Burden and Battista, 2019). To achieve these ends, it is worthwhile to have well-articulated principles and guidance for managers and stakeholders to help understand the approaches necessary to foster this resilience.

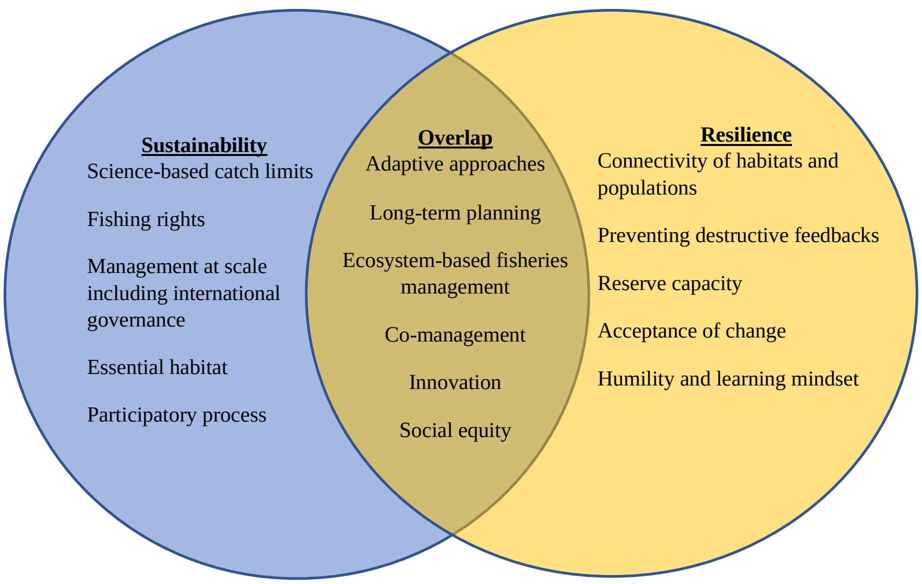

Figure 1: Management approaches based on sustainability and resilience, and their overlap. Sustainable fisheries management approaches include, but are not limited to, science-based catch limits, secure fishing rights, management at the appropriate scale, protection of essential habitat, and participatory policy-making processes. Resilience focuses on ensuring a level of redundancy and connectivity of habitats and populations, preventing negative impacts from becoming widespread through a system, managing conservatively with reserves, and developing a learning mindset that acknowledges and accepts change and uncertainty, among other considerations. Fisheries management elements that promote both sustainability and resilience include, but are not limited to, adaptive approaches, long-term planning, ecosystem-based fisheries management, co-management, innovation, and ensuring social equity in decision-making.

Science, management, and governance do not represent three distinct areas of resilience, as each is supported by and reinforces the others within the fishery. Science includes analysis and collection of data to inform and advise decision-making (e.g., fishery independent/dependent surveys, stock assessments, etc.). Management refers to the decision-making and implementation of rules and regulations for a fishery (e.g., allocation, catch limits, seasons, etc.). Governance refers to the laws and institutions of a fishery system (e.g., the Magnuson-Stevens Act, the U.S. Fishery Management Council system, ICCAT, etc.).

As we have discussed in preceding sections, climate change has already affected marine environmental conditions in the Atlantic and HMS distribution and abundance, and it is likely to have even more profound effects in the future, many of which are likely unknown to us at this time. These changes will result in mismatches between jurisdictions and management measures and the actual stock abundance and distribution, which could result in unintended overfishing, conflicts over access and allocation, and the need for industry to adjust fishing and business practices to remain viable. These impacts—and the uncertainty in predicting them—create an urgent need to manage not only for sustainability but also for resilience. While it is beyond the scope of this report to cover all the aspects of science, management, and governance needed to achieve resilient fisheries, we highlight a few key attributes below.

Science that fosters climate resilience

Investments in science will be critical for increasing fishery resilience. Better data collection in domestic and international fisheries (both commercial and recreational), including quantification of catch (including bycatch and discards), and more intensive monitoring of stock abundance and distribution and ecosystems will be needed to promote connectivity and inform adaptive approaches (Pinsky & Mantua, 2014). More research will be needed to understand the drivers of changes to distribution and productivity so that management measures have meaningful projections to follow and consequently avoid overfishing or spatial misalignment of management measures as stocks shift. Pairing research on complex species-environment relationships (including tipping points and feedback loops) with climate projections on various timescales can aid in scenario planning and developing a portfolio of climate-resilient management approaches (Holsman et al., 2019). Incorporating social and economic data will be crucial to understand opportunities, risks, and responses to change, and assess management scenarios for trade-offs (Holsman et al., 2019; Pinsky & Mantua, 2014). Additionally, diagnosis of the resilience status of supporting marine ecosystems and fishery management institutions will be required, since understanding the attributes that make a fishery resilient, and whether any are deficient or missing, is the first step toward building resilience (Ojea et al., 2017). This includes the drivers of resilience for any species, as well as the causes of gaps in resilience attributes in both the ecosystem and in the fishery management institutions.

Management that fosters climate resilience

Management can support climate resilience by recognizing the importance of previously under-acknowledged factors, such as age and genetic structure of different stocks, predator-prey interactions, and the conservation of key habitats within the ecosystem in order to protect system health and diversity (Free et al., 2020; Ojea et al., 2017; Sumaila & Tai, 2020). A key strategy for building ecological resilience is implementing best practices in fisheries management and effectively eliminating or reducing other stressors (e.g., overfishing, bycatch, habitat degradation, etc.), as well-managed fisheries will likely be more resilient to the impacts of climate change (Free et al., 2020;

Gaines et al., 2018; Pinsky & Mantua, 2014; Sumaila & Tai, 2020). Ecosystem-based fisheries management (EBFM) is an approach for addressing such issues that takes a holistic overview of the ecosystem and multiple fisheries sectors. By accounting for the different factors and interactions within the ecosystem rather than just individual species, management measures are more likely to promote resilience both for the ecosystem and the stocks it contains.

Management can also consider risk and uncertainty and integrate these considerations into a flexible and adaptive decision-making process. Management Strategy Evaluation (MSE) is a process that can be used to determine which approaches would best meet pre-defined objectives for a fishery. This may take the form of risk-averse harvest control rules (HCRs) and policies that allow fishermen to switch target species and fishing strategies in response to real-time information about changes in stock status (Gaines et al., 2018; Kritzer et al., 2019; Pinsky & Mantua, 2014).

Active participation of all affected stakeholder groups in the decision-making process can aid the design of practical and effective measures, foster buy-in, and reduce tension or resistance over policy decisions. Such an effort may include representation of actors from throughout the supply chain and other fishing sectors (such as recreational and artisanal) in advisory roles/committees and management meetings, with a particular focus on ensuring that the perspectives of marginalized groups are heard and valued (Biggs et al., 2012; Cochrane et al., 2011; Bennett, 2018). The exclusion of marginalized groups from decision-making may increase their vulnerability to climate change effects (Bennett, 2018).

Developing forward-looking policies that anticipate future changes will be an important component of climate resilient management. Considering future ecological states and socioeconomic consequences of future change will help to ensure that adaptation of management institutions is happening at a pace matching on-the-water change. Inevitably, some climate change effects will be unforeseen, and in this case, management should attempt to build measures robust to potential sources of climate-related risk and uncertainty. Examples include responsive HCRs that automatically adjust fishing pressure to match environmental conditions (Kritzer et al., 2019) and diverse portfolios of target species that allow fishermen to shift their focus as accessible stocks shift (Cline et al., 2017; Ojea et al., 2017).

More dynamic approaches could be promising for building resilience in fisheries. In Maxwell et al. (2015), dynamic ocean management is defined as "management that rapidly changes in space and time in response to changes in the ocean and its users through the integration of near real-time biological, oceanographic, social and/or economic data." Dynamic management approaches can incorporate the real-time, small-scale changes that culminate in large-scale shifts over time resulting from climate change (Lewison et al., 2015). Such approaches could improve performance around catch balancing efforts, including bycatch minimization, and increase climate-readiness. Technologies such as electronic monitoring (EM) and electronic reporting (ER) can provide catch data that can be integrated with oceanographic data to provide critical information for fishermen and scientists. Emerging EM/ER systems with real-time wireless transmission capabilities could give fishing fleets, managers, and scientists faster and unprecedented access to data to facilitate more dynamic approaches to management.

Governance that fosters climate resilience

When looking at the laws and institutions of a fishery system, several principles are key for promoting resilient governance. A governance system that is appropriately scaled to the ranges of the fish stock and the geographies of dependent stakeholders is essential for effective management of fisheries, including for achieving socioeconomic goals. Adequate science-based management is necessary at the relevant scales of the fishery (e.g., local, national, and international) (Biggs et al., 2012; Ojea et al., 2017; Pinsky & Mantua, 2014). Agreements and entities that span political boundaries will need to cover the existing range of the stock and adapt to the future range and future participants in the fishery as climate change causes stocks to shift.

Polycentric governance refers to a system with several different, generally nested centers of decision-making authority. Such a system can help increase resilience, particularly if the system is structured in a way that helps increase accountability and foster decentralized decision-making. Polycentric systems can provide opportunities for enhanced learning and broader levels of participation in governance at scale (Biggs et al., 2012). Where it is feasible and appropriate for the stock and community, governance systems should facilitate co-management to further promote stewardship of resources by communities. Local and regional fisheries stakeholders with more direct linkage to the resource can provide the basis for research and experimentation that provide valuable insights and can potentially be scaled across the system (Biggs et al., 2012).

Transparency and inclusiveness are key aspects of governance systems that foster resilience. Creating transparent decision-making processes in the development of rules and regulations (including the scientific justifications for decisions) and involving relevant affected parties can increase legitimacy, compliance, and trust (Bennett, 2018). As discussed in the management section, this transparency must also include a participatory process for stakeholders – including solicitation of comments, holding meetings, and consulting stakeholder groups on decisions. This should include all stakeholder groups. Ensuring broad participation also helps to link knowledge to action and promotes social equity and participatory processes (Biggs et al., 2012).

CONCLUSION

Climate change is already impacting HMS and will continue to do so at an increasing rate. The impacts of climate change are complex and affect HMS differently. However, even with this complexity, enhancing actions that help achieve sustainability and build the resilience capacity of the existing management regimes and scientific bodies for the Atlantic and GOM HMS fisheries will improve the ability to adapt to these impacts. In some cases, we could even achieve better outcomes than seen today.

To achieve a resilient future, expanding and building on our scientific understanding of how climate change will affect the marine environment of the Atlantic Ocean and surrounding seas, and consequently how HMS and HMS fisheries respond and adapt, will be essential for identifying solutions. More information is needed on vulnerable species including those that are currently data-limited, as well as improved data collection across all fisheries that interact with HMS. Management approaches that are ecosystem-based, forward-looking, adaptive/dynamic, inclusive, and hedge against unknown and unforeseen risks can increase resilience to climate change impacts. Electronic technologies present an opportunity to gather new insights, with the potential to greatly improve monitoring and data collection across many fisheries and opening new doors to science and management that is more responsive to changing ocean conditions. Lastly, among other attributes, governance that fosters resilience is appropriately scaled to cover the geographic range of the stock, has several different centers of decision-making at the appropriate levels, ensures participation and transparency in decision-making, and provides for continual learning and experimentation.

While this report discusses some science, management, and governance factors that can foster resilience, it does not address the social and economic resilience of HMS fisheries. A focused assessment of how climate change will affect HMS fishing communities and seafood markets is a critical next step for a holistic plan of how to build the resilience capacity. Climate change will affect communities differently. Understanding these disparate impacts alongside historical equity issues is necessary for crafting solutions that are fair and just.

Fishermen, policymakers, scientists, environmental groups, and others can work toward achieving a more profitable, sustainable, and resilient HMS fisheries. This collaboration needs to focus on approaches that are adaptive, well-informed, and have the buy-in of stakeholders, including fishermen. In doing so, we will develop the knowledge and tools for the successful management of transboundary stocks in a changing world – a model that can be replicated and adapted for other fisheries. Through such an effort, it is possible for fisheries to thrive for generations to come.

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