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Climate Impacts On Spatiotemporal Habitat Usage Of Mid-Atlantic Fishes

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Climate Impacts on Spatiotemporal Habitat Usage of Mid-Atlantic Fishes

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by

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APPROVAL PAGE

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This dissertation is dedicated to the one most impacted by all of my late nights and weekends spent working… Kini, the sweetest little cat in the world. Coming home to you was the best part of my day.

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ABSTRACT

Climate change has altered marine environments, most notably by increasing water temperatures and reducing dissolved oxygen concentrations. These persistent changes have impacted the phenology and spatiotemporal habitat usage of mobile species, often through distributional shifts poleward or to deeper water. Climate-driven distributional shifts have been documented for numerous species inhabiting the Atlantic Ocean along the US East Coast, a region disproportionately affected by climate change. Adjacent estuaries are experiencing similar alterations to their physical environments and biotic community composition. Many estuarine species are seasonal residents and changes to environmental conditions within an estuary can result in altered usage and residence times. The Chesapeake Bay is one such estuary experiencing these climate-associated effects. The bay serves as an important habitat for a diverse array of seasonally resident marine and estuarine taxa, providing valuable foraging, refuge, and spawning grounds. Concurrent with physical changes, survey data have indicated decreases in relative abundance of many finfishes. However, environmental drivers associated with these declines have not been fully quantified. To evaluate the role of climate change on spatiotemporal habitat usage of Chesapeake Bay fauna, state-of-the-art statistical models were applied to several long-term monitoring data sets.

Changes in Chesapeake Bay inhabitance by a suite of seasonally resident species were explored by evaluating estuarine-coastal ocean exchange and comparing the patterns to a more northern estuary, Delaware Bay. Relative habitat utilization of Chesapeake Bay declined for most species, while utilization patterns for Delaware Bay were largely constant or increasing over time. Broad-scale, multispecies analyses of relative habitat utilization time series revealed that the North Atlantic Oscillation, a signal of long-term warming, was an important driver of Chesapeake Bay exchange.

Baseline habitat associations for several seasonal resident species in Chesapeake Bay were quantified through the development of ecological niche models. Model output indicated that impacts of climate change on environmental conditions of the bay, including continued increases in temperature and hypoxic volume, will likely exacerbate the decline in relative abundance. The niche envelopes were paired with an estuarine-carbon-biogeochemical regional ocean model to derive estimates of habitat suitability. The temporal patterns in habitat suitability did not match abundance trends, indicating that dynamics outside of the physical conditions of Chesapeake Bay are likely driving the decreased utilization of this estuary.

Finally, the traditional mark-recapture modeling framework that includes catch-and-release fishing was extended to a subannual, multi-stock, spatially and temporally explicit version that allowed for simultaneous estimation of key parameters, including mortality rates and occupancy probabilities. Model estimated instantaneous natural mortality increased over time within Chesapeake Bay, particularly for older fish, but has not changed appreciably outside of the estuary, supporting previous findings of increased disease-associated mortality with age, and a possible role of climate change-associated suboptimal environmental conditions. Estimated occupancy probabilities exhibited differences in likelihood of estuarine inhabitance based on age, season, and producer region.

Collectively, the results demonstrate heterogeneous changes in spatiotemporal habitat use of several Mid-Atlantic species on various scales. This information can be used by managers tasked with temporally and spatially dynamic policy development in a changing environment.

AUTHOR'S NOTE

Chapters 2-4 of this dissertation have been prepared as manuscripts for peer-reviewed scientific journals. Therefore, the formatting for each chapter follows the guidelines of the scientific journal to which the manuscript was, or will be, submitted.

The citations are as follows:

Chapter 2
Schonfeld AJ, Gartland J, Latour RJ. 2022. Spatial differences in estuarine utilization by seasonally resident species in Mid-Atlantic Bight, USA. Fisheries Oceanography. 31(6):615–628. doi:10.1111/fog.12611.

Chapter 3
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Chapter 4
Schonfeld AJ, Wilberg MJ, Nehemiah S, Latour RJ. *In prep*. Use of multi-source tagging data to estimate regional age-varying striped bass mortality and movement.

Climate Impacts on Spatiotemporal Habitat Usage of Mid-Atlantic Fishes

CHAPTER 1

Introduction

Anthropogenic greenhouse gas emissions have resulted in unprecedented atmospheric warming (IPCC 2021) that has changed global climate patterns and increased sea surface temperatures in all ocean basins of the world (Levitus et al. 2000). Rates of warming have not been spatially uniform, however, and the Atlantic Ocean has been disproportionately affected compared to other ocean basins (Levitus 2005; Cheng et al. 2020). More specifically, sea surface temperatures along the northwestern Atlantic shelf (i.e., off the northeast coast of the United States) have increased at a rate that is three times faster than the global average (Saba et al. 2016). This region, the Northeast US Large Marine Ecosystem (NES LME), comprises three Ecological Production Units (EPU); listed south to north, those EPUs are the Mid-Atlantic Bight, Georges Bank, and the Gulf of Maine (Clark and Brown 1977; Lucey and Nye 2010; Lucey and Fogarty 2013).

Fishes are ectotherms, meaning that their internal body temperature is regulated by the surrounding environment. While these animals are unable to actively regulate their body temperatures, the physiological processes of each species are optimized within a preferred thermal range (Pörtner and Farrell 2008; Sunday et al. 2012; Freitas et al. 2015). Suboptimal environmental conditions, including temperatures that exceed their ideal range, cause fish to reallocate energy to stress responses, rather than towards growth and reproduction (Wendelaar Bonga 1997; Barton 2002). Motile marine species, therefore, shift poleward or to deeper water to remain within their preferred temperature range and optimize metabolic processes (Murawski 1993; Walther et al. 2002; Parmesan and Yohe 2003; Perry et al. 2005).

Due to the rapid warming documented in the NES LME, numerous studies have evaluated the role of climate change on the marine species inhabiting this region, and several have described shifts in the distributions of individual species, as well as the overall community composition. In species-specific investigations, significant shifts in spatial distribution associated with changing water temperature have been found for Atlantic herring (*Clupea harengus;* Thorne and Nye 2021), Atlantic mackerel (*Scomber scombrus;* Overholtz et al. 2011; Thorne and Nye 2021), black sea bass (*Centropristis striata*), and scup (*Stenotomus chrysops;* Bell et al. 2015). Further, an investigation of changes in the spatial distribution of 36 fish stocks found that two-thirds (i.e., 24 stocks) have shifted significantly poleward or to deeper water in association with long-term warming (Nye et al. 2009). At the community scale, species assemblages in the subunits of the NES LME more closely resemble the composition of the adjacent southern subregion during the 1960s, rather than that of the subregion itself (Lucey and Nye 2010).

The observed trends in these distributional shifts are expected to continue. Studies coupling species ecological niche models with climate projections have predicted northward shifts in the distribution of most species inhabiting the Mid-Atlantic Bight (Kleisner et al. 2017). Further, a vulnerability assessment conducted within the NES LME found that climate vulnerability is high or very high for approximately half of the species (Hare et al. 2016).

The directionality and extent of the shifts in assemblages of these individual EPUs are not homogenous throughout the entirety of the NES LME, even among species with shared life history characteristics. In the southern zone, and especially in the Mid-Atlantic Bight, species assemblages associated with shallower water have been found to shift poleward, while in the northern region, species have tended to shift west-southwest (Kleisner et al. 2016). This indicates that the influence of climate change varies spatially within the ecosystem.

While temperature is often a main focus of climate change research, the physical impacts extend beyond warming. Rising water temperatures result in a decline in dissolved oxygen concentrations, as dissolved oxygen has a lowered solubility in warmer waters. These reductions in dissolved oxygen have been suggested as an important driver of distributional shifts of marine species (Pörtner and Knust 2007; Deutsch et al. 2015). Other expected effects of climate change include increases in precipitation frequency and intensity, extreme climatic events, and sea level rise (Karl and Trenberth 2003; Trenberth 2005; Sun et al. 2007; Trenberth 2007), all of which can influence salinity and circulation patterns in marine environments. The oceanic uptake of atmospheric carbon dioxide also leads to changes in seawater chemistry and acidification (i.e., pH is lowered; Doney et al. 2009; Sokolova et al. 2016).

The effects of climate change on the NES LME are not limited to the continental shelf waters, but extend to adjacent estuarine systems as well. Indeed, the cumulative impacts of climate change are expected to be greatest in shallow, near-coastal and estuarine habitats (Najjar et al. 2010; Wetz and Yoskowitz 2013). An analysis of over 150 estuaries along the Australian coast found that the rate of warming was greater than that observed in the atmosphere and ocean (Scanes et al. 2020). Along the NES LME, warming has been documented within many estuarine environments, including Great Harbor (Woods Hole, Massachusetts; Nixon et al. 2004), Narragansett Bay (Rhode Island; Oviatt 2004; Collie et al. 2008), Long Island Sound (Connecticut and New York; Howell and Auster 2012), the Hudson River (New York; Seekell and Pace 2011), Delaware Bay (Delaware; Oleynik 2020), and Chesapeake Bay (Maryland and Virginia; Ding and Elmore 2015; Hinson et al. 2021; Tian et al. 2021).

Climate change has impacted the community composition within these estuarine environments in ways that mirror responses documented in the coastal ocean. In Narragansett Bay, there has been a supersession of resident species by seasonal migrants and a shift in dominance from demersal to pelagic fishes (Oviatt 2004; Collie et al. 2008). Further, there have been appreciable phenological impacts, with significant decreases in residence times for most cold-water species and significant increases for warm-water species (Langan et al. 2021). In Long Island Sound, there has been a significant decline in catches of cold-adapted species and a significant increase in catches of warm-adapted and subtropical species (Howell and Auster 2012). Thus, the impacts of warming on the fauna of estuarine systems reflect those documented coastwide, and globally: distributional shifts and subsequent alterations in community composition.

The Chesapeake Bay is the largest estuary within the NES LME, as well as the continental US. The bay is partially-mixed with estuarine circulation primarily driven by freshwater inputs (Pritchard 1956; Kemp et al. 2005), and is characterized by a deep central channel (20-30 m) surrounded by shallower (primarily < 10 m) environments (Boicourt et al. 1999; Kemp et al. 2005). The Chesapeake Bay serves as an important habitat for diverse marine and estuarine species. While a small number of resident species inhabit this estuary year-round, it is also utilized by an array of boreal, temperate, and subtropical species seasonally, typically from spring (March to May) through fall (September to November), as valuable foraging, refuge, and spawning habitat (Murdy et al. 1997).

The Chesapeake Bay is also a critical nursery habitat for several taxa, as it promotes increased growth, density, and survival of juveniles (Beck et al. 2001; Nagelkerken et al. 2015; Schloesser and Fabrizio 2019). Similarly, the Chesapeake Bay spawning stock of striped bass (*Morone saxatilis*), a high-value anadromous species, contributes disproportionately to the migrant coastal stock (Koo 1970; Fabrizio 1987; Hasegawa et al. 2022). The importance of the bay ecologically is also reflected economically, as several valuable recreational and commercial fisheries operate within this estuary (Kirkley et al. 2005; Lellis-Dibble et al. 2008; NMFS 2022).

However, the Chesapeake Bay is subjected to many of the same physical impacts of climate change as documented for the whole of the NES LME.

As described, Chesapeake Bay water temperatures are increasing (Ding and Elmore 2015; Hinson et al. 2021). There has also been a significant increase in hypoxic volume (Hagy et al. 2004; Murphy et al. 2011). Hypoxia is an especially acute issue in the bay during summer when warm, low salinity surface waters overlay cooler, more saline waters. The resultant strong pycnocline prevents mixing and resupply of dissolved oxygen to the bottom, contributing to hypoxia at depth (Boicourt 1992; Murphy et al. 2011; Scully 2013). Long-term fisheries-independent survey data have indicated a decrease in abundance of up to 90% for several species within the bay in recent years (Buchheister et al. 2013), although the factors driving these declines have not been fully evaluated.

Understanding potential shifts in distribution is pivotal for successful management of these species. Fishers follow the distributional shifts of their target species, but more slowly and lagged in time (Pinsky and Fogarty 2012), and conflicts over harvest allocation have already occurred, due to spatial changes in species' abundances (Dubik et al. 2019). With increased information on expected distributional changes, however, the socioeconomic ramifications of climate change and shifts in species distribution on fishers could be mitigated (Rogers et al. 2019). While extensive work has been conducted on the impacts of climate change on the physical environment of the Chesapeake Bay, and on the distribution and community composition of marine species along the coast of the NES LME, relatively little attention has been dedicated to the influence of climate change on the fauna of the bay. Thus, this dissertation seeks to address this knowledge gap and to provide important baseline information in a changing environment. The specific objectives of this body of work include:

(1) evaluating the role of environmental factors in driving the relative habitat usage of Chesapeake Bay compared to the coastal ocean and a more northern estuary,

(2) quantifying the ecological niches of a suite of species to obtain time series of habitat suitability in Chesapeake Bay and assessing the role of hypoxia,

(3) deriving estimates of age-, time-, and region-specific rates of mortality and occupancy for striped bass, a high-value and iconic species of Chesapeake Bay.

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CHAPTER 2

Spatial differences in estuarine utilization by seasonally resident species in Mid-Atlantic Bight, USA

Abstract

Climate-driven distributional shifts have been well-documented for fishery resources along the East Coast of the United States, yet little attention has been given to adjacent estuarine systems. The Chesapeake Bay is the largest estuary in the continental US and serves as important habitat for a diversity of fishes and invertebrates, many of which are seasonal residents. Survey data indicate that relative abundance of finfish in Chesapeake Bay has diminished substantially, while coastwide stock status has remained unchanged. In response to warming, seasonal estuarine residents may remain in coastal waters or inhabit a northerly estuary, but the extent to which changing environmental conditions may drive exchange between the coastal ocean and estuarine systems remains unresolved. This study analyzed data collected from 2008-2019 by three fisheries-independent trawl surveys to explore temporal patterns and associated environmental drivers of the estuarine-coastal ocean exchange in the Mid-Atlantic for eight economically and ecologically important species. Relative habitat utilization of Chesapeake Bay declined for most species, while utilization patterns for Delaware Bay were largely constant or increasing over time. Broad-scale, multispecies analyses of relative habitat utilization time series revealed that the North Atlantic Oscillation (NAO) was an important driver of Chesapeake Bay exchange, but that average Apr/May coastal ocean bottom temperature was significant for Delaware Bay. Collectively, the results demonstrate that several Mid-Atlantic species have altered their estuarine habitat use over time, climate drivers associated with estuarine-coastal ocean exchange operate on different time scales, and that the impacts of warming within the Mid-Atlantic vary spatially.

Introduction

Ocean basins serve as the predominant sink of the energy accumulated in response to anthropogenic greenhouse gas emissions, which has led to global increases in sea surface temperature (IPCC, 2015; Levitus et al., 2000). The Atlantic Ocean has been disproportionately impacted by warming (Cheng et al., 2020; Levitus et al., 2005), with temperatures increasing on the northwestern Atlantic shelf at rates nearly three times the global average (Saba et al., 2016). Adjacent estuaries along the east coast of the US also have been impacted by climate change, with systemic warming documented in Narragansett Bay (Collie et al., 2008; Langan et al., 2021; Oviatt, 2004), Long Island Sound (Howell & Auster, 2012), and Chesapeake Bay (Ding & Elmore, 2015; Hinson et al., 2021; Tian et al., 2021).

The Chesapeake Bay is the largest estuary in the continental United States and serves as an important habitat for an array of fish and invertebrate species that represent a variety of life history modes and occupy unique ecological niches. Several of these species support economically valuable recreational and commercial fisheries, as well as a host of non-market ecosystem services (Kirkley et al., 2005; Lellis-Dibble et al., 2008; NMFS, 2018). Although several species are resident to this estuary, the bay is also utilized seasonally by a diverse assemblage of boreal, temperate, and subtropical species as a foraging, spawning, nursery, and refuge habitat (Murdy et al., 1997).

Most of the seasonally resident species in Chesapeake Bay immigrate into the estuary during spring (Mar-May) and emigrate to the coastal ocean in the fall (Sep-Nov). The effects of climate change on this ecosystem have not only led to increased water temperatures year round, but have also impacted the seasonal temperature cycles that are associated with the timing of migratory patterns. Specifically, the rate of warming in the spring has increased (Friedland &

Hare, 2007), and the earlier physical onset of spring, defined by the thermal environment, is leading to altered timing of associated spring phenological events for many marine species (Burrows et al., 2011; Parmesan & Yohe, 2003; Thackeray et al., 2010; Thomas et al., 2017). These changes likely will affect residence times of migratory species, as has been documented in Narragansett Bay (Langan et al., 2021), and may ultimately lead to modifications of their seasonal usage of the Chesapeake Bay.

Numerous studies conducted along the northwestern Atlantic shelf have documented significant shifts in distribution of individual marine species and assemblages poleward or to deeper waters in response to warming temperatures (e.g., Bell et al., 2015; Kleisner et al., 2016; Lucey & Nye, 2010; Nye et al., 2009; Pinsky & Fogarty, 2012). For seasonal estuarine residents, the combination of distributional shifts, faster spring warming, and earlier spring onset may result in seasonal migrations that bypass Chesapeake Bay in favor of a more northern estuary. Furthermore, the lowered solubility of dissolved oxygen in warmer water temperatures is expected to cause an increase in the frequency, volume, and onset of hypoxia in this estuary (Irby et al., 2018; Najjar et al., 2010; Tian et al., 2021). This phenomenon has been suggested as a critical factor driving distributional shifts in other ecosystems (Deutsch et al., 2015; Pörtner & Knust, 2007), and fish hypoxia avoidance behaviors have been documented within Chesapeake Bay (Buchheister et al., 2013) and elsewhere (Eby & Crowder, 2002).

The Chesapeake Bay is considered a nursery habitat for many species due to the provisions afforded in support of increased density, growth, and survival for juveniles (Beck et al., 2001; Nagelkerken et al., 2015; Schloesser & Fabrizio, 2019). However, continued use of this estuary in light of the emerging suboptimal environmental conditions resulting from climate change could create negative impacts on vulnerable life stages that may cascade to population-level effects. The availability of more suitable nursery habitats is considered a key factor in driving the distributional shifts of demersal fishes in other coastal systems (Rijnsdorp et al., 2009). As there are several estuaries north of the Chesapeake Bay, estuarine-dependent Mid-Atlantic fishes may modify their seasonal migrations to inhabit a more amenable environment. Alternatively, some adult fishes less reliant on an estuarine system may forgo seasonal residency and instead remain in the coastal ocean.

For some fish species, declines in catch-per-unit-effort (CPUE) of up to 90% have been documented in Chesapeake Bay (Buchheister et al., 2013). However, these same precipitous drops in relative abundance are not apparent in coastwide stock assessments, which often indicate that populations are not overfished and overfishing is not occurring. The mismatch in realized relative abundance trends between localized and regional scales indicates that there may be ecological factors driving an exchange of these populations between the Chesapeake Bay and adjacent ecosystems, which have yet to be quantified. The term “exchange” is used throughout this manuscript to refer to within-stock habitat partitioning that occurs when a proportion of the population of a given marine species enters an estuary after overwintering in the ocean.

To gain insights into the interannual patterns of relative habitat usage and the potential drivers of exchange between the coastal ocean and Chesapeake Bay, this study paired catch data on several species collected from fisheries-independent surveys that were complementary in both space and time: a spring (Apr/May) survey conducted in nearshore coastal waters coupled with a Chesapeake Bay summer (May-Sep) survey provided measures of relative abundance for the same populations lagged in time. To explore spatial differences along the coast, analogous methods were applied to summer (Jun-Sep) survey data collected within Delaware Bay, a more northern estuary, and the same spring coastal survey. Overall, there were two objectives in this investigation: (1) to create time series of relative habitat usage representing estuarine-coastal ocean exchange for a suite of sampled species, and (2) to characterize the common trends shared amongst these time series with the goal of identifying the broad-scale factors associated with these trends. Results from this study can be used to better understand the nuances of distributional shifts of ecologically and economically important seasonal estuarine residents within the Mid-Atlantic.

Methods

Field sampling

Data for this study span 2008-2019 and were collected by the Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAP, May-Sep, 2008-2018), the Northeast Area Monitoring and Assessment Program (NEAMAP, Apr/May, 2008-2016, 2018-2019), and the Delaware Bay Adult Trawl Survey (DBATS, Jun-Sep, 2008-2019). All three programs are fisheries-independent bottom trawl surveys; NEAMAP and ChesMMAP are conducted by the Virginia Institute of Marine Science, while DBATS is administered by the Delaware Division of Fish & Wildlife. ChesMMAP data are restricted to 2018 due to a gear and vessel change in following years, while NEAMAP data excludes 2017 because of incomplete sampling during that year.

ChesMMAP samples at approximately 80 sites throughout the mainstem of Chesapeake Bay bimonthly from Mar-Nov each year. Sites are selected using a stratified random design based on depth (3.0-9.1 m, 9.1-15.2 m and > 15.2 m) and latitude (Figure 1). A four-seam bottom trawl (13.7 m headrope length with 7.6 cm codend mesh) is deployed for 20 minutes in the direction of the current at each site (Latour et al., 2003). NEAMAP samples the nearshore continental shelf waters from Cape Hatteras, North Carolina, to Martha’s Vineyard, Massachusetts. Two cruises are conducted annually, during spring (Apr/May) and fall (Sep/Oct), with 150 sites sampled each cruise. Sites are selected using a stratified random design, with stratification based on latitudinal/longitudinal regions and depth (6.1-12.2 m and 12.2-18.3 m south of Montauk, New York; 18.3-27.4 m and 27.4-26.6 m in Block Island Sound and Rhode Island Sound; Figure 1). At each site, a 400x12 cm (fishing circle circumference), three-bridle, four-seam bottom trawl with a 2.54 cm lined codend is towed for 20 minutes (Bonzek et al., 2017). DBATS conducts monthly cruises nearly year-round (Mar-Dec) where nine fixed stations are sampled throughout Delaware Bay (Figure 1). This survey utilizes a 9.3 m (headrope length) trawl with 5.1 cm codend mesh, and tow duration is 20 minutes (Greco, 2017).

Each survey records site variables and hydrographic measurements (e.g., bottom temperature) at every sampling location. Catches are sorted by species, with ChesMMAP and NEAMAP separating size-classes within species, if distinct. Specimens are enumerated, and individual length measurements are recorded. ChesMMAP subsamples five individuals of each species and size-class for age determination (Latour et al., 2017; Latour et al., 2003), while NEAMAP subsampling of species and size-classes for aging is restricted to those species with a Fisheries Management Plan (FMP; Bonzek et al., 2017).

Survey data on eight species (five demersal species, one pelagic, one elasmobranch, and one arthropod; Table 1) were included in this study, due to the ecological and economic importance of these taxa in the Mid-Atlantic Bight: Atlantic croaker (*Micropogonias undulatus*), scup (*Stenotomus chrysops*), spot (*Leiostomus xanthurus*), summer flounder (*Paralichthys dentatus*), windowpane flounder (*Scophthalmus aquosus*), weakfish (*Cynoscion regalis*), clearnose skate (*Raja eglanteria*), and horseshoe crab (*Limulus polyphemus*).

Data filtering

NEAMAP and the estuarine surveys (i.e., ChesMMAP or DBATS) provide measures of the same populations lagged in time. The NEAMAP data were spatially restricted to include only sites sampled between central New Jersey and Cape Hatteras, North Carolina, given that these boundaries encompass a biotic ecotone (Stratton, 2017). The species-specific datasets from each survey were filtered to remove catch data on young-of-year (YOY) animals, as only individuals actively undergoing migration (Murdy et al., 1997; Swan, 2005) were of interest. Age data are not routinely collected by DBATS, so ChesMMAP data were used to create an age-length key based on 5 mm length bins for each species, and these were applied to the DBATS length-frequency data to remove YOY specimens from survey collections. No survey captured horseshoe crab less than 20 mm prosoma width, which is the maximum size for YOY animals (Sekiguchi et al., 1988). While DBATS does not measure clearnose skate, the lengths observed in ChesMMAP and NEAMAP far exceeded the threshold of 33 cm total length to be considered age one (Packer et al., 2003).

The survey datasets for each species were also filtered to include only the key habitat regions, and thereby the most informative data, by removing locations where the species of interest was not expected to occur based on known life history characteristics and general absence in survey samples (Latour et al., 2017). Due to differences in sampling designs and the magnitude of catch rates, the definition of uninformative samples varied by survey. For ChesMMAP, these were defined as latitudinal regions in which less than approximately 5% of tows encountered the species of interest and contributed less than 5% of the total catch of the target species. For NEAMAP, the restriction was based on the joint region and depth strata, and the threshold for designation as uninformative was less than 2% for both frequency of encounter and overall catch. Due to the lower number of seasonal DBATS samples, sampling locations were excluded if they contributed less than 2% of the total catch or less than 5% and had a low number of positive occurrences. This filtering approach resulted in datasets that varied in size by species and survey.

Relative habitat usage

Species-specific catch data from spring NEAMAP and each estuarine survey's summer cruises were randomly paired within year, such that the maximum number of pairs per year was equal to the minimum number of tows in either survey during that year. Data on relative habitat usage ($H_{s,i,y}$) were generated as the ratio of catches from each paired tow:

$$H_{s,i,y} = \frac{E_{s,i,y}}{E_{s,i,y}+N_{s,i,y}}, \tag{1}$$

where $E_{s,i,y}$ represents the number of species s captured in the i^{th} estuarine tow in year y, and $N_{s,i,y}$ is the number in the complementary NEAMAP tow. Although there are differences in capture efficiency between NEAMAP and the estuarine surveys, the sampling gears and vessels have not changed during the time periods included in this investigation and thus support the assumption of constant gear efficiency within each survey. While the absolute value of the ratio is not meaningful, the trend of the ratio over time is indicative of changes in estuarine utilization as compared to the coastal ocean.

Generalized linear models (GLMs, McCullagh & Nelder, 1989) that included a fixed categorical year covariate were applied to estimate a time series of annual relative habitat usage:

$$g(H_{s,i,y}) = a + \alpha_{s,y} + \varepsilon_{s,i,y} \tag{2}$$

where g is the link function, a is the intercept representing year 2008, $\alpha_{s,y}$ is the estimated mean effect level y of the year covariate for species s and $\varepsilon_{s,i,y}$ is the error vector. Additionally, in the

Delaware Bay models, the station sampled by DBATS was included as a random effect to account for the fixed station sampling design.

The response data were assumed to follow a beta (BE) binomial (BI) distribution (Miller, 2013), which is a joint distribution in which the species-specific probability from the binomial distribution, π_s, follows a beta distribution. That is, $H_s \sim BI(n_s, \pi_s)$, where n_s is the known number of observations of species s and $\pi_s \sim BE(\alpha_s, \beta_s)$, such that $\alpha_s = \frac{\mu_s}{\sigma_s}$, $\beta_s = \frac{1-\mu_s}{\sigma_s}$, $0 < \mu_s < 1$, and $\sigma_s > 0$ (Rigby et al., 2019).

The process of random-stratified pairing of an estuarine dataset with the NEAMAP dataset and subsequent model fitting was repeated 1000 times. The final time series of annual indices of relative habitat usage for each species was calculated as the yearly means over the full set of model estimates. Subsequently, beta regression analyses (Ferrari & Cribari-Neto, 2004) were applied to each of these 16 final time series (i.e., eight species and two estuaries) to identify significant trends in the relative habitat usage.

Drivers of Ecosystem Exchange

Dynamic factor analysis (DFA) was used to estimate the underlying shared patterns among the time series of relative habitat usage. DFA is a multivariate analysis technique in which the common trends in temporal variation of *n* time series are quantified through linear combinations of *m* hidden random walks, where $1 \leq m < n$. The general form of a DFA is as follows (Holmes et al., 2012; Zuur et al., 2003a):

$$\mathbf{y}_t = \mathbf{\Gamma}\boldsymbol{\alpha}_t + \mathbf{D}\mathbf{x}_t + \boldsymbol{\varepsilon}_t \text{ where } \boldsymbol{\varepsilon}_t \sim MVN(0, \mathbf{R}) \tag{3}$$

$$\boldsymbol{\alpha}_t = \boldsymbol{\alpha}_{t-1} + \boldsymbol{\eta}_t \text{ where } \boldsymbol{\eta}_t \sim MVN(0, \mathbf{Q}),$$

where $\mathbf{y}_t$ is the z-scored (i.e., standardized to a mean of zero and variance of one) vector ($n \times 1$) of time series of estimated relative habitat usage for n species in year t, $\boldsymbol{\alpha}_t$ is the vector ($m \times 1$) of m common trends, $\mathbf{\Gamma}$ is the matrix ($n \times m$) of species-specific factor loadings on the common trends, $\mathbf{x}_t$ is the vector ($q \times 1$) of q covariates, $\mathbf{D}$ is the matrix ($n \times q$) of covariate effects, and $\mathbf{R}$ and $\mathbf{Q}$ are the variance-covariance matrices associated with the observation error vector $\boldsymbol{\varepsilon}_t$ ($n \times 1$) and process error vector $\boldsymbol{\eta}_t$ ($m \times 1$), respectively.

While $\mathbf{Q}$ is constrained to the identity matrix to ensure the model is identifiable, $\mathbf{R}$ may take several forms and is used to define the noise component of the model (Zuur et al., 2003a). The three forms of the variance-covariance matrix explored were diagonal with equal variance and zero covariance, diagonal with unequal variance and zero covariance, and nondiagonal with equal variance and equal covariance.

Twelve annualized covariates were considered as explanatory variables in the DFA model fitting, 10 of which were classified as climate variables, one as a biological covariate, and one as a metric of exploitation. Four of the climate variables considered reflect processes of broad spatial scales: the Atlantic Multidecadal Oscillation index (AMO; https://psl.noaa.gov/data/correlation/amon.us.data), the Gulf Stream Index (GSI; Bastille et al., 2021), the winter North Atlantic Oscillation index, defined as the average value from Dec-Mar (NAO; https://psl.noaa.gov/data/correlation/nao.data), and winter NAO lagged by one year. The remaining six climate variables reflect localized conditions: the sea surface temperature anomaly of the Mid-Atlantic Bight (Bastille et al., 2021), average bottom temperature and bottom salinity from the NEAMAP spring cruise (Apr/May) in the restricted geographical range, average winter-spring (Jan-May) precipitation and cooling degree days of the season, defined as the summation of the difference between average daily temperature and 18.3°C from six NOAA stations (the

Naval Air Station Oceana in Virginia Beach, VA, the Norfolk International Airport, VA, the Baltimore Washington International Airport, MD, the Ocean City Municipal Airport, MD, the Wilmington-New Castle Airport, DE, and the Atlantic City International Airport, NJ; https://www.ncdc.noaa.gov/cdo-web/), and the year-day of spring onset defined as the first day in a sequence of eight days that the sea surface temperature within the geographic range of the coastal waters considered exceeded a threshold temperature of 8°C (Thomas et al., 2017; https://www.ncei.noaa.gov/access). The biological metric was the small-large copepod abundance anomaly in the Mid-Atlantic Bight (Bastille et al., 2021) and exploitation was represented as the sum of recreational and commercial species-specific landings (lbs) coastwide for all species except windowpane flounder, which is managed as two stocks and thus New England landings were excluded (https://www.fisheries.noaa.gov/foss).

DFA model selection was based on Akaike's information criterion (AIC; Akaike 1973; Burnham & Anderson 2002) corrected for small sample sizes (AICc) and species-specific fit ratios, defined as $\sum \hat{\varepsilon}_t^2 \,/\, \sum \hat{y}_t^2$, where smaller values indicate better model fit (Zuur et al., 2003b). Models were first fitted with 1, 2, or 3 common trends for each of the variance-covariance error structures and no covariates. Model parameterizations where the mean of fit ratios was ≥ 0.6 or ΔAICc (i.e., AICc – minimum AICc) was greater than 10 were eliminated from consideration. The remaining parameterizations were then fitted with a single covariate or two covariates from different variable classifications. Final model selection was based on a combination of ΔAICc and mean fit ratio. All statistical analyses were performed using the R software program (v4.0.3, R Core Team, 2020). Packages 'gamlss' (Rigby & Stasinopoulos, 2005), 'betareg' (Cribari-Neto & Zeileis, 2010), and 'MARSS' (Holmes et al., 2012) were accessed to fit the beta-binomial time series models, the beta regressions, and DFAs, respectively.

Results

Time Series of Relative Habitat Usage

When comparing Chesapeake Bay and the coastal ocean, the beta regressions fit to the mean ratios of relative habitat usage (Figure S1) indicated a significant trend in relative habitat usage over time for six of the eight species: Atlantic croaker ($p < 0.001$), spot ($p < 0.001$), summer flounder ($p < 0.001$), weakfish ($p = 0.01$), clearnose skate ($p = 0.01$), and horseshoe crab ($p = 0.003$). The relationship was negative for each of these species, indicating a multispecies decrease in the usage of Chesapeake Bay relative to the coastal ocean over time. Compared to the baseline relative habitat usage value for Chesapeake Bay in 2008, seven species displayed largely negative changes, particularly since 2012 (Figure 2A). Although windowpane flounder exhibited an increase in relative usage of Chesapeake Bay for each year compared to 2008, peak estuarine usage occurred in 2010 followed by a notable decrease thereafter.

Only three species exhibited significant changes in relative habitat usage when comparing Delaware Bay to the coastal ocean over time: Atlantic croaker ($p = 0.002$), windowpane flounder ($p = 0.027$), and horseshoe crab ($p < 0.001$). Of these significant relationships, the trends for horseshoe crab and windowpane flounder were positive, and the trend for Atlantic croaker was negative. Five of the species displayed an increase in relative usage of Delaware Bay compared to the 2008 baseline for the majority of years (Figure 2B). Collectively, the general lack of significant relationships across species suggests fewer changes in the relative habitat usage of Delaware Bay when compared to Chesapeake Bay.

Time Series of Annualized Covariates

For the broad scale climate variables considered, NAO, NAO-lag-1, and GSI generally increased over time, whereas AMO displayed relatively large fluctuations but remained stable

(Figure 3A). The localized climate covariates were generally more variable than the broad scale metrics (Figure 3B). Average springtime bottom temperature from NEAMAP cruises, sea surface temperature anomaly in the Mid-Atlantic Bight, and average winter-spring precipitation have all steadily increased since 2014, 2013, and 2012, respectively. In contrast, average springtime bottom salinity from NEAMAP cruises increased from 2008-2016, then decreased in the most recent years. Cooling degree days increased rapidly between 2008 and 2011 and has fluctuated at these higher levels since. Spring onset has varied over time without a clear trend. The copepod abundance anomaly had a negative trend through 2017, but increased in recent years, while combined recreational and commercial landings of the species included in this investigation increased to a peak in 2013 and steadily declined after (Figure 3C).

Dynamic Factor Analysis: Drivers of Ecosystem Exchange

The final DFA model chosen for the Chesapeake Bay-coastal ocean exchange included one common trend, a diagonal and equal variance-covariance structure, and winter NAO as a covariate. The common trend peaked to its highest values during the first few years of the time series, before steadily declining from 2011-2014 and remaining low since 2014 (Figure 4A). Six of the species exceed the factor loading threshold of 0.2, and thus loaded strongly and positively on the common trend (Figure 4B). The usage of Chesapeake Bay by scup, windowpane flounder, and clearnose skate was significantly and negatively associated with NAO (Table S1).

For the Delaware Bay-coastal ocean comparison, the most empirically supported DFA model had two common trends, a diagonal and equal variance-covariance structure, and the average springtime coastal bottom temperature from NEAMAP cruises as a covariate. The first common trend showed an increase throughout the span of the time series (Figure 5A). Five species loaded strongly and positively and one strongly and negatively on the first common trend

(Figure 5B). The second common trend increased over the first two years of the time series, then followed a parabolic shape, decreasing until 2016, after which it increased (Figure 5C). Six species loaded strongly and positively on the second common trend (Figure 5D). Summer flounder, weakfish, clearnose skate, and horseshoe crab loaded strongly on both common trends while the remaining four species loaded strongly on one common trend. Average bottom temperature from the NEAMAP spring cruises had a significant and negative impact on the usage of Delaware Bay by weakfish and clearnose skate (Table S2). The model fits for both the Chesapeake Bay- and Delaware Bay-coastal ocean comparisons were generally good (Figures 6A and 6B). For the Chesapeake Bay DFA, only the time series of horseshoe crab relative habitat usage was considered to have a poor fit, with a fit ratio of 0.67. The remaining time series had fit ratios ranging from 0.05 (Atlantic croaker) to 0.3 (scup). The Delaware Bay DFA fit ratios were from 0.08 (spot) to 0.29 (Atlantic croaker).

Discussion

This investigation provides a quantitative evaluation of the patterns of estuarine utilization and ecosystem exchange for a suite of key fisheries resources in the southern Mid-Atlantic Bight. Gaining insight into the relative habitat usage of estuarine and coastal environments for these species contributes to the understanding of both their population dynamics and possible responses to climate change. Together, commercial landings of these species generate more than $20 million in revenue annually, and five of these species are among the most targeted by recreational fishers in the Mid-Atlantic (NMFS, 2018); thus an improved understanding is critical for the continued delivery of these desirable ecosystem services. Further, the information generated from this study can serve as a valuable baseline when evaluating the overall changes in the use of these three ecosystems over time, and may prove useful when considering benefits derived from these habitats, as these trends in relative usage identify systems that are seemingly becoming more (when positive) and less (when negative) favorable to these taxa.

A decrease (increase) in relative habitat usage of a given estuary can be attributed to one of four possible scenarios: (1) a decrease (increase) in estuarine relative abundance while coastal relative abundance is constant, (2) coastal relative abundance decreases (increases) at a slower rate than estuarine relative abundance, (3) an increase (decrease) in relative abundance in the coastal ocean while estuarine relative abundance remains constant, or (4) a relative abundance increase (decrease) in the estuary that is outpaced by an increase (decrease) in relative abundance in the coastal ocean. Given that the same NEAMAP datasets were used to evaluate exchange for both Chesapeake Bay and Delaware Bay, any changes in coastal abundance, including potential phenological shifts of earlier estuarine entrance affecting the availability to the NEAMAP spring survey, were captured in both ratios. If changes in relative habitat usage were being driven purely by a signal in coastal relative abundance, then the time series of relative habitat usage in the two estuaries would have been similar, which was not found, except for Atlantic croaker. Thus, it can be concluded that the observed trends in relative habitat usage were being driven by changes in proportional relative abundance within the estuaries. For the species analyzed, relative habitat usage of Chesapeake Bay compared to the coastal ocean has decreased since 2008, while relative usage of Delaware Bay by those taxa has either increased or remained constant.

Of the eight species included in this investigation, the stock status of five species (scup, summer flounder, windowpane flounder, clearnose skate, and horseshoe crab) was recently assessed as healthy at the regional scale (ASMFC, 2019a; NEFSC, 2020; Sosebee, 2020; Terceiro, 2021a, 2021b) and the remaining three (Atlantic croaker, spot, weakfish) displayed population characteristics that caused management concern (ASMFC, 2019b, 2021a, 2021b). This provides important context for the trends in relative habitat usage and further supports the conclusion that the trends are not driven by coastal abundance. Of the five species with healthy coastwide stock status, three species (summer flounder, clearnose skate, and horseshoe crab) displayed a significant decline in relative habitat usage in Chesapeake Bay, while the same declining relationship was not found in Delaware Bay relative habitat usage. Atlantic croaker was the only species that had a significant trend in the same direction (declining) in relative habitat usage in both estuaries. As abundance levels are of concern for Atlantic croaker, and associated management efforts have been implemented (ASMFC, 2021a), it is possible that the trends in relative habitat usage of this species is being driven by the dynamics of the coastwide stock.

Previous studies have documented significant northward shifts in the distributions of many species in the Mid-Atlantic Bight, including several evaluated in this study (e.g., Bell et al., 2015; Lucey & Nye, 2010; Nye et al., 2009). Additionally, seven of the eight species evaluated were considered to have a high potential to exhibit distributional shifts in response to climate change; only horseshoe crab was deemed to have low potential (Hare et al., 2016). These distributional changes likely would cause a decline in the localized abundance of these species in the vicinity of the mouth of Chesapeake Bay. As such, these shifts may have driven the trends of decreasing relative usage of Chesapeake Bay, as overwintering individuals would likely have to migrate well past this estuary to encounter amenable conditions for the summer season.

Additionally, long-term warming, rather than annual temperature fluctuations, has been found to drive the northward distributional shift of marine taxa in the northwest Atlantic Ocean (Nye et al., 2009). While NAO has not yet been implicated as the primary driver responsible for these shifts in the near coastal waters of the Mid-Atlantic region, NAO was found to be positively associated with the overall trend shared among several broad-scale climatic indices, which was significantly correlated with shifts in species assemblages (Lucey & Nye, 2010). Further, NAO was significantly correlated with a shift in an estuarine community in New England from primarily demersal to dominated by pelagic species (Collie et al., 2008), and was significantly related to the community composition and seasonal usage of estuarine environments by juvenile fishes elsewhere (Attrill & Power, 2002). NAO has also been shown to impact the population dynamics of several marine species by shaping recruitment, abundance, and predatory interactions (Drinkwater et al., 2003; Ottersen et al., 2001, 2010).

In recent decades, the NAO index has been primarily in a positive phase, which is associated with warmer conditions in the Mid-Atlantic (Hurrell, 1995; Hurrell et al., 2003; Visbeck et al., 2001). This investigation found that NAO was associated with exchange between the Chesapeake Bay and coastal ocean, while average spring bottom temperature from NEAMAP cruises was related to the Delaware Bay-coastal ocean exchange. Thus, the climatic variables related to relative habitat usage in the two estuaries are operating on different temporal scales: NAO is a signal of longer-term warming, while average spring bottom temperature from NEAMAP cruises represent annual fluctuations. For individuals in the vicinity of Delaware Bay, spring temperature may serve as a signal to begin estuarine migration, or to remain in coastal waters if temperatures are higher than preferred. The significant relationship between spring bottom temperatures measured during NEAMAP cruises and the Delaware Bay-coastal ocean exchange underscores the importance of local-scale processes driving relative habitat usage of this estuary.

NAO is a mesoscale climate pattern impacting multiple environmental factors, including wind speed and direction, precipitation, storm intensity, circulation patterns, and heat transport in the ocean (Hurrell, 1995; Hurrell et al., 2003). Thus, despite the difference in temporal scales, the significant covariates in each model were measures of water temperature, albeit indirectly for NAO. Overall, the results of this investigation contribute to the growing body of information on the influences of climate on marine taxa in the Mid-Atlantic by finding that NAO likely is an important driver of estuarine utilization at the boundaries of a species' range (i.e., edge-effects), while local-scale drivers influence relative estuarine usage within its range.

The varying degrees of site fidelity or natal homing exhibited by the species included in this investigation introduces added complexity when attempting to evaluate the impact of changes in relative habitat usage on overall population dynamics. Four of the species in this investigation (scup, windowpane flounder, weakfish, and horseshoe crabs) spawn within estuaries (Able & Fahay, 2010; ASMFC, 2019a). The reliance upon an estuarine environment to complete their reproductive cycle denotes some degree of estuarine dependency (Able, 2005; Whitfield, 2020). However, evidence suggests that scup spawn only in estuaries north of this study region (Able & Fahay, 2010; Eklund & Targett, 1990; NEFSC, 1999) and both windowpane flounder and weakfish can also spawn in ocean waters (Able & Fahay, 2010). The degree to which weakfish exhibit site fidelity is still not fully resolved, as some studies have found high levels of spawning site fidelity (e.g., Thorrold et al., 2001), while others have found low levels or evidence of a single panmictic population (Graves et al., 1992; Krause et al., 2020). Similarly, the level of site fidelity exhibited by horseshoe crabs is still unclear, as there is evidence that populations within estuaries are genetically distinct, indicating high rates of natal homing (Pierce et al., 2000). However, multiple long-term tagging studies have found that while horseshoe crabs remain close to their tagging sites for several days, the fraction recovered at the same spawning site the subsequent year diminished greatly, demonstrating a lack of site fidelity across years (McGowan, 2018; Swan, 2005).

In general, if strong site fidelity is a life history characteristic of a species, then the changes in estuarine relative habitat usage would likely be reflected in the future abundance of the overall coastwide population. That is, declines in relative usage of Chesapeake Bay would likely indicate a future decline in the localized coastal population of that species. However, changing environmental conditions could lead to improved survival and recruitment in the local population of a more northern estuary. In Delaware Bay, for example, this study has found that the relative habitat usage of horseshoe crabs has increased significantly over the time series. Thus, if horseshoe crabs do display strong natal homing, then the increase could result in the horseshoe crab population increasing overall. For windowpane flounder, studies have not yet been conducted on the site fidelity of the Mid-Atlantic or New England stocks, and so it is unclear if changes in relative habitat usage can be interpreted as influencing trends in the overall population.

Future work on estuarine fidelity of these non-obligate estuarine users (i.e., those that are not fully dependent upon estuaries; Able, 2005; Whitfield, 2020) would help contextualize the results of this study and the implications for the coastwide populations. An additional area of focus for future work is on the spawning location of coastal shelf spawners, as juvenile abundances of summer flounder and spot, two of three coastal shelf spawners included in this study, have declined in recent years (Tuckey & Fabrizio, 2021), while coastwide assessments have not found similar declines in adult biomass (Able et al., 2017; ASMFC, 2021b; NEFSC, 2019), although spot harvest levels have recently triggered management actions. Finally, while this investigation quantified ratios of relative habitat usage by pairing a spring coastal and summer estuarine survey, evaluating the within-season egress of migrant species back into coastal waters and the role of bay-specific covariates, such as measures of habitat quality (e.g., temperature or hypoxic volume) or fishing pressure, in driving that migration represent a valuable area of future research.

While this study cannot support explicit inference on abundance trends for the eight species included in an absolute sense, this work provides valuable information on relative habitat utilization and ecosystem exchange in the southern Mid-Atlantic Bight. For example, the relative usage of Delaware Bay by horseshoe crabs has increased significantly, while declining significantly within Chesapeake Bay. The trends can be used to provide a “ranking” of the relative usage of each ecosystem, with Delaware Bay usage the strongest, followed by the coastal ocean, and finally Chesapeake Bay.

Water temperatures are expected to continue to rise, and thus these general trends in relative habitat usage likely will continue. It is expected that Chesapeake Bay will be utilized less frequently, as important fisheries resources will instead inhabit coastal waters or more northerly estuaries. Shifting distributions of living marine resources have already caused management conflicts (Dubik et al., 2019), and the impacts of range changes on estuarine utilization will only further the discourse. This study contributes to the growing body of information focused on characterizing the dynamics in the Northwest Atlantic Ocean along the US continental shelf by resolving trends in relative habitat utilization and ecosystem exchange for two major estuaries in the southern Mid-Atlantic Bight.

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Tables

TABLE 1. Characterizations of species evaluated in this investigation. A. croaker: Atlantic croaker; S. flounder: summer flounder; W. flounder: windowpane flounder; C. skate: clearnose skate; H. crab: horseshoe crab

Species	**Family**	**Description**	**Spawning location** Able & Fahay, 2010	**Timing of spawning** Able & Fahay, 2010	**Focal Stock Range**	**Stock Status**
A. croaker	Sciaenidae	Demersal finfish	Ocean	Summer to Fall	ME - FL	Of concern ASMFC, 2019a
Scup	Sparidae	Demersal finfish	Estuaries	Spring to Summer	MA - NC	Not overfished, overfishing not occurring Terceiro, 2021a
Spot	Sciaenidae	Demersal finfish	Ocean	Fall to Winter	ME - FL	Of concern ASMFC 2021b
Summer Flounder	Paralichthyidae	Demersal finfish	Ocean	Fall	ME - NC	Not overfished, overfishing not occurring Terceiro, 2021b
W. Flounder	Scophthalmidae	Demersal finfish	Estuaries & ocean	Spring and Fall	MA - NC	Not overfished, overfishing not occurring NEFSC, 2020
Weakfish	Sciaenidae	Pelagic finfish	Estuaries & ocean	Spring to Summer	NY - NC	Depleted ASMFC, 2019b
C. skate	Rajidae	Elasmobranch	Unknown	Egg deposition in spring Packer et al., 2003	MA - NC	Not overfished, overfishing not occurring Sosebee, 2020
H. Crab	Limulidae	Marine arthropod	Estuaries ASMFC 2019a	Spring to Summer ASMFC, 2019a	ME - FL	Not overfished, overfishing not occurring ASMFC, 2019a

Note: Information on timing of spawning reflects the season(s) during which active spawning occurs within the Mid-Atlantic region. Each species included in this investigation is managed as one or more unit stocks, and focal stock range provides the geographic bounds of the unit stock evaluated in this study. Stock status provides the most recent classification given of the stock as determined by the governing management body.

Figures

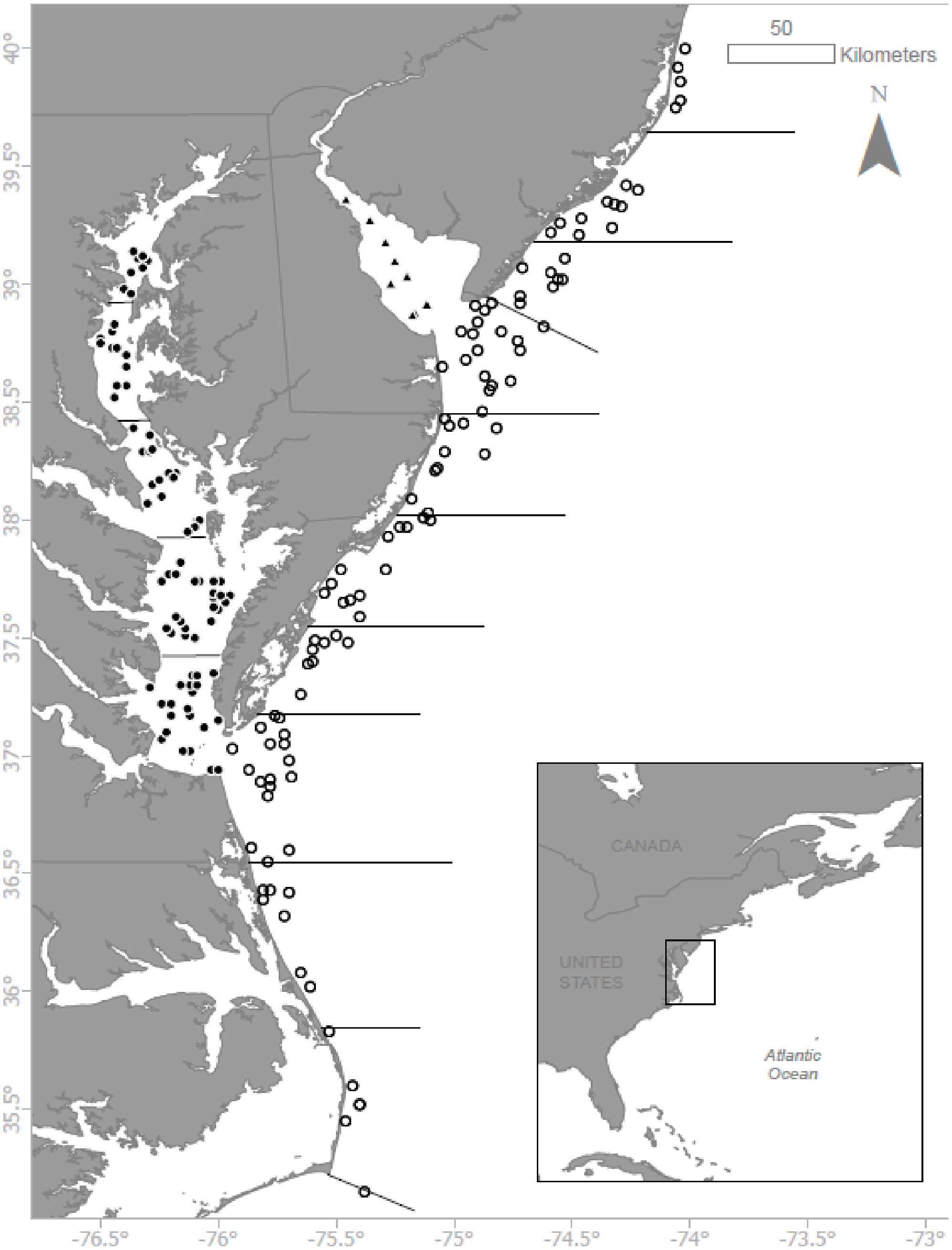
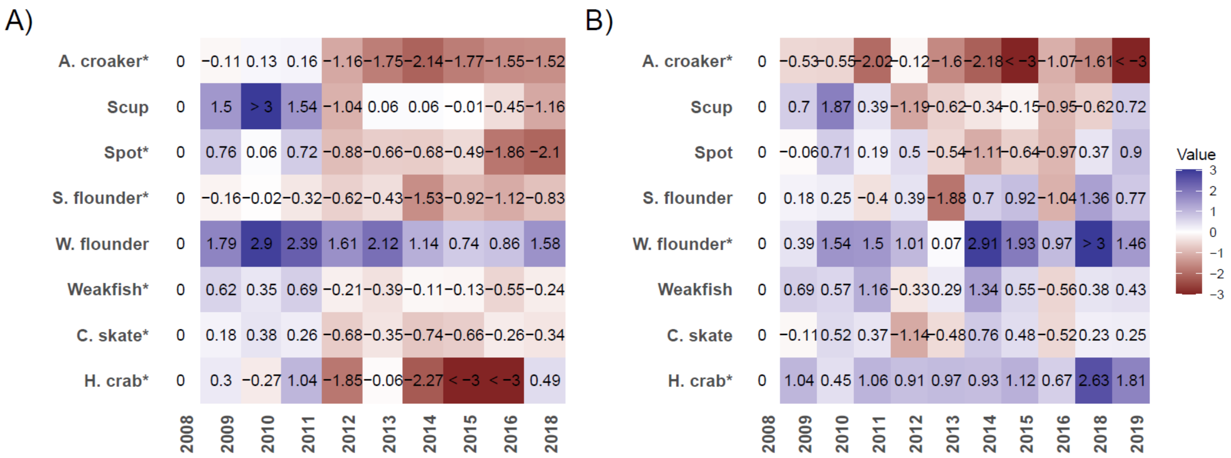


FIGURE 1 Sampling sites for the fisheries independent trawl surveys. The filled circles are the sampling locations from a representative Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAP) cruise (July 2018). The open circles are trawl sites from a representative Northeast Area Monitoring and Assessment Program (NEAMAP) cruise (spring 2018). The triangles are the nine fixed stations sampled by the Delaware Bay Adult Trawl Survey (DBATS). Horizontal lines delineate the sampling regions of ChesMMAP (lines within Chesapeake Bay) and NEAMAP (along US coastal waters).



A)

	2008	2009	2010	2011	2012	2013	2014	2015	2016	2018
A. croaker*	0	−0.11	0.13	0.16	−1.16	−1.75	−2.14	−1.77	−1.55	−1.52
Scup	0	1.5	> 3	1.54	−1.04	0.06	0.06	−0.01	−0.45	−1.16
Spot*	0	0.76	0.06	0.72	−0.88	−0.66	−0.68	−0.49	−1.86	−2.1
S. flounder*	0	−0.16	−0.02	−0.32	−0.62	−0.43	−1.53	−0.92	−1.12	−0.83
W. flounder	0	1.79	2.9	2.39	1.61	2.12	1.14	0.74	0.86	1.58
Weakfish*	0	0.62	0.35	0.69	−0.21	−0.39	−0.11	−0.13	−0.55	−0.24
C. skate*	0	0.18	0.38	0.26	−0.68	−0.35	−0.74	−0.66	−0.26	−0.34
H. crab*	0	0.3	−0.27	1.04	−1.85	−0.06	−2.27	< −3	< −3	0.49

B)

	2008	2009	2010	2011	2012	2013	2014	2015	2016	2018	2019
A. croaker*	0	−0.53	−0.55	−2.02	−0.12	−1.6	−2.18	< −3	−1.07	−1.61	< −3
Scup	0	0.7	1.87	0.39	−1.19	−0.62	−0.34	−0.15	−0.95	−0.62	0.72
Spot	0	−0.06	0.71	0.19	0.5	−0.54	−1.11	−0.64	−0.97	0.37	0.9
S. flounder	0	0.18	0.25	−0.4	0.39	−1.88	0.7	0.92	−1.04	1.36	0.77
W. flounder*	0	0.39	1.54	1.5	1.01	0.07	2.91	1.93	0.97	> 3	1.46
Weakfish	0	0.69	0.57	1.16	−0.33	0.29	1.34	0.55	−0.56	0.38	0.43
C. skate	0	−0.11	0.52	0.37	−1.14	−0.48	0.76	0.48	−0.52	0.23	0.25
H. crab*	0	1.04	0.45	1.06	0.91	0.97	0.93	1.12	0.67	2.63	1.81

FIGURE 2 Mean estimated coefficients associated with levels of the year covariate for the eight species derived from 1000 beta-binomial model fits for (A) Chesapeake Bay-coastal ocean comparison, and (B) Delaware Bay-coastal ocean comparison. Positive values (purple tones) represent an increase compared to the 2008 baseline, while negative values (red tones) signify a decrease. Species names followed by an asterisk indicate a significant trend in relative habitat usage over time based on beta regressions. A. croaker: Atlantic croaker; S. flounder: summer flounder; W. flounder: windowpane flounder; C. skate: clearnose skate; H. crab: horseshoe crab

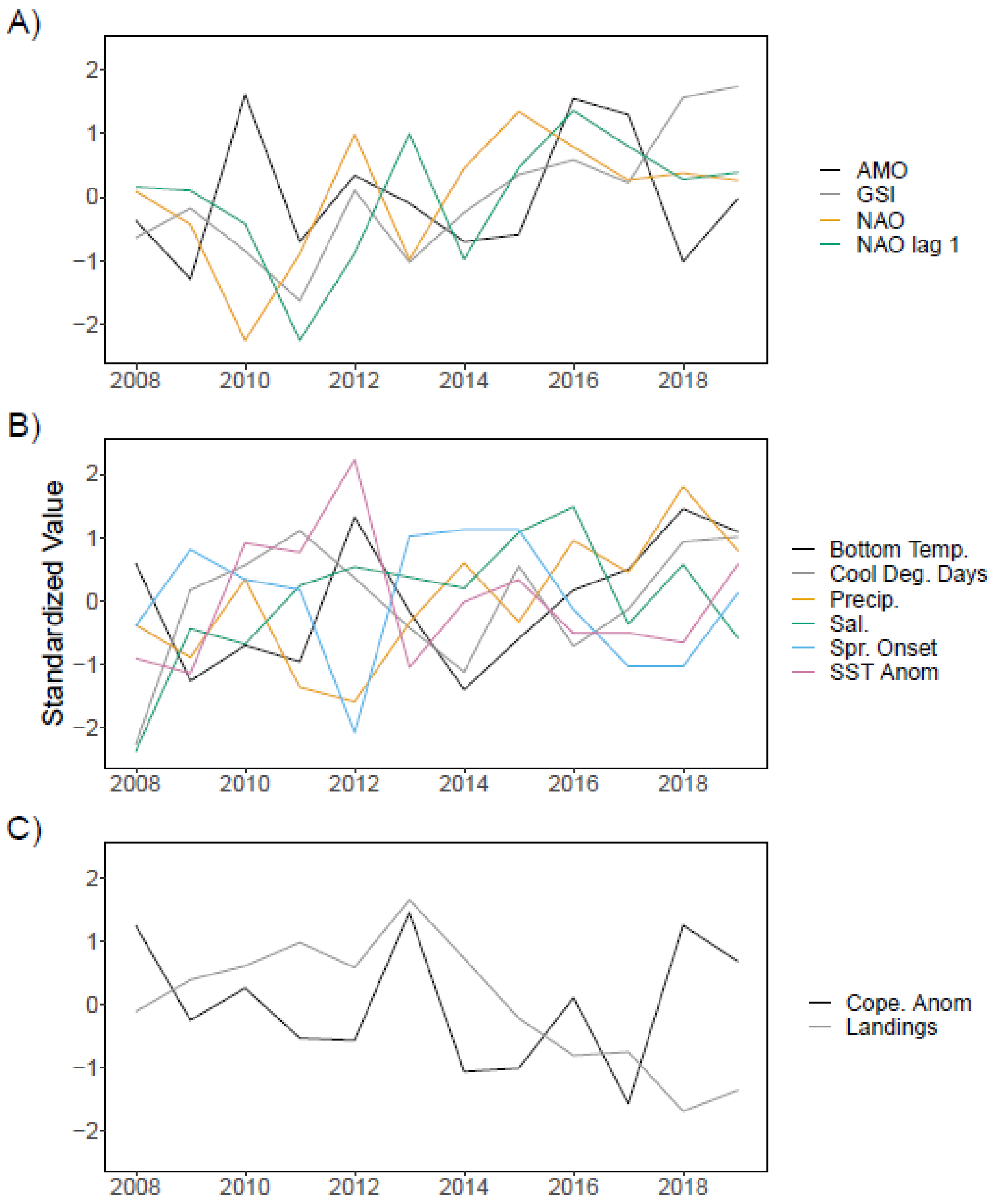


FIGURE 3 Time series of (A) broad-scale climate variables (Atlantic Multidecadal Oscillation [AMO]; Gulf Stream Index [GSI]; North Atlantic Oscillation [NAO]; North Atlantic Oscillation lagged by one [NAO lag 1]), (B) localized environmental variables (average spring bottom temperature from NEAMAP trawls [Bottom Temp.]; cooling degree days [Cool Deg. Days]; precipitation [Precip.]; average spring bottom salinity from NEAMAP trawls [Sal.]; spring onset [Spr. Onset]; sea surface temperature anomaly [SST Anom]), and (C) biological and exploitation covariates (copepod abundance anomaly [Cope. Anom]; landings of focal species [Landings]) considered in dynamic factor analysis (DFA). See Methods for descriptions and data sources

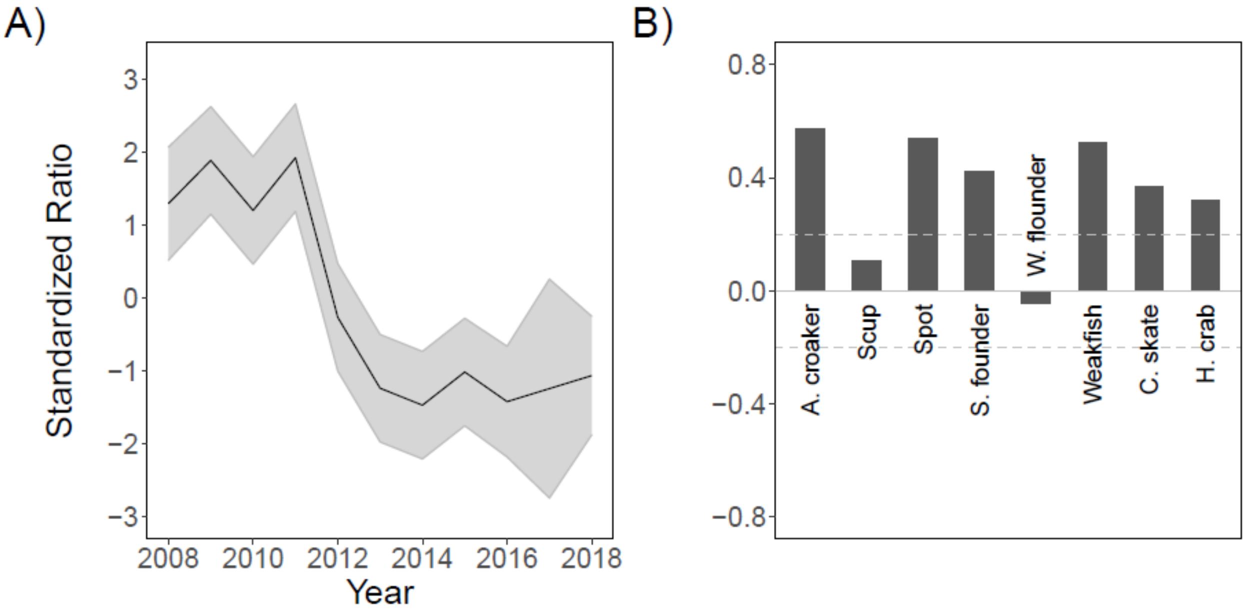


FIGURE 4 The (A) common trend from the Chesapeake Bay-coastal ocean dynamic factor analysis with the confidence interval represented by the gray ribbon, and (B) factor loadings, where the threshold (±0.2) indicating strong loading on the common trend is represented by the dashed lines. A. croaker: Atlantic croaker; S. flounder: summer flounder; W. flounder: windowpane flounder; C. skate: clearnose skate; H. crab: horseshoe crab

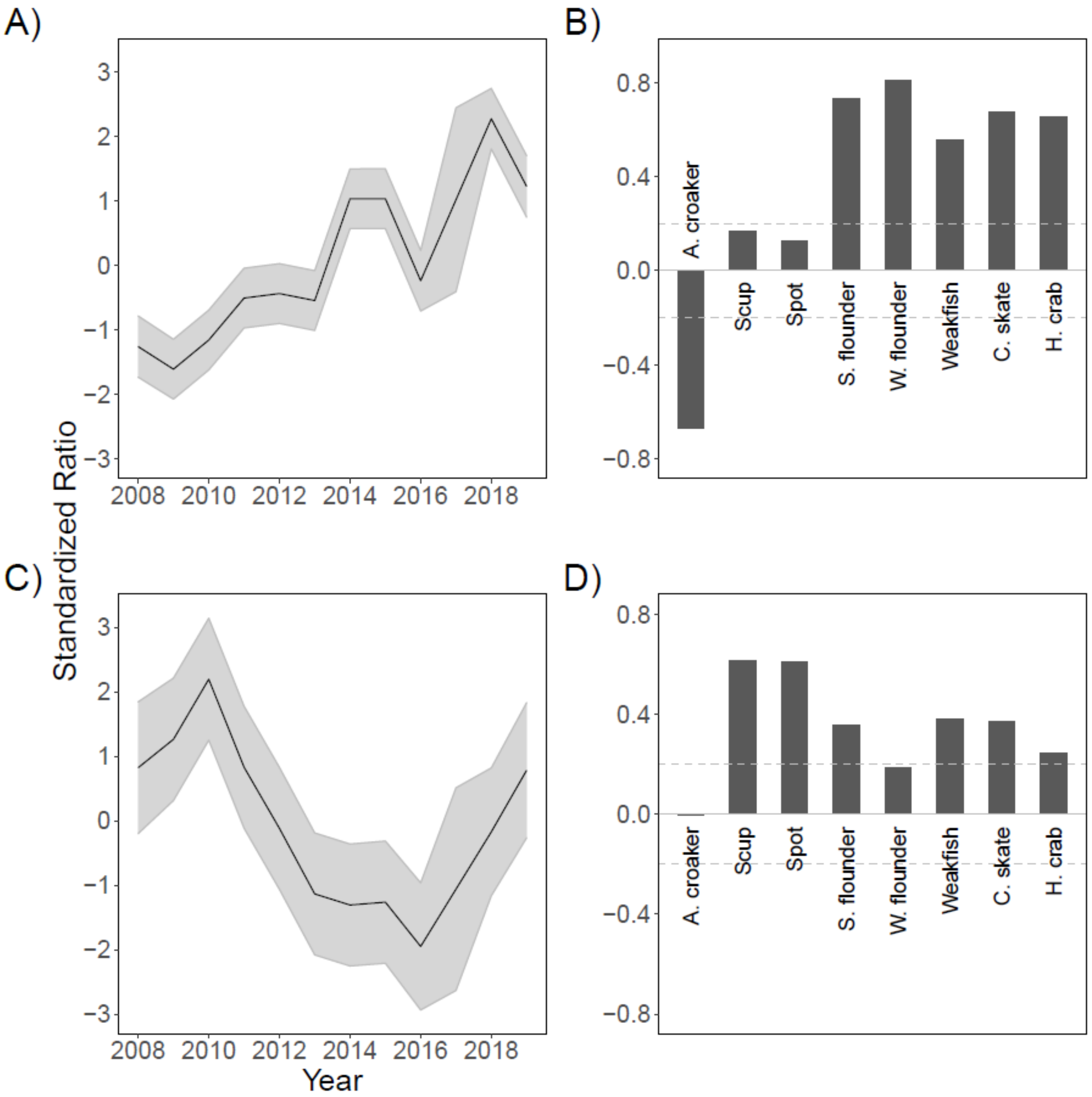


FIGURE 5 The (A) first common trend and (B) factor loadings on common trend one, and (C) the second common trend and (D) resultant factor loadings on common trend two from the Delaware Bay-coastal ocean dynamic factor analysis (DFA). The confidence intervals are represented by the gray ribbon in (A) and (B), and the threshold (±0.2) indicating strong factor loading on the common trend is represented by the dashed lines in (C) and (D). A. croaker: Atlantic croaker; S. flounder: summer flounder; W. flounder: windowpane flounder; C. skate: clearnose skate; H. crab: horseshoe crab

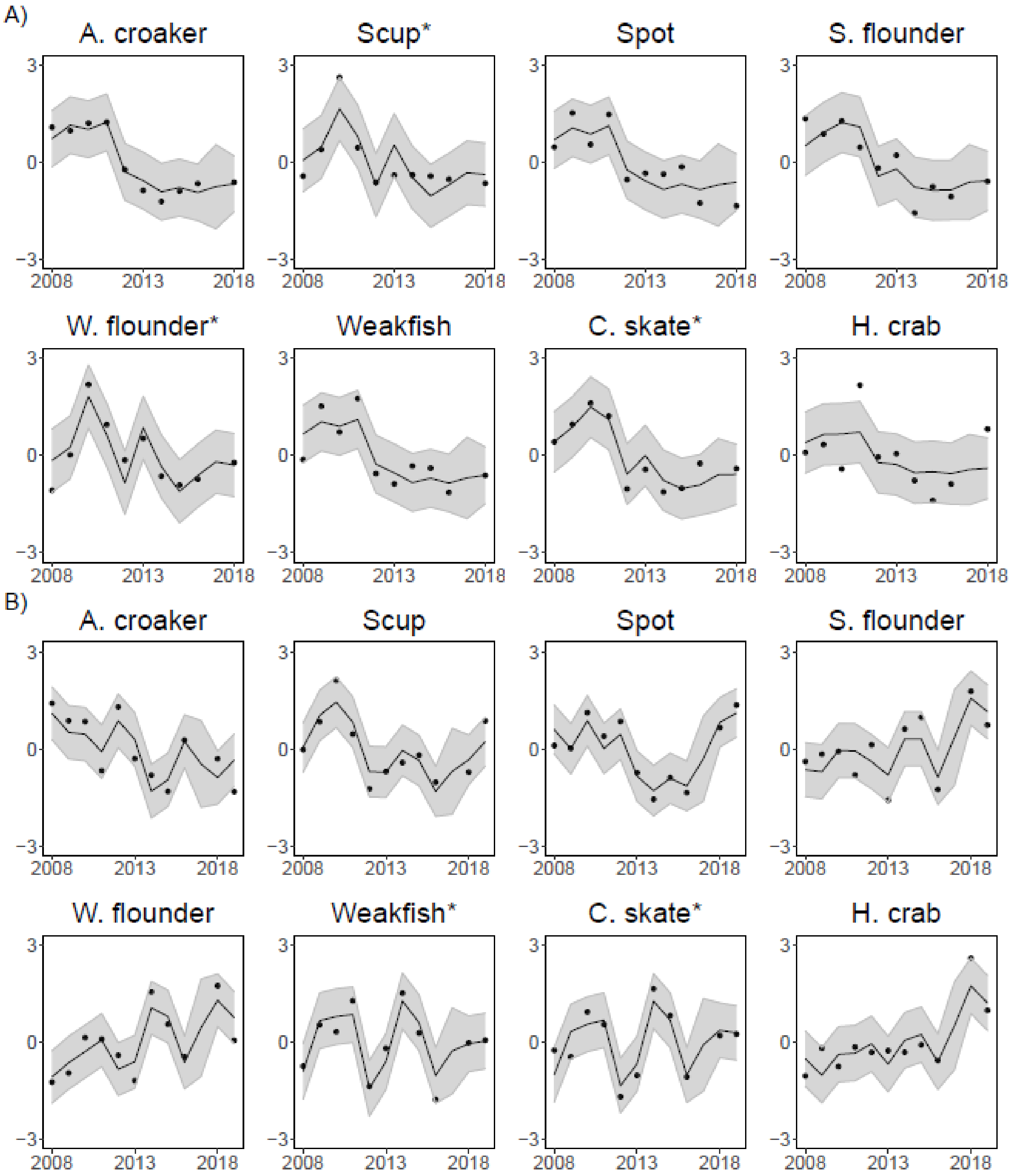


FIGURE 6 Model fits from the dynamic factor analysis (DFA) for (A) Chesapeake Bay-coastal ocean comparison and (B) Delaware Bay-coastal ocean comparison. The gray ribbons represent the confidence intervals and the points are the estimates from the beta-binomial time series models. Species names followed by an asterisk indicate a significant relationship between the time series of relative habitat usage and the covariate included in the selected DFA. A. croaker: Atlantic croaker; S. flounder: summer flounder; W. flounder: windowpane flounder; C. skate: clearnose skate; H. crab: horseshoe crab

Supplementary Materials

TABLE S1 Estimated coefficients, standard errors, and 95% confidence intervals from the selected dynamic factor analysis (DFA), displaying the relationship between the time series of relative habitat usage for a given species in Chesapeake Bay and the covariate of winter North Atlantic Oscillation (NAO). Species exhibiting a significant relationship are denoted with an asterisk.

Species	**Coefficient**	**SE**	**95% CI**
Atlantic croaker	-0.15	0.23	(-0.61, 0.30)
Scup*	-0.71	0.17	(-1.05, -0.37)
Spot	-0.10	0.23	(-0.55, 0.34)
Summer flounder	-0.34	0.21	(-0.74, 0.07)
Windowpane flounder*	-0.88	0.17	(-1.21, -0.54)
Weakfish	-0.13	0.22	(-0.57, 0.31)
Clearnose skate*	-0.49	0.20	(-0.88, -0.10)
Horseshoe crab	-0.13	0.19	(-0.51, 0.24)

TABLE S2 Estimated coefficients, standard errors, and 95% confidence intervals from the selected dynamic factor analysis (DFA), displaying the relationship between the time series of relative habitat usage for a given species in Delaware Bay and the covariate of average spring coastal bottom temperature, as measured by the Northeast Area Monitoring and Assessment Program (NEAMAP) in the utilized geographic range. Species exhibiting a significant relationship are denoted with an asterisk.

Species	**Coefficient**	**SE**	**95% CI**
Atlantic croaker	0.44	0.24	(-0.02, 0.90)
Scup	-0.42	0.23	(-0.88, 0.04)
Spot	0.44	0.23	(-0.01, 0.89)
Summer flounder	-0.02	0.26	(-0.54, 0.50)
Windowpane flounder	-0.34	0.27	(-0.87, 0.18)
Weakfish*	-0.86	0.24	(-1.32, -0.40)
Clearnose skate*	-0.76	0.25	(-1.26, -0.26)
Horseshoe crab	0.21	0.24	(-0.26, 0.68)

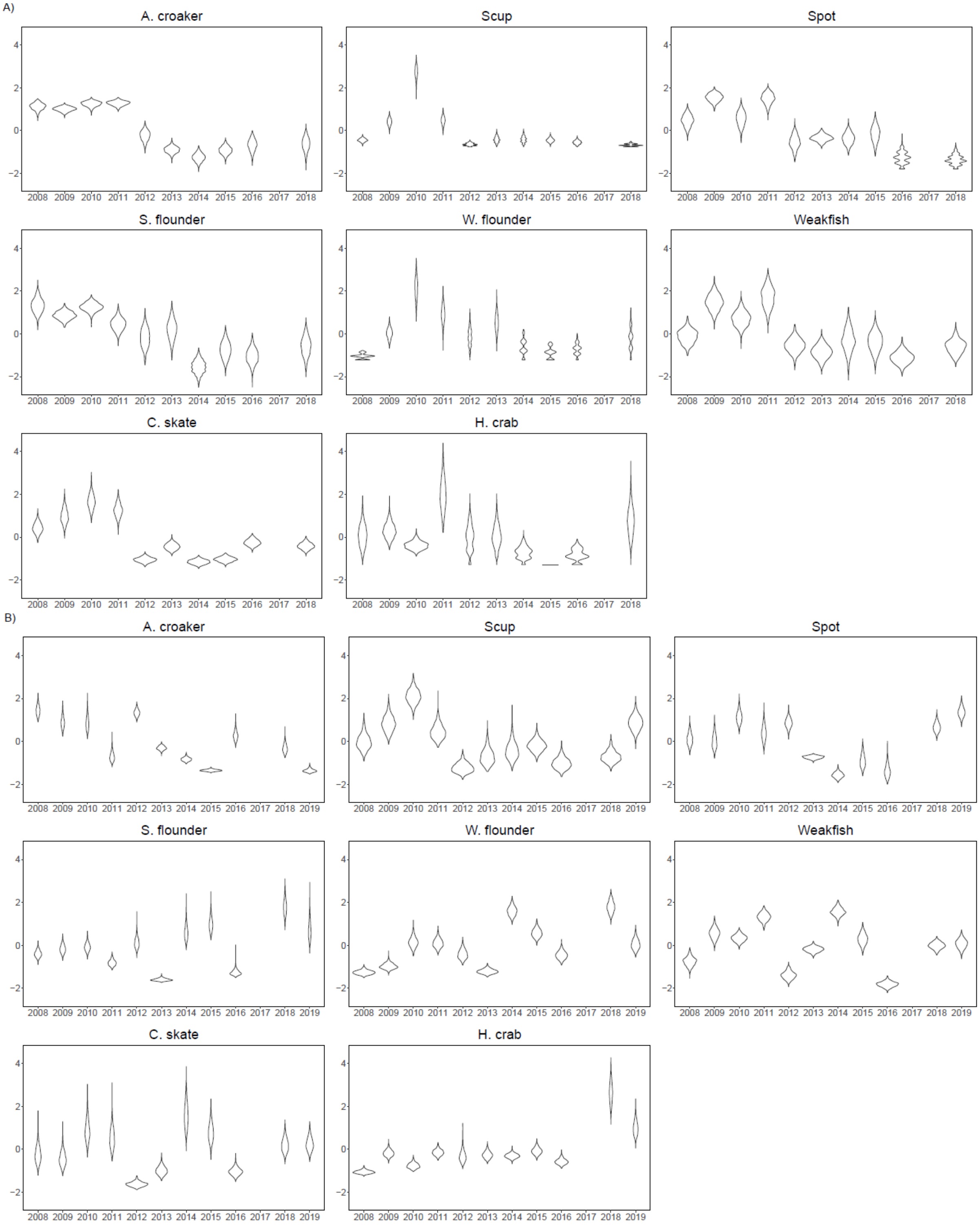


FIGURE S1 Violin plots displaying the z-scored (i.e., standardized to a mean of zero and variance of one) ratios of habitat usage from all 1000 iterations of model fitting for each species in (A) Chesapeake Bay and (B) Delaware Bay. A. croaker: Atlantic croaker; S. flounder: summer flounder; W. flounder: windowpane flounder; C. skate: clearnose skate; H. crab: horseshoe crab

CHAPTER 3

Hypoxia influences the extent and dynamics of suitable fish habitat in Chesapeake Bay

Abstract

Intra-annual patterns of hypoxia in Chesapeake Bay have been recorded since the mid-1900s, but anthropogenic inputs and climate change have exacerbated the volume and extent of hypoxic waters, which mobile marine fishes avoid. Given the documented declines in abundance and relative habitat usage of this estuary, which provides important habitat for many seasonally resident species, an understanding of the relationship between environmental conditions, habitat suitability and population dynamics could assist in elevating the stock status of these animals. To characterize baseline habitat associations for four fishes, ecological niche models were built relating catch-per-unit-effort from a fisheries-independent trawl survey conducted within Chesapeake Bay to environmental covariates. Model output indicated that impacts of climate change on the environmental conditions, including continued increases in temperature and hypoxic volume, will likely further the decline in estuarine utilization of these species. These niche envelopes were then paired with hindcasts from an estuarine-carbon-biogeochemical regional ocean model to derive estimates of spatiotemporal habitat suitability. The patterns in habitat suitability do not match those of declining abundance, indicating that dynamics outside of Chesapeake Bay are likely driving the shift. An auxiliary model was used to replace hypoxic dissolved oxygen concentrations with normoxic concentrations to determine the influence of hypoxia on habitat suitability. Both hypoxic severity and extent displayed clear trends in their associations with the quantity of suitable habitat available to each species in the bay. Results of this investigation demonstrate the complexity of the dynamics underpinning observed trends in habitat utilization.

1. INTRODUCTION

The influence of aquatic hypoxic zones, defined as areas with low dissolved oxygen (DO) concentrations, on both motile and sessile animals has long been of interest to ecologists, but that focus has become more pertinent in recent decades as anthropogenic nutrient inputs and climate change have amplified the extent of hypoxic events (Diaz & Rosenberg 2008, Rabalais et al. 2014, Altieri & Diaz 2019). Hypoxia can manifest seasonally (typically during warmer months), periodically (days to weeks), or episodically (infrequent, less than one event per year; Diaz & Rosenberg 2008). Seasonal oxygen depletion can cause mortality of sessile benthic organisms (Sagasti et al. 2001) and it influences the physiological processes of more mobile fishes, as evidenced by decreases in growth rates (Eby et al. 2005), reproduction (Wu et al. 2003), antipredator behaviors (Domenici et al. 2007, Chapman & McKenzie 2009), and swimming speeds (Craig et al. 2023). Thus, persistent hypoxia has the potential to impact the population dynamics of species and ecosystem functioning more broadly.

The Chesapeake Bay is the largest estuary in the continental United States and is characterized by a deep channel (20-30 m) that is surrounded by shallow (primarily < 10 m) water environments (Boicourt et al. 1999, Kemp et al. 2005). The bay is partially-mixed with estuarine circulation primarily driven by freshwater inputs (Pritchard 1956, Kemp et al. 2005). A strong salinity gradient (oligohaline to polyhaline) and riverine flow lead to stratification of the water column, particularly in summer months (Boicourt 1992, Hagy 2002, Kemp et al. 2005). The Chesapeake Bay also displays large intra-annual fluctuations in temperature, allowing it to serve as critical habitat seasonally, from the spring (March to May) through fall (September to November), for a diversity of post-juvenile (> age 1) marine fishes (Murdy et al., 1997). Specifically, during these warmer months, the bay is used by these taxa as a refuge, foraging, and spawning habitat (Murdy et al. 1997, Able & Fahay 2010), and several of these species support highly valuable recreational and commercial fisheries (Kirkley et al. 2005, Lellis-Dibble et al. 2008, Able & Fahay 2010, NMFS 2022).

Water temperatures in Chesapeake Bay have been increasing as a result of climate change (Ding & Elmore 2015, Hinson et al. 2021, Tian et al. 2021), consistent with documented changes occurring in other estuaries on the US East Coast, including Long Island Sound (Howell & Auster 2012) and Narragansett Bay (Oviatt 2004, Collie et al. 2008, Langan et al. 2021), as well as throughout the global ocean basins (Levitus et al. 2000, IPCC 2014). The cumulative impacts of climate change are expected to be greatest in coastal and estuarine systems (Najjar et al. 2010, Wetz & Yoskowitz 2013), and include additional effects on the physical environment such as decreasing DO, increasing frequency and intensity of precipitation, and changes to salinity and the seawater chemistry (e.g., Karl & Trenberth, 2003; Muhling et al., 2018; Najjar et al., 2010).

There has been a significant increase in hypoxic volume in the Chesapeake Bay since the 1950s (Hagy et al. 2004, Murphy et al. 2011), which is expected to continue in response to the decreased solubility of DO in warmer waters (Irby et al. 2018, Tian et al. 2021). Fish avoidance of hypoxic zones, in the form of spatial displacement, has been documented within the bay (Buchheister et al. 2013) and other systems (e.g., Eby & Crowder 2002, 2004, Craig et al. 2023). Further, temperature-related reductions in DO have been suggested as a main driver of distributional shifts of mobile marine species throughout the Atlantic Ocean (Pörtner & Knust 2007, Deutsch et al. 2015). Similarly, to maintain their optimal thermal range, fish are expected to shift poleward or to deeper water in response to warming (Murawski 1993, Walther et al. 2002, Parmesan & Yohe 2003, Perry et al. 2005), which has been extensively documented in coastal waters adjacent to Chesapeake Bay (e.g., Nye et al. 2009, Lucey & Nye 2010, Pinsky & Fogarty 2012, Bell et al. 2015, Kleisner et al. 2016).

The relative abundance of several fish species in Chesapeake Bay has decreased substantially in recent years, with declines in survey catch rates of up to 90% for some taxa (Buchheister et al. 2013). Over approximately the same time-period, the usage of this estuary relative to the coastal ocean has also declined for several species (Schonfeld et al. 2022). As fishery managers seek to improve the status of living marine resources in Chesapeake Bay, it is important to understand the relationship between environmental factors, habitat suitability, and the population dynamics and abundances of those species. This investigation seeks to (1) develop ecological niche models for several fish species inhabiting Chesapeake Bay, (2) pair these niche envelopes with an estuarine-carbon-biogeochemical regional ocean model to evaluate changes in suitable habitat in Chesapeake Bay over time (2002-2020), and (3) quantify the influence of hypoxia on spatiotemporal patterns of habitat suitability.

2. MATERIALS & METHODS

2.1 Data Sources

Four finfish species common to the Chesapeake Bay were included in this study due to their status as key recreational and commercial species in the Mid-Atlantic (NMFS 2022), as well as their ecological importance: Atlantic croaker (*Micropogonias undulatus*), spot (*Leiostomus xanthurus*), summer flounder (*Paralichthys dentatus*), and weakfish (*Cynoscion regalis*). The analyses were supported by 17 years (2002-2018) of data collected by the Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAP), a fisheries-independent trawl survey conducted within the mainstem of the bay. ChesMMAP cruises occur every other month from early spring to fall, sampling approximately 80 sites using a stratified random design based on latitude and depth (3.0-9.1 m, 9.1-15.2 m, and >15.2 m; Fig. 1). To gain insight into the relationship between habitat suitability and hypoxia, and how it has changed over time, data from ChesMMAP cruises conducted during three months; namely, May (pre-hypoxic peak), July (during hypoxic peak), and September (post-hypoxic peak; Smith et al. 1992, Kemp et al. 2005, Murphy et al. 2011), were included. Data collected during 2002, 2007, 2009, and 2010 were excluded due to incomplete cruises during the months of interest.

Environmental conditions, including bottom water temperature, bottom dissolved oxygen concentration, bottom salinity, and depth, are measured at each ChesMMAP sampling site. A four-seam bottom trawl (13.7 m headrope length with 7.6 cm codend mesh) is towed for 20 minutes in the direction of the current. Specimens are then sorted by species and enumerated (Latour et al. 2003). For each species, only regions in which the fish are expected to be present were included in the analysis to reduce the number of uninformative zeros in the data (Latour et al., 2017). Specifically, regions were excluded if < 5% of tows captured the species of interest and catch in the region represented < 5% of the overall catch.

Output from an implementation of the Regional Ocean Modeling System (ROMS; Shchepetkin & McWilliams, 2005) coupled with an Estuarine-Carbon-Biogeochemistry (ECB) module configured specifically for the Chesapeake Bay (ROMS-ECB; St-Laurent et al. 2020), was used to provide simulated values of the environmental parameters of interest (i.e., water temperature, dissolved oxygen concentration, and salinity) at 600 m resolution from 2002-2020. ROMS-ECB output for all months within the range of the ChesMMAP cruises was used (May-Sep), while the spatial grid of this model was trimmed to include only cells within the sampling frame of the ChesMMAP cruises used for each species. Although ROMS-ECB is a 3-

dimensional model with 20 vertical levels, only the bottom level was used in this analysis as the species included in this study are demersal and specimens were collected using a bottom trawl.

2.2 Ecological Niche Models

The habitat associations for the suite of species were characterized through the development of ecological niche models (ENMs; Peterson & Soberón 2012), whereby catch-per-unit-effort (CPUE), quantified as count per tow, is related to the four environmental parameters measured synoptically at each site: bottom water temperature (˚C), bottom dissolved oxygen concentration (mg/L), bottom salinity (psu), and depth (m). The generalized additive modelling (GAMs) framework was used to develop the ENMs, as these models can include both parametric (i.e., linear) and non-parametric (i.e., non-linear) components (Zuur et al. 2009). The count data were assumed to follow a negative binomial distribution and the natural logarithm of the area swept by the survey trawl, the measure of effort, was included as an offset variable. Akaike's information criterion (AIC; Akaike, 1973; Burnham & Anderson, 2002), the Bayesian information criterion (BIC; Burnham & Anderson 2004), and diagnostic plots (analysis of residuals) were used in model selection. For continuous covariates, the number of knots included in the smoothing function was adjusted based on information criteria to avoid extraneous smoothing without losing important information on the relationships. Marginal means (Searle et al. 1980) were then used to estimate the relationship between predicted abundance across the domain of each covariate of the selected models. All analyses were conducted using the software program R (v4.2.0, R Core Team, 2022). Package "mgcv" (Wood 2017) was accessed to fit the ENMs.

2.3 Habitat Suitability & Hypoxia

ROMS-ECB provided simulated environmental conditions for each individual cell in the 600 m sampling grid every day for five months (May-Sep) and 19 years (2002-2020). These water quality outputs were then coupled with the selected ENM of each species, and used to predict the expected count of the species based on those environmental conditions in each grid cell. These predicted counts were used as a proxy for suitable habitat, where a larger predicted count represented greater habitat suitability. After predicting this value in each grid cell daily, the estimates for each cell were averaged within each month and year. That is, a single value was calculated to represent the habitat suitability of each cell for a given month and year. Then, the overall annual habitat suitability index (HSI) for each species in Chesapeake Bay was calculated by summing the averaged values in the sampling frame across the five months. Annual HSI values were then scaled by dividing by the mean of the annual HSI estimates.

Spatial patterns of habitat suitability within Chesapeake Bay were also evaluated by calculating the average HSI value per cell on an annual scale (i.e., averaged across all months, May-Sep, within a given year), to allow for visualization of the suitability throughout the full sampling frame at an annual scale. For each species, quantiles were calculated from the estimates of all 19 years of estimated values and mapped. To derive a measurement of stability in the annual averages, the standard error of the predictions within a single cell across all months in a year was used to calculate 95% confidence intervals surrounding the mean. Dividing the range of the confidence interval by the annual average value in the corresponding cell provided a value akin to a coefficient of variation, which hereafter is referred to as the instability or variability of the suitability of the cell.

To evaluate the impacts of hypoxia on available habitat for each species, all ROMS-ECB dissolved oxygen values that were hypoxic were replaced with a normoxic value. While 2.0 mg/L is often used to categorize waters as hypoxic, the dissolved oxygen concentration that induces behavioral and physiological responses is more ecologically relevant. Species-specific thresholds of hypoxia tolerance vary and many finfishes have been shown to avoid areas with DO concentrations greater than 2.0 mg/L, including several in this study (Eby & Crowder 2002). Thus, a threshold value of 2.5 mg/L was used to better encapsulate the habitat association of each species in this analysis. The replacement of hypoxic values with normoxic values was accomplished by filtering the ROMS-ECB output to only include normoxic cells (i.e., > 2.5 mg/L) and subsequently fitting a GAM to this dataset, where dissolved oxygen (DO) concentration at space s and time t was the response variable, assumed to follow a gamma distribution:

$$DO_{s,t} = b + f_1(T_{s,t}) + f_2(SA_{s,t}) + f_3(D_{s,t}) + \alpha_t(MO_t) \tag{1}$$

and where b is the intercept, f_1, f_2, and f_3 are the smoothing functions for the other simulated environmental conditions: water temperature (T), salinity (SA), and depth (D). Additionally, α_t is the estimated mean effects for each month (MO). The R package “gamlss” (Rigby & Stasinopoulos 2005) was utilized to develop this model.

This model was then coupled with the ROMS-ECB output containing hypoxic values, to provide estimated normoxic dissolved oxygen concentrations ($\widehat{DO}_{s,t}$) at times and cells that were hypoxic. All other environmental conditions from the ROMS-ECB simulation (i.e., water temperature, salinity, and depth) were unchanged. These outputs with hypoxia “removed” were then paired with the selected ENM and the same methods as above were used to calculate the “no hypoxia” annual HSI. For comparison, the “no hypoxia” annual HSI was also scaled by dividing by the mean of the "true" annual HSI estimates (i.e., calculated from the outputs that included hypoxia).

The approximate area gained each month by removing hypoxia was calculated through the comparison of the average monthly predicted value in each cell in the sampling frame. Each estimate, for both "true" outputs and "hypoxia off" outputs, was divided by the mean "true" value within a month across years (e.g., mean cell estimate in May 2002-2020). Any values that were greater than or equal to the mean were considered to be good habitat. If a cell was below average in the "true" output calculations, but became suitable once hypoxia was removed, the cell was classified as area gained. The number of cells that changed from below average to equal or greater than average was summed in the month and multiplied by 0.36 km^2 (the area of a ROMS-ECB cell) to generate the total area gained in that month. The total area gained was also divided by the total area in the sampling frame for a given species (# of cells $\times$ 0.36 km^2) to calculate the proportional increase in suitable habitat area.

To further evaluate the influence of hypoxia on habitat suitability, ENM predictions for July were analyzed, since this month most often corresponds to the peak of hypoxia in Chesapeake Bay. The first several steps in calculating the annual HSI were followed, whereby a single value was calculated for each cell in a given year by predicting daily abundances and averaging across the month to generate a spatial field of averages for each July. The same calculations were applied to the ROMS-ECB output with "no hypoxia" and at each cell, the average value from the "true" outputs was subtracted from the average "no hypoxia" value, which populated the full sampling frame with the difference in suitability with no hypoxia. The quantiles were calculated from these differences and mapped. Then, the averaged values were summed to a get a single HSI value for the entire Chesapeake Bay sampling frame in July for each year. This calculation was performed for both the “true” ROMS-ECB outputs and the “no hypoxia” ROMS-ECB outputs. The proportional increase in July HSI was calculated by subtracting the “true” July HSI from the “no hypoxia” July HSI, then dividing by the “true” July HSI.

The influence of “removing” hypoxia on habitat suitability was evaluated through relating the proportion change in available habitat in July to two measures of environmental quality from the ROMS-ECB outputs: extent and severity of hypoxia. Hypoxic extent was represented as the proportion of hypoxic area in July, which was calculated by determining the total number of hypoxic cells in July of that year divided by the total number of cells in the spatial field and days in the month. Hypoxic severity was quantified as the average bottom DO concentration in July from the ROMS-ECB outputs. The temporal trends in the relationships between the proportion change without hypoxia and extent and severity were visualized by applying a locally weighted regression smoother (LOESS) to the estimates (Cleveland 1979, Cleveland & Devlin 1988).

3. RESULTS

3.1 Ecological Niche Models

The selected ENM for each species included all four covariates and all displayed nonlinearity in the relationships between survey count and the predictor variables (exception: the depth covariate was linear for the summer flounder ENM; Table S1). The marginal mean predicted catches for three of the four species (Atlantic croaker, spot, and summer flounder) displayed a bimodal relationship with temperature, with the second peak larger than the first (Fig. 2a). For spot and summer flounder, this second peak occurred at approximately 25°C, while for Atlantic croaker, the second maximum occurred at approximately 22.5°C. Although the relationship between the weakfish marginal mean prediction and temperature was not bimodal, this species also displayed a maximum predicted relative abundance at approximately 25°C (Fig. 2a). Marginal mean predictions for all four species were very low under hypoxic (< 2.5 mg O_2/L) conditions (Fig. 2b). Peak marginal mean predictions for Atlantic croaker, summer flounder, and weakfish in relation to salinity occurred at approximately 20-30 psu (Fig. 2c). For spot, the marginal mean prediction for salinity showed the highest association with areas < 10 psu and a secondary peak in the 20-30 psu range, as noted for the other species (Fig. 2c). The relationship between the marginal mean predictions and depth for all four species was highest at the lower to middle depth ranges sampled (Fig. 2d).

3.2 Habitat Suitability & Hypoxia

For the four focal species, annual estimates of habitat suitability generally fluctuated without a clear trend from 2002-2014 but showed a declining pattern thereafter (Fig. 3). For spot and weakfish, the minimum annual HSI occurred in 2003 (Figs. 3b, d), while the minima for Atlantic croaker and summer flounder were in 2018 (Figs. 3a, c). During both of those years, the Chesapeake Bay experienced high spring and summer freshwater inputs, as evidenced by having the two lowest average salinities from ROMS-ECB output during the time span of this investigation (i.e., May-Sep 2002-2020), and thus were classified as wet years. For spot, summer flounder, and weakfish, the maximum estimated annual HSI occurred in 2002 (Figs. 3b, c, d), while for Atlantic croaker the maximum was in 2009 (Fig. 3a). In terms of freshwater inputs to the bay, 2002 was a dry year (i.e., one of the highest average salinities from the ROMS-ECB output) and 2009 was drier than average, but more typical.

The most obvious difference in the spatial distribution of suitable habitats during years with high and low annual HSI for the four species was the increase in extent of high-quality habitat towards the head of Chesapeake Bay (Figs. 4a-d). There were some areas that remained low quality for a species regardless of whether the year was estimated as having a maximum or minimum annual HSI. For example, the waters in the northernmost region of Chesapeake Bay were consistently low-quality habitat for summer flounder (Fig. 4c). There was markedly more instability for all species during the years with the estimated minimum HSI compared to years of estimated maximum HSI (Figs. 4e-h). For both summer flounder and weakfish, estimated HSI was highly stable throughout most of the bay mainstem during 2002 (the high year; Figs. 4g-h) and the lower bay was relatively stable for all species during high and low years of estimated HSI (Figs. 4e-h). The most instability in estimated HSI for Atlantic croaker and spot was in the mainstem during low years (2018 and 2003, respectively; Figs. 4a-b).

The time series of proportional increase in suitable habitat when hypoxia was “removed” were highly similar among the four species, with the primary difference being the scale of the proportional increase (Fig. 5). Spot showed the largest increases in habitat with approximately a 70% increase in some years (Fig. 5b). Removing hypoxia appeared to have the smallest impact on the quantity of suitable habitat for weakfish, with less than a 25% increase over the years of this study (Fig. 5d). For both spot and weakfish, the maximum proportion increase occurred coincident with the minimum HSI (2003; Figs. 5b, d). Atlantic croaker and summer flounder exhibited a maximum proportion increase in suitable habitat in 2019 (Figs. 5a, c), which was not the same year associated with their respective minimum HSIs.

There was a clear seasonality in the potential increase in suitable habitat without hypoxia for all four species, with the highest increase occurring primarily in July, and in June for some years (Fig. 6). Spot exhibited the highest potential gains in suitable habitat under the no hypoxia scenario, reaching approximately 2,250 km^2 in June 2019, which is over 40% of the sampling frame (Fig. 6b). That increase was nearly three times the amount of area gained by summer flounder, which had the second highest increase of approximately 700 km^2 in July 2019 (Fig. 6c). While weakfish displayed the least amount of above-average habitat quality area to be potentially gained without hypoxia, namely a maximum of about 465 km^2 (June 2019), weakfish also had the smallest sampling frame included in the analyses (and therefore used to predict suitable habitat) due to the removal of the two northernmost regions in which they are not commonly found. Therefore, the largest increase in area for weakfish was about 12% of the Chesapeake Bay mainstem analyzed (Fig. 6d). Although Atlantic croaker displayed a larger potential increase in suitable habitat, nearly 540 km^2 in July 2003, that area comprised only about 10% of the area of the mainstem, the least of all four species (Fig. 6a).

The peak in hypoxic extent and severity in the Chesapeake Bay primarily occurred in July. According to the ROMS-ECB outputs within the ChesMMAP sampling frame, over 40% of the cells were hypoxic at some point throughout the month of July. Habitat gains from removing hypoxia for Atlantic croaker and spot were higher than those for summer flounder in the more northern regions of the bay (Figs. 7a-c, respectively). Removal of the small hypoxic areas off several main tributaries in the southern portion of the bay resulted in larger effects on the habitat suitability for Atlantic croaker and weakfish (Figs. 7a, d) when compared to spot and summer flounder (Figs. 7b, c).

The relationship between the proportion increase in habitat suitability when hypoxia was “removed” in July and both the severity and extent of hypoxia displayed clear trends for all species, as showcased by the fitted LOESS smoothers (Fig. 8). There was a positive trend in the proportional increase in suitable habitat when hypoxia was “removed” in years with increasing hypoxic extent (i.e., proportion of hypoxic cells; Fig.8a) and a declining pattern with decreasing hypoxic severity (i.e., an increase in average dissolved oxygen concentrations; Fig. 8b).

4. DISCUSSION

The Chesapeake Bay is undergoing alterations in its physical environment in response to climate change, which will affect whether the environmental conditions remain within the optimal ranges of the seasonally migrant species that inhabit the bay. This estuary has warmed significantly in recent years (Ding & Elmore 2015, Hinson et al. 2021), and despite the ENMs of all four species displaying the largest peak in the relationship between mean relative abundance and temperature at fairly high values (22.5-25°C), continued warming will result in temperatures that will surpass those upper values. Of the 19 years of ROMS-ECB bottom outputs used in this study, the three years with the highest number of cells reaching temperatures above 25°C occurred within the last five years. Accordingly, and based on the ENMs developed, those continued increases will correspond to lower relative abundance of all four species, as temperatures in a portion of the Chesapeake Bay will exceed their optimal ranges.

The ENMs for all species indicated low relative abundance or absence at the lowest dissolved oxygen concentrations (e.g., hypoxic waters, ≤ 2.5 mg O_2/L). Similarly, studies conducted individually on each of these species have documented hypoxia avoidance behaviors (Tyler 2004, Craig & Crowder 2005, Sackett et al. 2008, Brady & Targett 2013; Craig et al. 2023). Since the 1950s, dissolved oxygen concentrations in Chesapeake Bay have declined appreciably and hypoxic volume has increased (Hagy et al. 2004, Murphy et al. 2011). This trend is likely to continue, due to continued atmospheric warming and the lowered solubility of dissolved oxygen in warmer waters (Najjar et al. 2010, Irby et al. 2018, Tian et al. 2021), thus potentially leading to further declines in the relative abundance of these four species in this estuary.

The possible impacts of climate change on the salinity in Chesapeake Bay are highly variable and largely unpredictable. Climate change is expected to lead to increases in precipitation frequency and intensity, extreme climatic events, and sea level rise (Karl & Trenberth 2003, Trenberth 2005, 2007, Sun et al. 2007). Sea level rise is expected to increase salinity in Chesapeake Bay (Hilton et al. 2008, Hong & Shen 2012). However, the influence on salinity caused by the weather-based changes is dependent upon seasonality and the specifics of the events. For example, increased precipitation will increase stream flow and lead to a decrease in salinity. However, if heavy precipitation events are interspersed with periods of drought, salinity will increase during the drought periods. Current models predicting stream flow vary widely (Najjar et al. 2010), so concrete conclusions cannot be drawn about expected salinity trends in Chesapeake Bay relative to climate change, but it is likely that variability in salinity would increase. The ENMs for both summer flounder and weakfish display clear, discrete ranges of salinity associated with highest predicted relative abundances. Thus, any changes in salinity that extend beyond the bounds of these ranges would likely lead to a decrease in relative abundance of these species.

Overall, based on the ENMs, the expected changes to the physical environment of the Chesapeake Bay due to climate change will likely result in decreases of relative abundance of all four species, continuing trends of many species previously recorded (Buchheister et al. 2013). However, none of the effects of climate change are occurring individually. The occurrence of multiple stressors acting simultaneously can result in different physiological responses to the same stimuli. The presence of two stressors could dampen the individual effects (i.e., an antagonistic interaction), or it could diminish the individual's ability to respond to the stressors such that the negative consequences would be greater than the sum of the individual effects (i.e., a synergistic interaction; Côté et al., 2016; Folt et al., 1999). A plethora of studies have been dedicated to determining the influence of multiple stressors on the physiological response of an animal, including many on the four species included in this analysis. Such investigations have documented the influence of salinity on temperature tolerance of spot (Hodson et al. 1981), the interaction of temperature and salinity on feeding and growth rates of juvenile weakfish (Lankford & Targett 1994), and the interaction of temperature and pCO2 on hypoxia tolerance of summer flounder (Schwieterman et al. 2019). The concurrence of multiple stressors in Chesapeake Bay due to climate change could cause the expected declines in relative abundance to occur more rapidly than the ENMs would suggest.

One of the more interesting, and somewhat unexpected, relationships produced by the ENMs was the multimodal distribution of mean relative abundance as a function of temperature for all four species. The differences in the temperatures corresponding to the local maxima for each species indicates that this multimodal relationship is not solely due to the seasonality of the ChesMMAP sampling design. While the ranges of temperatures encountered vary based on the month of the cruise, peaks in abundance of the species occurring at different temperatures indicates a reflection of species-specific temperature associations, rather than representing a mean or mode associated with a cruise month.

For summer flounder, the predicted maximum mean relative abundance occurred at approximately 25°C, which is beyond the temperature (20°C) of waters they were most commonly distributed within and is near the maximum temperatures in which these fish were found during a tagging study conducted in Delaware Bay, a neighboring northern estuary (Sackett et al. 2008). Further, the movement rates of summer flounder in Chesapeake Bay peak at 24°C and decrease at higher temperatures (Henderson et al. 2014). Atlantic croaker exhibited a second peak in mean relative abundance at approximately 22.5°C, which is in contrast to two other studies conducted in estuarine environments of South Carolina and the Gulf of Mexico that found this species to be most abundant at temperatures above 24°C (Miglarese et al. 1982, Craig & Crowder 2005). Previously reported optimal temperature ranges for spot and weakfish are more similar to the temperature associated with the maximum predicted relative abundance in this study. Ideal temperatures for juvenile weakfish range from 27-29°C (Lankford & Targett 1994), and spot have been found in a wide range of temperatures, regularly exceeding 30°C (Parker 1971), with lab experiments showing the upper incipient lethal temperature for juvenile spot to be about 35°C (Hodson et al. 1981).

The Chesapeake Bay, as an estuarine system, experiences the influence and input of both saline ocean water and freshwater from its tributaries. The salinity difference between these two water sources is one of the major drivers of water column stratification, which prevents dissolved oxygen from mixing to the bottom and thereby contributing to hypoxia at depth (Boicourt 1992, Murphy et al. 2011, Scully 2013). As displayed by the ENMs developed in this study, as well as described in numerous other investigations, including those specific to the four focal species of this analysis and the Chesapeake Bay overall (Tyler 2004, Craig & Crowder 2005, Sackett et al. 2008, Buchheister et al. 2013, Brady & Targett 2013), fish avoid hypoxic areas. Given that hypoxia occurs in cooler, deeper waters of the bay, fish likely relocate to the periphery of these hypoxic areas, which are shallower and warmer. Such displacements may explain the peak in predicted relative abundance associated with higher temperatures exhibited in the ENMS, and may act as a hyperstabilizing phenomenon. That is, survey catch remains stable due to aggregation behaviors of the fish, thus presenting the illusion of a robust population, but the high and stable catches are not reflective of the true trends in abundance (Hilborn & Walters 1992). Displacement due to hypoxia and aggregation along the hypoxic edge have been associated with changes in the mean temperature occupied by several species, including Atlantic croaker in the Gulf of Mexico (Craig & Crowder 2005).

Anthropogenic nutrient runoff is correlated with hypoxia in Chesapeake Bay (Officer et al. 1984, Hagy et al. 2004, Murphy et al. 2011), as large nutrient inputs fuel phytoplankton blooms, and subsequent high benthic respiration rates at depth deplete oxygen as bacteria remineralize this organic matter (Kemp & Boynton 1992, Diaz & Rosenberg 1995, Rabalais et al. 2010). As such, historic total maximum daily load (TMDL) reductions of nutrients have had large impacts in reducing hypoxic volume in Chesapeake Bay (Frankel et al. 2022). Therefore, the maps displaying the largest increases in HSI when hypoxia was removed (Fig. 7), could be utilized by managers to guide policies related to the TMDL of various nutrients. For example, the hypoxic zones at the mouths of several main tributaries in the southern portion of Chesapeake Bay, namely the James River, the York River, Mobjack Bay, and the Rappahannock River, represent areas where TMDL restrictions might be most beneficial. These water bodies contribute freshwater flow to the bay, and therefore, also inputs of anthropogenic nutrient loads. Adjusting TMDLs in these areas could result in an increase in suitable habitat if the measures were able to reduce summertime hypoxia, especially for Atlantic croaker and weakfish since these species displayed the largest increases in habitat suitability by the mouths of these tributaries.

Further, the clear seasonality in the theoretical increase in area of suitable habitat with the potential elimination of hypoxia (Fig. 6) supports temporally dynamic TMDL policies, indicating that the limitation of nutrient inputs in the months preceding the highest habitat losses due to hypoxia could be advantageous. While climate change, as previously described, will have an impact on the extent of hypoxic areas and their persistence in Chesapeake Bay, TMDL reductions could nevertheless alleviate some adverse effects, with the largest amelioration occurring during dry years by decreasing the change in dissolved oxygen concentrations, particularly along the edge of the hypoxic zone (Irby et al. 2018).

This study has shown that hypoxia plays a large role in determining the quantity of suitable habitat for four ecologically and economically important species in Chesapeake Bay. The time series of HSIs developed in this analysis do not display a notable trend, but instead, results showed large annual fluctuations in the quantity of suitable habitat. Concurrently, however, trends in relative abundance of important species have declined in Chesapeake Bay (Buchheister et al. 2013, Bonzek et al. 2022) and the usage of this estuary relative to the coastal ocean has also decreased (Schonfeld et al. 2022). Therefore, it can be surmised that the environmental conditions of the Chesapeake Bay itself are likely not the only factor contributing to the documented declines in relative abundance and seasonal estuarine utilization patterns. As described, these species inhabit the Chesapeake Bay only seasonally, spending the remainder of the year in the coastal ocean. The Atlantic Ocean is also affected by climate change, and the rate of warming of the northwestern Atlantic shelf is nearly three times the global average (Saba et al. 2016). Many studies conducted using data from these coastal waters have documented significant shifts in distribution of fishes poleward or to deeper habitats in response to warming, several of which include the four species in this investigation (e.g., Bell et al., 2015; Kleisner et al., 2016; Lucey & Nye, 2010; Nye et al., 2009; Pinsky & Fogarty, 2012). Consequently, the dynamics of climate change and processes in the coastal ocean may contribute to the recent decrease in relative abundance and estuarine utilization of many fishes in Chesapeake Bay, in addition to the physical environment of the bay itself.

A valuable area of future research could involve the pairing of the ENMs developed in this analysis with projections of future conditions within Chesapeake Bay, as this study utilized 19 years of hindcasts from ROMS-ECB. While this analysis did not find notable trends in the time series of HSI, future environmental conditions under various climate change scenarios may result in forecasted values of the environmental covariates that are outside the optimal ranges estimated by the ENMs, and subsequent annual HSI estimates may begin to exhibit directionality. Such a study could be furthered by including potential TMDL policy adjustments with the climate change scenarios to quantify the value of specific management actions aimed at increasing suitable habitat. Additionally, the hypothesis that the hypoxic waters at depth are leading to aggregation at the periphery (i.e., hyperstabilization or edge effects) could be evaluated through more directed fieldwork.

This study has provided valuable information on the relationship between the physical environment of Chesapeake Bay and abiotic habitat of four key seasonally resident species that had previously not been quantified. Insight into these relationships allows for increased understanding of species-specific habitat utilization and the potential impacts of climate change. Additionally, this investigation analyzed the role of hypoxia as it relates to habitat suitability, and the resultant spatial HSI maps provide awareness of relative habitat quality within the bay mainstem that can aid directed management efforts. Although hypoxia in Chesapeake Bay remains problematic, this study did not find clear declining patterns in abiotic habitat quality, which raises important questions regarding impacts of larger scale, coastal ocean processes on the distribution and ecology of fishes commonly found in estuaries within the mid-Atlantic.

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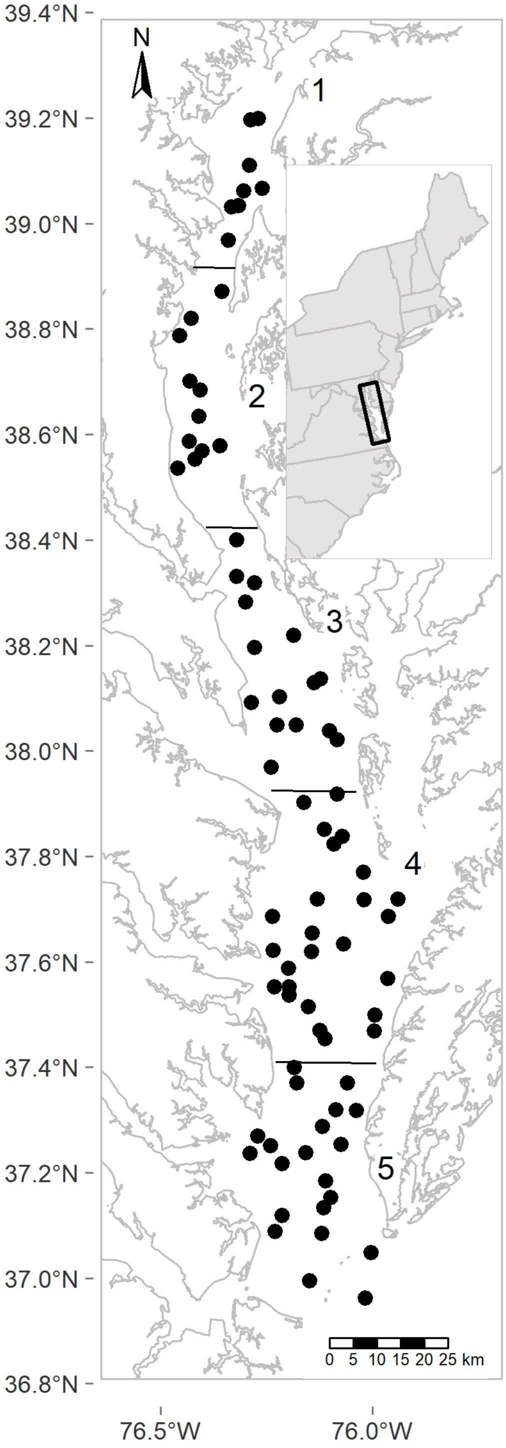
Figures


39.4°N
39.2°N
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38.8°N
38.6°N
38.4°N
38.2°N
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37.6°N
37.4°N
37.2°N
37.0°N
36.8°N
76.5°W
76.0°W
N
1
2
3
4
5
0 5 10 15 20 25 km

Fig. 1. Sampling sites for a representative cruise (July 2013) conducted by the Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAP). The circles represent tow locations and the horizontal lines delineate the stratification scheme (i.e., sampling regions), with regions labeled 1-5.

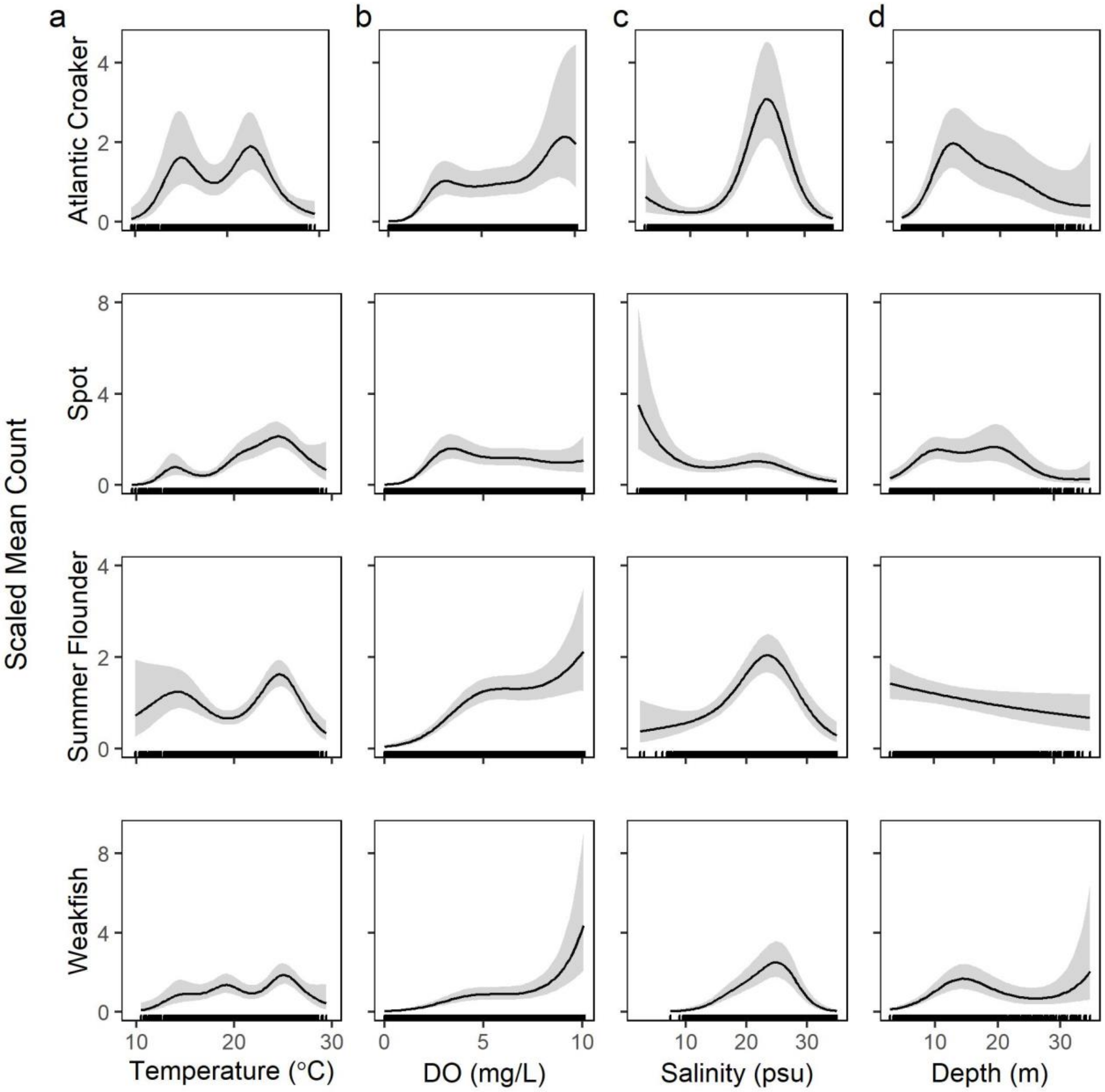


Fig. 2. Ecological niche model (ENM) output of the relationship between mean relative abundance and (a) temperature, (b) dissolved oxygen (DO), (c) salinity, and (d) depth for each species developed using survey data collected by the Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAP). Measurements of environmental covariates in sparsely recorded ranges (i.e., on the upper and/or lower bounds of the observed; ≤ 0.5% of values) were omitted for visualization purposes.

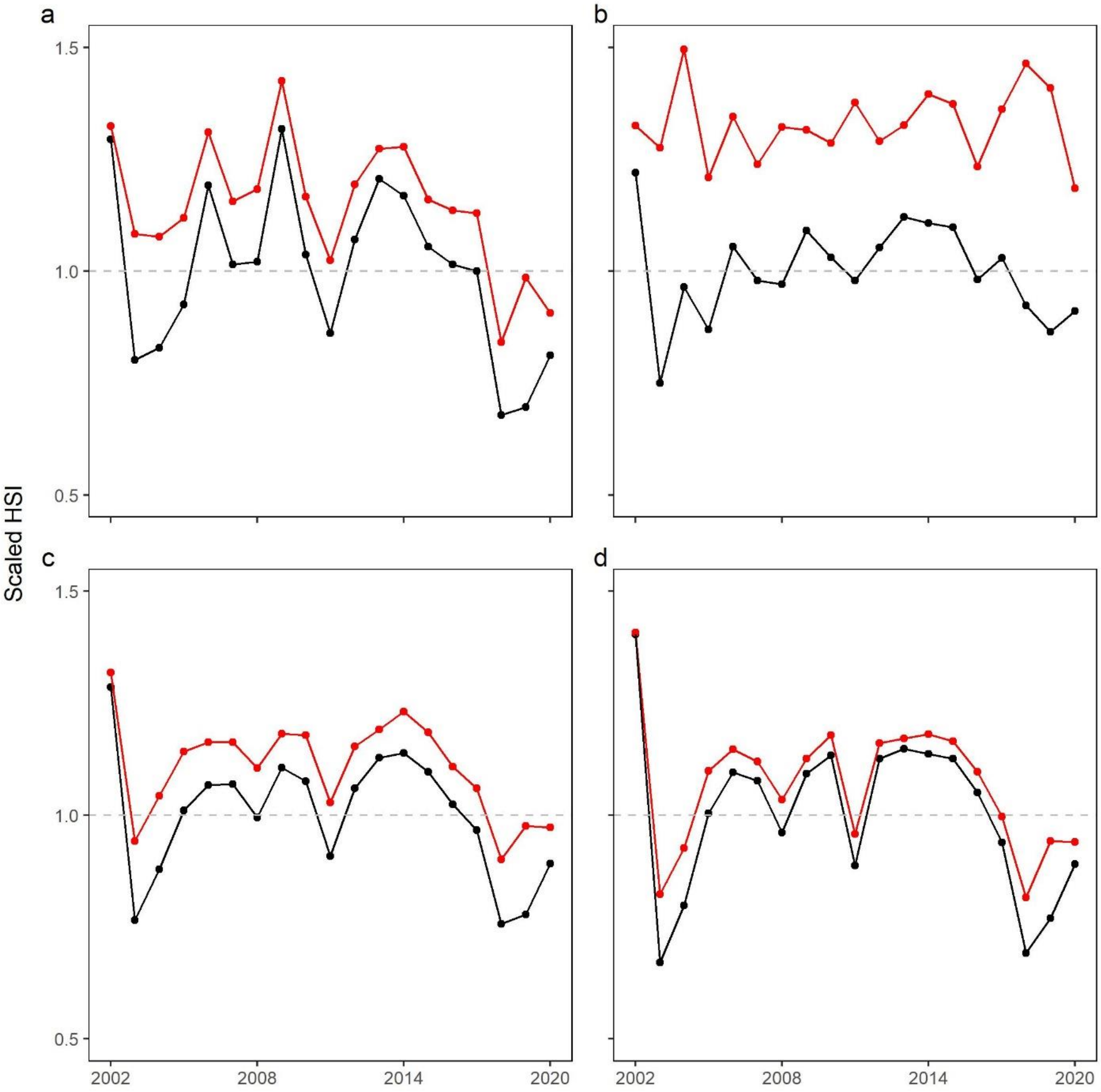


Fig. 3. Time series of habitat suitability indices (HSI) derived from the pairing of the ecological niche models (ENMs) and the simulated environmental conditions from the estuarine-carbon-biogeochemical Regional Ocean Modeling System (ROMS-ECB) for (a) Atlantic croaker, (b) spot, (c) summer flounder, and (d) weakfish. Black lines indicate the HSI based on the “true” values from ROMS-ECB and red lines indicate HSI based on the data with hypoxia “removed.”

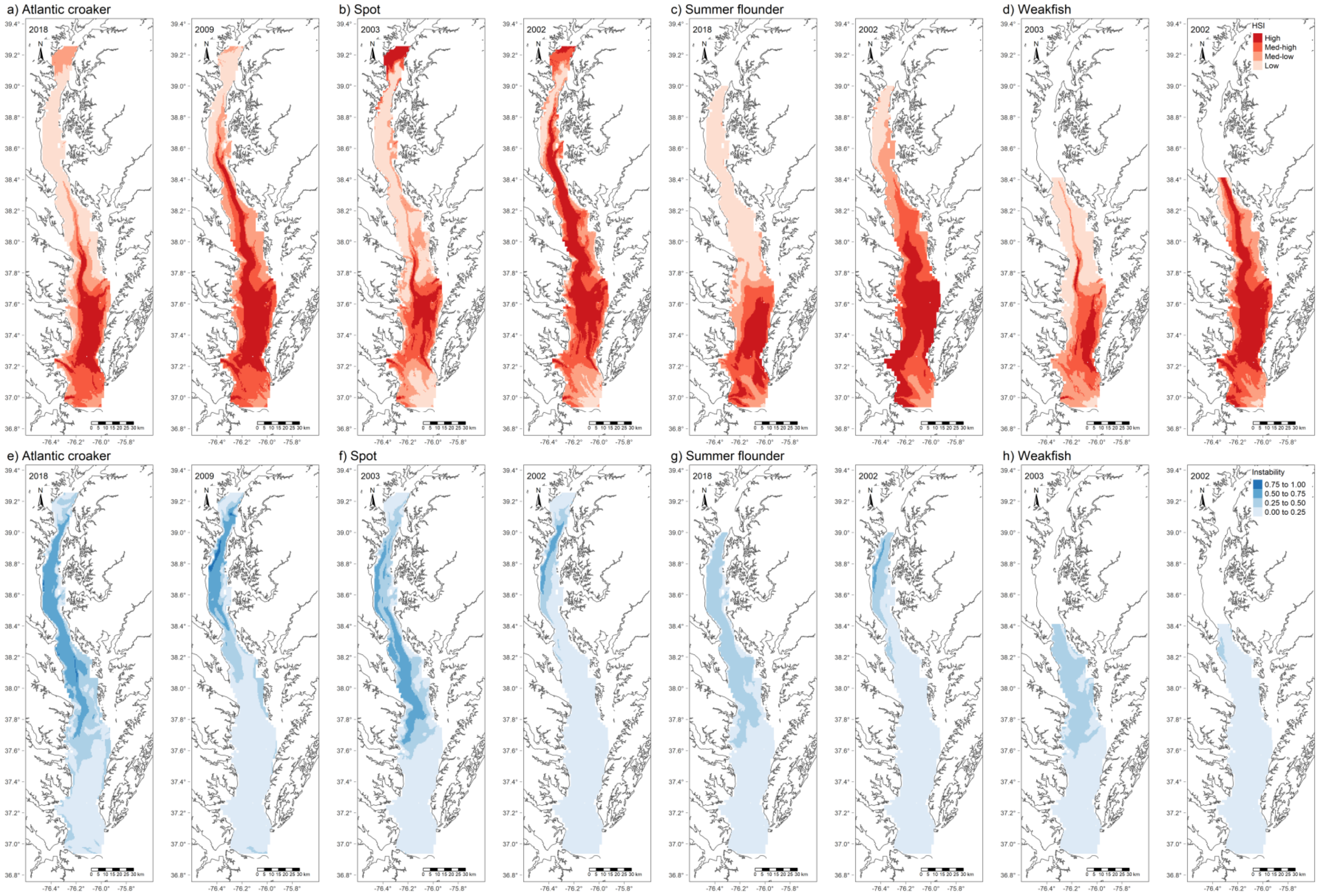

a) Atlantic croaker
2018
2009
b) Spot
2003
2002
c) Summer flounder
2018
2002
d) Weakfish
2003
2002
HSI
High
Med-high
Med-low
Low
e) Atlantic croaker
2018
2009
f) Spot
2003
2002
g) Summer flounder
2018
2002
h) Weakfish
2003
2002
Instability
0.75 to 1.00
0.50 to 0.75
0.25 to 0.50
0.00 to 0.25
N
0 5 10 15 20 25 30 km
39.4°
39.2°
39.0°
38.8°
38.6°
38.4°
38.2°
38.0°
37.8°
37.6°
37.4°
37.2°
37.0°
36.8°
-76.4°
-76.2°
-76.0°
-75.8°

Fig. 4. Maps displaying the spatial distribution of suitable habitat during years with the minimum and maximum annual habitat suitability indices (HSI) for (a) Atlantic croaker (min. 2018, max. 2009), (b) spot (min. 2003, max. 2002), (c) summer flounder (min. 2018, max. 2002), and (d) weakfish (min. 2003, max. 2000), generated by pairing the ecological niche model (ENM) with daily output from an estuarine-carbon-biogeochemical Regional Ocean Modeling System (ROMS-ECB). Mapped values represent averaged estimated suitability per cell from May-Sep. Quantiles were calculated using all years of habitat suitability, with the top 25% in the darkest red and the lowest quantile in the lightest. Instability values (e-h) were derived by dividing the range of the 95% confidence interval calculated in each ROMS-ECB cell by its corresponding mean suitability value. The highest instability (0.8 to 1.0) is displayed with the darkest shade of blue and the lowest instability (0 to 0.2) is in the lightest.

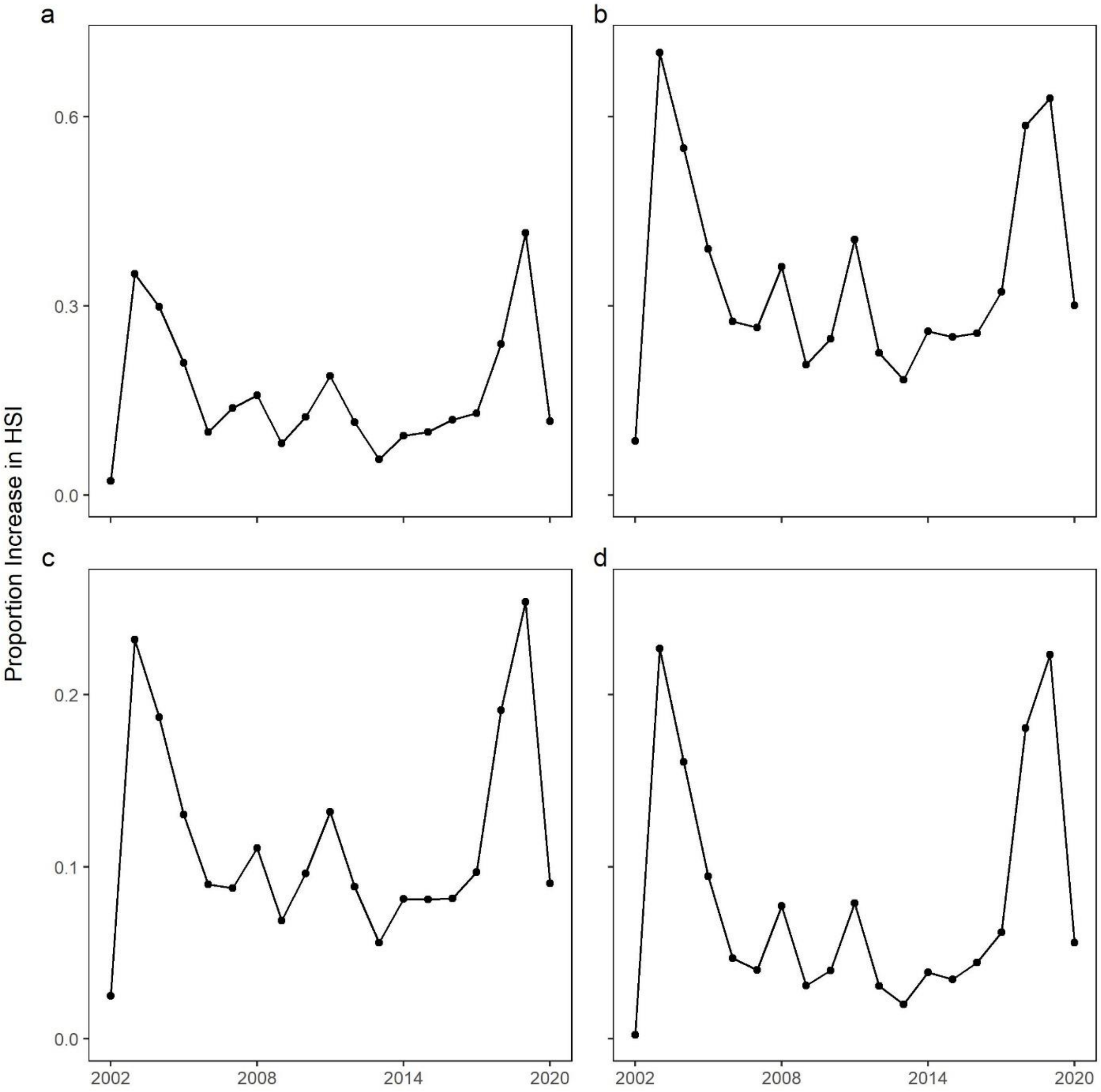


Fig. 5. The proportion increase in habitat suitability each year when hypoxia was “removed” for (a) Atlantic croaker, (b) spot, (c) summer flounder, and (d) weakfish.

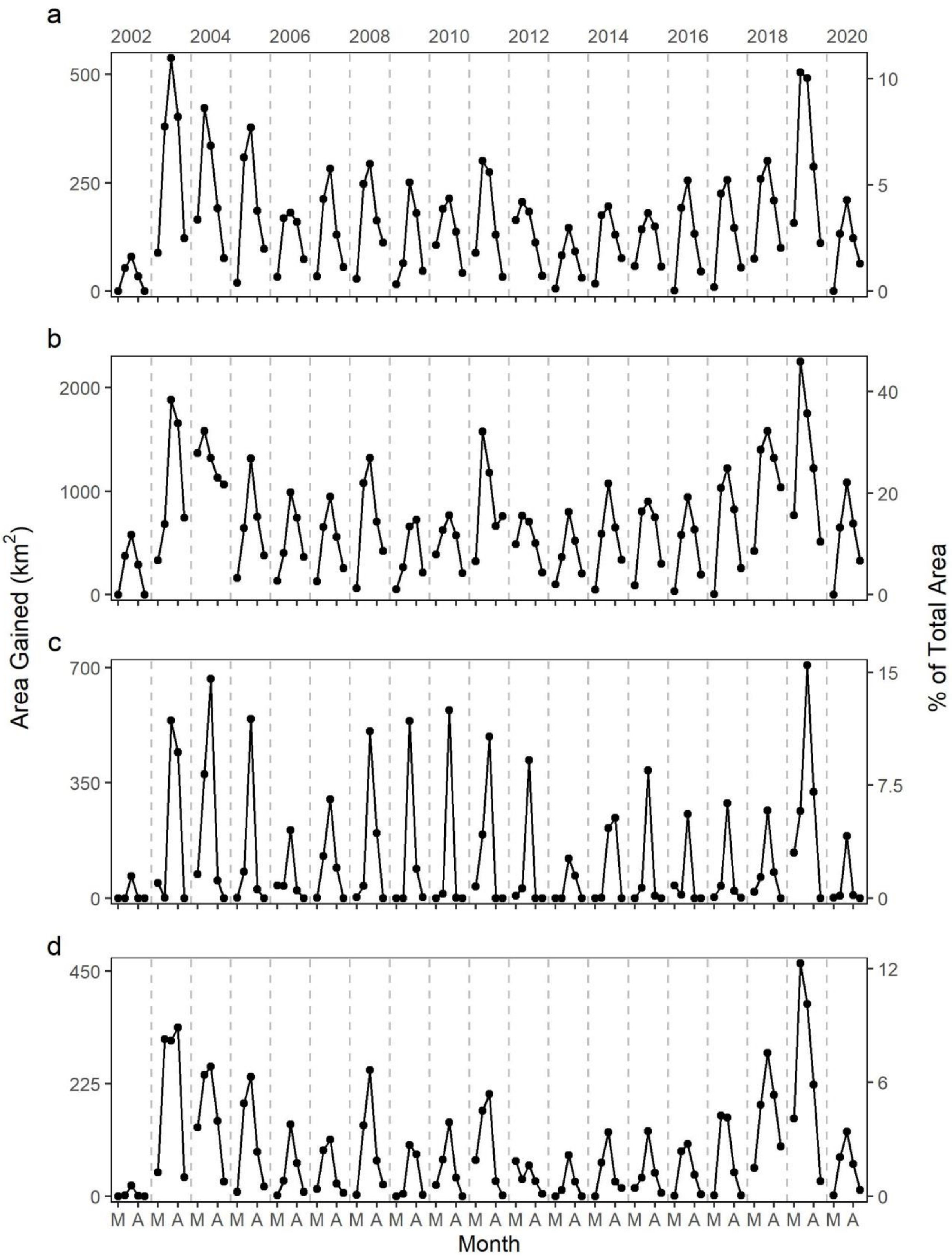
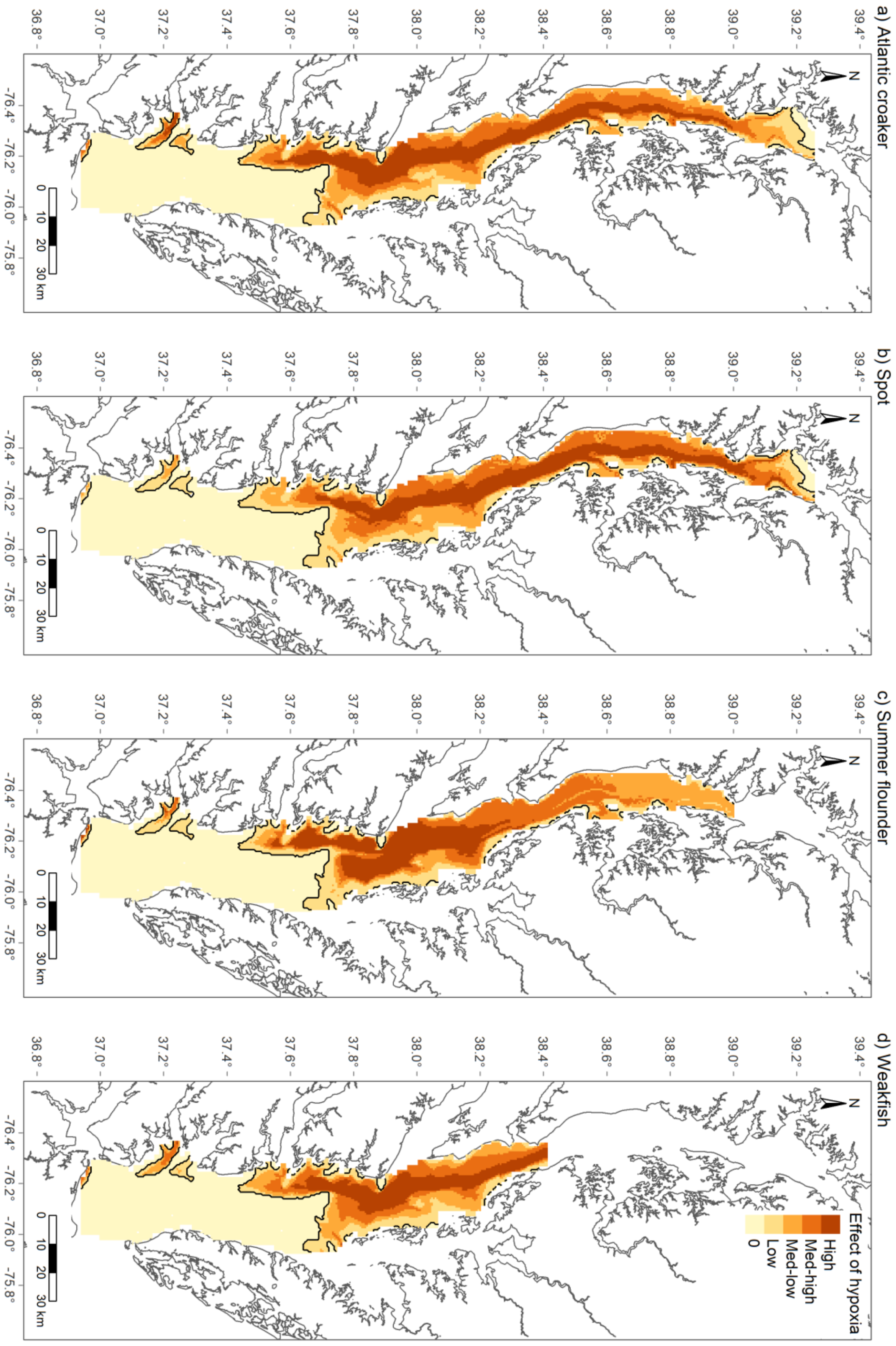

a
b
c
d
2002
2004
2006
2008
2010
2012
2014
2016
2018
2020
500
250
0
10
5
0
2000
1000
0
40
20
0
700
350
0
15
7.5
0
450
225
0
12
6
0
Area Gained (km^2)
% of Total Area
M A M A M A M A M A M A M A M A M A M A M A M A M A M A M A M A M A M A M A
Month

Fig. 6. The quantity of area gained each month (May-Sep) when hypoxia was “removed” for (a) Atlantic croaker, (b) spot, (c) summer flounder, and (d) weakfish. The second y-axis is the corresponding percentage of the total area of the sampling frame that was gained. The area gained was calculated by averaging each cell within a month and dividing by the average habitat suitability of the corresponding month across all years. Any cells that changed from below-average to average or above-average once hypoxia was “removed” were classified as area gained.


a) Atlantic croaker
b) Spot
c) Summer flounder
d) Weakfish
N
39.4°
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38.4°
38.2°
38.0°
37.8°
37.6°
37.4°
37.2°
37.0°
36.8°
-76.4°
-76.2°
-76.0°
-75.8°
0
10
20
30 km
Effect of hypoxia
High
Med-high
Med-low
Low
0

Fig. 7. Maps displaying the effects of “removing” hypoxia in July 2019, the year with the largest change, for (a) Atlantic croaker, (b) spot, (c) summer flounder, and (d) weakfish. The differences were calculated by averaging each cell within a month and year, and subtracting the estimated habitat suitability in each cell using the “true” estuarine-carbon-biogeochemical Regional Ocean Modeling System (ROMS-ECB) output from the estimated value in the corresponding cell with hypoxia “removed”. Quantiles were calculated based on all nonzero values (i.e., only cells where hypoxia occurred) and mapped. The largest changes in habitat suitability are represented with the darkest orange, and the lowest quantile in the lightest orange. All cells that were normoxic throughout July (i.e., no alterations in habitat suitability) are in yellow and the black outline surrounds the areas where hypoxia occurred.

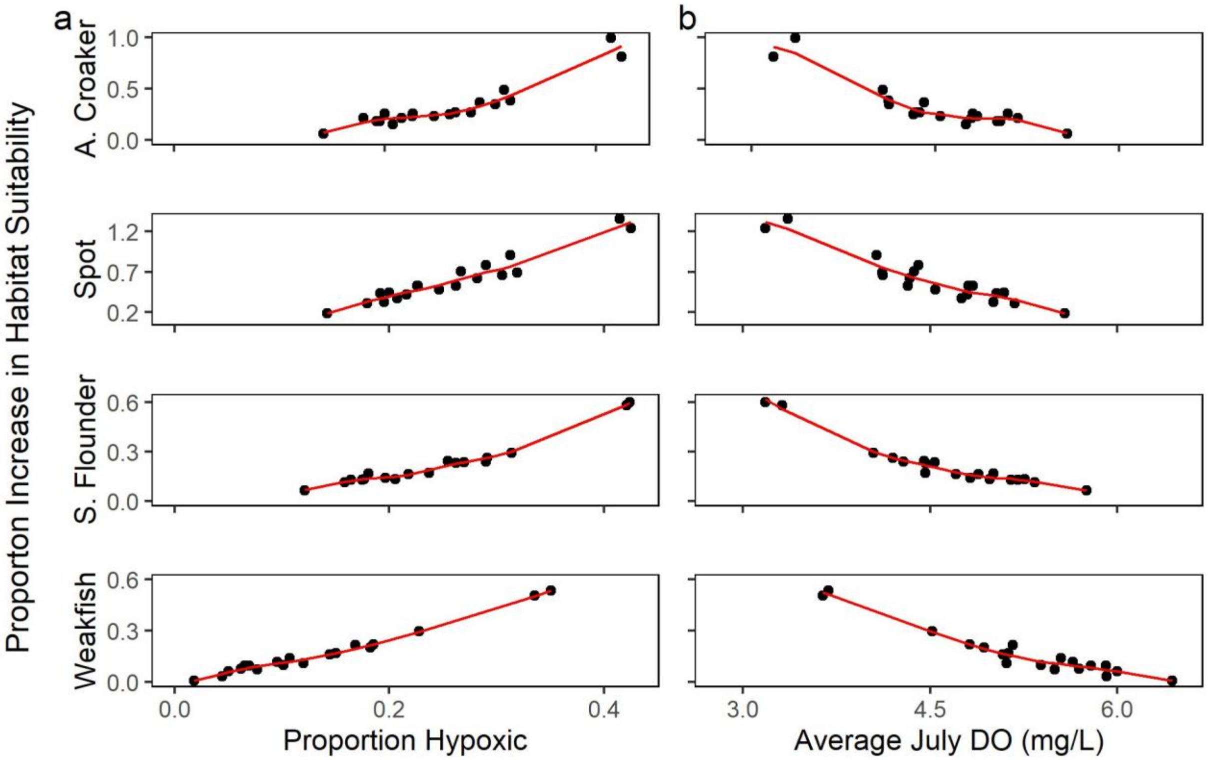

Fig. 8. The relationship between the proportional increase in habitat suitability in July with (a) hypoxic extent and (b) hypoxic severity for each species included in the analysis. Hypoxic extent was calculated as the proportion of the estuarine-carbon-biogeochemical Regional Ocean Modeling System (ROMS-ECB) cells that had simulated dissolved oxygen (DO) concentrations < 2.5 mg/L. Hypoxic severity was calculated as the average bottom DO in July. The proportion increase in habitat suitability was calculated by averaging each cell within a month/year and summing to get a single habitat suitability index (HSI) for each month and then calculating a proportion from the "true" HSI and the HSI with hypoxia "removed". The black dots are the calculated values and the red lines are locally weighted regression smoothers (LOESS). A. Croaker: Atlantic Croaker; S. Flounder: Summer Flounder

Supplementary Materials

Table S1. Data and structure of the selected ecological niche model (ENM) for each species. Regions refers to the stratification scheme used by the Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAP) trawl survey (Fig. 1). Covariates could be linear or nonlinear (i.e., smoothed), and the resulting number of knots for each smoother are listed after the nonlinear terms.

Species	Regions	Temperature	Dissolved Oxygen	Salinity	Depth
Atlantic croaker	1 – 5	Nonlinear, 6	Nonlinear, 7	Nonlinear, 4	Nonlinear, 6
Spot	1 – 5	Nonlinear, 8	Nonlinear, 6	Nonlinear, 4	Nonlinear, 6
Summer flounder	2 – 5	Nonlinear, 5	Nonlinear, 4	Nonlinear, 4	Linear
Weakfish	3 – 5	Nonlinear, 8	Nonlinear, 4	Nonlinear, 5	Nonlinear, 4

CHAPTER 4

Use of multi-source tagging data to estimate regional age-varying striped bass mortality and movement

Abstract

Tag-recovery models can be useful for estimating vital rates of harvested fish populations. However, complex life history characteristics of the tagged population and attributes of associated fisheries can challenge our ability to meet assumptions of mark-recapture models. We extended the instantaneous rates tag-recovery modeling framework to be subannual, multi-stock, spatially and temporally explicit, and to allow for catch-and-release fishing for analysis of 31 years (1990-2020) of Atlantic striped bass, *Morone saxatilis*, tag-recovery data collected from a coastwide coordinated tagging program. The model simultaneously estimates fleet-specific selectivity, annual commercial reporting rate, recreational catchability and annual adjustments for catch-and-release behaviors, instantaneous natural and fishing mortality rates, and age-based occupancy probabilities. Additionally, a time series of decreasing recreational tag reporting rates, mirroring patterns in angler behavior, was externally estimated and supplied to the model. Results indicated that natural mortality of striped bass increased over time and with age in Chesapeake Bay, a main producer region of the species, but was relatively stable elsewhere. Fishing mortality estimates generated by the model displayed substantial differences among fleet, disposition (fish or tag mortality), and region. Estimated producer stock-, time-, and age-based occupancy probabilities provide insight into the spatiotemporal distribution of the coastwide population.

Introduction

Traditional mark-recapture models (i.e., Brownie models) allow for the estimation of tag recovery and the total mortality rates experienced by a marked population (Brownie *et al.*, 1985). These two model parameters can be expressed as functions of other parameters, thereby allowing the investigation of factors contributing to changes in mortality or recovery rates. In the case when a fish population is tagged and tags are later recovered by fishers, the tag recovery rate is the product of the rates of the short-term tag-induced mortality/tag-shedding, tag reporting, and exploitation, with the latter assuming different functional forms depending on if the tagged population is subjected to a pulse or continuous fishery (Hoenig *et al.*, 1998a). For the typical situation of a continuous fishery, obtaining an estimate of the tag reporting rate is critical because it allows total mortality to be partitioned into its fishing and natural components (Hoenig *et al.*, 1998a; Pollock *et al.*, 2001). Movement probabilities are also of high interest to better understand life history and responses to natural and anthropogenic pressures exerted upon a fish population. The explicit estimation of movement probabilities from tag recovery data, however, is difficult due to an intrinsic link with mortality in traditional models (Hilborn, 1990; Brownie *et al.*, 1993; Schwarz *et al.*, 1993). Implementing a mark-recapture analysis in a Bayesian framework allows for the inclusion of data from published studies through priors placed on estimated parameters, additional penalizations for differences from previously reported values or alternative sources, and use of actual supplementary estimated parameters (Michielsens *et al.*, 2006; Liljestrand *et al.*, 2019). Such an extension, therefore, provides the ability to estimate additional parameters of interest without the risk of confounding from nuisance parameters.

Striped bass, *Morone saxatilis*, support extensive and economically valuable recreational and commercial fisheries along the east coast of the US (NMFS, 2022). Historically, commercial landings were variable from the 1950s-1970s but consistently declined thereafter to very low levels in the early 1980s, likely due to recruitment overfishing (Richards and Rago, 1999; NEFSC, 2019). Due to increasing concern over the potential loss of this valuable resource, the first striped bass Fisheries Management Plan (FMP) was developed in the early 1980s by the Atlantic States Marine Fisheries Commission (ASMFC). It was in this plan that the implementation of a tagging program to generate estimates of mortality and rates of migration of striped bass was first suggested (ASMFC, 1981). After the passage of the Atlantic Striped Bass Conservation Act, a federal law enacted in 1984 (16 U.S.C. §§ 5151), the management strategies suggested by the ASMFC Striped Bass Technical Committee became mandated. Thus, a coordinated, multijurisdictional tagging effort along the US coast began in the mid-1980s (Richards and Deuel, 1987; USDOI and USDOC, 1989) that provides a spatially explicit, long-standing time series of tagging data for analysis.

Although estimation of parameters of interest through mark-recapture analysis can be difficult for any species, the life cycle of striped bass introduces many complexities that exacerbate the challenge. While the distribution of striped bass encompasses nearly the entirety of the east coast of North America (Canada – Florida), the Atlantic coast migratory stock, which is managed as a single unit, extends from Maine to North Carolina (NEFSC, 2019). Striped bass are anadromous and undergo freshwater spawning migrations in early spring (Trent and Hassler, 1968; Setzler-Hamilton *et al.*, 1981; NEFSC, 2019) that are likely cued by temperature (Able and Grothues, 2007; Wingate and Secor, 2007). Residence time in estuaries is both sex- and age-dependent, with females entering the coastally migrating population earlier than males (Secor *et al.*, 2020).

Additionally, striped bass display homing behavior, returning to the same spawning grounds annually (Wingate and Secor, 2007; Callihan *et al.*, 2015; Secor *et al.*, 2020). The success of a spawning event and subsequent larval survival is highly dependent upon a myriad of biotic and abiotic factors, including: age and weight of female striped bass (Gervasi et al., 2019; Jackson & Tiller, 1952; Secor, 2000); freshwater flow (North & Houde, 2001; O'Connor et al., 2012); co-occurrence with zooplankton prey, through presence in the estuarine turbidity maximum (North & Houde, 2003) or cold, wet winters (Millette *et al.*, 2020); and mechanisms of density dependence and compensatory mortality (Martino and Houde, 2012). Thus, localized conditions in the spawning grounds could have varying influence on the health of the overall Atlantic coastal striped bass stock. There are three primary spawning stocks that contribute to the Atlantic coastal stock: Hudson River, Delaware River, and Chesapeake Bay, with the Chesapeake Bay stock contributing disproportionately (Koo, 1970; Fabrizio, 1987; ASMFC, 2022; Hasegawa *et al.*, 2022).

As a key recreational resource, the striped bass population experiences a substantial amount of recreational harvesting and also catch and release fishing (NMFS, 2022). The practice of catch and release fishing is well-established among recreational anglers and within fisheries management. Widespread in the striped bass tagging database are instances where a fish was caught, its tag was removed (streamer of the internal anchor tag clipped off), and then it was released alive back into the wild. This situation represents "mortality" of the tag and was the focus of work to extend tag recovery models to allow tag "mortality" to be modeled separately from mortality of the fish (Jiang *et al.*, 2007). First application of these extended models was to Chesapeake Bay striped bass tag recovery data and results provided evidence of increased rates of natural mortality, possibly due to the subacute and chronic bacterial disease mycobacteriosis

(Jiang *et al.*, 2007). A study unrelated to mycobacteriosis but also on Chesapeake Bay striped bass reported higher natural mortality within the resident fish compared to the coastal migrant population (Secor *et al.*, 2020).

Mycobacteriosis was first documented in Chesapeake Bay striped bass in 1997 (Vogelbein *et al.*, 1999). While detection rate of mycobacteriosis varies depending upon the technique used (Kaattari *et al.*, 2005), overall prevalence of visceral and dermal disease within Chesapeake Bay has exceeded 50% (Overton *et al.*, 2003; Rhodes *et al.*, 2004; Kaattari *et al.*, 2005), which is substantially higher than overall prevalence found in nearby estuaries (less than 20% in Delaware Bay; Ottinger et al. 2007) or in the coastal migrant population (less than 10%; Matsche et al. 2010). Disease prevalence in Chesapeake Bay fish also differs among sexes and is age/size-dependent, reaching over 80% for some age/size-classes (Rhodes *et al.*, 2004; Kaattari *et al.*, 2005; Gauthier *et al.*, 2008; Groner *et al.*, 2018). Studies have also shown lower relative survival rates of disease-positive fish compared to disease-negative fish through both the application of an epidemiology model to age-specific prevalence data (Gauthier et al. 2008) and from the analysis of tag recovery data from a disease-focused tagging study separate from the FMP mandated tagging efforts (Hoenig et al. 2017; Groner et al. 2018).

The goal of this study was to analyze the conventional striped bass tag recovery data to derive estimates of key parameters, including age-, region-, and time-varying fishing mortality rates, time- and producer stock-specific occupancy probabilities, and age-based natural mortality. The results of this work are intended to complement the routinely conducted age-structured integrated striped bass stock assessment and aid management efforts aimed at sustainable harvest of this valuable resource.

Methods

Tagging, fish disposition, and data filtering

Conventional tagging of striped bass along the US east coast began in 1986, however initial tagging efforts were sparse, so the data used in this study were limited to tags released from 1990-2020. During these three decades, a total of 23 agencies and institutions participated in the tagging program. Fish were captured by the agency and tagged with surgically implanted anchor tags in their abdomens and then released. Each tag had a unique number that was used to identify the individual. The timing and location of tagging varies by agency and encompasses most of the year and coast (ASMFC, 2013). To maximize the probability that the fish tagged were native to each of the three spawning stocks (Chesapeake Bay, Delaware River, and Hudson River), only tagging events that occurred within or near the spawning site during the months of March-June, the spawning season for striped bass (Trent and Hassler, 1968; Setzler-Hamilton *et al.*, 1981; NEFSC, 2019), were included. For similar reasons, fish tagged and released by hatcheries were excluded.

While most of the tagged fish were not aged at release, the length of the fish was recorded. Data from the Striped Bass Adult Spawning Stock Survey (1985-2020), administered by the Maryland Department of Natural Resources, include both length and age information for 37,371 striped bass and were used to create an age-length key, whereby an age was assigned to every 5 mm bin based on the largest proportion of fish-at-age recorded for that length bin. A single key was constructed based on all years of data and was then used to assign an age to tagged striped bass at time of release. Individuals that did not have length information were excluded from analysis.

When a tagged fish is recaptured, fishers report information regarding the capture, including the type of recapture (e.g., commercial or recreational; recreational fishers were those classified as sport or charter), the location, disposition of the fish (e.g., killed or released alive), and, if released alive, if the tag was removed from the fish. A recaptured fish released alive with the tag removed represents the tag "mortality" rather than death of the fish. This distinction was included in the analysis (Jiang et al. 2007), such that fishing mortality and tag mortality (i.e., disposition) were each tracked separately and by fleet. Thus, previously tagged striped bass were included in the analysis if they were killed during capture (i.e., fish mortality) or if the tag was removed and the fish was released alive (i.e., tag mortality).

Data were filtered and removed according to several criteria including encounter type outside of commercial or recreational (e.g., scientific survey), missing recapture/resighting location information, contradictions between release and recapture information (e.g., recapture or resighting date prior to date of tagging), and multiple resightings. All fish that had recapture information that led to their exclusion were also removed from the release data based on tag number.

Model

As noted previously, the release data of three producer regions were included in this analysis: (1) Chesapeake Bay, (2) Delaware River, and (3) Hudson River. Time steps were structured to reflect six-month periods (Jan-Jun, Jul-Dec) to allow estimated parameters to vary within a given year, and to capture the subannual migrations of striped bass. Ten age-classes were defined (2-11+) and all fish in the plus group (i.e., age 11 or older) were assumed to experience the same age-based dynamics regardless of their age within the group. Age 11 was chosen as the base of the plus group because of few observations of older fish tagged and re-encountered.

To derive age-, time-, and producer region-based occupancy probabilities, the recapture regions were defined to be outside of the Chesapeake Bay and within Chesapeake Bay. Recaptured fish were assigned a region of recapture based on the location information provided by the fisher. Occupancy probabilities were defined as the proportion of the total number of fish of a given age expected to be found within a region. Recaptures were categorized based on two fleets defined as commercial and recreational, and encounter disposition was tabulated for each fleet as either fish mortality or tag mortality. Finally, an annual reporting rate for the commercial fleet was estimated to allow for the derivation of the exploitation rate. Taken together, the model provided estimates of time-, region-, fleet-, and disposition-specific rates of fishing mortality, which were converted to age-based rates through the application of estimated fleet-specific selectivity functions. Also estimated were age-, time-, and region-varying rates of natural mortality. Model structure followed the instantaneous parameterization of the Brownie mark-recovery models (Brownie et al. 1985; Hoenig et al. 1998a; see Table 1 for parameter descriptions) and the program Automatic Differentiation Model Builder (ADMB; Fournier et al., 2012) was used for implementation.

The abundance of each cohort of striped bass tagged and released in producer region p at time T of age A, $I_{p,T,A}$, was tracked spatially and through time in six-month increments. The number of individuals of age a expected to be in region r at time t from the cohort released in producer region p at release time T of age A, $N_{p,T,A,t,r,a}$, was calculated through the application of mortality and occupancy probabilities. This model assumes no tag loss or tagging-induced mortality (Jiang *et al.*, 2007) such that the number of individuals expected at the time step of release is equivalent to the number released:

$$N_{p,T,A,t=T,r=p,a=A} = I_{p,T,A}.$$

Mortality and occupancy probabilities were applied sequentially, such that fish of age a must first survive at time t in region r, $S_{a,t,r}$, before dispersal to other regions:

$$N^*{}_{p,T,A,t,r,a} = N_{p,T,A,t,r,a} \times S_{a,t,r},$$

where N^* is the number of fish following survival, S, but prior to migration. During the same time step as release, fish were assumed to experience partial (0.5) mortality and exploitation due to survival for a portion of the six-month period before tagging occurred (Hoenig *et al.*, 1998b).

Applying the age-based occupancy probability of fish from producer region p during the migration period m to be in region r, $\varphi_{p,a,m,r}$, to N^* summed across all regions provided the calculation of the cohort abundance at time $t+1$, $N_{p,T,A,t+1,r,a}$:

$$N_{p,T,A,t+1,r,a} = \varphi_{p,a,m,r} \times \sum_r \left(N^*_{p,T,A,t,r,a}\right),$$

where m is the six-month period of time $t+1$ independent of the year.

The age of fish in a cohort was incremented following each complete year until reaching the plus group, a^*. Thus, the number of fish in the plus group at time $t + 1$ is the sum of fish in the plus group that survived time t and fish of age 10 that survived the year and entered into the plus group:

$$N_{p,T,A,t+1,r,a^*} = \varphi_{p,a^*,m,r} \times \left(\sum_r \left(N_{p,T,A,t,r,a^*-1} \times S_{a^*-1,t,r}\right) + \sum_r \left(N_{p,T,A,t,r,a^*} \times S_{a^*,t,r}\right)\right),$$

where $a^*- 1$ is the age class below the plus group and

$$N_{p,T,A,t,r,a^*-1} \times S_{a^*-1,t,r} = N^*_{p,T,A,t,r,a^*-1} \text{ and } N_{p,T,A,t,r,a^*} \times S_{a^*,t,r} = N^*_{p,T,A,t,r,a^*}.$$

To ensure the occupancy parameters were identifiable, only the occupancy probabilities outside the Chesapeake Bay (region 1) for all ages, producer regions, and migration periods were explicitly estimated. The corresponding occupancy probability inside Chesapeake Bay (region 2) was calculated by subtracting the estimated probability for outside the bay from 1, as the probabilities must sum to 1:

$$\varphi_{p,a,m,2} = 1 - \varphi_{p,a,m,1}.$$

Age-, time-, and region-specific survival, $S_{a,t,r}$, was calculated based on the total mortality experienced by fish of age *a* at time *t* in region *r*, $Z_{a,t,r}$:

$$S_{a,t,r} = e^{-Z_{a,t,r}}.$$

The total instantaneous mortality, $Z_{a,t,r}$, was the summation of instantaneous fishing mortality by fleet *f* on fish of age *a* at time *t* in region *r*, $F_{f,t,a,r}$, and instantaneous tag morality, $F'_{f,t,a,r}$, across fleets and natural mortality of fish of age a, M_a:

$$Z_{a,t,r} = \sum_f \left(F_{f,a,t,r} + F'_{f,a,t,r}\right) + M_a.$$

To address considerations regarding potential changes in natural mortality of Chesapeake Bay striped bass, additional model forms were developed that allowed natural mortality at age, M_a, to vary spatially and temporally. The time-varying forms of natural mortality explored include by decade (1990-1999, 2000-2009, and 2010-2020), fifteen-year periods (1990-2004 and 2005-2020), and prior- and post-mycobacteriosis discovery in Chesapeake Bay striped bass (1990-1999 and 2000-2020):

$$Z_{a,t,r} = \sum_f \left(F_{f,a,t,r} + F'_{f,a,t,r}\right) + M_{i,a,r},$$

where *i* indexes the time interval associated with natural mortality.

An age-specific estimate of fishing mortality was calculated through the application of age-based selectivity by fleet, $sel_{f,a}$, to fleet-, time-, and spatially-specific fishing mortality, $F_{f,t,r}$:

$$F_{f,a,t,r} = F_{f,t,r} \times sel_{f,a}.$$

For both fleets, age-based mortality of the tag, $F'_{f,a,t,r}$ was estimated following the same process:

$$F'_{f,a,t,r} = F'_{f,t,r} \times sel_{f,a}.$$

The selectivity of fleet *f* was assumed to be constant through time and for both dispositions within a fleet (i.e., fish mortality or tag mortality). Selectivity was assumed to follow an increasing logistic function of age:

$$sel_{f,a} = \frac{1}{1+ e^{-\alpha_f \times\left(a- \beta_f\right)}},$$

where α_f and β_f are fleet-specific parameters representing the age at which there is 50% selectivity and the slope of the curve, respectively, and *a* is the age.

Finally, the application of Baranov's catch equation (Quinn and Deriso, 1999) allowed for the calculation of the total number of striped bass of age *a* captured by fleet *f* at time *t* in region *r* from each cohort of fish (i.e., tagged and released in producer region *p* at time *T* and age *A*), for both dispositions:

$$C_{f,p,T,A,t,r,a} = N_{p,T,A,t,r,a} \times (1 - e^{-Z_{a,t,r}}) \times \frac{F_{f,a,t,r}}{Z_{a,t,r}} \times \lambda_{f,y}$$

$$C'_{f,p,T,A,t,r,a} = N_{p,T,A,t,r,a} \times (1 - e^{-Z_{a,t,r}}) \times \frac{F'_{f,a,t,r}}{Z_{a,t,r}} \times \lambda_{f,y},$$

where *C* is the calculated number of harvested striped bass, *C'* is the calculated number of harvested tags, $\lambda_{f,y}$ is the tag reporting rate of fleet *f* during year *y*, and *y* is the year associated with time *t*. The commercial reporting rate, $\lambda_{com,y}$, was estimated by the model simultaneously with all other parameters (see below for information on the recreational reporting rate, $\lambda_{rec,y}$).

As described, there were two dispositions of fleet-specific fishing mortality: fish mortality (*F*) and tag mortality (*F'*). Tag mortality represents the removal of the tag, but the fish was released alive. Thus, to convert the tag mortality to mortality experienced by the released fish, fleet-specific release-associated mortality, δ_f, was applied (Jiang *et al.*, 2007). Adding this product to the estimated fish mortality provided the total fishing mortality experienced by striped bass by fleet *f*, $F_{f_{tot},t,r}$:

$$F_{f_{tot},t,r} = F_{f,t,r} + \delta_f F'_{f,t,r}.$$

For the recreational fishery, release mortality has been estimated to be 9% (Diodati and Richards, 1996). The mortality associated with releasing a live striped bass from the commercial fishery is gear-dependent (NEFSC, 2019). Commercial gear for the striped bass fishery and the associated release mortalities include anchor gillnets (0.4275), drift gillnets (0.08), hook and line (0.09), pound nets (0.05), trawls (0.35), and uncategorized (0.2; ASMFC 2013). As commercial gear type was not considered in this analysis, release mortality was calculated by dividing the total annual estimated dead discards by the commercial fishery used in the stock assessment (NEFSC, 2019) by the annual total estimated commercial releases. This allowed for an estimated release mortality that varied annually, reflecting the composition of the commercial fishery within a given year.

Total fishing mortality experienced by striped bass in region *r* at time *t*, $F_{tot,t,r}$, can be calculated by summing across fleets:

$$F_{tot,t,r} = \sum_{f} F_{f_{tot},t,r},$$

where $F_{f_{tot},t,r}$ is calculated as described above.

Parameter Estimates

The parameters in this model were estimated by minimizing the sum of the negative log likelihood of the recovery data and priors:

$$P = NegLL_c + \rho_\varphi + \rho_E + \rho_H,$$

where ρ_φ, ρ_E, and ρ_H are the priors for the occupancy probabilities, effort data (see below), and harvest data, respectively. The estimated catches were assumed to follow a negative binomial distribution (Michielsens *et al.*, 2006):

$$NegLL_c = \sum_{f_d}\sum_{p}\sum_{T}\sum_{A}\sum_{t}\sum_{r} -\log_e\left(\frac{\Gamma\left(k + O_{f_d,p,T,A,t,r}\right)}{\Gamma(k)\Gamma\left(O_{f_d,p,T,A,t,r}\right)} \times \left(\frac{k}{k + C_{f_d,p,T,A,t,r}}\right)^{k} \times \left(\frac{C_{f_d,p,T,A,t,r}}{k + C_{f_d,p,T,A,t,r}}\right)^{O_{f_d,p,T,A,t,r}}\right),$$

where k is the overdispersion parameter, assumed to be 2.5 based on other studies (Liljestrand *et al.*, 2019) and evaluation of 0.5 increment adjustments, O represents the observed recaptures, and f_d is the disposition of the fish (i.e., released alive/tag mortality or harvested/fish mortality) of fleet f.

The occupancy probabilities were conditioned on a normal distribution, in log space, such that the sum of squares was calculated:

$$\rho_\varphi = \sum_{p} \log(\varphi_{p,a,m,r})^2.$$

This prevents the model from estimating values nearing infinity as the penalization is greater the farther a given occupancy probability is from zero.

Recreational fishing effort data were used as an external data source (i.e., auxiliary to the conventional tagging data) to provide additional baseline information in the estimation of fishing mortality by the recreational fleet. The incorporation of these data constrained the model to estimate values of recreational instantaneous fishing mortality and tag mortality that were in agreement with realized recreational fisher behavior. Data from the National Oceanic and Atmospheric Association (NOAA) Marine Recreational Information Program (MRIP; www.fisheries.noaa.gov/data-tools) were used, in the form of number of trips taken by the recreational fishing fleet. Fishing mortality can then take on the form:

$$F = qE,$$

where E is effort and q is the catchability coefficient (Ricker, 1975; Quinn and Deriso, 1999).

In this model, catchability of the recreational fleet was estimated regionally, q_r. A regional annual adjustment for the recreational tag mortality, $\theta'_{y,r}$, was also estimated and applied to catchability to account for differences in behavior of retaining the catch or releasing the fish alive:

$$q'_{y,r} = q_r \times \theta'_{y,r}.$$

The effort prior was conditioned such that the deviations of the two alternate calculations of instantaneous recreational fishing/tag mortality were log-normally distributed:

$$\rho_E = \sum_t \sum_r \left(\frac{\left(\log\left(q_r E_{t,r}\right) - \log\left(F_{rec,t,r}\right)\right)^2}{2\sigma^2} \right) + \sum_t \sum_r \left(\frac{\left(\log\left(q'_{y,r} E_{t,r}\right) - \log\left(F'_{rec,t,r}\right)\right)^2}{2\sigma^2} \right),$$

where y is the year corresponding to time t and σ^2 is the assumed variance of the distribution. A value of 0.2 was used for σ^2, in log space, which resulted in a coefficient of variation of ~45%.

The final external data source included in the model was the estimated harvest by recreational and commercial fishers, as calculated in the most recent striped bass stock assessment (NEFSC, 2019). The report provides annual estimates by region (Chesapeake Bay, ocean, and Delaware Bay) from 1990-2017. The harvest in Delaware Bay and the ocean were summed to represent the region outside of Chesapeake Bay. As the time series in the stock assessment was shorter than the time series considered in this study, the final three years of harvest (2018-2020) were calculated as the average of the last three years of harvest data. The deviation in the ratio of commercial harvest to recreational harvest in region *r* during year *y*, $H_{com,y,r}/H_{rec,y,r}$, to the ratio of estimated instantaneous fishing mortality by the commercial fleet to the recreational fleet during year *y* in region *r*, $F_{com,y,r}/F_{rec,y,r}$, constrained the model to estimate instantaneous fishing mortality rates by fleet that reflect external estimates of harvest. This deviation was assumed to follow a normal distribution:

$$\rho_H = \sum_y \sum_r \left(\frac{\left(\frac{H_{com,y,r}}{H_{rec,y,r}} - \frac{F_{com,y,r}}{F_{rec,y,r}} \right)^2}{2\sigma_r^2} \right),$$

where σ_r is the standard deviation associated with the time series of harvest ratios in region *r*, calculated to be 0.023 in region 1 (outside of Chesapeake Bay) and 0.147 in region 2 (inside the bay). The annual fishing mortality rate by fleet, $F_{com,y,r}$ and $F_{rec,y,r}$, was calculated by summing the instantaneous fishing mortality estimated in region *r* during the two six-month time steps that comprise a single year.

Vague uniform priors were placed on several of the parameters to constrain the estimates by limiting the parameter space explored by the model. Natural mortality, α_{com}, β_{com}, and β_{rec} were constrained between 0.0067 and 148.41 (-5 and 5 on the log scale),

$$M \sim U(0.0067, 148.41),$$

$$\alpha_{com} \sim U(0.0067, 148.41),$$

$$\beta_{com} \sim U(0.0067, 148.41),$$

$$\beta_{rec} \sim U(0.0067, 148.41),$$

α_{rec} was constrained between 0.0067 and 7.39 (-5 and 2 on the log scale),

$$\alpha_{rec} \sim U(0.0067, 7.39),$$

fishing mortality and tag mortality were constrained between 4.54×10^{-5} and 22026.47 (-10 and 10 on the log scale) for both fleets, *f*,

$$F_f \sim U(4.54 \times 10^{-5}, 22026.47),$$

$$F_f' \sim U(4.54 \times 10^{-5}, 22026.47),$$

the occupancy probabilities, φ, and the commercial reporting rate, λ, were constrained between 4.54×10^{-5} and 1 (-10 and 0 on the log scale),

$$\varphi \sim U(4.54 \times 10^{-5}, 1),$$

$$\lambda \sim U(4.54 \times 10^{-5}, 1),$$

the catchability of the recreational fleet was constrained between 2.06×10^{-9} and 1 (-20 and 0 on the log scale),

$$q \sim U(2.06 \times 10^{-9}, 1),$$

and the recreational tag mortality adjustment applied to catchability was constrained between 2.06×10^{-9} and 4.85×10^{8} (-20 and 20 on the log scale),

$$\theta' \sim U(2.06 \times 10^{-9}, 4.85 \times 10^{8})$$

Reporting Rate Estimation

As described, the reporting rate, λ, is confounded with the exploitation rate when estimating the recovery rate, and therefore, λ must be assumed to be known (Hoenig *et al.*, 1998a). An accurate estimate of λ is difficult to derive and often requires external data. The most common method for estimating λ is a high-reward tagging study, where known numbers of fish are tagged with high-reward tags and standard tags. Typically, it is assumed that there is a 100% reporting rate for high-reward tags, so the comparison of the number of high-reward tags returned to the number of standard tags returned allows for the derivation of the tag reporting rate for standard tags (Pollock *et al.*, 2001).

In the striped bass literature, the most commonly used value of λ is 0.43 (estimated by Kahn and Shirey 2000; used in Smith et al. 2000; Welsh et al. 2007; Jiang et al. 2007). However, several other high-reward tagging studies have been conducted and provided different estimates of the reporting rate. Two studies were conducted within the Chesapeake Bay specifically, and found the reporting rate to be 0.75 (Rugolo *et al.*, 1994) and 0.64 (Hornick *et al.*, 2000). Most recently, a high-reward tagging study was conducted in the mid-2000s to estimate the reporting rate regionally and by fleet, resulting in an estimated reporting rate of 0.11 for commercial fishers and 0.85 for recreational fishers (ASMFC, 2013).

It has also been suggested that the tag reporting rate may be decreasing over time (ASMFC, 2013). The striped bass tagging program has been occurring for over 30 years and angler fatigue related to the program and changes in efforts to encourage tag reporting (i.e., advertisements of the program) could be causing decreases in reporting rates. Significant declines in reporting rates have been found after only a year in a Florida fishery (Taylor *et al.*, 2006). To derive an annual tag reporting rate, and subsequently assess if the tag reporting rate is declining throughout the tagging program, the recreational recovery rate data were modeled over time.

In the analysis of the recreational recovery rate time series, only recaptures that occurred within the same year as release were considered. This was done to reduce the effect of a potential increase in natural mortality over time on the number of recaptured fish from a given cohort. The recreational fishery was chosen to be modeled because there are more tag returns from the recreational fishery than the commercial fishery, and because of the availability of the recreational effort data from MRIP.

A generalized linear model (GLM) was used to evaluate the relationship between the recreational recovery rate and time. The annual recovery rate was assumed to follow a beta distribution and annual effort was included as a covariate:

$$\frac{R_{yy}}{I_y} = b + \alpha_{1,y}(YR_y) + \alpha_{2,y}(E_y) + \varepsilon_y,$$

where R_{yy} is the number of recaptured striped bass in year y that were released in year y, I_y is the number of striped bass tagged and released in year y, b is the intercept, $\alpha_{1,y}$ and $\alpha_{2,y}$ are the estimated effects associated with year y, YR_y and effort in year y, E_y, and ε_y is the error. The R package "gamlss" was used to fit this model (Rigby and Stasinopoulos, 2005).

The marginal means approach (Searle *et al.*, 1980) was then used to derive information on the relationship between the annual recovery rate and year when effort was held constant. The proportional change in the estimated recovery rate was calculated for each subsequent year. Finally, this proportional change was applied to assumed starting values of the reporting rate from the literature (i.e., 0.85, ASMFC 2013; 0.75, Rugolo et al. 1994; 0.64, Hornick et al. 2000, and 0.43, Kahn and Shirey 2000). An initial maximum value of λ_{rec} was held constant for the first 10 years (1990-1999). This was done because the first coastwide high-reward tagging study concluded at the end of this period, providing the earliest estimated values of λ throughout the region (i.e., not localized within Chesapeake Bay). Further, at the beginning of the program it is likely that fishers are less aware of it, especially before a high-reward study with ample advertising is conducted, and may be less familiar with spotting a tag.

The externally estimated values of the reporting rate described above were used as these initial maximum values. Each time series of recreational reporting rate was used in the mark-recapture model and performance was evaluated through the use of diagnostic plots and Akaike's information criterion (AIC; Akaike 1973; Burnham and Anderson 2002):

$$AIC = 2\ \times NegLL + 2k,$$

where *NegLL* is the negative log likelihood and *k* is the number of parameters estimated. Due to the high complexity of this model, over 600 parameters were estimated and that number exceeded 700 in some formulations. Therefore, the penalization term for the number of parameters in the AIC calculation (+ 2k) was an important consideration in model selection as compared to using the raw negative log likelihood.

Results

Tagging

During 1990-2020, summed across all agencies participating in the coastwide tagging program, tags were deployed on more than 7,000 days and approximately 450,000 individual fish were tagged. When considering only those fish that were tagged in a producer region during a time in which they were most likely spawning or undergoing their freshwater spawning migration, included all necessary release information (e.g., length), and, if recaptured, met recapture criteria (e.g., recreational or commercial fisher, recapture ended in mortality of fish or tag, etc.), the overall dataset was reduced to 172,555 striped bass; 89,606 (51.9%) from the Chesapeake Bay spawning stock, 48,815 (28.3%) from the Delaware River, and 34,134 (19.8%) from the Hudson River. Of these, there were 28,019 recaptured fish reported, which is a recovery rate of 16.2%. The recovery rate of tagged fish from each producer region varied, with the highest recovery rate of fish from the Delaware River (20.6%; 10,080 fish), followed by Hudson River fish (17.7%; 6,033 fish), and the lowest recovery rate of Chesapeake Bay fish (13.3%;

11,906 fish). Of all the recaptures, 24,278 were caught and reported by the recreational fleet (57.8% fish mortality and 42.2% tag mortality) and 3,741 by the commercial fleet (72% fish mortality and 28% tag mortality).

Model

The most empirically supported model based on diagnostics and AIC estimated 695 parameters. This version included time-varying age-based natural mortality within Chesapeake Bay (30 parameters), time invariant natural mortality outside of the bay (10 parameters), time-, region-, fleet-, and disposition-varying rates of fishing mortality (496 parameters), an annual reporting rate for the commercial fishery (31 parameters), fleet-specific selectivity (4 parameters), regional catchability for the recreational fleet (2 parameters), an annual regional adjustment to catchability to account for changes in catch and release fishing behaviors (62 parameters), and age-, migration period-, and producer region-specific occupancy probabilities (60 parameters). Overall, the model fit the tag recovery data relatively well (Figure 1).

Similarly, the estimated parameters from the model reflected the external data sources used as priors (i.e., recreational effort data from MRIP and the ratio of commercial harvest to recreational harvest as estimated by the stock assessment, NEFSC 2019) fairly well. The estimated instantaneous fishing mortality by the recreational fleet, F_{rec}, reflected the external effort data from MRIP, represented as a calculated value of $F_{rec,calc}$ (the product of an estimated regional catchability and time- and regionally-specific recreational fishing effort), relatively well (Figure S1). While there are some years with substantial differences between the two values, overall, the confidence intervals primarily overlap. The estimated and calculated instantaneous tag mortality rates by the recreational fleet are highly similar throughout the time series (Figure S2). Outside of the Chesapeake Bay, the ratio of the estimated instantaneous fishing mortality from the commercial fleet to that of the recreational fleet fit the estimated harvest ratios from the stock assessment well (Figure S3a). In the Chesapeake Bay, however, the estimated harvest ratios from the stock assessment are outside of the 95% confidence intervals of the instantaneous fishing mortality ratios for several years (Figure S3b).

When summing across all fleets, dispositions, regions, and time steps, the total model misspecification of striped bass recaptures from the Chesapeake Bay producer region amounted to an overestimate of 5.7% of the total observed recaptures, an underestimate of 4.98% of fish from the Delaware River, and an overestimate of 3.68% of the Hudson River stock. Of the over 28,000 reported recaptures in this analysis, the model ultimately overestimated the number of fish by 1.42%.

Natural Mortality

The form of the age-based natural mortality in the selected model was allowed to vary regionally and temporally by decade within the Chesapeake Bay. In contrast, the selected form of natural mortality in the region outside of the bay was held constant throughout time. Allowing natural mortality outside of the bay to change by decade was also explored, but the AIC was better for time invariant M in this region (Table 2). Other forms of regionally- and temporally-varying forms of natural mortality were considered, including a time span of 15 years (instead of decades), and separating into prior- and post-mycobacteriosis discovery in Chesapeake Bay striped bass. Similarly, the AIC values of these models indicated that the chosen form of natural mortality (i.e., varying by decade within the bay and time invariant outside the estuary) provided the optimal explanation of the data (Table 2).

Natural mortality was estimated to primarily decrease with age (Figure 2) In the Chesapeake Bay, the estimated natural mortality increased each decade (Figure 2b). The confidence intervals at all ages overlapped during the second and third decade, indicating no substantial increases in natural mortality. In contrast, the confidence intervals did not overlap for ages 2, 5, and 6 between the first and second decade, nor did they for four ages (3, 5, 7, and 8) between the first decade and last decade; the later decade had a higher natural mortality rate in both comparisons (Figure 2b). When comparing the natural mortality at age outside of Chesapeake Bay to within the bay, natural mortality was higher within the estuary for only two ages (7 and 9) during the first decade (Figure 2c). By the third decade, almost all ages (2-3, 5, 7-11+) had substantially higher natural mortality rates in the Chesapeake Bay (Figure 2d).

Fishing Mortality

The estimated instantaneous fishing mortality rates varied widely between regions and associated six-month time steps (Figure 3). Outside of the Chesapeake Bay, the instantaneous fishing mortality experienced by striped bass was dominated by the recreational sector (Figure 3a and 3c), while inside the estuary, the commercial sector had a sizable contribution some years (Figures 3b, d). In both regions, the instantaneous fishing mortality was higher during the second six-month period (Jul-Dec; Figures 3c, d). While the instantaneous tag mortality by the commercial sector was low for both subannual periods and regions, the pattern in tag mortality by the recreational fleet varied between regions. Outside of the Chesapeake Bay, tag mortality was initially high relative to the other rates of instantaneous mortality before declining (Figure 3a, c), but tag mortality was estimated to be relatively low throughout the time series in Chesapeake Bay (Figure 3b, d).

The total instantaneous mortality rates experienced by striped bass by sector were calculated by applying fleet-specific proportions of mortality associated with catch and release fishing (Figure 4). The instantaneous fishing mortality by the commercial sector was estimated to be higher inside the Chesapeake Bay than outside the estuary, however, this difference was substantial for only a portion of the time series, primarily during the first 15 years (Figure 4a). In contrast, the instantaneous recreational fishing mortality rate was relatively similar across regions (Figure 4b). The estimated total instantaneous fishing mortality rates, summed across fleets, were higher in the Chesapeake Bay from 1993-2001, similar between the two regions for the next decade, before the rate was estimated to be higher in the bay for several years more recently (2014, 2015, 2018, and 2020; Figure 4c).

Occupancy Probabilities

For the striped bass from the Chesapeake Bay producer region, the probability of occupancy outside of the bay increased with age (Figure 5a). At the oldest ages (9-11+), there was an increase in probability for the fish to be outside of the bay during the second six-month period of the year (Jul-Dec), as compared to the portion of the year that includes spawning (Jan-Jun; Figure 5a). The reverse was displayed by striped bass from the Delaware River stock, with a decrease in probability of the oldest fish (7-11+) to be found outside of the Chesapeake Bay in the second half of the year (i.e., an increase in probability to be located within the bay; Figure 5b). Occupancy probabilities for striped bass from the Hudson River producer region indicated that those fish are rarely seen within Chesapeake Bay (Figure 5c).

Reporting Rate

The externally conducted beta regression analysis relating the annual recovery rate by recreational fishers to year and recreational effort found significant relationships with both covariates. The association of the annual recreational recovery rate with year was significantly negative, and with effort the relationship was significantly positive ($p < 0.05$). Of the various initial values of the recreational reporting rate explored and supplied to the mark-recapture model, 0.43 (based on Kahn and Shirey 2000) minimized the negative log likelihood (Table 3) and, therefore, was the selected value (Figure 6).

The commercial reporting rate was estimated within the mark-recapture model and was, expectedly, sensitive to the recreational reporting rate supplied. The model estimated a high commercial reporting rate during the first several years of the analysis, before falling sharply and fluctuating annually around relatively low values (Figure 6).

Discussion

The methods in this analysis extended the instantaneous formulation (Hoenig *et al.*, 1998a) of the traditional mark-recapture Brownie model (Brownie *et al.*, 1985) that accounts for catch and release fishing (Jiang *et al.*, 2007) to a subannual, multi-stock, spatially and temporally explicit version that allows for simultaneous estimation of key parameters, including occupancy and mortality. Further, this investigation utilized over thirty years of striped bass conventional tagging data from a coordinated coastwide effort in a comprehensive synthesis. This allowed for age-, region-, time-, and stock-specific estimates of natural mortality, fishing morality by fleet and disposition, and occupancy probabilities. These fine-scale and biologically relevant parameters can be used to inform management of a highly valuable species.

Moreover, this study estimated the commercial reporting rate simultaneously, rather than relying on an externally supplied value. Other studies have found direct estimation of reporting rate to be unstable (Hoenig *et al.*, 1998a; Jiang *et al.*, 2007) and so this methodology serves as a relatively novel approach to decrease the dependence on an externally supplied value. The reporting rate was also estimated to be time-varying for both the commercial and recreational fleet. This investigation was the first to implement a reporting rate time series in support of striped bass mark-recapture modeling.

Model output indicated that natural mortality at age has not changed substantially since 1990 outside of the Chesapeake Bay, but it appears to have increased within the estuary. As described, the outbreak of mycobacteriosis in Chesapeake Bay striped bass has been suggested to have caused an increase in natural mortality experienced by this species over time. Disease status was not incorporated in this model, nor are the data available for the full time-series, so the role of disease-associated mortality cannot be directly extrapolated from the natural mortality estimates, although it supports reported patterns of mycobacteriosis prevalence. A previous quantitative analysis (through 2003) of localized striped bass tagging data (only in Maryland waters) found an increase in natural mortality over time (Jiang *et al.*, 2007), and the mark-recapture analysis presented here has extended those findings to bay-wide. Additionally, this study was the first to include discrete regions, which indicated that natural mortality is increasing only within Chesapeake Bay and has likely not changed appreciably outside of the estuary.

Natural mortality of fishes is generally assumed to decrease with increasing size, and therefore age (Beverton and Holt, 1959; Pauly, 1980; Lorenzen, 1996). The model estimates of natural mortality followed this pattern outside of the Chesapeake Bay and during the first decade within the bay (Figure 2). Although the increasing trend in estimated natural mortality with age within the bay more recently contradicts classic life history theory, prevalence of mycobacteriosis in striped bass in the bay also increases with age until about age 4-5, after which prevalence declines (Rhodes *et al.*, 2004; Gauthier *et al.*, 2008). The first age at which the model estimates of natural mortality in the bay during recent decades begins increasing is age 5, which corresponds with the notion that disease-associated mortality may be occurring in older fish.

The magnitude of the natural mortality estimates in recent decades within Chesapeake Bay may be high, but there is evidence that currently accepted values of natural mortality may be substantially lower than the true experience of the species. An analysis accounting for disease prevalence in Chesapeake Bay striped bass found that the natural mortality rate may be nearly twice as high as previously accepted values (Hoenig *et al.*, 2017). Moreover, the mortality rate of mycobacteriosis-infected fish increases with sea surface temperature (Groner *et al.*, 2018), and the bay has warmed significantly as a result of climate change (Ding and Elmore, 2015; Hinson *et al.*, 2021). Additionally, hypoxic volume has increased in Chesapeake Bay (Hagy *et al.*, 2004; Murphy *et al.*, 2011), and oxy-thermal habitat compression has been documented for striped bass in the estuary (Itakura *et al.*, 2021), which has been suggested as a mode of increased disease transmission (Coutant, 1985). This is potentially further exacerbated by an increased concentration of *Mycobacterium* in warmer waters (Jacobs *et al.*, 2009). Taken together, this suggests that prior estimates of natural mortality rates experienced by striped bass in Chesapeake Bay may be increasingly underestimated with time.

The estimates of age-based natural mortality outside of the Chesapeake Bay were relatively similar to assumed values used in the most recent peer-reviewed stock assessment (Jiang *et al.*, 2007; NEFSC, 2019). The majority of ages (six of ten) used in population analyses by the stock assessment fall within the 95% confidence intervals of the age-based natural mortality for the region outside of the Chesapeake Bay estimated by this model, as well as within the 95% confidence intervals of natural mortality for the first decade within Chesapeake Bay. However, in the second and third decades, only one stock assessment value falls within the confidence intervals, suggesting that the calculations used to estimate population size and stock status may be overestimating the survival of striped bass.

The trends in fishing mortality over time were similar to the output in the most recent stock assessment update (ASMFC, 2022), with *F* increasing at the beginning of the time series (1990s), then fluctuating at relatively high levels throughout the 2000s, before declining over the past several years. The magnitudes of fishing mortality are also relatively similar between this analysis and the stock assessment. For much of the time series, this model estimated substantially higher fishing mortality within the Chesapeake Bay, as compared to outside the estuary. The stock assessment, however, consistently estimated markedly higher fishing mortality in coastal waters compared to within the bay.

This investigation tracked recaptures of tagged striped bass by fleet (recreational and commercial) and disposition (fish harvested and fish released alive), providing estimates of fish mortality (*F*) and tag mortality (*F'*) imposed by sector. To calculate the total fishing mortality by fleet, the tag mortality is converted by applying rates of fleet-specific mortality associated with release (Jiang *et al.*, 2007). These release-mortality rates are assumed to be constant through time, but they could vary intra- and inter-annually. A mortality rate of 9% has been applied to striped bass caught and released by hook and line since the 1990s (Diodati and Richards, 1996). The upper end of the preferred temperature of adult striped bass is only approximately 25°C, which the waters of the Chesapeake Bay often exceed seasonally (Coutant, 1985). Inhabitance of suboptimal water temperatures could cause stress and result in additional mortality after release. Such a phenomenon has been documented in numerous species (Gale *et al.*, 2013), and mortality in released striped bass was found to significantly increase at only 21°C (Nelson, 1998), which is below temperatures experienced in the Chesapeake Bay. Further, as described, the Chesapeake Bay is warming (Hinson *et al.*, 2021) and, thus, release-mortality could be chronically increasing over time, in addition to seasonal variation.

Key outputs of this model are the subannual stock- and age-specific occupancy probabilities, which represent time-integrated regional habitat usage. That is, there is a single occupancy probability representing the entire six-month period, although fish are likely moving during that time. For example, the first half-year period, which includes spawning times for each of the three producer regions, extends from Jan-Jun, which includes time before and after spawning. Thus, striped bass could be caught outside of their natal estuary while traveling towards it to spawn, or after they complete spawning and re-enter the coastal waters. This is likely why the model indicated that there was a relatively high probability of older fish (9-11+) from the Chesapeake Bay stock to be present outside of the estuary during the subannual time step that includes their spawning season. Striped bass display strong homing behaviors, returning to the same spawning grounds following coastal migrations, seemingly irrespective of producer region (Wingate and Secor, 2007; Callihan *et al.*, 2015; Secor *et al.*, 2020). While skipped spawning does occur in striped bass, it is uncommon (Callihan *et al.*, 2015; Secor *et al.*, 2020). Taken together, this indicates that the occupancy probability of striped bass from the Chesapeake Bay stock in coastal waters should be low during the spawning season. Therefore, these results are more likely due to the length of the subannual time step, rather than indicative of skipped spawning behaviors.

There are resident striped bass in the Chesapeake Bay, individuals that remain in the estuary throughout the year, comprised primarily of younger/smaller fish (Secor *et al.*, 2020). Larger fish are more likely to undergo coastal migrations (Dorazio *et al.*, 1994; Secor *et al.*, 2020), generally migrating farther with age (Secor and Piccoli, 2007). This model found that the first age of striped bass from the Chesapeake Bay stock to exhibit ≥ 50% occupancy probability outside of the estuary was age 9, which is slightly younger but within the age range found in an acoustic telemetry study (Secor *et al.*, 2020).

While these analyses sought to include many complexities to better reflect the realized dynamics of striped bass, there are many remaining aspects that could be considered in future work. As described above, shortening the subannual time steps could allow mortality and occupation probabilities to be tracked at a higher resolution, and could potentially allow for inferences to be made regarding spawning behavior through use of the occupancy probabilities. Similarly, striped bass migratory behavior varies seasonally during the non-spawning time. Upon leaving the estuary, Chesapeake Bay migrants typically travel north toward Massachusetts, where they remain through summer and into early fall (Oct), and thereafter travel south to overwinter (Secor *et al.*, 2020). By developing a model with both shorter subannual time steps and more regions, these migratory behaviors could be captured more fully. However, adjusting the length of the subannual time steps and the number of recapture regions would result in a simultaneous increase in parameters to be estimated and a decrease in data to support those estimations.

An additional aspect of striped bass life history that could not be included in the model is the sex-based dynamics of the species. Female striped bass reach larger sizes (Setzler *et al.*, 1980) and the sex ratio is increasingly female with age (Trent and Hassler, 1968; Setzler *et al.*, 1980). As larger individuals undergo ocean migrations (Dorazio *et al.*, 1994; Secor *et al.*, 2020), the majority of these migrants are female (Secor *et al.*, 2020). However, a high proportion of tagged striped bass were not sexed, which therefore precludes a sex-based analysis of occupancy probabilities.

All fisheries mark-recapture models require assumptions about the reporting rate of fishers, due to the confounded relationship of recovery rate with exploitation and reporting rates (Hoenig *et al.*, 1998a; Pollock *et al.*, 2001). While theoretically it is possible to estimate the reporting rate during the modeling process (Hoenig *et al.*, 1998a), in practice it often leads to unreasonable estimates of other parameters and low precision (Jiang *et al.*, 2007). The simultaneous estimation of the reporting rate was not feasible for all fleets within this model, which motivated the strategy to supply only a recreational-specific reporting rate and allow the model to estimate the commercial reporting rate. Further, the calculation of the recreational reporting rate by quantifying a decrease through time through use of a beta regression and effort data, circumvented the typical assumption that the reporting rate is constant through time. Finally, running the model with the various reporting rates estimated by external high-reward tagging studies facilitated a more objective determination of the most quantitatively supported reporting rate instead of an assumed true value.

The commercial reporting rates estimated simultaneously by the model were higher than the estimated value from the most recent striped bass high-reward tagging study (0.11), which is also the only study that separates the reporting rate by fleet (ASMFC, 2013). For approximately half of the years, the commercial reporting rate was estimated to be higher than the provided recreational reporting rate. While the high-reward fleet-specific estimates of reporting rate found the recreational reporting rate to be approximately eight times greater than the commercial reporting rate, the study was conducted after nearly 20 years after the establishment of the coordinated coastwide tagging program (ASMFC, 2013). Human behavior is complex, and the reporting rate could change rapidly in response to numerous unquantified factors. For example, the commercial fishing moratorium ended in 1990 (ASMFC, 1989; Richards and Rago, 1999), coincident with the first year in this investigation, and lower commercial allocations compared to before the moratorium, could affect fishers' willingness to participate in the tagging study.

The uncertainty surrounding the commercial reporting rates estimated by this model are high. Thus, the absolute value of the estimated commercial reporting rates should be interpreted with caution, but the patterning in them could reflect true reporting rate dynamics. Developing more accurate and recent tag reporting rates should be a priority to improve future analyses of striped bass tagging data owing to the bias introduced by an incorrectly specified tag reporting rate. However, the key parameters of interest in this investigation (i.e., natural mortality and occupancy probabilities) were relatively robust to the starting value of the recreational reporting rate.

An additional assumption of the model is that the tag reporting rate does not vary by fish length (Jiang *et al.*, 2007). Such an assumption is unable to be tested, but it is possible that it would be violated in practice. It would be reasonable to expect fishers to be less likely to report undersized tagged striped bass. Similarly, striped bass fishing in federal waters, in the Exclusive Economic Zone (EEZ; 3-200 nautical miles offshore) was prohibited in 1990 and the moratorium continues to the present (Nelson, 2018). Striped bass are further protected in federal waters through their federal gamefish status, granted in 2007, which precludes commercial fishing in the EEZ (Exec. Order No. 13449, 2007; Nelson, 2018). If any fishers, and particularly commercial fishers, were to catch tagged striped bass in federal waters, they may be less likely to report the tag, even if the catch was incidental.

Other important assumptions of the model are that there is no tag shedding (short-term or chronic), nor tag-induced mortality (Jiang *et al.*, 2007). Both immediate tag loss and tag-induced mortality of striped bass using internal anchor tags has not been documented (Dunning *et al.*, 1987). Estimates of short-term tag retention of internal anchor tags vary, but reported estimates for striped bass encapsulating the size range of the majority of tagged individuals of this study range from 73% (Sprankle *et al.*, 1996) to 98% (Dunning *et al.*, 1987; Waldman *et al.*, 1991). There is also evidence that tag retention varies with size of the striped bass (Waldman *et al.*, 1990). Although these results generally support the model configuration, alterations in the physical environment as related to climate change, as described above, could be causing suboptimal conditions for striped bass. This increase in stress could also cause subsequent increases in tag-induced mortality. Similarly, at the onset of the program, the agencies may be less skilled in deploying tags and there could be increased tag loss or tag-induced mortality. However, at this time, both values are unquantified at the scale necessary for this model (i.e., age/size specific) and, therefore, adjustments to the assumptions cannot be made.

Overall, this investigation has developed a highly complex mark-recapture model to better reflect true striped bass and fisher dynamics and has provided estimates of key parameters that can be used by fishery managers. The occupancy probabilities supplied by this model could aid the development of a stock-specific statistical catch-at-age model, which is a goal of the ASMFC Striped Bass Technical Committee (NEFSC, 2019). This analysis has also provided support for previously unquantified hypotheses of natural mortality of striped bass in Chesapeake Bay, and differences temporally and regionally. Continued alterations in the physical environment of the Chesapeake Bay in response to climate change could negatively affect striped bass in the estuary (Costantini *et al.*, 2008; Itakura *et al.*, 2021), thus, the parameters estimated here provide important baseline information on striped bass. Collectively, this study provides pertinent information to sustainably manage a highly important species while also contributing a model framework that could assist with analyses of mark-recapture data for other species.

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Tables

Table 1. Variables used in the mark-recapture model with descriptions and values.

Variable	Description	Value
p	Producer region	1-3: Chesapeake Bay, Delaware River, Hudson River
T	Time of release	1-31: 1990-2020, March-June
A	Age at release	2-11+
t	Time step; $t \geq T$	1-62: Jan-Jun/Jul-Dec 1990-2020
a	Age at time t	2-11+
r	Region at time t	1-2: Inside Chesapeake Bay, outside Chesapeake Bay
y	Year at time t	1-31: 1990-2020
i	Time intervals of varying lengths for exploration of natural mortality	Decades (1-3: 1990-1999, 2000-2009, 2010-2020); 15 years (1-2: 1990-2004, 2005-2020) Prior/post mycobacteriosis discovery (1-2: 1990-1999, 2000-2020)
m	Migration period	1-2: Jan-Jun, Jul-Dec
Likelihood Components		
$NegLL_c$	Negative log likelihood of the estimated recoveries	
ρ_{φ}	Prior for occupancy probabilities	
ρ_E	Prior for effort	
ρ_H	Prior for harvest	

Provided Quantities	
$I_{p,T,A}$	Number of fish tagged and released in producer region p at time T of age A
λ_{rec}	The rag reporting rate by the recreational fishery
$O_{f,p,T,A,t,r,a}$	The observed recaptured fish of age a by fleet f at time t in region r from the cohort tagged in producer region p of age A at time T
$E_{t,r}$	Recreational fishing effort from the Marine Recreational Information Program (MRIP) at time t in region r
$H_{f,y,r}$	Estimated harvest by fleet f in region r during year y by the stock assessment (NEFSC 2019)

Calculated Quantities	
$N_{p,T,A,t,r,a}$	Number of fish that were released in producer region p at time T of age A, expected to be present at time t in region r at age a
$S_{a,t,r}$	Survival of fish of age a at time t in region r
$Z_{a,t,r}$	Total instantaneous mortality experienced by a fish of age a at time t in region r
$sel_{f,a}$	Selectivity of fleet f on fish of age a
$F_{f,t,a,r}$	Instantaneous fishing mortality experienced by a fish of age a at time t in region r by fleet f
$F'_{f,t,a,r}$	Instantaneous tag mortality applied to a fish of age a in region r at time t by fleet f
$C_{f,p,T,A,t,r,a}$	The number of fish from the cohort tagged in producer region p of age A at time T expected to be recaptured by fleet f of age a at time t in region r
$q'_{y,r}$	Catchability of the recreational fleet in region r at year y, adjusted for annual changes catch and release behaviors

Directly Estimated Quantities	
$M_{i,a,r}$	Instantaneous natural mortality experienced by a fish of age a in region r during time interval i
α_f	Age at which selectivity is 50% for fleet f
β_f	Slope of the selectivity curve for fleet f
$\Phi_{p,a,t,r}$	Occupancy probability of a fish of age a from producer region p to be in region r at time t
$F_{f,t,r}$	Instantaneous fishing mortality applied by fleet f at time t in region r
$F'_{f,t,r}$	Instantaneous tag mortality applied by fleet f at time t in region r
λ_{com}	The tag reporting rate by the commercial fishery
q_r	Catchability of the recreational fleet in region r
$\theta'_{y,r}$	Annual region-specific adjustment to recreational catchability to account for changes in catch and release behaviors

Table 2. Forms of natural mortality explored. AIC is Akaike's information criterion and ΔAIC is the difference between the AIC value and the minimum. Subscript values are a for age, r for region, d for decade, and h for half. Year range subscripts represent time spans of differing lengths and values of 1 and 2 represent region 1 (outside of Chesapeake Bay) and region 2 (within the estuary) when treatments of M vary between the regions. The recreational reporting rate used in the final selected model (maximum of 0.43 at the beginning of the time series) was used for these model runs.

Form of M	**Description**	**AIC**	**ΔAIC**
M_a	Age-based Time- and region-invariant	70025.8	575.6
$M_{a,r}$	Region- and age-based Time-invariant	69797	346.8
$M_{d,a,r}$	Time-, region-, and age-based, Time separated by decade (1990-1999, 2000-2009, 2010-2020)	69479.4	29.2
$M_{a,1}$, $M_{d,a,2}$	Region- and age-based Time-invariant in region 1, time-based by decade in region 2	69450.2	0
$M_{1990\text{-}1999,2000\text{-}2020,a,r}$	Time-, region- and age-based Time separated into prior (1990-1999) and post (2000-2020) mycobacteriosis discovery in Chesapeake Bay striped bass	69522.8	72.6
$M_{a,1}$, $M_{1990\text{-}1999,2000\text{-}2020,a,2}$	Region- and age-based Time-invariant in region 1, time-based in region 2, separated into prior (1990-1999) and post (2000-2020) mycobacteriosis discovery in Chesapeake Bay striped bass	69548.8	98.6
$M_{h,a,r}$	Time-, region-, and age based Time separated into halves (1990-2004, 2005-2020)	69551.8	101.6

Table 3. The starting values for the first 10 years of the calculated recreational reporting rate, λ_{rec}, supplied to the mark-recapture model. AIC is Akaike's information criterion and ΔAIC is the difference between the AIC value and the minimum. The same proportional decline estimated through the beta regression relating recovery rate to year and recreational effort was applied to all reporting rate time series. The form of the age-based natural model used in the final selected model (time invariant outside of the Chesapeake Bay, time-based within the bay, varying be decade) was used in all model runs.

Initial λ_{rec}	**AIC**	**ΔAIC**
0.43 Kahn and Shirey 2000	69450.2	0
0.64 Hornick et al. 2000	69502	51.8
0.75 Rugolo et al. 1994	69503.8	53.6
0.85 ASMFC 2013	69505.6	55.4

Figures

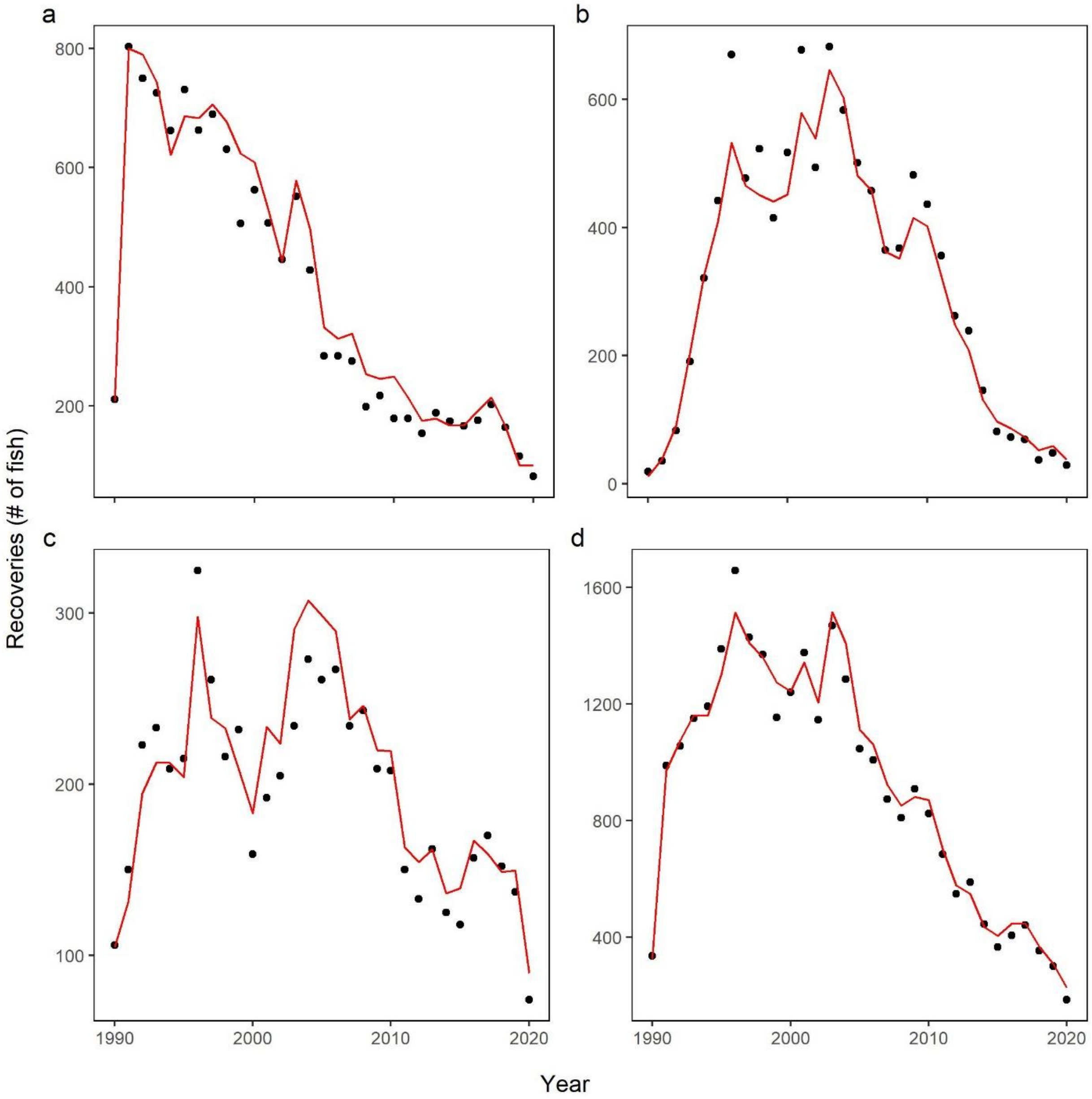

Figure 1. The number of predicted (red line) and observed (black dots) recoveries of tagged striped bass, summed across subannual time steps, fleets, and regions from (a) the Chesapeake Bay stock, (b) the Delaware River stock, and (c) the Hudson River stock, and (d) summed across producer regions.

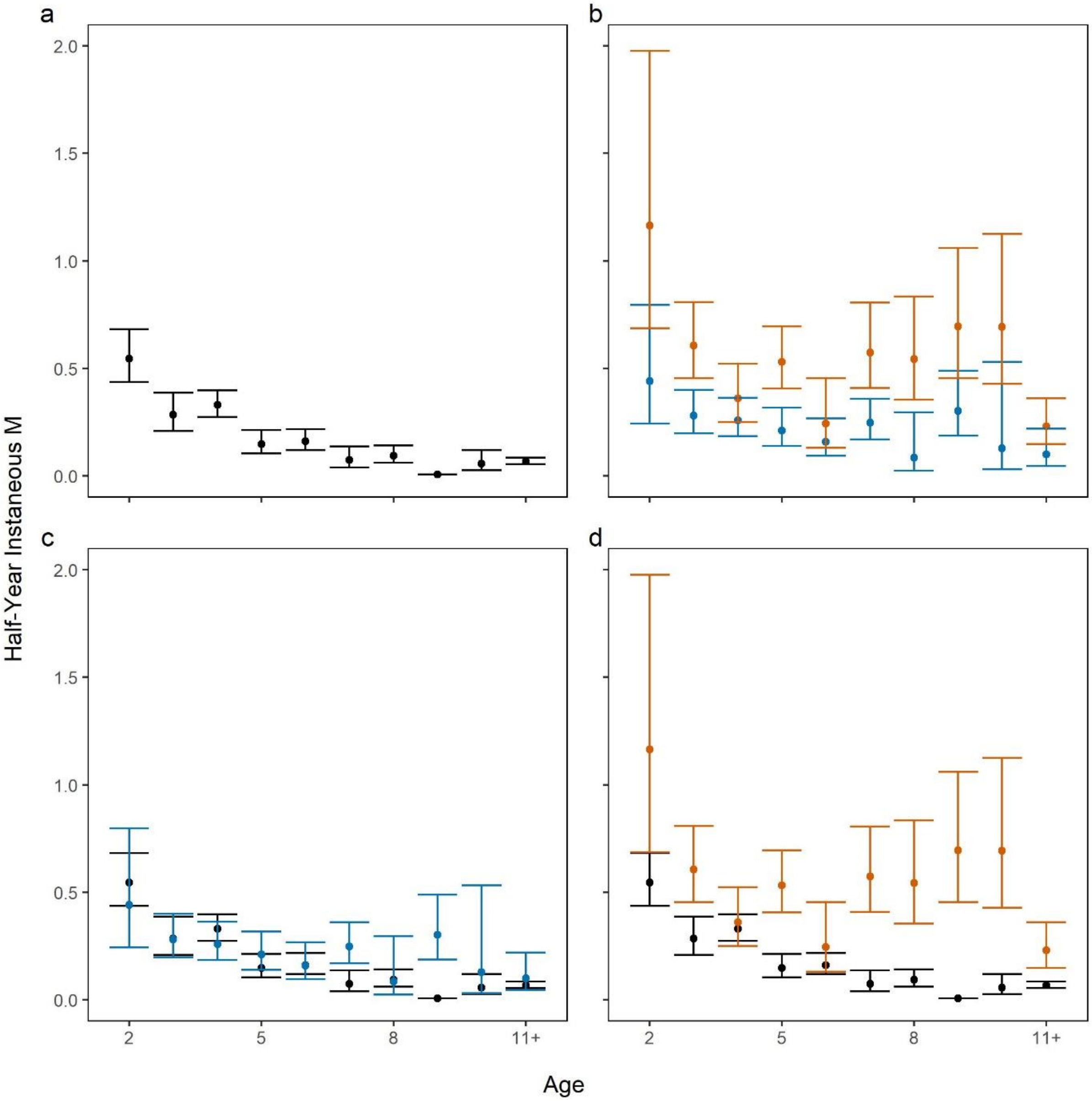

Figure 2. Estimated natural mortality by age during a 6-month time step (a) outside of the Chesapeake Bay, (b) inside Chesapeake Bay, with the first decade (1990-1999) in blue and the final decade (2010-2020) in orange, (c) outside the Chesapeake Bay (black) compared to the first decade inside the bay (blue), and (d) outside the Chesapeake Bay (black) compared to the final decade inside the bay (orange). The error bars represent the 95% confidence intervals surrounding the means.

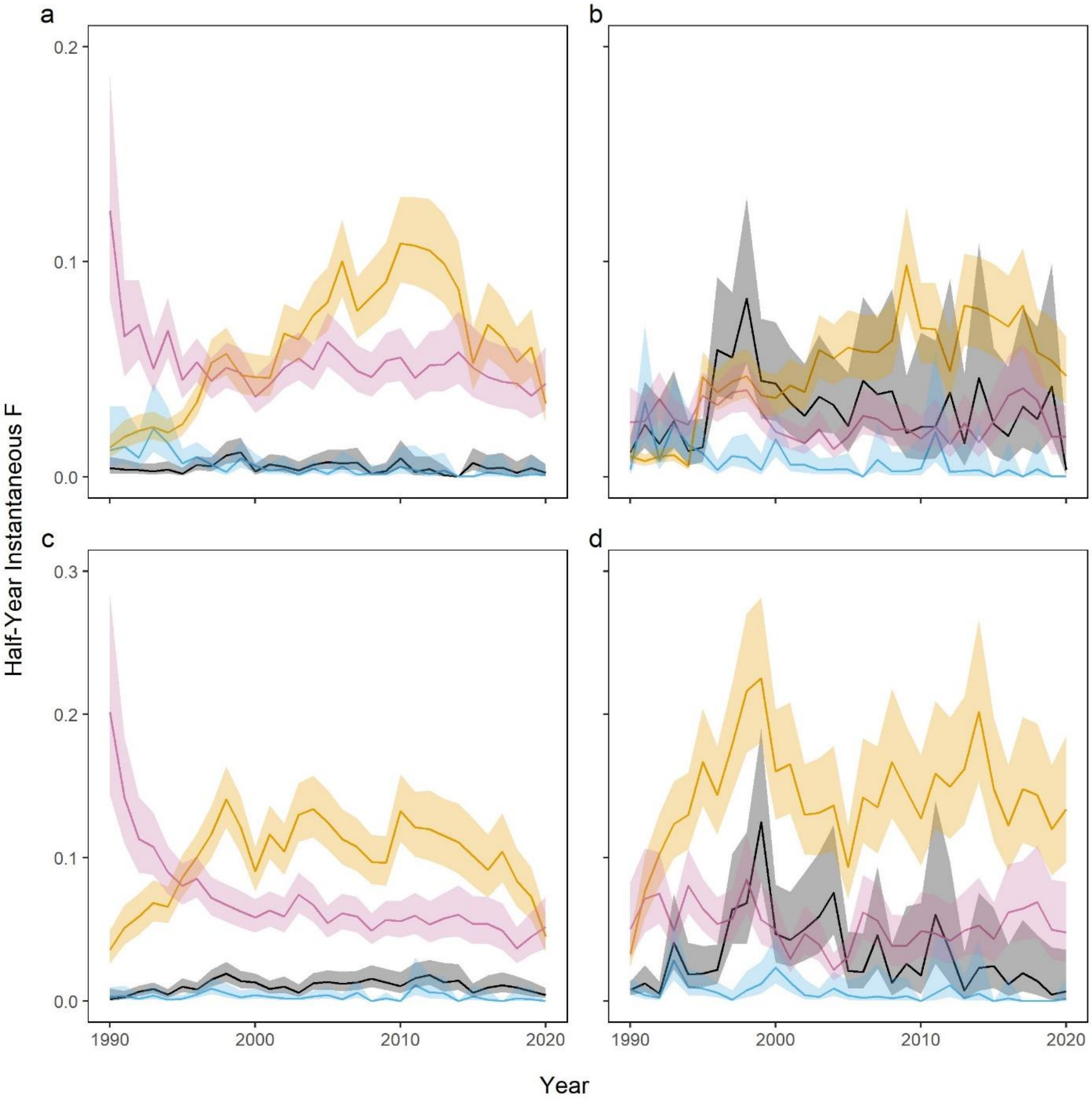

Figure 3. Model estimates of instantaneous fishing mortality experienced by striped bass during (a) the first 6-month period (Jan-Jun) outside Chesapeake Bay and (b) inside the bay, and (c) the second 6-month period (Jul-Dec) outside the bay and (d) within the estuary. The black lines represent the instantaneous fishing mortality by the commercial sector, the blue lines are the instantaneous tag mortality (i.e., a striped bass is recaptured, the tag is removed, and the fish is released alive) by the commercial sector, the orange lines are the instantaneous fishing mortality by the recreational sector, and the pink lines are the instantaneous tag mortality by the recreational sector. The ribbons represent the 95% confidence intervals.

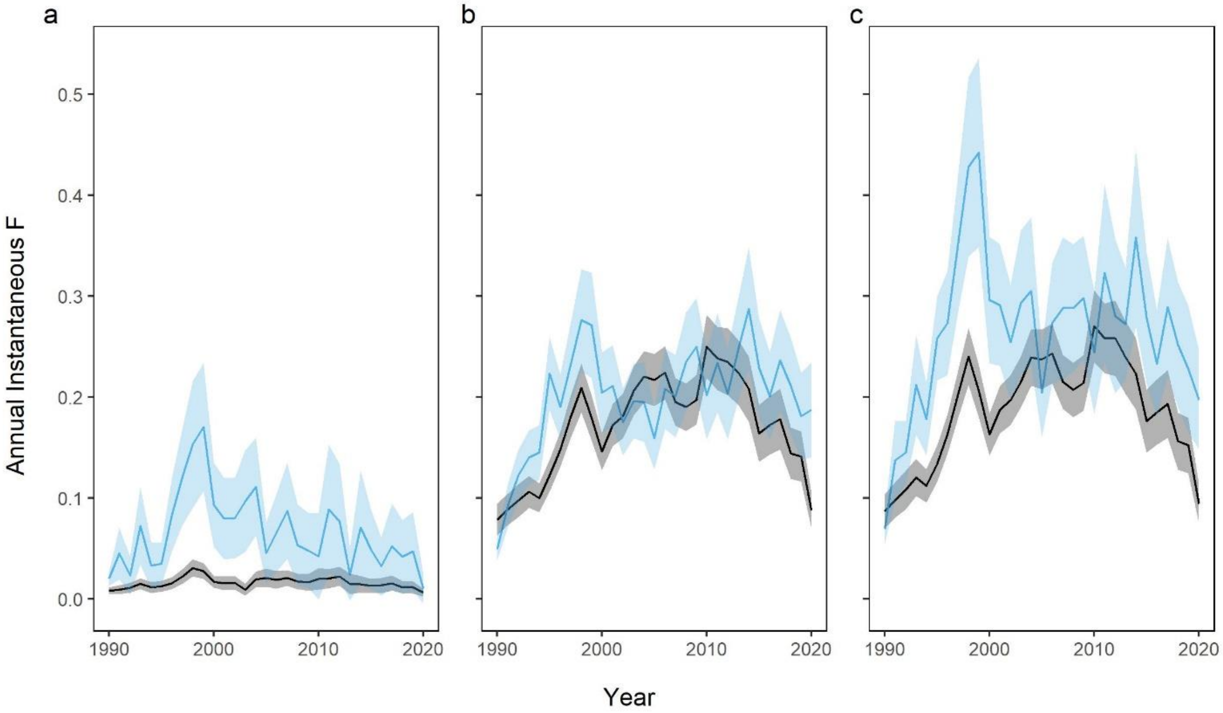

Figure 4. The total annual instantaneous fishing mortality experienced by striped bass from the (a) commercial sector, (b) recreational sector, and (c) combined recreational and commercial. The blue lines represent fishing mortality experienced inside the Chesapeake Bay and the black lines are outside of the bay, with the ribbons as the 95% confidence intervals. The contribution of the instantaneous tag mortality (*F'*) to striped bass mortality was calculated by applying assumed mortality rates related to catch and release fishery.

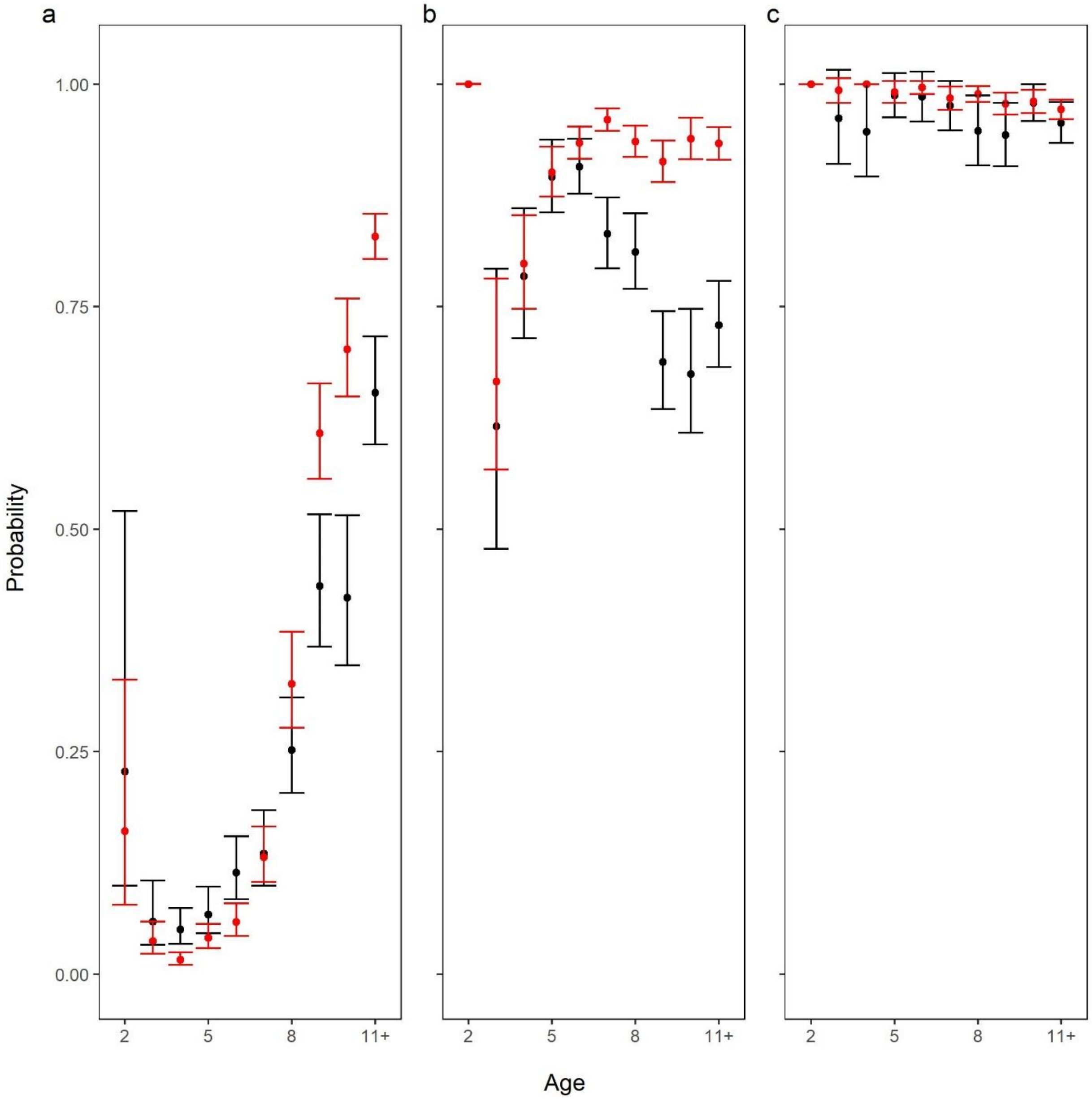

Figure 5. The estimated probability of occupancy outside of the Chesapeake Bay with age of striped bass from the (a) Chesapeake Bay, (b) Delaware River, and (c) Hudson River producer regions. The black lines are during the first six-month period (Jan-Jun) and the red lines are the second (Jul-Dec). The error bars represent the 95% confidence intervals.

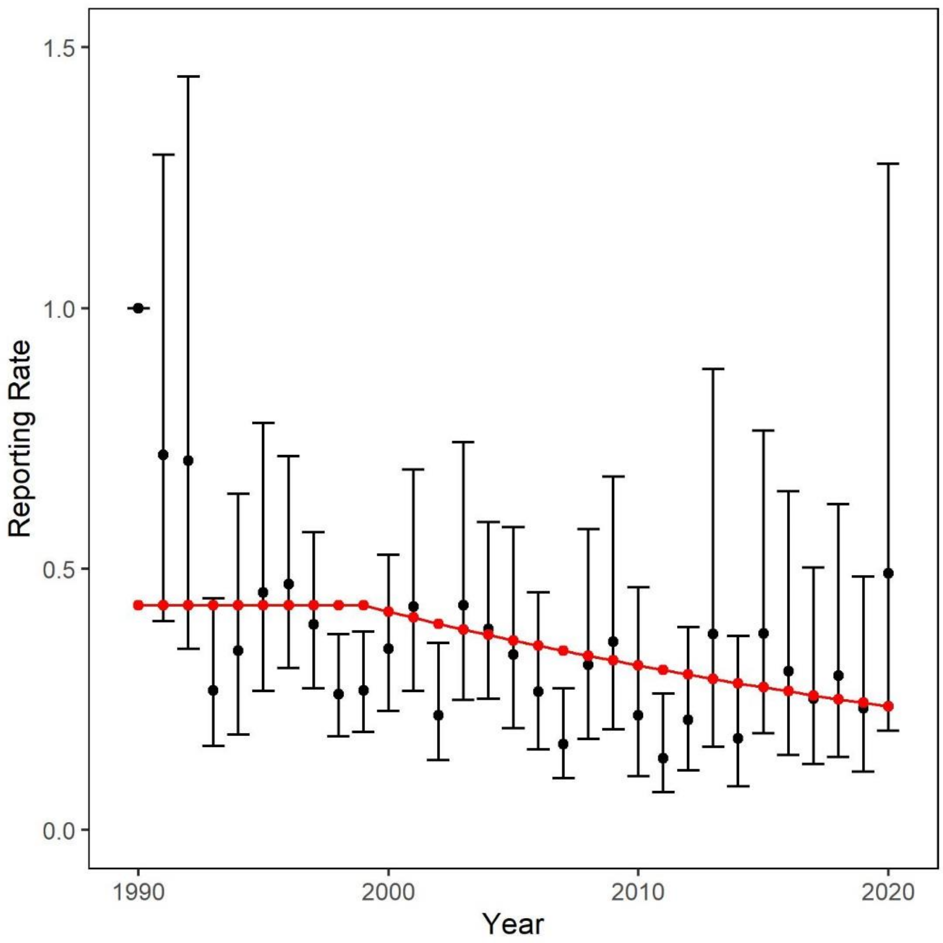

Figure 6. The annual reporting rate by commercial fishers as estimated by the mark-recapture model (black dots). The error bars represent the 95% confidence intervals. The red line is the annual recreational reporting rate externally calculated and supplied to the model. The first 10 years of the recreational reporting rate were held constant at a maximum value, based on external high-reward tagging studies, and the slope was derived through a beta regression relating the recovery rate to year and recreational fishing effort.

Supplementary Materials

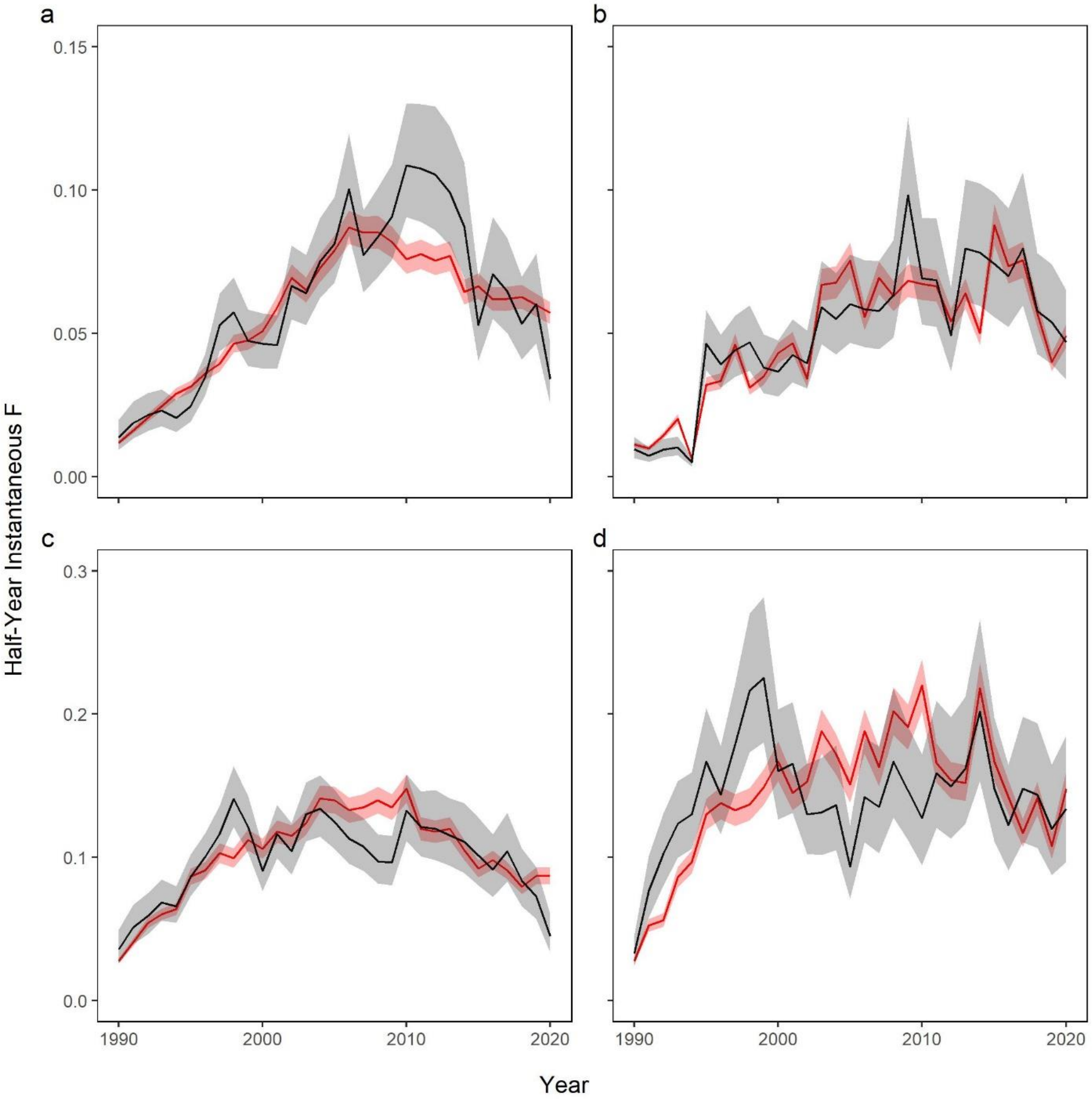

Figure S1. A comparison of the instantaneous recreational fishing mortality estimated directly by the model (black line) and the instantaneous recreational fishing mortality calculated as the product of regional catchability, an estimated parameter, and recreational effort supplied by the Marine Recreational Information Program (MRIP; red line) during (a) the first six-month period (Jan-Jun) outside of Chesapeake Bay and (b) inside the bay, and (c) the second six-month period (Jul-Dec) outside the bay and (d) inside the estuary. The ribbons represent the 95% confidence intervals.

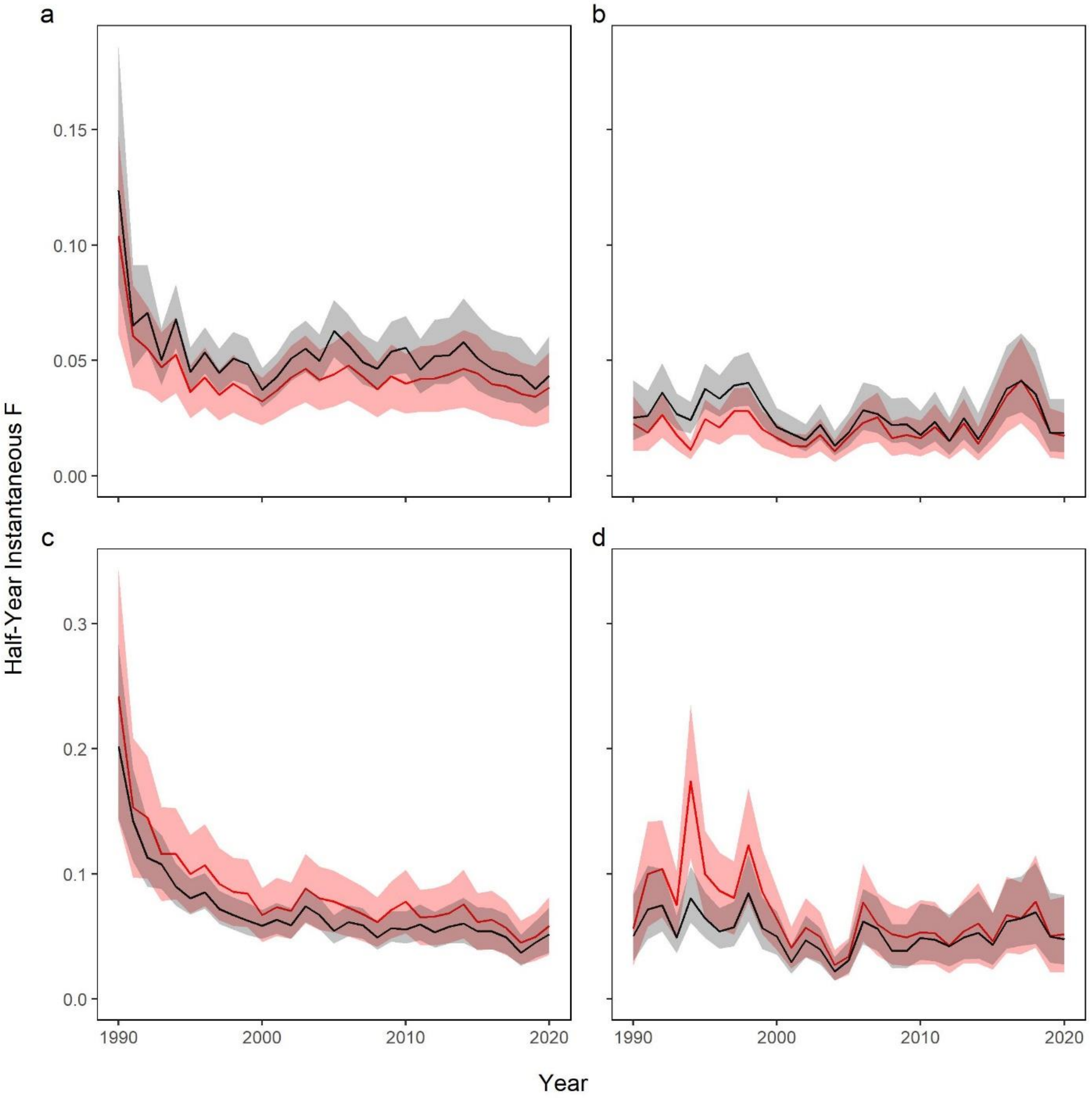

Figure S2. A comparison of the instantaneous recreational tag mortality estimated directly by the model (black line) and the instantaneous recreational tag mortality calculated using the recreational effort data supplied from the Marine Recreational Information Program (MRIP; red line). A regionally-specific annual catchability for recreational catch and release fishers was derived by estimating a regionally-specific annual adjustment to the regional catchability. The instantaneous tag mortality was then calculated as the product of the regionally-specific annual catchability and recreational effort. The comparisons are shown during (a) the first six-month period (Jan-Jun) outside of Chesapeake Bay and (b) inside the bay, and (c) the second six-month period (Jul-Dec) outside the bay and (d) inside the estuary. The ribbons represent the 95% confidence intervals.

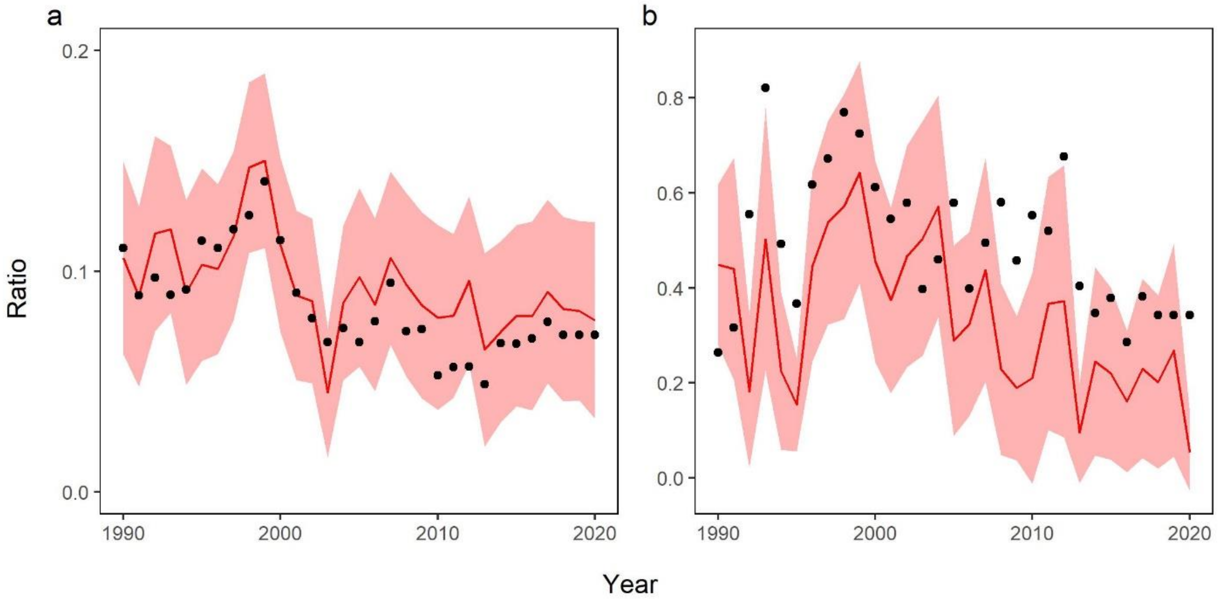

Figure S3. A comparison of the ratio of the estimated instantaneous fishing mortality by the commercial fleet to that of the recreational fleet (red line) and the ratio of the estimated harvest by the commercial fishery to the recreational harvest from the stock assessment (black dots; NEFSC 2019) (a) outside of the Chesapeake Bay and (b) inside the estuary. The red ribbon represents the 95% confidence interval of the model estimates.

CHAPTER 5

Conclusions

Understanding the influence of climate change on living marine resources has been a priority for both scientists and natural resource managers for decades, leading to a vast body of literature. Climate change is, however, a persistent problem, and warming will continue even if carbon emissions were to cease entirely (Solomon et al. 2009). Thus, even as knowledge grows on the effects of current conditions, environmental status is constantly changing, resulting in the need for subsequent investigations to fill ever-changing knowledge gaps.

This dissertation focused on a central theme: changes in spatiotemporal habitat usage by living marine resources in response to climate change, and thus contributes to the body of knowledge on faunal responses to changing environmental conditions. The associated research provided information on patterns and drivers of exchange between southern Mid-Atlantic estuaries and the coastal ocean (Chapter 2), habitat associations of several seasonal residents within Chesapeake Bay and impacts of localized bay conditions on habitat suitability (Chapter 3), and quantification of spatiotemporal patterns of mortality and occupancy probabilities of a valuable anadromous finfish (Chapter 4). Collectively, these studies can provide pertinent information to fisheries managers tasked with policymaking in a changing environment.

Importantly, the results of this work provide baseline information on a suite of species for the first two decades of the 21st century. Conflicts over harvest allocations currently exist (Dubik et al. 2019) and likely will become more prevalent as living marine resources continue to respond to climate change. This baseline information can be considered in current efforts to ameliorate quota conflicts and perhaps serve as a benchmark against which future quota reallocations could be evaluated.

Living marine resources are often assessed at coastwide or regional levels but managed at statewide or local levels; this mismatch can lead to discrepancies between the status of a resource and local policies aimed at protecting it. Results of this dissertation provide information on several assessed taxa that is congruent with their management, allowing for the alignment of the spatial scale of science and policy. Further, incorporating factors that influence population dynamics beyond harvest has gained popularity with both scientists and managers, and is required in some instances (NOAA 1996; NRC 1999). This work provides valuable information on climate and habitat associations for several taxa, which could be used in the development of policies in support of Ecosystem Approaches to Fisheries Management (EAFM).

More specifically, the results of all chapters could be used directly by managers in spatially and temporally dynamic policy development. Results from Chapter 2 can be used to understand shifting distributions and manage allocations accordingly. Maps of habitat suitability by species within Chesapeake Bay from Chapter 3 can be used in spatial management, allowing the visualization of where policies may provide the most benefit. Parameter estimates derived in Chapter 4, such as producer stock-, time-, and age-based occupancy probabilities, provide insight into the spatiotemporal distribution of the coastwide population, which could be used by managers in assessments conducted to estimate biomass, determine overfished/overfishing status, and to set quotas and allocations.

Collectively, this dissertation has highlighted heterogeneity in and impacts of climate change on spatiotemporal habitat usage, at multiple spatial scales and for a variety of species. Across all chapters, variability was quantified within a subunit of an ecological production unit (EPU), within a single estuary (the Chesapeake Bay), between species in the same estuarine system, and within a single species of high ecological and economic importance. Thus, any future investigations on the impacts of climate change must consider the scale at which the investigation occurs.

While this dissertation provided important information on spatiotemporal habitat usage of a suite of estuarine species in response to climate change, the work presented here could be extended by evaluating future habitat usage under various climate change scenarios. Future research in this area may also want to consider evaluating additional taxa. The Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAP) effectively samples numerous species beyond those considered in this dissertation. Individual habitat associations could be developed for species that are not managed, but are ecologically important to allow for inferences on expected changes to the overall ecosystem. Similarly, the inclusion of more taxa could allow for the grouping of similar species to elucidate shared patterns in habitat usage. The tag-recovery modeling framework developed in Chapter 4 could also be applied to additional species, allowing for the estimation of key parameters of those species, including mortality and occupancy.

The results of this dissertation are complementary to work conducted by numerous scientists in various subregions within the Northeast US Large Marine Ecosystem (NES LME), which, when integrated together, provides critical information to decision-makers charged with sustainable management of living marine resources. On a coastwide scale, many investigations have focused on shifting distributions of species assemblages in the coastal community (Lucey and Nye 2010; Nye et al. 2014; Kleisner et al. 2016). Studies have also focused on changing community composition and phenologies in more northern estuarine systems including Narragansett Bay (Oviatt 2004; Collie et al. 2008; Langan et al. 2021) and Long Island Sound (Howell and Auster 2012). The contribution of information provided by this dissertation on the estuarine usage in the southern portion of the NES LME complements these coastal and northern studies. Taken together, this provides a more holistic picture of the effects of climate change on living marine resources in the NES LME, supporting management efforts aimed at sustainability.

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VITA

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