# Coastal fish dynamics across scales: roles of warming and restoration, and interactions with fisheries

by

Sean B. Hardison

A Dissertation Submitted in Partial Fulfillment
of the Requirements for the Degree of
Doctor of Philosophy
in the Department of Environmental Sciences

*Supervisor:*

Max C. N. Castorani, PhD, Department of Environmental Sciences, University of Virginia

*Dissertation Committee:*

Michael Pace, PhD, Department of Environmental Sciences, University of Virginia

Patricia Wiberg, PhD, Department of Environmental Sciences, University of Virginia

Christopher Patrick, PhD, Section for Coastal & Ocean Processes, Virginia Institute of Marine Science

*Dean's Representative:*

Shan Yu, PhD, Department of Statistics, University of Virginia

University of Virginia
January 2024

# Table of Contents

# Acknowledgments

The completion of this dissertation would not have been possible without the support of my friends, collaborators, committee members, and family. I owe a debt of gratitude to the members of the Castorani Lab, past and present, for their friendship and support over the years that has helped me grow as a scientist and personally.

I am thankful to my advisor, Max Castorani, who, among many other things, graciously provided feedback on the numerous drafts that ultimately became the chapters in this dissertation, was always present and thoughtful during our meetings together, and provided unwavering support to me during my time at UVA. I am thankful to Michael Cornish for his boundless enthusiasm about ecology that pushed me to become a better natural scientist and for his friendship throughout graduate school. To Kinsey Tedford, whose dedication to her own work while balancing meaningful friendships during the completion of her degree was inspiring, and who never hesitated to help me work through the many challenges of graduate school.

To Rachel Smith, whose career guidance, nuanced feedback on ideas and drafts, and optimistic outlook on science (and life in general) were critical to me finishing this dissertation while holding onto my enthusiasm about science as a career. To Ethan Kadiyala, whose committed service to the department made for a more enjoyable experience as a graduate student, and whose attitude was always positive, even 15 hours into an 11 hour drive. To Lauren Brideau, whose friendship and support I valued highly, and whose baked goods I benefitted from consistently. To Maowei Liang and Jon Walter, whose guidance when it came to diversity-stability dynamics were essential to the completion of this work. I am also thankful to the many undergraduates and staff scientists supporting the Castorani Lab whose contributions in the lab and the field facilitated this research, as well as to the many other graduate students and faculty at UVA who contributed to the development of this dissertation in one way or another.

I am hugely grateful to my many collaborators and committee members who contributed intellectually to this work and supported me through my degree. To Jon Lefcheck, who was always willing to meet with me to share his knowledge of ecology and statistics and provided me with valuable life and career advice. To Stacy Zhang and Joel Fodrie, who, without knowing me, drove across the state of North Carolina to meet with me in person, and whose guidance was important to the development of this work. To Rob Latour and Jim Gartland, who provided ChesMMAP survey data and were invaluable resources in helping me to understand survey operations.

To Shelby White, who provided critical insights into Chesapeake Bay commercial fisheries, and Andrew Scheld, who never hesitated to provide me with feedback and allowed me to take his Marine Resource Economics course remotely without question. To Sean Anderson, who helped me troubleshoot and understand the spatiotemporal models used in this work. To Karen McGlathery, whose insights into seagrass biology were invaluable to the development of my last chapter. To Chris Patrick, whose thoughtful and nuanced feedback helped me to become a better scientist and scientific writer. Lastly, to Mike Pace and Pat Wiberg, whose comments on earlier drafts helped me to shape this dissertation into a presentable form, and whose service in the department and on my committee was an important part of my experience as a graduate student.

Finally, I am indebted to my family, without whom none of this would be possible.

# Abstract

Coastal fish population dynamics are highly variable in time and space, and in the Mid-Atlantic Bight (MAB) region of the U.S. Northeast Continental Shelf, many species migrate seasonally and ontogenically between the coastal zone and offshore shelf habitats. The seasonal timing of migrations and spawning, the survivorship of larvae and juveniles, the locations of inshore habitats that fishes move into, and the presence and quality of nursery habitats like seagrasses impact the abundances and species diversities of inshore fish communities and have implications for the small-scale commercial fisheries that depend on them. In Chapter 1 of this dissertation, I explored how ocean warming on the continental shelf due to climate change has impacted the abundances of fishes in inshore habitats across the MAB. I found that, on the spatial scale of the MAB, the population responses of fishes to warming were weakly mediated by life history characteristics, but that smaller-bodied, faster-lived species whose populations responded positively to warming tended to be warm-adapted, while populations of larger-bodied, slower-lived species responding negatively were cool-adapted. In Chapter 2, I evaluated how seasonal species asynchrony—the temporal offset in the population dynamics of species biomasses—related to seasonal asynchrony in the harvests of those species, and how harvest asynchrony contributed to the stability of small-scale commercial fisheries operating in the Chesapeake Bay (USA).

I showed that harvest asynchrony and stability were associated with both social and ecological dynamics, including fisher behaviors in response to management restrictions and changes in effort, and to the availability and variability of targeted species populations that contributed to species asynchrony. In Chapter 3, I studied the impacts of seagrass restoration on

the abundance and diversity of juvenile coastal fishes. I showed that fish communities within restored meadows were more abundant and diverse compared to nearby unvegetated habitats, further bolstering the case that seagrass restoration is a worthy endeavor. Together, this body of work provides novel insights into the impacts of continental shelf warming on inshore fish populations in the MAB, the consequences of population variability on small-scale commercial fisheries, and how seagrass restoration can enhance the function of inshore ecosystems.

# Introduction

Marine ecosystems are changing rapidly in response to climate change, leading to shifts in the distribution (Kleisner et al., 2016; Pinsky et al., 2013), productivity (Free et al., 2019; Friedland, Ganley, et al., 2023), and phenology (Asch et al., 2019; Walsh et al., 2015) of fishes worldwide. These impacts are well-documented on regional scales in continental shelf ecosystems (Asch et al., 2019; Free et al., 2019; Simpson et al., 2011), but have been less well studied on regional scales among inshore habitats like estuaries and coastal bays (Fujiwara et al., 2022; Oke et al., 2022). In general, the causes and consequences of variability in inshore fish population dynamics are important to understand because many species of commercially harvested fish inhabiting shelf habitats have migratory life histories, spending a substantial portion of their lives inshore where they also support large commercial and recreational fisheries (Schonfeld et al., 2022). A critical part of the life history of many such species that influences the variability of harvestable biomass in both inshore and offshore systems is the presence of inshore nursery habitats like seagrass meadows that enhance the growth and survival of larval and juvenile fishes (Lefcheck et al., 2019a).

In this dissertation, I explored the relationships between inshore fish populations, their habitats and environmental drivers, and the commercial fisheries that target them on spatial scales ranging from the tens to hundreds of kilometers. In Chapter 1, I tested the hypothesis that the responses of inshore fish populations to continental shelf sea-surface temperature (SST) anomalies were mediated by their positioning along the fast-slow continuum of life history strategies, an important biological characteristic of fishes that influences species' capacities to respond to climate change (Beukhof et al., 2019). This analysis considered inshore fish populations along the entire length of the Mid-Atlantic Bight (MAB) region of the Northeast U.S. Continental Shelf (NES) in the western Atlantic Ocean. In Chapter 2, I evaluated how the within-year asynchrony of inshore fish populations influenced the asynchrony and stability of commercial fisheries targeting those populations and their overall value in Chesapeake Bay, USA. Lastly, in Chapter 3, I examined the habitat provisioning function of restored seagrass for juvenile fishes relative to unvegetated habitats in the coastal bays of Virginia, USA.

The NES is warming rapidly (Friedland, Morse, et al., 2020) and as a result, populations of many fishes have shifted poleward and deeper (Friedland et al., 2021; Kleisner et al., 2016), while also becoming smaller-bodied and more abundant (Friedland, Ganley, et al., 2023). How the impacts of a warming ocean are reflected in the population dynamics of fishes in inshore habitats in the region is largely unknown, although recent work has found inshore community abundances and diversities to have increased with oceanic SSTs (Oke et al., 2022). In Chapter 1, I tested the hypothesis that the position of species along the fast-slow life history continuum (which I quantified as a composite index of species-specific natural mortalities, asymptotic biomasses, and maximum ages) mediated the inshore population responses of fishes to seasonal SST anomalies in offshore habitats in the MAB. I based this hypothesis on research from continental shelf ecosystems, which has shown that population distributions of faster-lived (smaller-bodied, shorter-lived) species have a greater capacity to respond to warming waters, in terms of distribution shifts or changes in abundances, than those of slower-lived species (larger-bodied, longer-lived) (Free et al., 2019; Perry et al., 2005; Simpson et al., 2011).

My results from this study showed that, first, there was a weakly mediating effect of the fast-slow continuum on inshore population responses to seasonal warming in offshore habitats. This meant that fish populations responding positively to warming tended to be faster-lived, and slower-lived responding negatively. This effect was weak, and further analyses indicated that there was high bay to bay variability in population responses to warming within species. However, in evaluating the populations of species who were faster-lived, we found that faster-lived species whose populations were responding positively to seasonal warming tended to be warm-adapted, while slower-lived fishes responding negatively to seasonal warming tended to be cool-adapted. This finding suggests that increased fish abundances in the inshore habitats of the MAB in response to SST anomalies (Oke et al., 2022) could be due to the population responses of primarily faster-lived species in the southerly, subtropical portion of the system. This work is among the first to explore how the responses of inshore fish populations to offshore SST anomalies are mediated by fish life history characteristics on a macroecological scale and provides important insights into how climate change is likely to shape future inshore fish assemblages in the MAB.

A key finding from this chapter was that the responses of inshore fish populations to offshore warming were highly variable across habitats within species. This suggests that, while some species were predicted to benefit from a warming ocean, other processes that went uncharacterized in this study (e.g., environmental conditions and species interaction) were likely highly important to “realized” population responses to warming. Understanding these dynamics has large implications for small-scale commercial fisheries in the MAB (White & Scheld, 2021) that directly or indirectly depend on these populations (e.g., through trophic linkages). This is because, for fishers operating on small spatial scales, declines in the local abundances of target species may be difficult to overcome if fishers lack the operational capacity to diversify their targets to different stocks that are abundant outside of historically fished areas (Thorson et al., 2018). However, fish populations in the inshore habitats of the Mid-Atlantic tend to fluctuate asynchronously within years according to species-specific seasonal migratory dynamics, and fishers may be able to stabilize their yields over the course of the year by asynchronously targeting these stocks as their availabilities fluctuate seasonally.

I explored these dynamics in Chapter 2 from the level of the regional commercial fishing harvest portfolio. Specifically, I evaluated how the temporal offset of seasonal fish population dynamics among species, or species asynchrony, in the Maryland and Virginia regions of the Chesapeake Bay (USA) contributed to asynchrony in the commercial fishing harvests drawn from these species. I then evaluated how seasonal harvest asynchrony contributed to the within-year economic stability and value of commercial harvest portfolios. This analysis ultimately linked species asynchrony occurring due to the seasonal migratory patterns of biomass-dominant species and interannual changes in their relative abundances to the economic stability of regional commercial fisheries.

Results from this study showed that both ecological and social dynamics were important contributing factors to harvest asynchrony and harvest portfolio stability. In Maryland, where the harvest of the most valuable species, striped bass *Morone saxatilis*, was restricted for part of the year, we found that seasonal harvest asynchrony and stability emerged due to effort compensation, or fishing effort being directed towards other species during the striped bass closure. However, these harvest portfolio effects did not stabilize the within-year economic value of the fishing portfolio likely due to the relatively low value of targeted stocks outside of striped bass in MD waters.

In Virginia, there were no analogous seasonal closures that significantly impacted harvests, resulting in the emergence of harvest asynchrony as fishers preferentially targeted species as they became seasonally abundant. Despite this seasonal harvest compensation that supported harvest stability, a decline in the abundance of fish entering into the Bay seasonally from the continental shelf (Schonfeld et al., 2022) counteracted seasonal harvest compensation and, in tandem with declining fishing effort, drove down the stability of the Virginia harvest portfolio. However, there exists a high diversity of commercial fishing opportunities outside of the demersal finfish species discussed here, as well as in related industries like seafood sales and processing, that are viable alternatives. Frequently, fishers already retain the necessary licenses that would allow them to take advantage of these opportunities (White & Scheld, 2021). For instance, wild caught shellfish and shellfish aquaculture, the blue crab *Callinectes sapidus* fishery, or the emerging commercial fishery surrounding the invasive blue catfish *Ictalurus furcatus* (Fabrizio et al., 2021; White & Scheld, 2021).

Ultimately, fisheries require fish populations to draw from, and the abundances of these populations are enhanced by inshore nursery habitats that support the survival and growth of larvae and juveniles prior to joining the adult population (Lefcheck et al., 2019a). In the MAB, seagrasses form undersea meadows that serve as important nursery habitats for larval and juvenile fishes. In the coastal bays of Virginia—the focus of my third chapter—seagrass was extirpated in the 1930s following wasting disease and hurricane disturbance (Orth &

McGlathery, 2012). Over six decades later, in the late 1990s, a seed-based restoration program was undertaken that by 2021 led to the re-establishment of ~36 km$^2$ of seagrass meadow in the bays (Orth et al., 2012). In Chapter 3, I examined the habitat provisioning function of the restored seagrass meadow for juvenile fish relative to nearby unvegetated areas and the direct and indirect effects of landscape-scale environmental variables on seagrass presence and fish community abundance and diversity. Using long-term survey data, I discovered that juvenile fish abundance and diversity during summer were substantially higher inside the meadow than in unvegetated areas, and that this effect was consistent despite strong interannual variation in fish counts. I also found that water residence time and depth were important predictors of seagrass presence, showing how environmental variability contributed to restoration success and the subsequent ecosystem function of restored habitat.

In this body of work, I explored how climate and habitat influence the dynamics of inshore fish populations along the coastline of the MAB, with implications for the impacts of warming oceans on fish communities and the stability of the fisheries that depend upon them. I showed how emergent properties of commercial fisheries in Chesapeake Bay, i.e., stability and asynchrony, are related to species asynchrony in the fish community and the behaviors of fishers in response to seasonal harvest restrictions. Lastly, I showed that restored seagrass habitat is important habitat for a diverse and abundant community of coastal fishes.

# Chapter 1

## *Evidence for a weakly mediating effect of life history characteristics on inshore fish population responses to offshore warming in the Mid-Atlantic Bight*

Anticipated authors of peer-reviewed manuscript:

Sean Hardison
Y. Stacy Zhang
F. Joel Fodrie
Christopher J. Patrick
Max C. N. Castorani

## Abstract

Marine ecosystems are experiencing rapid and unprecedented changes in response to ocean warming. The consequences of such warming for fishes, including altered population distributions, productivities, and phenologies, are usually studied in the context of continental shelf ecosystems where large-scale commercial fisheries operate and where governments support spatially comprehensive bottom trawl surveys. However, fishes in temperate continental shelf ecosystems often migrate seasonally to and from the coastal zone where population responses to warming are less well-understood. We explored how seasonal offshore sea-surface temperature (SST) anomalies across the Mid-Atlantic Bight region of the Northeast U.S. Continental Shelf impacted the dynamics of autumn fish assemblages in inshore habitats across 42 years (1982–2023), and how these effects were mediated by species' positioning along the "fast-slow" life history continuum. We found that the responses of fish populations to SST anomalies in the spring and summer months were weakly mediated by species' positioning along the fast-slow continuum ($P_{\mathrm{Spring}} = 0.08$, $P_{Summer} = 0.09$), meaning that inshore populations of smaller-bodied and shorter-lived species tended to respond positively to seasonal warming, and larger-bodied and longer-lived species negatively. However, there was uncertainty in these relationships following bay-to-bay variability in population SST responses. We also found that the direction of population responses to warming (positive or negative) tended to fall along a gradient of species thermal affinities—faster-lived populations who responded positively to warming tended to be warm-adapted species, and slower-lived populations responding negatively, cool-adapted. These findings showed that life history characteristics contributed to how inshore fish populations responded to warming, but also that the effects of warming are unlikely to be consistent across

inshore populations subjected to highly variable environments and species interactions impacting population abundances.

## Introduction

Globally, oceans are warming rapidly due to climate change with far-reaching consequences for the structure and function of marine ecosystems and the human systems that depend upon them (Baudron et al., 2020; Kleisner et al., 2017). For instance, ocean warming is responsible for expansions and contractions of fish species distributions into more suitable thermal habitats (Dulvy et al., 2008; Kleisner et al., 2016; Pinsky et al., 2013), contributing to changes in species richness (Batt et al., 2017; Friedland, Langan, et al., 2020), productivity (Free et al., 2019; Friedland, Langan, et al., 2020), and body size (Baudron et al., 2014; Friedland, Ganley, et al., 2023; Ikpewe et al., 2021). While most macroecological studies of marine fish responses to ocean warming have focused on continental shelf ecosystems given data availability and shelf contributions to fisheries (Free et al., 2019; Friedland, Ganley, et al., 2023; M. McLean et al., 2019; Simpson et al., 2011), many of the dominant species inhabiting continental shelves exhibit complex life histories with seasonally mediated migrations to and from coastal habitats, particularly at mid and lower latitudes (Pinsky et al., 2020; Walsh et al., 2015). Despite the ubiquity of migratory behavior in marine fishes, the macroecological patterns of inshore fish community responses to ocean warming in offshore habitats (Oke et al., 2022; Schonfeld et al., 2022) and how these effects may be mediated by fish functional traits remains understudied.

In the Northeast U.S. Continental Shelf (NES) region of the Northwest Atlantic Ocean, surface and bottom water temperatures are increasing at rates that far exceed the global average (Thomas et al., 2017). The NES is a transition zone between subtropical and subpolar biogeographic regions (Friedland et al., 2021), characterized by a steep latitudinal temperature gradient and marine fish populations whose distributions track local climate velocities, and oceanographic and physiographic features (Kleisner et al., 2016, 2017; Pinsky et al., 2013). In the southern region commonly referred to as the Mid-Atlantic Bight (MAB, Fig. 1a)—the focus of this study—population centers have shifted poleward along the predominant latitudinal temperature gradient (Kleisner et al., 2016). Fish distributions on the NES have also expanded, leading to increased local species richness and habitat overlap among species, as well as higher productivity and a shift towards smaller body sizes overall (Fisher et al., 2010a; Friedland, Ganley, et al., 2023). While there are some species whose biomasses have declined in recent years, biomass trends across diverse taxa on the NES have been mostly positive and synchronous with increasing water temperatures (Friedland, Tanaka, et al., 2023).

Given these trends on the NES, one might expect similar patterns of increased productivity and diversity to emerge across fish populations in MAB estuaries and coastal bays. Indeed, inshore fish communities along the U.S. east coast have become more abundant and diverse in response to increasing sea-surface temperatures (SSTs) in the region, suggesting that there may be a joint response to warming across species in both the inshore and offshore habitats of the MAB (Friedland, Ganley, et al., 2023; Oke et al., 2022). However, the effects of warming may not be consistent across or within species and inshore habitats in part due to interactions between warming and local environmental and trophic dynamics, but also due to the diversity of species' life history characteristics and thermal affinities (Kleisner et al., 2017) across latitudes in the NES.

Fish life history characteristics along the latitudinal temperature gradient of the west Atlantic continental shelf are not uniformly distributed (Fisher et al., 2010b). Instead, the maximum lengths of fish species tends to increase with latitude from the Southeast US

Continental Shelf, whose northern biogeographic boundary is the southern end of the MAB at Cape Hatteras, NC (Pappalardo et al., 2015, Fig. 1a), to the northern reaches of the NES and the Scotian Shelf (Fisher et al., 2010b). This gradient is important because body size and the life history parameters that covary with body size, e.g., longevity, age-at-maturity, growth, natural mortality, and generation time are mediating characteristics of population responses to environmental variability (Free et al., 2019; Fujiwara et al., 2022; M. McLean et al., 2019; M. J. McLean et al., 2019; Perry et al., 2005). Frequently, populations of smaller-bodied, shorter-lived fishes are shown to have greater capacities for tracking environmental variability, in terms of their abundance responses and population distributions, due to their rapid turnover of biomass following high natural mortalities and short generation times (M. McLean et al., 2019; Perry et al., 2005). Given the increased favorability of water temperatures in the MAB for more southerly distributed, smaller-bodied species, we would expect that these "faster-lived" species would be those whose population dynamics respond positively to warming SSTs.

Here, we explored how seasonally- and regionally-variable ocean SST anomalies from 1982 to 2023 impacted inshore fish populations across the MAB, and whether these effects were mediated by species' positioning along a continuum of life history parameters characterized by a composite index of body size, natural mortality, and maximum age (i.e., characterizing the "fast-slow" continuum of life history characteristics). We also evaluated how the species contributing most to relationships between population responses to seasonal SSTs and the fast-slow continuum differed according to their environmental temperatures (an average of typical water temperatures encountered by species across their ranges) (Pauly, 1980; Thorson et al., 2017), under the expectation that faster-lived species whose populations increased with positive SST anomalies would be associated with warmer waters and slower-lived species whose populations declined with SST anomalies with cooler waters. Our analysis integrated long-term bottom trawl surveys across five estuaries and coastal bays in the MAB (North Carolina to Massachusetts), providing important context for understanding how increasing SSTs impact the communities of fish occupying these habitats.

## Methods

### *Methods overview*

The analysis for this work involved four major steps: 1) We developed abundance indices for commonly collected species in each of five estuaries and coastal bays in the MAB (hereafter referred to as “bays”, and each bay-species combination a “population”). These indices were point estimates of inshore relative abundance for each population during the month of September. 2) We used satellite-derived SST measurements to create season-and bay-specific time series of offshore SST anomalies (within a 150 km radius of trawl survey locations on the continental shelf). We then related SST anomaly time series to abundance indices across all populations using mixed-effects models that included population-specific random slopes representing the effects of seasonal (winter, spring, and summer) offshore SST anomalies on September inshore population abundances. 3) We used principal components analysis (PCA) to ordinate species along three trait axes (natural mortality, M, asymptotic biomass, $W_{Inf}$, and maximum age, $T_{Max}$). We then extracted PC1 from this analysis, which we refer to as the “fast-slow index”, to relate to the population-specific random slopes from the previous step. 4) Lastly, we identified the species whose contributions drove relationships between population responses to seasonal SST anomalies and the fast-slow index and tested the hypothesis that the environmental temperatures of those species differed according to whether their populations were fast-lived and responding positively to warming, or slow-lived and responding negatively to warming.

*Trawl survey data sources*

Data were drawn from September fishery-independent bottom trawl surveys from lagoons and estuaries across the MAB. These bays included Buzzards Bay, Massachusetts (MA), Delaware Bay, New Jersey (NJ), a collection of connected bays in Maryland (MD; Sinepuxent, Assawoman, Chincoteague, and Isle of Wight Bays), South Bay, Virginia (VA), and Pamlico Sound, North Carolina (NC) (Fig. 1).

Massachusetts trawls were collected by the Massachusetts Department of Marine Fisheries between 1978 and 2019. These surveys used a 11.9 m otter trawl, were 20 minutes in duration, and typically targeted 4–7 sites per year in Buzzards Bay (mean annual number of Buzzards Bay trawls = 5.9). New Jersey trawls were collected by the New Jersey Bureau of Marine Fisheries as part of the Delaware Bay Juvenile Finfish Trawl Survey between 1997 and 2018. This survey used a 4.9 m otter trawl towed for 10 minutes and targeted 11 sites per year in September (except 6 sites in 2017). In Maryland, trawl surveys were performed using a 4.9 m otter trawl by the Maryland Department of Natural Resources between 1990 and 2018 (19–20 trawls per year). Trawls in this survey were 6 minutes in duration and targeted four connected coastal bays that fell along roughly 50 km of coastline.

Virginia bottom trawls were collected by the Virginia Institute of Marine Science between 2012 and 2023 using a 4.9 m otter trawl. Trawls in this survey were 2 minutes in duration and surveyed 5–6 sites per year. Lastly, the North Carolina bottom trawl survey was conducted between 1987 and 2019 in Pamlico Sound by the North Carolina Department of Marine Fisheries using double-rigged 9.1 m head rope mongoose trawls. We excluded five of 34 survey years in Pamlico Sound where the September survey was disrupted by hurricanes and vessel repairs. The remaining 29 years of data included between 36 and 44 trawls annually, each lasting 20 minutes in duration. Prior to developing abundance indices from these data, catches across surveys were standardized to catch per minute by dividing catch numbers by trawl duration (we refer to this metric as "tCPUE").

### *Abundance indices*

We chose to analyze September bottom trawls because surveys within all states occurred during the month of September (other months were not sampled in all states). For each survey, we used statistical models to estimate the relative abundances of each collected species across years. These models varied according to the complexity of the trawl survey, but all treated the year of sampling as a fixed-effect variable for which abundances were derived. For surveys where information regarding survey locations were available (i.e., "stations" in Buzzards Bay, Delaware Bay, Maryland Coastal Bays, and Pamlico Sound), we developed a model selection routine that fitted six models of varying observation error distribution and random effects structure for each species. For the Maryland Coastal Bays, we pooled catches together prior to fitting these models and did not model catches from the four bays separately because they were adjacent to one another within a relatively small area (roughly 50 km distance).

Three of these models were generalized linear mixed models (GLMMs) with either a Tweedie, negative binomial, or Poisson observation error distribution and a random intercept term for "station". The other three models were generalized linear models (GLMs) corresponding to Tweedie, negative binomial, and Poisson observation error distributions and no random intercept term for station. For each model of the six that converged, we evaluated residual patterns using the DHARMa R package (Hartig, 2020), excluding models from further analysis that displayed significant ($P < 0.05$) deviations from expected residual behaviors (specifically, regarding residual uniformity, dispersion, and zero-inflation). We then used AIC to select the best-fitting model that passed these thresholds for residual behavior. Lastly, we used the selected model to predict September abundance for each year of the trawl survey (excluding random intercepts from this prediction to generate a single annual index for each population). In the case of the South Bay survey that had the fewest years of data and lacked "stations" for which to model using random intercepts, we repeated the above analytical workflow but only for the three GLMs of varying observation error distribution. GLMMs/GLMs were fitted using maximum likelihood with the *glmmTMB* R package (Brooks et al., 2017a). This process yielded 77 time series of abundance corresponding to 45 different species across the five bays.

There are several species of fish found in the inshore habitats of the MAB that are considered inshore residents and are not found in high abundances offshore. To ensure that our analysis relating offshore SSTs to inshore population abundances was biologically relevant, we cross-referenced the list of species that we developed abundance indices for with a list of species collected offshore in the MAB by the Northeast Fisheries Science Center Bottom Trawl Survey (NEFSC BTS) (Wigley et al., 2003). If species were infrequently collected in the NEFSC BTS, meaning that their abundance or biomass fell outside the 75th percentile of abundances or biomasses across species collected by the survey between 1963-2023, then we excluded them from further analysis.

### *The fast-slow continuum and environmental temperatures*

We generated a composite index of life history parameters to serve as our measure of individual species' positioning along the fast-slow continuum. The life history index was the first principal component (PC1) extracted from a principal component analysis (PCA) of species-specific life history parameters including natural mortality (M; the fraction of the population lost to natural causes annually), asymptotic mass ($W_{Inf}$), and maximum age ($T_{Max}$). Life history parameters were derived from the R package *FishLife* (Thorson et al., 2017). *FishLife* leverages the public database *FishBase* when life history characteristics are provided in published lab or field studies (Froese et al., 2010). When life history parameters are unknown for a particular species, *FishLife* provides predicted values based on empirically derived parameters from other species belonging to the same taxonomic grouping (e.g., genus, family, order) (Thorson et al., 2017). We found that PC1 explained 89.9% of the total variance across species, and how species fell along PC1 therefore served as our measure of the fast-slow continuum (Fig. 2). There were several different life history parameters that we could have used in creating this index (see Thorson et al., 2017), but they were highly correlated with those chosen here and did not greatly alter the proportion of total variance explained by PC1 or the interpretation of the index. Switching between correlated variables, such as exchanging the von Bertalanffy growth parameter (K) with M and age-at-maturity with maximum age, did not alter our conclusions from later analyses involving this index, nor did only exchanging age-at-maturity with maximum age in the PCA. However, exchanging K for M while leaving maximum age in the PCA increased uncertainty in our final conclusion, indicating this analysis was sensitive to the inclusion of K vs. M in the creation of the fast-slow index.

Among the life history parameters available for each species in *FishLife* is a measure of environmental temperature, which is an average of water temperatures used within population growth studies listed on *FishBase*, reflecting mean water temperatures within the regions where a particular population was studied. These values are derived from maps of global water temperatures (Pauly, 1980), and represent environmental temperatures encountered by fishes in the habitats where they are commonly found. When environmental temperatures are unavailable on *FishBase*, *FishLife* provides predictions as for other life history characteristics.

*Ocean temperature data and anomaly calculation*

We related population abundance indices to seasonal SST anomalies on the MAB continental shelf across the study period. To calculate seasonal SST anomalies, we first drew a 150 km radius circle around each survey location that we then intersected with a polygon of the NES whose eastern boundary was defined by the 100 m isobath (this radius was arbitrary, but re-analyses using radii of 100 km and 200 km did not alter conclusions regarding inshore fish population responses to seasonal SSTs). Using these polygons, we cropped rasters of daily SSTs between 1982 and 2023 (using the NOAA Optimum Interpolation SST V2 data set [Reynolds et al., 2007]) to specific regions "local" to inshore habitats (Fig. 1a). We then split this set of daily raster layers into seasons, where we defined winter as January–March, spring as April–June, and summer as July–September. We calculated baseline SSTs for each region as the average of all raster cells and days within that season between 1982 and 2010. We then calculated the seasonal anomaly each year by subtracting this seasonal baseline from the average of all raster cells and days within that buffer area, year, and season (Fig. 1b). We then used trend analysis to evaluate how SST anomalies within the vicinities of surveyed habitats on the continental shelf have changed over the study period. We tested for linear trends in the SST time series using linear regression or generalized least squares (GLS) with various error structures if model residuals were correlated (Table 1).

*Species responses to seasonal SST anomalies*

We fitted three GLMMs to model September population responses to seasonal SST anomalies (the SSTs in the preceding winter, spring, and summer; summer included SST anomalies from the month of September). For each season, we fitted the following Tweedie GLMM:

$$\begin{aligned} \mu_{ijk} &= \exp(bay_i + species\colon bay_{0ij} + \\ &\qquad species\colon bay_{1ij} \cdot SSTA_{ik}), \\ species\colon bay_{0ij} &\sim N\left(0, \sigma^2_{species:bay_0}\right), \\ species\colon bay_{1ij} &\sim N\left(0, \sigma^2_{species:bay_1}\right), \end{aligned} \tag{1}$$

where $\mu_{ijk}$ is the abundance of species *j* in bay *i* and year *k*, $bay_i$ is a bay-specific fixed effect intercept, $species\colon bay_{0ij}$ is the population-specific random intercept, $species\colon bay_{1ij}$ is the population-specific random effect of seasonal SST anomalies, $SSTA_{ik}$ (random slope). Measures of summer SST anomalies included September data, and so the summer model partly reflected species responses to September SST conditions when sampling occurred. These models were fitted using restricted maximum likelihood (REML) (Brooks et al., 2017). After modeling population responses to seasonal SST anomalies, we extracted population-specific random slopes ($species\colon bay_{1ij}$) to relate to the fast-slow continuum index described above using a Gaussian GLMM with random intercepts on bay and species. If the inclusion of these intercepts prevented the model from converging, they were removed.

Lastly, for each of these latter models relating population-specific SST anomaly effects to the fast-slow continuum, we identified the species driving these patterns by isolating the populations whose random slopes exceeded the 75th percentile of slopes and whose value for PC1 (the fast-slow index) was less than the 25th percentile of PC1. In terms of life history characteristics and direction of responses to SST anomalies, these species represented the "fast/positive" group. Alternatively, we selected the populations whose random slopes were ≤25th percentile of slopes and those whose value for PC1 was ≥75th percentile of PC1, representing the "slow/negative" group. We tested the hypothesis that the environmental temperatures of species comprising these groups were different using a *t* test. Our results for this analysis were robust to the choice of percentiles used to classify species groupings. Selecting the median or 20th/80th percentiles rather than the 25th/75th percentiles as cut-off values for slope and PC1 did not change our conclusions. Selecting the 10th/90th percentiles altered our conclusions, but greatly reduced the number of species within each group (to between 2-4), so we suggest that the 25th/75th percentile cut-offs are reasonable (providing 6-7 species in both "fast/positive" and "slow/negative" groups.)

## Results

### *Seasonal warming trends in the offshore vicinities of inshore habitats*

Our analysis of seasonal offshore SST anomaly trends within the offshore vicinities of surveyed inshore habitats revealed that SST anomaly trend magnitude was seasonally and spatially variable (Fig. 1b, Table 1). In the winter months, SST anomalies were increasing only in the offshore vicinity of Buzzards Bay (linear trend = 0.02 °C $yr^{-1}$, $P = 0.031$). During the spring, the magnitude of warming trends followed a latitudinal gradient (from North to South): near Buzzards Bay (trend = 0.034 °C $yr^{-1}$, $P = 0.06$), Delaware Bay (trend = 0.028 °C $yr^{-1}$, $P = 0.004$), and the Maryland Coastal Bays (trend = 0.023 °C $yr^{-1}$, $P = 0.023$), but spring trends were not evident near South Bay or Pamlico Sound. Warming trends were most spatially consistent during the summer months with positive trends occurring across all regions, and trend magnitudes declined with latitude (from North to South): near Buzzards Bay (trend = 0.059 °C $yr^{-1}$, $P < 0.001$), Delaware Bay (trend = 0.042 °C $yr^{-1}$, $P < 0.001$), the Maryland Coastal Bays (trend = 0.04 °C $yr^{-1}$, $P < 0.001$), South Bay (trend = 0.034 °C $yr^{-1}$, $P < 0.001$), Pamlico Sound (trend = 0.034 °C $yr^{-1}$, $P < 0.001$). We include a discussion of these trends to show that inshore fish population responses to SST anomalies reflected population responses to increasing water temperatures, particularly in the summer months when significant warming occurred offshore within the vicinities of all bays, rather than solely interannual variability in water temperatures around a long-term mean.

*Inshore fish population responses to seasonal SST anomalies*

Our analyses relating the inshore abundances of fishes in the MAB to seasonal SST anomalies offshore revealed that population responses (meaning positive or negative abundance responses within species and bays) were weakly mediated by species' positioning along the fast-slow continuum (Fig. 3, Table 2, $P_{\mathrm{Spring}} = 0.08$, $P_{Summer} = 0.087$). These relationships were uncertain due to population-level variability in species responses to seasonal SST anomalies—for species that were found in least three of five bays over the study period (whose abundances we modeled, in total, nine species), the range of population responses to SST anomalies included zero for 56% of species (n = 5) in the spring SST anomaly model and for 89% of species (n = 8) in the summer SST anomaly model (Fig. 4). This suggested that the mediating effects of life history on how populations responded to seasonal SST anomalies were highly variable across bays.

Lastly, we identified the faster-lived species responding positively to seasonal SST anomalies (the "fast/positive" group) and the slower-lived species responding negatively to seasonal SST anomalies (the "slow/negative" group). In comparing the environmental temperatures of these species, we found that the fast/positive group had significantly higher environmental temperatures ($P_{Spring} = 0.008$, $P_{Summer} = 0.051$) than the slow/negative group (Fig. 5). While the life history effect mediating inshore population responses to seasonal SST anomalies was weak, the fastest-lived species responding positively and slowest-lived species responding negatively to SST anomalies were organized along an environmental temperature gradient. This finding aligns with the expectation that populations of warm-adapted and faster-lived species benefit more from a warming MAB than cool-adapted and slower-lived species, as the spatial gradient of warming trends in the region shows that SSTs in cooler, northern regions are increasing more rapidly than in warmer, southern regions.

## Discussion

Our study shows that SST anomalies increased across the offshore habitats of the MAB (1982–2023), and that this changing environment tended to promote the autumn population abundances of faster-lived species, while the abundances of slower-lived species tended to decline in response to increasing SSTs in the spring and summer. However, these relationships were weak ($P_{\mathrm{Spring}} = 0.08$, $P_{Summer} = 0.087$), indicating that population-level responses to warming differed in sign (positive/negative) between the inshore habitats of the MAB within species. This bay-to-bay variability in population responses to warming could have been due to differential population responses to region-specific environmental variability or species interactions that went uncharacterized in this study. In addition, we found that the fastest-lived species whose abundances were positively associated response with warming were warm-adapted, whereas the slowest-lived species whose abundances were negatively associated with warming were cool-adapted. Together, our work shows that the autumn population dynamics of inshore fishes in the MAB are being altered by warming waters, and that the magnitude of population responses to warming were weakly dependent on species' positioning along the fast-slow life history continuum, thermal preferences, and local scale processes mediating the integration of these characteristics into population dynamics.

Life history-mediated changes in the population dynamics and distributions of fishes in response to warming are well-documented in continental shelf habitats (Free et al., 2019; M.

McLean et al., 2019; Perry et al., 2005). In the North Sea, those species whose populations shifted or became more abundant in response to warming waters were found to be shorter-lived and smaller-bodied than those populations that did not, suggesting that the faster turnover of these species served as an adaptive response to a warming environment (Perry et al., 2005; Simpson et al., 2011). However, the evidence provided from these studies that fast-lived species shifted their distributions (Perry et al., 2005) and increased in abundances (Simpson et al., 2011) in response to warming to a greater degree than slow-lived species identified these patterns by comparing life history parameters (e.g., maximum body size) between groups of species that shifted or were more abundant following warming. In the latter study of abundance changes, the authors found no relationship between the magnitude of abundance changes and maximum body sizes (Simpson et al., 2011), and this hypothesis is most like the one tested in our study—that the magnitudes of abundance responses to warming fell along a gradient of fast-slow life histories.

The differential within-species responses to warming in our study contributed to the uncertainty around the relationship between magnitudes of warming responses and life history characteristics, but this response variability could shed light on why the potentially mediating effects of life history characteristics on the magnitude of abundance changes in response to warming is elusive on shelf-wide spatial scales. That is, region-specific dynamics may confound patterns of warming responses mediated by life history characteristics evaluated at larger spatial scales. Of course, fish population distributions that are not constrained by the physiographic features of inshore environments will reasonably be expected to respond more homogenously to warming. However, a more explicit consideration of population structures and the spatial variability of population responses to warming in continental shelf habitats, where available data sources are more highly resolved spatially than in inshore environments, may yield insights into how abundance responses to warming fall along life history gradients like the fast-slow gradient evaluated in this study.

While our analysis did not touch on population distribution shifts, other work in the adjacent NES has shown that suitable habitat area has expanded for many commonly collected species (Friedland, Langan, et al., 2020; Friedland, Tanaka, et al., 2023) and that marine fish population centers in the MAB have generally shifted poleward (Kleisner et al., 2016). Our findings that the species contributing most positively to the relationship between population responses to warming and life history characteristics were warm-adapted while those contributing most negatively were cool adapted supports an analogous interpretation to those findings from the NES—an increase in suitable thermal habitat for warm-adapted species in the MAB may have promoted increased abundances of those species in inshore habitats, whereas a decline in suitable thermal habitat for cool-adapted species promoted population declines for those species. However, this interpretation does not speak to the mechanisms through which changes in autumn population abundances in inshore habitats occurs in response to warming. While discerning the specific mechanisms through which warming impacts coastal fish populations falls outside the scope of this study, there are several avenues through which inshore population dynamics may hypothetically respond to warming on the continental shelf.

For instance, an important mechanism that is sensitive to offshore warming and could explain patterns of increased September abundances of warm-adapted species following warming is the phenology of migratory and spawning behaviors of coastal fishes. Many fishes common to the MAB will leave coastal embayments for the continental shelf to spawn in the summer and/or fall months, e.g., spot *Leiostomus xanthurus* and Atlantic croaker *Micropogonias undulatus* (Bucheister et al. 2013; Schonfeld et al. 2022). An explanation for why September population abundances in southerly inshore habitats tend to respond positively to warming could be related to the timing of this migration. That is, a later onset of seasonal cooling during the fall could promote fishes to remain in inshore habitats for longer, therefore increasing September abundances of inshore fishes.

Water temperatures also influence the timing of spawning (Norcross & Austin, 1988) and larval ingress (Thaxton et al., 2020) from the continental shelf into inshore habitats. The availability of food resources is critical for the survival of larval fishes (Cushing, 1990), and so changes in spawning and ingress phenology may threaten the spatiotemporal overlap between larvae and their food, ultimately impacting their recruitment and population abundances in inshore habitats. Warming in offshore habitats is also expected to be correlated with warming in inshore habitats, and warming has been documented in several embayments along the NES (Nixon et al., 2009; Rheuban et al., 2016; Rice et al., 2015; Woodland et al., 2021). However, regardless of spawning location, regional warming may enhance fish population abundances up to a point but may also eventually lead to declines in abundances as temperatures increase outside of species' optimal thermal ranges; non-linear relationships that we did not quantify in our work (Auth et al. 2020). This may help to explain the declining patterns of abundances among cool-adapted species found in our study. Future work may better understand the mechanisms behind population responses to SST anomalies by considering these non-linear effects between abundances and temperatures, the age-structure of collected fishes, as well as a broader range of months when trawl surveys occurred to characterize interactions between warming and migratory and spawning phenologies.

In this work, we analyzed five disparate bottom trawl surveys from across the Mid-Atlantic Bight to understand how autumn inshore fish populations responded to SST anomalies in offshore habitats, and how these responses were mediated by species' positioning along the fast-slow life history continuum. Our results showed that there was high bay-to-bay variability in population responses to warming, but also that population responses to warming were mediated by their thermal affinities and weakly by their life history characteristics. September population abundances of faster-lived, smaller-bodied species that are warm-adapted have tended to increase in response to spring and summertime warming, whereas populations of larger-bodied, longer-lived species that are cool-adapted have tended to decline in response. This work advances our understanding of how climate change influences the dynamics of inshore fish populations in the MAB, and provides insights into the species likely to become more abundant in the region under continued warming.

## Acknowledgements

This project was made possible by financial support from Virginia Sea Grant through their graduate research fellowship. We are extremely grateful to the research staff and scientists who collected and organized the trawl survey data used in this study.

## Figures

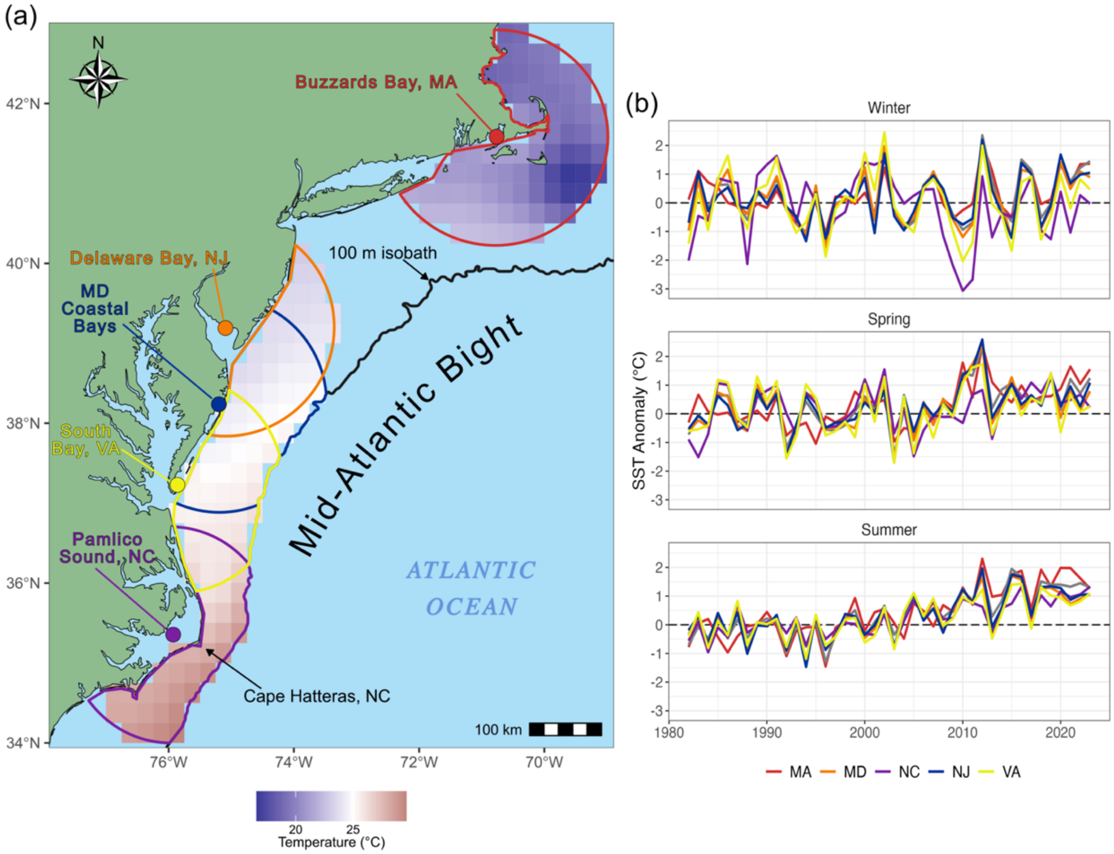


*Figure 1.* Map of the study region shown with the centroid locations of bottom trawl surveys and the names of the bays where trawls occurred (a). Abbreviations are for US states: MA = Massachusetts, NJ = New Jersey, MD = Maryland, VA = Virginia, NC = North Carolina. “MD Coastal Bays” refers to the centroid of trawls performed across four connected coastal bays spanning ~50 km of coastline. The colored polygons associated with survey locations are the 150 km radius circles on the NES that were intersected with the 100 m isobath boundary. The filled grid cells within those polygons show summer 2023 SSTs (°C) from the NOAA OISST V2 data set. Data corresponding to these grid cells were used to calculate bay-specific seasonal SST anomalies, the time series of which are shown in (b), where line colors correspond to the different regions identified on the map.

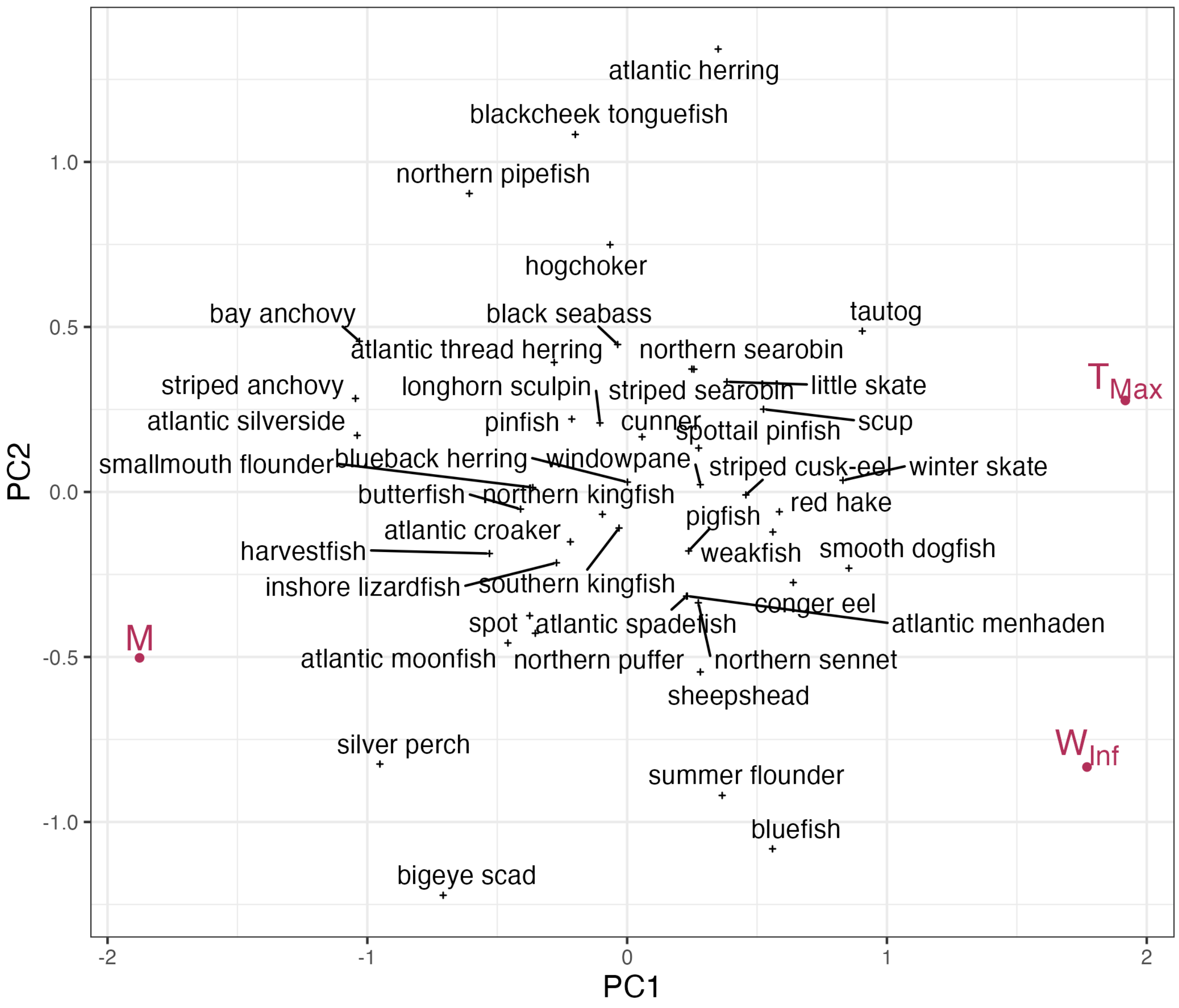


*Figure 2.* PCA biplot showing the multivariate positioning of species considered in our SST anomaly analysis in relation to their life history parameters: natural mortality (M), maximum age ($T_{Max}$), and asymptotic biomass ($W_{Inf}$).

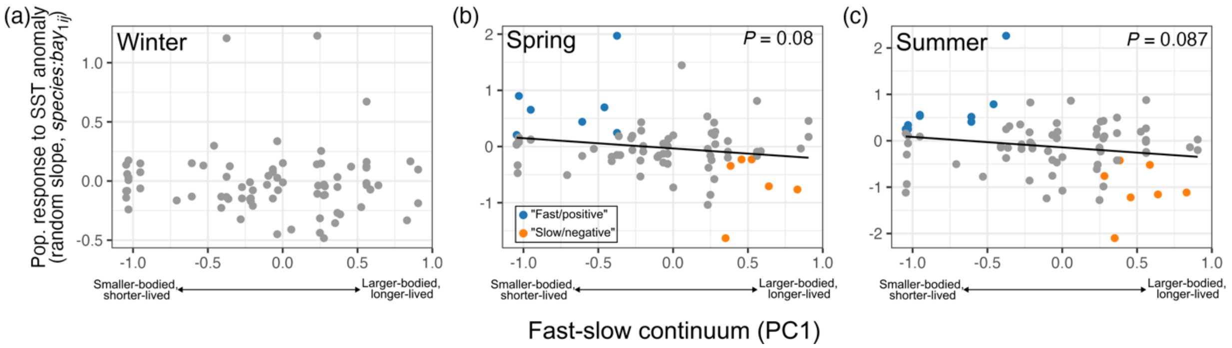


*Figure 3.* The relationship between autumn inshore fish population responses to seasonal SST anomalies in winter (a), spring (b), and summer (c) and the fast-slow continuum. The blue points represent "fast/positive" populations whose SST responses exceed the 75th percentile for slopes and whose PC1 value is in the lower 25th percentile of PC1. Alternatively, the orange points correspond to "slow/negative" populations whose SST responses fall inside the bottom 25th percentile of slopes and whose PC1 values exceed the 75th percentile for PC1.

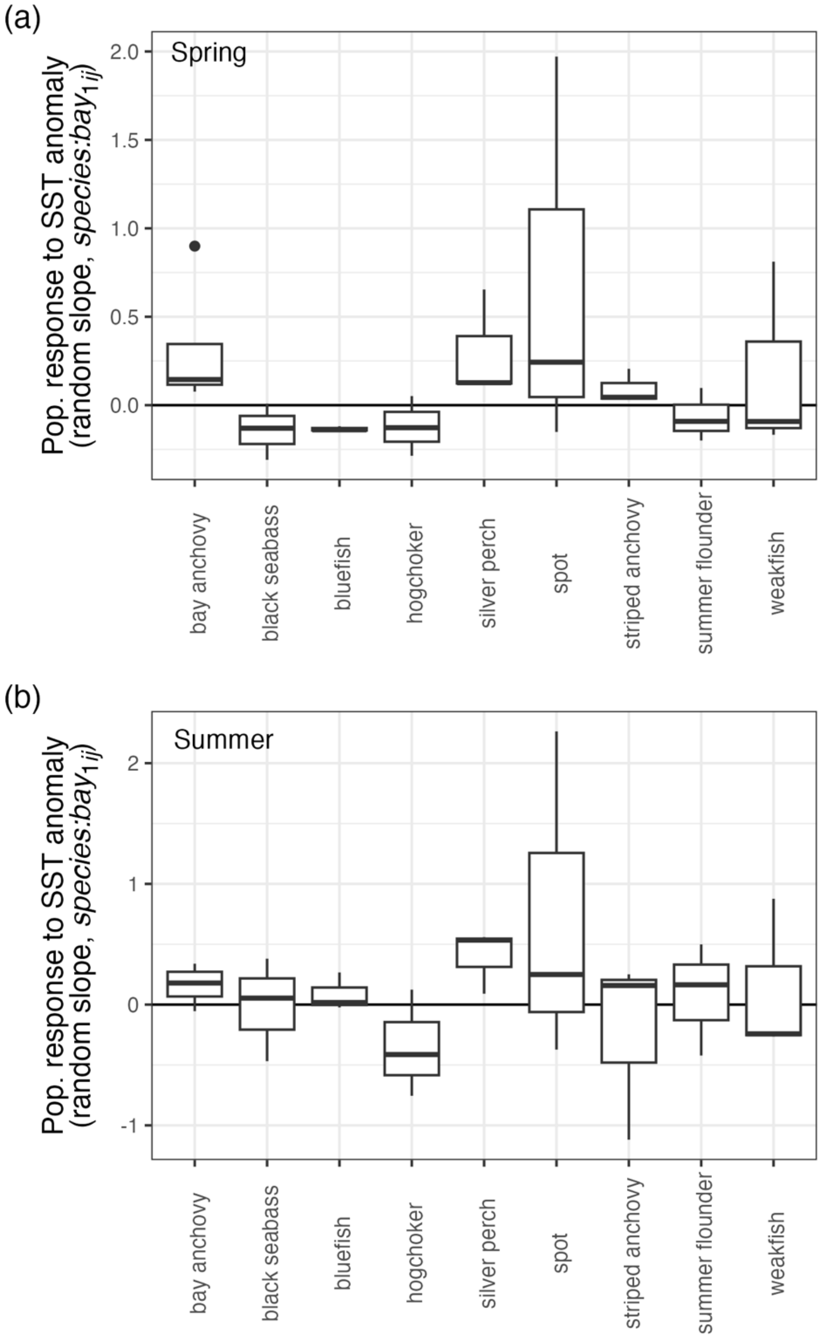
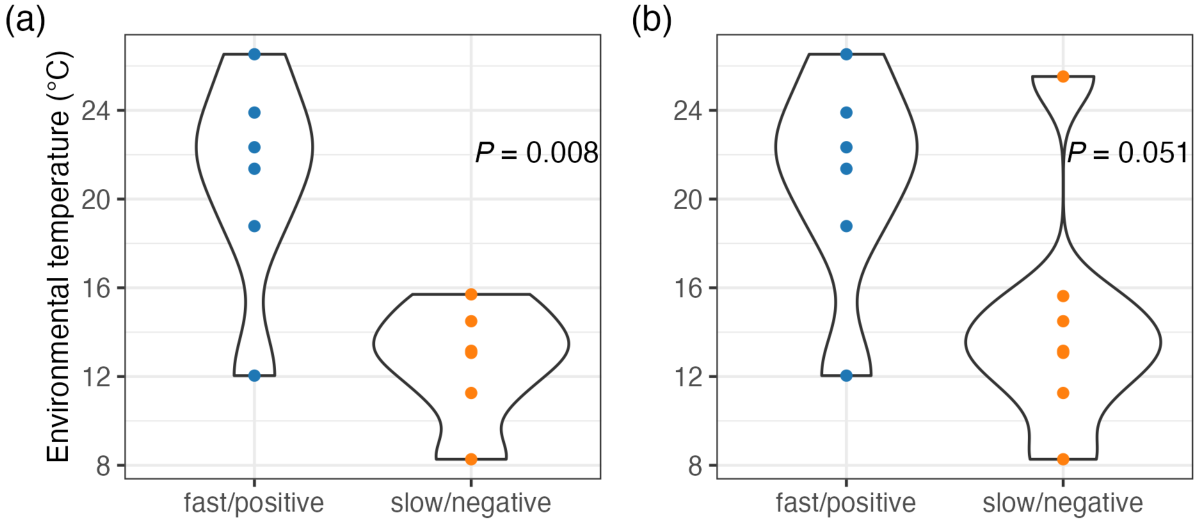


*Figure 4.* Population responses to spring (a) and summer (b) shown by species to visualize their variability around zero effect (black horizontal line). Only species with population estimates in three or more bays were included here.



596

597 *Figure 5.* Violin plots show the distribution of environmental temperatures associated with

598 species driving patterns between population responses to spring (a) and summer (b) SST

599 anomalies on the continental shelf and the fast-slow continuum (Fig. 3). *P* values are from *t* tests

600 between the "fast/positive" and "slow/negative" groups.

601

*Table 1:* Trend statistics for seasonal SST anomalies on the continental shelf by region, reflecting trends within the boundaries on the continental shelf identified in Figure 1. Trends with $P < 0.01$ are highlighted. “iid” refers to independent and identically distributed error.

| *State* | *Season* | *Trend (°C yr$^{-1}$)* | *SE* | *T statistic* | *P* | *Error structure* |
|---|---|---|---|---|---|---|
| **MA** | **Winter** | **0.020** | **0.009** | **2.239** | **0.031** | **iid** |
| **MA** | **Spring** | **0.034** | **0.018** | **1.930** | **0.061** | **AR(2)** |
| **MA** | **Summer** | **0.059** | **0.007** | **8.267** | **0.000** | **iid** |
| NJ | Winter | 0.015 | 0.011 | 1.433 | 0.160 | iid |
| **NJ** | **Spring** | **0.028** | **0.009** | **3.071** | **0.004** | **iid** |
| **NJ** | **Summer** | **0.042** | **0.008** | **5.462** | **0.000** | **iid** |
| MD | Winter | 0.013 | 0.011 | 1.162 | 0.252 | iid |
| **MD** | **Spring** | **0.023** | **0.010** | **2.363** | **0.023** | **iid** |
| **MD** | **Summer** | **0.040** | **0.008** | **5.260** | **0.000** | **iid** |
| VA | Winter | 0.000 | 0.014 | -0.011 | 0.991 | iid |
| VA | Spring | 0.010 | 0.009 | 1.088 | 0.283 | AR(3) |
| **VA** | **Summer** | **0.034** | **0.007** | **4.563** | **0.000** | **iid** |
| NC | Winter | -0.009 | 0.024 | -0.395 | 0.695 | AR(1) |
| **NC** | **Spring** | 0.017 | 0.009 | 1.853 | 0.071 | **iid** |
| **NC** | **Summer** | **0.034** | **0.005** | **6.470** | **0.000** | **iid** |

*Table 2.* Model summary from mixed effects model relating inshore fish population responses to winter, spring, and summer SST anomalies (within 150 km of the centroid of trawl survey locations on the continental shelf and within the 100 m isobath) to the fast-slow continuum (PC1). Here, $\tau_{00,bay}$ and $\tau_{00,species}$ are random intercepts for bay and species respectively, and $N_{bay}$ indicates the number of bays and $N_{species}$ the number of species. When random intercepts are excluded, their inclusion meant that they prevented the model from converging.

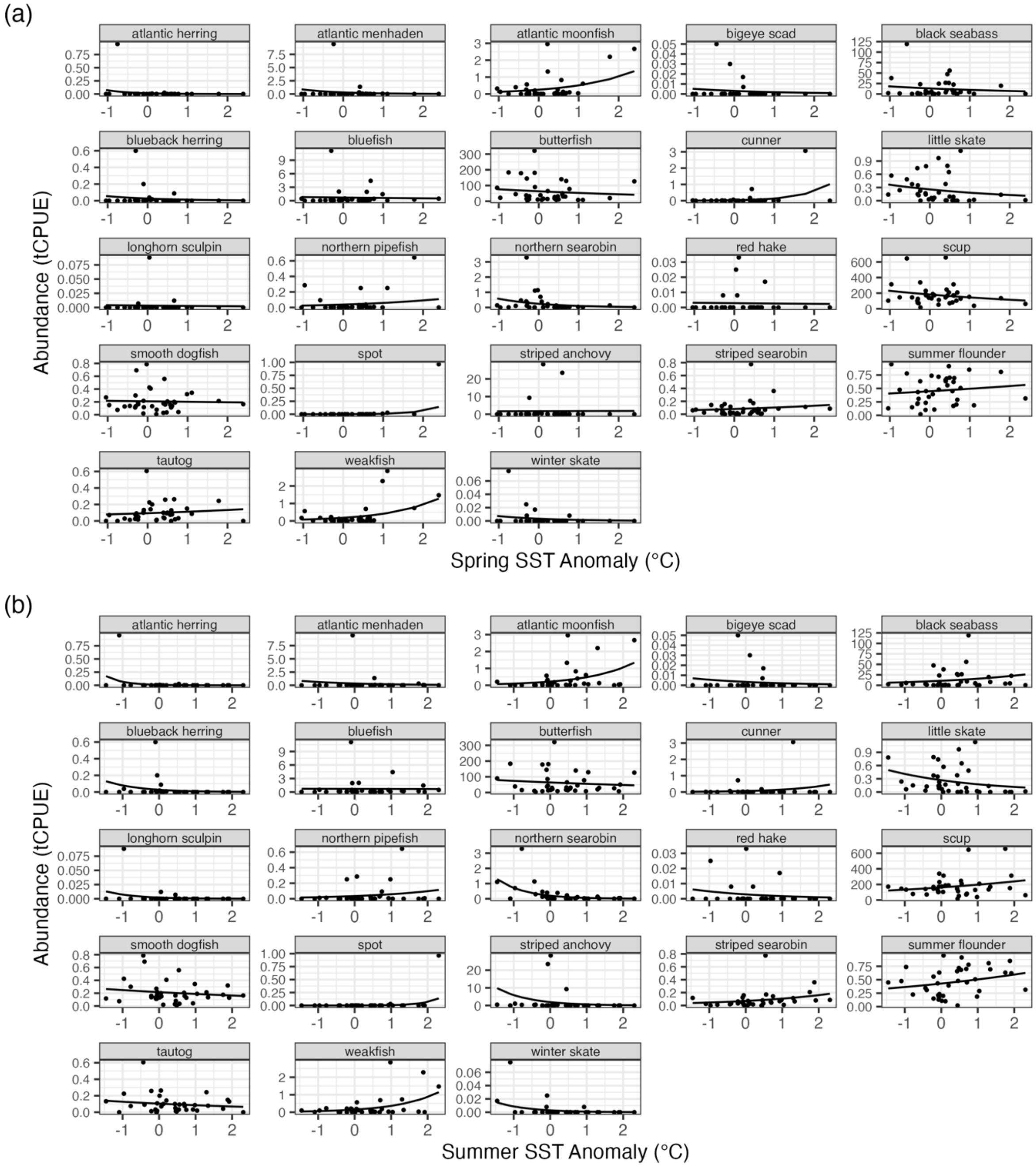
| *SST anomaly season* | *Predictors* | *Estimates* | *CI* | *P* |
|---|---|---|---|---|
| Winter | (Intercept) | -0.00 | -0.08– 0.05 | 0.676 |
| | Fast-slow continuum (PC1) | -0.01 | -0.13 – 0.10 | 0.829 |
| | **Random Effects** | | | |
| | $\sigma^2$ | 0.08 | | |
| | $\tau_{00,bay}$ | 0.00 | | |
| | $\tau_{00,species}$ | 0.00 | | |
| | $N_{bay}$ | 5 | | |
| | $N_{species}$ | 45 | | |
| | Observations | 77 | | |
| | Marginal $R^2$ | 0.001 | | |

| *SST anomaly season* | *Predictors* | *Estimates* | *CI* | *P* |
|---|---|---|---|---|
| Spring | (Intercept) | -0.02 | -0.15 – 0.08 | 0.551 |
| | Fast-slow continuum (PC1) | -0.18 | -0.39 – 0.02 | 0.080 |
| | **Random Effects** | | | |
| | $\sigma^2$ | 0.22 | | |
| | $\tau_{00, bay}$ | 0.00 | | |
| | $\tau_{00, species}$ | 0.01 | | |

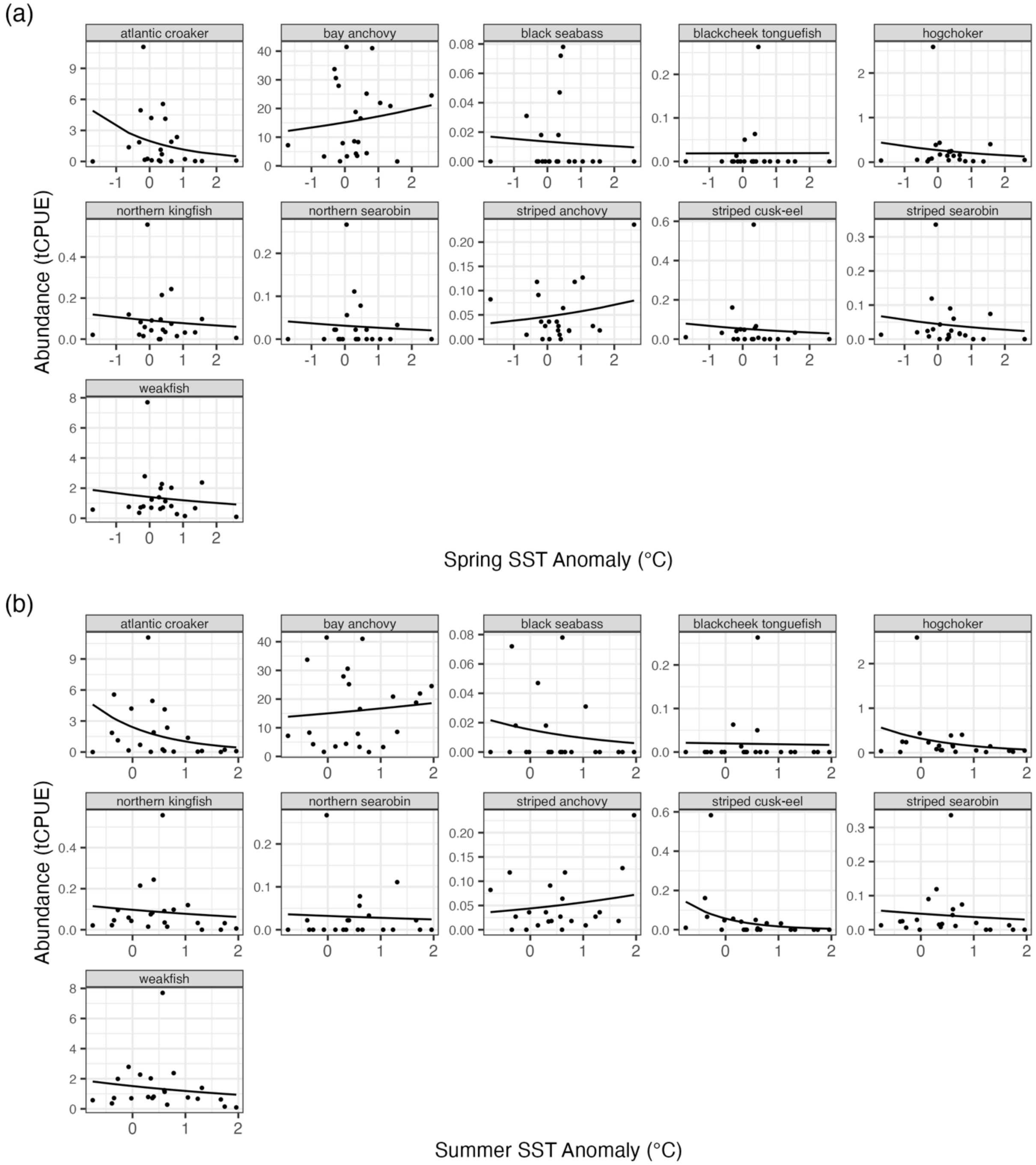
|  |  |  |  |  |
|---|---|---|---|---|
|  | $N_{bay}$ | 5 |  |  |
|  | $N_{species}$ | 45 |  |  |
|  | Observations | 77 |  |  |
|  | Marginal $R^2$ | 0.045 |  |  |

| *SST anomaly season* | *Predictors* | *Estimates* | *CI* | *P* |
|---|---|---|---|---|
| Summer | (Intercept) | -0.14 | -0.29 – -0.01 | 0.002 |
|  | Fast-slow continuum (PC1) | -0.22 | -0.48 – -0.03 | 0.087 |
|  | **Random Effects** |  |  |  |
|  | $\sigma^2$ | 0.38 |  |  |
|  | $\tau_{00, species}$ | 0.00 |  |  |
|  | $N_{bay}$ | 5 |  |  |
|  | $N_{species}$ | 45 |  |  |
|  | Observations | 77 |  |  |
|  | Marginal $R^2$ | 0.038 |  |  |

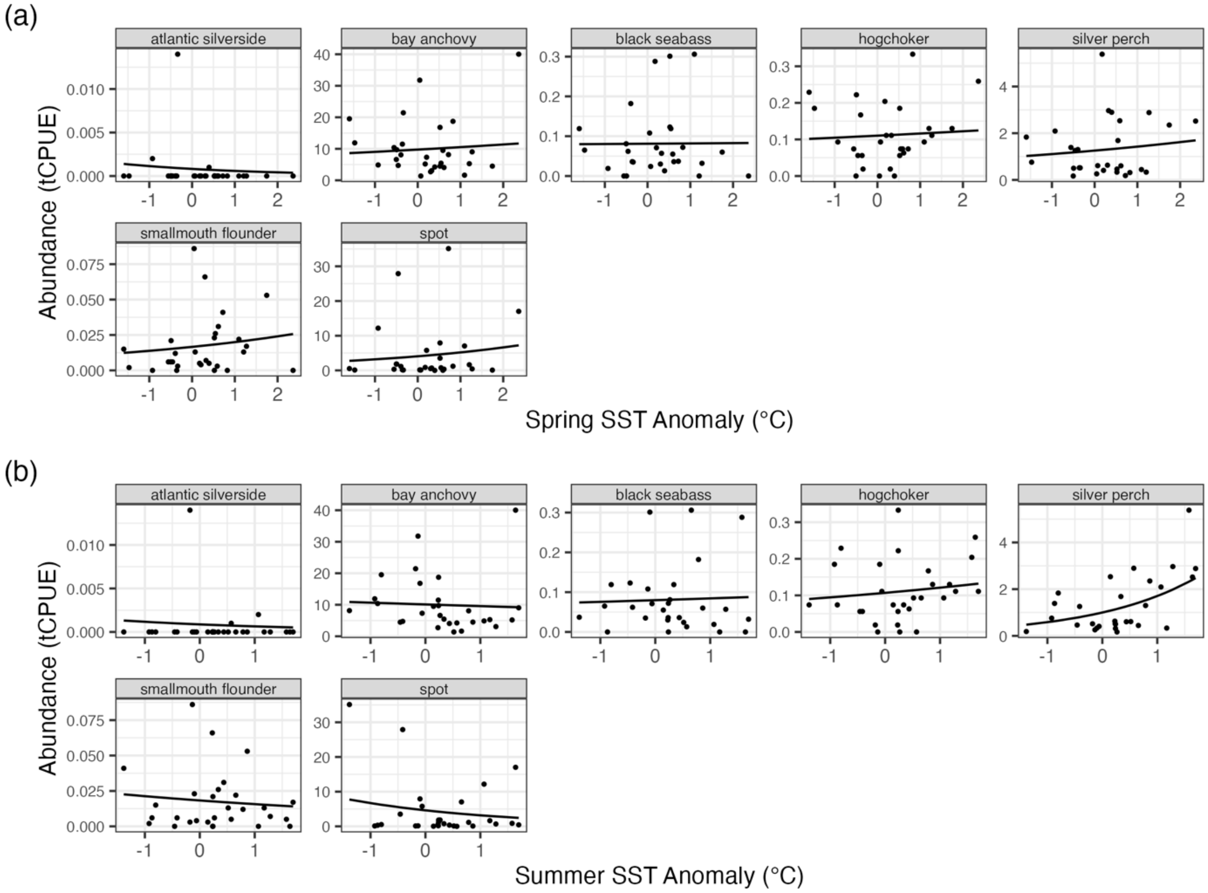
# Appendix



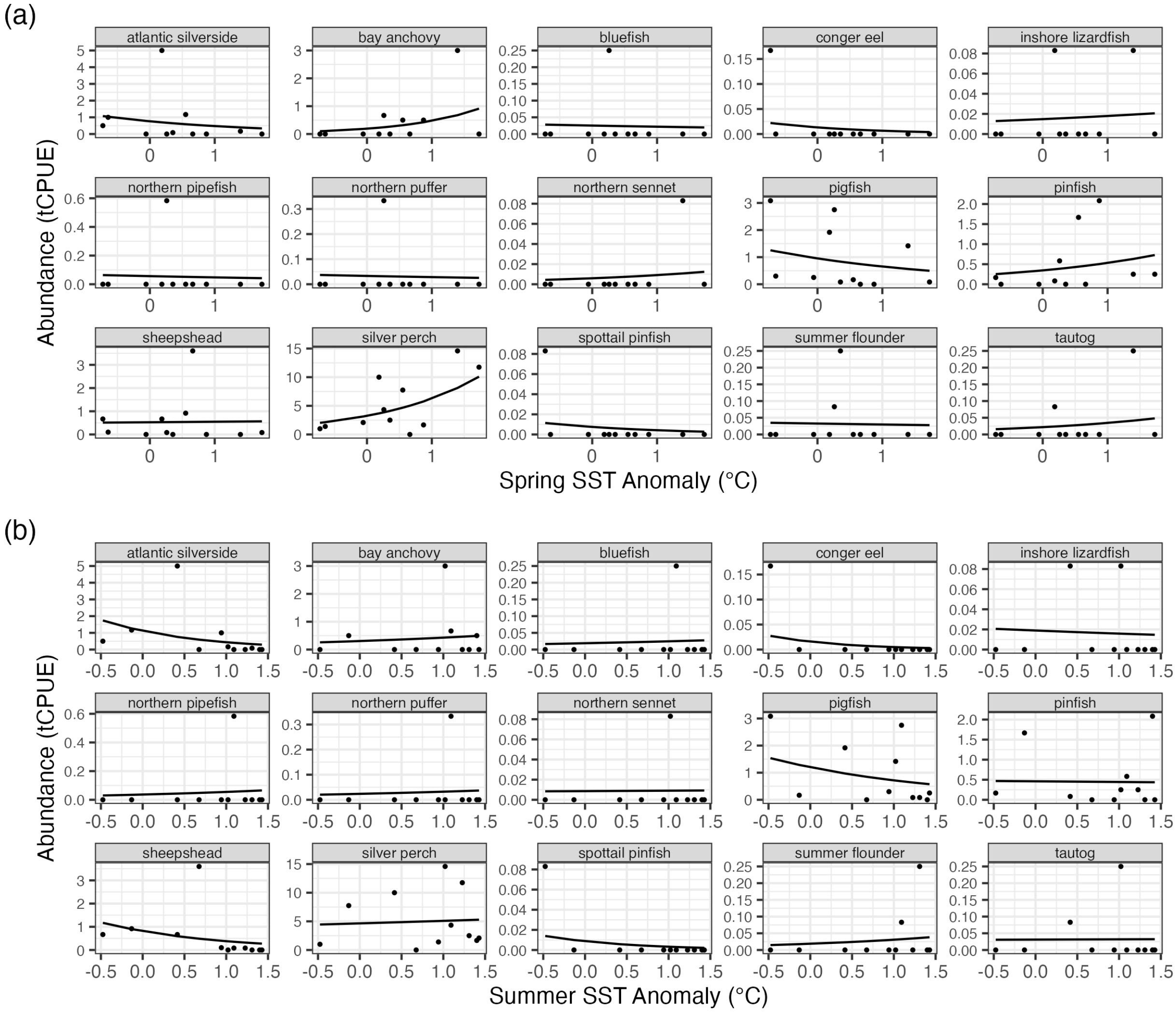
*Appendix 1.* Species-level predictions for the relationship between autumn inshore tCPUE (modeled time series of catch per trawling minute) and spring (a) and summer (b) SST anomalies in the offshore habitat near Buzzards Bay, Massachusetts.



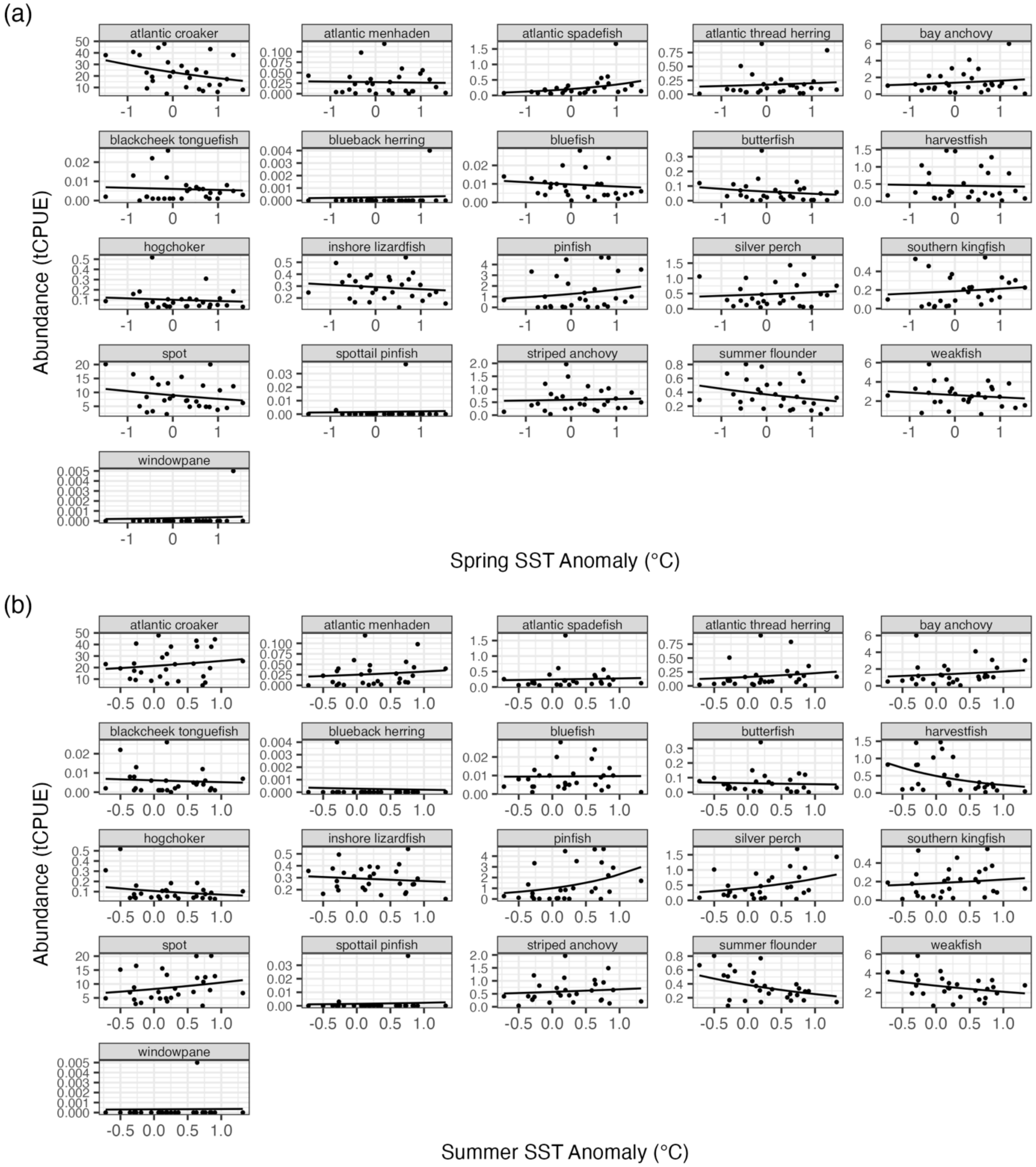
*Appendix 2.* Species-level predictions for the relationship between autumn inshore tCPUE (modeled time series of catch per trawling minute) and spring (a) and summer (b) SST anomalies in the offshore habitat near Delaware Bay, New Jersey.



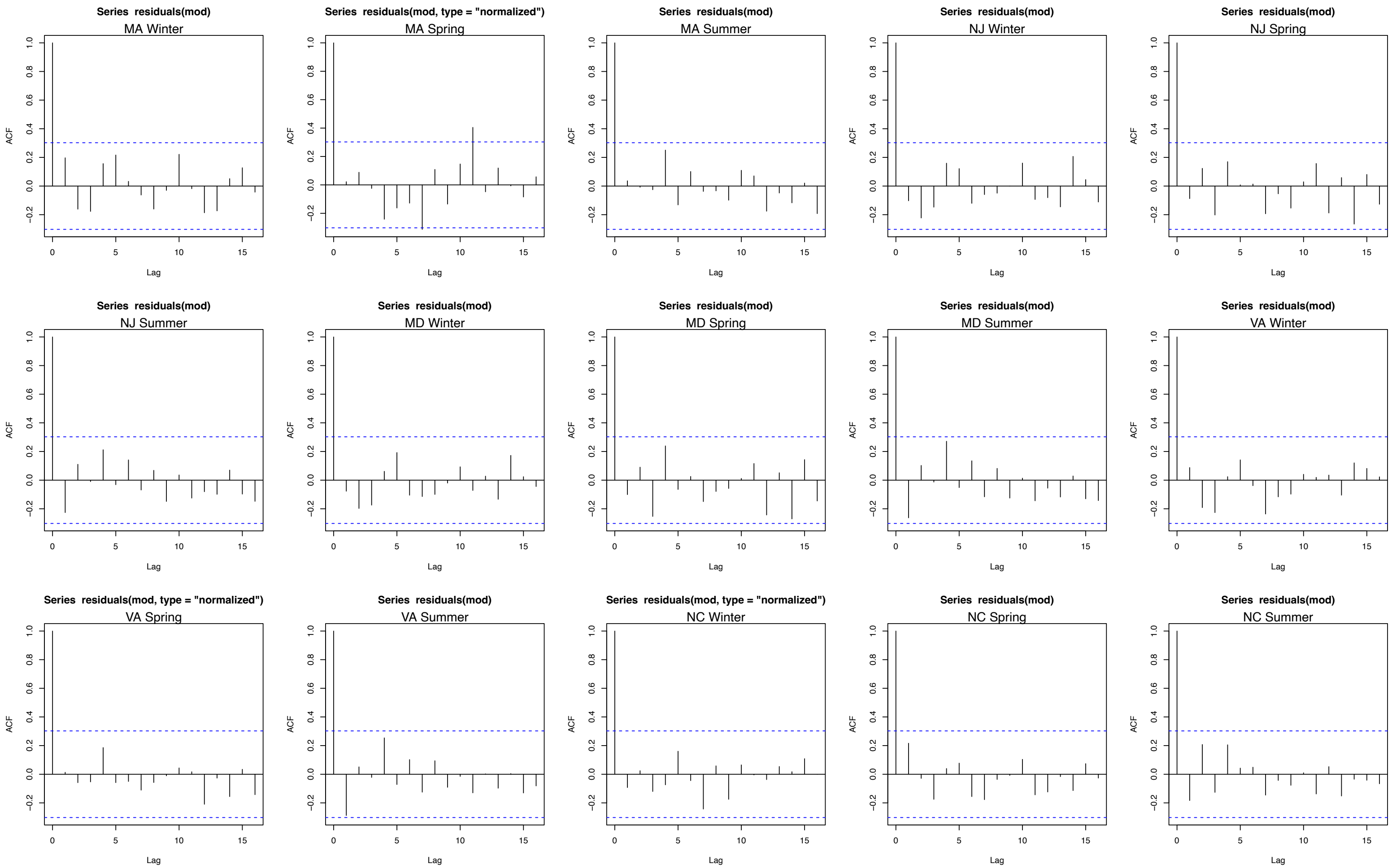
*Appendix 3.* Species-level predictions for the relationship between autumn inshore tCPUE (modeled time series of catch per trawling minute) and spring (a) and summer (b) SST anomalies in the offshore habitat near the coastal bays of Maryland.



*Appendix 4.* Species-level predictions for the relationship between autumn inshore tCPUE (modeled time series of catch per trawling minute) and spring (a) and summer (b) SST anomalies in the offshore habitat near South Bay, Virginia.



*Appendix 5.* Species-level predictions for the relationship between autumn inshore tCPUE (modeled time series of catch per trawling minute) and spring (a) and summer (b) SST anomalies in the offshore habitat near Pamlico Sound, North Carolina.



*Appendix 6.* Autocorrelation of residuals from trend models of seasonal SST anomalies. Figures with “type = normalized” show the autocorrelation of normalized residuals after fitting the trend model using generalized least squares with various error structures (see Table 1).

*Appendix 7.* Summary statistics from the three mixed-effects models used to model population responses to warming in the winter, spring, and summer months. “CI” is the 95% confidence interval for the estimates.

| ***Season*** | ***Predictors*** | ***Estimates*** | ***CI*** | ***P*** |
|---|---|---|---|---|
| Winter | (Intercept) | 0.15 | 0.05 – 0.48 | 0.001 |
| | *bay* [Delaware Bay] | 0.94 | 0.12 – 7.16 | 0.951 |
| | *bay* [MD Coastal Bays] | 1.2 | 0.11 – 13.16 | 0.88 |
| | *bay* [Pamlico Sound] | 0.8 | 0.15 – 4.27 | 0.794 |
| | *bay* [South Bay] | 0.59 | 0.09 – 3.78 | 0.58 |
| | | | | |
| | **Random Effects** | | | |
| | (intercept) $species{:}bay_{0ij}$ | 7.846 | | |
| | (slope) $species{:}bay_{1ij}$ | 0.164 | | |
| | $N_{species}$ | 45 | | |
| | $N_{bay}$ | 5 | | |
| | Observations | 2049 | | |

| ***Season*** | ***Predictors*** | ***Estimates*** | ***CI*** | ***P*** |
|---|---|---|---|---|
| Spring | (Intercept) | 0.13 | 0.04 – 0.43 | 0.001 |
| | *bay* [Delaware Bay] | 1.14 | 0.15 – 8.96 | 0.9 |
| | *bay* [MD Coastal Bays] | 1.36 | 0.12 – 15.38 | 0.805 |
| | *bay* [Pamlico Sound] | 0.94 | 0.17 – 5.17 | 0.948 |
| | *bay* [South Bay] | 0.59 | 0.09 – 3.89 | 0.584 |
| | | | | |
| | **Random Effects** | | | |
| | (intercept) $species{:}bay_{0ij}$ | 8.066 | | |
| | (slope) $species{:}bay_{1ij}$ | 0.426 | | |
| | $N_{species}$ | 45 | | |
| | $N_{bay}$ | 5 | | |
| | Observations | 2049 | | |

| ***Season*** | ***Predictors*** | ***Estimates*** | ***CI*** | ***P*** |
|---|---|---|---|---|
| Summer | (Intercept) | 0.12 | 0.04 – 0.40 | 0.001 |
| | bay [Delaware Bay] | 1.31 | 0.16 – 10.57 | 0.801 |
| | bay [MD Coastal Bays] | 1.47 | 0.13 – 17.09 | 0.76 |
| | bay [Pamlico Sound] | 0.99 | 0.18 – 5.55 | 0.995 |
| | bay [South Bay] | 0.71 | 0.10 – 4.88 | 0.731 |

| | |
|---|---|
| **Random Effects** | |
| (intercept) $species{:}bay_{0ij}$ | 8.263 |
| (slope) $species{:}bay_{1ij}$ | 0.681 |
| $N_{species}$ | 45 |
| $N_{bay}$ | 5 |
| Observations | 2049 |

# Chapter 2

## *Asynchrony drives stability across coupled social-ecological systems: an example from Chesapeake Bay demersal fisheries*

Anticipated authors of peer-reviewed manuscript:

Sean B. Hardison
Jonathan S. Lefcheck
Shelby B. White
Maowei Liang
Y. Stacy Zhang
Christopher J. Patrick
Andrew M. Scheld
Robert J. Latour
F. Joel Fodrie
Sean C. Anderson
Max C. N. Castorani

## Abstract

Ecological diversity can confer temporal stability of ecosystem processes through asynchrony in species' abundances. This stability can also translate to stability of ecosystem services, for example in fisheries, by distributing harvest pressure among asynchronous populations that are also exploited. Coupled investigations that consider both naturally- and anthropogenically-induced asynchrony are rare, but have the potential to greatly inform the management of resource systems. Here, we used harvest data and fisheries-independent trawl surveys in two regions (Maryland and Virginia) of the Chesapeake Bay, USA from 2002–2018 to explore how seasonal (within-year) asynchrony among targeted fish species contributed to: 1) seasonal asynchrony in the harvests of these species, and 2) the within-year stability and economic value of harvests. In Maryland, seasonal closure of striped bass (*Morone saxatilis*) fishing resulted in asynchrony by forcing the harvest of alternative stocks. In Virginia, the natural emigration of target species from the system was positively associated with harvest asynchrony, although this effect was driven largely by the increase in relative evenness among remaining species that constituted a much lower exploitable biomass. Our findings show that both social (management) and ecological factors influence asynchrony in the harvests of fished populations, which goes onto affect the stability of regional harvest portfolios.

## Introduction

The management of social-ecological systems like commercial fisheries is challenged by their immense complexity that limits the comprehension of the drivers of system dynamics (Levin et al., 2013; Link, 2018) and ultimately their predictability (Boettiger & Hastings, 2013). However, in commercial fishing harvest portfolios, defined as dynamic collections of harvests drawn from multiple species and/or populations within a region (i.e, “stocks”), as well as in the ecosystems those portfolios depend upon, it is interestingly the fostering and conservation of complexity that has long been advocated for as a strategy to reduce variability in aggregate system properties like total harvest yield and revenue (Cline et al., 2017; Hilborn et al., 2001; Schindler et al., 2010) or community biomass production (Tilman, 1996; Tilman et al., 1998). When commercial fishing portfolios or biological communities are composed of diverse species assemblages, the asynchronous dynamics of these “assets” leads to reduced variability (enhanced stability) over time in the aggregate system relative to the average asset, otherwise known as a “portfolio effect” (S. C. Anderson et al., 2017; Link, 2018; Schindler et al., 2015). Despite the dependence of commercial fisheries on the population dynamics of the species they target, the relationships between asynchrony among species populations in the environment (species asynchrony) and the asynchrony of harvests drawn from those species (harvest asynchrony) are not well integrated. Clarifying these relationships will shed light on the stabilizing role of biodiversity in social-ecological systems like commercial fisheries.

The stabilizing effect of asynchrony is a common feature of complex, hierarchical, and dynamic systems that are composed of species populations whose abundances fluctuate through time (Link, 2018). Understanding how asynchrony in harvest portfolios and the biological communities they depend upon relate to each other benefits from first considering how asynchrony emerges from within these systems. While there are many ways to quantify asynchrony (Doak et al., 1998; J. W. Moore et al., 2021; Siple et al., 2020; Thorson et al., 2018), we adopt an approach developed in community ecology where, in the context of a community of species, asynchrony ($\phi$) is quantified as the ratio comparing community stability ($S_{Community}$) to an average across-species stability ($S_{Species}$), such that $S_{Community} = \phi S_{Species}$ (Thibaut & Connolly, 2013; Wang & Loreau, 2016; Zhao et al., 2022). While this approach has only previously been applied in an ecosystem context, we extend its application to fishery harvest portfolios that share similar hierarchical structures to communities, i.e., populations (stocks) that comprise a portfolio (harvest) (Link, 2018). In all cases, stability is the inverse temporal variability (i.e., the inverse coefficient of variation = 1/CV) of system properties. In this formulation, $\phi$ cannot be < 1, meaning that stability of the community will almost always be higher than average across-species stability due to asynchrony (Doak et al., 1998; Link, 2018). This measure of asynchrony integrates two related processes whose effects can be partitioned mathematically: statistical averaging and compensation (Fig. 1, Zhao et al., 2022).

Statistical averaging is the enhancement of system stability that occurs when system components fluctuate independently of one another through time, thereby reducing variability of the system in aggregate (Doak et al., 1998; Link, 2018). In the mathematical partitioning of $\phi$, Zhao et al. (2022) showed that statistical averaging depends on the quantity and evenness of species variances. For example, the contribution of statistical averaging to $\phi$ will be low in a community characterized by few species whose population dynamics are independent and with highly unequal variances. This unevenness in variances is a common feature of communities, which are almost universally skewed in abundances among species (Avolio et al., 2019; Pedersen et al., 2019) and where population variances tend to increase non-linearly with their means (S. C. Anderson et al., 2013; Mikkelson et al., 2011). In contrast, compensation effects also contribute to $\phi$, but increase when species' dynamics in a community are negatively correlated. In other words, different species may rise to (and fall from) dominance through time in response to, for example, changing conditions in the environment or availability of resources, such that any given ecosystem property is steadily provided by a rotating cast of characters. Compensation effects can occur in ecosystems due to species interactions (Del Río et al., 2017) or due to the differential responses of species to their environments (Brown et al., 2016).

While asynchrony among species dynamics within a community—or among harvest dynamics within a harvest portfolio—will stabilize the aggregate properties of these systems, how asynchrony within a community relates to asynchrony in the harvests derived from that community depends on both ecological and social factors (J. W. Moore et al., 2021; Oken et al., 2021). Asynchrony in stock population dynamics can enhance the stability of the fishery portfolios derived from those stocks, as fishing effort can switch among individual stocks as they become more or less productive from year to year (Hilborn et al., 2003; J. W. Moore et al., 2021; Nesbitt & Moore, 2016; Oken et al., 2021; Schindler et al., 2010). Similarly, seasonal (within-year) compensatory dynamics among stocks extend fishing seasons as harvestable biomass remains accessible to fishers for longer (Nesbitt & Moore, 2016; Schindler et al., 2010). However, the stability imparted to the fishery portfolio by stock population asynchrony is mediated by fisher behaviors in response to regulatory and economic factors. For example, if the harvest of a particular stock is limited due to management regulations, if many fishers are unable to attain licenses to target a particular stock, or if diversifying across stocks is cost prohibitive or not profitable (Kasperski & Holland, 2013; Sethi et al., 2014), stability may arise not from inherent asynchrony in the population dynamics of targeted stocks, but rather from societal changes in how fishing effort is distributed across stocks. We note that these processes are not mutually exclusive, and in fact may operate in tandem to further bolster fisheries stability.

In this study, we tested the hypothesis that within-year asynchrony in commercial fishing harvest portfolios is driven by within-year asynchrony among the species comprising the harvest portfolio. To accomplish this, we partitioned asynchrony into compensatory and statistical averaging effects among species and then among harvests. We predicted that seasonal compensation in population dynamics would be positively associated with the seasonal compensation of harvests. We then extended this analysis to test the hypothesis that within-year harvest asynchrony increased within-year fishery economic stability and the overall value of the harvest portfolio.

We explored these hypotheses within communities of demersal finfish and the associated commercial fisheries in the mainstem of Chesapeake Bay, USA (Fig. 2). The Chesapeake Bay (hereafter, ‘the Bay’) is among the largest and most economically and ecologically valuable estuaries in the world and supports numerous economically and culturally valuable fisheries (Sanchirico et al., 2008). Like many other temperate estuaries, fishes in the Bay are transient and migrate into and out of the estuary seasonally (Buchheister et al., 2013; Schonfeld et al., 2022). The fish community in the Bay is also heavily structured by salinity, with distinct communities dominating more saline waters near the mouth versus those in the comparably fresher headwaters (Lefcheck et al., 2014), and commercial fisheries operating in these regions fall under different management regimes, although several species within the portfolio of stocks are collectively overseen by a regional authority. The relatively low estuarine diversity, naturally asynchronous dynamics among harvested species through time, and well-documented regulatory structuring along a prominent spatial environmental gradient make the Chesapeake Bay an ideal test case for evaluating how asynchrony among populations of exploited species relates to asynchrony in dependent fisheries.

## Methods

### *Methods overview*

To test the hypotheses that within-year species asynchrony among targeted fishes in Chesapeake Bay led to within-year harvest asynchrony and harvest portfolio yield, stability, and economic value, we first developed monthly time series of species-specific total biomass estimates ("biomass indices") for six species of finfish commonly targeted by commercial fishing in the Maryland and Virginia regions of the Bay mainstem (Fig. 2). We used these indices to calculate within-year species asynchrony and its components—species compensation and species statistical averaging effects—within both regions.

We then used the total monthly harvests of these six species from the mainstem of the Bay in Maryland and Virginia to calculate harvest asynchrony and its components—harvest compensation and harvest statistical averaging effects. Next, we related seasonal species compensation and statistical averaging effects to seasonal harvest compensation and statistical averaging effects using structural equation models (SEMs). We predicted that harvest and species compensation would be positively associated given strong seasonal patterns in fish abundances in the Bay and the expectation that seasonal harvests from these species would correlate with their seasonal abundances. In Maryland, the striped bass (*Morone saxatilis*) fishery is closed for part of the year, so we expected that harvest diversification outside of striped bass during this closure would increase harvest asynchrony.

Lastly, we summed harvest yields and harvest values across species within-years to create monthly indices of portfolio harvests and value. We used these indices to calculate annual harvest yield and value stability, as well as total annual harvest yields and value. We extended the SEMs from the previous analysis to evaluate the indirect linkages between species asynchrony (partitioned as species compensation and statistical averaging effects) and harvest portfolio yield, stability, and economic value. We identified that commercial fishing effort declined over the study period, and so we related an index of overall fishing effort to the components of harvest asynchrony in SEMs.

### *Fish community dynamics and commercial fishing in the Bay*

In the northern mainstem of the Chesapeake Bay (blue region in Fig. 2), fisheries management falls under the jurisdiction of the US state of Maryland (MD; via the Maryland Department of Natural Resources [MD-DNR]), and long-term average salinities within this region vary from fresh to mesohaline (0–15 PSU) with proximity to freshwater inputs to the north and west (Harding et al., 2019). Demersal fish biomass in MD waters is dominated by anadromous white perch (*Morone americana*) and striped bass (*Morone saxatilis*), especially in spring prior to moving into Bay tributaries to spawn and in autumn when these fishes aggregate in deeper waters (Buchheister et al., 2013). In the mainstem alone, striped bass harvests in 2002–2018 were valued at $3.1 million USD per year, making them the most valuable finfish harvested in this region, and white perch $276,000 USD per year, the third most valuable species (this study; data from MD-DNR). In the MD waters of Chesapeake Bay, commercial striped bass harvests are prohibited during the spring spawning season (March–May).

In the southern mainstem of the Bay (orange region in Fig. 2), fisheries management falls to the commonwealth of Virginia (VA; via the Virginia Marine Resources Commission [VMRC]). Salinities in this region increase to euhaline at the interface of the Bay and Atlantic Ocean, and demersal fish biomass is frequently dominated by species that seasonally migrate onto the adjacent continental shelf to spawn (Buchheister et al., 2013). These species include the major fishery targets Atlantic croaker (*Micropogonis undulatus*) and spot (*Leiostomus xanthurus*), whose biomasses tend to peak in the spring and summer following the migration and recruitment of adults and young-of-the-year fish into the Bay from the continental shelf, as well as the ontogenic movement of juveniles from shallow Bay nurseries to the Bay mainstem (Buchheister et al., 2013). In the VA mainstem, the three most valuable commercial finfish fisheries include Atlantic croaker (average harvest value in 2002–2018 was \$2.3 million USD/year), striped bass (\$1.65 million USD/year), and spot (\$1.27 million USD/year) (this study; data from VMRC). Regulations in the Bay prevent commercial harvest of Atlantic croaker prior to January 15 of each calendar year, striped bass prior to January 16, and spot prior to April 15 or after December 8. Given the unique regulatory, environmental, and ecological characteristics of the northern (MD) and southern (VA) regions of the Bay, we considered the ecosystems and fisheries in these regions to be distinct and analyzed them separately.

### *Bottom-trawl survey and commercial harvest data*

In order to characterize demersal finfish population dynamics, we derived within-year biomass indices from the Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAP) bottom trawl survey (Latour et al., 2003). During 2002–2018, ChesMMAP cruises usually surveyed the entire Bay mainstem five times annually (targeting March, May, July, September, and November), sampling 300–400 locations per year. However, surveys in some month-year combinations did not occur, and in others sample coverage was relatively sparse (detailed below). The survey followed a stratified random design within three depth ranges (3.0–9.1 m, 9.1–15.2 m, and >15.2 m) (Buchheister et al., 2013).

We estimated biomass indices (see below) for demersal finfishes that were both well-sampled by the bottom trawl survey (see Buchheister et al., 2013) and for whose cumulative commercial harvests made up >90% of total harvest yield over the study period. In MD, these species included Atlantic croaker, striped bass, white perch, gizzard shad (*Dorosoma cepedianum*), and channel catfish (*Ictalurus punctatus*). While gizzard shad and channel catfish were only found in ~5% and ~2% of ChesMMAP trawls, respectively, these species are considered well-sampled in the Bay mainstem by the bottom trawl (Buchheister et al. 2013). After excluding blue crabs and Atlantic menhaden (a pelagic species poorly-sampled by the bottom trawl [Bucheister et al., 2013]), the combined harvests of these five species contributed to ~94% of total harvests in the MD mainstem over the study period. In VA, these species included Atlantic croaker, spot, and striped bass. We selected these species because their combined harvests accounted for ~93% of total harvests over the study period after excluding blue crab and Atlantic menhaden.

We evaluated commercial harvest dynamics for these species in the regions of MD and VA that overlapped with ChesMMAP surveys using monthly harvest yield and value data provided by MD-DNR and VMRC (Fig. 3). We also received data on fishing effort in the form of the number of trips per month that fishers encountered each species in both MD and VA. We created a combined index of trips across species within each region that was the mean number of trips across species annually. To understand how the closure of the striped bass fishery, the most valuable fishery in the MD harvest portfolio, impacted the stability and value of the portfolio, we created an index called the seasonal harvest ratio (SHR). The SHR was the ratio of the average monthly harvests occurring during the striped bass fishery closure to the average monthly harvests occurring outside the striped bass fishery closure. When the SHR was high, harvests of species other than striped bass were compensating for the absence of striped bass harvests during the closure.

*Biomass index modeling*

We used generalized additive mixed models (GAMMs) to develop within-year biomass indices for these species in MD and VA waters to compare with harvests in these regions. The GAMMs included penalized smooth terms and spatial and spatiotemporal Gaussian Markov random fields. We modeled biomass indices with Tweedie observation error and a log link (Tweedie, 1984). All models included categorical predictors corresponding to each of five target sampling months for the ChesMMAP survey. We allowed for interannual variability in month-year predictions by including factor-smooth interactions (bs = “fs” in the R package *mgcv* [S. N. Wood, 2006]) for numeric month by year; treating month as numeric because surveys sometimes occurred in months adjacent to the “target” month. For the spot biomass model, we included a thin-plate regression smoother for the numeric year-month combination (S. N. Wood, 2006), and for the gizzard shad and channel catfish models, we included categorical predictors for year factors. These changes improved convergence and residual behavior for these models.

There were four instances where cruises did not occur in 2002–2018 (out of 85 possible; 4.7%). In fitting each model, we also excluded trawls collected from regions where a given species was not found throughout all surveys (Commander et al., 2022). This reduced the number of observations available for fitting these models, especially for anadromous fishes whose distributions were limited to the northern mainstem. However, the inclusion of smooth terms allowed us to interpolate reasonable biomass estimates representing typical seasonal densities for each species during these periods and for when there were relatively few observations (e.g., in 3 of 85 month-year combinations, there were fewer than 30 trawls available for fitting the white perch model). To calculate area-weighted biomass indices, we predicted from each model over a grid with 2 km$^2$ cells derived from the boundary of the ChesMMAP survey (Fig. 2) and summed these predictions within months. The model for species besides spot, gizzard shad, and channel catfish can be represented as

$$\begin{aligned} \mathbb{E}[y_{\mathbf{s},t}] &= \mu_{\mathbf{s},t}, \\ \mu_{\mathbf{s},t} &= \exp\left(\alpha_{\text{season}} + f_{\text{year}}(\text{month}) + \omega_{\mathbf{s}} + \epsilon_{\mathbf{s},t}\right), \\ \omega_{\mathbf{s}} &\sim \text{MVN}(\mathbf{0}, \mathbf{\Sigma}_{\omega}), \\ \epsilon_{\mathbf{s},t} &\sim \text{MVN}(\mathbf{0}, \mathbf{\Sigma}_{\epsilon}), \end{aligned} \tag{1}$$

where $\mu_{\mathbf{s},t}$ represents the mean at location *s* and time *t*, $\alpha_{\text{season}}$ an overall mean for each target month, $f_{\text{year}}(\text{month})$ the numeric month-year factor-smooth interaction with common wiggliness, $\omega_{\mathbf{s}}$ a spatial random field value (varies by space but is constant with time), and $\epsilon_{\mathbf{s},t}$ a spatiotemporal random field value that is independent each year. The Gaussian random fields were approximated as Gaussian Markov random fields using the Stochastic Partial Differential Equation (SPDE) approach (Lindgren et al., 2011) with covariance matrices $\mathbf{\Sigma}_{\omega}$ and $\mathbf{\Sigma}_{\epsilon}$, each constrained by a Matérn covariance function (Cressie & Huang, 1999).

We fitted these models in R using the package *sdmTMB* (S. C. Anderson et al., 2022) via maximum marginal likelihood. sdmTMB integrates SPDE matrices from R-INLA (Lindgren & Rue, 2015) with marginal log likelihood calculations and random effect integration via the Laplace approximation with TMB (Kristensen et al., 2015). Our ‘mesh’ for the SPDE calculations was constructed in R-INLA with an inner mesh near the data and an outer mesh further away from the data to reduce boundary effects (Lindgren & Rue, 2015). Our inner and outer meshes had an ‘offset’ of 3 km and 8 km from the data, maximum triangle edge lengths of 3 km and 15 km, and a minimum triangle edge length of 3 km. We assessed model convergence by checking that the maximum absolute gradient of the marginal log likelihood with respect to all fixed effects was < 0.001 and the Hessian matrix was positive definite. The time series derived from these models are shown in Figure 4.

*Partitioning stability and asynchrony and hypothesis testing*

We applied the stability and asynchrony partitioning framework developed by Thibault & Connolly (2013; who considered the related quantities of variability and synchrony) that is commonly used in ecological contexts (Lamy et al., 2019; Wang et al., 2019) to both the communities of species being targeted by commercial fisheries in the Bay and to the harvest portfolios in MD and VA. When applied to the fishery harvest portfolio, the stability of intra-annual portfolio harvests is $S_{Portfolio}$, or the inverse of total harvest variability, given by

$$S_{Portfolio} = \left(\frac{\sigma_R}{\mu_R}\right)^{-1}. \qquad (2)$$

Here, $\sigma_R$ is the temporal standard deviation of total harvests and $\mu_R$ the temporal mean of total harvests in a region $R$. $S_{Portfolio}$ is equivalent to the product of harvest asynchrony ($\phi_{Harvest}$) and species stability ($S_{Harvest}$), the latter term being given by

$$S_{Harvest} = \left(\sum_i^n CV_i \times \frac{\mu_i}{\mu_R}\right)^{-1}, \qquad (3)$$

where $CV_i$ is the temporal coefficient of variation of harvests of species i, and $CV_i$ is weighted by species harvest contributions to $\mu_R$ . Stated plainly, $S_{Harvest}$ is the inverse of weighted average harvest variability (Zhao et al., 2022). We calculated $S_{Portfolio}$ twice: once corresponding to the 5 months for which biomass estimates were available ($S_{Portfolio,S}$), and again for all 12 months of the year ($S_{Portolio,L}$). We similarly calculated the stability of portfolio value by calculating the inverse temporal variability of summed harvest values (all months included).

We next partitioned species asynchrony $\left(\phi_{Species}\right)$ and harvest asynchrony ($\phi_{Harvest}$) into compensation ($CPE$) and statistical averaging effects ($SAE$) (Zhao et al., 2022). Continuing in the context of the commercial harvest portfolio, harvest asynchrony is given by $\phi_{Harvest} = \frac{\sum_i \sigma_i}{\sigma_R} = SAE_{Harvest} \times CPE_{Harvest}$. In the theory of Zhao et al. (2022),

$$SAE_{Harvest} = \frac{\sum_i \sigma_i}{\sqrt{\sum_i \sigma_i^2}}, \qquad (4)$$

where the $SAE_{Harvest}$ is the ratio comparing the portfolio harvest stability if all species harvests were uncorrelated and independent to the portfolio harvest stability if species harvests were perfectly synchronous. $CPE_{Harvest}$ is then

$$CPE_{Harvest} = \frac{\sqrt{\sum_i \sigma_i^2}}{\sigma_R}. \qquad (5)$$

Zhao et al. (2022) note that the $CPE$ is equivalent to the inverse of the square-rooted variance ratio (Schluter, 1984), a commonly used measure of synchrony/asynchrony in the ecological literature. $CPE_{Harvest} > 1$ indicates greater portfolio harvest stability than what would be expected if species harvests fluctuated independently of one another. We partitioned $\phi_{Species}$ identically to $\phi_{Harvest}$ (Table 1).

We used piecewise structural equation models (SEMs) to relate asynchrony and stability indices across ecosystem and fishery systems (Lefcheck, 2016). Within each SEM, we evaluated sub-models for residual independence, normality, and homogeneity of variances. When residual autocorrelation was present, we modeled residual error as an AR(1) process using generalized least squares (Pinheiro et al., 2017). All stability and asynchrony indices were log-transformed prior to fitting models relating these indices across systems given their multiplicative relationships within-systems. To provide context to these results, we used linear models to model interannual trends in population and harvest dynamics. We used generalized least squares models with varying error structures to account for residual autocorrelation when evident.

## Results

*Relationships between the components of species and harvest asynchrony*

Across the Chesapeake Bay, we found that harvest compensation was an important driver of harvest asynchrony and the stability of fisheries yields. However, the drivers of harvest asynchrony differed geographically. In MD (Fig. 5, MD SEM 1), harvest compensation was positively associated with the seasonal harvest ratio (SHR) —or the degree to which species other than striped bass dominated the fishery during closed season. This result therefore represents the diversification of harvests during the annual striped bass fishery closure that compensate for the engineered loss of harvestable biomass of this fish (Fig. 6). In contrast, there were no relationships between compensation and statistical averaging in the MD community and fishery portfolio, indicating that seasonal compensation among populations of target species was not responsible for enhancing the portfolio effect in this state. Ultimately, then, asynchrony in MD fisheries harvests was found to be largely promoted by fisher behaviors occurring in response to management strategies, rather than natural fluctuations among exploited species here.

During the study period in VA, the total annual biomass of all three dominant species (Atlantic croaker, spot, and striped bass) declined significantly in the lower mainstem of the Bay (Table 1, Fig. 7). However, these biomass declines were not equivalent in magnitude: Atlantic croaker saw the largest declines overall (linear trend = $-1.22\text{x } 10^5$ kg year$^{-1}$, $P < 0.001$), followed by spot ($-1.91 \text{ x } 10^4$ kg year$^{-1}$, $P = 0.003$) and lastly striped bass ($-3.5 \text{ x } 10^3$ kg year$^{-1}$, $P = 0.04$). After the substantial loss of Atlantic croaker biomass, the variabilities of species biomasses became more evenly distributed, thereby increasing the species statistical averaging effect over the study period (Fig. 8a). Increases in the species statistical averaging effect due to increased evenness of biomass variabilities among species were then positively associated with species compensation ($P < 0.001$, Fig. 5, VA SEM 1). In other words, following the steep declines in Atlantic croaker biomass, species population dynamics became more seasonally compensatory and therefore asynchronous (Fig. 8b), albeit with substantially lower biomass overall.

While species statistical averaging and compensation increased in the VA fish community over the study period, harvest compensation effects showed a weak negative trend ($P = 0.079$, Fig. 8d, Table 2), and harvest compensation was most strongly associated with species statistical averaging ($\beta_{std} = -0.834$, $P = 0.017$, Fig. 5, VA SEM 1). This suggests that declines in the availability of target species biomass in the Bay were associated with shifts in the timing of harvests that resulted in a decline of harvest compensation. This was supported by the finding that the timing of Atlantic croaker and striped bass harvests shifted to later and earlier the year, respectively (both $P < 0.001$, Fig. 9, Table 3), such that the timing of Atlantic croaker harvests became more similar to that of spot, whereas striped bass harvests became more dominated by harvests in the spring months. In addition to species statistical averaging being associated with a shift in harvest timing, we also found a strong correlative association between species statistical averaging and the average number of fishing trips across species ($P < 0.001$, VA SEM 1, Fig. 5), which declined throughout the 2002-2018 period across stocks (Fig. 10a). We characterized this relationship as correlated error because effort changes in response to biomass declines may be related to exogenous factors like harvest prices, which we did not consider. Interestingly, despite steep declines in biomass availability, catches per trip did not show significant trends across the study period (Fig. 10b). This suggests that changes in harvest effort played a substantial role in the decline in harvests overall in VA.

We found that harvest compensation was positively associated with species compensation ($\beta_{std} = 0.636$, $P = 0.032$, Fig. 5, VA SEM 1), suggesting that seasonal compensatory dynamics in population biomasses drove seasonal harvest compensation. However, the magnitude of the standardized partial effect of species statistical averaging on harvest compensation was greater than that of species compensation on harvest compensation and opposite in sign ($SAE_{\beta_{std}} = -0.834$ vs $CPE_{\beta_{std}} = 0.636$). This result means that the stabilizing effects of seasonal species dynamics on harvest compensation were overwhelmed by the destabilizing effects of species statistical averaging, representing the decline in target species biomasses that was associated with more temporally synchronous harvests (Fig. 8d, 9).

### *Portfolio harvest stability and economic performance*

We find that portfolio harvest stability was enhanced by harvest asynchrony, which the previously discussed results show was driven by fisher behavioral responses to the striped bass closure (MD) and to the relative biomasses and variabilities of fish populations as they naturally migrate into and out of the Bay mainstem seasonally (VA). Using two additional SEMs, we expanded this analysis to evaluate how portfolio harvest stability associated with portfolio value stability and overall value.

In MD (Fig. 5, MD SEM 2), we found that portfolio harvest stability quantified at the same temporal resolution as the population biomass indices (i.e., $S_{\text{Portfolio, S}}$) was positively associated with portfolio harvest stability quantified using all months of harvest data ($S_{\text{Portfolio, L}}$). We quantified harvest stability at both resolutions because biomass indices were only resolved at the five-month timescale, whereas fishing harvest data were available for all 12 months. This finding shows that harvest asynchrony induced by fisher target diversification in response to the striped bass fishery closures (Fig. 6) was positively linked to the within-year harvest stability of the portfolio. However, portfolio harvest stability was not linked to the economic stability of harvests. In other words, active switching by fishers buffered the stability of the portfolio against regulatory measures, in the form of the seasonal closure, but that this stabilizing effect did not translate to enhanced economic stability. Lastly, we identified a strong positive relationship between total yield and total value ($P < 0.001$), showing that years with greater harvests were associated with greater portfolio value (Fig. 5, MD SEM 2).

In VA (Fig. 5, VA SEM 2), where we also identified a positive link between portfolio harvest stability at the 5-month and 12-month temporal resolutions, portfolio harvest stability ($S_{\text{Portfolio, L}}$) declined substantially over the study period (Fig. 11, Table 4, $P < 0.001$) in response to diminished harvest compensation (Figs. 8b) and species harvest stability, the latter of which was associated with fishing effort (Fig. 10). In other words, the loss of harvestable biomass, primarily of Atlantic croaker, was associated with more temporally synchronous harvests, and this coincided with decreasing fishing effort that drove more temporally variable and lower harvests within-years. Both of these factors contributed to interannual declines in harvest portfolio stability overall. Portfolio harvest stability was positively associated with the stability of portfolio value, as well as total harvest yield (Fig. 5, VA SEM 2).

## Discussion

Asynchronous dynamics among different species can promote community stability over time, but this effect could be translated to—or compromised by—the active exploitation of these species by humans. We approached this problem by analyzing 17 years of data from fisheries-independent surveys (i.e., community data) and fisheries landings across one of the largest and most economically valuable estuaries in the world, the Chesapeake Bay. We found that asynchrony in Chesapeake Bay fish harvests within a given year emerged from two sources:

fisher-behavior responses to management strategies (i.e., the closure of the striped bass fishery in Maryland), and from the components of asynchrony among fish species that emerged due to seasonal population dynamics (compensation) and the unevenness of population variabilities (statistical averaging effects). However, while species compensation was a positive contributor to harvest compensation, these effects were counteracted by the negative effect of species statistical averaging on harvest compensation, which reflected a decline in overall biomass availability and increased evenness of variabilities in the ecosystem. In Virginia, we also found that the stability of the harvest portfolio was positively associated with the stability of the value of the harvest portfolio. These findings demonstrate that conserving asynchronously fluctuating exploited natural resources can enhance the within-year stability of their associated harvest portfolios and their value, but that these stabilizing effects can be overwhelmed by the relative availability and variability of targets in the environment, human behavior, and management regulations.

Our application of this framework to a coupled social-ecological system is highly relevant, as it more fully considers the mechanisms through which asynchrony among species in a biological community contributes to stability while the system is simultaneously being both exploited and actively managed. Several authors have explored similar relationships between community dynamics and harvest asynchrony (J. W. Moore et al., 2021; Nesbitt & Moore, 2016; Schindler et al., 2010), but have not treated the populations targeted by fisheries and their associated harvests as hierarchically structured portfolios that are linked by asynchrony. By conceptualizing these systems separately, we were able to identify the specific components of asynchrony that contributed to (in the case of MD) or diminished (as in VA) these coupled systems.

Cross-system asynchrony relationships were limited in MD, where harvest asynchrony was strongly related to the adaptive response of fishers to management strategies limiting access to the valuable striped bass fishery. During the closure, fishers targeted species like Atlantic croaker, white perch, and gizzard shad. In this sense, the striped bass closure ultimately enhanced the stability of the regional harvest portfolio that became more diversified as a result, although this stabilizing effect did not translate to stability of the value of the harvest portfolio, possibly due to the lower value of species being targeted during the striped bass closure compared to striped bass.

Portfolio harvest stability in VA waters declined over the study period, and this decline was related to ecological and social factors impacting species and harvest asynchrony and species harvest stability. First, through the declines in the biomass of Atlantic croaker and spot in the lower Bay (also documented in Buchheister et al., 2013; Schonfeld et al., 2022), a relationship that was captured in VA SEM 1 (Fig. 5) through the effect of species statistical averaging on harvest compensation. When species biomasses were most uneven (high biomass availability), their harvests tended to be more seasonally compensatory, contributing to the stability of the harvest portfolio overall. However, as population variabilities became more even (low biomass availability), species harvests became more synchronous, and this contributed to declining harvest stability interannually.

Second, we identified a clear decline in the number of commercial fishing trips occurring in VA over the study period. While understanding the complete suite of factors influencing this decline is beyond the scope of our study, our finding is supported by recent work showing declines in finfish fishery participation in VA (in terms of the number of licensed fishers) (White & Scheld, 2021), although that study found that these declines may be due largely to demographic factors. Declining trends in effort may also be due to market factors that we did not characterize (e.g., prices), with commercial fishers being tempted to other fisheries and marine-related industries that may be more profitable and with greater promise of future reliability in harvest, including but not limited to the growing aquaculture industry, as well as fisheries for blue crabs (*Callinectes sapidus*) and hard clams (*Mercenaria mercenaria*) (White & Scheld, 2021). Increasing participation in these industries by fishers at the expense of effort in the finfish fisheries documented here could help explain effort declines, but further work is needed to better understand the drivers of effort declines.

Like many fishes inhabiting temperate ecosystems, the life histories of Atlantic croaker, spot, and striped bass involve a seasonal migratory phase wherein fishes seasonally move into and out of inshore habitats from the coastal ocean (Buchheister et al., 2013; Murdy & Musick, 2013). Importantly, the peak abundances of these species in VA waters are typically seasonally compensatory, implying that their harvest dynamics may also be seasonally compensatory, and that this compensation would stabilize the harvest portfolio. We found evidence for this effect, although the positive contribution of seasonal species compensation to harvest asynchrony was overwhelmed by the negative effect of species statistical averaging. This finding suggests that seasonal species compensation was and is not effective in stabilizing within-year harvests in the face of fewer fish entering into the Bay (Schonfeld et al., 2022). Such biomass declines challenge the capacity for fishers to diversify among finfish species since fishers in the Bay typically do not operate outside of Bay waters where these species may be found in higher numbers (Schonfeld et al., 2022).

However, one diversification opportunity that may prove important for providing stability to commercial fishers in the Bay that would also not require leaving the Bay to fish is the emerging blue catfish (*Ictalurus furcatus*) fishery. Blue catfish is an invasive species whose abundances have increased dramatically in Bay tributaries in recent years, and in VA waters, harvests of blue catfish have exceeded those of striped bass since 2015 (Fabrizio et al., 2021). The governments of Maryland and Virginia have recently put forth legislative efforts supporting the development of a commercial fishery around this species (Senate Joint Resolution 4, 2021; Blue Catfish Processing, Flash Freezing, and Infrastructure Grant Program, 2023).

The substantial yield of blue catfish in Bay tributaries in recent years demonstrates the increasing importance of this fishery and raises a limitation of the presented analysis. First, the Bay is home to several species of finfish and invertebrates that are not considered within this study. For instance, beyond blue catfish whose low abundances in the Bay mainstem were inconsequential during our study period (2002–2018), the Bay supports relatively enormous blue crab fisheries that, at a regional scale, are valued at $80–$100 million USD annually (Scheld et al., 2021). Additionally, in the MD portion of the Bay mainstem, the pelagic Atlantic menhaden (*Brevoortia tyrannus*) is the second most valuable finfish after striped bass, the harvests of which were valued at ~$700,000 USD annually over the study period. While we focused our analyses on fishes that were well-sampled in ChesMMAP bottom trawl surveys and so excluded these important species, if comparable biomass estimates can be made to those presented here, then it would be reasonable to include these species in a future analysis.

Similarly, our analyses were geographically constrained to ensure the overlap between commercial harvest data and the ChesMMAP survey. Future work should consider expanding this approach to Bay tributaries and their associated commercial and recreational fisheries. Lastly, we assumed a unidirectional relationship between species abundances and species harvests, although harvesting will certainly influence the population dynamics of harvested species (Arlinghaus et al., 2017; J. W. Moore et al., 2021). Future work should explore these bidirectional dynamics, but doing so here is beyond the scope of this paper.

In the present analysis, we have presented novel insights into how species asynchrony relates to harvest asynchrony to stabilize commercial fishing harvest portfolios. In a system like MD where the dominant fishery target was seasonally closed to harvesting, we showed that harvest asynchrony arose due to the diversification of harvests occurring during the closure, and that this diversification stabilized the within-year harvest portfolio overall, but harvest stability was not associated with the stability of portfolio value. In VA, declines in the biomass of target species in the Bay played a key role in how within-year species asynchrony related to harvest asynchrony. With biomass declines came a greater evenness of population variabilities that was associated with declines in harvest compensation, and a coincident decline in effort that was associated with declines in species harvest stability. These relationships drove a negative trend in the stability of the harvest portfolio, although periods of high portfolio stability were associated with high portfolio value stability.

Understanding how stability arising from ecosystem processes contributes to the stability of dependent social-ecological systems has the potential to unlock novel management strategies that leverage these stabilizing features while concurrently conserving biodiversity.

## Acknowledgements

We are grateful to Virginia Sea Grant for their financial support that made this study possible through a graduate research fellowship, and to the staff and scientists at the Virginia Institute of Marine Science who collected the data used in this study. We also thank the staff at VMRC and MD-DMF for providing the commercial harvest data.

## Figures

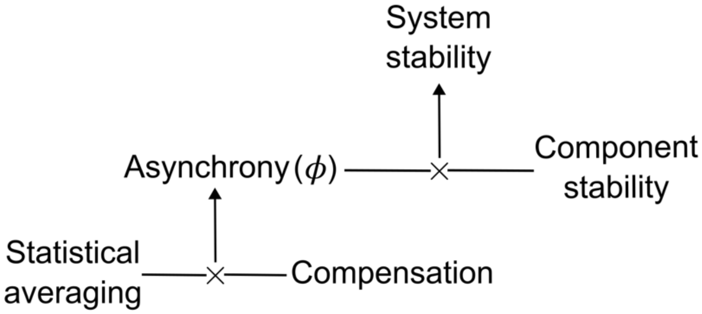


*Figure 1*. Conceptual model describing the generalization of a stability partitioning framework originally applied in an ecological context (Thibaut & Connolly, 2013), and extended to consider the asynchrony partitioning method introduced by Zhao et al. 2022. Variables connected by "×" indicate a multiplicative relation between those variables, where their product is given by the variable indicated with an arrow.

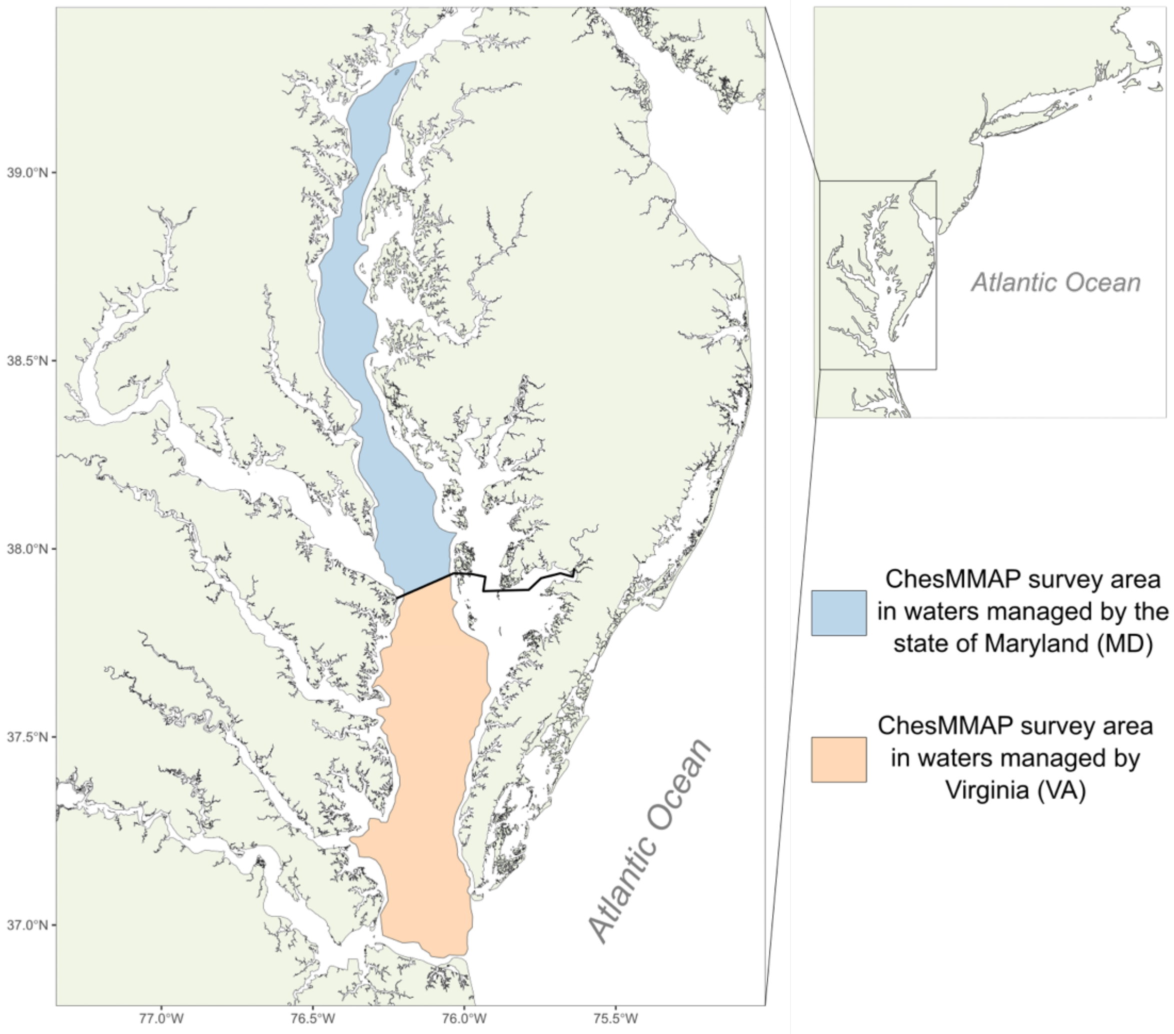


*Figure 2*. Map of Chesapeake Bay and its location along the east coast of the United States (inset). The light blue area refers to the area of the ChesMMAP survey falling within waters managed by the state government of Maryland (MD), and the light orange area the area falling within the management jurisdiction of Virginia (VA). The black line denotes the boundary between MD and VA waters.

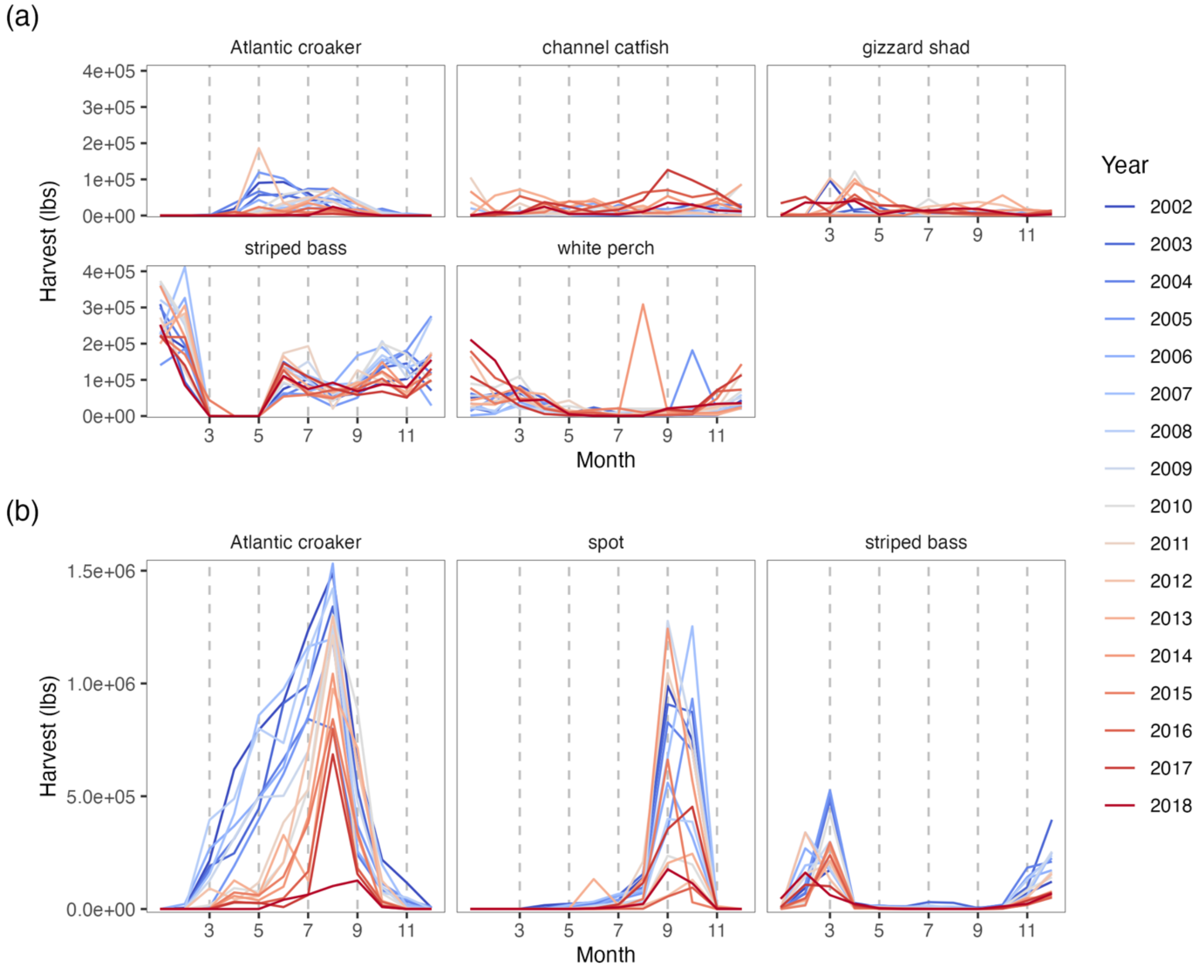


*Figure 3*. Within-year time series of commercial fishing harvests in Maryland (top, a) and Virginia (bottom, b), where each line corresponds to a different year. Vertical lines correspond to the months where biomass indices for each species were estimated.

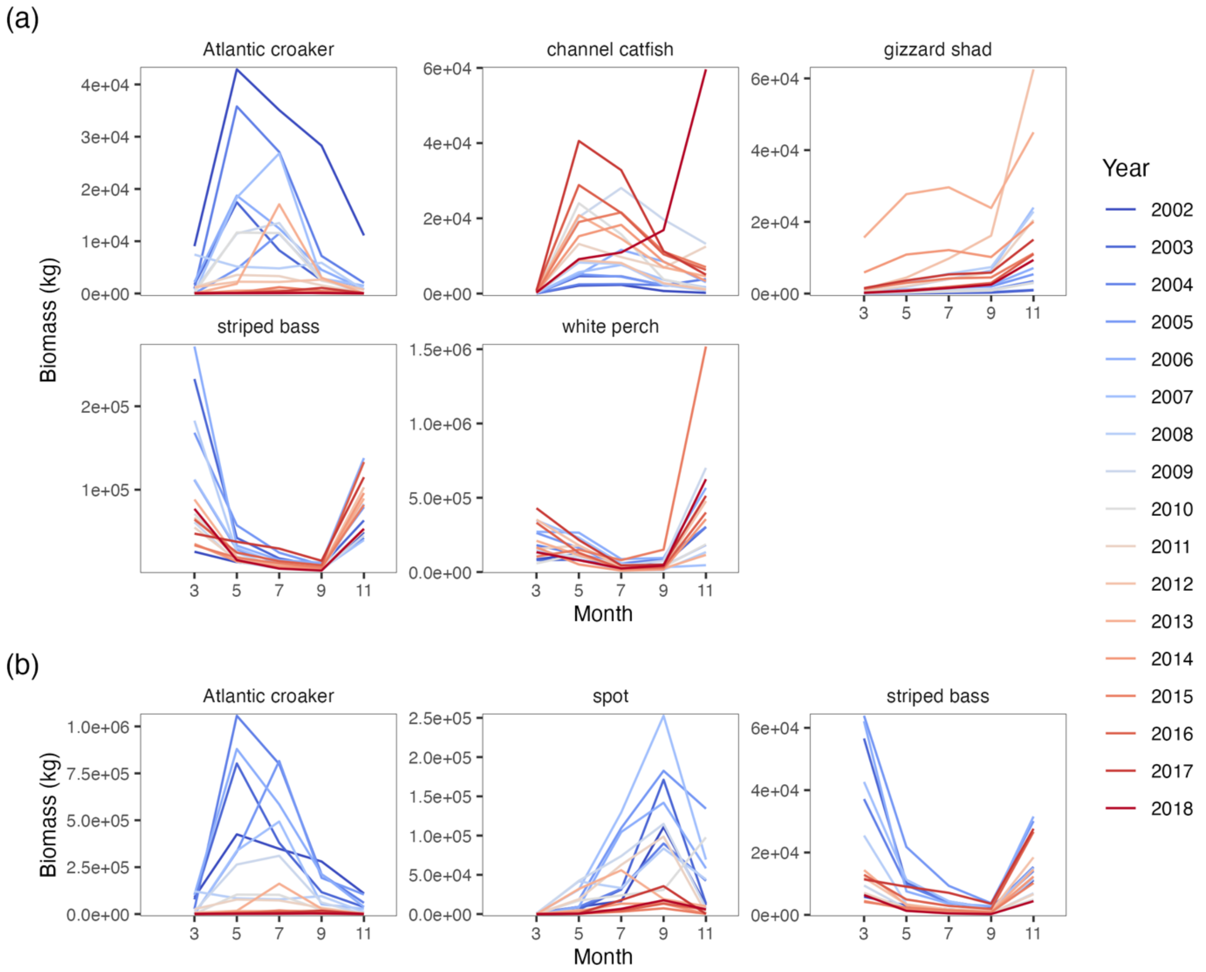


*Figure 4.* Within-year time series of modeled species biomasses in Maryland (top, a) and Virginia (bottom, b), where each line corresponds to a different year. Note the change in y-axis scales between species.

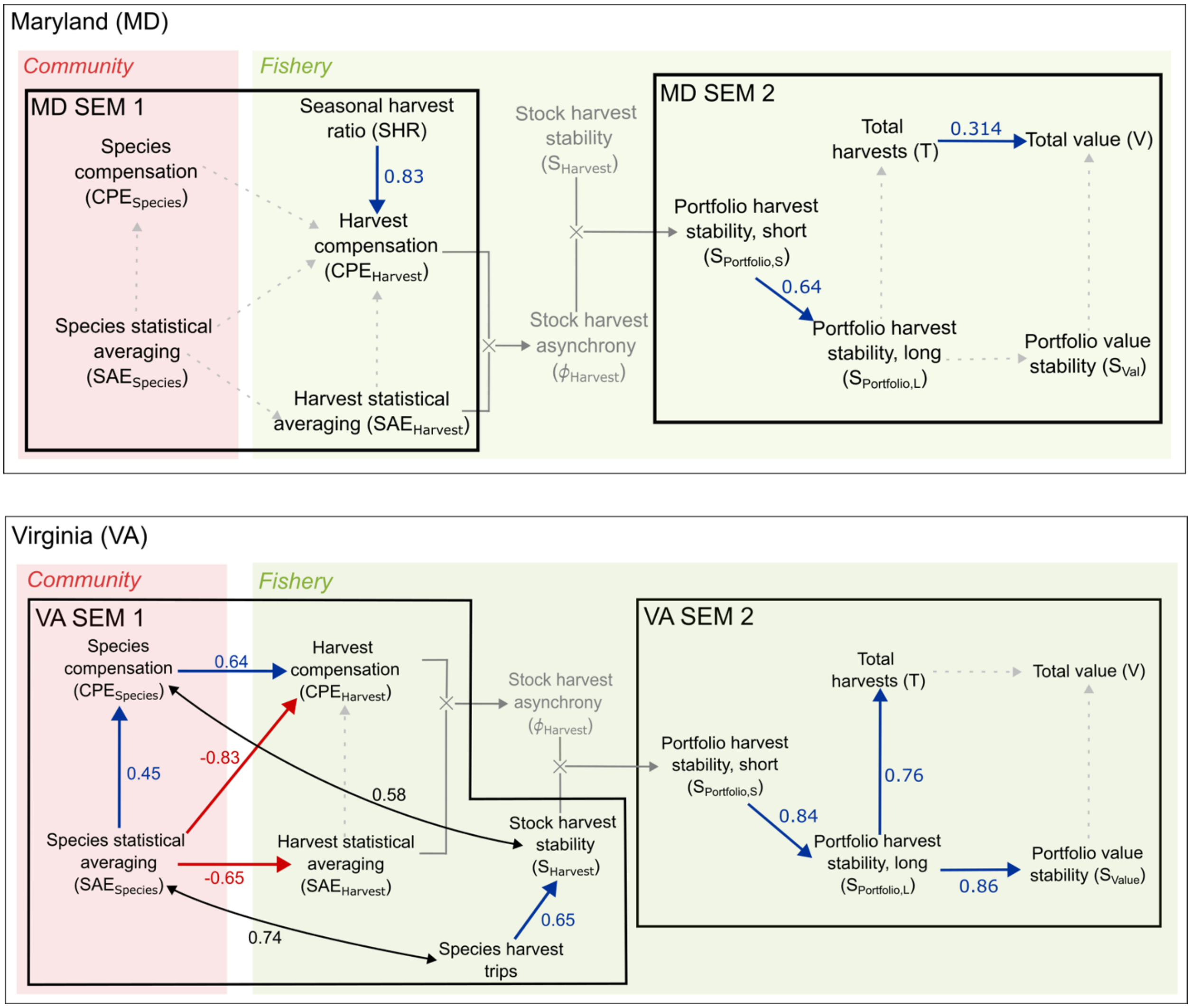


*Figure 5.* Linked path diagrams showing the relationships between asynchrony in the community (red) and harvest portfolio (green) in MD (top) and VA (bottom) waters. Variables connected by an "×" indicate a multiplicative relation between those variables, the product of which is given by the variable following the arrow. Statistical relationships were modeled using SEMs, the hypothesized paths of which are shown in the black boxes: dark blue arrows indicate positive relationships ($P < 0.05$), red arrows negative, double-headed black arrows correlated errors, and dotted grey lines no relationship. Numbers next to paths show standardized coefficients. See Table 1 for definitions of terms.

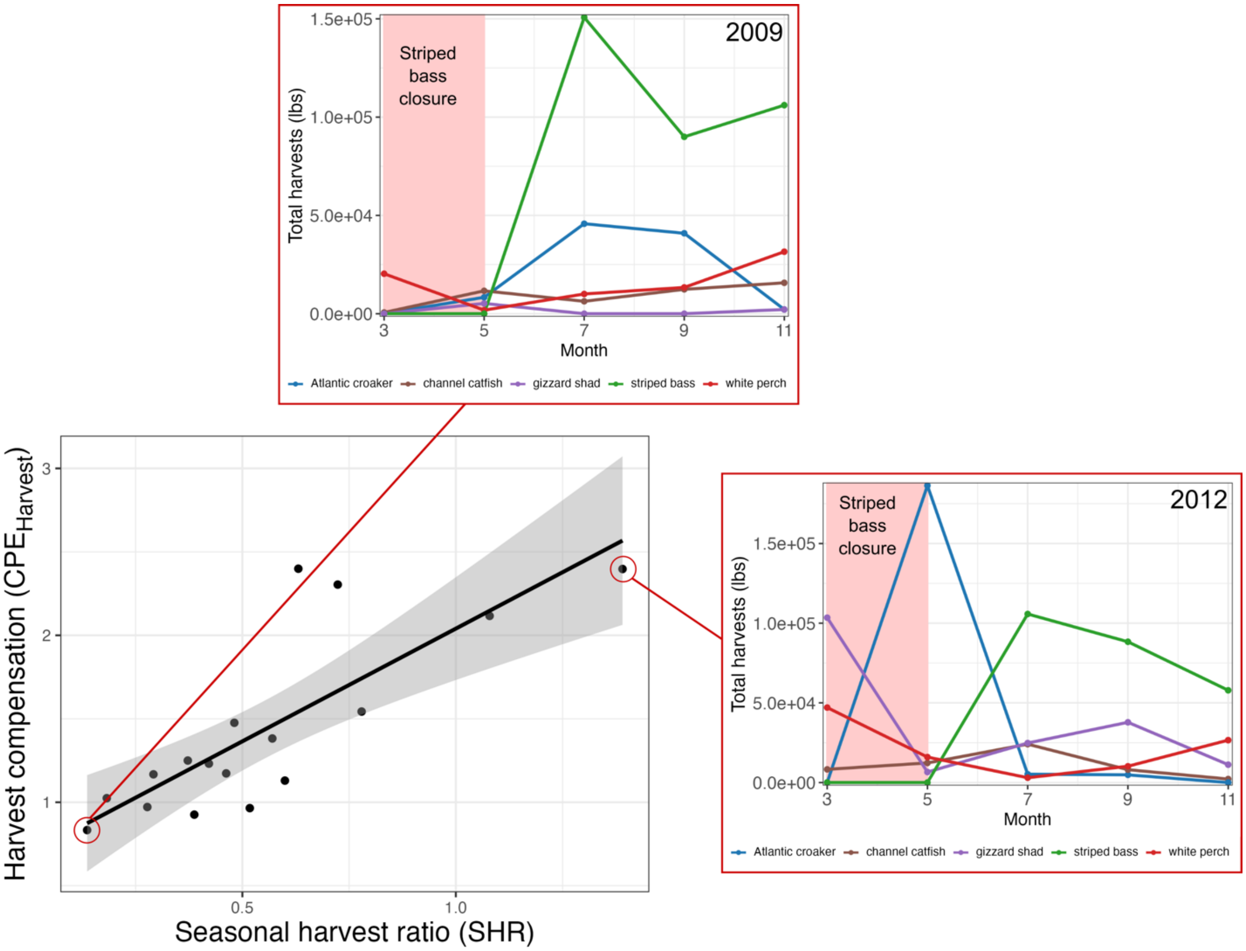


*Figure 6.* The relationship between the harvest compensation effect ($CPE_{Harvest}$) and the seasonal harvest ratio (SHR) in MD (bottom left; $R^2 = 0.64$). Also shown are harvest time series from Maryland during years when the SHR was highest (right; 2012) and lowest (top; 2009). Red shaded areas show the months during which the striped bass fishery was closed.

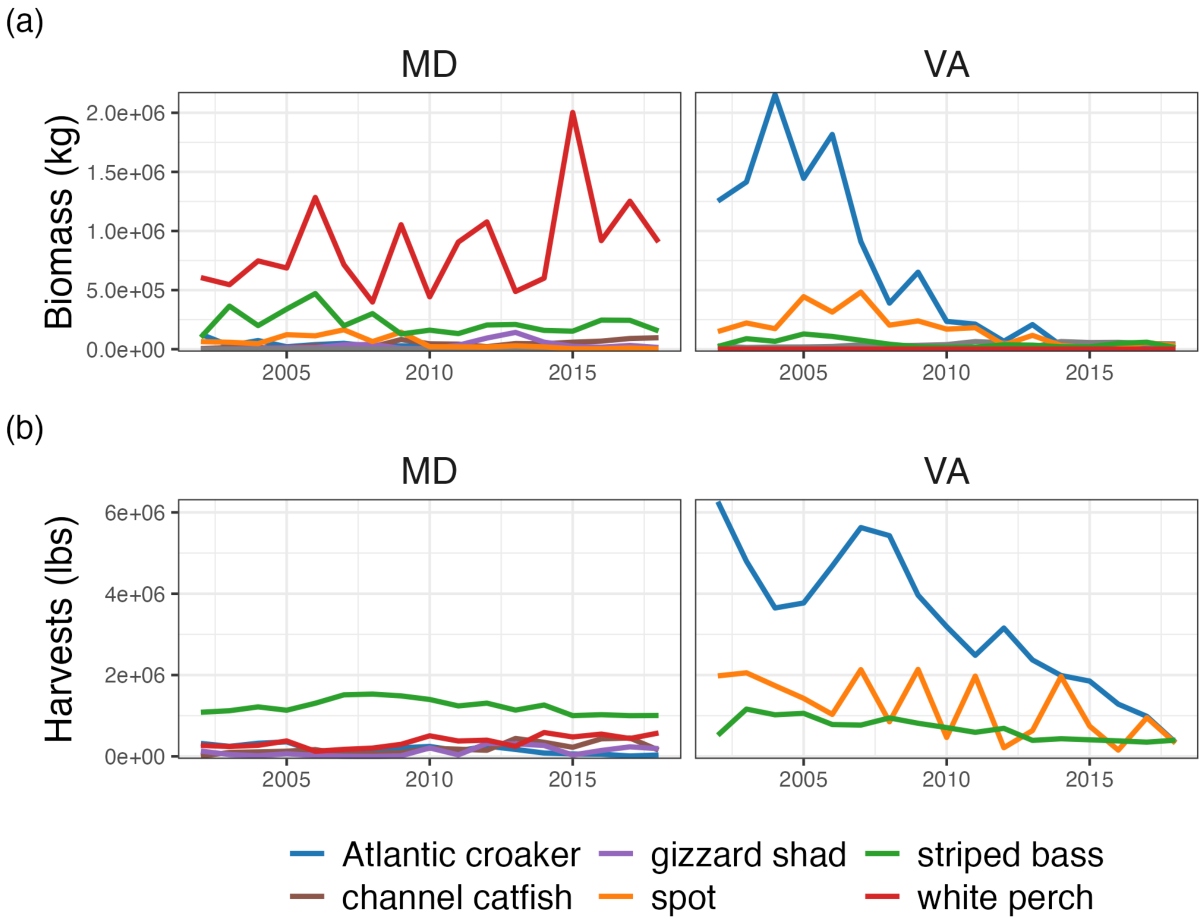


*Figure 7.* Time series of annual biomass (a) and harvests (b) in the Virginia and Maryland regions of the Chesapeake Bay mainstem between 2002-2018.

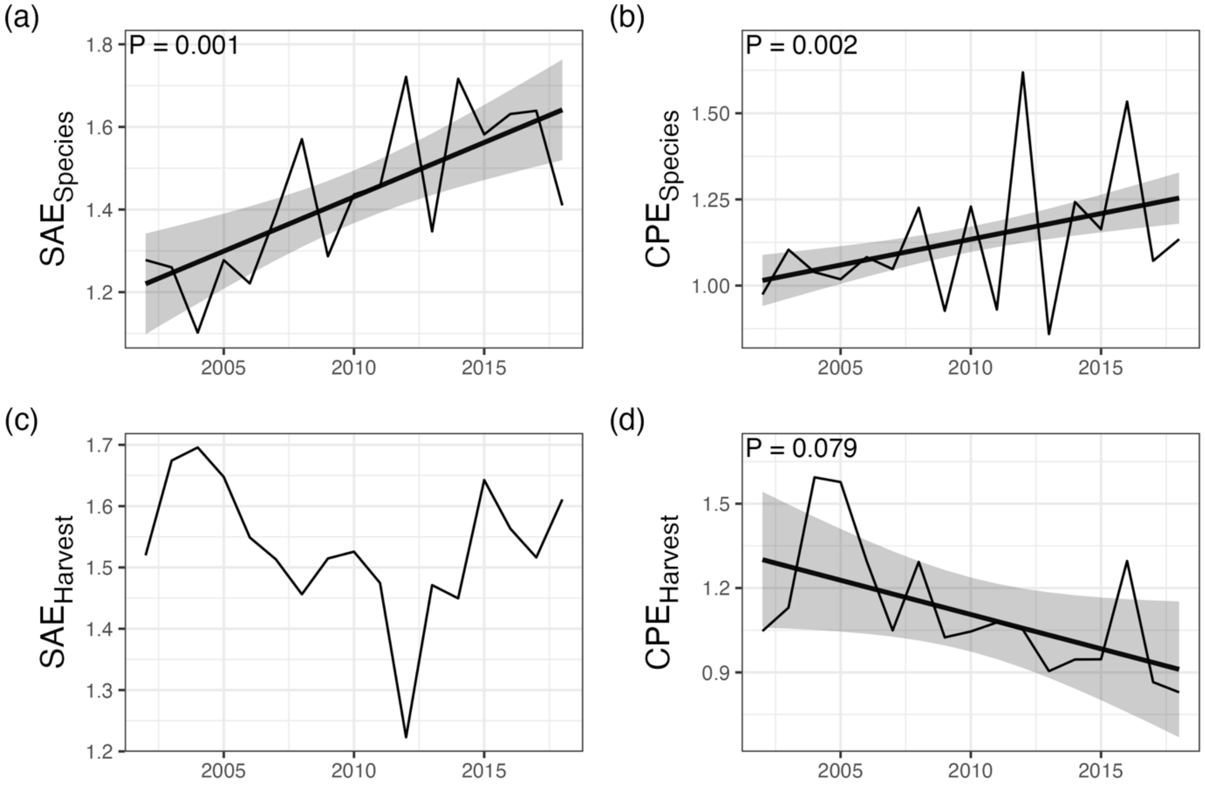


*Figure 8.* Interannual time series of annual species statistical averaging (a, $\mathrm{SAE}_{\mathrm{Species}}$), species compensation effects (b, $\mathrm{CPE}_{\mathrm{Species}}$), harvest statistical averaging (c, $\mathrm{SAE}_{\mathrm{Harvest}}$), and harvest compensation effects (d, $\mathrm{CPE}_{\mathrm{Harvest}}$) in Virginia. Trend lines are from linear models shown with 95% confidence intervals (see Table 2 for details).

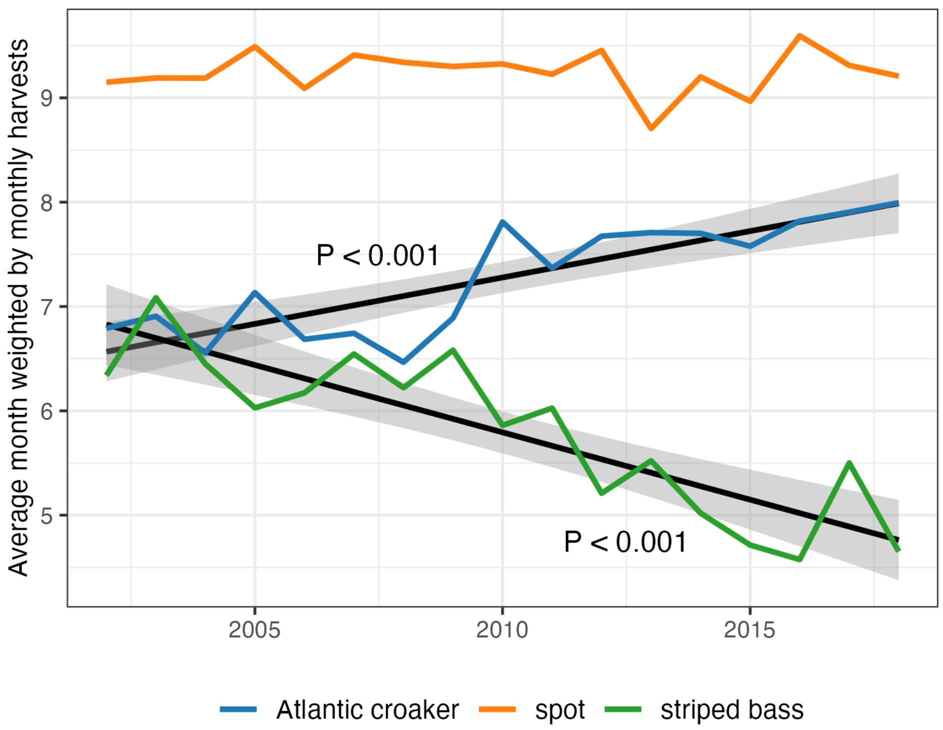


*Figure 9.* Species-specific time series of the weighted-average month of harvest in Virginia, where weights are given by monthly harvests. A positive linear trend indicates that the timing of harvests shifted to be later in the year, and a negative trend, earlier.

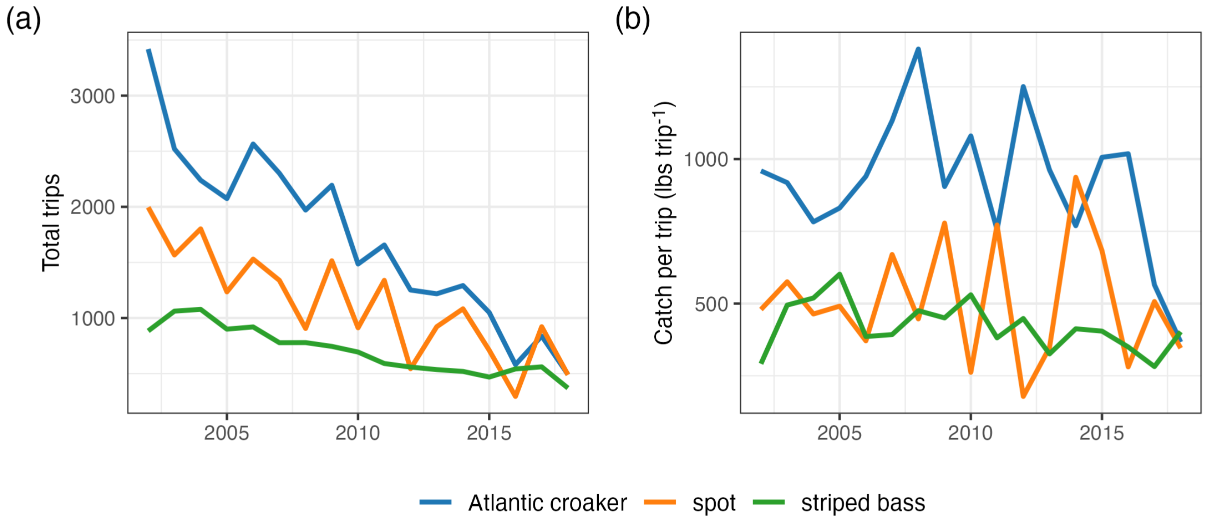


*Figure 10*. Time series of total annual fishing trips across months (a) and total harvest per trip (b) in the Virginia portion of Chesapeake Bay. The across-species annual average of these time series is used in VA SEM 1, shown in Fig. 5.

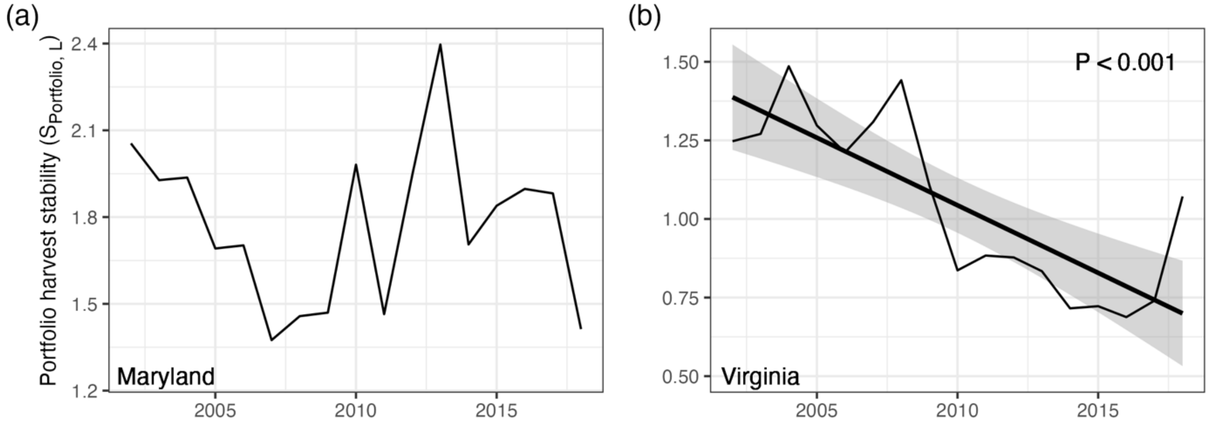


*Figure 11*. Time series of portfolio harvest stability in Maryland (a) and Virginia (b). Virginia portfolio harvest stability declined significantly over the study period ($P < 0.001$), as shown by the trend line with 95% confidence interval.

Table 1. Definitions of asynchrony and stability terms, their abbreviations, and general mathematical formulas.

| ***Term*** | ***Abbreviation*** | ***Formula*** | ***Description*** |
|---|---|---|---|
| Total harvest stability (all months) | $S_{Portfolio,L}$ | $\left(\frac{\sigma_R}{\mu_R}\right)^{-1}$ | The stability of total harvests across all species and months. |
| Total harvest stability (5 months) | $S_{Portfolio,S}$ | $\left(\frac{\sigma_R}{\mu_R}\right)^{-1}$ | The stability of total harvests across all species during the five months when biomass estimates are available. |
| Species harvest stability | $S_{Harvest}$ | $\left(\sum_{i}^{n} CV_i \times \frac{\mu_i}{\mu_R}\right)^{-1}$ | The inverse of weighted-average harvest variability across species. We calculated this index for the five months when biomass estimates are available. |
| Asynchrony | $\phi$ | $\frac{\sum_i \sigma_i}{\sigma_R}$ | A measure of the stabilizing effects of compensation and statistical averaging; either among harvests of multiple stocks $(\phi_{Harvest})$ or among the biomass dynamics of multiple species $(\phi_{Species})$. |
| Statistical averaging effect | $SAE$ | $\frac{\sum_i \sigma_i}{\sqrt{\sum_i \sigma_i^2}}$ | The enhancement of harvest or community stability following independent fluctuations among species harvests $(SAE_{Harvest})$ or population dynamics $(SAE_{Species})$. |
| Compensation effect | $CPE$ | $\frac{\sqrt{\sum_i \sigma_i^2}}{\sigma_R}.$ | The enhancement of harvest or community stability following negatively correlated dynamics among species harvests $(CPE_{Harvest})$ or population dynamics $(CPE_{Species})$. |

Table 1. Statistics from linear models evaluating interannual temporal trends in Atlantic croaker, spot, and striped bass annual biomass (summed across months) in the Virginia portion of Chesapeake Bay over 2002-2018.

| **Species** | **Trend (kg year$^{-1}$)** | **Std. error** | **T statistic** | **P value** | **Error structure** |
|---|---|---|---|---|---|
| Atlantic croaker | -122,256 | 18,549 | -6.591 | <0.001 | iid |
| spot | -19,140 | 5,320 | -3.598 | 0.003 | iid |
| striped bass | -3,497 | 1,546 | -2.262 | 0.039 | iid |

Table 2. Statistics from linear models evaluating interannual temporal trends in within-year species and harvest statistical averaging ($\text{SAE}_{\text{Species}}$ and $\text{SAE}_{\text{Harvests}}$) and within-year species and harvest compensation effects ($\text{CPE}_{\text{Species}}$ and $\text{CPE}_{\text{Harvests}}$) in the Virginia portion of Chesapeake Bay over 2002-2018.

| **Term** | **Trend (SAE/CPE year$^{-1}$)** | **Std. error** | **T statistic** | **P value** | **Error structure** |
|---|---|---|---|---|---|
| $\text{SAE}_{\text{Species}}$ | 0.026 | 0.007 | 3.976 | 0.001 | iid |
| $\text{CPE}_{\text{Species}}$ | 0.014 | 0.005 | 2.994 | 0.009 | AR(1) |
| $\text{SAE}_{\text{Harvests}}$ | -0.005 | 0.005 | -0.994 | 0.336 | iid |
| $\text{CPE}_{\text{Harvests}}$ | -0.024 | 0.013 | -1.887 | 0.079 | AR(1) |

Table 3. Statistics from linear models evaluating interannual temporal trends in within-year weighted-average month of harvest, where weights are monthly harvests in the Virginia portion of Chesapeake Bay over 2002-2018.

| **Species** | **Trend (month year$^{-1}$)** | **Std. error** | **T statistic** | **P value** | **Error structure** |
|---|---|---|---|---|---|
| Atlantic croaker | 0.089 | 0.014 | 6.241 | <0.001 | iid |
| spot | -0.001 | 0.011 | -0.092 | 0.928 | iid |
| striped bass | -0.129 | 0.019 | -6.694 | <0.001 | iid |

Table 4. Statistics from linear models evaluating interannual temporal trends in within-year portfolio harvest stability ($S_{Portfolio,L}$) in Maryland and Virginia regions of the Chesapeake Bay over 2002-2018.

| **Region** | **Term (stability year $^{-1}$)** | **Trend** | **Std. error** | **T statistic** | **P value** | **Error structure** |
|---|---|---|---|---|---|---|
| Maryland | $S_{Portfolio, L}$ | -0.002 | 0.014 | -0.158 | 0.877 | iid |
| Virginia | $S_{Portfolio, L}$ | -0.043 | 0.008 | -5.130 | 0.000 | iid |

# Chapter 3

## Effects of seagrass restoration on coastal fish abundance and diversity

Citation: Hardison, S., McGlathery, K., & Castorani., C. N. (2023) Effects of seagrass restoration on coastal fish abundance and diversity. *Conservation Biology*, *e14147*.

## Abstract

Restoration is accelerating to reverse global declines of key habitats and recover lost ecosystem functions, particularly in coastal ecosystems. However, there is high uncertainty about the long-term capacity of restored ecosystems to provide habitat and increase biodiversity, and the degree to which these ecosystem services are mediated by spatial and temporal environmental variability. We addressed these gaps by sampling fishes biannually for 5–7 years (2012–2018) at 16 sites inside and outside of a rapidly-expanding restored seagrass meadow in coastal Virginia, USA. Despite substantial among-year variation in abundance and species composition, seine catches in restored seagrass beds were consistently more numerous (6.4× more fish, $P < 0.001$) and speciose (2.6× greater species richness, $P < 0.001$; 3.1× greater Hill-Shannon diversity, $P = 0.03$) than adjacent unvegetated areas, with larger catches particularly during summer (vs. autumn, $P < 0.01$). Structural equation modeling revealed that depth and water residence time interacted to control seagrass presence, leading to higher fish abundance and richness in shallow, well-flushed areas that supported seagrass. Together, our results indicate that seagrass restoration yields large and consistent benefits for many coastal fishes, but that restoration and its benefits are sensitive to the dynamic seascapes within which it is established. Consideration of how seascape-scale environmental variability impacts both the success of

habitat restoration as well as subsequent ecosystem function will improve restoration outcomes and the provisioning of ecosystem services.

## Introduction

Human activities have led to global degradation of ecosystem structure and function over the past century (Ellison et al. 2005; Barbier et al., 2011). In response, habitat restoration has increasingly been investigated as a tool for combating these declines (Guan et al., 2019), although there remains uncertainty about the long-term capacity of restored ecosystems to consistently provide ecosystem services such as habitat provisioning (Lamb 2018). Restored ecosystems may fail to enhance and sustain ecosystem services due to site-specific environmental constraints that limit restoration success or the suitability of restored habitat for associated fauna (Raposa and Talley, 2012; England and Wilkes, 2018). For example, the direction (positive/negative/zero) and magnitude of effects of salt marsh restoration on nekton were found to be highly variable and site-dependent at a regional scale due to local-scale environmental variability and anthropogenic impacts (Raposa and Talley, 2012). Similarly, while river restorations have been successful in reinstating physical functioning to degraded waterways, these improvements were not always associated with the rehabilitation of associated macroinvertebrate communities subject to local- and catchment-scale environmental variability (Leps et al., 2016; England and Wilkes, 2018). Evaluating how spatial and temporal variation impacts communities in restored habitats is critical to maximizing the success of restorations and the ecosystem services they provide.

Following declines of seagrass meadows in shallow coastal ecosystems worldwide (Dunic et al., 2021), restoration efforts have increased to recover these habitats and their associated ecosystem services (Duarte et al., 2020; Orth et al., 2020). While numerous studies have shown the benefits of seagrass for fish and fisheries (e.g., Gilby et al., 2018; Unsworth et al., 2019; Orth et al., 2020), there is still uncertainty about how spatial environmental variability directly and indirectly mediate the capacity of restored meadows to yield more numerous and diverse fish assemblages. Moreover, it is unclear how the enhancement of fish communities by restoring seagrass meadows varies over longer time scales, as studies that compare habitat provisioning by restored meadows and reference habitats are almost always less than five years in duration (e.g., Fonseca et al., 1996; Sheridan et al. 2003; Sheridan, 2004; McSkimming et al. 2016). Fish populations are highly variable over space and time (Auth et al., 2020), and so positive trends in fish abundance or diversity associated with seagrass restoration may be overwhelmed by seasonal, interannual, and spatial variability in relation to environmental conditions, such as nearshore oceanography (Shanks, 2020). Quantifying the spatial and temporal variability in the enhancement of fish communities by restored seagrass meadows is valuable to guiding restoration and is especially urgent as climate change intensifies a variety of factors that may have direct and indirect effects on coastal fishes, including ocean warming, sea-level rise, and storm disturbance (Ummenhofer and Meehl, 2017; Castorani et al., 2018; von Biela et al., 2019; Aoki et al., 2020a).

Seagrass restoration may be particularly beneficial to juvenile fishes because meadows commonly function as nursery habitats (Heck et al., 2003; Lefcheck et al., 2019) that offer shelter from predation (Hindell et al., 2002; Smith et al., 2011) and enhance food availability (Nakamura and Sano, 2005; Alfaro, 2006). Numerous coastal fishes recruit to seagrass meadows as larvae and remain in or near meadows until maturity (Rooker et al., 1998; ASMFC, 2010; Faletti et al., 2019). Seasonal recruitment results in distinct assemblages of juvenile fishes inhabiting meadows throughout the year (Rooker et al., 1998; Sobocinski et al., 2013). Overlaid on these seasonal patterns are typically large year-to-year variations in recruitment and community composition due to variability in climate drivers, currents, and lower trophic-level production, among other factors (Wood, 2000; Woodland et al., 2021; Schonfeld et al. 2022). Further, within seagrass meadows, the distributions and diversities of fishes and mobile invertebrates vary spatially in response to meadow attributes (Yeager et al., 2011, 2016; Cheng et al., 2022) that are mediated by environmental context. For example, the density and patchiness of seagrass meadows are affected by wave exposure, current speed, and water depth (Fonseca and Bell, 1998; Carr et al., 2010, Uhrin and Turner, 2018), and these meadow characteristics contribute to the structure of associated fish communities (Yeager et al., 2011, 2016). However, studies have rarely considered the direct and indirect effects of the abiotic conditions associated with the seagrass niche on fish communities explicitly (e.g., Giacomazzo et al., 2020).

To address these gaps, we determined (1) how seagrass restoration affects fish abundance and diversity, (2) the extent to which this effect varies among seasons, years, and locations, and (3) the direct and indirect effects of spatial variation in abiotic conditions on the distribution of seagrass and the fish community. We carried out a long-term and spatially replicated study (5–7 years at 16 sites) to characterize fish community dynamics across a rapidly expanding restored seagrass meadow in coastal Virginia, USA. Our findings indicate that despite pronounced seasonal and interannual variation, seagrass restoration increases fish abundance and diversity, and that coastal hydrodynamics (water residence time) and bathymetry (depth) constrain fish communities by mediating seagrass distributions. A greater consideration of how ecosystem service provisioning varies in response to direct and indirect environmental forcing will improve the success and value of future restoration projects.

## Methods

### *Study system*

We conducted our investigation in a network of coastal bays along the Atlantic coastline of Virginia, USA, studied by the Virginia Coast Reserve Long Term Ecological Research project. The bays are shallow (1 – 2 m below mean sea level, MSL) and punctuated by deep inlets connecting them to the Atlantic Ocean (McGlathery et al., 2001; Oreska et al., 2021). Salinities are euhaline (typically >30 PSU) due to limited freshwater inputs from the Delmarva Peninsula bordering the western margin of the bays (Oreska et al., 2021), and low nutrient loading from the coastal watersheds results in general oligotrophy and consistently high water quality (McGlathery et al., 2001; Anderson et al., 2010). These factors combine to provide an estimated >100 km$^2$ of suitable habitat for the dominant species of seagrass in the coastal bays, eelgrass *Zostera marina* (Oreska et al., 2021).

Seagrass was extirpated from the coastal bays in the 1930s due to wasting disease and hurricane disturbance. The discovery of a small patch of naturally occurring seagrass spurred the creation of a large-scale, seed-based restoration program that since 1999 has deposited >75 million seeds across the coastal bays (Orth et al., 2012, 2020). The total area restored now exceeds 36 km$^2$ and the meadows have contributed to improvements in water quality, carbon and nitrogen sequestration, and finfish and epifaunal invertebrate biomass and diversity (Lefcheck et al., 2017; Aoki et al., 2020b; Oreska et al., 2020; Orth et al., 2020).

We focused on two restored bays: South Bay (median depth = 0.85 m below MSL) and Hog Island Bay (median depth = 1 m below MSL). The two bays have similar tidal ranges of 1.32 m in South Bay and 1.24 m in Hog Island Bay (McGlathery et al., 2012). Aerial surveys (Moore et al., 2009) show that seagrass cover expanded 83% in South Bay (from 10.7 km$^2$ to

19.6 km$^2$) and 80% in Hog Island Bay (1.8 km$^2$ to 3.3 km$^2$) from the start to end of our study (2012–2018). We sampled fish at each of 16 fixed locations (sites): 4 vegetated sites within the South Bay meadow and 4 nearby unvegetated sites outside the meadow; 4 vegetated sites within the Hog Bay meadow and 4 nearby unvegetated sites (Fig. 1).

Within the two bays, we used observations of seagrass presence at fish sampling sites to evaluate relationships between abiotic drivers, seagrass, and the fish community. As the initial sampling design established a total of eight sites inside and eight sites outside the meadows, we assumed that seagrass was present or absent at these sites until noted otherwise during field sampling. When unvegetated sites were overtaken by seagrass encroachment or seagrass was lost from vegetated sites, we assumed that these altered states persisted at each site until another change was noted (see Appendix 1 for seagrass presence through time).

### *Fish sampling*

To examine the effects of seagrass restoration on fish communities over time, we sampled fish at each site once or twice per year using beach seines (7.6 m wide × 1.8 m tall; 1.5 m deep pocket with 6.4 mm mesh) pulled along 25 m transects in the summer (May or June) and autumn (September or October) from 2012 through 2018. Researchers stopped sampling at the 4 initially unvegetated sites in South Bay after 2015 when sites were colonized by seagrass, although seining occurred once more at these sites during the autumn of 2017. We counted, measured (total length, TL), and identified fish to the lowest possible taxon in the field prior to release. All seine pulls occurred during the day and within three hours of low tide for logistical reasons (N = 204).

Catch data were analyzed in terms of catch per unit effort (CPUE), richness per seine haul, and diversity per seine haul as Hill-Shannon diversity (D) (Hill, 1973). Hill-Shannon diversity can be interpreted as an index of mean rarity, where a seine haul containing many species in low abundance (i.e., many rare species) would have a larger Hill-Shannon diversity than a seine haul with few species in high abundance. D is given by

$$\mathrm{D} = \exp\left(-\sum_{i=1}^{S} p_i \ln(p_i)\right), \qquad (1)$$

where $p_i$ is the proportion of individuals belonging to species $i$ and $S$ is the number of species (Roswell et al., 2021).

All fish sampling methods have some degree of bias. Our sampling method likely represents a conservative estimate of the effect of seagrass restoration on fish communities because the capture efficiency of beach seines is generally lower within structured habitat relative to unstructured habitats (Connolly 1994; Jenkins and Sutherland 1997). Benthic fishes in seagrass meadows may avoid capture in seine nets because they are positioned deeper within the vegetation (Connolly 1994). The strength of undersampling varies among species; for instance, fish associated with the upper seagrass canopy and middle of the water column are sampled in seines more efficiently than seafloor-associated species that may avoid the net capture area (Jenkins and Sutherland 1997). Therefore, reduced capture efficiency within the seagrass meadow likely resulted in our data underestimating fish densities for segments of the fish community.

### *Abiotic variables*

To address our third goal of determining the influence of spatial variation in abiotic conditions on seagrass and the fish community, we modeled the effects of wind fetch, water residence time, and bathymetry on seagrass presence/absence, fish CPUE, and fish species richness. Specifically, we used piecewise structural equation models (SEMs, described below) to test the hypotheses that wind fetch, water residence times, and depth have direct effects on seagrass occurrence, which in turn mediates indirect effects between these environmental variables and fish community responses. SEMs are a class of modeling techniques that allow for testing hypotheses about causal relationships within multivariate systems (Grace, 2008).

Recent spatial niche modeling in the Virginia coastal bays found that wind fetch and water residence times are important predictors of seagrass recruitment and survival, respectively (Oreska et al., 2020). We chose to include bathymetry in SEMs because water depth constrains seagrass growth through light limitation in turbid habitats (McGlathery et al., 2012; Aoki et al., 2020a) and desiccation, temperature stress, and wave disturbance cause mortality in shallow zones (Marsh et al., 1986; Boese et al., 2005; Castorani et al., 2014). We also tested the hypothesis that water residence times directly affect fish abundance and richness, as sites closer to inlets may be more suitable for fishes due to the higher stability of abiotic conditions associated with more frequent tidal flushing (Martino and Able, 2003).

We created the wind fetch predictor by averaging wind fetch lengths within 150 m of seine sampling sites from raster layers of fetch calculated across the coastal bays for the summers of 2014 and 2015 (Kremer and Reidenbach, 2021). Fetch was calculated as the maximum distance wind may travel unobstructed over water in a constant direction and was weighted by observed wind directions from a nearby meteorological station. Despite variability in fetch between 2014 and 2015 due to changes in wind direction, fetch lengths at sampling sites were highly correlated ($R^2 = 0.97$), and so we assumed that the average fetch length across years was representative of site-specific fetch lengths over the study period. We followed a similar approach to estimate water residence times, which were developed with a three-dimensional numerical coastal circulation model (Safak et al., 2015). Here, residence time refers to the amount of time a Lagrangian particle, released during high tide, spent at a particular location within the coastal bays before leaving through a tidal inlet (Safak et al., 2015; data from Wiberg et al., 2015). Variability in residence times within the inlet bays—where our seining sites were located—is largely mediated by distance to the bay inlet, bay geometry, and tidal phase (Safak et al., 2015), factors that do not show large interannual variation on the timescale of our study. Therefore, we assumed that the residence times used here were broadly representative of residence times over the study period. We extracted depths within 150 m of each site using bathymetric maps of the Virginia coastal bays (Richardson et al., 2014; Barnes and Wiberg, 2020).

### *Statistical analyses*

We used generalized linear mixed models (GLMMs) to quantify the effects of seagrass (inside vs. outside of meadows) and season (summer vs. autumn) on fish CPUE, richness, and Hill-Shannon diversity. We also evaluated whether the meadow where sampling occurred mediated changes in the fish community by modeling the interactions between meadow location (Hog Island or South Bay) and abundance, richness, and diversity, with sampling sites and years treated as random intercepts (Zuur et al., 2009). Hill-Shannon diversities had a high frequency of ones due to seine hauls where zero or one species of fish were caught, so we subtracted one from calculated catch diversities to model the data as zero-inflated (Zuur et al., 2009) and modeled non-zero Hill Shannon diversities using the gamma distribution with log-link. We used a negative binomial distribution with log-link in community- and species-level models of CPUE, and a Poisson distribution with log-link to model richness. When comparing the catches of multiple species across habitats or seasons, we adjusted P values according to Benjamini and Hochberg (1995). We used a residual simulation approach to confirm that fitted model residuals met expectations of dispersion, zero-inflation, the abundance of outliers, and residual normality using the *DHARMa* package (Hartig, 2017). We fit GLMMs using the *glmmTMB* package in R (Brooks et al., 2017).

We next applied permutational multivariate analysis of variance using distance matrices (PERMANOVA) to the fish catch data to test the hypothesis that fish community composition differed between meadow locations (South Bay vs. Hog Island Bay) and sampling habitats (inside vs. outside of meadows) (Anderson, 2005). We log transformed catches according to $ln(\text{CPUE} + 1)$ for $\text{CPUE} > 0$ within the community matrix and then converted the catch matrix to Bray-Curtis dissimilarities for hypothesis testing. We included sampling habitat, meadow location, season, and year as model covariates, and blocked permutations within sampling sites ($N = 5000$). We used the R package *vegan* for these analyses (Oksanen et al., 2020).

Lastly, we used piecewise SEMs to evaluate the strengths of relationships among direct and indirect predictors of CPUE and species richness. We used piecewise SEMs because they provided for the inclusion of hierarchical data structures and non-Gaussian response distributions in evaluating model paths (Lefcheck, 2016). For SEMs of both CPUE and richness, we created path diagrams encoding hypothesized relationships between seagrass presence, physical variables (fetch, residence time, and depth), and fish community variables (CPUE, richness) (see *Physical Variables*, above). All covariates in SEMs were scaled and centered prior to model fitting.

We used Fisher's C to determine if the proposed model structures were appropriate given the data and that no important paths were excluded (Shipley, 2000; Lefcheck, 2016), in which large P values derived from Fisher's C ($P > 0.05$) indicated a well-fitting model. We modeled the probability of seagrass occurrence using a binomial GLMM with a logit-link and modeled CPUE and richness using negative binomial and Poisson GLMMs with log-links, respectively. We found standardized path coefficients for the binomial GLMM submodel using the latent-theoretical approach, and for the Poisson and negative binomial models using the observation-empirical approach (Grace et al., 2018). We fitted piecewise SEMs using the R package *piecewiseSEM* and mixed models using *lme4* (Bates et al., 2015; Lefcheck 2016).

## Results

### *Total fish CPUE and diversity*

On average, total fish CPUE was 6.4× greater inside than outside of seagrass meadows (Wald $\chi_1^2$=59.14, P < 0.001). Likewise, estimates of Hill-Shannon diversity were 3.1× greater (Wald $\chi_1^2$=4.68, P = 0.03), and estimates of species richness were 2.6× greater (Wald $\chi_1^2$=38.67, P <0.001) inside than outside of seagrass meadows (Fig. 2a, c, e). We also found that CPUE, diversity, and species richness were consistently elevated within the seagrass meadow relative to outside the meadow regardless of whether samples were collected in Hog Island or South Bay. However, the interaction model for species richness showed that richness was significantly higher overall in South Bay compared to Hog Island Bay (Wald $\chi_1^2$=5.39, P = 0.02). Summary tables for community-level statistical models are available in Appendices 2 and 3.

### *Community composition across habitats and meadows*

Fish community composition differed between vegetated and unvegetated habitats (SS = 4.61, Pseudo *F* = 15.84, P = 0.02). Inside of seagrass meadows, pipefish (*Syngnathus* spp.; N = 610) and silver perch (*Bairdiella chrysoura*; N = 486) were the most common taxa. Outside of seagrass meadows, anchovies (*Anchoa* spp.; N = 210) and Atlantic silversides (*Menidia menidia*; N = 78) were most common (Figs. 3 and 4). Together with pinfish (*Lagodon rhomboides*) and spot (*Leiostomus xanthurus*), these six taxa accounted for 91.8% of the total catch. 28 additional taxa comprised the remaining 8.2% of catch (see Appendix 4 for complete list). Of the 2664 fish collected over the 2012–2018 sampling period, 86.7% were collected in seagrass habitats (Fig. 3a). Significant ($P < 0.05$) species-level differences in CPUE between habitats were also evident in four of the six most common taxa. Species-specific pairwise comparisons showed that 11.7× more pinfish, 57× more pipefish, 24.8× more silver perch, and 14× more spot were collected inside vs. outside of seagrass (all $P_{adj.} < 0.01$; Fig. 4b). Despite increased richness in the South Bay meadow, we did not detect any differences in community composition between the two meadows ($P = 0.3$).

*Fish lengths*

The lengths of collected fishes ranged from 2.5 mm (Gobiidae) to 400 mm (bluespotted cornetfish, *Fistularia commersonii*). We found that the lengths of the majority of Atlantic silverside, pinfish, silver perch, and spot were below respective lengths-at-maturity as indicated by the literature (anchovy: Stevenson, 1958; Atlantic silverside: Fay et al., 1983; pipefish: Ripley and Foran, 2006; pinfish: Ohs et al., 2011; silver perch: Grammer et al., 2009; spot: ASMFC, 2010), suggesting that the majority of collected fish were juveniles or post-larvae (Fig. 5).

*Season and interannual variation in fish communities*

Pairwise comparisons showed that CPUE during the summer months significantly exceeded those in the autumn (Wald $\chi_1^2 = 7.45$, $P < 0.01$), and catch data suggested that this effect was mostly due to a decline in October CPUE rather than September (Fig. 2a). In contrast, Hill-Shannon catch diversity was not significantly different between seasons ($P = 0.8$), although species-level models of catch across sampling seasons revealed strong within-year patterns in catch composition. Within the top six most collected taxa, we found that pipefish, pinfish, and spot were significantly more abundant in the summer rather than autumn months (all $P_{adj.} < 0.001$; Fig. 4a).

Species-specific catches also varied greatly among years. For example, pinfish made up 69% of catch during June 2015, but were absent from collections in June 2016. Similar patterns emerged for catches of silver perch, which were absent from May 2017 collections but made up 69% of catch in May 2018. Pipefish were the only taxa present across all years and sampling months, while Atlantic silversides were present in all sampling years and months except for October of 2018.

*Seascape-scale environmental drivers*

Fisher's C indicated that no paths were missing from SEMs modeling CPUE ($C = 0.9$, $P = 0.9$, $df = 4$), but identified a missing path in the richness SEM between depth and richness that we updated the model to include ($C = 1.04$, $P = 0.6$, $df = 2$). We found that the best fitting sub-model of seagrass presence included an interaction between depth and residence time ($\beta_{\text{unstd.}} = -3.13$, $SE = 1.24$, $P = 0.01$) with a significant main effect of depth ($\beta_{\text{unstd.}} = -2.55$, $SE = 1.0$, $P = 0.01$), indicating that seagrass presence was more likely in shallow areas, and particularly when those shallower areas were more frequently flushed.

In the CPUE SEM, seagrass presence was the most important contributor to CPUE ($\beta_{\text{unstd.}} = 1.82$, $SE = 0.23$, $P < 0.001$), whereas residence time did not influence catch. However, in the richness SEMs, seagrass presence ($\beta_{\text{unstd.}} = 0.83$, $SE = 0.13$, $P < 0.001$), residence time ($\beta_{\text{unstd.}} = -0.11$, $SE = 0.05$, $P = 0.03$), and depth ($\beta_{\text{unstd.}} = -0.17$, $SE = 0.07$, $P = 0.01$) were each found to be significant contributors to richness. Standardized coefficients for the richness sub-model showed that seagrass presence had a larger influence on mean richness ($\beta_{\text{std.}} = 0.44$) than residence time ($\beta_{\text{std.}} = -0.12$) or depth ($\beta_{\text{std.}} = -0.18$).

## Discussion

Using a spatially replicated, multiyear seine survey, we found that restored seagrass meadows were associated with large gains in fish abundance and diversity relative to adjacent unvegetated areas. Catches within restored meadows were 6.4 times more abundant and 3.1 times more diverse, with substantial differences in community composition attributable to the presence of seagrass and seasonal patterns in abundance. The seine method that we used undersamples fishes that closely associate with the seafloor, where they may avoid the net capture area (Connolly, 1994; Jenkins & Sutherland, 1997); therefore, our assessment of the benefits of seagrass restoration for the abundance and diversity of juvenile fishes is likely an underestimate. We found that patterns of enhanced abundance and richness were stable through both space and time despite environmental variability across seagrass meadows and seasonal-to-interannual variability in species composition. SEM results showed that seagrass presence was influenced by coastal hydrodynamics and bathymetry. Deeper areas with longer residence times (less frequent flushing) were less likely to have seagrass, and an absence of seagrass was associated with less diverse and abundant catches. By considering the environmental constraints limiting restoration success and the provisioning of ecosystem services by restored habitats, practitioners may better optimize site selection during the initial phases of restoration and reduce the risk 95estoringg habitats that fail to meet benchmarks for recovering lost ecosystem functions. For instance, our results from coastal Virginia indicate that the success of seagrass restoration and the associated benefits for fish production and diversity will be maximized at shallow, frequently flushed sites; optimal site selection guidelines for other regions will differ with variation in the relationships between environmental conditions and seagrass restoration success, and the associated direct and indirect effects on fishes.

Our findings showed that fish were more numerous within the restored seagrass meadows than outside of them, supporting short-term studies documenting higher densities of fishes in seagrass meadows relative to unvegetated habitats (Orth and Heck, 1980; Heck et al., 1989; Arrivillaga and Baltz, 1999; Gilby et al., 2018). Importantly, we found that these patterns held over long periods (5–7 years) despite spatial, between-year, and within-year variability in community composition. Catches were largest during the summer months when new and recently recruited fishes could be found in high densities. For example, pinfish (*Lagodon rhomboides*) recruit to seagrass meadows from offshore spawning grounds in the winter and spring months (Faletti et al., 2019). Likewise, the most abundant taxa in our collections, pipefish (*Syngnathus* spp.), migrate from offshore into estuaries during the spring and summer where spawning and brooding of eggs occurs (Campbell and Able, 1998). We also documented spot (*Leiostomus xanthurus*) in higher abundance in seagrass meadows during the summer months, which aligns with the timing of spot larval migration from offshore into nearshore nurseries (spring to early summer in the Mid-Atlantic) (ASMFC, 2010).

Silver perch (*Bairdiella chrysoura*) were also collected in higher abundance within the meadow, although catches were similar across seasons, aligning with previous work from the northern Gulf of Mexico identifying silver perch as permanent residents of estuaries with a peak spawning period between mid-March and June (Grammer et al., 2009). Similarly, there was a weakly significant, positive effect of meadow presence on Atlantic silverside abundance ($P_{Adj.} = 0.06$), and silverside catches did not differ between seasons. Within the U.S. mid-Atlantic region, both juvenile and adult Atlantic silverside are found in coastal habitats in high abundance in all seasons except winter, when migration to deeper or offshore waters occurs (Fay et al., 1983). Our results and the life histories of these species suggest that silver perch and Atlantic silverside may contribute less to seasonal differences in community composition than other species inhabiting the meadows.

Length-frequency distributions for these common fishes suggest that the majority of collected Atlantic silverside, pinfish, silver perch, and spot were juveniles, with fish lengths also tending to be smaller during the summer months than in the autumn (Appendix 5). This interpretation was less well-supported for pipefish, possibly because two species of pipefish with distinct length-frequencies—*Syngnathus fuscus* and *Syngnathus floridae* (Ripley and Foran, 2006)—are found in this region and we only identified pipefish to genus. Given increases in water temperatures in the Mid-Atlantic that favor the more southerly distributed *S. floridae* (Sobocinski et al., 2013), understanding the relative abundance dynamics of these species in the restored meadows may provide insights into the responses of seagrass-associated fish communities to climate change. While our findings suggest that the restored meadows act as preferred habitat for juvenile fishes over nearby unvegetated areas, the vegetated-versus-unvegetated dichotomy oversimplifies the complexity of fish movement patterns within the meadow and broader seascape mosaic (Nagelkerken et al., 2015; Litvin et al., 2018). The coastal bay seascape is composed of a variety of structured habitats used by fishes in addition to seagrass meadows, including intertidal marshes and oyster reefs, as well as hydrodynamically and bathymetrically complex areas like oceanic inlets, channels, and tidal creeks. The proximity of these habitats to seagrass meadows, as well as the capacity for fishes to move between habitats, influences fish abundance and biodiversity patterns (Yeager et al., 2016; Gilby et al. 2018). Expanding these analyses to consider interactions between restored meadows and features of the seascape more broadly would further refine our understanding of how environmental context shapes ecosystem services associated with seagrass restoration.

SEM analyses showed how seascape-scale environmental covariates affected fish-habitat relationships indirectly by influencing seagrass distributions. We found a negative effect of depth on the probability of seagrass occurrence, indicating a lower likelihood of seagrass presence in deeper areas, where deep, turbid water restricts seagrass growth through light limitation (Carr et al., 2010; Aoki et al., 2020a). Further, we identified an interaction effect of depth and water residence time on the probability of seagrass occurrence, indicating a greater likelihood of seagrass presence in shallower areas, especially those with frequent tidal flushing. Frequently flushed areas tend to have larger sediment grain sizes that are favorable for seagrass growth (Koch, 2001; Wiberg et al., 2015) and may be less susceptible to the disturbance effects of marine heatwaves through more frequent exchange with the cooler coastal ocean (Aoki et al., 2021, Berger et al. 2020).

While we show that depth and an interaction between depth and residence time mediate seagrass presence and habitat provisioning for juvenile fishes, our analyses were limited by only considering seagrass presence within the immediate vicinity of sampling sites. Seagrass-associated fish communities will also organize along gradients of seagrass patchiness and areal coverage (Yeager et al., 2011, 2016; McCloskey and Unsworth, 2015). In the species richness SEM, we found that depth had a direct negative effect on species richness, indicating a greater diversity of fishes at shallower sites. This could be due to correlations between depth and unmeasured characteristics of the meadow, such as meadow area, patchiness, or shoot density (Aoki et al., 2020a; Belgrad et al., 2021). For example, in the shallower and more frequently flushed South Bay meadow, average seagrass shoot densities were 4.4× greater than in Hog Island Bay during the study period (365 vs. 84 shoots/$m^2$; Appendix 6; McGlathery 2017; Aoki et al., 2020a). Alternatively, physical properties of the water column that scale with depth, such as light availability or water temperature (Aoki et al., 2020a) may alter local habitat suitability and subsequent community structure (Belgrad et al., 2021).

We also found that catches at sites with shorter water residence times (more frequent tidal flushing) tended to be more species rich, a pattern largely due to high richness in the South Bay meadow where residence times were approximately three hours. Comparatively, residence times at all other sites exceeded 20 hours (Appendix 7). Beyond the consistent presence of seagrass in South Bay, this finding may be due to higher stability in environmental conditions afforded by more frequent flushing by the coastal ocean (Martino and Able, 2003), which has been hypothesized to mitigate the negative effects of marine heatwaves on seagrass (Aoki et al., 2021). Alternatively, more frequent water exchange with the coastal ocean may simply introduce more larvae into the meadow, where the presence of dense structured habitat (Grol et al., 2011) and an abundance of food (Lefcheck et al., 2017) could improve survivorship of recruits and lead to a more diverse species assemblage relative to Hog Island Bay.

Through long-term study, we discovered a diverse and abundant coastal fish community that is highly dynamic over space and time yet is consistently enhanced by restored seagrass. Such increases in abundance and diversity add to the numerous ecosystem services shown to recover with large-scale seagrass restoration (Orth et al. 2020). Continued long-term study may further contextualize how local to regional scale environmental variation mediates the benefits of seagrass restoration for fish production and biodiversity. The acceleration of marine habitat restoration in recent decades (Duarte et al. 2020) should serve as motivation for new studies to evaluate the functional services of restored habitats, advise restoration planning, and inform policies that incentivize restoration (e.g., Smith and Castorani, 2023). For example, the seagrass restoration that we studied will soon be the first of its kind to enter a ‘blue carbon’ market with payments for ecosystem services, which involves a spatial accounting of carbon sequestered by the restored meadow (Oreska et al., 2021; Shilland et al., 2021). Understanding how ecosystem services beyond carbon sequestration, such as provisioning habitat and supporting biodiversity, could contribute to such markets is nascent but interest in these services is growing (Shilland et al. 2021).

## Acknowledgements

This study was funded by the U.S. National Science Foundation through support of the Virginia Coast Reserve Long Term Ecological Research Project (VCR LTER; award DEB- 1237733, DEB-1832221). We thank the many participants of the VCR LTER for their assistance in collecting and curating the data, especially C. Baird, D. Boyd, L. Cole, D. Lee, J. Mor- reale, J. Porter, M. Reidenbach, A. Schwarzschild, T. Barnes, and P. Wiberg. We are grateful to R. Smith and M. Cornish for comments that improved this manuscript.

## Figures

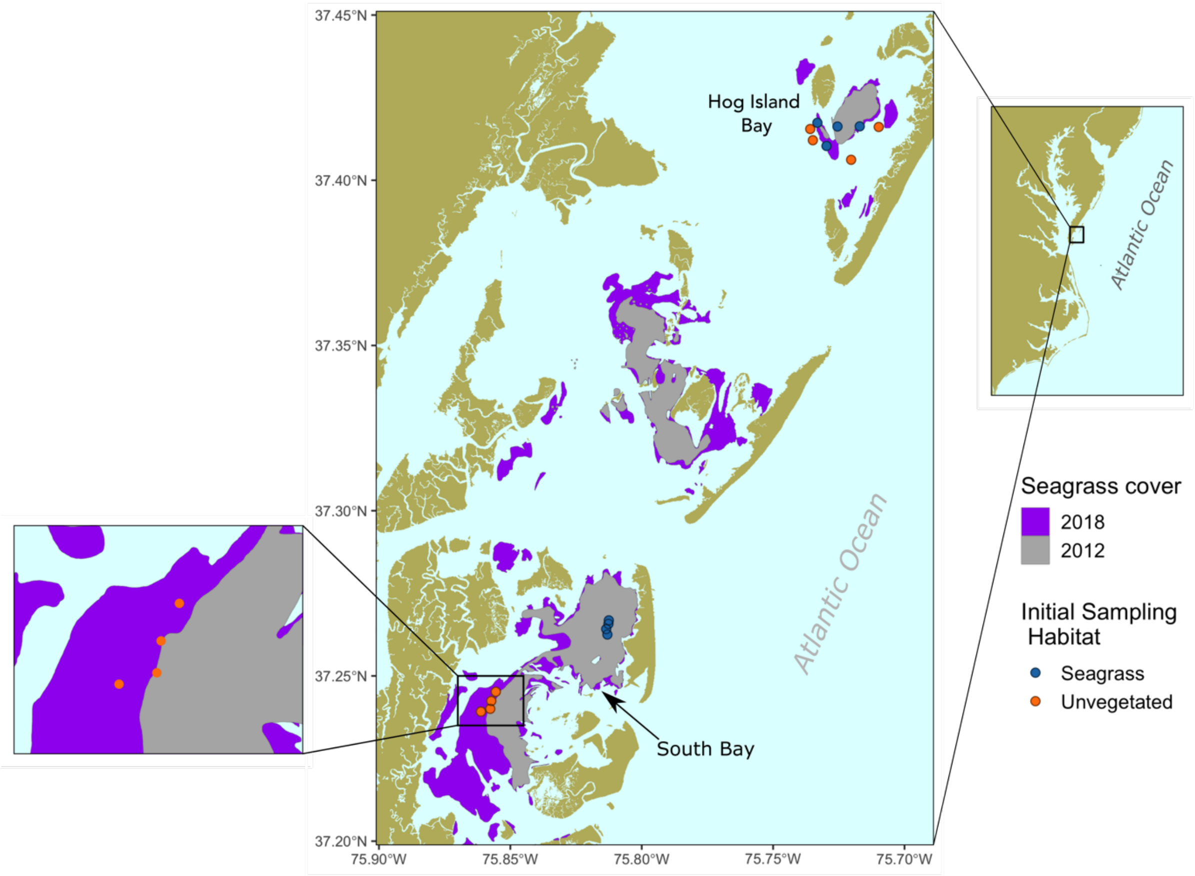


*Figure 1.* Fish sampling sites in Hog Island and South Bay seagrass meadows within the Virginia Coast Reserve (VCR) along the Atlantic coast of Virginia, USA. Grey and purple shading shows the extent of seagrass in 2012 and 2018, respectively, from aerial imagery. Points show sampling sites. The color of points indicate the presence (blue) or absence (orange) of seagrass at sampling sites when fish surveys began in 2012. Note that some sites that were initially unvegetated became vegetated during the study period (e.g., see bottom left inset).

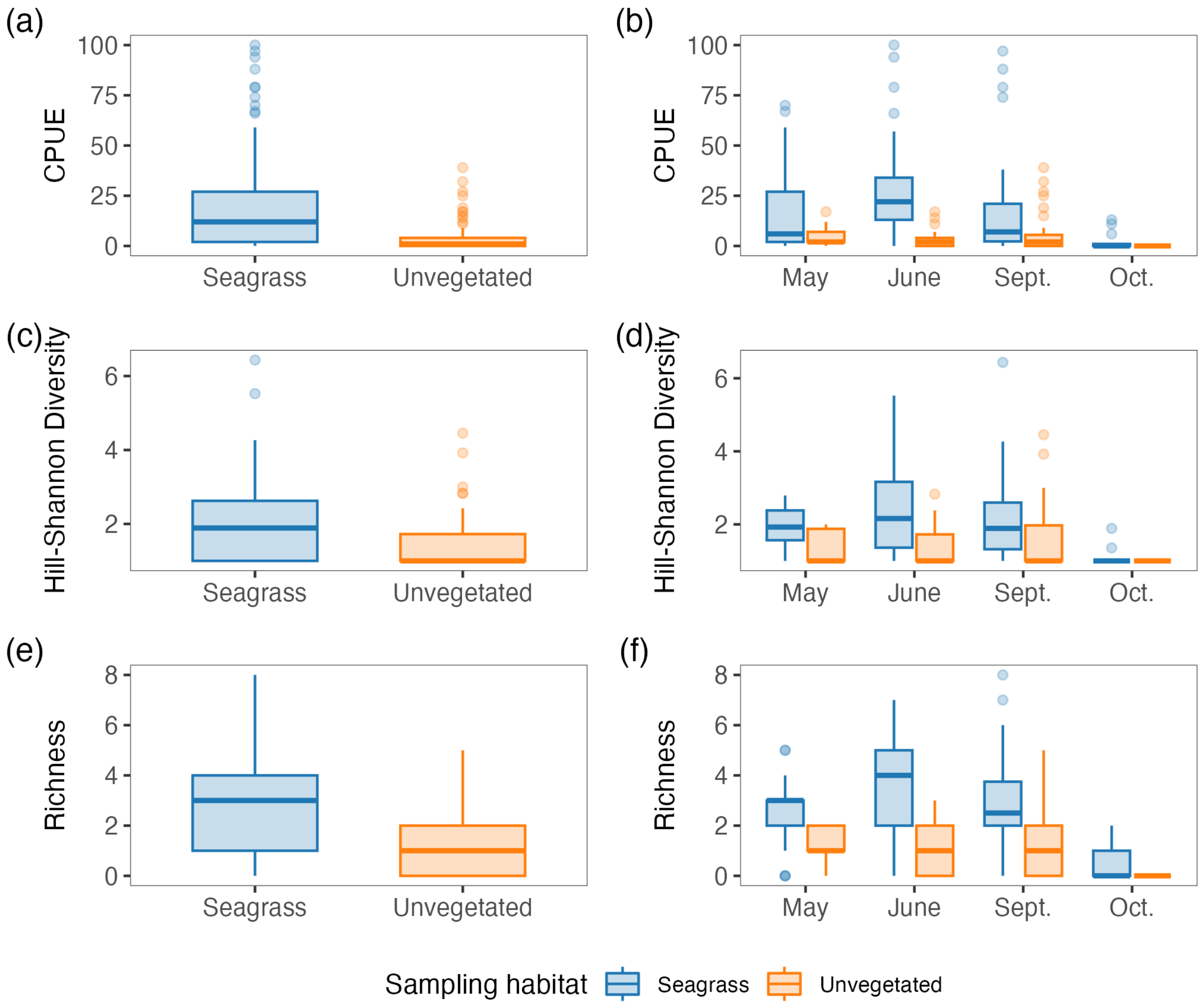


*Figure 2.* Boxplots showing fish catch per unit effort (CPUE; a, b), Hill-Shannon diversity (c, d), and species richness (e, f) inside and outside seagrass meadows across all sampling months (a, c, e) and specific to each sampling month (b, d, f). Boxplots include all years of data ($N_{May} = 28$, $N_{June} = 72$, $N_{Sept.} = 80$, $N_{Oct.} = 24$), and show median values (bold lines) and interquartile ranges (IQR; boxes), with outliers (transparent points) greater than 1.5 × the interquartile range (whiskers).

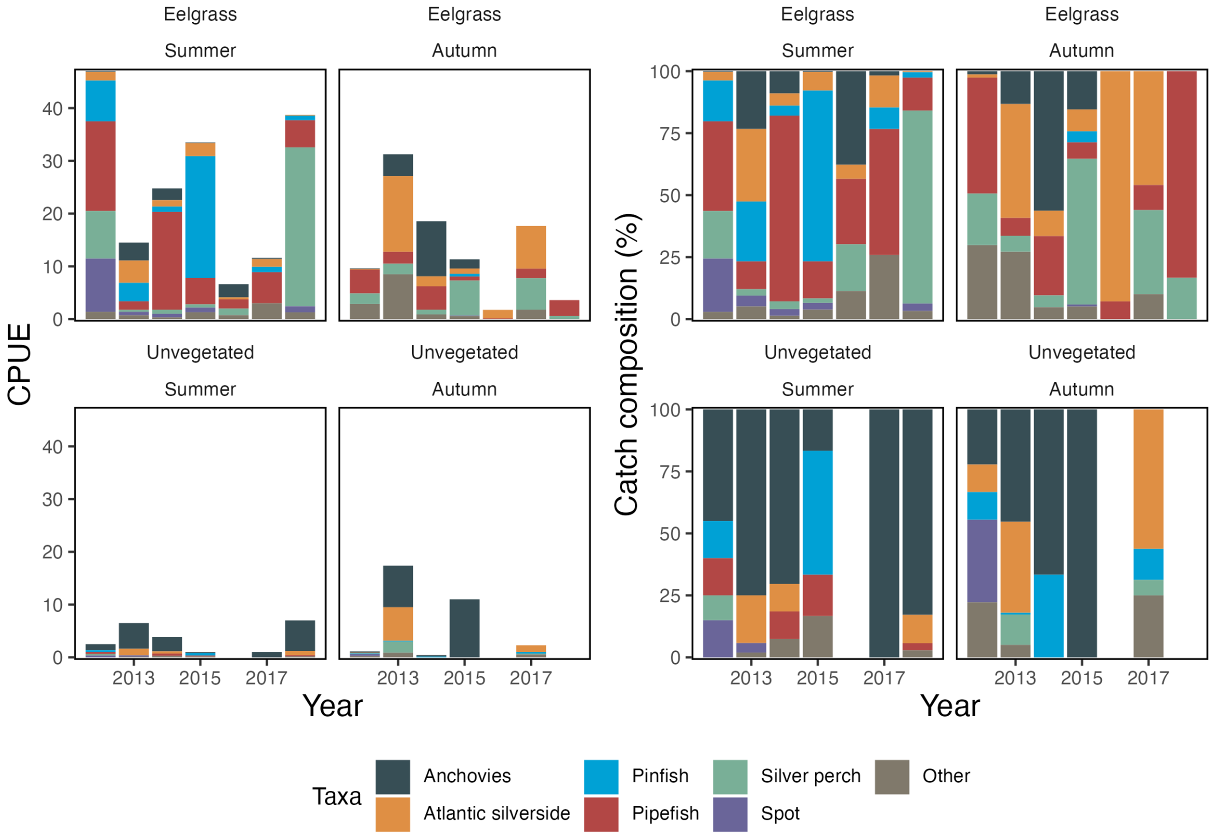


*Figure 3.* Catch per unit effort (CPUE) of the six most common taxa and all other taxa ("Other") in the summer (May and June) and autumn (September and October) inside and outside of restored seagrass meadows. Panels (a) and (b) show the total and proportional contribution, respectively, of taxa to aggregate CPUE. Empty bars indicate a year-season-habitat combination in which sampling occurred but no fish were captured.

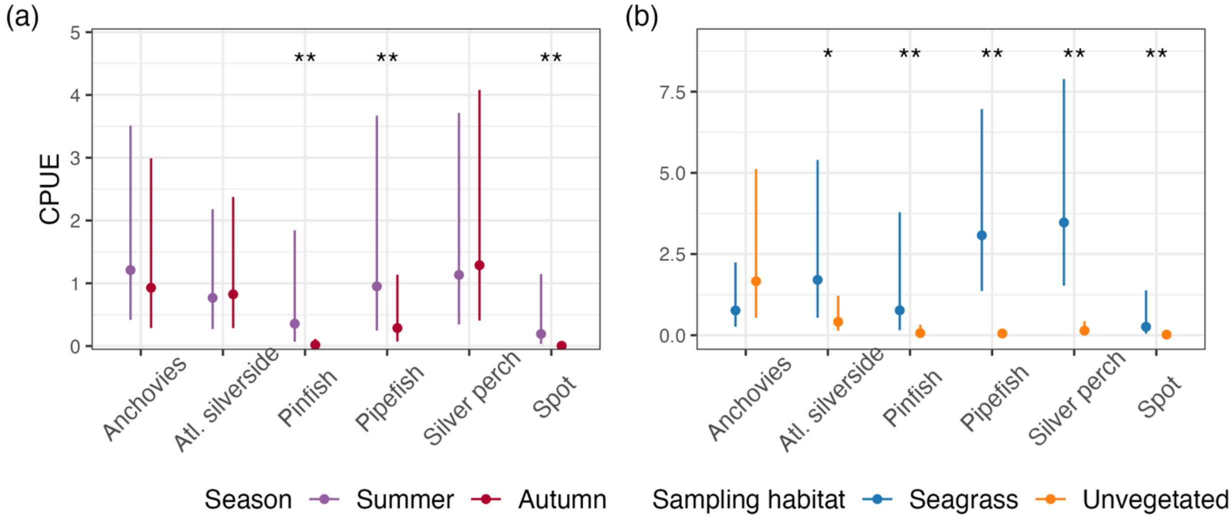


*Figure 4.* Predicted catch per unit effort (CPUE) for the six most commonly collected taxa in summer and autumn months (a) and inside and outside of seagrass habitat (b). Points indicate marginal means and bars show 95% confidence intervals. Asterisks indicate significant differences in mean CPUE between seasons or habitats at P < 0.1 (*) and P < 0.05 (**) after adjusting for multiple comparisons.

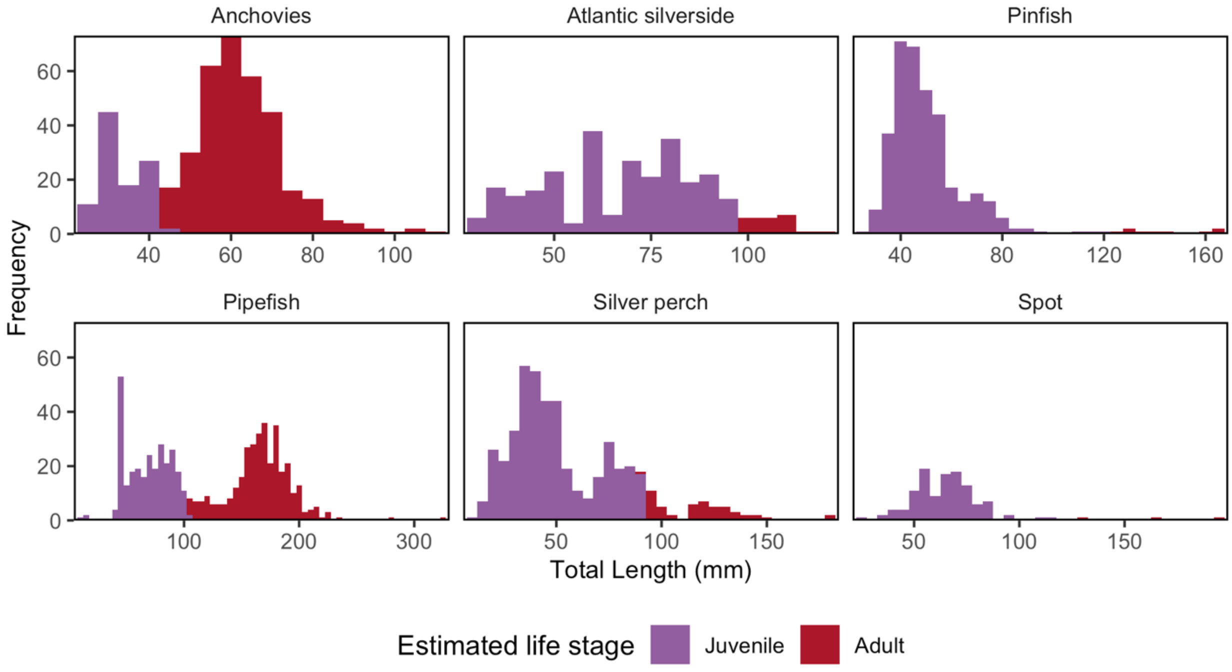


*Figure 5.* Length-frequency histograms for the six most common taxa in seine collections, segregated into estimated life stages based on available estimates of lengths at maturity (purple vs. red). Life stage splits are reported as total lengths-at-maturity except for pipefish and silver perch where length-length conversions were unavailable and reported as standard lengths-at-maturity. The pipefish length-at-maturity is the minimum of reported lengths for mature *Syngnathus floridae* females (Ripley and Foran 2006). For anchovies, we report length-at-maturity for the highly abundant bay anchovy, *Anchoa mitchilli*. These data represent lengths measured during all sampling periods and locations both inside and outside of seagrass.

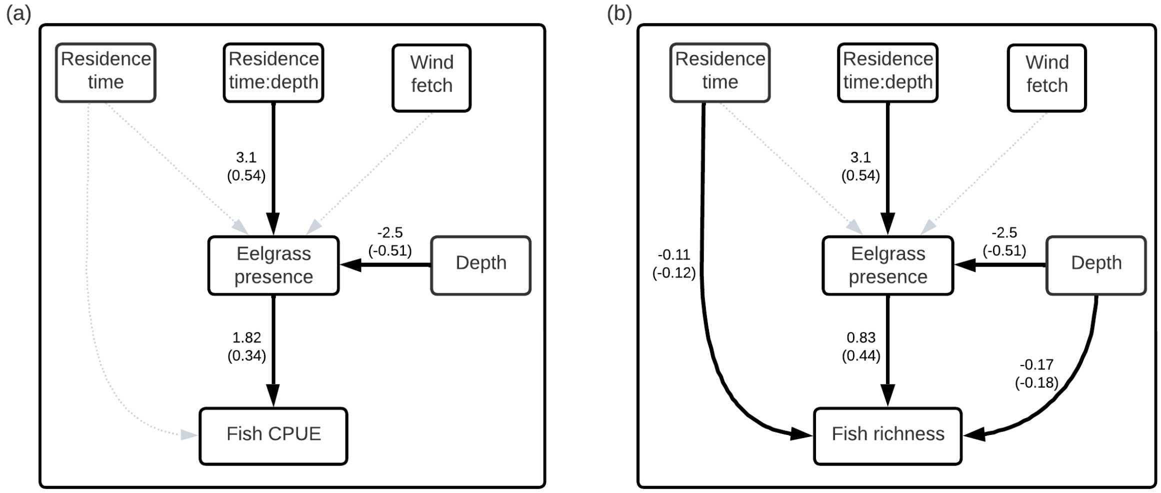
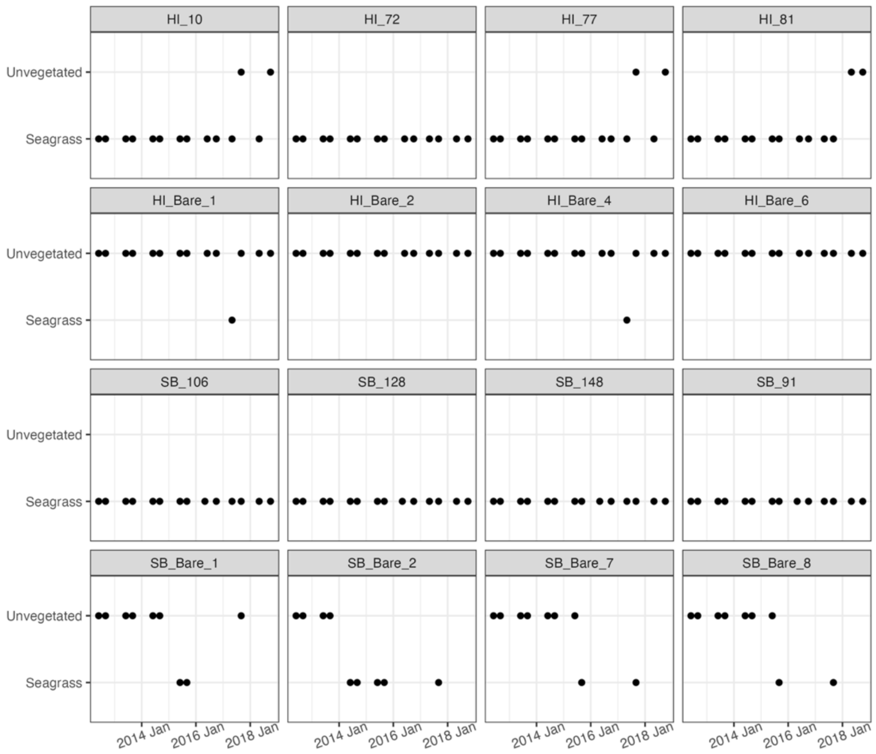


*Figure 6.* Path diagrams for community-level fish catch per unit effort (CPUE; a) and taxa richness (b). Black arrows with solid lines are significant at P < 0.05. Grey dotted lines indicate non-significant paths. Coefficients are reported next to black lines where P < 0.05; standardized coefficients are included in parentheses next to unstandardized coefficients. The interaction between residence time and depth is indicated by ‘Residence time:depth’.

# Appendix



*Appendix 1.* Time series of presence-absence of seagrass at each seine sampling site from 2012-2018. Each subplot represents a different site, and those with "Bare" in the subplot title were unvegetated in 2012 at the beginning of the study. "SB" or "HI" refers to the South Bay or Hog Island Bay meadows, respectively. Note that sampling did not occur consistently at initially unvegetated South Bay sites after 2015.

*Appendix 2.* Model summaries from comparisons of catch abundance, Hill-Shannon diversity, and species richness inside and outside of seagrass, the interaction between habitat and meadow location on species richness, and the effect of sampling season on total CPUE. Factor reference levels are given in brackets, and reported P values are those returned by Wald z tests.

Model 1: Catch (across species) inside vs. outside seagrass

| *Predictors* | *Log-Mean* | *95% CI* | *Wald* $\chi^2_1$ | *Wald* z | *P* |
|---|---|---|---|---|---|
| Intercept | 2.87 | 2.27 – 3.46 | - | - | **<0.001** |
| Vegetated vs. unvegetated [Unvegetated] | -1.86 | -2.33 – -1.38 | 59.14 | -7.69 | **<0.001** |
| **Random Effects** | | | | | |
| $\sigma^2_{site}$ | 0.04 | | | | |
| $\sigma^2_{year}$ | 0.49 | | | | |

Model 2: Catch diversity (Hill-Shannon) inside vs. outside seagrass

| *Predictors* | *Log-Mean* | *95% CI* | *Wald* | *Wald* z | *P* |
|---|---|---|---|---|---|
| **Count Model** | | | | | |
| Intercept | 0.31 | 0.08 – 0.54 | - | 2.63 | **0.008** |
| Vegetated vs. unvegetated [Unvegetated] | -0.29 | -0.55 – -0.03 | 4.68 | -2.16 | **0.03** |

| | | | | | |
|---|---|---|---|---|---|
| **Probability Model** | | | | | |
| Intercept | -1 | -1.41 – -0.59 | - | -2.86 | **0.004** |
| Vegetated vs. unvegetated [Unvegetated] | 1.76 | 1.15 – 2.38 | - | 5.67 | **<0.001** |
| **Random Effects** | | | | | |
| $\sigma_{site}{}^2$ | 0 | | | | |
| $\sigma_{year}^2$ | 0.07 | | | | |

Model 3: Catch richness inside vs. outside seagrass

| *Predictors* | *Log-Mean* | *95% CI* | *Wald* $\chi_1^2$ | *Wald* z | *P* |
|---|---|---|---|---|---|
| Intercept | 0.9 | 0.54 – 1.25 | - | 4.96 | **<0.001** |
| Vegetated vs. unvegetated [Unvegetated] | -0.95 | -1.25 – -0.65 | 38.67 | -6.22 | **<0.001** |
| **Random Effects** | | | | | |
| $\sigma_{site}{}^2$ | 0.02 | | | | |
| $\sigma_{year}^2$ | 0.17 | | | | |

Model 4: Catch richness inside vs. outside seagrass (× meadow)

| *Predictors* | *Log-Mean* | *95% CI* | *Wald* $\chi_1^2$ | *Wald* z | *P* |
|---|---|---|---|---|---|
| Intercept | 0.77 | 0.40 – 1.14 | - | 4.1 | **<0.001** |

| | | | | | |
|---|---|---|---|---|---|
| Vegetated vs. unvegetated [Unvegetated] | -0.93 | -1.29 – -0.58 | 47.00 | -5.16 | **<0.001** |
| Meadow [SB] | 0.26 | 0.02 – 0.51 | 5.39 | 2.12 | **0.034** |
| Vegetated vs. unvegetated [Unvegetated] × Meadow [SB] | -0.05 | -0.55 – 0.46 | 0.03 | -0.182 | 0.856 |
| | | | | | |
| **Random Effects** | | | | | |
| ${\sigma_{site}}^{2}$ | 0 | | | | |
| $\sigma_{year}^{2}$ | 0.17 | | | | |

Model 5: Catch (across species) by season (summer vs. autumn)

| *Predictors* | *Log-Mean* | *95% CI* | *Wald* $\chi_1^2$ | *Wald* z | *P* |
|---|---|---|---|---|---|
| Intercept | 2.39 | 1.68 – 3.10 | - | 6.56 | **<0.001** |
| Season [Fall] | -0.62 | -1.06 – -0.17 | 7.45 | -2.73 | **0.006** |
| | | | | | |
| **Random Effects** | | | | | |
| ${\sigma_{site}}^{2}$ | 0.72 | | | | |
| $\sigma_{year}^{2}$ | 0.44 | | | | |

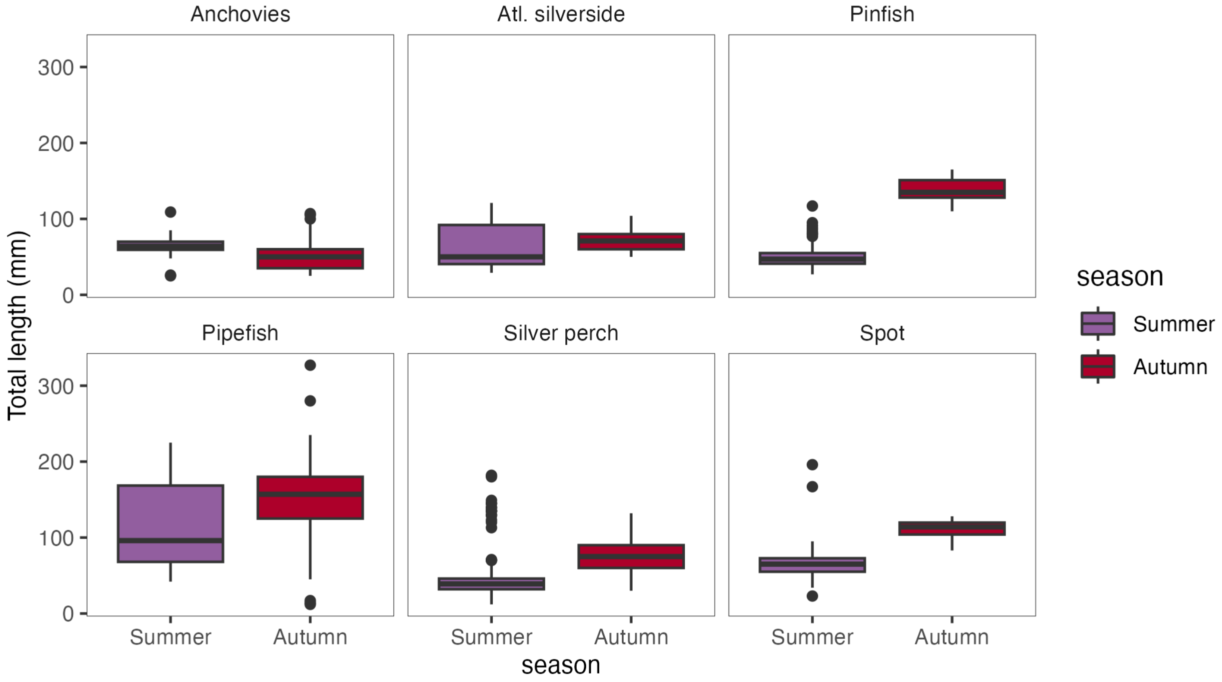
*Appendix 3*. Summary from PERMANOVA test for differences in sample species composition inside vs. outside seagrass habitat, across seasons and years.

| PERMANOVA | | | | | |
|---|---|---|---|---|---|
| *Predictors* | *DF* | *Sum of Sqs.* | *Pseudo-$R^2$* | *F* | *P* |
| Vegetated vs. unvegetated | 1 | 4.61 | 0.09 | 15.84 | **0.02** |
| Season | 1 | 1.72 | 0.03 | 5.91 | **<0.001** |
| Meadow (HI vs. SB) | 1 | 1.27 | 0.02 | 4.37 | 0.32 |
| Year | 1 | 0.72 | 0.01 | 2.4 | **<0.01** |
| Residual | 148 | 43.1 | 0.82 | | |
| Total | 152 | 52.58 | 1 | | |

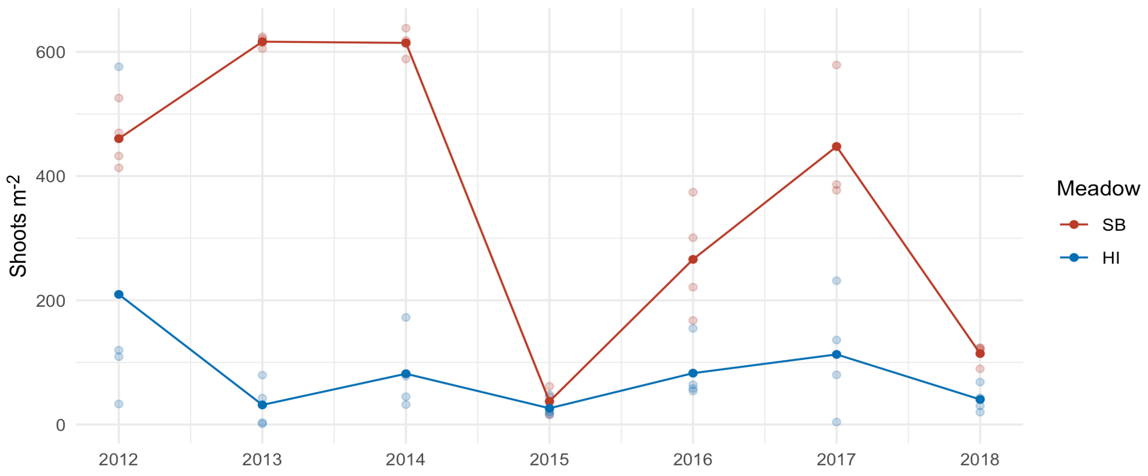
*Appendix 4*. Catches inside and outside of eelgrass meadows with mean, minimum, and maximum lengths for all collected fishes.

| Fish taxa | Unvegetated | Eelgrass | Mean length (mm) | Min. length (mm) | Max length (mm) |
|---|---:|---:|---|---|---|
| *Syngnathus* spp. | 8 | 610 | 123 | 12 | 327 |
| *Bairdiella chrysoura* | 20 | 486 | 56.3 | 12 | 182 |
| *Anchoa* spp. | 210 | 220 | 55.7 | 25 | 109 |
| *Menidia menidia* | 78 | 333 | 68.8 | 29 | 121 |
| *Lagodon rhomboides* | 11 | 352 | 52.4 | 27 | 165 |
| *Leiostomus xanthurus* | 8 | 110 | 66.9 | 23 | 196 |
| *Archosargus probatocephalus* | 1 | 43 | 76.8 | 53 | 115 |
| *Orthopristis chrysoptera* | 0 | 37 | 103.7 | 15 | 127 |
| *Micropogonias undulatus* | 1 | 34 | 36.6 | 21 | 240 |
| *Centropristis striata* | 1 | 17 | 86.2 | 20 | 160 |
| *Hippocampus erectus* | 1 | 14 | 92.9 | 80 | 111 |
| Gobiidae | 4 | 10 | 36.6 | 2 | 61 |
| *Eucinostomus argenteus* | 1 | 6 | 45.3 | 31 | 88 |
| *Chilomycterus schoepfii* | 0 | 5 | 167.6 | 80 | 236 |
| *Pomatomus saltatrix* | 2 | 2 | 92 | 65 | 155 |
| *Tautoga onitis* | 0 | 4 | 74.5 | 18 | 105 |
| *Fistularia commersonii* | 1 | 2 | 325 | 195 | 400 |

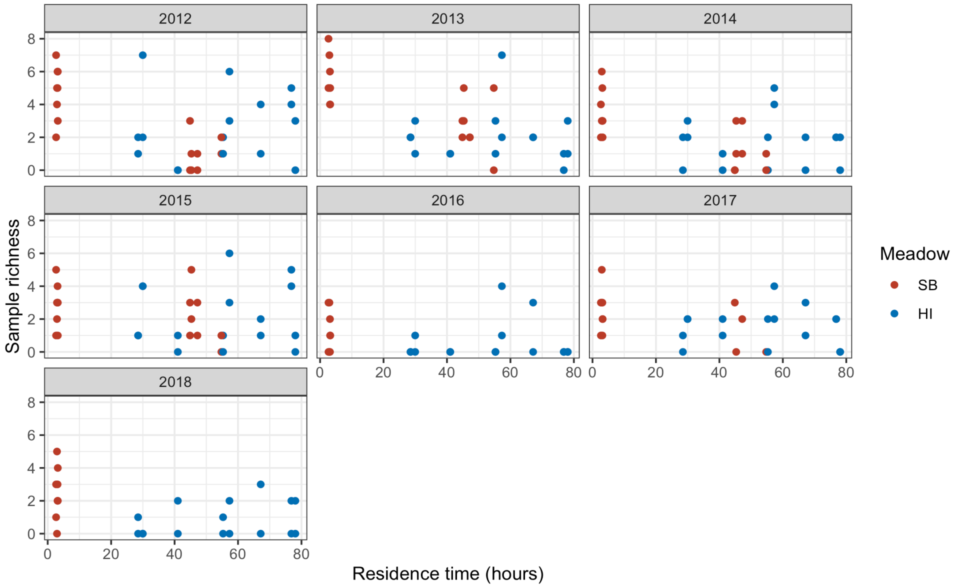
| Fish taxa | Unvegetated | Eelgrass | Mean length (mm) | Min. length (mm) | Max length (mm) |
|---|---|---|---|---|---|
| Mugilidae | 0 | 3 | 83 | 55 | 109 |
| *Paralichthys dentatus* | 0 | 3 | 78.7 | 71 | 86 |
| Sciaenidae | 0 | 3 | 30 | 30 | 30 |
| *Sphoeroides maculatus* | 0 | 3 | 37.7 | 13 | 80 |
| *Strongylura marina* | 1 | 2 | 171.7 | 80 | 285 |
| *Hyporhamphus meeki* | 0 | 2 | 84 | 71 | 97 |
| *Lolliguncula brevis* | 2 | 0 | 43 | 35 | 51 |
| *Lutjanus griseus* | 0 | 2 | 58 | 56 | 60 |
| *Opsanus tau* | 0 | 2 | 113.5 | 112 | 115 |
| *Stephanolepis hispidus* | 0 | 2 | 35 | 30 | 40 |
| *Brevoortia tyrannus* | 0 | 1 | 52 | 52 | 52 |
| *Chasmodes bosquianus* | 0 | 1 | 60 | 60 | 60 |
| *Cynoscion nebulosus* | 0 | 1 | 38 | 38 | 38 |
| *Gobiesox strumosus* | 1 | 0 | 120 | 120 | 120 |
| *Peprilus triacanthus* | 1 | 0 | 10 | 10 | 10 |
| *Sphyraena borealis* | 0 | 1 | 75 | 75 | 75 |
| *Stenotomus chrysops* | 1 | 0 | 174 | 174 | 174 |
| Total | 353 | 2,311 | - | - | - |



*Appendix 5.* Boxplots showing the distribution of fish lengths (TL) in the summer (purple) and autumn (red) months by most common species. The data shown here include fish collected both inside and outside the meadow and across years/seasons.



*Appendix 6.* Eelgrass shoot densities at sites within South Bay (red) and Hog Island Bay (blue where fish seining occurred between 2012-2018. Density observations were made annually during July. Bold points indicate annual mean densities. See Aoki et al. (2020) for more information.



*Appendix 7*. Sample richness against residence times across years and meadows. Samples collected in South Bay are shown in red and Hog Island Bay in blue.

# Discussion

In this work, I explored how SST anomalies influence inshore fish populations on the spatial scale of the Mid-Atlantic Bight (MAB), how stability and asynchrony within commercial fisheries relates to asynchrony in the ecological communities that they depend upon in the Chesapeake Bay, and how seagrass restoration enhances the abundance and diversity of juvenile fishes in the coastal bays of Virginia. A unifying aspect of these studies is that they yield insights into the give and take of societal interactions with fish populations. Society manages the extraction of fish biomass from inshore ecosystems while also advocating for the restoration of fish habitats that support these populations. The effects of ocean warming on fish populations, which are an indirect effect of societal greenhouse gas emissions (Frölicher et al., 2014), are another pathway through which humans have impacted inshore fish populations. However, while these research foci are connected in the sense that they are all related to human drivers of ecological change, the differing spatial scales of their human-ecological interactions cannot be overstated.

In Chapter 1, I showed that the responses of inshore fish population dynamics within the MAB were weakly mediated by species life history characteristics, displaying high variability in their responses to warming from bay to bay. However, the species whose populations responded positively to warming and maintained the "fastest" life histories, meaning that they were smaller-bodied and faster-lived, tended to be warm-adapted. Alternatively, the species whose populations responded negatively to warming and were the "slowest" lived, or were larger-bodied and longer-lived, tended to be cool-adapted. For species whose populations are "moving" northwards in the MAB (I was not able to differentiate between the possible drivers of population responses, so an increase/decline could indicate the movement of individuals to new habitats or changes in productivity or phenology) along with their suitable thermal habitats, the conservation and restoration of nursery habitats like seagrass meadows is unlikely to be enough to prevent population declines in the long-term. This is because the spatial scale of seasonally averaged warming occurs on hundreds to thousands of kilometers, whereas habitat restoration, even when hugely successful, falls on the scale of tens of kilometers, and can be further complicated by temperature variability associated with climate change like a greater occurrence of marine heatwaves (Spillman et al. 2021). This is not to say that seagrass restoration efforts are unlikely to benefit fish communities in a warming climate; quite the opposite, as many warm-adapted species whose populations are increasing will likely benefit from an abundance of inshore nursery habitat in the future. However, the composition of species occupying inshore nursery habitats may shift towards those species that are more well-suited to the local thermal environment.

Nowhere is confronting and understanding variability in fish population dynamics more important than in fisheries management. In the Chesapeake Bay, for example, many of the most commercially valuable finfish move into and out of the Bay mainstem seasonally, and in recent years, the biomasses of these species have declined, particularly in the southern regions of the Bay. These declines have been attributed to reductions in the exchange of finfish biomass with the adjacent continental shelf due to climatic variability—e.g., the North Atlantic Oscillation and its impacts on regional oceanographic dynamics—processes that manifest on spatial scales far exceeding that of Chesapeake Bay, but also due to coastwide declines in abundance for species like Atlantic croaker (Schonfeld et al. 2022).

In Chapter 2, I showed that these biomass declines mitigated the stabilizing effects of within-year harvest diversification for the commercial fishing portfolio in the Virginia portion of Bay, as the within-Bay biomasses of targeted species in this region displayed synchronous declines on interannual time scales, and small-scale fishing operations in the Bay typically do not extend their operations into adjacent offshore habitats where populations may be more abundant. Stated differently, the within-year stability of commercial harvest portfolios in the lower Bay benefit less from diversification if the species in the portfolio, while retaining unique migratory patterns leading to within-year biomass asynchrony, are synchronously declining in their within-Bay availabilities from year to year. This situation requires creative management strategies to ensure the stability of commercial fisheries operating in the Virginia portion of the Bay. These strategies are being enacted in the form of legislative initiatives supporting the development of the blue catfish fishery, but other approaches like management strategies that support fishers transitioning from finfish harvesting to related industries like shellfish and crab fisheries are likely to be beneficial for the stability of the regional harvest portfolio.

In addition to the population dynamics of targeted fishes impacting the stability of the commercial harvest portfolio in the Virginia region of the Bay, we found that the stability of the harvest portfolio in both Virginia and Maryland was impacted by fishing behaviors in the form of declines in harvest effort in Virginia and target species diversification during the striped bass closure in Maryland. In Virginia, the social context of this declining effort is important to consider, and declines in fishing effort may also be rooted in changes in the composition of the fishing fleet, as recent research has shown that the number of licensed fishers in Virginia has declined in recent decades (White & Scheld, 2021), but also changes in market forces and demand for certain fishes. In Maryland, behavioral patterns in fishing effort were stabilizing for the portfolio, but within-year harvest portfolio effects did not translate to economic stability: during the striped bass closure, the targeting of other species like Atlantic croaker, white perch, and gizzard shad created harvest compensation that stabilized within-year fishery harvests, but the relatively low value of these species compared to striped bass ultimately meant that diversification during the closure did not stabilize the within-year value of the harvest portfolio. These findings showed that asynchrony in population dynamics was not guaranteed to be associated with asynchrony and stability in the portfolio of harvests derived from those populations, as social and management-related factors can influence how fishing effort is distributed across target stocks.

For many fishes that inhabit inshore environments for a portion or all of their life cycles, the use of nursery habitats like seagrasses enhances the survivorship of juveniles (Lefcheck et al., 2019a) and so indirectly supports the fisheries that depend on those species (Unsworth et al., 2019). For this reason, and that the high diversity and abundance of invertebrates and non-target fish species that inhabit seagrasses contribute to fisheries production through trophic pathways (Jackson et al., 2001), funding seagrass restoration efforts is one way that governments can support commercial and recreational fisheries. In Chapter 3, I considered how fish biodiversity and abundance differed between restored seagrass (*Zostera marina*) meadow and unvegetated habitats in the coastal bays of Virginia. I showed that both the abundance and diversity (species richness and Hill-Shannon diversity) were significantly higher within the restored meadow compared to unvegetated areas. I also found that this pattern of increase abundance and diversity was temporally stable throughout the year when sampling occurred, and that most of the collected fish were juveniles. In the context of my other chapters, this work showed that restoring seagrass meadows was effective for increasing local fish biodiversity in the coastal bays of Virginia, although the composition of species inhabiting the restored meadows may change under continued ocean warming.

In this dissertation, I have provided novel insights into how a warming continental shelf has impacted populations of fishes in the inshore habitats of the MAB, how within-year species asynchrony among commercially fished species in Chesapeake Bay impacts the stability of fisheries portfolios associated with those species, and lastly, that restored seagrasses in the coastal bays of Virginia were associated with substantial and temporally consistent increases in fish biodiversity and abundance within those meadows relative to nearby unvegetated areas. Understanding these interactions is essential to the successful management of these highly interconnected systems in the Anthropocene.

# References

Alfaro, A. C. (2006). Benthic macro-invertebrate community composition within a mangrove/seagrass estuary in northern New Zealand. *Estuarine, Coastal and Shelf Science*, *66*(1–2), 97–110.

Anderson, I. C., Stanhope, J. W., Hardison, A. K., & McGlathery, K. J. (2010). Sources and fates of nitrogen in Virginia coastal bays. *Coastal Lagoons: Critical Habitats of Environmental Change. CRC Press, Boca Raton, FL*, 43–72.

Anderson, M. J. (2005). Permutational multivariate analysis of variance. *Department of Statistics, University of Auckland, Auckland*, *26*, 32–46.

Anderson, S. C., Cooper, A. B., & Dulvy, N. K. (2013). Ecological prophets: Quantifying metapopulation portfolio effects. *Methods in Ecology and Evolution*, *4*(10), 971–981.

Anderson, S. C., Ward, E. J., English, P. A., & Barnett, L. A. (2022). sdmTMB: an R package for fast, flexible, and user-friendly generalized linear mixed effects models with spatial and spatiotemporal random fields. *bioRxiv*, 2022–03.

Anderson, S. C., Ward, E. J., Shelton, A. O., Adkison, M. D., Beaudreau, A. H., Brenner, R. E., Haynie, A. C., Shriver, J. C., Watson, J. T., & Williams, B. C. (2017). Benefits and risks of diversification for individual fishers. *Proceedings of the National Academy of Sciences*, *114*(40), 10797–10802.

Aoki, L. R., McGlathery, K. J., & Oreska, M. P. (2020). Seagrass restoration reestablishes the coastal nitrogen filter through enhanced burial. *Limnology and Oceanography*, *65*(1), 1–12.

Aoki, L. R., McGlathery, K. J., Wiberg, P. L., & Al-Haj, A. (2020). Depth affects seagrass restoration success and resilience to marine heat wave disturbance. *Estuaries and Coasts*, *43*, 316–328.

Aoki, L. R., McGlathery, K. J., Wiberg, P. L., Oreska, M. P., Berger, A. C., Berg, P., & Orth, R. J. (2021). Seagrass recovery following marine heat wave influences sediment carbon stocks. *Frontiers in Marine Science*, *7*, 576784.

Arlinghaus, R., Alós, J., Beardmore, B., Daedlow, K., Dorow, M., Fujitani, M., Hühn, D., Haider, W., Hunt, L., Johnson, B., & others. (2017). Understanding and managing freshwater recreational fisheries as complex adaptive social-ecological systems. *Reviews in Fisheries Science & Aquaculture*, *25*(1), 1–41.

Arrivillaga, A., & Baltz, D. M. (1999). Comparison of fishes and macroinvertebrates on seagrass and bare-sand sites on Guatemala's Atlantic coast. *Bulletin of Marine Science*, *65*(2), 301–319.

Asch, R. G., Stock, C. A., & Sarmiento, J. L. (2019). Climate change impacts on mismatches between phytoplankton blooms and fish spawning phenology. *Global Change Biology*, *25*(8), 2544–2559.

ASFMC. (2010). *Spot Life History Report*.

Auth, T. D., Arula, T., Houde, E. D., & Woodland, R. J. (2020). Spatial ecology and growth in early life stages of bay anchovy *Anchoa mitchilli* in Chesapeake Bay (USA). *Marine Ecology Progress Series*, *651*, 125–143.

Avolio, M. L., Forrestel, E. J., Chang, C. C., La Pierre, K. J., Burghardt, K. T., & Smith, M. D. (2019). Demystifying dominant species. *New Phytologist*, *223*(3), 1106–1126.

Barbier, E. B., Hacker, S. D., Kennedy, C., Koch, E. W., Stier, A. C., & Silliman, B. R. (2011). The value of estuarine and coastal ecosystem services. *Ecological Monographs*, *81*(2), 169–193.

Barnes, T., & Wiberg, P. (2020). *Bathymetry of South Bay* (knb-lter-vcr.382.1) [dataset]. Virginia Coast Reserve Long-Term Ecological Research Project Data Publication.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). Fitting linear mixed-effects models using lme4. *arXiv Preprint arXiv:1406.5823*.

Batt, R. D., Morley, J. W., Selden, R. L., Tingley, M. W., & Pinsky, M. L. (2017). Gradual changes in range size accompany long-term trends in species richness. *Ecology Letters*, *20*(9), 1148–1157.

Baudron, A. R., Brunel, T., Blanchet, M.-A., Hidalgo, M., Chust, G., Brown, E. J., Kleisner, K. M., Millar, C., MacKenzie, B. R., Nikolioudakis, N., & others. (2020). Changing fish distributions challenge the effective management of European fisheries. *Ecography*, *43*(4), 494–505.

Baudron, A. R., Needle, C. L., Rijnsdorp, A. D., & Tara Marshall, C. (2014). Warming temperatures and smaller body sizes: Synchronous changes in growth of North Sea fishes. *Global Change Biology*, *20*(4), 1023–1031.

Belgrad, B. A., Correia, K. M., Darnell, K. M., Darnell, M. Z., Hayes, C. T., Hall, M. O., Furman, B. T., Martin, C. W., & Smee, D. L. (2021). Environmental drivers of seagrass-associated nekton abundance across the northern Gulf of Mexico. *Estuaries and Coasts*, 1–12.

Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society: Series B (Methodological)*, *57*(1), 289–300.

Berger, A. C., Berg, P., McGlathery, K. J., & Delgard, M. L. (2020). Long-term trends and resilience of seagrass metabolism: A decadal aquatic eddy covariance study. *Limnology and Oceanography*, *65*(7), 1423–1438.

Beukhof, E., Frelat, R., Pecuchet, L., Maureaud, A., Dencker, T. S., Sólmundsson, J., Punzón, A., Primicerio, R., Hidalgo, M., Möllmann, C., & others. (2019). Marine fish traits follow fast-slow continuum across oceans. *Scientific Reports*, *9*(1), 17878.

Boese, B. L., Robbins, B. D., & Thursby, G. (2005). Desiccation is a limiting factor for eelgrass *(Zostera marina L.)* distribution in the intertidal zone of a northeastern Pacific (USA) estuary.

Boettiger, C., & Hastings, A. (2013). From patterns to predictions. *Nature*, *493*(7431), 157–158.

Brooks, M. E., Kristensen, K., Van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Machler, M., & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, *9*(2), 378–400.

Brown, B. L., Downing, A. L., & Leibold, M. A. (2016). Compensatory dynamics stabilize aggregate community properties in response to multiple types of perturbations. *Ecology*, *97*(8), 2021–2033.

Buchheister, A., Bonzek, C. F., Gartland, J., & Latour, R. J. (2013). Patterns and drivers of the demersal fish community of Chesapeake Bay. *Marine Ecology Progress Series*, *481*, 161–180.

Campbell, B. C., & Able, K. W. (1998). Life history characteristics of the northern pipefish, *Syngnathus fuscus*, in southern New Jersey. *Estuaries*, *21*, 470–475.

Carr, J., D'odorico, P., McGlathery, K., & Wiberg, P. (2010). Stability and bistability of seagrass ecosystems in shallow coastal lagoons: Role of feedbacks with sediment resuspension and light attenuation. *Journal of Geophysical Research: Biogeosciences*, *115*(G3).

Castorani, M. C., Reed, D. C., & Miller, R. J. (2018). Loss of foundation species: Disturbance frequency outweighs severity in structuring kelp forest communities. *Ecology*, *99*(11), 2442–2454.

Cheng, S. L., Tedford, K. N., Smith, R. S., Hardison, S., Cornish, M. R., & Castorani, M. C. (2022). Coastal vegetation and bathymetry influence blue crab abundance across spatial scales. *Estuaries and Coasts*, *45*(6), 1701–1715.

Cline, T. J., Schindler, D. E., & Hilborn, R. (2017). Fisheries portfolio diversification and turnover buffer Alaskan fishing communities from abrupt resource and market changes. *Nature Communications*, *8*(1), 1–7.

Commander, C. J., Barnett, L. A., Ward, E. J., Anderson, S. C., & Essington, T. E. (2022). The shadow model: How and why small choices in spatially explicit species distribution models affect predictions. *PeerJ*, *10*, e12783.

Connolly, R. M. (1994). Comparison of fish catches from a buoyant pop net and a beach seine net in a shallow seagrass habitat. *Marine Ecology-Progress Series*, *109*, 305–309.

Cressie, N., & Huang, H.-C. (1999). Classes of nonseparable, spatio-temporal stationary covariance functions. *Journal of the American Statistical Association*, 1330–1340.

Cushing, D. (1990). Plankton production and year-class strength in fish populations: An update of the match/mismatch hypothesis. In *Advances in marine biology* (Vol. 26, pp. 249–293). Elsevier.

Del Río, M., Pretzsch, H., Ruíz-Peinado, R., Ampoorter, E., Annighöfer, P., Barbeito, I., Bielak, K., Brazaitis, G., Coll, L., Drössler, L., & others. (2017). Species interactions increase the temporal stability of community productivity in Pinus sylvestris–Fagus sylvatica mixtures across Europe. *Journal of Ecology*, *105*(4), 1032–1043.

Doak, D. F., Bigger, D., Harding, E., Marvier, M., O'malley, R., & Thomson, D. (1998). The statistical inevitability of stability-diversity relationships in community ecology. *The American Naturalist*, *151*(3), 264–276.

Duarte, C. M., Agusti, S., Barbier, E., Britten, G. L., Castilla, J. C., Gattuso, J.-P., Fulweiler, R. W., Hughes, T. P., Knowlton, N., Lovelock, C. E., & others. (2020). Rebuilding marine life. *Nature*, *580*(7801), 39–51.

Dulvy, N. K., Rogers, S. I., Jennings, S., Stelzenmüller, V., Dye, S. R., & Skjoldal, H. R. (2008). Climate change and deepening of the North Sea fish assemblage: A biotic indicator of warming seas. *Journal of Applied Ecology*, *45*(4), 1029–1039.

Dunic, J. C., Brown, C. J., Connolly, R. M., Turschwell, M. P., & Côté, I. M. (2021). Long-term declines and recovery of meadow area across the world's seagrass bioregions. *Global Change Biology*, *27*(17), 4096–4109.

Ellison, A. M., Bank, M. S., Clinton, B. D., Colburn, E. A., Elliott, K., Ford, C. R., Foster, D. R., Kloeppel, B. D., Knoepp, J. D., Lovett, G. M., & others. (2005). Loss of foundation species: Consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment*, *3*(9), 479–486.

England, J., & Wilkes, M. A. (2018). Does river restoration work? Taxonomic and functional trajectories at two restoration schemes. *Science of the Total Environment*, *618*, 961–970.

Fabrizio, M. C., Nepal, V., & Tuckey, T. D. (2021). Invasive blue catfish in the Chesapeake Bay region: A case study of competing management objectives. *North American Journal of Fisheries Management*, *41*, S156–S166.

Faletti, M. E., Chacin, D. H., Peake, J. A., MacDonald, T. C., & Stallings, C. D. (2019). Population dynamics of Pinfish in the eastern Gulf of Mexico (1998-2016). *PLoS One*, *14*(8), e0221131.

Fay, C. W., Neves, R. J., & Pardue, G. B. (1983). Species profiles: Life histories and environmental requirements of coastal fishes and invertebrates (mid-Atlantic): Atlantic silverside. *82*(11.1).

Fisher, J. A., Frank, K. T., & Leggett, W. C. (2010a). Breaking Bergmann's rule: Truncation of Northwest Atlantic marine fish body sizes. *Ecology*, *91*(9), 2499–2505.

Fisher, J. A., Frank, K. T., & Leggett, W. C. (2010b). Global variation in marine fish body size and its role in biodiversity–ecosystem functioning. *Marine Ecology Progress Series*, *405*, 1–13.

Fonseca, M. S., & Bell, S. S. (1998). Influence of physical setting on seagrass landscapes near Beaufort, North Carolina, USA. *Marine Ecology Progress Series*, *171*, 109–121.

Fonseca, M. S., Meyer, D. L., & Hall, M. O. (1996). Development of planted seagrass beds in Tampa Bay, Florida, USA. II. Faunal components. *Marine Ecology Progress Series*, *132*, 141–156.

Free, C. M., Thorson, J. T., Pinsky, M. L., Oken, K. L., Wiedenmann, J., & Jensen, O. P. (2019). Impacts of historical warming on marine fisheries production. *Science*, *363*(6430), 979–983.

Friedland, K. D., Ganley, L. C., Dimarchopoulou, D., Gaichas, S., Morse, R. E., & Jordaan, A. (2023). Change in body size in a rapidly warming marine ecosystem: Consequences of tropicalization. *Science of The Total Environment*, 166117.

Friedland, K. D., Langan, J. A., Large, S. I., Selden, R. L., Link, J. S., Watson, R. A., & Collie, J. S. (2020). Changes in higher trophic level productivity, diversity and niche space in a rapidly warming continental shelf ecosystem. *Science of the Total Environment*, *704*, 135270.

Friedland, K. D., Morse, R. E., Manning, J. P., Melrose, D. C., Miles, T., Goode, A. G., Brady, D. C., Kohut, J. T., & Powell, E. N. (2020). Trends and change points in surface and bottom thermal environments of the US Northeast Continental Shelf Ecosystem. *Fisheries Oceanography*, *29*(5), 396–414.

Friedland, K. D., Smoliński, S., & Tanaka, K. R. (2021). Contrasting patterns in the occurrence and biomass centers of gravity among fish and macroinvertebrates in a continental shelf ecosystem. *Ecology and Evolution*, *11*(5), 2050–2063.

Friedland, K. D., Tanaka, K. R., Smoliński, S., Wang, Y., Hodgdon, C., Mazur, M., Wiedenmann, J., Goetsch, C., & Pendleton, D. E. (2023). Trends in Area of Occurrence and Biomass of Fish and Macroinvertebrates on the Northeast US Shelf Ecosystem. *Marine and Coastal Fisheries*, *15*(2), e10235.

Froese, R., Pauly, D., & others. (2010). *FishBase*. Fisheries Centre, University of British Columbia Vancouver, BC, Canada.

Frölicher, T. L., Winton, M., & Sarmiento, J. L. (2014). Continued global warming after $CO_2$ emissions stoppage. *Nature Climate Change*, *4*(1), 40–44.

Fujiwara, M., Simpson, A., Torres-Ceron, M., & Martinez-Andrade, F. (2022). Life-history traits and temporal patterns in the incidence of coastal fishes experiencing tropicalization. *Ecosphere*, *13*(8), e4188.

Garrido, S., Cristóvão, A., Caldeira, C., Ben-Hamadou, R., Baylina, N., Batista, H., Saiz, E., Peck, M., Re, P., & Santos, A. (2016). Effect of temperature on the growth, survival, development and foraging behaviour of *Sardina pilchardus* larvae. *Marine Ecology Progress Series*, *559*, 131–145.

Giacomazzo, M., Bertolo, A., Brodeur, P., Massicotte, P., Goyette, J.-O., & Magnan, P. (2020). Linking fisheries to land use: How anthropogenic inputs from the watershed shape fish habitat quality. *Science of The Total Environment*, *717*, 135377.

Gilby, B. L., Olds, A. D., Connolly, R. M., Maxwell, P. S., Henderson, C. J., & Schlacher, T. A. (2018). Seagrass meadows shape fish assemblages across estuarine seascapes. *Marine Ecology Progress Series*, *588*, 179–189.

Gillanders, B. (2006). Seagrasses, fish, and fisheries. *Seagrasses: Biology, Ecology and Conservation*, 503–536.

Senate Joint Resolution 4, (2021). https://mgaleg.maryland.gov/2021RS/Chapters_noln/JR_1_sj0004t.pdf.

Grace, J. B. (2008). Structural equation modeling for observational studies. *The Journal of Wildlife Management*, *72*(1), 14–22.

Grace, J. B., Johnson, D. J., Lefcheck, J. S., & Byrnes, J. E. (2018). Quantifying relative importance: Computing standardized effects in models with binary outcomes. *Ecosphere*, *9*(6), e02283.

Grammer, G. L., Brown-Peterson, N. J., Peterson, M. S., & Comyns, B. H. (2009). Life history of silver perch *Bairdiella chrysoura* (Lacepède, 1803) in north-central Gulf of Mexico estuaries. *Gulf of Mexico Science*, *27*(1), 7.

Grol, M. G., Nagelkerken, I., Rypel, A. L., & Layman, C. A. (2011). Simple ecological trade-offs give rise to emergent cross-ecosystem distributions of a coral reef fish. *Oecologia*, *165*, 79–88.

Guan, Y., Kang, R., & Liu, J. (2019). Evolution of the field of ecological restoration over the last three decades: A bibliometric analysis. *Restoration Ecology*, *27*(3), 647–660.

Harding, L. W., Mallonee, M. E., Perry, E. S., Miller, W. D., Adolf, J. E., Gallegos, C. L., & Paerl, H. W. (2019). Long-term trends, current status, and transitions of water quality in Chesapeake Bay. *Scientific Reports*, *9*(1), 1–19.

Hartig, F. (2020). DHARMa: Residual diagnostics for hierarchical (multi-level/mixed) regression models. *R Package Version 0.3*, *3*.

Heck, K., Able, K., Fahay, M., & Roman, C. (1989). Fishes and decapod crustaceans of Cape Cod eelgrass meadows: Species composition, seasonal abundance patterns and comparison with unvegetated substrates. *Estuaries*, *12*, 59–65.

Heck, K., Hays, G., & Orth, R. J. (2003). Critical evaluation of the nursery role hypothesis for seagrass meadows. *Marine Ecology Progress Series*, *253*, 123–136.

Hilborn, R., Maguire, J.-J., Parma, A. M., & Rosenberg, A. A. (2001). The precautionary approach and risk management: Can they increase the probability of successes in fishery management? *Canadian Journal of Fisheries and Aquatic Sciences*, *58*(1), 99–107.

Hilborn, R., Quinn, T. P., Schindler, D. E., & Rogers, D. E. (2003). Biocomplexity and fisheries sustainability. *Proceedings of the National Academy of Sciences*, *100*(11), 6564–6568.

Hill, M. O. (1973). Diversity and evenness: A unifying notation and its consequences. *Ecology*, *54*(2), 427–432.

Hindell, J. S., Jenkins, G. P., & Keough, M. J. (2002). Variability in the numbers of post-settlement King George whiting (Sillaginidae: *Sillaginodes punctata*, Cuvier) in relation to predation, habitat complexity and artificial cage structure. *Journal of Experimental Marine Biology and Ecology*, *268*(1), 13–31.

Ikpewe, I. E., Baudron, A. R., Ponchon, A., & Fernandes, P. G. (2021). Bigger juveniles and smaller adults: Changes in fish size correlate with warming seas. *Journal of Applied Ecology*, *58*(4), 847–856.

Jackson, E. L., Rowden, A. A., Attrill, M. J., Bossey, S. J., & Jones, M. B. (2001). The importance of seagrass beds as a habitat for fishery species. *Oceanography and Marine Biology*, *39*, 269–304.

Jenkins, G. P., & Wheatley, M. J. (1998). The influence of habitat structure on nearshore fish assemblages in a southern Australian embayment: Comparison of shallow seagrass, reef-algal and unvegetated sand habitats, with emphasis on their importance to recruitment. *Journal of Experimental Marine Biology and Ecology*, *221*(2), 147–172.

Jenkins, G., & Sutherland, C. (1997). The influence of habitat structure on nearshore fish assemblages in a southern Australian embayment: Colonisation and turnover rate of fishes associated with artificial macrophyte beds of varying physical structure. *Journal of Experimental Marine Biology and Ecology*, *218*(1), 103–125.

Kasperski, S., & Holland, D. S. (2013). Income diversification and risk for fishermen. *Proceedings of the National Academy of Sciences*, *110*(6), 2076–2081.

Kleisner, K. M., Fogarty, M. J., McGee, S., Barnett, A., Fratantoni, P., Greene, J., Hare, J. A., Lucey, S. M., McGuire, C., Odell, J., & others. (2016). The effects of sub-regional climate velocity on the distribution and spatial extent of marine species assemblages. *PloS One*, *11*(2), e0149220.

Kleisner, K. M., Fogarty, M. J., McGee, S., Hare, J. A., Moret, S., Perretti, C. T., & Saba, V. S. (2017). Marine species distribution shifts on the US Northeast Continental Shelf under continued ocean warming. *Progress in Oceanography*, *153*, 24–36.

Koch, E. W. (2001). Beyond light: Physical, geological, and geochemical parameters as possible submersed aquatic vegetation habitat requirements. *Estuaries*, *24*, 1–17.

Kremer, M., & Reidenbach, M. (2021). Modeled wind fetch for the bays of the Virginia Coast Reserve. *Virginia Coast Reserve Long-Term Ecological Research Project Data Publication Knb-Filter-Vcr*, *300*.

Kristensen, K., Nielsen, A., Berg, C. W., Skaug, H., & Bell, B. (2015). TMB: automatic differentiation and Laplace approximation. *arXiv Preprint arXiv:1509.00660*.

Lamb, D. (2018). Undertaking large-scale forest restoration to generate ecosystem services. *Restoration Ecology*, *26*(4), 657–666.

Lamy, T., Wang, S., Renard, D., Lafferty, K. D., Reed, D. C., & Miller, R. J. (2019). Species insurance trumps spatial insurance in stabilizing biomass of a marine macroalgal metacommunity. *Ecology*, *100*(7), e02719.

Latour, R. J., Brush, M. J., & Bonzek, C. F. (2003). Toward ecosystem-based fisheries management: Strategies for multispecies modeling and associated data requirements. *Fisheries*, *28*(9), 10–22.

Lefcheck, J. S. (2016). piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, *7*(5), 573–579.

Lefcheck, J. S., Buchheister, A., Laumann, K. M., Stratton, M. A., Sobocinski, K. L., Chak, S. T., Clardy, T. R., Reynolds, P. L., Latour, R. J., & Duffy, J. E. (2014). Dimensions of biodiversity in Chesapeake Bay demersal fishes: Patterns and drivers through space and time. *Ecosphere*, *5*(2), 1–48.

Lefcheck, J. S., Hughes, B. B., Johnson, A. J., Pfirrmann, B. W., Rasher, D. B., Smyth, A. R., Williams, B. L., Beck, M. W., & Orth, R. J. (2019b). Are coastal habitats important nurseries? A meta-analysis. *Conservation Letters*, *12*(4), e12645.

Lefcheck, J. S., Marion, S. R., & Orth, R. J. (2017). Restored eelgrass (*Zostera marina L.*) as a refuge for epifaunal biodiversity in mid-western Atlantic coastal bays. *Estuaries and Coasts*, *40*, 200–212.

Leps, M., Sundermann, A., Tonkin, J. D., Lorenz, A. W., & Haase, P. (2016). Time is no healer: Increasing restoration age does not lead to improved benthic invertebrate communities in restored river reaches. *Science of the Total Environment*, *557*, 722–732.

Levin, S., Xepapadeas, T., Crépin, A.-S., Norberg, J., De Zeeuw, A., Folke, C., Hughes, T., Arrow, K., Barrett, S., Daily, G., & others. (2013). Social-ecological systems as complex adaptive systems: Modeling and policy implications. *Environment and Development Economics*, *18*(2), 111–132.

Lindgren, F., & Rue, H. (2015). Bayesian spatial modelling with R-INLA. *Journal of Statistical Software*, *63*(19).

Lindgren, F., Rue, H., & Lindström, J. (2011). An explicit link between Gaussian fields and Gaussian Markov random fields: The stochastic partial differential equation approach. *Journal of the Royal Statistical Society Series B: Statistical Methodology*, *73*(4), 423–498.

Link, J. S. (2018). System-level optimal yield: Increased value, less risk, improved stability, and better fisheries. *Canadian Journal of Fisheries and Aquatic Sciences*, *75*(1), 1–16.

Litvin, S. Y., Weinstein, M. P., Sheaves, M., & Nagelkerken, I. (2018). What makes nearshore habitats nurseries for nekton? An emerging view of the nursery role hypothesis. *Estuaries and Coasts*, *41*, 1539–1550.

Blue Catfish Processing, Flash Freezing, and Infrastructure Grant Program, HB 1664, 2023 (2023). https://law.lis.virginia.gov/vacodeupdates/title3.2/section3.2-312/.

Marsh Jr, J. A., Dennison, W. C., & Alberte, R. S. (1986). Effects of temperature on photosynthesis and respiration in eelgrass (*Zostera marina* L.). *Journal of Experimental Marine Biology and Ecology*, *101*(3), 257–267.

Martino, E. J., & Able, K. W. (2003). Fish assemblages across the marine to low salinity transition zone of a temperate estuary. *Estuarine, Coastal and Shelf Science*, *56*(5–6), 969–987.

McCloskey, R. M., & Unsworth, R. K. (2015). Decreasing seagrass density negatively influences associated fauna. *PeerJ*, *3*, e1053.

McGlathery, K. (2019). Fish Counts and Lengths in South Bay and Hog Island Bay, Virginia 2012-2018. https://doi.org/10.6073/pasta/cae6c1c3f90b1f7d65ec0c1ae9b94398

McGlathery, K. J., Anderson, I. C., & Tyler, A. C. (2001). Magnitude and variability of benthic and pelagic metabolism in a temperate coastal lagoon. *Marine Ecology Progress Series*, *216*, 1–15.

McGlathery, K. J., Reynolds, L. K., Cole, L. W., Orth, R. J., Marion, S. R., & Schwarzschild, A. (2012). Recovery trajectories during state change from bare sediment to eelgrass dominance. *Marine Ecology Progress Series*, *448*, 209–221.

McLean, M. J., Mouillot, D., Goascoz, N., Schlaich, I., & Auber, A. (2019). Functional reorganization of marine fish nurseries under climate warming. *Global Change Biology*, *25*(2), 660–674.

McLean, M., Mouillot, D., Lindegren, M., Villéger, S., Engelhard, G., Murgier, J., & Auber, A. (2019). Fish communities diverge in species but converge in traits over three decades of warming. *Global Change Biology*, *25*(11), 3972–3984.

McSkimming, C., Connell, S. D., Russell, B. D., & Tanner, J. E. (2016). Habitat restoration: Early signs and extent of faunal recovery relative to seagrass recovery. *Estuarine, Coastal and Shelf Science*, *171*, 51–57.

Mikkelson, G. M., McGill, B. J., Beaulieu, S., & Beukema, P. L. (2011). Multiple links between species diversity and temporal stability in bird communities across North America. *Evolutionary Ecology Research*, *13*(4), 361–372.

Moore, J. W., Connors, B. M., & Hodgson, E. E. (2021). Conservation risks and portfolio effects in mixed-stock fisheries. *Fish and Fisheries*, *22*(5), 1024–1040.

Moore, K. A., Orth, R. J., & Wilcox, D. J. (2009). Assessment of the abundance of submersed aquatic vegetation (SAV) communities in the Chesapeake Bay and its use in SAV management. In *Remote Sensing and Geospatial Technologies for Coastal Ecosystem Assessment and Management* (pp. 233–257). Springer.

Murdy, E. O., & Musick, J. A. (2013). *Field guide to fishes of the Chesapeake Bay*. JHU Press.

Nagelkerken, I., Sheaves, M., Baker, R., & Connolly, R. M. (2015). The seascape nursery: A novel spatial approach to identify and manage nurseries for coastal marine fauna. *Fish and Fisheries*, *16*(2), 362–371.

Nakamura, Y., & Sano, M. (2005). Comparison of invertebrate abundance in a seagrass bed and adjacent coral and sand areas at Amitori Bay, Iriomote Island, Japan. *Fisheries Science*, *71*, 543–550.

Nesbitt, H. K., & Moore, J. W. (2016). Species and population diversity in Pacific salmon fisheries underpin indigenous food security. *Journal of Applied Ecology*, *53*(5), 1489–1499.

Nixon, S. W., Fulweiler, R. W., Buckley, B. A., Granger, S. L., Nowicki, B. L., & Henry, K. M. (2009). The impact of changing climate on phenology, productivity, and benthic–pelagic coupling in Narragansett Bay. *Estuarine, Coastal and Shelf Science*, *82*(1), 1–18.

Norcross, B. L., & Austin, H. M. (1988). Middle Atlantic Bight meridional wind component effect on bottom water temperatures and spawning distribution of Atlantic croaker. *Continental Shelf Research*, *8*(1), 69–88.

Ohs, C. L., DiMaggio, M. A., & Grabe, S. W. (2011). Species Profile: Pinfish, *Lagodon rhomboides*. Southern Regional Aquaculture Center.

Oke, T. A., Zhang, S. Y., Keyser, S. R., & Yeager, L. A. (2022). Sea-surface temperature anomalies mediate changes in fish richness and abundance in Atlantic and Gulf of Mexico estuaries. *Journal of Biogeography*, *49*(9), 1609–1617.

Oken, K. L., Holland, D. S., & Punt, A. E. (2021). The effects of population synchrony, life history, and access constraints on benefits from fishing portfolios. *Ecological Applications*, *31*(4), e2307.

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Stevens, M. H. H., Oksanen, M. J., & Suggests, M. (2007). The vegan package. *Community Ecology Package*, *10*(631–637), 719.

Oreska, M. P., McGlathery, K. J., Aoki, L. R., Berger, A. C., Berg, P., & Mullins, L. (2020). The greenhouse gas offset potential from seagrass restoration. *Scientific Reports*, *10*(1), 7325.

Oreska, M. P., McGlathery, K. J., Wiberg, P. L., Orth, R. J., & Wilcox, D. J. (2021). Defining the *Zostera marina* (eelgrass) niche from long-term success of restored and naturally colonized meadows: Implications for seagrass restoration. *Estuaries and Coasts*, *44*, 396–411.

Orth, R. J., & Heck, K. L. (1980). Structural components of eelgrass (*Zostera marina*) meadows in the lower Chesapeake Bay—Fishes. *Estuaries*, *3*, 278–288.

Orth, R. J., Lefcheck, J. S., McGlathery, K. S., Aoki, L., Luckenbach, M. W., Moore, K. A., Oreska, M. P., Snyder, R., Wilcox, D. J., & Lusk, B. (2020). Restoration of seagrass habitat leads to rapid recovery of coastal ecosystem services. *Science Advances*, *6*(41), eabc6434.

Orth, R. J., & McGlathery, K. J. (2012). Eelgrass recovery in the coastal bays of the Virginia Coast Reserve, USA. *Marine Ecology Progress Series*, *448*, 173–176.

Orth, R. J., Moore, K. A., Marion, S. R., Wilcox, D. J., & Parrish, D. B. (2012b). Seed addition facilitates eelgrass recovery in a coastal bay system. *Marine Ecology Progress Series*, *448*, 177–195.

Pappalardo, P., Pringle, J. M., Wares, J. P., & Byers, J. E. (2015). The location, strength, and mechanisms behind marine biogeographic boundaries of the east coast of North America. *Ecography*, *38*(7), 722–731.

Parsley, M. J., Palmer, D. E., & Burkhardt, R. W. (1989). Variation in capture efficiency of a beach seine for small fishes. *North American Journal of Fisheries Management*, *9*(2), 239–244.

Pauly, D. (1980). On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *ICES Journal of Marine Science*, *39*(2), 175–192.

Pedersen, E. J., Miller, D. L., Simpson, G. L., & Ross, N. (2019). Hierarchical generalized additive models in ecology: An introduction with mgcv. *PeerJ*, *7*, e6876.

Perry, A. L., Low, P. J., Ellis, J. R., & Reynolds, J. D. (2005). Climate change and distribution shifts in marine fishes. *Science*, *308*(5730), 1912–1915.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Heisterkamp, S., Van Willigen, B., & Maintainer, R. (2017). Package 'nlme.' *Linear and Nonlinear Mixed Effects Models, Version*, *3*(1), 274.

Pinsky, M. L., Selden, R. L., & Kitchel, Z. J. (2020). Climate-driven shifts in marine species ranges: Scaling from organisms to communities. *Annual Review of Marine Science*, *12*, 153–179.

Pinsky, M. L., Worm, B., Fogarty, M. J., Sarmiento, J. L., & Levin, S. A. (2013). Marine taxa track local climate velocities. *Science*, *341*(6151), 1239–1242.

Raposa, K. B., & Talley, D. M. (2012). A meta-analysis of nekton responses to restoration of tide-restricted New England salt marshes. *Tidal Marsh Restoration: A Synthesis of Science and Management*, 97–118.

Reynolds, R. W., Smith, T. M., Liu, C., Chelton, D. B., Casey, K. S., & Schlax, M. G. (2007). Daily high-resolution-blended analyses for sea surface temperature. *Journal of Climate*, *20*(22), 5473–5496.

Rheuban, J. E., Williamson, S., Costa, J. E., Glover, D. M., Jakuba, R. W., McCorkle, D. C., Neill, C., Williams, T., & Doney, S. C. (2016). Spatial and temporal trends in summertime climate and water quality indicators in the coastal embayments of Buzzards Bay, Massachusetts. *Biogeosciences*, *13*(1), 253–265.

Rice, E., Dam, H. G., & Stewart, G. (2015). Impact of climate change on estuarine zooplankton: Surface water warming in Long Island Sound is associated with changes in copepod size and community structure. *Estuaries and Coasts*, *38*, 13–23.

Richardson, D., Porter, J., Oertel, G., Zimmerman, R., Carlson, C., & Overman, K. (n.d.). *Integrated topography and bathymetry for the eastern shore of Virginia* [dataset]. https://doi.org/doi:10.6073/pasta/63a22558d6650fae8232b6a8814a90d5

Ripley, J. L., & Foran, C. M. (2006). Population structure, growth rates, and seasonal abundance of two Syngnathus pipefish species. *Estuaries and Coasts*, *29*, 1161–1171.

Rohweder, J. J., Rogala, J. T., Johnson, B. L., Anderson, D., Clark, S., Chamberlin, F., & Runyon, K. (2008). *Application of wind fetch and wave models for habitat rehabilitation and enhancement projects*. Geological Survey (US).

Rooker, J. R., Holt, S. A., Soto, M. A., & Joan Holt, G. (1998). Postsettlement patterns of habitat use by sciaenid fishes in subtropical seagrass meadows. *Estuaries*, *21*, 318–327.

Roswell, M., Dushoff, J., & Winfree, R. (2021). A conceptual guide to measuring species diversity. *Oikos*, *130*(3), 321–338.

Safak, I., Wiberg, P., Richardson, D., & Kurum, M. (2015). Controls on residence time and exchange in a system of shallow coastal bays. *Continental Shelf Research*, *97*, 7–20.

Sanchirico, J. N., Smith, M. D., & Lipton, D. W. (2008). An empirical approach to ecosystem-based fishery management. *Ecological Economics*, *64*(3), 586–596.

Scheld, A. M., Bilkovic, D. M., & Havens, K. J. (2021). Evaluating optimal removal of derelict blue crab pots in Virginia, US. *Ocean & Coastal Management*, *211*, 105735.

Schindler, D. E., Armstrong, J. B., & Reed, T. E. (2015). The portfolio concept in ecology and evolution. *Frontiers in Ecology and the Environment*, *13*(5), 257–263.

Schindler, D. E., Hilborn, R., Chasco, B., Boatright, C. P., Quinn, T. P., Rogers, L. A., & Webster, M. S. (2010). Population diversity and the portfolio effect in an exploited species. *Nature*, *465*(7298), 609–612.

Schluter, D. (1984). A variance test for detecting species associations, with some example applications. *Ecology*, *65*(3), 998–1005.

Schonfeld, A. J., Gartland, J., & Latour, R. J. (2022a). Spatial differences in estuarine utilization by seasonally resident species in Mid-Atlantic Bight, USA. *Fisheries Oceanography*, *31*(6), 615–628.

Sethi, S. A., Reimer, M., & Knapp, G. (2014). Alaskan fishing community revenues and the stabilizing role of fishing portfolios. *Marine Policy*, *48*, 134–141.

Shanks, A. L. (2020). Mechanisms of cross-shelf dispersal of larval invertebrates and fish. In *Ecology of Marine Invertebrate Larvae* (pp. 323–367). CRC Press.

Sheridan, P. (2004). Comparison of restored and natural seagrass beds near Corpus Christi, Texas. *Estuaries*, *27*(5), 781–792.

Sheridan, P., Henderson, C., & McMahan, G. (2003). Fauna of natural seagrass and transplanted *Halodule wrightii* (shoalgrass) beds in Galveston Bay, Texas. *Restoration Ecology*, *11*(2), 139–154.

Shilland, R., Grimsditch, G., Ahmed, M., Bandeira, S., Kennedy, H., Potouroglou, M., & Huxham, M. (2021). A question of standards: Adapting carbon and other PES markets to work for community seagrass conservation. *Marine Policy*, *129*, 104574.

Shipley, B. (2000). A new inferential test for path models based on directed acyclic graphs. *Structural Equation Modeling*, *7*(2), 206–218.

Simpson, S. D., Jennings, S., Johnson, M. P., Blanchard, J. L., Schön, P.-J., Sims, D. W., & Genner, M. J. (2011). Continental shelf-wide response of a fish assemblage to rapid warming of the sea. *Current Biology*, *21*(18), 1565–1570.

Siple, M. C., Essington, T. E., Barnett, L. A., & Scheuerell, M. D. (2020). Limited evidence for sardine and anchovy asynchrony: Re-examining an old story. *Proceedings of the Royal Society B*, *287*(1922), 20192781.

Smith, R. S., & Castorani, M. C. (2023). Meta-analysis reveals drivers of restoration success for oysters and reef community. *Ecological Applications*, e2865.

Smith, T. M., Hindell, J. S., Jenkins, G. P., Connolly, R. M., & Keough, M. J. (2011). Edge effects in patchy seagrass landscapes: The role of predation in determining fish distribution. *Journal of Experimental Marine Biology and Ecology*, *399*(1), 8–16.

Sobocinski, K. L., Orth, R. J., Fabrizio, M. C., & Latour, R. J. (2013). Historical comparison of fish community structure in lower Chesapeake Bay seagrass habitats. *Estuaries and Coasts*, *36*, 775–794.

Spillman, C. M., Smith, G. A., Hobday, A. J., & Hartog, J. R. (2021). Onset and decline rates of marine heatwaves: Global trends, seasonal forecasts and marine management. *Frontiers in Climate*, *3*.

Stevenson, R. A. (1958). The biology of the anchovies, *Anchoa mitchilli mitchilli* Cuvier and Valenciennes 1848 and *Anchoa hepsetus hepsetus* Linnaeus 1758 in Delaware Bay [PhD Thesis]. University of Delaware.

Thaxton, W. C., Taylor, J. C., & Asch, R. G. (2020). Climate-associated trends and variability in ichthyoplankton phenology from the longest continuous larval fish time series on the east coast of the United States. *Marine Ecology Progress Series*, *650*, 269–287.

Thibaut, L. M., & Connolly, S. R. (2013). Understanding diversity–stability relationships: Towards a unified model of portfolio effects. *Ecology Letters*, *16*(2), 140–150.

Thomas, A. C., Pershing, A. J., Friedland, K. D., Nye, J. A., Mills, K. E., Alexander, M. A., Record, N. R., Weatherbee, R., & Henderson, M. E. (2017). Seasonal trends and phenology shifts in sea surface temperature on the North American northeastern continental shelf. *Elem Sci Anth*, *5*, 48.

Thorson, J. T., Munch, S. B., Cope, J. M., & Gao, J. (2017). Predicting life history parameters for all fishes worldwide. *Ecological Applications*, *27*(8), 2262–2276.

Thorson, J. T., Scheuerell, M. D., Olden, J. D., & Schindler, D. E. (2018). Spatial heterogeneity contributes more to portfolio effects than species variability in bottom-associated marine fishes. *Proceedings of the Royal Society B*, *285*(1888), 20180915.

Tilman, D. (1996). Biodiversity: Population versus ecosystem stability. *Ecology*, *77*(2), 350–363.

Tilman, D., Lehman, C. L., & Bristow, C. E. (1998). Diversity-stability relationships: Statistical inevitability or ecological consequence? *The American Naturalist*, *151*(3), 277–282.

Tweedie, M. C. (1984). An index which distinguishes between some important exponential families. *Statistics: Applications and New Directions: Proc. Indian Statistical Institute Golden Jubilee International Conference*, *579*, 579–604.

Uhrin, A. V., & Turner, M. G. (2018). Physical drivers of seagrass spatial configuration: The role of thresholds. *Landscape Ecology*, *33*, 2253–2272.

Ummenhofer, C. C., & Meehl, G. A. (2017). Extreme weather and climate events with ecological relevance: A review. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *372*(1723), 20160135.

Unsworth, R. K., Nordlund, L. M., & Cullen-Unsworth, L. C. (2019). Seagrass meadows support global fisheries production. *Conservation Letters*, *12*(1), e12566.

von Biela, V. R., Arimitsu, M. L., Piatt, J. F., Heflin, B., Schoen, S. K., Trowbridge, J. L., & Clawson, C. M. (2019). Extreme reduction in nutritional value of a key forage fish during the Pacific marine heatwave of 2014-2016. *Marine Ecology Progress Series*, *613*, 171–182.

Walsh, H. J., Richardson, D. E., Marancik, K. E., & Hare, J. A. (2015). Long-term changes in the distributions of larval and adult fish in the northeast US shelf ecosystem. *PLoS One*, *10*(9), e0137382.

Wang, S., Lamy, T., Hallett, L. M., & Loreau, M. (2019). Stability and synchrony across ecological hierarchies in heterogeneous metacommunities: Linking theory to data. *Ecography*, *42*(6), 1200–1211.

Wang, S., & Loreau, M. (2016). Biodiversity and ecosystem stability across scales in metacommunities. *Ecology Letters*, *19*(5), 510–518.

White, S. B., & Scheld, A. M. (2021). Characterizing Changes in Participation and Diversification in Small-Scale Fisheries of Virginia, USA. *Coastal Management*, *50*(1), 3–28.

Wiberg, P. L., Carr, J. A., Safak, I., & Anutaliya, A. (2015). Quantifying the distribution and influence of non-uniform bed properties in shallow coastal bays. *Limnology and Oceanography: Methods*, *13*(12), 746–762.

Wigley, S. E., McBride, H. M., & McHugh, N. J. (2003). Length-weight relationships for 74 fish species collected during NEFSC research vessel bottom trawl surveys, 1992-99.

Wood, R. J. (2000). *Synoptic scale climatic forcing of multispecies fish recruitment patterns in Chesapeake Bay*. The College of William and Mary.

Wood, S. N. (2006). *Generalized additive models: An introduction with R*. Chapman and Hall/CRC.

Woodland, R. J., Buchheister, A., Latour, R. J., Lozano, C., Houde, E., Sweetman, C. J., Fabrizio, M. C., & Tuckey, T. D. (2021). Environmental drivers of forage fishes and benthic invertebrates at multiple spatial scales in a large temperate estuary. *Estuaries and Coasts*, *44*, 921–938.

Yeager, L. A., Keller, D. A., Burns, T. R., Pool, A. S., & Fodrie, F. J. (2016). Threshold effects of habitat fragmentation on fish diversity at landscapes scales. *Ecology*, *97*(8), 2157–2166.

Yeager, L. A., Layman, C. A., & Allgeier, J. E. (2011). Effects of habitat heterogeneity at multiple spatial scales on fish community assembly. *Oecologia*, *167*, 157–168.

Zastrow, C., Houde, E., & Morin, L. (1991). Spawning, fecundity, hatch-date frequency and young-of-the-year growth of bay anchovy *Anchoa mitchilli* in mid-Chesapeake Bay. *Marine Ecology Progress Series*, 161–171.

Zhao, L., Wang, S., Shen, R., Gong, Y., Wang, C., Hong, P., & Reuman, D. C. (2022). Biodiversity stabilizes plant communities through statistical-averaging effects rather than compensatory dynamics. *Nature Communications*, *13*(1), 7804.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., Smith, G. M., & others. (2009). *Mixed effects models and extensions in ecology with R* (Vol. 574). Springer.