Linking Fish Community Dynamics and Trophic Interactions with Ecological Processes on the Northeast US Continental Shelf

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This dissertation is dedicated to my wife, Kristin, and my daughters, Caroline and Molly. You three have always stood by me in my ‘whatever it takes’ approach to building my career, both on the water and behind a computer, and for that I am forever grateful. Love you guys.

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ABSTRACT

Extensive and largely unregulated fisheries operating on the Northeast US continental shelf during the 20th century resulted in widespread overfishing. Single-species stock assessments and management have been used to end overfishing and rebuild these resources, yet as stocks recover the influences of biophysical forcing and trophic interactions play a greater role in shaping their dynamics. Infrastructure for including these ecosystem processes into assessment and management activities began emerging during the 1990s and has led to a gradual transition toward Ecosystem Approaches to Fisheries Management (EAFM) in the Northeast. By creating spaces to improve communication, enhancing data collection, synthesizing ecosystem indicators, developing system-level caps on harvest, and monitoring outcomes, management agencies should be well-positioned to accelerate this evolution to EAFM.

Operationalizing EAFM requires quantifying community ecology with a focus on developing ecosystem indicators. Northeast shelf coastal ecosystems have received little attention, so 12 years (2008 – 2019) of fisheries-independent bottom trawl survey data were used to characterize and synthesize the spatiotemporal patterns of species assemblages inhabiting the nearshore Mid-Atlantic Bight (MAB). All 178 species collected by the survey were allocated among nine ecomorphotype (EMT) groups: demersal fishes; pelagic fishes; flatfishes; skates; rays; dogfishes; other sharks; cephalopods; and benthic arthropods. Univariate hurdle models were used to quantify annual time-series and seasonal, spatial distributions of EMT relative biomass, and a multivariate state-space model revealed that the nine time-series were effectively summarized by three common trends. Model fits to the EMT time-series represented a new suite of indicators for this ecosystem. MAB winter sea surface temperature was a significant predictor of relative biomass trends for several EMTs, suggesting that winter environmental conditions structure this system on an annual scale. Multivariate ordination uncovered a north-to-south gradient in EMT seasonal, spatial distributions and a distinct area of elevated biomass for several assemblages along Long Island, NY.

Exploited forage species support directed fisheries and predator productivity, so both harvest and trophic removals should be considered when developing EAFM. Shelf-wide predator catch and stomach content data collected by two fisheries-independent bottom trawl surveys over 42 years (1978 – 2019) were combined within multivariate spatiotemporal models to estimate consumptive removals during spring and fall each year for four commercially-exploited prey; Atlantic herring (*Clupea harengus*), silver hake (*Merluccius bilinearis*), butterfish (*Peprilus triacanthus*), and longfin squid (*Doryteuthis pealeii*). Seasonal consumption trends were mostly synchronous for Atlantic herring and silver hake and were asynchronous for butterfish and longfin squid. Consumption increased since the 1990s for most prey, which coincided with the widespread implementation of harvest constraints meant to rebuild fisheries resources. State-space regression models linking these time-series with hypothesized drivers revealed that prey availability (bottom-up; positive relationships) and commercial catch (top-down; primarily negative relationships) were the strongest predictors of consumption.

Overall, this body of research yielded novel insights on the community and predator-prey dynamics of the Northeast shelf ecosystem by illuminating key linkages with biophysical, trophic, and harvest processes that govern fisheries resource productivity. Such information could be used by managers to further advance EAFM strategies meant to improve resource sustainability and stakeholder outcomes.

AUTHOR'S NOTE

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

The citations are as follows:

Chapter 2
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Chapter 4
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Linking Fish Community Dynamics and Trophic Interactions with Ecological Processes on the Northeast US Continental Shelf

CHAPTER 1

Introduction

Marine fisheries have existed for millennia, providing societies with a valuable array of market goods and nonmarket services such as food resources, recreational opportunities, and cultural cohesion (Holland et al. 2010, Li & Fang 2014, Tam et al. 2017). Technological advances during the 20th century expanded the spatial footprint of fishery harvest activities and improved operational efficiencies which, along with a lack of adequate governance structures, has threatened the sustainability of marine fisheries on a global scale (Link & Watson 2019). In particular, contemporary harvest practices have overfished stocks of numerous predator and prey species worldwide, which has diminished profits, threatened food security, and altered the structure and function of many exploited ecosystems (Jennings & Kaiser 1998, Pauly et al. 2005, Sumalia et al. 2012).

The Northeast US continental shelf is among the most productive and diverse marine ecosystems on the planet, given its relatively unique hydrology and geology (Link et al. 2008). This system extends from Cape Hatteras, North Carolina in the south to the US/Canadian border in the north and is comprised of three Ecological Production Units (EPUs): namely (from south to north), the Mid-Atlantic Bight, Georges Bank, and Gulf of Maine (Lucey & Fogarty 2013). Fisheries resources in this ecosystem were subject to widespread, intense exploitation beginning with international fleets in the mid-1960s and followed by expanding domestic operations in the early 1980s (Fogarty & Murawski 1998). The biomass of living marine resources on the shelf was reduced by more than 50% during this period, and a multitude of stocks was overfished in each of the EPUs (e.g., Richards & Rago 1999, Hart & Rago 2006, Hayden et al. 2015, Latour & Gartland 2020).

Efforts to end overfishing and rebuild overfished stocks on the Northeast shelf began in earnest with the passage (and reauthorization) of US federal legislation calling for a nationwide

science-based approach to fisheries management (Methot et al. 2014). In response to this mandate, single-species frameworks for assessing stocks and implementing management strategies, where the evaluation and mitigation of harvest impacts are the paramount considerations, have served as the basis for rebuilding populations and achieving sustainable fisheries (Dolan et al. 2016). This single-species approach has been quite successful at ending overfishing and recovering overfished stocks (e.g., Peterson et al. 2017, Gaichas et al. 2018, NMFS 2023). There are concerns, however, that these reductionist approaches to stock assessment and management yield inefficiencies with respect to foregone long-term harvest and economic yield, since single-species frameworks typically fail to consider environmental influences on stock dynamics, interactions among species in the system, or the broader societal impacts of candidate management strategies (Larkin 1996, Botsford et al. 1997, Link & Marshak 2022).

In response to these concerns, the three entities primarily responsible for managing fisheries resources on the Northeast shelf (i.e., Mid-Atlantic Fishery Management Council, New England Fishery Management Council, Atlantic States Marine Fisheries Commission) have committed to incorporating ecosystem considerations into their stock assessment and management processes, following the Ecosystem Approach to Fisheries Management (EAFM) framework (NEFMC 2010, MAFMC 2019, ASMFC 2023). Each organization has made incremental progress on implementing EAFM for the Northeast shelf ecosystem (e.g., Feeney et al. 2019, Anstead et al. 2021, Muffley et al. 2021), and remain dedicated to transitioning their management frameworks toward EAFM as foundational scientific information becomes available (Biedron & Knuth 2016).

The overarching goal of this dissertation is therefore to facilitate the evolution toward EAFM on the Northeast US shelf by exploring how fish communities and interspecific interactions link with a myriad of ecological processes. Chapter 2 provides a historical overview of fisheries exploitation, management, and science in this ecosystem, chronicles the development and implementation of EAFM, and concludes by providing five specific recommendations to promote further integration of ecosystem considerations into regional stock assessment and fishery management activities. Information on spatiotemporal patterns in the community structure of marine systems serve as the foundation of effective ecosystem management, so Chapter 3 uses catch data from a relatively new fisheries-independent bottom trawl survey to (1) quantify relative annual, seasonal, and spatial trends in aggregate biomass for nine multispecies groups in the nearshore zone of the Mid-Atlantic Bight EPU; (2) evaluate the coherence among the annual time-series, trends in assemblage productivity, and the influence of biophysical forcing and exploitation on shaping these trends; and (3) assess patterns in the seasonal, spatial distribution of these groups. This work generated a new series of biological ecosystem indicators for the coastal ocean of the Mid-Atlantic that can inform system-level assessment activities and delineated an approach to synthesize information across an ever-increasing number of these indicators (e.g., NEFSC 2023).

Exploited forage species serve a dual role in marine ecosystems by supporting directed fisheries and predator productivity, such that both harvest and predatory removals should be accounted for when developing stock assessments and evaluating management tradeoffs for these species. Thus, Chapter 4 was designed to support forage assessments and management by using 42 years of shelf-wide predator catch and stomach content data from two fisheries-independent bottom trawl surveys to estimate time-series of aggregate fish consumption during

spring and fall for four key prey species: Atlantic herring (*Clupea harengus*), silver hake (*Merluccius bilinearis*), butterfish (*Peprilus triacanthus*) and longfin squid (*Doryteuthis pealeii*). Relationships between these time-series of predatory removals and a suite of covariates representing potential bottom-up (i.e., biophysical forcing, prey availability) and top-down (i.e., fishery harvest) controls were quantified to illuminate key factors shaping predator-prey interactions on the shelf and highlight linkages among the three main drivers of systemic productivity: i.e., trophodynamics, biophysical processes, and harvest (Gaichas et al. 2012, Link & Marshak 2022). Taken together, these studies contribute to the scientific underpinnings needed to continue the evolution toward EAFM on the Northeast shelf, which in turn is expected to improve resource sustainability and stakeholder welfare while streamlining the management process.

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CHAPTER 2

EAFM on the Northeast US shelf: history, status, and guiding recommendations for the future

Abstract

Extensive and largely unregulated fisheries operating on the Northeast US continental shelf during the middle 20th century resulted in widespread overfishing of living marine resources. Single-species approaches to the assessment and management of these fish stocks, underpinned by Federal legislation, have been mostly successful in ending overfishing and rebuilding these resources. As these stocks recover, however, the influences of biophysical forcing and interspecific interactions play a larger role in shaping their dynamics, while the potential for technical interactions among fisheries and between fisheries and protected species has increased. Appreciation for the need to include these broader ecosystem considerations into stock assessments and regulatory frameworks to ensure sustainability reemerged during the 1990s, and since then fisheries science and management in the Northeast US have been evolving toward Ecosystem Approaches to Fisheries Management (EAFM). While the activities undertaken by management agencies in the Northeast have varied, each has successfully implemented EAFM in some form and remains committed to advancing toward a more holistic approach to managing fisheries resources. A myriad of challenges remains, but by creating spaces to improve communication, enhancing data collection and modeling frameworks, synthesizing ecosystem indicators, developing system-level caps on harvest, and monitoring outcomes and adjusting approaches, these agencies should be well-positioned to accelerate the evolution toward EAFM, and by doing so continue to improve resource sustainability and stakeholder welfare while streamlining the management process.

The overfishing problem

Marine ecosystems supply an array of goods and services that are vital to society, including food resources, recreational opportunities, energy production, minerals, waste storage and detoxification, climate stability, cultural sites and a host of others valued at more than $112 trillion USD (Holland et al. 2010, Li & Fang 2014, Tam et al. 2017). Marine fisheries contribute over $140 billion USD to the global economy (Essington et al. 2016) and have existed for millennia. Technological advances during the 20th century such as diesel engines, shipboard freezers, and sonar fueled expansion of both the scale and impact of harvest activities, however, which has jeopardized the sustained delivery of a myriad market and non-market economic benefits derived from marine environments. Specifically, stocks of many living marine resources have been severely overfished throughout the globe (Link & Watson 2019). As the abundance of target predator species declined and both catch rates and profits diminished, new harvest opportunities were identified, resulting in increased fishing pressure on lower trophic-level species and a pattern of either sequential depletion of stocks or fishing through food webs (Pauly et al. 1998, Essington et al. 2006). This approach has reduced biodiversity in some ecosystems, in turn threatening the biological stability of these systems (Worm et al. 2006).

Widespread fishing operations began on the Northeast US continental shelf with the arrival of Western European fleets during the 15th century (Link et al. 2011). While detailed landings information is nonexistent, these harvest activities primarily focused on groundfishes and were likely sustainable. In contrast, whaling operations that occurred during the 1800s overfished the resource (Smith et al. 2012), the effects of which have persisted into the 21st century (Meyer-Gutbrod & Greene 2018). Fishing pressure in this ecosystem increased markedly with the arrival of industrialized trawl fleets from Europe, Asia, and Central America following

the Second World War. These 'distant water' operations targeted species across a broad range of trophic levels, harvested more than 750,000 metric tons annually, and reduced the biomass of living marine resources on the Northeast shelf by at least 50% (Fogarty & Murawski 1998). Initially unregulated, these foreign fleets were eventually required to comply with mesh size regulations and then harvest quotas, although enforcement was scant and populations of several groundfish and pelagic forage species either declined appreciably or collapsed.

These international operations were replaced by an expanding domestic fleet throughout the 1980s which prevented the recovery of some species and caused others, for example Atlantic cod (*Gadus morhua*), striped bass (*Morone saxatilis*), several shark species, and Atlantic sea scallop (*Placopecten magellanicus*), to decline to lower levels (Richards & Rago 1999, Hart & Rago 2006, Hayden et al. 2015, Latour & Gartland 2020). While management measures based on improved scientific understanding of stock dynamics have since been successful in reversing many of these trends (e.g., Peterson et al. 2017, Gaichas et al. 2018, NMFS 2023), threats to the sustainability of marine fishery resources have yet to be fully resolved (Hilborn 2007).

US fisheries legislation & management framework

Management of marine fisheries in the United States was formalized in 1976 with the passage of the Fishery Conservation and Management Act, later renamed the Magnuson-Stevens Fishery Conservation and Management Act (MSA) (16 United States Code [USC] 1801). This legislation extended US jurisdiction over natural resources in the marine environment from 12 NM to 200 NM off the coast, established eight Regional Management Councils (RMCs) responsible for the stewardship of living marine resources in this Exclusive Economic Zone (EEZ), and defined seven (later, 10) National Standards (NS) to serve as the foundation of

Fishery Management Plans (FMPs) developed by the RMCs (Methot et al. 2014). These NS call for a management process that is open to the public and based on the best scientific information available, uses the stock concept to define primary management units, requires fair allocation of fishing privileges and the preservation of fishing communities, promotes efficiency as well as safety at sea, allows for contingencies, and considers bycatch issues (NSG 2016).

NS1 is perhaps the most consequential of these directives, however, as it states that the primary objective of fisheries management is to achieve optimum yield (OY), defined as "the amount of fish which will provide the greatest overall benefit to the Nation...taking into account the protection of marine ecosystems" (16 USC §1802(33)). The term "optimum" was specifically defined as maximum sustainable yield (MSY), reduced by an appropriate amount to account for economic, social, and ecological considerations (Healy 1984, Patrick & Link 2015a). It is worth highlighting that the incorporation of a broad, ecosystem perspective to managing fisheries was woven into the concept of OY and thus effectively mandated as part of this early legislation (MacPherson 2001). Given the limited scientific information available to support management in the early 1980s, however, RMCs defined OY as average domestic harvest to exclude foreign fishing from the US EEZ and encourage the expansion of domestic fleets (Methot et al. 2014).

The Sustainable Fisheries Act (SFA) amended the MSA in 1996, emphasized the precautionary approach for managing US fisheries, specified OY as MSY reduced by an amount necessary to account for scientific uncertainty in stock status, and mandated an end to overfishing and rebuilding of overfished stocks (Darcy & Matlock 1999, Methot et al. 2014). This definition of OY enshrined a science-based approach to fisheries management in the US. The SFA also directed the formation of the Ecosystem Principles Advisory Panel (EPAP), charged with developing recommendations on incorporating ecosystem considerations into the

stock assessment and management processes (EPAP 1999, Patrick & Link 2015a). Arguably the most substantial recommendation of the EPAP was a call for RMCs to craft Fishery Ecosystem Plans (FEPs) for their jurisdictions. These FEPs would delineate and prioritize system-level management goals and objectives, outline strategies to evaluate tradeoffs among objectives, and monitor the effectiveness of regulatory measures designed to achieve these goals (Essington et al. 2016). Although not required, FEPs were envisioned as a tool to capture and integrate systemic issues that are otherwise difficult to address within individual FMPs.

The need for science-driven management was reinforced with the 2007 MSA reauthorization, which established a tiered system for the development of fisheries harvest quotas (Figure 1). Specifically, catch associated with MSY or a proxy measure is the Overfishing Limit (OFL), which can be reduced to account for scientific uncertainty by the Scientific and Statistical Committee (SSC) of a given RMC, yielding Acceptable Biological Catch (ABC). The Council then can set an Annual Catch Limit (ACL) at an amount less than the ABC to address management uncertainty. Annual Catch Targets (ACT) may also be specified below the ACL to serve as a management trigger, slowing the rate of harvest as total removals approach the ACL. While this tiered mechanism is currently used to manage nearly all fisheries in US federal waters (Methot et al. 2014), there were concerns that this strict hierarchical structure obfuscated the original definition of OY, and in particular obscured the mandate to incorporate ecosystem considerations into fisheries management (Patrick & Link 2015a).

The single-species approach

Given the legal directives for science-based management of US fisheries, single-species stock assessments have served as the primary source of scientific information underpinning

management advice, harvest quota development, and fishing regulations (Dolan et al. 2016). In short, data on a stock are used to quantify the status of the resource, relative to reference levels designed to signify whether the stock is in a desirable or undesirable state. These biological reference points are typically related to the biomass (or abundance) and fishing mortality rates of the stock (Restrepo et al. 1998, Methot et al. 2014). Data on the stock may be derived from the fishery (i.e., fisheries-dependent data), scientific monitoring programs (i.e., fisheries-independent data), focused research investigations, or a combination of these sources. These data can include information on catch, spatial distribution, relative abundance, size- or age-structure, recruitment, growth, and a host of other population vital rates (Hilborn & Walters 1992). Assessment complexity ranges from simple catch- and index-based approaches, primarily used when data on a stock are relatively limited, to detailed cohort-based methods that employ a variety of advanced statistical modelling techniques to yield information on stock status (Quinn & Deriso 1999). The single-species approach to the assessment and management of living marine resources has achieved notable success (Richards & Rago 1999, Hart & Rago 2006, Peterson et al. 2017, Latour & Gartland 2020). As of 2022, only 7% of the 492 federally-managed stocks were experiencing overfishing, 19% were overfished and, since 2000, 49 have been rebuilt (NMFS 2023).

While the single-species approach has been relatively effective in achieving the mandates set forth in the MSA, there are concerns that this framework yields inefficient management with respect to foregone long-term harvest and economic yield, as this approach typically fails to consider environmental impacts on stock dynamics, interactions among species, or the human component of the system beyond harvest removals (Link & Marshak 2022). For example, climate variability and ocean circulation regulate recruitment success, phenology, and spatial

distributions of motile species (Houde 2008, Morley et al. 2018, Langan et al. 2021). Local abiotic factors influence fish behavior and physiology, which cumulatively shape population vital rates such as growth, fecundity, and natural mortality. It is worth noting that some single-species, cohort-based assessments do incorporate time-varying size-at-age, which can capture environmental (and likely other) influences on fish growth, albeit indirectly (Gaichas et al. 2016). The structure and function of ecological communities in marine environments is typically molded by predator-prey interactions through both top-down and bottom-up controls. Lower trophic level dynamics regulate system-level production (Ware & Thompson 2005), while removals due to predation can exceed fishery harvest for many forage species (Tyrrell et al. 2011). Overexploitation of predator taxa has resulted in trophic cascades in some systems, drastically altering food web dynamics (Salomon et al 2010). Data on trophic interactions can be directly included into assessment models to estimate time-varying (either annually or by age) natural mortality rates, but this is not yet a common practice.

Within the single-species framework, the evaluation of management trade-offs to optimize economic, social, and cultural considerations has been very rare (MAFMC 2022). Further, while technical (i.e., between-fishery) interactions are quantified in approximately 40% of federal stock assessments by tabulating the bycatch of a stock in fisheries targeting other resources (Marshall et al. 2019), impacts of catch quotas, gear restrictions, and closed areas or seasons in other fisheries on a stock of interest has received little attention (Link & Marshak 2022). The discovery that system-level MSY typically is less than the sum of individual stock MSYs has further reinforced the need to evolve beyond single-species assessment and management of marine fisheries (Fogarty et al. 2012). Indeed, evaluating fisheries while considering the ecosystem linkages can improve management of living marine resources by

identifying more sustainable, stable, and socially acceptable harvest strategies that could improve economic outcomes by reducing foregone yield (Link 2018). And finally, the successes of the single-species approach in curbing fishing mortality have actually made these ecosystem considerations more important, as the influence of harvest activities on stock dynamics continues to decline relative to biophysical forcing and trophodynamics.

(Re)Emergence of ecosystem approaches: guiding philosophy & policy

The need to consider biotic and abiotic influences on stock dynamics has been advocated for more than a century (Baird 1873, Hjort 1914). Widespread recognition of the value of ecosystem-scale assessment and management of living marine resources, however, emerged in the early 1990s and several US government agencies began mandating this approach (Buck 1993, Griffis & Kimball 1996). The legal authorities to pursue these ecosystem approaches also began to take shape, rooted in the original OY definition in the MSA and the recommendations of the EPAP from the 1996 SFA. The result was a proliferation of scientific literature defining these ecosystem approaches (Link 2002a, Link 2002b, Pikitch et al. 2004), discussing whether an evolution from vetted single-species management was necessary (Hilborn 2004), and developing modelling frameworks to support the transition (Hollowed et al. 2000, Plagányi 2007, Collie et al. 2016). At the time, however, efforts to operationalize these ecosystem approaches were hampered by a myriad of factors, including the limited availability of high-quality, long-term ecological datasets, insufficient computing power, inconsistent terminology, lingering questions regarding legal mandates and governing frameworks, and debates as to whether increased uncertainty associated with the estimation of additional ecological parameters represented an advance over single-species assessments (Hilborn 2004, Patrick & Link 2015b).

Over the next two decades, many data deficiencies were overcome with the development of new or expansion of existing sampling programs, requisite computing power became readily available and, for the most part, terminology was clarified. Reviews of extant law and policy identified unequivocal mandates for incorporating ecosystem considerations into the management process, and the benefits of this approach were clearly articulated (Link et al. 2020). Indeed, the discussion on adopting a more holistic, ecosystem approach to assessing and managing living marine resources evolved from 'what it is and why we should do it' (e.g., Link 2002b, Browman & Stergiou 2004) to 'how can we do it and when can we operationalize it' (e.g., Link & Browman 2014, DePiper et al. 2017).

It is valuable to note that frameworks for assessing and managing fisheries in an ecosystem context range across a continuum that spans from excluding these considerations altogether (i.e., single-species) to Ecosystem Management (EM), which operates at the full-system scale, across multiple use sectors, and seeks to optimize sustained delivery of all goods and services. Between these extremes are Ecosystem Approaches to Fisheries Management (EAFM) and Ecosystem-Based Fisheries Management (EBFM). EAFM essentially extends the single-species framework to incorporate information on biophysical, trophodynamic, and technical interactions, as well as socioeconomic data, while EBFM endeavors to consider all fisheries in an ecosystem simultaneously (Dolan et al. 2016). Both approaches view fisheries as part of a broader socio-ecological system, involve the evaluation of trade-offs to achieve ecosystem-scale objectives, and thus are similar (Woods 2022). To date, however, most efforts to incorporate ecosystem considerations into US fisheries management are best categorized as EAFM (Link & Browman 2014, Dolan et al. 2016).

The philosophy guiding delineation of geographic boundaries for assessment and subsequent management of living marine resources fundamentally differs between the single-species framework and ecosystem approaches (Link et al. 2011). In the single-species approach, the spatial unit encompasses the area occupied by the stock of interest, and thus can vary widely among stocks. Ecosystem approaches are place-based, however, such that the area of interest is defined by meaningful ecological boundaries (FAO 2003), and the communities of living marine resources within those boundaries are subject to management (Pikitch et al. 2004, Fogarty 2014). A global system of Large Marine Ecosystems (LMEs) has been defined to delineate these ecologically meaningful spatial boundaries. Each LME covers an area of approximately 200,000 km^2 and is characterized by a relatively distinct hydrography, bathymetry, and community of living marine resources relative to adjoining LMEs (Sherman 1991). The National Oceanographic and Atmospheric Administration (NOAA) has identified nine LMEs along the US coastline, including the Northeast US LME encompassing the Northeast US shelf, which serve as the spatial units for the development and implementation of EAFM. Some of the LMEs have been subdivided into smaller regions called Ecological Production Units (EPUs) to facilitate assessment and management (Lucey & Fogarty 2013).

Research efforts underpinning the implementation of EAFM intensified in response to the development of the US National Ocean Policy (EO 13547, 2010; since rescinded) and NOAA Policy on Ecosystem-Based Fisheries Management (NMFS 2016). The NOAA Policy defined EAFM/EBFM as an:

"approach to fisheries management in a geographically specified area that: contributes to the resilience and sustainability of the ecosystem; recognizes the physical, biological, economic, and social interactions among the affected fishery-related components of the ecosystem, including humans; and seeks to optimize benefits among a diverse set of societal goals."

Six associated guidelines were developed that directed the RMCs to: (1) implement ecosystem-level planning; (2) advance understanding of ecosystem processes; (3) prioritize vulnerabilities and risks to ecosystems and their components; (4) explore and address tradeoffs within an ecosystem; (5) implement ecosystem considerations into management; and (6) support ecosystem resilience via monitoring and adjusting management actions.

While these policies apply throughout the US EEZ, notable advances toward EAFM have been made on the West Coast (i.e., Gulf of Alaska, Eastern Bering Sea, and California Current LMEs) and the Northeast US shelf (NEUS LME). The concept that system-level MSY is less than the sum of single-species MSYs is used by the North Pacific Fishery Management Council (NPFMC) to set Bering Sea/Aleutian Island groundfish harvest quotas. Specifically, system-level reference points are estimated and used as a constraint on total groundfish harvest, which then requires trade-offs in setting quotas on the individual groundfish stocks (Patrick & Link 2015a). This RMC also pioneered the development and evaluation of ecosystem indicators, measures of the status of various biological, physical, and social components of the system provided in an annual Ecosystem Considerations report, that serve as a qualitative guide in the quota setting process (Zador et al. 2017). Developing new fisheries on forage species is not permitted, in recognition of the role that these species play in the transfer of energy from lower trophic levels to harvested predator species (Witherell et al. 2000). Farther south, an interdisciplinary conceptual model of the California Current LME has been crafted to guide the implementation of EAFM by the Pacific Fishery Management Council (Levin et al. 2016), and indicators of system status are updated in an annual State of the California Current Ecosystem Report (Harvey et al. 2023). Both RMCs have developed FEPs for their respective regions.

Ecosystem science & management in the Northeast US

Fisheries resources on the Northeast US shelf are managed primarily by three entities: namely, the Mid-Atlantic Fishery Management Council (MAFMC), the New England Fishery Management Council (NEFMC), and the Atlantic States Marine Fisheries Commission (ASMFC). The MAFMC has jurisdiction over living marine resources in the EEZ of most of the Mid-Atlantic Bight (MAB) EPU, while the NEFMC regulates fisheries in the northeast MAB, Georges Bank, and the Gulf of Maine EPUs (Figure 2). Both RMCs derive their regulatory authority from the MSA, and management measures must be approved by the US Department of Commerce prior to implementation. The ASMFC manages fishery resources out to 3 NM (i.e., state waters) between Maine and Florida as authorized by the Atlantic Coastal Fisheries Cooperative Management Act of 1993. While each organization operates independently, some species are co-managed between two or more of these groups, and each has committed to implementing EAFM within their respective jurisdictions. The following sections provide an overview of the progress that each has made toward this goal.

Mid-Atlantic Fishery Management Council

Efforts to transition fisheries management toward EAFM in the Mid-Atlantic EEZ began in earnest in 2011. The MAFMC had just conducted a visioning exercise to gain input on future priorities, and both stakeholders and Council members emphasized the need to incorporate ecosystem considerations into the assessment and management of Mid-Atlantic fisheries resources (Gaichas et al. 2018). At the same time, their SSC hosted a national workshop to delineate approaches for including ecosystem considerations into the federal fisheries stock assessment and management processes (Seagraves & Collins 2012). The confluence of these events led to the development of the MAFMC EAFM Guidance Document, which was designed

to serve as the foundation for the transition to EAFM (MAFMC 2019). This document specified a clear goal, 'to enhance the Council's species-specific management programs with more ecosystem science, broader ecosystem consideration, and management policies that coordinate Council management actions across its FMPs and relevant ecosystems', and stated that the incorporation of ecosystem considerations would occur within the existing FMP frameworks. Four focal areas served as pillars for the implementation of EAFM, including (1) forage/low trophic level species considerations; (2) ecosystem-level habitat conservation and management; (3) oceanographic influences on stock abundance and distribution; and (4) sustainable harvest policy in the context of species, fleet, habitat, and climate interactions. The Council convened a series of workshops to both communicate their commitment to operationalizing EAFM and devise approaches to address each focal area, which culminated in the development of a strategic plan that identified implementation of EAFM as a top priority (Muffley et al. 2021). Council members, the SSC, and stakeholders agreed that this transition should occur gradually and at a rate commensurate with the availability of requisite scientific information (Biedron & Knuth 2016).

Given the stated commitment to implement EAFM for the Mid-Atlantic, a systematic research effort was undertaken to yield the scientific underpinnings required to support this transition, and has mainly followed the Integrated Ecosystem Assessment (IEA) framework (Levin et al. 2009, Muffley et al. 2021). An IEA is designed to efficiently incorporate ecosystem information into fisheries science and management through a six-step process that includes (1) defining goals and targets; (2) developing indicators of system status; (3) assessing the system; (4) analyzing uncertainty and risk; (5) evaluating management strategies; and (6) implementing

and monitoring management actions (Woods 2022). This framework was designed to be flexible, rather than prescriptive, and thus can be modified as necessary to suit organizational needs.

Due to the novelty of EAFM approaches and the overwhelming number of ecosystem considerations to pursue, the MAFMC chose to modify the original IEA framework and begin with a system-wide risk assessment (step 4) to identify the greatest threats to maintaining sustainable fisheries (Figure 3; Gaichas et al. 2018). This assessment included an array of biological, environmental, and socioeconomic risk elements, was completed in a matter of months, and identified relatively high risks to the summer flounder stock and fishery. Following the risk assessment, a conceptual model was created for this species that linked risk elements to key ecological, climate, habitat, fleet, and socio-economic factors (DePiper et al. 2021). The model included 57 elements and factors with 138 linkages among them, was coupled with indicators of system status (combining steps 2 & 3) found in the RMC's State of the Ecosystem Report (NEFSC 2023a), and served as a valuable tool for Council members and scientists to collaboratively identify research needs and data gaps. The Council used the conceptual model to identify several management objectives (step 1) and chose to pursue evaluation of the 'biological and economic benefits of minimizing discards and converting discards into landings in the [summer flounder] recreational sector.' (DePiper et al. 2021). A formal management strategy evaluation (MSE) was developed by linking a summer flounder population model with an angler behavior model (step 5; Punt et al. 2016) and quantifying the biological and socio-economic performance of candidate management measures (MAFMC 2022). Harvest regulations that included a slot limit consistently outperformed the current minimize size approach in terms of reducing discards and increasing angler welfare.

While the case above provides a concrete example of progress toward EAFM, the MAFMC has and continues to take several additional steps to incorporate ecosystem considerations into the scientific and management enterprises. In recognition of the important role that forage species play in maintaining system structure and function, the Council approved the Omnibus Unmanaged Forage Amendment in 2017 that protects over 50 forage species from the development of new fisheries without a thorough review (MAFMC 2019). The stock assessment for butterfish (*Peprilus triacanthus*) uses water temperature to quantify availability to regional trawl surveys (NEFSC 2014), while the OFL for this species acknowledges its forage role by scaling the fishing mortality rate to natural mortality. The recent bluefish (*Pomatomus saltatrix*) assessment incorporated spatiotemporal information on prey distribution to account for the availability of this species to the recreational fishery (Gaichas et al. 2024), and was the first in the region to develop an Ecosystem and Socio-Economic Profile (ESP) in conjunction with the stock assessment (Tyrrell et al. 2022). This ESP was created in response to the now-standard Term of Reference (TOR) 1 for all federal stock assessments in the Northeast US, which requires identification of 'relevant ecosystem and climate influences on the stock', and included a conceptual bluefish model along with indicators of stock performance. Finally, the MAFMC SSC created the Ecosystem Working Group to further operationalize EAFM by providing recommendations on incorporating ecosystem information into OFL specification, developing processes to provide multispecies and multi-fleet advice, improving ESPs, and including additional ecosystem considerations into the management process. Taken together, these activities enabled the MAFMC to advance toward their EAFM goals while satisfying mandates defined within the MSA.

New England Fishery Management Council

Efforts by the NEFMC to incorporate ecosystem considerations into New England fisheries management began in 2010 with the development of a white paper by their SSC (NEFMC 2010). In line with the NOAA EBFM Policy and consistent with the later MAFMC EAFM Guidance Document, this paper noted that plans to include ecosystem information into the management process needed to be adaptive, tailored to specific geographic areas, and able to account for external influences on stocks, uncertainty, and a myriad of social objectives. The approach outlined to achieve these objectives followed the IEA framework and was expected to yield several benefits including: simplified management plans, greater protections for stocks, habitats, and biodiversity, and enhanced ability to adapt to a changing climate, to name a few. In response, the NEFMC created the EBFM Committee and Plan Development Team which pursued the development of an example FEP (eFEP) for the Georges Bank EPU (NEFMC 2019). The purpose of the eFEP was to compile information designed to evaluate management strategies (through formal MSE) that would regulate fisheries in this system as stock complexes. This path was ultimately abandoned in 2023 in favor of developing an EAFM Guidance Document, mirroring the approach used by the MAFMC.

Nevertheless, the NEFMC has made progress on integrating ecosystem considerations into assessment and management activities, particularly through the development of their annual State of the Ecosystem Report (NEFSC 2023b) and an MSE for the Atlantic herring (*Clupea harengus*) fishery (Feeney et al. 2019). Like the MAFMC, this RMC has recognized the important role that forage species play in maintaining ecosystem integrity. The Atlantic herring MSE coupled population models for this and three predator species with an economics model to evaluate biological and economic metrics under a range of management scenarios (Townsend et al. 2019). As a result, the Atlantic herring FMP now accounts for its role as forage by specifying

the maximum allowable fishing mortality rate to be 80% of that expected to yield MSY. It is likely that ecosystem linkages will be incorporated into additional NEFMC assessments and management strategies in response to the new TOR1 detailed above.

Atlantic States Marine Fisheries Commission

State fishery managers that compose the ASMFC Interstate Fisheries Management Program Policy Board are in general agreement on the need to evolve management strategies toward EAFM (Safiq et al. 2021), and these sentiments are reflected in the Commission's most recent strategic plan (ASMFC 2023). Consistent with the MAFMC and NEFMC focus on harvested forage species, the ASMFC has been incorporating quantitative information on the role of Atlantic menhaden (*Brevoortia tyrannus*) as a food source for predators for the past 20 years (Anstead et al. 2021). Atlantic menhaden support the largest commercial fishery by volume on the US East Coast and are consumed by an array of upper trophic level predators. Initially, predation mortality on this species was quantified by using an extended multispecies virtual population analysis (MSVPA-X) model that linked a series of single-species VPA models with a predator consumption model. The results of the MSVPA-X were used to estimate time- and age-varying natural mortality rates, which were then included in the single-species Atlantic menhaden assessment model. The ASMFC formed the Ecological Reference Point Work Group (ERP WG) in 2012, tasked with developing assessment methods that would ensure the sustainability of the Atlantic menhaden fishery and dependent predator populations. Five ecosystem models were evaluated, and from those a Model of Intermediate Complexity for Ecosystem Assessment (i.e., MICE model; Chagaris et al. 2020) was selected to develop reference points. The target fishing mortality rate for Atlantic menhaden was defined as the maximum that would maintain striped bass at their biomass target when harvested at their target

fishing mortality rate. This assessment approach and associated reference points were adopted for management in 2020, representing the first case where quantitative ecosystem models were used in a management context on the US East Coast.

Future directions

Ecosystem approaches to the assessment and management of marine fisheries in the US are considered to be in a 'trial-and-error' phase (Woods 2022). Nevertheless, the MAFMC, NEFMC, and ASMFC have each made meaningful progress toward implementing EAFM on the Northeast US shelf. The need to manage fisheries in the context of the broader ecosystem is only becoming more urgent, however. As successes mount in rebuilding overfished stocks and the number subjected to overfishing decline, abiotic environmental processes and predator-prey interactions will play an increasing role in shaping stock dynamics, and technical interactions among fisheries and with protected species will become more likely. The diversity and magnitude of both direct (e.g., sand mining and wind energy) and indirect (e.g., coastal population growth and shoreline development) anthropogenic uses of the system are increasing, although the extent to which these activities will impact fisheries resources remains mostly unknown (Byrnes et al. 2004, Methratta et al. 2023). Further, these pressures are operating on a backdrop of climate change, which in the Northeast US is occurring at among the highest rates in the world. Climate change is expected to continue to increase water temperatures, accelerate rates of sea level rise, reduce pH, alter storm intensity, precipitation patterns, and salinity regimes, and impact phytoplankton productivity on the continental shelf (Kemp et al. 2005, Bates & Peters 2007, Najjar et al 2010, Sallenger et al. 2012). Threats to achieving and

maintaining sustainable fisheries clearly remain, so we offer five recommendations below to extend and accelerate the evolution toward EAFM on the Northeast US shelf.

Recommendation 1: Create spaces for improved communication & idea exchanges

Incorporating ecosystem considerations into fisheries management is inherently more complex than the traditional single-species framework in terms of assessment model output, the consideration of trade-offs among management strategies, and the potential to impact a broader range of stakeholders. The need to create communication spaces that include scientists, managers, stakeholders, and the public to vet the utility of scientific products and evaluate management options therefore becomes more critical under EAFM. Given the mandates of the MSA, both RMCs and the ASMFC (although not bound by the MSA) developed single-species management as an inclusive process, where all Council and Commission meetings are open to the public, SSC deliberations include a public comment period, and Advisory Panels comprised of interested stakeholders provide input on specific FMPs. The scientific process is also conducted in an open format, where stock assessment working group meetings and peer reviews are open to the public, and several scientific teams have begun to hold stakeholder meetings early in the assessment cycle to gain buy-in. While these efforts have established and maintained effective lines of communication, they tend to be somewhat siloed. The composition and extent of stakeholder participation varies based on the species under consideration, public attendance is often sparse, and except in the case of co-managed species, coordination among management entities can be somewhat limited.

Given the more complex and cross-cutting nature of EAFM, we recommend that the MAFMC, NEFMC, and ASMFC begin to conduct joint, semi-annual 'Ecosystem Meetings' designed to serve as fora for the exchange of ideas on incorporating ecosystem considerations

into fisheries stock assessment and management. The MAFMC held a series of workshops when developing their EAFM Guidance Document, and what we are proposing here is an extension and broadening of that effort. These venues could serve as 'trading spaces' (Johnson & McCay 2012), where stakeholder/public preferences can be clearly conveyed to managers, and in turn management needs can be linked with scientific capacity. One possible result could be greater inclusion of EAFM at each phase of the process: stock assessment, OFL determination, and management strategy development. Further, while the portfolio of species managed by each entity mostly differ, they share common challenges in evolving toward EAFM, such that these meetings could serve as a space to evaluate what has and has not worked, and to develop solutions for overcoming these challenges by leveraging a greater diversity of perspectives. While the ecosystems managed by each agency have unique characteristics, climate-driven shifts in species distributions have shown that system boundaries can be quite porous (Morley et al. 2018), which has complicated management. These meetings could provide a valuable opportunity to address this and other shelf-wide issues. Finally, these venues could be used to showcase successful outcomes associated with the myriad implementations of EAFM on the Northeast shelf, which could be used to reinforce the 'business case' for this approach and generate buy-in on this evolution (Link et al. 2019). The use of professional facilitation services is highly recommended to increase the likelihood of achieving acceptable compromises and successful meeting outcomes (e.g., Miller et al. 2010).

Recommendation 2: Enhance data collection & integrate modeling frameworks

The Northeast US shelf is a data-rich ecosystem, characterized by well-established, long-term fisheries-independent monitoring of both the biotic and abiotic components of the system (e.g., Politis et al. 2014, Gartland et al. 2023), along with comprehensive fisheries-dependent

sampling of the commercial and recreational harvest sectors. While these and other datasets have been instrumental in advancing EAFM across the region, sampling inconsistencies, spatiotemporal gaps in coverage, and limited availability of biological data have impeded the incorporation of ecosystem considerations into management. Currently, the Northeast shelf is sampled during spring and fall by four relatively large-scale, long-term bottom trawl surveys. Unfortunately, the sampling protocols and gears differ among the four surveys, and while recent statistical advances have made combining their datasets more feasible (e.g., Perretti & Thorson 2019), integrating the information generated by these programs remains a challenge. Further, while the combined sampling frame of these monitoring programs encompasses most of the shelf, some notable gaps remain including Nantucket Shoals, the shore zone, and regions with extensive amounts of glacial moraines and fixed fishing gear, among others. The dynamics of the Northeast shelf vary seasonally, such that the lack of sampling during summer and winter months represents a major knowledge gap that has particularly hampered efforts to generate annual estimates of prey consumption and predatory demand needed to inform extended single-species and ecosystem-scale stock assessment models (Deroba 2018, Chapter 4). While some of these challenges could be overcome with innovate collections of biological data from fisheries-dependent sources, future efforts to operationalize EAFM would benefit greatly from spatiotemporal expansions of the current fisheries-independent surveys, improved coordination of their sampling protocols, dedicated ship time for data collection to support process-oriented studies, and the development of new programs designed to sample habitats that are inaccessible to trawls.

Enhancing efforts to collect, analyze, and incorporate socioeconomic data into the fisheries assessment and management processes will also be necessary to advance EAFM in the

region. While the semi-annual Ecosystem Meetings could provide managers with insights on stakeholder and public preferences among possible management strategies, quantifying these preferences with discrete choice surveys or analogous approaches would provide scientists with requisite data to parameterize MSEs meant to evaluate welfare tradeoffs (Holland et al. 2010). Indeed, these methods were successfully used to quantify angler welfare in the recent summer flounder MSE (MAMFC 2022), which could serve as a template for including this type of information for other fisheries. Additional data are also needed on the various other non-market values provided by the Northeast shelf ecosystem (e.g., aesthetics, non-fishing recreation, climate buffering) to better inform evaluations of costs and benefits associated with management strategy options.

Since ecosystem approaches reemerged in the 1990s, an array of modeling frameworks has been developed that can incorporate environmental influences on stock dynamics, predator-prey data, and technical interactions. To further advance EAFM, it is recommended that stock assessment teams routinely evaluate several of these modeling frameworks, in addition to various parameterizations of each model type, perhaps as part of a new standard TOR. This approach led to the successful development of ERPs for the Atlantic menhaden fishery (Anstead et al. 2021) and represents a paradigm that could be repeated for other fisheries, extended to incorporate economic information and quantify structural (i.e., model form) uncertainty, and possibly combined in an ensemble modeling framework to yield management advice (Link & Browman 2014, Jardim et al. 2021).

Recommendation 3: Synthesize ecosystem indicators

Both the MAFMC and NEFMC generate annual State of the Ecosystem reports that outline ecosystem management goals and objectives and include a host of indicators conveying

the status of the biological, physical, and socioeconomic components of the systems under their jurisdictions. These reports have been refined through an exemplary collaboration between managers and scientists, and most of the current indicators are linked to an ecosystem management objective. Only a few of these indicators have been used in the stock assessment process (e.g., Gaichas et al. 2024), however, and none have been used to modify OFLs, ABCs, or ACLs. This disconnect may be due simply to the overwhelming number of ecosystem indicators now available to managers (e.g., >90 indicators in the Mid-Atlantic). A potential remedy is to begin to synthesize information across the available indicators. For example, a recent study recommended evaluating trends among a suite of indicators for each ecosystem objective or fishery, identifying potential concerns based on a qualitative synthesis of trends, and then developing management strategies to address those concerns (Link et al. 2020). As an alternative, statistical multivariate methods such as dynamic factor analysis could be used to synthesize indicators by identifying common trends and potential drivers (Gartland et al. 2023). Other approaches could include calculating ratios of indicators to evaluate system-level productivity (e.g., landings * primary production^{-1}; Link & Marshak 2019) and combining indicators that represent topology, resiliency, and distortive pressures to yield an 'ecosystem traits index' to assess system status (Fulton & Sainsbury 2024). While each of these approaches has the potential to efficiently synthesize information from multiple indicators, management utility may remain limited until indicator target and threshold values are established that give clear indication of states to be avoided and serve as a trigger for management action (Large et al. 2015). Evaluating indicator status relative to its threshold could also provide the quantitative underpinnings for the risk designations developed as part of the IEA process (Gaichas et al 2018).

Recommendation 4: Develop system-level caps on harvest

Specifying multispecies harvest caps, whether at the system-level or for functional groups (e.g., demersal fishes), represents an ambitious yet achievable goal for the implementation of EAFM on the Northeast shelf. Modeling approaches ranging from simple aggregate surplus production models (e.g., Mueter & Megrey 2006) to full ecosystem models could be used to quantify MSY for a system or species complex, and quotas could be set for each constituent taxa by combining information on its (preferably extended) single-species assessment, market demand, and stakeholder preferences (Zador et al. 2017). Simultaneous consideration of taxa-specific and aggregate OFLs guards against overfishing at both the species and ecosystem level, could result in a more efficient utilization of fisheries resources (i.e., stakeholders could capitalize on species 'booms' and underutilized resources), and may yield a more balanced harvest approach where removals are more closely aligned with species productivity (Collie et al. 2022). As fisheries scientists and managers borrowed the risk assessment concept from business practices to advance EAFM, so too could they integrate the concepts of operations research to optimize tradeoffs in single-species quotas under an aggregate harvest cap (Bhunia et al 2019).

While this recommended 'cap-and-trade' system for quota specification represents a major change to the process by which fisheries resources are assessed and managed on the Northeast shelf, this approach is not without precedent. The NPFMC has successfully used this framework to set groundfish quotas in the Bering Sea/Aleutian Islands and Gulf of Alaska for several years (Patrick & Link 2015a). Council and SSC members of the MAFMC have expressed interest in applying this approach in the Mid-Atlantic (Biedron & Knuth 2016) and the SSC Ecosystem Working group is exploring mechanisms to begin providing multispecies advice. While the MSA does not prevent the specification of system-level harvest caps (Patrick & Link

2015a), future reauthorizations that explicitly codify this concept would be helpful in facilitating the transition toward EAFM. Implementing such an approach for the Northeast shelf would be challenging, but could pay dividends in terms of controlling overfishing, improving stakeholder welfare, and streamlining the management process.

Recommendation 5: Monitor outcomes & adapt

The MAFMC, NEFMC, and ASMFC have each recorded successes in developing management strategies that incorporate EAFM concepts, and these entities remain committed to continuing this evolution. A key step in any management process, and one that is often overlooked, is to periodically evaluate strategies that have been implemented (Dickey-Collas et al. 2022). Specifically, the NEFMC and ASMFC should monitor the efficacy of harvest quotas designed to acknowledge the forage roles of Atlantic herring and Atlantic menhaden, perhaps by monitoring the diet compositions or condition indices of their key fish predators. These evaluations should be conducted every 3 – 5 years, and management strategies should be adjusted if performance metrics fall short of desired outcomes. The MAFMC should conduct similar evaluations of the temperature-based stock assessment for butterfish and associated harvest control rule that accounts for its role as forage. By incorporating a management monitoring program as a routine part of the process, each of these entities would gain greater insight on what works and what does not, which in turn should improve future tradeoff analyses and decision-making.

Several authors have noted the slow progress on implementing EAFM on the Northeast shelf and elsewhere (e.g., Link & Browman 2017, Townsend et al. 2019). The transition has and continues to be evolutionary, yet there is cause for optimism. The MAFMC, NEFMC, and ASMFC have all incorporated ecosystem approaches to stock assessment and management for at

least some of the fisheries under their jurisdiction, and momentum toward operationalizing EAFM seems to be increasing as scientists, managers, and stakeholders become more familiar with the process and its benefits. We hope that the recommendations provided here further stimulate the evolution toward EAFM, and by so doing, continue to improve resource sustainability and stakeholder welfare while streamlining the management process.

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Figure 1. Framework developed under the 2007 reauthorization of the Magnuson-Stevens Fishery Conservation and Management Act to guide the specification of harvest quotas.

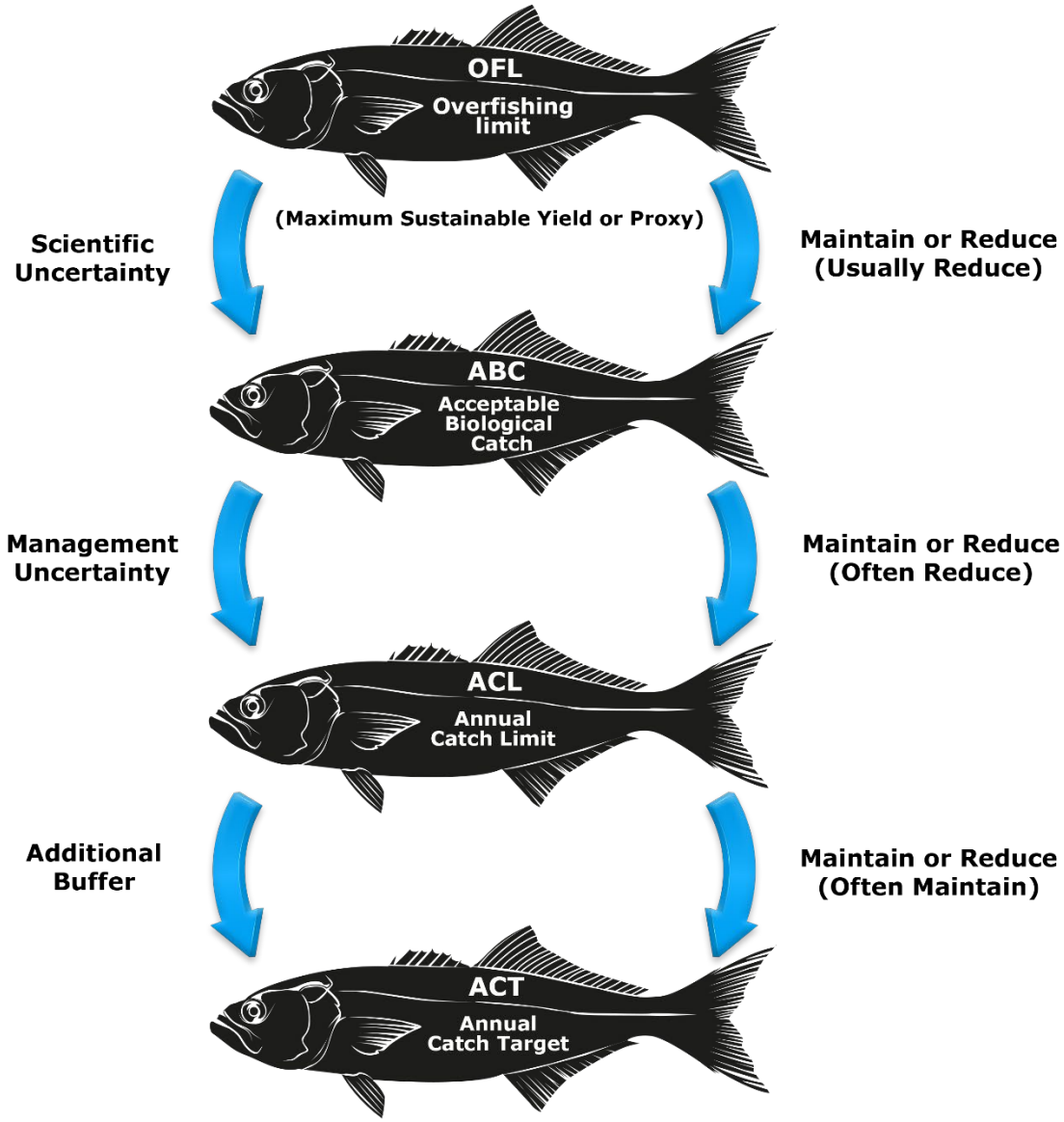


Figure 2. Extent of the Northeast US continental shelf ecosystem, denoting the locations of the Mid-Atlantic, Georges Bank, and Gulf of Maine ecological production units.

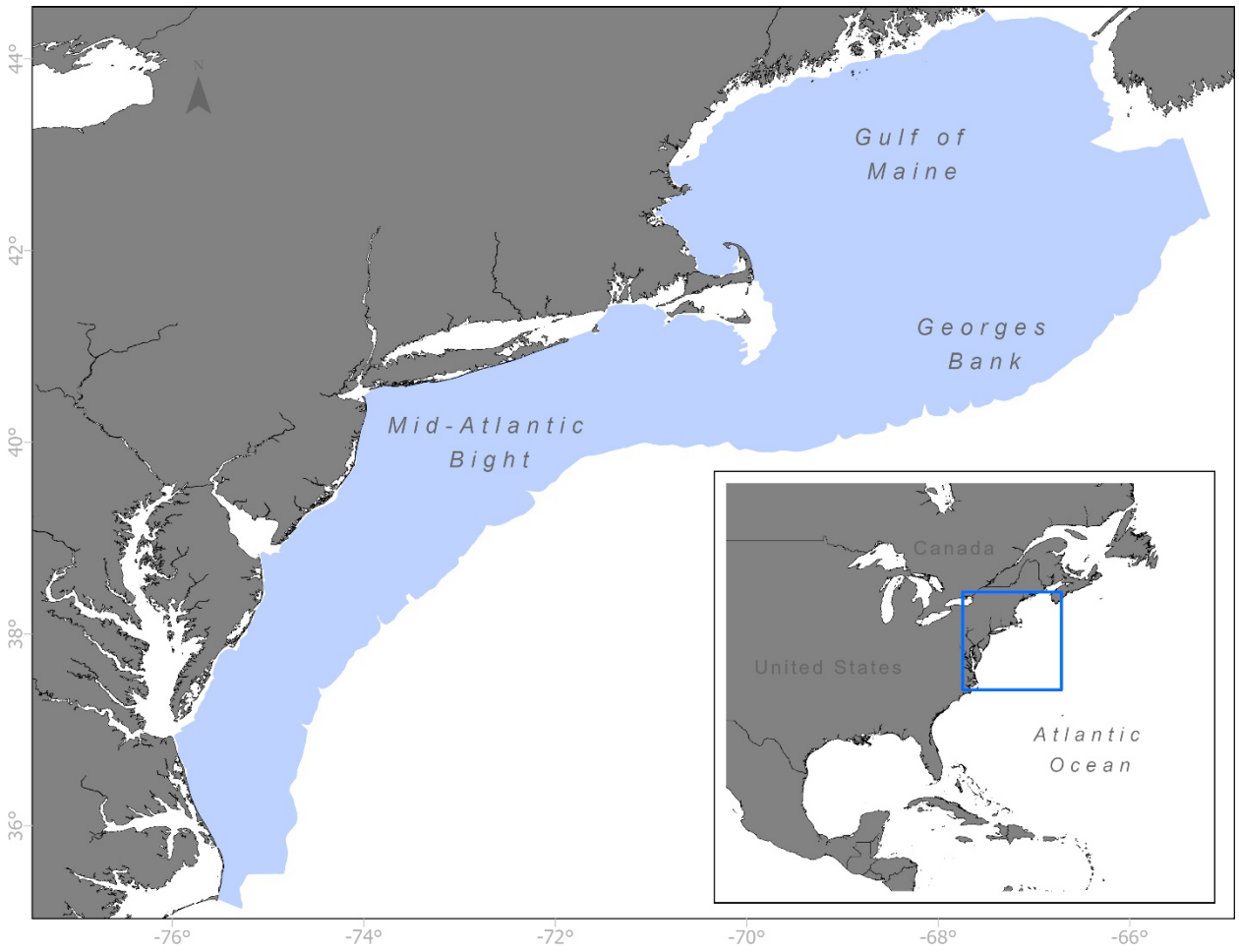
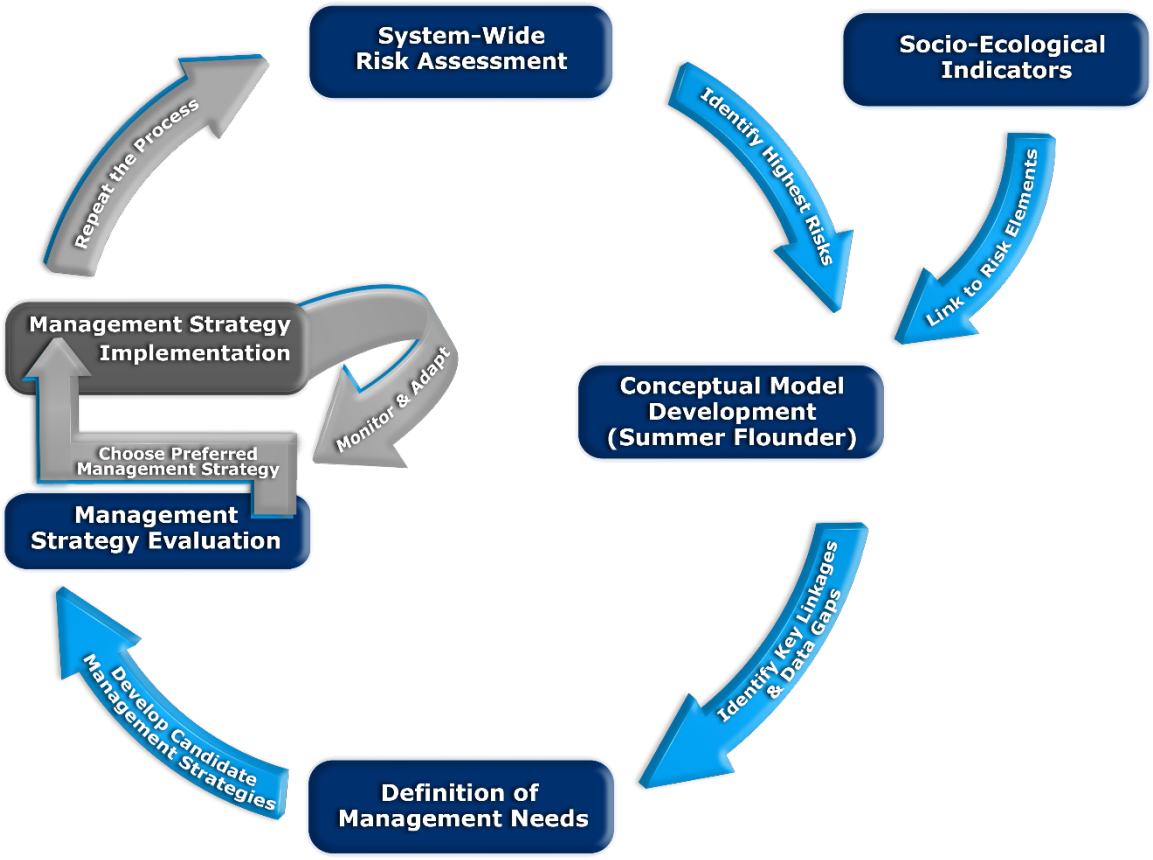


Figure 3. Schematic of the modified integrated ecosystem assessment loop used by the Mid-Atlantic Fishery Management Council to begin operationalizing ecosystem approaches to fisheries management in the Mid-Atlantic Bight Ecological Production Unit. Gray areas represent steps that have yet to be implemented.



CHAPTER 3

Spatiotemporal patterns in the ecological community of the nearshore Mid-Atlantic Bight

Abstract

Recognition of the need for a more holistic, ecosystem approach to the assessment and management of living marine resources has renewed interest in quantitative community ecology and fueled efforts to develop ecosystem metrics to gain insight on system status. This investigation utilized 12 years (2008 – 2019) of fisheries-independent bottom trawl survey data to quantify and synthesize the spatiotemporal patterns of species assemblages inhabiting the nearshore Mid-Atlantic Bight (MAB). Assemblages were delineated by ecomorphotype (EMT), and all species collected by the survey were allocated among nine EMTs: demersal fishes; pelagic fishes; flatfishes; skates; rays; dogfishes; other sharks; cephalopods; and benthic arthropods. Annual time-series and seasonal, spatial distributions of relative aggregate biomass were quantified for each EMT using delta-generalized additive models. Dynamic factor analysis (DFA) revealed that the information content of the nine annual time-series was effectively summarized by three common trends, and DFA model fits to each EMT time-series represented a new suite of ecosystem indicators for this system. Mean sea surface temperature during winter in the MAB was included in the selected DFA model, suggesting that winter environmental conditions influence the structure of this system at an annual scale. Principal component analysis uncovered a north-to-south gradient in the seasonal, spatial distributions of these EMTs and identified a distinct area of elevated biomass for several assemblages along the south shore of Long Island, NY. Taken together, these results characterize the community structure of the nearshore MAB and yield requisite information to support ongoing ecosystem-scale assessment and management activities for this region.

Introduction

Societies depend on marine ecosystems as a source of both market goods and non-market services, and the magnitude and diversity of the demands on these systems have increased as the human population and associated economies continue to expand (Holland et al. 2010, Tam et al. 2017). Concomitant with this growth, rising anthropogenic pressures have altered the structure and function of living marine resource communities inhabiting these systems, often jeopardizing sustained delivery of desired economic outputs (Link et al. 2020). For example, land use practices have increased turbidity, contaminants, and the extent of hypoxia in many adjacent marine ecosystems, disrupting systemic habitat utilization patterns and predator-prey dynamics (Craig 2012, Buchheister et al. 2013, Ortega et al. 2020). Climate change has altered the spatiotemporal distributions of marine species at broader scales as taxa shift poleward and to deeper waters in response to warming, which likely has impacted population vital rates, phenologies, and interactions (Nye et al. 2009, Doney et al. 2012, Langan et al 2021). Meanwhile, harvest activities have had perhaps the most direct and demonstrable effects on ecological communities through overfishing and sequential exploitation of target stocks (Essington et al. 2006), bycatch of non-target species (Kennelly 1995), fisheries-induced evolution (Walsh et al. 2006), and habitat alteration due to fishing practices (Collie et al. 1997). In response, governments have implemented fisheries management frameworks to reduce harvest and promote sustainable utilization of these resources.

Efforts to curb overfishing and rebuild overfished stocks in the US have achieved measurable successes since the passage of the Fishery Conservation and Management Act in 1976, and primarily have relied on single-species approaches to assess the status of living marine resources and develop regulations for the associated fisheries (Methot et al. 2014, NMFS 2022). A notable

shortcoming of this reductionist approach, however, is that while stock productivity is molded by an integrated series of drivers that broadly represent biophysical forcing, trophodynamics, and exploitation, single-species assessment and management typically only have considered the influence of exploitation (Link 2010, Gaichas et al. 2012). As harvest is constrained, natural environmental processes, trophic interactions, and non-fishing human impacts that include the aforementioned examples play a greater role in shaping population dynamics (Tyrrell et al. 2011, Fogarty 2014). Further, the breadth of current assessment and management activities primarily encompasses species targeted by fisheries, such that the structure, function, and dynamics of the broader ecological community remain unresolved even in many well-managed systems. The recognized need for a more holistic, integrated approach to the stewardship of fisheries resources has fueled a renewed interest in quantitative community ecology designed to support development of Integrated Ecosystem Assessments (IEA) and operationalization of Ecosystem Approaches to Fishery Management (EAFM) for Large Marine Ecosystems (LMEs) under US jurisdiction (Levin et al. 2014, Link et al. 2020, Muffley et al 2021).

The Mid-Atlantic Bight (MAB) is the southernmost Ecological Production Unit (EPU) in the Northeast US LME, and includes the continental shelf and estuarine ecosystems bounded by Cape Cod, MA and Cape Hatteras, NC (Lucey & Fogarty 2013). Given the broad and increasing intra-annual temperature ranges that occur in this region (Forsyth et al. 2015) and rather complex hydrography defined primarily by the Gulf Stream, remnants of the Labrador Current, and freshwater inputs to the estuaries, this EPU is a dynamic and productive system that supports a diverse ecological community and numerous fisheries. There is a wealth of data on living marine resources inhabiting the MAB, given the array of fisheries-independent monitoring surveys that have been sampling the shelf and estuaries of this system for decades (Howell & Auster 2012,

Politis et al. 2014, Latour et al. 2017, Langan et al. 2021). Early efforts to quantify community dynamics in the offshore waters (i.e., > 27 m isobath) of the shelf revealed distinct species assemblages that exhibited notable seasonal and spatial dynamics (Gabriel 1992), and these assemblages have been shifting primarily northeastward since the 1960s (Lucey & Nye 2010, Kleisner et al. 2016). Many faunal groups inhabiting the shelf also have experienced appreciable changes in relative abundance through time (Methratta & Link 2006, NEFSC 2022), while assemblages in Narragansett Bay (Collie et al. 2008, Langan et al. 2021), Long Island Sound (Howell & Auster 2012), and Chesapeake Bay (Jung & Houde 2003, Buchheister et al. 2013) have exhibited distinct spatiotemporal patterns shaped by natural and anthropogenic drivers. Taken together, these data on shelf and estuarine communities have formed the basis for the development of ecological metrics, particularly time-series indicators, that yield insight into the status of system structure and productivity, which in turn facilitate development of IEAs for the region (Muffley et al. 2021).

While the ecological communities of the estuarine and outer shelf regions of the MAB EPU have been the focus of intense research efforts, the structure and dynamics of species assemblages in the coastal ocean (i.e., < 27 m isobath) have yet to be explored in a holistic, synthetic manner given the lack of directed and consistent sampling throughout this zone prior to 2008. The inner shelf represents a valuable foraging, spawning, and nursery area for an array of species, and serves as a transitional ecosystem between offshore and estuarine environments (Malek et al. 2014). The physical oceanography of this region is dynamic, influenced by estuarine outflows, seasonal upwelling events, and rapid temperature changes characteristic of shallow water environments, and this system experiences additional direct and indirect anthropogenic disturbances comparable with those observed in estuaries, due to the proximity to

land (Farr et al. 2021). Given the unique nature of this coastal ocean, documented spatial variability of community-based, ecosystem indicators within the MAB EPU (Heim et al. 2021), and the recent establishment of a fisheries-independent trawl survey in this nearshore zone, an evaluation of the community dynamics in this ecosystem could yield valuable information needed to support ecosystem assessment efforts for the MAB.

As such, this investigation used 12 years of trawl survey data collected from the nearshore MAB to (1) quantify relative annual, seasonal, and spatial trends in aggregate biomass for several multispecies groups; (2) answer relevant ecological questions on the degree of coherence among the annual time-series, trends in productivity of these assemblages, and the influence of biophysical forcing and exploitation in shaping these trends; and (3) assess patterns in ecosystem usage through synthesis of the seasonal, spatial distributions of these groups. This approach provides insight into the dynamics of the ecological community in the coastal ocean of this EPU, yields several ecological indicators that reflect temporal patterns of system status, and generates baseline spatiotemporal information against which to evaluate future system states.

Materials & Methods

Field sampling

Data for this investigation were collected by the Northeast Area Monitoring and Assessment Program (NEAMAP) Nearshore Bottom Trawl Survey from 2008 – 2019. NEAMAP is a fisheries-independent monitoring program designed to sample the late juvenile and adult stages of the living marine resources inhabiting the MAB coastal ocean (Figure 1) through annual spring (Apr – May) and fall (Sep – Nov) cruises (ASMFC 2009). The sampling frame encompasses 12,097 km^2 and is bounded by the 6.1 m and 18.3 m depth contours between

Montauk, NY and Cape Hatteras, although sampling in the vicinity of Delaware Bay extends to 27.4 m to maintain spatial continuity. Survey activities in Block Island Sound (BIS) and Rhode Island Sound (RIS) occur from 18.3 – 36.6 m depth. Sites are selected from a grid of 772 ha sampling cells using a stratified-random design, where stratification is delineated by latitudinal or longitudinal regions and depth (6.1 – 12.2, 12.2 – 18.3, 18.3 – 27.4, and 27.4 – 36.6 m), and effort is allocated in proportion to the surface area of each stratum. NEAMAP sampled at 150 sites during each cruise, except during spring 2017 when only 63 sites were sampled.

A three-bridle, four-seam bottom trawl with a 48 m (c) fishing circle and 2.54 cm knotless lined codend is towed during daylight hours at 1.5 m s^{-1} for 20 min at each sampling location. NEAMAP uses a net mensuration system to collect trawl geometry data and ensure consistent gear performance on each tow. Vessel position also is recorded throughout trawl hauls and used to calculate tow distance, which is coupled with wingspread data to estimate the area swept by the trawl at a site (range: 0.012 – 0.033 km^2). While a suite of additional variables is recorded synoptically with each haul, the most relevant for this investigation were sample time of day and water depth (to the nearest 0.05 m). Catch data are collected on each species captured at a site, and include aggregate weight (to the nearest 2 g) and count, as well as length data (to the nearest 0.5 cm) for all or a subsample of individuals. NEAMAP animal handling protocols were approved by the William & Mary Institutional Animal Care and Use Committee (IACUC-2020-02-24-14108-jxgart).

Species assemblages

Species assemblages can be defined using an array of approaches, but often have been structured based on taxonomy, habitat associations, life history, morphology, or trophic mode. Here, species were grouped based on coarse similarities in taxonomy, morphology, and habitat

usage, and thus generally represent ecomorphotypes (EMT; *sensu* Compagno 1990). In designating these EMTs, consideration was given to maintaining alignment with the primary modes of fishing in this ecosystem and consistency with assemblage definitions used in previous studies of the Northeast US LME. All taxa sampled by NEAMAP were allocated among nine EMT assemblages that included three bony fish, four elasmobranch, and two invertebrate groups (Table S1 in the Supplement), and each species was assigned to an assemblage based on information in the literature (Murdy et al. 1997, Collette & Klein-MacPhee 2002). This qualitative approach was used to delineate EMTs in lieu of quantitative methods, such as cluster analysis or multivariate ordination, based on concerns that using NEAMAP catch data to both partition these assemblages and subsequently quantify the spatiotemporal patterns of these groups would represent a circular analysis.

All bony fishes collected by the survey were partitioned among the demersal fishes, pelagic fishes, and flatfish categories. These EMTs separated fishes that primarily inhabit the water column from those typically associated with the seafloor, divided the latter taxa based on general body form, and broadly aligned with the fishery categories in the MAB (Gaichas et al. 2014). Further, the assemblage designations for these bony fishes mirrored groupings used in prior studies that focused on quantifying the community structure of and developing ecosystem indicators for the offshore waters of the Northeast US LME (Link & Brodziak 2002, Methratta & Link 2006).

Elasmobranch species were grouped into the skate, ray, dogfish, and other shark EMTs. Note that while skates and rays share morphological similarities in that component species of both groups are dorsoventrally compressed, several skate taxa are harvested by directed commercial fisheries while rays usually are encountered as bycatch in this ecosystem (NEFSC

2020). The decision to evaluate skates and rays as separate EMTs was based on these fishery differences, and because temporal patterns of the skate assemblage had been previously assessed for Georges Bank, an adjacent EPU north of the MAB (Fogarty & Murawski 1998). Similar reasoning supported the decision to separate the dogfish and other shark EMTs. Dogfish included smaller-bodied sharks and, as with skates, the historical dynamics of this assemblage have been evaluated for Georges Bank (Fogarty & Murawski 1998). The species composing this EMT are also subjected to directed fisheries (NEFSC 2006, SEDAR 2015). In contrast, the other shark category encompassed medium-to-larger bodied animals that are either targeted by smaller-scale directed harvest, encountered as bycatch, or are prohibited to possess (Mandelman et al. 2008). Finally, the invertebrate taxa collected by NEAMAP were allocated among two EMTs that separated soft-bodied cephalopods from benthic arthropods (Link & Brodziak 2002).

Spatiotemporal modeling of ecomorphotype relative aggregate biomass

Annual trends and seasonal, spatial distributions of relative aggregate biomass were quantified for each EMT assemblage by employing model-based approaches commonly used to standardize fisheries-independent survey catch-per-unit-effort (CPUE) data (Maunder & Punt 2004). Site-specific CPUE for an assemblage was given by:

$$CPUE_k = \frac{\sum_{i=1}^{S} B_{i,k}}{a_k} \quad (1)$$

where $B_{i,k}$ was the biomass (kg) of the i^{th} species of the EMT collected at sampling site k, S represented the number of taxa included in that assemblage, and a_k was the area swept by the trawl.

Generalized additive models (GAMs) were used to relate CPUE data for each group to a suite of covariates recorded synoptically at the NEAMAP sampling sites. The GAM framework represents a flexible univariate approach that allows a response variable to be modeled as a

function of both parametric (similar to generalized linear models) and non-parametric components, where the latter incorporate smoothing functions for continuous covariates and thus permit a nonlinear relationship between the response and predictor variable that is informed by the available data (Wood 2017). Covariates considered in these GAMs included: year (categorical), season (categorical), depth (m, continuous), solar zenith (angle, continuous), and a season-coastal position interaction (km, continuous) that accounted for the seasonally-varying spatial distributions of each EMT. The coastal position variable was created given the need for a spatial metric, and because latitude and longitude are highly colinear within the NEAMAP survey area (Figure 1). The first step in creating this variable was to generate a near-continuous contour that mirrored the MAB coastal shoreline. Given that the inshore boundary of the NEAMAP sampling frame is comprised of sampling cells that follow this shoreline, the landward three positions of each of these inshore cells (i.e., south -, central -, and northwest for cells south of New York Harbor, and northwest, - central, and - east otherwise) were selected from the full survey sampling grid. Linear regression models were then fitted to consecutive pairs of these points, 1000 location predictions were generated between each pair, and predictions were concatenated to yield a near-continuous contour of ~1.4 m resolution at the inshore margin of the sampling frame that paralleled the coastal shoreline (Figure 1). This approach was akin to applying a LOESS smoothing spline to these inshore positions using a very small span width such that a curve (i.e., straight line) is fitted between each pair of points, resulting in a contour that tracks the shoreline (Zuur et al. 2007). Next, all sites sampled by NEAMAP were assigned to the nearest location on this contour. Finally, the distances along the contour from Cape Hatteras (the 0 km reference) to these assigned locations were calculated and used to represent the coastal positions (distances) of the sampling sites (*sensu* Nye et al. 2009).

All distance calculations were performed using the 'geosphere' package in R (v3.6.3, R Core Team 2020).

Some trawl hauls resulted in no catch for a given assemblage, and thus most of the EMT datasets contained several CPUE observations equal to zero. Initial attempts to fit GAM models for each group using the Tweedie distribution, which has positive mass at zero, were unsuccessful based on an evaluation of diagnostic plots and likely due to an insufficient number of zero observations in the EMT datasets (Shono 2008). A delta-GAM framework therefore was used to model CPUE of these assemblages (Lo et al. 1992). Delta-GAMs are hurdle models suitable for continuous response data that include zero values and contain two components; namely, a binomial model fitted to presence/absence data to estimate the probability of encountering the assemblage, and a conditional component fitted to CPUE data for the subset of sites where the EMT was encountered. Delta-GAM models were expressed as:

$$logit(\boldsymbol{\pi}) = \boldsymbol{X\beta} + \sum_{j=1}^{p} s_j\,(x_j) \qquad (2)$$

$$g(E(\boldsymbol{y})) = \boldsymbol{X\beta} + \sum_{j=1}^{p} s_j\,(x_j)$$

where $\boldsymbol{\pi}$ represented of probability of encountering the EMT, $E(\boldsymbol{y})$ was the expected value of the response vector CPUE for the subset of sites where the assemblage was captured, $\boldsymbol{X}$ was the fixed-effects model matrix containing observations of the categorical covariates, $\boldsymbol{\beta}$ was the vector of fixed-effects coefficients, s_j was the smoothing function for continuous covariate j, and g was the monotonic link function. Representatives of the demersal fishes and skate EMT assemblages were collected at approximately 99% of NEAMAP sites and thus were modeled using the conditional component of equation (2) only, where a small quantity (0.2 kg for demersal fishes, 10 kg for skate) was added to all catches given that the domains of the available response distributions were defined on the positive real line.

The delta-GAM models were fitted for each EMT using generalized additive models for location, scale, and shape (GAMLSS) regressions (Rigby & Stasinopoulos 2005). GAMLSS extends traditional GAM models by incorporating distributions of the response variable beyond the exponential family. For each EMT, the most supported distribution of the CPUE data in the conditional component of the model (or overall model for demersal fishes and skates) was identified by fitting a model with all candidate covariates (i.e., full model) using each available continuous distribution defined on the positive real line and evaluating competing forms using Akaike's Information Criterion (AIC; Akaike 1973, Burnham & Anderson 2002). Once the most supported conditional distribution was identified, four forms of both the binomial and conditional models were fitted (Table 1), and the most supported parameterization within each component was identified by AIC and evaluation of model diagnostic plots. Note that analyses of residuals yielded no evidence of appreciable spatial (correlogram) or temporal (partial autocorrelation function) autocorrelation in these EMT datasets (Zuur et al. 2009).

While the covariates included in the delta-GAM models for each assemblage were allowed to vary between the binomial and conditional components, given that the processes that influence probability of encounter and conditional relative abundance may differ (Lo et al. 1992, Rubec et al. 2016), the year covariate and the season-coastal position interaction were included in all candidate models, since an objective of this investigation was to evaluate annual trends in and the seasonal, spatial distributions of relative biomass for each EMT. Predictions of annual and seasonal-spatial probability of encounter and conditional CPUE were generated using marginal means (Searle et al. 1980), and these component values were multiplied to yield both an annual index of relative abundance and to estimate the seasonal, spatial distribution for each EMT. For the latter metric, CPUE was predicted at 1000 points spaced evenly over the domain

of the coastal position contour (~1 km resolution) for each season. Coefficients of variation (CVs) for these annual and seasonal, spatial predictions were quantified from 1000 nonparametric bootstrapped samples (Efron & Tibshirani 1993). Resampling was conducted with replacement and stratified by year to characterize uncertainty in annual CPUE indices and by season and survey region for seasonal, spatial relative abundance.

Coherence among and drivers of annual trends

Dynamic factor analysis (DFA) is a multivariate, dimension reduction technique designed to extract common trends (i.e., latent variables) from a suite of relatively short, nonstationary time-series, evaluate coherence among the time-series by illuminating relationships with these trends, and quantify the influence of measured covariates on the collection of time-series (Zuur et al. 2003). Because the DFA framework is structured to incorporate time-series information, survey catch data and hypothesized covariates must be summarized on some time interval (often annual) prior to analysis (Nye et al. 2010, Peterson et al. 2017). Thus, DFA was used in this investigation to synthesize the commonalities among and evaluate the influence of biophysical forcing and exploitation covariates on the time-series of annual CPUE predictions generated for the nine EMTs from the delta-GAMs. The DFA model was given by:

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

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

where $\boldsymbol{y}_t$ was the vector (9 x 1) of the standardized (Z-scored) CPUE predictions for the nine EMTs in year t, $\boldsymbol{\alpha}_t$ the vector (r x 1) of r common trends ($r < 9$) modeled as stochastic random walks, $\boldsymbol{\Gamma}$ the matrix (9 x r) of EMT-specific loadings, $\boldsymbol{x}_t$ the vector (q x 1) of q covariates, $\boldsymbol{D}$ the matrix (9 x q) of covariate effects, and $\mathbf{R}$ and $\mathbf{Q}$ the variance-covariance matrices associated with the observation error vector $\boldsymbol{\varepsilon}_t$ (9 x 1) and process error vector $\boldsymbol{\eta}_t$ (r x 1), respectively, both of

which were assumed to follow a multivariate normal distribution with mean zero. **Q** was set to the identity matrix so that the model parameterizations were identifiable (Zuur et al. 2003).

Twelve annualized covariates representing physical forcing, biological processes, and fishery removals were evaluated within the DFA models. Specifically, the hypothesized physical drivers of the MAB ecological community included the principal components-based winter (Dec – Mar) North Atlantic Oscillation (NAO) index of atmospheric pressure differences between Iceland and the Azores (Hurrell et al. 2003), the Atlantic Multidecadal Oscillation (AMO) which quantifies decadal-scale variability in sea surface temperature, and the Gulf Stream Index (GSI) which measures the position of the north wall of this boundary current and has been shown to impact physical processes on the shelf (Joyce et al. 2019). The volume of the MAB Cold Pool (MCP) was included as this feature can affect recruitment (Miller et al. 2016), while the influence of mean sea surface temperature in the MAB at both annual (SSTA) and seasonal scales (winter: Jan – Mar [SSTWI]; spring: Apr – Jun [SSTSP]; summer: Jul – Sep [SSTSU]; fall: Oct – Dec [SSTFA]) was also evaluated (Reynolds et al. 2007). The primary production anomaly (PPD) ratio measures annual fluctuations in primary productivity (NEFSC 2022), while the small-large copepod (SLC) ratio characterizes the size-structure and quality of the zooplankton community (Perretti et al. 2017), and these two metrics were used to explore bottom-up biological controls on the MAB assemblages. Finally, total commercial landings (COM) served as a measure of fishing pressure and was used to evaluate top-down controls (NEFSC 2022). Given that each of these processes could impact faunal recruitment and availability to the survey, and that NEAMAP primarily samples the late juvenile and adult stages of species in the MAB, all physical and biological covariates were lagged 0, 1, and 2 years, and

exploitation was lagged 0 and 1 year. These predictor variables were Z-scored prior to inclusion in the DFA models.

In the DFA framework, the **R** matrix specifies the variance and covariance structure among time-series (Zuur et al. 2003). The mean of the annual CV estimates generated from the bootstrapped delta-GAMs was calculated for each EMT and incorporated as the diagonal elements of the **R** matrix to propagate time-series uncertainty (Peterson et al. 2021). Models including one, two, and three common trends were fitted and included either no covariate, a single covariate, or a lagged covariate. This approach yielded 114 candidate DFA models. Model selection occurred by evaluating AIC corrected for small sample size (AICc) to identify empirically supported forms, where those with ΔAICc < 10 were considered further (Latour et al. 2017). The FitRatio, which is the ratio of the sum-of-squared residuals and sum-of-squared observations ($\sum \hat{\boldsymbol{\varepsilon}}_t^2 / \sum \boldsymbol{y}_t^2$) for the DFA model fits to the EMT time-series, was evaluated for each aggregate group as well as across these EMTs (i.e., Mean Fit) for the remaining models and coupled with a visual evaluation of residuals to identify the 'final' model. Statistical significance of factor loadings and covariate coefficients was assessed for this model using 95% confidence intervals (CIs), and the fits of this DFA model to each EMT time-series represented a suite of ecosystem indicators for the nearshore MAB (e.g., Nye et al. 2010, Latour et al. 2017).

Synthesis of seasonal, spatial distributions

Principal component analysis (PCA) was applied to the predicted seasonal, spatial distributions of CPUE generated for the nine EMTs from the delta-GAM models to synthesize spatiotemporal patterns of these assemblages. PCA is an ordination technique routinely used to achieve dimension reduction and signal isolation for complex, multivariate datasets, that relies on singular value decomposition to quantify principal components [PCs] as linear combinations

of the original variables, such that a subset of these PCs capture an appreciable proportion of the variability in the dataset (Zuur et al. 2007). While the application of PCA to observed (i.e., 'raw') species abundance information is usually not recommended given the typical dominance of zero observations and violation of multivariate normality in these datasets (Clarke et al. 2014), model-derived, ecological community data are much less prone to these issues. As such, the use of PCA for exploring patterns in ecological metrics generated using various analytical approaches is appropriate and has proven valuable when assessing system status in the Northeast US LME (Link et al. 2002).

In this investigation, the input dataset for the PCA was a 1000 x 16 site-by-assemblage matrix, where the 16 columns represented a given EMT-season combination (spring data on rays and other sharks excluded, see Results for details), and rows were predictions of CPUE at each of the 1000 locations along the coastal contour. The relationships among factor loadings (representing EMT-season combinations) and scores (representing locations along the contour) were visualized using a correlation biplot (Zuur et al. 2007). Uncertainty in the factor loading vectors for each EMT-season combination, which represented gradients in relative aggregate biomass for each assemblage, were characterized using a nonparametric approach that incorporated bootstrapped predictions from the GAMs (Mehlman et al. 1995). All statistical analyses were performed using the R software program (v3.6.3, R Core Team 2020). Packages 'gamlss' (Rigby & Stasinopoulos 2005), 'MARSS' (Holmes et al. 2018), and 'stats' were accessed to fit the delta-GAMs, DFAs, and PCA, respectively.

Results

Ecomorphotype catch summaries

NEAMAP completed 24 survey cruises and collected data at 3532 sites from 2008 – 2019. A total of 178 species was encountered, and the aggregate catch was comprised of 13,436,602 individuals weighing 851.7 t. The demersal fishes category included 82 species and was encountered at 99.5% of the sites sampled. This EMT encompassed the largest number of taxa and had the highest frequency of occurrence among all groups, which was not unexpected given the bottom-tending, mobile nature of the sampling gear. Although previous studies of marine communities based on bottom trawl survey data have excluded information on pelagic fishes due to catchability concerns (e.g., Buchheister et al. 2013), the high-rise nature of the NEAMAP trawl and sampling of relatively shallow depths combined to yield appreciable, consistent catches of this assemblage. A total of 37 pelagic fish species was collected across 96.4% of NEAMAP trawls. Although only four species of skate were sampled, this group was quite ubiquitous as the frequency of encounter was 98.8% and second only to demersal fishes.

Flatfishes were collected at 86.1% of sites and included 11 species. The five taxa that composed the cephalopod EMT were captured at a frequency (88.8%) similar to that of the flatfishes. Benthic arthropod was a relatively diverse EMT comprised of 17 taxa and encountered in 73.9% of hauls, while dogfishes included only two species that were caught at 68.3% of sites. Encounter frequencies of rays (nine species) and other sharks (11 species) were relatively low, as these EMTs were collected in 28.2% and 14.8% of trawl hauls, respectively. Both of these EMTs were rarely encountered during NEAMAP spring surveys, and thus the early season catch data on these assemblages were excluded from subsequent modelling efforts. Rays were captured in 46.8% of tows that occurred in the fall, while other sharks were sampled at 23.8% of these sites, and the fall species compositions for each of these EMTs mirrored those observed at the annual scale.

Spatiotemporal modeling of ecomorphotype relative aggregate biomass

GAM models were successfully fitted for each of the nine EMTs, as no convergence or estimation problems occurred for any of the candidate parameterizations. The generalized beta type-2 (GB2) was the most supported distribution for modelling non-zero CPUE data associated with demersal fishes, pelagic fishes, benthic arthropods, and skates, while the Box-Cox *t* (BCTo) distribution was chosen for the flatfish, cephalopod, dogfish, and ray EMTs (Table S2 in the Supplement). The non-zero CPUE data for other sharks was assumed to follow the generalized inverse gaussian (GIG) distribution. The most supported parameterizations for each assemblage were considered reliable for estimating the annual trends and seasonal, spatial distributions of these EMTs based on a thorough evaluation of the associated model diagnostics, which included worm plots (detrended quantile-quantile plots), histograms of residuals, and relationships between residuals and fitted values as well as between residuals and the covariates.

Model M_1, the full model (Table 1), was the most supported parameterization for both the binomial and conditional models for the flatfish, benthic arthropod, and dogfish assemblages, as well as for the binomial component of pelagic fishes and the conditional model for cephalopods (Table S3 in the Supplement). This formulation also yielded the lowest AIC values for both the demersal fish and skate EMTs. In each of these cases, depth and solar zenith explained appreciable variation in the encounter or non-zero CPUE of these EMTs. The selected parameterization for the binomial component of the cephalopod model and conditional component of the pelagic fishes model included the depth covariate, but not solar zenith (i.e., M_2). Given that the datasets for the ray and other sharks EMTs were restricted to the fall cruises, model M_6 received the most empirical support for both components of the ray model and for the

binomial component for other sharks, while M_8 was chosen for the conditional model of the latter group.

Coefficients of variation (CVs) associated with predicted annual CPUE estimates were less than 0.33, indicative of good precision, for all of the EMTs except pelagic fishes, rays, and other sharks. For these three groups, maximum annual CVs were 0.40, 0.41, and 0.51, respectively. The CVs of the spatial predictions during spring ranged from 0.09 to 0.63 and were between 0.08 and 0.91 for most EMTs in fall. The CVs associated with the other sharks CPUE during fall were as high as 9.63 in the northern extent of the survey range, likely due to the sporadic catches of relatively few large animals that occur in this region during fall.

Coherence among and drivers of annual trends

The DFA model receiving the most empirical support and thus used for inference included three common trends and SSTWI (i.e., MAB mean sea surface temperature during winter; Figure 2) as a covariate. Although a competing model with three common trends and NAO had a ΔAICc value of 0.4 and a slightly lower Mean Fit (Table S4 in the Supplement), FitRatios of DFA model fits for seven out of nine EMTs were larger than those from the selected model, and thus this model was not considered further. The first common trend indicated a notable shift in CPUE from slightly above average prior to 2014 to a period of lower values through 2017 (Figure 3a). Relative aggregate biomass then increased throughout the remainder of the time-series. The factor loading of demersal fishes on this common trend was statistically significant and positive, while those of the cephalopod, ray, and other shark assemblages were significant and negative, revealing contrasting responses of relative aggregate biomass over the 2008-2019 period between the demersal fishes and these latter three groups (Figure 3b). The SSTWI covariate had a significant, positive effect on the CPUE of the demersal fishes, and the

influence on the ray group also was positive and nearly significant (ray 95% lower confidence limit [LCL]: -0.06; Table S5 in the Supplement). The DFA model fit to demersal fishes showed a gradual decline early in the time-series, a peak in 2012 that was followed by a sharp decrease from 2013 – 2014, and then a gradual increase through 2019 with a secondary peak during 2016 (Figure 3c). Fits to both the cephalopod and other sharks EMTs exhibited increasing trends in relative abundance between 2008 and 2019 and, in contrast with demersal fishes, the CPUE of both assemblages spiked in 2014. The relative aggregate biomass of these two groups also was high in 2017. The abundance of the ray group varied throughout the time-series with little discernable trend. These model fits represent a new suite of ecosystem indicators for these EMTs in the nearshore MAB ecosystem. Fits to the demersal fishes, cephalopod, and other shark EMTs were good as FitRatios ranged from 0.12 to 0.21, while that of the rays was relatively poor at 0.66 and likely responsible for the equivocal trend.

Common trend two reflected below-average CPUE values during 2008 and 2009, a somewhat parabolic trend between 2009 and 2015 where relative aggregate biomass increased sharply and then declined gradually, and a subsequent stable period through 2019 (Figure 4a). The three EMTs with significant factor loadings on this common trend again displayed conflicting patterns in their time-series of CPUE. The factor loading of pelagic fishes was positive, and those of the benthic arthropods and dogfishes were negative (Figure 4b). The DFA model fit for pelagic fishes exhibited a cuneate trend from 2009 to 2015, and the highest CPUE for this assemblage occurred during 2012 (Figure 4c). Similar to the demersal fishes, pelagics were abundant during 2016 and this group was significantly and positively influenced by SSTWI. Unlike the demersal fishes, however, the abundance of this EMT mostly declined after 2012. Model fits indicated that the highest CPUE values for dogfishes occurred during the early

and late periods of the time-series, with below-average values during most of the intervening years. The relative aggregate biomass of benthic arthropods peaked in 2009, and in contrast with pelagic fishes exhibited consistently low CPUE between 2010 and 2013. A secondary peak occurred in 2014 and was followed by a steady decline. The FitRatios of the ecosystem indicators for these three EMTs ranged from 0.07 – 0.41, indicative of good model fits.

The third common trend showed a slight increase at the beginning of the time-series, followed by a consistent decline thereafter (Figure 5a), and both the flatfish and skate EMTs were significantly and positively coherent with this trend (Figure 5b). Although the DFA model fits for these groups displayed notable declines through time, the exact patterns exhibited by these assemblages varied (Figure 5c). The rate of decrease for the flatfish ecosystem indicator was relatively gradual and somewhat consistent after 2009. Conversely, while the skate indicator also trended lower after 2009, CPUE showed peaks in both 2012 and 2016, likely due to the influence of the SSTWI covariate on this group, which was positive and nearly significant (skate 95% LCL: -0.01; Table S5 in the Supplement). DFA model fits for both of these EMTs were good, as the FitRatios associated with the flatfishes and skates were 0.07 and 0.11, respectively.

Synthesis of seasonal, spatial distributions

The PCA applied to the seasonal, spatial predictions of CPUE for the nine EMTs revealed appreciable differences in the locations of the nearshore MAB associated with the largest relative aggregate biomasses of these groups as well as seasonal contrasts within most assemblages. The first principal component (PC1) accounted for 37.6% of the variation in the seasonal, spatial distributions of these EMTs and effectively divided the northern and southern areas of this ecosystem at approximately Delaware Bay (Figure 6). PC2, which delineated a gradient that separated the boundaries of this EPU from its central region, captured 28.7% of the

variance in the seasonal distributions of the groups. During fall, the CPUE of demersal fishes, rays, and other sharks increased toward the southern zone of the nearshore MAB and generally peaked in the vicinity of Oregon Inlet, NC. Relative aggregate biomass of demersal fishes was highest near the northern and southern boundaries of this ecosystem in spring as indicated by the central position of and relatively large uncertainty associated with the factor loading of this group on PC1, along with the strong negative loading on PC2.

Spatial patterns of relative abundance for pelagic fishes during fall mirrored those of the demersal category in spring, and while spring catches of the pelagic assemblage were also elevated in the northern and southern extents of this EPU, relative abundance of this EMT tended to be greater in RIS (i.e., between Block Island, RI and Martha's Vineyard, MA). The CPUE of benthic arthropods peaked during both seasons in the vicinity of Delaware Bay, and the dogfish group was also most abundant in this area during spring. Cephalopod relative aggregate biomass was greatest between central Long Island and about Delaware Bay in spring, while the abundance of dogfishes was highest in this area during fall, indicating that these EMTs exhibit alternating seasonal use of this area. The south shore of Long Island, and particularly the region between Moriches Inlet, NY and Montauk, represented a hotspot of elevated biomass for skates, flatfishes, and cephalopods. The gradient of CPUE for skates peaked in this area during both seasons, while this zone was associated with the largest abundances of flatfishes in spring and cephalopods during the fall season. The relative aggregate biomass of flatfishes was highest west of Moriches Inlet in the fall.

Discussion

This investigation quantified and synthesized temporal and spatial patterns of the ecological community inhabiting the nearshore MAB, a system that serves as a vital spawning, nursery, foraging, and refuge habitat for an array of economically and ecologically important living marine resources (Wuenschel et al. 2013, Malek et al. 2014). The annual time-series and seasonal-spatial distributions of relative aggregate biomass quantified for the nine EMTs using delta-GAM modelling provided insights into spatiotemporal trends in the productivity and partitioning of biomass among these groups (Buchheister et al. 2013). These patterns both illuminated the community structure of the EMTs and complimented prior ecological investigations that focused on the offshore and estuarine environments of this EPU. Identifying the commonalities among and drivers of the annual trends using DFA offered a key framework for summarizing the often-overwhelming number of time-series available for consideration when evaluating ecosystem status. This approach effectively reconciled seemingly disparate temporal trends among multiple species assemblages while yielding a new suite of ecosystem indicators for this system. The synthesis of EMT seasonal, spatial distributions using PCA represented a novel, albeit somewhat coarse, system-level approach to quantifying community spatial gradients that could be used by decision makers charged with mitigating risks to important marine habitats and balancing trade-offs among multiple use sectors in marine spatial planning activities.

Evaluating the spatiotemporal patterns of species assemblages in an ecosystem first requires the implementation of a classification scheme to group taxa based on similarities across traits of interest. The approach used to define these assemblages represents a vitally important decision, as it both influences the perceived structure of the ecosystem and shapes inference on system processes (Frost et al. 1992). To our knowledge, none of the myriad approaches commonly used to delineate assemblages has been identified as superior to the others (Link &

Brodziak 2002) and thus, much like the EAFM process itself (Link 2010), selecting an appropriate grouping framework involves the consideration of trade-offs. However, because these assemblages often serve as the basis for developing ecosystem metrics, including time-series indicators that underpin ecosystem assessments, it is critical that the approach used to define these groups maintains coherence with as much of the established guidance for indicator development as possible (e.g., Dale & Beyeler 2001, Rice & Rochet 2005). The common themes of this guidance are that the measures be: (1) based in ecological theory; (2) relatively inexpensive to produce; (3) generated consistently over time; (4) responsive to abiotic, biotic, and anthropogenic drivers; and (5) easily understood by the scientific community, fishery managers, and stakeholders, among others.

All species collected by NEAMAP from 2008 to 2019 were assigned to one of nine EMTs, which effectively mirrored assemblage definitions used previously to evaluate community status in the broader Northeast US LME, although the groupings in these prior studies were not described as EMTs (Fogarty & Murawski 1998, Link & Brodziak 2002, Methratta & Link 2006). This EMT framework follows many of the themes associated with the development of informative and reliable ecosystem metrics. First, this classification system allowed for the incorporation of all taxa sampled by NEAMAP which, although the contributions of some species to the aggregate biomass of their assigned EMT was relatively small, was critical to support a holistic evaluation of the spatiotemporal patterns of the entire ecological community as represented by the survey trawl (Theme 1 [T1] listed above; Methratta & Link 2006). Assigning taxa to the nine EMTs was based on information available in the literature and thus was low-cost (T2), and unlike with other modes of classification, species EMT assignments likely are robust to systemic changes (e.g., demersal fishes remain demersal) which should

promote longer-term consistency in the species composition of the resulting metrics (T3). These EMTs also generally align with the fisheries operating in the MAB ecosystem (Gaichas et al. 2014), and therefore are likely to be responsive to fisheries management measures (T4) and intuitive to fishery managers, stakeholders, and the public (T5). Note that further subdividing these nine EMTs to gain greater alignment of assemblages with MAB fisheries (e.g., divide demersal fishes into warm- and cold-adapted species), perhaps by applying DFA at the species-level to identify these groupings, represents a potentially fruitful area of future research. Finally, and perhaps most importantly, this relatively simple EMT classification approach can be implemented for any ecosystem with at least a modest data collection program. As the value of EAFM gains greater appreciation and efforts to quantify ecosystem dynamics become more widespread, developing standard metrics (and first, assemblage delineations) based on relatively simple criteria and minimal data requirements will help to facilitate cross-system comparisons meant to illuminate common themes in ecosystem structure and function (Link & Marshak 2019).

As noted above, the choice of an assemblage framework to serve as the basis for quantifying ecological communities and developing ecosystem indicators involves trade-offs. Given similarities in habitat usage within each assemblage, spatiotemporal abundance patterns of EMTs are expected to be responsive to environmental cues and harvest pressures. Note, however, that these groupings likely would mask any trends in the ecological community driven primarily by changing trophic interactions, since most of the EMTs contain a myriad of both predators and prey as well as potential competitors (Garrison & Link 2000, Link & Auster 2013). The classification framework currently underpinning aggregate biomass indicator development for the offshore waters of the MAB shelf relies on the trophic guild concept as the basis for

assemblage definition (Garrison & Link 2000, NEFSC 2022), which offers the advantage of being more likely to detect trends driven by changes in these species interactions. Drawbacks of the trophic guild approach include increased costs to generate the diet data required to delineate these groups and, at times, misalignment of these assemblages with established fisheries and associated management. The question as to which of these assemblage frameworks is preferable for quantifying ecological communities in support of EAFM is not new (Link & Brodziak 2002). Because these two approaches focus on different aspects of an ecosystem, we contend that both should be considered in the development and maintenance of EAFM, with research directed toward synthesis of the metrics generated from each.

The annual trends and seasonal, spatial distributions of relative aggregate biomass were quantified for the nine EMTs using delta-GAMs. Given the prevalence of nonlinear relationships between community measures and hypothesized synoptic localized drivers, recognition of the value of GAMs in standardizing and quantifying ecosystem metrics is increasing (Buchheister et al. 2013, Large et al. 2015). The availability of a broad array of candidate distributions in GAMLSS represented a key advancement over frameworks that limit choices to the exponential family of distributions (Rigby & Stasinopoulos 2005), as the ability to model CPUE data using the GB2, BCTo, and GIG distributions yielded marked improvements in model diagnostics, and presumably greater accuracy and precision in predicted measures of central tendency. This framework also permits the modelling of scale (variance) and shape (skewness and kurtosis) as a function of covariates which, although based on model diagnostics was not necessary in this study, could prove useful in other applications and thus represents a valuable area of future research in the development of ecosystem indicators.

Evaluating trends in and patterns of relative aggregate biomass for species assemblages has received criticism following the revelation that these metrics are prone to bias and can be hypersensitive when catchability of the component species is not constant (Kleiber & Maunder 2008). The catch data underpinning this study were derived from a fisheries-independent monitoring program that has maintained consistency in both the fishing system and sampling protocols since its inception, such that the assumption of constant species-specific catchability over space and time was reasonable and thus any bias or hypersensitivity in these metrics likely was minimal. Indeed, preliminary analyses showed that the spatiotemporal patterns in the aggregate biomass indicators were consistent with those of many component species within these EMTs, and the value of such metrics for quantifying ecosystem structure and function has been well-documented (Link et al. 2002, Methratta & Link 2006, Buchheister et al. 2013, Latour & Gartland 2020), meaning that the aforementioned concerns were outweighed by the need to gain insight into the spatiotemporal patterns of the community assemblage in this system. Likewise, the restricted sampling frame and short time-series of available data represented potential constraints on the applicability of this investigation. While generating information on ecosystem status at the LME (or at least EPU) level had been assumed to be an appropriate scale to support IEAs, delineating system metrics such as assemblage indicators at multiple spatial scales congruent with the hierarchal structure of the ecosystem (e.g., estuary vs. coastal ocean vs. offshore shelf) may be more relevant to these IEA efforts (Heim et al. 2021). Following guidance to avoid inference based on statistically significant annual trends in time-series of less than 30 years (Hardison et al. 2019), this study instead employed an approach designed for use with short, nonstationary time-series typically associated with relatively new fisheries-independent monitoring programs.

The time-series of relative aggregate biomass for the EMTs inhabiting the nearshore MAB were characterized by three common trends, which effectively represented latent, unmeasured variables that influenced the relative abundances of these assemblages (Zuur et al. 2003). The first common trend was characterized by an abrupt shift from positive to negative values during the 2013 – 2014 timeframe, which likely reflected a severe, system-level disturbance that impacted nearly half of the assemblages. Because SSTWI was included in the model that received the most empirical support, the effect of this covariate was removed from all of the common trends, and as such the source of this perturbation remains unresolved. An ideal DFA model would include multiple identifiable covariates that explain nearly all of the variation in the time-series of interest, yielding a single common trend with no prominent features (Zuur et al. 2003). Attempts to include more than one covariate in a DFA model resulted in convergence issues that likely were due to the relatively short time-series of available data, and thus represented a limitation of this analysis. The second common trend was approximately parabolic during the first half of the time-series, while the third reflected a steady decline. Each of these latent variables was associated with multiple EMTs, meaning that the annual indices of these nine assemblages primarily reflected three relatively simple trends.

To be clear, the DFA model fits to the EMT time-series, and not these common trends, constituted the new suite of ecosystem indicators generated for the nearshore MAB from this investigation. Nevertheless, DFA common trends could prove valuable to assessments of ecosystem status in support of EAFM, as they group ecosystem indicators by identifying coherence (or conflict) among these metrics and provide synthetic information on the underlying patterns in the groups of indicators. Efforts to assess system status and implement EAFM are becoming overwhelmed by the myriad of indicators that must be considered (Bundy et al. 2019).

The ability to synthesize the information content of multiple indicators based on a smaller number of latent measures (common trends) therefore represents a critical step towards promoting efficient ecosystem assessment and management activities, and one that likely will become more important as the number of indicators available for consideration continues to increase. Further, although this investigation was unable to identify the three latent covariates driving the annual trends in EMT relative aggregate biomass, information provided by the common trends could be used in a qualitative manner during ecosystem assessments to identify events such as perturbations (e.g., first common trend) or other concerning patterns (e.g., third common trend) that should be prioritized for further exploration. Process-oriented studies designed to unmask the covariates underlying these common trends represent a very important future direction for investigations focused on understanding community dynamics in the MAB.

The factor loadings of the EMTs associated with these three common trends provided insight on the responses of assemblage time-series to system-level forcing (Zuur et al. 2003, Nye et al. 2010). Notably, the seven groups associated with the first and second common trends showed conflicting patterns in relative abundance during the study period. Trends in relative aggregate biomass for the cephalopod, ray, and other shark EMTs generally opposed that of the demersal fishes category, while the pelagic fishes trend contrasted with those of the benthic arthropod and dogfish groups. A central tenet of ecosystem-based management is that trade-offs must be evaluated to sustain an optimized delivery of desirable market goods and nonmarket services from these systems (Link 2010). Quantifying these conflicting responses among EMTs in the nearshore MAB illuminated some of the potential trade-offs, and as such highlighted the value of DFA as a synthetic tool for suites of ecosystem indicators, even when these indicator time-series are relatively short. The annual patterns of the flatfish and skate assemblages were

not in conflict, but instead both mirrored the third common trend, and the general decline in the relative abundance of these two EMTs may have reflected actual trends in the abundances of the component species (Perretti & Thorson 2019, NEFSC 2020), changing availability to the NEAMAP survey as these taxa respond to climate change (Nye et al. 2009, Morley et al. 2018), or a combination of these hypotheses. The statistically significant influence of SSTWI on the demersal and pelagic fishes EMTs, and near significance for skates and rays, was somewhat unexpected given that NEAMAP samples these assemblages during spring and fall. While it is plausible that warmer winter temperatures trigger earlier migrations into the nearshore MAB that in turn yield increased catches during spring, trends in aggregate biomass were generated annually for most EMTs and were limited to the fall for rays, indicating that winter temperatures may drive observed community patterns at an annual scale in this coastal zone.

As noted previously, the DFA model fits to the time-series of EMT relative aggregate biomass represent a new suite of ecosystem indicators for the nearshore MAB meant to support the continued development and implementation of EAFM for this EPU. An array of indicators has been quantified for this ecosystem and are updated annually in Mid-Atlantic State of the Ecosystem (SOE) reports (NEFSC 2022). Following the IEA framework for EAFM, the indicators in this report are used to inform risk assessments, where the highest risk elements are explored further through the development of conceptual models, and the performance of measures designed to mitigate these risks is tested via management strategy evaluation (Gaichas et al 2016, Muffley et al. 2021). While the time-series of many of the current ecosystem indicators span decades, several measures are reported on time-scales that are equal to or shorter than those of the EMT indicators developed in this study, and have been included in risk assessments. As such, it is anticipated that these EMT ecosystem indicators could be

incorporated into the SOE reports, where they would then be used during the annual risk assessment process specifically to evaluate ecosystem status relative to the objective of maintaining system biomass (NEFSC 2022). A 'high risk' designation could result in the development of conceptual models and testing of management strategies to minimize the identified risk. Continued monitoring of these indicators would provide feedback on the efficacy of implemented management measures, and thus aid in advancing EAFM in the MAB. Given that risk assessments currently are based on somewhat qualitative evaluations of indicator trends, developing target (i.e., desired state) and threshold (i.e., state to be avoided) reference points for these metrics, including those generated from this investigation, is an important area of future research (Large et al. 2015).

Much of the research associated with the development of ecosystem metrics for species assemblages has focused on evaluating inter-annual trends in these measures, whereas quantifying seasonal patterns and spatial variability of these groups have received less attention (Buchheister et al. 2013). A clear north-to-south gradient was evident in the seasonal community structure of the nearshore MAB, with the nuance that assemblage compositions at the ecosystem boundaries generally were more similar relative to the central regions. Interestingly, the relative aggregate biomass of most EMTs appeared to cluster near the entrances to estuaries (i.e., Oregon Inlet for Pamlico Sound, NC; the mouth of Delaware Bay, and Moriches Inlet associated with the Moriches Bay estuary). A host of species inhabiting the MAB utilize estuaries during the warmer months (Murdy et al. 1997, Able & Fahay 2010), such that these results may reflect the composite distributions of EMT component species as they undertook seasonal migrations to (spring) or from (fall) these systems. Alternatively, estuarine outflows may create areas of elevated habitat suitability in the coastal ocean, and the implementation of multispecies

ecological niche modelling to explore the distributions uncovered here from a mechanistic perspective represents a promising area of future research (Roberts et al. 2022). It is worth noting, however, that none of the factor loadings of the EMT seasonal-spatial distributions were associated with Chesapeake Bay, one of the largest estuaries in the United States. These findings are consistent with documented, appreciable declines in the relative usage of this system by several seasonally resident taxa in recent years (Schonfeld et al. 2022).

The synthesis of the seasonal, spatial distributions of the EMTs was based on fisheries-independent bottom trawl data, which necessitated a somewhat coarse treatment of these distributions given that each trawl haul likely sampled over a range of unique bottom types and other environmental conditions (Sullivan et al. 2006). Nevertheless, this information on the general distributions of these assemblages could be used to inform the development of more-refined, future investigations of multispecies or assemblage essential fish habitat either by directing the focus of these studies toward areas associated with large relative abundances of several EMTs or those where alternating seasonal use of a region occurs. Further, given the expected continuing impacts of climate change and increased uses of the MAB ecosystem for non-fishing human activities (Methratta 2020), these seasonal, spatial distributions could be valuable to future climate vulnerability assessments and in the context of marine spatial planning activities, both of which contribute to advancing EAFM (Malek et al 2014, Farr et al. 2021). For example, the region along the south shore of Long Island, NY, and specifically along the eastern half of the island, appeared to represent a distinct subunit of the nearshore MAB ecosystem that supported elevated biomass of three EMTs across both spring and fall. This aggregation of multiple assemblages, coupled with the declining trends in the ecosystem indicator time-series of two of these three EMTs, suggests that this zone could be especially sensitive to the impacts of

climate change and should receive particular consideration by decision-makers tasked with managing current and planned use sectors in this area.

Fishery managers in the MAB have expressed the desire to move toward EAFM at a rate that is commensurate with the available science (Muffley et al. 2021). Overall, this investigation provided a classification scheme for generating ecological metrics of species assemblages that required minimal auxiliary information, built on previous efforts, and was designed to promote consistency and comparisons among ecosystems. Synthesizing the spatiotemporal patterns in the relative aggregate biomass of the resulting assemblages yielded, to our knowledge, the first integrated evaluation of the structure of the nearshore MAB ecological community and thus much-needed baseline information against which to evaluate future system states. Further, when coupled with comparable ecosystem information derived from the offshore waters and estuaries of this EPU, these results generate a holistic characterization of this ecosystem that likely will prove instrumental to advancing EAFM in the MAB.

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Table 1. Generalized additive model parameterizations evaluated for the analysis of presence/absence and conditional catch-per-unit-effort data on nine ecomorphotypes collected by the Northeast Area Monitoring and Assessment Program (NEAMAP) from 2008 – 2019. Model selection for the demersal fishes, pelagic fishes, flatfish, skate, dogfish, cephalopod, and benthic arthropod groups used parameterizations M_1 – M_4, and for the ray and other shark categories used M_5 – M_8.

Model	Covariates
M_1	Year, Season, Season*Coastal Position, Depth, Solar Zenith
M_2	Year, Season, Season*Coastal Position, Depth
M_3	Year, Season, Season*Coastal Position, Solar Zenith
M_4	Year, Season, Season*Coastal Position
M_5	Year, Coastal Position, Depth, Solar Zenith
M_6	Year, Coastal Position, Depth
M_7	Year, Coastal Position, Solar Zenith
M_8	Year, Coastal Position

Figure 1. Sampling frame of the Northeast Area Monitoring and Assessment Program (NEAMAP) Nearshore Bottom Trawl Survey. Boundaries of the 17 regional strata (numbered 1-17, north to south) are provided by the black lines, while the four depth strata are denoted by the orange shading. The coastal position line developed for this investigation is provided in blue and includes select locations along the coast for reference. CH: Cape Hatteras, NC; OI: Oregon Inlet, NC; CB: Chesapeake Bay; CI: Chincoteague, VA; DB: Delaware Bay; BN: Barnegat Inlet, NJ; NY: New York Harbor; MI: Moriches Inlet, NY; MK: Montauk, NY; BI: Block Island, RI; MV: Martha's Vineyard, MA.

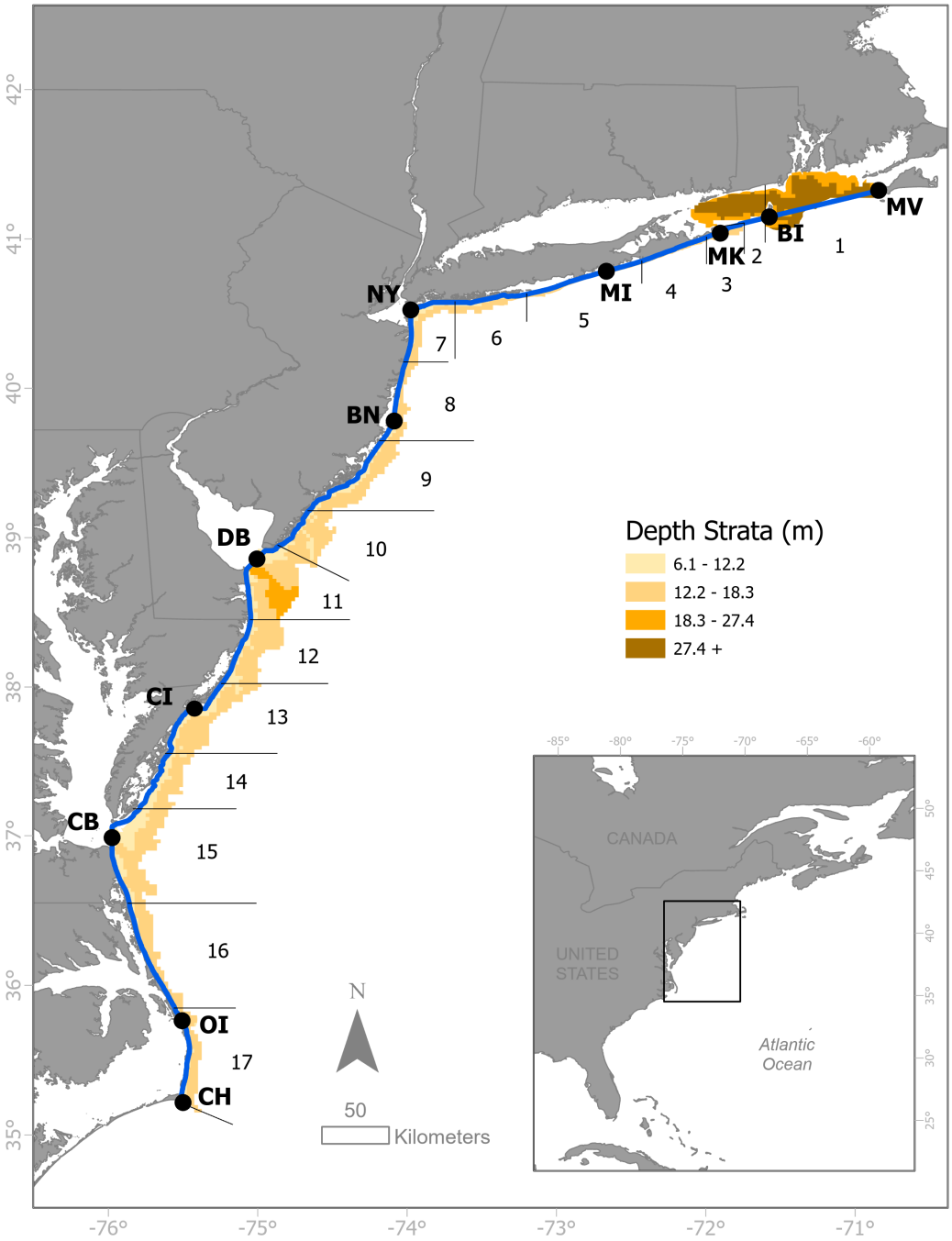


Figure 2. Standardized time-series of the Mid-Atlantic Bight mean sea surface temperature during winter (SSTWI) covariate included in the most supported dynamic factor analysis model of predicted annual catch-per-unit effort values for nine ecomorphotypes inhabiting the coastal ocean of this ecosystem.

Figure 3. (a) First common trend (solid line) and 95% confidence intervals (CIs; dashed lines) generated from a dynamic factor analysis (DFA) using predicted annual catch-per-unit effort (CPUE) values from delta-generalized additive models for nine ecomorphotypes (EMT) inhabiting the coastal ocean of the Mid-Atlantic Bight. (b) Factor loadings on this common trend for each EMT. Statistically significant loadings based on 95% CIs are denoted by an asterisk. Dem: demersal fishes; Pel: pelagic fishes; Fla: flatfish; Ska: skate; Ray: ray; Dog: dogfish; Shk: other shark; Cep: cephalopod; Art: benthic arthropod. (c) DFA model fits to the CPUE time-series for each EMT with a statistically significant loading on the first common trend.

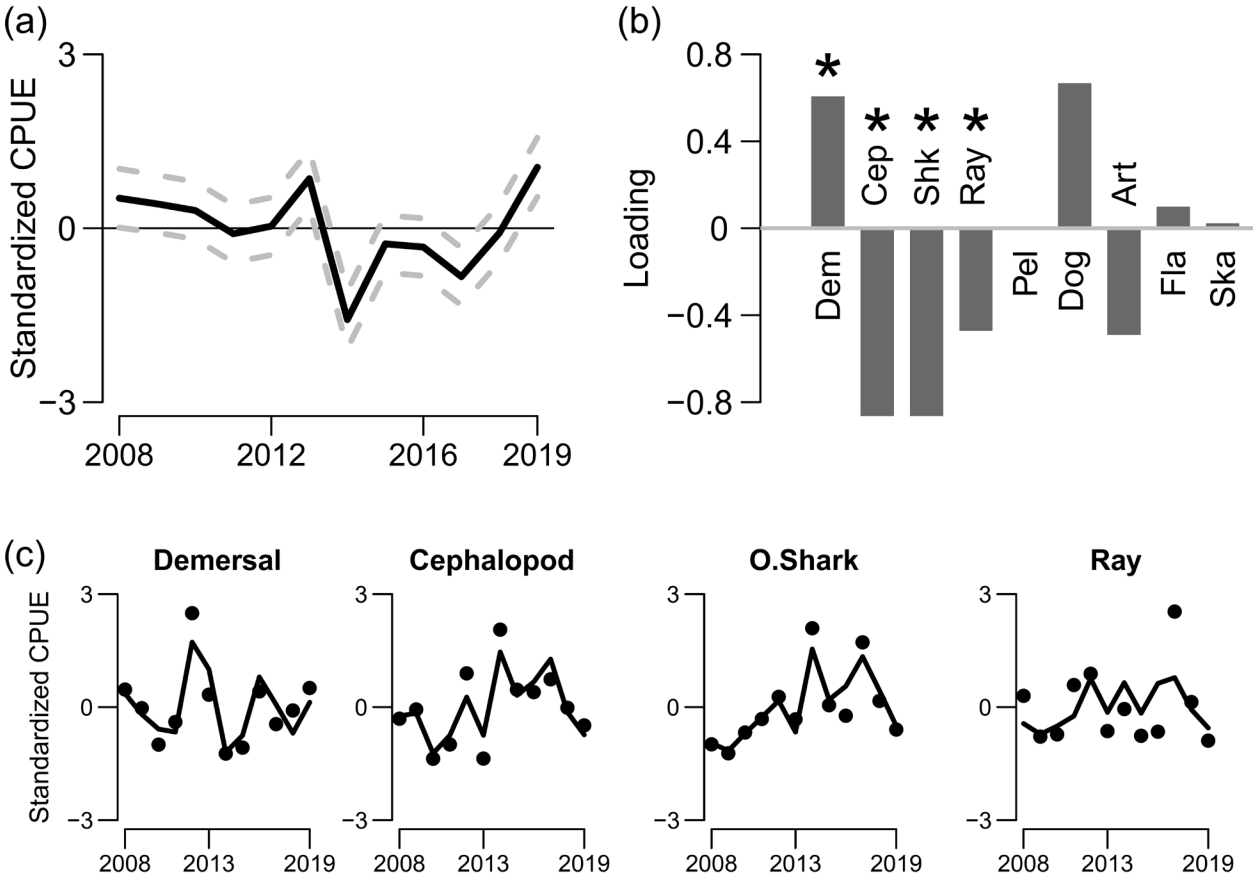


Figure 4. (a) Second common trend (solid line) and 95% confidence intervals (CIs; dashed lines) generated from a dynamic factor analysis (DFA) using predicted annual catch-per-unit effort (CPUE) values from delta-generalized additive models for nine ecomorphotypes (EMT) inhabiting the coastal ocean of the Mid-Atlantic Bight. (b) Factor loadings on this common trend for each EMT. Statistically significant loadings based on 95% CIs are denoted by an asterisk. Dem: demersal fishes; Pel: pelagic fishes; Fla: flatfish; Ska: skate; Ray: ray; Dog: dogfish; Shk: other shark; Cep: cephalopod; Art: benthic arthropod. (c) DFA model fits to the CPUE time-series for each EMT with a statistically significant loading on the second common trend.

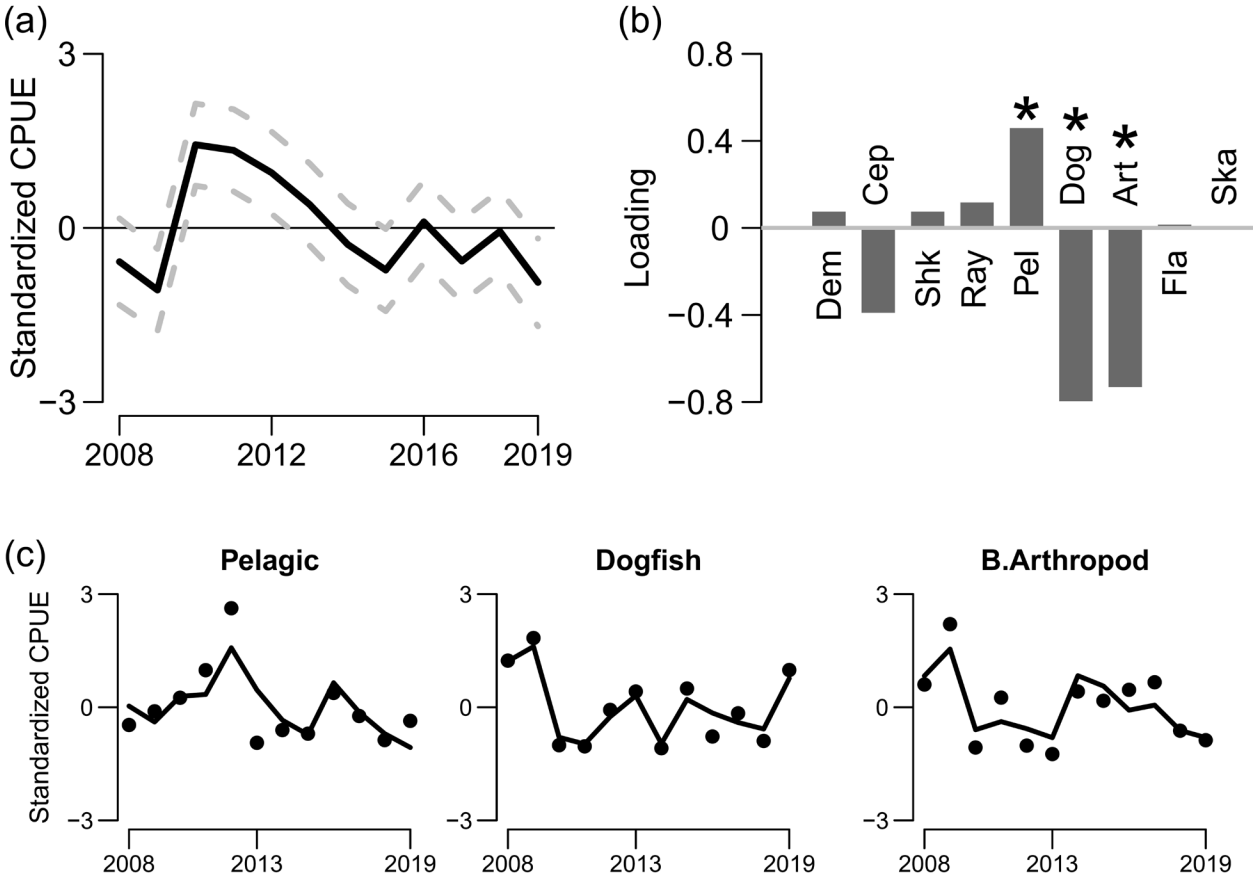


Figure 5. (a) Third common trend (solid line) and 95% confidence intervals (CIs; dashed lines) generated from a dynamic factor analysis (DFA) using predicted annual catch-per-unit effort (CPUE) values from delta-generalized additive models for nine ecomorphotypes (EMT) inhabiting the coastal ocean of the Mid-Atlantic Bight. (b) Factor loadings on this common trend for each EMT. Statistically significant loadings based on 95% CIs are denoted by an asterisk. Dem: demersal fishes; Pel: pelagic fishes; Fla: flatfish; Ska: skate; Ray: ray; Dog: dogfish; Shk: other shark; Cep: cephalopod; Art: benthic arthropod. (c) DFA model fits to the CPUE time-series for each EMT with a statistically significant loading on the third common trend.

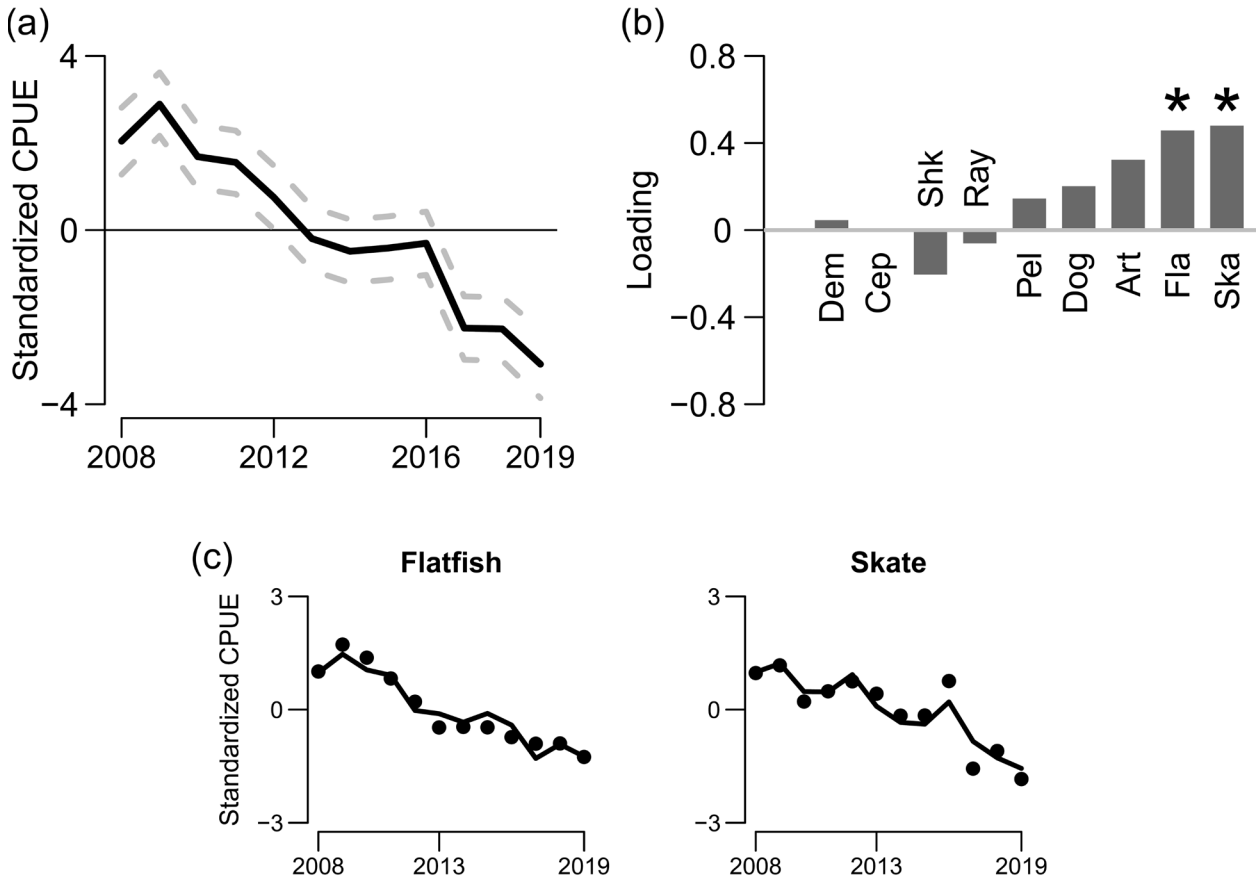
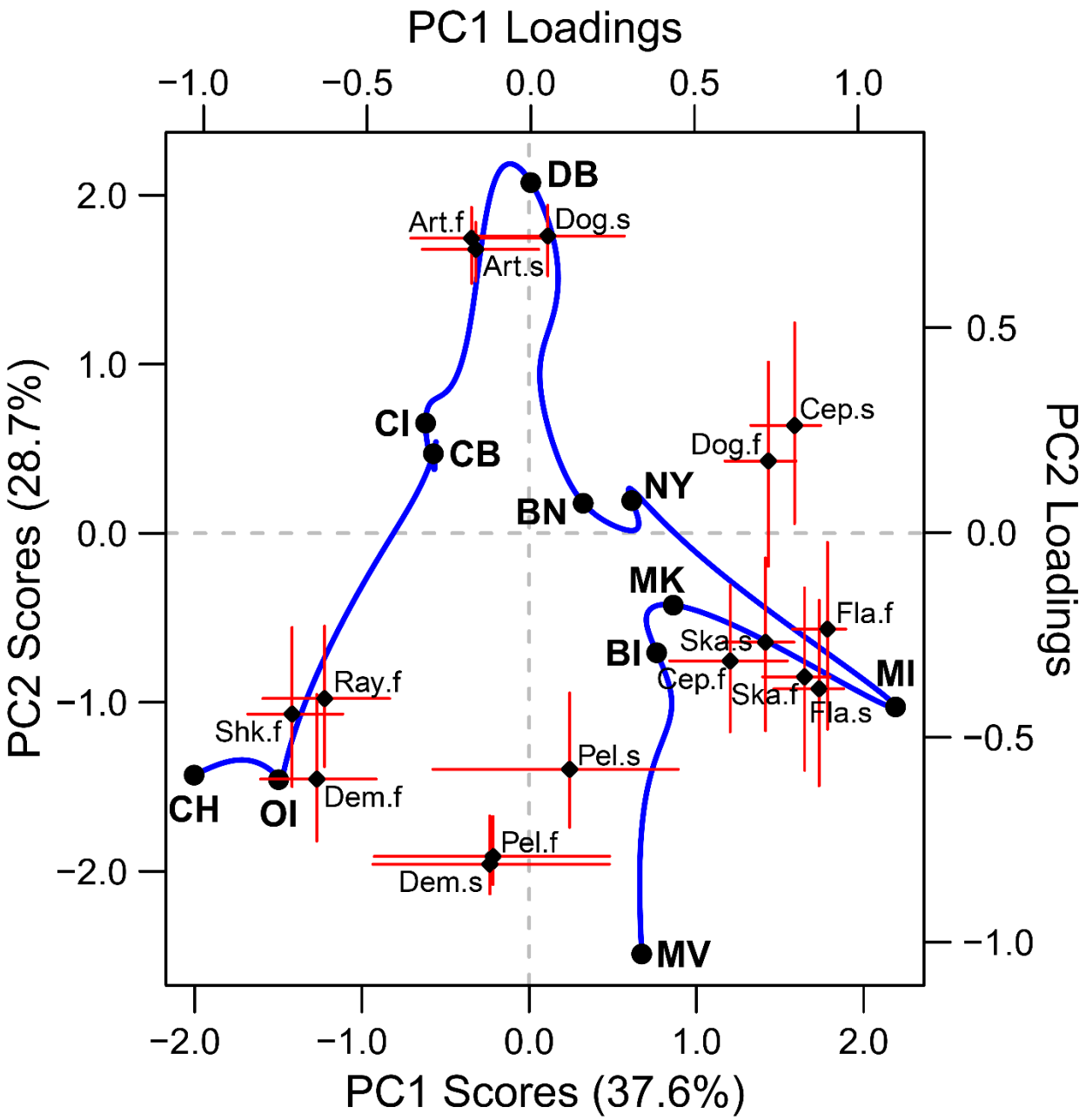


Figure 6. Principal component analysis biplot of the predicted seasonal, spatial distribution of catch-per-unit-effort for nine ecomorphotypes (EMT) inhabiting the coastal ocean of the Mid-Atlantic Bight from delta-generalized additive models. Each EMT/season combination represents principal component (PC) factor loadings and is given by a point and associated uncertainty. Dem: demersal fishes; Pel: pelagic fishes; Fla: flatfish; Ska: skate; Ray: ray; Dog: dogfish; Shk: other shark; Cep: cephalopod; Art: benthic arthropod; s: spring; f: fall. PC scores (in blue) represent 1000 coastal position values and location markers are included for reference, while the proportion of variance accounted for by each PC is provided in the axis labels. CH: Cape Hatteras, NC; OI: Oregon Inlet, NC; CB: Chesapeake Bay; CI: Chincoteague, VA; DB: Delaware Bay; BN: Barnegat Inlet, NJ; NY: New York Harbor; MI: Moriches Inlet, NY; MK: Montauk, NY; BI: Block Island, RI; MV: Martha's Vineyard, MA.



Supplementary Materials

Table S1. Catch data for the nine ecomorphotypes (EMTs) and component species sampled by the Northeast Area Monitoring and Assessment Program (NEAMAP) Nearshore Bottom Trawl Survey, 2008-2019. The number of individuals collected (count) and aggregate biomass (kg) are provided, along with the number and percentage (% frequency of occurrence [FO]) of sites at which the EMT or species was encountered.

Ecomorphotype	Species	Count	Biomass (kg)	No. Sites	% FO
Demersal Fish		*5,880,232*	*331,424.81*	*3514*	*99.5*
	Atlantic croaker (Micropogonias undulatus)	1,089,291	81,884.01	1065	30.2
	Weakfish (Cynoscion regalis)	1,113,584	72,698.90	1871	53.0
	Scup (Stenotomus chrysops)	1,814,077	53,032.16	2273	64.4
	Spot (Leiostomus xanthurus)	928,445	50,213.99	1103	31.2
	Kingfishes (Menticirrhus spp.)	170,524	20,243.34	2034	57.6
	Striped bass (Morone saxatilis)	3,701	12,425.23	268	7.6
	Spotted hake (Urophycis regia)	164,543	5,512.83	2147	60.8
	Silver perch (Bairdiella chrysoura)	176,043	5,306.89	713	20.2
	Silver hake (Merluccius bilinearis)	160,325	5,286.68	1438	40.7
	Atlantic sturgeon (Acipenser oxyrinchus)	244	4,858.67	157	4.4
	Black seabass (Centropristis striata)	10,674	4,008.48	1221	34.6
	Sheepshead (Archosargus probatocephalus)	873	2,881.21	190	5.4
	Striped searobin (Prionotus evolans)	8,730	2,175.24	910	25.8
	Northern searobin (Prionotus carolinus)	10,919	1,312.72	823	23.3
	Red drum (Sciaenops ocellatus)	98	1,269.72	37	1.0
	Red hake (Urophycis chuss)	11,500	1,225.66	564	16.0
	Ocean pout (Macrozdarces americanus)	922	906.03	102	2.9
	Atlantic cutlassfish (Trichiurus lepturus)	68,138	759.51	467	13.2
	Goosefish (Lophius americanus)	296	670.77	204	5.8
	Atlantic moonfish (Selene setapinnis)	97,905	616.18	646	18.3
	Northern puffer (Sphoeroides maculatus)	4,627	601.12	1047	29.6
	Pigfish (Orthopristis chrysoptera)	9,918	561.70	348	9.9
	Tautog (Tautoga onitis)	715	537.77	140	4.0
	Banded drum (Larimus fasciatus)	14,444	341.87	300	8.5
	Black drum (Pogonias cromis)	514	322.18	163	4.6
	Northern sennet (Sphyraena borealis)	3,653	290.12	422	11.9
	Striped burrfish (Chilomycterus schoepfii)	1,041	269.17	383	10.8
	Inshore lizardfish (Synodus foetens)	1,955	219.39	455	12.9
	Pinfish (Lagodon rhomboides)	3,875	200.57	368	10.4

Ecomorphotype	Species	Count	Biomass (kg)	No. Sites	%FO
Demersal (cont.)					
	Haddock (Melanogrammus aeglefinus)	1,425	159.92	42	1.2
	Longhorn sculpin (*Myoxocephalus octodecemspinosus*)	554	156.74	103	2.9
	Northern stargazer (*Astroscopus guttatus*)	102	141.78	88	2.5
	Sea raven (*Hemitripterus americanus*)	102	72.05	70	2.0
	Atlantic spadefish (*Chaetodipterus faber*)	1,379	53.33	135	2.8
	Cunner (*Tautogolabrus adspersus*)	254	52.37	49	1.4
	Atlantic cod (*Gadus morhua*)	39	46.19	30	0.9
	Gray triggerfish (*Balistes capriscus*)	50	32.99	37	1.1
	Striped cusk-eel (*Ophidion marginatum*)	346	14.71	153	4.3
	Spotted seatrout (*Cynoscion nebulosus*)	121	14.02	42	1.2
	American eel (*Anguilla rostrata*)	44	10.77	26	0.7
	Spotfin mojarra (*Eucinostomus argenteus*)	385	5.36	92	2.6
	Sand lances (*Ammodytes* spp.)	3,080	3.80	28	0.8
	Silver jenny (*Eucinostomus gula*)	212	3.73	73	2.1
	Florida pompano (*Trachinotus carolinus*)	24	2.42	10	0.3
	Lookdown (*Selene vomer*)	80	2.32	23	0.7
	Silver seatrout (*Cynoscion nothus*)	16	1.80	7	0.2
	Star drum (*Stellifer lanceolatus*)	173	1.69	8	0.2
	Feather blenny (*Hypsoblennius hentz*)	7	1.68	1	<0.1
	Bluespotted cornetfish (*Fistularia tabacaria*)	58	1.66	51	1.4
	Orange filefish (*Aluterus schoepfii*)	15	1.66	15	0.4
	African pompano (*Alectis ciliaris*)	8	1.40	7	0.2
	Red goatfish (*Mullus auratus*)	36	1.12	27	0.8
	Pollock (*Pollachius virens*)	12	1.08	12	0.3
	Fourbeard rockling (*Enchelyopus cimbrius*)	21	1.00	7	0.2
	Oyster toadfish (*Opsanus tau*)	3	0.89	2	0.1
	Conger eel (*Conger oceanicus*)	2	0.85	2	0.1
	Gizzard shad (*Dorosoma cepedianum*)	10	0.76	9	0.3
	Lumpfish (*Cyclopterus lumpus*)	1	0.76	1	<0.1
	Planehead filefish (*Stephanolepis hispida*)	11	0.63	11	0.3
	Carolina hake (*Urophycis earllii*)	3	0.52	2	0.1
	Permit (*Trachinotus falcatus*)	2	0.50	2	0.1
	White hake (*Urophycis tenuis*)	4	0.49	2	0.1
	Spotfin butterflyfish (*Chaetodon ocellatus*)	27	0.33	16	0.5
	Bigeye (*Priacanthus arenatus*)	5	0.24	5	0.1
	Atlantic needlefish (*Strongylura marina*)	3	0.23	2	0.1
	Short bigeye (*Pristigenys alta*)	9	0.19	9	0.3
	Gag (*Mycteroperca microlepis*)	1	0.12	1	<0.1
	Scrawled filefish (*Aluterus scriptus*)	1	0.12	1	<0.1
	Black grouper (*Mycteroperca bonaci*)	2	0.08	2	0.1
	Pipefishes (*Syngnathus* spp.)	11	0.06	5	0.1
	Lined seahorse (*Hippocampus erectus*)	7	0.05	6	0.2
	Fawn cusk-eel (*Lepophidium cervinum*)	2	0.05	2	0.1
	Dotterel filefish (*Aluterus heudeloti*)	1	0.05	1	<0.1
	Dwarf goatfish (*Upeneus parvus*)	2	0.04	2	0.1
	Fringed filefish (*Monacanthus ciliatus*)	1	0.04	1	<0.1
	Naked goby (*Gobiosoma bosc*)	1	0.02	1	<0.1

Ecomorphotype	Species	Count	Biomass (kg)	No. Sites	%FO
Demersal (cont.)					
	Red snapper (*Lutjanus campechanus*)	1	0.02	1	<0.1
	Snowy grouper (*Epinephelus niveatus*)	1	0.02	1	<0.1
	Silver porgy (*Diplodus argenteus*)	1	0.02	1	<0.1
	Bandtail puffer (*Spheroides spengleri*)	1	0.01	1	<0.1
	Spotted driftfish (*Ariomma regulus*)	1	0.01	1	<0.1
	Horned boxfish (*Lactoria cornuta*)	1	0.01	1	<0.1
Pelagic Fish		*5,744,444*	*108,726.82*	*3406*	*96.4*
	Butterfish (*Peprilus triacanthus*)	3,308,558	72,952.12	3201	90.6
	Striped anchovy (*Anchoa hepsetus*)	1,174,584	14,545.69	1102	31.2
	Bluefish (Pomatomus saltatrix)	83,015	8,298.74	1416	40.1
	Atlantic menhaden (*Brevoortia tyrannus*)	57,840	2,633.75	504	14.3
	Blueback herring (*Alosa aestivalis*)	170,506	2,414.67	753	21.3
	Bay anchovy (*Anchoa mitchilli*)	794,159	2,344.53	1219	34.5
	Alewife (*Alosa pseudoharengus*)	42,571	2,230.77	867	24.5
	Atlantic herring (*Clupea harengus*)	23,724	884.17	358	10.1
	American shad (*Alosa sapidissima*)	22,283	675.12	915	25.9
	Harvestfish (*Peprilus paru*)	12,710	507.38	221	6.3
	Atlantic thread herring (*Opisthonema oglinum*)	23,866	387.36	155	4.4
	Round herring (*Etrumeus teres*)	19,117	373.93	188	5.3
	Rough scad (*Trachurus lathami*)	4,460	158.71	351	9.9
	Cobia (*Rachycentron canadum*)	8	54.26	2	0.1
	Hickory shad (*Alosa mediocris*)	431	52.09	63	1.8
	Blue runner (*Caranx crysos*)	988	51.43	199	5.6
	Atlantic mackerel (*Scomber scombrus*)	499	45.96	182	5.2
	Round scad (*Decapterus punctatus*)	1,769	33.69	157	4.4
	Spanish mackerel (*Scomberomorus maculatus*)	283	31.75	40	1.1
	Bigeye scad (*Selar crumenophthalmus*)	448	20.21	92	2.6
	Crevalle jack (*Caranx hippos*)	54	5.12	26	0.7
	Spanish sardine (*Sardinella aurita*)	937	5.04	36	1.0
	King mackerel (*Scomberomorus cavalla*)	1	4.62	1	<0.1
	Silver anchovy (*Engraulis eurystole*)	1,171	4.51	11	0.3
	Atlantic bonito (*Sarda sarda*)	10	3.36	2	0.1
	Banded rudderfish (*Seriola zonata*)	11	1.64	8	0.2
	Cero (*Scomberomorus regalis*)	76	1.25	3	0.1
	Atlantic bumper (*Chloroscombrus chrysurus*)	321	1.19	17	0.5
	White mullet (*Mugil curema*)	13	1.18	4	0.1
	Sharksucker (*Echeneis naucrates*)	6	0.71	3	0.1
	Chub mackerel (*Scomber japonicus*)	5	0.63	5	0.1
	Mackerel scad (*Decapterus macarellus*)	1	0.46	1	<0.1
	Guaguanche (*Sphyraena guachancho*)	9	0.20	1	<0.1
	Barrelfish (*Hyperoglyphe perciformis*)	6	0.19	3	0.1
	Striped mullet (*Mugil cephalus*)	1	0.16	1	<0.1
	Smooth puffer (*Lagocephalus laevigatus*)	2	0.12	2	0.1
	Remora (*Remora remora*)	1	0.11	1	<0.1

Ecomorphotype	Species	Count	Biomass (kg)	No. Sites	%FO
Flatfish		*55,038*	*17,079.83*	*3041*	*86.1*
	Summer flounder (*Paralichthys dentatus*)	13,390	7,155.94	2556	72.4
	Winter flounder (*Pseudopleuronectes americanus*)	18,640	5,881.48	984	27.9
	Windowpane (*Scophthalmus aquosus*)	15,611	3,004.16	2050	58.0
	Fourspot flounder (*Hippoglossina oblonga*)	3,659	749.38	467	13.2
	Hogchoker (*Trinectes maculatus*)	1,983	166.26	217	6.1
	Yellowtail flounder (*Pleuronectes ferruginea*)	158	68.22	38	1.1
	Blackcheek tonguefish (*Symphurus plagiusa*)	684	32.79	150	4.2
	Gulf Stream flounder (*Citharichthys arctifrons*)	910	21.33	98	2.8
	Witch flounder (*Glyptocephalus cynoglossus*)	1	0.22	1	<0.1
	Naked sole (*Gymnachirus melas*)	1	0.03	1	<0.1
	Ocellated flounder (*Ancylopsetta ommata*)	1	0.02	1	<0.1
Cephalopod		*1,309,723*	*28,233.56*	*3138*	*88.8*
	Longfin inshore squid (*Doryteuthis pealeii*)	1,275,827	27,744.52	3025	85.6
	Northern shortfin squid (*Illex illecebrosus*)	11,446	308.72	103	2.9
	Atlantic brief squid (*Lolliguncula brevis*)	22,437	177.88	331	9.4
	Atlantic shore octopus (*Octopus vulgaris*)	12	2.43	12	0.3
	Bobtail squid (*Semirossia tenera*)	1	0.01	1	<0.1
Benthic Arthropod		*167,737*	*34,842.82*	*2611*	*73.9*
	Horseshoe crab (*Limulus polyphemus*)	26,968	30,684.48	1706	48.3
	White shrimp (*Litopenaeus setiferus*)	123,786	2,517.03	264	7.5
	American lobster (*Homarus americanus*)	3,312	920.68	483	13.7
	Common spider crab (*Libinia emarginata*)	2,148	226.81	475	13.4
	Atlantic rock crab (*Cancer irroratus*)	2,549	199.64	515	14.6
	Brown shrimp (*Farfantepenaeus aztecus*)	4,764	103.77	339	9.6
	Blue crab (*Callinectes sapidus*)	560	62.60	196	5.5
	Lady crab (*Ovalipes ocellatus*)	2,139	54.61	423	12.0
	Six spine spider crab (*Libinia dubia*)	417	43.92	157	4.4
	Jonah crab (*Cancer borealis*)	163	17.45	58	1.6
	Iridescent swimming crab (*Portunus gibbesii*)	541	4.98	61	1.7
	Mantis shrimp (*Squilla empusa*)	179	4.00	52	1.5
	Lesser blue crab (*Callinectes similis*)	63	1.74	12	0.3
	Pink shrimp (*Farfantepenaeus duorarum*)	15	0.41	8	0.2
	Speckled crab (*Arenaeus cribrarius*)	13	0.37	6	0.2
	Roughneck shrimp (*Rimapenaeus constrictus*)	119	0.33	18	0.5
	Peppermint shrimp (*Lysmata wurdemanni*)	1	<0.01	1	<0.1
Skate		*227,578*	*194,399.67*	*3490*	*98.8*
	Little skate (*Leucoraja erinacea*)	150,820	82,103.28	2409	68.2
	Winter skate (*Leucoraja ocellata*)	40,651	65,972.97	2001	56.7
	Clearnose skate (*Raja eglanteria*)	36,082	46,304.39	2411	68.3
	Barndoor skate (*Dipturus laevis*)	25	19.03	17	0.5

Ecomorphotype	Species	Count	Biomass (kg)	No. Sites	%FO
Dogfish		*35,206*	*65,070.42*	*2411*	*68.3*
	Spiny dogfish (*Squalus acanthias*)	21,308	38,404.63	1287	36.44
	Smooth dogfish (*Mustelus canis*)	13,898	26,665.79	1966	55.66
Ray		*15,401*	*56,121.54*	*997*	*28.2*
	Cownose ray (*Rhinoptera bonasus*)	5,674	18,195.64	256	7.25
	Spiny butterfly ray (*Gymnura altavela*)	831	11,385.97	278	7.87
	Bullnose ray (*Myliobatis freminvillii*)	5,965	10,326.29	682	19.31
	Bluntnose stingray (*Dasyatis say*)	1,432	9,966.85	269	7.62
	Roughtail stingray (*Dasyatis centroura*)	234	2,787.00	152	4.30
	Smooth butterfly ray (*Gymnura micrura*)	941	1,949.05	269	7.62
	Atlantic torpedo (*Torpedo nobiliana*)	32	645.15	27	0.76
	Southern stingray (*Dasyatis americana*)	92	641.66	34	0.96
	Atlantic stingray (*Dasyatis sabina*)	200	223.93	98	2.77
Other Shark		*1,243*	*15,755.84*	*524*	*14.8*
	Thresher shark (*Alopias vulpinus*)	138	6,742.34	128	3.6
	Sand tiger shark (*Carcharias taurus*)	92	3,606.40	75	2.1
	Atlantic angel shark (*Squatina dumeril*)	304	2,904.73	191	5.4
	Sandbar shark (*Carcharhinus plumbeus*)	604	1,767.21	234	6.6
	White shark (*Carcharodon carcharias*)	7	339.10	6	0.2
	Atlantic sharpnose shark (*Rhizoprionodon terraenovae*)	84	337.17	39	1.1
	Dusky shark (*Carcharhinus obscurus*)	6	34.66	6	0.2
	Spinner shark (*Carcharhinus brevipinna*)	4	16.29	4	0.1
	Scalloped hammerhead shark (*Sphyrna lewini*)	2	5.56	2	0.1
	Smooth hammerhead shark (*Sphyrna zygaena*)	1	1.81	1	<0.1
	Bonnethead shark (*Sphyrna tiburo*)	1	0.57	1	<0.1

Table S2. Model selection statistics associated with the evaluation of candidate response variable distributions for the conditional component of the delta-generalized additive models (delta-GAMs) fitted to catch-per-unit-effort (CPUE) data on nine ecomorphotypes (EMTs) collected by the Northeast Area Monitoring and Assessment Program (NEAMAP) Nearshore Bottom Trawl Survey, 2008 – 2019. Results are given for the five most supported distributions when fitting a model with all candidate covariates (i.e., full model). Bold denotes the distribution selected for each EMT. Distribution abbreviations are: BCPEo, Box-Cox Power Exponential; BCTo, Box-Cox t; GA, Gamma; GB2, Generalized Beta Type-2; GG, Generalized Gamma; GIG, Generalized Inverse Gaussian; IG, Inverse Gaussian; LOGNO, Log Normal; LOGNO2, Log Normal 2; PARETO2, Pareto 2; PARETO2o, Pareto 2 Original; WEI, Weibull; WEI3, Weibull Type 3.

Distribution	-2log(L)	*df* for Model Fit	AIC	ΔAIC
		Demersal Fish		
GB2	**59012.6**	**53.7**	**59120.0**	**0.0**
BCTo	59021.1	53.8	59128.6	8.6
GG	59056.6	52.6	59161.7	41.7
Pareto2o	59059.4	53.0	59165.3	45.3
Pareto2	59060.9	52.4	59165.6	45.6
		Pelagic Fish		
GB2	**50094.8**	**55.9**	**50206.6**	**0.0**
BCTo	50106.8	55.8	50218.4	11.8
GG	50129.4	53.4	50236.3	29.7
WEI3	50256.5	50.2	50357.0	150.4
WEI	50256.5	50.2	50357.0	150.4
		Flatfish		
BCTo	**34360.5**	**59.2**	**34478.9**	**0.0**
GG	34369.2	58.6	34486.3	7.5
GA	34437.4	56.4	34550.3	71.4
WEI3	34487.6	56.0	34599.6	120.7
WEI	34487.6	56.0	34599.6	120.7

Cephalopod				
BCTo	**39568.0**	**60.8**	**39689.5**	**0.0**
GG	39571.1	59.3	39689.7	0.2
GB2	39570.0	61.3	39692.6	3.1
LOGNO2	39604.6	58.0	39720.5	31.0
LOGNO	39604.6	58.0	39720.5	31.0
Benthic Arthropod				
GB2	**34564.3**	**55.4**	**34675.1**	**0.0**
BCTo	34568.0	54.2	34676.4	1.3
GG	34644.4	54.4	34753.1	78.0
WEI	34647.3	53.4	34754.0	78.9
WEI3	34647.3	53.4	34754.0	78.9
Skate				
GB2	**57760.8**	**61.3**	**57883.5**	**0.0**
BCTo	57782.1	55.3	57892.7	9.2
BCPEo	57857.7	62.6	57982.8	99.3
GG	57894.2	53.4	58001.0	117.5
LOGNO	57993.4	59.3	58112.0	228.5
Dogfish				
BCTo	**36682.9**	**50.4**	**36783.6**	**0.0**
GB2	36683.6	50.1	36783.8	0.2
GG	36720.7	50.4	36821.6	38.0
LOGNO2	36732.4	49.0	36830.5	46.9
LOGNO	36732.4	49.0	36830.5	46.9
Ray				
BCTo	**13119.0**	**24.1**	**13167.2**	**0.0**
GB2	13119.3	24.2	13167.6	0.4
GG	13121.9	23.0	13167.9	0.7
LOGNO	13126.1	22.3	13170.7	3.5

LOGNO2	13126.1	22.3	13170.7	3.5
		Other Shark		
GIG	**6702.0**	**22.7**	**6747.4**	**0.0**
GG	6704.9	23.1	6751.1	3.7
IG	6707.5	21.9	6751.2	3.8
BCTo	6705.2	24.2	6753.5	6.1
GB2	6707.3	24.2	6755.8	8.4

Table S3. Model selection statistics associated with delta-generalized additive models (delta-GAMs) fitted to presence/absence (i.e., binomial) and conditional catch-per-unit-effort (CPUE) data on nine ecomorphotypes (EMTs) collected by the Northeast Area Monitoring and Assessment Program (NEAMAP) Nearshore Bottom Trawl Survey, 2008-2019. Bold represents model parameterizations chosen for inference.

Model	-2log(L)	*df* for Model Fit	AIC	ΔAIC
		Demersal Fish		
		Conditional		
M1	**59012.6**	**53.7**	**59120.0**	**0.0**
M2	59052.8	52.1	59156.9	36.9
M3	59125.4	48.6	59222.5	102.5
M4	59168.6	46.6	59261.7	141.7
		Pelagic Fish		
		Binomial		
M1	**940.2**	**28.3**	**996.9**	**0.0**
M2	944.2	27.7	999.6	2.7
M3	954.0	25.0	1004.1	7.2
M4	958.7	24.2	1007.1	10.2
		Conditional		
M1	50094.8	55.9	50206.6	1.6
M2	**50094.9**	**55.0**	**50205.0**	**0.0**
M3	50236.0	46.8	50329.7	124.7
M4	50237.5	45.9	50329.4	124.4
		Flatfish		
		Binomial		
M1	**1927.8**	**37.5**	**2002.8**	**0.0**
M2	1942.9	34.8	2012.5	9.7
M3	1941.4	31.6	2004.5	1.7
M4	1956.9	29.1	2015.0	12.2

		Conditional		
M1	**34360.5**	**59.2**	**34478.9**	**0.0**
M2	34385.4	57.1	34499.6	20.7
M3	34451.3	52.6	34556.4	77.5
M4	34472.9	50.2	34573.2	94.3
		Cephalopod		
		Binomial		
M1	2042.5	42.1	2126.7	0.9
M2	**2043.5**	**41.1**	**2125.8**	**0.0**
M3	2127.6	41.0	2209.6	83.8
M4	2134.0	37.9	2209.8	84.1
		Conditional		
M1	**39568.0**	**60.8**	**39689.5**	**0.0**
M2	39581.8	55.0	39691.8	2.3
M3	39952.7	51.1	40055.0	365.5
M4	39966.8	47.0	40060.8	371.3
		Benthic Arthropod		
		Binomial		
M1	**3472.1**	**45.3**	**3562.7**	**0.0**
M2	3512.7	42.6	3597.8	35.1
M3	3607.5	37.2	3681.9	119.2
M4	3645.2	34.9	3715.0	152.3
		Conditional		
M1	**34564.3**	**55.4**	**34675.1**	**0.0**
M2	34589.6	53.3	34696.2	21.1
M3	34598.6	52.8	34704.0	28.9
M4	34625.6	50.5	34726.6	51.5
		Skate		
		Conditional		

M1	**57761.7**	**61.2**	**57884.1**	**0.0**
M2	57794.9	60.2	57915.2	31.1
M3	57816.4	52.7	57921.9	37.8
M4	57852.4	51.6	57955.7	71.6
		Dogfish		
		Binomial		
M1	**3331.5**	**39.7**	**3410.8**	**0.0**
M2	3335.0	38.6	3412.2	1.4
M3	3364.3	38.5	3441.3	30.5
M4	3366.1	37.5	3441.0	30.2
		Conditional		
M1	**36682.9**	**50.4**	**36783.6**	**0.0**
M2	36695.4	45.2	36785.7	2.1
M3	36690.9	49.0	36788.8	5.2
M4	36703.8	43.8	36791.4	7.8
		Ray		
		Binomial		
M5	1437.0	28.8	1494.7	0.2
M6	**1438.8**	**27.8**	**1494.5**	**0.0**
M7	1465.7	26.7	1519.2	24.7
M8	1469.6	25.7	1521.0	26.5
		Conditional		
M5	13117.0	25.0	13167.0	1.6
M6	**13117.3**	**24.0**	**13165.4**	**0.0**
M7	13130.5	26.7	13183.9	18.5
M8	13131.2	25.8	13182.8	17.4
		Other Shark		
		Binomial		
M5	1396.5	25.9	1448.4	1.9

M6	**1396.6**	**24.9**	**1446.5**	**0.0**
M7	1406.1	21.3	1448.8	2.3
M8	1406.2	20.4	1446.9	0.4
		Conditional		
M5	6695.8	25.3	6746.4	2.0
M6	6696.4	24.2	6744.9	0.5
M7	6695.6	25.0	6745.6	1.2
M8	**6696.5**	**23.9**	**6744.4**	**0.0**

Table S4. Model structure, fit statistics, and model selection statistics for the dynamic factor analysis (DFA) models fitted to predicted annual catch-per-unit-effort (CPUE) data from delta-generalized additive models (delta-GAMs) for nine ecomorphotypes (EMTs) collected by the Northeast Area Monitoring and Assessment Program (NEAMAP) Nearshore Bottom Trawl Survey, 2008 – 2019. Models are limited to those with ΔAICc < 10 and bold identifies the model chosen for inference.

Covariates	Lag	m	-2log(L)	AICc	ΔAICc	Mean Fit
SSTWI	**0**	**3**	**241.3**	**307.3**	**0.0**	**0.227**
NAO	0	3	241.7	307.7	0.4	0.221
SSTA	0	3	248.8	314.8	7.5	0.242

Table S5. Estimated coefficients, standard errors, and 95% confidence intervals associated with the winter mean sea surface temperature (SSTWI) covariate in the dynamic factor analysis (DFA) selected for inference. This DFA was fitted to predicted annual catch-per-unit-effort (CPUE) data on nine ecomorphotypes (EMTs) collected by the Northeast Area Monitoring and Assessment Program (NEAMAP) Nearshore Bottom Trawl Survey, 2008 – 2019.

EMT	Coefficient	SE	95% CI
Demersal fish	0.78	0.21	(0.37, 1.20)
Pelagic Fish	0.50	0.22	(0.07, 0.94)
Flatfish	-0.19	0.15	(-0.49, 0.11)
Cephalopod	0.33	0.26	(-0.18, 0.83)
Benthic Arthropod	-0.05	0.27	(-0.57, 0.48)
Skate	0.28	0.15	(-0.01, 0.56)
Dogfish	0.16	0.27	(-0.37, 0.69)
Ray	0.35	0.21	(-0.06, 0.76)
Other Shark	0.14	0.30	(-0.45, 0.73)

CHAPTER 4

Disentangling bottom-up and top-down controls on fish consumption of key prey in the Northeast US shelf ecosystem

Abstract

Exploited forage fishes serve a dual role in marine ecosystems by supporting directed fisheries and predator productivity, so both harvest and predatory removals should be accounted for when developing stock assessments and evaluating management trade-offs. Predator catch and stomach content data collected on the Northeast US shelf from 1978 – 2019 by two fisheries-independent surveys were combined within multivariate spatiotemporal models to estimate time-series of consumptive removals during spring and fall for four commercially-exploited prey; Atlantic herring (*Clupea harengus*), silver hake (*Merluccius bilinearis*), butterfish (*Peprilus triacanthus*), and longfin squid (*Doryteuthis pealeii*). Seasonal consumption trends were mostly synchronous for both Atlantic herring and silver hake, asynchronous for butterfish and longfin squid, and predatory removals were generally greater during fall. Consumption increased since the 1990s for all prey except Atlantic herring and butterfish during fall, which coincides with the widespread implementation of harvest constraints meant to rebuild predator and prey populations. These time-series were linked to hypothesized drivers using state-space regression models; prey availability (bottom-up; positive relationships) and commercial catch (top-down; primarily negative relationships) were the strongest predictors of consumption. Although the mechanisms underlying these relationships remain unresolved, these linkages highlight connections among the systemic drivers of productivity on the Northeast shelf.

Introduction

Efforts to develop and operationalize ecosystem approaches to fisheries management (EAFM) for living marine resources have been driven in large part by a renewed appreciation for the role that trophodynamics and biophysical forcing play in governing the dynamics of exploited taxa (Gaichas et al., 2012; Link and Marshak, 2022). Trophic interactions regulate the transport of matter and energy through ecosystems while shaping productivity and mortality rates for both predators and prey (Garrison and Link, 2000). Information on predator-prey relationships is thus critical to advancing ecosystem-based stock assessments and management strategies (Link and Marshak, 2022). Although a myriad of data sources can be used to quantify these interactions, information derived from stomach content sampling has yielded an array of valuable insights on system trophodynamics (Garrison and Link, 2000; Bundy et al., 2011; Buchheister and Latour, 2016). Indeed, stomach content data have been used to estimate diet compositions, functional responses, and consumption rates (among others), which have then parameterized a host of models designed to quantify ecosystem organization, status, and management trade-offs (Gaichas et al., 2010; Smith and Smith, 2020; de Moor, 2023).

Appreciable progress has been made over the past several decades in designing and improving modeling frameworks that include data derived from predator stomach contents, yet many of these approaches provide heuristic or strategic information on trophic groups, rather than species-specific tactical management advice needed for EAFM (Plagányi et al., 2014). As a result, focus has shifted toward integrating predator-prey interactions into stock assessment models that produce tactical advice (e.g., Curti et al., 2013; Gaichas et al., 2024). Particular attention has been given to incorporating the impacts of predator consumption on the dynamics of exploited prey, since these forage species underpin the productivity of both predator

populations and directed fisheries, and management strategies need to optimize trade-offs between the ecological and economic values of the prey to be effective (Pikitch et al., 2014; de Moor, 2023).

Consumptive removals of prey are often estimated by combining information on predator abundance, stomach contents, and gastric evacuation rates across a suite of predators in an ecosystem (Overholtz et al., 2000; Link and Sosebee, 2008). These removals can be included in assessment models ranging in complexity from extended single-species to multispecies statistical-catch-at-age frameworks, typically as an additional 'fishing fleet', to account for natural mortality due to predation (M_2; Collie and Gislason, 2001; Moustahfid et al., 2009). Given that predator consumption usually rivals or exceeds the harvest of prey and varies through time, adding this large and often nonstationary source of mortality to assessments can result in drastic changes to perceived stock dynamics, biological reference points, and management advice, and thus yields the tactical information needed to advance EAFM (Tyrrell et al., 2011; Trijoulet et al., 2020). However, current management of prey species largely relies on traditional single-species assessments that do not explicitly account for M_2 and likely supply risk-prone management advice (Tyrrell et al., 2011).

The Northeast US Large Marine Ecosystem (NEUS LME) encompasses the Gulf of Maine, Georges Bank, and Mid-Atlantic Bight and ranks among the most productive and diverse marine ecosystems worldwide (Link et al., 2008). Fisheries in this LME are managed primarily by two regional councils (i.e., New England and Mid-Atlantic) and an interstate commission. Each organization has prioritized the implementation of EAFM, with particular emphasis on developing ecosystem-based assessments and management strategies for fisheries targeting prey species (Gaichas et al., 2016). Several studies have quantified predator consumption rates in this

LME (Overholtz et al., 2000; Overholtz and Link, 2007; Link and Idoine, 2009; Moustahfid et al., 2009), although data on predator removals are only routinely included in stock assessments for Atlantic menhaden (*Brevoortia tyrannus*; SEDAR, 2020). In most cases, predator abundance and diet data were aggregated across broad spatiotemporal scales, which may have biased consumption estimates by obscuring the fine-scale variability in the predator-prey interactions (Deroba, 2018). Only one study quantified uncertainty in consumption (Overholtz and Link, 2007), and a comprehensive evaluation of the connectivity between predatory removals and other ecosystem processes is currently lacking. While trophodynamics play a major role in defining the structure and function of an ecosystem, exploring the potential impacts of bottom-up (e.g., biophysical forcing, prey availability) and top-down (e.g., fishery harvest) processes on the consumption of exploited prey could illuminate key factors shaping these interactions and highlight linkages among systemic drivers of productivity (Buchheister and Latour, 2016).

The goal of this study was to provide contemporary information on predatory removals of key prey on the Northeast US continental shelf, based on a 42-year time-series of catch and stomach content data from two fisheries-independent monitoring surveys. Specifically, these datasets were used to (1) estimate time-series of aggregate fish consumption of Atlantic herring (*Clupea harengus*), silver hake (*Merluccius bilinearis*), butterfish (*Peprilus triacanthus*), and longfin squid (*Doryteuthis pealeii*) during spring and fall by leveraging the spatiotemporal structure of the data and (2) quantify relationships between seasonal predatory removals and a suite of covariates representing hypothesized bottom-up and top-down controls. Atlantic herring and silver hake support valuable directed fisheries in New England, while butterfish and longfin squid do so in the Mid-Atlantic. Quantifying predator consumption and drivers of prey removals could support the development of ecosystem-based assessment models designed to yield tactical

management advice for each species, offer greater insight into system function, and facilitate the implementation of EAFM in the Northeast US.

Methods

Data sources

Information on predator relative abundances, stomach contents, and gastric evacuation rates needed for prey consumption modeling were acquired from two bottom trawl surveys (BTS) with long-term, consistent time-series of catch and diet data; namely, the National Oceanographic and Atmospheric Administration (NOAA) Northeast Fisheries Science Center (NEFSC) BTS and the Northeast Area Monitoring and Assessment Program (NEAMAP) Nearshore BTS (Politis et al., 2014; Gartland et al., 2023).

The NEFSC has been sampling on the continental shelf of the NEUS LME since 1963 (Azarovitz, 1981; Politis et al., 2014). Surveys occur during spring (Mar – May) and fall (Sep – Nov), and 350 – 400 sites are sampled during each season. Sites are selected using a stratified-random design, where the sampling frame is stratified primarily by depth and latitude (~270,000 km^2; Figure 1). Site-specific data on year, season, sampling location, area swept by the trawl (constant, 0.0384 km^2), bottom water temperature (BT; 0.1 ^{0}C), depth (m), species-specific catch weights (2 g), individual predator weights (g), and prey weights (0.1 g) from stomach samples were used in this study. The NEFSC adopted a new vessel and trawl in 2009, so calibration coefficients derived from paired-tow experiments were used to generate consistent time-series of catch data (Miller, 2013).

Shelf-wide sampling of fish predator stomach contents was initiated in 1978. At each site, a subsample of priority species is selected for diet analysis (see Smith and Link, 2010 for

prioritization), and the individual length (cm) and weight (g) of each predator is recorded. When individual predator weight data were not available (26.1% of records), species-specific seasonal length-weight relationships were used to predict weight (Wigley et al., 2003). Stomach contents were quantified by wet weight prior to 1981 and volume (0.1 cm^3) thereafter, so a linear regression specifying a 1.1:1 conversion factor was used to translate prey volumes to masses (r^2 = 0.906, $p < 0.0001$; Link and Almeida, 2000). All NEFSC sampling complied with US Animal Welfare Act laws, guidelines, and policies as approved by NOAA Fisheries which determined that no animal use protocol was required.

NEAMAP began sampling the nearshore strata of the Mid-Atlantic Bight in 2008 (~12,000 km^2; Figure 1), in part because the new NEFSC vessel could not operate in these shallow depths. This survey samples during spring (Apr – May) and fall (Sep – Nov), sites are selected using a stratified-random design, and 150 sites are sampled during each cruise (Gartland et al., 2023). NEAMAP records each of the data elements listed above and collects stomach content data on 30 fish species from a subsample of individuals captured at each location (ASMFC, 2009). Wet weight is recorded for each prey item encountered in these stomachs. NEAMAP animal handling protocols were approved by the William & Mary Institutional Animal Care and Use Committee (current protocol: 2023-0098).

Data filtering

The NEFSC and NEAMAP datasets were combined and restricted to the 1978 – 2019 period, since the spatial domain of the predator catch and diet sampling has been relatively consistent since 1978 and both surveys were interrupted during the global pandemic in 2020. Data were collected from 31,615 sites (27,683 NEFSC / 3,932 NEAMAP), and the stomach

contents of 458,191 fishes (362,384 NEFSC / 95,807 NEAMAP) were quantified during these 42 years.

Separate spring and fall datasets were developed for each prey species to estimate time-series of consumption, given the distinct seasonal trophodynamics of the NEUS LME (Deroba, 2018; Ng et al., 2021). Because this study sought to quantify total predatory removals of prey, catch and stomach content data were aggregated across a suite of predators for each prey (Table S1 in the Supplement). Two criteria were used to identify the fish predators of a prey species: (1) the prey must have been encountered in predator stomachs at five or more sites sampled by the two surveys across all years and (2) the predator must have been sampled consistently for diet by both surveys over their time-series. The first criterion eliminated predators that did not feed on the prey or did so very rarely. Marginal increases to the five-site threshold were explored and did not alter predator compositions. The second criterion was meant to ensure that inconsistencies in sample prioritization did not impact consumption trends. Predation by conspecifics was excluded to avoid circularity when modeling relationships between consumption and prey abundance (Section 3.4). Only silver hake exhibited appreciable cannibalism. Finally, if a prey species was not encountered in stomachs collected from a survey stratum across the full spring or fall time-series, then all predator catch and stomach data for that season – stratum combination were removed from the corresponding prey dataset to minimize uninformative zeros.

Consumption modeling

For each prey, the mean daily minimum biomass consumed (C_t) in year t was estimated for spring and fall separately by coupling predator catch and stomach content data with gastric evacuation rate estimates (Eggers, 1977; Elliott and Persson, 1978):

$$C_t = \sum_{g=1}^{n_g} PBD_{g,t} \cdot PCC_{g,t} \cdot a_g, \quad (1)$$

where $PBD_{g,t}$ was model predicted aggregate predator biomass-density at time t and cell g of a grid overlaid on the Northeast shelf, $PCC_{g,t}$ was the predicted per capita daily consumption of the prey in the cell, and a_g was the surface area of the cell ($\bar{a}_g$ = 10.2 km^2).

Aggregate predator biomass-density (PBD_i) at each survey site i was calculated using predator catch data:

$$PBD_i = \frac{\sum_{d=1}^{n_d} cp_{d,i}}{as_i}, \quad (2)$$

where $cp_{d,i}$ was the catch weight of predator species d and as_i was the area swept by the trawl. The per capita daily consumption (PCC_i) of the prey at site i relied on predator diet data:

$$PCC_i = \frac{\sum_{p=1}^{n_p} py_{p,i} \cdot E_{p,i} \cdot 24}{\sum_{p=i}^{n_p} pd_{p,i}}, \quad (3)$$

where $py_{p,i}$ was the prey biomass in the stomach of individual predator p and n_p included those with empty stomachs, $pd_{p,i}$ was individual predator weight, and 24 expanded consumption to a daily timescale. The hourly evacuation rate of each predator ($E_{p,i}$) was estimated using:

$$E_{p,i} = \alpha_p \cdot exp^{\beta_p \cdot T_i}, \quad (4)$$

where T_i was BT (see '*Modeling Bottom Temperature*' in the Supplement), and α_p and $\beta_p$were constants that varied between teleosts (α = 0.004; β = 0.115) and elasmobranchs (α = 0.002; β = 0.110) owing to the metabolic differences between these groups (Overholtz et al., 2000; Link and Sosebee, 2008). Consumption data were combined across all predators at a site since the stomach contents of fishes collected at the same location and time were likely not independent (Grüss et al., 2020; Ng et al., 2021).

Multivariate spatiotemporal models were fitted to PBD_i and PCC_i data for each prey – season combination to estimate mean daily minimum consumption for each year using the vector autoregressive spatiotemporal (VAST) package (version 3.10.0; Thorson, 2019) in R (v4.3.1, R

Core Team, 2023). VAST is a two-stage delta model that can incorporate multiple georeferenced response variables (e.g., PBD and PCC) as categories (c) that are modeled separately, but simultaneously (Grüss et al., 2020). A Poisson link framework was used to model each category as the product of two linear predictors representing numbers-density ($n_{s,t,c}$) and biomass-per-individual ($w_{s,t,c}$) at knot locations s (see below; Thorson, 2018). For the PBD data (c = 1, 'predators'), $n_{s,t,c}$ reflected predator count-per-unit-area while $w_{s,t,c}$ was the weight of an individual predator. These terms represented prey count-per-predator-biomass and individual prey weight, respectively, for the PCC (c = 2, 'prey') data. Multiplying $n_{s,t,c}$ and $w_{s,t,c}$ for a given category yielded expected values of the response that equal the product of the probability of encounter ($\rho_{s,t,c}$) and biomass-density given encounter ($r_{s,t,c}$) found in typical logit-link delta models (Thorson, 2018). The Poisson link framework assumes that the spatial distribution of individuals in the vicinity of sample collection is random, such that the probability of encounter follows a Poisson distribution and is related to the unobserved quantity $n_{s,t,c,i}$ by:

$$\rho_{s,t,c,i} = 1 - exp^{-as_i \cdot n_{s,t,c,i}}, \tag{5}$$

and in turn, biomass-density given encounter is a function of both $n_{s,t,c.i}$ and $w_{s,t,c,i}$:

$$r_{s,t,c,i} = \frac{n_{s,t,c,i}}{\rho_{s,t,c,i}} \cdot w_{s,t,c,i}. \tag{6}$$

In effect, the Poisson link relaxes the traditional assumption that the encounter and conditional components of the delta model are independent (Thorson, 2018). Given these relationships, the probability of observing quantity D (i.e., either PCC or PBD) at sampling site i was:

$$f(d_i = D) = \begin{cases} 1 - \rho_i & \text{if D} = 0 \\ \rho_i \cdot h(D|r_i; \sigma_r^2) & \text{if D} > 0 \end{cases} \tag{7}$$

where $h()$ was the probability density function for unexplained variation in the positive catch rate, σ_r^2 was residual variation, and $f(d_i = D)$ was the likelihood function (Grüss et al., 2023).

The linear predictors for numbers-density and biomass-per-individual were expressed as:

$$log(n_{s,t,c,i}) = \beta_{n_{t,c,i}} + \omega_{n_{s,c,i}} + \varepsilon_{n_{s,t,c,i}} + \sum_{k=1}^{n_k}(\lambda_{n_k} + \varphi_{n_{s,k,i}}) \cdot q_{n_{k,i}} \quad (8)$$

$$log(w_{s,t,c,i}) = \beta_{w_{t,c,i}} + \omega_{w_{s,c,i}} + \varepsilon_{w_{s,t,c,i}} + \sum_{k=1}^{n_k}(\lambda_{w_k} + \varphi_{w_{s,k,i}}) \cdot q_{w_{k,i}}.$$

Both predictors used the log-link function, $\beta_{n_{t,c,i}}$ and $\beta_{w_{t,c,i}}$ were the annual intercepts for each category estimated as fixed effects, $\omega_{n_{s,c,i}}$ and $\omega_{w_{s,c,i}}$ represented latent time-invariant spatial processes, and $\varepsilon_{n_{s,t,c,i}}$ and $\varepsilon_{w_{s,t,c,i}}$ were time-varying spatial processes (Thorson, 2019). Each spatial and spatiotemporal term was estimated as a random effect, specified as a Gaussian Markov random field, and assumed to follow a multivariate normal distribution:

$$\omega_{n_c} \sim MVN\left(0, \sigma^2_{n,\omega_c} \boldsymbol{R}(\kappa_n)\right), \varepsilon_{n_{t,c}} \sim MVN\left(0, \sigma^2_{n,\varepsilon_c} \boldsymbol{R}(\kappa_n)\right), \quad (9)$$

$$\omega_{w_c} \sim MVN\left(0, \sigma^2_{w,\omega_c} \boldsymbol{R}(\kappa_w)\right), \varepsilon_{w_{t,c}} \sim MVN\left(0, \sigma^2_{w,\varepsilon_c} \boldsymbol{R}(\kappa_w)\right).$$

The $\boldsymbol{R}(\kappa_n)$ and $\boldsymbol{R}(\kappa_w)$ terms represented correlations among locations that were a function of decorrelation distances κ_n and κ_w, respectively, σ^2_{n,ω_c} and σ^2_{w,ω_c} were pointwise variances of spatial variation in numbers-density and biomass-per-individual for each category, and $\sigma^2_{n,\varepsilon_c}$ and $\sigma^2_{w,\varepsilon_c}$ were pointwise variances of the spatiotemporal variation. Both $\boldsymbol{R}(\kappa_n)$ and $\boldsymbol{R}(\kappa_w)$ were estimated from Matérn correlation functions that specified either geometric anisotropy, where correlation depended on direction, or isotropy, where correlation was independent of direction (Thorson and Haltuch, 2018). Spatial and spatiotemporal terms were estimated at discrete locations (s) within the sampling frame, the number of which depended on the quantity of knots specified for each model. Knot locations were determined through a *k*-means clustering algorithm that distributed these points in proportion to sampling density.

The remaining terms in Equation (8) modeled the effects of catchability covariates on the linear predictors. The $q_{n_{k,i}}$ and $q_{w_{k,i}}$ terms represented covariate k, λ_{n_k} and λ_{w_k} reflected the

average effect of the covariate on the predictors, and $\varphi_{n_{s,k,i}}$ and $\varphi_{w_{s,k,i}}$ quantified the spatial variation in the covariate effect, where:

$$\varphi_{n_k} \sim MVN\left(0, \sigma^2_{\varphi,n_k} \boldsymbol{R}(\kappa_n)\right),\ \varphi_{w_k} \sim MVN\left(0, \sigma^2_{\varphi,w_k} \boldsymbol{R}(\kappa_w)\right), \quad (10)$$

and σ^2_{φ,n_k} and σ^2_{φ,w_k}were pointwise spatial variances. Estimates of the annual intercept, spatial, and spatiotemporal terms were used to predict PBD and PCC at each knot for each year, while catchability covariates were set to mean values (continuous) or a reference level (categorical).

A four-step modeling approach was used to estimate time-series of consumption for each prey – season combination. First, the most supported distribution of the response variables was identified by fitting three models using each continuous distribution available in VAST: lognormal, gamma, and generalized gamma. These models included only the β, ω, and ε terms in the linear predictors, parameters were estimated using maximum likelihood (ML), and the appropriate distribution was selected using Akaike's Information Criterion (AIC; Akaike, 1973; Burnham and Anderson, 2002). The second step involved fitting nine models to evaluate the spatial and spatiotemporal random effects, including whether spatial correlations reflected anisotropy or isotropy (Table 1; Ng et al., 2021; Gaichas et al., 2024). Each model was fitted using restricted maximum likelihood (REML) and the parameterization with the lowest marginal AIC value was selected. This model was used in step three to assess two catchability covariates: (1) a categorical survey identifier that used the NEFSC as the reference level and (2) a continuous day-of-year covariate, mean-centered for each season, to account for interannual changes in survey timing. Twenty-one model formulations were explored to assess effects of these covariates, including those that allowed the survey effect to vary spatially and between PBD and PCC by specifying a survey-by-category interaction (Table 2). These models were fitted using ML and the most supported was identified by AIC. All models in steps 1 – 3

included 100 knots, and convergence was verified by evaluating parameter gradients (i.e., all < 10^{-4}) and confirming that the Hessian matrix was positive definite.

The most supported model from the third step was selected as the final model and refitted in step four using REML and specifying 500 knots to increase spatial resolution (Thorson, 2019). Predictions of PBD_g and PCC_g were generated for each Northeast shelf grid cell using bilinear interpolation between knots and subsequently used to estimate bias-corrected time-series of C_t following Equation (1) (Thorson and Kristensen, 2016). Uncertainty was quantified using the delta method (Kass and Steffey, 1989), and both C_t and their standard errors were multiplied by 91.25 (i.e., 365/4) to translate estimates from a daily to seasonal timescale.

Ecological linkages

Univariate dynamic linear models (DLMs) were used to link consumption time-series to covariates representing biophysical processes, prey availability, and fishery harvest. The DLM framework represents a state-space linear regression, where a normally distributed response and associated candidate predictors are time-ordered, and parameter estimation follows a temporal autoregressive process (Holmes et al., 2023). Seasonal estimates of biomass consumed for each prey were log-transformed ($log(C_t * 91.25)$) and related to the annualized covariates by:

$$log(C_t \cdot 91.25) = \boldsymbol{F}_t^{\mathrm{T}} \cdot \boldsymbol{\theta}_t + v_t \tag{11}$$

$$\boldsymbol{\theta}_t = \boldsymbol{\theta}_{t-1} + \boldsymbol{w}_t$$

where $\boldsymbol{F}_t$ and $\boldsymbol{\theta}_t$were vectors of covariates and parameters for year t, respectively, v_t were the observation errors ($v_t \sim N(0, r)$), and $\boldsymbol{w}_t$were process errors ($\boldsymbol{w}_t \sim MVN(\boldsymbol{0}, \boldsymbol{Q})$) that governed parameter stochasticity.

Nine annualized covariates were evaluated as possible drivers of consumption. Each of the five physical indicators considered impact biotic processes in the NEUS LME and represent

potential bottom-up controls on predatory removals. The North Atlantic Oscillation (NAO) and Southern Oscillation Index (SOI) are winter (Dec – Mar) indices of atmospheric pressure anomalies (NAO: Azores v. Iceland; SOI: Tahiti v. Darwin, Australia) that differentially impact temperature regimes, precipitation patterns, and storm intensity in the LME (Joyce, 2002; Hurrell et al., 2003). The Gulf Stream Index (GSI) tracks the position of this boundary current, which affects shelf oceanography (Joyce et al., 2019), while the spatial extent of the Mid-Atlantic Cold Pool (CPE) measures an important ephemeral nursery habitat (Miller et al., 2016). The proportion of warm slope water (WSW) entering the Gulf of Maine regulates nutrient availability in this system (Du et al., 2022), and therefore was evaluated as a predictor of consumption for northern prey (Atlantic herring and silver hake) only. The small-large copepod ratio (SLR) is a biological covariate that quantifies the size structure, and thus quality, of the zooplankton community on the Northeast shelf (Perretti et al., 2017), which may exert a bottom-up control on consumption.

Survey indices of relative abundance for each prey species during spring (SIA) and fall (FIA) characterized prey availability to the predators and were hypothesized to exert bottom-up influences on consumption. SIA and FIA were generated by combining biomass catch data for each prey from the NEFSC and NEAMAP surveys in VAST. Development of these univariate VAST models followed the four-step approach outlined above (see '*Modeling Prey Relative Abundance*' in the Supplement). Harvest covariates quantified annual fishery catch (CAT) for each prey and represented potential top-down controls on predator consumption through resource competition (NOAA Fisheries, 2023).

The DLMs fitted to the consumption time-series included one biophysical, prey availability, or harvest covariate, or no covariates (i.e., null model; Table S8). When a predictor

variable was species-specific (SIA, FIA, or CAT), that covariate was only included in models for that prey. Covariates were lagged 0, 1, and 2 years for all prey except for the short-lived longfin squid, where lag-2 covariates were excluded. When modeling spring consumption, lag-0 for CPE was also omitted since this index primarily reflects conditions during warmer months. Finally, models of spring consumption included SIA at lag-0 and FIA at lag-1, while fall models incorporated SIA and FIA at lag-0. SIA and FIA were log-transformed given the variability in these indices (*sensu* Stratton et al., 2018), all covariates were z-scored prior to modeling, and models were fitted using the 'MARSS' package in R (Holmes et al., 2023).

For each prey – season combination, the observation error term in the DLMs was fixed at the average standard error of the seasonal consumption estimates to propagate uncertainty from the VAST modeling (Peterson et al., 2021). The process error associated with the slope was estimated by the model, while the intercept error was set to zero to facilitate convergence (Stratton et al., 2018). Model selection was based on AIC corrected for small sample size (AIC_c), and covariates from all converged models with $\Delta AIC_c < 10$ ($\Delta AIC_c = AIC_c - \min(AIC_c)$) were retained. One-year forecasts of expected values of consumption and uncertainty were generated for the model with $\Delta AIC_c = 0$ using a Kalman filter algorithm.

The persistence of each retained covariate was quantified by removing successive years of data from the time-series, refitting DLMs, and evaluating ΔAIC_c at each iteration (*sensu* Mohn, 1999). Ten truncated 'peels' were created, where each year removed alternated between the beginning and end of the time-series. Covariate persistence (γ_v) was estimated as:

$$\gamma_v = \sum_{m=1}^{n_m} \left(\frac{o_{v,m}}{10}\right) z_m \cdot 100, \quad (12)$$

where $o_{v,m}$ was the number of retained occurrences of covariate v in 10 peels of the untruncated retained model m, and z_m was Akaike weight (Burnham and Anderson, 2002). Note that if a set

of untruncated retained models included a variable at multiple lags, then $m > 1$ for that predictor and γ_v was combined across lags. Covariate prevalence was also quantified to assess the relative importance of the variables in predicting consumption across prey – season combinations:

$$\Phi_v = \frac{\sum \gamma_v}{\sum \gamma} \cdot 100 \,, \tag{13}$$

where $\sum \gamma_v$ summed persistence values for covariate v, and $\sum \gamma$ summed across covariates.

Results

Consumption modeling

VAST models were successfully fitted to the PBD and PCC data for each prey – season combination, and the generalized gamma was the most supported distribution for modeling the non-zero data in each case (Table S9). Likewise, when evaluating random effects, model R_1 received the most empirical support across all prey and seasons (Table S10), indicating that the inclusion of latent spatial and spatiotemporal terms in both linear predictors, and anisotropy in the correlation functions, was appropriate. The most supported catchability covariate parameterizations varied among the prey and seasons, however (Table S11). Model Q_5 had the lowest AIC value for the spring model of Atlantic herring consumption, while the most supported fall model was Q_{20}. This parameterization was also selected for the fall models of silver hake and longfin squid. The most supported spring model of silver hake consumption was Q_{18}, while that of longfin squid was Q_6. The butterfish models with the lowest AIC values for spring and fall were Q_{16} and Q_{21}, respectively.

Atlantic herring were encountered in predator stomachs at 6.6% of the sampling sites included in the spring dataset and resulting consumption estimates ranged from 275.9 – 19,069.8 metric tons (t) (Figure 2a). Consumption was relatively low from 1978 – 1983, where these early

season estimates varied around 927.5 t (1981 excluded). The anomalously high value in 1981 was due to large quantities of herring encountered in goosefish (*Lophius americanus*) stomachs that spring. Consumption increased from the mid-1980s to between 13,253.1 and 17,383.7 t during 1999 – 2002, fluctuated around 5,575.0 t from 2003 – 2010, reached 17,601.7 t in 2011, and declined thereafter. Coefficients of variation (CVs) were all less than 0.54. Fall consumption estimates for herring were 0.0 – 53,131.5 t and greater than spring consumption during 34 of 42 years (Figure 2b). Predatory removals were again low early in the time-series, increased to around 15,802.2 t during 1987 – 2001, and peaked in 2002. Estimates varied from 4,665.4 – 37,390.6 t, with a declining trend, since 2008. The encounter rate was 8.7%, and CVs were between 0.22 and 0.71.

Spring consumption of silver hake was between 475.4 and 19,183.9 t. While the time-series showed no obvious trends, estimates varied around 13,452.9 t before 1982 and 11,493.3 t after 2009, and around 6,685.1 t during the intervening years (Figure 2c). These hake were encountered in predator stomachs at 7.4% of the sampling sites, and CVs were all less than 0.56. Fall consumption ranged from 1,751.8 – 38,884.5 t, which was comparable to predatory removals during spring, and encounter rates were 10.1% (Figure 2d). The time-series again showed no obvious trends, but consumption was mostly higher from 1982 – 1987 and after 2009, varying around 17,937.2 t and 15,308.3 t respectively, and lower at around 8,385.9 t from the late-1980s – 2009. CVs ranged from 0.18 – 0.57.

The consumption of butterfish during spring was 0.0 – 14,065.2 t, and the encounter rate in predator stomachs was only 3.5% (Figure 2e). As observed with silver hake, butterfish consumption was greater during the early and later years of the time-series. Specifically, these removals varied around 3,849.2 t from 1982 – 1986 and 5,006.2 t since 2008, but fluctuated

around 761.3 t from 1987 – 2007. CVs ranged between 0.31 and 0.72. Consumption during fall was consistently greater than that in the spring until 2011 and ranged from 547.4 – 19,612.7 t, while the encounter rate of butterfish in predator stomachs was more than double that during spring at 7.3% (Figure 2f). Consumption was highest prior to 1985, varying around 9,472.6 t, but then declined and remained relatively consistent for much of the remaining time-series. There is evidence of a further decline in more recent years. CVs were 0.22 – 0.59.

Consumption of longfin squid during spring generally increased over the time-series, with distinct peaks occurring in 2012 (21,184.5 t) and 2019 (19,585.0 t; Figure 2g). These squid were encountered in predator stomachs at 8.3% of sampling sites, and CVs were all less than 0.59, similar to other prey – season combinations. Fall encounter rates were 13.8%, and consumption ranged from 1,299.5 – 31,877.3 t (Figure 2h). As observed for butterfish during spring and silver hake in both seasons, consumption was higher in the early and latter parts of the time-series. Estimates fluctuated around 10,492.5 t from 1978 – 1985 and 10,056.8 t since 1999, while varying around 2,737.8 t from 1986 – 1998. All CV estimates were less than 0.42.

Ecological linkages

The most supported DLM linking spring consumption of Atlantic herring to annualized covariates included the survey-derived, within-season index of relative abundance for this species (i.e., SIA) at lag-0 (Figure 3a, Table S12). The slope of the regression was time-varying, positive, and statistically significant prior to 2008, while SIA persistence was 74.6%, meaning that it was included in the suite of retained models in about three-quarters of the time-series peels, adjusted for Akaike weight. Similarly, the model with the lowest AICc value for fall consumption of herring included the within-season index of relative abundance (FIA, lag-0), which had a constant and significant positive effect on consumption, and persistence was 100%

(Figure 3b). The forecast bias, quantified as Root Mean Squared Error (RMSE) of the model fit (zero indicates no bias), was lower for the fall model (0.45) than for the spring (0.78). Similarly, the models receiving the most empirical support for consumption of silver hake in spring and fall included the within-season indices of relative abundance for each (i.e., SIA lag-0 for spring, FIA lag-0 for fall; Figure 4a&b). Both covariates had constant and significant positive effects on silver hake consumption, and persistence values were 79.6% and 36.7% while the RMSEs were 0.69 and 0.55, respectively.

The CAT covariate at lag-1 was included in the most supported DLM model of spring butterfish consumption (Figure 5a). Fishery catch of this species had a negative effect on consumption from 1978 – 1980, a positive effect from 1981 – 1996, and a negative effect thereafter, although these effects were not significant until after 2007. The persistence of this covariate was very high (96.1%), but the RMSE was also high at 1.04. The most supported DLM for fall consumption of butterfish included CAT at lag-0 (Figure 5b). Persistence was only 46.7%, although the model fit had lower bias (0.71), and the covariate effect was constant, positive, and significant. The lag-0 CAT covariate was also included in the model receiving the most empirical support for longfin squid spring consumption. This variable had a constant, statistically significant negative effect on the predatory removals of squid (Figure 6a), and the persistence was 63.4%. The model with the lowest AIC_c value for fall squid consumption included SLR, lag-0. This covariate had a constant and significant negative effect on longfin consumption (Figure 6b), meaning that as the proportion of small copepods increased in the ecosystem, predatory removals of these squid declined. SLR persistence was very high (93.2%). The RMSEs of these spring and fall models were 0.74 and 0.67, respectively.

While the majority of the annualized covariates were not represented in any of the most supported DLM models, each was included in the retained models (i.e., those with $\Delta AICc < 10$) for at least some prey – season combinations (Table S12). The prevalence of the within-season indices of relative abundance (WSI; i.e., SIA for spring models, FIA for fall models) was 37.8% (Table 3), which was the highest among the covariates. These 'now' measures of prey availability were included in the retained models for all prey and seasons except longfin squid during spring. The CAT covariate had a prevalence value of 27.8% and was retained in butterfish and longfin squid models for both seasons, and for silver hake during fall. The prevalence value of the SLR variable was 12.4%, while those of the climate covariates were all less than 7%.

Discussion

This study combined fish predator catch and stomach content data collected over four decades by two fisheries-independent BTS operating in the NEUS LME to estimate the seasonal consumption of four prey species targeted by commercial fisheries. The multivariate VAST modeling framework used to quantify consumption was developed only recently to estimate predator diet composition and 'snapshot' consumption in the Eastern Bering Sea (EBS; Grüss et al., 2020; Goodman et al., 2022), and represents a departure from the deterministic approaches typically used to estimate predatory removals for the Northeast shelf ecosystem (e.g., Overholtz et al., 2000; Link and Idoine, 2009). The spatiotemporal consumption models developed here extend those applied to the EBS in two important ways; (1) this study combined catch and diet data from two complimentary BTS and used catchability covariates to adjust for relative capture efficiency, and (2) gastric evacuation rates were incorporated at the individual fish level. These evacuation rates translated observed stomach contents (i.e., the snapshots) into daily rations

(Holsman and Aydin, 2015), that yielded seasonally integrated estimates of consumption. These time-series of predatory removals were linked to annualized covariates using DLMs, which revealed that both prey availability (bottom-up; positive relationships) and fishery catch (top-down; primarily negative relationships) were the strongest predictors of consumption across most prey and seasons. While the mechanisms underlying these relationships remain unclear, they do provide insight into possible linkages among the drivers of productivity on the Northeast shelf.

Modeling consumption of prey using VAST offers several advantages over the deterministic approaches applied in past studies. Perhaps the most important benefit associated with this statistical framework is the ability to explicitly model fine-scale spatial and temporal variability in the input data as random effects. In doing so, the model accounts for spatiotemporal autocorrelation in the catch and diet data, which likely reduces bias and increases the precision of the resulting consumption estimates (Grüss et al., 2020). Similarly, while deterministic models have been used to estimate the uncertainty associated with predatory removals by sampling the distributions of the input data (Overholtz and Link, 2007), simultaneous estimation of PBD and PCC in a statistical multivariate spatiotemporal model offers an efficient means to propagate uncertainty from the observed data to consumption estimates. When predator catch and stomach content data are available from multiple sources in an ecosystem, VAST can combine these data streams using catchability covariates that quantify the fishing power of each (i.e., NEAMAP) relative to a reference (NEFSC) if there is some spatiotemporal overlap between the sources. In this study, both the NEFSC and NEAMAP operated in the inshore strata of the Mid-Atlantic Bight during 2008, and since 2009 each survey has sampled at the mouth of Delaware Bay and in Rhode Island Sound. This overlap effectively represents the ‘opportunistic paired sampling’

required to estimate relative catchability in VAST (Grüss et al., 2023), as opposed to the extensive, expensive paired tows that would be needed to develop predator-specific calibration coefficients and combine survey data in a deterministic model.

Trends in the consumption time-series for each of the northern prey species, Atlantic herring and silver hake, were similar between spring and fall. For Atlantic herring, predatory removals during both seasons were low during the late 1970s and early 1980s, following the intense overfishing that occurred on this stock in the early 1970s (Overholtz and Friedland, 2002). Consumption of herring increased throughout the 1980s to relatively high levels in the 2000s and 2010s as the stock rebuilt, but has declined again in recent years coincident with a series of poor recruitment events (NEFSC, 2018). Trends in silver hake removals were less remarkable, although both seasons reflected a period of depressed consumption from about the mid-1980s through the 2000s. While predation on silver hake by conspecifics is quite appreciable (Link et al., 2012), cannibalism was not included in consumption models for this species to avoid circularity in the DLMs. Excluding silver hake predation impacted the magnitude of seasonal consumption but did not notably alter the trends (J. Gartland, unpubl. data), which reinforces that temporal patterns in aggregated predatory removals are often robust to the exclusion of even an important consumer (Gaichas et al., 2024).

In contrast to the inter-seasonal coherence observed for the northern prey, consumption trends differed markedly between spring and fall for both butterfish and longfin squid. While the true mechanism underlying these seasonal inconsistencies is unknown, it is possible that interannual patterns in the availability of these prey to their predators varied between spring and fall, perhaps due to climate-induced shifts in spatial distributions or migration phenologies (Langan et al., 2021; Goodman et al., 2022). Differential changes in predator availability (and

thus stomach sample availability) to the surveys could also have accounted for mismatch between spring and fall consumption trends, while the inconsistencies for longfin squid, a species with a sub-annual life cycle (Macy and Brodziak, 2001), may reflect disparate predator-prey dynamics between the early and late-season cohorts. For all prey except for silver hake, consumption was generally greater in the fall than in the spring, which could be attributed to higher predator evacuation rates during the warmer season (metabolic effect), increased encounters between predators and prey when species are widely distributed across the shelf (behavioral effect), or both. Likewise, consumption was relatively low during the late 1980s and throughout the 1990s for all species except Atlantic herring, which coincides with the period when many predator stocks were at low levels prior to the widespread implementation of rebuilding plans in the mid-1990s (Wiedenmann and Legault, 2022).

While estimates of total annual consumption would be most useful to prey stock assessment models designed to incorporate data on predatory removals, constraints imposed by the predator stomach content data available for the Northeast shelf precluded quantifying consumptive removals at an annual scale. Specifically, these diet data are only collected during spring and fall, and given the documented intra-annual trophodynamics of this ecosystem (e.g., Deroba, 2018; Gaichas et al., 2024), extending daily estimates of consumption beyond these sampling seasons would represent an out of sample prediction. Adding survey sampling during summer and winter months would alleviate these temporal constraints, although financial resource limitations would likely prevent implementation. Since VAST can integrate multiple data streams, including those from fisheries-dependent sources, a viable alternative to achieve year-round predator diet sampling would be to collect information on stomach contents as part of the existing Northeast Fisheries Observer Program. Such observer-based diet collections occur

on the US West Coast (Holsman and Aydin, 2015), and previous investigators have called to expand these efforts to the Northeast shelf (e.g., Overholtz et al., 2000; Deroba, 2018). Extending predator stomach sampling into adjacent estuaries and inshore areas north of the NEAMAP, whether on extant surveys (Latour et al., 2023) or observed commercial trips, should further improve consumption estimates by encompassing the full extent of the NEUS LME.

It is also important to note that limitations of the predator stomach content and catch data likely resulted in underestimates of seasonal predatory removals. This study quantified consumption by trawl-collected fish predators, but the four prey species are also consumed by fauna that are not routinely sampled, including marine mammals, seabirds, and large pelagic fishes (Overholtz et al., 2007). Because consistent, long-term sampling of the diet of these taxa does not occur, removals by these predator groups will likely remain a cryptic source of prey natural mortality. While seasonal consumption of each prey was estimated by combining catch and diet data across several consumers, it is possible that some important fish predators were missed due to inadequate sampling by the survey trawls or the prioritization strategies for stomach collections. Further, predator catch data were not adjusted for trawl capture efficiency, which therefore assumes that all fishes in the trawl path were caught (efficiency = 1.0) and in turn likely underestimates predator biomass and resulting consumption. Experiments designed to quantify capture efficiency for the broad range of species sampled by the NEFSC and NEAMAP survey trawls (e.g., Miller et al., 2023) could improve consumption estimates and thus represent an important area of future research.

Patterns in the seasonal consumption of prey reflected trends in the relative abundance of these taxa measured within the same season by the NEFSC and NEAMAP survey trawls. Indeed, these WSI covariates were included in the most supported DLM models for Atlantic herring and

silver hake for both seasons, as well as in retained models for butterfish (spring and fall) and longfin squid (fall only), and thus had the highest prevalence value of the annualized covariates evaluated in this study. These results indicated that prey availability could have a strong influence on predator consumption, which adds to a growing body of evidence that bottom-up processes (i.e., donor control) regulate trophodynamics in the NEUS LME (Buchheister and Latour, 2016). Further, the positive relationships between consumption and survey-derived relative abundance lends support to the use of consumption trends as an additional, or alternative, source of information on prey abundance. The concept of using predators as samplers of prey populations (i.e., Mills et al., 2007), where each predator represents a survey of prey and their stomach the sampling gear, has received much attention in the Northeast US (e.g., Buchheister and Latour, 2016; Ng. et al., 2021; Gaichas et al., 2024). Although most predators in this ecosystem exhibit a Type III functional response where feeding should be proportional to prey abundance (i.e., prey-switching; Smith and Smith, 2020), efforts to link trends in prey abundance derived from stomachs of individual predator species with those from surveys have shown equivocal results, perhaps due to fine-scale variability in predator feeding behavior or predator-prey overlap (Buchheister and Latour, 2016; Ng et al., 2021). In contrast, combining diet data across predators effectively created an ensemble of the more-variable individual predator-prey interactions, which appeared to have a stabilizing effect on the prey abundance information generated from predator stomachs.

The fishery catch covariate was included in the most supported DLMs of butterfish consumption during both seasons and longfin squid in spring, while this predictor occurred in the suite of retained models for both longfin squid and silver hake in fall. Fishery catch was inversely related to each of these seasonal consumption estimates, except for butterfish during

spring. While the mechanism underpinning these inverse relationships is unknown, it is possible that harvest activities exert a top-down control on predator consumption by limiting prey availability (Hjermann et al., 2004). Alternatively, these results could be a byproduct of stock rebuilding efforts that began on the Northeast shelf in the 1990s (Wiedenmann and Legault, 2022). As constraints were placed on harvest, stock sizes of many predators and prey increased, likely augmenting interactions and consumption. Each prey – season combination that showed a negative relationship with catch also exhibited an increase in predatory removals during the latter part of the time-series. The positive relationship between fall butterfish consumption and catch could reflect synchronous trends in the availability of this prey both to predators and the fishery. None of the climate covariates evaluated in this study were included in the most supported DLMs of prey consumption, but each had a prevalence value greater than zero, meaning that they were included among the retained models for at least some prey. The influence of physical forcing on biological processes in this ecosystem is well-documented (Nye et al., 2014), and it is possible that these covariates influenced consumption indirectly, for example by shaping prey abundance or predator – prey overlap, which may have obscured linkages between the abiotic drivers and consumption. Nevertheless, continued exploration of the relationships between predatory removals and physical processes is an important future direction of research, particularly considering the expected impacts of climate change in the NEUS LME (Saba et al., 2023).

Maintaining an adequate prey base to support directed fisheries and predators can be attained by including predation mortality in stock assessments and quantifying trade-offs between the market and nonmarket values of prey. Both activities have been identified as achievable first steps toward operationalizing EAFM (Howell et al., 2021). Most stock

assessments for prey species in the Northeast US, including for the four evaluated here, now call for incorporating predatory removals to account for the appreciable, variable, and likely increasing role that M_2 plays in shaping population dynamics and to address the strong retrospective patterns that have recently emerged in many assessments (Wiedenmann and Legault, 2022). The model-based seasonal consumption estimates generated in this study, although likely biased low, provide requisite data to support these assessments and inform management strategy evaluations on the trade-offs between harvest and predation (de Moor, 2023). The linkages between predator consumption, prey availability, and fishery harvest documented here offer valuable insights into the relationships among the drivers of productivity in the NEUS LME and serve as a useful starting point for future research on the mechanisms by which top-down and bottom-up forcing shape trophodynamic processes in this ecosystem.

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Data Availability

The NEFSC BTS data underlying this article were provided by NOAA Fisheries by permission. Data will be shared on request to the corresponding author with permission of NOAA Fisheries. All other data analyzed for this study are available from the corresponding author upon reasonable request.

Author Contributions

Both authors conceptualized this study and developed the analytical approach. JG acquired the data, conducted the analyses, and wrote the first version of the manuscript. RJL reviewed and edited the manuscript. Both authors approved of the final manuscript.

Conflict Of Interest Statement

The authors have no conflicts of interest to declare.

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Table 1. Multivariate spatiotemporal model parameterizations used to assess the support for including spatial (ω) and spatiotemporal (ε) random effects in the first (LP1) and second (LP2) linear predictors when modeling predator catch and stomach content data collected by the National Oceanographic and Atmospheric Administration, Northeast Fisheries Science Center and Northeast Area Monitoring and Assessment Program bottom trawl surveys (1978 – 2019) to estimate prey consumption. Support for modeling spatial correlation among locations using geometric anisotropy (A) or isotropy (I) was also evaluated.

Model	LP1	LP2	Correlation
R_1	ω, ε	ω, ε	A
R_2	ω, ε	ω, ε	I
R_3	ω, ε	ω	A
R_4	ω, ε	ω	I
R_5	ω, ε	-	A
R_6	ω, ε	-	I
R_7	ω	-	A
R_8	ω	-	I
R_9	-	-	-

Table 2. Multivariate spatiotemporal model parameterizations used to assess support for including catchability covariates in the first (LP1) and second (LP2) linear predictors when modeling predator catch and stomach content data collected by the National Oceanographic and Atmospheric Administration, Northeast Fisheries Science Center and Northeast Area Monitoring and Assessment Program bottom trawl surveys (1978 – 2019) to estimate prey consumption. Survey represented a categorical covariate used to account for differences between the monitoring programs. This survey effect was permitted to vary spatially, indicated by $Survey_s$, and between the predator catch and stomach content data through a Survey * Category (Cat) interaction. Day was a continuous day-of-year covariate, mean-centered for spring and fall separately, meant to address interannual variability in survey timing.

Model	LP1	LP2
Q_1	-	-
Q_2	Survey	-
Q_3	Survey	Survey
Q_4	$Survey_s$	-
Q_5	$Survey_s$	Survey
Q_6	$Survey_s$	$Survey_s$
Q_7	Survey * Cat	-
Q_8	Survey * Cat	Survey
Q_9	Survey * Cat	Survey * Cat
Q_{10}	$Survey_s$ * Cat	$Survey_s$
Q_{11}	$Survey_s$	$Survey_s$ * Cat
Q_{12}	Day + Survey	-
Q_{13}	Day + Survey	Day + Survey
Q_{14}	Day + $Survey_s$	-
Q_{15}	Day + $Survey_s$	Day + Survey
Q_{16}	Day + $Survey_s$	Day + $Survey_s$

Q_{17}	Day + Survey * Cat	-
Q_{18}	Day + Survey * Cat	Day + Survey
Q_{19}	Day + Survey * Cat	Day + Survey * Cat
Q_{20}	Day + $Survey_s$ * Cat	Day + $Survey_s$
Q_{21}	Day + $Survey_s$	Day + $Survey_s$ * Cat

Table 3. Prevalence values for the biophysical, prey availability, and fishery harvest covariates linked to seasonal time-series of consumption (1978 – 2019) for four prey species on the Northeast shelf using dynamic linear models. CAT: fishery catch; CPE: cold pool extent; GSI: Gulf Stream index; NONE: no covariate model; NAO: North Atlantic Oscillation; SLR: small-large copepod ratio; SOI: Southern Oscillation Index; WSW: proportion of warm slope water entering the Gulf of Maine. WSI was the within-season index of prey relative abundance, represented by the spring index at lag-0 for spring consumption time-series and the fall index at lag-0 for fall consumption series. PSI was the prior-season index of prey relative abundance, which was the fall index at lag-1 for spring consumption and spring index at lag-0 for fall consumption.

Covariate	Prevalence
WSI	37.8
CAT	27.8
SLR	12.4
GSI	6.9
PSI	5.4
CPE	3.3
NONE	2.6
SOI	1.8
WSW	1.2
NAO	0.9

Figure 1. Sampling frames of the National Oceanographic and Atmospheric Administration, Northeast Fisheries Science Center (light blue) and Northeast Area Monitoring and Assessment Program (dark blue) bottom trawl surveys used to estimate time-series of consumption for four prey species on the Northeast US continental shelf.

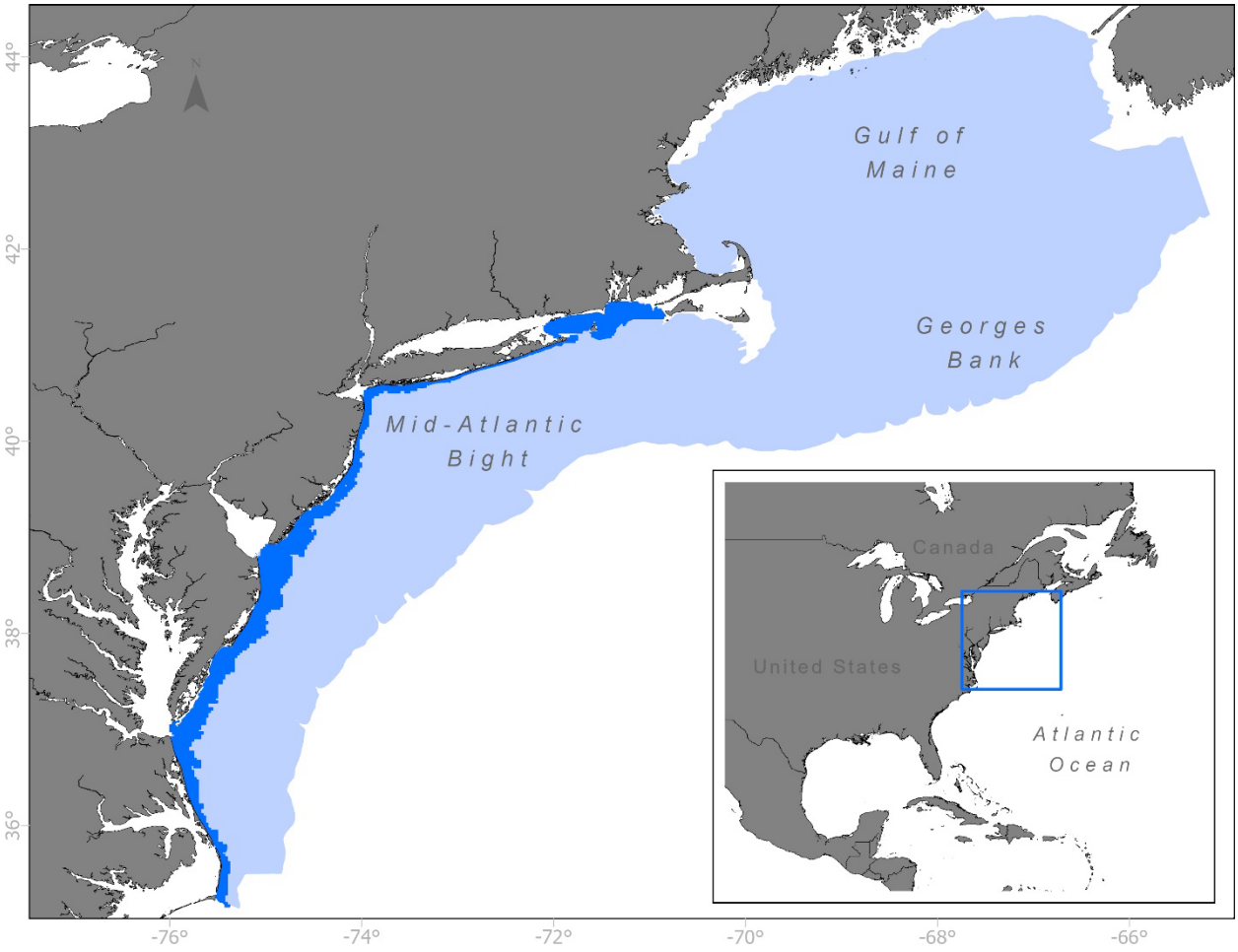


Figure 2. Seasonal time-series of consumption (black lines) for Atlantic herring (a: spring; b: fall), silver hake (c: spring; d: fall), butterfish (e: spring; f: fall), and longfin squid (g: spring; h: fall) in thousands of metric tons (t) with 95% confidence intervals (gray shading). Consumption was estimated by combining data on predator catch and stomach contents collected by the National Oceanographic and Atmospheric Administration, Northeast Fisheries Science Center and Northeast Area Monitoring and Assessment Program bottom trawl surveys (1978 – 2019) in a multivariate spatiotemporal modeling framework.

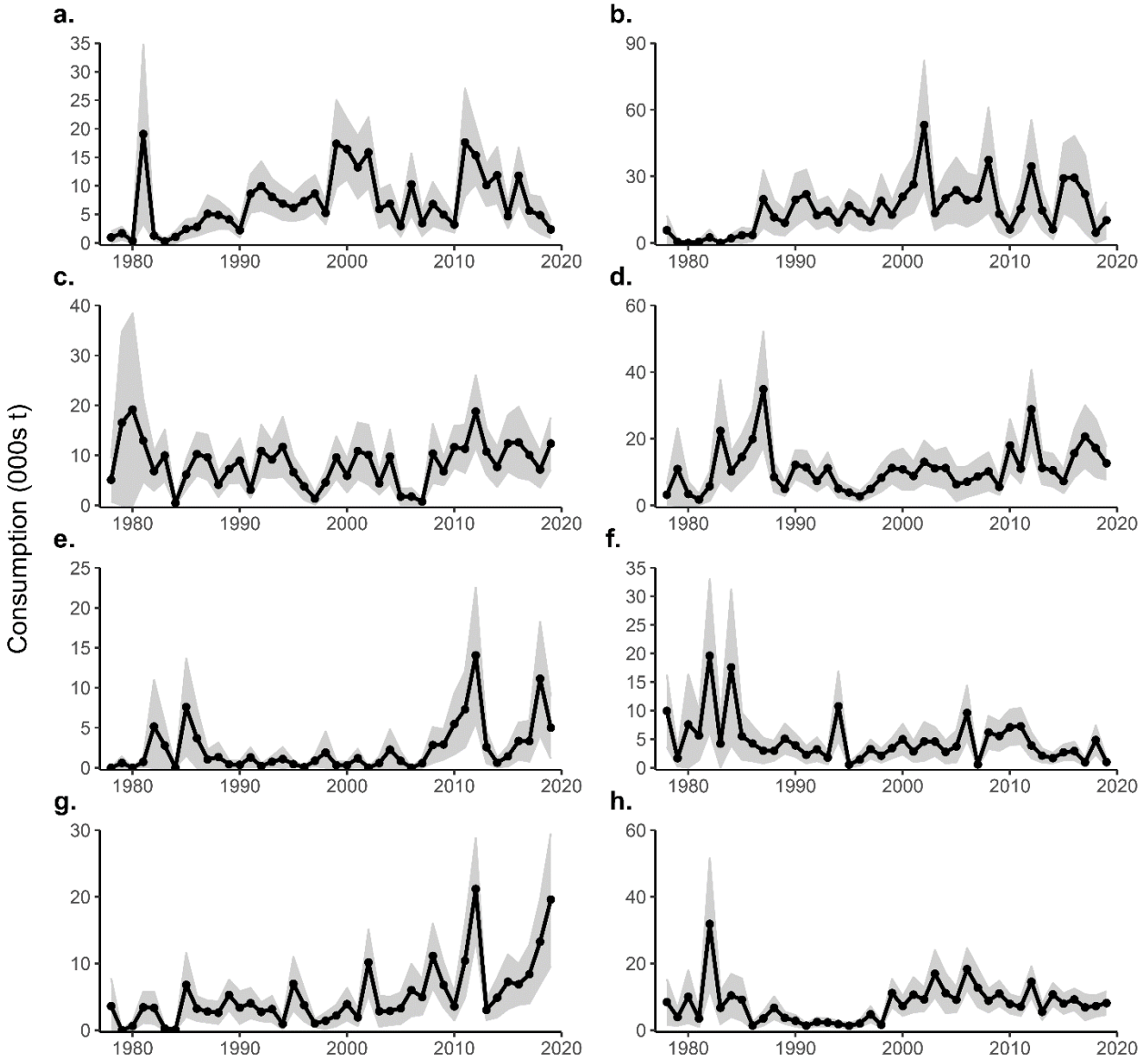


Figure 3. Dynamic linear model (DLM) fits (left panels, black lines) and 95% prediction intervals (grey shading) from relating (a.) the spring time-series of Atlantic herring consumption (blue points) to the spring index of relative abundance for this species at lag-0 (SIA, L0) and (b.) the fall time-series of consumption (blue points) to the fall index of relative abundance at lag-0 (FIA, L0). Root Mean Square Error (RMSE) of the model fits are given for each season. The right panels provide the associated time-series of coefficient estimates for SIA, L0 and FIA, L0 (a. spring; b. fall). Closed circles represent years in which the 95% confidence intervals of these estimates did not overlap zero. Model fits and parameter estimates are provided only for the most supported ($\Delta AIC_c = 0$) DLM from each season.

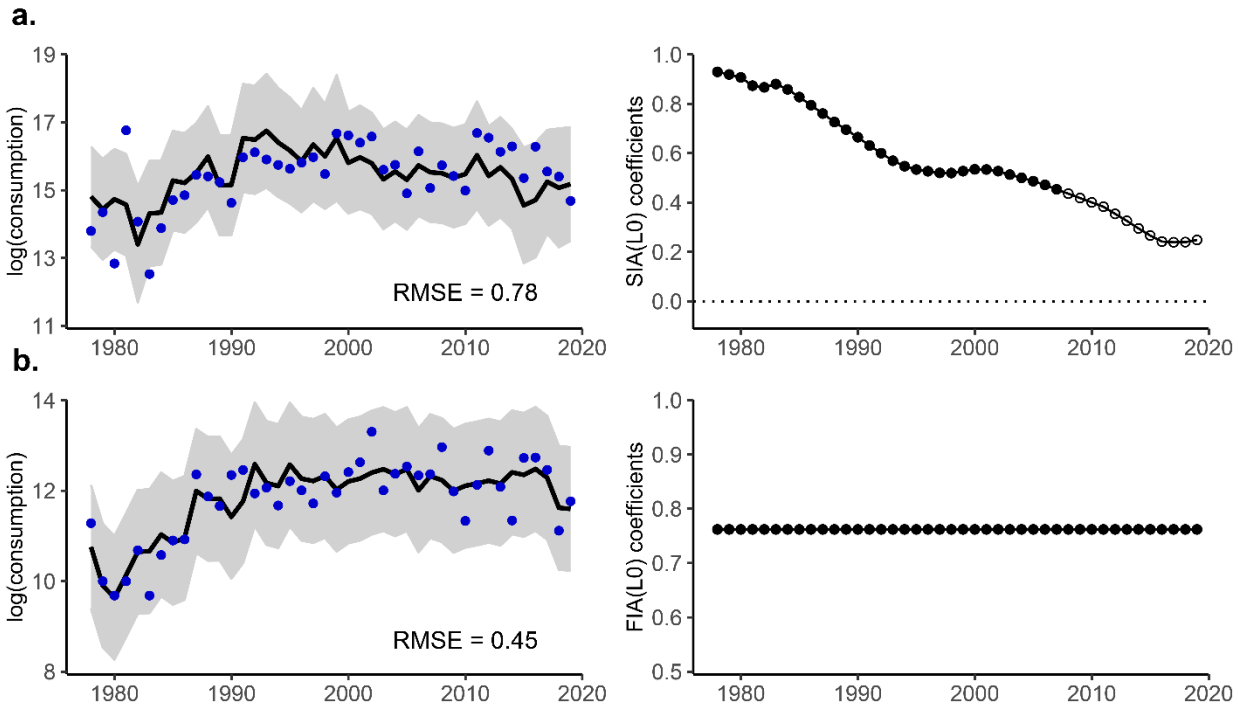


Figure 4. Dynamic linear model (DLM) fits (left panels, black lines) and 95% prediction intervals (grey shading) from relating (a.) the spring time-series of silver hake consumption (blue points) to the spring index of relative abundance for this species at lag-0 (SIA, L0) and (b.) the fall time-series of consumption (blue points) to the fall index of relative abundance at lag-0 (FIA, L0). Root Mean Square Error (RMSE) of the model fits are given for each season. The right panels provide the associated time-series of coefficients for SIA, L0 and FIA, L0 (a. spring; b. fall). Closed circles represent years in which the 95% confidence intervals of these estimates did not overlap zero. Model fits and parameter estimates are provided only for the most supported ($\Delta AIC_c = 0$) DLM from each season.

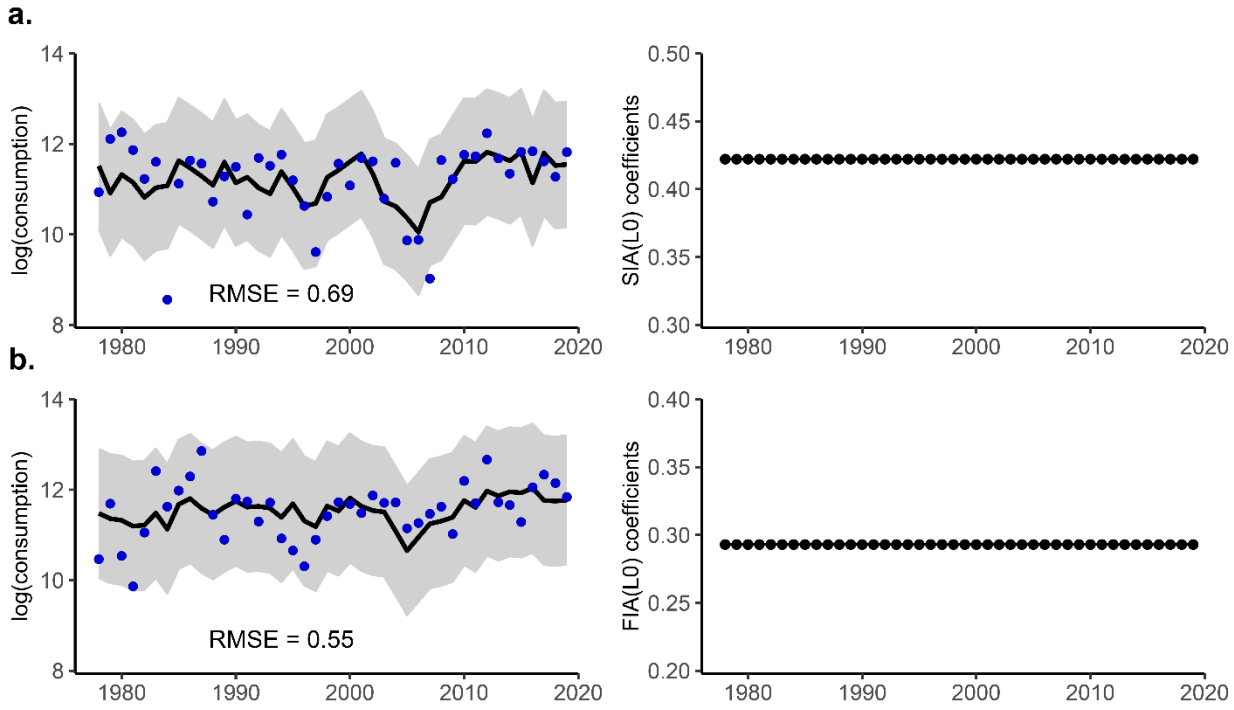


Figure 5. Dynamic linear model (DLM) fits (left panels, black lines) and 95% prediction intervals (grey shading) from relating (a.) the spring time-series of butterfish consumption (blue points) to the fishery catch of this species at lag-1 (CAT, L1) and (b.) the fall time-series of consumption (blue points) to the fishery catch at lag-0 (CAT, L0). Root Mean Square Error (RMSE) of the model fits are given for each season. The right panels provide the associated time-series of coefficients for CAT, L1 and CAT, L0 (a. spring; b. fall). Closed circles represent years in which the 95% confidence intervals of these estimates did not overlap zero. Model fits and parameter estimates are provided only for the most supported ($\Delta AIC_c = 0$) DLM from each season.

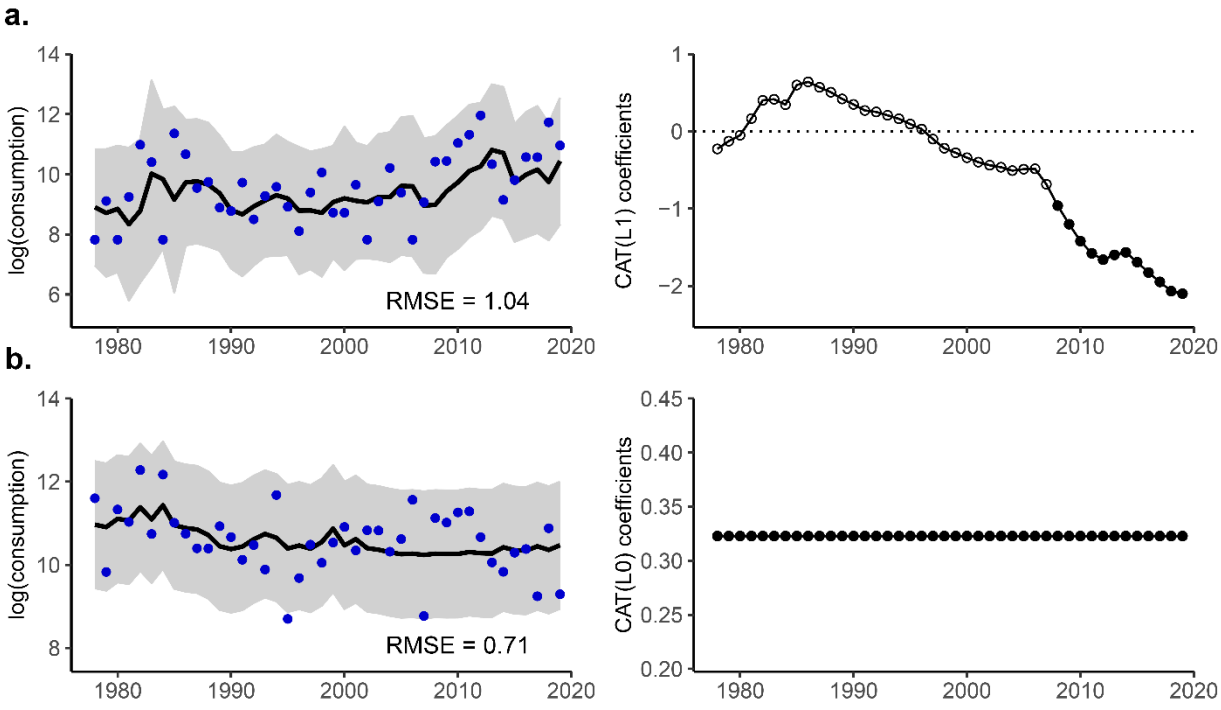
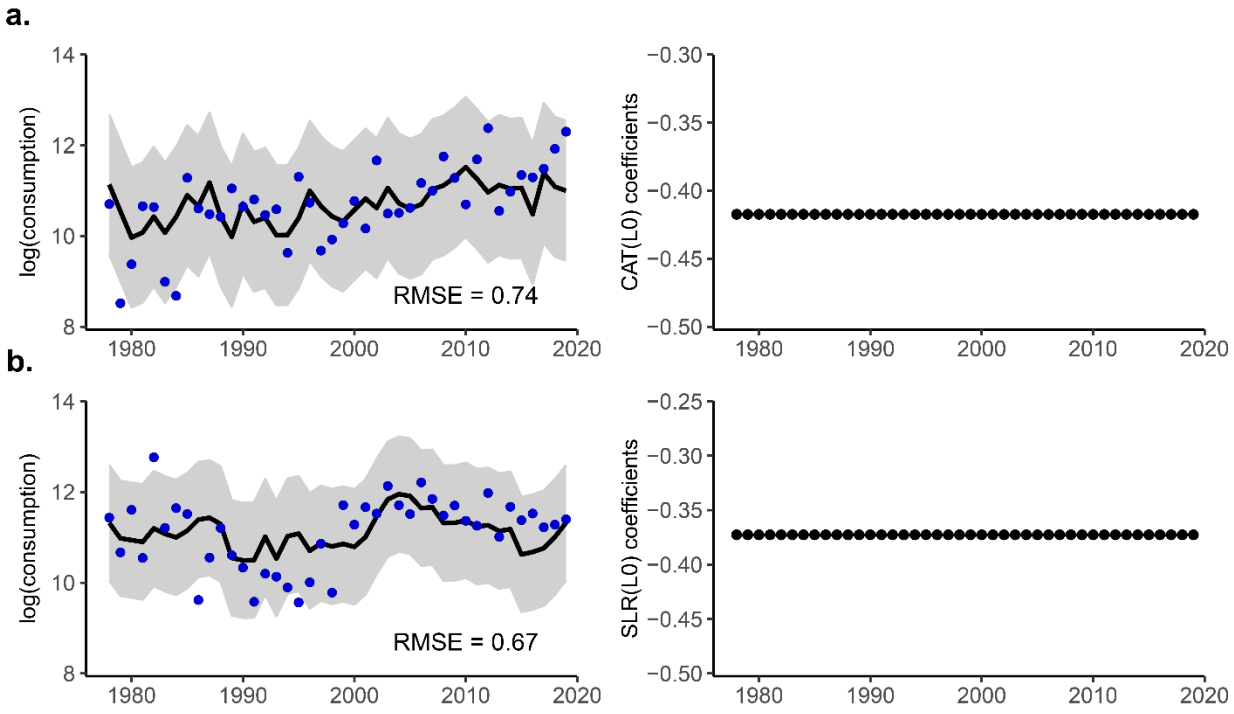


Figure 6. Dynamic linear model (DLM) fits (left panels, black lines) and 95% prediction intervals (grey shading) from relating (a.) the spring time-series of longfin squid consumption (blue points) to the fishery catch of this species at lag-0 (CAT, L0) and (b.) the fall time-series of consumption (blue points) to the small-large copepod ratio at lag-0 (SLR, L0). Root Mean Square Error (RMSE) of the model fits are given for each season. The right panels provide the associated time-series of coefficients for CAT, L0 and SLR, L0 (a. spring; b. fall). Closed circles represent years in which the 95% confidence intervals of these estimates did not overlap zero. Model fits and parameter estimates are provided only for the most supported ($\Delta AIC_c = 0$) DLM from each season.



Supplementary Materials

1. Data Filtering (Methods, Section 3.2)

Table S1. Predator species included to estimate consumption of four prey on the Northeast US continental shelf by combining data on predator catch and stomach contents collected by the National Oceanographic and Atmospheric Administration, Northeast Fisheries Science Center and Northeast Area Monitoring and Assessment Program bottom trawl surveys from 1978 – 2019 in a multivariate spatiotemporal modeling framework.

Predator	Atlantic herring	Silver hake	Butterfish	Longfin squid
Acadian redfish (*Sebastes fasciatus*)		x		
American plaice (*Hippoglossoides platessoides*)		x		
Atlantic cod (*Gadus morhua*)	x	x	x	x
Atlantic croaker (*Micropogonias undulatus*)				x
Atlantic halibut (*Hippoglossus hippoglossus*)	x	x		
Atlantic herring (*Clupea harengus*)		x		
Atlantic mackerel (*Scomber scombrus*)	x	x	x	x
Black sea bass (*Centropristis striata*)		x	x	x
Bluefish (*Pomatomus saltatrix*)	x	x	x	x
Clearnose skate (*Raja eglanteria*)	x	x	x	x
Goosefish (*Lophius americanus*)	x	x	x	x
Haddock (*Melanogrammus aeglefinus*)	x	x		
Little skate (*Leucoraja erinacea*)	x	x	x	x
Offshore hake (*Merluccius albidus*)				x
Pollock (*Gadus chalcogrammus*)	x	x	x	x
Scup (*Stenotomus chrysops*)				x
Silver hake (*Merluccius bilinearis*)	x		x	x
Smooth dogfish (*Mustelus canis*)	x	x	x	x
Smooth skate (*Malacoraja senta*)		x		
Spiny dogfish (*Squalus acanthias*)	x	x	x	x
Striped bass (*Morone saxatilis*)	x	x	x	x

Predator	Atlantic herring	Silver hake	Butterfish	Longfin squid
Summer flounder (*Paralichthys dentatus*)	x	x	x	x
Thorny skate (*Amblyraja radiata*)	x	x		
Weakfish (*Cynoscion regalis*)	x	x	x	x
White hake (*Urophycis tenuis*)	x	x	x	x
Windowpane (*Scopthalmus aquosus*)	x	x		x
Winter skate (*Leucoraja ocellata*)	x	x	x	x

2. Modeling Bottom Temperature (Methods, Section 3.3)

Bottom temperature (BT) data collected by the NEFSC and NEAMAP surveys were used to estimate predator gastric evacuation rates. Approximately 14.8% of sites sampled by the NEFSC (highest rates: 1984 – 1995) and 1.0% sampled by NEAMAP (highest rate: 2014) were missing BT measurements, so the generalized additive models for location, scale, and shape (GAMLSS) framework was used to predict these missing data (Rigby and Stasinopoulos, 2005). Like generalized additive modeling (GAM), GAMLSS permits a response variable to be modeled as a function of parametric and non-parametric components, where the latter can include smoothing functions on continuous variables. However, GAMLSS extends traditional GAMs by incorporating distributions of the response variable beyond the exponential family and allowing the mean, scale (variance), skewness, and kurtosis of the response to be modeled as a function of covariates. The general form of the GAMLSS model is given by:

$$g_1(\boldsymbol{\mu}) = \boldsymbol{X}_1\boldsymbol{\beta}_1 + \sum_{j=1}^{n_j} s_{j1}(x_{j1}) \tag{S1}$$

$$g_2(\boldsymbol{\sigma}) = \boldsymbol{X}_2\boldsymbol{\beta}_2 + \sum_{j=1}^{n_j} s_{j2}(x_{j2})$$

$$g_3(\boldsymbol{\nu}) = \boldsymbol{X}_3\boldsymbol{\beta}_3 + \sum_{j=1}^{n_j} s_{j3}(x_{j3})$$

$$g_4(\boldsymbol{\tau}) = \boldsymbol{X}_4\boldsymbol{\beta}_4 + \sum_{j=1}^{n_j} s_{j4}(x_{j4}) ,$$

where $\boldsymbol{\mu}$, $\boldsymbol{\sigma}$, $\boldsymbol{\nu}$, and $\boldsymbol{\tau}$ represented the mean, variance, skewness, and kurtosis parameters, respectively, $\boldsymbol{X}_{1-4}$ were fixed-effects model matrices, $\boldsymbol{B}_{1-4}$ were fixed-effects coefficients, $s_{j,1-4}$ were smoothing functions for continuous covariate *j*, and g_{1-4} were monotonic link functions.

Initial attempts to model all BT data collected in both seasons by the NEFSC and NEAMAP yielded poor diagnostics, so each season was modeled separately, but across surveys. Candidate predictors included year, location (i.e., latitude x longitude interaction), depth, and sea

surface temperature (SST; 0.1 ^{0}C). SST data were acquired from the NOAA Optimum Interpolation SST (OI SST) V2 High Resolution Dataset, which contains daily global SST on a 25 km grid extending back to 1981 (Reynolds et al., 2007). An OI SST value was assigned to each site sampled by the surveys using sampling date and a spatial nearest neighbor approach (Gaichas et al., 2024). GAMLSS models were fitted to BT data following a two-step approach. The most supported distribution of these data for each season was first identified by fitting a suite of models with all candidate covariates related to the mean parameter using each available continuous distribution defined on the positive real line and evaluating competing forms using Akaike's information criterion (AIC; Akaike, 1973; Burnham and Anderson, 2002). Using these distributions, five parameterizations were then fitted for each seasonal model (Table S2), and the most supported form for each was identified by AIC and evaluating diagnostic plots. These models were used to predict missing BT data; observed values were retained when available. Predictions were not made for sites missing BT data and sampled prior to 1981 (n = 62), so these were removed from prey consumption datasets.

GAMLSS models were successfully fitted to BT data for each season, as no convergence or estimation problems occurred for any of the parameterizations. The Box-Cox t (BCT) distribution was the most supported for modeling spring BT data, while the generalized beta type-2 (GB2) was selected for the fall (Table S3). The full model (M_1) was the most supported parameterization for both seasons (Table S4), and initial model explorations indicated that modeling the variance, skewness, and kurtosis of the spring BT data as a function of OISST improved model diagnostics. Including covariates for parameters other than the mean was not warranted for fall models, based on AIC and diagnostic plots. Slopes of linear regressions fitted to predicted and observed BT data were 0.838 ($p < 0.0001$, $r^2 = 0.799$) for the spring and 0.900

for fall ($p < 0.0001$; $r^2 = 0.873$) indicating that these models performed reasonably well in predicting BT (Figure S1).

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Table S2. Generalized additive model for location, scale, and shape parameterizations evaluated for modeling spring and fall bottom temperature data collected by the National Oceanographic and Atmospheric Administration (NOAA), Northeast Fisheries Science Center and Northeast Area Monitoring and Assessment Program bottom trawl surveys from 1981 – 2019. Lat is latitude, Lon is longitude, and OISST is sea surface temperature obtained from the NOAA Optimum Interpolation Sea Surface Temperature, V2 High Resolution dataset.

Model	Covariates
M_1	Year, Lat*Lon, Depth, OISST
M_2	Lat*Lon, Depth, OISST
M_3	Year, Depth, OISST
M_4	Year, Lat*Lon, OISST
M_5	OISST

Table S3. Model selection statistics associated with the evaluation of candidate response variable distributions for modeling spring and fall bottom temperature data collected by the National Oceanographic and Atmospheric Administration, Northeast Fisheries Science Center and Northeast Area Monitoring and Assessment Program bottom trawl surveys, 1981 – 2019. Results are given for the five most supported distributions when fitting a generalized additive model for location, scale, and shape with all candidate covariates (i.e., full model) to the mean parameter. Bold denotes the distribution selected for each season. BCPE, Box-Cox Power Exponential; BCPEo, Box-Cox Power Exponential – original; BCT, Box-Cox t; BCTo, Box-Cox t – original; GB2, Generalized Beta Type-2.

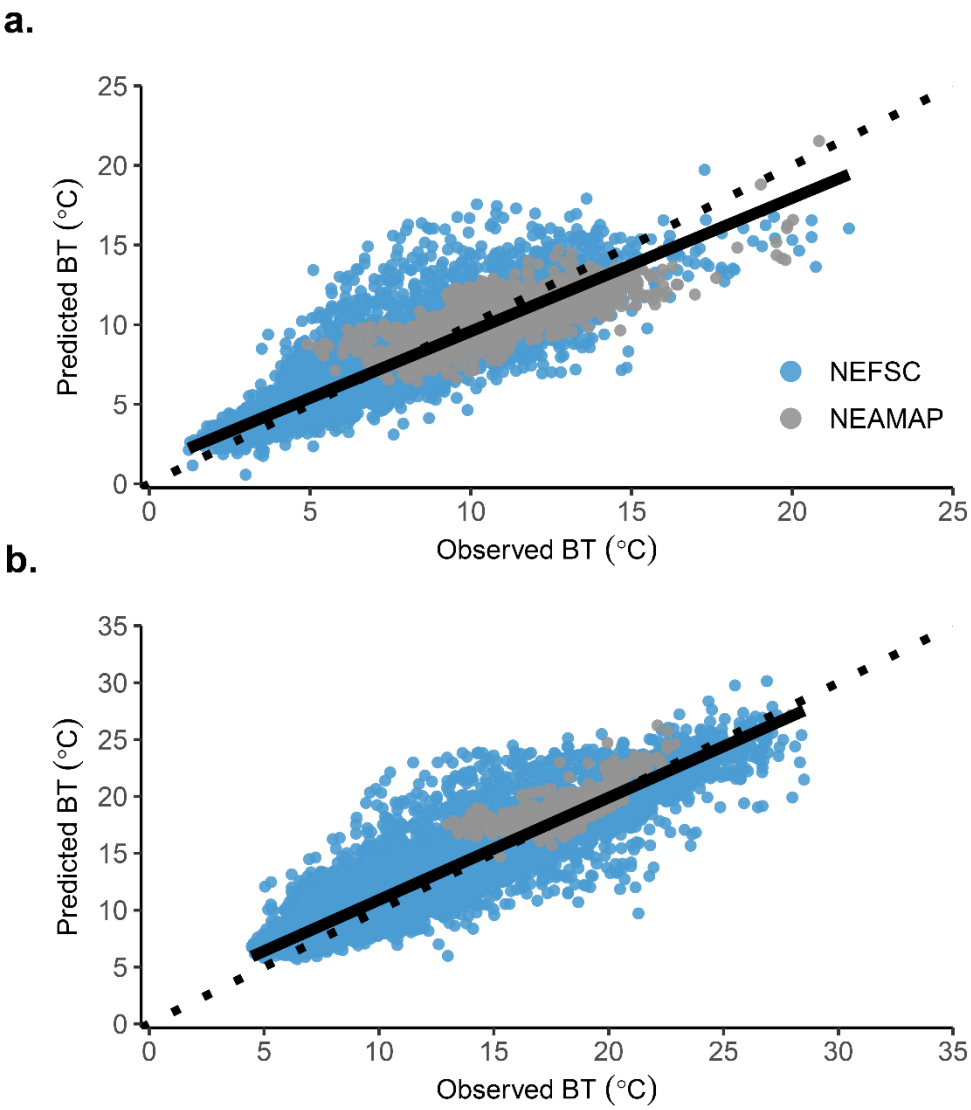
Distribution	-2log(L)	*df* for Model Fit	AIC	ΔAIC
		Spring		
BCT	**35836.7**	**155.6**	**36147.8**	**0.0**
BCPE	35932.3	156.2	36224.8	77.0
GB2	36349.6	156.3	36677.8	530.0
BCTo	36365.2	156.3	36710.3	562.5

BCPEo	36397.8	156.3	36761.3	613.5
		Fall		
GB2	**44404.9**	**156.3**	**44717.6**	**0.0**
BCTo	44475.4	154.9	44785.3	67.7
BCPEo	44489.6	155.4	44800.4	82.8
BCT	44807.9	155.8	45119.5	401.9
BCPE	44940.2	156.2	45252.7	535.1

Table S4. Model selection statistics associated with generalized additive models for location, scale, and shape fitted to spring and fall bottom temperature data collected by the National Oceanographic and Atmospheric Administration, Northeast Fisheries Science Center and Northeast Area Monitoring and Assessment Program bottom trawl surveys, 1981-2019. Bold represents model parameterizations chosen for inference.

Model	-2log(L)	*df* for Model Fit	AIC	ΔAIC
		Spring		
M_1	**35395.5**	**179.4**	**35754.4**	**0.0**
M_4	36097.4	170.4	36438.3	683.9
M_2	38026.4	138.3	38303.1	2548.7
M_3	43625.1	61.4	43747.8	7993.4
M_5	48556.2	15.9	48587.9	12833.5
		Fall		
M_1	**44390.3**	**156.1**	**44702.4**	**0.0**
M_2	45576.5	118.5	45813.4	1111.0
M_4	45874.8	146.7	46168.2	1465.8
M_3	51825.9	58.9	51943.6	7241.2
M_5	59342.0	12.4	59366.7	14644.3

Figure S1. Predicted versus observed bottom temperature (BT) data collected by the National Oceanographic and Atmospheric Administration, Northeast Fisheries Science Center (NEFSC, blue points) and Northeast Area Monitoring and Assessment Program (NEAMAP, gray points) bottom trawl surveys during (a) spring and (b) fall, 1981 – 2019. A linear regression was fitted to predicted and observed BT for each season (solid black line). A 1:1 line that intersects the origin (dotted black line) was provided for reference.



3. Modeling Prey Relative Abundance (Methods, Section 3.4)

The prey indices of relative abundance for spring (SIA) and fall (FIA) used as covariates in the dynamic linear models (DLM) were generated by combining catch data from the NEFSC and NEAMAP surveys in VAST. The modeling framework followed Equations 1 – 10 (see *Methods, Section 3.3*), except that the response variable was comprised of only a single category (i.e., prey biomass density) which was fitted using univariate spatiotemporal models. For each prey – season combination, prey biomass density was calculated at each sampling site by dividing the weight of the prey species collected by the trawl area swept (following Equation 2), and strata were filtered to mirror the corresponding consumption datasets. Spring data were restricted to 1978 – 2019, while fall ranged from 1977 – 2019 so that FIA, lag-1 could be included as a covariate for spring consumption.

A four-step modeling approach analogous to that used to estimate time-series of consumption was implemented to generate indices of relative abundance for each prey – season combination. Again, the most supported distribution of the response variable was identified by fitting models using the lognormal, gamma, and generalized gamma distributions. As with the consumption models, these models included only the β, ω, and ε terms in the linear predictors, parameters were estimated using maximum likelihood (ML), and the appropriate distribution was selected using Akaike's Information Criterion (AIC; Akaike, 1973; Burnham and Anderson, 2002). Likewise, the second step involved fitting nine models using restricted maximum likelihood (REML) to evaluate the spatial and spatiotemporal random effects, including whether spatial correlations reflected anisotropy or isotropy, and the parameterization with the lowest marginal AIC value was retained (Table 1; Ng et al., 2021; Gaichas et al., 2024). This model was used in step three to assess the two catchability covariates that were used in the consumption

models: (1) a categorical survey identifier that used the NEFSC as the reference level and (2) a continuous day-of-year covariate, mean-centered for each season, to account for interannual changes in survey timing. Eleven model formulations were explored to assess effects of these covariates (Table 2; $Q_1 – Q_6$, $Q_{12} – Q_{16}$). Parameterizations with survey-by-category interactions were not needed when modeling a single category. These models were fitted using ML and the most supported was identified by AIC. All models in steps 1 – 3 included 100 knots, and convergence was verified by evaluating parameter gradients (i.e., all $< 10^{-4}$) and confirming that the Hessian matrix was positive definite.

The most supported model from the third step was selected as the final model and refitted in step four using REML and specifying 500 knots to increase spatial resolution (Thorson, 2019). Predictions of prey biomass density were generated for each Northeast shelf grid cell using bilinear interpolation between knots, combined with grid cell area, and summed across cells to estimate bias-corrected time-series of SIA or FIA (Thorson and Kristensen, 2016). Uncertainty was quantified using the delta method (Kass and Steffey, 1989).

VAST models were successfully fitted to the prey biomass density data for all prey – season combinations except for butterfish in spring. The generalized gamma was the most supported distribution for modeling the non-zero data for silver hake and longfin squid during both seasons, while the lognormal distribution was selected for Atlantic herring during spring and fall and butterfish in fall (Table S5). All three models fitted to butterfish spring catch data failed to converge, so the generalized gamma distribution was used in the subsequent model selection steps. When evaluating random effects, model R_1 received the most empirical support across all prey and seasons (Table S6). The most supported catchability covariate parameterizations varied among the prey – season combinations (Table S7). Model Q_{16} had the

lowest AIC value for the spring model of Atlantic herring relative abundance, as well as for silver hake in the spring and fall, butterfish in the fall, and longfin squid in the spring. The most supported fall model of Atlantic herring relative abundance was Q_3, while the only model that converged for butterfish in spring was Q_{14}. Although model Q_{16} had the lowest AIC value for longfin squid in fall, Q_{15} was selected because the ΔAIC of this simpler model was 0.9. Relative abundance indices generated for each prey – season combination (Figure S2) were used as covariates in the DLMs of prey consumption.

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Table S5. Model selection statistics associated with univariate vector autoregressive spatiotemporal models fitted to prey catch data collected by the National Oceanographic and Atmospheric Administration, Northeast Fisheries Science Center and Northeast Area Monitoring and Assessment Program bottom trawl surveys during spring (1978 – 2019) and fall (1977 – 2019). These models were used to identify the most supported distribution of the non-zero catch data for each prey-season combination. Bold indicates the distribution chosen for inference. GAMMA: gamma distribution; G.GAMMA: generalized gamma distribution; LOGNO: lognormal distribution.

Model	Convergence	Objective	AIC	ΔAIC
		Atlantic herring		
		Spring		
LOGNO	**Y**	**40674.7**	**81543.5**	**0.0**
GAMMA	Y	41264.5	82723.1	1179.6
G.GAMMA	N	-	-	-
		Fall		
LOGNO	**Y**	**19583.0**	**39360.8**	**0.0**
GAMMA	Y	19814.5	39823.1	462.3
G.GAMMA	N	-	-	-
		Silver hake		
		Spring		
G.GAMMA	**Y**	**54927.6**	**110051.3**	**0.0**
LOGNO	Y	55014.0	110222.0	170.7
GAMMA	Y	55140.5	110474.9	423.6
		Fall		
G.GAMMA	**Y**	**51776.4**	**103749.0**	**0.0**
GAMMA	Y	51847.6	103889.2	140.2
LOGNO	Y	51998.6	104171.2	422.2
		Butterfish		
		Spring		
G.GAMMA	**N**	**-**	**-**	**-**

GAMMA	N	-	-	-
LOGNO	N	-	-	-
		Fall		
LOGNO	**Y**	**57404.5**	**115003.0**	**0.0**
GAMMA	Y	58069.3	116332.5	1329.5
G.GAMMA	N	-	-	-
		Longfin Squid		
		Spring		
G.GAMMA	**Y**	**33405.8**	**67007.7**	**0.0**
LOGNO	Y	33472.5	67138.9	131.2
GAMMA	Y	33519.8	67233.6	225.9
		Fall		
G.GAMMA	**Y**	**69910.3**	**140016.6**	**0.0**
GAMMA	Y	69971.0	140136.0	119.4
LOGNO	Y	70166.0	140525.9	509.3

Table S6. Model selection statistics associated with univariate vector autoregressive spatiotemporal models fitted to prey catch data collected by the National Oceanographic and Atmospheric Administration, Northeast Fisheries Science Center and Northeast Area Monitoring and Assessment Program bottom trawl surveys during spring (1978 – 2019) and fall (1977 – 2019). These models were used to evaluate support for including spatial and spatiotemporal random effects, as well as anisotropy. Bold indicates the model chosen for inference.

Model	Convergence	Objective	AIC	ΔAIC
		Atlantic herring		
		Spring		
R_1	**Y**	**40685.1**	**81388.2**	**0.0**
R_2	Y	40745.0	81504.1	115.9
R_3	Y	40767.7	81551.5	163.3
R_4	Y	40826.6	81665.2	277.0

R_5	Y	41080.1	82172.1	783.9
R_6	Y	41145.3	82298.5	910.3
R_7	Y	42550.9	85111.8	3723.6
R_8	Y	42570.0	85146.0	3757.8
R_9	Y	43680.7	87363.3	5975.1
		Fall		
R_1	**Y**	**19579.7**	**39177.4**	**0.0**
R_2	Y	19584.4	39182.8	5.4
R_3	Y	19611.1	39238.3	60.9
R_4	Y	19614.9	39241.7	64.3
R_5	Y	19758.3	39528.6	351.2
R_6	Y	19762.1	39532.2	354.8
R_7	Y	20035.8	40081.6	904.2
R_8	Y	20039.7	40085.5	908.1
R_9	Y	23402.5	46806.9	7629.5
		Silver hake		
		Spring		
R_1	**Y**	**54908.3**	**109836.6**	**0.0**
R_2	Y	54965.2	109946.4	109.8
R_3	Y	55126.4	110270.9	434.3
R_4	Y	55172.6	110359.1	522.5
R_5	Y	55667.1	111348.2	1511.6
R_6	Y	55702.6	111415.3	1578.7
R_7	Y	57203.2	114418.4	4581.8
R_8	Y	57211.9	114431.7	4595.1
R_9	Y	60759.7	121523.4	11686.8
		Fall		
R_1	**Y**	**51746.4**	**103512.8**	**0.0**
R_2	Y	51757.7	103531.3	18.5
R_3	Y	51935.4	103888.7	375.9

R_4	Y	51947.4	103908.8	396.0
R_5	Y	52675.2	105364.3	1851.5
R_6	Y	52683.6	105377.2	1864.4
R_7	Y	53450.8	106913.7	3400.9
R_8	Y	53453.5	106915.0	3402.2
R_9	Y	59085.1	118174.3	14661.5
		Butterfish		
		Spring		
R_1	**Y**	**26080.2**	**52180.4**	**0.0**
R_3	Y	26133.7	52285.3	104.9
R_2	Y	26190.2	52396.5	216.1
R_4	Y	26250.4	52514.8	334.4
R_6	Y	26519.9	53049.9	869.5
R_7	Y	27247.9	54507.8	2327.4
R_8	Y	27255.0	54518.1	2337.7
R_9	Y	28857.0	57717.9	5537.5
R_5	N	-	-	-
		Fall		
R_1	**Y**	**57441.1**	**114900.2**	**0.0**
R_2	Y	57468.6	114951.1	50.9
R_3	Y	57581.5	115179.1	278.9
R_4	Y	57603.8	115219.7	319.5
R_5	Y	58210.9	116433.9	1533.7
R_6	Y	58226.0	116460.0	1559.8
R_7	Y	59029.7	118069.4	3169.2
R_8	Y	59039.8	118085.6	3185.4
R_9	N	-	-	-
		Longfin Squid		
		Spring		
R_1	**Y**	**33403.2**	**66826.4**	**0.0**

R_3	Y	33484.2	66986.5	160.1
R_2	Y	33531.6	67079.1	252.7
R_4	Y	33616.1	67246.2	419.8
R_5	Y	34389.4	68792.9	1966.5
R_6	Y	34487.0	68984.0	2157.6
R_7	Y	35321.9	70655.7	3829.3
R_8	Y	35329.3	70666.6	3840.2
R_9	Y	38483.8	76971.6	10145.2
		Fall		
R_1	**Y**	**69988.4**	**139996.8**	**0.0**
R_2	Y	70006.5	140028.9	32.1
R_3	Y	70141.6	140301.2	304.4
R_4	Y	70155.7	140325.5	328.7
R_5	Y	70516.2	141046.3	1049.5
R_6	Y	70525.7	141061.5	1064.7
R_7	Y	71259.3	142530.6	2533.8
R_8	Y	71263.0	142534.0	2537.2
R_9	Y	76321.9	152647.8	12651.0

Table S7. Model selection statistics associated with univariate vector autoregressive spatiotemporal models fitted to prey catch data collected by the National Oceanographic and Atmospheric Administration, Northeast Fisheries Science Center and Northeast Area Monitoring and Assessment Program bottom trawl surveys during spring (1978 – 2019) and fall (1977 – 2019). These models were used to evaluate support for including catchability covariates. Bold indicates the model chosen for inference.

Model	Convergence	Objective	AIC	ΔAIC
		Atlantic herring		
		Spring		
Q_{16}	**Y**	**40369.4**	**80944.9**	**0.0**

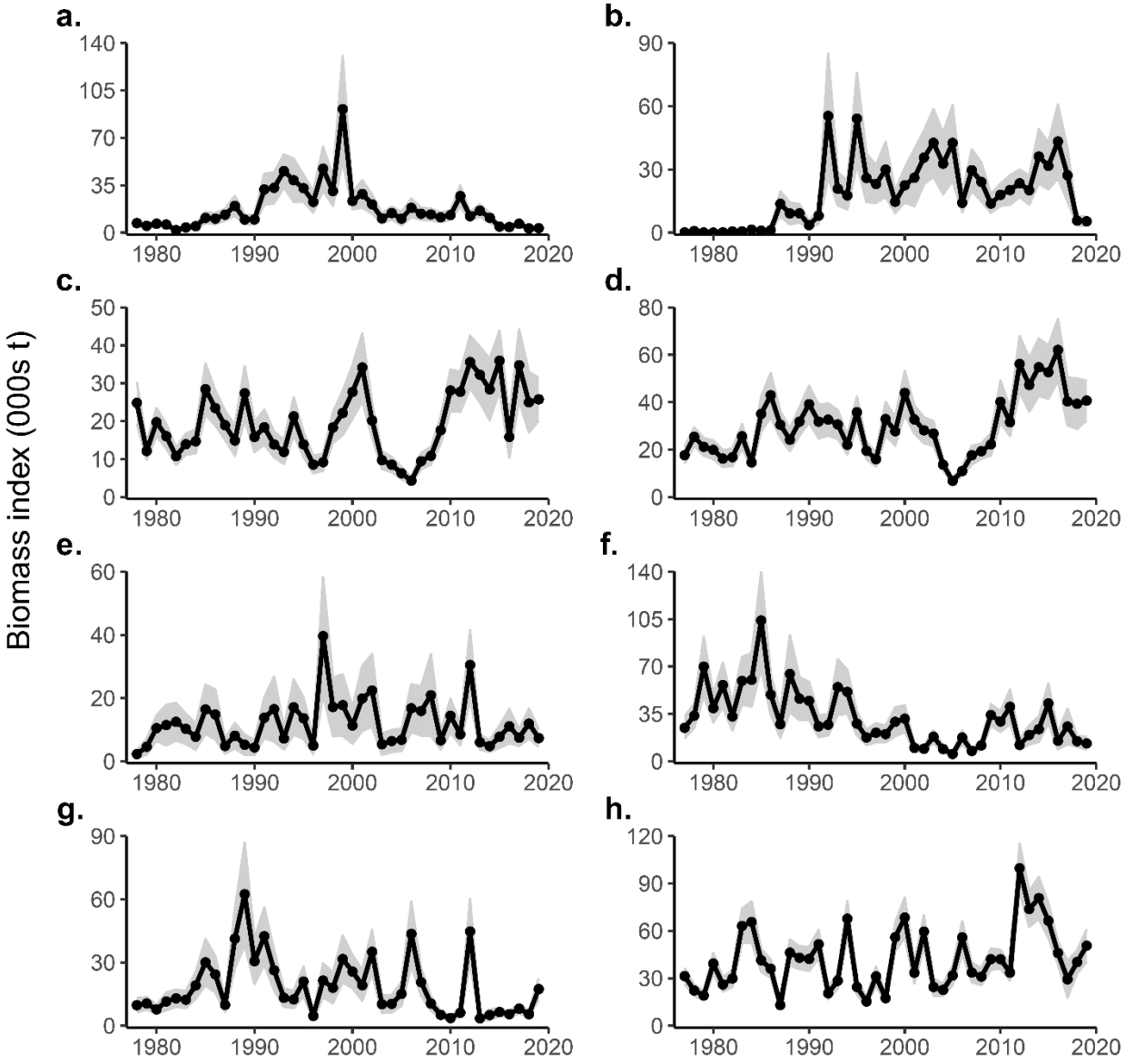
Q_{15}	Y	40372.0	80948.0	3.1
Q_6	Y	40373.9	80949.7	4.8
Q_5	Y	40376.4	80952.9	8.0
Q_{14}	Y	40381.4	80962.8	17.9
Q_4	Y	40384.1	80966.1	21.2
Q_{13}	Y	40442.6	81087.2	142.3
Q_3	Y	40446.6	81091.1	146.2
Q_{12}	Y	40456.8	81111.5	166.6
Q_2	Y	40458.3	81112.5	167.6
Q_1	Y	40674.7	81543.5	598.6
		Fall		
Q_3	**Y**	**19580.2**	**39358.5**	**0.0**
Q_{13}	Y	19579.2	39360.5	2.0
Q_5	Y	19580.2	39360.5	2.0
Q_1	Y	19583.4	39360.8	2.3
Q_2	Y	19582.8	39361.7	3.2
Q_6	Y	19580.2	39362.5	4.0
Q_{12}	Y	19582.6	39363.2	4.7
Q_4	Y	19582.8	39363.7	5.2
Q_{14}	N	-	-	-
Q_{15}	N	-	-	-
Q_{16}	N	-	-	-
		Silver hake		
		Spring		
Q_{16}	**Y**	**54385.5**	**108979.0**	**0.0**
Q_{15}	Y	54401.8	109009.7	30.7
Q_6	Y	54410.8	109025.6	46.6
Q_5	Y	54426.5	109055.1	76.1
Q_{13}	Y	54523.1	109250.2	271.2
Q_3	Y	54545.7	109291.4	312.4

Q_{14}	Y	54661.3	109524.6	545.6
Q_4	Y	54673.8	109547.7	568.7
Q_{12}	Y	54826.1	109852.3	873.3
Q_2	Y	54837.3	109872.6	893.6
Q_1	Y	54885.2	109966.4	987.4
		Fall		
Q_{16}	**Y**	**51633.8**	**103475.6**	**0.0**
Q_6	Y	51637.9	103479.8	4.2
Q_{15}	Y	51640.6	103487.1	11.5
Q_5	Y	51645.2	103492.5	16.9
Q_{13}	Y	51653.2	103510.5	34.9
Q_3	Y	51661.7	103523.4	47.8
Q_{14}	Y	51679.7	103561.3	85.7
Q_4	Y	51683.2	103566.4	90.8
Q_{12}	Y	51699.1	103598.1	122.5
Q_2	Y	51704.9	103607.7	132.1
Q_1	Y	51707.3	103610.5	134.9
		Butterfish		
		Spring		
Q_{14}	**Y**	**25359.8**	**50921.7**	**0.0**
Q_1	N	-	-	-
Q_2	N	-	-	-
Q_3	N	-	-	-
Q_4	N	-	-	-
Q_5	N	-	-	-
Q_6	N	-	-	-
Q_{12}	N	-	-	-
Q_{13}	N	-	-	-
Q_{15}	N	-	-	-
Q_{16}	N	-	-	-

		Fall		
Q_{16}	**Y**	**57109.2**	**114424.4**	**0.0**
Q_6	Y	57124.7	114451.5	27.1
Q_{15}	Y	57130.3	114464.6	40.2
Q_5	Y	57154.0	114508.1	83.7
Q_{13}	Y	57161.7	114525.4	101.0
Q_3	Y	57189.5	114577.0	152.6
Q_{14}	Y	57288.2	114776.4	352.0
Q_4	Y	57290.5	114779.0	354.6
Q_2	Y	57367.5	114930.9	506.5
Q_{12}	Y	57366.7	114931.4	507.0
Q_1	Y	57404.5	115003.0	578.6
		Longfin Squid		
		Spring		
Q_{16}	**Y**	**32419.0**	**65046.0**	**0.0**
Q_{15}	Y	32421.3	65048.5	2.5
Q_6	Y	32451.7	65107.4	61.4
Q_5	Y	32453.4	65108.7	62.7
Q_{14}	Y	32520.5	65243.0	197.0
Q_{13}	Y	32544.5	65293.0	247.0
Q_4	Y	32549.3	65298.5	252.5
Q_3	Y	32589.1	65378.2	332.2
Q_{12}	Y	32648.2	65496.3	450.3
Q_2	Y	32685.6	65569.3	523.3
Q_1	Y	33405.8	67007.7	1961.7
		Fall		
Q_{16}	Y	69478.7	139165.3	0.0
Q_{15}	**Y**	**69480.1**	**139166.2**	**0.9**
Q_6	Y	69503.2	139210.4	45.1
Q_5	Y	69504.5	139211.0	45.7

Q_{13}	Y	69507.8	139219.6	54.3
Q_3	Y	69537.8	139275.6	110.3
Q_{14}	Y	69643.3	139488.5	323.2
Q_4	Y	69670.2	139540.4	375.1
Q_{12}	Y	69702.0	139603.9	438.6
Q_2	Y	69727.8	139653.7	488.4
Q_1	Y	69934.6	140065.1	899.8

Figure S2. Time-series of relative abundance (black lines) in thousands of metric tons (t) and 95% confidence intervals (gray shading) estimated from univariate spatiotemporal models that combined prey catch data from the National Oceanographic and Atmospheric Administration, Northeast Fisheries Science Center and Northeast Area Monitoring and Assessment Program bottom trawl surveys during spring (1978 – 2019) and fall (1977 – 2019). Time-series are provided for Atlantic herring (a: spring; b: fall), silver hake (c: spring; d: fall), butterfish (e: spring; f: fall), and longfin squid (g: spring; h: fall).



4. Dynamic Linear Models; Covariates (Methods, Section 3.4)

Table S8. Covariates evaluated as predictors for each of the seasonal time-series of prey consumption using dynamic linear models. NONE: no covariate model; CPE: cold pool extent; GSI: Gulf Stream Index; NAO: North Atlantic Oscillation; SLR: small-large copepod ratio; SOI: Southern Oscillation Index; WSW: proportion of warm slope water entering the Gulf of Maine; CAT: fishery catch; SIA: spring index of relative prey abundance; FIA: fall index of relative prey abundance. AHS: Atlantic herring, spring; AHF: Atlantic herring, fall; SHS: silver hake, spring; SHF: silver hake, fall; BFS: butterfish, spring; BFF: butterfish, fall; LFS: longfin squid, spring; LFF: longfin squid, fall.

Covariate	Lag	AHS	AHF	SHS	SHF	BFS	BFF	LFS	LFF
NONE	-	x	x	x	x	x	x	x	x
CPE	0		x		x		x		x
	1	x	x	x	x	x	x	x	x
	2	x	x	x	x	x	x		
GSI	0	x	x	x	x	x	x	x	x
	1	x	x	x	x	x	x	x	x
	2	x	x	x	x	x	x		
NAO	0	x	x	x	x	x	x	x	x
	1	x	x	x	x	x	x	x	x
	2	x	x	x	x	x	x		
SLR	0	x	x	x	x	x	x	x	x
	1	x	x	x	x	x	x	x	x
	2	x	x	x	x	x	x		
SOI	0	x	x	x	x	x	x	x	x
	1	x	x	x	x	x	x	x	x
	2	x	x	x	x	x	x		
WSW	0	x	x	x	x				
	1	x	x	x	x				
	2	x	x	x	x				
CAT, AH	0	x	x						
	1	x	x						

Covariate	Lag	AHS	AHF	SHS	SHF	BFS	BFF	LFS	LFF
CAT, AH	2	x	x						
CAT, SH	0			x	x				
	1			x	x				
	2			x	x				
CAT,BF	0					x	x		
	1					x	x		
	2					x	x		
CAT, LF	0							x	x
	1							x	x
SIA, AH	0	x	x						
SIA, SH	0			x	x				
SIA, BF	0					x	x		
SIA, LF	0							x	x
FIA, AH	0		x						
	1	x							
FIA, SH	0				x				
	1			x					
FIA, BF	0						x		
	1					x			x
FIA, LF	0							x	
	1								

5. Consumption Model Selection (Results, Section 4.1)

Table S9. Model selection statistics associated with multivariate vector autoregressive spatiotemporal models fitted to predator biomass and stomach content data collected by the National Oceanographic and Atmospheric Administration, Northeast Fisheries Science Center and Northeast Area Monitoring and Assessment Program bottom trawl surveys, 1978 – 2019, to estimate consumption of four prey species during spring and fall. These models were used to identify the most supported distribution of the non-zero data for each prey-season combination. Bold indicates the distribution chosen for inference. GAMMA: gamma distribution; G.GAMMA: generalized gamma distribution; LOGNO: lognormal distribution.

Model	Convergence	Objective	AIC	ΔAIC
		Atlantic herring		
		Spring		
G.GAMMA	**Y**	**125495.6**	**251353.1**	**0.0**
GAMMA	Y	125642.4	251642.9	289.8
LOGNO	Y	125814.4	251986.7	633.6
		Fall		
G.GAMMA	**Y**	**95759.0**	**191856.9**	**0.0**
LOGNO	Y	95796.6	191929.1	72.2
GAMMA	Y	96182.5	192701.0	844.1
		Silver hake		
		Spring		
G.GAMMA	**Y**	**127829.3**	**256016.6**	**0.0**
LOGNO	Y	127998.8	256351.6	335.0
GAMMA	Y	128075.4	256504.9	488.3
		Fall		
G.GAMMA	**Y**	**108821.5**	**218005.0**	**0.0**
LOGNO	Y	108859.8	218077.6	72.6
GAMMA	Y	109425.2	219208.4	1203.4
		Butterfish		
		Spring		

G.GAMMA	**Y**	**93116.6**	**186569.2**	**0.0**
GAMMA	Y	93204.2	186740.3	171.1
LOGNO	Y	93269.5	186870.9	301.7
		Fall		
G.GAMMA	**Y**	**110920.5**	**222206.9**	**0.0**
LOGNO	Y	110982.7	222327.5	120.6
GAMMA	Y	111445.0	223252.0	1045.1
		Longfin Squid		
		Spring		
G.GAMMA	**Y**	**107534.6**	**215417.2**	**0.0**
GAMMA	Y	107680.1	215704.3	287.1
LOGNO	Y	107717.2	215778.4	361.2
		Fall		
G.GAMMA	**Y**	**113957.7**	**228279.5**	**0.0**
LOGNO	Y	114026.4	228412.8	133.3
GAMMA	Y	114760.8	229881.6	1602.1

Table S10. Model selection statistics associated with multivariate vector autoregressive spatiotemporal models fitted to predator catch and stomach content data collected by the National Oceanographic and Atmospheric Administration, Northeast Fisheries Science Center and Northeast Area Monitoring and Assessment Program bottom trawl surveys, 1978 – 2019, to estimate consumption of four prey species during spring and fall. These models were used to evaluate support for including spatial and spatiotemporal random effects, as well as anisotropy. Bold indicates the model chosen for inference.

Model	Convergence	Objective	AIC	ΔAIC
		Atlantic herring		
		Spring		
R_1	**Y**	**125524.1**	**251080.1**	**0.0**
R_2	Y	125557.4	251142.8	62.7

R_3	Y	125622.3	251272.7	192.6
R_4	Y	125650.1	251324.2	244.1
R_5	Y	125725.5	251473.1	393.0
R_6	Y	125747.3	251512.6	432.5
R_7	Y	127391.6	254801.2	3721.1
R_8	Y	127405.2	254824.4	3744.3
R_9	Y	128533.1	257074.2	5994.1
		Fall		
R_1	**Y**	**95780.4**	**191592.8**	**0.0**
R_3	Y	95795.6	191619.1	26.3
R_2	Y	95798.5	191625.0	32.2
R_4	Y	95811.1	191646.1	53.3
R_5	Y	95871.3	191764.6	171.8
R_6	Y	95884.9	191787.8	195.0
R_7	Y	96660.2	193338.3	1745.5
R_8	Y	96668.6	193351.2	1758.4
R_9	Y	99664.2	199336.5	7743.7
		Silver hake		
		Spring		
R_1	**Y**	**127861.6**	**255755.2**	**0.0**
R_2	Y	127908.8	255845.6	90.4
R_3	Y	127916.8	255861.6	106.4
R_4	Y	127961.9	255947.7	192.5
R_5	Y	128140.1	256302.2	547.0
R_6	Y	128182.4	256382.8	627.6
R_7	Y	129714.9	259447.7	3692.5
R_8	Y	129729.8	259473.7	3718.5
R_9	Y	131167.5	262343.0	6587.8
		Fall		
R_1	**Y**	**108556.5**	**217144.9**	**0.0**

R_2	Y	108573.5	217175.0	30.1
R_3	Y	108620.0	217268.1	123.2
R_4	Y	108632.7	217289.5	144.6
R_5	Y	108820.1	217662.2	517.3
R_6	Y	108827.8	217673.5	528.6
R_7	Y	109702.2	219422.5	2277.6
R_8	Y	109706.9	219427.7	2282.8
R_9	Y	114861.0	229730.0	12585.1
		Butterfish		
		Spring		
R_1	**Y**	**93111.3**	**186254.6**	**0.0**
R_2	Y	93165.3	186358.6	104.0
R_3	Y	93168.0	186364.0	109.4
R_4	Y	93217.1	186458.1	203.5
R_5	Y	93243.7	186509.3	254.7
R_6	Y	93289.3	186596.7	342.1
R_7	Y	94422.5	188863.0	2608.4
R_8	Y	94439.8	188893.5	2638.9
R_9	Y	95111.3	190230.7	3976.1
		Fall		
R_1	**Y**	**110942.3**	**221916.7**	**0.0**
R_2	Y	110985.6	221999.2	82.5
R_3	Y	111059.3	222146.5	229.8
R_4	Y	111097.7	222219.4	302.7
R_5	Y	111479.0	222980.0	1063.3
R_6	Y	111512.6	223043.2	1126.5
R_7	Y	112620.9	225259.7	3343.0
R_8	Y	112631.4	225276.7	3360.0
R_9	Y	118330.2	236668.3	14751.6
		Longfin Squid		

		Spring		
R_1	**Y**	**107539.7**	**215111.3**	**0.0**
R_3	Y	107601.4	215230.9	119.6
R_2	Y	107614.9	215257.9	146.6
R_4	Y	107666.7	215357.4	246.1
R_5	Y	107715.5	215453.1	341.8
R_6	Y	107759.5	215536.9	425.6
R_7	Y	109142.0	218301.9	3190.6
R_8	Y	109155.4	218324.8	3213.5
R_9	Y	110211.1	220430.2	5318.9
		Fall		
R_1	**Y**	**114022.1**	**228076.1**	**0.0**
R_2	Y	114052.6	228133.2	57.1
R_3	Y	114120.4	228268.8	192.7
R_4	Y	114148.0	228320.0	243.9
R_5	Y	114650.5	229323.1	1247.0
R_6	Y	114675.3	229368.7	1292.6
R_7	Y	115778.9	231575.9	3499.8
R_8	Y	115792.3	231598.6	3522.5
R_9	Y	121655.0	243318.1	15242.0

Table S11. Model selection statistics associated with multivariate vector autoregressive spatiotemporal models fitted to predator catch and stomach content data collected by the National Oceanographic and Atmospheric Administration, Northeast Fisheries Science Center and Northeast Area Monitoring and Assessment Program bottom trawl surveys, 1978-2019, to estimate consumption of four prey species during spring and fall. These models were used to evaluate support for including catchability covariates. Bold indicates the model chosen for inference.

Model	Convergence	Objective	AIC	ΔAIC
Atlantic herring				
		Spring		
Q_5	**Y**	**125198.2**	**250764.3**	**0.0**
Q_6	Y	125198.2	250766.3	2.0
Q_9	Y	125204.1	250776.2	11.9
Q_8	Y	125214.2	250796.4	32.1
Q_7	Y	125220.5	250806.9	42.6
Q_{15}	Y	125221.4	250814.9	50.6
Q_{19}	Y	125224.1	250820.2	55.9
Q_4	Y	125231.3	250828.6	64.3
Q_{14}	Y	125235.9	250839.7	75.4
Q_{17}	Y	125236.3	250840.5	76.2
Q_{18}	Y	125235.2	250842.5	78.2
Q_3	Y	125261.5	250889.0	124.7
Q_{13}	Y	125282.9	250935.8	171.5
Q_2	Y	125298.0	250960.0	195.7
Q_{12}	Y	125310.0	250986.1	221.8
Q_1	Y	125495.6	251353.1	588.8
Q_{10}	N	-	-	-
Q_{11}	N	-	-	-
Q_{16}	N	-	-	-
Q_{20}	N	-	-	-

Q_{21}	N	-	-	-
		Fall		
Q_{20}	**Y**	**95434.7**	**191225.5**	**0.0**
Q_{16}	Y	95452.5	191257.0	31.5
Q_{15}	Y	95453.7	191257.5	32.0
Q_{14}	Y	95459.3	191264.6	39.1
Q_{18}	Y	95458.9	191267.9	42.4
Q_{19}	Y	95458.9	191267.9	42.4
Q_{17}	Y	95466.8	191279.6	54.1
Q_{13}	Y	95475.5	191299.0	73.5
Q_{12}	Y	95481.3	191306.5	81.0
Q_{11}	Y	95486.2	191324.4	98.9
Q_3	Y	95494.3	191332.6	107.1
Q_8	Y	95493.6	191333.2	107.7
Q_9	Y	95493.6	191333.2	107.7
Q_7	Y	95498.3	191340.5	115.0
Q_5	Y	95499.5	191345.1	119.6
Q_6	Y	95499.5	191347.1	121.6
Q_4	Y	95505.7	191355.4	129.9
Q_2	Y	95515.1	191372.2	146.7
Q_1	Y	95758.5	191856.9	631.4
Q_{10}	N	-	-	-
Q_{21}	N	-	-	-
		Silver hake		
		Spring		
Q_{18}	**Y**	**127468.5**	**255305.0**	**0.0**
Q_{16}	Y	127468.1	255306.1	1.1
Q_{15}	Y	127469.8	255307.6	2.6
Q_{17}	Y	127491.6	255347.3	42.3
Q_{11}	Y	127489.7	255349.4	44.4

Q_{12}	Y	127501.9	255365.8	60.8
Q_{13}	Y	127501.6	255369.2	64.2
Q_4	Y	127525.1	255412.1	107.1
Q_5	Y	127524.8	255413.7	108.7
Q_6	Y	127524.8	255415.7	110.7
Q_8	Y	127528.3	255420.6	115.6
Q_9	Y	127528.3	255420.6	115.6
Q_7	Y	127550.2	255462.3	157.3
Q_2	Y	127561.1	255482.2	177.2
Q_3	Y	127561.0	255483.9	178.9
Q_1	Y	127829.3	256016.6	711.6
Q_{10}	N	-	-	-
Q_{14}	N	-	-	-
Q_{19}	N	-	-	-
Q_{20}	N	-	-	-
Q_{21}	N	-	-	-
		Fall		
Q_{20}	**Y**	**108128.1**	**216640.2**	**0.0**
Q_{15}	Y	108137.4	216652.9	12.7
Q_{16}	Y	108136.6	216653.1	12.9
Q_{14}	Y	108143.1	216660.2	20.0
Q_{19}	Y	108155.7	216689.4	49.2
Q_{17}	Y	108166.7	216707.4	67.2
Q_{18}	Y	108165.9	216709.8	69.6
Q_{13}	Y	108168.3	216712.7	72.5
Q_{12}	Y	108171.8	216715.6	75.4
Q_6	Y	108216.0	216808.0	167.8
Q_5	Y	108218.1	216810.1	169.9
Q_9	Y	108221.1	216816.3	176.1
Q_4	Y	108224.5	216820.9	180.7

Q_3	Y	108235.6	216843.1	202.9
Q_1	Y	108509.7	217387.4	747.2
Q_2	N	-	-	-
Q_7	N	-	-	-
Q_8	N	-	-	-
Q_{10}	N	-	-	-
Q_{11}	N	-	-	-
Q_{21}	N	-	-	-
		Butterfish		
		Spring		
Q_{16}	**Y**	**92655.3**	**185658.5**	**0.0**
Q_5	Y	92667.9	185677.7	19.2
Q_6	Y	92667.9	185679.7	21.2
Q_{10}	Y	92666.9	185681.8	23.3
Q_{14}	Y	92674.9	185691.9	33.4
Q_4	Y	92684.6	185709.1	50.6
Q_{19}	Y	92721.8	185789.7	131.2
Q_{13}	Y	92730.9	185805.8	147.3
Q_{17}	Y	92732.7	185807.5	149.0
Q_9	Y	92734.2	185810.3	151.8
Q_{12}	Y	92742.1	185824.2	165.7
Q_3	Y	92742.9	185825.7	167.2
Q_8	Y	92742.6	185827.1	168.6
Q_7	Y	92743.8	185827.5	169.0
Q_2	Y	92752.3	185842.6	184.1
Q_1	Y	93120.7	186577.4	918.9
Q_{11}	N	-	-	-
Q_{15}	N	-	-	-
Q_{18}	N	-	-	-
Q_{20}	N	-	-	-

Q_{21}	N	-	-	-
		Fall		
Q_{21}	**Y**	**110366.7**	**221115.4**	**0.0**
Q_{16}	Y	110393.4	221164.8	49.4
Q_{15}	Y	110411.0	221198.1	82.7
Q_{11}	Y	110420.4	221218.8	103.4
Q_{14}	Y	110427.0	221226.0	110.6
Q_{19}	Y	110438.1	221252.2	136.8
Q_{10}	Y	110439.9	221257.9	142.5
Q_{18}	Y	110446.0	221267.9	152.5
Q_{13}	Y	110447.3	221268.6	153.2
Q_6	Y	110450.7	221275.4	160.0
Q_{17}	Y	110459.1	221290.2	174.8
Q_{12}	Y	110462.2	221294.3	178.9
Q_5	Y	110474.6	221321.2	205.8
Q_4	Y	110477.6	221325.2	209.8
Q_9	Y	110504.7	221381.3	265.9
Q_7	Y	110510.6	221391.2	275.8
Q_8	Y	110510.6	221393.2	277.8
Q_3	Y	110514.4	221398.8	283.4
Q_2	Y	110517.4	221402.8	287.4
Q_1	Y	110920.5	222206.9	1091.5
Q_{20}	N	-	-	-
		Longfin Squid		
		Spring		
Q_6	**Y**	**106962.4**	**214280.8**	**0.0**
Q_{11}	Y	106960.7	214281.4	0.6
Q_{21}	Y	106959.3	214282.7	1.9
Q_{16}	Y	106961.9	214283.7	2.9
Q_{15}	Y	106963.9	214285.7	4.9

Q_5	Y	106967.0	214288.0	7.2
Q_4	Y	106990.2	214332.5	51.7
Q_{14}	Y	106991.2	214336.3	55.5
Q_3	Y	107071.8	214495.6	214.8
Q_8	Y	107070.9	214495.8	215.0
Q_9	Y	107070.9	214495.8	215.0
Q_{18}	Y	107069.4	214496.7	215.9
Q_{19}	Y	107069.4	214496.7	215.9
Q_{13}	Y	107070.7	214497.4	216.6
Q_7	Y	107074.4	214500.8	220.0
Q_{17}	Y	107073.9	214501.9	221.1
Q_2	Y	107091.6	214533.2	252.4
Q_{12}	Y	107094.0	214540.1	259.3
Q_1	Y	107534.6	215417.2	1136.4
Q_{10}	N	-	-	-
Q_{20}	N	-	-	-
		Fall		
Q_{20}	**Y**	**113747.6**	**227875.3**	**0.0**
Q_{10}	Y	113776.4	227928.8	53.5
Q_{16}	Y	113786.7	227949.4	74.1
Q_{14}	Y	113799.6	227969.1	93.8
Q_{15}	Y	113799.0	227971.9	96.6
Q_{19}	Y	113806.1	227986.2	110.9
Q_{18}	Y	113812.0	227998.0	122.7
Q_6	Y	113813.3	227998.6	123.3
Q_4	Y	113823.2	228014.3	139.0
Q_{17}	Y	113822.3	228014.6	139.3
Q_5	Y	113823.1	228016.3	141.0
Q_9	Y	113825.3	228020.6	145.3
Q_{12}	Y	113830.8	228029.6	154.3

Q_8	Y	113830.3	228030.6	155.3
Q_{13}	Y	113830.1	228032.2	156.9
Q_7	Y	113839.4	228046.7	171.4
Q_2	Y	113847.9	228061.8	186.5
Q_3	Y	113847.9	228063.8	188.5
Q_1	Y	113955.3	228274.6	399.3
Q_{11}	N	-	-	-
Q_{21}	N	-	-	-

6. Dynamic Linear Model Selection (Results, Section 4.2)

Table S12. Model selection statistics associated with dynamic linear models fitted to seasonal time-series of consumption for four prey species on the Northeast shelf, 1978 - 2019. Results are limited to retained models ($\Delta AIC_c < 10$). Bold indicates the model chosen for inference. CAT: fishery catch; CPE: cold pool extent; GSI: Gulf Stream Index; NONE: no covariate model; NAO: North Atlantic Oscillation; SLR: small-large copepod ratio; SOI: Southern Oscillation Index; WSW: proportion of warm slope water entering the Gulf of Maine; SIA: spring index of relative prey abundance; FIA: fall index of relative prey abundance. The effect of the covariate is indicated by a "+" when covariate coefficients are positive throughout the time-series, "-" when they are negative, and "+/-" when both positive and negative.

Covariate	Lag	log(L)	AICc	ΔAICc	Effect	Persistence
Atlantic herring						
		Spring				
SIA	**0**	**-49.3**	**105.3**	**0.0**	**+**	**74.6**
FIA	1	-50.9	108.5	3.2	+	16.3
WSW	1	-54.0	114.6	9.3	+	0.5
		Fall				
FIA	**0**	**-31.8**	**70.3**	**0.0**	**+**	**100.0**
Silver hake						
		Spring				
SIA	**0**	**-43.7**	**94.1**	**0.0**	**+**	**79.6**
FIA	1	-45.1	96.9	2.8	+	19.6
GSI	0	-48.3	103.2	9.1	+	0.3
		Fall				
FIA	**0**	**-36.8**	**80.2**	**0.0**	**+**	**36.7**
NONE	-	-40.2	82.6	2.4	N/A	10.9
GSI	0	-38.5	83.7	3.5	+	6.3
SIA	0	-38.8	84.2	4.0	+	4.8
WSW	1	-38.8	84.3	4.1	+	4.7
WSW	0	-38.8	84.3	4.1	+	4.5

CPE	2	-39.1	84.8	4.6	-	3.6
CAT	0	-39.2	85.0	4.8	-	3.2
CAT	2	-39.2	85.0	4.8	-	3.2
CPE	1	-39.3	85.2	5.0	-	3.0
CPE	0	-39.3	85.2	5.0	-	2.9
CAT	1	-39.5	85.6	5.4	-	2.4
GSI	2	-39.7	85.9	5.7	+	2.0
GSI	1	-39.9	86.4	6.2	+	1.6
SLR	0	-39.9	86.5	6.3	-	1.5
SOI	1	-40.0	86.6	6.4	+	1.4
SOI	0	-40.1	86.9	6.7	-	1.3
SOI	2	-40.1	86.9	6.7	+	1.2
NAO	1	-40.2	87.0	6.8	+	1.2
NAO	2	-40.2	87.1	6.9	-	1.2
SLR	1	-40.2	87.1	6.9	+	1.1
NAO	0	-40.2	87.1	6.9	+	1.1
			Butterfish			
			Spring			
CAT	**1**	**-59.7**	**126.0**	**0.0**	**+/-**	**35.2**
CAT	0	-59.7	126.1	0.1	+/-	34.5
CAT	2	-60.0	126.6	0.6	+/-	26.4
SOI	1	-63.3	133.1	7.1	+	1.0
NONE	-	-65.6	133.3	7.3	N/A	0.9
SIA	0	-63.8	134.1	8.1	+	0.6
GSI	2	-63.8	134.2	8.2	+	0.6
CPE	2	-64.2	135.0	9.0	-	0.4
GSI	0	-64.2	135.1	9.1	+	0.4
			Fall			
CAT	**0**	**-45.3**	**97.2**	**0.0**	**+**	**25.4**

CPE	1	-46.0	98.7	1.5	+	13.3
CAT	2	-46.2	99.0	1.8	+	11.3
CAT	1	-46.3	99.3	2.1	+	9.9
NONE	-	-49.0	100.0	2.8	N/A	6.9
GSI	1	-46.7	100.1	2.9	-	6.8
GSI	2	-46.9	100.4	3.2	-	5.8
FIA	0	-47.1	100.9	3.7	+	4.6
CPE	2	-48.1	102.7	5.5	+	1.8
NAO	0	-48.2	103.1	5.9	-	1.5
NAO	2	-48.3	103.1	5.9	-	1.5
SOI	0	-48.3	103.2	6.0	+	1.4
GSI	0	-48.3	103.3	6.1	-	1.3
SLR	0	-48.7	104.0	6.8	-	0.9
SOI	1	-48.8	104.2	7.0	-	0.9
NAO	1	-48.8	104.3	7.1	-	0.8
SIA	0	-48.9	104.3	7.1	+	0.8
SLR	1	-48.9	104.4	7.2	-	0.8
CPE	0	-48.9	104.5	7.3	+	0.7
SOI	2	-49.0	104.6	7.4	-	0.7
Longfin squid						
		Spring				
CAT	**0**	**-46.8**	**100.3**	**0.0**	**-**	**59.2**
GSI	1	-48.1	102.8	2.5	+	16.8
GSI	0	-48.4	103.5	3.2	+	11.9
CAT	1	-49.4	105.5	5.2	-	4.3
SOI	0	-49.7	106.1	5.8	+	3.2
SOI	1	-50.0	106.6	6.3	+	2.5
NONE	-	-52.8	107.8	7.5	N/A	1.4
FIA	1	-51.1	108.9	8.6	+	0.8

		Fall				
SLR	**0**	**-43.1**	**92.8**	**0.0**	**-**	**82.1**
SLR	1	-45.1	96.9	4.1	-	11.0
CAT	0	-46.9	100.4	7.6	-	1.7
CAT	1	-46.9	100.4	7.6	+/-	1.7
FIA	0	-47.1	100.9	8.1	+	0.9
SOI	0	-47.6	101.8	9.0	+	0.7
NONE	-	-50.2	102.5	9.7	N/A	0.3

VITA

James Gartland

Jim was born in Philadelphia, Pennsylvania. He earned a Bachelor of Science in Marine Science and Biology from the University of Miami in May 1999, and a Master of Science in Marine Science from the School of Marine Science, William & Mary in May 2002. He has been employed by the Virginia Institute of Marine Science since January 2002 and entered the doctoral program at the School of Marine Science, William & Mary in August 2016.