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Structure, Drivers, and Trophic Interactions of the Demersal Fish Community in Chesapeake Bay

Andre Buchheister

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Structure, Drivers, and Trophic Interactions
of the Demersal Fish Community in Chesapeake Bay

A Dissertation

Presented to

The Faculty of the School of Marine Science
The College of William and Mary in Virginia

In Partial Fulfillment

Of the Requirements for the Degree of

Doctor of Philosophy

by

Andre Buchheister

2013

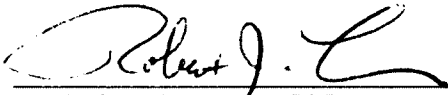
APPROVAL SHEET

This dissertation is submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy




Andre Buchheister

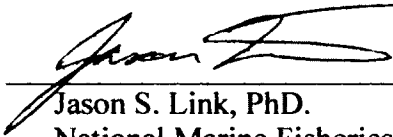
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DEDICATION

This dissertation is dedicated to my parents Roberto Max and Mara. May they realize the depth of my gratitude for all of the love and support they have bestowed throughout my life.

Esse trabalho é dedicado aos meus pais Roberto Max e Mara, para que eles possam saber da minha profunda gratidão por todo amor e apoio prestado ao longo da minha vida.

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AUTHOR'S NOTE

The chapters that comprise this dissertation were written in manuscript format for scientific publication. Thus, the formatting of each chapter follows the guidelines of the publication to which the manuscript was or will be submitted. At the time of writing, citations for individual chapters are as follows:

CHAPTER 1

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CHAPTER 2

Buchheister, A., and R.J. Latour. In Review. Food habits and trophic guild structure of a diverse fish assemblage in Chesapeake Bay, USA. *Estuarine, Coastal and Shelf Science*.

CHAPTER 3

Buchheister, A., and R.J. Latour. In Prep. Dynamic trophic linkages in a large estuarine system – support for supply-driven dietary changes using delta generalized additive mixed models. To be submitted to *Marine Ecology Progress Series*.

CHAPTER 4

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DISSERTATION ABSTRACT

Management of fisheries resources is increasingly broadening its scope from single-species approaches to more holistic, ecosystem-based approaches that account for interactions of fish with a variety of ecological factors, such as predators, prey, and habitat. This ecosystem based fisheries management (EBFM) approach requires thorough biological and ecological understanding of systems pertaining to community structure, habitat suitability, and food web interactions. To strengthen the ecological underpinnings of EBFM efforts in Chesapeake Bay, the largest estuary in the USA, I conducted synoptic analyses examining the structure, function, and patterns of the bay's demersal fish community. This research relied on 10 years of data from a multi-species, bimonthly bottom trawl survey of the Chesapeake Bay mainstem. The unifying objectives of this work were to 1) synthesize basic biological and ecological information of many Chesapeake Bay fishes, and 2) examine the environmental drivers of community structure and trophic interactions in the Bay. One major hypothesis underlying the more detailed research objectives for each component was that bay-wide patterns in biomass and feeding habits of Chesapeake Bay fishes were mostly driven through bottom-up processes governed by a blend of small- and large-scale environmental factors.

As food web structure and trophic interactions are governed by the presence, distribution, abundance, and behavior of species, Chapter 1 focused on evaluating patterns for these basic biological characteristics for a large suite of 50 species and investigating environmental factors that influence the community trends. Univariate and multivariate statistical modeling revealed that the demersal fish community (dominated by five species) was strongly structured along a salinity gradient, and other factors (e.g. dissolved oxygen, temperature, month, and year) helped regulate biomass and diversity trends. Chapter 2 synthesized diet information for 47 fish species, demonstrated the role of five prey groups (mysids, fishes, bivalves, polychaete worms, and crustaceans) in differentiating feeding guilds, and highlighted the importance of non-pelagic prey groups (especially the hyper-benthic mysids) in supporting the nutritional needs of fishes. Diets of 12 predator species were investigated in more detail in Chapter 3 to infer the dynamics of four important prey groups (mysids, bay anchovy, polychaetes, and bivalves) using advanced statistical modeling techniques. Results revealed generally coherent consumption trends across predators for a given prey, suggestive of prey availability driving consumptive patterns. Synchronous annual peaks in prey consumption were indicative of pulses in prey production (particularly mysids and bivalves) that were exploited by predator populations. To evaluate the population-scale effects of these bottom-up alterations in prey productivity, Chapter 4 relied on a simulation model to examine the potential effects that these annual changes in prey availability could have on consumption and production of one representative predator species. The model indicated that enhanced individual growth resulting from pulses in prey production could generate substantial gains in predator spawning stock biomass, recruitment, and fishery yield. However, the bottom-up effects on predator production had only modest effects on rebuilding times of a depleted population relative to controls on fishing mortality.

This research represents one of the largest studies on community structure and trophic interactions for demersal fishes in an estuarine environment, contributing to a broader understanding of fish ecology within a complex and dynamic system. By filling research gaps identified for EBFM in Chesapeake Bay, this body of work also supports a more holistic management approach for the sustainable use of resources from the Chesapeake Bay and coastal waters of the Northwest Atlantic Ocean.

STRUCTURE, DRIVERS, AND TROPHIC INTERACTIONS
OF THE DEMERSAL FISH COMMUNITY IN CHESAPEAKE BAY

INTRODUCTION

Fisheries management

Sustainability of living marine resources is a central objective for resource management, but there are concerns regarding the sustainability and status of global marine fisheries. Many fish stocks around the world are depleted or have collapsed (Jackson et al., 2001; Pauly et al., 2002; Myers and Worm, 2003; Rosenberg et al., 2005). Recovery of some stocks from overfishing is uncertain and may take exceedingly long times despite reductions in fishing effort (Hutchings and Reynolds, 2004; Neubauer et al., 2013). Mean trophic level of catches in many ecosystems have decreased due to serial replacement of fisheries from high- to low-trophic-level fishes or to expansion of fisheries throughout the food web (Pauly et al., 1998; Essington et al., 2006). Size-selective fishing practices truncate size distributions and can induce evolutionary changes in populations towards smaller sizes and slower growth rates (Conover and Munch, 2002; Walsh et al., 2006). And declines in marine and estuarine biodiversity are hindering the ability of ecosystems to provide various services such as sustaining fisheries (Worm et al., 2006). Although some of these concerns have been criticized as being overly pessimistic or relying on faulty methodology (e.g., Hilborn 2007), the general trends of these various concerns are more robust and highlight the serious and complex nature of global fisheries (Worm et al., 2009).

The status of global fisheries and marine ecosystems has contributed to the ongoing evaluation of the best practices for managing fisheries. Traditionally, fisheries

management has relied on a single-species (SS) framework, focused on establishing reference points related to the abundance, biomass, recruitment, or fishing mortality of an individual stock. A common fishery management objective is to achieve maximum sustainable yield (MSY), which typically requires stocks to be maintained at relatively low levels (20-40%) of virgin biomass (Hilborn and Walters, 1992). Despite the depletion of many fisheries far below MSY levels, there are various examples of stocks that have been successfully managed or rebuilt (Richards and Rago, 1999; Hart and Rago, 2006; Gutiérrez et al., 2011). Indeed, some argue that the tools and means to rebuild global fisheries exist, and they are needed to overcome the overcapacity, inappropriate incentive structures, and lack of adequate governance that appear as common issues with failed fisheries (Beddington et al., 2007; Hilborn, 2007b). However, at its core, traditional SS approaches neglect ecological and technical interactions among species and among ecosystem components, and thus they do not typically address the tradeoffs inherent in managing more than a single resource within an ecosystem (Link, 2010a).

Sustainable practices hinge on a complex interplay among biological, physical, social, and economic factors, and awareness of this has fostered increasing support for ecosystem-based fisheries management (EBFM) (Larkin, 1996; Botsford et al., 1997; Link, 2010a). EBFM strives to “balance diverse societal objectives by taking into account the knowledge and uncertainties about biotic, abiotic, and human components of ecosystems and their interactions and applying an integrated approach to fisheries within ecologically meaningful boundaries” (FAO Fisheries Department 2003). By taking a more holistic and integrative perspective, EBFM is better suited than SS management to

address several issues including: ecological interactions among species (e.g. predation, competition); environmental processes that can modulate mortality rates, recruitment, and stock biomass (e.g. habitat suitability, climate change); technical interactions within fisheries (e.g., multispecies fisheries, bycatch); habitat alteration from fishing gears; conflicts among fisheries that target different species that may depend on one another; and balancing fisheries interests with those of other sectors deriving services from an ecosystem (Pikitch et al., 2004; Link, 2010a). As a simple example for the need of ecosystem considerations in fisheries management, the MSY from an ecosystem as a whole must be less than the sum of the individual species' MSYs (Jennings et al., 2001; Gamble and Link, 2009; Link et al., 2012b); therefore optimizing the yield of an individual species is inextricably linked to other species (e.g., prey and predators) and SS fisheries management doesn't account for such interactions.

Established SS concepts and methodologies are indeed being adapted to incorporate ecosystem considerations. For example, predation mortalities can be modeled explicitly, SS models can be modified for multispecies and aggregate biomass applications, and environmental factors can be built in as covariates into stock assessment models (Hollowed et al. 2000a, Keyl & Wolff 2008, Garrison et al. 2010). This expansion of SS approaches, cognizant of the broader ecosystem, has been termed an ecosystem approach to fisheries management, or EAFM (Link, 2010a). As opposed to EAFM, the term EBFM can imply more of a focus on the broader ecosystem effects on fisheries from the start, but EBFM and EAFM are commonly used interchangeably. My use of EBFM throughout the dissertation is intended to also include the EAFM perspective. Regardless of the term used, many proponents acknowledge that the

incorporation of ecosystem principles and multi-species interactions into fisheries management should involve an evolutionary and adaptive change from the traditional SS approaches (Francis et al., 2007; Marasco et al., 2007).

Science for ecosystem-based fisheries management

As attention continues to shift towards more holistic ecosystem-based approaches to management, scientific understanding of the ecological, environmental, and anthropogenic processes structuring ecosystems must be advanced to support the development and application of tools and strategies for EBFM (Whipple et al., 2000; Latour et al., 2003; Link, 2010a). Understandably, long lists of research priorities and questions can be developed to support EBFM, given the complexity of ecosystems and their functioning (e.g., Link 2002, Marasco et al. 2007, Leslie & McLeod 2007). However, for this dissertation, one unifying framework has been to focus on a triad of main drivers that control ecosystem and fisheries production: trophic dynamics, exploitation, and biophysical factors (Link et al., 2010; Gaichas et al., 2012).

Trophic dynamics is one of the most critical features governing the structure and function of ecosystems. Predator-prey relationships provide the topographic structure of food webs by identifying the energy flows within the system, and they establish the most direct lines of control on prey populations. From a fisheries perspective, dietary habits of organisms are responsible not only for connecting abiotic forcing factors to production of fisheries through bottom-up processes, but also for regulating top-down effects of fishery exploitation (Kaiser and Jennings, 2002; Frank et al., 2005). In wild populations, predation can be the strongest mechanism governing mortality for fishes, exceeding

fishing mortality in many of the world's most exploited ecosystems (Bax 1991, 1998, Hollowed, et al. 2000b, Tyrrell et al. 2011).

Biophysical factors have long been identified as crucial regulators of population dynamics and ecosystem processes. Fundamentally, biophysical factors regulate the nutrients and resources available for primary production at the base of all food webs, and thus have substantial control on the overall production capacity of any system (e.g., Longhurst et al. 1995, Ware & Thomson 2005). At small scales, basic environmental factors (e.g., temperature, salinity, dissolved oxygen) regulate metabolic rates, growth, survival, habitat suitability, and food resources that catalyze physiological and behavioral responses of individual organisms (Houde, 1987; Levin, 1992; Wootton, 1998; Mason and Brandt, 1999). These responses by individuals are aggregated over space and time to drive population-level changes in mortality, production, abundance, and distribution (e.g., Hofmann & Powell 1998, MacKenzie & Koster 2004, Nye et al. 2009). For example, many of the prevailing theories pertaining to the control of fish recruitment relate to biophysical factors, especially how they interact with trophic dynamics (Houde, 2009). At even broader temporal scales, environmental conditions such as climate can dictate ecosystem states that favor certain species or assemblages over others, drastically altering community structure, biodiversity, fishery yields, and other ecosystem services (Anderson and Piatt, 1999; Attrill and Power, 2002; Chavez et al., 2003).

Although fisheries resources were once thought to be inexhaustible (Smith, 1994), exploitation is known and understood to be a dominant factor regulating fish populations and ecosystem productivity. As stated previously, there are many concerns regarding the effects of exploitation on the sustainability of fisheries. Although the direct effects of

exploitation can be easier to detect, the indirect effects (e.g., on predators, prey, and other ecosystem services) are more challenging to discern and quantify (Jennings and Kaiser, 1998; Estes et al., 2011). Continued research on the role of fisheries in regulating system dynamics and production is vital for EBFM, particularly given that fishing is the one component (relative to trophic dynamics and biophysical factors) that can be most directly controlled and managed.

Chesapeake Bay background

Continued scientific research is needed to advance EBFM in a variety of systems around the globe, and this dissertation focuses on Chesapeake Bay. Chesapeake Bay is the largest estuary in the U.S. and one of the largest in the world (Boesch et al., 2001; Kemp et al., 2005b). The Chesapeake Bay watershed spans parts of Virginia, Maryland, Delaware, West Virginia, Pennsylvania, and New York states (~166,000 km²), and it accommodates an increasing population currently at ~16 million people (Boesch et al., 2001; Kemp et al., 2005b). The bay is a relatively young (10-12,000 year old) environment characterized by dynamic biophysical conditions. For example, the bay has a progressive salinity gradient from freshwater to ocean water along its 320 km length, and it experiences some of the most drastic temperature ranges (1-30°C) of any coastal ecosystem (Murdy et al., 1997). Chesapeake Bay provides a variety of ecosystem services that includes commercial and recreational fisheries, trade-routes for global commerce, attractions for tourism, filtering and detoxification of water and sediments, a habitat for diverse flora and fauna, locations for human recreation, and provision of general aesthetic value.

Chesapeake Bay acts as vital habitat for a diverse fish fauna that supports many fisheries. Approximately 300-350 species of fishes are known to occur in Chesapeake Bay, although only a small fraction resides in the system year-round (Murdy et al., 1997). The seasonally dynamic nature of the fish community is largely due to its utilization as a juvenile nursery and foraging habitat for adults. Typical of coastal estuaries, the bay supports high levels of primary and secondary production, driven by nutrient inputs from rivers and land runoff (Longhurst et al., 1995; Breitburg et al., 2009). Many species spawn in waters on the continental shelf and rely on physical processes to transport larvae into the bay, whereas other species spawn directly in the tributaries or estuary (Murdy et al., 1997; Able and Fahay, 2010).

Since colonial times, Chesapeake Bay has supported many commercially important fisheries regionally, including those targeting the Atlantic menhaden (*Brevoortia tyrannus*), blue crab (*Callinectes sapidus*), river herring (*Alosines*), eastern oyster (*Crassostrea virginica*), and a variety of other fishes. However, the bay is also vital to the recruitment and production of coast-wide populations of migratory fishes found throughout the eastern U.S. seaboard (Able and Fahay, 2010). Landings in the bay have reached in excess of 250,000 metric tons (Secor and Austin, 2006), but many fisheries have declined, compromising the economic welfare of the fishing industry (and related enterprises) and altering ecosystem structure and function.

As with other coastal environments, Chesapeake Bay has been affected by many stressors that operate within the triad of drivers. Land-use practices, eutrophication, and water pollution are inter-related stressors that have contributed to seasonal hypoxia, increased turbidity and sedimentation, loss of wetlands and submerged aquatic

vegetation, degradation of benthic habitats, blooms of harmful algae, shifting of production to pelagic habitats, and alteration of food webs (Boesch et al., 2001; Kemp et al., 2005b). Climate change and increased CO₂ concentrations are predicted to accelerate sea level rise, increase water temperatures (2-6°C), decrease water pH, increase winter-spring precipitation, and intensify storms with various potential consequences for habitat quality and ecosystem structure (Najjar et al., 2010). Industrialization of finfish and shellfish exploitation since the late 19th century has drastically altered the Chesapeake Bay community. For example, American shad (*Alosa sapidissima*) fisheries collapsed and are under a continued moratorium due to overfishing and restriction from spawning habitat (Olney and Hoenig, 2001); eastern oyster populations have been reduced to ~1% due to overexploitation and habitat loss (Rothschild et al., 1994); striped bass (*Morone saxatilis*) populations collapsed but have since recovered (Richards and Rago, 1999); and Atlantic menhaden experience intensive fishing making it one of the largest fisheries in the country (ASMFC, 2011).

Dissertation rationale and objectives

The complexity of the Chesapeake Bay system, the variety of stressors, and the multitude of derived resources have helped motivate regional interest in EBFM, acknowledging that single-species approaches may be insufficient for balancing varied objectives. EBFM efforts in the bay are exemplified by the collaborative development of a fishery ecosystem plan (FEP) by a team of federal, state, and academic scientists and managers (CBFEAP 2006). The FEP reviewed the status of the system, formulated consensus recommendations for management and research, and provided strategic

guidance for implementation of EBFM. This dissertation addresses aspects of six of the stated research needs and recommendations identified by the FEP:

- 1) quantify species abundance, distribution, and population structure,
- 2) quantify major predator-prey interactions and significant sources of food and mortality,
- 3) determine food web approaches to quantify effects of dynamically important linkages
- 4) model anthropogenic and natural processes influencing trophic interactions,
- 5) develop multispecies and ecosystem models, and
- 6) develop indicators for assessing ecosystem status.

In order to address these research needs, my work leveraged 10 years of fishery-independent data collected by the Chesapeake Bay Multispecies Assessment and Monitoring Program (ChesMMAP). Since 2002, the fishery-independent ChesMMAP bottom trawl survey has seasonally sampled late-juvenile and adult fishes in the bay's mainstem, contributing valuable quantitative data to inform management regulations, stock assessments, and ecosystem models. This dissertation represents the first broad, multi-species analysis of the ChesMMAP database, and it is unified by two over-arching objectives: 1) synthesize basic biological and ecological information of many Chesapeake Bay fishes, and 2) examine the drivers of community structure and trophic interactions in Chesapeake Bay. The triad of productivity drivers (trophic dynamics, biophysical factors, and exploitation) acted as an underlying theme to guide investigations that pertained to the six stated research needs for EBFM in Chesapeake Bay. Specifically, Chapter 1 focused on evaluating the patterns in the distribution, abundance, and dynamics

of demersal fishes in the bay, as influenced by environmental and anthropogenic factors. Chapter 2 synthesized diet information for 47 fishes to characterize food web structure, trophic gradients, and resource partitioning. Chapter 3 examined dominant predator-prey linkages in more detail to evaluate their biophysical drivers, to infer dynamics of four key prey groups, and to explore the role of prey availability on interannual trends. And lastly, Chapter 4 relied on a population simulation model to evaluate the effects of changes in prey availability on the population-scale production of a representative predator.

As a whole, this research represents one of the largest studies on community structure and trophic interactions for demersal fishes in an estuarine environment, contributing to a broader understanding of fish ecology within a complex and dynamic system. By filling research gaps identified by the FEP, this work strengthens the scientific underpinnings for EBFM within Chesapeake Bay and the coastal waters of the Northwest Atlantic Ocean. The ultimate goal is for this dissertation to play a role in the sustainable management of the resources derived from these valuable environments.

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CHAPTER 1

PATTERNS AND DRIVERS OF THE DEMERSAL FISH COMMUNITY OF
CHESAPEAKE BAY

ABSTRACT

Large-scale research on the environmental, biological, and anthropogenic drivers of fish distributions, abundances, and community structure can identify patterns and trends within systems, provide mechanistic insight into ecosystem functioning, and contribute to ecosystem-based fisheries management. This study synthesized 10 years of extensive fisheries-independent bottom trawl data (2002-2011) to evaluate drivers of demersal fish community structure in Chesapeake Bay, the largest estuary in the U.S. Changes in community composition were assessed using constrained correspondence analysis. Also, aggregate community metrics (species richness, Simpson diversity, and catch-per-unit-effort (CPUE) of species groups) were modeled using generalized additive models. Five species (Atlantic croaker, white perch, spot, striped bass, and summer flounder) accounted for >75% of the total trawled biomass. The demersal fish community was primarily structured by the latitudinal salinity gradient that largely differentiated anadromous fishes from coastal shelf spawning species and elasmobranchs, with low overall CPUE and richness in mesohaline waters. Low dissolved oxygen concentrations ($\sim <4 \text{ mg l}^{-1} \text{ O}_2$) greatly suppressed CPUE and diversity metrics and appeared to displace fish biomass towards the northern and southern edges of the bay's mainstem channel. Water temperature and month strongly influenced the seasonal dynamics of community composition and metrics. Community composition and biomass shifted following 2007 with a substantial decline in annual CPUE of some species groups. Recruitment and fishing indices for the dominant species were the best predictors of the interannual patterns in community metrics, outperforming various other climatic and biological annual-scale covariates.

INTRODUCTION

Understanding the influences of environmental and biological factors on fish abundance, distribution, population dynamics, and catch has been an integral objective of fisheries science since the inception of the field (Smith 1994). Information on these ecological processes and relationships helps inform management actions designed to promote sustainable use of fisheries resources, particularly in an ecosystem-based fisheries management (EBFM) context (Link 2010). The growing attention and even mandated utilization of EBFM approaches has fostered renewed appreciation of multispecies and community-based research within ecosystems and highlights the need for continued research and monitoring to support ecosystem modeling efforts (Latour et al. 2003, Link 2010). Research linking environmental and anthropogenic drivers with fish dynamics is particularly important in estuarine and coastal waters where productivity, fishing pressure, and anthropogenic stresses are most intense (Longhurst et al. 1995, Jackson et al. 2001, Worm et al. 2009).

Within the United States, the Chesapeake Bay is a model system to study the many factors influencing fish dynamics in an estuarine environment given its large area, high productivity, well-studied nature, and long fishing history. The Chesapeake Bay ecosystem supports a large number of fish species and is a critical nursery and foraging habitat for many migratory fishes (Murdy et al. 1997, Able & Fahay 2010). As with most estuarine and coastal environments, the system is influenced by a multitude of stressors that include eutrophication, fishing, and climate change. Eutrophication has promoted

phytoplankton growth, shifted production from benthic to pelagic habitats, contributed to the growing hypoxia problems, decreased water clarity, and also degraded important submerged vegetated habitats (Nixon 1995, de Leiva Moreno et al. 2000, Kemp et al. 2005). Industrialized exploitation of finfish and shellfish since the late 19th century has drastically modified the fish community and fish habitat, as exemplified by the collapse and moratorium on several fisheries (e.g., American shad, river herring, and Atlantic sturgeon), reductions of eastern oyster populations to ~1% of virgin abundance (Rothschild et al. 1994, Wilberg et al. 2011), and the collapse and recovery of striped bass populations (Richards & Rago 1999). Climate change is predicted to affect water temperature, CO₂ concentrations, water acidity, sea level, precipitation, and storm intensity in Chesapeake Bay, with consequences for the physiological suitability of the bay for species, the extent of juvenile fish habitats, the quality and timing of plankton production, and the severity of bottom hypoxia (Najjar et al. 2010). The various stressors of the bay combine with natural environmental conditions to structure the occupying fish community in terms of abundance, distribution, and diversity of member species. Evaluation of these ecological relationships and the dynamics of the fish community is an important component to facilitating EBFM (Link 2010), aiding in the ongoing development of ecosystem models (e.g., Christensen et al. 2009), and predicting community responses to changes in the severity of system stressors.

Despite the large research efforts within Chesapeake Bay, the majority of studies examining fish community structure have concentrated on smaller spatial and temporal scales (e.g., Orth & Heck 1980), riverine systems (Carmichael et al. 1992, Wagner & Austin 1999, Wagner 1999), or juvenile fishes (Jung & Houde 2003, Woodland et al.

2012). Only one study focused on bay-wide patterns in species assemblages and community structure (Jung & Houde 2003); however, it was restricted to ecological patterns of small (3-26 cm), non-benthic fishes as sampled with a midwater trawl. To date, no published study has quantitatively examined and described the factors influencing community structure of the bay's benthic and demersal fish fauna at a large spatial scale, mostly due to the lack of available data. This monitoring and research gap contributed to the initiation in 2002 of the Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAP), a large-mesh bottom trawl survey designed to capture late juvenile and adult demersal fishes in the bay. The survey provides critical biological and ecological data in support of ecosystem modeling and fisheries management (Latour et al. 2003, Bonzek et al. 2011).

The current study utilized 10 years of extensive ChesMMAP trawl data to examine patterns in community structure of fishes in the mainstem of the bay, and evaluated the role of different environmental, biological, and anthropogenic factors in affecting structural changes. Several catch and biodiversity metrics were used to characterize community structure in a multispecies context. Community metrics were modeled as functions of various explanatory covariates hypothesized or documented to influence fish populations or system dynamics. Dominant species in Chesapeake Bay were grouped based on life history characteristics to capture different modes of bay utilization. The specific objectives were to 1) characterize spatial and temporal patterns in demersal fish community structure and aggregate community metrics and 2) relate community structure and metrics to physical and biological factors at both smaller and larger spatio-temporal scales. These analyses benefit ongoing EBFM and modeling

efforts in Chesapeake Bay by providing basic information on community ecology, time-series of CPUE trends, simple indicators of ecosystem status, and a 10-year frame of reference for evaluating ongoing community responses to natural and anthropogenic stressors.

MATERIALS AND METHODS

Study area.

Chesapeake Bay, located in the Mid-Atlantic region of the U.S. East Coast (Fig. 1), is the largest estuary in the U.S. and one of the largest in the world (Kemp et al. 2005). Large freshwater inputs from the Susquehanna River in the north and multiple rivers along the western shore generate an increasing salinity gradient along the bay's 320 km length. The bay is relatively shallow with an average depth of 6.5 m (Kemp et al. 2005), but a deeper (20-30 m) narrow channel runs along its center north of the Rappahannock River. The annual temperature range of bay waters (0-30°C) is one of the most drastic of any coastal ecosystem (Murdy et al. 1997).

Field data.

Data for this study were collected by the ChesMMAAP bottom-trawl survey from 2002-2011. The survey operates five cruises a year (March, May, July, September, and November), sampling approximately 80 stations per cruise. Stations were selected based on a stratified random design, with strata defined by water depth (3.0-9.1 m, 9.1-15.2 m, and >15.2 m) and latitude (five latitudinal regions; Fig. 1). Sampling locations for each cruise were selected randomly (limited to trawlable areas) and sampling intensity was proportional to the surface area of the stratum. The survey utilizes a 13.7 m (headrope length) 4-seam balloon trawl with 7.6 cm mesh in the codend to target late juvenile and

adult fishes (Bonzek et al. 2011). At each station, temperature, salinity, dissolved oxygen (DO), and depth were measured using a Hydrolab MS5 sonde prior to sampling. Real-time net mensuration equipment (NETMIND trawl monitoring system, Northstar Technical, Inc.) was used to monitor net geometry, ensure consistent gear behavior, and allow for accurate estimation of area swept. Tows were conducted in daylight hours in the direction of the tidal current at speeds of approximately 3 kts (5.6 km/h) and were typically 20 minutes in duration. However, duration of tows at stations with hypoxic bottom waters ($DO < 2 \text{ mg l}^{-1}$) were generally restricted to 10 minutes to maximize cruise efficiency as the catches at these stations are typically zero or very low. Some tows were also reduced to avoid interactions with commercial fishing gears. Immediately after collection, the catch was sorted by species and size class (if distinct size classes were evident), enumerated, and weighed. Subsamples of captured species and size classes were processed for individual length and weight.

For this study, analyses were restricted to demersal fishes and excluded pelagic fishes which are not sampled effectively by the bottom trawl. Demersal species with <10 individuals or $<1\text{kg}$ captured were omitted from analyses as these represent rare species or species that are not adequately sampled by the survey gear. Catch-per-unit-effort (CPUE, kg km^{-2}) was calculated for each tow from area swept measurements (mean net width multiplied by towed distance measured by onboard GPS) for the following species groups: all fishes (FISH), anadromous fishes (ANAD), coastal shelf spawners (COAS), and elasmobranchs (ELAS). Catchability was assumed to be constant over time, space, and species. Species classified as ANAD or COAS were restricted to those that accounted for $>5\%$ of total biomass, and ELAS species were restricted to $>0.5\%$ of total

biomass. The ANAD, COAS, and ELAS groupings were chosen because they 1) segregate species by life history characteristics, 2) exhibit differential recruitment patterns (Wood & Austin 2009), 3) represent distinct patterns of habitat usage (Murdy et al. 1997), and 4) account for >90% of total biomass sampled.

Multivariate analysis.

A multivariate statistical technique was used to explore patterns within the demersal fish community inhabiting Chesapeake Bay. Relationships among species CPUE and environmental variables were assessed using constrained (or canonical) correspondence analysis, CCA (Ter Braak 1986). CCA, commonly used in ecological studies of communities, is an ordination technique that extracts the major gradients in a multivariate dataset that can be explained by different explanatory variables (McGarigal et al. 2000). CCA combines a weighted multiple linear regression with ordination, and assumes that species have a unimodal response across the gradient of each explanatory variables (Borcard et al. 2011). The explanatory variables in the current study included physical characteristics of bottom water (temperature, salinity, dissolved oxygen), spatial attributes (depth, latitude), and temporal periods (month, year). Significance of explanatory factors (at the 5% significance level) was evaluated using a permutation test (Legendre and Legendre 1998). Prior to analysis, individual species that accounted for less than 0.5% of total trawled biomass were grouped together as “minor” species, as CCA can be sensitive to rare species (Borcard et al. 2011).

Univariate analyses.

Community characteristics were summarized into three general univariate community metrics for analysis: species richness, Simpson's index of diversity, and aggregate CPUE (for FISH, ANAD, COAS, and ELAS groups). These metrics were chosen because they 1) describe different aspects of assemblages such as biological diversity and biomass, 2) are commonly measured and reported, facilitating comparisons with other studies, and 3) have been proposed (or are considered) as useful ecosystem indicators for EBFM and ecosystem modeling (Rice 2000, Methratta & Link 2006, Link 2010). Although aggregate CPUE metrics can be biased and hyper-responsive indices of community abundance if species catchabilities are not constant (Maunder et al. 2006, Kleiber and Maunder 2008), we chose to include them because they 1) rely on fishery-independent data that are less prone to temporal or spatial change in species catchabilities than fishery-dependent data, 2) have a precedent of use in EBFM literature (Rice 2000, Methratta & Link 2006, Link 2010), 3) preserve the directionality of community changes (Kleiber and Maunder 2008), and 4) accurately represented the trends of the dominant individual species (A. Buchheister, unpublished data). Biological diversity was described with two common diversity metrics: species richness (S ; the number of species in a tow) and Simpson's diversity index (D) calculated at each station. D was calculated as:

$$D = 1 - \sum_{i=1}^S p_i^2$$

(1)

where p is the fraction of the total biomass belonging to the i^{th} species at a station, given that at least one species was captured (Magurran 2004). Diversity values, D , are constrained between 0 and 1, and increase with greater S or with a more even biomass

distribution across captured species. As is commonly done, stations with no species captured ($S=0$) were omitted from D calculations because they would result in high diversity estimates ($D=1$) at those stations.

Generalized additive models (GAM) were used to model the response of the three univariate community metrics as functions of explanatory variables. GAMs provide a general and powerful modeling framework that allows for responses to be modeled with both a parametric component (equivalent to generalized linear modeling) and also with a non-parametric component (Wood 2006, Zuur et al. 2009). The non-parametric component relies on smoothing functions for covariates, permitting the covariates to have non-linear effects on the response that are dictated by the data and not by *a priori* assumptions of relationships among the response and covariate. Explanatory variables were identical to those used for the multivariate analyses. Year and month of sampling (YR and MO , respectively) were modeled parametrically as categorical factors. The continuous covariates included latitude (LAT , decimal degrees), depth (DE , m), bottom dissolved oxygen (DO , mg l^{-1}), bottom salinity (SA), and bottom water temperature (T , $^{\circ}\text{C}$). These continuous covariates were smoothed non-parametrically and were chosen because they are commonly measured and known to influence fish distribution and abundance (Murdy et al. 1997). The full GAM was defined as:

$$y_i = a + \alpha_1(YR) + \alpha_2(MO) + g_1(LAT) \cdot MO + g_2(SA) + g_3(T) + g_4(DO) + g_5(DE) + e_i \quad (2)$$

where y_i is a given response variable for station i , the α s are the estimated mean effects for each level of YR and MO , and the g s are nonparametric smoothing functions for each covariate. A space-time interaction was included in the model (i.e., separate latitude smoothers for each month) because this was the only first-order interaction of concern

based on thorough graphical analyses. Thin-plate regression splines were used as the basis to smooth all covariates. The intercept, a , scales the model prediction to the appropriate level of the response because each smooth estimate (g) is constrained to average to 0 over the entire dataset (Ciannelli et al. 2008). The residual error, e_i , is assumed to be independent and identically distributed with a mean of zero and constant variance. Both CPUE and D were modeled using a normal distribution; however, CPUE was log transformed ($\log_e(\text{CPUE}+0.1)$) prior to analysis to account for the positively skewed distribution of these data. Species richness data were modeled with a negative binomial distribution, appropriate for overdispersed count data (Zuur et al. 2009). Graphical and statistical analyses indicated that differences in sampling effort (area swept) did not have discernible effects on S or D across stations and that all tows were sufficiently long to capture a representative sample of biological diversity; therefore no sampling effort adjustments were needed in GAMs for S or D (e.g., an offset *sensu* Zuur et al. (2009) was not included in the GAMs).

Model selection was employed to determine the best combination of explanatory variables for predicting changes in the response metrics. Akaike's Information Criterion (AIC) was used to determine whether reduced models were more strongly supported by the data than the full model in equation 2 (Burnham & Anderson 2002, Zuur et al. 2009). For all models, stations with incomplete water quality information ($n = 230$; 6.3% of stations) were omitted from the analysis. Collinearity among covariates was examined with Pearson correlation coefficients and variance inflation factors (VIF) (Zuur et al. 2009). Although correlated, salinity and latitude were both retained because VIF values

were not above the cutoff of 5 (Zuur et al. 2009) and because they provide information on different environmental characteristics.

Examining interannual patterns in data.

Several annual-scale covariates were hypothesized to contribute to interannual variability in species composition and community metrics of the Chesapeake Bay demersal fish fauna (Table 1). Model selection approaches were used to compare among different annual covariates to infer which variables best explained the interannual trends in the community metrics and to evaluate the strength of evidence for different mechanisms influencing fish community structure.

Annual-scale covariates were classified into categories representing the predominant mode of influence on fishes: climate, fishing, population size, and recruitment (Table 1). Climate variables included: the principal components-based index of the North Atlantic Oscillation for winter months (Hurrell 2012); mean daily discharge from the Susquehanna River (the bay's largest tributary) from February to May (Schubel & Pritchard 1986, Kemp et al. 2005, USGS 2012); summertime volume of hypoxic water ($<2 \text{ mg O}_2 \text{ l}^{-1}$) in the bay (Donald Scavia & Mary Anne Evans, University of Michigan, personal communication); minimum of monthly mean temperatures for winter months (December-March) at Gloucester Point VA following Hare & Able (2007) (SERCC 2012, VIMS 2012); and mean daily chlorophyll-a (ug l^{-1}) estimates (March-August) of bay-wide surface waters interpolated from Chesapeake Bay Program data (Mark Brush, Virginia Institute of Marine Science, unpublished data). The fishing category of covariates included annual Chesapeake Bay (MD and VA) and coast-wide (NC-MA)

landings calculated as the sum of recreational and commercial catches as reported by the National Marine Fisheries Service (NOAA 2012). The sum of female spawning stock biomasses (SSB) was used as an indicator of coast-wide population size for the ANAD and COAS groups. SSB estimates were restricted to species with available data from stock assessments: Atlantic croaker, summer flounder, and striped bass (ASMFC 2010, ASMFC 2011, Terceiro 2011). Recruitment covariates included composite young of the year (YOY) recruitment indices for the ANAD and COAS separately and for the two groups combined (ANAD + COAS). Composite indices were calculated as the average of z-standardized recruitment indices for appropriate species weighted by each species' relative biomass from all ChesMMAP cruises. Recruitment indices were obtained from MD Department of Natural Resources (ANAD species; Durrell & Weedon 2011) and the Virginia Institute of Marine Science (VIMS) Juvenile Fish and Blue Crab Trawl Survey (COAS species; Tuckey & Fabrizio 2011). All annual covariates were standardized to have a mean of zero and standard deviation of one for consistency in model comparisons.

The community metrics (*S*, *D*, CPUE) were aggregates of many species and year classes of fishes. Effects of annual covariates on adult and community metrics may have been delayed by several years if the mechanism of control was through recruitment processes. To account for multiple year classes and delayed effects, annual covariates were calculated as a single year value, or a mean of two years (i.e., a span of 1 or 2 years). Covariates were also lagged 0, 1, or 2 years. All combinations of these spans and lags were calculated. Some covariates (hypoxic volume, landings, and SSB) were restricted to a zero-year lag and one-year span (Table 1), as these covariates were hypothesized to have weak or negligible delayed effects on the measured response

variables. GAMs of ANAD and COAS CPUE did not include the landings, SSB, or YOY indices for the opposing group.

The evaluation of the annual covariates involved replacing the year factor of the best GAM with each of the annual covariates individually. Each annual covariate was modeled with a smoothing function, but was constrained to have no more than two degrees of freedom to avoid over-parameterization of the 10-year time-series. Competing models for each response variable were fitted and ranked using AIC and Akaike weights (Burnham & Anderson 2002). Pearson product-moment correlations were calculated between the estimated effect of each annual covariate and the original estimated year effect to indicate the strength and directionality of the relationships. All statistical analyses for this study were performed using the ‘vegan’ and ‘mgcv’ libraries in the software package R (version 2.13.2; R Development Core Team 2012)

RESULTS

Basic catch information

ChesMMAP sampled 3640 stations during 48 cruises from 2002-2011. Two cruises were not conducted (September 2007, May 2009), and upper bay stations were not sampled during the May 2003 and July 2010 cruises. A total of 98 species were collected during this 10-year period, however the analyses were limited to 50 demersal species based on the previously specified criteria (Tables 2 and 3). The number of species captured at each station ranged from 0 to 19 species with an overall mean of 3.4 species. Simpson's diversity averaged 0.30 across all stations and 0.42 if diversity values of zero were excluded. A total of 57.9 metric tons and 272,084 individuals were collected from the Chesapeake Bay. The top five species ranked by weight (Atlantic croaker, white perch, spot, striped bass, and summer flounder) accounted for 75% of all trawled biomass, with Atlantic croaker alone contributing 38% by both biomass and abundance (Table 2).

Species composition of trawl catches varied considerably across year, month, region, and depth strata, reflecting the dynamic spatiotemporal characteristics of the Chesapeake Bay fish community (Fig. 2). Monthly differences in species composition were dominated by changes in Atlantic croaker, striped bass, white perch, and spot. Atlantic croaker accounted for over 50% of sampled fish biomass in May and July, but relative contributions decreased in the fall (September and November) as this species is known to migrate to the continental shelf for spawning. Biomass proportions of striped

bass and white perch were highest in November and March, corresponding with their winter-spring spawning. Although proportional spot catches were high from July to November, their contribution to total biomass peaked in September. Trawled biomass peaked in July, with that month accounting for 31% of the total. Species dominance in the five survey regions shifted spatially from white perch in the upper bay to striped bass in the mid bay and Atlantic croaker in the lower bay. Region 5 in the lower bay accounted for 43% of total trawled biomass and had a more equitable contribution from various species. Patterns by depth stratum indicated higher catches of white perch in the shallow reaches of the bay, whereas croaker dominated in intermediate and deeper bay areas. Relative to the other factors, annual variability in catch composition was less pronounced, but showed decreased contribution by Atlantic croaker in the later years. Concomitant increases in proportional biomass contributions by ELAS and other fishes were also observed in later years. Overall, trawled biomasses were higher before 2007 (with peaks in 2004 and 2006) whereas 2008-2011 had relatively low biomasses. However, these trends were slightly confounded due to the missing and incomplete cruise in 2009 and 2010 respectively.

Constrained correspondence analysis of community composition.

Species composition within the Chesapeake Bay community was largely driven by latitudinal and salinity gradients which were strongly correlated with the first CCA axis (CCA1; Fig. 3). The CCA explained 18% of the total inertia in the multivariate dataset due to the high variability and noise common in survey catch data. ANAD species (white perch and striped bass) had strong negative loadings on CCA1,

highlighting their higher catch rates in the lower salinity waters of the upper bay, especially during November and March. Cownose ray, spot and the minor species held an intermediate position reflecting a broader and more equitable distribution throughout the bay. The second CCA axis (CCA2) differentiated among the many marine-dominated species that tend to be centered in the higher salinity waters of the lower bay. One of the strongest factors driving the patterns in community composition along this axis was a clear separation among years before and after 2008 (2002-2007 and 2008-2011 with more negative and positive loadings, respectively). There was also separation among spring and early fall (September) catches. Atlantic croaker loaded negatively on CCA2 corresponding with higher CPUE in the early period (2002-2007) of the time series, while the relative contribution of many other species to total catch increased in the later period of the time series. September also was a strong driver of species composition, with many of the elasmobranchs loading with warmer water in September. Although a significant factor in the model, DO did not correspond strongly with gradients in species composition.

Generalized additive models of community metrics

With only two exceptions, the full generalized additive model provided the best fit to the univariate community metrics (Table 4). Inclusion of a space-time interaction helped account for the dynamic seasonal movements of different species within the Chesapeake Bay. Models explained between 33.9 and 51.2% of the null deviance.

Species richness exhibited the largest changes in magnitude as a function of latitude, with mid-latitudes having substantially lower values particularly in July and

September (Fig. 4). Dissolved oxygen also strongly depressed S at values below $\sim 4 \text{ mg l}^{-1}$ (Fig. 5). Species richness was greatest at intermediate depths ($\sim 16\text{-}22 \text{ m}$) and greater depths ($>30 \text{ m}$), but precision at the greater depths was poor. Mean station-level S increased at lower salinities and increased linearly with warmer temperatures (Fig. 4). Species richness progressively increased by month with the largest positive effect in November (Fig. 6). Annually, S peaked in 2007, but the magnitudes of the year effects were generally low (Fig. 6).

The model for Simpson's diversity index only explained 33.9% of the deviance, but had similar responses to the modeled covariates as did S (Table 4). For example, D increased with temperature and depth, decreased as DO declined below $\sim 4 \text{ mg l}^{-1}$ (Fig. 4), and exhibited minima at mid-latitudes (Fig. 5). Salinity was dropped from the GAM as a non-significant covariate (Table 4). Temporally, November yielded the highest relative effect on D , but D was relatively consistent across years (Fig. 6).

Results of GAMs fitted to CPUE data clearly demonstrated different influences of environmental and spatial factors on catch rates of different species groups (Figs. 4-6). Trends for the FISH group were generally a combination of the predicted patterns for the other groups, but the FISH trends tended to mirror COAS patterns more closely (e.g. Fig. 4) due to the biomass dominance of COAS fishes in the total catch (Table 2). Catches of COAS and ANAD fishes generally showed contrasting trends with temperature and latitude; ANAD fishes preferred colder waters below 15°C and higher latitudes, opposing the trends for COAS species (Figs. 4-5). These inverse trends acted to dampen the responses of the FISH patterns with these factors. The Potomac River mouth (at 38°N) represented a transitional point for COAS below which catches increased dramatically in

most months, with a clear peak at approximately 37.5°N in the spring and summer months (Fig. 4). Catches of ELAS increased monotonically with decreasing latitude. Salinity had strong positive effects on CPUE of ANAD and ELAS fishes in low and high salinities, respectively, whereas the effect on COAS fishes was only slightly positive at lower salinities (Fig. 5). COAS fishes preferred intermediate depths whereas ANAD fishes preferred shallower waters. The effect of DO was detected only at levels $<3.5 \text{ mg l}^{-1}$, but this was most strongly evident with the COAS group. Month effects on CPUE were generally smaller than other factors and lacked precision (Fig. 6), suggesting that the majority of changes by month were captured by water temperature or by the latitude-month interaction. The annual trends showed peaks in ANAD, COAS, and FISH catches in 2005 and 2006 followed by declines during the latter half of the time series. Back-transformed, bias-corrected CPUE values (calculated at the medians of all the explanatory variables) indicated that COAS and ANAD catch rates (in kg km^{-2}) declined dramatically from their respective peaks (90% decline in COAS CPUE from 2005-2011; 80% decline in ANAD CPUE from 2005-2009). These estimates of percent decline exceeded estimates for individual COAS species (declines of 85-88%) and ANAD species (declines of 43-77% for white perch and striped bass respectively) (A. Buchheister, unpublished data), likely due to the characteristics of aggregate CPUE metrics (Kleiber and Maunder 2008); however all of these values represent substantial decreases in catch rates in recent years, especially for COAS species. ELAS CPUE remained more consistent over the time series although values were slightly higher after to 2006.

Annual covariates

The categorical year factor typically described annual trends in community metrics far better than the various covariates hypothesized to influence community dynamics (Table 5). Of the examined covariates, fishery landings and recruitment indices tended to have greater predictive power across metrics and species groups. Landings tended to be positively correlated with interannual trends in FISH, ANAD, and COAS CPUE, suggesting that fisheries may have been responding to changes in fish abundance as represented by ChesMMAP data. YOY indices ranked within the top three models for several metric-group combinations, but effects could be positive or negative. For example, ANAD CPUE was positively correlated with the ANAD YOY index (with a relatively longer lag and span), whereas COAS CPUE was negatively correlated with a composite YOY index (i.e., high levels of recruitment corresponded with lower predicted COAS catch).

DISCUSSION

Environmental filtering of Chesapeake Bay demersal fish community

Salinity was the major environmental gradient structuring community composition, biodiversity, and catch rates within Chesapeake Bay. This gradient was captured by two related covariates: direct measures of salinity and latitude. Latitude indicated the general salinity regime (e.g., oligohaline to polyhaline) and acted as a spatial locator, whereas salinity was a higher-resolution (and more variable) measure of water quality. Particularly in estuarine environments, salinity is frequently found to be a dominant structuring factor (Day et al. 1989), separating freshwater and marine species. Typically, species richness and total biomass tend to have parabolic, nonlinear relationships with salinity, displaying a minimum in mesohaline waters owing to the physiological demands of living in these brackish waters (Odum 1988, Wagner 1999). Consequently, mesohaline waters act as an obstacle to marine and freshwater species that limits the distribution of those species groups within the bay, translating to the documented parabolic trends in S , D , and total fish CPUE (with a transitional point at ~20 psu and 38-38.5°N). These patterns suggest that bay-wide community assembly is largely driven through environmental filtering processes (i.e., general habitat suitability) whereby species inhabiting the different regions of the bay are restricted by unique tolerances to and preferences for certain habitat and environmental characteristics (e.g., Mouillot et al. 2007). A mid-bay reduction in fish biomass indices was also observed consistently over years for the pelagic fish community (Jung & Houde 2003). Thus, both

demersal and pelagic environments of the mesohaline Chesapeake Bay mainstem act as suboptimal habitats for bay fishes and support a relative paucity of fish biomass.

The mid-bay minima in biomass and diversity metrics may also be related to reduced habitat quality stemming from hypoxia. Fitted GAMs accounted for the direct effects of low DO concentrations (discussed below), but other indirect effects are possible. Research suggests that benthic macro- and meiofauna (important food for benthivorous species like Atlantic croaker, spot, and white perch) are degraded in the mid-bay relative to other bay regions due to hypoxia and eutrophication stress (Hagy 2002, Kemp et al. 2005). Prolonged exposure of the mesohaline benthos to hypoxic conditions could have lasting consequences on the quality of foraging habitat for benthivores that restricts the suitability of the region even after bottom waters become oxygenated.

The spatial gradient in community composition was largely driven by the ANAD species (white perch and striped bass) but also reflected broader spatiotemporal trends in biodiversity. Ecologists frequently partition biodiversity into various components (α , β , and γ diversity) to better understand the processes that structure communities, particularly along environmental gradients (Magurran 2004). The demersal fish community of Chesapeake Bay exhibits an overarching trend of increasing regional species richness (i.e., γ diversity) from the upper bay to the lower bay (19 vs. 45 species encountered respectively; A. Buchheister unpublished data); however, our station-level estimates of S (i.e., α diversity) were highest in the upper bay based on the GAMs. Thus, upper bay stations tend to have a consistently higher number of species caught at each station despite a smaller regional species pool than other bay regions. This pattern indicates that

species turnover (i.e., β diversity – a measure of the change in species biodiversity over time or space) is low; in other words, species composition is more consistent and the fish community more homogenous across upper bay stations, likely due to the relative ubiquity of white perch throughout the year in the upper bay. The mid-bay stations had a lower predicted S , a higher regional pool, and thus a much higher species turnover across stations. Generally, the middle and lower bays have a more diverse and dynamic fauna due to the migration of many species, making these regions more heterogeneous over space and time. Higher turnover in the mesohaline portion of the bay mainstem opposes the patterns documented in the Chesapeake Bay tributaries for smaller littoral fishes where turnover was highest at the tidal freshwater interface (Wagner 1999). Thus, community patterns in species turnover may differ by estuarine region (tributaries vs. mainstem) or by the size range of the fish assemblage.

Seasonal regulation of community patterns

As in most temperate estuaries, the fish assemblage within Chesapeake Bay is known to be seasonally dynamic as different species migrate into and out of the bay given their life history strategies (Murdy et al. 1997, Able & Fahay 2010). Dividing the biomass dominant species into ANAD, COAS, and ELAS groups effectively separated ~90% of the assemblage's biomass into different modes of life history and estuarine usage. Spawning by striped bass and white perch in freshwater and tidal tributaries during spring concentrates anadromous individuals in the upper bay, especially when water temperatures are low. For white perch, this is due to fish residing in deeper channels and bay areas during winter prior to their upstream spawning migration in the

spring. Striped bass are also caught in higher numbers during cold months (March), when the resident contingent (mostly male fish) is overwintering in Chesapeake Bay and as coastal migrants are moving to the rivers for spawning (Fay et al. 1983). Catches of ANAD fishes also increased in November as white perch and striped bass residents generally aggregate in deeper waters in preparation for winter.

Both the COAS and the majority of the ELAS species demonstrated alternative usage of the bay's mainstem (relative to ANAD fishes), with greatest residence and utilization during summer and fall when water temperatures are the warmest. The COAS trends are likely linked to 1) the migrations of COAS species that forage in the estuary during warmer months prior to offshore spawning (Murdy et al. 1997, Able & Fahay 2010), 2) the movement of winter/spring-settled juveniles from shallow estuarine nursery areas and tributaries to the mainstem during ontogeny (Rogers et al. 1984, Sackett et al. 2008), and 3) the recruitment of age-0 COAS juveniles to the trawl gear when sufficient fish sizes (~100-150 mm) are attained in the summertime (Bonzek et al. 2011). ELAS life histories are more varied given the larger number of species; however, several species spawn in spring or summer within estuarine waters or forage in the bay in summer and fall (Wourms 1977, Murdy et al. 1997).

The warmest temperatures (in July) promote greater bay utilization by many species, including ELAS, COAS, and subtropical species that use the bay as a foraging ground. Late summer and early autumn temperatures also allow rarer tropical species to join the warm-temperate and subtropical summer residents in the bay (Murdy et al. 1997), thus increasing biological diversity. Despite cooler temperatures, species richness and Simpson diversity was relatively high in November because cold temperate and even

boreal species (e.g., striped bass, spotted hake) become more prevalent in the bay while many species are migrating out to overwinter in coastal waters.

Community responses to hypoxia

Low dissolved oxygen produced one of the strongest negative responses of any of the modeled variables. Within Chesapeake Bay, the effects of hypoxia on distribution and abundance of zooplankton and fish larvae have been demonstrated in several locations (Roman et al. 1993, Keister et al. 2000, Ludsin et al. 2009). However, research on effects of hypoxia on adult fishes has been restricted to tributaries and smaller areas within the bay (Pihl et al. 1991, Carmichael et al. 1992, Breitburg et al. 2001) or it has focused on effects on pelagic and mainly planktivorous fishes (Jung & Houde 2003, Ludsin et al. 2009). To our knowledge, this is the first study in Chesapeake Bay to document the large-scale effects on demersal fish biodiversity and catch rates that are predominantly driven by chronic influence of low dissolved oxygen concentrations. The drastic decline in *S*, *D*, and CPUE documented here was consistent with work from other systems (e.g., Breitburg et al. 2002, Eby & Crowder 2002, Keller et al. 2010), and suggests that from a multispecies, community perspective, there is a strong threshold avoidance response that begins when DO drops below $\sim 4 \text{ mg l}^{-1}$. This threshold suggests that habitat quality for the demersal fish assemblage begins to be reduced at values greater than 2 mg l^{-1} (the typical definition for hypoxia), as fish exhibit elevated respiration and metabolism, reduced growth, or other signs of physiological stress that drive mobile animals to emigrate from the affected area (Breitburg et al. 2002, Gray et al. 2002).

Emigration from and avoidance of low DO waters was detected in the spatial distribution of fishes in July when hypoxic conditions are most extreme. The latitudinal effects predicted by the GAMs (Fig. 4) included apparent indirect effects of low DO (i.e. after the direct DO effects were explicitly accounted for by the models). FISH CPUE, COAS CPUE, and species richness showed the steepest declines with latitude in July at $\sim 37.75^{\circ}\text{N}$ near the southern edge of the bay's deeper mainstem channel (Fig. 1), suggesting an aggregated edge effect due to the southern displacement of fishes. The bathymetry of this area near the mouth of the Rappahannock River promotes a strong oxycline (Hagy et al. 2004), and similar aggregations of fish catch rates have been shown surrounding hypoxic areas in the Gulf of Mexico (Craig et al. 2012). A concurrent northward displacement of fishes was evidenced by the steep increase in FISH CPUE in July and September at the northern edge of the mainstem channel (at $\sim 39^{\circ}\text{N}$). These patterns in CPUE combined the effects of multiple species which may respond differently to low DO. For example, the northward displacement of COAS fishes was caused almost exclusively by spot in July and September. Interestingly, the displacement of ANAD fishes did not appear as drastic in July (more so in September). However, these ANAD trends may be a result of a longitudinal displacement resulting from greater utilization of shallower stations and habitats at those latitudes (e.g., Eby & Crowder 2002). Additionally, the lack of a steeper increase in ANAD CPUE to the north could be the result of the smoothing function fitting data from two species; white perch catch rates alone (without striped bass) were much greater north of 39°N where the mainstem channel ends and hypoxia is less problematic. Slightly elevated CPUE (FISH, ANAD,

and COAS groups) at DO levels of $\sim 4 \text{ mg l}^{-1}$ also provide some support for aggregation of fish biomass at DO levels that are sufficiently oxygenated.

Biomass and biodiversity trends with DO and latitude primarily reflect the seasonally chronic, large-scale effects of low DO. This study documented notable, drastic shifts in large-scale fish distributions and catches, which represents a substantial reduction in available fish habitat for demersal fishes. From a system-wide perspective, it remains unclear whether the tradeoffs of increased production from eutrophication combine with the negative effects of low DO to hinder or promote overall secondary fish production (Caddy 1993, Breitburg et al. 2009). Jung & Houde (2003) found bay-wide pelagic fish biomass to increase as mean annual depth-integrated DO decreased, which is supported by large-scale studies documenting higher pelagic productivity with increased eutrophication (de Leiva Moreno et al. 2000, Breitburg et al. 2009). However, it is also possible that the Jung & Houde (2003) patterns could be influenced by vertical displacement of fishes away from hypoxic bottom waters (Hazen et al. 2009). Demersal production does not benefit as much from eutrophication-induced increases in pelagic productivity due to the resulting degradation of benthic habitats (de Leiva Moreno et al. 2000, Breitburg et al. 2009). In our study, the localized negative effects of hypoxia were much more evident in the demersal community whereas there was little evidence of annual patterns in demersal productivity being strongly related to hypoxic volume or other climatic variables related to eutrophication (e.g., river discharge, chl-a).

Large-scale factors influencing interannual community patterns

Species composition and community metrics changed dramatically within the 10-year dataset with later years characterized by low CPUE of COAS, ANAD, and FISH species groups and decreased proportional contributions by Atlantic croaker. Strong annual shifts in community composition and structure have previously been documented for the Bay's pelagic fish community (Jung & Houde 2003). The pelagic community exhibited resilience to a strong environmental perturbation (in the form of very high annual precipitation), progressively returning to the pre-disturbance structure as time passed (Jung & Houde 2003). In this study, several climate, fishing, population size, and recruitment covariates were evaluated to identify the dominant drivers of the documented interannual patterns for the demersal community, based on different hypotheses. Multiple ecosystem processes act simultaneously on the various constituents of the community (species, age-classes, etc.) and can complicate relationships between individual covariates and community metrics. Given this complexity and the greater flexibility (i.e., degrees of freedom) of the categorical year factor, models with single covariates tended to be outperformed by models with the year factor. However, there is value in ranking the relative explanatory power of considered variables to help elucidate and evaluate different underlying mechanisms regulating community dynamics (e.g., Jung & Houde 2003, Keller et al. 2012). Overall, the annual patterns were most strongly linked to fishing pressure and recruitment processes, but it is unclear whether the trends represent natural fluctuations in community dynamics or if these changes are symptomatic of continued stresses on the bay ecosystem (e.g. Boesch et al. 2001, Kemp et al. 2005).

Coastwide landings ranked as some of the best annual predictors of CPUE and biodiversity metrics. Coastwide landings for the COAS group (primarily Atlantic croaker and summer flounder) have been decreasing since ~2004 and 2005, while landings of white perch and striped bass have remained relatively consistent during the study period (ASMFC 2010, ASMFC 2011, Terceiro 2011). The positive correlation between fishery landings and survey CPUE is complicated by the vagaries of using landings data (e.g., lack of effort data, influence of management regulations, discards); however, part of these concerns are minimized as landings for Atlantic croaker (the dominant species) are not restricted by a catch quota as they are for some of the other species (ASMFC 2010). The correlated pattern in coastwide landings and CPUE metrics underscores the fact that relationships among independent and dependent variables in the GAMs are not necessarily causative, but they may be both responding to some other latent variable(s). Interestingly, the general decline in COAS CPUE (since 2005/2006) and COAS landings does not appear to be driven by changes in total population size given that SSB for Atlantic croaker and summer flounder have continued to grow (ASMFC 2010, Terceiro 2011). A likely explanation is that spatial and distributional dynamics of species could alter the theoretically positive relationship among survey CPUE, landings, and SSB. Such changes in fish distributions can occur at large scales as a consequence of environmental climate drivers (Nye et al. 2009, Pinsky and Fogarty 2012), or they could result from local factors such as habitat quality, prey availability, etc. (e.g. Caddy 1993, Craig 2012). Linkages between survey CPUE, landings, and the coastwide stock are also influenced by the degree of spatial connectivity and exchange among the many estuarine and coastal systems that contribute to the total stock of each species.

Recruitment indices also ranked highly as some of the best predictors of CPUE. Surprisingly, the sign of the relationship was not positive for COAS fishes, contrary to the typical expectation. Given the dominance of Atlantic croaker in the ChesMMAAP catch and the weighting scheme of the YOY composite index calculations, the Atlantic croaker YOY index drove the patterns in the COAS and ANAD + COAS YOY indices. The negative relationship between recruitment and future adult CPUE could be indicative of density dependent effects on mortality (Rose et al. 2001); however recent work has demonstrated a relatively weak correspondence between YOY Atlantic croaker indices and future CPUE of croaker age-classes using the ChesMMAAP data (Woodward 2009). This poor correlation may be related to low site fidelity by adult Atlantic croaker and highlights the importance of spatial scale in looking at such relationships. CPUE of ANAD fishes was positively correlated with the group's recruitment index with a longer lag, which is consistent with ANAD fishes recruiting to the trawl gear at slightly older ages (approx. age 2-3; Bonzek et al. 2011). The strong correlation between ANAD CPUE and the ANAD recruitment index may also have been influenced by the spatially constrained nature of the white perch population whose migrations are smaller in scale; any white perch recruitment signals would be more easily detected in adults with less environmental and ecological noise.

Within the Chesapeake Bay and other coastal systems, several studies have linked climatic variables with patterns in fish populations and community metrics (e.g., Hofmann & Powell 1998, Attrill & Power 2002, Nye et al. 2009). Despite the several climatic covariates examined and the multiple iterations of time lags and spans for each, these covariates consistently performed worse than variables related to fishing and

recruitment. The only exception was river discharge, but it was used to model Simpson diversity which lacked variability and contrast among years.. These general patterns do not negate the importance of climatic variables as drivers of community metrics, but instead indicate that other processes, such as recruitment (which can be influenced by climate), may be more directly related over the 10-year time scale investigated.

Additionally, community responses to climatic forcing may be harder to detect than those for individual species. For example, Hare & Able (2007) linked recruitment indices, adult abundance, and landings of Atlantic croaker to the NAO and to minimum winter temperatures at decadal time scales. These relationships were not strongly evident in our analysis, perhaps due to our shorter time series or to the added influence of the other COAS species.

Implications and significance

Concerns over long-term environmental and anthropogenic stressors and their impacts on the Chesapeake Bay ecosystem have helped foster interest in EBFM in Chesapeake Bay (Houde 2006). Management of Chesapeake Bay in an ecosystem-based framework will rely on a suite of suitable indicators to capture the many components that define ecosystem status (Brodziak & Link 2002, Link 2002) and to overcome the limitations of any individual metric (e.g. Kleiber and Maunder 2008). Given its distinct annual and spatial trends in Chesapeake Bay and emphasis on biomass-dominant species, total fish CPUE (as an index of demersal fish biomass) appears to be a useful ecosystem indicator as suggested by many authors in other systems (e.g., Rice 2000, Methratta & Link 2006). However, we have demonstrated that aggregate biomass metrics for

anadromous fishes, coastal spawners, and elasmobranchs provide greater resolution of community patterns, capturing distinct life history and bay utilization patterns for dominant demersal species. Both species richness and Simpson diversity were sensitive to the environmental covariates and exhibited similar functional responses to the modeled variables, suggesting that both are useful indicators of general biological diversity of the Chesapeake Bay fish community.

This study provides a 10-year frame of reference for the bay-wide demersal fish community that can be used to evaluate future changes to species composition, distribution, or abundance at a large scale. The documented trends and influences of each explanatory factor may also provide tentative relationships to help inform predictions regarding the influence of different stressors on the Chesapeake Bay fish community. Continued large-scale monitoring of the Chesapeake Bay will be critical for detecting ecosystem-level responses to continued stresses and is an essential component to a successful management strategy for the many resources of the Chesapeake Bay and western Atlantic waters.

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TABLE CAPTIONS

Table 1. Details and justifications for the annual-scale covariates included in statistical models of fish community patterns in Chesapeake Bay. Annual covariates were grouped into four categories (climate, fishing, population size, and recruitment) and were calculated for different lags (yrs) and spans (yrs) using data for identified months. Fishing, population size, and recruitment covariates were calculated separately for anadromous species (ANAD), coastal shelf spawners (COAS), and both of these groups combined.

Table 2. Catch information for demersal fish species captured in Chesapeake Bay by the ChesMMAP survey. Values are totals of all cruises from 2002-2011. The top five species are classified as either a coastal shelf spawner (COAS) or an anadromous species (ANAD). Elasmobranchs (ELAS) contributing at least 0.5% of the total biomass were also classified as a distinct group. Mean body size (with standard deviation) was calculated from fork length for teleosts, pre-caudal length for sharks, and disc width for batoids.

Table 3. Fishes excluded from analyses due to low catches or poor sampling by the ChesMMAP bottom trawl. P – pelagic, D – demersal.

Table 4. Best fit generalized additive models (GAMs) of species richness (S), Simpson's diversity (D), and catch-per-unit-effort (CPUE, kg km^{-2}) from bottom trawl survey data in Chesapeake Bay for different species groups (FISH – all fishes, ANAD – anadromous fishes, COAS – coastal shelf spawners, and ELAS – elasmobranchs). Models include an intercept (a), coefficients for the parametric components (α), smoothing functions for the nonparametric components (g), residual error (e) for each station (i), and various explanatory variables: year (YR), month (MO), latitude (LAT), salinity (SA), water temperature (T), dissolved oxygen (DO), and water depth (DE). Percent of total deviance (% Dev) explained by each model is also presented.

Table 5. Summaries of the highest-ranking competing generalized additive models of catch-per-unit-effort (CPUE), species richness, and species diversity modeled with different annual covariates. Models were constructed by replacing the Year factor from the best fit models of Table 4 with each annual covariate from Table 1. Response metrics were modeled separately for each species group (FISH – all species combined, ANAD – anadromous species, COAS – coastal shelf spawners, ELAS – elasmobranchs). Covariates were calculated for different lags (yrs), spans (yrs), and species groups (A+C represents ANAD and COAS groups combined). Akaike weights (w) provide the weight of evidence, or probability that a model is the best model of the models compared within each Metric-Group pair. Pearson product-moment correlations (R) between the covariate and the estimated year effect in the null model (as plotted in Fig. 6) indicate the strength and direction of the relationship of the covariate and the response variable.

FIGURE CAPTIONS

Figure 1. All stations (n = 3640) sampled by the Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAAP) in March, May, July, September, and November from 2002-2011. Dark horizontal lines delineate five regional strata (Region 1 in the upper bay and Region 5 in the lower bay) and the 15 m depth contour is represented.

Figure 2. Fish biomass composition from ChesMMAAP bottom trawls by a) year, b) month, c) region, and d) depth stratum. Species groups are identified by bar color (white – coastal shelf spawners (COAS), gray – anadromous species (ANAD), dark gray – elasmobranchs (ELAS), black – other species). Region values are for 30-minute latitude intervals from the upper bay (region 1) to the lower bay (region 5). Depth strata 1, 2, and 3 are defined as 3.0-9.1 m, 9.1-15.2 m, and >15.2 m respectively. Numbers on the top of each bar represent the percentage of total biomass captured for that factor level.

Figure 3. Constrained correspondence analysis (CCA) ordination diagram for station-level catch-per-unit-effort of species captured by the ChesMMAAP survey from 2002-2011. Arrows indicate the increasing gradient of the significant continuous explanatory variables (LAT – latitude, DEPTH, TEMP – temperature, SAL – salinity, DO – dissolved oxygen). Squares and bold text identify the centroids for each year and month of sampling. Species scores in ordination space are indicated by dots (bass – striped bass,

bdrum – black drum, blunt – bluntnose stingray, bulln – bullnose ray, cown – cownose ray, croak – Atlantic croaker, flou – summer flounder, kingf – kingfish, minor – species <0.5% total biomass, perch – white perch, sheep – sheepshead, skate – clearnose skate, smbfly – smooth butterfly ray, smdog – smooth dogfish, spbfly – spiny butterfly ray, spdog – spiny dogfish, spot, ssray – southern stingray, weakf – weakfish).

Figure 4. Partial, smoothed effects of latitude on diversity metrics (upper panels) and log-transformed catch-per-unit-effort ($\log_e(\text{CPUE}+0.1)$) (lower panels) by sampling month, as estimated from generalized additive models of Chesapeake Bay trawl survey data. Upper panels display mean partial effects (± 2 SE) of latitude on species richness (S ; thin line with gray shading; left scale) and Simpson's diversity index (D ; thick lines; right scale) for each month separately. Lower panels display mean monthly partial effects on CPUE of different species groups: all fishes (FISH; thin solid line), anadromous fishes (ANAD; thick solid line), dominant coastal shelf spawners (COAS; dashed line), and elasmobranchs (ELAS; dotted line). For clarity, confidence intervals (± 2 SE; gray shading) are only plotted for FISH, but the magnitudes were similar for other species groups. Sampling intensity for each covariate is indicated by tick marks on the x-axis.

Figure 5. Effects of salinity, temperature, dissolved oxygen (DO), and depth on diversity metrics (upper panels) and log-transformed catch-per-unit-effort ($\log_e(\text{CPUE}+0.1)$) (lower panels), as estimated from generalized additive models of Chesapeake Bay trawl survey data. Upper panels display mean partial effects (± 2 SE) of covariates on species

richness (S ; thin line with gray shading; left scale) and Simpson's diversity index (D ; thick lines; right scale). Lower panels display mean partial effects of each covariate on CPUE of different species groups: all fishes (FISH, thin solid line), anadromous fishes (ANAD, thick solid line), dominant coastal shelf spawners (COAS, dashed line), and elasmobranchs (ELAS, dotted line). For clarity, confidence intervals (± 2 SE; gray shading) are only plotted for FISH, but the magnitudes were similar for other species groups. Sampling intensity for each covariate is indicated by tick marks on the x-axis.

Figure 6. Parametric partial effects of month and year on diversity metrics (upper panels) and log-transformed catch-per-unit-effort ($\log(\text{CPUE}+0.1)$) (lower panels), as estimated from generalized additive models of Chesapeake Bay trawl survey data. Upper panels display mean partial effects (± 2 SE) on species richness (S ; thin line with gray shading; left scale) and Simpson's diversity index (D ; thick lines; right scale). Lower panels display mean partial effects on CPUE of different species groups: all fishes (FISH; thin solid line), anadromous fishes (ANAD; thick solid line), dominant coastal shelf spawners (COAS; dashed line), and elasmobranchs (ELAS; dotted line). For clarity, confidence intervals (± 2 SE; gray shading) are only plotted for FISH in the lower panels, but the magnitudes were similar for other species groups. Note that standard errors are inestimable for the reference (i.e., first) level of each factor.

Covariate	Months	Lag	Span	Justification	Examples	Source
Climate						
North Atlantic Oscillation index	DJFM	0,1,2	1,2	Indicator of climate conditions; linked to changes in fish communities and stocks	Hofmann & Powell 1998, Attril & Power 2002, Hurrell et al. 2003, Hare & Able 2007	Hurrell 2012
River discharge	FMAM	0,1,2	1,2	Alters availability of low salinity habitat; affects nutrient loading, hypoxia, and food web structure	Jung & Houde 2003, Kemp et al. 2005, Purcell & Decker 2005	USGS 2012
Hypoxic volume	July	0	1	Alters habitat quality, fish distribution, prey availability; potential increase in mortality	Pihl et al. 1991, Keister et al. 2000, Breitbart 2002, Stierhoff et al. 2006	D. Scavia & M. A. Evans, pers. comm.
Minimum winter temp	DJFM	0,1,2	1,2	Affects overwinter mortality; linked to croaker recruitment	Norcross & Austin 1981, Hare & Able 2007, Lankford & Targett 2001	SERCC 2012, VIMS 2012
Chlorophyll a	MAMJJA	0,1,2	1,2	Proxy for primary productivity; influences food availability; related to eutrophication intensity	Harding et al. 2002, Kemp et al. 2005	M. Brush, pers. comm.
Fishing						
Landings, Bay	all	0	1	Direct biomass removal and source of mortality (local scale)	Richards & Rago 1999, Worm et al. 2009	NOAA 2012
Landings, coast-wide	all	0	1	Direct biomass removal and source of mortality (larger scale)	Richards & Rago 1999, Worm et al. 2009	NOAA 2012
Population size						
Spawning stock biomass	all	0	1	Estimate of coastwide population size	Richards & Rago 1999, Worm et al. 2009	ASMFC 2010, ASMFC 2011, Terceiro 2011
Recruitment						
YOY Index	*	0,1,2	1,2	Measure of age-0 production; source of biomass for population	Hare & Able 2007	Durrell & Weedon 2011, Tuckey & Fabrizio 2011

* Months used for index calculation vary depending on the species included in the index.

Table 1. Details of annual-scale covariates used to model fish community patterns.

Table 2. Catch information for ChesMMA demersal species.

Species	Group	No. stations	Biomass (kg)	Biomass (%)	Count (no. fish)	Count (%)	Size (mm)
<i>Micropogonias undulatus</i> (Atlantic croaker)	COAS	1347	22068.7	38.1	104624	38.5	239 (52)
<i>Morone americana</i> (white perch)	ANAD	522	8347.8	14.4	61230	22.5	188 (30)
<i>Leiostomus xanthurus</i> (spot)	COAS	1574	5228.4	9	56715	20.8	162 (33)
<i>Morone saxatilis</i> (striped bass)	ANAD	994	5166.5	8.9	7275	2.7	347 (117)
<i>Paralichthys dentatus</i> (summer flounder)	COAS	1517	3035.3	5.2	6097	2.2	329 (103)
<i>Raja eglanteria</i> (clearnose skate)	ELAS	356	2447.3	4.2	1678	0.6	404 (62)
<i>Cynoscion regalis</i> (weakfish)		1119	2105.1	3.6	17023	6.3	213 (61)
<i>Dasyatis say</i> (bluntnose stingray)	ELAS	175	1607.8	2.8	424	0.2	395 (128)
<i>Rhinoptera bonasus</i> (cownose ray)	ELAS	113	990.6	1.7	196	0.1	585 (216)
<i>Gymnura altavela</i> (spiny butterfly ray)	ELAS	110	918.3	1.6	318	0.1	566 (220)
<i>Myliobatis freminvillii</i> (bullnose ray)	ELAS	96	825.6	1.4	234	0.1	511 (215)
<i>Pogonias cromis</i> (black drum)		92	766.7	1.3	178	0.1	448 (326)
<i>Dasyatis americana</i> (southern stingray)	ELAS	85	655.3	1.1	151	0.1	423 (164)
<i>Mustelus canis</i> (smooth dogfish)	ELAS	137	439.1	0.8	368	0.1	593 (162)
<i>Archosargus probatocephalus</i> (sheepshead)		65	427.6	0.7	115	<0.05	478 (155)
<i>Gymnura micrura</i> (smooth butterfly ray)	ELAS	114	412.3	0.7	220	0.1	514 (156)
<i>Squalus acanthias</i> (spiny dogfish)	ELAS	33	376.5	0.7	147	0.1	727 (97)
<i>Menticirrhus</i> spp. (kingfish)		407	336.0	0.6	1905.5	0.7	233 (63)
<i>Sphoeroides maculatus</i> (northern puffer)		408	223.1	0.4	1941	0.7	151 (34)
<i>Dorosoma cepedianum</i> (gizzard shad)		127	195.1	0.3	420	0.2	285 (88)
<i>Ictalurus punctatus</i> (channel catfish)		40	178.6	0.3	159	0.1	382 (78)
<i>Stenotomus chrysops</i> (scup)		355	137.3	0.2	3158	1.2	120 (22)
<i>Dasyatis sabina</i> (Atlantic stingray)		52	130.4	0.2	73	<0.05	314 (102)
<i>Chaetodipterus faber</i> (Atlantic spadefish)		182	129.9	0.2	409	0.2	126 (103)
<i>Carcharhinus plumbeus</i> (sandbar shark)		43	104.6	0.2	54	<0.05	555 (109)
<i>Sciaenops ocellatus</i> (red drum)		6	101.9	0.2	11	<0.05	892 (185)
<i>Tautoga onitis</i> (tautog)		21	73.2	0.1	48	<0.05	419 (68)
<i>Chilomycterus schoepfii</i> (striped burrfish)		127	54.9	0.1	166	0.1	191 (48)
<i>Opsanus tau</i> (oyster toadfish)		103	50.0	0.1	151	0.1	226 (90)
<i>Prionotus carolinus</i> (northern searobin)		405	49.6	0.1	2252	0.8	121 (23)
<i>Scophthalmus aquosus</i> (windowpane)		251	48.5	0.1	427	0.2	191 (53)
<i>Dasyatis centroura</i> (rougetail stingray)		7	48.1	0.1	16	<0.05	440 (44)
<i>Trinectes maculatus</i> (hogchoker)		344	46.5	0.1	974	0.4	124 (24)
<i>Urophycis regia</i> (spotted hake)		255	39.4	0.1	1216	0.4	137 (44)
<i>Ameiurus catus</i> (white catfish)		21	38.2	0.1	42	<0.05	346 (129)
<i>Centropristis striata</i> (black seabass)		163	21.3	<0.05	285	0.1	155 (50)
<i>Leucoraja erinacea</i> (little skate)		16	19.4	<0.05	25	<0.05	288 (33)
<i>Bairdiella chrysoura</i> (silver perch)		156	17.1	<0.05	396	0.1	140 (26)
<i>Prionotus evolans</i> (striped searobin)		162	11.7	<0.05	257	0.1	135 (43)
<i>Larimus fasciatus</i> (banded drum)		36	10.1	<0.05	142	0.1	157 (60)
<i>Ameiurus nebulosus</i> (brown bullhead)		4	5.6	<0.05	28	<0.05	244 (18)
<i>Orthopristis chrysoptera</i> (pigfish)		43	5.6	<0.05	84	<0.05	147 (27)
<i>Astroscopus guttatus</i> (northern stargazer)		17	5.1	<0.05	17	<0.05	220 (72)
<i>Synodus foetens</i> (inshore lizardfish)		28	3.5	<0.05	34	<0.05	223 (42)
<i>Lagodon rhomboides</i> (pinfish)		9	3.0	<0.05	39	<0.05	139 (14)
<i>Selene vomer</i> (lookdown)		30	3.0	<0.05	72	<0.05	110 (23)
<i>Selene setapinnis</i> (Atlantic moonfish)		73	2.4	<0.05	200	0.1	81 (21)
<i>Cynoscion nebulosus</i> (spotted seatrout)		15	2.2	<0.05	17	<0.05	224 (60)
<i>Etropus microstomus</i> (smallmouth flounder)		9	2.0	<0.05	13	<0.05	115 (93)
<i>Trichiurus lepturus</i> (Atlantic cutlassfish)		20	1.2	<0.05	59	<0.05	290 (93)

Table 3. Fishes excluded from analyses.

Species	Habitat	Count	Biomass
		(no. fish)	(kg)
<i>Peprilus triacanthus</i> (butterfish)	P	5502	378.6
<i>Peprilus paru</i> (harvestfish)	P	5502	285.3
<i>Brevoortia tyrannus</i> (Atlantic menhaden)	P	1422	257.9
<i>Pomatomus saltatrix</i> (bluefish)	P	562	138.7
<i>Cyprinus carpio</i> (common carp)	D	9	82.0
<i>Alosa pseudoharengus</i> (alewife)	P	624	79.8
<i>Acipenser oxyrinchus</i> (Atlantic sturgeon)	D	4	17.2
<i>Alosa aestivalis</i> (blueback herring)	P	138	14.1
<i>Carcharias taurus</i> (sand tiger shark)	P	3	13.0
<i>Anchoa mitchilli</i> (bay anchovy)	P	13299	10.2
<i>Alosa sapidissima</i> (American shad)	P	69	10.0
<i>Alosa mediocris</i> (hickory shad)	P	40	9.4
<i>Rachycentron canadum</i> (cobia)	P	1	6.5
<i>Carcharhinus brevipinna</i> (spinner shark)	P	1	6.4
<i>Leucoraja ocellata</i> (winter skate)	D	1	5.2
<i>Trachinotus carolinus</i> (Florida pompano)	P	30	4.8
<i>Squatina dumeril</i> (Atlantic angel shark)	D	2	4.1
<i>Scomberomorus maculatus</i> (Spanish mackerel)	P	7	3.3
<i>Sphyrna tiburo</i> (bonnethead)	D	1	3.2
<i>Rhizoprionodon terraenovae</i> (Atlantic sharpnose shark)	D	1	2.7
<i>Caranx hippos</i> (crevalle jack)	P	22	1.6
<i>Clupea harengus</i> (Atlantic herring)	P	9	1.5
<i>Caranx crysos</i> (blue runner)	P	24	1.2
<i>Notropis hudsonius</i> (spottail shiner)	P	1	0.8
<i>Symphurus plagiusa</i> (blackcheek tonguefish)	D	43	0.7
<i>Opisthonema oglinum</i> (Atlantic thread herring)	P	37	0.7
<i>Hippocampus erectus</i> (lined seahorse)	D	33	0.6
<i>Urophycis chuss</i> (red hake)	D	12	0.4
<i>Merluccius bilinearis</i> (silver hake)	D	3	0.4
<i>Pseudopleuronectes americanus</i> (winter flounder)	D	1	0.4
<i>Anchoa hepsetus</i> (striped anchovy)	P	120	0.3
<i>Perca flavescens</i> (yellow perch)	D	4	0.3
<i>Etropus</i> spp. (left-eye flounders (Etropus))	D	9	0.1
<i>Mugil</i> spp. (gray mullets)	P	1	0.1
<i>Lepomis gibbosus</i> (pumpkinseed)	D	1	0.0
<i>Hippoglossina oblonga</i> (fourspot flounder)	D	1	0.0
<i>Eucinostomus argenteus</i> (spotfin mojarra)	D	3	0.0
<i>Syngnathus fuscus</i> (northern pipefish)	D	30	0.0
<i>Hypsoblennius hentz</i> (feather blenny)	D	23	0.0
<i>Fistularia tabacaria</i> (bluespotted cometfish)	D	1	0.0
<i>Gobiosoma bosc</i> (naked goby)	D	17	0.0
<i>Sardinella aurita</i> (Spanish sardine)	D	1	0.0
Serranidae (unidentified sea basses)	D	1	0.0
<i>Gobiesox strumosus</i> (skilletfish)	D	7	0.0
<i>Stellifer lanceolatus</i> (star drum)	D	1	0.0
<i>Sphyraena borealis</i> (northern sennet)	D	1	0.0
<i>Acipenser brevirostrum</i> (shortnose sturgeon)	D	1	—
<i>Ammodytes</i> spp. (sand lancees)	D	1	—

Table 4. Best-fit GAMs of community metrics.

Metric	Group	Model	% Dev
Richness	FISH	$S_i = a + \alpha_1(YR) + \alpha_2(MO) + g_1(LAT) \cdot MO + g_2(SA) + g_3(T) + g_4(DO) + g_5(DE) + e_i$	50.9
Diversity	FISH	$D_i = a + \alpha_1(YR) + \alpha_2(MO) + g_1(LAT) \cdot MO + g_2(T) + g_3(DO) + g_4(DE) + e_i$	33.9
CPUE	FISH	$\ln(\text{CPUE}_i + 0.1) = a + \alpha_1(YR) + \alpha_2(MO) + g_1(LAT) \cdot MO + g_2(SA) + g_3(T) + g_4(DO) + g_5(DE) + e_i$	35.0
	ANAD	$\ln(\text{CPUE}_i + 0.1) = a + \alpha_1(YR) + \alpha_2(MO) + g_1(LAT) \cdot MO + g_2(SA) + g_3(T) + g_4(DO) + g_5(DE) + e_i$	51.2
	COAS	$\ln(\text{CPUE}_i + 0.1) = a + \alpha_1(YR) + \alpha_2(MO) + g_1(LAT) \cdot MO + g_2(SA) + g_3(T) + g_4(DO) + g_5(DE) + e_i$	48.3
	ELAS	$\ln(\text{CPUE}_i + 0.1) = a + \alpha_1(YR) + g_1(LAT) \cdot MO + g_2(SA) + g_3(T) + g_4(DO) + e_i$	47.6

Table 5. Summaries for GAMs with different annual covariates.

Metric	Group	Rank	Covariate	Lag	Span	w	R
Richness	FISH	1	Year	0	1	0.9945	1.000
		2	Landings, coast-wide (COAS)	0	1	0.0032	0.316
		3	YOY Index(A+C)	1	2	0.0011	-0.747
Diversity	FISH	1	River discharge	2	2	0.5042	0.725
		2	YOY Index(ANAD)	1	1	0.0921	-0.258
		3	Landings, coast-wide (ANAD)	0	1	0.0793	0.617
CPUE	FISH	1	Year	0	1	0.9913	1.000
		2	Landings, coast-wide (A+C)	0	1	0.0086	0.809
		3	Landings, coast-wide (COAS)	0	1	9E-05	0.734
	ANAD	1	Year	0	1	0.8105	1.000
		2	Landings, coast-wide (A+C)	0	1	0.172	0.938
		3	YOY Index(ANAD)	2	2	0.0156	0.903
	COAS	1	Year	0	1	0.9832	1.000
		2	YOY Index(A+C)	0	2	0.0127	-0.921
		3	Landings, coast-wide (COAS)	0	1	0.0028	0.755
	ELAS	1	Year	0	1	0.5108	1.000
		2	Landings, Bay (COAS)	0	1	0.4622	-0.378
		3	YOY Index(ANAD)	1	2	0.0098	-0.659

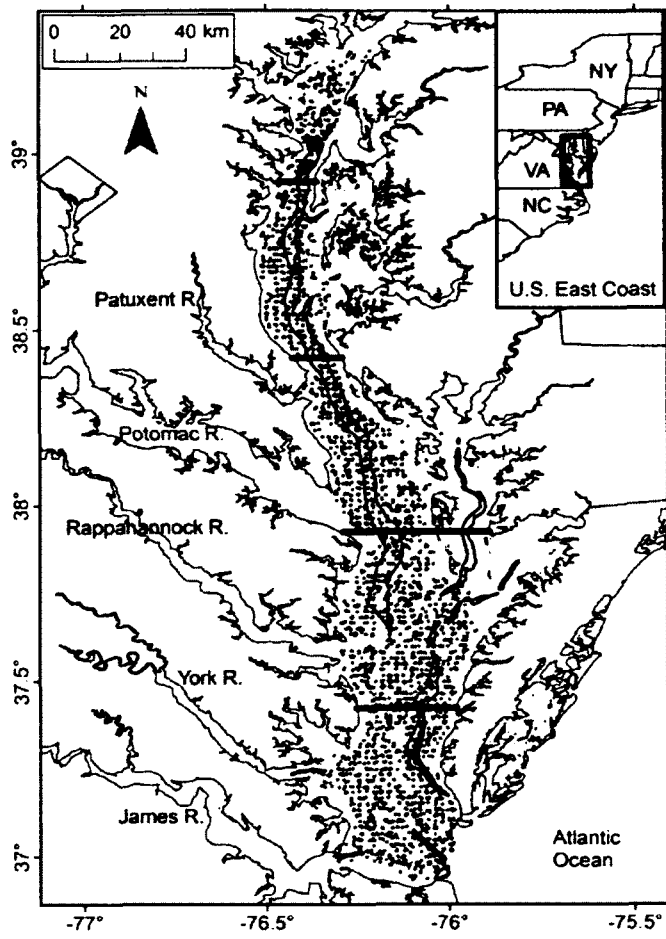


Figure 1.

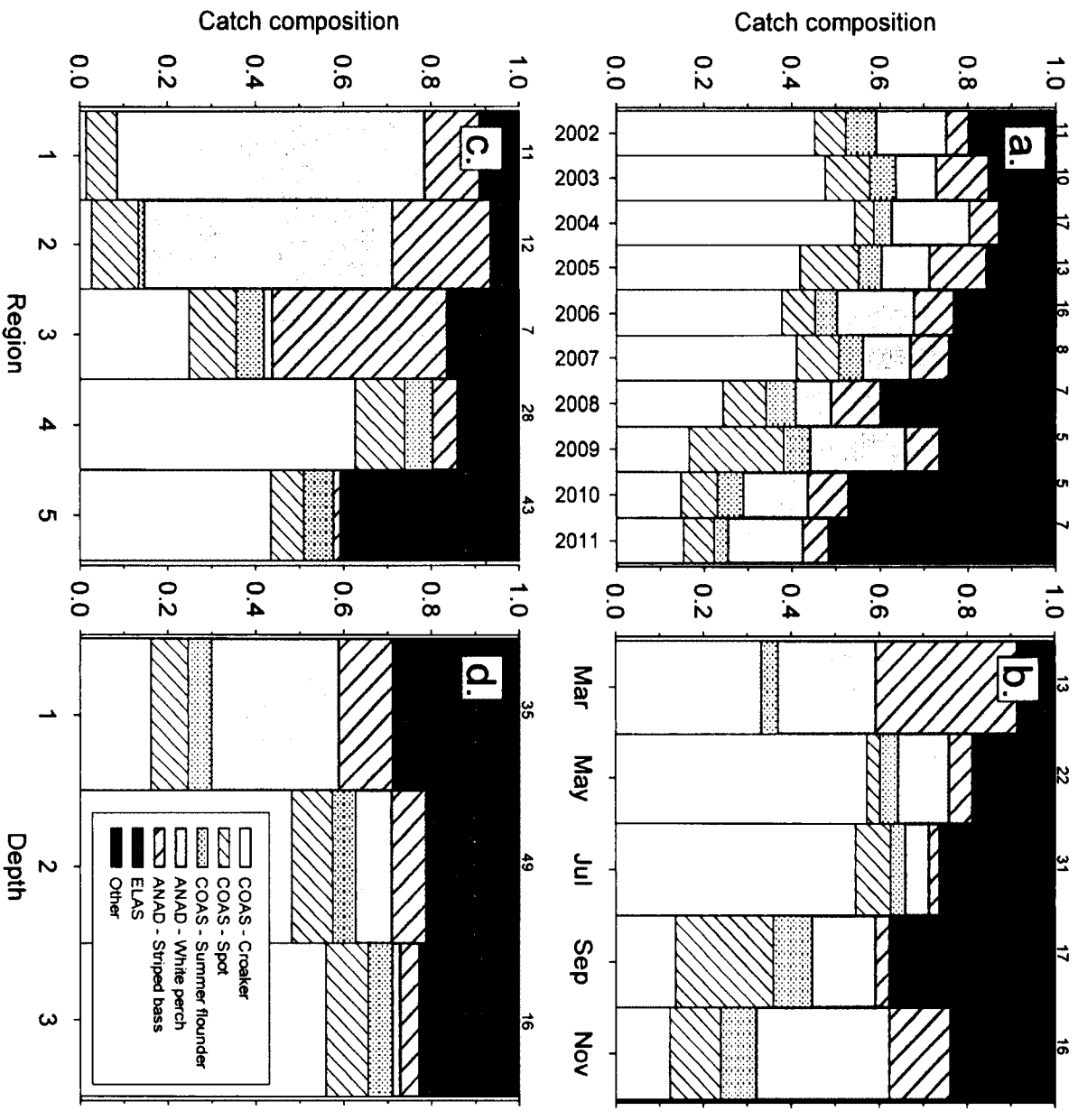


Figure 2.

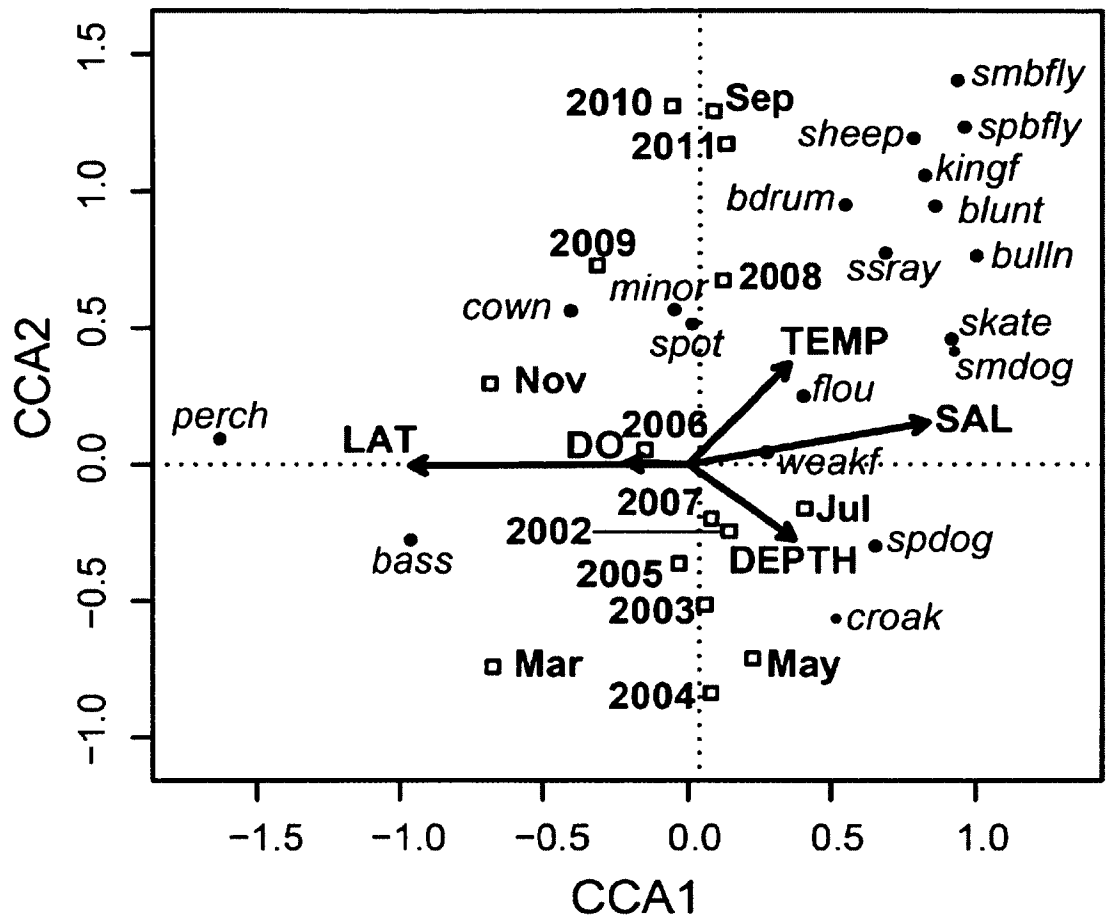


Figure 3.

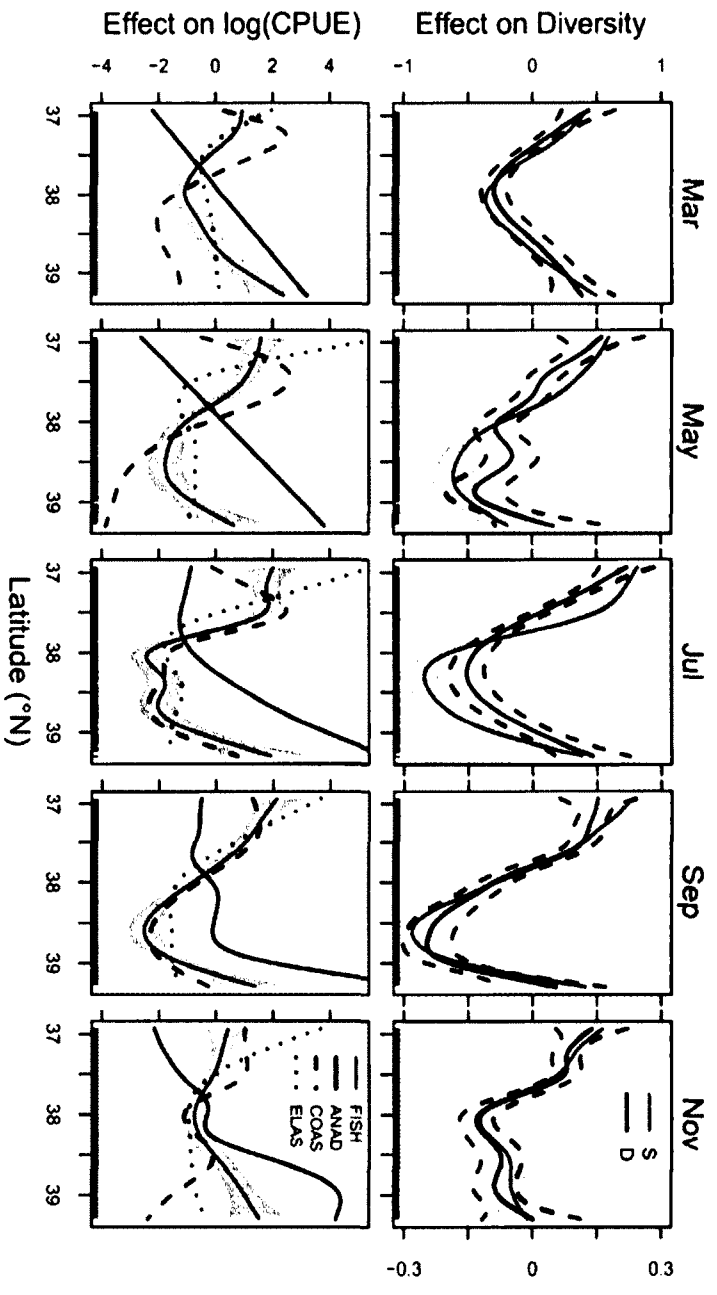


Figure 4.

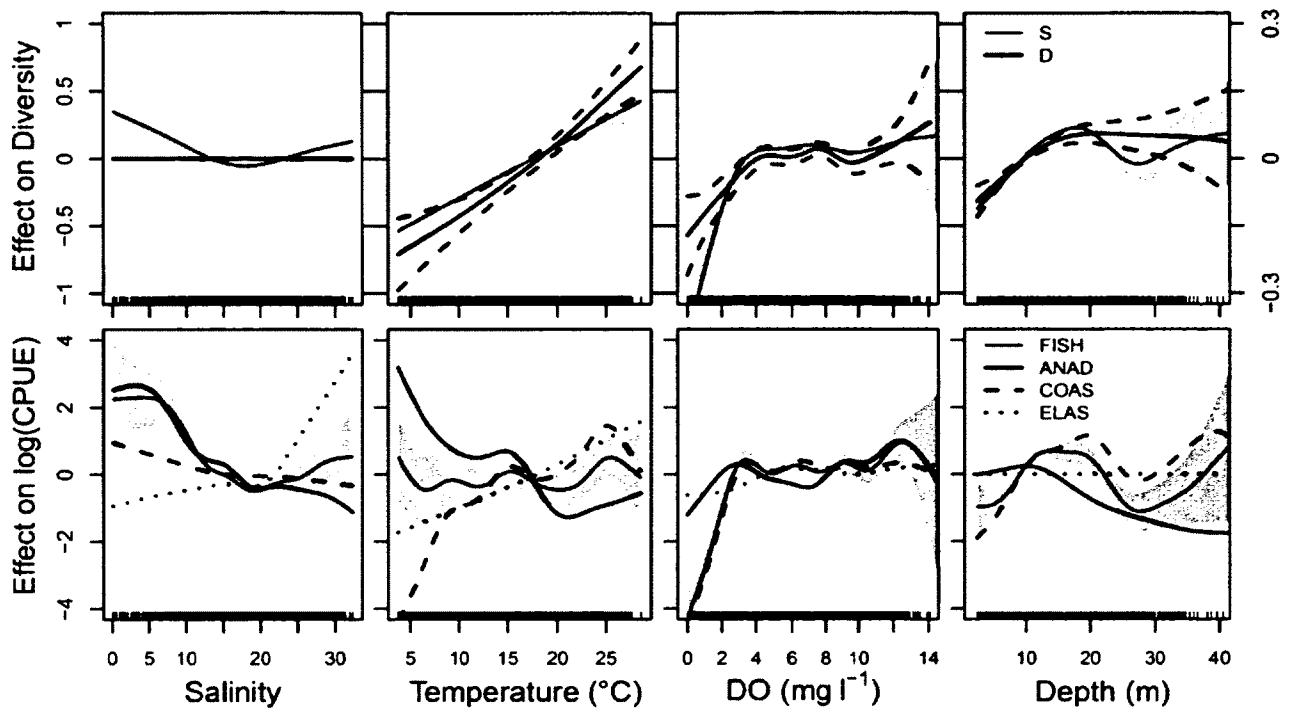


Figure 5.

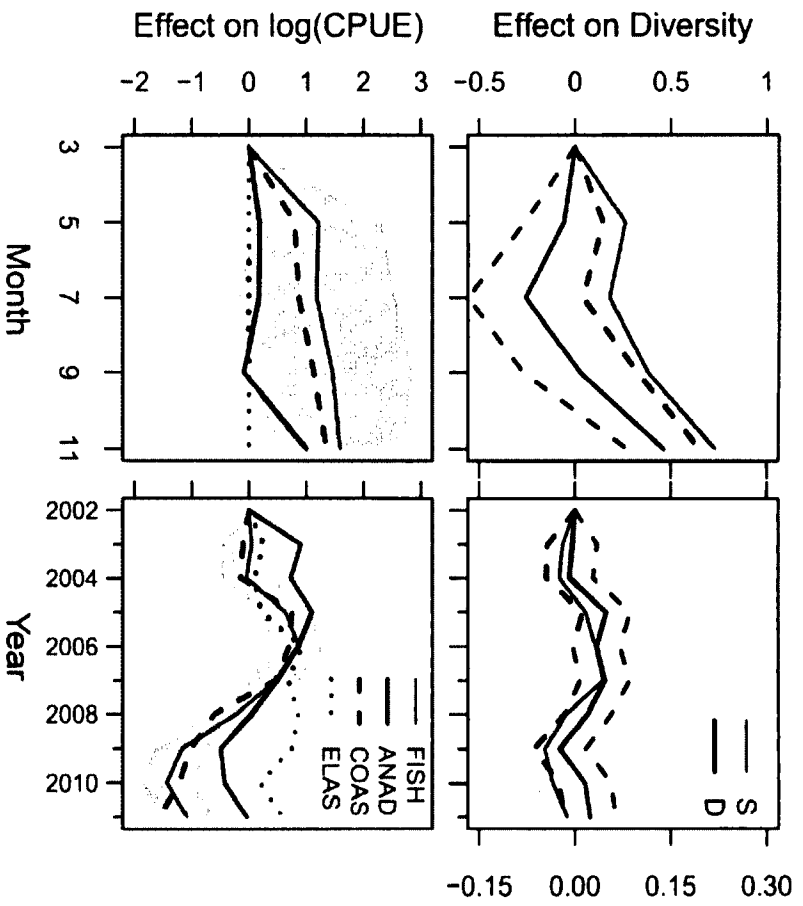


Figure 6.

CHAPTER 2

FOOD HABITS AND TROPHIC GUILD STRUCTURE OF A DIVERSE FISH ASSEMBLAGE IN CHESAPEAKE BAY, USA

ABSTRACT

Shifting from single-species fisheries management to ecosystem-based approaches necessitates a thorough understanding of trophic dynamics because predation governs the natural mortality of fishes, regulates direct and indirect food web effects, and controls the transfer of energy within a system. Using data from a 10-year multi-season trawl survey, this study examined dietary habits and trophic guild structure in an assemblage of 47 species of fish in the Chesapeake Bay, the largest estuary in the USA. The assemblage was divided statistically into 10 significant trophic guilds that were principally differentiated by the relative amounts of Mysida, Bivalvia, Polychaeta, Teleostei, and other Crustacea in the diets. These guilds were broadly aggregated into 5 trophic categories: piscivores, zooplanktivores, benthivores, crustacivores, and miscellaneous consumers. Food web structure was largely dictated by gradients in habitat (benthic to pelagic) and prey size. Size classes within piscivorous species were more likely to be classified into different guilds, reflecting stronger dietary changes through ontogeny relative to benthivores and other guilds. Relative to predator species and predator size, the month of sampling had negligible effects on dietary differences within the assemblage. Mysida (predominantly *Neomysis americana*) contributed substantially to the diets of over 25% of the sampled predator groups, indicating that this species is likely a critical, but underappreciated node in the Chesapeake Bay food web. A majority of fishes derived most of their nutrition from non-pelagic prey sources, suggesting a strong coupling of fish production to benthic and demersal food resources. As one of the largest trophic studies conducted on an estuarine fish assemblage (with >25,000 non-empty stomachs), this work contributes to the general understanding of estuarine trophic ecology and to efforts in developing ecosystem approaches to fisheries management in Chesapeake Bay and the coastal ocean.

INTRODUCTION

The continued development and application of ecosystem-based fisheries management (EBFM) approaches rely in large part on accounting for ecological processes that are known to influence fishery systems and resources (Larkin, 1996; Link, 2002a; Latour et al., 2003). Identifying and quantifying trophic interactions within the fishery ecosystem are fundamental requirements for EBFM, as they govern its structure and function (Whipple et al., 2000; Tyrrell et al., 2011). Predator-prey relationships provide the topographic structure of food webs, regulate the flow of energy in the system, and mediate most of the direct and indirect effects among species (Carpenter et al., 1985; Northcote, 1988; Wootton, 1998; Ware and Thomson, 2005; Link, 2010a). Predation can be the strongest mechanism governing mortality and biomass loss for fishes, exceeding losses to fishing mortality and harvest in many of the world's most exploited ecosystems (Bax, 1991, 1998; Hollowed et al., 2000b; Gamble and Link, 2009; Tyrrell et al., 2011). From a fisheries perspective, dietary habits of organisms are responsible not only for linking abiotic forcing factors to production of fisheries through bottom-up processes, but also for regulating top-down and indirect effects of fishery exploitation (Kaiser and Jennings, 2002). As fisheries management becomes more holistic in its application, detailed dietary information for fishes in managed systems is critical.

One approach to simplifying and synthesizing dietary information across a diverse assemblage of organisms is to focus on trophic guild structure. Root (1967) formally defined a guild as “a group of species that exploit the same class of environmental

resources in a similar way”. Development of the trophic guild concept has provided a useful framework for simplifying species complexes within systems into meaningful ecological units based on the food they consume. Trophic guild characterizations describe the functional roles of species within the system, facilitate comparison across systems, and identify species most likely to compete for food resources (Garrison and Link, 2000; Elliott et al., 2007; Franco et al., 2008).

Diet and trophic guild analyses aid EBFM efforts by supplying critical inputs for ecosystem models, informing suitable species groupings within these models, and establishing useful indicators of ecosystem status. Ecosystem models are the principal tools in EBFM for evaluating the tradeoffs associated with different management decisions (Sainsbury et al., 2000; Christensen and Walters, 2004), comparing dynamics across various ecosystems (Monaco and Ulanowicz, 1997; Megrey et al., 2009), and generating and testing hypotheses related to ecosystem function (Harvey et al., 2003). Predatory-prey diet matrices are necessary inputs into these types of models, and trophic guild classifications can establish ecological guidance for species aggregations that can be used to simplify complex food webs. Additionally, diet and guild analyses can provide more objective criteria for determining size or age thresholds when modeling important species that exhibit substantial ontogenetic shifts in ecological function (Wootton, 1998; Specziár and Rezsú, 2009). Lastly, a variety of reliable and meaningful ecosystem indicators depend on trophic guild concepts (e.g. trophic guild biomasses or their ratios) because they summarize basic ecological functions served by species within the broader ecosystem context (Rice, 2003; Methratta and Link, 2006). Such indicators can operate within a suite of metrics to help establish ecosystem reference points, control

rules, or decision criteria to inform management actions (Link, 2005; Rice and Rochet, 2005).

Countless trophic studies have been conducted in marine and estuarine waters of the northwest Atlantic, but the most extensive work in this area has focused on the continental shelf where the USA and Canada have large fishery-independent surveys with food habits programs (Bundy et al., 2011; Link et al., 2012a). Although these programs provide ample data for parameterizing ecosystem models on the shelf, they neglect estuarine and nearshore waters that are essential foraging and nursery habitats for numerous migratory species. Many of these species support important commercial and recreational fisheries in the eastern USA (e.g. striped bass *Morone saxatilis*, Atlantic menhaden *Brevoortia tyrannus*, summer flounder *Paralichthys dentatus*, Atlantic croaker *Micropogonias undulatus*, bluefish *Pomatomus saltatrix*). Within estuaries, the trophic interaction information for ecosystem modeling endeavors or comprehensive analyses of fish diets is typically garnered from a litany of disparate sources (Baird and Ulanowicz, 1989; Marancik and Hare, 2007; Christensen et al., 2009; Frisk et al., 2011); however most estuarine trophic studies are typically limited in sample size, number of species, spatial coverage, annual duration, seasonal representation, and at times in the statistical rigor of sampling design.

In this study, dietary habits are synthesized for a diverse collection of estuarine fishes from Chesapeake Bay, the largest estuary in the USA. Extensive diet data were obtained from a fishery-independent trawl survey of the bay in which samples were collected over 10 years, multiple seasons, and a 3900 km² area. This study represents the most comprehensive study of fish diets in Chesapeake Bay, and it may also be one of the

largest trophic studies of any estuarine fish assemblage in the world. Given the ongoing interests in developing EBFM in Chesapeake Bay and other estuarine and coastal systems (Pikitch et al., 2004; Houde, 2006; Essington and Punt, 2011), our objectives were to i) quantify dietary patterns for a large suite of estuarine fishes, ii) characterize trophic guilds within the assemblage of fishes, and iii) evaluate the dominant factors and gradients regulating resource partitioning. This work is intended to be a source of information for basic estuarine trophic ecology, comparative studies among systems, development of ecosystem models, and EBFM in Chesapeake Bay and the northwest Atlantic.

METHODS

Data sources

This study relied on 10 years of data (2002-2011) obtained from the bottom trawl survey conducted by the ongoing Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAP) of the Virginia Institute of Marine Science. Full details of the survey gear and sampling design are available elsewhere (Bonzek et al., 2008; Buchheister et al., 2013). Briefly, the survey operated bimonthly from March to November and sampled the mainstem of the Chesapeake Bay using an otter trawl designed to target late juvenile and adult fishes (13.7 m headrope length, 7.6 cm codend mesh). The survey area was stratified by latitude (five regional strata) and depth (three strata: 3.0-9.1 m, 9.1-15.2 m, and >15.2 m) (Fig. 1). Each cruise sampled approximately 80 stations during daylight hours, with tows typically lasting 20 minutes. Fishes captured at each station were identified, enumerated, and weighed. If a species exhibited a broad length range or distinct length groups, it was divided into 2-4 size classes. Random subsamples of these species-size-class groups were processed for size (length and weight), and their stomachs were excised and preserved in Normalin™ fixative for later diet determination. If stomachs were visually confirmed to be empty in the field, additional specimens (when available) were processed to obtain 3-5 non-empty stomachs for the species and size class. *Menticirrhus saxatilis* and *M. americanus* are very similar species most easily differentiated by the presence or absence of an elongate dorsal spine that was commonly damaged by trawling. To avoid potential problems of

misidentification, these species were combined, although the majority of samples were likely northern kingfish.

In the laboratory, stomach contents were sorted, identified to the lowest possible taxon, enumerated, weighed, and measured for length (when possible) following standardized ChesMMAP protocols. For this study, prey were aggregated into 59 prey groups (Table 1) to 1) account for the difficulty in identifying some prey to species (due in part to variability in prey digestive state), 2) simplify the >400 unique prey codes recorded, and 3) achieve a balance between capturing individual prey species of significance and providing broader functional groupings when individual species were not of importance. Particularly important prey that accounted for a substantial portion of the mean diet for a predator were retained at the species level (e.g. *Brevoortia tyrannus*, *Cynoscion regalis*, and *Leiostomus xanthurus*) or at a lower taxonomic level such as genus or family. In some cases, a prey group was predominantly represented by a single species (e.g. *Anchoa mitchilli* in Engraulidae, and *Neomysis americana* in Mysida) although other rarer species were included. When possible, prey groups were defined at the family level; however, broader resolution was needed for some categories, notably the non-crustacean invertebrates. Our number of prey groups (n=59) and level of prey resolution is consistent with other similar studies (Garrison and Link, 2000; Baldo and Drake, 2002; Colloca et al., 2010; French et al., 2013), while some authors have opted (or been constrained) to base analyses on a smaller number of general functional groups (Bulman et al., 2001; Marancik and Hare, 2007; Dolbeth et al., 2008; Reum and Essington, 2008). All statistical analyses were based on the 59 prey groups, but these groups were aggregated into 12 broad taxonomic and functional categories to simplify the

presentation of results while still preserving the major dietary differences among predators (Table 1). For summaries of diets using the broad prey categories, any unidentified teleosts were apportioned to the pelagic and demersal fish categories based on their relative percentages.

Data for this study were restricted to fish species with non-empty stomachs sampled from >15 stations, yielding 47 species (36 teleosts, 11 elasmobranchs) with a total of 25,952 non-empty stomachs (Table 2). Where appropriate, predators were divided into multiple size classes (see “Size class determination” below). For each predator and size class combination, diets were summarized gravimetrically as percent composition of each prey group (k) by weight ($\%W_k$) using a cluster sampling estimator (Bogstad et al., 1995a; Buckel et al., 1999; Latour et al., 2008):

$$\%W_k = \frac{\sum_{i=1}^n M_i q_{ik}}{\sum_{i=1}^n M_i} * 100,$$

where $q_{ik} = \frac{w_{ik}}{w_i}$,

and where n = the number of trawls containing the predator;

M_i = the number of individuals of the predator collected at sampling site i ;

w_i = the total weight of all prey groups encountered in the stomachs of the predator from sampling site i ; and

w_{ik} = the total weight of prey group k occurring in the predator stomachs from sampling site i .

This cluster sampling estimator accounts for the lack of independence among fish collected at the same sampling location; individuals from the same station typically have

diets that are more similar to one another and are thus pseudoreplicates (Bogstad et al., 1995a). Given the approximately equal stomach-sampling effort across stations, this estimator also provides a more accurate population-level description of diet than a simple mean because the estimate is weighted by the number of fish caught at each station (Bogstad et al., 1995a). Diet indices were developed for each predator-size-class combination, using data pooled across years, months, and regions, unless otherwise indicated.

Size class determination

Ontogenetic shifts in feeding are common among fishes, and individuals can occupy substantially different ecological niches in the environment as they grow and mature (Wootton, 1998; Scharf et al., 2000; Specziár and Rezsú, 2009). To account for discernible ontogenetic differences in feeding habits, hierarchical agglomerative cluster analysis (with group-average linkage) was used to identify size classes whose diets were dissimilar. Within each species, diets were calculated for 25-mm length bins using all available data, and a cluster analysis was run based on a Bray-Curtis similarity matrix for the size groups (e.g. Latour et al., 2008; Specziar and Rezsú, 2009). Designation of size classes (S-small; M-medium; L-large) were determined from cluster analysis results, provided that 1) size-based groupings were evident, 2) sample sizes within a size class were adequately large (>15 stations), and 3) prey saturation curves for each size class approached a stable maximum. This relatively objective analytical approach to determining size classes was used to avoid delineating size groups subjectively with length delineations that do not have ecological significance (Specziár and Rezsú, 2009).

Of the 47 species included in the study, 20 species were divided into two or three size classes using this methodology (Table 2). This yielded 71 species-size-class combinations (hereafter “predator groups”) that were treated as functionally distinct predators for all remaining analyses.

Multivariate analyses of trophic guilds

Two multivariate statistical methods were used to aggregate predator groups into trophic guilds. First, hierarchical agglomerative clustering with group-average linkage was used to identify trophic guilds of fishes. Cluster analysis relied on Bray-Curtis dissimilarities and sequentially aggregated predator groups together based on dietary similarity. Statistically significant cluster groupings were identified using a bootstrap randomization technique in which the non-zero values in the predator-prey diet matrix were resampled (with replacement) and used to generate pseudovalues of Bray-Curtis dissimilarities under the null hypothesis of there being no structure in the diet matrix (Jaksic and Medel, 1990). A frequency distribution of pseudovalues was generated from 100 randomizations of the diet matrix, and the 95th percentile was used as the critical value to determine significance in the cluster analysis of the observed data (Jaksic and Medel, 1990). Second, non-metric multidimensional scaling (NMDS) was used to corroborate and visualize trophic guild designations from the cluster analysis. NMDS is a non-parametric ordination technique that relies on the rank order of response values (dietary Bray-Curtis dissimilarities), and thus does not make any underlying distributional assumptions of the data in contrast to many other ordination approaches

(Clarke and Warwick, 2001). Predators were plotted in ordination space with distance among points being positively related to dissimilarity.

Two approaches were used to identify the most influential prey groups within and across trophic guilds. First, to identify the prey groups most responsible for the significant trophic guild classifications, a similarity percentage analysis (SIMPER) routine was used to decompose the average similarity between all pairs of predators within a guild into percentage contributions from each prey group (Clarke and Warwick, 2001). This method highlights the prey groups most responsible for within-guild dietary similarity. Second, the importance of individual prey groups to the fish assemblage as a whole was evaluated based on the number of predators deriving an appreciable amount of nutrition from each prey group. The number of predator groups whose diets were comprised of at least 20% of a prey group was calculated. Analysis focused on only those prey groups (n=9) with $\geq 20\%$ dietary contribution to at least three predator groups. The percent occurrence of each of these nine prey groups across the fish assemblage was also calculated, based on the presence/absence of the prey in the mean diet of each predator group.

Fish diets are known to vary over time and space largely due to variability in prey availability, particularly in biophysically dynamic environments such as temperate estuaries. The primary goal of this study was to provide a broad characterization of dietary habits of Chesapeake Bay fishes, pooling across years, months, and regions, because this spatiotemporal scale is most directly pertinent to general ecological description of fishes and to ecosystem modeling efforts in the bay. However, to assess the relative influence of month effects on diets (compared to species and size class

effects), additional analyses were conducted for the six most sampled species (*M. undulatus*, *P. dentatus*, *C. regalis*, *M. saxatilis*, *Morone americana*, *L. xanthurus*). These six species accounted for 65% of total stomachs analyzed in this study (Table 2) and comprised 79% of the total biomass captured by the survey (Buchheister et al., 2013). For this species subset, NMDS was conducted using a Bray-Curtis dissimilarity matrix derived from diet estimates by species, size class, and month. Analysis of similarity (ANOSIM) was used in PRIMER to test for significant differences in diet similarity among the three factors (species, size classes, and months) using one-way and two-way crossed analyses (e.g. Bundy et al., 2011; French et al., 2013). ANOSIM is a multivariate permutation test (conceptually similar to a univariate ANOVA) that relies on the test statistic R, whose value determines a factor's significance and can be used to assess the relative importance of factors (Clarke and Warwick, 2001). For a two-way crossed ANOSIM, the effect of one factor is tested after accounting for the effect of the second factor. All multivariate analyses were conducted with either the statistical package R using the 'stats' and 'cluster' packages (R Core Development Team, 2011) or with PRIMER (Clarke and Warwick, 2001).

RESULTS

Dietary patterns and trophic guilds

The trophic guild analyses yielded robust groupings of fishes that displayed significantly different food habits. The cluster analysis and bootstrap randomization identified 10 unique trophic guilds that characterize the diversity of feeding modes among Chesapeake Bay fishes (Fig. 2). A dissimilarity value of 0.69 was determined to be the critical value for group significance; any groupings with a dissimilarity less than 0.69 were unlikely to have occurred by chance ($p < 0.05$; Jaksic and Medel, 1990).

Dietary differences among trophic guilds were largely evident when prey were grouped into broad categories (Fig. 2). However, some guilds were differentiated by taxonomic differences at finer scales, as seen in the full predator-prey diet matrix with all 59 prey groups (Appendix A). To classify broader patterns in consumptive habits, pairs of guilds (designated “a” and “b”) were aggregated into five major feeding categories (Fig. 2): piscivores (PISC), zooplanktivores (ZOOP), benthivores (BENT), crustacivores (CRUS; defined as predominant consumers of Crustacea, excluding Mysida and Copepoda), and miscellaneous consumers (MISC). To facilitate discussion and interpretation of our results, we did not fully conform to the standardized guild nomenclature proposed by Elliott et al. (2007). However, for comparative or meta-analytical purposes our trophic guilds can be classified as follows based on their Table 2 (Elliott et al., 2007): PISC-a and PISC-b = PV; ZOOP-a = ZB-H; ZOOP-b = ZP; BENT-a, BENT-b, and CRUS-a = ZB-I; CRUS-b = ZB-E; MISC-a = ZB-E; MISC-b = ZP.

The broad piscivore category included 15 predator groups (10 species) that mostly consumed fishes but were differentiated by the size and type of fish consumed (Figs. 2, 3). The PISC-a guild, included higher trophic-level predators (L *C. regalis*, L *M. saxatilis*, M *P. saltatrix*, and the sharks *Carcharhinus plumbeus* and *Squalus acanthias*) and was characterized by consumption of large pelagic fishes (Figs. 2, 3). *B. tyrannus* in particular was the prey most strongly responsible for the intra-guild dietary similarity (contributing 61.1% of the total) based on the SIMPER analysis (Table 3). The PISC-b guild consumed greater proportions of smaller pelagic fishes (mostly *A. mitchilli* in the Engraulidae prey group) and demersal fishes including juvenile sciaenids (Figs. 2, 3 and Table 3). PISC-b predators included smaller size classes of three PISC-a species (M *C. regalis*, S *P. saltatrix*, S and M *M. saxatilis*) as well as M and L *P. dentatus*, *Synodus foetens*, *Alosa mediocris*, *Gymnura altavela*, and *Gymnura micrura*. Large *P. dentatus* and *Gymnura* rays consumed a large proportion (58-83%) of demersal fishes (mainly *L. xanthurus* and *M. undulatus*), and this cluster was close to being sufficiently different to constitute a separate trophic guild (Fig. 2). Diets of fishes from the two significant piscivore guilds were augmented predominantly by Mysida and other crustacean prey, most notably for *C. regalis* (M and L), *C. plumbeus*, *P. dentatus* (M and L), and *M. saxatilis* (S and M) (Fig. 2).

Zooplanktivores, including 17 predator groups (14 species), consumed large amounts of zooplankton, primarily Mysida and Copepoda. The ZOOP-a guild was the larger of the two zooplanktivore guilds (14 predator groups, 11 species) and relied heavily on Mysida (28-94% of diet by weight). *N. americana* was the overwhelmingly dominant mysid species, accounting for 99% of all mysid occurrences identifiable to

species. Mysida alone accounted for 79.6% of the similarity within the ZOOB-a guild (Table 3). This guild included small size classes of some piscivores (*C. regalis*, *P. dentatus*), as well as *Bairdiella chrysoura*, *Selene setapinnis*, *Scophthalmus aquosus*, *Larimus fasciatus*, *Urophycis regia*, *Prionotus carolinus*, *Prionotus evolans*, *Selene vomer*, and *Dasyatis sabina*. Three alosines (*Alosa pseudoharengus*, *Alosa sapidissima*, and *Alosa aestivalis*) comprised the ZOOB-b guild and had diets dominated by Copepoda (18-66%), Mysida (7-46%), and other unidentified material (16-25%; Figs. 2, 3). Each of these prey groups contributed substantially to the intra-guild similarity (Table 3).

Benthivores represented the largest feeding category, including 23 predator groups from 16 species. All benthivores consumed a blend of Polychaeta, Bivalvia, unidentified material, and Crustacea in varying proportions (Figs. 2, 3). Some of the major bivalve species consumed included *Ensis directus*, *Gemma gemma*, *Macoma spp.*, *Mercenaria mercenaria*, *Mya arenaria*, and *Tagelus plebeius*. The eastern oyster *Crassostrea virginica* was only identified twice in the stomachs, but its densities are greater in shallower habitats that were not sampled. Fishes commonly foraged on bivalve siphons, preventing detailed identification. Some of the most commonly consumed polychaete annelids included the *Nereis*, *Pectinaria*, and *Glycera* genera, with additional representation from the Maldanidae, Terebellidae, Chaetopteridae, and Capitellidae families. The two significant benthivore guilds were largely differentiated by the predominance of Polychaeta (BENT-a) or Bivalvia (BENT-b) in the stomachs (Figs. 2, 3, Table 3). The BENT-a guild consumed Polychaeta (1-76%) and unidentified material (2-63%) to a larger extent than the BENT-b guild (Fig. 3) and included a variety of predator species: *M. undulatus* (all sizes), *L. xanthurus* (M and L), *Stenotomus chrysops*, *Trinectes*

maculatus, *S Menticirrhus*, *Dasyatis say* (S and M), *Orthopristis chrysoptera*, *S Dasyatis americana*, *M. americana* (S and M), *Chaetodipterus faber* (S and M), and *Pogonias cromis* (Fig. 2). The BENT-b guild generally exhibited higher consumption of *Bivalvia* (21-63%; Fig. 3) and included the *Sphoeroides maculatus*, *Archosargus probatocephalus*, *Tautoga onitis*, *Rhinoptera bonasus* (M and L), and *Chilomycterus schoepfii* (Fig. 2).

Crustacivores were the fourth identified trophic category and contained 12 predator groups (9 species), all of whom fed on a variety of Crustacea, particularly decapod shrimp, decapod crabs, and Squillidae. The CRUS-a guild diets were variable with no single unifying prey group, but the SIMPER analysis indicated that Squillidae, *Bivalvia*, Portunidae, unidentified Teleostei, and other decapod crabs were the prey most responsible for dietary similarity within the guild (Table 3). Some CRUS-a predators had appreciable (~20%) consumption of *Bivalvia* (*Raja eglanteria*, *M Menticirrhus*, and *Ictalurus punctatus*) or Polychaeta (*M D. sabina* and *M D. americana*) that were similar to the benthivores (Figs. 2, 3). The CRUS-b guild (*Centropristis striata*, *Opsanus tau*, *S I. punctatus*, and *Ameiurus catus*) shared a stronger reliance on panopeid mud crabs (11-29% of diets) (Figs. 2, 3). Unidentified Teleostei, unidentified material, decapod crabs, and Corophiida also contributed to the intraguild similarity (Table 3).

The fifth general trophic category of miscellaneous consumers included two guilds that were grouped for convenience as opposed to dietary similarity. The MISC-a guild (S and M *Myliobatis freminvillii*) was more closely related to the crustacivores and benthivores, but they fed predominantly on Gastropoda (60-83%; Figs. 2, 3), which alone accounted for 81.8% of the guild's similarity (Table 3). The MISC-b guild consisted of

two *Peprilus* congeners that can be classified as gelatinous zooplanktivores, with 77-86% of the diet coarsely identified as schyphozoan cnidarians.

Non-metric multidimensional (NMDS) scaling corroborated the cluster analysis results, establishing clear multivariate differences in predator diets among the five major trophic categories and the 10 guilds (Fig. 4). Slight overlap among trophic categories or guilds reflected the gradual and transitional nature of dietary differences among predators that was not as visually prominent in the discretized approach of cluster analysis. Unlike parametric ordination plots that are constrained to be plotted in a specific two-dimensional orientation, NMDS plots can be rotated in any direction within the established plane. But as presented, the x-axis of the NMDS largely segregated guilds along a benthic to pelagic habitat gradient. Consumers of infaunal and epifaunal benthic organisms (the benthivores and crustacivores) grouped together to the left of consumers of more pelagic prey (zooplanktivores and piscivores) (Fig. 4). The y-axis represented a size gradient from smaller to larger prey, with consumers of Polychaeta, Copepoda, Mysida, and gelatinous zooplankton plotted below consumers of Squillidae, portunid crabs, and teleosts (Fig. 4).

Few individual prey groups were consistently important (i.e., dietary contribution $\geq 20\%$ by weight) across multiple predators, even if the prey occurred in a majority of predators. Mysida was the most essential prey, accounting for $\geq 20\%$ of the mean diet in 27% of predator groups (19 out of 71) and occurring in 85% of predators groups (60 out of 71) (Fig. 5A). Polychaeta, Bivalvia, and unidentified material each contributed substantially to the diet of $\sim 17\text{-}18\%$ of sampled predator groups. Engraulidae, *B. tyrannus*, Squillidae, unidentified Teleostei, and *L. xanthurus* were each important in the

diets of 4-7% of sampled predators. Many of these prey groups occurred in a majority of the predators (70-96%; Fig. 5B). Only *B. tyrannus*, Squillidae, and *L. xanthurus* occurred in less than half of the sampled predators (28-48%; Fig. 5B).

Ontogenetic and seasonal variability

Length-based, ontogenetic differences in diets were substantial for several of the species examined. Of the 20 species divided into multiple size classes, eight species had size classes designated into different trophic guilds (*D. sabina*, *P. saltatrix*, *I. punctatus*, *Menticirrhus*, *D. americana*, *M. saxatilis*, *P. dentatus*, and *C. regalis*), although three of these remained within the same broad trophic category (*P. saltatrix*, *I. punctatus*, and *M. saxatilis*) (Fig. 4B). For twelve species, all size classes grouped within the same guild (*M. undulatus*, *R. eglanteria*, *L. xanthurus*, *M. americana*, and others). However, larger size classes within all 20 species always plotted higher than smaller size classes in the NMDS plot, consistent with the prey size gradient (Fig. 4B). Thus, some species undergo more drastic ontogenetic changes in feeding, whereas size-based differences in other species are relatively minor when compared to the broad spectrum of resource use within the demersal fish community.

Analyses focused on the subset of predators with the largest sample sizes indicated that monthly differences in diets tended to be minimal with respect to the differences observed across species or across size classes. All one- and two-way ANOSIM tests of species effects on diets were significant (Table 4). Size-class effects were significant in the one way test and also after accounting for any species effects. In contrast, all tests of the month effect were not significant, even after accounting for

differences among species or size classes. The relative values of the test statistic R (Table 4) suggest that the effect of species was the strongest, followed by size class, and lastly by month whose effects were negligible within the context of this analysis. ANOSIM results were corroborated visually by an NMDS plot of diet data summarized by predator, size class, and month (Fig. 6). The multiple monthly points for each species-size-class combination were typically more similar to one another than plots using other factor groupings. The plot more clearly demonstrated the influence of species on guild membership, particularly separating benthivores from piscivores along a habitat gradient (Fig. 6). The influence of body size along the vertical gradient was also evident particularly for *M. undulatus*, *M. saxatilis*, *C. regalis*, and *P. dentatus*, with larger sizes typically plotting higher. The main exceptions to this size gradation for *C. regalis* and *P. dentatus* were caused by above average consumption of Crangonidae in March and May (Fig. 6).

DISCUSSION

Trophic structure and trophodynamic gradients

The Chesapeake Bay fish assemblage was highly carnivorous, with trophic guild structure largely defined by the consumption of a small number of broad prey categories, particularly Mysida, Teleostei, Bivalvia, Polychaeta, and epi-benthic Crustacea. Fish diets were relatively general and usually included various prey groups from multiple trophic levels (median of 22 prey groups per predator). Herbivory, which is typically rare in temperate and higher latitudes (Horn, 1989; Franco et al., 2008), was not observed, and only two species (*A. mediocris* and *S. C. faber*) consumed appreciable amounts (> 10%) of plant material. Direct detritivory was also not prevalent in this study, consistent with a broad survey of European estuaries (Franco et al., 2008) and the observation that this trophic guild is more common in lower latitudes (Gerking, 1994). However, our study did not include two common Chesapeake Bay fishes (gizzard shad, *Dorosoma cepedianum*, and common mummichog, *Fundulus heteroclitus*) that are known to consume detritus (Allen et al., 1994; Yako et al., 1996).

Resource utilization is typically thought to be partitioned among species along three major gradients (food, habitat, and time) to minimize competition among species, with the food axis often the most important (Ross, 1986; Wootton, 1998). Our study focused on resource partitioning with respect to food, and it indicates that food resources are partitioned along two dominant trophodynamic gradients: prey habitat and prey size. These two gradients appear to be consistent characteristics of food partitioning in aquatic

systems (Garrison and Link, 2000; Marancik and Hare, 2007; French et al., 2013), and these trophodynamic gradients are a mechanism for minimizing competition and niche overlap among or within species.

The prey habitat gradient was arranged from benthic to pelagic environments, but the majority of consumption was directly derived from non-pelagic sources. As shown in other studies, the habitat gradient distinguished benthivores from zooplanktivores and piscivores (Garrison and Link, 2000; Marancik and Hare, 2007; Reum and Essington, 2008). Although the habitat gradient was largely explained by the two-dimensional benthic to pelagic gradient, this gradient can be arranged along other habitat parameters of importance such as depth (Colloca et al., 2010), benthic structure (e.g. seagrasses, reefs; Marancik and Hare, 2007), or sediment type (Holland et al., 1987). The main pelagic prey resources were *B. tyrannus*, Engraulidae, Copepoda, and Scyphozoa, whereas most other prey groups were benthic, hyperbenthic (e.g. Mysida), or demersal. After apportioning unidentified Teleostei to pelagic and demersal components, only 10/71 predator groups derived >50% of their diets from pelagic sources, with most of these predators in the piscivore guilds. Thus, 61 predator groups were primarily supported through non-pelagic food resources. Strong reliance on benthic and hyperbenthic food sources has been noted in various other similar systems in the US and Europe (Barry et al., 1996; Franco et al., 2008; Reum and Essington, 2008; Woodland and Secor, 2013). As a whole, the Chesapeake Bay is a system dominated by pelagic primary production (Baird and Ulanowicz, 1989; Diaz and Schaffner, 1990; Kemp et al., 2005b), and coastal eutrophication acts to further increase these rates (Nixon, 1995; Kemp et al., 2005b). Our data suggest that most of the carbon directly fueling the studied

fishes (at the sizes examined) is funneled through the benthic food web via filter feeding or detritivorous invertebrates, even if the indirect sources of fish production are more pelagically-derived from phytoplankton (Baird and Ulanowicz, 1989). However, Mysida (in addition to forage fishes and Copepoda) can act as a more direct pathway of pelagic carbon to predators given their vertical migrations to feed in the water column and their more pelagic isotopic signatures (Jumars, 2007; Woodland and Secor, 2013).

Chesapeake Bay fishes also partitioned prey resources along a size gradient, which is another common character by which food resources are allocated across species in a community (Scharf et al., 2000; Kerr and Dickie, 2001). There is generally a positive relationship between prey size and predator size (Scharf et al., 2000; Colloca et al., 2010), particularly for gape-limited predators, making it difficult to separate the effect of prey vs. predator size. This general size gradient in foraging was particularly evident in comparisons among size classes of each species as well as the analysis of the species subset; all analyses captured the progressive dietary shifts to larger prey as the predators grew. The dispersion of each species within ordination space can also be considered a measure of trophic niche breadth (Fig. 6), suggesting that the intra-species breadth was larger for each of the piscivores (relative to the benthivores), particularly along the size gradient. Piscivorous foraging tends to be more gape-limited than benthivorous feeding, allowing for individuals to exploit a larger range of prey sizes and types through ontogeny. Estuarine benthivores on the other hand, consume prey that have a more constrained size range with the largest prey being larger portunid crabs, bivalves, and Squillidae.

Ontogenetic shifts in diets are well established in fishes, and are largely linked to indirect effects of increased size (changes in prey vulnerability, increased capture success, etc.), but can also be related to changes in habitat and behavior (Juanes, 1994; Wootton, 1998; Scharf et al., 2000). From a guild classification perspective, ontogenetic effects on fish diets were more significant for piscivores. PISC-a acted as a terminal guild which could be achieved by progressing through zooplanktivory (ZOOP-a) and piscivory on smaller fishes (PISC-b). In this regard the ZOOP-a, and PISC-b can be considered as largely transitional guilds for many fishes as they are growing. The ontogenetic signal in benthivorous species was present but less ecologically significant, as a larger proportion of these species remained within the same trophic guild as they grew. Only two predators (*Menticirrhus* and *D. americana*) transitioned through the BENT-a guild into the CRUS-a guild, demonstrating a shift to larger prey types. Thus, some guilds (particularly the BENT-a, ZOOP-a, and PISC-b) can be considered transitional guilds that characterize smaller individuals of a given species that are ultimately adapted to be a crustacivore or piscivore, provided they manage to grow and survive. The increasing degree of piscivory by some crustacivores (e.g. *R. eglanteria* and *I. punctatus*), suggests that, although not observed in our study, CRUS can also be a transitional trophic phase to PISC as documented for some fishes in coastal waters (Garrison and Link, 2000; Scharf et al., 2000). The concept of transitional guilds would be even more evident if the full size range of each species was adequately sampled; for example, the majority of all fishes are zooplanktivorous at larval stages (Nunn et al., 2011). These patterns reinforce the dominant role that body size plays in structuring food webs (Kerr and Dickie, 2001).

Key estuarine prey groups

Mysida was the single most important prey group, establishing a key trophic link supporting fish production within Chesapeake Bay, but their importance to the food web is likely even greater than suggested by our diet results. An entire trophic guild was defined by mysid consumption, and could be more aptly named the mysivore guild. *N. americana*, the overwhelmingly dominant mysid species consumed, is predominant throughout estuarine and coastal waters of the Northeast US (Wigley and Burns, 1971; Nemerson and Able, 2004). As with most other mysid species, they make frequent migrations into the water column from the benthos (thus termed “hyperbenthos”), linking benthic and pelagic food webs with their migrations and highly omnivorous diets which include detritus, microalgae, protists, and small animals such as copepods (Mauchline, 1980; Jumars, 2007). Mysida is consumed by a wide range of fishes, mammals, cephalopods, crustaceans, and other aquatic fauna (Mauchline, 1980). It is particularly dominant in diets of small and juvenile fishes (~30-150mm) in temperate estuaries and coastal waters (Mauchline, 1982; Baldo and Drake, 2002; Nunn et al., 2011). Consequently, mysids are likely even more important to Chesapeake Bay fishes at sizes below those captured by our survey gear. However, our work suggests that Mysida continue to be of importance to fishes at substantially larger sizes >300mm. Based on stable isotope data, the dietary contribution of *N. americana* to fish production can be underestimated from stomach contents (Buchheister and Latour, 2011a), due to rapid digestion of mysids (Lankford and Targett, 1997; Andersen, 1999) and the potential for greater mysid consumption during crepuscular and night hours when *N. americana* are

more active (Hulburt, 1957; Herman, 1963). Laboratory studies on juvenile *C. regalis* suggest that there can be a high degree of selectivity for *N. americana* over alternative prey (Lankford and Targett, 1997), and growth and condition of *C. regalis* in the wild may be linked to mysid consumption (Grecoy and Targett, 1996). Given the typically large biomass and relatively high production rates of Mysida, it is unlikely that demersal fish communities exert significant top-down control (Hostens and Mees, 1999); instead, fishes may be regulated through bottom-up processes with respect to Mysida. All of these lines of evidence suggest that *N. americana* could be a particularly important prey influencing recruitment, growth rates, and condition of fishes (Nunn et al., 2011) as well as benthic-pelagic coupling (Jumars, 2007). Thus, this single species can be considered a critical node in the Chesapeake Bay food web.

Despite the prevalence of mysids in diets of fishes and other animals, the central role they play in estuarine and marine food webs, and their ability to link benthic and pelagic productivity, mysids are regularly neglected or under-represented in ecosystem models. This trend appears to be widespread throughout estuaries and coastal systems and is largely due to difficulties in sampling caused by evasive behaviors, swarming and patchiness of aggregations, vertical migration, and gears that inadequately sample their habitats (Mauchline, 1980; Jumars, 2007). Within Chesapeake Bay, this issue is evident in Baird and Ulanowicz's (1989) seminal network model in which mysids are unmentioned, and in the Chesapeake Bay Fisheries Ecosystem Model in which mysids are broadly grouped with a large suite of infaunal and epifaunal species (Christensen et al., 2009). Undoubtedly, increasing resolution of such ecosystem models at lower trophic levels is partially predicated on obtaining adequate data to parameterize biomass and

production rates of the group. Future research and monitoring efforts focused on mysids are warranted given their key role in transferring energy to a large variety of fishes, including several species of current or historic economic value in the region (e.g., *M. saxatilis*, *P. dentatus*, *C. regalis*, and Alosines).

Bivalvia and Polychaeta were two significant macrobenthic prey groups in the diets of Chesapeake Bay fishes. The relative specialization of some fishes on either of these two groups was also noted in other estuarine studies (Reum and Essington, 2008), and may be a common mechanism for partitioning macrobenthic resources in temperate estuaries. Both groups are ubiquitous, though bivalves are typically a larger proportion of infaunal benthic biomass (Diaz and Schaffner, 1990). Bivalve consumption is often limited by morphological adaptations, especially oral and pharyngeal dentition, as evidenced by the molariform or plate-like dentition found in many of the bivalve predators (*P. cromis*, *A. probatocephalus*, *L. xanthurus*, *R. bonasus*) (Chao and Musick, 1977; Clifton and Motta, 1998; Grubich, 2003). The BENT-a fishes that consume polychaetes and other benthos in larger amounts tend to be less morphologically specialized than BENT-b bivalve predators. This generalism in morphology and diet is facilitated by the diversity of polychaete feeding behaviors (carnivores, detritivores, planktivores) and lifestyles (from sessile tube builders to mobile predators) which offers a wider range of foraging options to predatory fishes (Diaz and Schaffner 1990, Gillett and Schaffner 2009). Thus, polychaetes can be considered a more general benthic prey, accessible to predators of various sizes and morphologies.

Crustaceans can be the most taxonomically and trophically diverse group of benthic animals encountered in estuaries (Gillett and Schaffner, 2008), and they

contributed significantly to diets of many Chesapeake Bay fishes. Within the crustacean prey category (which excludes Mysida and Copepoda), Squillidae (mostly *Squilla empusa*), Panopeidae, and Portunidae (including the blue crab, *Callinectes sapidus*) were particularly important, and their presence in diets reflected the structuring gradients of size and habitat. Larger predator body sizes tended to be a pre-requisite for consumption of Squillidae (which can grow to 20-25 cm), as evidenced by its dominant predators: several elasmobranchs and larger size classes of some teleosts, consistent with previous work (Ellis and Musick, 2006; Latour et al., 2008). Likewise, portunid crabs tended to be eaten by larger predators, but we did not sample shallow creek and seagrass habitats where juvenile *C. sapidus* densities are higher (Heck and Thoman, 1984; Ralph et al., 2013) and where predation by smaller fishes would be possible. Consumption of Panopeid mud crabs was greatest for fishes (*C. striata*, *O. tau*, *I. punctatus*, and *A. catus*) associated with the structured or hard-bottom habitats in which these crabs generally reside (e.g. shell, cobble, hard reefs, sponges, hydroids). Crangonidae provided the strongest example of seasonality in foraging habits of Chesapeake Bay fishes. Crangonid consumption (by *P. dentatus*, *C. regalis*, *U. regia*, *Prionotus*, *Menticirrhus*, and others) was seasonally opportunistic with peak consumption occurring in March and May when *Crangon septemspinosa* are aggregated and most abundant in the lower Chesapeake Bay before they move to shallower areas (Price, 1962; Haefner, 1976).

The two most important forage fishes in Chesapeake Bay, *A. mitchilli* and *B. tyrannus*, are also the most abundant and most commercially valuable fishes (respectively) in the bay (Houde and Zastrow, 1991; Murdy et al., 1997; Able and Fahay, 2010). Although few predators' diets contained >20% of each of these fishes, the critical

role that these prey fishes play in supporting several commercially and recreationally important fishes (e.g. *M. saxatilis*, *C. regalis*, *P. saltatrix*, *P. dentatus*) is unquestioned (Hartman and Brandt, 1995a; Walter III and Austin, 2003; Latour et al., 2008; Overton et al., 2009). For example, up to 80% of seasonal *A. mitchilli* secondary production in Chesapeake Bay is estimated to be consumed by the bay's piscivores (Baird and Ulanowics 1989). Some authors have highlighted the potential for long-term shifts in the contribution of *B. tyrannus* to the diet and production of striped bass, resulting from fishery-induced changes in their respective populations (Griffin and Margraf, 2003; Hartman and Margraf, 2003; Pruell et al., 2003). These types of concerns are part of the motivation behind the increasing interest in managing these species in an EBFM framework to better handle the ecosystem tradeoffs in setting catch limits for individual species (Houde, 2006; Garrison et al., 2010; Link, 2010a).

Dietary variability

The aggregation of diet information across seasons, years, and habitats contributed to dietary variability but yielded a broad, general characterization of the trophic dynamics of the Chesapeake Bay fish assemblage. The month of sampling had a negligible effect on diets (relative to the effect of species and size class), which is consistent with a seasonal network analysis of the bay's food web in which the topology was found to be largely consistent across seasons, even though the magnitude of overall energy flow varies (Baird and Ulanowicz, 1989). Other studies have also documented a relatively small or non-significant seasonal effect on dietary structure of fish assemblages (Bulman et al., 2001; Reum and Essington, 2008; Colloca et al., 2010; Bundy et al., 2011;

French et al., 2013), but the opposite has also been observed (Hajisamae and Ibrahim, 2008; Horinouchi et al., 2012; Kellnreitner et al., 2012). The discrepancy among these studies may be partially attributed to the size of the system. For example, larger systems like Chesapeake Bay exhibit greater inherent variability due to patchiness of prey, predators, and habitats as well as the migrations of interacting species; this heterogeneity may dampen any seasonal signal in food habits. Habitat heterogeneity beyond the benthic-pelagic gradient (e.g., seagrasses, structured reefs, depth, and salinity) can also strongly influence prey availability, foraging success, and realized diets (Orth et al., 1984; Nemerson and Able, 2004; Marancik and Hare, 2007; Colloca et al., 2010). The majority of the Chesapeake Bay mainstem can be classified as muddy or sandy bottom (Diaz and Schaffner, 1990); therefore the majority of structural diversity in the trawlable habitats sampled can be attributed to the various invertebrate organisms (e.g., tunicates, hydrozoans, bryozoans, bivalves, and Porifera), which can also alter feeding.

Natural and anthropogenic perturbations to aquatic food webs can contribute to inter-annual and longterm variability in fish diets (e.g., Link et al., 2002; Jin et al., 2010; Palsson and Bjornsson, 2011). Anthropogenic stressors of major concern in Chesapeake Bay include eutrophication (increased phytoplankton, decreased water clarity, hypoxia, reduction in benthic primary productivity, SAV declines), land use (urbanization, loss of wetlands, shoreline modifications), fishing (collapse of several species, modified predation pressure), and climate change (increasing temperatures, water acidity, precipitation, storm intensity) (Kemp et al., 2005b; Najjar et al., 2010). These anthropogenic stressors act in combination with natural processes and variability to regulate recruitment, mortality, and interaction strengths of the many species occupying

the system. Consequently, the trophic structure described for Chesapeake Bay is the current, decadal realization of a dynamic system that may differ from previous or future ecosystem states (Griffin and Margraf, 2003; Hartman and Margraf, 2003; Kemp et al., 2005b; Najjar et al., 2010).

The large sample sizes and broad spatiotemporal coverage underlying this study integrate various sources of variability to provide robust and general dietary characterizations for a relatively large fraction of the Chesapeake Bay fish fauna. Our study examined 18% of the 267 Chesapeake Bay fishes described by Murdy et al. (1997), but the proportion would be larger (~25-35%) if rare and transient species to the mainstem are excluded. With the principal exceptions of Atlantic menhaden and bay anchovy, the majority of biomass-dominant Chesapeake Bay fishes commonly found in the bay's mainstem were represented in this dataset (Jung and Houde, 2003; Buchheister et al., 2013). Although sample sizes were relatively low for more pelagic species (e.g. bluefish, alosines) and structure-oriented species (e.g. Atlantic spadefish, Sheepshead, Tautog), the results were comparable and representative of expectations from previous diet studies (Murdy et al., 1997; Marancik and Hare, 2007; Able and Fahay, 2010). Despite the influence of a myriad of hierarchical factors regulating fish foraging, these factors are largely subordinate to two paramount variables: species and body size (Gerking, 1994; Scharf et al., 2000; Kerr and Dickie, 2001; Bundy et al., 2011; Reecht et al., 2013). Segregating the assemblage into species accounted for the unique combination of functional morphologies and foraging behaviors that each fish has evolved, while body size accounted for intra-species, size-mediated changes that help regulate the prey types and prey sizes that are vulnerable to predation. The population-

level estimates of diets are generated at relevant scales for multispecies and ecosystem modeling efforts (e.g., Christensen et al., 2009; Garrison et al., 2010), but extrapolation of the detailed predator diet estimates to other ecosystems should be made cautiously, given the influence of habitat and prey availability on foraging outcomes, as indicated by dietary differences between conspecifics in estuaries and coastal waters (e.g., Link et al., 2002; Marancik and Hare, 2007). However, the trophic guild designations and relative species differences are more robust as they are indicative of the general prey types, prey sizes, and benthic-pelagic habitats that constrain each species' successful foraging.

Utility and application to ecosystem based fisheries management

The most direct application of trophic studies to EBFM is through the parameterization of ecosystem models and development of ecosystem indicators. Diet data are necessary for establishing the magnitude of the linkages within ecosystem models such as Ecopath with Ecosim (Pauly et al., 2000), ATLANTIS (Fulton et al., 2011), and others. Although model outputs may be more sensitive to biomass and production inputs than to diet inputs (Essington, 2007), models undoubtedly benefit from using reliable and robust dietary information. Ecosystem indicators are needed in EBFM implementation to determine management actions, and several indicators rely on trophic structure (Rice, 2003; Link, 2005). For example, trophic guild biomasses (of planktivores and benthivores) were identified as two of the best indicators of ecosystem status in the northwest Atlantic Ocean (Methratta and Link, 2006). Ratios of trophic guild biomasses (e.g. piscivorous:zooplanktivorous fishes) have also been shown to vary in response to ecosystem changes and fishing pressure (de Leiva Moreno et al., 2000;

Cury et al., 2005). Mean trophic level, which can be estimated from diet information, has also been used as an ecosystem indicator (e.g., Pauly et al., 1998), though other related indices may be more appropriate or useful (Jennings, 2005).

This study provides and synthesizes detailed dietary information gathered over 10 years by the ChesMMAP trawl survey for many of the dominant Chesapeake Bay fishes. To continue advancing ecosystem modeling efforts and development of ecosystem indicators in Chesapeake Bay and northwest Atlantic waters, the detailed trophic interactions data used for this study are available to researchers, modelers, and managers through two primary mechanisms: the supplemental material of this paper (Appendix A), and an online data interface. Customizable dietary summaries by predator species, year, age, state, and prey species are accessible online at www.vims.edu/fisheries/fishfood. Similar diet summaries are also available for ChesMMAP's sister survey, the Northeast Area Monitoring and Assessment Program (NEAMAP), which samples nearshore coastal waters (6.1-36.6 m) from NC to MA. Accessibility to these datasets (and other data collected by the surveys) is intended to advance research on estuarine and marine trophic dynamics and to improve single species, multispecies, and ecosystem management by state and federal agencies.

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TABLE CAPTIONS

Table 1. Prey groups used for the diet analysis, organized by the broad categories that are used to summarize results.

Table 2. Size classes, sample sizes (number of non-empty stomachs [No. Stom.] and stations [No. Stat.]), and abbreviations for the 47 fish species included in the current study. The six biomass dominant species from the trawl survey (79% of total catch) are in bold. Sizes were measured as fork length for teleosts, pre-caudal length for sharks, and disc width for batoids.

Table 3. Prey species contributions (%) to the average percent similarity within each of the 10 trophic guilds, based on the similarity percentage routine (SIMPER) results. Contributions <5% are indicated with dashes. See Figure 2 for trophic guild definitions.

Table 4. Results of one-way and two-way analysis of similarity (ANOSIM) tests for species, size class, and month differences in the diets of the six most sampled fishes. The global test statistic (R) and significance level for Factor 1 are presented after accounting for effects of Factor 2. One-way ANOSIM results are indicated with "--" for Factor 2, and significant results are in bold.

FIGURE CAPTIONS

Figure 1. Chesapeake Bay sampling locations for a typical month (filled circles, n=80) and year (all circles, n=398) for the Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAP) trawl survey. Major western tributaries are labeled, and horizontal lines delineate the five regional strata.

Figure 2. Dietary relationships and dietary composition for species and size classes of fishes in Chesapeake Bay. Fishes are identified by a four letter abbreviation (see Table 2) followed by the size class (S-small, M-medium, L-large). Predators were grouped into ten significant trophic guilds at a dissimilarity of 0.69 (vertical red line), based on a bootstrap randomization test ($\alpha=0.05$). Trophic guilds were aggregated into five broader categories (PISC – piscivores, ZOOP – zooplanktivores, BENT – benthivores, CRUS – crustaceivores, MISC – miscellaneous consumers). Within each broad trophic category, significant guilds are indicated with letters (a,b), a horizontal red line, and vertical black lines (to the right). Gravimetric dietary compositions (%W) for the predator groups are summarized by broad prey categories (legend), with prey organized along a benthic to pelagic gradient.

Figure 3. Contribution of broad prey categories to the diets of predators within each of 10 trophic guilds (a-j) as labeled in Fig. 2. Boxes denote the interquartile range with the

median indicated. Whiskers extend to the most extreme value that is no further than 1.5x the interquartile range from the box. Outliers are marked as circles.

Figure 4. Non-metric multi-dimensional scaling ordination plot of diets for all predator groups with habitat and prey size gradients denoted along axes. A) Data are coded by trophic guilds with colors denoting broad category and shapes indicating sub-guild as shown in the legend. B) NMDS plot of predator diets differentiating species with multiple size classes (color and symbol scheme identical to A) from species without multiple size classes (small open circles). Species with more drastic ontogenetic diet shifts had size classes designated into different trophic guilds (filled symbols) whereas other species did not (open colored symbols). Arrows join the multiple size classes of each species sequentially, leading to the largest size class that is labeled with the species code from Table 2.

Figure 5. Summary of key prey groups in Chesapeake Bay fish diets. A) Frequency of predator groups (species-size-class combinations) whose diets consist of at least 20% of a given prey group. Prey groups were restricted to those with a value greater than 2. B) Percentage of all 71 predator groups that consumed each of the prey groups.

Figure 6. Non-metric multi-dimensional scaling ordination plot of diets for the six most sampled species. Species are coded by color, and size classes are indicated by shape (see legend). Multiple, identical symbols denote different months. Ellipses and labels designate trophic guild classification based on the predator and size class. March and

May diets with high contributions of crangonid shrimp (12-56%) are demarked with the dashed polygon.

Table 1.

Broad category name	Scientific name	Common Name	
Bivalvia	Bivalvia	Bivalves	
Copepoda	Copepoda	Copepods	
Crustacea ¹	Amphipoda	Unclassified amphipod	
	Anomura	Anomuran crabs	
	Brachyura	True crabs	
	Cancridae	Cancer crabs	
	Caridea	Caridean shrimp	
	Cirripedia	Barnacles	
	Corophiida	Corophiidan amphipods	
	Crangonidae	Crangonid shrimp	
	Crustacea	Unclassified crustacean	
	Cumacea	Hooded shrimps	
	Decapoda - crab	Decapod crabs	
	Decapoda - shrimp	Decapod shrimps	
	Dendrobranchiata	prawns	
	Gammaridea	Gammaridean amphipods	
	Isopoda	Isopods	
	Paguridae	Pagurid hermit crabs	
	Panopeidae	Mud crabs	
	Panaeidae	Panaeid shrimp	
	Portunidae	Portunid crabs	
	Squillidae	Mantis shrimps	
	Tanaidacea	Tanaids	
	Thalassinidea	Ghost shrimps	
	Gastropoda	Gastropoda	Snails
Miscellaneous	Anthozoa	Corals and anemones	
	Ascidacea	Sea squirts	
	Branchiostomidae	Lancelets	
	Bryozoa	Moss animals	
	Cephalopoda	Cephalopods	
	Ctenophora	Comb jellies	
	Echinodermata	Echinoderms	
	Hydrozoa	Hydroids	
	Insecta	Insects	
	Miscellaneous	Miscellaneous or inorganic item	
	Miscellaneous zooplankton	Miscellaneous zooplankton	
	Plant matter	Plant matter	
	Unidentified or other mollusca	Unidentified or other mollusca	
	Mysida	Mysida (mostly <i>Neomysis americana</i>)	Mysid shrimp
	Polychaeta	Polychaeta	Polychaete worms
		Other annelida	Other worms
	Scyphozoa	Scyphozoa	True jellyfish
Teleostei-demersal	<i>Cynoscion regalis</i>	Weakfish	
	<i>Leiostomus xanthurus</i>	Spot	
	<i>Micropogonias undulatus</i>	Atlantic croaker	
	Moronidae	Temperate basses	
	Other Sciaenidae	Other drum	
	Other Teleostei and Elasmobranchii	Other fishes	
	Phycidae	Phycid hakes	
	Pleuronectiformes	Flatfish	
	Sparidae	Porgies	
	Syngnathidae	Seahorses and pipefishes	
	Triglidae	Sea robins	
	Teleostei-pelagic	<i>Brevoortia tyrannus</i>	Menhaden
		Engraulidae (mostly <i>Anchoa mitchilli</i>)	Anchovies
		Other Clupeidae	Herrings
		Pomatomidae	Bluefishes
	Teleostei-unidentified	Unidentified teleostei	Unidentified fish
Unidentified	Unidentified material	Unidentified material	

¹Excluding Copepoda and Mysida

Table 2.

Latin name	Common name	Abbrev.	No. Stom.	No. Stat.	Size classes (mm)		
					Small	Med	Large
<i>Alosa aestivalis</i>	blueback herring	Aaes	73	35	—	75-274	—
<i>Alosa mediocris</i>	hickory shad	Amed	29	28	—	75-374	—
<i>Alosa pseudoharengus</i>	alewife	Apse	360	162	—	50-299	—
<i>Alosa sapidissima</i>	American shad	Asap	53	35	—	100-499	—
<i>Ameiurus catus</i>	white catfish	Acat	28	16	—	175-624	—
<i>Archosargus probatocephalus</i>	sheepshead	Apro	84	51	—	—	425-649
<i>Bairdiella chrysoura</i>	silver perch	Bchr	217	114	—	75-224	—
<i>Carcharhinus plumbeus</i>	sandbar shark	Cplu	26	22	—	375-874	—
<i>Centropristis striata</i>	black sea bass	Cstr	225	141	—	50-274	—
<i>Chaetodipterus faber</i>	Atlantic spadefish	Cfab	250	136	25-124	125-549	—
<i>Chilomycterus schoepfii</i>	striped burrfish	Csch	150	117	—	75-299	—
<i>Cynoscion regalis</i>	weakfish	Creg	5060	1301	25-99	100-324	325-624
<i>Dasyatis americana</i>	southern stingray	Dame	108	71	200-349	350-924	—
<i>Dasyatis sabina</i>	Atlantic stingray	Dsab	52	41	150-349	350-599	—
<i>Dasyatis say</i>	bluntnose stingray	Dsay	246	152	175-399	400-774	—
<i>Gymnura altavela</i>	spiny butterfly ray	Galt	57	39	—	375-2124	—
<i>Gymnura micrura</i>	smooth butterfly ray	Gmic	38	31	—	350-874	—
<i>Ictalurus punctatus</i>	channel catfish	Ipun	103	50	200-449	450-549	—
<i>Larimus fasciatus</i>	banded drum	Lfas	58	31	—	25-224	—
<i>Leiostomus xanthurus</i>	spot	Lxan	1597	645	—	50-199	200-249
<i>Menticirrhus spp.</i>	kingfishes	Ment	893	417	25-199	200-399	—
Micropogonias undulatus	Atlantic croaker	Mund	2949	1095	25-149	150-349	350-499
<i>Morone americana</i>	white perch	Mame	1853	560	75-149	150-374	—
<i>Morone saxatilis</i>	striped bass	Msax	2639	970	25-199	200-599	600-1074
<i>Mustelus canis</i>	smooth dogfish	Mcan	301	155	—	300-649	650-1224
<i>Myliobatis freminvillii</i>	bullnose ray	Mfre	138	86	225-549	550-1330	—
<i>Opsanus tau</i>	oyster toadfish	Otau	96	74	—	25-424	—
<i>Orthopristis chrysoptera</i>	pigfish	Ochr	55	31	—	75-224	—
<i>Paralichthys dentatus</i>	summer flounder	Pden	2867	1695	125-249	250-374	375-724
<i>Pepnilus paru</i>	harvestfish	Ppar	123	67	—	25-199	—
<i>Pepnilus triacanthus</i>	butterfish	Ptri	90	38	—	25-224	—
<i>Pogonias cromis</i>	black drum	Pcro	64	45	150-299	—	—
<i>Pomatomus saltatrix</i>	bluefish	Psal	244	149	100-274	275-549	—
<i>Prionotus carolinus</i>	northern searobin	Pcar	764	338	—	25-224	—
<i>Prionotus evolans</i>	striped searobin	Pevo	194	147	25-149	150-274	—
<i>Raja eglanteria</i>	clearnose skate	Regl	826	387	75-374	375-524	—
<i>Rhinoptera bonasus</i>	cownose ray	Rbon	82	61	—	225-599	600-1024
<i>Scophthalmus aquosus</i>	windowpane	Saqu	300	204	50-174	175-349	—
<i>Selene setapinnis</i>	Atlantic moonfish	Sset	70	38	—	25-174	—
<i>Selene vomer</i>	lookdown	Svom	33	23	—	50-149	—
<i>Sphoeroides maculatus</i>	northern puffer	Smac	995	384	—	25-274	—
<i>Squalus acanthias</i>	spiny dogfish	Saca	70	30	—	600-949	—
<i>Stenotomus chrysops</i>	scup	Schr	733	314	—	50-224	—
<i>Synodus foetens</i>	inshore lizardfish	Sfoe	25	21	—	100-324	—
<i>Tautoga onitis</i>	tautog	Toni	40	19	—	225-599	—
<i>Trinectes maculatus</i>	hogchoker	Tmac	178	124	—	75-199	—
<i>Urophycis regia</i>	spotted hake	Ureg	516	255	50-149	150-324	—
<i>Total</i>			25952	10945			

Table 3.

Prey Category	Prey Group	PISC		ZOOB		BENT		CRUS		MISC	
		a	b	a	b	a	b	a	b	a	b
Bivalvia	Bivalvia	--	--	--	--	10.9	60.2	18.6	--	--	--
Copepoda	Copepoda	--	--	--	40.0	--	--	--	--	--	--
Crustacea	Corophiida	--	--	--	--	--	--	--	5.2	--	--
	Crangonidae	--	--	6.2	--	--	--	--	--	--	--
	Decapoda - crab	--	--	--	--	--	6.2	5.5	9.9	--	--
	Paguridae	--	--	--	--	--	--	--	--	8.6	--
	Panopeidae	--	--	--	--	--	--	--	32.4	--	--
	Portunidae	--	--	--	--	--	--	14.5	--	--	--
Teleostei-demersal	Squillidae	--	--	--	--	--	--	25.3	--	--	--
	<i>Cynoscion regalis</i>	--	6.1	--	--	--	--	--	--	--	--
Teleostei-pelagic	<i>Leiostomus xanthurus</i>	--	10.0	--	--	--	--	--	--	--	--
	<i>Brevoortia tyrannus</i>	61.1	--	--	--	--	--	--	--	--	--
Teleostei-unidentified	Engraulidae	--	37.6	--	--	--	--	--	--	--	--
	Unidentified teleostei	18.5	14.0	--	--	--	--	6.6	12.5	--	--
Scyphozoa	Scyphozoa	--	--	--	--	--	--	--	--	--	88.1
Miscellaneous	Unidentified or other Mollusca	--	--	--	--	--	7.6	--	--	--	--
Mysida	Mysida	--	14.7	79.6	21.0	--	--	--	--	--	--
Gastropoda	Gastropoda	--	--	--	--	--	--	--	--	81.8	--
Unidentified	Unidentified material	--	--	--	30.4	28.4	7.9	--	12.5	--	11.3
Polychaeta	Polychaeta	--	--	--	--	41.3	--	--	--	--	--
<i>Average within guild similarity</i>		50.0	41.2	61.0	58.8	46.0	47.9	38.2	39.6	73.2	87.6

Table 4.

Factor 1	Factor 2	R	Sig. level (%)
Species	--	0.57	0.1
Species	Size Class	0.694	0.1
Species	Month	0.546	0.1
Size Class	--	0.2	0.1
Size Class	Species	0.454	0.1
Size Class	Month	0.125	5.8
Month	--	0.026	20.5
Month	Species	0.012	45.6
Month	Size Class	-0.053	79.2

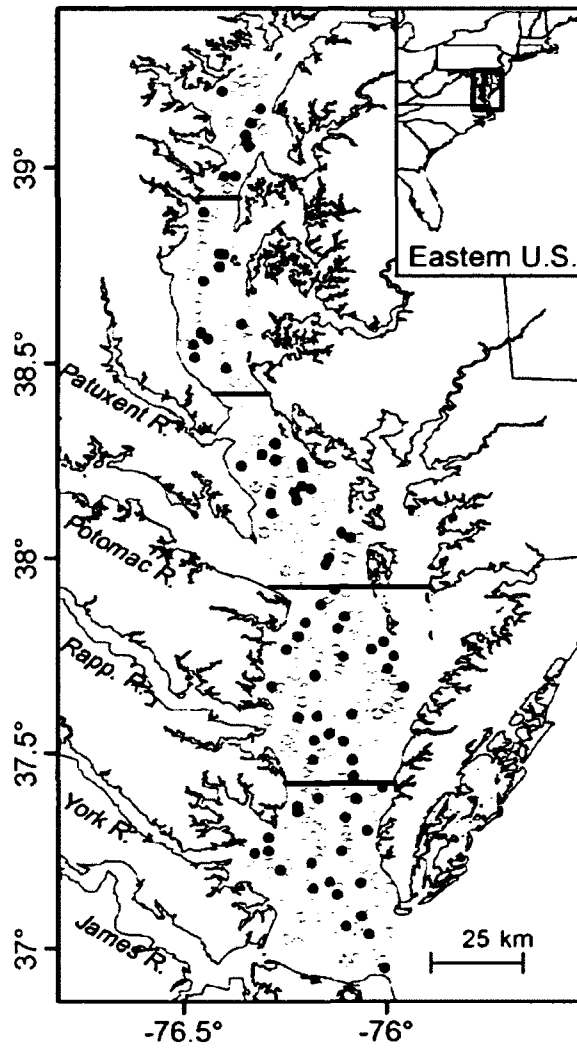


Figure 1.

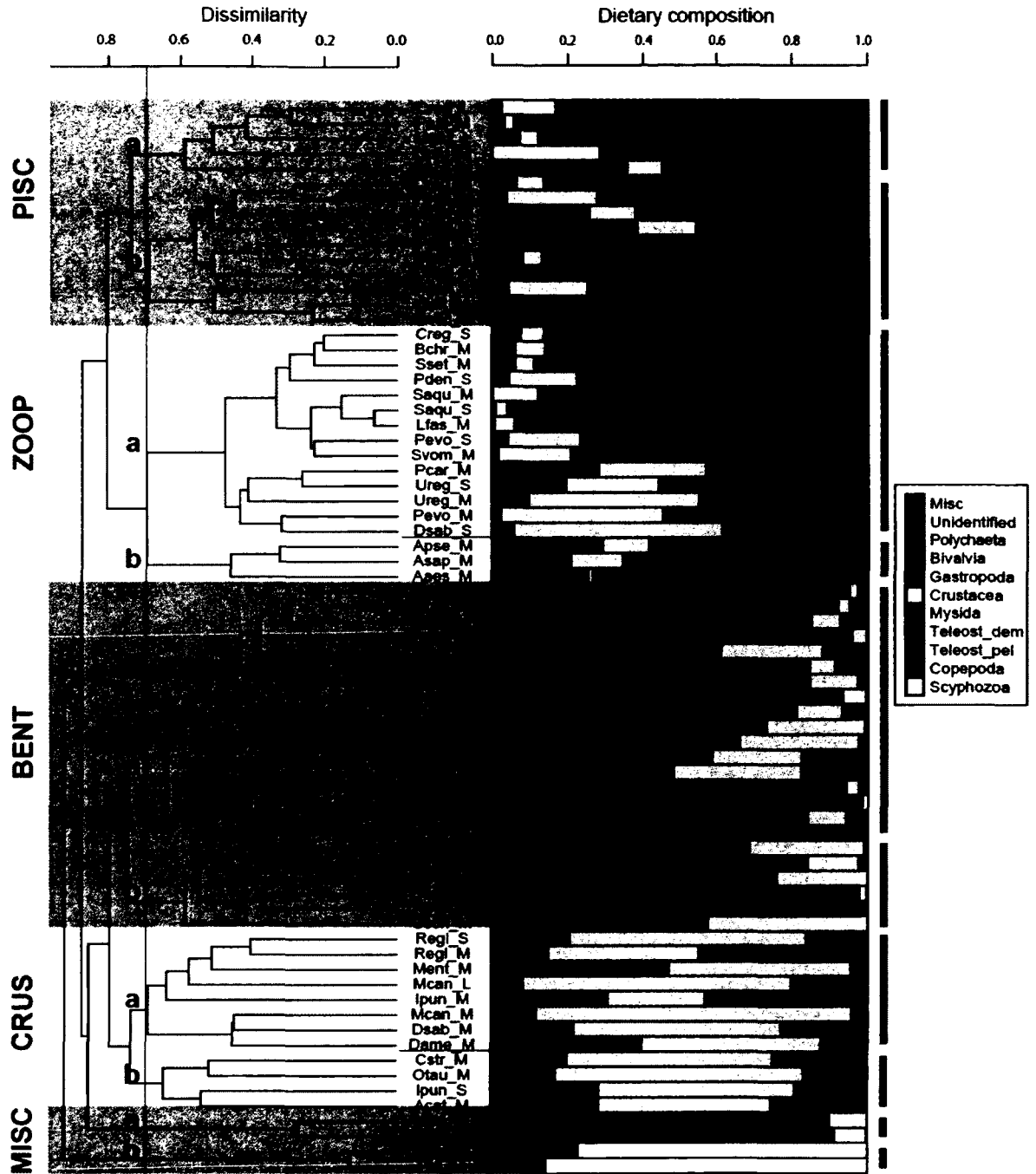


Figure 2.

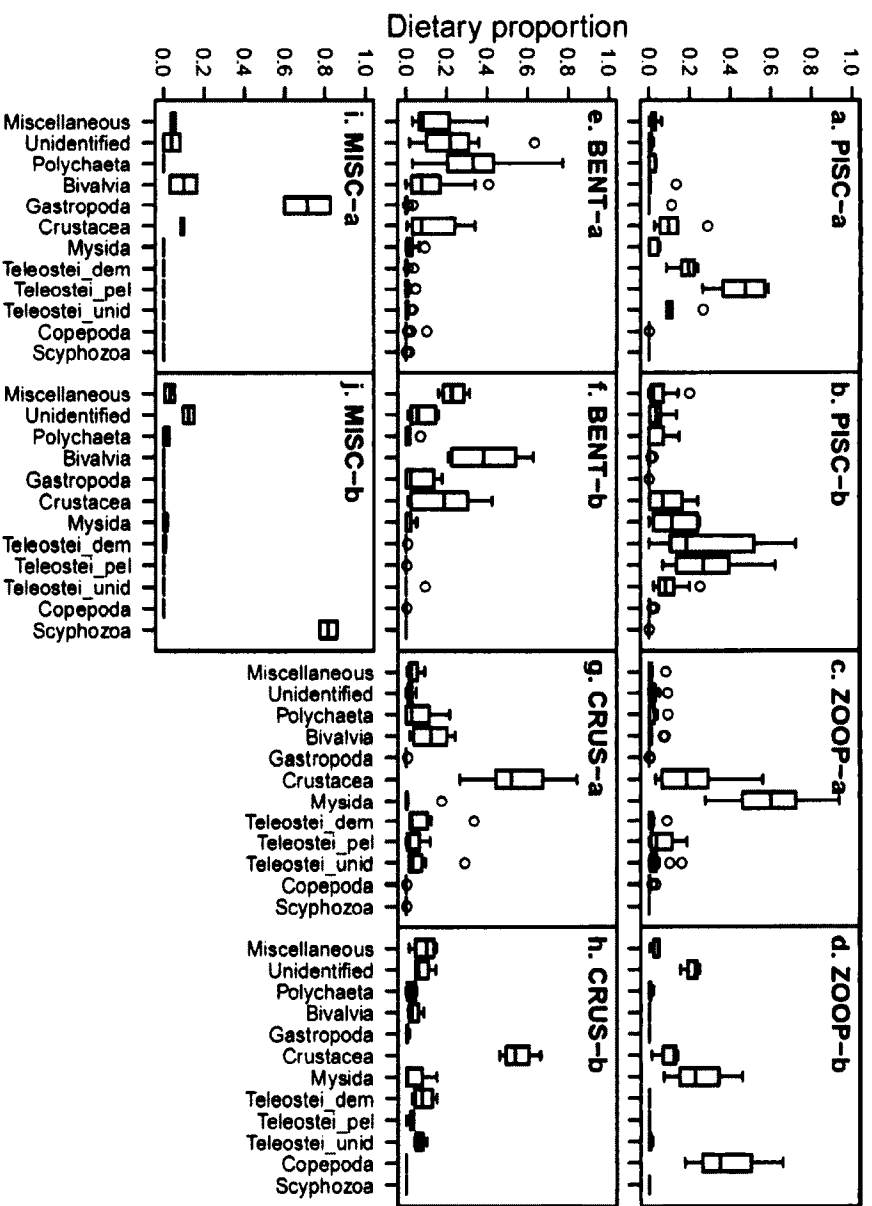


Figure 3.

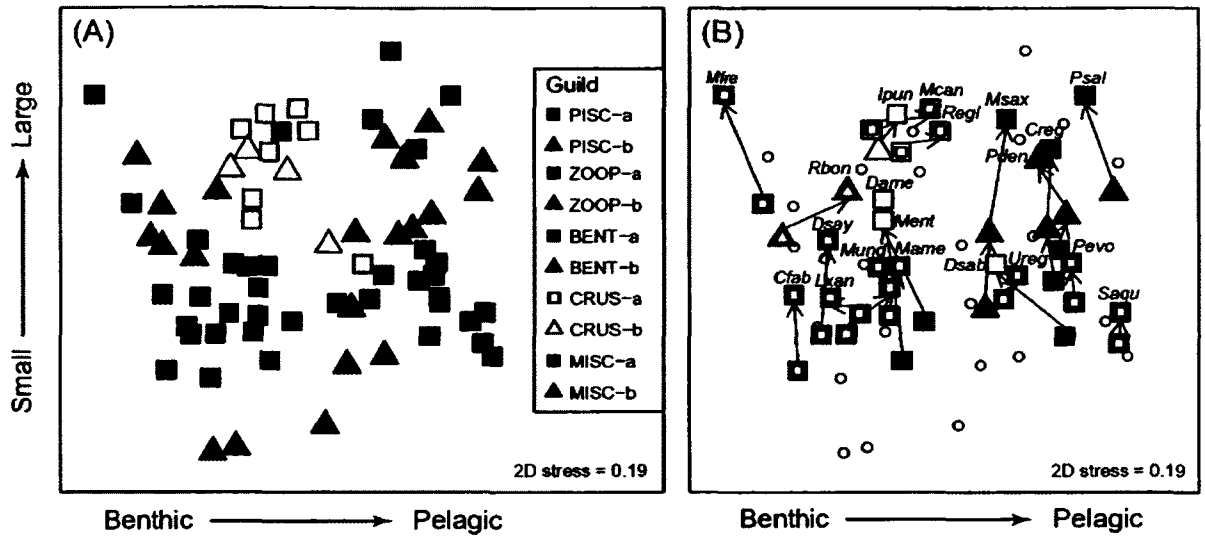


Figure 4.

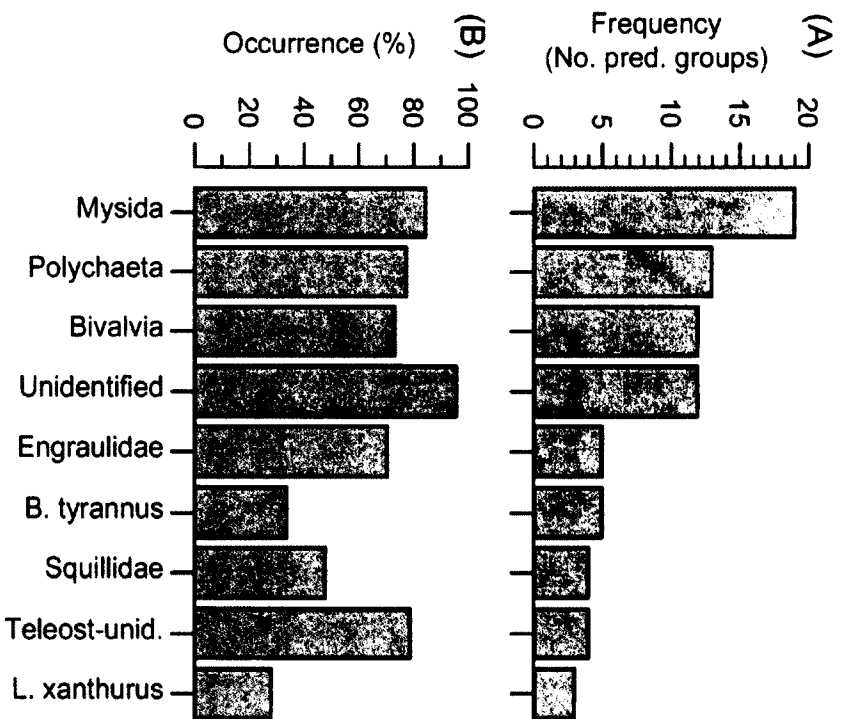


Figure 5.

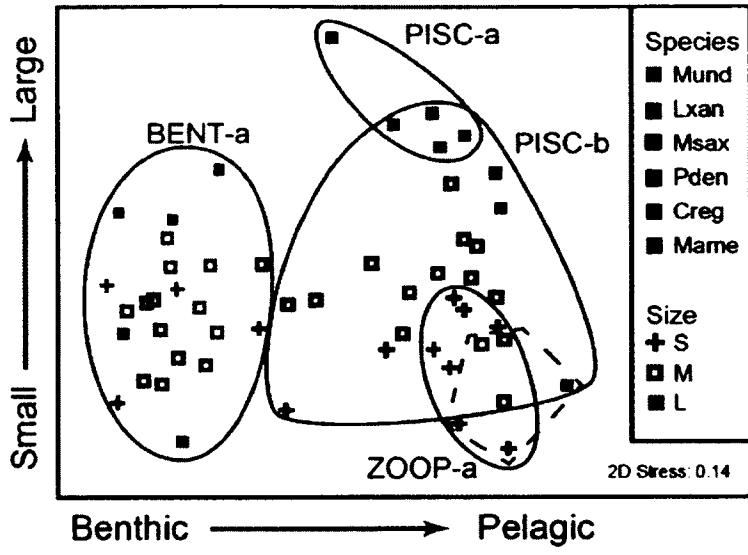


Figure 6.

CHAPTER 3

DYNAMIC TROPHIC LINKAGES IN A LARGE ESTUARINE SYSTEM – SUPPORT FOR SUPPLY-DRIVEN DIETARY CHANGES USING DELTA GENERALIZED ADDITIVE MIXED MODELS

ABSTRACT

Trophic dynamics within aquatic systems are a predominant regulator and modifier of fisheries production, and thus research on food web linkages is an integral component to ecosystem-based fisheries management (EBFM). A diet composition database from a 10-year, multi-seasonal bottom trawl survey conducted in the largest estuary in the United States, Chesapeake Bay, was used to 1) evaluate the effects of various biological and environmental variables on trophic interactions of 12 common predatory fishes, 2) infer dynamics of four key prey groups (bay anchovy, mysids, bivalves, and polychaetes), and 3) evaluate whether interannual dietary trends are regulated by prey availability. The underlying assumption was that commonalities in dietary trends across predators would be driven by bottom-up effects, specifically changes in prey availability. Two-part, delta generalized additive mixed models (GAMM) were used to achieve the research objectives while accounting for various statistical issues commonly encountered with stomach content data. The most consistently important covariate in the models was predator length, and its effect on prey occurrences exhibited either linear or parabolic (dome-shaped) forms depending on the prey. When significant, the effects of latitude, temperature, and depth were largely similar across predators for a given prey, suggestive of prey availability driving consumptive patterns. Annual patterns of mysid, bivalve, and bay anchovy consumption each showed a single, dramatic peak shared by a majority of predators, despite predators having varied feeding preferences and distributional characteristics. The coherence of annual consumption trends was consistent with supply-driven dynamics, where annual pulses in prey availability yielded greater consumption. However, interannual trends were not significantly correlated with available survey-based measures of prey availability, likely due to various factors including survey sampling bias, discrepancies in the macrobenthic species sampled, and scale-related differences. When taken together, the results highlight the overall variability in predator-prey linkages, the utility of using multiple predators to infer prey dynamics, and the role of interannual changes in prey availability in regulating consumptive changes of a broad suite of estuarine fishes.

INTRODUCTION

Trophic dynamics have been described as one of the three principal drivers of fisheries production, in addition to environmental and exploitative drivers (Link, 2010a; Gaichas et al., 2012). Trophic dynamics control not only the direct consequences of predation (e.g., mortality, survival, growth, changes in population biomass, and modified size structure) but also a myriad of indirect ecological effects (e.g., changes in behavior, distribution, habitat utilization, foraging, and competition), all of which are critical to governing the structure and function of aquatic food webs (Brooks and Dodson, 1965; Werner and Hall, 1977; Carpenter et al., 1985; Northcote, 1988; Whipple et al., 2000; Tyrrell et al., 2011). Consequently, understanding the factors regulating predator-prey interactions is an important consideration in applying a more holistic, ecosystem-based approach to managing fisheries resources (Larkin, 1996; Link, 2002a; Latour et al., 2003). One of the challenges to advancing knowledge on predator-prey interactions is to continue moving beyond basic diet descriptions by evaluating the factors regulating the dynamics of food web linkages, including how environmental conditions and prey availability alter foraging patterns in dynamic, open systems (Link, 2002a; Hunsicker et al., 2011).

One basic prediction from foraging theory is that prey consumption rate for an unsatiated predator generally increases with the prey's density, and thus predator diets can be used as indicators of prey availability. Density-dependent feeding is a foundational and well-tested principle within ecology (Holling, 1959; Jeschke et al., 2002), and such

supply-driven consumptive changes are also favored by the relatively opportunistic feeding strategies of most fishes (Dill, 1983; Gerking, 1994). Indeed, functional responses are typically a central component in many multispecies and ecosystem models, used to estimate per capita consumption rates based on prey density (e.g., Hollander et al. 2000, Garrison et al. 2010). These relationships and their functional forms can be modified by a variety of factors, including predator satiation (Holling, 1959; Dill, 1983), predator-dependent effects (Abrams and Ginzburg, 2000; Essington and Hansson, 2004), prey selectivity (Eggers, 1977; Juanes, 1994), and prey switching among alternative prey (Murdoch, 1969; Koen-Alonso, 2007). However, the premise of greater consumption with an increase in a prey's density (prior to satiation) generally holds fast at a broad, fundamental level, particularly when foraging is strongly regulated by encounter rates (Breck, 1993; Juanes, 1994). Consequently, fish diets have been successfully used to: estimate prey distributions (Fahrig et al., 1993; Link, 2004), derive annual indices of relative prey abundance (Link, 2004; Mills et al., 2007), evaluate prey demographics and length-weight relationships (Rachlin et al., 1997), determine benthic community composition (Frid and Hall, 1999; Dell et al., 2013), assess spatiotemporal trends in biodiversity (Cook and Bundy, 2012; Staudinger et al., 2012), and corroborate long term changes in prey availability (Dwyer et al., 2010; Jin et al., 2010; Pálsson and Björnsson, 2011).

Fish may act as environmental samplers. But, much like traditional fish survey gears, they can introduce sampling biases in what they capture, most notably due to differences in selectivity and efficiency (Eggers, 1977; Juanes, 1994). Approaches for addressing statistical challenges in the analysis of survey data are more advanced and

more available than they are for stomach contents data. Two approaches are often used to deal with sampling concerns in fishery-independent surveys used in stock assessments. First, indices of relative abundance can be standardized using statistical models that partition and account for the effects of variation associated with different environmental covariates (Maunder and Punt, 2004; Kimura and Somerton, 2006) and secondly, multiple gear types with different sampling properties can be used synoptically to derive more robust estimates of a desired response variable. Extension of this reasoning to trophic studies suggests that indices of prey consumption would be more representative of prey availability once standardized for heterogeneous environmental conditions that introduce variability into predator-prey interactions, and also that synchronous patterns across multiple predators would strengthen the robustness of conclusions for individual prey. An added benefit of this prey-centric analytical approach is that when limited biological data exist for the prey, the effects of modeled covariates can be used to draw inference on prey distribution, availability, and dynamics.

In order to statistically model stomach content data, whether by univariate or multivariate approaches, three major data complications must be addressed. First, diet data often suffer from an overabundance of zero values that does not conform to standard statistical distributions. Approaches to deal with excessive zeros in diet data include applying transformations (e.g., proportions, $\log(x+1)$, arc sin, presence/absence; Hyslop 1980, Cortes 1997), relying on non-parametric statistical models (Cortes, 1997; Jaworski and Ragnarsson, 2006), fitting zero-inflated models (also known as mixture models; Zuur et al. 2009, Santos et al. 2013), and using delta models (also known as two-part, hurdle, or zero-altered models; Stefánsson & Pálsson 1997, Zuur et al. 2009). A second

statistical complication with stomach contents data is the violation of the independence assumption that often occurs when multiple individuals are captured at the same location (e.g., in the same trawl haul) or when individuals are sampled repeatedly through time (e.g., in experimental studies), but are treated as independent samples in the analyses. Hierarchical or longitudinal sampling designs such as these can yield fish with correlated diets because they are auto-correlated in time and space rather than because they are responding to the same external drivers independently (Hurlbert, 1984; Bogstad et al., 1995b; Millar and Anderson, 2004). Solutions for this problem include using cluster sampling estimators to calculate diet indices (e.g., Buckel et al., 1999), modeling spatial or temporal autocorrelation with repeated measures ANOVA (Chipps and Garvey, 2007), or using mixed models that are more flexible at modeling compound error structures (Millar and Anderson, 2004; Michalsen et al., 2008). A third statistical complication is that the effects of covariates (e.g., temperature, predator size) on diets are often non-linear. Solutions here include data transformations and use of discrete factor levels in place of continuous data, but more recently, additive modeling approaches that rely on non-parametric smoothers have become more common (Stefánsson and Pálsson, 1997; Adlerstein, 2002; Trenkel et al., 2005). Despite the many statistical approaches to analyzing patterns in fish diet data and dealing with the issues identified, to our knowledge the efficacy of applying delta generalized additive mixed models (GAMM) to diet data has not been assessed.

Here we apply delta-GAMMs to evaluate the dynamic trophic interactions among several dominant fishes and key prey groups in a large estuarine system. Chesapeake Bay is the largest nursery and estuarine foraging ground in the northwest Atlantic Ocean,

and it contributes greatly to the production of many important commercial and recreational fisheries (Kohlenstein, 1981; Murdy et al., 1997; Able and Fahay, 2010). Previous work highlighted the broad importance of four key prey groups (mysids, bay anchovy, bivalves, and polychaetes) in supporting the bay's diverse fish assemblage (Chapter 2), but there is limited information on the basic biological characteristics of some of these prey groups, particularly mysids, at larger spatiotemporal scales in estuaries. Also, researchers and managers are interested in understanding how environmental conditions and prey availability regulate the dynamic predator-prey interactions at both small and large scales (Hartman and Margraf, 2003; Latour et al., 2003; Lipcius and Latour, 2006; Christensen et al., 2009). This work used data from an extensive, multi-seasonal bottom trawl and diet composition survey of Chesapeake Bay fishes to address three objectives: 1) evaluate the influence of predator length, spatiotemporal factors, and environmental drivers on prey consumption by 12 common Chesapeake Bay predators, 2) compare patterns across predators to infer dynamics of four key prey groups, and 3) evaluate whether interannual consumption trends were coherent among predators and regulated by prey availability. In addition to representing general estuarine food web dynamics, these detailed analyses support ongoing efforts in ecosystem modeling and EBFM within Chesapeake Bay and along the continental shelf (Latour et al., 2003; Houde, 2006; Christensen et al., 2009; Link et al., 2011).

METHODS

Field and laboratory methods

Data were obtained from the Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAAP), operated by the Virginia Institute of Marine Science. Since 2002, this bottom trawl survey has sampled the Chesapeake Bay mainstem using a random-stratified design with stations stratified by depth and latitude (Fig. 1). Typically, five cruises were conducted per year (bimonthly from March to November), with approximately 80 stations sampled per cruise. Data on latitude, longitude, water depth, bottom temperature, salinity, and dissolved oxygen were collected at each station. Parameters on gear deployment were also recorded. After catches were sorted, species with broad length distributions or discrete length groups were further sorted into 2-4 size classes, random individual subsamples from the species-size-class groups were processed for weight and length (fork length for teleosts; disc width for batoids), and stomachs were removed for diet analysis. If stomachs were visually confirmed to be empty in the field, additional specimens (when available) were processed to obtain 3-5 nonempty stomachs per species and size class. In the laboratory, contents from preserved stomachs were sorted, identified to the lowest possible taxon using dissection microscopes, and prey categories weighed to the nearest 0.001 g. Additional survey and methodological details are provided by Buchheister et al. (2013) and in Chapter 2.

We focused on four prey groups for this study: 1) mysid shrimp (primarily *Neomysis americana*), 2) bay anchovy (*Anchoa mitchilli*, with very minor contribution of

Anchoa hepsetus), 3) bivalves (including *Ensis directus*, *Gemma gemma*, *Macoma spp.*, *Mercenaria mercenaria*, *Mya arenaria*, and *Tagelus plebeius*), and 4) polychaete worms (including families Capitellidae, Chaetopteridae, Glyceridae, Maldanidae, Nereidae, Pectinariidae, Terebellidae). These four prey groups were chosen because they represent relatively unique functional morphologies and are largely responsible for differentiating among fish trophic guilds within Chesapeake Bay (Chapter 2). The bivalve and polychaete groups were defined at a coarser taxonomic level to alleviate the disparity in the resolution of prey identifications and to bolster predator sample sizes. Predators for each of the four prey groups were restricted to species with >15% frequency occurrence and a minimum sample size of 140 stomachs that contained the prey group. These two criteria excluded predators that rarely consumed a given prey group and omitted predators with low sample sizes. These restrictions yielded a total of 12 predator species with a total of 29,350 analyzed stomachs (Table 1). Depending on the species, 9-42% of sampled fish stomachs were empty (27% overall). Each predator-prey combination was represented by at least 146 fish and up to 2,301 fish that contained the prey of interest. Summaries of general diet compositions (% weight) for the selected predators were calculated using a cluster sampling estimator by pooling across all available non-empty stomach data (see Chapter 2 for equations).

Statistical analysis

The consumption of prey by individual predators and its response to multiple covariates were modeled using a GAMM framework. The use of a generalized additive model (GAM) allows for the effect of covariates to take flexible, nonlinear forms that are

dictated by a smoothing function. GAMs rely on the assumptions of independent and identically distributed errors with constant variance. To account for the intra-station (i.e., intra-haul) correlation that stems from the nested nature of the sampling design, station was included as a random effect in the model (Wood, 2006; Zuur et al., 2009). Following Stefánsson and Pálsson (1997), a two-part, delta approach was used to deal with the high frequency of zero values. First, the presence-absence of a given prey in the stomachs of a predator was modeled (termed the “binomial” model henceforth), and second, the weight of prey consumed was modeled, provided that the prey occurred in the stomach (termed the “positive” model henceforth).

The binomial models estimated the probability that a stomach contains the prey of interest, relying on a logit link between the response and the explanatory variables. This was analogous to modeling the frequency of occurrence of a given prey. There was no differentiation among the various ecological and methodological processes that may have led to the lack of prey (e.g., the habitat was not suitable, mis-identification error, design error) or to “false zeros” as is done in zero-inflated models (Zuur et al., 2009). The first, binomial stage of the delta-GAMM was defined as:

$$\text{logit}(p_{ij}) = \log(p_{ij}/(1-p_{ij})) = \alpha + \beta(YR_i) + f_1(L_i) + f_2(LA_i) + f_3(T_i) + f_4(D_i) + b_j + \varepsilon_{ij}$$

(1)

where p_{ij} is the expected probability that fish i from station j contains the prey of interest, α is the overall intercept, β is a vector of parametric effects for the categorical year (YR) factor, and f_{1-4} are smooth functions for each covariate (Wood, 2006; Zuur et al., 2009). The continuous covariates included predator fork length (L) in mm, latitude (LA) in decimal degrees, water temperature (T) in °C, and water depth (D) in m. The b_j term is

the independent and identically distributed random station effect which is assumed to be normally distributed with mean of zero and variance of σ_h^2 , and ε_{ij} is the residual error for each fish and station that was assumed to have a binomial (more specifically, Bernoulli) distribution. Available data on longitude, salinity, dissolved oxygen, and month were not included in the model to avoid convergence issues resulting from overly complex models and to avoid slight collinearity among some variables. Models with interactions among variables (including variable coefficient GAMM; Wood 2006) were not formally evaluated because 1) graphical analyses did not indicate the presence of strong interactions (Zuur et al., 2010), 2) they would decrease sample sizes and precision of covariate effects, and 3) they could prohibit model convergence based on preliminary analyses.

The second, positive component of the delta-GAMM excludes all zeros and models the quantity of prey consumed, relying on an appropriate data distribution. We chose to model the biomass of prey consumed because this measure is more meaningful than prey counts in dictating the transfer of energy through food webs (e.g., Pauly et al. 2000). We did not back-calculate the fresh weights of consumed prey, but instead assume that the modeled covariate effects on the measured weights would be representative of the processes regulating consumption of fresh prey. As a continuous variable, prey biomass can be modeled using a gamma distribution (Stefánsson and Pálsson, 1997); however this distribution resulted in convergence issues for many predator-prey combinations in the GAMMs. Instead, we used a log-transformation of the biomass data in conjunction with a Gaussian distribution to alleviate the convergence issues and to homogenize the originally heteroscedastic residuals. The model for the

second stage of the delta-GAMM, restricted to fish stomachs that contained a given prey, was defined as:

$$\log(\mu_{ij}) = \alpha + \beta(YR_i) + f_1(L_i) + f_2(LA_i) + f_3(T_i) + f_4(D_i) + b_j + \varepsilon_{ij}$$

(2)

where μ_{ij} is the expected mass (in g) of a prey group in the stomach of fish i from station j , given the random effect b_j , and ε_{ij} is the residual error for each fish and station assumed to be normally distributed with a mean of zero and variance of σ_ε^2 (Wood, 2006; Zuur et al., 2009). Definitions for all remaining components of the model are identical to those for equation 1.

All GAMMs were fitted to data from each of the 22 predator-prey combinations (Table 1), and Akaike's Information Criterion (AIC) was used to select the optimal fixed effects structure (Burnham and Anderson, 2002). Models with all possible combinations of explanatory variables were evaluated, with the exception that YR was retained in all iterations to evaluate interannual consumption trends (objective 3). Partial effects plots for the best-fit models were used to demonstrate the effect of each covariate on the response after accounting for all other covariates in the model, and they were presented on the scale of the linear predictor (logit scale for binomial model results; log scale for positive model results). Goodness-of-fit measures (e.g., percent of deviance explained or R^2) are still being developed for mixed models (Nakagawa and Schielzeth, 2013) and there is no standard summary statistic for overall GAMM fit, so these measures were not estimated. However, as a general proxy for overall goodness of fit, a fixed-effects version of each model (without the random station effect) was fitted to estimate the percent of deviance explained by the model.

One consideration in modeling consumption of individual prey is that there can be indirect effects of one prey on the consumption of another, resulting from foraging selectivity by predators or ecological interactions among prey (Stefánsson and Pálsson, 1997). To evaluate the potential for interactions between prey groups, a Chi-square test was conducted on contingency tables of prey presence for each predator (Stefánsson and Pálsson, 1997). These tests were conducted separately for the predators that consumed each of the following prey pairs: 1) mysids and bay anchovy, and 2) bivalves and polychaetes. Interactions were most likely to occur for these two prey pairs given their consumption by different trophic guilds (Chapter 2). To coarsely account for ontogenetic changes in diets, each predator was divided into 1-3 size classes based on the classification scheme used in Chapter 2.

A combined index of prey consumption for year y (C_y) was obtained for each predator-prey combination by multiplying predictions for the binomial and positive components of the best-fit delta-GAMMs. The consumption index was calculated as $C_y = p_y * \mu_y$ where p_y is the expected probability that a predator from year y consumed a given prey, and μ_y is the expected mass of the prey in a predator's stomach in year y . Predictions were standardized for the other covariates by holding them at constant values ($L = 200$ mm; $LA = 38^\circ$; $D = 10$ m; $T = 20^\circ\text{C}$). All μ_y values were bias-corrected for back transformation from lognormal space (Sprugel, 1983). To evaluate the similarity in prey consumption patterns across predators and the influence of prey availability, Pearson correlations (R) were calculated among predator estimates of logged C_y and indices of prey abundance. Indices of annual biomass for polychaetes and bivalves were calculated as geometric means (mean of $\log(x+0.001)$, where x = biomass density in g m^{-2}) using

data from the Chesapeake Bay Benthic Monitoring Program for the randomly selected stations surveyed within the bay mainstem (Versar, Inc., www.baybenthos.versar.com). Bivalves from this dataset were restricted to the most common species found in predator stomachs (*Ensis directus*, *Gemma gemma*, *Macoma spp.*, *Mercenaria mercenaria*, *Mya arenaria*, and *Tagelus spp.*); however only *Macoma spp.* and *Gemma gemma* were regularly sampled (occurring in 49% and 13% of stations, respectively). Annual abundance indices for bay anchovy were obtained from the Virginia Institute of Marine Science Juvenile Fish and Blue Crab Trawl Survey (Tuckey and Fabrizio, 2012). Data on patterns of mysid annual abundance were not available from any existing Chesapeake Bay monitoring program. Significance of Pearson correlations were determined from critical R values based on Bonferroni-adjusted α values ($\alpha_{adjusted} = 0.05/n$, where n is the number of pairwise correlations for a given prey group). Spots were omitted from correlation analysis due to lack of sampling stomach content data from 2002-2007. To facilitate visual comparison of annual consumption and prey indices across predators, all C_y values and prey indices were standardized to range from 0-1. For example, standardized C_y values were calculated as $(C_y - C_{min}) / (C_{max} - C_{min})$, where C_{min} and C_{max} are the minimum and maximum values for C_y across the time series. As an indicator of broad-scale, indirect interactions among prey, the significance of Pearson correlations between consumption indices of prey pairs for each predator was also tested using Bonferroni-adjusted α values. All statistical analyses were conducted using R 3.0.1 (R Core Team 2013), with the `gamm4` package used to fit the delta-GAMMs (Wood, 2012).

RESULTS

The four prey groups of focus contributed substantially to predator diets, and their consumption by predators was well-modeled with GAMMs. Collectively, bay anchovy, mysids, bivalves, and polychaetes accounted for large fractions of the fish diets (13-64%), reinforcing the broad importance of these prey in the Chesapeake Bay food web (Fig. 2). Individual prey groups contributed as much as 41% to the overall diet of a predator, though these dietary contributions can be greater for specific predator size classes (Chapter 2).

Generalized additive mixed modeling

The best-fitting binomial and positive GAMMs included various combinations of the explanatory variables, ranging from all variables to none of the variables (except *YR*, which was forced; Table 2). Generally, the binomial models were more complex than the positive models; however, this may be partially attributed to lower samples sizes for positive models which may have restricted the ability to detect significant covariate effects. Proxies for the deviance explained by models varied among predator-prey combinations, ranging from 4.3-36.7% (mean 14.1%) for binomial models and 5.4-49.3% (mean 19.6%) for positive models. These goodness of fit values are comparable to other dietary studies that employed additive models and reflect the relatively large amount of variability inherent in diet composition data (Stefánsson and Pálsson, 1997; Santos et al., 2013).

Most binomial models of prey consumption included length and latitude as significant covariates (Table 2), indicating the importance of both size limitation and spatial dynamics in trophic interactions. Best-fitting models that did not include length were typically for predators with relatively smaller length ranges. Significance of depth and temperature varied by prey; depth was not important for bivalves, and temperature was typically excluded from polychaete models. For the positive models, predator length was again a consistently critical covariate, yet few models included latitude or temperature. Only two positive models revealed significant effects of water depth.

Consumption of mysids by predators was strongly influenced by the modeled covariates. Predator length produced the strongest effect on the probability of mysids being consumed, with larger individuals far less likely to consume this small-bodied prey (Fig. 3). The prey biomass consumed tended to increase across predators at smaller sizes prior to declining, with this transition occurring between ~150-300 mm (Fig. 3). Both the occurrence and the biomass consumed indicated greater mysid availability at lower latitudes for the predators with the largest sample sizes (Fig. 3). Temperature effects on mysid occurrence and biomass were inconsistent across predators, preventing clear conclusions regarding the influence of temperature on mysid dynamics. Mysid occurrences in stomachs were slightly greater at shallower depths, but weakfish contradicted this pattern.

Bay anchovy consumption was strongly influenced by predator length (Fig. 4). The parabolic shape for the binomial model indicates a strong peak in prey occurrence at sizes ~175-300 mm, with weakfish targeting bay anchovy at slightly smaller sizes than summer flounder and striped bass. The mass of bay anchovy found in stomachs

increased with predator size until leveling off at sizes that corresponded to the peaks in bay anchovy occurrence (Fig. 4). A size effect on biomass consumed was not detected for striped bass. Effects of latitude on the probability of bay anchovy consumption differed by predator, with striped bass opposing the trend of greater bay anchovy occurrence at higher latitudes. Temperature effects varied by predator, and again striped bass opposed the general trend detected for the other species. Weakfish and summer flounder results indicated greater probability of bay anchovy consumption at lower temperatures. Depth effects on occurrence were negligible, although there was some evidence for increased bay anchovy occurrence in shallower water.

Consumption of bivalves by Chesapeake Bay predators was strongly influenced by predator length and latitude. Dietary occurrence of bivalves increased with length for Atlantic croaker, white perch, and northern puffer, but appeared to reach an asymptote for Atlantic croaker (Fig. 5). The biomass consumed also increased steeply with predator size. When viewed in unison, the latitude effects for all predators demonstrated a decreased occurrence of bivalves in stomachs at mid-latitudes, with increases in both the lower and upper bays (Fig. 5). For Atlantic croaker, the mass of consumed bivalves also supported this parabolic latitudinal trend in prey availability. Water temperature had a positive effect on bivalve occurrence in fish stomachs for three species, but only white perch showed a similar positive relationship when modeling prey biomass. Depth was not a significant covariate for any of the bivalve GAMMs.

Patterns of polychaete consumption showed varied responses to covariates depending on the predator. Dietary occurrence of polychaetes varied greatly by predator length depending on the species, but tended to increase with size before decreasing at

larger sizes (Fig. 6). The biggest exception to this pattern was for kingfish for which occurrence decreased monotonically. The biomass of consumed polychaetes increased with predator length at similar rates across predators, with only striped bass showing a reliable indication of saturation at larger sizes (Fig. 6). Latitudinal effects on the probability of polychaete consumption tended to show an inverse pattern to bivalve occurrence by latitude (Figs. 5, 6). Polychaete occurrences tended to be greatest in mid-latitudes, but latitude did not have significant effects on biomass of consumed polychaetes for the majority of modeled predators (Fig. 6). Temperature effects on polychaete occurrence and biomass were largely negligible across the majority of predators (Fig. 6). Depth effects on polychaete occurrence were inconclusive as a whole at shallow depths, but most fishes indicated decreasing occurrence as depth increased beyond ~10 m (Fig. 6).

Annual trends in consumption indices

Standardized indices of annual prey consumption varied through the time-series but demonstrated some synchronous and coherent trends across predators. Generation of the annual consumption index clarified the interpretation of the year effects from individual binomial and positive GAMM models (Fig. S1). Five of seven predators (Atlantic croaker, northern searobin, scup, summer flounder, weakfish) exhibited a distinct annual peak in consumption of mysids in 2003, with a magnitude dramatically greater than other years (Fig. 7). Correlations among annual trends for these five species ranged from 0.55-0.94, with 4 of 10 values being significant (Bonferroni-corrected $p < 0.05$; Table 3). Only striped bass and spotted hake did not conform to this pattern.

Consumption of bay anchovy by summer flounder and striped bass were strongly, though not significantly, correlated ($R=0.73$), exhibiting largely synchronous changes in directionality (Fig. 7). Although consumption indices were not correlated with the bay anchovy index (Table 3), the highest consumption values for summer flounder and weakfish (and second highest value for striped bass) were obtained in 2010 when the prey index was at its highest. Bivalve consumption had a peak in 2008 that was shared by all predators, although overall trends were not significantly correlated with one another or with the prey index (Fig. 7). Consumption indices of polychaetes were highly variable among predators; however the highest values occurred in the last 5 years of the time series and 4 of the 7 predators (Atlantic croaker, scup, spot, and white perch) consumed the greatest amount of polychaetes in 2010 (Fig. 7). None of the pairwise polychaete correlations among predators and prey index were significant (Table 3).

Interactions among prey

Results indicated that some level of interaction among prey occurred. Several Chi-square tests were significant for presence of mysids and bay anchovy in predator stomachs, indicating a likely interaction among these two prey (Table 4). Typically, presence of one of these prey in the stomach reduced the frequency of occurrence of the other prey by approximately 7-33%. Lack of significance for the large size classes was due to the negligible consumption of mysids at these sizes. Only two of the bivalve-polychaete tests were significant (Table 4) but the effects were smaller; consumption of one prey reduced the frequency of occurrence of the other by 3-10%. At the broader, annual scale, consumption indices for prey were typically not correlated with one another

for individual predators, with only two exceptions: annual consumption of mysids was significantly inversely correlated with polychaete consumption for Atlantic croaker, and mysid consumption was inversely correlated (though not significantly) with bay anchovy consumption for summer flounder (Table 5).

DISCUSSION

General

Biological, environmental, and spatiotemporal factors strongly regulated predatory consumption of four key prey groups in Chesapeake Bay. Despite the notorious variability of fish diet data generated from the complex processes that influence trophic dynamics (Gerking, 1994; Wootton, 1998), the use of an extensive data set and multiple opportunistic predators aided in illuminating more robust commonalities in feeding patterns that appear to be linked to prey availability at both small and large scales. Coherent annual peaks in mysid, bay anchovy, and bivalve consumption are suggestive of episodic annual pulses in prey productivity that may be mediated by bottom-up processes. The dynamic nature of trophic linkages reinforces the variability in energy pathways within aquatic food webs. However, the consequences of these regional and annual dietary changes on the magnitude of annual prey consumption, the productivity of predator populations, and the relative strength of bottom-up and top-down regulation remain intriguing topics for future research in Chesapeake Bay and the Northwest Atlantic (see Chapter 4).

Predator length as a strong determinant of diet

Predator length was the most consistently important determinant of prey consumption, supporting a vast literature that emphasizes the significance of body size in

structuring trophic interactions (e.g., Juanes 1994, Scharf et al. 2000, Kerr & Dickie 2001). Among other things, body size regulates the foraging process by controlling the physical constraints on the size and types of prey that can be ingested, the speed and endurance of a predator, the relative success of foraging attacks, and the visual limit for prey detection (Webb, 1976; Eggers, 1977; Blaxter, 1986; Mittelbach and Persson, 1998; Scharf et al., 2002). In this study, the binomial GAMM effects for predator length provide information on the continuous functional forms of relative prey consumption by predators of varying sizes. The forms of these size-based consumption curves were either linear, asymptotic, or dome-shaped (which translate to sigmoidal, asymptotic, and dome shapes when converted to the 0-1 probability scale). The sigmoidal decline in consumption of mysids supports their greater importance to juveniles and smaller sized individuals (Mauchline, 1980; Hostens and Mees, 1999), while the sigmoidal or asymptotic increase in bivalve consumption suggests this prey is a “terminal” prey for which occurrence is greatest at the most advanced ages and sizes that were sampled (Chapter 2). The dome shapes for bay anchovy and polychaetes identified these prey as being transitional forage resources as predators grew (through the examined sizes), reaching consumption optima at intermediate sizes. Generally, these bay anchovy optima corresponded with significant shifts in diet composition based on discrete size-class cutoffs (Latour et al. 2008, Chapter 2), and they also corresponded with published distributions of predator-prey size ratios for summer flounder and weakfish (Scharf et al., 2000). The empirically-derived consumption curves can thus help inform the parameterization of size-based components of prey suitability functions that are used in foraging or multispecies models (Garrison et al., 2010).

Prey dynamics

Mysids are critical links within estuarine and coastal food webs due to their predominance in fish diets (Hostens & Mees 1999, Chapter 2) and their role in coupling benthic and pelagic production pathways (Mauchline, 1980; Jumars, 2007). Within Chesapeake Bay and other estuaries, the role of mysids as a key component of the fish forage base has been underappreciated (Jumars 2007, Chapter 2), and relatively little is known about the regional dynamics of this group, highlighting the basic research needed for this key prey group. *Neomysis americana* is the predominant mysid species within the bay (Chapter 2), and it is well suited to a range of environmental conditions with congeners tolerant of salinities from 1-45‰ and temperatures from 0-35°C (Mauchline, 1980). For example, although endemic to Chesapeake Bay and the northwest Atlantic, the physiological adaptability of *N. americana* has facilitated its invasion of many South American estuaries and coastal waters (Jumars, 2007). Within the neighboring Delaware Bay, *N. americana* densities peaked at mesohaline salinities ~50-90 km away from the mouth of the estuary (Hulburt, 1957; Cronin et al., 1962), whereas our study (from a much larger estuary) indicates mysid availability and presumably density was highest at lower latitudes towards the mouth of the bay. This trend is consistent with the premise that coastal waters act as the major source for estuarine mysid populations (Whitely, 1948; Hulburt, 1957; Hopkins, 1965), and suggests that physical advection and distance from the coastal population source may be more important than specific salinity regimes in dictating estuarine mysid distributions in large estuaries like Chesapeake Bay. However, it should be noted that mysid consumption did occur throughout the entire

sampled area, likely supported by local estuarine reproduction that can occur through their 2-3 annual reproductive cycles (Hulburt, 1957). Although mid-Atlantic estuarine populations tend to peak in summer months with warmer temperatures, mysids can be found throughout the year in estuaries (Hulburt, 1957; Hopkins, 1965). This seasonal ubiquity contributes to the lack of consistent dietary occurrence trends with temperature and supports the importance of mysids as a food resource throughout the year to a variety of resident and seasonally migrating predators (Hartman & Brandt 1995, Latour et al. 2008, Chapter 2). Analyses suggested greater mysid availability in relatively shallower bay areas (4-15 m) based on the diets, contrary to trends in Delaware Bay where Hulburt (1957) noted low mysid concentration in areas <5.5 m. However, his study sampled during daylight hours in surface waters when mysids typically reside on the benthos (Herman, 1963).

Bay anchovy are the most abundant fish in the Chesapeake Bay and they contribute substantially to the production of commercially and recreationally important piscivorous species like striped bass, summer flounder, weakfish, and bluefish (Baird and Ulanowicz, 1989; Houde and Zastrow, 1991; Able and Fahay, 2010). For many piscivores, bay anchovy acts as a critical forage species that bridges the transition from small zooplanktonic and benthic prey to larger forage fishes (e.g., Atlantic menhaden and various sciaenids) (Hartman & Brandt 1995, Latour et al. 2008, Chapter 2). The discrepancy in bay anchovy consumption trends between striped bass and the other predators, as influenced by latitude and temperature, are likely related to differences in spatiotemporal overlap of prey and predator populations. Bay anchovy tend to be more abundant in the mid- and upper-bay as juvenile production increases in the summer

months prior to a biomass peak in October (Wang and Houde, 1993). During these warm summer months, resident striped bass also inhabit the upper bay, north of the Potomac River (Fig. 1; A. Buchheister unpublished data), likely contributing to the relatively high dietary occurrence of bay anchovy in the summertime temperatures. As temperatures cool thereafter, the bay anchovy, now of larger size, tend to migrate to the lower bay and inner continental shelf to overwinter (Luo and Musick, 1991; Wang and Houde, 1993; Jung and Houde, 2004b), with lower-bay trawl catches peaking in December (T. Tuckey, Virginia Institute of Marine Science, personal communication). In late fall and winter months, striped bass are found throughout the bay and may encounter relatively higher anchovy densities of more consumable sizes in the lower bay, explaining the increased dietary occurrence at those latitudes. Summer flounder and weakfish, on the other hand, exhibit life history strategies that favor the lower bay with biomass peaking in late summer and fall, opposing the distributional patterns of the anadromous striped bass (Murdy et al., 1997; Latour et al., 2008). Thus their relative spatiotemporal overlap with bay anchovy differs from striped bass and contributes to the conflicting latitudinal and temperature trends among predators. Regarding depth, although bay anchovy occur at a variety of depths in the bay, they tend to be more rare in deeper waters >25 m (Houde and Zastrow, 1991), corresponding with the dietary trends observed.

The trends of bivalve and polychaete consumption revealed broad-scale patterns in the availability of macrobenthic prey for demersal fishes in Chesapeake Bay. The decline of bivalve consumption and increase of polychaete consumption in mid-latitude, mesohaline waters could be influenced by two principal mechanisms relating to prey availability. First, regional biogeography and physico-chemical preferences (e.g.,

salinity, sediment type) largely dictate the bay regions in which individual macrobenthic species reside (Holland et al., 1987; Diaz and Schaffner, 1990). For example, *Macoma* and *Gemma* clams favor the more moderate salinities of the mid- to upper-bay (with biomass peaks from 38.5-39.25°N based on the benthic monitoring data), while *Ensis* and *Tagelus* reside in more polyhaline, low-latitude waters (Diaz and Schaffner, 1990). Thus, latitudinal trends of bivalve and polychaete prey are an amalgamation of effects generated from individual species that comprise each of the macrobenthic prey groups. The second mechanism potentially influencing prey consumption relates to chronic and acute habitat degradation. Extensive seasonal hypoxia caused by eutrophication, physical stratification, and bacterial remineralization of organic matter is a dominant environmental feature in the bay from June to August, persisting up to 3 months in some areas (Murphy et al., 2011). Hypoxia diminishes macrobenthic productivity and biomass more strongly in deeper mid-bay waters relative to upper and lower bay regions during the summer months (Holland et al., 1987; Kemp et al., 2005a; Seitz et al., 2009). This decreased production can contribute to the declines in mid-bay bivalve consumption, whereas the increased dietary occurrence of polychaetes in the mid-bay could be partially attributed to their greater tolerance of low oxygen conditions relative to bivalves (Vaquer-Sunyer and Duarte, 2008; Sturdivant et al., 2013) or their tendency to more quickly recolonize benthic habitats once waters become re-oxygenated (Lu and Wu, 2000; Rosenberg et al., 2002). Effects of hypoxia on mid-bay macrobenthic prey availability are not isolated to summer, as habitat degradation and seasonal hypoxia-induced mortality have shifted the annual benthic community to smaller, shorter-lived species with lower standing stock biomass (Holland et al., 1987; Kemp et al., 2005a).

Indeed, the latitudinal trend in bivalve consumption was detected in all sampled months (A. Buchheister, unpublished data), suggesting that species biogeographical distributions and long-term degradation of mid-bay habitats may be more influential on macrobenthic consumption than direct seasonal hypoxic effects, particularly considering that fishes avoid the low oxygen waters (Buchheister et al., 2013).

Annual patterns in prey consumption

Despite the lack of concordance between indices of prey abundance and consumption overall, there was strong evidence of prey availability regulating annual consumption indices of individual Chesapeake Bay predators, as supported in many other systems (Fahrig et al., 1993; Mills et al., 2007; Dwyer et al., 2010; Schückel et al., 2010; Pálsson and Björnsson, 2011). The strongest empirical indication that prey availability was involved in the annual trends was the coherence in peak consumption of mysids, bivalves, and bay anchovy by predators with varied feeding preferences, foraging modes, and distributional patterns. For example, two benthivorous species (Atlantic croaker and scup) exhibited the same 2003 peak in mysid consumption as other zooplanktivorous and piscivorous species (Northern searobin, summer flounder, weakfish), despite having diets that do not typically target these small, hyperbenthic crustacean (Chapter 2). Also, fishes that predominantly reside in upper bay waters (white perch and striped bass) demonstrated similar bivalve and bay anchovy consumption peaks as the other predators that primarily inhabit the lower third of the bay. These synchronous dietary patterns relate largely to 1) the density-dependent feeding behavior of animals (Holling, 1959), and 2) the opportunistic feeding strategies that evolved to allow fishes to exploit

spatiotemporally-patchy prey resources in dynamic, heterogeneous environments (Gerking, 1994). Presumably, different environmental or ecological conditions supported large pulses in prey production during certain years (mysids – 2003; bivalves – 2008; bay anchovy – 2010) that were utilized by a variety of predators that adapted to the greater prey availability. For example, based on bay monitoring data, 2003 was an anomalous year in the time series yielding the lowest mean daily temperatures and salinities for spring (April – June), the highest annual estimate of mean surface chlorophyll, and the second largest volume of summertime hypoxia (A. Buchheister, unpublished data). Some of these conditions could have contributed to greater mysid production through bottom-up processes including improved local reproduction during the spring spawning event, greater overall phytoplankton food availability that improved juvenile or adult survival, or greater immigration of mysids from coastal waters (Hopkins, 1965; Ezzack and Corey, 1979). Indeed, bottom-up mechanisms have been implicated as drivers of ecosystem structure, fish recruitment, and fisheries landings in the Chesapeake Bay and Mid-Atlantic Bight (Frank et al., 2007; Hare and Able, 2007; Wood and Austin, 2009), and the dietary trends documented are consistent with such donor control in food webs. However, any speculations on specific mechanisms driving pulses in production of mysids, bay anchovy, or bivalves require more directed and targeted research.

The general lack of concordance between prey abundance indices and the consumption indices can partially be explained by sampling issues. Prey sampling methodologies, whether by survey gear or by predatory consumption, are biased to some degree and may not be representative of annual prey dynamics and density. Examples of temporal and spatial survey biases include 1) the long-term benthic monitoring program

excluding Maryland waters >12 m, 2) that survey sampling from July to September after the macrobenthic biomass is affected by summertime hypoxia, and 3) the bay anchovy index being derived from a bottom trawl survey that is not optimal for sampling the pelagic species. Consumption biases from the predators largely take the form of prey selectivity, which is most strongly affected by predator species and by body size (Eggers, 1977; Ney, 1990; Juanes, 1994). Concerns regarding the effect of prey selectivity are minimized by the fact that annual trends were mirrored by the annual effects from the binomial models, which relied on presence/absence data that are less biased by selectivity than gravimetric diet estimates (Link, 2004; Baker et al., 2013). The aggregation of various prey species into the bivalve and polychaete groups could also hinder the ability to resolve the linkages between prey availability and predator consumption. For example, the 2008 consumption peak was largely dominated by *Ensis* and *Tagelus* clams in the lower bay and *Macoma* clams in the upper bay, whereas the abundance index was driven by *Macoma* clams.

The second explanation for the incongruence between prey consumption and abundance indices relates to the scale of investigation which differs from the inherently small-scale nature of predator-prey interactions (Levin, 1992; Hunsicker et al., 2011). Inference at the broad, annual scale can be obfuscated by variation in distributional changes and spatiotemporal overlap of predators and prey. For example, the absence of peaks in mysid consumption by striped bass and spotted hake in 2003 is likely due to the absence of these predators in lower latitudes from July to September, where mysids appear more concentrated and when mysid biomass peaks (Hulburt, 1957; Hopkins, 1965). Use of multiple predators with contrasting life histories helped identify

incongruous overlap situations such as this, but interpretation of patterns is more challenging when both predator and prey are highly mobile (as was the case for bay anchovy and their predators). Inadequate contrast in annual prey densities has been identified as another complicating factor in detecting density-dependent diet signals (Greenstreet et al., 1998; Pinnegar et al., 2003); in our study, peaks in bay anchovy consumption in 2010 corresponded with the highest abundance index documented in 23 years (Tuckey and Fabrizio, 2012), but other years exhibited weak contrast. Preciado et al. (2008) also note that discrepancies in length distributions between the prey consumed and the population in the wild alter the effective prey availability, potentially contributing to poor correlations between prey abundance and predator diets. Lastly, indices of prey standing stocks may not be fully representative of prey production rates, particularly for shorter lived prey groups with multiple or continuous recruitment events throughout the year. For example, it is estimated that Chesapeake Bay piscivores can consume up to 80% of seasonal bay anchovy secondary production (Baird and Ulanowicz, 1989). However, predation pressure is unlikely to overwhelm and mask annual trends in standing stocks and production for most of the examined prey groups (macrobenthos – Holland et al. 1987; mysids – Hostens & Mees, 1999).

Methodological considerations

When modeling the consumption of an individual prey group, there is a potential for interactions among prey caused largely by prey selectivity and prey switching (Murdoch, 1969; Eggers, 1977; Juanes, 1994), but robust empirical tests of this are challenging in the field at broad scales (Fahrig et al., 1993; Stefánsson and Pálsson, 1997;

Santos et al., 2013). The strongest indication of prey interaction in this study was between mysids and bay anchovy, but the tests conducted were confounded by the strong opposing ontogenetic trends in consumption for these two prey. The decreased likelihood of mysid consumption when bay anchovy are present in a stomach could be driven more by the size-based shifts in feeding as opposed to active prey selection (Juanes 1994). The patchiness of prey may also expose individual predators to a single prey group at any given time, reducing the likelihood of joint occurrence of prey. The scale-dependent nature of potential interactions among prey is reinforced by the few cases of negative correlations in annual consumption. Undoubtedly, prey selectivity and the choices predators make at small scales can influence broader consumptive trends, but disentangling these effects from other system interactions, indirect food web effects, and spatiotemporal changes in predator-prey overlap require continued research. One promising approach to address prey interaction effects is by explicitly building them into the GAMM structure. However, insufficient sample sizes can hinder the ability to draw robust conclusions, as we discovered with unreported analyses.

Generalized additive mixed effects models provided a powerful and flexible approach for drawing more robust statistical inferences from stomach content data. The biggest advantages of these models included the ability to 1) appropriately handle the excessive number of zeros in an approach that is ecologically meaningful, 2) account for the correlation structure of the hierarchical sampling designs common in fisheries surveys, 3) incorporate a variety of categorical and continuous explanatory variables, 4) account for nonlinear effects of covariates on the response, and 5) maintain diet information at the individual fish level, to avoid pooling data as is needed for average-

based analytical methods (e.g., pooling predators into size classes was not required). However, as with other statistical modeling, GAMM convergence was largely predicated on having sufficient sample sizes for models of greater complexity. Proxies for goodness of fit and precision of covariate effects were poor in some cases, but this is largely attributable to the large variability of ecological datasets that are typically noisy. The major dietary patterns and general conclusions of the study were not altered by the exclusion of the random station effect (nor replacing it with a random stratum effect), but accounting for the non-independence of fish is more statistically valid and helps avoid erroneous conclusions (Hurlbert, 1984; Millar and Anderson, 2004). Although GAMMs have been described as being on “the frontier of statistical research” (Zuur et al., 2009), these and related methods are being advanced quickly and are becoming more accessible to researchers (Wood, 2006; Zuur et al., 2009); thus, they are rapidly being integrated into the statistical toolboxes of many ecologists and fisheries scientists (Venables and Ripley, 2002; Dichmont, 2004; Ciannelli et al., 2008; Bailey et al., 2009; Viana et al., 2009; Gilman et al., 2012; Philippart et al., 2012).

Implications

Comprehensive, spatiotemporally-extensive trophic studies such as this work help elucidate the trophic relationships and drivers that structure ecosystems, and can contribute to implementation of ecosystem-based fisheries management. The coherence in annual prey consumption indices of multiple predators supports their utility as indicators of relative prey abundance that could augment current prey sampling surveys (e.g., Mills et al. 2007, Einoder 2009), and such diet metrics may be particularly useful

for monitoring or hindcasting of key prey groups, such as mysids, for which systematic sampling does not exist. EBFM applications of this type of research include use of dietary indices as ecosystem indicators (Dwyer et al., 2010), parameterization of multispecies and ecosystem models (Pauly et al., 2000), empirical information for parameterizing prey vulnerabilities within foraging sub-models (Garrison et al., 2010), fitting of functional response curves if consumptions are expressed as rates (Moustahfid et al., 2010), and potentially the use of diet time-series as additional tuning indices for ecosystem models. Continued research on trophic dynamics, particularly focused on long time periods and broader spatial extents, can provide valuable information for EBFM at the scales most pertinent to resource management.

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TABLE CAPTIONS

Table 1. Sample summaries for Chesapeake Bay predators collected for dietary analysis. Length measurements were recorded as fork length (teleosts) or disc width (batoids). N_s = Number of stations with predator captured, N_f = Number of individual fish sampled for stomachs, P_e = percentage of fish stomachs that were empty. Numbers of fish containing key prey groups are indicated.

Table 2. Best binomial and positive generalized additive mixed models (GAMM) for each predator-prey combination. Inclusion (+) and exclusion (blank) of covariates for the best fit models (YR = Year; L = Length; LA = Latitude; T = Temperature; D = Depth) were determined through model selection using Akaike's Information Criterion. Inclusion of the YR was forced in all models. A proxy for the deviance explained (% Dev) by each model was determined by fitting a fixed-effects generalized additive model with the specified covariates.

Table 3. Pearson correlations among annual predator consumption indices and prey abundance indices (when available) for each of four prey groups (a – bay anchovy; b – mysids; c – bivalves; d – polychaetes). Correlations calculated from logged values of unstandardized consumption indices from Figure 7. Gray shading used to denote significance ($\alpha=0.05$) without Bonferroni correction; bold used to denote significance

with Bonferroni correction. Spot were omitted from polychaete correlations due to lack of sampling over the whole time series.

Table 4. Chi-square test results of prey dependencies in stomachs of predator size classes. Significant p-values (bold) indicate lack of independence of prey pair presences within each predator and size-class (S-small, M-medium, L-large). Predators not classified into a size class are denoted with dashes.

Table 5. Pearson correlations between annual consumption indices of specific prey pairs by individual predators. Correlations were calculated from logged values of consumption indices from Figure 7. Gray shading used to denote significance ($\alpha=0.05$) without Bonferroni correction; bold used to denote significance with Bonferroni correction. Prey groups were mysids, bay anchovy (Anch.), bivalves (Biv.), and polychaetes (Poly.).

FIGURE CAPTIONS

Figure 1. Map of Chesapeake Bay mainstem areas sampled by the Chesapeake Bay Multispecies Monitoring and Assessment Program. Survey area is divided into 1 km² grid cells and classified into three depth strata. Areas in white are not sampled by the survey.

Figure 2. Composition of predator diets (as % of stomach content weight) for select Chesapeake Bay fishes consuming four key prey groups (bay anchovy, mysids, bivalves, and polychaetes). The remainder of stomach contents were comprised of other prey.

Figure 3. Modeled effects of continuous covariates on consumption of mysids based on delta generalized additive mixed-effects models (GAMMs) for multiple Chesapeake Bay predators. Upper panels depict covariate effects on the relative probability of a predator stomach containing a mysid, based on a binomial GAMM. Lower panels depict covariate effects on the relative amount of mysids consumed (log of biomass) based on the positive GAMM. Dashed lines represent 95% confidence limits for the estimated effects. Predator curves are not plotted if a covariate was not included in the best model.

Figure 4. Modeled effects of continuous covariates on consumption of bay anchovy based on delta generalized additive mixed-effects models (GAMMs) for multiple Chesapeake Bay predators. See Figure 3 for full description of plot.

Figure 5. Modeled effects of continuous covariates on consumption of bivalves based on delta generalized additive mixed-effects models (GAMMs) for multiple Chesapeake Bay predators. See Figure 3 for full description of plot.

Figure 6. Modeled effects of continuous covariates on consumption of polychaetes based on delta generalized additive mixed-effects models (GAMMs) for multiple Chesapeake Bay predators. See Figure 3 for full description of plot.

Figure 7. Annual indices of prey consumption derived from the delta generalized additive mixed-effects models (GAMMs). Consumption of each prey by a predator was standardized to range from 0-1 (solid, colored lines). Standardized prey abundance index denoted with dashed line, but not available for mysids.

Supplemental Figure S1. Modeled effects of year on consumption of 4 key prey groups by multiple Chesapeake Bay predators, based on delta generalized additive mixed-effects models (GAMMs). See Figure 3 for full description of plot.

Table 1.

Predator	Length (mm)		N _s	N _f	P _e	No. fish containing prey				
	Range	Mean				Any Prey	Mysid	Anchovy	Bivalve	Polychaete
Atlantic croaker (<i>Micropogonias undulatus</i>)	20 - 478	242	977	3374	14	2914	458	--	550	1753
clearnose skate (<i>Raja eglanteria</i>)	84 - 519	412	355	941	13	821	--	--	146	--
kingfishes (<i>Menticirrhus spp.</i>)*	45 - 383	236	399	1077	18	882	--	--	179	178
northern puffer (<i>Sphoeroides maculatus</i>)	49 - 272	156	407	1087	9	990	--	--	292	180
northern searobin (<i>Prionotus carolinus</i>)	40 - 223	127	387	941	20	751	381	--	--	--
scup (<i>Stenotomus chrysops</i>)	69 - 223	123	347	879	17	732	150	--	--	268
spot (<i>Leiostomus xanthurus</i>)	40 - 311	156	616	2217	29	1581	--	--	--	556
spotted hake (<i>Urophycis regia</i>)	50 - 318	147	244	609	19	491	323	--	--	--
striped bass (<i>Morone saxatilis</i>)	92 - 1051	372	1005	3868	33	2590	549	638	--	707
summer flounder (<i>Paralichthys dentatus</i>)	129 - 750	344	1501	4874	42	2828	1119	663	--	--
weakfish (<i>Cynoscion regalis</i>)	15 - 616	211	1128	6699	25	4994	2301	1951	--	--
white perch (<i>Morone americana</i>)	68 - 351	202	524	2784	38	1739	--	--	278	510

**Menticirrhus saxatilis* and *M. americanus* combined.

Table 2.

Prey	Predator	Binomial GAMM						Positive GAMM					
		YR	L	LA	T	D	% Dev	YR	L	LA	T	D	% Dev
Bay anchovy	Summer flounder	+	+	+	+	+	13.5	+	+				5.4
	Striped bass	+	+	+	+	+	17.0	+		+			9.4
	Weakfish	+	+	+	+		8.7	+	+				7.6
Bivalve	Atlantic croaker	+	+	+			13.5	+	+	+			24.6
	Clearence skate	+		+			16.9	+					22.3
	Kingfish	+		+	+		22.6	+	+				35.4
	Northern puffer	+	+	+	+		15.0	+	+				20.0
	White perch	+	+	+	+		12.6	+	+				15.0
Mysid	Atlantic croaker	+	+		+		16.5	+					8.8
	Northern searobin	+		+			6.8	+	+		+	+	15.7
	Scup	+			+	+	13.5	+					6.0
	Spotted hake	+	+		+	+	19.3	+	+		+	+	29.1
	Striped bass	+	+	+	+		19.0	+	+	+			24.3
	Summer flounder	+	+	+	+	+	36.7	+	+	+			9.1
	Weakfish	+	+	+	+	+	18.8	+	+				12.8
Polychaete	Atlantic croaker	+	+	+	+	+	8.9	+	+				28.5
	Kingfish	+	+				6.9	+	+				49.3
	Northern puffer	+		+		+	9.5	+	+				32.4
	Scup	+	+	+		+	8.0	+	+				22.8
	Spot	+	+	+			4.3	+	+				16.7
	Striped bass	+	+	+		+	13.5	+	+				10.6
	White perch	+	+	+		+	8.2	+	+	+			25.5

Table 3.

a. Mysids	Scup	Flounder	Croaker	Weakfish	N. searobin	Str. bass
Flounder	0.81					
Croaker	0.88	0.71				
Weakfish	0.84	0.70	0.94			
N. searobin	0.87	0.55	0.73	0.75		
Str. bass	-0.11	-0.28	-0.08	-0.21	0.21	
Sp. Hake	-0.15	-0.45	-0.09	-0.05	0.04	0.37

b. Bay anchovy	Flounder	Str. bass	Weakfish
Str. bass	0.73		
Weakfish	-0.02	0.08	
Index	0.43	0.29	0.44

c. Bivalves	Kingfish	Cl. skate	W. perch	Croaker	N. puffer
Cl. skate	0.69				
W. perch	0.43	0.73			
Croaker	0.22	0.51	0.34		
N. puffer	0.23	0.29	0.39	0.37	
Index	-0.12	-0.13	-0.09	0.20	0.75

d. Polychaetes	Index	Scup	Kingfish	W. perch	Croaker	N. puffer
Scup	0.49					
Kingfish	0.31	0.04				
W. perch	0.37	0.64	0.12			
Croaker	0.23	0.50	0.68	0.55		
N. puffer	0.14	0.24	-0.38	0.25	0.14	
Str. bass	-0.69	-0.66	0.34	-0.34	0.05	-0.35

Table 4.

Prey pair	Predator	Size class		
		S	M	L
Mysid - bay anchovy	Summer flounder	<0.01	<0.01	0.42
	Striped bass	0.02	0.26	0.91
	Weakfish	<0.01	<0.01	0.77
Bivalve - polychaete	Atlantic croaker	0.24	<0.01	0.30
	Kingfish	0.23	0.37	–
	Northern puffer	–	0.62	–
	White perch	0.39	0.02	–

Table 5.

Predator	Prey pairs				
	Mysid - Anch.	Biv. - Poly.	Mysid - Poly.	Anch. - Poly.	Mysid - Biv.
Atlantic croaker		0.20	-0.86		-0.28
Kingfish		0.42			
Northern puffer		-0.23			
Scup			-0.12		
Striped bass	0.07		-0.03	-0.27	
Summer flounder	-0.64				
Weakfish	-0.11				
White perch		0.12			

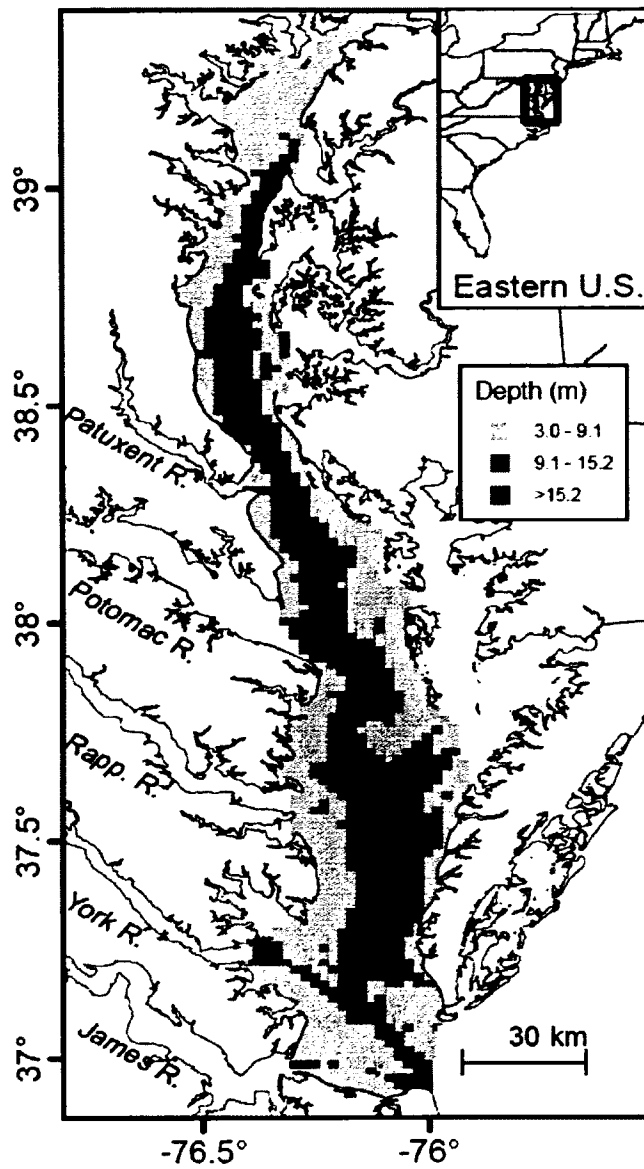


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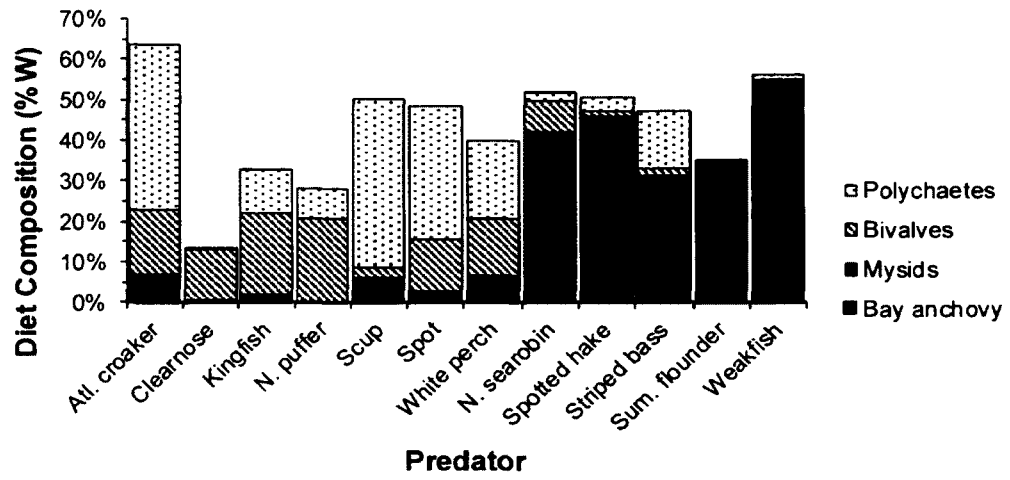


Figure 2.

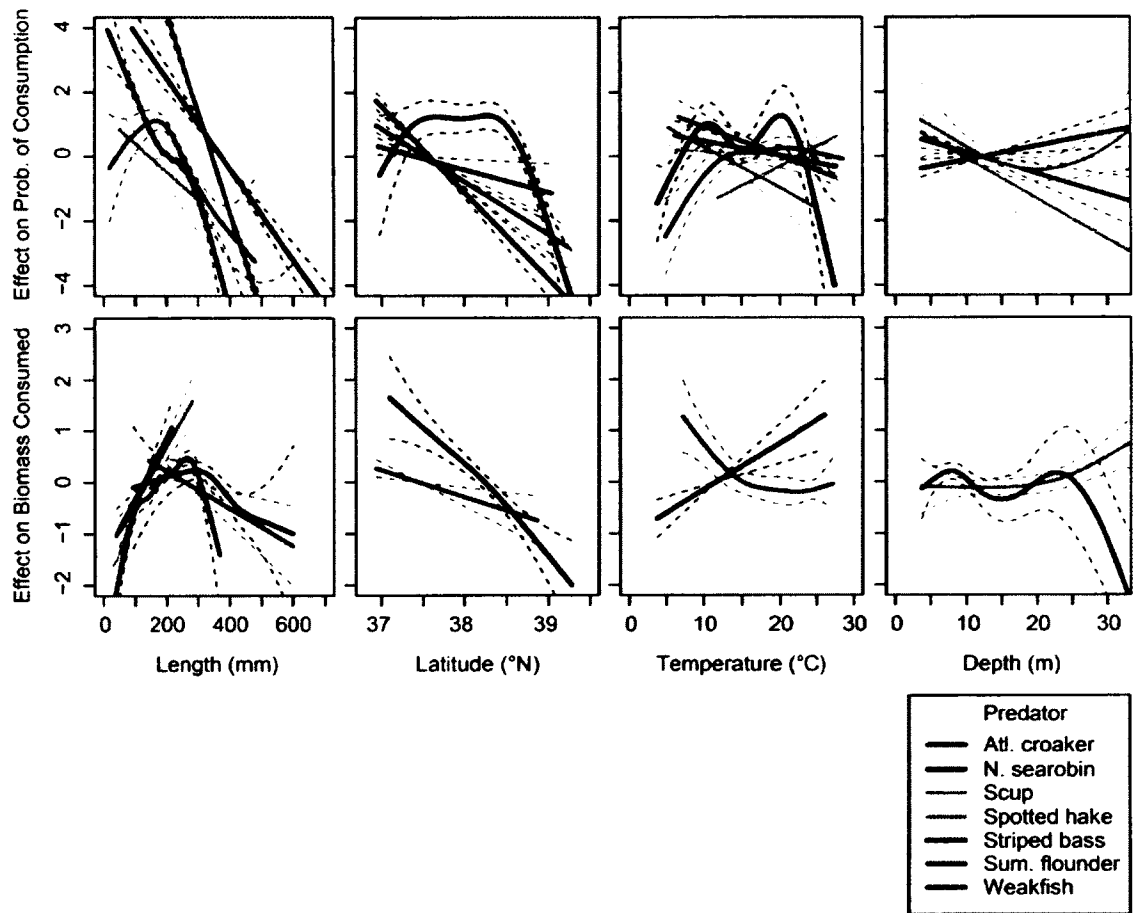


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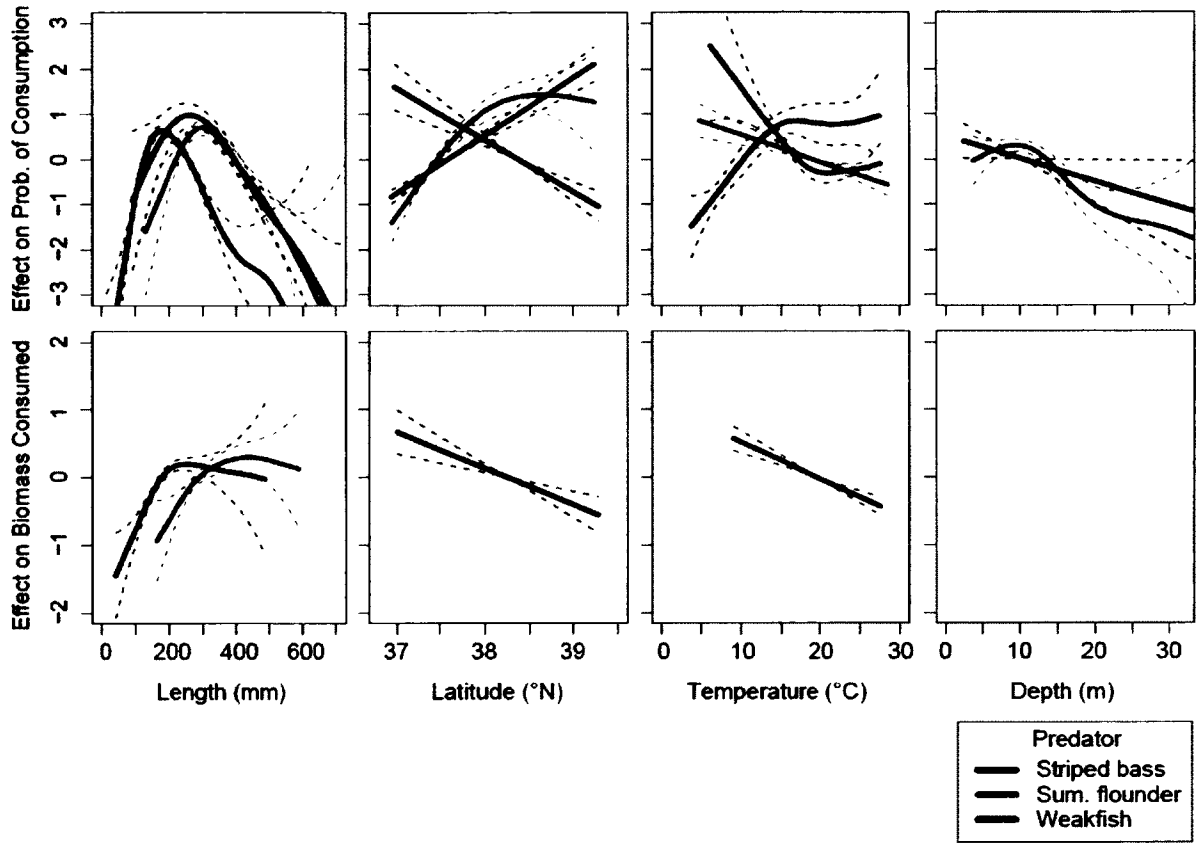


Figure 4.

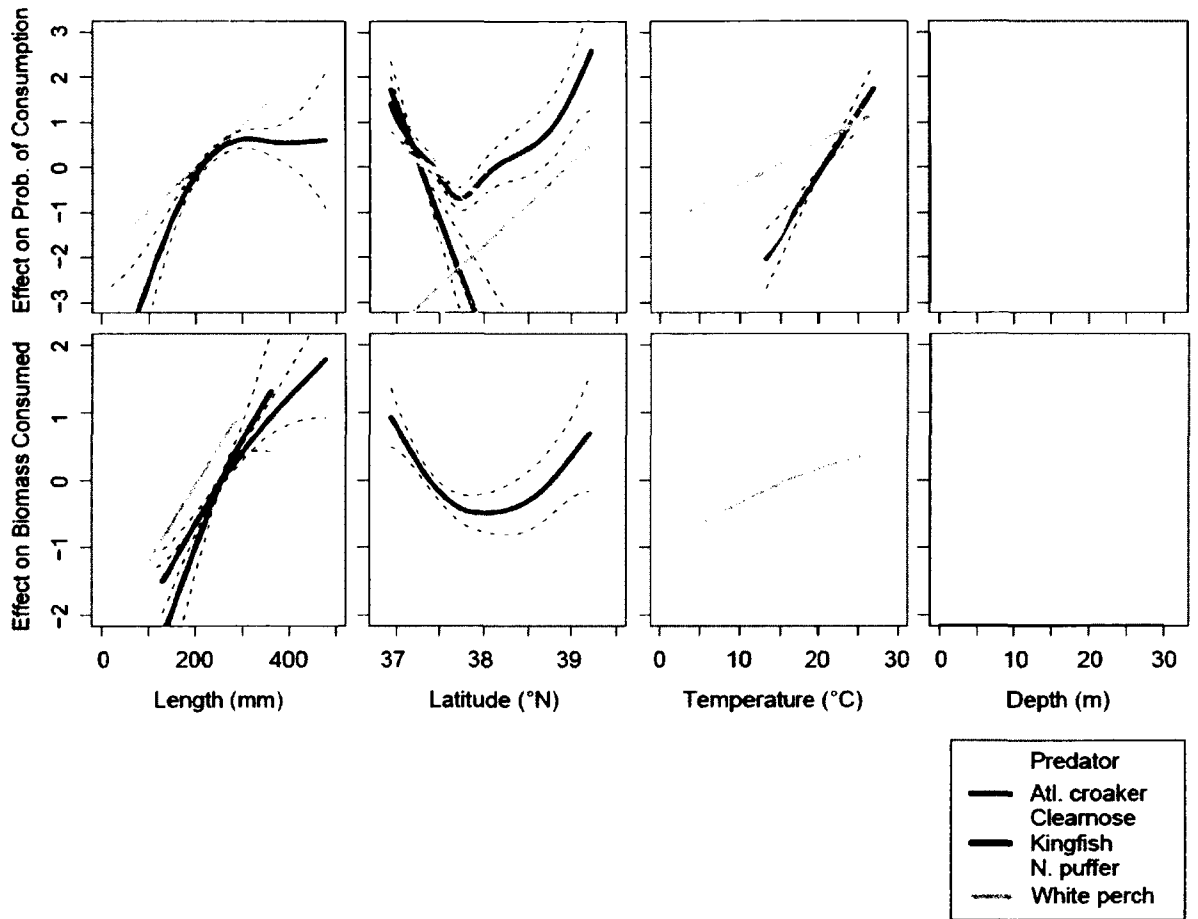


Figure 5.

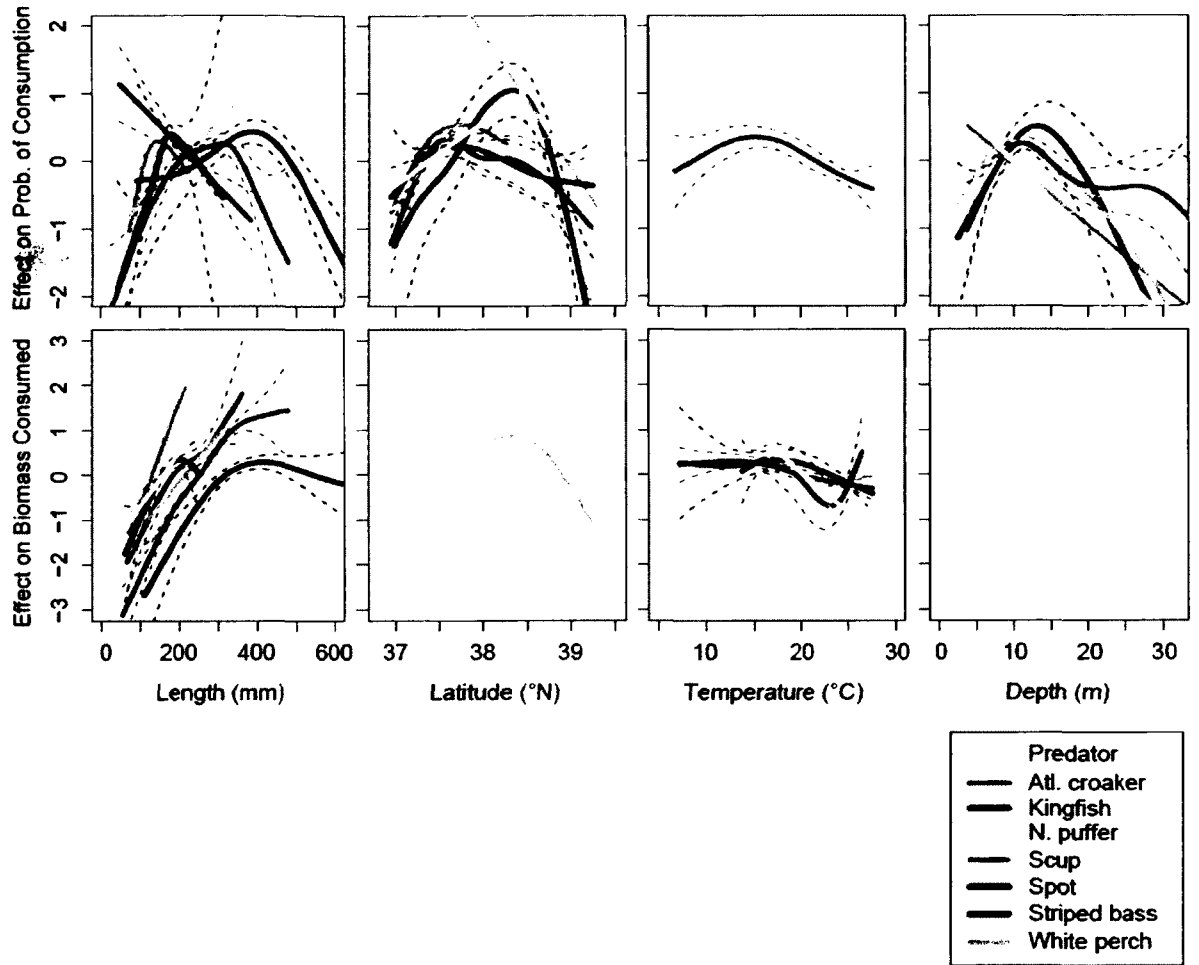


Figure 6.

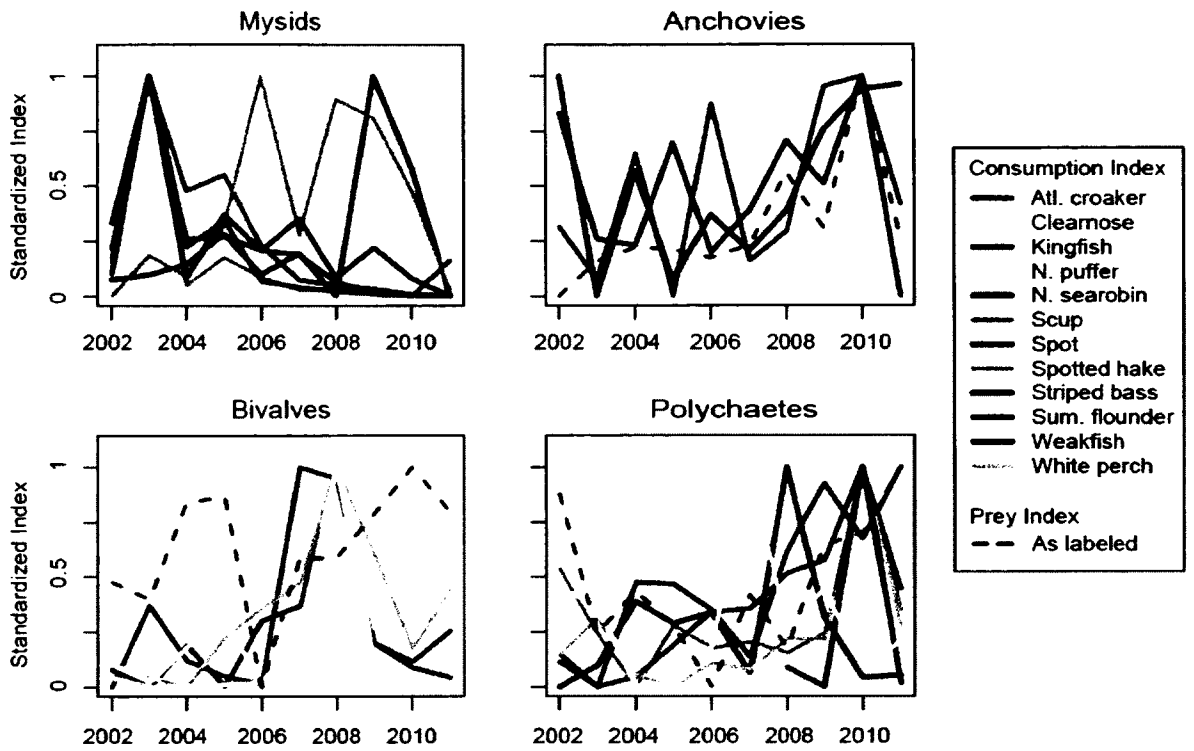
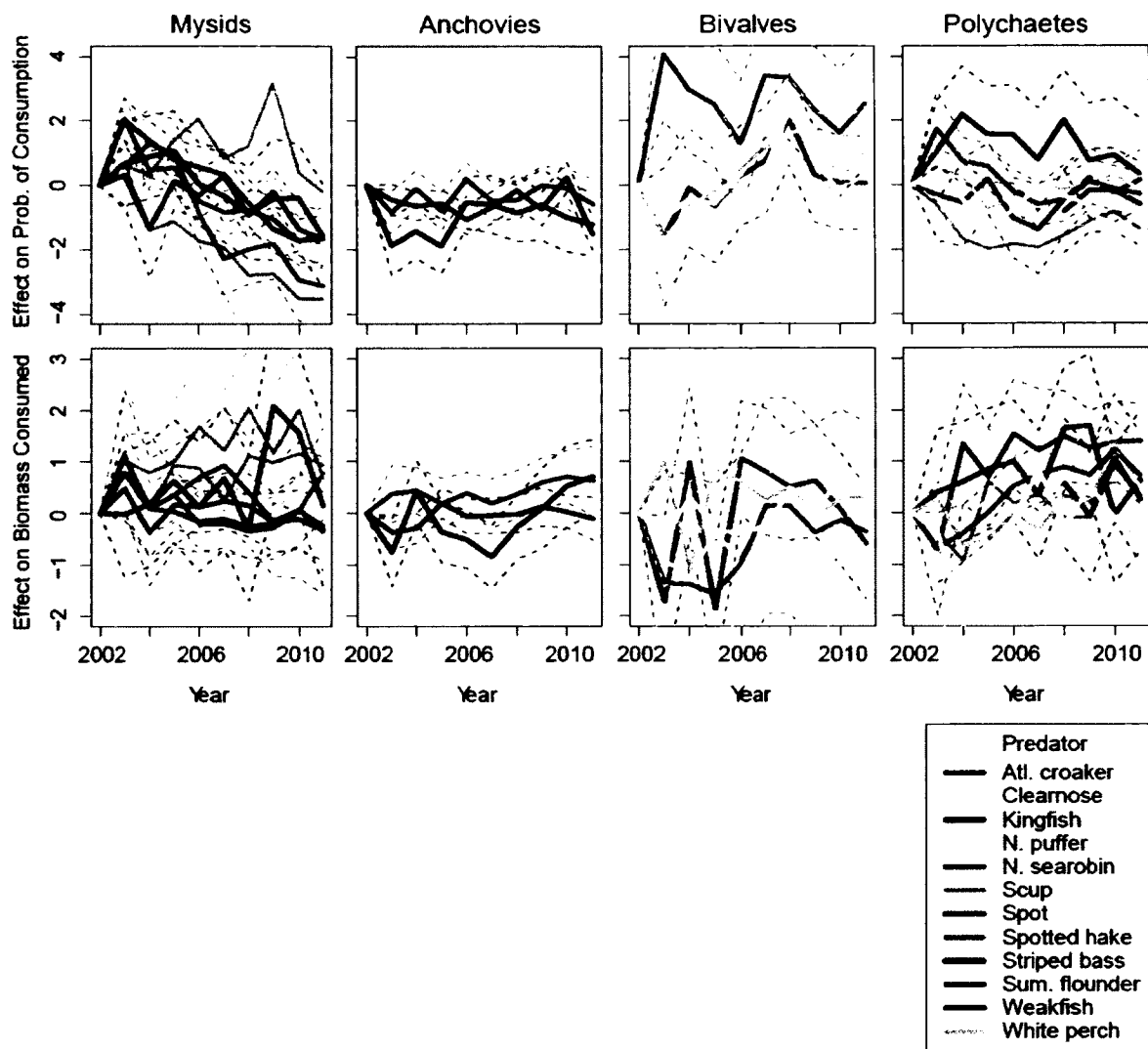


Figure 7.



Supplemental Figure S1.

CHAPTER 4

SIMULATING BOTTOM-UP EFFECTS ON PREDATOR PRODUCTIVITY AND CONSEQUENCES FOR THE REBUILDING TIMELINE OF A DEPLETED POPULATION

ABSTRACT

Bottom-up control within ecosystems relies, in part, on predator populations exhibiting growth and recruitment changes in response to variability in prey density or production. Annual prey availability can vary more than 10-fold in marine ecosystems, with prey experiencing a dramatic increase or pulse in production in some years. In order to assess the bottom-up effects of such pulses on predator growth, production, and fisheries management, we developed an age-specific, predator-prey simulation model (parameterized for summer flounder, *Paralichthys dentatus*) based on simple hypothesized mechanisms for consumption, growth, and population dynamics. Pulses in each of the three modeled prey groups generated differing magnitudes of change in predator weight-at-age (w), spawning stock biomass (S), fishery yield (Y), and recruitment (R), due to ontogenetic differences in growth potential and dietary composition across predator age classes. Increases in productivity of small forage fishes generated the greatest gains in predator w , S , Y , and R , relative to pulses of either small crustaceans or larger fish prey. Median increases in R following a prey pulse were minimal (<4%) except under high fishing rates that stimulated a stronger compensatory response in the population (8-11% increase in R), demonstrating the interactive role of top-down and bottom-up effects on predator productivity. Seasonal migration patterns determined the degree of spatiotemporal predator-prey overlap with the spatially constrained pulses in prey production. Prey pulses reduced the median time required for depleted populations to be rebuilt by 0-5% following declines in fishing pressure, but reductions were highly variable due to recruitment stochasticity and stock recovery was more sensitive to the severity of harvest control measures. Understanding the relative magnitudes of such bottom-up processes, particularly in the presence of varied fishing pressure can aid in developing ecosystem approaches to fisheries management that account for such ecological interactions more explicitly.

INTRODUCTION

Bottom-up control in ecosystems is characterized by productivity and variability of higher trophic levels being largely regulated by processes acting on lower trophic levels. Although other forms of control (top-down and wasp-waist) can be dominant in some systems or under certain conditions (Hunt and Stabeno, 2002; Cury and Shannon, 2004; Hunt and McKinnell, 2006), bottom-up structuring of ecosystems is supported in various marine systems (Aebischer et al., 1990; Verheye, 2000; Chavez et al., 2003; Frederiksen et al., 2006). A simple mechanism supporting such bottom-up control can consist of: 1) environmentally-mediated increases in prey production and density, 2) enhanced foraging by predators, 3) improved growth, survival, and fecundity of predators, and 4) greater recruitment to the following generation of the predator population. The relationship between predator density and prey density (at adjacent trophic levels) that would link the two ends of this mechanistic progression has been described in terrestrial literature as a predator's reproductive numerical response (Solomon, 1949; Holling, 1959). For marine fishes, direct empirical support for this numerical response mechanism is stronger for steps 1-3 (e.g., McGowan et al., 1998; Ringuette et al., 2002; Castonguay et al., 2008), but wanes through its progression to step 4 (e.g., McFarlane and Beamish, 1992; Beaugrand et al., 2003), particularly as the scale of inference expands to the population (Hunsicker et al., 2011). Thus, at broad scales, support for reproductive numerical responses by fishes tends to be more correlative in nature (Aebischer et al., 1990; Ware and Thomson, 2005; Frank et al., 2007), with the

mechanistic components corroborated empirically at smaller spatiotemporal scales or supported theoretically.

Aside from observation error, two of the main difficulties in linking prey densities and predator densities at system-wide scales involve the high degree of interannual variability in predator-prey populations and the adaptive foraging behaviors of most fishes. Populations of fishes and other organisms commonly experience 10-fold variability in recruitment, but variations can be even more drastic (>100-fold) as recruitment and mortality are influenced by a complex suite of climatic, oceanographic, ecological, and anthropogenic factors (Rothschild, 1998; Hunt and Stabeno, 2002; Houde, 2009). In certain years or periods, an aggregation of ameliorative conditions can cause dramatic increases, or pulses, in production (Holland et al., 1987; Rothschild, 1998; Jung and Houde, 2004b). These pulses in production can be targeted and consumed heavily by predators, especially by relatively opportunistic fishes that can switch to these prey as they become more available (Gerking, 1994; Ringuette et al., 2002; Castonguay et al., 2008). However, the ability of predators to exploit pulses in prey production is partially mediated by the ontogenetic changes in preferences and diets they exhibit as they age and grow (Gerking, 1994; Wootton, 1998; Scharf et al., 2000). Understanding a predator's growth and numerical responses to the large inherent variability in prey production can be an important component to characterizing the trophodynamic mechanisms controlling fisheries production.

The potential benefits of increased prey production to predators can also interact with top-down fishing pressure and be influenced by spatiotemporal overlap of the interacting species. For exploited predator populations, fishery removals are a dominant

source of mortality, and a reproductive numerical response could be dissipated by the harvest of any surplus predator production that results from prey pulses. Movement of predatory populations also has the potential of obscuring any bottom-up effects, given that prey production can be regionally confined. For example, many marine fishes have life histories dependent on estuaries, where prey production can be greater relative to alternative offshore habitats (Beck et al., 2001; Able, 2005). Thus, the degree of movement between estuarine and offshore regions could influence predator-prey overlap, predatory growth, and the numerical response.

In this study, we evaluated the population-scale consequences of increased prey availability on a predator stock. We applied a mechanistic, multi-species simulation modeling approach to standardize for recruitment and natural variability and to isolate the effects of prey pulses on a predator population. The age-specific, spatially-explicit predator-prey model linked consumption, growth, and population dynamics sub models. The model was parameterized for summer flounder, *Paralichthys dentatus*, because it is an important fisheries resource in the Northwest Atlantic Ocean (Terceiro, 2002), and its life history (e.g., migration, ontogenetic diet shifts, life span) is representative of several other commercially exploited species. Previous research from the Chesapeake Bay, which is the largest estuarine nursery area serving the coastal summer flounder population (Able and Kaiser, 1994), demonstrated strong episodic increases in prey consumption likely driven by prey availability (Chapter 3). These annual periods of increased consumption were also correlated with larger weight-at-age (A. Buchheister, unpublished data). The simulation model provided a controlled environment for examining questions regarding the potential population-scale response to these prey

pulses. We were specifically interested in examining the relative effects of three different prey groups that are consumed and targeted at varying rates through ontogeny, as is common in the diets of many fishes (Latour et al., 2008, Chapter 2). Multiple modeling scenarios were used to address three major research questions: 1) How do pulses in productivity of different prey populations influence the growth, production, and reproductive numerical response of a migratory predator? 2) How do fishing rates and migration patterns interact with a population's ability to harness regionally-localized increases in prey production? 3) What influence would these prey pulses have on rebuilding timelines of an overfished predator population? Understanding the relative magnitudes of these bottom-up processes, particularly in the presence of varied fishing pressure can aid in developing ecosystem approaches to fisheries management that account for such ecological interactions more explicitly (Link, 2010a).

METHODS

Base model formulation

We developed a spatially-explicit, age-specific simulation model that consisted of linked population, growth, and consumption submodels. Within the population submodel, the key abundance fluxes modeled were decreases in abundance due to fishing and natural mortality, movement between regions, and additions through recruitment. The growth submodel calculated mean individual weight as a function of consumption and was linked to the population submodel by its effect on the spawning stock biomass of the population. We modeled consumption using a multispecies type II functional response model that was dependent on forced biomasses of three functional prey groups: prey 1 – small crustaceans such as mysids (e.g., *Neomysis americana*) and shrimps, prey 2 – small forage fishes (e.g., *Anchoa mitchilli*), and prey 3 – larger fishes (e.g. *Leiostomus xanthurus*) and cephalopods (e.g. *Doryteuthis pealeii*, *Illex illecebrosus*). Although the diversity of prey species consumed is greater (Chapter 2, 3), these three prey groups capture the majority of general prey types summer flounder consume in the wild (Link et al., 2002; Staudinger, 2006; Latour et al., 2008; Buchheister and Latour, 2011b). Biomasses of prey species were forced in the model under the simplifying assumption that top down control of prey by the single modeled predator was negligible. We coded the model for two linked spatial domains or ecosystems: 1) nearshore estuaries and bays and 2) offshore continental shelf waters. We treated time discretely, using a seasonal (three month) time-step to account for the highly seasonal dynamics of summer

flounder movement, spawning, and growth. The order of processes within each time step was as follows: recruitment, mortality, consumption, growth, and movement (with the census taken at the end of each season). We divided summer flounder into 8 age-classes from age-0 to age-7+, following the convention of recent stock assessments (Terceiro, 2011). With the simulation model, we explored a three-way factorial combination of scenarios involving different prey pulses, fishing pressure, and movement conditions. All symbols and equations used in the simulation model are described in Tables 1 and 2. The equations in Table 2 are referenced by Tx.y, with x denoting the table number and y indicating the equation number within the table. All default parameter values are presented in Appendix Table A1.

Population submodel

We modeled the summer flounder population abundance (P) as an exponential decrease following initial recruitment (R). Recruitment was regulated by Beverton-Holt stock recruitment (SR) dynamics, and declines in population abundance were dictated by instantaneous rates of natural mortality (M) and fishing mortality (F). At each time step, the net movement (I) of fish was calculated as a proportion of individuals within a region that moved to the neighboring region. The population submodel is described by:

$$P_{y,a=0,s=1,r} = R_{y,r} = \frac{\alpha_{SR} S_{y,s'}}{(1 + S_{y,s'} / \kappa_{SR})^{\beta_{SR}}} \theta_r e^{\delta_y} L_{y,a,s} \quad (1)$$

$$P_{y,a,s,r} = (P_{y,a,s-1,r} + I_{y,a,s,r}) L_{y,a,s} \quad (2)$$

$$P_{y,A,s=1,r} = (P_{y-1,A-1,A,r} + P_{y-1,A,A,r} + I_{y,A,1,r}) L_{y,a,s} \quad (3)$$

where $P_{y,a,s,r}$ is the age a predator abundance in year y , season s , and region r . Recruitment was dependent on: the coast-wide annual spawning stock biomass ($S_{y,s}$; eq. T2.8) during the spawning season (s); the SR parameters α_{SR} , β_{SR} , and κ_{SR} (Rothschild et al., 2012); the fraction of the total recruitment that occurs in region r (θ_r); a stochastic error term $\delta_y \sim N(0, \sigma_\delta^2)$; and the fraction of juvenile fish that is not lost to natural and fishing mortality during the season ($L_{y,a,s}$; eq. T2.9). Following a recent stock assessment (Terceiro, 2011), the instantaneous natural mortality rate was held constant ($M=0.25$), whereas annual fishing mortality rates ($F_{y,a}$) were age-specific based on age-dependent selectivities (eq. T2.10). The net immigration of age- a fish into region r during year y and season s ($I_{y,a,s,r}$) was estimated using assumed parameters for the proportions of regional pools that migrate into the neighboring region (eq. T2.7). When $s=1$, P is evaluated based on P for the age $a-1$ fish from season four of the previous year (eq. T2.1-3). Age- A (the plus group) predator abundance during $s=1$ ($P_{y,A,s=1,r}$) was calculated using the abundances of the surviving members of age- A fish plus age $a-1$ individuals that joined the group (eq. T2.3). The initial population abundances by age in the first year were set to the stock assessment estimates for 1989 (Terceiro, 2011), divided evenly between regions and constant across seasons.

Growth submodel

We used a simple conversion efficiency approach to model the changes in mean weight-at-age of summer flounder through time and space. Prior to accounting for mixing between regions, weight-at-age was defined as:

$$w_{y,a,s,r} = w_{y,a,s-1,r} + f_{s,r} K_{y,a,s,r} \sum_{j=1}^k C_{j,y,a,s,r} \quad (4)$$

where $w_{y,a,s,r}$ is the mean weight (kg) for age- a fish in season s and region r , $K_{y,a,s,r}$ is the gross conversion efficiency by which consumed prey mass is converted to somatic mass (T2.15; Brett, 1979; Ney, 1993), $C_{j,y,a,s,r}$ is the biomass consumed (kg) of each prey j by an age a predator in season s and region r , and f is a temperature-dependent function that scales the consumption and growth of fish to account for the physiological changes in maximum consumption and growth attainable in different seasons (T2.16; Hanson et al., 1997). We set the initial weight of an age-0 individual in the first season as a constant (w_0) derived from empirical data from the Chesapeake Bay (Table A1). We modeled the conversion efficiency ($K_{y,a,s,r}$) as a decreasing logistic function of weight to account for the physiological decline in growth rate and greater energy allocation to reproduction that occurs through ontogeny (T2.15; Brett, 1979). The parameterization of conversion efficiency is described below (see *Base model calibration*). To account for mixing of fish from the two regions following their movement, the final seasonal weight-at-age within a region was calculated as an abundance-weighted mean of the individuals that ended in that location (T2.12), but equation 4 describes the growth process prior to population mixing.

Consumption submodel

We modeled predatory consumption ($C_{j,a,s,r}$) using a multispecies functional response (Koen-Alonso 2007):

$$C_{j,y,a,s,r} = \frac{C_{a,s}^{\max} \alpha_{j,a,s} N_{j,y,s,r}^h}{C_{a,s}^{\max} + \sum_{j=1}^k \alpha_{j,a,s} N_{j,y,s,r}^h} \quad (5)$$

where $C_{a,s}^{\max}$ is the maximum consumption (in kg) for age- a predators in season s , $\alpha_{j,a,s}$ is the attack rate or suitability of prey j to age- a predators, $N_{j,y,s,r}$ is the stochastically variable biomass (kg) of prey j in year y , season s , and region r (eq. T2.25), and h is a shape parameter assumed to be $h=1$ which corresponds with a hyperbolic Type-II functional response (Koen-Alonso, 2007). To account for the ontogenetic shifts in feeding and diet (Chapter 3), we modeled the attack rates as a logistic decline for prey 1 (eq. T2.23), a dome-shaped double logistic curve for prey 2 (eq. T2.24), and a logistic increase for prey 3 (eq. T2.23). See *Base model calibration* below for parameterization of the functional response model. We estimated $C_{a,s}^{\max}$ as an allometric function of mean body weight using parameters for striped bass (Hartman and Brandt, 1995b) that reproduced empirical trends in summer flounder stomach fullness (eq. T2.22; A. Buchheister, unpublished data).

Base model calibration

Parameterization of the base model was informed by fishery independent survey data, stock assessment reports, and available literature (Table A1). Few suitable empirical values existed for parameterizing the growth and consumption submodels, so we calibrated them to two relationships: 1) the empirical weight-at-age of summer flounder captured over 10 years in a fishery-independent trawl survey from Chesapeake Bay (n=4849 individuals; Bonzek et al., 2011); and 2) a general, simplified ontogenetic

trend in diet composition by predator age that was informed by empirical stomach content data (Chapter 3). We used a stepwise approach in the calibration to select suitable parameters. First, we optimized the conversion efficiency parameters (K^{max} , KR , KW) to minimize the mean square error of weight-at-age estimates (relative to modeled means from empirical data), assuming a constant consumption of 40% of C^{max} . We then simultaneously optimized functional response parameters (λ , ρ) for the three prey by minimizing the sum of the mean square errors for dietary composition from survey results and the weight-at-age data. Thus, the unknown consumption parameters were chosen to replicate dietary trends and growth trajectories for wild summer flounder.

Model scenarios

Prey scenarios

The three prey scenarios (Table 3) involved introducing random pulses in prey production that elevated the standing stock biomass of each prey ($N_{j,y,s,r}$) above its long-term mean value based on the equation:

$$N_{j,y,s,r} = \bar{N}_2 \tau_j \psi_{j,y,r} e^{\gamma_{j,y,s,r}} \quad (6)$$

where \bar{N}_2 is the mean biomass for prey 2, τ_j is the biomass of prey j relative to prey 2, $\psi_{j,y,r}$ is a biomass multiplier for prey j in year y and region r , and $\gamma_{j,y,s,r}$ is a stochastic error term $\sim N(0, \sigma_\gamma^2)$. The \bar{N}_2 term was set at 30 kmt (Jung and Houde, 2004a), and τ_j was set assuming prey 1 and prey 3 biomasses were an order of magnitude higher and lower than \bar{N}_2 , respectively, based on their different trophic levels (Link, 2010b). For the base model, the biomass multiplier was forced to be constant at $\psi=1$. For each prey scenario,

five years ($n_{pulse}=5$) were randomly-selected within a 25-year “experimental” period (within years 26-50, following a 25-yr burn in period) during which ψ was assigned a random number between two and six for the nearshore region ($r=1$) only. This range for ψ was chosen because, on average, it generated a maximum increase of 10-fold for prey biomass levels across simulations (after accounting for the random stochastic variability, which alone generated 2-3 fold differences in N); a 10-fold variability in prey biomass and recruitment is not uncommon (Houde, 2009). In summary, each prey oscillated randomly around its respective mean, but for a given prey scenario, that prey would experience a 2-6 fold increase in biomass (in addition to the stochastic variability) within the nearshore region during 5 random years (Fig. 1).

Fishing sub-scenarios

We developed three sub-scenarios that examined the influence of fishing pressure on the population’s response to the simulated prey pulses (Table 3). These sub-scenarios simulated fishing mortality rates that were constant and high (“H”, $F_{max}=1.5$), constant and low (“L”, $F_{MSY}=0.31$), or decreasing through time (“D”, linear decline from F_{max} to F_{MSY} over 12 years, starting at year 26). We chose these F values to mimic the trends observed in the Northwest Atlantic summer flounder population in which F averaged 1.5 from 1982 to 1996 before management actions reduced F to a target value ($F=0.255$) over a period of ~12 years (Terceiro, 2011). For our simulations, the target F value was set at F_{MSY} , the fishing mortality that achieved maximum sustainable yield (MSY) in the base model when stochasticity was set to 0 (Fig. A1). Spawning stock biomass for MSY (S_{MSY}) was defined as the equilibrium S when F_{MSY} was maintained. For assessing the

time required to rebuild depleted stocks, two additional fishing scenarios were generated for comparison with sub-scenario D: F was reduced twice as fast (“D2”, linear decline from F_{\max} to F_{MSY} over 6 years), and F mimicked a moratorium (“M”, immediate shift from F_{\max} to $F=0$ at year 26).

Movement sub-scenarios

To evaluate the role of spatial connectivity in transferring the bottom-up pulses in prey production to the predator population, two movement sub-scenarios were constructed (Table 3). The migration (“mig”) sub-scenario relied on proportional movements of fish between the two regions that are in line with their seasonal life history strategies, moving nearshore during summer and offshore for winter (Table A1; Packer et al., 1999; Terceiro, 2002). We treated movements as constant across ages, assuming that effects of age-specific differences in movement (e.g., overwintering of age-0 fish in the nearshore area) were negligible. This seasonal movement pattern was contrasted with a fully mixed (“mix”) sub-scenario in which recruitment to regions and migration between regions was held constant at 50%.

Model evaluation

Output

The output metrics of interest were classified at individual- and population-level scales. Each simulation of a scenario was run with identical stochastic perturbations (in recruitment and prey biomass) as the base model, and we evaluated the difference

between the two models. As an individual-scale response metric, we calculated the mean percent increase in weight-at-age (Δw) during the pulse years, defined as:

$$\Delta w = 0.2 \sum_{y^*} \frac{w_{y^*,a,s=4,r=1}^{scen} - w_{y^*,a,4,1}^{base}}{w_{y^*,a,4,1}^{base}} \times 100 \quad (7)$$

where y^* are the years in which a prey pulse occurred, $w_{y^*,a,s=4,r=1}^{scen}$ is the weight-at-age of fish in years y^* in season 4 and region 1 for either a simulated scenario (*scen*) or for the base model (*base*), and the coefficient 0.2 represents the inverse of the number of years in which a pulse occurred ($1/n_{pulse}$). In this fashion, we isolated the change in mean individual body size that was solely due to the change in prey availability. As population-scale metrics, we calculated the mean percent increase in the spawning stock biomass (ΔS), the annual fishery yield (ΔY), and the following year's recruitment (ΔR) using equation 6, but substituting $S_{y^*,s}$, Y_{y^*} , and $\sum_r R_{y^*+1,r}$ for $w_{y^*,a,4,1}$ respectively. Annual fishery yield (Y_y) was calculated as the sum of all catches across seasons, regions, and ages, using Baranov's catch equation (eq. T2.11).

To assess the influence of the prey pulses on achieving management rebuilding goals, we calculated the percent decrease in the time needed to achieve S_{MSY} (Δt) as:

$$\Delta t = \frac{t_{rebuild}^{base} - t_{rebuild}^{scen}}{t_{rebuild}^{base}} \times 100 \quad (8)$$

where $t_{rebuild}$ is the rebuilding time (yrs) needed for a depleted population to reach S_{MSY} following a reduction in F for either a simulated scenario (*scen*) or for the base model (*base*). For this metric, examined scenarios were restricted to combinations of the three prey pulse scenarios, the three non-constant F sub-scenarios (De-F, D2-F, and Mo-F), and

the migration sub-scenario. Larger Δt values indicate that S_{MSY} was attained more rapidly in the scenario compared to the base model.

The stochastic simulation model was run 100 times for each unique combination of scenarios. The output metrics are presented as boxplots depicting the distribution of values across the 100 simulation runs. Cumulative frequency plots of $t_{rebuild}$ across the 100 simulation runs were also used to quantify the probability of reaching S_{MSY} based on the number of years following the reduction in F. We ran all models for 80 years, with the first 25 years as a burn-in period. Prey pulses occurred randomly from years 26-50, and the final 30 years allowed for the population to equilibrate.

Sensitivity

Sensitivity of the model output was investigated using two approaches. First, to evaluate the relative sensitivity to each model parameter, we re-ran the simulation 100 times after increasing or decreasing an individual parameter by 20%. This was done repeatedly for each parameter, holding all of the other values at their default values. For the ψ values, the default range of a 2-6 fold increase in production was modified to be either a 2-4 fold or a 4-6 fold increase in production. We calculated the mean difference of each output metric (Δw , ΔS , ΔY , ΔR , Δt) from the default scenario models, restricting the models to the De-F and migration sub-scenarios. For the second, Monte-Carlo sensitivity approach, we simultaneously varied all parameter values randomly (uniformly within 20% of their defaults) to examine the influence of parameter uncertainty and potential parameter interactions on the model results and conclusions.

RESULTS

The calibrated base model reproduced the mean weight-at-age of wild summer flounder and the general dietary trends with relatively high precision. Temporal stochasticity in prey biomasses generated variability in the dietary composition of simulated fish (± 10 -20%; Fig. 2A), as seen in normal conditions in the field (Chapter 3). Seasonal consumption by predator age did not attain the maximum value, but averaged 28-73% of the maximum consumption (across years), which are reasonable values based on bioenergetics studies for other fishes (Fig. 2B; Hartman and Brandt, 1995b; Stevens et al., 2006). These trends in consumption translated into weight-at-age trajectories that corresponded strongly with mean empirical values from the field (Fig. 2C), suggesting that the consumption and growth submodels generated reasonable results.

Scenario results

Pulses in prey production were utilized by predators and increased their weight-at-age to varying degrees (Fig. 3). Patterns in the percent increase in weight-at-age followed trends in dietary composition (Fig. 2A); the weight of an age-class increased the most when its most-consumed prey experienced a pulse in production. During pulse years, pulses in prey 1 generated median increases in weight of 16-18% for age-0 and age-1 fish and declined for older age classes. Pulses in prey 2 caused a median peak increase of 21% in weight of age-1 fish with a subsequent decline. Prey 3 pulses generated a median peak of 13% at age-3 and slowly tapered off at older sizes. The

relatively large increases in weight-at-age generated by prey pulses were well within the range of observed body sizes from wild fish suggesting that such changes in weight are feasible in natural environments (Fig. 4). The model also reproduced the seasonality in growth patterns that are observed for summer flounder and other fishes (Fig. 4; Powell, 1982). The mixed sub-scenario generated nearly identical trends to the migration sub-scenario presented, although the magnitudes of the increases were lower (by as much as 8%). Fishing sub-scenarios had no effect on weight-at-age changes because there were no density-dependent controls on individual growth.

The patterns in the three population-scale metrics (ΔS , ΔY , and ΔR) were similar across the simulated scenarios, although the magnitudes varied (Fig. 5). Relative to the base model, the simulated scenarios generated median increases in S , Y , and R as high as 19%, 11%, and 11% respectively. Generally, ΔS values were higher than ΔY or ΔR . In comparing across the prey scenarios, pulses in prey 2 consistently yielded stronger increases in ΔS , ΔY , and ΔR (with medians up to 13% higher) relative to pulses in prey 1 and 3, regardless of the fishing or movement sub-scenarios. However, an interaction between the effect of prey pulses and fishing pressure was observed; prey 1 pulses generated greater increases in S , Y , and R than prey 3 pulses in the high F sub-scenario, yet the opposite was true for the low F sub-scenario. The two movement sub-scenarios demonstrated that median increases in S for a given prey pulse were significantly greater (1-3.5%) for the mig sub-scenario relative to the mix scenario.

The influence of the different prey pulses on the recovery time of the overfished stock was highly variable, yielding 0-75% reductions in $t_{rebuild}$ (Fig. 6). The median declines in $t_{rebuild}$ for the Pulse 1 and Pulse 3 scenarios were 0% and the declines were

modest for pulses in prey 2 (4-5%, or 1 year). However, reductions in $t_{rebuild}$ of 10% were not uncommon across scenarios. The largest outliers occurred in simulations where a prey pulse increased S sufficiently to achieve S_{MSY} prior to a random period of poor recruitment that otherwise maintained the base model run below S_{MSY} for an extended length of time (Fig. A2).

Expressing $t_{rebuild}$ values as cumulative probabilities demonstrated the relatively modest declines in $t_{rebuild}$ that resulted from pulses in prey production compared to the different implementations of fishing mortality controls (Fig. 7). For example, prey pulses in fishing sub-scenario D increased the probability of achieving S_{MSY} within 14 years by ~5-8% whereas more stringent implementation of fishing controls (sub-scenario D2) would increase that probability of success by 38%. Under the most drastic fishing sub-scenario (M), prey pulses exhibited no detectable effect on achieving the management target. Under moratorium there was a 50% probability of rebuilding the stock within 4-5 years, compared to 15 and 19 years for the same probability benchmark under the D2 and D base scenarios, respectively.

Sensitivity results

Simulation outputs and conclusions were not overly sensitive to the choice of parameter values. Monte-Carlo sensitivity runs generated similar patterns in Δw , ΔS , ΔY , and ΔR to those presented in Figures 3 and 5, although the variability across simulations increased (~2-fold increase in the interquartile spread), and the median responses tended to decrease slightly (Figs. A3 and A4). Based on perturbations of individual parameters (Fig. A5), Δw , ΔS , and ΔY were most sensitive to prey biomass and consumption

parameters (specifically ψ , \bar{N}_2 , η_3 , and CTO), whereas ΔR was most sensitive to parameters of the population submodel (α_{SR} , β_{SR} , M), prey biomass time series (ψ , \bar{N}_2), and the growth submodel (KL , KR , KW , CTO). However, the Δw , ΔS , ΔY , and ΔR typically varied by no more than $\pm 3\%$ due to the parameter perturbations. The Δt estimates were most sensitive to growth (KL , KR , KW , CTO) and population dynamics (α_{SR} , β_{SR} , κ_{SR} , M) parameters, with perturbations often translated to median values of zero for Δt .

DISCUSSION

Patterns in the population-scale responses to prey pulses integrated the individual growth benefits with population mortality losses and reproductive additions. Physiologically, younger fish have a greater scope for growth facilitating larger proportional increases in weight-at-age than older conspecifics (Brett and Groves, 1979); however this did not necessarily correspond to greater increases in S , Y , and R . The scaling of the weight-at-age responses to the population-level relied on integrating these biomass gains demographically across ages, while addressing the diversion of predatory production gains to natural mortality, fishing, or spawning stock biomass accumulation. Although some prey groups such as mysids and small crustaceans (prey 1) generated relatively strong increases in weight-at-age, these gains were constrained to a more narrow age range than the other prey, and a greater proportion of this production was lost through natural mortality before fish could mature to contribute to increased S and R . Increased production of small forage fishes (prey 2) translated into the largest increases in S , Y , and R because young predators exhibited greater growth, the prey was consumed over a broader range of ages, and many of these fish matured and spawned prior to becoming vulnerable to fishing. Overall, this suggests that the proportional magnitude of bottom-up effects on predatory production reflects a balance between the predator's growth potential (with greater scope at smaller sizes) and the total dietary contribution across age classes, with the increased production routed to natural mortality losses,

fishery removal, or S accumulation based on the rates of mortality, fishing, and maturation.

Top-down pressure on the predator population, in the form of fishery removals, regulated the capacity of the population to respond to the resource-driven, bottom-up forcing. Similar interactions between bottom-up and top-down forces are common in natural ecosystems and demonstrate the dynamic nature of ecosystem structure and control (Hunter and Price, 1992; Hunt and McKinnell, 2006). In our model, this interaction was caused by the density-dependent processes underlying the SR function. By maintaining S at lower levels, higher fishing rates produced stronger population compensation whereby the recruits per spawner was larger (Rose et al., 2001), thus facilitating greater increases in S and R within pulse 1 and 2 scenarios. In the pulse 3 scenario with high F , the additional predatory production was shunted more to the fishery, restricting the accumulation of S and future recruitment. Thus, top down fishing pressure can regulate a population's ability to capitalize on bottom-up forcing by regulating the density-dependent production (i.e., compensation) expected at lower stock sizes.

Recruitment is one of the most critical processes regulating population dynamics, but it remains a challenge to predict given the complex interactions among various density-independent and density-dependent factors that govern recruitment strength (Sissenwine, 1984; Houde, 2009). The reproductive numerical response in this simulation model relied on the density-dependent nature of the SR function, but it was not overly sensitive to the parameterization of the SR function. Although summer flounder recruitment data can appear independent of S in the wild (Maunder, 2012), the

empirical realization of an underlying density-dependent relationship is obscured by large natural variability in recruitment, in addition to sampling and estimation errors of those values. In our simulations, we could rely on broader theoretical and empirical support for compensatory mechanisms operating on fish populations (Rose et al., 2001), while also standardizing and accounting for uncertainty through the inclusion of the stochastic recruitment deviations. Summer flounder and other flatfishes have relatively high steepness values for SR relationships (Maunder, 2012; steepness=0.74 in this study) indicating that recruitment remains relatively high at low S compared to other commercial species (Myers et al., 1999; Rose et al., 2001). Therefore, other species with lower steepness could be expected to exhibit stronger proportional increases in R due to prey pulses, given similar conditions to our simulation.

From a fisheries management perspective, the numerical responses of predators to increases in prey production had relatively minor effects on rebuilding time relative to recruitment variability and fishing pressure. Recruitment stochasticity, which represented various climatic, oceanographic, and ecological processes known to influence recruitment (Houde, 2009), generated far greater variability in rebuilding time than prey pulses alone. The role of strong recruitment years can facilitate the recovery of overfished stocks (Richards and Rago, 1999; Hart and Rago, 2006), but in the wild any numerical responses of the form we have investigated would be imbedded within a complex mosaic of environmental and anthropogenic controls on recruitment. However, our simulations emphasized the predominant role that curbing top-down fishing pressure has on the speed at which target stock sizes are attained (Safina et al., 2005; Rosenberg et al., 2006). Given the greater accumulation of S and stronger reproductive numerical

responses of predators to pulses in prey 1 and 2 (at high F), conservation of prey for younger age-classes of an overfished predatory stock could provide some benefits for rebuilding the population. But, one important caveat is that our simulation assumed that none of the prey resources were depleted or limiting. For example, if prey 3 represented a depleted forage fish population, then that trophic linkage could be a bottleneck for predator nutrition, preventing suitable growth and recovery (e.g., Hartman and Margraf, 2003).

The movement patterns of the simulated population regulated the degree of spatial-temporal overlap of predators with the spatially constrained pulses in prey production. A fully mixed population was less able to capitalize on improved foraging conditions in the nearshore environment. The availability of diverse and abundant prey resources within estuarine and nearshore habitats is an important component selecting for the estuarine-dependent life history strategies of summer flounder and many other coastal fishes (Beck et al., 2001; Able, 2005). Although summer flounder are managed as a unit stock in the Northwest Atlantic, as many as three populations have been proposed (Terceiro, 2002). In cases of increased spatial structure among subpopulations, we would anticipate any reproductive numerical responses of the population to be similarly controlled by the extent of spatiotemporal overlap of predators with areas of increased prey productivity but potentially modified by any spatial patterns in fishing.

The level of complexity for the simulation model was chosen to simplify the mechanistic processes governing consumption, growth, and population dynamics while accounting for the major factors of influence. For example, our simple consumption and growth submodels accounted for the effects of temperature, prey availability, predator

size, and diet ontogeny, which rank as some of the most dominant regulators of prey consumption and growth (Brett and Groves, 1979). We aborted attempts to incorporate greater physiological detail into the growth process using a bioenergetics model (BEM) due to insufficient empirical parameters for anchoring growth estimates to realistic values across the range of ages modeled. One advantage of the BEM approach would have been to account for differences in prey quality, but any prey quality effects on our conclusions are minimized given the similarity in energy densities (within 10%) among summer flounder and representative species from the three prey groups (Hartman and Brandt, 1995b; A. Horodysky and R. Schloesser, unpublished data).

Two model assumptions could potentially have a larger influence on the model dynamics and our conclusions. First, we assumed that the predator-prey system was adequately described using three prey groups. Marine food webs can be highly complex and connected, characterized by a multitude of trophic linkages and high degree of omnivory (Link, 2002b). However, trophic complexity is reduced when prey are aggregated into size or functional groups as we have done (French et al., 2013; Chapter 3), and omnivory and prey switching was incorporated at this coarse resolution of prey (with the multi-species functional response). Our model formulation did not account for any indirect effects among the modeled groups (e.g., pulses affecting other prey groups and their predators), assuming that these effects would be minimal and potentially delayed relative to the modeled direct effects. Second, we assumed that natural mortality was constant as commonly employed in population models and stock assessments (e.g., Terceiro, 2011). However, improved foraging and growth can alter mortality rates and can be part of the mechanism regulating recruitment strength and reproductive numerical

responses (Cushing, 1990; Houde, 2009). These foraging effects on survival appear most drastic and notable on early life history stages of fishes (Sissenwine, 1984; Caddy, 1991), therefore the majority of this effect would occur prior to the initiation of our predator population. Generally, there is limited empirical, quantitative information to parameterize the ecological regulation of natural mortality across ages at the population-scale (e.g., Caddy, 1991; Maunder and Wong, 2011), therefore we were unable to justify the form and magnitude of any effects of prey pulses and improved growth on natural mortality. Consequently, we consider our estimates to be conservative measures of the effects that pulses in prey production have on a predator population.

Age-specific predator-prey models like the one developed here provide a simple framework for testing the effects of bottom-up and top-down influences on a predator population. Given that ecosystem approaches to fisheries management ideally rely on a blend of model types (Link, 2010a), this age-specific approach can complement more complex ecosystem models. Ecosystem models can provide a broader assessment of system-wide consequences (both direct and indirect) of changes in production or fishing, but they do not typically provide high ontogenetic resolution within modeled species groups. As shown in our study, the ontogenetically variable feeding habits of fishes have bearing on the individual- and population-scale responses of predators to bottom-up forcing, particularly for species with varying degrees of historical fishing pressure (Hunt and McKinnell, 2006). In the simulations, depleted populations were the most sensitive to episodic pulses in prey production, but detection of such effects would be easily obscured in wild populations due to other factors influencing recruitment variability which is particularly high at low stock sizes (Myers, 2001). While these bottom-up

effects of prey pulses can benefit rebuilding plans of overfished populations, their small magnitude relative to changes in fishing mortality supports the primacy of regulating fishing for stock recovery.

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TABLE CAPTIONS

Table 1. Description of symbols in Table 2 that were used for the simulation model.

Table 2. Equations for summer flounder (*Paralichthys dentatus*) simulation model consisting of population, growth, and consumption submodels.

Table 3. Description of simulation scenario levels for prey pulses, fishing mortality, and movement.

FIGURE CAPTIONS

Figure 1. Prey biomass time-series (kmt) for a base model run (black line) and a prey pulse scenario (red line) whereby base values are multiplied 2-6 fold for five randomly-selected years between years 25 and 50 (dotted lines).

Figure 2. Growth, consumption, and diet output from one stochastic 80-year run of the base simulation model for summer flounder. A) Diet composition by age for each simulated year (prey 1 – black; prey 2 – red; prey 3 – blue) with the target values (used for calibration) overlaid as smooth thick lines. B) Per capita seasonal consumption for simulated cohorts (C , black lines) relative to the maximum consumption (C^{max} , green line). C) Weight-at-age data for wild summer flounder (gray points) with mean empirical growth curve (red line) and simulated cohort growth curves (blue lines) overlaid.

Figure 3. Percent increase in weight-at-age (Δw) of simulated populations experiencing pulses in prey production relative to the base model populations that experience no pulse. At each age, boxplots are staggered for each of the prey pulse scenarios (prey 1 – gray; prey 2 – red; prey 3 – blue). Boxplots show the distribution of mean values across 100 stochastic simulation runs (colored bar – interquartile range, horizontal line – median, notches – approximate 95% confidence interval for the median, whiskers – furthest value from the quartile within $1.5 \times$ (interquartile range), individual points – outliers).

Figure 4. Simulated growth trajectories for the single fastest-growing cohorts, from all model runs, for each of the pulse scenarios (prey 1 – black; prey 2 – red; prey 3 – blue). Mean growth of all base runs (dashed line) and empirical weight-at-age data (points) also presented. Simulations used a migration sub-scenario with a constant, high fishing mortality (Hi-F subscenario).

Figure 5. Population-scale output metrics of simulated summer flounder (*Paralichthys dentatus*) populations. Percent increase in the A) spawning stock biomass (ΔS), B) fishery yield (ΔY), and C) following year's recruitment (ΔR) for various scenarios were calculated relative to base model runs. Scenarios were comprised of different combinations of fishing mortality trends (high – H; decreasing – D; low – L), prey pulses (prey 1 – gray; prey 2 – red; prey 3 – blue), and movement patterns (migration – Mig; full mixing – Mix). See Figure 4 for boxplot description.

Figure 6. Percent decrease in the time (Δt) needed for simulated depleted populations to rebuild to target spawning stock biomass, relative to the base model. Scenarios were comprised of different combinations of fishing mortality trends (decreasing – D; rapid decrease – D2; and moratorium – M) and prey pulses (prey 1 – gray; prey 2 – red; prey 3 – blue). Results plotted for the migration sub-scenario only. See Figure 4 for boxplot description.

Figure 7. Cumulative probability of achieving the target spawning stock biomass (S_{MSY}) under different simulated pulse and fishing scenarios. Prey pulse scenario indicated by

solid line color (prey 1 – gray; prey 2 – red; prey 3 – blue) relative to its base model (dashed line). Each group of curves reflects a different fishing mortality sub-scenario (moratorium – M, rapid decrease – D2, decrease – D), with black triangles marking the year in which the target F (F_{MSY}) was achieved for each F sub-scenario.

Table 1.

Symbol	Description	Units
Subscript indicators (range/level)		
<i>a</i>	Predator age (0-7+)	years
<i>A</i>	Maximum predator age, plus group (7+)	years
<i>j</i>	Prey type (crustaceans = 1, small fishes = 2, larger fishes = 3)	
<i>r</i>	Region (nearshore estuaries and bays = 1, offshore shelf = 2)	
<i>n</i>	Neighboring region (nearshore estuaries and bays = 1, offshore shelf = 2)	
<i>s</i>	Season (Jan-Mar, winter = 1; Apr-Jun, spring = 2; Jul-Sep, summer = 3; Oct-Dec, fall = 4)	
<i>s'</i>	Spawning season (fall)	
<i>y</i>	Year (1-80)	
<i>y*</i>	Year in which a pulse occurs (5 random years selected from y=26-50)	
Calculated values		
$P_{y,a,s,r}$	Predator abundance by year, age, season, and region	fish
$I_{y,a,s,r}$	Net immigration by year, age, season, and region	fish
$R_{y,r}$	Abundance of surviving recruits by year and region in season 1	fish
S_s	Predator spawning biomass in the spawning season	kg
$L_{y,a,s}$	Fraction of fish that survive by year, age, and season	
$F_{y,a,s}$	Instantaneous fishing mortality rate by year, age, and season	year ⁻¹
$G_{y,a,s,r}$	Somatic growth by year, age, season, and region	kg
$w_{y,a,s,r}$	Average individual weight-at-age by year, season, and region	kg
$K_{y,a,s,r}$	Gross conversion efficiency by year, age, season, and region	
$C_{j,y,a,s,r}$	Per capita consumption by prey, year, age, season, and region	kg prey (kg pred) ⁻¹ s ⁻¹
$C_{\alpha,a,s}$	Maximum per capita consumption by age and season	kg prey (kg pred) ⁻¹ s ⁻¹
$\bar{w}_{s,s}$	Mean empirical weight-at-age by season	kg
$\alpha_{j,a,s}$	Functional response attack rate coefficient by prey, age, and season	(kg prey) ⁻¹
$N_{j,y,s,r}$	Prey <i>j</i> biomass year, season, and region	kg
$f_{s,r}$	Proportion of max consumption attainable by season and region	
<i>V, X, Y, Z</i>	Intermediate calculations for <i>f</i>	
Y_y	Biomass yield to the fishery by year	kg
Parameters		
$\phi_{s,n \rightarrow r}$	Proportion of predators migrating from region <i>n</i> into region <i>r</i> by age and season	
$\phi_{s,r \rightarrow n}$	Proportion of predators migrating from region <i>r</i> into region <i>n</i> by age and season	
F_y	Instantaneous fishing mortality rate by year	year ⁻¹
sel_a	Selectivity of fishery by age	
<i>M</i>	Instantaneous natural mortality rate	year ⁻¹
α_{SR}	Maximum recruitment-per-unit biomass for stock-recruitment relationship	10 ⁶ recruits (kmt) ⁻¹
	Threshold biomass above which the density-dependent effects dominate the density-independent effects.	
K_{SR}		kmt
β_{SR}	Shape parameter for degree of density compensation ($\beta=1$ for Beverton Holt)	
θ_r	Fraction of total recruitment that recruits to region <i>r</i> .	
δ_y	Stochastic recruitment error term $\sim N(0, \sigma_\delta^2)$ by year	
$m_{a,s'}$	Proportion of fish that are mature by age during the spawning season	
w_0	Average individual weight of age-0 predator in first season	kg
<i>KL</i>	Maximum gross conversion efficiency	
<i>KR</i>	Rate parameter for change in gross conversion efficiency	g ⁻¹
<i>KW</i>	Weight at which <i>K</i> is 50% of <i>KL</i>	g
<i>h</i>	Shape parameter for functional response (Type II when <i>h</i> =1)	
λ_j	Scale parameter for maximum attack rate by prey	(kg prey) ⁻¹
ρ_j	Rate parameter for change in attack rate with age for prey <i>j</i>	years ⁻¹
η_j	Age at which attack rate is 50% of λ_j	years
η_{1j}, η_{2j}	Inflection points for ascending and descending limbs of double logistic equation	years
<i>CA</i>	Intercept for the allometric relationship between <i>C</i> and predator mass	
<i>CB</i>	Rate parameter for the allometric relationship between <i>C</i> and predator mass	
\bar{N}	Mean biomass for prey 2	kg
τ_j	Biomass of prey <i>j</i> relative to biomass of prey 2	
$\psi_{j,r}$	Prey biomass multiplier by year and region;	
$v_{j,y,s,r}$	stochastic error term $\sim N(0, \sigma_v^2)$ for prey <i>j</i> biomass by year, season, and region	
$T_{s,r}$	Mean bottom water temperature by season and region	C
<i>CTM</i>	Maximum water temperature above which consumption ceases	C
<i>CTO</i>	Optimal water temperature for maximum consumption	C
<i>CQ</i>	Rate parameter for temperature function	

Table 2.

Equation	Reference
Population submodel	
<i>Population dynamics (s = 1)</i>	
$P_{y,a=0,s=1,r} = R_{y,r} = \frac{\alpha_{SR} S_{y,s'}}{(1 + S_{y,s'} / \kappa_{SR})^{\beta_{SR}}} \theta_r e^{\delta_y} L_{y,a,s}$	T2.1
$P_{y,a,s=1,r} = (P_{y-1,a-1,4,r} + I_{y,a,s,r}) L_{y,a,s}$	T2.2
$P_{y,A,s=1,r} = (P_{y-1,A-1,4,r} + P_{y-1,A,4,r} + I_{y,A,1,r}) L_{y,a,s}$	T2.3
$I_{y,a,s=1,r} = \varphi_{s,n \rightarrow r} P_{y-1,a-1,4,n} - \varphi_{s,r \rightarrow n} P_{y-1,a-1,4,r}$	T2.4
$I_{y,A,s=1,r} = \varphi_{s,n \rightarrow r} (P_{y-1,A-1,4,n} + P_{y-1,A,4,n}) - \varphi_{s,r \rightarrow n} (P_{y-1,A-1,4,r} + P_{y-1,A,4,r})$	T2.5
<i>Population dynamics (s > 1)</i>	
$P_{y,a,s,r} = (P_{y,a,s-1,r} + I_{y,a,s,r}) L_{y,a,s}$	T2.6
$I_{y,a,s,r} = \varphi_{s,n \rightarrow r} P_{y,a,s-1,n} - \varphi_{s,r \rightarrow n} P_{y,a,s-1,r}$	T2.7
<i>Supporting equations</i>	
$S_{y,s'} = \sum_{r=1}^2 \sum_{a=0}^A P_{y,a,s',r} w_{y,a,s',r} m_{a,s'}$	T2.8
$L_{y,a,s} = e^{-0.25(M+F_{y,a})}$	T2.9
$F_{y,a} = F_y \cdot sel_a$	T2.10
$Y_y = \sum_{s=1}^4 \sum_{r=1}^2 \sum_{a=0}^A \frac{F_{y,a}}{M + F_{y,a}} (1 - L_{y,a,s}) P_{y,a,s,r} w_{y,a,s,r}$	T2.11
Growth submodel	
<i>Growth</i>	
$w_{y,a,s,r} = \frac{1}{P_{y,s,r,a}} \left(\frac{P_{y,a,s-1,r} L_{y,a} (1 - \varphi_{s,r \rightarrow n}) (w_{y,a,s-1,r} + G_{y,a,s,r}) +}{P_{y,a,s-1,n} L_{y,a} \varphi_{s,n \rightarrow r} (w_{y,a,s-1,n} + G_{y,a,s,n})} \right)$	T2.12
$G_{y,a,s,r} = f_{s,r} K_{y,a,s,r} \sum_{j=1}^k C_{j,y,a,s,r}$	T2.13
$w_{a=0,s=1,r} = w_0$	T2.14
$K_{y,a,s,r} = \frac{K^{\max}}{(1 + e^{-KR(1000w_{y,a,s,r} - KW)})}$	T2.15
<i>Temperature dependence</i>	
$f_{s,r} = V^X e^{(X(1-V))}$	T2.16
$V = (CTM - T_{s,r}) / (CTM - CTO)$	T2.17

$$X = \frac{Z^2 \left(1 + \sqrt{(1 + 40/Y)}\right)^2}{400} \quad \text{T2.18}$$

$$Y = \ln(CQ) \cdot (CTM - CTO + 2) \quad \text{T2.19}$$

$$Z = \ln(CQ) \cdot (CTM - CTO) \quad \text{T2.20}$$

Consumption submodel

Functional response

$$C_{j,y,a,s,r} = \frac{C_{a,s}^{\max} \alpha_{j,a,s} N_{j,y,s,r}^h}{C_{a,s}^{\max} + \sum_{j=1}^k \alpha_{j,a,s} N_{j,y,s,r}^h} \quad \text{T2.21}$$

$$C_{a,s}^{\max} = 91 \cdot \bar{w}_{a,s-1} \cdot CA(\bar{w}_{a,s-1})^{CB} \quad \text{T2.22}$$

$$\alpha_{j,a,s} = \frac{\lambda_j}{(1 + e^{-\rho_j(a_s - \eta_j)})} \quad \text{T2.23}$$

$$\alpha_{j=2,a,s} = \lambda_j \left(\frac{1}{(1 + e^{-\rho_j(a_s - \eta_{1j})})} \right) \left(1 - \frac{1}{(1 + e^{-\rho_j(a_s - \eta_{2j})})} \right) \quad \text{T2.24}$$

Prey biomass

$$N_{j,y,s,r} = \bar{N}_2 \tau_j \psi_{y,r} e^{y_{j,y,s,r}} \quad \text{T2.25}$$

Table 3.

Scenarios	Description
<i>Pulse Scenario</i>	
Prey 1	5 annual increases in biomass (2-6 fold) of prey group 1, representing small crustaceans (e.g. mysids, shrimps)
Prey 2	5 annual increases in biomass (2-6 fold) of prey group 2, representing small forage fishes (e.g. anchovies)
Prey 3	5 annual increases in biomass (2-6 fold) of prey group 3, representing larger fishes & cephalopods (e.g. sciaenids, squids)
<i>Fishing Sub-scenarios</i>	
H	Constant, high fishing mortality (F_{max})
L	Constant, low fishing mortality for maximum sustainable yield (F_{MSY})
D	Linear decrease in fishing mortality from F_{max} to F_{MSY} over 12 years
D2*	Linear decrease in fishing mortality from F_{max} to F_{MSY} over 6 years
M*	Immediate, knife-edge decrease in fishing mortality from F_{max} to zero
<i>Movement Sub-scenarios</i>	
Mig	Seasonal migrations between offshore and nearshore habitats
Mix	Spatially mixed population with equal distribution and movement between offshore and nearshore habitats

*These fishing sub-scenarios only used as contrasts to the D sub-scenario for estimating time to recovery.

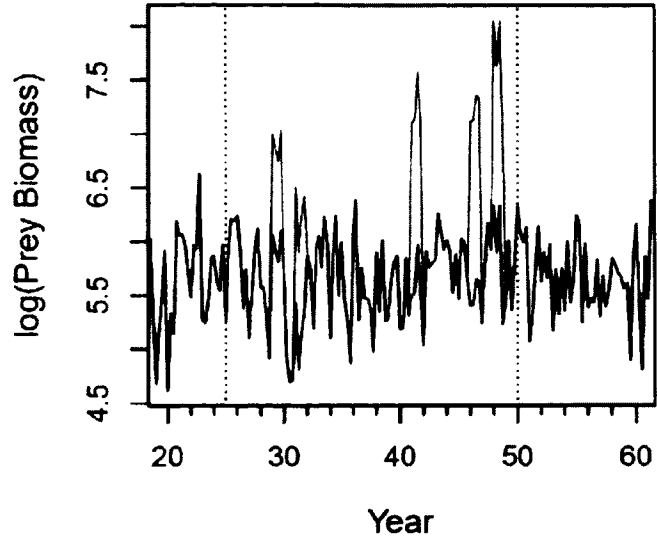


Figure 1.

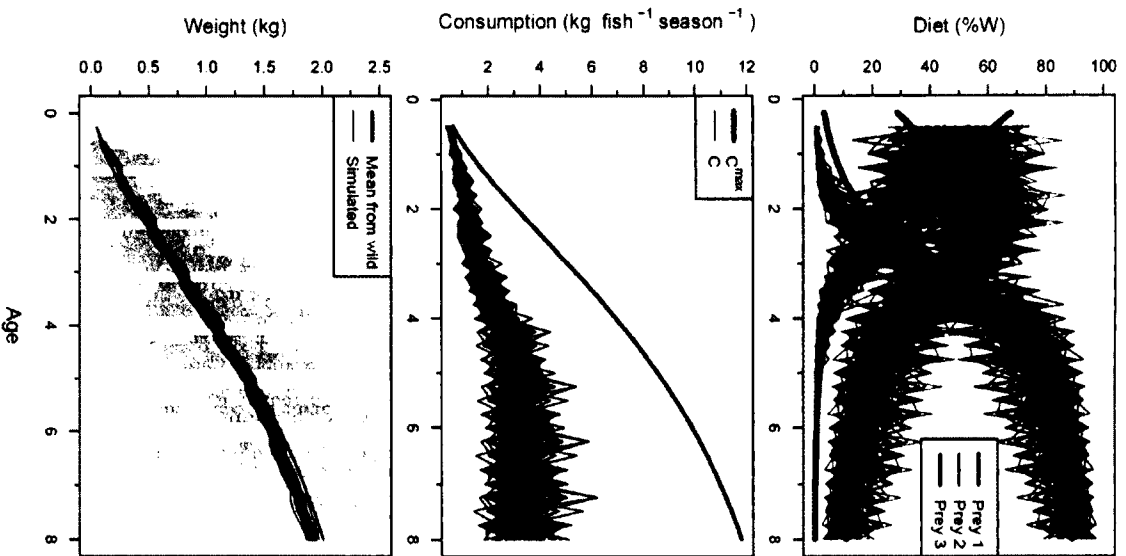


Figure 2.

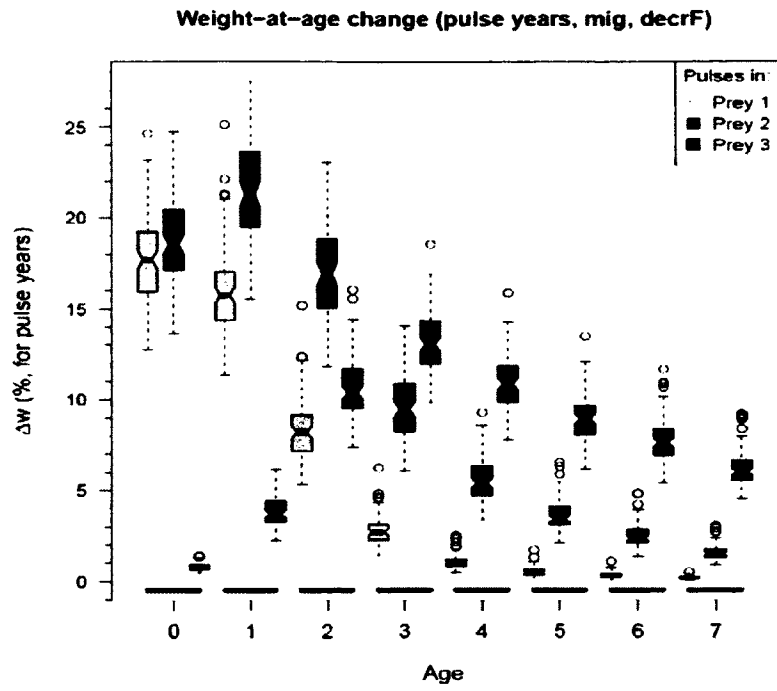


Figure 3.

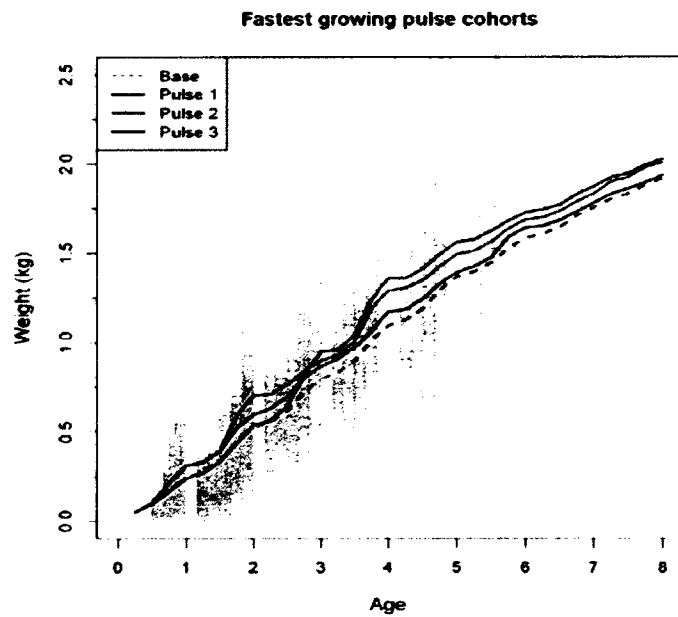


Figure 4.

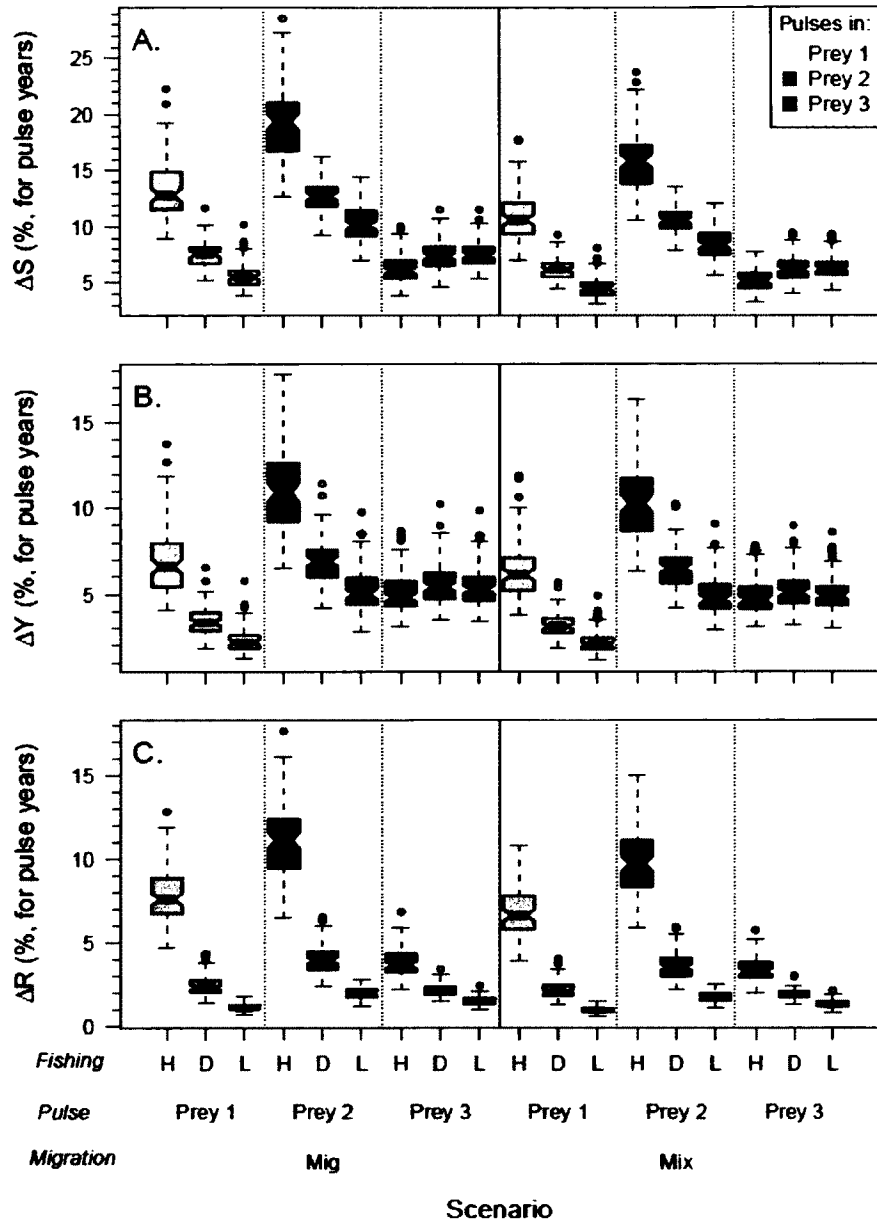


Figure 5.

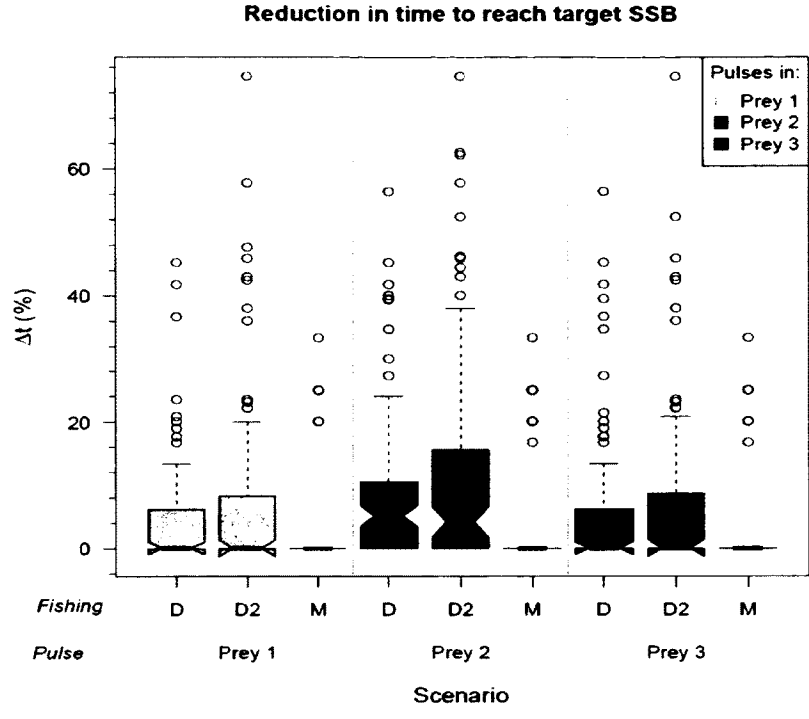


Figure 6.

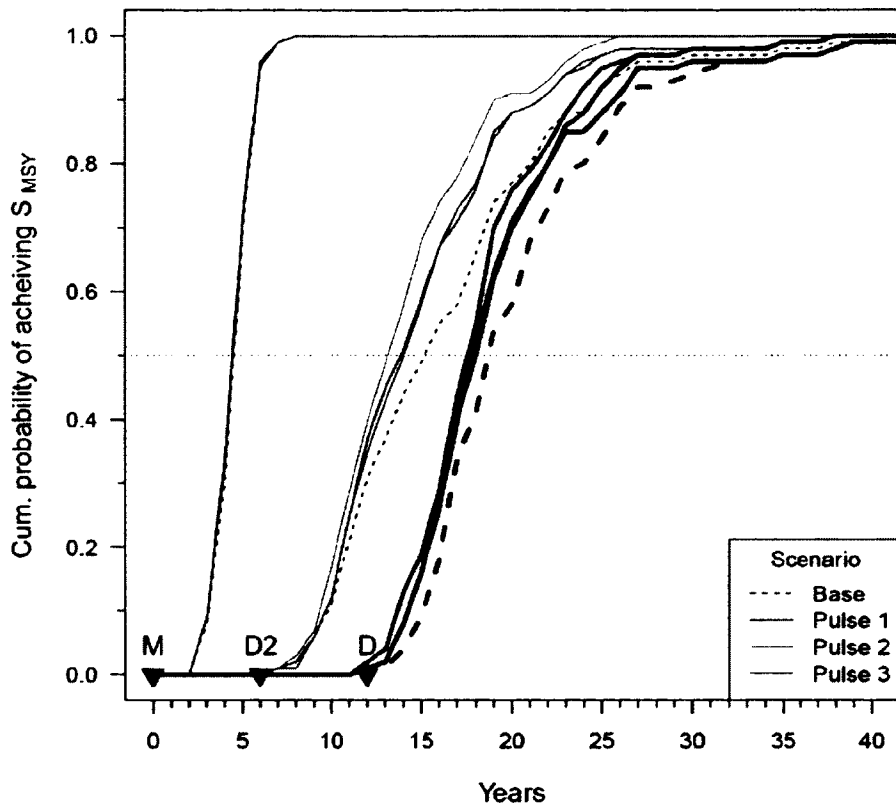


Figure 7.

APPENDIX TABLE CAPTIONS

Appendix Table A1. Default parameter values for base simulation model. See Tables 1 and 2 for symbol definitions and model equations.

APPENDIX FIGURE CAPTIONS

Appendix Figure A1. Sustainable fishery yield (kmt) at varying levels of instantaneous fishing mortality (F). Results were generated from the simulation model with all stochasticity removed. Maximum sustainable yield (MSY) was achieved at $F_{MSY}=0.31$.

Appendix Figure A2. Recovery of spawning stock biomass (S) for a simulated population under the decreasing fishing mortality sub-scenario. This outlier simulation run yielded the biggest difference in the time to reach S_{MSY} (horizontal dashed line) between a pulse scenario (black line) and the base model (red line). Vertical dotted lines denote the start and end of the period in which prey pulses could occur.

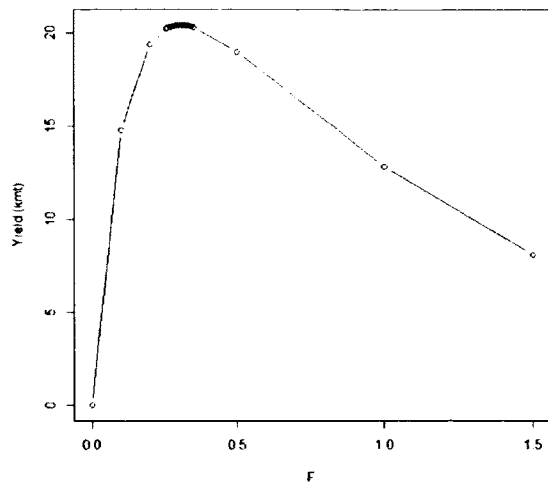
Appendix Figure A3. Monte-Carlo sensitivity results for population-scale output metrics of simulated summer flounder (*Paralichthys dentatus*) populations. Percent increase in the A) spawning stock biomass (ΔS), B) fishery yield (ΔY), and C) following year's recruitment (ΔR) for various scenarios were calculated relative to base model runs. Scenarios were comprised of different combinations of fishing mortality trends (high – H; decreasing – D; low – L), prey pulses (prey 1 – gray; prey 2 – red; prey 3 – blue), and movement patterns (migration – Mig; full mixing – Mix), with model parameters randomly selected within $\pm 20\%$ of default values. See Figure 4 for boxplot description.

Appendix Figure A4. Monte-Carlo sensitivity results for the difference in rebuilding times (Δt) relative to the base model. Models were run by randomly selecting all parameters within $\pm 20\%$ of default values. Scenarios were comprised of different combinations of fishing mortality trends (decreasing – D; rapid decrease – D2; and moratorium – M) and prey pulses (prey 1 – gray; prey 2 – red; prey 3 – blue). Results were plotted for the migration sub-scenario only. See Figure 4 for boxplot description.

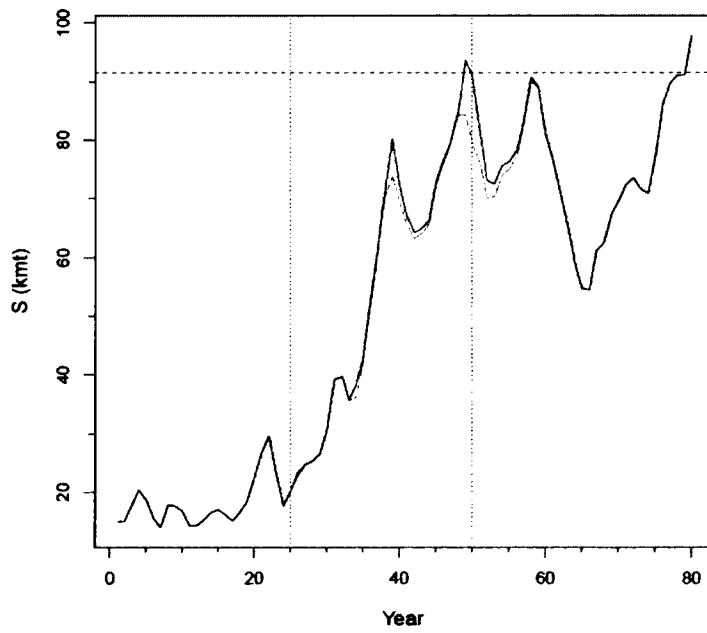
Appendix Figure A5. Sensitivity of model outputs to perturbations of individual model parameters. Each parameter was shifted $\pm 20\%$ (see legend) while holding all other parameters at default values. Mean or median differences in weight-at-age (Δw), spawning stock biomass (ΔS), fishery yield (ΔY), recruitment (ΔR), and rebuilding time (Δt) are presented relative to the standard simulation scenario runs (zero line). Standard simulation scenario runs included pulses in prey 1 (P1), prey 2 (P2), and prey 3 (P3), using the migration and decreasing fishing mortality sub-scenarios. Parameters are grouped based on the process they most directly influence (consumption, growth, prey biomass, or population dynamics). Weight-at-age plot is for age-1 fish which was representative of other age-classes. See Table 1 for parameter definitions. Positive values indicate a stronger effect of a pulse relative to the default simulation.

Appendix Table A1.

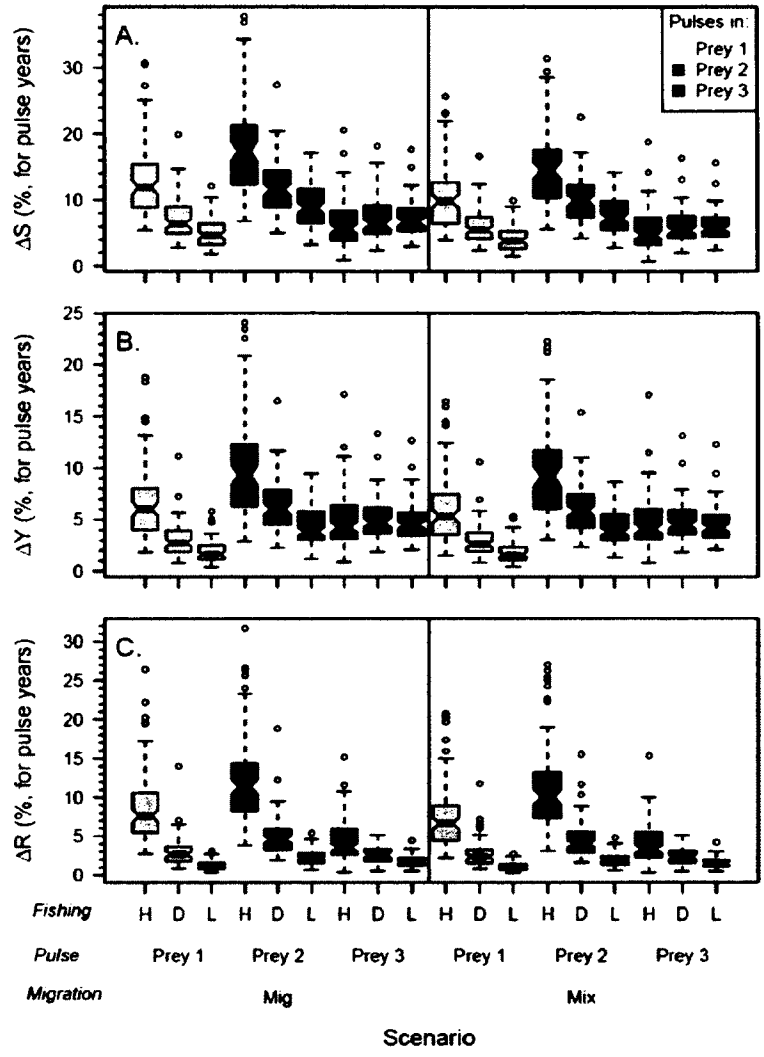
Symbol	Parameter Value	Sources
$\phi_{s,n \rightarrow r}$	$\phi_{s,1 \rightarrow 2}=0.0, 0.0, 0.4, 0.9$	Packer et al. 1999; Terceiro 2002
$\phi_{s,r \rightarrow n}$	$\phi_{s,2 \rightarrow 1}=0.3, 0.95, 0.0, 0.0$	Packer et al. 1999; Terceiro 2002
F_y	see F scenarios	Terceiro 2011
sel_a	$sel_a=0.0, 0.1, 0.5, 1, 1, 1, 1, 1$	Terceiro 2011
M	0.25	Terceiro 2011
α_{SR}	3.4	Rothschild et al. 2012
K_{SR}	27	Rothschild et al. 2012
β_{SR}	1	Rothschild et al. 2012
θ_r	$\theta_1=0.9, \theta_2=0.1$	assumed
δ_y	$\sigma_\delta=0.4$	Terceiro 2011
$m_{a,s'}$	$m_{a=0-3+}=0.38, 0.72, 0.90, 1.0$	Terceiro 2011
w_0	0.051	A. Buchheister unpublished
KL	0.5	optimized
KR	-0.0014	optimized
KW	-600	optimized
h	1	assumed
λ_j	$\lambda_1=e^{-19.5}, \lambda_2=e^{-16.3}, \lambda_3=e^{-13.5}$	optimized
ρ_j	$\rho_1=-1.1, \rho_2=0.46, \rho_3=1.9$	optimized
η_j	$\eta_1=2, \eta_3=3.5$	optimized
η_{1j}, η_{2j}	1, 4	optimized
CA	0.3	modified from Hartman and Brandt 1995
CB	-0.2	modified from Hartman and Brandt 1995
\bar{N}	3×10^{10}	Jung and Houde 2003
τ_j	$\tau_1=10, \tau_3=0.1$	assumed
$\psi_{y,r}$	$\psi_{y^*,1}=U(2,6)$; otherwise $\psi=1$	assumed
σ_v	$\sigma_v=0.4$	assumed
$T_{s,r}$	$T_{s,1}=4.4, 13.6, 24.4, 14.8$; $T_{s,2}=7.6, 10.8, 13.5, 15.2$	Chesapeake Bay Program and NEFSC databases
CTM	35	assumed
CTO	22	assumed
CQ	2.5	Modified from Burke and Rice 2002



Appendix Figure A1.

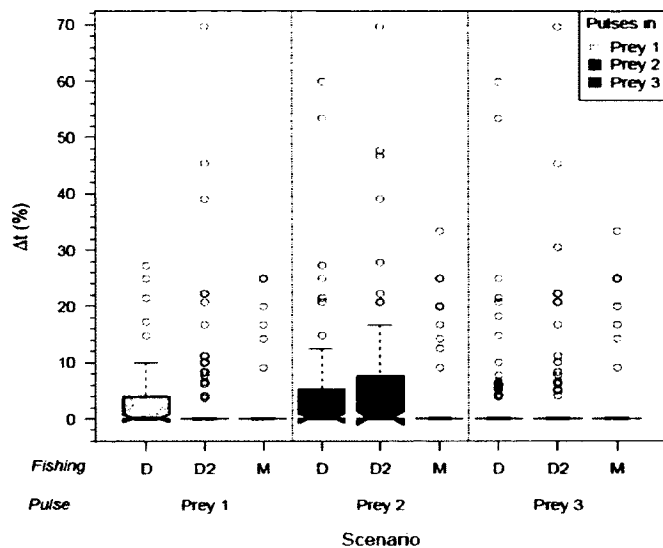


Appendix Figure A2.

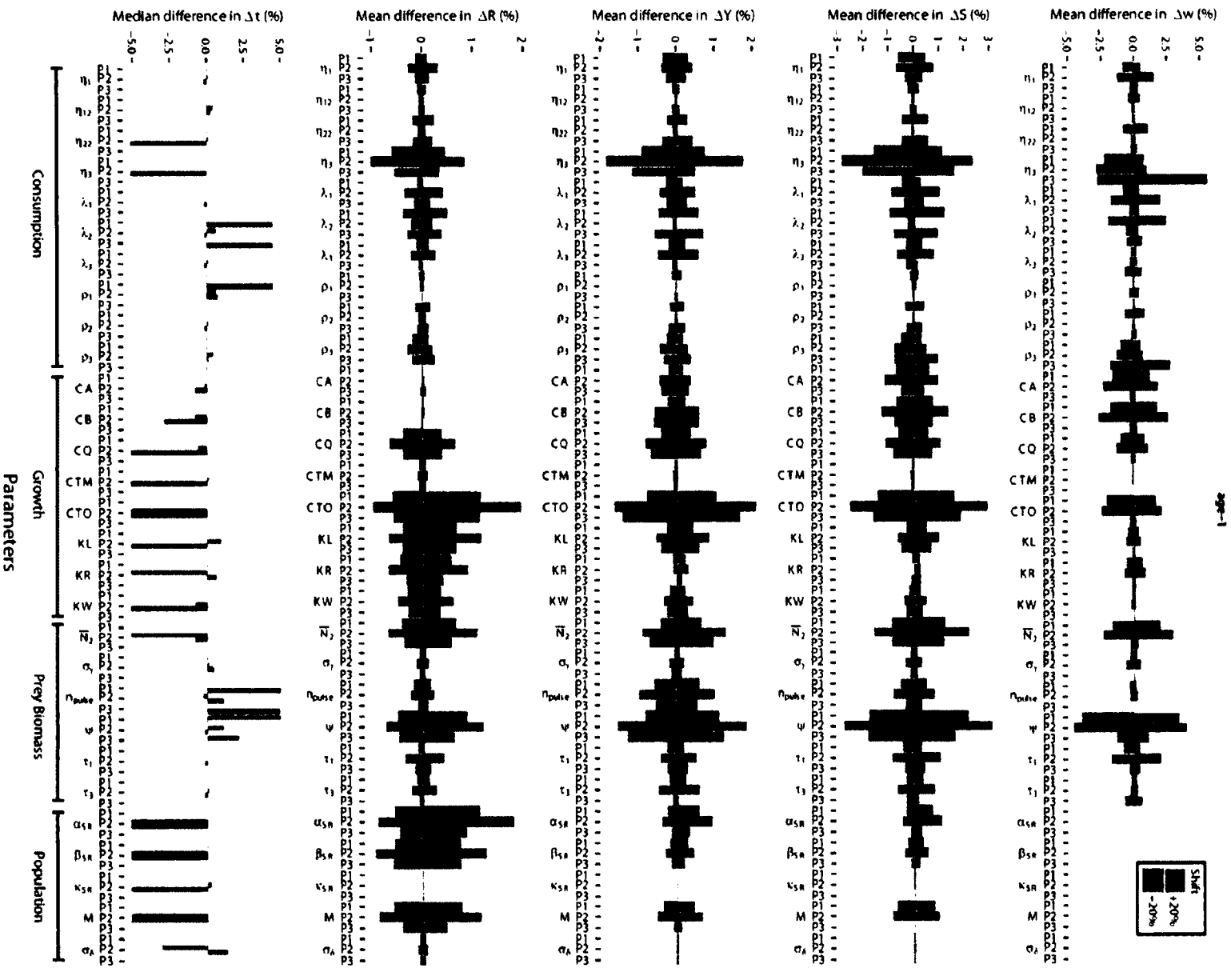


Appendix Figure A3.

SENSITIVITY: Reduction in time to reach target SSB



Appendix Figure A4.



Appendix Figure A5.

CONCLUSION

This dissertation set out to achieve two over-arching objectives, 1) synthesize basic biological and ecological information for the demersal fish community of Chesapeake Bay and 2) examine the drivers of its structure and trophic dynamics. By utilizing a rich, 10-year dataset of fishery-independent bottom trawl catches, water quality, and fish diet composition, I was able to conduct some of the largest studies of their kind on community and trophic dynamics in an estuarine environment.

A theme that was reinforced across the individual studies was the dynamic, variable, and heterogeneous nature of fish populations and trophic interactions. Small- and large-scale patterns in fish distribution and abundance were predominantly established by biophysical drivers, with community structure largely dictated by the latitudinal salinity gradient that separated fishes by life history characteristics (e.g., anadromous vs. coastal shelf spawners). Dissolved oxygen was also a causal driver for distributional heterogeneity as noted with analyses that represented one of the first quantitative demonstrations of the strong negative effect of hypoxia on demersal fish catches and distribution at a broad-scale in Chesapeake Bay, confirming a variety of other studies conducted at smaller scales or in the pelagic environment. The role of environmental factors was also evident in the variable consumption patterns of fishes; however, the similarity of consumption trends across predators supported a generally opportunistic predation strategy that facilitated the use of predators as prey sampling

“devices”. Despite the heterogeneity of trophic interactions, food web linkages were simplified by aggregating prey into broader groups of which mysids, bay anchovy, bivalves, polychaetes, and other crustaceans were the most important. Food resources were largely partitioned among fishes by body size and habitat, demonstrating that the complexity in trophic interactions can be simplified when the processes underlying ecological patterns are identified.

Interannual patterns in community and trophic dynamics were evident across the studies, although identifying their drivers and underlying processes was challenging. Following 2007, Chesapeake Bay experienced a decline in overall catches and a shift in species composition, corresponding with declines in fisheries landings. Recruitment levels were implicated as a potential driver, but the directionality of the relationship for one major species group opposed the hypothesized relationship, potentially indicative of a more complex underlying process. Annual trends in prey consumption by diverse predators were suggestive of opportunistic diets that responded to dramatic changes in prey availability. However, this hypothesis could not be confirmed by independent indices of annual prey abundance due to lack of available data, observation error, scaling issues, or species aggregation. The distinct annual patterns in community structure and trophic interactions likely indicate broad-scale forcing of system dynamics, but natural variability, data issues, observation or process error, and a relatively short time series hindered uncovering strong support for the underlying processes. Maintaining long-term monitoring of demersal fishes in Chesapeake Bay would alleviate many of these problems.

Another emergent theme from the dissertation was the role of bottom-up and top-down processes in controlling system dynamics and production. As mentioned, biophysical drivers helped establish the conditions that regulated species distributions, abundances, and dietary trends through bottom-up processes. However, the magnitude of prey pulses on predator productivity (i.e., a bottom-up effect) was modest compared to the control by fishing for rebuilding a simulated, overfished population. The severity of fishing also regulated the compensation capacity of the population, altering its ability to exploit any prey pulses; thus, bottom-up and top-down forces acting on populations and systems can form a dynamic equilibrium that varies under different conditions (e.g., Hunter & Price 1992, Hunt & McKinnell 2006).

One of the most important extensions from this work in more of an ecological context would be to continue investigating the role and dynamics of mysids within Chesapeake Bay. This work solidifies mysids as one of the most critically important prey groups in the bay, joining copepods and bay anchovy in this regard (Baird and Ulanowicz, 1989). Although predator diets were useful in describing relative patterns in mysid distribution and abundance, more targeted research would be needed to elucidate their population dynamics. For example, the presumed pulse in mysid production in 2003 corresponded with anomalous temperature, salinity, and chlorophyll measurements, indicating that mysids may be sensitive to large-scale environmental drivers and climate change. Mysids not only couple benthic and pelagic environments (Jumars, 2007), but they also act as a transitional prey item (e.g., between copepod and bay anchovy prey) for larger predators. Much like bay anchovy, mysids (*Neomysis americana*) are a critical single-species node within the Chesapeake Bay food web with no ecologically functional

equivalents. Consequently, changes in the mysid population (stemming from natural or stress-induced variability) could have significant consequences for ecosystem structure and functioning, but there is currently little information available to gauge their relative impacts.

The broad motivation behind the dissertation was to advance the science for implementation of ecosystem-based fisheries management (EBFM) in Chesapeake Bay. Previous work by a multi-institutional panel of experts identified research needs for EBFM within a fishery ecosystem plan (FEP; CBFEP 2006). This dissertation addressed several of the research recommendations that pertained to population and community structure, trophic interactions, natural and anthropogenic drivers, multi-species modeling, and ecosystem indicators. Much of the dissertation helps provide a fuller, quantitative description of the patterns and drivers of the system, which is needed for understanding the processes regulating the system (Underwood et al., 2000). Such information can be used to help characterize changes in the system that might result from natural or anthropogenic stressors, while also providing a 10-year frame of reference for ongoing monitoring. The diet synthesis provides valuable dietary data that can augment ongoing ecosystem modeling efforts within the bay using Ecopath with Ecosim and Atlantis software. The simulation model developed can be used as a complement to these ecosystem models to evaluate the effects of prey conditions on management of a predator species. And lastly, the results contribute to the development of ecosystem indicators by either quantifying simple indicators (e.g., aggregate species CPUEs and biodiversity metrics) or providing trophic data to inform development of trophic guild indicators.

One logical next step for this research would be to leverage its unique products, in conjunction with the wealth of other available studies, and move towards policy-forming advice and research for EBFM. The dissertation generated community- and system-level data and information to support EBFM, but implementation of EBFM in Chesapeake Bay requires strategic and tactical advances in its framework. Link (2010) advocates a three-stage decision-theoretic framework for EBFM implementation: 1) define goals (e.g., prioritization, biomass allocation), 2) assess the system, and 3) establish decision criteria (e.g., reference points matched to control rules). Guidance and recommendations for EBFM goals for Chesapeake Bay are available in the *Chesapeake 2000* agreement (CBP 2000) and the FEP, though they are more strategic in nature. System assessments exist in the form of the FEP and products from the Chesapeake Bay Program; additionally, assessments can utilize data from the varied monitoring programs or analyses like those from Chapter 1. The third stage of the EBFM framework, establishing decision criteria, is one area that requires substantial development, but is dependent on the formulation of clear tactical goals.

Two of the challenges hindering EBFM implementation in Chesapeake Bay are 1) the complexity of the system and EBFM approaches, and 2) buy-in from stakeholders (fishers, conservationists, managers, scientists). One approach to deal with the complexity of EBFM approaches has been to incrementally incorporate ecosystem considerations into fishery management plans (e.g., accounting for predation mortality in Atlantic menhaden assessment). Focusing on some focal species and their interactions may provide a simpler and more tangible approach to EBFM to minimize the jurisdictional, stakeholder, and implementation complexity of whole-system

management. As an example, my post-doctoral research will use ecosystem models to develop ecosystem-based reference points for Atlantic menhaden cognizant of their key ecosystem services (e.g., food for predators), and it will use a management strategy evaluation (MSE) approach to evaluate the trade-offs associated with different harvest levels. In a broad sense, tactical MSE applications that engage stakeholders and a focus on certain species groups may be two strategies to facilitate greater buy-in from stakeholders that are resistant to transitioning from the status quo (e.g., scientists, managers) or those that are commonly frustrated with top-down regulation (e.g., fishers).

Despite the challenges and complexities of EBFM, there is growing consensus that accounting for ecological and technical interactions within ecosystems is merited for fisheries management (Link, 2010a; Essington and Punt, 2011). Research on community structure, trophic dynamics, and their drivers, as addressed in this dissertation, fortifies the scientific underpinnings for more holistic management of aquatic systems. These integrative ecosystem approaches to fisheries management will facilitate the sustainable and responsible use of the diverse and valuable resources derived from Chesapeake Bay and other similar ecosystems.

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