2018

Consumption Patterns of Chesapeake Bay Fishes

Christopher James Sweetman
College of William and Mary - Virginia Institute of Marine Science, cjsweetman@vims.edu

Consumption Patterns of Chesapeake Bay Fishes

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

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by

Christopher James Sweetman

August 2018

APPROVAL PAGE

This dissertation is submitted in partial fulfillment of

the requirements for the degree of

Doctor of Philosophy

Christopher James Sweetman

Approved by the Committee, July 2018

Robert J. Latour, Ph.D.
Committee Chair / Advisor

Jan R. McDowell, Ph.D.

Eric J. Hilton, Ph.D.

Mark J. Brush, Ph.D.

Andrij Z. Horodysky, Ph.D.
Hampton University
Hampton, Virginia, USA

DEDICATION

To my parents, James and Claire Sweetman, for their constant support and decades spent nurturing my passion of nature. You made me believe that I can do anything I want if I set my mind to it. Also, to my grandparents, Charles and Dorothy Sweetman and Richard and Lucille Langevin; may your light always shine through.

TABLE OF CONTENTS

ACKNOWLEDGEMENTS

The process of completing a doctoral dissertation can be challenging in a multitude of ways. The guidance, direction, and support I have received throughout the years have been instrumental in shaping me as a person and as a researcher. I am extremely thankful for each of my committee members for their help in developing my dissertation. First, I would like to thank Robert Latour for always challenging me to do more than I thought I was capable of. I also thank him for his tutelage, academic support, and patience in guiding me through hours of scientific discourse and statistical lessons. Jan McDowell was a constant source of encouragement during a period of time when I sorely needed it. Her enthusiasm towards my research and mentorship in the genetics laboratory enabled me to implement and complete a project that I had spent years developing. I am truly honored to have collaborated with her and consider her both a respected colleague and a friend. The teachings of Eric Hilton and Mark Brush throughout their courses and in personal communications have kept me grounded in my research. Often times we try to think about the bigger picture in our research efforts, but if we ignore the details then our inferences can be biased and both Eric and Marc served as reminders to never stop thinking mechanistically. I also would like to thank Andrij Horodysky for constantly challenging me to improve myself as a scientist and his physiological insight was pivotal in designing experiments and interpreting subsequent results.

In addition to my committee, I received help from many other VIMS faculty and staff. I'd especially like to thank the VIMS Multispecies Research Group for their help in collecting and managing much of the data that I used in my research. I especially thank Jim Gartland and Jameson Gregg for their help in developing, logistically organizing, and implementing a new survey on top of their constantly rigorous field schedules. To this point, I also thank Dustin Gregg, Greg Mears, Cameron Ward, Ben Davis, Taylor Moore, Rebecca Hailey, Jeffrey Eckert and Evan McComber for spending extra days away from their family and friends to help me with data collection for my research. I also thank Melanie Chattin for her expertise in stomach content identification, which formed the basis for much of the work in my dissertation. Additionally, Debra Gauthier also assisted with stomach content analyses and provided her knowledge of GIS to better illustrate the scope of my research. I also thank Chris Bonzek for his help with my many database queries and always being available to answer any questions I had. To the captains and crew that operate the VIMS large vessel fleet, including Durand Ward, John Olney Jr., Keith Mayer, and Voight "Bubba" Hogge, I cannot begin to explain how invaluable your insight was and how much of a pleasure it has been to work with you. To Mary Fabrizio and Troy Tuckey, I thank you for your willingness to collaborate on several projects and for your support. I thank Wendy Lowery and the crew of the Juvenile Fish and Blue Crab Survey for their meticulous collection of data that was incredibly important in my dissertation.

VIMS has provided me with a unique opportunity to interact with many intelligent and enjoyable people and I thank them for their conversations that have meant so much to me, both

personally and professionally. I am grateful for my lab mates, past and present, including: Jeanna Hudson for her genuine kindness and support; Cassidy Peterson for her many contributions in my dissertation development and for being a great friend; Mark Stratton, also for his friendship, and many late-night discussions about all walks of life; Carissa Gervasi for reminding me to not take life so seriously all the time; Kathryn Sobocinski for her bioenergetics modeling teachings and her love of all things New England; Andre Buchheister for laying the foundation as to how dietary analyses should be performed and for allowing me to pick his brain throughout the years, and Patrick Lynch for setting the bar so high. I also would like to thank other VIMSers whom I have shared a laugh with or whom I have had the pleasure of conversing with. There are far too many to be named but some include Kristy and Kevin Spanik, Cassie Lovall, Matt Whalen, Gina Ralph, Gabby Saluta, Amy Then, Kattie McMillan, Wes Hudson, Kristen Omori, Leeza Ailloud, Brandon Conroy, Lela Schlenker, Sean Charles, Heidi Brightman, Hamish Small, Nadya Mamoozadeh, Toddy Clardy, Ali Deary, Kate Bemis, Diego Vaz, Peter Konstantinidis, Peter Warth, Cindy Marin, Andrew Wozniak, and Tony Nalovik,

My journey to VIMS was strongly influenced by several mentors including Ann Bucklin, Tracey Sutton, Brian Ortman, and Paola Batta-Lona. I am humbled by the opportunities and experiences that each of you provided me to help guide my academic career. Their advocacy and willingness to take a chance on a kid fresh out of college helped steer me towards doing what I've always wanted to do since I was seven years old. I am forever in your debt.

I am especially grateful to my family James, Claire, Josh, and Ashleigh Sweetman. You all believed in me and helped nourish my passion for the sea. You taught me to fight for what I believe in and to be proud of what I do. Having family that is unconditionally supportive not only helped me in times of need, but also served as a driving force to complete this dissertation. I strive to make you proud in all walks of life, as a professional and as a person. I also want to thank my godparents, Rob Sweetman and Lynn Langevin, for their unwavering support and interest in what I have chosen to do as a profession and for their words of encouragement throughout the years. I also want to thank the rest of my extended family for their love throughout my life. Finally, I want to extend the largest thanks to my partner in all walks of life, Kristene Parsons. You inspire me every day and I could not have done this without you. From the bottom of my heart, thank you for being you. "In high tides or in low tides, I'll be by your side."

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

CHAPTER 2

DISSTERTATION ABSTRACT

As fisheries management moves away from single-species approaches and towards more holistic, ecosystem-based approaches, physiological and ecological interactions need to be explicitly considered and mechanistically understood. Accurate portrayals of food web interactions and the direction and magnitude of energy flow between predator and prey populations are fundamental components to further develop ecosystem-based fisheries management (EBFM). To bolster information that is required within an EBFM framework in the Chesapeake Bay, I conducted research designed to advance traditional dietary studies and better understand the form and structure within the Bay's food web. This research relied on controlled feeding experiments, comprehensive sampling of predator and prey communities, and over 10 years of data from the Chesapeake Bay Monitoring and Assessment Program (ChesMMAP) and the Juvenile Fish and Blue Crab surveys. The dissertation presented here has two main objectives: 1) incorporate additional methodologies to improve stomach content identification, and 2) examine the drivers of trophic interactions and consumption within a suite of abundant and economically valuable predatory fishes in the Chesapeake Bay.

Prey that is considered unidentifiable is often ignored in stomach content analyses, but can account for a significant proportion of fish diets. In Chapter 1, I demonstrate the use of molecular techniques to detect specific prey consumed by Atlantic croaker (*Micropogonias undulatus*) and evaluate factors that influence the rate of gastric evacuation. Molecular protocols developed to identify specific prey DNA from stomach contents determined that DNA from blue mussel (*Mytilus edulis*) can be detected as long as prey resides in the stomach (~30 hours), which is long after prey can be considered visually identifiable. Furthermore, temperature significantly influenced gastric evacuation rates and therefore should be considered throughout the collection process to ensure accurate identification of prey. Chapter 2 evaluated prey selection patterns among three sympatric predators in the Chesapeake Bay: weakfish (*Cynoscion regalis*), summer flounder (*Paralichthys dentatus*), and Atlantic croaker. Comprehensive sampling of predator and prey (midwater, zooplankton, benthic) populations revealed selection patterns on dominant prey selection taxa driven by a variety of mechanisms. Bay anchovy selection was significantly influenced by predator size in both weakfish and summer flounder. Mysid selection was driven by both fish size and Julian Day in weakfish and by temperature in summer flounder. Atlantic croaker select for both polychaetes and bivalves, with selection patterns relating to predator size and Julian Day. To evaluate how trophic linkages and environmental conditions influence consumption, bioenergetics models were developed in Chapter 3 for young-of-the-year Atlantic croaker and weakfish. Annual consumption from 2006 – 2016 was estimated and subsequent

analyses demonstrated that prey abundance metrics significantly influenced the observed consumption patterns.

This research represents a comprehensive study on predator-prey interactions within the Chesapeake Bay and contributes to a broader understanding of fish ecology and production patterns. The results from this dissertation provides a better understanding of food web structure and aids in the development EBFM strategies towards the sustainable use of marine living resources.

CONSUMPTION PATTERNS OF CHESAPEAKE BAY FISHES

INTRODUCTION

Fisheries management

The status and sustainability of the world's marine fish stocks are of great concern to managers as many are depleted or have ultimately collapsed (Jackson et al. 2001; Pauly et al. 2002; Rosenberg et al. 2005). As global human populations continue to increase, so has the demand for living marine resources. Systematic practices of overfishing of top predators (Myers and Worm 2003; Baum and Myers 2004) have led to a reallocation of effort that has had cascading effects throughout marine ecosystems. For example, the mean trophic level of catches has declined around the globe as upper-level predators are overfished and sequentially replaced by less valuable, lower trophic level species and has been described as 'fishing down the food web' (Pauly et al. 1998). Conversely, some lower trophic level fisheries within marine ecosystems have increased despite the maintenance of high fishing pressure on upper trophic level fisheries (Essington et al. 2006). The implications of such fishing practices are likely to have major impacts on the structure of marine food webs and their ability to maintain resiliency in the face of anthropogenic and environmental perturbations.

Current management of fisheries has largely relied on single-species models with an emphasis placed on biological reference points such as abundance, biomass, recruitment, and fishing mortality. These models typically seek to obtain estimates for a maximum sustainable yield that can be harvested from a particular stock. However, traditional single-species management often neglects ecological and technical interactions, which are essential for estimating current and potential production patterns of a stock (Link 2010; Link et al. 2012). Many fisheries scientists and managers of aquatic resources believe that management approaches that explicitly account for ecological interactions, especially those of a trophic nature, are better suited to sustainably manage living marine resources (Pauly and Christensen 2002). The development of a more holistic approach to management, termed ecosystem-based fisheries management (EBFM), requires knowledge of complex, interacting factors including biological, physical, social, and economic considerations. By definition, the goals of EBFM are 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 meaningful ecological boundaries" (Garcia et al. 2003). Within the framework of EBFM, an understanding of ecological, environmental, and anthropogenic processes must be advanced to provide empirical support for the development and application of management strategies (Whipple et al. 2000; Latour et al. 2003; Link 2010).

An important process within the EBFM framework involves the fate and fluxes of nutrients and energy within a food web. The quantitative descriptions of energy flow allow for insights into the fundamental structure of an ecosystem (Baird and Ulanowicz 1989) and provide a reference point to evaluate the impact of far-reaching ecosystem effects such as overfishing, environmental variability, and climate effects. Food webs are formed by the trophic interactions between species within an ecological community and can ultimately dictate the fate and flux of both predator and prey populations within an ecosystem (Pimm 1982). Without understanding the mechanisms that structure food webs, be it through bottom-up or top-down forcing factors, the ability to implement EBFM is difficult.

Trophic interactions and consumption

At the most basic level, determining the structure of food webs relies on understanding the diets of predators. Predator-prey interactions play a pivotal role in structuring marine food webs through the regulation of energy flow within systems, and can have direct and indirect influences on both predator and prey assemblages (Wootton 1998; Ware and Thomson 2005; Buchheister and Latour 2015). The production and ability of fish populations to recover from perturbations can be strongly influenced by species interactions (Baum and Worm 2009; Gamble and Link 2009; Essington 2010; Tyrell et al. 2011). Production in marine fisheries is largely regulated by three main drivers: 1) fisheries exploitation, 2) biophysical processes, and 3) trophodynamics (Link et al. 2010; Gaichas et al. 2012). Although conditions vary amongst different marine ecosystems, ecological effects (e.g. trophodynamics) can often be the dominant driver of fisheries production (Link et al. 2012). To this point, effects of competition and predation have been shown to exceed the removals from fisheries (Gamble and Link 2009; Tyrell et al. 2011), thus the accurate identification and quantification of interactions are of great importance.

Accurate characterization of trophic interactions and subsequent ecosystem-scale food web analyses relies on the assumption that stomach content analyses are unbiased. Visual identification of prey from fish stomach contents has yielded considerable insight into food web dynamics and remains the standard approach to understanding trophic interactions (Hyslop 1980). Despite this, a large component of the marine food web is not amenable to the standard visual approach. Prey items may be cryptic or damaged during ingestion, rapidly digested beyond recognition, or lack diagnostic hard parts, rendering visual identification extremely challenging, if not impossible. In these instances, the results are a biased picture of food web interactions at best, such that there is a clear need for alternative tools to accurately characterize food web relationships.

Predation consists of a sequence of actions including detection, pursuit, attack, capture, retention, and ingestion (Holling 1959). At each step in the predation process, fishes must "choose" or select among all possible prey. The feeding patterns of fishes can be related to a multitude of factors that are not necessarily independent of each other, including fish size, environmental conditions, prey quality, and prey availability, amongst others (Lankford and Targett 1997; Juanes et al. 2001; Nye et al. 2011; Buchheister and Latour 2016). Most fishes show some sort of morphological or behavioral preference for a particular prey type, but may also demonstrate foraging flexibility in response to the seasonal availability of different food items (Barton, 2007). Patterns of selection by predator fishes reduce levels of competition and predation, thereby maximizing energy intake, growth, and survival. Diet switching and prey preferences are essential to our understanding of optimal foraging theory, and the mechanisms that drive these feeding patterns play an important role in carbon flow throughout the food web (Gerking, 1994). Additionally, when prey selection estimates are combined with known consumption rates, predator biomass or prey biomass, then critical fisheries and ecological issues can be addressed (Link, 2004).

Fish consumption estimates are valuable for informing fisheries managers, as numerous multispecies and ecosystem models that rely on understanding how much fish consume are becoming more frequently used in management (Bogstad et al. 1997; Whipple et al. 2000; Plaganyi 2007; Link 2010; Link et al. 2011). Estimates of fish consumption are important for three main reasons: 1) to assess the demands that predatory fishes make on their prey, 2) to assess the extent to which growth, reproduction, and survival are influenced by prey availability,

and 3) to quantify the energy obtained from feeding and understand how that energy is allocated between maintenance, growth, and reproduction (Wootton 1998). Consumption patterns at the individual and population level can have direct implications on mortality, survival, and growth as well as indirect effects on behavior, habitat utilization, foraging, and competition (Carpenter et al. 1985). Therefore, understanding factors that influence consumption in abundant, high-trophic level fishes are important considerations in ecosystem-based approaches to fisheries management. Additionally, drivers of annual consumption rates can provide useful insight into predictions of food web structure as they fluctuate over time with changes in environmental conditions and prey abundance.

Many methodologies to estimate fish consumption have been developed due to their utility in a multispecies and/or ecosystem framework (Link et al. 2012). Two of the most common approaches for estimating fish consumption rely on the utilization of gastric evacuation rates (Eggers 1977; Elliott and Persson 1978) and a mass-balance approach (Winberg 1956), both of which are discussed in this dissertation. The Elliott and Persson (1978) method is widely used (Jobling 1981; Durbin et al. 1983; Bromley 1994; Overholtz and Link 2007; Tyrrell et al. 2007) and relatively simplistic, requiring only knowledge about feeding patterns over diel cycles, gastric evacuation rates, and ambient water temperatures. Once daily per capita consumption rates are obtained, those estimates can be scaled up to population-scale estimates with additional knowledge about abundance patterns. Conversely, bioenergetics models are complex and involve laboratory-derived estimates of metabolic and consumption rates in order to parameterize the models. Each model is species-specific and can be conditioned on field-based growth observations to provide robust estimates of consumption at individual and population-level scales (Stewart et al. 1983; Luo and Brandt 1993; Hartman and Brandt 1995; Sobocinski and Latour 2015). Factors that influence consumption can subsequently be determined and used to evaluate ecosystem level energy flow as abundances of predator and prey change over time.

Chesapeake Bay

Numerous ecosystems around the globe require additional data to move EBFM forward, and the Chesapeake Bay, which is the focus of this dissertation, is one such system. The Bay is the largest estuary in the United States and its watershed spans six states, including Virginia, Maryland, Delaware, West Virginia, Pennsylvania, and New York (Boesch et al. 2001). The Bay

is a highly productive, dynamic ecosystem characterized by highly variable biophysical conditions. Major inputs of freshwater flow are dominated by the Susquehanna River, accounting for approximately 48% of freshwater entering the Bay (Schubel and Pritchard 1987). Seasonal river inflow influences salinity gradients in the Bay, which in turn drive species distribution patterns. The mainstem of the Bay is typified by three major salinity zones, including oligohaline (0 – 5 ppt, upper Bay), mesohaline (5-18 ppt, middle Bay), and polyhaline (>18 ppt, lower Bay) regions. The lower Bay (e.g. Virginia waters) is of intermediate depth and is clearer than the middle and upper Bay. During summer, hypoxic zones are frequent in the middle Bay and extend into the northern portion of the lower Bay where they are less severe in terms of magnitude and duration (Zhou et al. 2014).

The Chesapeake Bay supports over 350 species of resident and migratory fishes (Murdy and Musick 2013). The high degree of productivity in the Bay, which is driven in part by nutrient input from rivers and land runoff (Breitbrug et al. 2009), contributes to the importance of the estuary as nursery and foraging habitat for many species (Able and Fahay 2010). Owing in large part to the high primary and secondary production within the estuary, the Bay has supported many important commercial and recreational fisheries, including the invertebrates blue crab (*Callinectes sapidus*) and eastern oyster (*Crossostrea virginica*), and numerous finfish species such as Atlantic menhaden (*Brevoortia tyrannus*), striped bass (*Morone saxatilis*), summer flounder (*Paralichthys dentatus*), and Atlantic croaker (*Micropogonias undulatus*) amongst many others. Commercial fisheries landings in the Bay have reached an excess of 200,000 metric tons in 2016 (https://www.st.nmfs.noaa.gov/st1/commercial/landings/annual_landings.html), and despite management efforts, the abundance of many species has declined in recent years (Buchheister et al. 2013).

Analogous to other coastal environments, the Chesapeake Bay has undergone dramatic transformations over the last several decades. Combined effects of nutrient loading, eutrophication, and overfishing have contributed to large seasonal hypoxia events, increased turbidity, and a decline in submerged aquatic vegetation (Boesch et al. 2001; Kemp et al. 2005; Diaz and Rosenberg 2008). The degradation of the Bay ecosystem via changes in suitable foraging habitat has presumably altered the community structure and the productivity of both fish and their prey (Breitburg 2002). Furthermore, climate change is predicted to impact a multitude of environmental variables in the Chesapeake Bay (Najjar et al. 2010). While the

implications of climate change to the Bay's food web remains unknown, physiological constraints and resulting distributional shifts of both predator and prey, combined with the availability of suitable habitat and the quality and timing of primary productivity, may have significant ecosystem effects.

Dissertation rationale and objectives

The multitude of stressors that are currently impacting the Chesapeake Bay has the potential to influence fisheries that support the economic welfare of the fishing industry, while also altering ecosystem structure and function. In support of advancing EBFM, the scope of this dissertation addresses research needs of a fishery ecosystem plan developed by academic, state, and federal scientists, and living resource managers (CBFEAP 2006). Specifically, this dissertation focuses on components related to the trophodynamics of predatory fishes where the stated research needs for the fishery ecosystem plan include quantifying predator-prey interactions and sources of food and mortality, quantification of dynamic linkages within the Bay's food web, and modeling of natural processes that influence trophic interactions. To address these research needs, my work utilized fishery-independent datasets collected by the Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAP), the Juvenile Fish and Blue Crab Survey, and a prey sampling survey throughout the lower Bay developed during this study. ChesMMAP is bottom trawl survey designed to sample early juvenile and adult fishes in the Bay's mainstem since 2002. The Juvenile Fish and Blue Crab Survey is also a bottom trawl survey but targets juvenile fishes throughout the lower Bay's tributaries and mainstem and has been operating since 1955. One of the overarching themes of this dissertation to gain a better understanding as to how prey dynamics influence the diets of predatory fishes. While stomach content analysis alone can be incredibly informative, the application of prey metrics can further elucidate potential drivers that have wide-ranging effects on the ecosystem scale.

This dissertation has two main objectives: 1) to incorporate additional methodologies to improve fish stomach content identification, and 2) to examine the drivers of trophic interactions and consumption within a suite of abundant and economically valuable predatory fishes in the Chesapeake Bay. Specifically, Chapter 1 focused on developing molecular techniques for identifying important prey that are, at times, not amenable to visual identification at the species-

level, and determining gastric evacuation rates. Chapter 2 examined the influence of temporal patterns in relative abundance of prey on the diets of Atlantic croaker, weakfish, and summer flounder based on concurrent benthic, midwater, and zooplankton prey and predator sampling. And lastly, Chapter 3 synthesized 11 years of survey data from the Juvenile Fish and Blue Crab Survey and ChesMMAP to derive annual patterns and drivers of consumption via a bioenergetics modeling framework.

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CHAPTER 1

CHARACTERIZATION OF MOLECULAR DIGESTION AND GASTRIC EVACUATION RATES IN ATLANTIC CROAKER, *MICROPOGONIAS UNDULATUS*

ABSTRACT

Shifting from single-species fisheries management to ecosystem-based approaches requires a detailed understanding of food webs interactions, from accurate characterizations of trophic interactions to factors causing variability in consumption. Prey that is considered unidentifiable is often ignored in stomach content analyses, but can account for a significant proportion of fish diets. I demonstrate the use of molecular techniques to detect specific prey consumed by Atlantic croaker (*Micropogonias undulatus*) and evaluate factors that influence the rate of gastric evacuation. A molecular protocol was developed to isolate prey DNA from stomach contents. The isolated DNA was amplified using quantitative polymerase chain reaction (qPCR) with PCR primers designed to target specific prey taxa. Feeding experiments determined that DNA from blue mussel (*Mytilus edulis*) can be detected for as long as prey is in the stomach (~30 hours); long after prey has been rendered visually unidentifiable due to the effects of digestion. Temperature significantly influenced gastric evacuation rates and therefore should be considered throughout the collection process to ensure accurate identification of prey. I found that molecular techniques offer accurate and reproducible taxonomic identification of prey in the stomach contents of predators and provides a complimentary approach to traditional dietary analyses in field-based applications. Furthermore, the gastric evacuation rates determined in this study provides essential information to evaluate consumption patterns within the Chesapeake Bay. Overall, the material presented here contributes to better understanding trophic interactions and feeding rates within a complex and dynamic ecosystem.

INTRODUCTION

Atlantic croaker, *Micropogonias undulatus*, are an abundant inshore demersal fish species along the Atlantic and Gulf coasts ranging from Massachusetts to Mexico, however, they are not common north of New Jersey due to thermal tolerances (Nye et al. 2008). Throughout its range, Atlantic croaker support important commercial and recreational fisheries (ASMFC 2010). Atlantic croaker are estuarine-dependent and spawning occurs in coastal waters where larvae enter nursery habitats within estuaries in the fall and winter. In the Chesapeake Bay region, spawning occurs at age two to three along the continental shelf from July through February, with peak spawning occurring in August and September (Barbieri et al. 1994). Young-of-the-year (YOY) fish reside in low-salinity tributary waters and freshwater creeks where they overwinter and leave the Bay with adults the following autumn (Murdy and Musick 2013). Atlantic croaker have been observed to be the biomass dominant fish species within the Chesapeake Bay (Buchheister et al. 2013), but display large interannual variability in abundance (Norcross 1983; Murdy and Musick 2013). Mortality of YOY croaker due to low temperatures in the winter is thought to predict recruitment success (Hare and Able 2007). Over the last decade, data from the fishery-independent Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAP) have demonstrated a significant decline in abundance, particularly in fish over 200 mm (Buchheister et al. 2013), and the causes are poorly understood.

Understanding the food web dynamics of predatory fishes has long been a research area garnering immense interest due to the broad implications for overall ecosystem functioning, carbon transport, and fisheries management (Latour et al. 2008; Link et al. 2010). Given the historical abundance of patterns of Atlantic croaker in the Chesapeake Bay, this species has the potential to strongly influence food web dynamics. The decline in Atlantic croaker abundance in recent years has undoubtedly impacted the utilization of carbon from the benthos and further research is needed to better understand how changes in dietary patterns and post-consumptive processes (e.g., gastric evacuation) influence carbon flow in the Bay. At the most basic level, accurate characterizations of trophic interactions and subsequent ecosystem-scale food web analyses relies on the assumptions that stomach content analyses are unbiased and species-

specific physiological constraints pertaining to digestion are well understood. The visual identification of prey from fish stomach contents has yielded considerable insight into food web dynamics, and remains the standard approach to understanding trophic interactions (Hyslop 1980). Despite this, a large component of the marine food web is not amenable to the standard visual approach. Prey items may be cryptic or damaged during ingestion, rapidly digested beyond recognition, or lack diagnostic hard parts, thus rendering visual identification extremely challenging if not impossible. In these instances, the results from traditional stomach contents analysis are, at best, an incomplete picture of food web interactions such that there is a clear need for alternative tools to accurately characterize food web relationships.

Previous research on the trophic interactions of Atlantic croaker has largely relied on visual stomach content analysis (Homer and Boynton 1978; Nye et al. 2011; Buchheister and Latour 2015). Generally, Atlantic croaker are considered opportunistic bottom-feeders consuming a variety of invertebrates, including polychaetes, bivalves, mysids, decapods, and occasionally fishes (ASMFC 2010; Buchheister and Latour 2015). Throughout the 15-year time-series of dietary information of Atlantic croaker stomach content analysis from ChesMMAP, bivalves accounted for 14.7% of the dietary composition by weight (Buchheister and Latour 2015). Highlighting the limitations of visual stomach content analysis, only 3.4% of bivalves were identified to species-level in Atlantic croaker stomachs, presumably due to feeding strategies of croaker and the relatively rapid digestion of soft-bodied prey. The feeding strategies of Atlantic croaker, in particular the mastication of their prey and their preponderance for siphon nipping of bivalves (Long and Seitz 2008), likely has contributed to a lack of species-level taxonomic resolution in these important prey taxa. To better understand how croaker abundance and production patterns are influenced by seasonal and annual changes in food webs, it is important to have a comprehensive understanding of food-web interactions resolved to species-level taxonomic resolution.

Problems associated with traditional diet analysis can be overcome using molecular techniques targeting unique nucleotide sequences in prey DNA and thus can be viewed as a key for detailed and quantitative end-to-end food web analyses. The use of quantitative Polymerase Chain Reaction (qPCR) is faster, more sensitive, and offers improved specificity to studies of trophic interactions relying solely on visual stomach content analysis. In qPCR, the application of species-specific genetic markers target conserved sequences of nucleotides unique to a species

or taxa, thus enabling highly specific and sensitive assays to be developed (Albaina et al. 2010). Quantitative PCR has been successfully applied to identify visually indistinguishable prey in predatory fish diets (Taylor et al. 2002; Carreon-Martinez et al. 2011; Fox et al. 2012), and may provide important information on trophic interactions that are difficult if not impossible to obtain in any other way. Prior to application of any molecular method to field predation studies, it is important to understand the specificity of the assay and how digestion rates of prey taxa influence our ability to accurately identify prey in the stomachs of predatory fishes (Rosel and Kocher 2002). The best approach to determining sensitivity of a qPCR assay attempting to identify prey consumption is through feeding experiments that establish how long post-ingestion prey DNA can be detected within a predator stomach (King et al. 2008).

The goals of this project were twofold in the scope of post-consumptive processes in Atlantic croaker. Firstly, I aimed to determine the impact of digestion on the detection rates of blue mussel (*Mytilus edulis*), which is a common prey item in Atlantic croaker stomachs, at different temperatures utilizing qPCR assays and experimental feeding trials. Secondly, I aimed to estimate the gastric evacuation rates of blue mussels in Atlantic croaker stomachs where subsequent comparisons can be made between successful identification between visual and molecular assessments as a function time post-consumption.

METHODS

Prey detection assay development

Mitochondrial and nuclear genes were investigated for primer design. Ultimately, mitochondrial cytochrome oxidase subunit I (COI) was utilized due to high level of nucleotide sequence divergence between the predator and the selected prey taxa (~43%). DNA was extracted from tissue samples obtained from Atlantic croaker and blue mussel using a DNeasy® Blood & Tissue Kit (QIAGEN) following the manufacturer's protocol. About 700 bp of the mitochondrial COI gene region were then PCR-amplified using the universal mitochondrial primers 1490-(L)-GGTCAACAAATCATAAAGATATTGG-3' and 2198-(H)-TAAACTTCAGGGTGACCAAAAAATCA-3' (Folmer et al. 1994) for blue mussel, and FishF1-(L)-TCAACYAATCAYAAAGATATYGGCAC-3' and FishR1-(H)-ACTTCYGGGTGRCCRAARAATCA-3' for Atlantic croaker (Weigt et al. 2012) before direct sequencing using a BigDye™ Terminator v3.1 Cycle Sequencing Kit (Thermo Fisher Scientific,

Waltham, MA). Sequencing products were separated an ABI 3130*xl* Genetic Analyzer (Applied Biosystems). The resulting sequences were then imported in Sequencher v4.8 (Gene Codes Corp, Ann Harbor, MI) and checked for quality and accuracy in nucleotide base assignment. Non-target prey sequences that contribute significantly to the diets of Atlantic croaker were obtained either through direct sequencing or from GenBank and included *Glycera dibranchiata* (direct sequencing), *Nereis succinea* (accession # KU906105), *Pectinaria gouldii* (accession # KU906029), *Neomysis americana* (accession # KT209500), *Macoma balthica* (accession # KR084828), *Ensis directus* (accession # KU905877). All sequences were then aligned in MacVector version 8.1.2 (MacVector, Inc., California, USA) using Clustal W multiple alignment algorithm (Thompson et al. 1994). Species-specific primers, COI400F-(L)-CTTGCATTTAGCTGGGTTAAG-3' and COI534R-(H)-AATACGGCAGTAACTCTAATCCT-3' were then designed for blue mussel to amplify a 134 bp of the mCOI gene from the target prey taxa using SP-Design and Primer Express 3.0 software packages (Lei et al. 2008). Thermocycling conditions for these primers were optimized and the PCR protocol was 94°C for 30 seconds, 52°C for 40 seconds, and 72°C for 50 seconds, for 40 cycles. Primers were then tested for specificity against target and non-target taxa and subsequently utilized in a qPCR assay using a PowerUp SYBR Green Master Mix (ThermoFisher Scientific). Ten, ten-fold serial dilutions utilizing a known concentration of synthetic oligo fragment as the standard (gBlock gene fragment; 5'-TTGCATTTAGCTGGGTTAAGTTCTTTGGTGGGTGCTATTAAT TTTGCCAGTACTAACAAAAACATACCAGTTTTAGAGATAAAAGGAGAACGAGCTGA GCTTTATGTCCTAAGGATTAGAGTTACTGCCGTATT-3') were used for subsequent quantification of prey DNA in predator stomachs. Preliminary investigations revealed that the qPCR-based SYBR Green assays tested negative against Atlantic croaker and other non-target prey DNA (e.g. *Glycera dibranchiata*, *Nereis succinea*, *Pectinaria gouldii*, *Neomysis americana*, *Macoma balthica*, and *Ensis directus*), whereas it tested positive in detecting target prey DNA during all runs. Therefore, the specificity experiment validated the species-specific nature of the two SYBR Green assay primers and its utility for analyzing the molecular digestion rates of blue mussel in the stomachs of Atlantic croaker.

Feeding trials for molecular digestion and gastric evacuate rate determination

Wild-caught Atlantic croaker (n = 32 per trial) approximately 23.0 – 25.0 cm fork length (FL) were sampled by hook and line from the York River and transported to the VIMS Seawater Research Laboratory. All fish were initially placed into a 1,000 gallon flow-through system for acclimation to laboratory settings. During the acclimation period, fish were fed a daily diet of longfin inshore squid (*Doryteuthis pealii*). After one week, all fish were transferred into an experimental system and four fish were placed into one of eight, 300 gallon recirculating tanks. Any fish that showed signs of injury or poor condition were not used in experiments. Blue mussel prey was introduced during this time to allow for familiarity of prey taxa to be used in the feeding trials. Water quality (ammonia, nitrite, nitrate, pH, alkalinity, and temperature) was monitored daily to ensure optimal conditions for feeding.

The temperature of the recirculating systems was adjusted by 1°C every other day until the desired experimental temperature was reached (18°C, 22°C, and 26°C for molecular experiments; 18°C, 20°C, 22°C, 24°C, and 26°C for gastric evacuation experiments). Prior to commencement of feeding trials, food was withheld from the croaker for approximately 48-72 hours to allow time for gut clearance. Upon initiation of the feeding experiments, fish were fed a diet of blue mussel until satiation at all temperature regimes. Individuals were then sequentially euthanized (n = 3) in 1-2 hour intervals and fish were measured (FL), sexed, and maturity stage was recorded. Stomach contents were then immediately dissected, weighed to the nearest 0.001 g, assessed for visual identification, and a DNA sample was obtained from the stomach contents of each fish and preserved in 100% ethanol. Assessment for visual identification was based on the relative degree of digestion and its impact on the potential for successful identification. Prey that was considered visually unidentifiable had little to no musculature remaining with no diagnostic characters present. The experiments were then repeated at each of the remaining temperature regimes. All protocols for sampling and euthanizing fish were approved by the College of William & Mary's Institutional Animal Care and Use Committee (IACUC protocol #: IACUC-2017-08-15-12294).

Quantitative PCR on dissected stomach contents

Immediately following dissection and preservation of stomach contents, DNA was extracted using a DNeasy® Blood & Tissue Kit (QIAGEN) following the manufacturer's protocol. DNA quantity from each sample was assessed using a NanoDrop 2000 (Thermo

Scientific) and DNA quality was determined by via gel electrophoresis on a 1% agarose gel and visualized after staining with ethidium bromide. Each reaction was performed in duplicate to ensure reproducibility and contained 0.09µL of 100 nM forward and reverse primers, 5 µl of PowerUp SYBR Green Master Mix (2X), 1 µl of DNA, and 3.82 µl H_20. All SYBR Green assays were performed on a 7500 Fast Real-Time Fast PCR System (Applied Biosystems). Reactions were run in MicroAmp EduraPlate Optical 96-well plates (Applied Biosystems) under default real-time conditions, which consisted of an initial UDG activation stage of 50°C for 2 minutes and a Dual-Lock DNA polymerase stage of 95°C for 2 minutes to prevent carryover from previous reactions, followed by 40 cycles of a denaturing stage of 95°C for 3 seconds and an annealing/extension stage of 60°C for 30 seconds. A dissociation step was added to perform a melt curve analysis to determine whether the qPCR assay produced a single, specific product using the following procedure: 95°C for 15 seconds, 60°C for 1 minute, and 95°C for 15 seconds. A no template control (NTC) was used for each plate row to detect contamination. A positive fluorescence threshold was automatically calculated at ~0.1 ΔRn for the assays. Results from feeding trials were then compared to the standard and an absolute DNA quantification was determined and tracked over time to determine molecular digestion rates and how long post-consumption that a SYBR Green assay can detect prey DNA in a predator stomach.

Effects of time and temperature on gastric evacuation

To investigate the effect of time on the gastric evacuation of Atlantic croaker, five candidate models, including linear, exponential, power, logistic, and Weibull, were fitted to the gastric evacuation data (e.g. weight of prey remaining in Atlantic croaker stomachs at each time interval) using ordinary least squares (Table 1). Model comparisons were made at each temperature using Akaike's Information Criterion corrected for small sample size (AIC_c):

$$AIC_c = -2\log(\hat{L}) + 2k + \frac{2k(k+1)}{n-k-1} \quad (1)$$

where $\hat{L}$ is the estimated maximum likelihood value, k is the number of model parameters, and n is the total sample size. The most parsimonious model of a given set has the lowest AIC_c value, and because AIC_c is on a relative scale, it is important to calculate AIC_c differences ($\Delta AIC = AIC_c - AIC_{c\ min}$). Generally, ΔAIC values between 0 and 2 are indicative of substantial empirical

support for the fitted model, values between 4 and 7 are associated with models that have considerably less empirical support, and values >10 suggest virtually no empirical support (Burnham and Anderson 2002).

To evaluate the significance of the effect of temperature on the gastric evacuation rates in Atlantic croaker, the model with the most empirical support (e.g., Weibull) was fitted to the data via non-linear least squares pooled across temperature and compared results to the model parameterized with a temperature covariate (following Kimura 2008). The Kimura approach used temperature as a binary covariate coded in the gastric evacuation analysis. For each evacuation analysis, model parameterizations included: 1) no temperature effect and 2) effect of temperature on gastric evacuation rates. This approach enabled model-based inference, significance testing of temperature covariates, and comparisons of multiple model parameterizations based on model fit (Kimura 2008). Model support was evaluated utilizing Akaike's information criterion adjusted for small sample size (Akaike 1974).

Researchers have utilized gastric evacuation rates (E) to inform daily consumption models by utilizing the statistical model following Elliott and Persson (1978):

$$E = a \times e^{bT_{i,t}} \quad (2)$$

where a and b are fitted constants and $T_{i,t}$ is the water temperature for predator i in time period t. Typically the a and b constants are set to 0.04 and 0.115, respectively, as these are viewed as conservative values for teleostean fishes (Durbin et al. 1983) and have been widely used in similar studies (Overholtz et al. 2000; Link and Garrison 2002; Link and Idoine 2009). A secondary consideration of the present study was to empirically derive constants for Atlantic croaker required in Elliott and Persson's (1978) gastric evacuation equation for comparison purposes to further evaluate the efficacy of applying standard a and b constants across all teleosts.

RESULTS

Molecular digestion rate

DNA was successfully amplified in 100% of qPCR assays using species-specific primers for blue mussels digesting in the stomachs of Atlantic croaker at water temperatures of 18°C,

22°C, and 26°C. Preliminary examination determined that the primers used in this study were specific for blue mussel and did not amplify DNA from the tested non-target prey organisms or DNA from the predator itself. Melt-curve analysis further indicated that the primers designed in the qPCR assays only amplified DNA from a single amplicon and were therefore considered suitable for the experimental design (Figures 4, 5, and 6, respectively). Standard curves were generated utilizing gBlock standards for each temperature regime and were plotted against the mean cycle number for each iteration of the feeding trials (Figures 7a, 8a, and 9a). Mean DNA quantity (copies/µL) for each iteration of the feeding trials was also plotted for each temperature (Figures 7b, 8b, 9b). Throughout the duration of the feeding trials, prey was consistently detected in the stomachs of Atlantic croaker until gastric evacuation was complete. Prey detection generally followed the trend where DNA amplified at earlier cycle numbers corresponded to a shorter digestion time and vice versa. For all experiments and assays, no negative controls (PCR no template controls) tested positive. Reproducibility within and between runs was high, with 31 repeated analyses of the same sample having a standard deviation of less than 0.4 Ct.

Progression of gastric evacuation during the course of the digestion experiments showed that the weight of the stomach contents decreased with increasing digestion time. At the final stage before complete evacuation, although stomach contents were consistently visually unidentifiable and often had less than 0.1 g remaining, all tested positive for blue mussel DNA. Standard curve comparisons allowed for quantification of the DNA remaining in the stomach contents of Atlantic croaker. Exponential models were fitted to qPCR data and demonstrated an increasing instantaneous molecular digestion rate with increasing temperature. For example, at 18°C, the instantaneous molecular digestion rate was determined to be 0.104 copies/µL/hour (Figure 10a), whereas at 22°C and 26°C the instantaneous molecular digestion rate was 0.134 copies/µL/hour (Figure 10b) and 0.349 copies/µL/hour (Figure 10c), respectively. Prior to complete evacuation, the lowest amplified DNA quantity observed was $8.04e^3$ copies/µL.

Gastric evacuation rate determination

Atlantic croaker feeding trials were completed at five temperature regimes typical of the estuarine thermal habitat of the Chesapeake Bay. Based on model selection criteria (AIC_c), the Weibull model consistently received the most empirical support at all temperature regimes, followed by the logistic model ($\Delta AIC_c < 2.4$ across temperature; Table 2). Linear, exponential,

and power models all performed poorly relative to the Weibull model. Results from a one-way ANOVA at each temperature demonstrated no significant tank effect at an alpha value of 0.05 (26°C: $F = 0.79$; 24°C; $F = 0.45$; 22°C; $F = 0.34$; 20°C; $F = 0.41$; 18°C; $F = 0.91$), and therefore data were pooled to investigate the effect of temperature on evacuation rates. Following Kimura (2008), Weibull models (Figure 2) demonstrated that gastric evacuation of Atlantic croaker was significantly influenced by temperature ($p<0.05$, Table 3), where evacuation rates were faster at higher temperatures than at lower temperatures, as expected. At 26°C, croaker gastric evacuation was completed relatively quickly after approximately 10 hours. Conversely, gastric evacuation took longer until completion at 24°C, 22°C, 20°C, and 18°C with times approximated at 15 hours, 22 hours, 26 hours, and 30 hours, respectively. At all temperatures, visual identification of remaining prey was deemed unidentifiable prior to complete gastric evacuation. Prey was visually unidentifiable after 7 hours of digestion at 26°C. At lower temperatures, prey was visually unidentifiable after 12 hours, 18 hours, 22 hours, and 24 hours at 24°C, 22°C, 20°C, and 18°C, respectively.

To determine the efficacy of using standard *a* and *b* estimates for all teleostean fishes as characterized Elliott and Persson (1978), exponential models were fit to the gastric evacuation data for each of the five temperature regimes. Instantaneous gastric evacuation rates (*b* estimates from exponential models) were estimated and plotted against the corresponding temperatures (Figure 3). The subsequent *a* and *b* estimates determined from the relationship of instantaneous gastric evacuation rate and temperature were $a = 0.05$ and $b = 0.152$.

DISCUSSION

Molecular digestion and detection of prey DNA

The detection of prey DNA in the stomach of predatory fishes depends upon the ability of the DNA to resist digestion in the predator gut and on the capacity of PCR to amplify a prey specific region of DNA from digested material (Jarman et al. 2002; Nejstgaard et al. 2003; Parsons et al. 2005). Bivalves represent an important component in the diet of Atlantic croaker, but are challenging to visually identify to species-level due to feeding strategies (Chao and Musick 1977; Deary and Hilton 2016) and the influence of rapid digestion rates of soft-bodied prey. However, molecular techniques offer a precise and reproducible technique for identifying taxa down to species-level. SYBR Green assays for predation studies tend to target short-

sequences of DNA in order to improve their effectiveness with degraded material (Symondson 2002; King et al. 2008; Troedsson et al. 2009). The design of my assay, with a targeted 134 bp of the mtCOI gene, shows that prey DNA can be isolated and detected from Atlantic croaker stomach contents throughout the entire process of digestion. In a couple instances, prey DNA was detected even when stomachs were appeared empty. These results demonstrate that the detection of trace levels of prey DNA is achievable, even when digestion or stomach clearance is nearly complete. Furthermore, previous research has demonstrated that molecular techniques can identify fish prey after longer digestion times than possible with visual methods (Carreon-Martinez et al. 2011), thus highlighting the practical use of these techniques for informing food web analyses.

Accurate depictions of prey digestion rates are important for both the design of field-sampling to detect predation and for the utilization of stomach content data to estimate broader ecological processes (Hunter et al. 2012). Water temperature is an important factor that must be taken into account in relating detectability by visual or molecular means to digestion time (Albaina et al. 2010; Moran et al. 2016). Utilizing qPCR, Albaina et al. (2010) showed that 90% detectability of juvenile plaice DNA in brown shrimp stomachs decreased from ~5 hours at temperatures < 16°C to ~2 hours at 19-20°C. Similarly, Carreon-Martinez et al. (2011) observed an increased number of failed qPCRs with an increase in water temperature. The results from this study did not illustrate the same trends that were observed in the previous studies as I had 100% detection across all temperature regimes. This could be an artifact of the highly specific nature of the assay designed relative to the other experiments, but more likely due to differential molecular digestion rates of various prey taxa in predator stomachs. Differential digestion rates among prey taxa are primarily related to nutritional content (Bromley 1994), however, at the molecular level digestion rates of different prey are less understood and require further research. Nonetheless, temperature had a significant effect on the molecular digestion rate of prey in Atlantic croaker stomachs. As expected, when temperature increased from 18°C to 26°C, molecular digestion rates subsequently increased from 0.104 copies/µL/hour to 0.349 copies/µL/hour, respectively. At all temperatures, molecular digestion of prey DNA decayed in a nonlinear fashion. No studies, to our knowledge, have evaluated the rate of molecular digestion in fish stomachs as most studies focus on the efficacy of applying various methodologies for detecting prey DNA in predator stomachs (Greenstone et al. 2014). However, previous research on the influence of

elapsed time post-consumption on detection ability of insect prey DNA also demonstrated a nonlinear trend in DNA degradation (Weber and Lundgren 2009). Ultimately I found that prey identification by molecular techniques were able to detect and amplify prey DNA as long as any residual prey material was found in stomach contents, therefore outperforming visual identification methods. To this point, the specificity and reproducibility of the assay used in this study demonstrated its viability for field-based identification of unidentifiable prey. When used in conjunction with field-based trophic measurements (e.g., prey weight), accurate depictions of food web interactions can be used to further parameterize ecosystem-level analyses. However, sampling frequency relative to water temperature should be taken into consideration as the ability to detect prey DNA in Atlantic croaker stomachs can fluctuate from 10- 30 hours post-consumption depending on environmental conditions. To further develop our knowledge of trophic interactions in the Chesapeake Bay, future research should develop additional assays for other major dietary components that are challenging to visually identify. As reported in previous studies, I recommend targeting multi-copy DNA in short amplicons (e.g. <300 bp) while testing for specificity against a wide range of other prey taxa commonly observed in predator diets (Symondson et al. 2002; King et al. 2008).

Gastric evacuation rate model selection

The two most common patterns of gastric evacuation found in experiments are linear and exponential (Bromley 1994). Linear evacuation models have demonstrated that the rate of evacuation can be constant and independent of time post-consumption and stomach fullness and has often been attributed to digestion patterns in piscivorous fishes (Adams et al. 1982; Olson and Boggs 1986; Bromley 1988; Sweka et al. 2004) and larval fishes (Wuenschel and Werner 2004). However, linear models did not fit the gastric evacuation data well in this study because the amount of prey digested per unit time was not constant. Conversely, exponential models account for a non-linear evacuation per unit time and operate under the assumption that evacuation begins immediately following consumption of prey. However, the exponential models consistently overestimated gastric evacuation rates at early and later stages of digestion in the present study. The overestimation at the early stages and later stages is likely attributed to a small lag phase that was observed over the course of the first and last few hours of the experiment, where the rate of evacuation was much more rapid at intermediate stages. Lag

phases, at the beginning and end of gastric evacuation, has been observed in laboratory studies where fish consumed large meals as well as in fish that consumed bivalves (Persson 1986; Hopkins and Larson 1990), which corresponds to the patterns observed in this study. Logistic and Weibull models are less commonly used to explain gastric evacuation, but they allow for the incorporation of the lag phase at the beginning of digestion, a lower asymptote at the end of digestion, and allow for an asymmetric shape in the relationship between evacuation and time (Medved 1985; Nelson and Ross 1995; Tekinay et al. 2003; Berens and Murie 2008; Redd 2015). Generally, both models explained the data; however, the Weibull model consistently received the most empirical support. The patterns of gastric evacuation observed in this study illustrate that evacuation is not entirely a volume-dependent function in Atlantic croaker. Instead, evacuation rates in croaker are depressed at early and late stages of digestion and are most rapid during the middle stages, described as pulses by Jobling (1987). While the patterns of gastric evacuation observed here are specific to Atlantic croaker fed to satiation on bivalves, they may not fully represent the opportunistic nature of croaker feeding in natural environments. Future studies would benefit from investigating the evacuation rates of other prey taxa as well how evacuation rates are influenced by the consumption of multiple prey groups. Regardless, the characterization of gastric evacuation rates of dominant prey taxa is an essential component to better understand population-level consumption rates, predation impact, energy budgets, and trophic dynamics within the Chesapeake Bay ecosystem.

Effect of temperature on gastric evacuation

Temperature had a significant effect on the gastric evacuation rate of Atlantic croaker as demonstrated by the better fit of models containing the temperature covariate compared to the null model that did not consider the effect of temperature. Results demonstrated that gastric evacuation rates significantly increased with increasing temperature. Numerous other studies have shown similar effects of temperature on gastric evacuation rates in a wide variety of teleost fishes ranging from salmonids (Elliott 1972; He and Wurtsbaugh 1993; Handeland et al. 2008) to flatfishes (Jobling 1979; Morais 1986; Vinagre et al. 2007) to grouper (Berens and Murie 2008; De et al. 2016). Gastric evacuation rates are impacted by periods of food deprivation, predator size, nutritional composition of prey, but above all by water temperature (Elliott and Persson 1978). Periods of food deprivation, fish size, and nutritional composition of prey were kept

relatively constant throughout the study to prevent potential confounding factors in interpreting the effect of temperature on gastric evacuation. In general, the results from this study agree with findings for other temperate teleostean fishes. Buckel and Conover (1998) found that 90% gastric evacuation in bluefish ranged from 5 hours at 30°C to 10 hours at 21°C. Red drum that were fed crustacean prey illustrated a 3.4% h^{-1} increase in gastric evacuation rates as temperatures increased from 17°C to 27°C (Gillum et al. 2012). Despite the fact that gastric evacuation rates generally increase with temperature, direct comparisons between species may be complicated due to the form and type of models used to predict rates of evacuation.

The influence of temperature on gastric evacuation rates has direct implications for consumption rates of fish populations (Wootton 1998). The use of daily consumption rates following Elliott and Persson's (1978) consumption model has enabled the quantification of predation and the magnitude of feeding interactions between populations (Durbin et al. 1983). However, accurate gastric evacuation rates relative to temperature are a prerequisite for subsequent modeling efforts. The temperatures utilized in this study represent the thermal regime Atlantic croaker encounter during their seasonal migration to Chesapeake Bay feeding grounds and therefore give a range of conservative evacuation rate estimates found throughout the spatial and temporal extent of the Bay. The estimates of *a* (0.05) and *b* (0.152) are in line with previous estimates of teleost fishes (Durbin et al. 1983).

Direct comparisons of gastric evacuation rates can be difficult given the numerous models utilized in laboratory and field-based experiments. Model fit among different gastric evacuation models have often involved a combination of Y-intercept values, residual plots, and residual mean square values, however, most predominantly utilize the coefficient of determination (R^2), which is inappropriate for nonlinear regression models. With this caveat in mind, only a few studies have investigated gastric evacuation rates among sciaenids and no studies have estimated gastric evacuation rates for Atlantic croaker. Figueiredo and Veira (2005) estimated that whitemouth croaker (*Micropogonias furnieri*) gastric evacuation rates were 0.11 g h^{-1}, whereas bigtooth corvina (*Isopisthus parvipinnis*) and shorthead drum (*Larimus breviceps*) evacuation rates were estimated to range from 0.073-0.215 g h^{-1} and 0.015-0.201 g h^{-1}, respectively, by Soares (2003). The values derived from the present study are similar and therefore may be useful for parameterizing broader ecological models (e.g. population-level consumption, production, etc.) for Atlantic croaker (Nye 2008). Overall, this study empirically

derived post-consumptive digestion rates to better understand the factors that influence them in a numerically abundant fish in the Chesapeake Bay. The methods developed here and the subsequent findings have direct implications for future dietary and consumption analyses and contribute to a better understanding trophic interactions and feeding rates within a complex and dynamic ecosystem.

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Table 1. Candidate models for Atlantic croaker gastric evacuation rate determination.

Model	Equation
Linear	$y = A - B_t$
Exponential	$y = Ae^{-Bt}$
Power	$y = At^{(B)}$
Logistic	$y = 100 - (\frac{A}{1 + e^{B(t+C)}})$
Weibull	$y = Ae^{(-\left(\frac{t}{B}\right)^{C})}$

Table 2. Summary statistics with standard error estimates for linear and non-linear gastric evacuation models of Atlantic croaker consuming blue mussels at (a) 26°C, (b) 24°C, (c) 22°C, (d) 20°C, and (e) 18°C. AIC values in bold indicate models with high empirical support.

Model	*a* ± S.E.	*b* ± S.E.	*c* ± S.E.	AIC	Δ AIC
(a) 26°C					
Linear	7.60 ± 0.22	0.85 ± 0.04	-	54.9	26.5
Exponential	10.45 ± 0.53	0.28 ± 0.02	-	60.2	31.7
Power	8.31 ± 0.65	-0.77 ± 0.08	-	100.0	71.5
Logistic	8.53 ± 0.63	0.11 ± 0.04	-0.59 ± 0.06	30.4	1.9
Weibull	7.42 ± 0.26	5.05 ± 0.15	1.99 ± 0.16	28.5	0
(b) 24°C					
Linear	6.08 ± 0.24	0.47 ± 0.03	-	58.1	52.1
Exponential	8.83 ± 0.45	0.21 ± 0.01	-	46.4	40.4
Power	9.46 ± 0.99	-0.82 ± 0.09	-	88.1	82.1
Logistic	**6.98 ± 0.41**	**0.09 ± 0.03**	**-0.45 ± 0.04**	**6.8**	**0.8**
Weibull	**6.18 ± 0.19**	**7.00 ± 0.18**	**2.03 ± 0.14**	**6.0**	**0**
(c) 22°C					
Linear	6.35 ± 0.24	0.31 ± 0.02	-	76.7	72.1
Exponential	9.32 ± 0.38	0.13 ± 0.01	-	51.7	47.1
Power	13.02 ± 1.51	-0.78 ± 0.08	-	109.8	105.2
Logistic	8.21 ± 0.52	0.15 ± 0.04	-0.26 ± 0.02	7.0	2.4
Weibull	**6.85 ± 0.18**	**10.34 ± 0.25**	**1.82 ± 0.11**	**4.6**	**0**
(d) 20°C					
Linear	6.67 ± 0.24	0.30 ± 0.02	-	88.0	59.9
Exponential	9.55 ± 0.41	0.12 ± 0.01	-	66.9	38.8
Power	13.39 ± 1.55	-0.74 ± 0.07	-	125.8	97.8
Logistic	**8.49 ± 0.63**	**0.15 ± 0.05**	**-0.24 ± 0.02**	**29.5**	**1.4**
Weibull	**7.12 ± 0.23**	**11.38 ± 0.33**	**1.82 ± 0.13**	**28.1**	**0**
(e) 18°C					
Linear	6.87 ± 0.19	0.26 ± 0.01	-	88.3	47.4
Exponential	9.30 ± 0.31	0.09 ± 0.01	-	68.1	27.2
Power	13.36 ± 1.34	-0.66 ± 0.06	-	142.0	101.0
Logistic	9.96 ± 1.07	0.29 ± 0.10	-0.16 ± 0.01	42.2	1.3
Weibull	**7.43 ± 0.25**	**13.67 ± 0.46**	**1.58 ± 0.11**	**41.0**	**0**

Table 3. Parameter estimates with standard error from Weibull models fitted to investigate the effects of temperature on Atlantic croaker gastric evacuation rates using the Kimura approach (2008). Parameter subscripts refer to temperature (T, °C). AIC values in bold indicate the model with empirical support.

Parameter	Estimate ± SE	AIC	ΔAIC
$Pooled_T$		560.2	424.0
a	8.51 ± 0.90		
b	7.15 ± 0.97		
c	0.98 ± 0.15		
$Kimura_T$		**136.2**	**0**
a	7.09 ± 0.11		
b_{18}	14.20 ± 0.29		
b_{20}	11.41 ± 0.31		
b_{22}	10.08 ± 0.31		
b_{24}	6.34 ± 0.28		
b_{26}	5.18 ± 0.27		
c	1.79 ± 0.06		

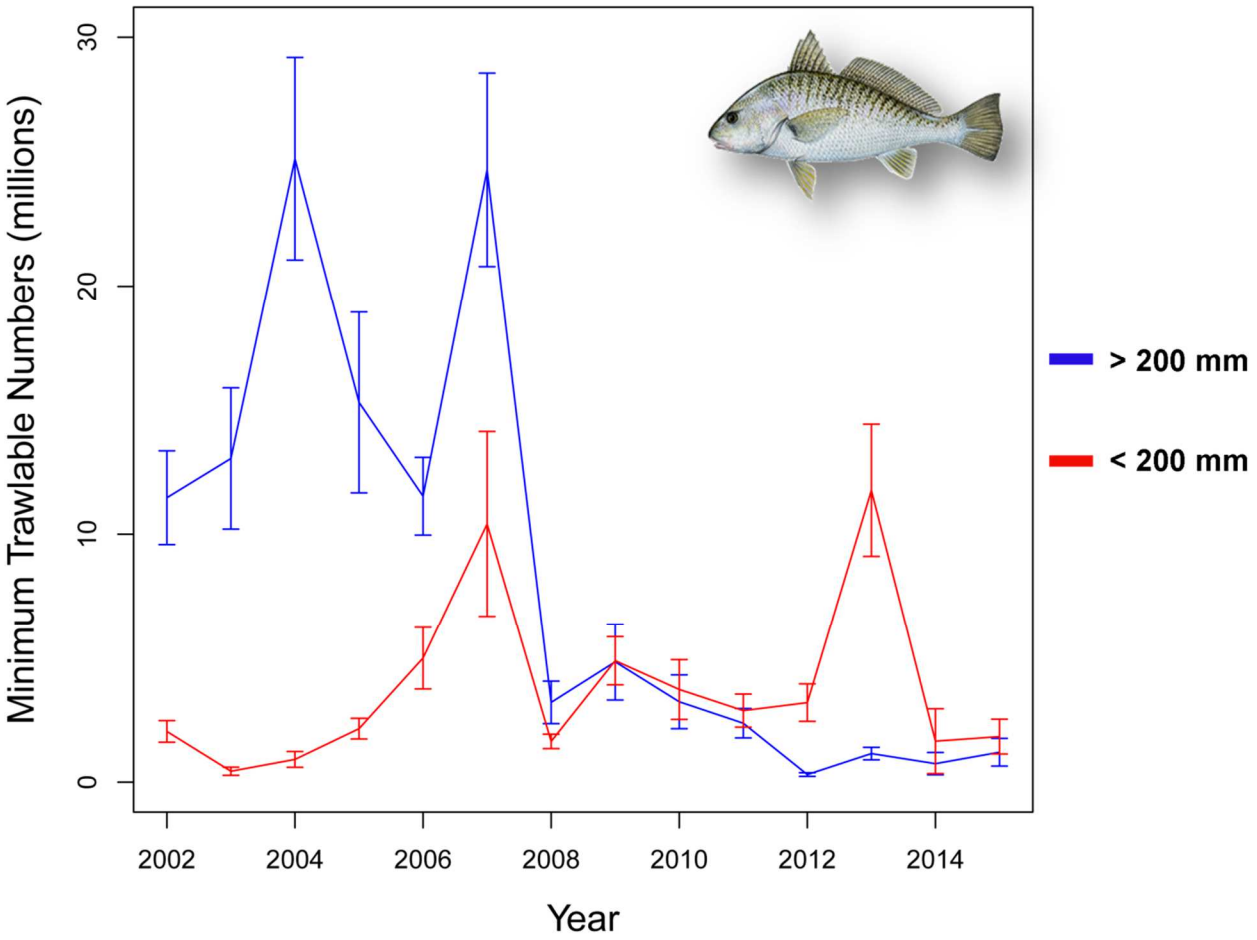

Figure 1. Minimum swept-area abundance estimates of small (S) and medium (M) Atlantic croaker in the mainstem of the Chesapeake Bay based on random-stratified geometric mean annual indices from ChesMMAP catch data. Error bars represent SE.

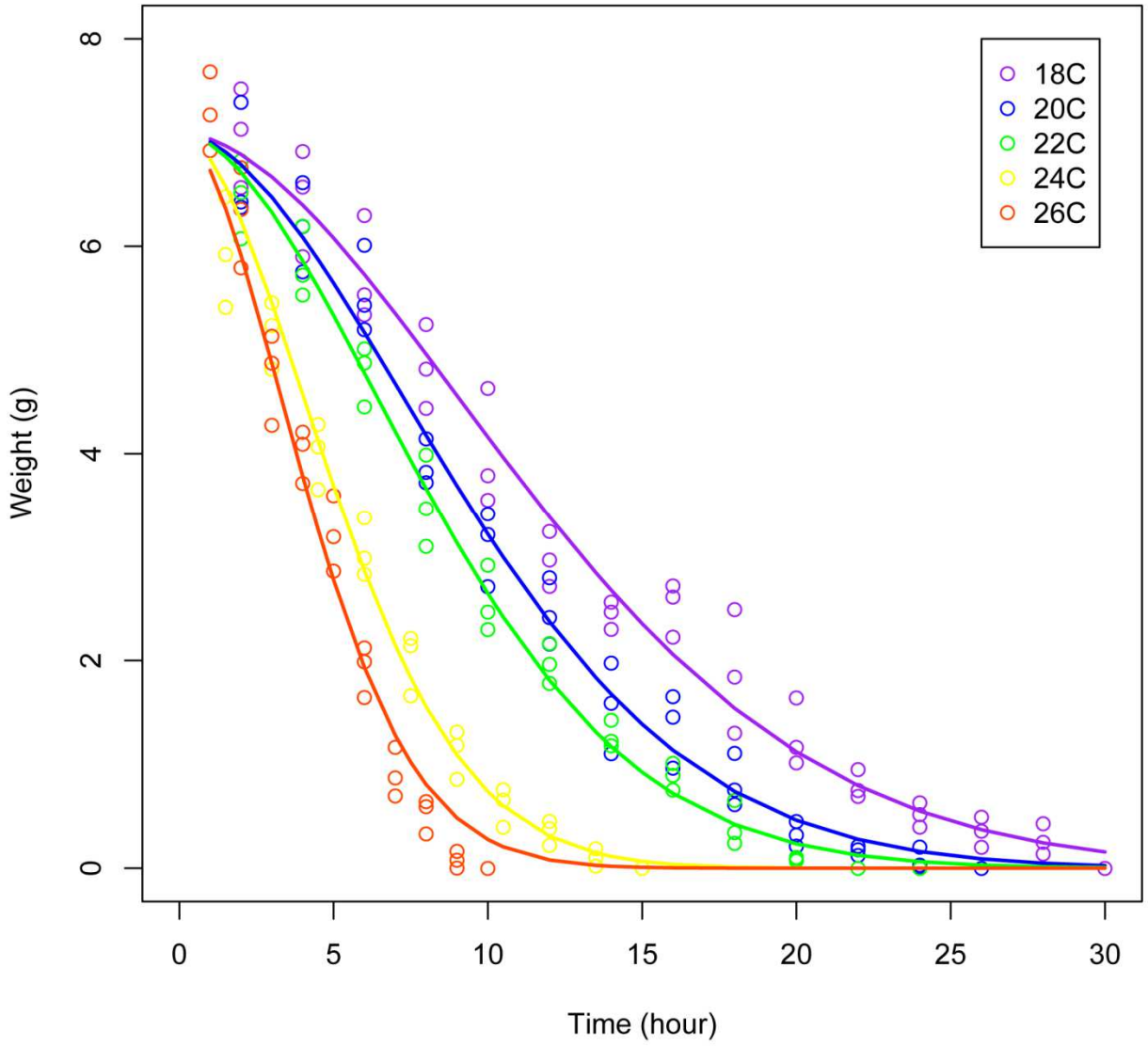

Figure 2. Gastric evacuation rates for blue mussel in Atlantic croaker stomachs at 18°C (purple), 20°C (blue), 22°C (green), 24°C (yellow), and 26°C (red) from fitting Weibull models to evacuation data utilizing Kimura's method (2008).

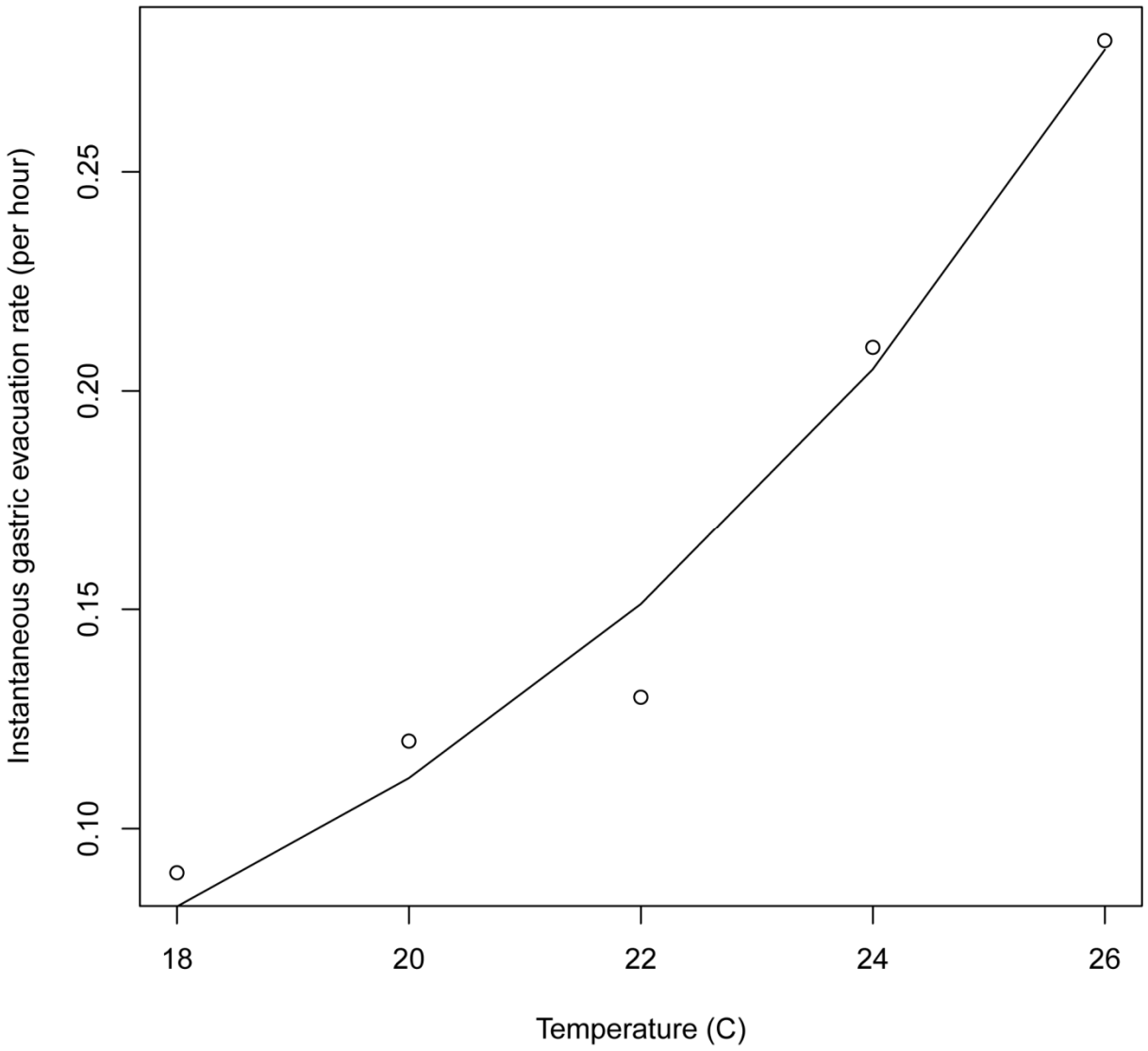

Figure 3. The relationship between instantaneous gastric evacuation rate (per hour) and temperature (°C) in Atlantic croaker. Trend line based on the exponential relationship between instantaneous gastric evacuation rate (per hour) and temperature (°C).

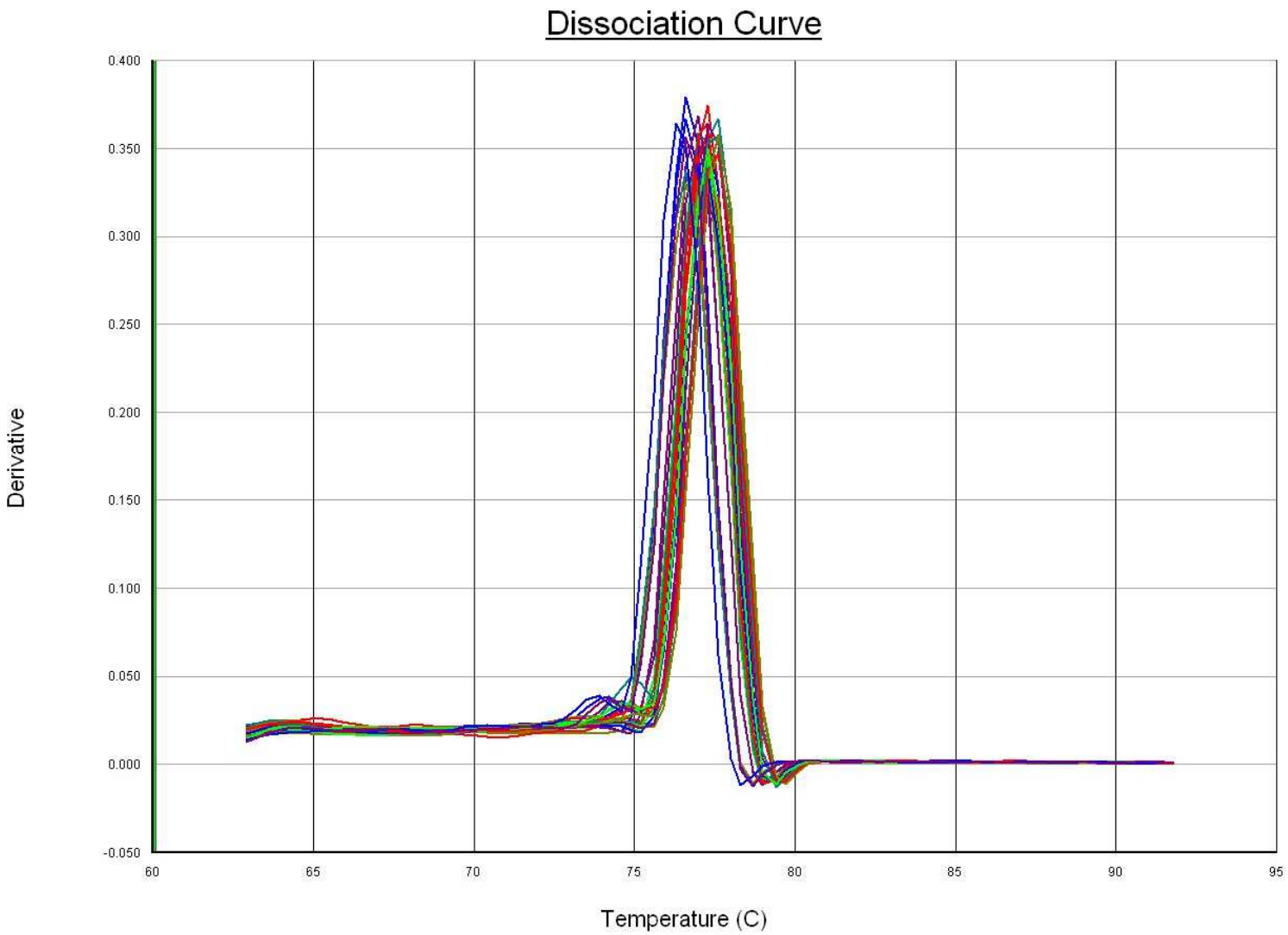

Figure 4. Melt curve analysis for qPCR at 18°C demonstrating a single targeted amplicon in Atlantic croaker feeding trials.

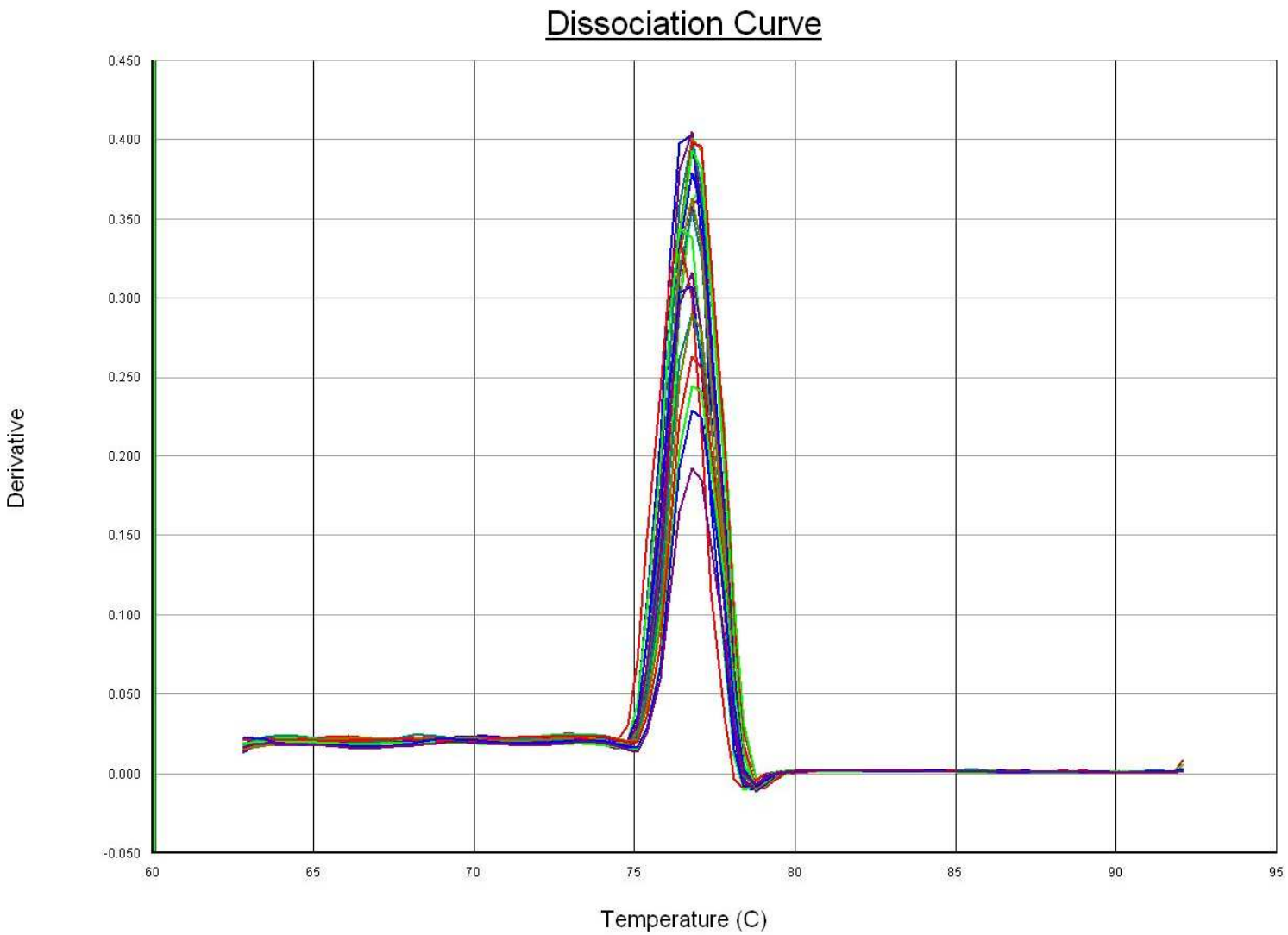

Figure 5. Melt curve analysis for qPCR at 22°C demonstrating a single targeted amplicon in Atlantic croaker feeding trials.

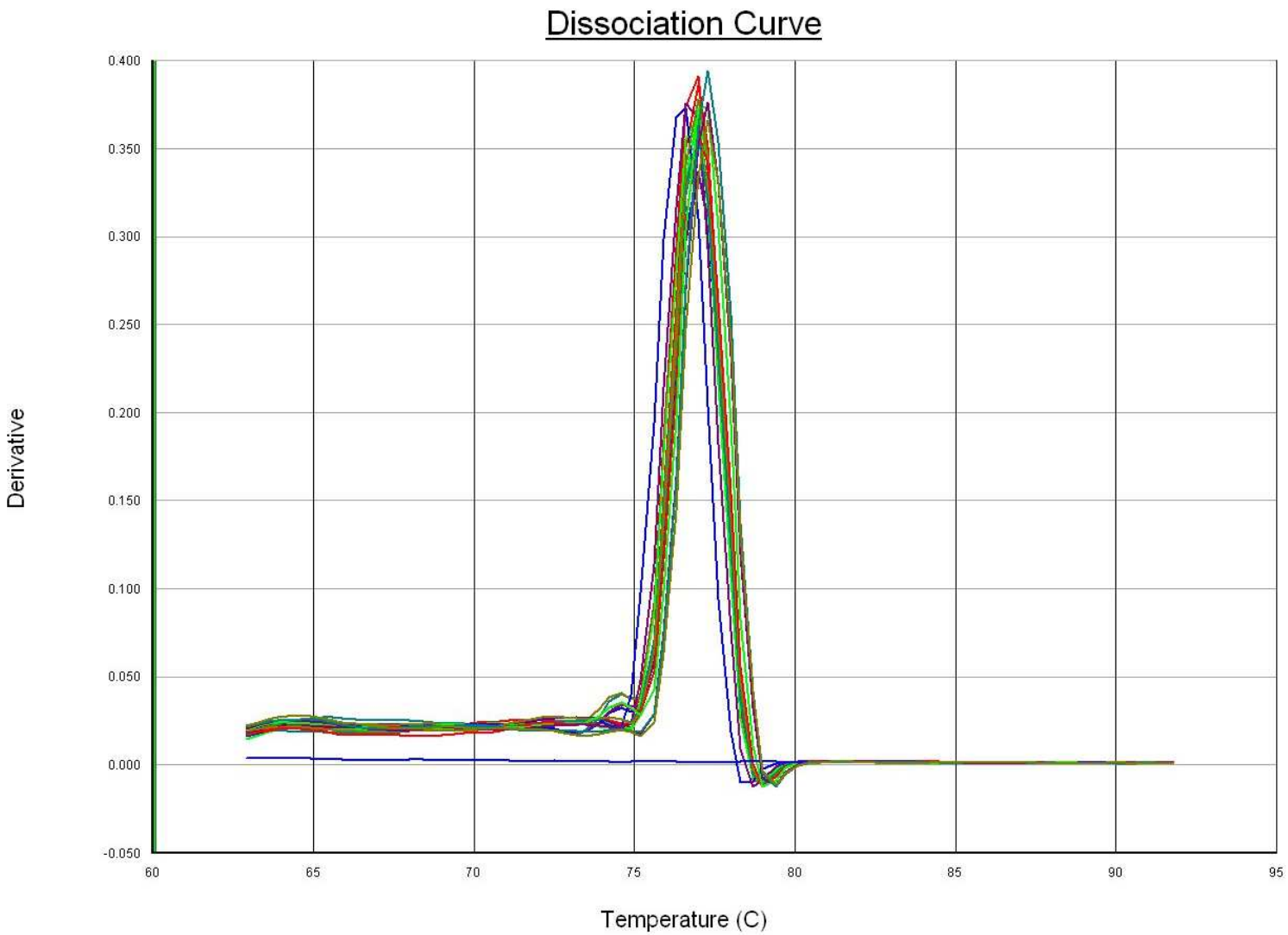

Figure 6. Melt curve analysis for qPCR at 26°C demonstrating a single targeted amplicon in Atlantic croaker feeding trials.

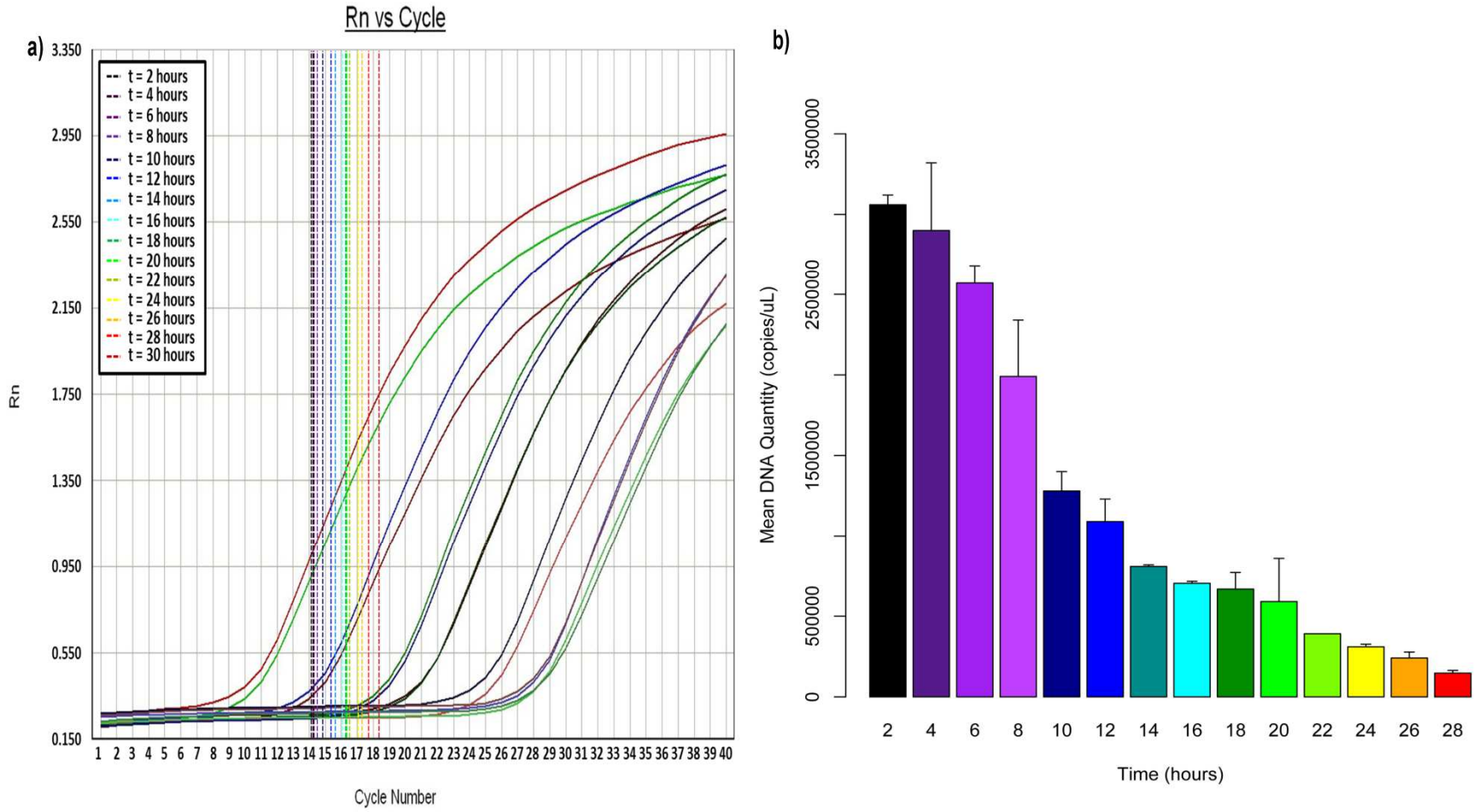

Figure 7. a) Standard curve amplification plot for Atlantic croaker feeding trials at 18°C. Vertical dashed lines represent mean cycle number of prey DNA amplification in Atlantic croaker stomachs across the iterations of the feeding trials; b) Mean DNA quantity (copies/µL) for each iteration of Atlantic croaker feeding trials at 18°C.

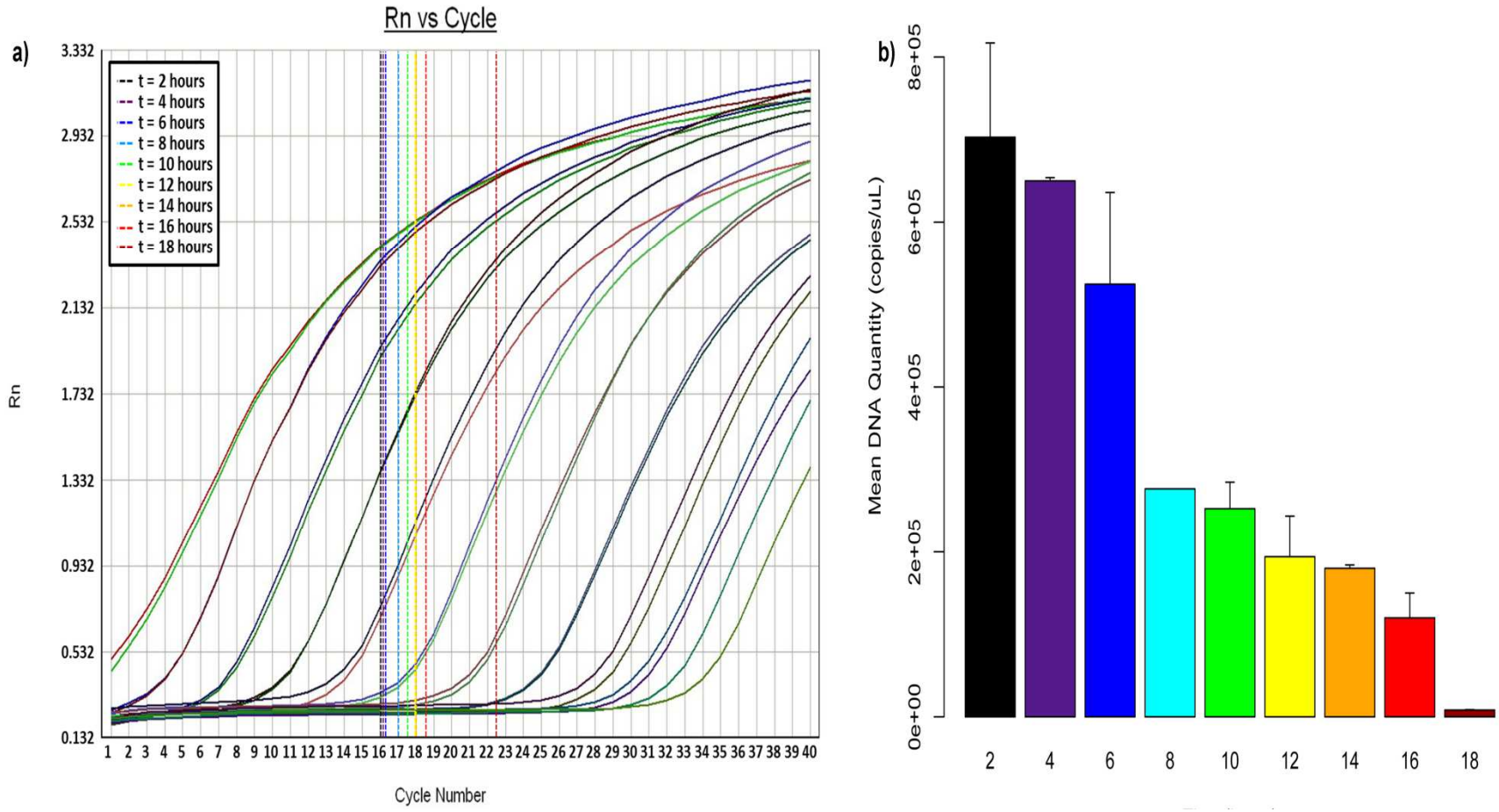

Figure 8. a) Standard curve amplification plot for Atlantic croaker feeding trials at 18°C. Vertical dashed lines represent mean cycle number of prey DNA amplification in Atlantic croaker stomachs across the iterations of the feeding trials; b) Mean DNA quantity (copies/µL) for each iteration of Atlantic croaker feeding trials at 22°C.

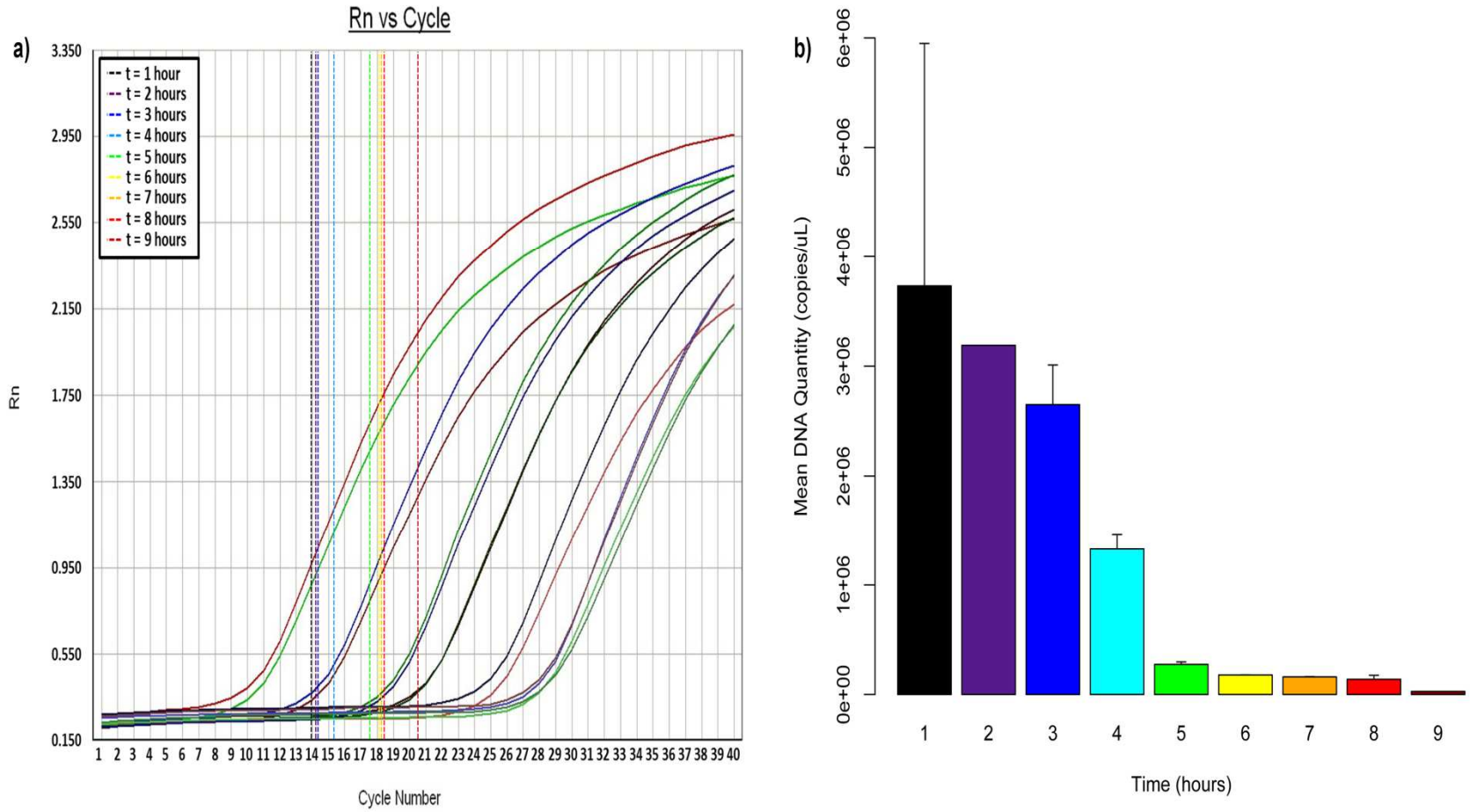

Figure 9. a) Standard curve amplification plot for Atlantic croaker feeding trials at 18°C. Vertical dashed lines represent mean cycle number of prey DNA amplification in Atlantic croaker stomachs across the iterations of the feeding trials; b) Mean DNA quantity (copies/µL) for each iteration of Atlantic croaker feeding trials at 26°C.

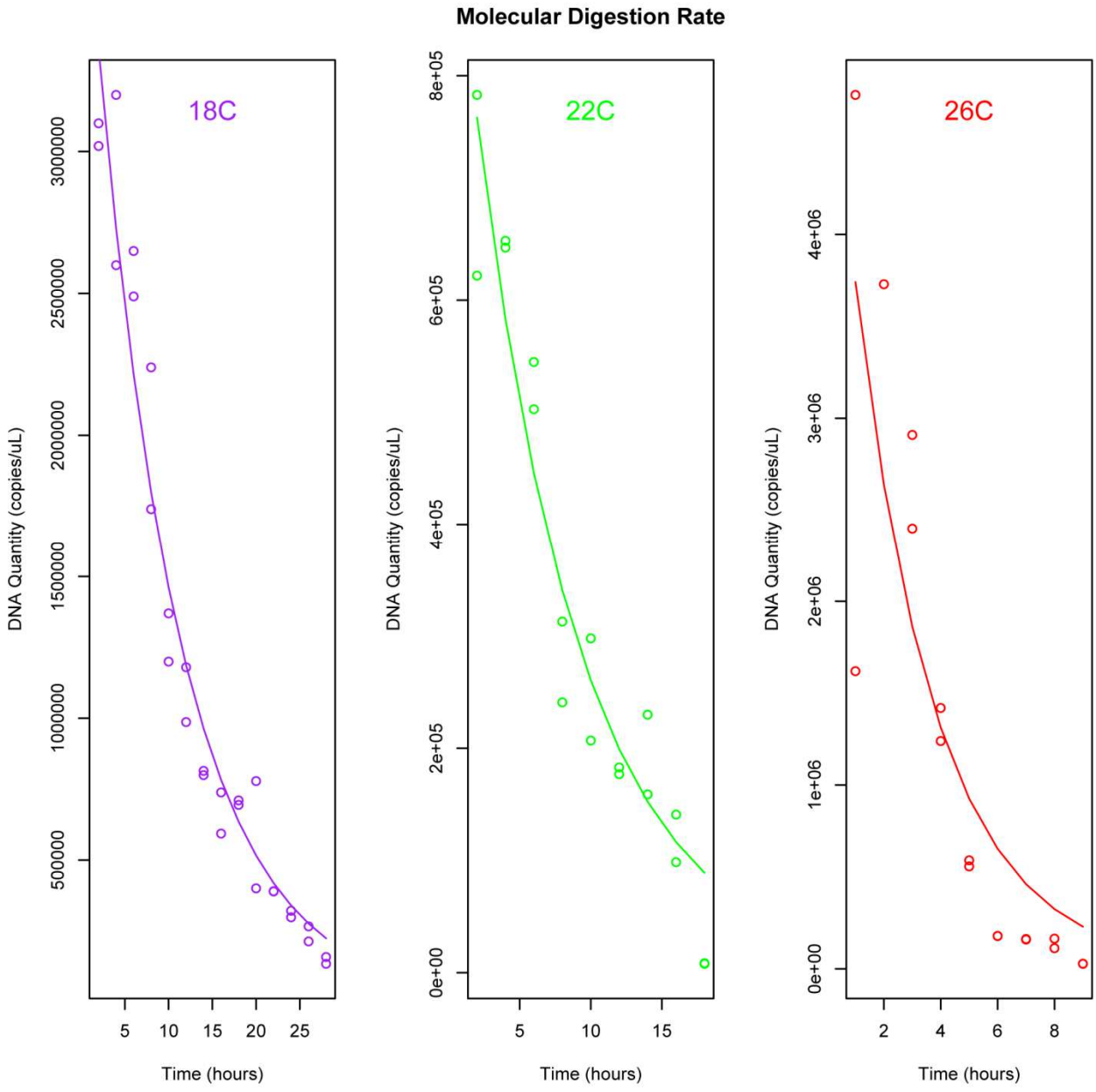

Figure 10. Molecular digestion rate of blue mussel in Atlantic croaker stomachs at a) 18°C, b) 22°C, and c) 26°C.

CHAPTER 2

PREY SELECTION OF THREE SYMPATRIC TELEOSTEAN PREDATORS IN THE LOWER CHESAPEAKE BAY: WEAKFISH (*CYNOSCION REGALIS*), SUMMER FLOUNDER (*PARALICHTHYS DENTATUS*), AND ATLANTIC CROAKER (*MICROPOGONIAS UNDULATUS*)

ABSTRACT

The feeding patterns of fishes have yielded key insights into the dynamics of aquatic ecosystems, and the mechanisms that drive underlying patterns are important drivers of energy flow within these ecosystems. I collected stomach contents from weakfish (*Cynoscion regalis*), summer flounder (*Paralichthys dentatus*), and Atlantic croaker (*Micropogonias undulatus*) from the lower Chesapeake Bay, during July 2014 through May 2015 to characterize diet and prey type selectivity. The prey field was evaluated utilizing midwater trawls, plankton tows, and benthic grabs at randomly selected stations where predatory fish were sampled. Bay anchovy, mysids, and shrimps dominated the diets of weakfish and summer flounder, whereas polychaetes and bivalves were the most important prey taxa observed in Atlantic croaker. Prey selection was calculated for each species using Chesson's Index of Selectivity based on relative abundance data. Selection of bay anchovy was influenced by predator size in weakfish and summer flounder, where selectivity increased with predator size in weakfish and decreased in summer flounder. Selection of mysids significantly decreased with predator size in weakfish and also increased as the year progressed. In summer flounder, mysid selection was mainly driven by increasing water temperatures. Amongst the benthic prey, polychaete and bivalve selection by Atlantic croaker were inversely related to predator size and Julian Day, where polychaete selection decreased with increasing predator size and Julian Day and vice versa for bivalves. Results of analysis of prey selection patterns across a broad spatial scale highlight the utility of incorporating prey availability data to infer mechanisms driving feeding patterns in three sympatric predators and will be useful for subsequent ecosystem-based modeling efforts.

INTRODUCTION

The trophic dynamics of fishes and their prey are critical features that underpin the structure and functioning of marine ecosystems. Generally, fishes will consume a wide variety of prey while operating under species specific anatomical and physiological constraints. However, fishes can adapt to focus on groups of prey that are spatially or temporally available, easy to capture, and provide a high net gain of energy for growth (Ware 1971; Reiriz et al. 1998; Wootton 1998). Optimal foraging theory predicts that predators will choose prey that minimizes the ratio of costs to benefits (Schoener 1971). Benefits include growth from nutrients and calories ingested, whereas costs include energy lost during each step of the predation sequence, including post-consumptive processes, as well as exposure to predators (Gerking 1994; Lankford and Targett 1997; Ahrens et al. 2012). While the species-specific mechanisms that drive selective feeding patterns in natural populations of predatory fishes remain poorly understood, the outcome of prey selectivity can have direct and indirect community effects (Sogard 1997; Juanes et al. 2001) and can elucidate how predator-prey relationships vary temporally with changing environmental conditions (Rudershausen et al. 2005).

Feeding patterns of fishes can be related to a variety of factors that are not necessarily independent of each other, including fish size, environmental conditions, prey quality, and prey availability, amongst others (Lankford and Targett 1997; Juanes et al. 2001; Nye et al. 2011; Buchheister and Latour 2016). Most fishes show some sort of morphological or behavioral preference for a particular prey type, but may also demonstrate foraging flexibility in response to the seasonal availability of different food items (Barton 2007). Patterns of prey selection by predator fishes reduce levels of competition, thereby maximizing energy intake, growth, and survival. Diet switching and diet preferences are essential to our understanding of optimal foraging theory and the mechanisms that drive these feeding patterns play an important role in carbon flow throughout the food web (Gerking 1994). Additionally, when prey selection estimates are further combined with known consumption rates, predator biomass or prey biomass, critical fisheries and ecological issues can be addressed (Link 2004). However, due to

the high cost and effort associated with evaluating predator diets and ambient prey abundance patterns, prey preference and selection patterns are seldom addressed.

Weakfish (*Cynoscion regalis*), summer flounder (*Paralichthys dentatus*), and Atlantic croaker (*Micropogonias undulatus*) are abundant, seasonal predators in the Chesapeake Bay and represent critical links in regulating the flow of energy within the Bay's food web (Baird and Ulanowicz 1989). All three species are recreationally and commercially important and contribute substantially to state and regional economies (ASMFC 2010; ASMFC 2013; ASMFC 2016). Evidence of significant declines in the relative abundance of weakfish, summer flounder, and Atlantic croaker in the Bay over the last decade has been observed through fishery-independent sampling (Buchheister et al. 2013). Given the complex nature of ecosystem structure within the Bay (i.e. interaction of species, habitat types, and environment over space and time), little is known about the mechanisms contributing to the observed decline in abundance of these three important species. As attention gains towards adopting ecosystem-based fisheries management (EBFM), identifying and quantifying trophic interactions, and patterns within these interactions, is a fundamental requirement for parameterizing ecosystem-based models for the Chesapeake Bay (Whipple et al. 2000; Nye et al. 2011; Tyrell et al. 2011).

Despite the implications that selective feeding can have at the individual (Fraser et al. 2008), population (Herwig and Zimmer 2007), and community levels (Schleuter and Eckmann 2008) and its importance in an ecosystem framework, few studies have been published on feeding selectivity in the Chesapeake Bay. To contribute to the growing body of research on prey selectivity, I conducted concurrent predator/prey sampling in the lower Chesapeake Bay. Previous research has hypothesized that bottom-up control regulates the magnitude of trophic interactions in the Bay (Buchheister and Latour 2016), however, they lacked synoptic prey data and assumed diet composition was reflective of relative abundance patterns of prey in the environment. This study aimed to examine the relationship of temporal abundance patterns of important prey taxa in the lower Chesapeake Bay and its influence on the diets of three important, sympatric estuarine predators: weakfish, summer flounder, and Atlantic croaker.

METHODS

Study Area

The Chesapeake Bay is the largest estuary in the United States and among the largest in the world (Boesch et al., 2001). The mainstem of the Bay is characterized by three major salinity

zones, including oligohaline (0 – 5 ppt, upper Bay), mesohaline (5 – 18 ppt, middle Bay), and polyhaline (>18 ppt, lower Bay) regions. The lower Bay (e.g. Virginia waters) is of intermediate depth and is clearer than the middle and upper Bay. Hypoxic zones, which are frequent in the summer in the mid Bay, extend into the northern portion of the lower Bay, where they are less severe in terms of magnitude and duration (Zhou et al. 2014). The Chesapeake Bay supports over 350 species of resident and migratory fishes (Murdy and Musick 2013). The high degree of productivity in the Bay, in part, contributes to the estuary serving as an important nursery and foraging habitat for many species (Able and Fahay 2010). However, the Chesapeake Bay has undergone dramatic transformations over the last several decades. Combined effects of nutrient loading and eutrophication have contributed to large seasonal hypoxic events, increased turbidity, and a decline in submerged aquatic vegetation (Boesch et al. 2001; Kemp et al. 2005; Diaz and Rosenberg 2008). The degradation of the Chesapeake Bay ecosystem via changes in suitable foraging habitat has presumably altered the community structure and the productivity of both fishes and their prey (Breitburg 2002). Furthermore, climate change is predicted to impact a multitude of environmental variables in the Chesapeake Bay (Najjar et al. 2010). While the implications of climate change to the Bay's food web remains unknown, the physiological constraints of both predator and prey and the resulting distributional shifts, the availability of suitable habitats, and the quality and timing of primary productivity has potential to have significant ecosystem effects.

Predator Collection

Abundance and dietary data of predatory fishes were collected in the lower Chesapeake Bay by the Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAP) bottom-trawl survey from July 2014 – May 2015 (Figure 11). The survey performed five research cruises (March, May, July, September, and November), sampling 36 stations per cruise. Stations were selected based on a random stratified design and strata were defined by water depth (3.1 – 9.1-m, 9.1 – 15.2-m, and >15.2-m) and latitude (two 30-latitudinal-minute regions of the Bay; Figure 11). Sampling intensity was proportional to the surface area of each stratum. At each station, a 13.7-m 4-seam balloon trawl, with 15.2-cm stretched mesh in the wings and the body, was set by boat during daylight hours to target late juvenile and adult fishes. The net was typically towed with the tidal current along the bottom for twenty minutes at 3.0-3.3 knots.

Prior to sampling, environmental parameters, including temperature, were measured from the surface to the bottom using a Hydrolab MS5 sonde. At stations where hypoxic bottom waters (DO < 2 mg l^{-1}) were observed, tows were limited to 10 minutes as catches at these stations are predominantly very low, if not zero. Following each sampling event, the catch was sorted by species and size class (if applicable) and enumerated. Subsamples of each species/size class were then processed for dietary determination.

Prey Collection

Two approaches were used to sample the prey fish community. A 9.1-m × 2.4-m Aluette midwater trawl, with 38-mm stretched Dyneema mesh in the wings and body, was deployed at 18 randomly selected ChesMMAP stations within 18 hours of predator sampling. Floating 'mullet' doors were utilized for shallow depths and high aspect ratio Hendricksson midwater doors were used for stations deeper than 3.1-m. Deployment of the midwater trawl was set to just above the Bay floor. Once the gear reached the desired depth, the trawl was stepped obliquely to the surface for a total tow duration of 20 minutes. The second approach targeted juvenile fishes and invertebrates by the Juvenile Fish and Blue Crab Trawl Survey, using a 9.1-m semi-balloon otter trawl, with a 38.1-mm stretched mesh and 6.4-mm cod-end liner trawl, and towed along the bottom for five minutes during daylight hours. A total of 17 randomly selected stations were sampled during each cruise within 2 weeks of predator sampling.

Sampling of the planktonic and benthic infauna community occurred within 16 hours of predator sampling at the same 18 randomly selected prey fish stations. Sampling took place at night to capture the diel vertical migration patterns that are common to many important prey taxa in the Chesapeake Bay food web. A plankton net (0.9-m diameter, 750 μm mesh) was deployed with a mechanical flowmeter and set into the current on the surface for a duration of five minutes. Following retrieval, the net was immediately washed down and the catch was preserved in the field for further analysis in the laboratory. To characterize benthic infauna and epifauna, three replicate Ponar benthic grabs (0.1 m^2 area) were taken at each station. Upon retrieval of the grab, benthic material was sieved to separate biological specimens from benthic substrate. Catch data from all trawls were standardized to 10,000 m^3 water filtered for subsequent comparison purposes. All potential prey captured with the various sampling gears were identified to the lowest taxonomic resolution possible and enumerated.

Predator Diets

Predatory fish stomachs from ChesMMAP sampling were removed for identification of stomach contents to the lowest possible taxonomic resolution. Prey observed in the esophagus and buccal cavity were included in dietary analysis because prey is not thought to be retained in the large mesh otter trawl, and therefore, minimal net feeding is assumed to occur. All prey items encountered were enumerated. Diets were quantified for each predatory fish species by proportion by number for each prey type (Hyslop 1980). Dietary indices were estimated for each month at three depth strata using the following cluster sampling estimator (Bogstad et al. 1995; Buckel et al. 1999):

$$I_k = \frac{\sum_{i=1}^{n} M_i q_{ik}}{\sum_{i=1}^{n} M_i} \times 100, \quad (1)$$

such that,

$$q_{ik} = \frac{m_{ik}}{m_i} \quad (2)$$

where I_k is the dietary index of concern, n is the number of ChesMMAP trawls containing a predator species of interest, M_i is the total catch of the predator species collected at station i, and q_{ik} represents the diet proportion by number at each station, m_i is the total abundance of all prey in the stomachs of the predator species at station i, and m_{ik} is the total abundance of prey type k in these stomachs.

Prey Selection

Prey type selectivity by predatory fishes was determined by comparing the proportion of prey abundance in the predator diets with the proportion of prey abundance in the environment. Prey taxa used for selectivity calculations were determined by analyzing the dominant prey (>5% contribution by number) in each collection period. Seasonal dietary indices were determined for comparison and calculation of prey selectivity patterns following Chesson's Index of Selectivity (Chesson 1978):

$$\alpha_k = \frac{r_k/p_k}{\sum r_m/p_m}, \quad k = 1,\ldots,m \tag{3}$$

where α_k is the selectivity index for prey type k in a species of predatory fish from a given month/depth combination, r_k is the abundance proportion of prey type k in the stomach of a species of predatory fish from a given month/depth combination, and p_k is the abundance proportion of prey type k in the environment, and m is the number of prey types available. Selectivity values can range from 0 to 1, with values of α_k greater than $1/m$ indicating active selection for prey type k. Random feeding occurs when α_k equals $1/m$. Chesson's index assumes that different prey types are equally identifiable at each time point post-consumption and that catchability among different prey is the same for each gear type (Chesson 1978), but the latter assumption is likely violated in most instances. To mitigate inherent biases associated with differences in gear catchability, prey abundance for each gear type were divided by their respective annual means, thereby placing data from all gear types on a common scale.

I also analyzed the relationship between selectivity of dominant prey types relative to environmental and biological variables (e.g. temperature, salinity, Julian Day, predator size) using a beta regression analysis. Beta regression models can be used where the dependent variable is measured continuously on the standard unit interval, i.e. $0 < y < 1$ and this approach allows for flexible modeling of proportions and rates (Ferrari and Cribari-Neto 2004). The response variable was the selectivity value for each prey type in a given month/depth combination and covariates analyzed represented the mean across the same month/depth combination. Only dominant prey taxa were included in the analysis, such that mysids and bay anchovy were considered in prey selection patterns for weakfish and summer flounder. In Atlantic croaker, polychaetes and bivalves were the major prey taxa analyzed in the beta regression analysis. Multiple model parameterizations were considered and Akaike's information criterion (AIC) was used to select the best fitting model (Burnham and Anderson 2002). Significant relationships between prey selection and environmental covariates allow for a better understanding of the potential mechanisms that influence predator-prey interactions.

RESULTS

Prey Collection

The prey fish community differed markedly between the two gear types and between months. A total of 41,430 midwater prey were sampled across 90 midwater trawls and was dominated by bay anchovy, *Anchoa mitchilli*, accounting for 94.9% of the total catch by number (Figure 12). With the exception of September, where a large pulse of *Menidia menidia* was observed, bay anchovies were the most abundant prey taxa sampled in every month. Catches from 68 trawls performed by the Juvenile Fish and Blue Crab Survey were slightly smaller (n = 25,221) when compared to the midwater trawl, but the species diversity was higher (Figure 13). Similar to the midwater trawl, bay anchovies were the most abundant taxa sampled, ranging from 36.8% of the catch by number in July to 77.7% in May. Weakfish (6.8%) and kingfish (3.8%) were the second and third most abundant taxa sampled, respectively, and all other taxa sampled represented less than 3% of the total catch composition.

An even larger species diversity in the prey community was observed during the 80 plankton tows and a total of 47,913 organisms were sampled (Figure 14). In total, mysid shrimps were the most abundant prey, accounting for 44.6% of the total catch, followed by crab larvae (17.1%), and decapod shrimps (12.6%). All other prey categories accounted for less than 10% of the total catch composition by number. Relative to monthly catch composition, mysids were the most abundant taxa sampled with the exception of the month of March, where amphipods ranked the highest. Amongst the benthic epi- and infauna prey, polychaetes (44.5%) and bivalves (39.0%) were the most abundant taxa sampled across 270 benthic grabs (Figure 15). Amphipods (10.4%) were the only other prey taxa sampled that accounted for more than 10% of the total catch. When the monthly catch composition of benthic prey is considered, polychaetes were the most abundant taxa sampled aside from the month of May, where bivalves were the most abundant taxa.

Predator Diets

Across the spatial and temporal extent of the predator and prey community surveys, a total of 164 weakfish, 64 summer flounder, and 102 Atlantic croaker were used for dietary analysis. Empty stomachs were observed in 40.9% for weakfish, 42.2% for summer flounder, and 30.4% for Atlantic croaker (Table 4). In weakfish, crustacean prey and, to a lesser degree,

fish prey dominated the diet (Figure 16a). Dominant crustacean prey taxa in weakfish stomach contents included mysid shrimps, mainly *Neomysis americana*, and decapod shrimps, mainly *Crangon septemspinosa*; whereas the majority of fish prey taxa were bay anchovy, *Anchoa mitchilli*. The diets of summer flounder were dominated by over 60% fish prey, with bay anchovy being the major contributor (Figure 16b). Invertebrate crustaceans accounted for a majority of the remaining prey in summer flounder, with mysid shrimps and sand shrimps representing the dominant invertebrate taxa. Conversely, Atlantic croaker displayed a more benthic-oriented dietary composition (Figure 16c). Polychaetes, predominately *Nereis* spp., *Glycera* spp., and *Pherusa affinis*, were the most important prey taxa to Atlantic croaker, followed by bivalves, being mainly represented by razor and macoma clams and blue mussels.

Prey Selection

Weakfish prey selection patterns varied temporally, with selectivity values for bay anchovy and mysid shrimps highest in the summer (Figure 17). Mean selectivity values for each month/depth combination generally showed selection for bay anchovy and selection against invertebrate crustaceans, with the exception of one collection (Table 5). However, during the spring, bay anchovies were not present in the diet of weakfish and selection patterns demonstrated a consistent selection of shrimps over other prey taxa at the 9.1–15.4-m and >15.4-m depth strata. Of the identifiable prey, bay anchovies were less prevalent in weakfish diets than mysids or shrimps (8.1% versus 39.7% and 35.2%, respectively). Beta regression analyses revealed a significant influence of mean predator size on bay anchovy and mysid selection patterns ($p = 0.05$ and $p < 0.001$, respectively), such that selection increased for bay anchovy and decreased for mysid shrimps with increasing predator size (Table 6; Figure 20). A significant relationship was also determined between Julian Day and the selection of mysid shrimps ($p = 0.004$) where selection increased with an increase in Julian Day.

Summer flounder displayed varied patterns of selection across all months and depths (Table 5). Bay anchovies were regularly selected for over mysid shrimps in July, September, and November at intermediate depths of 9.1 – 15.2-m (Figure 18). Conversely, mysids were selected over bay anchovies in September at shallower depths of 3.1 – 9.1-m. The high levels of selection towards bay anchovies corroborate the magnitude of their contribution in the diets of summer flounder where bay anchovies were more prevalent than all other identified fishes and mysids

(37.4% versus 11.7% and 17.0%, respectively). Larger flounder were sampled in fall and spring, typically in shallow habitats, and selected for larger prey, such as weakfish and spot rather than bay anchovy. Results from beta regression analyses revealed a significant relationship between anchovy selection and predator size ($p = 0.038$), where anchovy selection gradually decreased with increasing predator size (Table 7; Figure 20). Additionally, a significant relationship was observed between mysid selection and water temperature ($p = 0.013$), where mysid selection increased with increasing temperature.

Atlantic croaker selection patterns displayed a high degree of temporal variability across the sampling period (Figure 19). Mean selectivity values across month and depth strata elucidated positive selection for bivalves and brittle stars in September, and above the random feeding cutoff for polychaetes in the spring (Table 6). Relative to the diet of Atlantic croaker, polychaetes and bivalves were the most abundant taxa observed in the stomach contents, accounting for 42.8% and 20.9%, respectively. Hydroids were the only other prey group to account for more than 10% of the dietary composition. Selection of polychaetes and bivalves by Atlantic croaker were significantly explained by predator size and Julian Day (Table 7; Figure 20). Predicted polychaete selection by Atlantic croaker demonstrated a significant relationship with predator size ($p = <0.001$) and Julian Day ($p = <0.001$), such that selection for polychaetes decreased with increasing predator size and Julian Day. The opposite relationship were predicted for bivalve selection by Atlantic croaker where selectivity increased with increasing predator size ($p = 0.001$) and Julian Day ($p<0.001$).

DISCUSSION

Temporal abundance patterns of dominant prey taxa

Although not the direct focus of the present study, the fluctuating availability of important prey taxa across the temporal duration of sampling was assumed to be representative of the prey field available to predatory fishes. I observed monthly differences in the prey community for each of the sampling methodologies. A wide diversity of prey taxa were sampled with the midwater trawl, however, bay anchovies were the most important component to the diets of the predatory fishes sampled across the temporal extent of the study. The midwater trawl was highly effective at sampling small schooling fishes, such as bay anchovies, silversides, and YOY menhaden, but larger size-classes of prey fishes were largely absent from trawls and may

be underrepresented due to gear selectivity. Bay anchovy is the most abundant fish in the Chesapeake Bay, where it represents a key forage species to many predators (Jung and Houde 2004; Murdy and Musick 2013; Buchheister and Latour 2015). In the lower Bay, bay anchovy abundance nearly doubled in the fall relative to the summer and these findings agree with previous spatio-temporal distribution research of bay anchovy and likely are attributable to a seasonal southward migration in the Bay (Wang and Houde 1995; Jung and Houde 2004).

Samples from the juvenile fishes trawl were also dominated by bay anchovies, but to a lesser degree than the midwater trawl. Relative to previous years of sampling in the lower Bay, data from the VIMS Juvenile Fish and Blue Crab Survey indicated that bay anchovy abundance was at a 26-year time-series low across the sampling range for this study (Tuckey and Fabrizio 2015). The time-series low of bay anchovy abundance correlates with a large hypoxic water volume in the Chesapeake Bay during the 2014 summer (Friedrichs personal communication). Previous research has shown that planktivorous fishes, such as bay anchovy, avoid hypoxic water conditions thereby impacting their behavior, spatial distribution, and food web interactions (Eby and Crowder 2002; Ludsin et al. 2009; Zhang et al. 2009). Findings from the Neuse River Estuary and Chesapeake Bay suggest that low oxygen levels compress the spatial distribution of bay anchovy into shallow, warm waters, which has the potential to simultaneously reduce suitable habitat for feeding and increase overlap with competitors and predators (Ludsin et al. 2009; Ebby and Crowder 2011). Regardless of the mechanism driving the time-series low of bay anchovy abundance in the Bay, the low levels likely influenced the predator foraging patterns observed in the present study. Aside from bay anchovy, juvenile weakfish and spot were the only other fish prey groups that were important to the diets of the predatory fishes (e.g. >10% dietary contribution), mainly for large summer flounder.

Amongst the plankton community, mysid shrimps represented the most abundant prey taxa sampled and are an important component to the diet of many estuarine predatory fishes (Benfield 2013). Abundance of zooplankton was highest in the spring and summer, corresponding to the spring and summer phytoplankton blooms in the Chesapeake Bay (Roman et al. 2005). With the exception of March, mysid shrimps were the dominant component of the zooplankton community. Mysids often constitute a large fraction of zooplankton numbers and biomass in estuaries (Benfield 2013). Furthermore, they play a key role in structuring estuarine food webs as they are important in the transfer of carbon from microzooplankton,

mesozooplankton, and the detrital pool into small zooplanktivorous fishes and other higher trophic level predators (Vilas et al. 2008). Despite the importance of mysids to the diet of numerous commercially and recreationally important fish species in the Bay, particularly in juvenile fishes, there are little data regarding distributional and seasonal abundance patterns in the Chesapeake Bay. Mayor et al. (2017) observed peaks in *Neomysis americana* in coastal lagoons of Maryland in spring and summer, which agrees with the findings of this study. Mysid shrimps remain near the bottom during the day and vertically migrate to the surface at night (Cuker and Watson 2002). The lack of comparable seasonal mysid data in the Bay is likely attributable to previous zooplankton sampling occurring at the surface during the day, and therefore largely missing the mysid component of the zooplankton community. Continued monitoring of mysid shrimp distribution and abundance patterns would be informative from a variety of ecological perspectives, including, but not limited to, a better understanding of drivers of prey selection by predatory fishes.

Benthic communities play important roles in energy flow, cycling of nutrients, and in trophic transfer in estuaries (Wilson and Fleeger 2013). Polychaetes often dominate the benthos in terms of density (Seitz et al. 2008), whereas bivalves can contribute up to 90% of the benthic biomass (Diaz and Schaffner 1990). Results from benthic grab sampling further illustrated the numerical dominance of polychaetes and bivalves in the lower Chesapeake Bay as they accounted for at least 80% of the total combined abundance in each month. Polychaetes were the most abundant taxa sampled and were prevalent throughout all months, with maximum abundance observed in the spring. Bivalve abundance also peaked in spring, but showed an appreciable decline in abundance throughout the summer and fall. The decline in bivalve abundance during the summer is likely, in part, a product of predation by bottom-feeding fishes and blue crabs which has been well documented in controlling the distribution and abundance of macrobenthic invertebrates (Virnstein 1977; Peterson 1979; Holland et al. 1980, Seitz et al. 2003). The patterns of both seasonal predator abundance and polychaete and bivalve abundance in the present study further support these previous findings. Presumably, the abundance of bivalves and polychaetes are reduced during periods in the summer when predation levels are highest and also due to mortality of r-selected species following their recruitment peaks (Baird and Ulanowicz 1989; Hines 1990).

Diet composition

The diets of the predatory fishes investigated in this study were assumed to reflect the prey that was available to them spatially and temporally. Although we sampled both predator and prey populations at given location within 16 hours, it should be noted that it is possible predators fed in a different area than where they were captured. Regardless, the comparison of diets from one study to another is likely to yield varying results due to different sampling methodologies or temporal changes in prey distribution and abundance between the time periods of the two studies. However, accurate diet characterizations are essential for interpretation of feeding selectivity patterns, and thus, variability in diets can lend insight into potential predator-prey dynamics (Buchheister and Latour 2016). Diets of weakfish observed in this study were similar to previously reported diet composition analyses in previous years in the Chesapeake Bay (Buchheister and Latour 2015). Mysid shrimps dominated the diet of weakfish, followed by decapod shrimps, and bay anchovy. Grecay and Targett (1996) found similar patterns in Delaware Bay, but this is in contrast to findings from Hartman and Brandt (1995) where bay anchovies were the most important dietary component. The use of different dietary estimation methods and the limited spatial scope of the study by Hartman and Brandt (1995) likely accounts for the discrepancy in diet composition between the studies.

Summer flounder diets were found to be mainly comprised of bay anchovies, mysids, decapod shrimps, and crabs. Longer term dietary analyses of summer flounder in Chesapeake Bay have revealed a similar dietary makeup, however, mysid shrimps were found to be the dominant prey in that study (Latour et al. 2008). In recent years, the dietary importance of bay anchovies has nearly doubled from 25% to 50% in medium-sized summer flounder (225-375 mm). Correspondingly, the mean size of fish used in our dietary characterization was 291.8 mm, so our results concur with more recent findings from diet studies (Buchheister and Latour 2015). Another potential explanation in the discrepancy in dietary composition is the spatio-temporal extent of the dietary analyses. Spatially, this study focused on the diet of summer flounder within the lower Chesapeake Bay whereas the previously mentioned dietary analyses focused on the entire mainstem of the Bay. A higher degree of bay anchovy consumption was observed in the late summer/early fall and this coincides with a down Bay migration and an increase in production of bay anchovy in the lower Chesapeake Bay (Wang and Houde 1995; Rilling and Houde 1999). Buchheister and Latour (2016) contend that changes observed in dietary habits are

supply-driven, however, they lacked synoptic prey data from the environment to formally test their hypothesis. While large pulses in prey availability can influence consumption and growth patterns in opportunistic predators, I contend that additional selective mechanisms operate at a finer-scale which subsequently can influence dietary composition changes in predatory fishes.

Atlantic croaker diets were generally similar to what has been seen in previous analyses (Nye et al. 2011; Buchheister and Latour 2015). Polychaetes were the most important component of the diet in all studies, including this one. However, there were some departures from previous findings amongst the prey of secondary importance in the present study. For example, I found bivalves were the second most important prey taxa in Atlantic croaker in the lower Bay, but were found to be less important when the entire mainstem of the Chesapeake Bay was considered (Nye et al. 2011; Buchheister and Latour 2015). In recent years, however, dietary results from ChesMMAP have detected a similar increase in the dietary importance of bivalves when compared to diet data taken before 2014. Whether this increase in bivalve consumption is an artifact of increased bivalve abundance or a change in foraging behavior remains to be seen due to a lack of consistent concurrent predator/prey sampling in previous years. Additionally, a majority of the Atlantic croaker sampled during this study were mature according to size-at-maturity metrics (Barbieri et al. 1994), which has been shown to correspond with an increased bivalve dietary contribution (Nye et al. 2011) thus further supporting findings from this study.

Prey selection - influence of predator size

Body size regulates foraging patterns by controlling the morphological constraints on sizes 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 (Eggers 1977; Scharf et al. 2002; Buchheister and Latour 2016). Each predatory species operates under its own morphological, behavioral, and physiological constraints that drive selection for particular prey taxa that enables maximum growth rates while minimizing the risk of predation. Weakfish undergo an ontogenetic shift in their diets where smaller fish consume mysids and larger fish (~200 mm) switch to piscine prey, primarily bay anchovy (Buchheister and Latour 2015). Our results corroborate the ontogenetic shift in prey importance and assume that this switch is the result of active prey selection. At small predator sizes, mysid shrimps represent a profitable prey for juvenile weakfish due to high encounter rates, ease of capture, and minimal post-consumptive

processes, therefore, maximizing growth rates (Lankford and Targett 1997). Our results provide field-based corroboration of the laboratory-based observations by Lankford and Targett (1997) of mysid selection in juvenile weakfish. As fish grow, increases in gape size and improvements in locomotory and sensory abilities allow for subsequent increases in reactive field and size of prey that can be ingested (Gerking 1994; Wootton 1998). Furthermore, growth rates can increase markedly after switching from an invertebrate diet to a piscivorous diet (Buckel et al. 1998; Galarowicz and Wahl 2005). I suspect the difference in energy density between mysid shrimps and bay anchovy (4.8 kJ g^{-1} and 5.9 kJ g^{-1}, respectively) (Cummins and Wuycheck 1971; Steimle and Terranova 1985) is a driving mechanism for the shift from mysid to bay anchovy selection observed in the present study. Further research is required, however, to examine the energy expended by weakfish during pre- and post-consumptive processes to determine the extent to which net energy is gained by selecting for specific prey taxa as they grow.

In summer flounder, selection of bay anchovy decreased with increasing predator size, although the decrease in selection pressure was still above random feeding levels. Similar to weakfish, summer flounder undergo an ontogenetic shift in their diet where they switch from primarily feeding on mysids at small sizes to increasingly larger fish as they grow (Latour et al. 2008; Buchheister and Latour 2015). I observed relatively consistent active selection of bay anchovy over mysids throughout the duration of the study, which has been observed in other flatfish species (Roberts et al. 1982). As they grow, a decrease in the importance of bay anchovy in summer flounder diets corresponds with an increase in the dietary importance of larger demersal fishes, like spot (Latour et al. 2008; Buchheister and Latour 2015). Positive selection for spot was observed in the spring by the largest summer flounder sampled throughout this study. I believe that the decreased selection of bay anchovy as flounder grow is a function of increased selection and consumption of spot. One potential explanation for the observed increase in prey size as predators grow is simply that smaller prey are less profitable than larger prey in terms of net energy gained (Hartman 2000; Scharf et al. 2003). Another potential explanation is changes to the foraging behavior as summer flounder grow. Small summer flounder have been observed making vertical migrations up in the water column at night, which is thought to be related to foraging behavior, where important dietary components, such as mysids and bay anchovy are abundant (Yergey 2012; Henderson and Fabrizio 2014). Conversely, larger individuals primarily use ambush tactics to capture prey and remain sedentary for long periods

where encountering demersal teleosts, like spot, is more likely (Staudinger and Juanes 2010). To better understand the specific mechanisms driving the observed selective patterns, additional sampling of large summer flounder as well as research into predator/prey habitat overlap and predator/prey behavior is required.

Atlantic croaker are typically considered opportunistic predators given their large dietary breadth (Willis et al. 2015). Overall our results agree with this general characterization, but at a finer-scale I observed seasonal selective patterns among dominant prey taxa that appeared to be related to changes in abundance. Atlantic croaker consumed polychaetes during the spring at a higher proportion than they were found in the environment, which was significantly influenced by predator size. Small croaker had a higher feeding preference for polychaetes when compared to larger individuals. Conversely, smaller croaker were less selective towards bivalves than larger individuals. Previous research has shown a decrease in the importance of polychaetes to the diets of Atlantic croaker as they grow (Buchheister and Latour 2015). Although not empirically tested in this study, I suspect one mechanism partially responsible for the observed selective patterns is their morphological development. At small sizes, gape limitation and crushing ability of pharyngeal toothplates negatively impacts their ability to consume large or hard-bodied prey (Chao and Musick 1977; Deary and Hilton 2016), therefore, croaker likely seek out prey that are easier to consume such as polychaetes or mysid shrimps. As croaker grow, their dietary breadth increases and they become more opportunistic feeders (Parker 1971; Chao and Musick 1977), consuming increasing levels of bivalves and crustaceans (Nye et al. 2011).

Temporal selection patterns

I observed a significant increase in mysid selection by weakfish with increasing Julian Day that may be related to seasonal migration patterns. Weakfish are thought to migrate out of the Bay in fall (ASMFC 2016), which is when selection for mysids was at its highest. During that period, weakfish mean size sampled was 150.1-mm, which corresponds to immature fish based on size-at-maturity metrics (Lowerre-Barbieri et al. 1996). As stated previously, small weakfish primarily selected for mysid shrimps. Based on seasonal length-frequency comparisons, I suspect that larger weakfish are either not present or emigrate out of the Bay earlier than smaller weakfish, which allow for continued mysid selection prior to themselves migrating south before winter. Lankford and Targett (1997) demonstrated that juvenile weakfish

select mysids over larger prey due to differential prey digestibility, thus resulting in maximized growth rates. By residing longer in the Bay and selectively targeting mysids, small weakfish can potentially enhance their growth rate prior to expending extensive amounts of energy on their southward migration. However, migration patterns of weakfish are poorly understood and size-based patterns of weakfish emigration from the Chesapeake Bay into coastal waters is largely unknown and additional analysis is warranted. Regardless, results from this study demonstrate that weakfish selection for mysids is influenced by a multitude of factors, which further confirms the importance of mysids in supporting growth and survival of a species that has seen dramatic declines in abundance within the Chesapeake Bay over the last decade (Buchheister and Latour 2013; ASMFC 2016).

A seasonal selection pattern for mysids was observed in summer flounder where selection significantly increased with temperature, dramatically increasing from 24–26°C, which corresponds to summer water temperatures in the Chesapeake Bay. Previous research has demonstrated that the maximum growth rate of *Neomysis americana*, the dominant mysid in the Bay and in flounder diets, peaks at 25°C in saline waters (Pezzack and Corey 1979). The high growth rate of *N. americana* in summer likely supports the abundance maximums observed in the Chesapeake Bay in this study. As such, the extent of mysid feeding does appear to be correlated with their abundance relative to other prey taxa. As mysid abundance peaks around 24–26°C, the consumption by summer flounder increased. Conversely, the relative abundance and consumption of other important prey taxa, such as bay anchovy, subsequently decreased. These patterns suggest that the relative consumption of mysids is opportunistic and the selection pattern is a passive process. However, similar to weakfish, it should be noted the seasonal component of mysid selection by summer flounder corresponds with flounder catches that had the smallest average size (230-260 mm) throughout the duration of the study. Although no significant trend was observed for selection of mysids relative to predator size, I suspect this is due to inadequate diet sample size of larger summer flounder. With additional sampling of larger summer flounder, I can tease out the dominant prey selection mechanisms for this recreationally and commercially important species.

Two opposing temporal selection patterns were observed for Atlantic croaker. Polychaete selection decreased with increasing Julian Day, whereas bivalve selection increased with increasing Julian Day. Contrastingly, I observed a large increase in the relative abundance of

bivalves, mainly *Macoma balthica*, during spring sampling. The increase in spring bivalve abundance corresponds to the timing of peak settlement of *M. balthica* in the Bay (Hines et al. 1990). Despite the increased relative abundance of bivalves, polychaetes were selected by Atlantic croaker. Polychaetes have a higher energy density than bivalves (Cummins and Wuycheck 1971) and handling time is comparatively reduced, potentially indicative of a pre-consumptive energetic selective mechanism. Selection of polychaetes decreased over time and I observed a corresponding increase in the selection of bivalves. Enhanced predation of bivalves by epibenthic predators has been observed during and after seasonal hypoxic events in the Chesapeake Bay (Seitz et al. 2003; Long et al. 2014). Although hypoxic events are more severe and prolonged in the upper Chesapeake Bay, the northern portion of the lower Bay experiences localized depletion of oxygen in bottom waters in the summer (Zhou et al. 2014). These temporary hypoxic events have the capacity to reduce bivalve antipredator responses and also induce behavioral responses, such as reduced burial depth and extension of siphons, thus enhancing susceptibility to predation (Seitz et al. 2003; Long and Seitz 2008; Wang et al. 2010). Even in normoxic regions of the lower Bay, intensified predation on benthic infauna is evident due to exclusion of benthic predators from adjacent deep hypoxic waters (Kemp and Boynton 1981). The selective patterns on bivalves observed in this study appear to indicate that Atlantic croaker take advantage of the enhanced vulnerability, and therefore availability, during and after hypoxic events beginning in early summer. Due to the foraging patterns known for Atlantic croaker combined with prey abundance data observed here, I characterize Atlantic croaker as opportunistic foragers that select for polychaetes and bivalves as they become more available within the food web.

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Table 4. Total fish analyzed, number with food, mean size, and size range of weakfish, summer flounder, Atlantic croaker sampled in Chesapeake Bay from July 2014 – May 2015.

Species	Month	Number analyzed	Number with food	Mean FL	FL range
Weakfish	July	31	23	181.77	35-230
	Sept	40	15	145.50	50-260
	Nov	35	21	150.14	90-295
	May	58	49	194.05	130-260
Summer flounder	July	7	4	232.86	145-200
	Sept	22	12	260.68	160-520
	Nov	22	12	296.59	245-415
	May	12	9	368.08	220-520
Atlantic croaker	July	32	25	191.25	155-260
	Sept	29	13	222.24	160-335
	Nov	5	3	174.00	65-255
	May	36	30	189.86	135-240

Table 5. Mean prey type selectivity (Chesson's index, α_i) relative to month/depth combinations for weakfish, summer flounder, and Atlantic croaker collected in July 2014-May 2015 in lower Chesapeake Bay. Values of $\alpha_i = 1/m$ represent random feeding, $\alpha_i > 1/m$ represent selection for prey type *i*, and $\alpha_i < 1/m$ represent selection against prey type *i*, where *m* is the number of prey types. MW/JT/PT = standardized midwater trawl/juvenile fish trawl/plankton tow, BG = benthic grab.

Predator	Gear	1/*m*	Month	Depth (ft)	Prey type	Selectivity Index (α_i)
Weakfish	MW/JT/PT	0.33	July	30-50	Bay anchovy	0.669
					Mysids	0.241
					Shrimps	0.090
	MW/JT/PT	0.5	September	30-50	Bay anchovy	0.295
					Mysids	0.705
	MW/JT/PT	0.5	September	50+	Bay anchovy	0.599
					Mysids	0.401
	MW/JT/PT	0.5	November	30-50	Bay anchovy	0.572
					Mysids	0.428
	MW/JT/PT	0.5	May	30-50	Shrimps	0.989
					Mysids	0.011
	MW/JT/PT	0.5	May	50+	Shrimps	0.915
					Mysids	0.085
Summer flounder	MW/JT/PT	0.5	July	30-50	Bay anchovy	0.889
					Mysids	0.284
	MW/JT/PT	0.5	September	10-30	Bay anchovy	0.263
					Mysids	0.737
	MW/JT/PT	0.5	September	30-50	Bay anchovy	0.865
					Mysids	0.135
	MW/JT/PT	0.5	November	10-30	Bay anchovy	0.012
					Weakfish	0.988
	MW/JT/PT	0.5	November	30-50	Bay anchovy	0.882
					Mysids	0.118
	MW/JT/PT	0.5	May	10-30	Bay anchovy	0.014
					Spot	0.986
	MW/JT/PT	0.5	May	30-50	Bay anchovy	0.062
					Shrimps	0.938
Atlantic croaker	BG	0.25	July	30-50	Bivalves	0.789
					Polychaetes	0.211
	BG	0.5	September	30-50	Bivalves	0.840
					Polychaetes	0.160
	BG	0.5	September	50+	Brittle stars	0.910
					Polychaetes	0.090
	BG	0.5	May	10-30	Bivalves	0.103
					Polychaetes	0.897
	BG	0.5	May	30-50	Bivalves	0.366
					Polychaetes	0.634

Table 6. Beta regression analysis parameter estimates for prey selection covariates in weakfish, summer flounder, and Atlantic croaker. Beta regression analysis performed with a complementary log log link function and * indicates significant explanatory parameters (p = 0.05).

Predator	Prey	Covariates (parameter estimates)
Weakfish	Bay anchovy	Predator size (0.019)*
	Mysids	Predator size (-0.037)*
	Mysids	Julian Day (0.009)*
Summer flounder	Bay anchovy	Predator size (-0.134) *
	Mysids	Temperature (2.281)*
Atlantic croaker	Polychaetes	Predator size (-0.041)* + Julian Day (-0.034)*
	Bivalves	Predator size (0.031)* + Julian Day (0.022)*

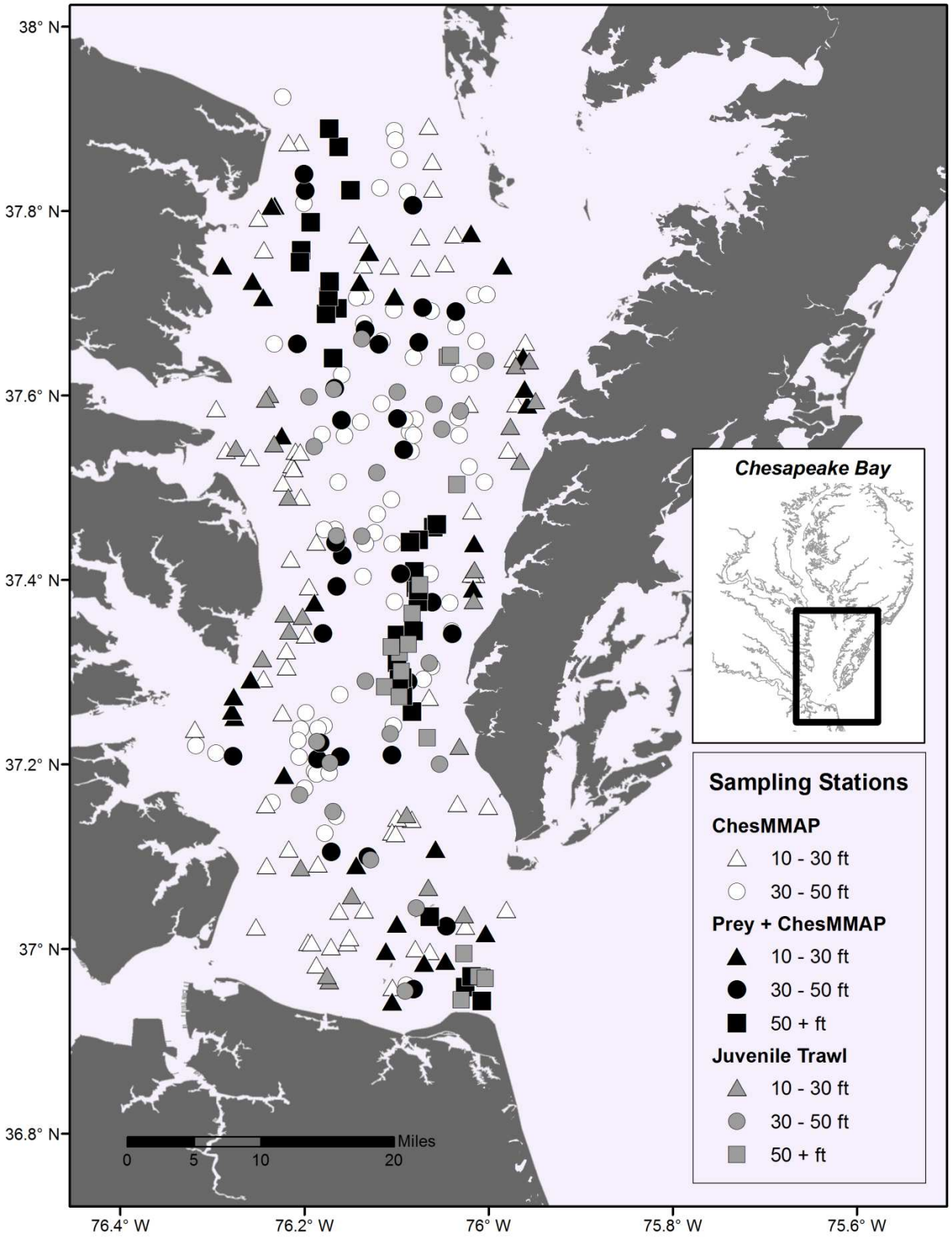

Figure 11. All stations sampled by the Chesapeake Bay Multispecies Monitoring and Assessment Program for predatory (n = 160) and prey community (n = 90) in July 2014 - May 2015.

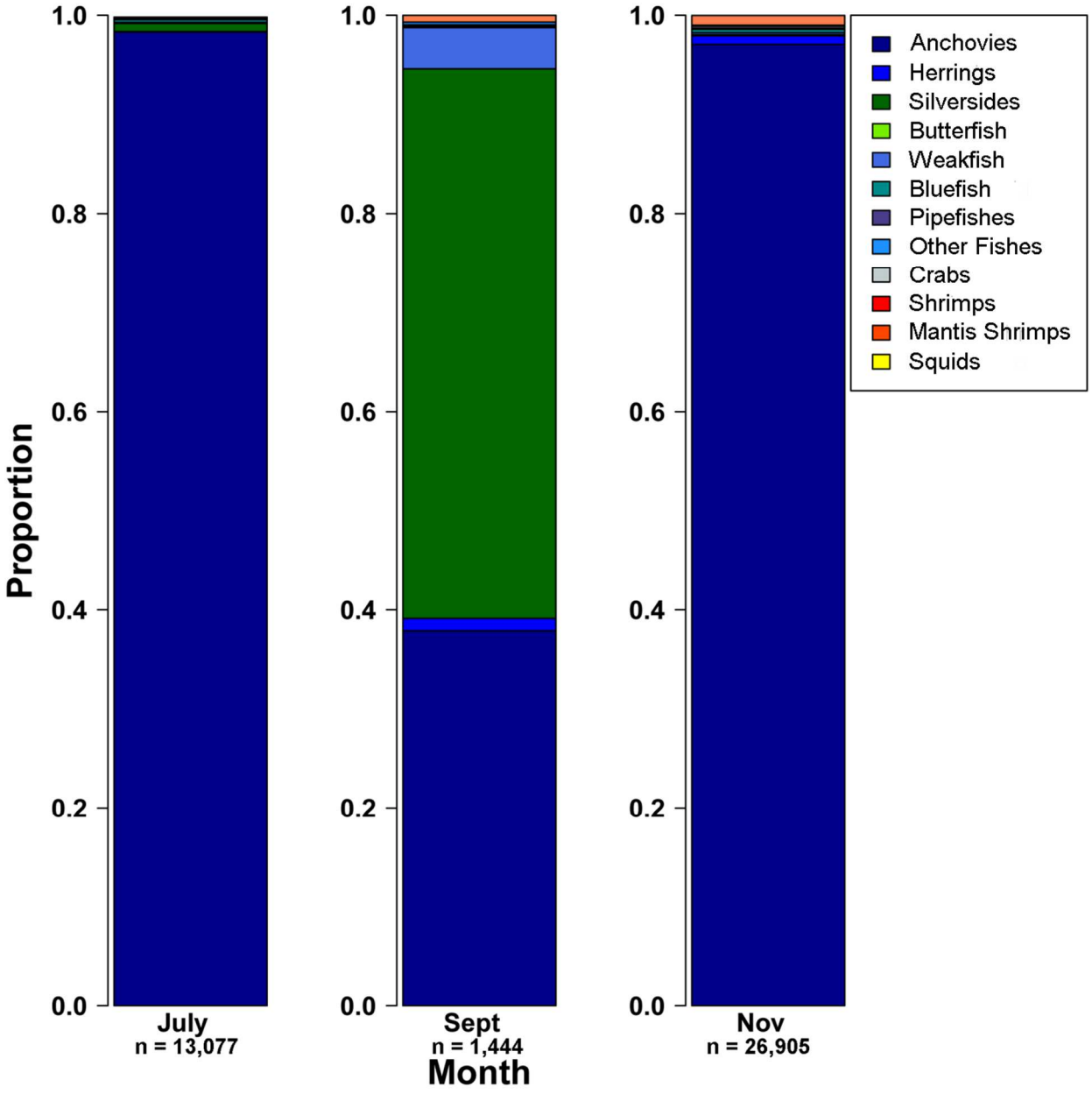

Figure 12. Monthly relative abundance (proportion) of prey groups collected with a midwater trawl in the lower Chesapeake Bay.

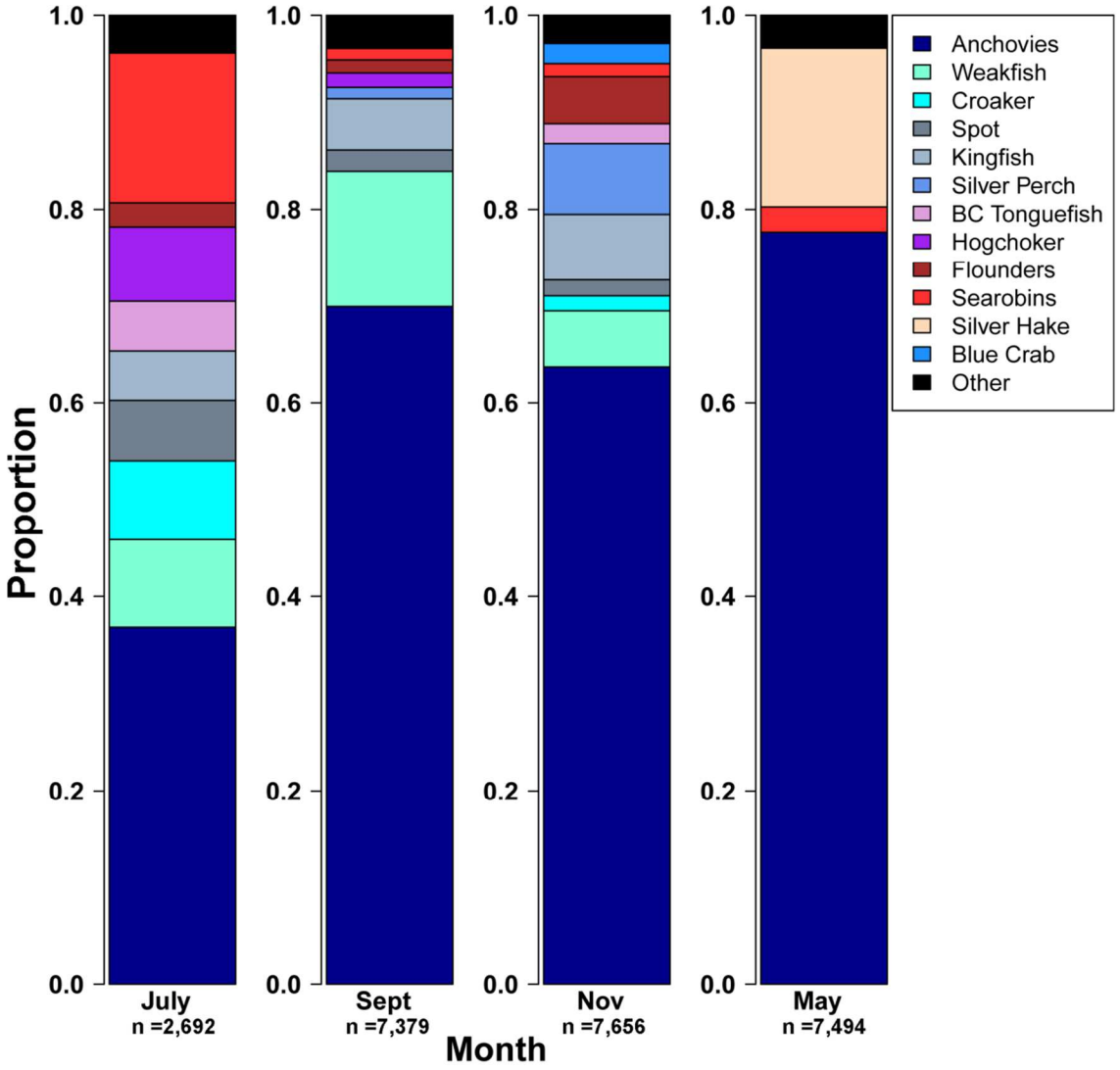

Figure 13. Monthly relative abundance (proportion) of prey groups collected by the Juvenile Fish and Blue Crab Trawl Survey in the lower Chesapeake Bay.

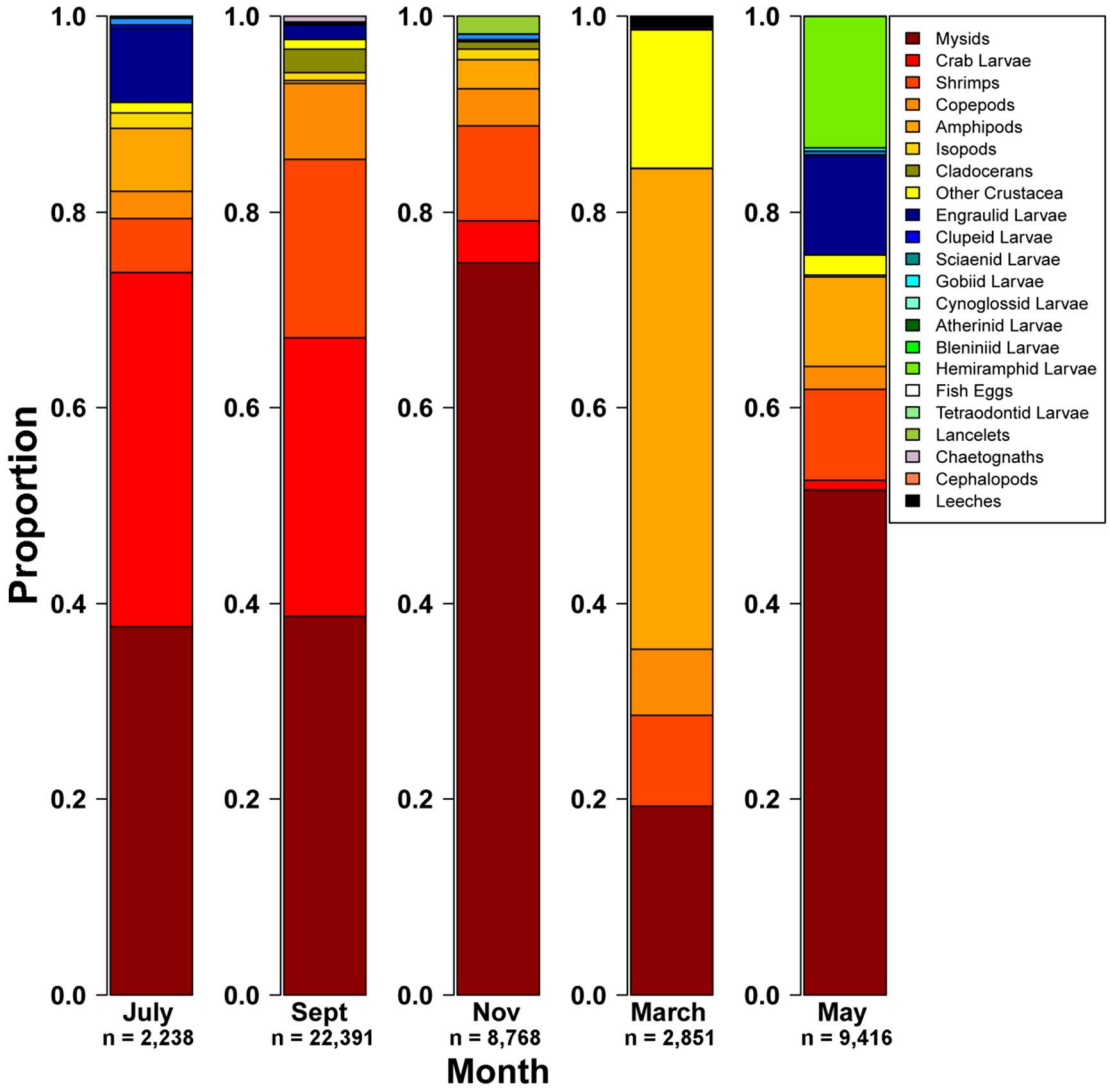

Figure 14. Monthly relative abundance (proportion) of prey groups collected with a plankton net in the lower Chesapeake Bay.

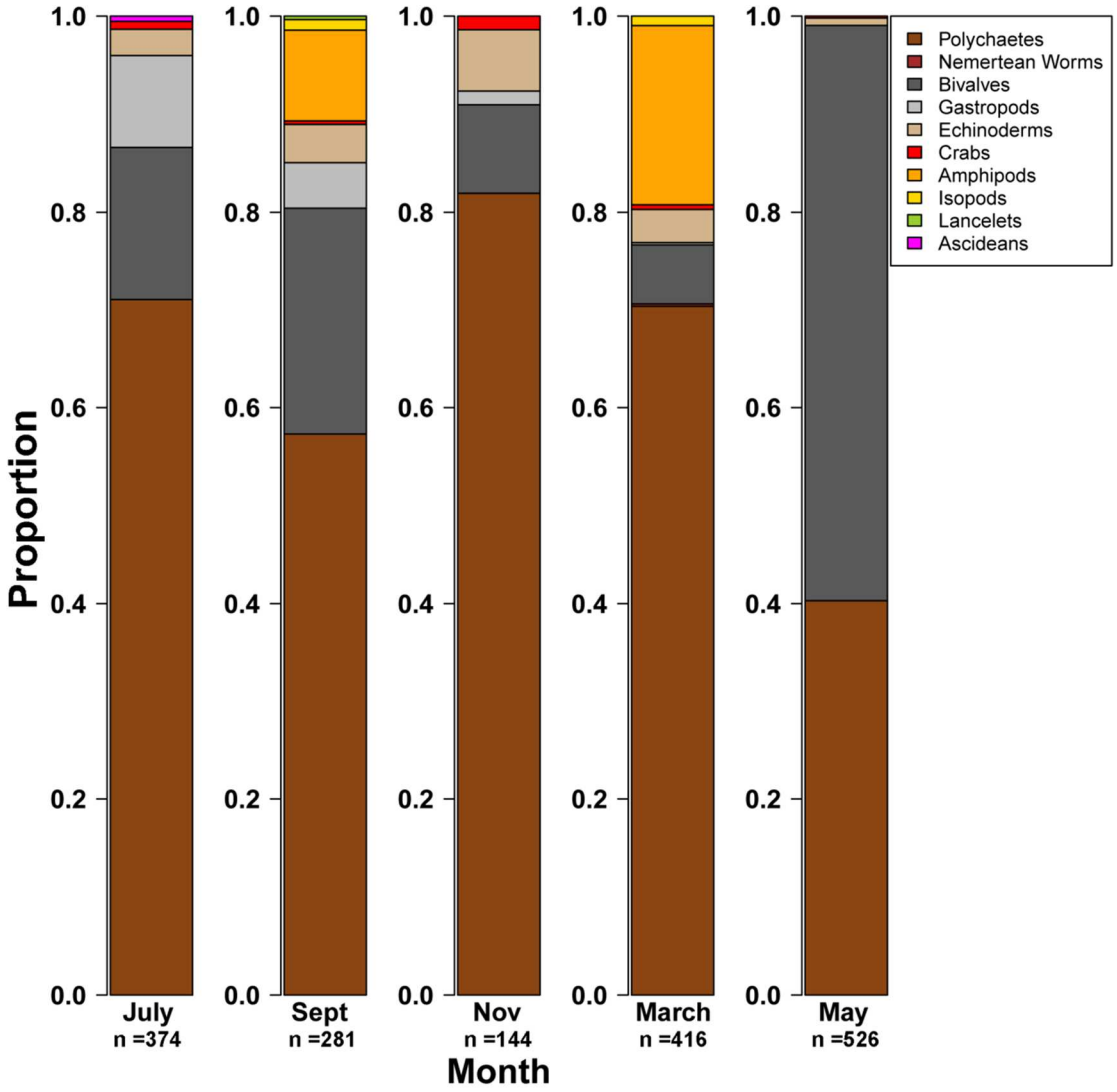

Figure 15. Monthly relative abundance (proportion) of prey groups collected with a Ponar benthic grab in the lower Chesapeake Bay.

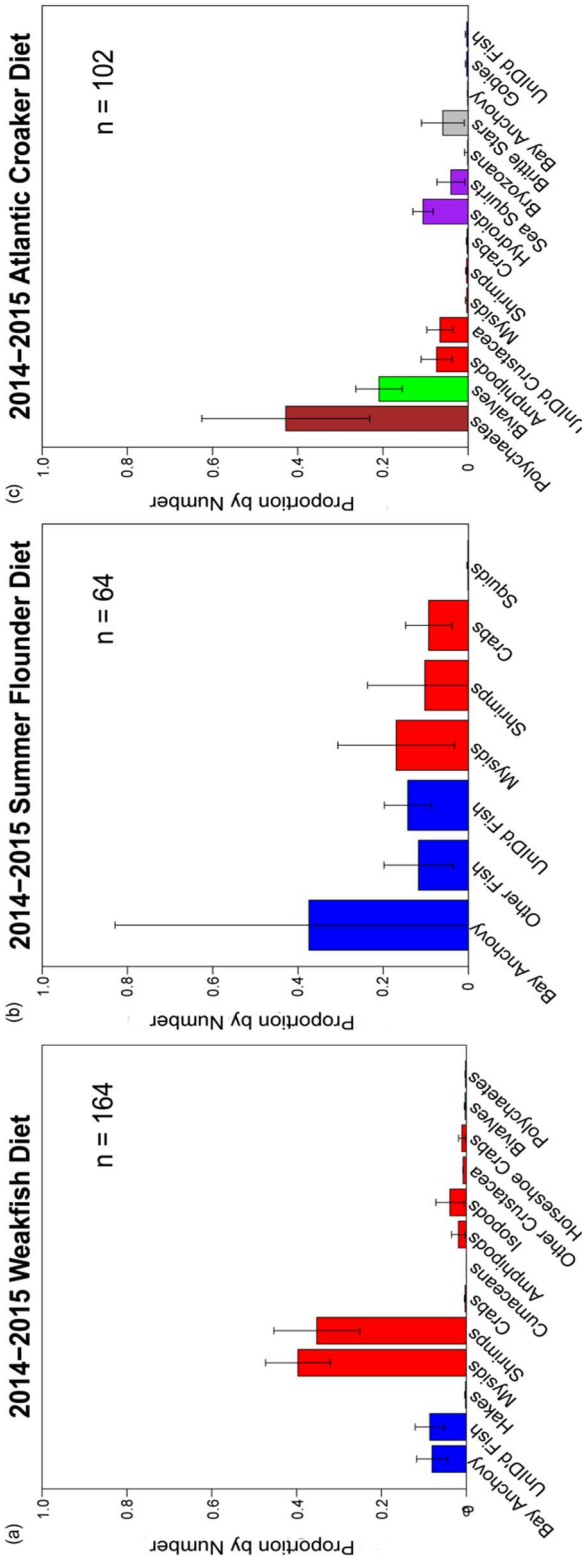

Figure 16. Diet proportion by number of prey groups consumed by a) weakfish, b) summer flounder, and c) Atlantic croaker in the lower Chesapeake Bay.

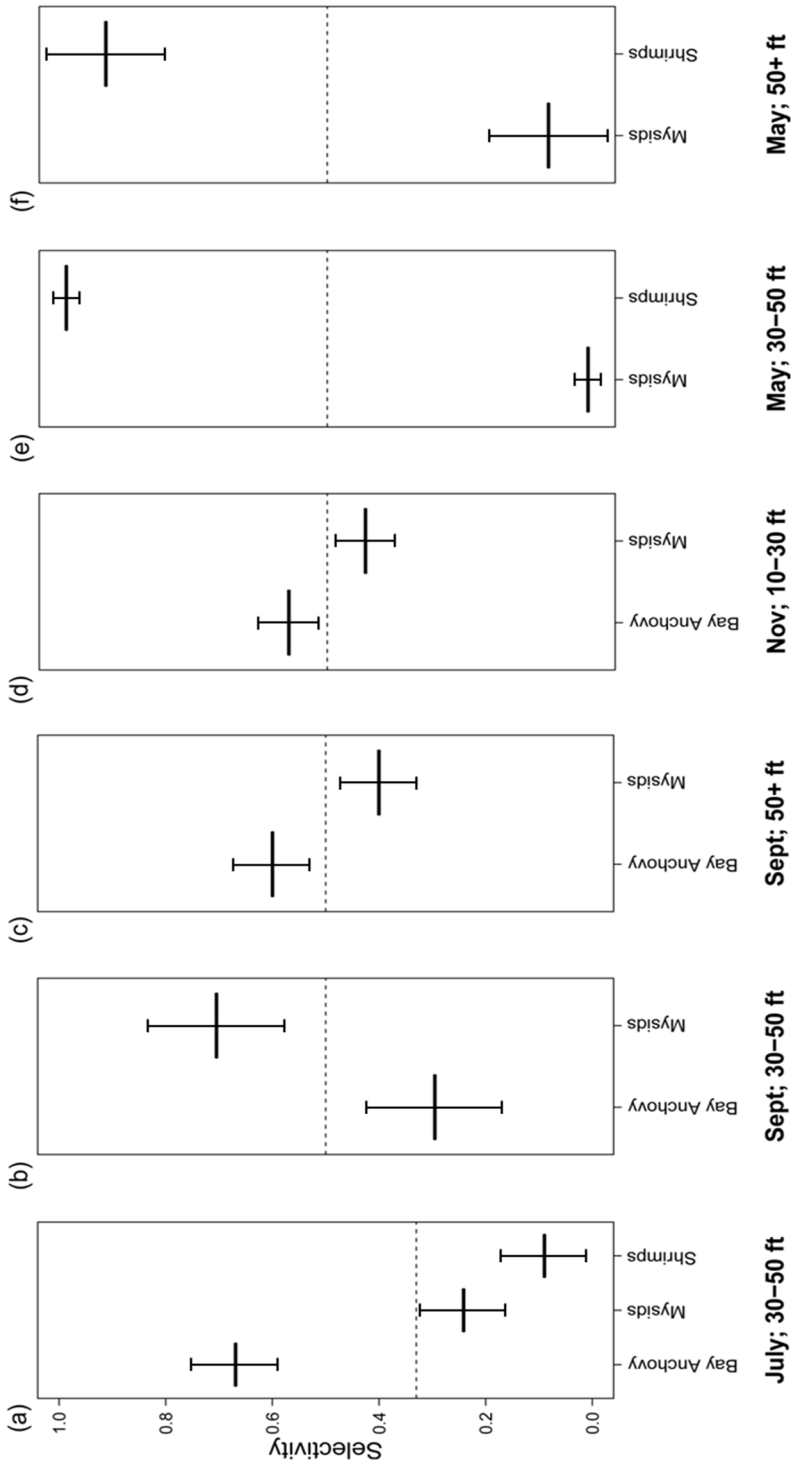

Figure 17. Mean selectivity (Chesson's index α ± SE) versus month and depth combinations for the dominant prey groups of weakfish collected in the lower Chesapeake Bay by standardized midwater trawl, juvenile fish trawl, and plankton net. Dashed line represents level of random feeding.

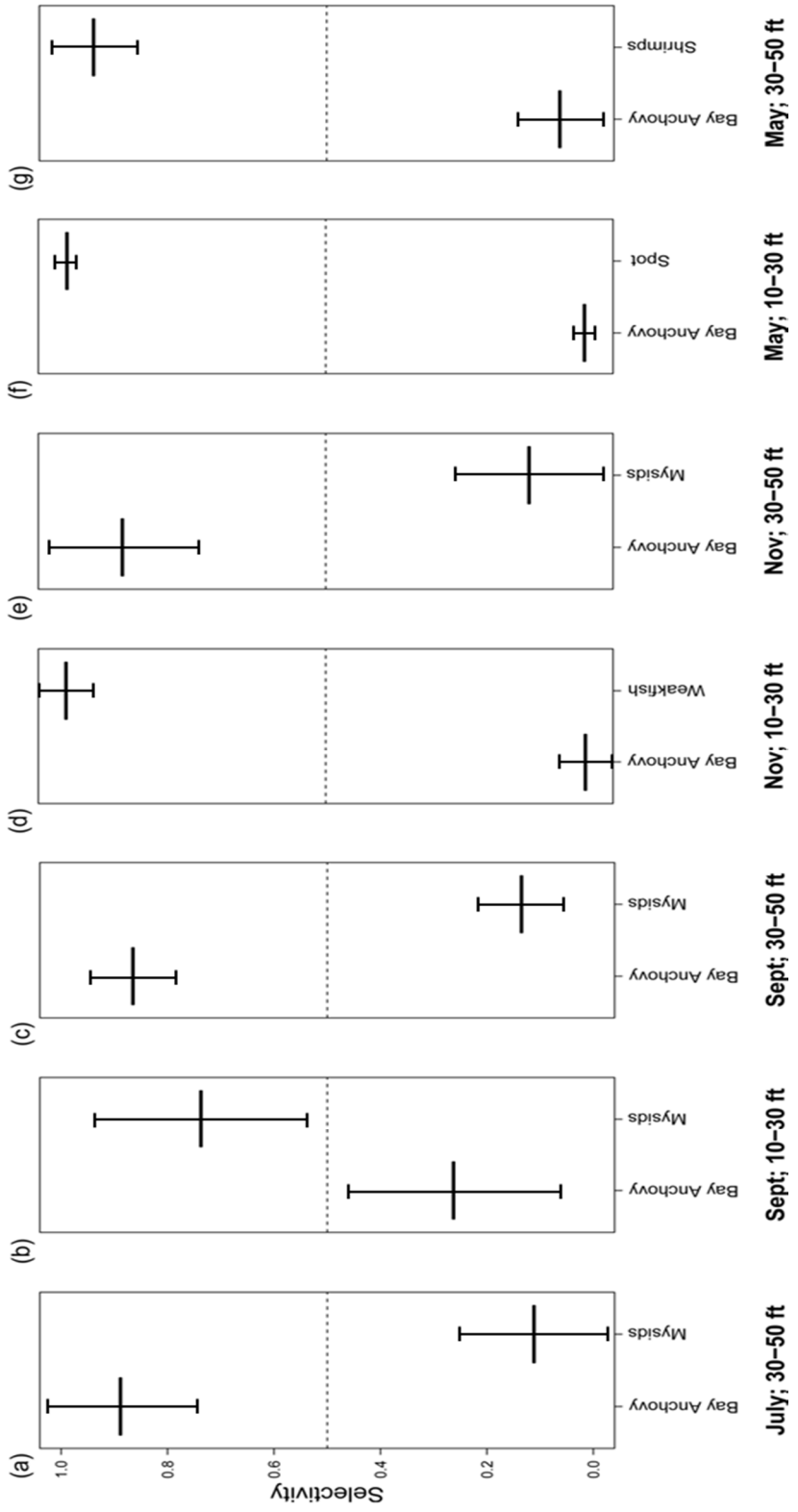

Figure 18. Mean selectivity (Chesson's index α ± SE) versus month and depth combinations for the dominant prey groups of summer flounder collected in the lower Chesapeake Bay by standardized midwater trawl, juvenile fish trawl, and plankton net. Dashed line represents level of random feeding.

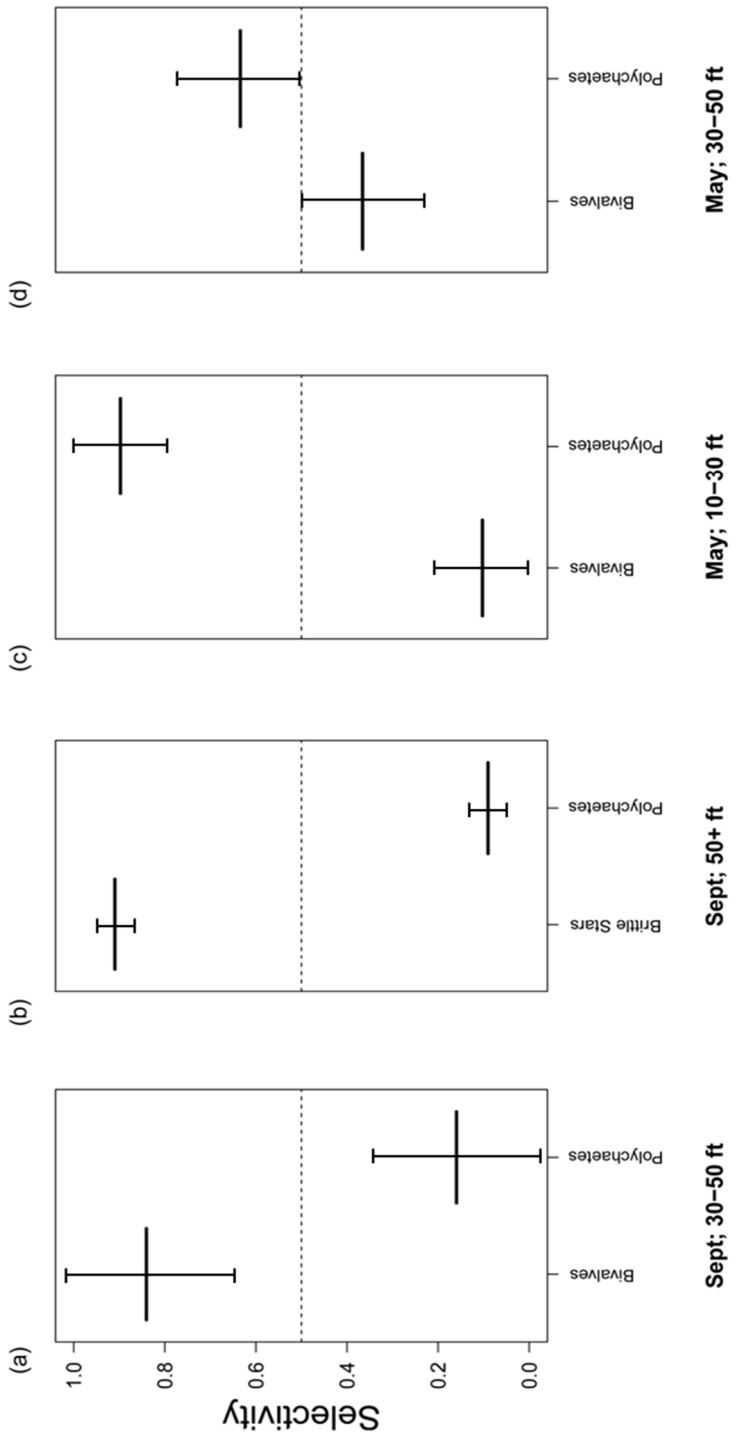

Figure 19. Mean selectivity (Chesson's index $\alpha \pm$ SE) versus month and depth combinations for the dominant prey groups of weakfish collected in the lower Chesapeake Bay by standardized benthic grabs. Dashed line represents level of random feeding.

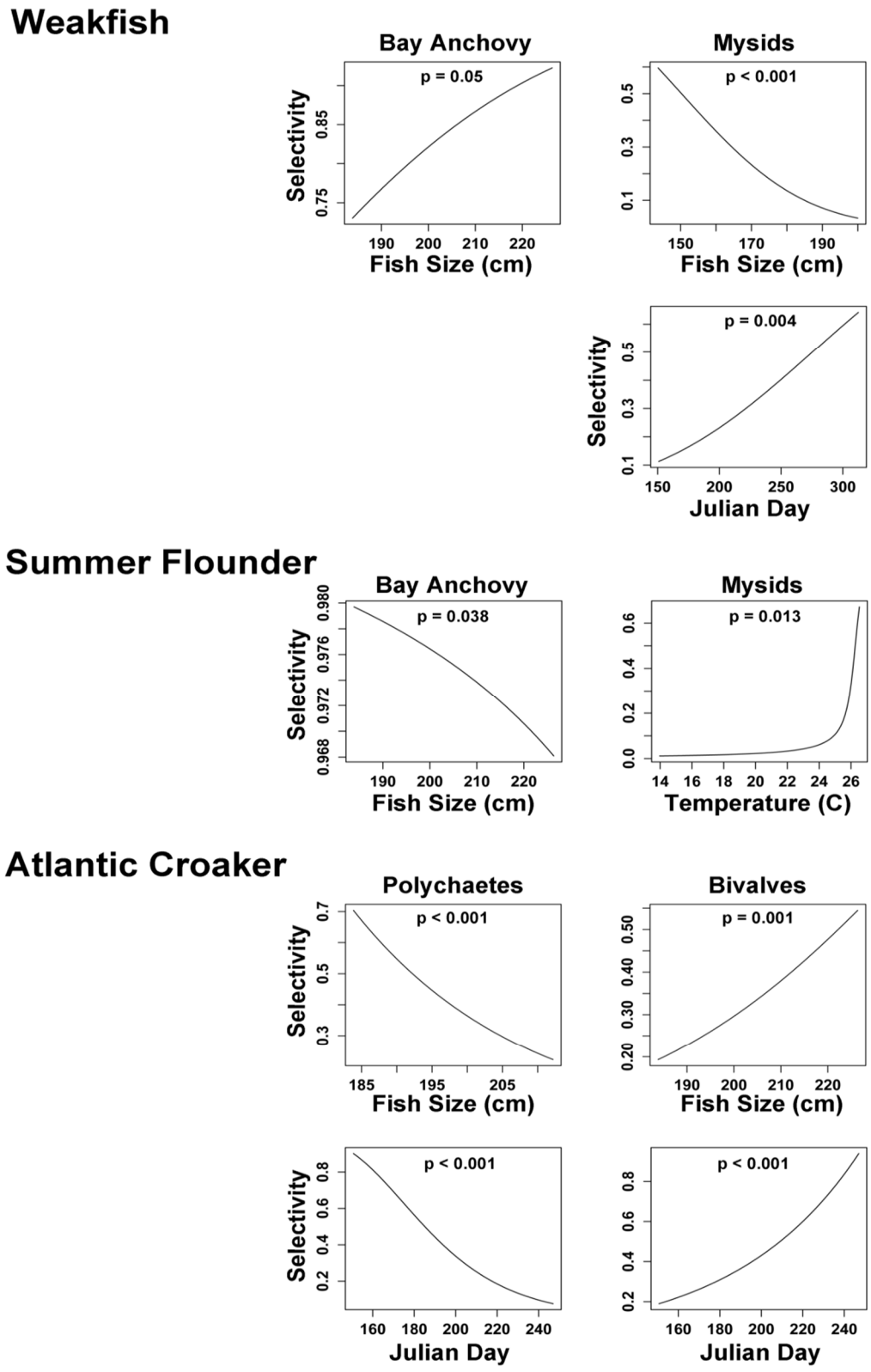

Figure 20. Predator size and temporal feeding selectivity patterns predicted from beta regression analyses for weakfish, summer flounder, and Atlantic croaker in the lower Chesapeake Bay.

CHAPTER 3

PATTERNS AND DRIVERS OF CONSUMPTION IN ATLANTIC CROAKER (*MICROPOGONIAS UNDULATUS*) AND WEAKFISH (*CYNOSCION REGALIS*) IN THE LOWER CHESAPEAKE BAY

ABSTRACT

I applied bioenergetics models for two sympatric, numerically abundant Chesapeake Bay predators, Atlantic croaker (*Micropogonias undulatus*) and weakfish (*Cynoscion regalis*), to examine trophic linkages and the drivers of observed annual consumption rates from 2006 – 2016. Mysids were important dietary components at small sizes in both species, and as fish grew, ontogenetic dietary shifts were observed such that polychaetes and bivalves became more important in Atlantic croaker and fish prey, mainly bay anchovy, became more important in weakfish. A single cohort was identified based on field observations and growth was tracked across a timeframe that encapsulated the main growing season for each species. Bioenergetics models were then conditioned on observed growth rates to estimate annualized specific consumption rates and subsequent modeling efforts revealed significant relationships between consumption and prey metrics. In Atlantic croaker, polychaete density in the lower Chesapeake Bay explained 88.78% of the variation in annual consumption rates whereas bay anchovy relative abundance explained 84.18% of the variance in weakfish consumption rates. Results from this study demonstrate that bottom-up forcing factors can have a direct impact on fish consumption, and therefore growth, within nursery habitats of the Chesapeake Bay.

INTRODUCTION

Estuaries are dynamic ecosystems that provide habitat for about two-thirds of recreational and commercial fisheries along the Atlantic coast (Tyus 2012). Large numbers of larval and juvenile fishes inhabit estuaries mainly for two reasons: 1) estuaries have high primary and secondary productivity, which allows for elevated consumption by juveniles to meet high metabolic demands and 2) there are also many habitat types that provide refuge from predators that seasonally utilize the area for feeding grounds (Able 2005; Baltz and Yáñez-Arancibia 2011; Cowhan et al. 2013). The Chesapeake Bay is the largest estuary in the US and accordingly supports a variety of predatory fishes, including Atlantic croaker (*Micropogonias undulatus*) and weakfish (*Cynoscion regalis*).

The Chesapeake Bay has undergone dramatic changes over the last several decades that may impact behavior, such as consumption patterns, of predatory fishes. For example, the summer depletion of oxygen in benthic waters due to eutrophication alters macrobenthic production and reduces zooplankton abundance, which are important prey groups for juvenile fishes, at a time when energy demands for fishes are high (Kemp et al. 2005; Keister et al. 2000; Sturdivant et al. 2014). Additionally, pelagic forage prey species, such as bay anchovy, have been postulated to increase as a result of benthic habitat loss (Caddy 1993; Caddy 2000). Climate change may decouple current relationships within the food web as seasonal abundances of predators and prey adjust to environmental conditions via changes in distribution or phenology (Najjar et al. 2010). Accordingly, annual estimates of prey availability are often highly variable and drivers are poorly understood. In addition to fluctuations in abundance of lower trophic levels, dramatic decreases in abundance and biomass of many upper-level predators over the last decade have been observed in the Chesapeake Bay, according to catch data from the fishery-independent Chesapeake Bay Multispecies Monitoring and Assessment Survey (ChesMMAP)(Buchheister et al. 2013). Within this large estuary, there is a clear need to better understand the population dynamics that support vital commercial and recreational fisheries.

Fish consumption and growth dynamics across broad temporal scales are of critical importance to inform ecosystem functioning processes and effective fisheries management. Consumption patterns at the individual and population level can have direct impacts on

mortality, survival, and growth as well as indirect effects on behavior, habitat utilization, foraging, and competition (Carpenter et al. 1985). Additionally, drivers of annual consumption rates can provide useful insight into food web structures and aid predictions as they fluctuate over time with changes in environmental conditions and prey abundance.

Atlantic croaker and weakfish are two numerically abundant, sympatric sciaenids that sustain pressure from both recreational and commercial fisheries. Both species are protracted spawners in the mid-Atlantic region, such that young-of-the-year (YOY) individuals can be found in the Bay throughout most of the year. Both species utilize the lower Bay and its tributaries for rapid growth and development within their first year. Atlantic croaker are opportunistic benthic predators feeding mainly on polychaete worms, molluscs and a multitude of small crustaceans, and typically spawn offshore between July – December (Barbieri et al. 1994, Buchheister and Latour 2015). YOY Atlantic croaker begin entering the Bay in August and initially occupy low-salinity habitats. In fall, they move into deeper portions of tidal rivers where they overwinter before migrating out of the Bay the following fall (Murdy and Musick 2013). During overwintering, mortality in this species likely results in interannual variability in abundance patterns (Norcross 1983). Weakfish spawning takes place at the mouth of the Chesapeake Bay from April – August with peak spawning occurring from May to June (Lowerre-Barbieri et al. 1996). YOY fishes are consistently present in low-salinity habitats in July based on catch data from the Virginia Institute of Marine Science (VIMS) Juvenile Fish and Blue Crab Survey (Tuckey and Fabrizio 2017). Growth is rapid through October before they move to more saline waters and apparently out of the Chesapeake Bay prior to the onset of winter (Murdy and Musick 2013). To achieve high growth rates, early YOY weakfish primarily consume energy-rich prey such as mysids and other large zooplankton before becoming more piscivorous with increasing size and preying heavily on forage fish such as bay anchovy (Buchheister and Latour 2015).

Consumption rates of fishes are typically estimated through one of two methodologies. Field-based methods utilize stomach content analysis over diel cycles requiring knowledge about gastric evacuation rates (Elliott and Persson 1978; Durbin et al. 1983; Overholtz et al. 2000; Link and Idoine 2009). The second methodology utilizes a mass-balance approach based on the balanced energy equation (Winberg 1956), where growth occurs after accounting for metabolic costs. Bioenergetics models have been successfully applied to a wide range of ecological issues,

ranging from growth and production to consumption and predatory demand (Kitchell et al. 1977; Rice et al. 1983; Luo and Brandt 1993; Hartman and Brandt 1995*a*; Nye 2008; Sobocinski and Latour 2015). Furthermore, robust estimators of consumption have been obtained from bioenergetics models when adequate growth information is available (Stewart et al 1983; Luo and Brandt 1993; Hartman and Brandt 1995*a*; Sobocinski and Latour 2015).

Given the relative abundance of Atlantic croaker and weakfish in the lower Chesapeake Bay, combined with extensive growth and dietary data across 10+ years, bioenergetics models can serve to inform growth and consumption patterns across a large temporal scale to gain a better understanding of the factors that influence these important processes. Using YOY Atlantic croaker and weakfish as model species, I seek to 1) develop bioenergetics models for each species calibrated using growth data from field surveys, 2) estimate yearly consumption over the residence period in the Bay for each species, and 3) evaluate relationships among consumption estimates and a suite of biological (prey abundance), environmental (temp, DO, salinity), and climate (AMO) covariates. Insight into factors that contribute to the variability in consumption patterns of fishes allows for better understanding of large-scale ecosystem processes and subsequent fisheries production.

MATERIALS AND METHODS

Field Collection

All sampling was conducted from 2006 – 2016 in the major tributaries (James River, York River, and Rappahannock River) and the mainstem of the lower Chesapeake Bay (Fig. 1). Continuous water quality data, including water temperature, were collected from the Goodwin Island Chesapeake Bay National Estuarine Research Reserve (CBNERR).

To estimate abundance of YOY Atlantic croaker and weakfish, fish were sampled by the VIMS Juvenile Fish and Blue Crab Survey using a trawl with a 5.8-m head line, 40-mm stretch-mesh body, and a 6.4-mm liner towed along the bottom for 5 minutes during daylight hours. Sampling occurred monthly from 2006 – 2016, from May – September for Atlantic croaker and July – October for weakfish. Stations in the mainstem were selected via a random stratified design based on regions separated by 15 latitudinal minutes that consisted of six strata: western and eastern shore shallow (1.2–3.7 m), western and eastern shoal (3.7–9.1 m), central plain (9.1–12.8 m), and deep channel (> 12.8 m). Stations within each tributary were selected based on both

random stratified design and historical fixed (mid-channel) stations. Each tributary was partitioned into four regions of about ten longitudinal minutes, with four depth strata in each (1.2–3.7 m, 3.7–9.1 m, 9.1–12.8 m, and > 12.8 m; Figure 21).

Fish were brought onboard and identified to species level, enumerated, and measured to the nearest millimeter total length (TL). In instances where large catches of varying size ranges were encountered, each size class was randomly subsampled, measured, and the remaining unmeasured catch was enumerated. To generate biomass data for the weakfish collected, a length-weight regression was developed utilizing data from the ChesMMAP and from the previous studies (Grecay and Targett 1996; Nye 2008). The length-weight regression was based on only YOY Atlantic croaker and weakfish (e.g., starting in May for Atlantic croaker that were <135 mm TL and July for weakfish that were <120 mm TL). Dietary compositions of both fishes were determined relative to size and season for subsequent analyses based on percent composition by weight.

Daily means of water temperature were compiled from the Virginia Estuarine and Coastal Observing System (VECOS) autonomous sensors (CHE19.38), located at the Goodwin Island CBNERR.

Field-based Growth Analysis

Cohort Identification

To inform the bioenergetics model of annual starting and ending weights for each year, I used field collections to model cohort growth. Accordingly, one cohort was identified per year, and its growth was tracked in the lower Chesapeake Bay throughout the duration of its seasonal residency. Each cohort was identified during a time period in which I observed constant recruitment in the catch data encompassing the primary growing season. Cohorts were identified by analyzing daily and monthly length-frequency data and known growth rates, utilizing the R package 'mclust', which applies Gaussian mixture models to identify modal peaks (Fraley and Raftery 2007). 'Mclust' uses an iterative approach where maximum likelihood estimation is used to fit the optimal mixture model to a single complex distribution. Model fits were then compared using Bayesian Information Criterion. I defined a probable cohort as an identified modal peak from the monthly length-frequency data ± one standard deviation. Observed lengths were then converted to weight using species-specific length-weight regressions. The dataset were pooled across tributaries and the mainstem, because both species are known to transition from lower-

salinity rivers early in the growing season to higher-salinity mainstem waters in the fall prior to emigration out of the Bay (Murdy and Musick 2013).

Cohort Growth Analysis

For each year, the species-specific cohort was used to develop field-based growth models. For Atlantic croaker, I set our cohort growth analysis from May 1 – September 31, whereas for weakfish, the time-period of interest was July 1 – October 31. For each year, I fit linear ($Weight \sim Julian\ Day$), exponential ($Weight \sim a \times \exp(Julian\ Day \times b)$), and Gompertz ($Weight \sim a\ \times \exp(b \times \exp(Julian\ Day\ \times c))$) growth models to survey observations of each cohort. Akaike's Information Criterion (AIC) was used to determine the model with the most empirical support (Burnham and Anderson 2002). Modeled growth curves were used to condition our bioenergetics models through optimization of proportion of maximum consumption (described below).

Bioenergetics Model

A Wisconsin modeling framework (Kitchell et al. 1977) was used to retroactively model seasonal fish consumption patterns, conditioned on field-based growth patterns, of YOY Atlantic croaker and weakfish for each year in the lower Chesapeake Bay. Field collected data were used to condition the bioenergetics model to our empirical observations. The Wisconsin bioenergetics model relies on the mass balanced energy equation of Winberg (1956), where specific consumption rates can be modeled as:

$$\frac{\mathrm{d}C}{d\mathrm{C}t} = G + (R + U + F + S) \quad (1)$$

where C is the consumption, t is the model time step (1 day), G is growth, R is respiration, U is excretion, and F is egestion. The 'Wisconsin model' has been widely used to model consumption, growth, and predatory impact under varying environmental conditions (Hanson et al. 1997). While this modeling framework has been used for various applications of fish population dynamics within the Bay (Luo and Brandt 1993; Hartman and Brandt 1995*a*; Nye 2008, Sobocinski and Latour 2015), the use of output from a time-series spanning 10+ years to subsequently evaluate drivers of consumption across broad temporal scales is a novel approach.

To develop our bioenergetics models, I used parameters from existing models developed by Nye (2008) for Atlantic croaker and Hartman and Brandt (1995*a*) for weakfish, along with bioenergetics models for similar species, life history stages, and habitats to achieve similar growth patterns observed in the field (Rice et al. 1983; Johnson 1995; Sobocinski and Latour 2015). Bioenergetics models were run using Fish Bioenergetics 4.0 (Deslauriers et al. 2017). All parameter values for Atlantic croaker and weakfish are provided in Table 9 and Table 10, respectively, and further described below.

Consumption

Consumption (C, g g^{-1} d^{-1}) was modeled as a function of temperature (°C), fish wet weight (W, g), and feeding, such that:

$$C = C_{max} \times p \times f(T) \quad (2)$$

and

$$C_{max} = CA \times W^{CB} \quad (3)$$

where consumption is defined as the maximum consumption rate (C_{max}) adjusted by a temperature function, $f(T)$, and the proportion of maximum consumption realized in the field (p). The maximum consumption rate is an allometric function of body mass (equation 3) at the optimum temperature for consumption, where CA and CB are species-specific and size-specific constants that represent the intercept and exponent, respectively.

To best describe the influence of temperature on consumption in each species, a separate temperature-dependent function was utilized. For Atlantic croaker, I followed Nye (2008) using the Thornton and Lessem (1978) equation:

$$f(T) = K_a \times K_b \quad (4)$$

where $K_a = (C_{K1} \times L_1)/(1 + C_{K1} \times (L_1 - 1))$

$L1 = e^{(G_1 \times (T - CQ))}$

$G1 = (1/(C_{TO} - CQ)) \times \ln(0.98 \times (1 - C_{K1}))/(C_{K1} * 0.02))$

$K_b = (C_{K4} \times L_2)/(1 + C_{K4} \times (L_2 - 1))$

$L2 = e^{(G_2 \times (CTL - T))}$

$$G2 = (1/(C_{TL} - C_{TM})) \times \ln(0.98 \times (1 - C_{K4}))/(C_{K4} * 0.02))$$

and C_{K1} is a small fraction of the maximum consumption rate, T is water temperature, CQ is the lower water temperature at which dependence is a small fraction, C_{TO} is the water temperature that corresponds to 98% of the maximum consumption rate, C_{K4} is a reduced fraction of the maximum consumption rate, C_{TL} is the temperature at which dependence is some reduced fraction (C_{K4}) of the maximum rate, and C_{TM} is the water temperature at which dependence is 0.98 of the maximum consumption rate (Hanson et al 1997).

For weakfish, I used the temperature-dependence function following (Kitchell et al. 1997):

$$f(T) = V^X \times e^{(X \times (1-V))} \quad (5)$$

where $V = (C_{TM} - T)/(C_{TM} - C_{TO})$

$Z = \ln(CQ) \times (C_{TM} - C_{TO})$

$Y = \ln(CQ) \times (C_{TM} - C_{TO} + 2)$

$X = Z^2 \times (1 + (1 + 40 / Y)^{0.5})^2) / 400$

and C_{TM} is the temperature above which consumption stops, C_{TO} is the optimal temperature for consumption, CQ is an approximation of the rate of consumption that increases as a function of temperature. Daily mean temperatures (T) from the VECOS water quality sensors were used as input. Hartman and Brandt (1995*b*) estimated the temperature for which consumption approaches cessation in YOY weakfish to be 24.3°C; however, feeding rates actually increase from 20-28°C (Lankford and Targett 1994). Furthermore, Cinelli and McIntosh (2011) found that juvenile weakfish approach their thermal tolerance around 34°C. I assumed that consumption would cease before lethal temperatures were experienced (Elliott and Persson 1978) and therefore set the C_{TM} to 32°C.

Respiration

Respiration (R; g O_2 g^{-1} d^{-1}) was modeled as a function of wet weight and temperature following the temperature-dependent function:

$$R = RA \times W^{RB} \times f(T) \times ACT \quad (9)$$

where *RA* and *RB* are the intercept and exponent, respectively, of the allometric mass function, temperature is the daily mean determined from VECOS sensors, *f*(*T*) is a temperature-dependent respiration function, and *ACT* is an activity multiplier that accounts for fish movement. *ACT* was assumed to be 1.25 for both species (Hartman and Brandt 1995*a*; Nye 2008), which are conservative estimates as most standard-energy-demand fish have values ranging from 1-3 (Madon et al. 2002; Sobocinski and Latour 2015).

In Atlantic croaker, the temperature-dependent respiration function with an activity multiplier following Stewart et al. (1983) took the form:

$$f(T) = e^{RQ \times T} \quad (10)$$

where *RQ* approximates the rate at which the function increases over relatively low temperatures (*T*).

In weakfish, the temperature-dependent respiration function following Kitchell et al. (1977) took the form:

$$f(T) = V^X \times e^{(X \times (1-V))} \quad (11)$$

where $V = (R_{TM} - T)/(R_{TM} - R_{TO})$

$Z = \ln(RQ) \times (R_{TM} - R_{TO})$

$Y = \ln(RQ) \times (R_{TM} - R_{TO} + 2)$

$X = Z^2 \times (1 + (1 + 40 / Y)^{0.5})^2) / 400$

and R_{TO} is the optimum water temperature for respiration, R_{TM} is the maximum (lethal) water temperature, and *RQ* approximates the rate at which the function increases with temperature.

The energetic cost of processing food (*S*) is another respiration component and represented by the equation:

$$S = SDA \times (C - F) \quad (12)$$

where *SDA* is specific dynamic action (assumed rate), F is the specific egestion rate (g g^{-1} d^{-1}), and C is as defined above.

Waste Losses

Egestion (*F*) and excretion rates (*U*, g g^{-1} d^{-1}) were modeled as constant proportions of consumption and assimilation following Kitchell et al. (1977):

$$F = FA \times C \quad (13)$$

$$U = UA \times (C - F) \quad (14)$$

where *FA* and *UA* for both bioenergetics models were based on previously derived values (Rice et al. 1983).

Stomach content analyses

To incorporate dietary patterns for both Atlantic croaker and weakfish into the Fish Bioenergetics 4.0 software, stomach content analyses were performed on fish sampled within the mainstem of the Bay by ChesMMAP. ChesMMAP is a bottom-trawl survey that performs five research cruises (March, May, July, September, and November) with 36 stations sampled in the lower Chesapeake Bay per cruise. Stations were selected based on a random stratified design and strata defined by water depth (3.1 – 9.1-m, 9.1 – 15.2-m, and >15.2-m) and latitude (two 30-latitudinal-minute regions of the Bay). Sampling intensity was proportional to the surface area of each stratum. At each station, a 13.7-m 4-seam balloon trawl, with 15.2-cm stretched mesh in the wings and the body, was set by boat during daylight hours to target late juvenile and adult fishes. The net was typically towed with the tidal current along the bottom for twenty minutes at 3.0-3.3 knots. Following each sampling event, the catch was sorted by species and size class (if applicable) and enumerated. Subsamples of each species/size class were then processed for dietary determination. Predatory fish stomachs were removed for identification of stomach contents were identified to the lowest possible taxonomic resolution. Prey observed in the esophagus and buccal cavity were included in dietary analysis because prey is not thought to be retained in the large mesh otter trawl, and therefore, net feeding is assumed to not occur. All prey items encountered were weighed and diets were quantified for each predatory fish species by percent weight for each prey type (Hyslop, 1980). Cluster sampling estimators (Bogstad et al.

1995) were used to calculate seasonal and size-specific dietary indices (%W) for each year from 2006 – 2016.

Energy Density

Predator and prey energy densities are also important components in the bioenergetics model framework. The energy densities (J g^{-1}) of Atlantic croaker and weakfish increase with increasing fish size, and therefore energy density was modeled as a function of fish weight (Wuenschel et al. 2006). I used previously reported seasonal estimates of Atlantic croaker energy densities (Hartman 1993) to arrive at the relationship between energy density and fish wet weight:

$$Energy\ density\ = 3108.7\ \times W^{0.20779} \quad (15)$$

Similarly, I used seasonal estimates of energy density of weakfish (Hartman and Brandt 1995*c*) to arrive at the relationship of energy density and wet weight:

$$Energy\ density\ = 3668\ \times W^{0.09761} \quad (16)$$

Prey energy densities utilized in this study were derived from prey energetic values in previous studies for prey taxa commonly observed in the diets of YOY Atlantic croaker and weakfish (Cummins and Wuycheck 1971; Hartman and Brandt 1995*b*). The prey energy densities were then used to inform the net energy consumed for YOY Atlantic croaker and weakfish as they grow throughout the main growing season.

Drivers of Annual Consumption Estimates

Annual specific consumption rate estimates derived from the bioenergetics model output for Atlantic croaker and weakfish, which were calculated as mean daily consumption over the respective analysis period, were further analyzed using general linear models (GLM). Four model parameterizations were fitted (Table 11), where each reflected a unique hypothesis about the effects of various explanatory variables, including prey effects, environmental effects, and climatological effects on annual consumption. The optimal model parameterization was selected using AIC.

For Atlantic croaker, three annualized covariates were included in the GLM analysis: 1) polychaete density (g ash-free dry weight cm^{-2}), 2) mean summer hypoxic volume, and 3) unsmoothed Atlantic Multidecadal Oscillation Index (AMO,

www.esrl.noaa.gov/psd/data/correlation/amon.us.data). Polychaete density, which are the dominant prey for Atlantic croaker (Buchheister and Latour 2015), was determined from box core samples collected in the Chesapeake Bay mainstem and tributaries by the Versar Chesapeake Bay Benthic Monitoring Program (Llansó and Zaveta 2017) and annual mean polychaete density from 2006 – 2016 was estimated using a delta-lognormal generalized linear model that included the covariates year, month, and Bay region (Latour et al. 2017). Hypoxic volume (DO < 2 mg l^{-1}) estimates, which has been shown to impact Atlantic croaker feeding and behavior (Pihl et al. 1991; Powers 2005), were based on Scavia et al. (2017). The effect of mean annual bottom salinity, daily freshwater discharge from the Susquehanna River (mean from February to May), and Atlantic croaker year-class strength on consumption were also investigated, but did not explain more deviance than the previously listed covariates and were therefore not included in final GLM analysis.

For weakfish, three explanatory variables were utilized in the GLM modelling efforts: 1) bay anchovy relative abundance, 2) spring surface chlorophyll *a*, and 3) unsmoothed AMO. Bay anchovy relative abundance, which are the dominant prey for weakfish (Buchheister and Latour 2015), was estimated as weighted geometric means from a randomly stratified survey design based on collections from the VIMS Juvenile Fish and Blue Crab Survey (Tuckey and Fabrizio 2017). Spring surface chlorophyll *a* concentration estimates were calculated using multiple linear regression models (with explanatory variables year, month, latitude, and longitude) from the Chesapeake Bay Program data following Latour et al. (2017). As with Atlantic croaker; salinity, Susquehanna River discharge, and weakfish year-class strength were initially evaluated to determine their effect on weakfish consumption patterns, but were not included in final GLM analysis due to a lack of deviance explanation.

RESULTS

Growth

Atlantic croaker

Length-weight measurements were recoded for 1,057 age-0 Atlantic croaker. The length-weight regression for all biomass conversions (TL and wet weight) for YOY Atlantic croaker was:

$$W = 0.00000001 \times L^{3.035} \quad (17)$$

with sizes ranging from 56 to 237 mm TL.

For the field-based weight-over-time growth models derived from the Juvenile Fish and Blue Crab Survey cohort analysis, the Gompertz model received the most empirical support for Atlantic croaker (Table 7) from 2006 – 2016. New Atlantic croaker recruits were present in all rivers in May in all years except for 2011 and 2015, presumably due to recruitment dynamics. The Gompertz model fit the field data well at earlier dates, but divergence from the fitted model increased over time, which was expected due to individual variation in growth rates (Figure 22). Additionally, an asymptote was not reached across the time period of interest, thus causing a higher standard error in the estimated asymptote of the Gompertz function in some years.

Weakfish

The length-weight measurements on 2,693 YOY weakfish yielded the biomass conversion relationship:

$$W = 0.00000001 \times L^{3.001} \quad (18)$$

with sizes ranging from 15 to 294 mm TL.

The Gompertz growth model was the most supported model for weakfish (Table 8) from 2006 – 2016. New recruits were present in all rivers in July and growth was tracked via cohort analysis through October. Similar to Atlantic croaker, the Gompertz growth model fit well at early dates, but deviation from the fitted model increased with increasing fish size (Figure 23).

Bioenergetics model

Atlantic croaker

I analyzed the stomach contents of 1,914 YOY Atlantic croaker, ranging in size from 24 to 200 mm TL, and characterized the diets such that they were temporally representative and size-specific relative to the cohort analysis. YOY Atlantic croaker fed on a wide variety of prey, but polychaetes and bivalves were the most important prey taxa, followed by mysid and sand shrimps. Mysid shrimps were consistently important in small Atlantic croaker, but less so in larger fish as their diet became more generalized (Appendix 1).

I evaluated annual model output using the Fish Bioenergetics 4.0 software (Deslauriers et al. 2017). The annual difference between the predicted weight from the bioenergetics model and the field-based observed weight ranged from 1.31% to 10.01%, differing by no more than 15% body weight on any given day (Figure 22). The proportion of realized consumption in the field (p), which is used to adjust consumption to fit the predicted growth patterns, ranged from 0.87 – 1.04 and was on average 0.95.

After fitting the bioenergetics models, I evaluated annual output related to consumption, growth, and metabolic losses (Appendix 3). Mean annual consumption was lowest in 2006 with a mean daily consumption rate of 10.43% body weight, ranging from 6.45% to 16.18% throughout the model period. Conversely, mean annual consumption was highest in 2014 averaging 13.36% body weight per day, ranging from 7.04% to 20.31% throughout the year. Smaller fish ate a greater proportion of body weight per day than larger fish throughout the time series, consuming a maximum 0.26 g g^{-1} d^{-1} in 2014, before the rate declined to 0.06 g g^{-1} d^{-1} at the end of the 2014 simulation period. This size-specific consumption rate pattern was observed in all years, with the patterns and magnitude of the values similar to what was previously observed in laboratory settings (Nye 2008). Across all years, total consumption over the 152 day simulation period ranged from 327 g in 2010 to 366 g in 2014.

Total growth ranged from 62.26 g to 71.27 g over the 152 day model period, which resulted in annual specific growth rates (g g^{-1} d^{-1}) ranging from 0.04 – 0.06 from 2006 – 2016. Mean annual metabolic losses accounted for 56.50 to 58.26% of consumption throughout the time-series, with a maximum daily value of 84.09% and a minimum value of 53.31%. Throughout all years, respiration accounted for approximately half of all metabolic losses across the simulation period, ranging from 40.53% to 58.41%. Specific respiration rates tended to be higher in smaller fish when compared with larger fish.

Weakfish

I analyzed the stomach contents of 1,852 YOY weakfish ranging in size from 29 to 200 mm TL. YOY weakfish displayed a varied diet, primarily consuming mysids, copepods, and sand shrimp at small sizes before transitioning to a more piscivorous diet, feeding heavily on bay anchovy and other small fishes (Appendix 2).

The calibrated bioenergetics models reproduced the modeled growth patterns from field data and produced output related to growth, consumption, and respiration patterns. The average

daily difference between the predicted weight and the modeled weight from field data ranged from 3.49% to 9.45% across all years, and differed by no more than 13% on any given day (Figure 23). The *p* term ranged from 0.37 to 0.46 and, on average, was 0.40.

Annual output from the weakfish bioenergetics related to consumption, growth, and metabolic losses are reported in Appendix 4. Mean annual consumption was lowest in 2016 at 10.14 % body weight per day ranging from 3.13% to 23.64% throughout the simulation period. Although 2016 had the lowest specific consumption rates, 2014-2015 had similar rates at 10.40% and 10.32%, respectively. Mean annual consumption was highest in 2010 at 16.18% body weight per day, and ranged from 3.54% to 67.38% annually. Small weakfish ate more per unit weight than larger weakfish, with specific consumption rates as high as 0.67 g g^{-1} d^{-1} at the beginning of the simulation period, before decreasing to 0.02 g g^{-1} d^{-1} at the end. Although specific consumption rates of 0.67 g g^{-1} d^{-1} are high for fishes, values of similar magnitude have been observed in YOY weakfish (Targett and Lankford 1994) and consumption rates in the early life history of some fishes can exceed their body weight (Houde 1997). Furthermore, the decline in per capita consumption with increasing size is consistent with previous studies fish consumption (Hartman and Brandt 1995*a*). Across the 11 year period, total consumption across the simulation period ranged from 276 g to 312 g in 2013 and 2011, respectively.

Total growth ranged from 27.73 g to 33.95 g over the 122 day model period with annual mean specific growth rates ranging from 0.04 – 0.07 g g^{-1} d^{-1} between 2006 – 2016, which were comparatively higher than Atlantic croaker. Mean annual metabolic losses for weakfish accounted for 67.50 to 71.07% of consumption from 2006 – 2016, with a maximum daily value of 86.02% and a minimum daily value of 54.24%. Respiration accounted for over half of the metabolic losses annually, ranging from 55.02% to 61.67% across the time-series. Among the other metabolic processes, specific dynamic action typically accounted for ~20% of the remaining losses, with egestion and excretion accounting for ~10% and <10%, respectively.

Drivers of Annual Consumption

Atlantic croaker

I compared four candidate GLM models to describe annual patterns observed in specific consumption rate estimates of Atlantic croaker using AIC (Table 11). The model with the most empirical support included only the polychaete density term and explained 88.7% of the deviance in the annual patterns of consumption (Figure 24a). Polychaete density was found to significantly

describe the relationship of Atlantic croaker consumption rates from 2006 – 2016 ($p < 0.001$, Figure 24b). Model parameterizations including all terms and polychaete density/hypoxic volume did receive some empirical support; however, each parameterization had slightly higher ΔAIC values, suggesting that the addition of hypoxic volume and AMO did not explain appreciably more deviance in the data and may not be as important as polychaete density in explaining Atlantic croaker consumption.

Weakfish

Similar to Atlantic croaker, I compared four candidate models to describe the annual patterns of consumption in weakfish using AIC from 2006 – 2016 (Table 11). The model with the most empirical support contained only the prey covariate for bay anchovy relative abundance, and explained 84.1% of the deviance (Figure 25a). Bay anchovy relative abundance significantly described the patterns of weakfish consumption observed throughout the duration of the study ($p < 0.001$, Figure 25b). Model parameterizations including all terms and bay anchovy relative abundance/chlorophyll *a* concentration each had high empirical support; however, the prey covariate was the major driver of weakfish consumption patterns in both parameterizations.

DISCUSSION

The use of field-collected catch data in conjunction with individual-based bioenergetics models for Atlantic croaker and weakfish enabled us to model consumption patterns from 2006 – 2016 in the lower Chesapeake Bay. I constrained our analyses to the main growing season for each species to encapsulate consumption patterns that are likely indicative of the majority of the total consumption for a YOY fish in a given year. As such, our estimates of consumption in the lower Chesapeake Bay are useful for annual comparisons.

Bioenergetics models

Atlantic croaker

Bioenergetics models for Atlantic croaker provided growth, metabolic, and consumption rates that were also similar to estimates from previous analyses (Nye 2008; Horodysky et al. 2011). To approximate growth trajectories observed in the field, our bioenergetics models estimated a high proportion of realized maximum consumption (p) values, based on the theoretical bound of 1 (Deslauriers et al. 2017), and ranged from 0.87 – 1.04, with an average of

0.95. Our estimates of the proportion of realized maximum consumption in the field were similar to estimates for Atlantic croaker in Nye's (2008) bioenergetics models, although generally high compared to other sciaenids and weakfish in this study (Sobocinski and Latour 2015). Available consumption parameters were mainly derived from previous laboratory-based experiments; however, if the full prey field was not included in previous studies then maximum consumption estimates could be biased low and subsequent *p* estimates could be inflated. Nye (2008) conducted Atlantic croaker consumption experiments where fish <100 g were fed mysid shrimps and fish >100 g were fed bay anchovy (Nye 2008). Both prey taxa represent the most energy dense food sources observed in the Atlantic croaker diets. However, dietary analyses from the present study found that they mainly fed on less energy dense prey, such as polychaete worms and molluscs. As a result, our *p* estimates were likely inflated comparatively to compensate for the prey energy differential to meet the metabolic demands. The interpretation of *p* estimates can be useful in exploring factors such as prey availability (Rice et al. 1983; Robel and Fisher 1999).

Previous research has demonstrated that bioenergetics models are most sensitive to the consumption and respiration sub-equations, specifically the functions that describe the effects of body mass and temperature (Bartell et al. 1986). The utilization of additional data on respiration relative to life history for closely related species (e.g. Wuenschel et al. 2004 and Sobocinski and Latour 2015) and from other bioenergetics analyses (e.g. Rice et al. 1983), allowed for the parameterization of annual bioenergetics models that realistically explained growth. I were fortunate to have published metabolic parameters (Hartman and Brandt 1995*a*; Nye 2008; Horodysky et al. 2011) that allowed for model building to be based on realistically, laboratory derived values.

Atlantic croaker growth rates were rapid within the first year, with fish growing in some years in excess of 70 g (~185 mm). This magnitude of growth agrees with previous findings, which has shown that growth is fastest within the first year, accounting for 64% of cumulative total growth where YOY Atlantic croaker reach 107-187 mm TL (Knudsen and Herke 1978; Ross 1988; Barbieri et al 1994). Specific growth rates reported here were higher for smaller fish than larger fish, which is consistent with general patterns of growth in early life history (Jobling 1994). High growth rates at small sizes is likely linked to ontogenetic dietary patterns, where fish fed predominantly on polychaete worms and mysid shrimps, with mysids representing the highest energy rich prey (4815 J g^{-1}). As Atlantic croaker continue to grow, their dietary breadth

increases and includes less energy rich prey items, such as bivalves (2292 J g^{-1}), polychaetes (3552 J g^{-1}), and sand shrimps (3138 J g^{-1}), and growth rates subsequently decline. Across the growing season (late spring – summer), Atlantic croaker average growth was ~0.5 g d^{-1} (~1.21 mm d^{-1}) ranging from 0.07 – 1.25 g d^{-1}, similarly observed by Nye (2008). Overall, the reported growth rates for Atlantic croaker from previous research are variable and dependent upon the time period for which growth was measured. Knudesen and Herke (1978) estimated growth rates to be 0.32 – 0.41 mm d^{-1} based on length-frequency catch data, and Nixon and Jones (1997) estimated that growth of larval and YOY Atlantic croaker ranged from 0.18 – 0.41 mm d^{-1}, both of which are lower than the rates estimated in this study. The difference in growth rates between these studies is likely a function of the inclusion of winter months, when little growth occurs (Chao and Musick 1977; Miller et al. 2003). Our results reflect growth rates determined by Miller et al. (2003) for the May – August period, which ranged from 0.6 – 1.3 mm d^{-1}. Thus, it is important to consider the temporal scale over which consumption and growth are examined to accurately describe the early life history of Atlantic croaker.

Weakfish

The bioenergetics models developed for weakfish in this study produced realistic growth estimates. The *p* term ranged from 0.37 – 0.46, and averaged 0.40 across all years, which is similar in magnitude to other species (Kitchell et al 1977; Hartman and Margaf 1992; Sobocinski and Latour 2015). Annual averages of respiration rates ranged from 0.0167 – 0.0212 g O_2 g^{-1} d^{-1}, although daily values varied throughout the year as fish grew and temperature changed. These rates were somewhat higher than those observed by Hartman and Brandt (1995*a*) for age-0 weakfish. However, the estimates of Hartman and Brandt (1995*a*) were standardized for a 30 g fish, which approaches the maximum size observed considered in this study. As a result, a vast majority of the sizes and subsequent energetic rates modeled in this study pertain to fish smaller than those used by Hartman and Brandt (1995*a*). Larger fish generally consume less oxygen than smaller conspecifics on a per-unit-weight basis (Jobling 1994) and the allometric relationship between fish size and specific metabolic rates likely accounted for the differences between the two studies. Comparatively, weakfish had higher metabolic rates than Atlantic croaker throughout the time-series, and agrees with findings from Horodysky et al. (2011).

Weakfish had high growth rates throughout the duration of their first year of life in residency in the Bay compared to most other sciaenids (Horodysky et al. 2011; Sobocinski and

Latour 2015). Cohort analysis and subsequent bioenergetics models revealed that YOY weakfish can grow up to ~ 35 g (~155 mm) from July – October prior to emigration out of the Bay, which is similar to previous findings (Hartman and Brandt 1995*a*). Growth rates were most rapid early in the simulation period compared to later dates and this is likely attributed to ontogenetic diet switching. Prior to becoming heavily reliant on bay anchovy as a food source, mysid shrimps were the main prey at small fish sizes (Buchheister and Latour 2015) as their high energy content provides an ideal food source to accommodate high metabolic demands. Across the time-series, weakfish grew about 0.25 g d^{-1}, which equates to approximately 1.21 mm d^{-1}. Otolith and scale increment analysis on juvenile weakfish in Delaware and Chesapeake Bay had previously estimated growth rates of 0.69 – 0.97 mm d^{-1} and 0.76 – 1.13 mm d^{-1}, respectively (Szedlmayer et al. 1990; Paperno et al. 2000). Additional methods, such as length-frequency analysis and laboratory growth experiments, have elucidated growth rates of 1.00 mm d^{-1} and 0.30 – 1.50 mm d^{-1} (Shlossman and Chittenden 1981; Lankford and Targett 1994). The reported growth rates in YOY weakfish are likely variable due to different estimation methods, but also due to the protracted spawning period of adults. For example, new recruits sampled in July are likely to have different growth rates than new recruits sampled in October due to environmental conditions and prey availability, amongst other potential drivers. Nonetheless, the growth rates observed in this study are similar to those previously observed and are likely reflective of the primary growing season in the Chesapeake Bay for weakfish.

Consumption Patterns

Atlantic croaker

The total estimated consumption of prey by a single YOY Atlantic croaker during the 152 day simulation period ranged from 327 – 377 g throughout the time-series. The estimates for Atlantic croaker, which are higher than previously estimated consumption rates for other YOY fishes in Chesapeake Bay, highlight the considerable predatory demand of YOY Atlantic croaker. For example, Sobocinski and Latour (2015) estimated 93 g total consumption for YOY silver perch; however, the growing season is shorter, and YOY silver perch only achieve a weight of 23 g during that time such that total consumption is comparatively reduced. Hartman and Brandt (1995*a*) estimated total consumption for YOY striped bass and weakfish to be 192 g and 54 – 296 g, respectively. Differences in total consumption between Atlantic croaker and these species can also be attributed to relative timing of recruitment. Survey data from this study

revealed that Atlantic croaker appear as new recruits in the tidal tributaries of the Bay earlier than weakfish (April – May vs. June – July, respectively). Due to this 1 to 2 month difference in growing period, total consumption is expected to be larger for Atlantic croaker. Finally, the dietary habits of YOY Atlantic croaker observed in this study are similar to previous research (Buchheister and Latour 2015) and indicate that they consume prey that has less energy density (e.g. polychaetes and molluscs) relative to the energy rich prey of YOY striped bass and weakfish (e.g. bay anchovy). To compensate for the difference in energy gained from targeted prey, Atlantic croaker need to consume comparatively more prey relative to YOY striped bass and weakfish. The elevated total consumption by Atlantic croaker is likely a function of a suite of interacting variables including growth patterns, duration of growing season, environmental conditions, and the energetics of prey taxa consumed. Relative to growth patterns, YOY Atlantic croaker accrue more biomass within their first year than silver perch, striped bass, and weakfish, thus total consumption is correspondingly larger.

Weakfish

Young-of-year weakfish consumed an estimated 276 – 312 g during the 122 day simulation period. The growing season for YOY weakfish was the same in this study as Hartman and Brandt's (1995*a*), where they estimated 296 g total consumption by a YOY weakfish recruited in July. The differences between the two estimates are not large, but the small variations are likely due to annual differences in dietary characterizations. For example, Hartman and Brandt (1995*a*) found that over 70% of YOY weakfish diet was composed of bay anchovy from day 1 – 60 of the simulation period. Conversely, I found through extensive dietary analysis that the majority of the diet of small weakfish during that same period was composed of mysid shrimps, mainly *Neomysis americana*, which was also supported by previous research (Grecay 1990). It is believed that juvenile weakfish selectively feed on mysid shrimps due to their post-consumptive handling efficiency, and therefore represent an important prey group at early life stages (Lankford and Targett 1997). The differences in methodologies used to calculate dietary indices likely accounted for the small variations between Hartman and Brandt (1995*a*) and this study. The seasonal and annual changes in YOY weakfish diets undoubtedly played a large role in the variation of consumption estimates throughout the time series, and highlight the importance of robust, temporal dietary characterizations.

Drivers of Annual Consumption Rates

The use of GLMs to analyze drivers of annualized mean consumption rates across the time-series elucidated a significant effect of prey abundance on both predator species. The importance of prey availability in regulating the consumption and dietary patterns of predatory fishes has been documented in many marine systems (Fahrig et al. 1993; Pinnegar et al. 2003; Mills et al. 2007; Dwyer et al. 2010; Schückel et al. 2010; Pálsson and Björnsson 2011). In the Chesapeake Bay, Buchheister and Latour (2016) demonstrated that bottom-up control largely regulates the diets of some estuarine fishes. Our study corroborates their findings and highlights the importance of synoptically examining multiple trophic levels to elucidate broad-scale trends within an ecosystem. Concurrence in consumption patterns and prey availability are related, in part, to opportunistic feeding behaviors that enable fishes to exploit spatiotemporally patchy prey distributions (Holling 1959; Gerking 1994). Variations in environmental and ecological conditions across spatial and temporal gradients clearly influence patterns in prey production, and require further research to identify specific mechanisms driving prey production patterns.

Annual differences in the density of polychaetes in the lower Chesapeake Bay were reflected in the diet, consumption, and growth rates of Atlantic croaker throughout the time-series. In years when polychaete density was low, Atlantic croaker consumption rates were also low. Polychaete worms are a dominant component of the benthos in the Chesapeake Bay (Diaz and Schaffner 1990) and are heavily exploited by Atlantic croaker (Buchheister and Latour 2015). Diversity of polychaete worms is high in the Chesapeake Bay and patterns of distribution and abundance appear to be related, in part, to salinity zones (Gillett and Schaffner 2009). However, a majority of the dietary characterizations and subsequent consumption estimates for Atlantic croaker were derived from the polyhaline region of the Bay; thus, salinity is not likely to be a strong driver of the patterns observed in this study. Previous research has hypothesized that low oxygen levels facilitate the transfer of benthic secondary production to mobile predators through behavioral responses of benthic macrofauna to hypoxic stress (Diaz and Schaffner 1990; Diaz and Rosenberg 1995). Some polychaete worms can be tolerant of short-lived oxygen levels (Pihl et al. 1991), whereas others migrate to shallower depths, potentially increasing their vulnerability to predation (Long et al. 1991; Nestlerode and Diaz 1998). However, at a broad scale, hypoxia can lead to mass mortality and reduced production in polychaetes (Sturdivant et al. 2014), thereby reducing overall availability to fish predators (Seitz et al. 2009). Greater

understanding of the link between polychaete and Atlantic croaker production would benefit from the identification of drivers of polychaete density, which was beyond the scope of the present study.

I found that hypoxic volume did not significantly influence Atlantic croaker consumption rates; however, Seitz et al. (2009) observed that dissolved oxygen levels in the summer had the greatest impact on benthic density with depth. Although I investigated large-scale driving factors of annual consumption patterns in Atlantic croaker, shorter term evaluations (e.g. weekly or monthly) of environmental variables, such as dissolved oxygen concentrations, could reveal significant fine-scale patterns that are obfuscated by pooling across longer time periods. Considering Atlantic croaker have historically been one of the most abundant fishes in the Bay (Murdy and Musick 2013) and play a key role in ecosystem function and face substantial fishing pressure from recreational and commercial fisheries (Baird and Ulanowicz 1989; ASMFC 2010), further research is needed to better understand how bottom-up mechanisms are manifested into consumption and ultimately production of Atlantic croaker.

Consumption patterns estimated for weakfish revealed that relative abundance indices of bay anchovy significantly explained much of the variation throughout the time-series. Previous research has shown that weakfish will selectively forage on bay anchovy (Chapter 2), which further highlights the magnitude of the two species' linkages within the Chesapeake Bay food web. Bay anchovy are the most abundant fish in the Chesapeake Bay and are of great importance to production patterns in commercially and recreationally important species such as weakfish, striped bass, summer flounder, and bluefish (Baird and Ulanowicz 1989; Able and Fahay 2010). Additionally, bay anchovy serve a critical role in the Bay's food web, linking lower trophic levels such as phytoplankton and zooplankton to economically valuable predators.

Recruitment patterns and year-class strength of bay anchovy have been linked to a multitude of factors, although specific driving mechanisms remain poorly understood. Jung and Houde (2004) postulated that recruitment patterns are related to variability in hydrological conditions (e.g. salinity and dissolved oxygen) and the spatial distribution of the spawning stock biomass. Bay anchovy spawn throughout most of the Bay between April – August and are more abundant in the mid- and upper-Bay in the summer (Wang and Houde 1993). Rapid growth causes bay anchovy to mature in as little as 3 months (Luo and Musick 1991). A down Bay ontogenetic migration occurs in the fall (Wang and Houde 1995) and results in a spatiotemporal

overlap with YOY weakfish in the lower Bay as they transition from tidal tributaries into more saline waters of the mainstem, and become available for consumption.

Predation is also thought to play a major role in regulating recruitment strength of bay anchovy. Seasonal predation by gelatinous predators, mainly *Chrysaora quinquecirrha*, which can consume as much as 60% of available bay anchovy eggs and larvae per day (Cowan and Houde 1993; Purcell et al. 1994). As adults, gelatinous zooplankton are direct competitors with zooplanktivorous fishes like bay anchovy, and may therefore have indirect effects on fish populations (Decker et al. 2007). Potential increases in gelatinous zooplankton abundance have been postulated to be influenced by habitat degradation and climate change (Richardson et al. 2009), which may have indirect effects on weakfish consumption. However, other researchers argue such increases are unsubstantiated (Condon et al. 2012). Given the findings from this study, factors that influence bay anchovy production and recruitment could have a cascading effect on weakfish and other upper level predators.

The impacts of Atlantic croaker and weakfish consumption patterns are important for improved understanding of the ecosystem dynamics within the Chesapeake Bay. The combined use of juvenile fish catch data and bioenergetics models supported the important role that prey abundance patterns can have on consumption, and therefore growth, of predatory fishes. Determining ecological patterns that drive fish consumption is an important component that controls fisheries production. To this point, recent evidence suggests that the abundance of both species has declined drastically over the last decade (Buchheister et al. 2013). Furthermore, the predatory demand of weakfish is much higher than prey supply (Hartman and Brandt 1995*b*), and competition for prey has been proposed to explain the failure of the weakfish stock to recover (Uphoff 2006). Less is known regarding the observed decline in Atlantic croaker stocks within the Chesapeake Bay, but ongoing research seeks to elucidate potential causes (Schonfeld, personal communication). Although bioenergetics models have traditionally been used to understand growth and consumption of particular species, this work illustrates that they can be useful in understanding ecosystem dynamics across a broad temporal scale when patterns of prey abundance are considered.

As interest continues in ecosystem-based approaches to fisheries management, factors that drive consumption and subsequent impacts on growth and abundance are critically important. Like many estuarine systems, the Chesapeake Bay has experienced considerable

change due to increased rates of nutrient loading, climate change, and overfishing which may shift production to pelagic habitats and alter food webs (Rothschild et al 1994; Olney and Hoenig 2001; Kemp et al. 2005; Najjar et al. 2010). Physiogeochemical changes such as these highlight the importance of understanding fish consumption patterns, as well as the direct and indirect mechanisms driving them.

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Table 7. Growth models of YOY Atlantic croaker cohorts on May 1 - September 31 from 2006 - 2016 with parameter and standard error estimates, residual sums of squares AIC, and Δ AIC. Note: Cohort was not present in 2011 and 2015. Δ AIC values were used to determine models with the most empirical support.

Model	Parameter values			RSS	AIC	Δ AIC
	a ± S.E.	*b* ± S.E.	*c* ± S.E.			
		2006				
Linear	-6.73 ± 0.19	0.41 ± 0.003	-	223914	29743	3714
Exponential	3.99 ± 0.06	0.02 ± 0.001	-	143300	27782	1753
Gompertz	151.13 ± 5.96	-5.63 ± 0.06	-0.01 ± 0.001	96101	26029	0
		2007				
Linear	-3.81 ± 0.15	0.38 ± 0.002	-	215503	32845	3179
Exponential	4.09 ± 0.06	0.02 ± 0.001	-	154116	31179	1513
Gompertz	130.49 ± 5.42	-5.05 ± 0.05	-0.01 ± 0.001	113624	29666	0
		2008				
Linear	-11.17 ± 0.12	0.45 ± 0.001	-	698634	103292	4483
Exponential	4.28 ± 0.04	0.02 ± 0.001	-	635290	101815	3006
Gompertz	123.01 ± 3.14	-5.18 ± 0.03	-0.01 + 0.001	523565	98809	0
		2009				
Linear	-3.56 ± 0.08	0.36 ± 0.001	-	255760	58782	5685
Exponential	3.88 ± 0.04	0.02 ± 0.001	-	257121	58833	5736
Gompertz	109.87 ± 1.99	-4.98 ± 0.03	-0.01 ± 0.001	141471	53097	0
		2010				
Linear	-6.70 ± 0.41	0.47 ± 0.004	-	249357	18285	535
Exponential	5.66 ± 0.18	0.02 ± 0.001	-	231070	18098	348
Gompertz	175.33 ± 17.96	-4.98 ± 0.09	-0.01 ± 0.001	200277	17750	0
		2012				
Linear	-7.49 ± 0.16	0.46 ± 0.001	-	368140	54974	1778
Exponential	7.04 ± 0.07	0.02 ± 0.001	-	387129	55391	2195
Gompertz	109.56 ± 2.71	-4.44 ± 0.05	-0.01 ± 0.001	297005	53196	0
		2013				
Linear	-5.26 ± 0.14	0.42 ± 0.002	-	749338	71809	5155
Exponential	4.04 ± 0.06	0.02 ± 0.001	-	571666	69091	2437
Gompertz	125.55 ± 3.77	-5.82 ± 0.08	-0.02 ± 0.001	448375	66654	0
		2014				
Linear	-6.46 ± 0.90	0.47 ± 0.011	-	38579	3486	65
Exponential	7.94 ± 0.35	0.02 ± 0.001	-	37828	3477	56
Gompertz	120.70 ± 21.64	-4.10 ± 0.21	-0.01 ± 0.002	33568	3421	0
		2016				
Linear	-4.40 ± 0.24	0.35 ± 0.003	-	108533	15123	1361
Exponential	2.95 ± 0.07	0.02 ± 0.001	-	68442	14086	324
Gompertz	258.91 ± 36.24	-5.75 ± 0.07	-0.01 ± 0.001	59235	13762	0

Table 8. Growth models of YOY weakfish cohorts on July 1 - October 31 from 2006 – 2016 with parameter and standard error estimates, residual sums of squares, AIC and Δ AIC. Δ AIC values were used to determine models with most empirical support.

Model	Parameter values			RSS	AIC	Δ AIC
	a ± S.E.	*b* ± S.E.	*c* ± S.E.			
			2006			
Linear	-4.28 ± 0.15	0.26 ± 0.002	-	10610	6401	382
Exponential	1.70 ± 0.06	0.03 ± 0.001	-	10143	6343	324
Gompertz	41.60 ± 2.93	-5.12 ± 0.14	-0.02 ± 0.001	7889	6019	0
			2007			
Linear	-3.98 ± 0.15	0.24 ± 0.002	-	41588	15430	1103
Exponential	1.62 ± 0.04	0.03 ± 0.001	-	33507	14829	502
Gompertz	49.22 ± 3.08	-6.04 ± 0.17	-0.02 ± 0.001	27957	14327	0
			2008			
Linear	-11.47 ± 0.15	0.33 ± 0.002	-	42824	23575	505
Exponential	1.28 ± 0.03	0.03 ± 0.001	-	46543	23963	893
Gompertz	35.79 ± 1.11	-8.78 ± 0.31	-0.03 + 0.001	38408	23070	0
			2009			
Linear	-5.23 ± 0.17	0.27 ± 0.002	-	27663	11463	374
Exponential	2.06 ± 0.06	0.02 ± 0.001	-	29285	11584	495
Gompertz	44.35 ± 2.75	-5.38 ± 0.14	-0.02 ± 0.001	23163	11089	0
			2010			
Linear	-8.89 ± 0.19	0.31 ± 0.003	-	101288	26705	1600
Exponential	1.26 ± 0.03	0.03 ± 0.001	-	81905	25752	647
Gompertz	47.18 ± 2.03	-8.48 ± 0.31	-0.03 ± 0.001	70860	25105	0
			2011			
Linear	-3.71 ± 0.11	0.27 ± 0.002	-	43873	16969	1230
Exponential	1.93 ± 0.05	0.03 ± 0.001	-	43081	16912	1173
Gompertz	46.79 ± 1.52	-6.06 ± 0.15	-0.02 ± 0.001	29450	15739	0
			2012			
Linear	-4.32 ± 0.12	0.24 ± 0.002	-	41720	19466	1798
Exponential	1.76 ± 0.03	0.03 ± 0.001	-	35607	18880	1212
Gompertz	39.11 ± 1.21	-6.43 ± 0.16	-0.03 ± 0.001	25647	17668	0
			2013			
Linear	-5.48 ± 0.16	0.23 ± 0.002	-	54938	19400	804
Exponential	1.28 ± 0.04	0.03 ± 0.001	-	47166	18912	316
Gompertz	64.57 ± 6.51	-6.19 ± 0.14	-0.02 ± 0.001	34837	18596	0
			2014			
Linear	-4.45 ± 0.08	0.25 ± 0.001	-	31528	21862	1495
Exponential	1.53 ± 0.03	0.03 ± 0.001	-	30713	21742	1375
Gompertz	44.99 ± 1.63	-5.34 ± 0.06	-0.02 ± 0.001	22751	20367	0
			2015			
Linear	-2.86 ± 0.11	0.24 ± 0.002	-	37348	19193	1922
Exponential	1.53 ± 0.03	0.03 ± 0.001	-	32812	17800	529
Gompertz	78.51 ± 6.22	-5.61 ± 0.06	-0.02 ± 0.001	27009	17271	0
			2016			
Linear	-3.97 ± 0.09	0.24 ± 0.002	-	44720	16159	976
Exponential	1.79 ± 0.04	0.03 ± 0.001	-	40735	15768	585
Gompertz	51.58 ± 2.92	-5.14 ± 0.09	-0.02 ± 0.001	35093	15183	0

Table 9. Parameters used in bioenergetics models for Atlantic croaker. See methods for a description of the parameter symbols and their functional relationships.

Component	Parameter	Parameter value
Consumption	***C*** **(g g^{-1} d^{-1})**	
	CA	0.405
	CB	-0.342
	CQ	12.26
	C_{TO}	29
	C_{TM}	39
	C_{TL}	28.82
	C_{K1}	0.359
	C_{K4}	0.899
Respiration	***R*** **(g O_2 g^{-1} d^{-1})**	
	RA	0.008352
	RB	-0.355
	RQ	0.0313
	ACT	1.25
	SDA	0.172
Egestion	***F***	
	FA	0.104
Excretion	***U***	
	UA	0.068
	O_2 Conversion	13560
	Predator energy density (J g-1 wet weight)	5100
	Prey energy density (J g-1 wet weight)	
	Bay anchovy	3937 - 4146
	Mysid shrimps	4816
	Sand Shrimp	3138
	Polychaetes	3552
	Other invertebrates	3138

Table 10. Parameters used in bioenergetics models for weakfish. See methods for a description of the parameter symbols and their functional relationships.

Component	Parameter	Parameter value
Consumption	**(*C*) (g g-1 d-1)**	
	CA	0.492
	CB	-0.268
	CQ	2.8615
	C_{TO}	27
	C_{TM}	32
Respiration	**(*R*) (g O2 g-1 d-1)**	
	RA	0.0132
	RB	-0.265
	RQ	2.1059
	R_{TO}	27
	R_{TM}	32
	ACT	1.25
	SDA	0.172
Egestion	***F***	
	FA	0.104
Excretion	***U***	
	UA	0.068
	O_2 Conversion	13560
	Predator energy density (J g-1 wet weight)	3811
	Prey energy density (J g-1 wet weight)	
	Bay anchovy	3870 - 4146
	Mysid shrimps	4816
	Sand shrimp	3138
	Other fishes	7163 - 7221
	Other invertebrates	3138

Table 11. Model fit of four linear models based on annualized specific consumption rate (g g^{-1} d^{-1}) estimates derived from bioenergetics model output for Atlantic croaker and weakfish from 2006 - - 2016.

Species	Parameters	-2 log($\hat{L}$)	AIC	Δ AIC
Atlantic croaker	Polychaete density, hypoxic volume, AMO	83.43	73.23	0.13
	Polychaete density, hypoxic volume	79.73	71.73	1.63
	Hypoxic volume	79.36	53.82	19.54
	Polychaete density	59.82	73.36	0
Weakfish	Bay anchovy abundance, chlorophyll *a*, AMO	79.68	69.68	1.18
	Bay anchovy abundance, chlorophyll *a*	77.36	69.36	1.5
	Chlorophyll *a*	76.86	50.75	20.11
	Bay anchovy abundance	56.75	70.86	0

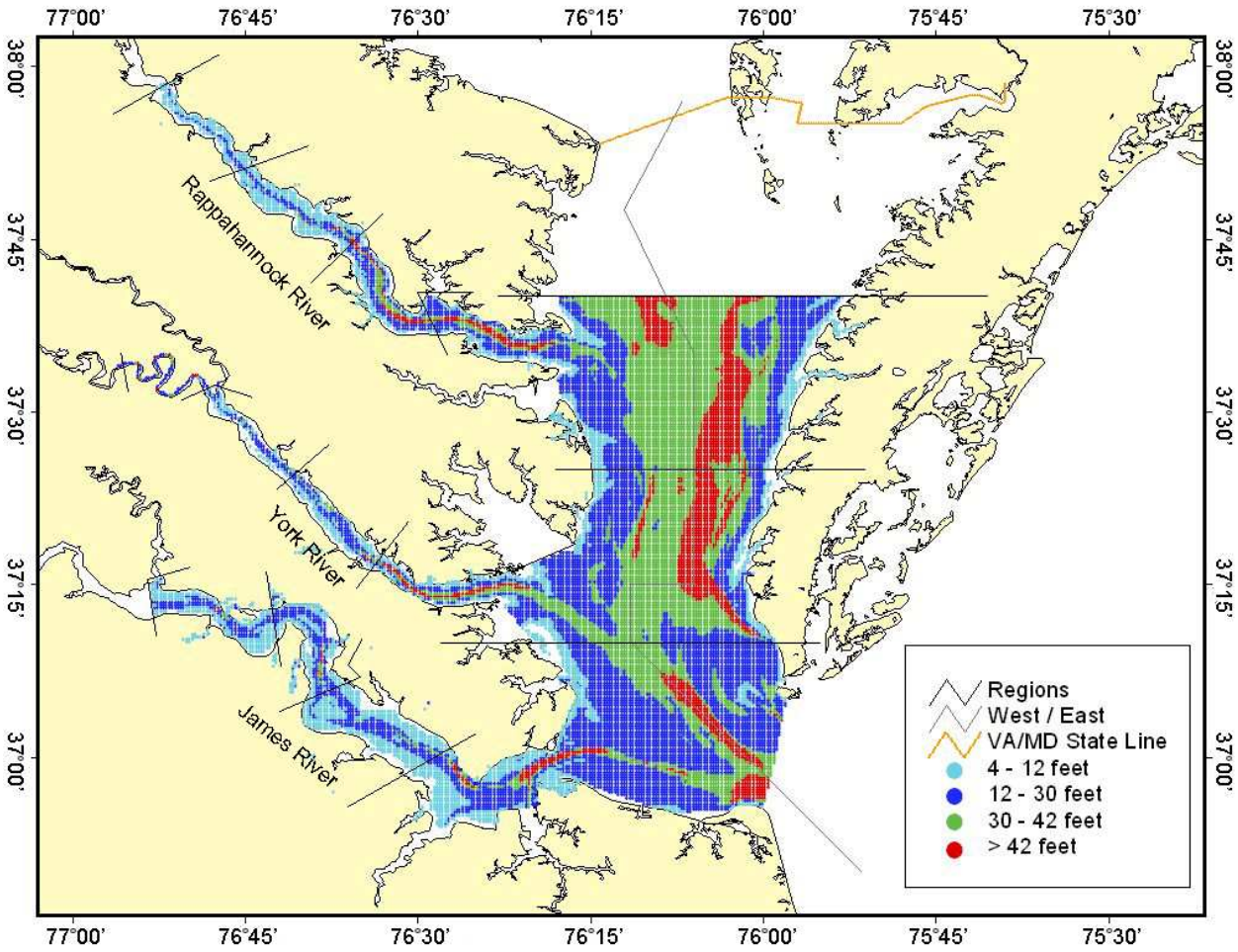

Figure 21. VIMS Juvenile Fish and Blue Crab Survey random stratified design in the Chesapeake Bay. Transect lines indicate geographic sampling regions in the Rappahannock River, York River, James River, and mainstem across four depth strata.

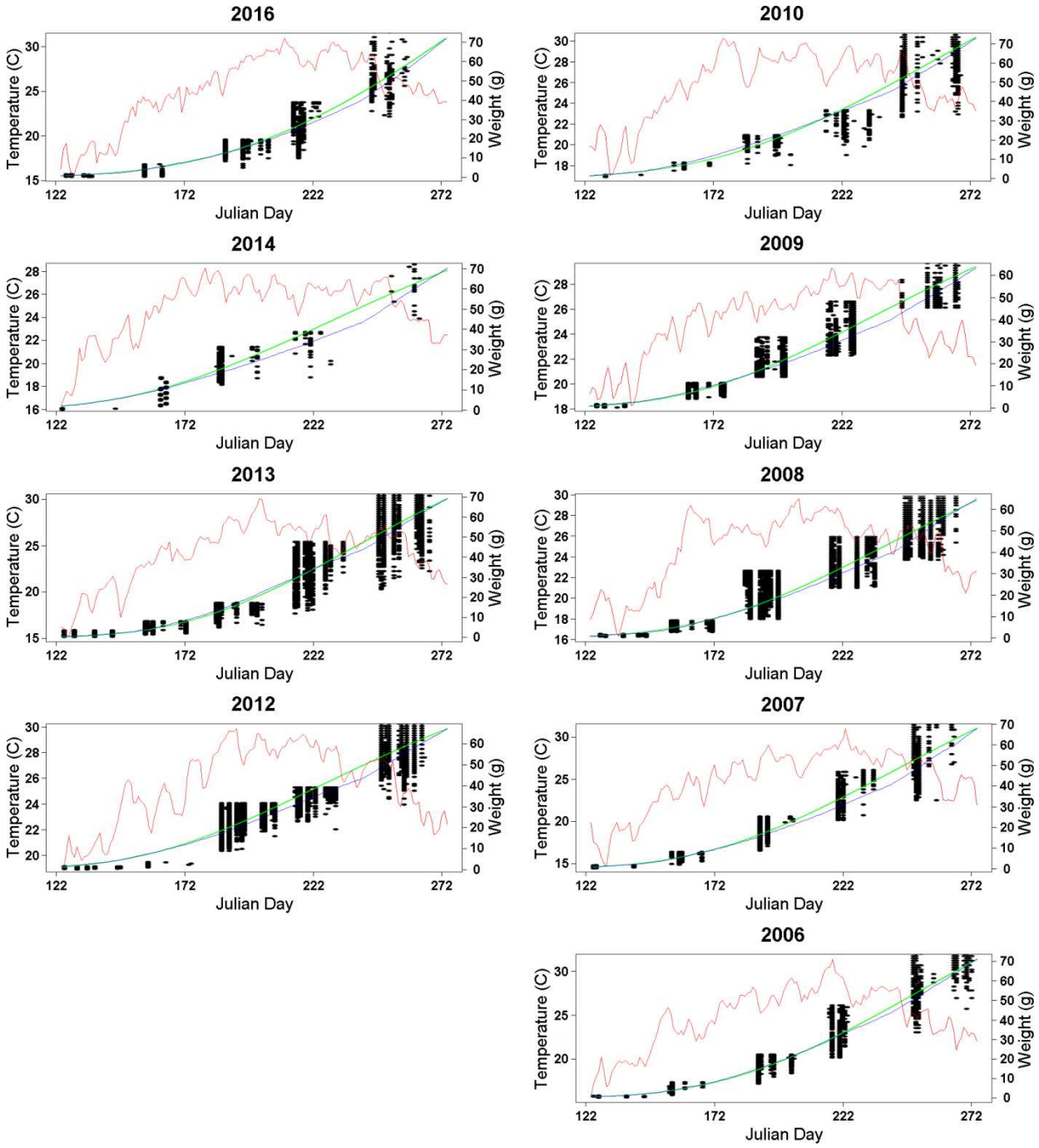

Figure 22. Atlantic croaker bioenergetics models calibrated to Chesapeake Bay field-based data. Green line: observed individual fish weight from Gompertz growth model fit to field data. Red line: daily mean temperature from VECOS sensor at Goodwin Islands. Blue line: bioenergetics model output once fit to the observed curve (calibrated model).

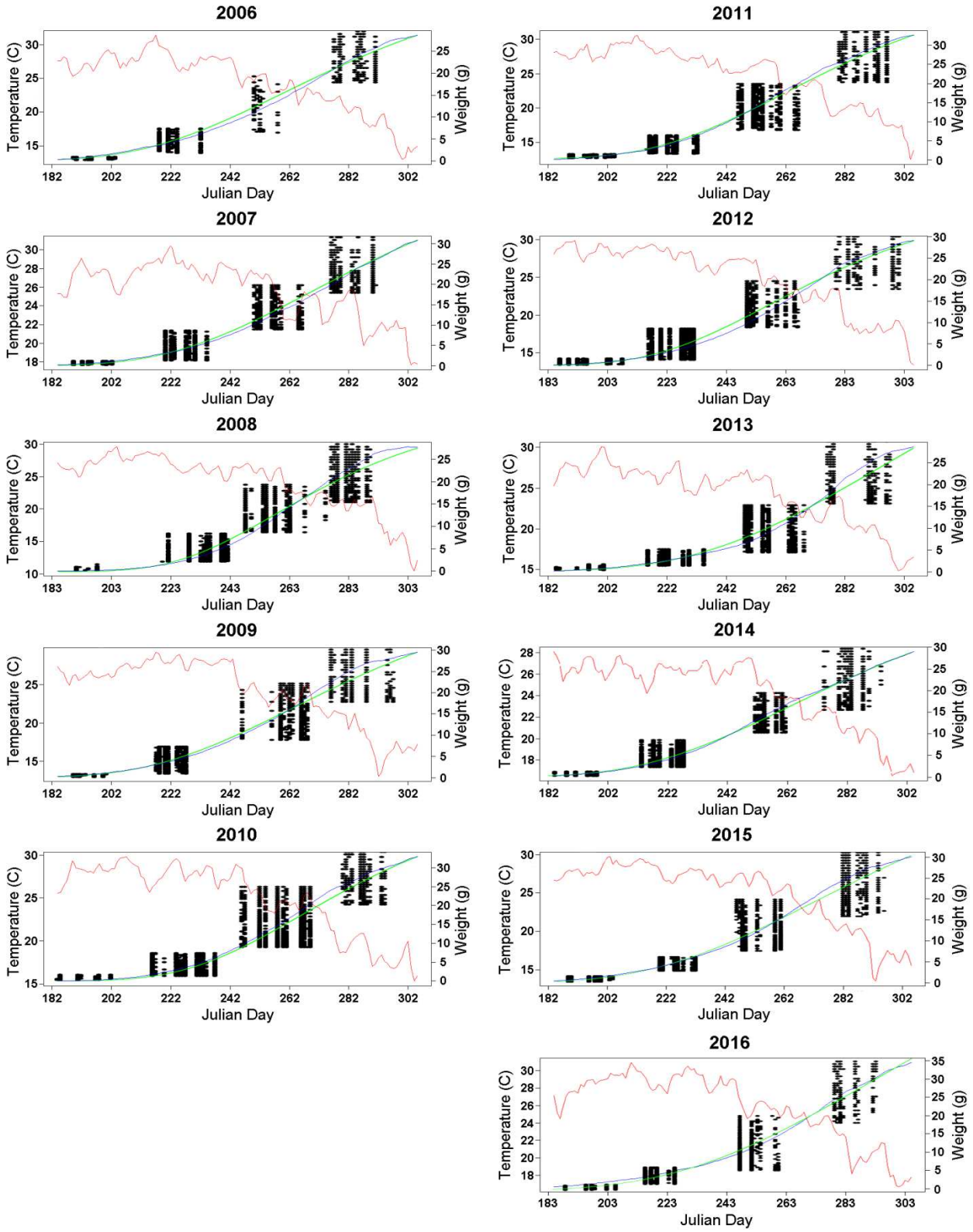

Figure 23. Weakfish bioenergetics models fit to Chesapeake Bay field-based data. Green line: observed individual fish weight from Gompertz growth model fit to field data. Red line: daily mean temperature from VECOS sensor at Goodwin Islands. Blue line: bioenergetics model output once fit to the observed curve (calibrated model).

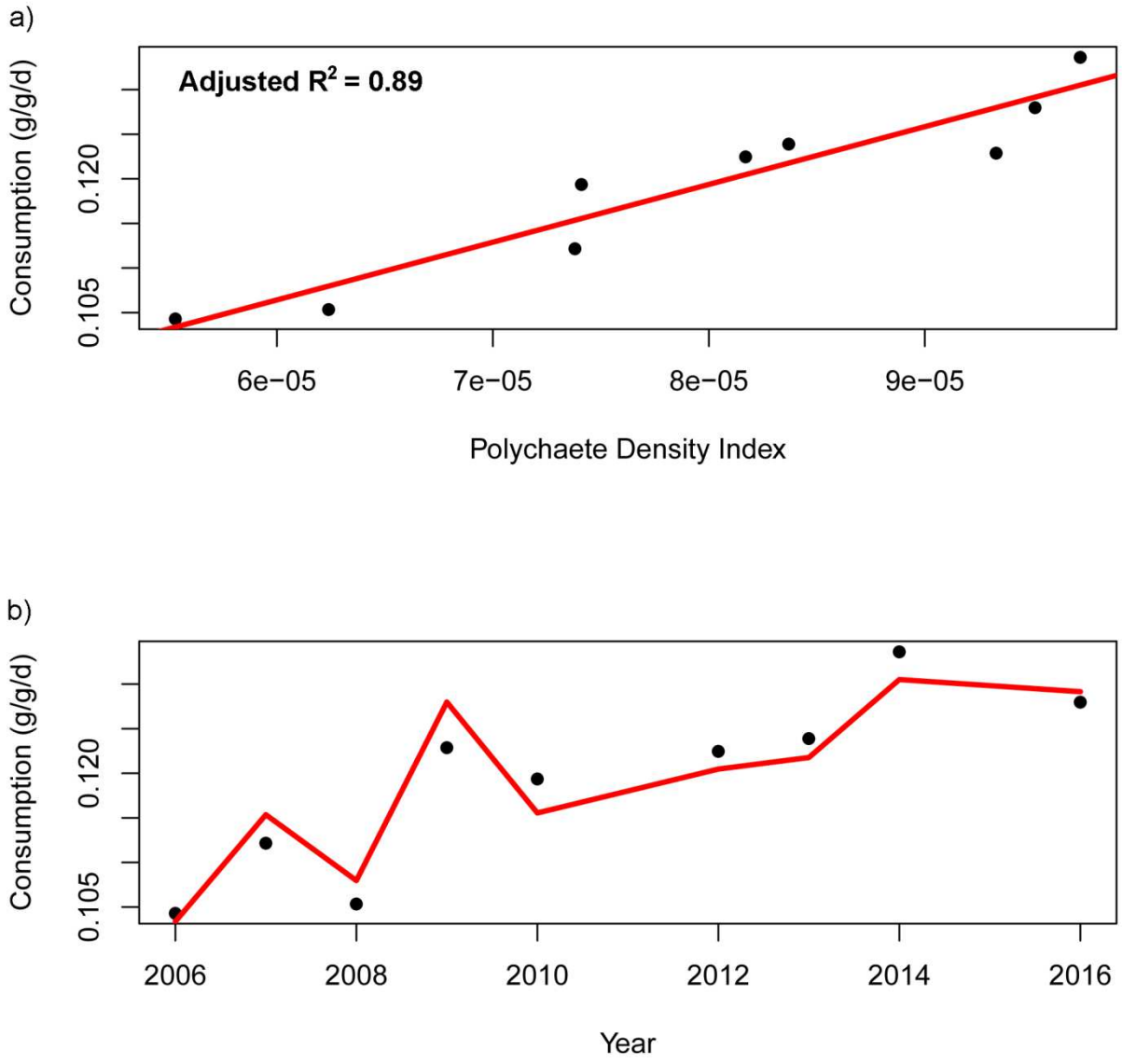

Figure 24. a) Linear model containing polychaete density as covariate (red line) fit to Atlantic croaker consumption (g/g/d) output from bioenergetics models (black dots) and b) model prediction (red line) for each year relative to estimated Atlantic croaker consumption rates (black dots).

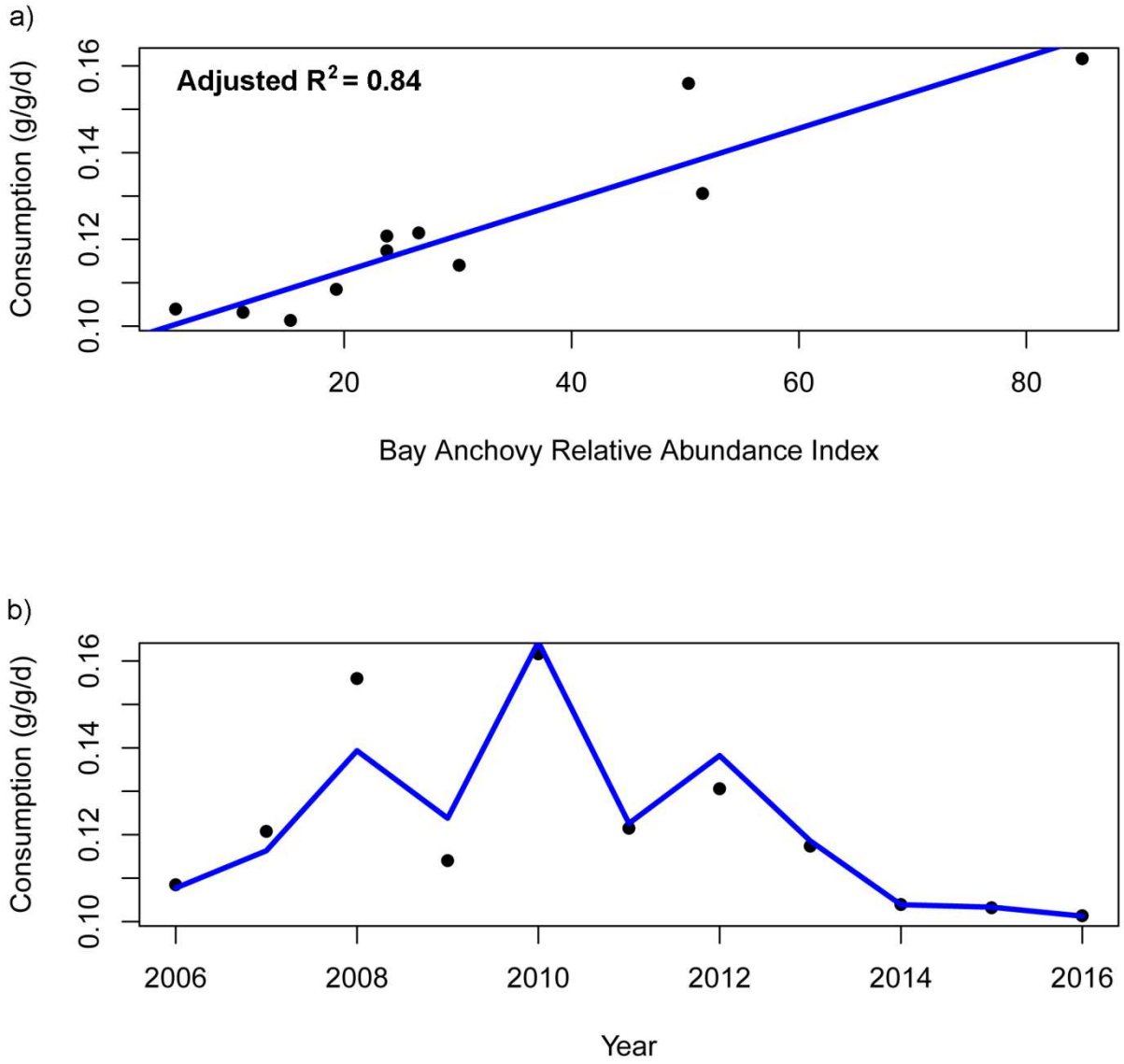

Figure 25. a) Linear model containing bay anchovy relative abundance index as covariate (blue line) fit to weakfish consumption (g/g/d) output from bioenergetics models (black dots) and b) model prediction (blue line) for each year relative to estimated weakfish consumption rates (black dots).

Appendix 1. Diet composition by weight of Atlantic croaker from 2006 - 2016 during the bioenergetics modeling simulation period (May 1 – September 31).

Day	Year	Mysids	Anchovies	Polychaetes	Sand shrimp	Other inverts	Molluscs
1	2016	0.31	0	0.45	0.1	0.04	0.1
60	2016	0	0	0.43	0	0.12	0.45
120	2016	0	0	0.79	0	0.15	0.06
1	2014	0.35	0	0.42	0.06	0.12	0.05
60	2014	0	0.01	0.18	0	0.55	0.26
120	2014	0.01	0.03	0.68	0	0.2	0.08
1	2013	0.29	0	0.41	0.15	0.15	0
60	2013	0.09	0	0.11	0.01	0.76	0.03
120	2013	0.01	0.01	0.53	0	0.18	0.17
1	2012	0.45	0	0.32	0.08	0.15	0
60	2012	0	0.01	0.69	0	0.25	0.05
120	2012	0.03	0.02	0.34	0	0.59	0.02
1	2010	0.38	0	0.15	0.12	0.35	0
60	2010	0	0	0.35	0.01	0.53	0.11
120	2010	0.01	0.01	0.68	0.01	0.18	0.11
1	2009	0.36	0	0.45	0.05	0.04	0.1
60	2009	0.01	0.06	0.3	0	0.4	0.23
120	2009	0.01	0.02	0.55	0	0.23	0.19
1	2008	0.43	0	0.44	0	0.13	0
60	2008	0	0.04	0.4	0	0.26	0.3
120	2008	0.01	0.07	0.28	0	0.54	0.1
1	2007	0.39	0	0.31	0.1	0.2	0
60	2007	0.01	0.02	0.54	0	0.12	0.31
120	2007	0	0.01	0.5	0	0.24	0.25
1	2006	0.52	0	0.37	0.07	0.04	0
60	2006	0.04	0.03	0.65	0	0.22	0.06
120	2006	0.06	0.04	0.45	0	0.34	0.11

Appendix 2. Diet composition by weight of weakfish from 2006 - 2016 during the bioenergetics modeling simulation period (July 1 - October 31).

Day	Year	Mysids	Anchovies	Other fish	Sand shrimp	Other inverts
1	2016	0.5	0.4	0	0.1	0
60	2016	0.2	0.75	0	0.05	0
120	2016	0.05	0.7	0.25	0	0
1	2015	0.47	0.37	0	0.02	0.14
60	2015	0.05	0.7	0.25	0	0
120	2015	0.01	0.74	0.25	0	0
1	2014	0.63	0.26	0	0	0.11
60	2014	1	0	0	0	0
120	2014	0	0.27	0.54	0	0.18
1	2013	0.55	0.25	0	0.1	0.1
60	2013	0.36	0.11	0	0	0.53
120	2013	0	0.79	0.21	0	0
1	2012	0.5	0.5	0	0	0
60	2012	0.34	0.33	0	0	0.33
120	2012	0	0.95	0.05	0	0
1	2011	0.62	0.28	0	0.03	0.07
60	2011	0.38	0.4	0	0	0.22
120	2011	0.25	0.18	0.15	0	0.42
1	2010	0.46	0.33	0	0.06	0.15
60	2010	0.34	0.37	0.03	0	0.26
120	2010	0.02	0.82	0.04	0	0.12
1	2009	0.26	0.37	0	0	0.37
60	2009	0.63	0	0	0.02	0.35
120	2009	0.09	0.81	0.04	0.03	0.03
1	2008	0.55	0.18	0	0.06	0.21
60	2008	0.28	0.33	0.29	0.05	0.05
120	2008	0.09	0.81	0	0.03	0.07
1	2007	0.5	0.4	0	0.1	0
60	2007	0.43	0.45	0.02	0.05	0.05
120	2007	0.38	0.28	0.05	0	0.29
1	2006	0.67	0.19	0	0	0.14
60	2006	0.26	0.25	0.01	0	0.48
120	2006	0.2	0.55	0.22	0	0.03

Appendix 3. Output from Atlantic croaker bioenergetics models. Mean values are averages across the 152 day simulation period; ranges are the minimum and maximum during the same period. *C* = consumption, *R* = respiration, *S* = coefficient for specific dynamic action, F = egestion, U = excretion, *p* = proportion of maximum consumption.

2016	Mean	Range
Temperature (°C)	25.23	(15.54, 30.91)
Weight (g)	23.22	(0.95, 71.74)
C (g g^{-1} d^{-1})	0.13	(0.07, 0.20)
C (g d^{-1})	2.31	(0.12, 4.97)
C (J d^{-1})	7602.02	(461.8, 16958.5)
R (J g^{-1} d^{-1})	207.83	(92.66, 346.49)
S (J g^{-1} d^{-1})	64.66	(36.29, 113.52)
F (J g^{-1} d^{-1})	43.63	(24.49, 76.61)
U (J g^{-1} d^{-1})	25.56	(14.35, 44.88)
Prey energy density (J g^{-1})	3287.47	(2935.8, 3746.0)
Predator energy density (J g^{-1})	5639.81	(3258.6, 7221.6)
Specific growth (g g^{-1} d^{-1})	0.05	(0.03, 0.09)
Total growth (g)	70.79	
p	0.99	

2014	Mean	Range
Temperature (°C)	24.24	(15.21, 30.04)
Weight (g)	25.16	(0.47, 69.09)
C (g g^{-1} d^{-1})	0.13	(0.06, 0.26)
C (g d^{-1})	2.43	(0.07, 4.88)
C (J d^{-1})	7448.47	(258.9, 14265.9)
R (J g^{-1} d^{-1})	209.34	(98.52, 350.78)
S (J g^{-1} d^{-1})	68.50	(29.32, 91.53)
F (J g^{-1} d^{-1})	46.23	(17.95, 99.79)
U (J g^{-1} d^{-1})	27.08	(10.51, 58.46)
Prey energy density (J g^{-1})	3240.69	(2924.8, 3752.4)
Predator energy density (J g^{-1})	5639.81	(3258.6, 7221.6)
Specific growth (g g^{-1} d^{-1})	0.06	(0.02, 0.11)
Total growth (g)	68.63	
p	1.04	

2013	Mean	Range
Temperature (°C)	24.83	(16.32, 29.58)
Weight (g)	23.54	(0.85, 64.91)
C (g g^{-1} d^{-1})	0.12	(0.05, 0.23)
C (g d^{-1})	2.20	(0.14, 4.42)
C (J d^{-1})	7090.06	(538.6, 14350.7)
R (J g^{-1} d^{-1})	205.27	(109.88, 314.99)
S (J g^{-1} d^{-1})	63.16	(27.47, 128.94)
F (J g^{-1} d^{-1})	42.62	(18.53, 87.01)
U (J g^{-1} d^{-1})	24.97	(10.86, 50.98)
Prey energy density (J g^{-1})	3280.27	(3087.2, 3748.6)
Predator energy density (J g^{-1})	5639.81	(3258.6, 7221.6)
Specific growth (g g^{-1} d^{-1})	0.05	(0.02, 0.10)
Total growth (g)	64.06	
p	0.97	

2012	Mean	Range
Temperature (°C)	24.80	(15.69, 31.38)
Weight (g)	25.09	(0.64, 71.02)
C (g g^{-1} d^{-1})	0.12	(0.06, 0.23)
C (g d^{-1})	2.24	(0.08, 4.41)
C (J d^{-1})	7621.13	(3057, 14841.7)
R (J g^{-1} d^{-1})	207.70	(100.01, 333.90)
S (J g^{-1} d^{-1})	66.27	(28.86, 134.56)
F (J g^{-1} d^{-1})	44.72	(20.04, 84.81)
U (J g^{-1} d^{-1})	26.20	(11.41, 53.20)
Prey energy density (J g^{-1})	3476.11	(3364.1, 3754.8)
Predator energy density (J g^{-1})	5639.81	(3258.6, 7221.6)
Specific growth (g g^{-1} d^{-1})	0.05	(0.02, 0.10)
Total growth (g)	70.37	
p	0.94	

2010	Mean	Range
Temperature (°C)	24.92	(18.24, 29.26)
Weight (g)	23.81	(0.94, 63.20)
C (g g^{-1} d^{-1})	0.12	(0.06, 0.21)
C (g d^{-1})	2.17	(0.17, 4.31)
C (J d^{-1})	7011.74	(642.7, 13962.5)
R (J g^{-1} d^{-1})	202.72	(101.15, 316.93)
S (J g^{-1} d^{-1})	61.38	(28.81, 117.89)
F (J g^{-1} d^{-1})	41.42	(19.44, 79.56)
U (J g^{-1} d^{-1})	24.27	(11.39, 46.61)
Prey energy density (J g^{-1})	3299.08	(3140.3, 3749.6)
Predator energy density (J g^{-1})	5639.81	(3258.6, 7221.6)
Specific growth (g g^{-1} d^{-1})	0.05	(0.02, 0.09)
Total growth (g)	62.26	
p	0.93	

2009	Mean	Range
Temperature (°C)	25.01	(14.68, 30.96)
Weight (g)	24.17	(1.05, 67.70)
C (g g^{-1} d^{-1})	0.12	(0.06, 0.22)
C (g d^{-1})	2.33	(0.11, 4.85)
C (J d^{-1})	7380.65	(392.4, 15244.3)
R (J g^{-1} d^{-1})	204.09	(100.67, 314.58)
S (J g^{-1} d^{-1})	62.33	(29.69, 125.67)
F (J g^{-1} d^{-1})	42.06	(20.04, 84.81)
U (J g^{-1} d^{-1})	24.64	(11.74, 49.68)
Prey energy density (J g^{-1})	3257.94	(3135.0, 3749.4)
Predator energy density (J g^{-1})	5639.81	(3258.6, 7221.6)
Specific growth (g g^{-1} d^{-1})	0.05	(0.01, 0.09)
Total growth (g)	66.66	
p	0.98	

2008	Mean	Range
Temperature (°C)	25.48	(19.15, 29.84)
Weight (g)	26.56	(1.63, 66.93)
C (g g^{-1} d^{-1})	0.11	(0.05, 0.18)
C (g d^{-1})	2.23	(0.23, 3.97)
C (J d^{-1})	7522.81	(874.8, 13218.3)
R (J g^{-1} d^{-1})	196.29	(101.19, 279.54)
S (J g^{-1} d^{-1})	56.29	(27.63, 103.63)
F (J g^{-1} d^{-1})	37.99	(18.64, 69.93)
U (J g^{-1} d^{-1})	22.25	(10.92, 40.97)
Prey energy density (J g^{-1})	3436.80	(3328.3, 3753.8)
Predator energy density (J g^{-1})	5639.81	(3258.6, 7221.6)
Specific growth (g g^{-1} d^{-1})	0.04	(0.02, 0.07)
Total growth (g)	65.30	
p	0.87	

2007	Mean	Range
Temperature (°C)	25.77	(17.02, 30.25)
Weight (g)	27.35	(1.45, 72.72)
C (g g^{-1} d^{-1})	0.11	(0.07, 0.20)
C (g d^{-1})	2.41	(0.24, 4.69)
C (J d^{-1})	8000.38	(858.6, 15718.9)
R (J g^{-1} d^{-1})	198.11	(101.48, 289.35)
S (J g^{-1} d^{-1})	58.50	(31.45, 112.98)
F (J g^{-1} d^{-1})	39.48	(21.22, 76.24)
U (J g^{-1} d^{-1})	23.13	(12.43, 44.67)
Prey energy density (J g^{-1})	3364.88	(3190.0, 3750.3)
Predator energy density (J g^{-1})	5639.81	(3258.6, 7221.6)
Specific growth (g g^{-1} d^{-1})	0.05	(0.03, 0.08)
Total growth (g)	71.27	
p	0.91	

2006	Mean	Range
Temperature (°C)	24.78	(16.32, 28.26)
Weight (g)	27.41	(2.27, 70.08)
C (g g^{-1} d^{-1})	0.10	(0.06, 0.16)
C (g d^{-1})	2.35	(0.20, 4.17)
C (J d^{-1})	7724.89	(765.8, 14155.9)
R (J g^{-1} d^{-1})	190.88	(100.24, 354.62)
S (J g^{-1} d^{-1})	53.17	(29.32, 91.53)
F (J g^{-1} d^{-1})	35.88	(19.78, 61.77)
U (J g^{-1} d^{-1})	21.02	(11.59, 36.18)
Prey energy density (J g^{-1})	3306.02	(3002.1, 3747.2)
Predator energy density (J g^{-1})	5639.81	(3258.6, 7221.6)
Specific growth (g g^{-1} d^{-1})	0.04	(0.02, 0.07)
Total growth (g)	67.81	
p	0.91	

Appendix 4. Output from weakfish bioenergetics models. Mean values are averages across the 122 day simulation period; ranges are the minimum and maximum during the same period. *C* = consumption, *R* = respiration, *S* = coefficient for specific dynamic action, F = egestion, U = excretion, *p* = proportion of maximum consumption.

2016	Mean	Range
Temperature (°C)	25.77	(16.66, 30.91)
Weight (g)	12.83	(0.50, 34.45)
C (g g^{-1} d^{-1})	0.10	(0.03, 0.23)
C (g d^{-1})	2.48	(0.1, 4.88)
C (J d^{-1})	8941.04	(458.4, 15339.9)
R (J g^{-1} d^{-1})	227.36	(53.08, 376.41)
S (J g^{-1} d^{-1})	68.54	(23.81, 156.95)
F (J g^{-1} d^{-1})	46.25	(16.07, 105.92)
U (J g^{-1} d^{-1})	27.10	(9.41, 62.05)
Prey energy density (J g^{-1})	4451.41	(4129.7, 4803.7)
Predator energy density (J g^{-1})	4643.31	(3828.5, 5514.5)
Specific growth (g g^{-1} d^{-1})	0.04	(0.01, 0.09)
Total growth (g)	33.95	
p	0.38	

2015	Mean	Range
Temperature (°C)	24.82	(13.53, 29.69)
Weight (g)	12.25	(0.40, 30.05)
C (g g^{-1} d^{-1})	0.10	(0.02, 0.24)
C (g d^{-1})	2.43	(0.09, 4.65)
C (J d^{-1})	8537.26	(382.5, 15315.1)
R (J g^{-1} d^{-1})	231.57	(43.90, 391.83)
S (J g^{-1} d^{-1})	69.53	(16.62, 161.41)
F (J g^{-1} d^{-1})	46.92	(11.21, 108.93)
U (J g^{-1} d^{-1})	27.49	(6.57, 63.81)
Prey energy density (J g^{-1})	4450.86	(4129.7, 4803.7)
Predator energy density (J g^{-1})	4650.50	(3824.5, 5528.2)
Specific growth (g g^{-1} d^{-1})	0.04	(0.006, 0.09)
Total growth (g)	29.65	
p	0.37	

2014	Mean	Range
Temperature (°C)	24.13	(15.90, 28.08)
Weight (g)	12.07	(0.30, 29.21)
C (g g^{-1} d^{-1})	0.10	(0.03, 0.25)
C (g d^{-1})	2.42	(0.07, 4.28)
C (J d^{-1})	8499.87	(289.4, 15073.1)
R (J g^{-1} d^{-1})	236.31	(52.03, 412.54)
S (J g^{-1} d^{-1})	72.80	(24.80, 166.33)
F (J g^{-1} d^{-1})	49.13	(16.73, 112.24)
U (J g^{-1} d^{-1})	28.78	(9.81, 65.76)
Prey energy density (J g^{-1})	4585.97	(3944.9, 5554.5)
Predator energy density (J g^{-1})	4650.50	(3824.5, 5528.2)
Specific growth (g g^{-1} d^{-1})	0.04	(0.01, 0.1)
Total growth (g)	28.91	
p	0.36	
2013	Mean	Range
Temperature (°C)	24.26	(14.82, 30.04)
Weight (g)	9.85	(0.18, 28.64)
C (g g^{-1} d^{-1})	0.12	(0.03, 0.28)
C (g d^{-1})	2.26	(0.05, 4.13)
C (J d^{-1})	8173.27	(201.6, 15341.1)
R (J g^{-1} d^{-1})	249.99	(48.50, 453.11)
S (J g^{-1} d^{-1})	80.50	(19.67, 191.42)
F (J g^{-1} d^{-1})	54.32	(13.27, 129.18)
U (J g^{-1} d^{-1})	31.82	(7.78, 75.68)
Prey energy density (J g^{-1})	4681.56	(3838.2, 6212.0)
Predator energy density (J g^{-1})	4650.50	(3824.5, 5528.2)
Specific growth (g g^{-1} d^{-1})	0.05	(0.008, 0.11)
Total growth (g)	28.46	
p	0.37	

2012	Mean	Range
Temperature (°C)	24.87	(14.82, 30.04)
Weight (g)	11.30	(0.10, 29.07)
C (g g^{-1} d^{-1})	0.13	(0.03, 0.39)
C (g d^{-1})	2.45	(0.03, 4.76)
C (J d^{-1})	8350.26	(147.4, 15507.6)
R (J g^{-1} d^{-1})	247.73	(43.02, 421.95)
S (J g^{-1} d^{-1})	84.87	(14.94, 263.27)
F (J g^{-1} d^{-1})	57.27	(10.09, 177.66)
U (J g^{-1} d^{-1})	33.55	(5.91, 104.08)
Prey energy density (J g^{-1})	4189.38	(3870.2, 4452.2)
Predator energy density (J g^{-1})	4650.50	(3824.5, 5528.2)
Specific growth (g g^{-1} d^{-1})	0.05	(0.006, 0.17)
Total growth (g)	28.97	
p	0.42	

2011	Mean	Range
Temperature (°C)	24.72	(12.51, 30.57)
Weight (g)	13.28	(0.17, 32.58)
C (g g^{-1} d^{-1})	0.12	(0.02, 0.34)
C (g d^{-1})	2.56	(0.05, 5.01)
C (J d^{-1})	8783.90	(215.2, 16165.9)
R (J g^{-1} d^{-1})	235.99	(38.84, 468.16)
S (J g^{-1} d^{-1})	78.80	(14.45, 231.53)
F (J g^{-1} d^{-1})	53.18	(9.75, 156.24)
U (J g^{-1} d^{-1})	31.15	(5.71, 91.53)
Prey energy density (J g^{-1})	4156.51	(3919.0, 4375.9)
Predator energy density (J g^{-1})	4650.50	(3824.5, 5528.2)
Specific growth (g g^{-1} d^{-1})	0.05	(0.006, 0.15)
Total growth (g)	32.41	
p	0.43	

2010	Mean	Range
Temperature (°C)	24.85	(15.34, 29.78)
Weight (g)	12.36	(0.02, 32.83)
C (g g^{-1} d^{-1})	0.16	(0.03 0.67)
C (g d^{-1})	2.50	(0.01, 4.93)
C (J d^{-1})	8683.00	(44.0, 15574.8)
R (J g^{-1} d^{-1})	266.61	(48.38, 668.81)
S (J g^{-1} d^{-1})	105.27	(20.27, 454.55)
F (J g^{-1} d^{-1})	71.04	(13.68, 306.75)
U (J g^{-1} d^{-1})	41.62	(8.01, 179.71)
Prey energy density (J g^{-1})	4122.17	(3919.0, 4375.9)
Predator energy density (J g^{-1})	4650.50	(3824.5, 5528.2)
Specific growth (g g^{-1} d^{-1})	0.07	(0.01, 0.31)
Total growth (g)	32.82	
p	0.46	

2009	Mean	Range
Temperature (°C)	24.02	(13.00, 29.26)
Weight (g)	12.18	(0.28, 29.49)
C (g g^{-1} d^{-1})	0.11	(0.2, 0.28)
C (g d^{-1})	2.41	(0.07, 4.46)
C (J d^{-1})	8440.35	(285.8, 15299.3)
R (J g^{-1} d^{-1})	235.13	(42.19, 420.89)
S (J g^{-1} d^{-1})	73.09	(15.21, 172.88)
F (J g^{-1} d^{-1})	49.32	(10.26, 116.67)
U (J g^{-1} d^{-1})	28.90	(6.01, 68.35)
Prey energy density (J g^{-1})	4241.43	(3950.7, 4689.2)
Predator energy density (J g^{-1})	4650.50	(3824.5, 5528.2)
Specific growth (g g^{-1} d^{-1})	0.05	(0.006, 0.11)
Total growth (g)	29.21	
p	0.40	

2008	Mean	Range
Temperature (°C)	24.04	(10.43, 29.58)
Weight (g)	10.46	(0.01, 27.78)
C (g g^{-1} d^{-1})	0.16	(0.02, 0.67)
C (g d^{-1})	2.32	(0.006, 4.55)
C (J d^{-1})	8102.71	(26.8, 15939.2)
R (J g^{-1} d^{-1})	287.75	(34.14, 777.92)
S (J g^{-1} d^{-1})	112.89	(9.57, 456.52)
F (J g^{-1} d^{-1})	76.18	(6.46, 308.07)
U (J g^{-1} d^{-1})	44.63	(3.78, 108.48)
Prey energy density (J g^{-1})	4754.62	(3882.1, 5120.3)
Predator energy density (J g^{-1})	4650.50	(3824.5, 5528.2)
Specific growth (g g^{-1} d^{-1})	0.07	(0.002, 0.28)
Total growth (g)	27.73	
p	0.39	

2007	Mean	Range
Temperature (°C)	25.64	(17.68, 30.96)
Weight (g)	11.26	(0.17, 30.74)
C (g g^{-1} d^{-1})	0.12	(0.04, 0.30)
C (g d^{-1})	2.44	(0.006, 4.81)
C (J d^{-1})	8600.43	(199.1, 15697.7)
R (J g^{-1} d^{-1})	246.97	(58.57, 460.51)
S (J g^{-1} d^{-1})	80.71	(24.39, 204.32)
F (J g^{-1} d^{-1})	54.47	(16.46, 137.88)
U (J g^{-1} d^{-1})	31.91	(9.64, 80.78)
Prey energy density (J g^{-1})	4311.17	(4184.8, 4379.6)
Predator energy density (J g^{-1})	4650.50	(3824.5, 5528.2)
Specific growth (g g^{-1} d^{-1})	0.05	(0.01, 0.12)
Total growth (g)	30.57	
p	0.39	

2006	Mean	Range
Temperature (°C)	24.36	(12.94, 31.38)
Weight (g)	11.72	(0.35, 28.57)
C (g g^{-1} d^{-1})	0.11	(0.02, 0.27)
C (g d^{-1})	2.43	(0.08, 4.71)
C (J d^{-1})	8359.39	(361.1, 6577.9)
R (J g^{-1} d^{-1})	229.84	(41.87, 404.19)
S (J g^{-1} d^{-1})	70.03	(16.45, 180.51)
F (J g^{-1} d^{-1})	47.26	(11.10, 121.81)
U (J g^{-1} d^{-1})	27.69	(6.50, 71.36)
Prey energy density (J g^{-1})	4244.25	(3833.5, 4774.7)
Predator energy density (J g^{-1})	4650.50	(3824.5, 5528.2)
Specific growth (g g^{-1} d^{-1})	0.04	(0.007, 0.11)
Total growth (g)	28.22	
p	0.40	

VITA

Christopher J. Sweetman

Born in New Haven, Connecticut on 26 May 1984. Graduated from Daniel Hand High School in Madison, Connecticut in 2002. Graduated *cum laude* from University of New Hampshire with a Bachelor of Science in Marine and Freshwater Biology. Worked as a molecular genetics research specialist at the University of Connecticut – Avery Point from 2006-2007. Earned a Master of Science degree in Marine Science from the College of William and Mary, School of Marine Science in 2012. Entered the doctoral program at the College of William and Mary, School of Marine Science in 2013.