

Feeding Ecology of Invasive Catfishes in Chesapeake Bay Subestuaries
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Academic Abstract

Blue Catfish *Ictalurus furcatus* are native to tributaries of the Mississippi River but are now invasive in several Atlantic slope drainages. This includes subestuaries of the Chesapeake Bay, where their feeding ecology and potential impact on native species was largely unknown. We collected stomach contents from 16,110 Blue Catfish at 698 sites in three large subestuaries of the Chesapeake Bay (James, York, Rappahannock rivers). Cumulative prey curves revealed that sample size was sufficient for diet description, though 1,000 – 1500 stomachs were needed per river. Blue Catfish are opportunistic generalists that feed on a broad array of plant and animal material. Logistic regression models reveal that Blue Catfish undergo significant ontogenetic diet shifts to piscivory at larger sizes ($P<0.01$) though the lengths at which these shifts occur varies by river system (500 – 900 mm total length; TL). Over 60% of Blue Catfish stomachs contained other invasive species, primarily *Hydrilla verticillata* and Asian clams *Corbicula fluminea*. Canonical Correspondence Analysis (CCA) revealed that salinity and season explained the most variation in Blue Catfish diet, while Generalized Additive Models (GAMs) demonstrated that there is considerable spatiotemporal and length-based variation in predation of species of concern. Species of concern include American Shad, American Eel, and river herring, which are imperiled, and blue crab, which support valuable fisheries in Chesapeake Bay. Predation of American Shad, American Eel, and river herring was rare (max predicted occurrence in Blue Catfish diets = 8%), while blue crab was much more common in the diet (max predicted occurrence = 28%). Predation of American Shad and river herring peaks in freshwater areas in April, while predation of blue crab peaks in brackish areas in October. Predation of all species of concern is highest for large catfish (500 – 1000 mm TL). Field and laboratory-based estimates of consumption rate revealed that Blue Catfish feed at similar rates as Channel Catfish *Ictalurus punctatus*, and daily ration is estimated to be 2-5% bodyweight per day during warm temperatures, while peak feeding (maximum daily ration) can approach 10% bodyweight per day. While consumption of imperiled species is rare, Blue Catfish could still have negative impacts on these species due to dense catfish populations.

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General Audience Abstract

Native to the Mississippi River basin, Blue Catfish *Ictalurus furcatus* are the largest catfish species in North America; they can exceed 100 lbs and live for over 30 years. They were stocked in Chesapeake Bay as a sportfish 40 years ago and are now considered invasive. We performed a series of experiments to describe how invasive Blue Catfish fit in the food web, including diet and consumption rate analyses. Most of the Blue Catfish population is comprised of opportunistic generalists that feed on a diverse array of plant and animal material. We experimentally demonstrated that Blue Catfish tend to feed on whatever species are locally abundant. The most common prey were other species considered invasive in Chesapeake Bay; primarily Asian clams and *Hydrilla verticillata*, which is an invasive aquatic plant. Blue Catfish also eat other types of vegetation, clams, snails, crabs, fish, small invertebrates, mammals, birds, reptiles, and amphibians. Consumption of imperiled native fishes (like American Shad, American Eel, and river herring) was uncommon while consumption of the commercially-valuable blue crab was common, especially in brackish areas during the autumn. Blue Catfish consumption rates were similar to a closely related species, the channel catfish, and blue catfish can consume an estimated 2 – 5% of their body weight per day during the summer months, and up to 10% of their body weight per day during times of peak feeding. While consumption of imperiled species is rare, Blue Catfish could still have negative impacts on these species due to dense catfish populations

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Important Note to Readers

The Blue Catfish invasion is a highly controversial topic in eastern Virginia (Schmitt et al. 2017) and has received a great deal of media publicity during this project (Springston 2015, Carman 2017). Because of this, it is imperative that our research is published as quickly as possible so that the best available information is available to managers and policymakers.

Because of this, each chapter of this dissertation is designed to be a stand-alone manuscript to save time during the publication process. This results in some redundancy and lack of formatting consistency between chapters. Redundancy will be especially evident in the introductions of each chapter, since I will cover much of the same background information on Blue Catfish in Chesapeake Bay.

The formatting and style will also vary from chapter to chapter, especially with regard to figures, tables, and references since chapters have different target journals. Style within the body of each chapter will also vary, depending on the requirements of each target journal. For example, in Chapter 1 “Blue Catfish” is capitalized throughout to adhere with journal guidelines for *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science*, while lowercase “blue catfish” is used in Chapter 2 (target journal is *Environmental Biology of Fishes*). More inconsistencies will be apparent in Chapters 3 and 4 since they also have different target journals (*Biological Invasions* and *Transactions of the American Fisheries Society*, respectively). The introduction and conclusion chapters will follow AFS formatting guidelines, thus will be consistent with Chapters 1 and 4.

I apologize for any inconvenience this may cause, and I appreciate your patience

Chapter 1: Introduction

Invasive species are a global problem.— Invasive species have long been recognized as having negative ecological and economic impacts (Elton 1958; Simberloff 1996; Sakai et al. 2001). Invasive species in the United States cause an estimated \$100 billion in economic damages per year, while global losses exceed \$1 trillion per year (Pimental et al. 2005). Next to habitat degradation, invasive species are often cited as the second greatest threat to global biodiversity, and have resulted in hundreds of extinctions worldwide (Sakai et al. 2001; Mack et al. 2000; Light and Marchetti 2007). Successful invasions often lead to a homogenization of flora and fauna, which may ultimately yield a “global biomonotony” (Mooney and Cleland 2001; Devin and Beisel 2007; Moyle and Mount 2007). With time, invasive species are expected to become problematic throughout all ecosystems, as increasing global trade and human mobility increases the likelihood of introductions (Sakai et al. 2001). The U.S. government recognized the danger of invasive species nearly two decades ago, and implemented Executive Order #13112, which directed several agencies to “prevent the introduction of invasive species, provide for their control, and to minimize the economic, ecological, and human health impacts that invasive species cause” (Federal Register 64:6183-6186).

The Chesapeake Bay is the largest estuary in the United States and has a long history of invasion. It currently supports reproducing populations of nearly 150 nonnative aquatic species, including 27 nonnative fishes (Ruiz and Reid 2007). Habitat degradation and invasive species may contribute to native species declines within the estuary (Boesch et al. 2001; Orth et al. 2006), which is problematic as the Chesapeake Bay supports numerous fisheries that are economically valuable to the region. Many fisheries have waned in recent years (DeWar et al. 2009), including the collapse of the oyster fishery (Rotschild et al. 1994), the decline of blue crab harvest (Lipcius

et al. 2002), and the closures of the American Shad *Alosa sapidissima*, Alewife *A. pseudoharengus*, and Blueback Herring *A. aestivalis* fisheries (Onley et al. 2003; Limburg and Waldman 2009; Bethony et al. 2013). While failing Chesapeake Bay fisheries have largely been attributed to Bay-wide nutrient enrichment and its associated effects on seagrass and dissolved oxygen (Kemp et al. 2005; Orth et al. 2006), increases in the abundance of nonnative, predatory fish may also be contributing to these declines (MacAvoy et al. 2000; Brown et al. 2005; Jiao et al. 2009; Schloesser et al. 2011).

Non-native catfish stocked in Virginia's tidal rivers.— During the 1970s and 1980s, Blue Catfish *Ictalurus furcatus* were introduced into the Chesapeake Bay watershed to create new recreational fisheries (Jenkins and Burkhead 1994), a time when many fisheries had collapsed or were on the brink of collapse (Rothschild et al. 1994; Richards and Rago 1999). The Department of Game and Inland Fisheries stocked hundreds of thousands of Blue Catfish fingerlings in the early and mid-1970s, starting with the James and Rappahannock Rivers (Orth et al. 2017). More stockings continued over several years, expanding to the Pamunkey River and later to the Mattaponi River. It is important to note that Blue Catfish were the second “invasive” Ictalurid in these rivers, as channel catfish *Ictalurus punctatus* were stocked sometime during the 1800s (Jenkins and Burkhead 1994). Anecdotal information suggests that the population grew slowly and catfish harvesters noticed little difference in catfish species catch composition. Blue Catfish populations became well-established during the 1990s (Bob Greenlee, *personal communication*), and by the early 2000s dense populations existed in all of Virginia's tidal rivers (Greenlee and Lim 2011). Populations have expanded further and Blue Catfish now inhabit the Potomac, Patuxent, Elk, and Nanticoke river systems in Maryland. Blue Catfish have also been captured in the Susquehanna Flats area of the northern Chesapeake Bay (Aguilar et al. 2017).

Blue Catfish are a large, long-lived species that can live for over 25 years and weigh in excess of 50 kg (Graham 1999). They are native to the Mississippi River and its tributaries, and populations extend southward into Mexico and Central America (Graham 1999). Blue Catfish have been widely introduced into many water bodies along the Atlantic and Pacific coasts, and are now found in 29 states (Graham 1999), but are only considered “invasive” in the Chesapeake watershed (Schloesser et al. 2011). Blue Catfish populations expanded after introduction, and the species is now very common in Virginia’s tidal rivers (Greenlee and Lim 2011). They have expanded into brackish areas and have been captured in salinities as high as 21.5 ppt (*unpublished data*, cited in Fabrizio et al. 2017). Blue Catfish routinely inhabit brackish waters in their native range, thus further range expansion within the Chesapeake is likely (Perry 1969; Schloesser et al. 2011), particularly the less saline waters of the upper Chesapeake Bay. Blue Catfish now support expanding commercial fisheries and trophy recreational fisheries in several of these rivers (Greenlee and Lim 2011; Orth et al. 2017).

Flathead Catfish *Pylodictis olivarus* were introduced to the James River sometime during the 1960s or 1970s, though no official record exists (Jenkins and Burkhead 1994). They are now established in the James, Potomac, and Susquehanna drainages (Jenkins and Burkhead 1994; Brown et al. 2005; Orrell et al. 2005). We also captured several juvenile and mature individuals (N=22) from the York River, where Flathead Catfish had not yet been documented (Schmitt et al. 2017). Both catfish species are well-equipped for foraging in the muddy, high-productivity rivers of their native range, as they possess advanced olfactory, gustatory, electroreceptory, and mechanoreceptory systems (Graham 1999; Jackson 1999). This may partially explain their success in the present day Chesapeake Bay, which has been transformed into a turbid, nutrient-rich system by agricultural runoff and other anthropogenic disturbances (Boesch et al. 2001).

Moreover, Blue Catfish thrive in estuarine habitats in their native range, such as the Mississippi River estuary in Louisiana (Baltz and Jones 2003).

While diet studies are limited in their native range, Blue Catfish are omnivores that consume vegetation, mollusks, insects, and crustaceans, with larger individuals shifting to piscivory (Edds et al. 2002; Eggleton and Schramm 2004). Conversely, Flathead Catfish are almost exclusively piscivorous, even at small sizes (Jackson 1999; Herndon and Waters 2002; Pine et al. 2005). Their piscivorous nature has also earned them a reputation as a dangerous invasive (Fuller et al. 1999), and food-web simulation models have projected up to 50% declines in native fish biomass after Flathead Catfish become established (Pine et al. 2007). Both catfish species can inhabit brackish waters, though Flathead Catfish seem to prefer lower salinity areas, while Blue Catfish routinely inhabit estuarine waters (Bringolf et al. 2005; Schloesser et al. 2011). The diverse food habits of these two non-native catfishes have the potential to impact a multitude of imperiled or commercially-valuable native species including American Shad, river herring, blue crab *Callinectes sapidus*, and American Eel *Anguilla rostrata*. While Blue Catfish and Flathead Catfish have been in the watershed for decades, regional diet information for these species is limited (Schmitt et al. 2017).

Feeding ecology of invasive species.— Food web structure is often altered following an invasion, which can lead to changes in species assemblages and ecosystem function (Mack et al. 2000; Clavel et al. 2010). While invasive species can alter ecosystems in a variety of ways, feeding strategy is a primary determinant for predicting how an invasive will change a given system (Brandner et al. 2012; Garvey and Whiles 2017). In summary, apex predators can restructure food webs through top-down control, herbivores can enhance bottom-up forces by reducing plant biomass, and mid-trophic level species can generate forces in either direction (Simon and

Townsend 2003). Moreover, omnivore-generalist species are capable of restructuring food webs using mechanisms that don't require direct mortality, including competitive interactions and other indirect effects, particularly in bottom-up controlled systems (van Riel et al. 2006; Garvey and Whiles 2017). Unfortunately, the Chesapeake Bay is now home to hundreds of exotic species at a variety of trophic levels, which can complicate species-level analyses (Mooney and Cleland 2001; Ruiz and Reid 2007); consequently, native species might be affected by top-down forces, bottom-up forces, or a combination of the two (Keeler et al. 2006). In essence, catfish diet analysis will provide evidence of what is being eaten and can provide information on which native species are most likely to be affected by these invasive species through herbivory, predation, or competition.

Feeding strategy analysis can also help predict whether or not an invasive species will have lasting impacts on an ecosystem (Moyle and Light 1996). Generalist species are most likely to be successful long-term invaders within degraded or disturbed systems (Clavel et al. 2010), which has implications within the Chesapeake Bay watershed, as it has a long history of pollution and anthropogenic disturbance (Boesch et al. 2001). For freshwater fish invasions, piscivores are most likely to cause long-term ecological changes while omnivore/detritivores are least likely to do so; however, this is not without exception (Moyle and Light 1996). The situation with Blue Catfish may be particularly confusing, as they have been demonstrated to be herbivores, detritivores, and piscivores within their native range (Edds et al. 2002; Eggleton and Schramm 2004), and literature pertaining to large, invasive fishes within estuaries is limited.

Are Blue Catfish “invasive”? — Introductions of non-native fishes are a growing concern for fisheries managers as they can threaten native aquatic biodiversity and alter food web dynamics (Jelks et al. 2008). Conversely, many freshwater fish introductions have been demonstrated to

have minimal ecological impacts while providing benefits to society (Gozlan 2008). The attention the Blue Catfish has received as an “invasive” in Virginia waters has been the center of much controversy, as the James River now supports a nationally-recognized trophy fishery, which financially supports numerous guides and tackle shops. In addition, Blue Catfish support viable commercial fisheries in several of Virginia’s tidal rivers and harvest has been increasing steadily since the early 2000’s (VMRC 2010, *cited in* Schloesser et al. 2011). The establishment of Blue Catfish in Virginia’s tidal rivers has had a polarizing effect and has resulted in much controversy, as many rely on this resource for their livelihood. While some argue that all non-native fish introductions should be considered “guilty until proven innocent” (Simberloff 2007), others insist that conclusions pertaining to the impact of non-natives should be based on “quantifiable empirical evidence and not *a priori* statements” (Gozlan 2008).

Defining an invasive species is not as straightforward as you would think. Definitions of “invasive” vary broadly, and definitions are inconsistent even among the invasion scientists (Valéry et al. 2008; Heger et al. 2013). The U.S. government defines an invasive species as an introduced organism that results in “harm, either to the environment, to the economy, or to human health”. Moreover, for a species to be considered invasive, the negative impacts associated with it must outweigh any benefits that it provides (ISAC 2006). Many ecologists have adopted a broader definition, and consider an organism “invasive” if its population is reproducing and expanding geographically from its point of introduction (Lockwood et al. 2013). Management agencies; however, generally adhere to an impact-based definition (Simberloff 2003).

For definitions based on impact, further complications arise from differing interpretations or from inconsistencies in underlying value systems (Russell and Blackburn 2017). Furthermore,

scientific uncertainty regarding impact is often inevitable, opening the door for more debate (Russell and Blackburn 2017). While intellectual debate is welcomed and often results in scientific progress, “denialism” has been a prevalent societal response to invasive species in recent years. Science denialism differs from debate in that “deniers” completely disregard scientific evidence, while scientific debate generally focuses on uncertainty associated with scientific discovery (Russell and Blackburn 2017).

Blue Catfish narrative in Chesapeake Bay. — On the other end of the spectrum, society can overreact to introduced species through different forms of “xenophobia”, where public response is characterized by panic, sensationalism, and irrational rhetoric (Peretti 1998; Sagoff 1999; Subramaniam 2001). For example, Verbrugge et al. (2016) reported that numerous metaphors (e.g. ‘explosive growth’) are used in narratives examining science, policy, and management of invasive species. While metaphors such as ‘invasional meltdown’ and ‘nateness’, may expedite change and create a sense of urgency, there is always the risk that these metaphors will replace science in informing policy (Orth et al. 2017). Furthermore, the use of ‘nateness’ and ‘invasiveness’ metaphors can result in automatic management positions that are not necessarily supported by scientific evidence. Jumping to conclusions without supporting evidence is the antithesis of the scientific method, and should be avoided.

The narrative surrounding Blue Catfish in Chesapeake Bay played developed in the press and social media far ahead of any evidence of impact (Orth et al. 2017). Blue Catfish have been vilified, and most of the media’s coverage of this animal has been filled with hyperbole and alarmist narratives. Newspapers have made wild claims like “behind pollution, Blue Catfish are the biggest threat to the Chesapeake Bay” and “the Blue Catfish is one of the greatest environmental threats the Chesapeake Bay has ever faced” (Springston 2015), with no

supporting evidence. Many more examples of emotional rhetoric and negative language exist. For example, Harper (2010) wrote “up close and in person, Blue Catfish are gruesome creatures. They grow big and ugly and grey. They croak like pigs. And because they have no scales, they are especially slimy, even as fish go”. Other examples include bold (and often incorrect) claims about the feeding ecology and trophic position this species. Springston (2015) stated that “Blue Catfish live at the top of the food chain and eat everything that can fit into their huge mouths” and are “Bengal tigers of the Chesapeake”, while Carman (2017) said they have “black hole like mouths… are vacuuming up whatever gets in their way”. Our diet work demonstrates that much of this is hyperbole.

There is clearly a disconnect between science and the media, and efforts should be made to improve communication in the future. Much of the public relies on the media as their primary information source, therefore this lack of communication can be dangerous. The public is a key player in the invasion process and invasive species management (Pasko and Goldberg 2013; Carballo-Cárdenas 2015), making invasion science both a sociologic and scientific endeavor. Science communication is inextricably linked to public perception of invasive species risk, and scientists often fail to communicate clearly or don’t communicate at all. Scientists should make more intentional efforts to communicate effectively with policy makers, the media, and the public moving forward (Gozlan et al. 2013).

Invasive species: drivers or passengers of change? — While the negative impacts of invasives have been well documented worldwide, the high co-occurrence of invasive species and anthropogenic disturbance (e.g. habitat destruction or degradation) make it difficult to distinguish which mechanism is driving observed ecosystem changes (MacDougal and Turkington 2005). Some have suggested that the success of many invaders is due to their ability

to cope with adverse conditions, and that they are just symptoms of underlying ecological problems (MacDougal and Turkington 2005; Layman and Allgeier 2011). This theory is supported by worldwide declines of specialist species, which have been unable to adapt to changing conditions (Clavel et al. 2010). Specialists are being replaced by generalist species, which can adapt to a variety of adverse conditions, and global replacement is occurring at an alarming rate (McKinney and Lockwood 1999; Olden et al. 2004; Clavel et al. 2010). Successful generalists typically have broad diets, are tolerant of a variety of environmental conditions, disperse rapidly, and have high fecundity (McKinney and Lockwood 1999). Blue Catfish have been demonstrated to be successful across broad spatial scales and in a variety of habitats; moreover, they are a highly mobile, migratory catfish that can make seasonal migrations in excess of 500 km (Graham 1999). Blue Catfish have generalist food habits within their native range (Edds et al. 2002; Eggleton and Schramm 2004), and have higher fecundity and larval hatching success than other Ictalurids (Graham 1999). Considering these attributes, the success of Blue Catfish within the Chesapeake Bay may be due to their ability to adapt to adverse conditions. If this is the case, it would be prudent to address the underlying cause(s), rather than simply attempting to control the species (Didham 2007).

Predicting long-term ecological impacts. —While the ecological impact of these catfishes is largely unknown, concern about these species is well-justified. In a review of case studies pertaining to introduced fish species, Moyle and Light (1996) were able to make several generalizations. First, piscivores, omnivores, or detritivores are the most likely to be successful invaders; second, introduced piscivores are more likely to alter the native fish community than omnivores or detritivores. Additionally, the authors claim that long-term success and integration of nonnatives is more likely in aquatic systems that are continually disturbed by anthropogenic

activities. All of these generalizations are concerning as Flathead Catfish and Blue Catfish can act as detritivores, omnivores, and/or piscivores, and the Chesapeake Bay is far from pristine, having a long history of anthropogenic disturbance (Graham 1999; Jackson 1999; Kemp et al. 2005). Ultimately, characterizing the trophic role of these nonnative catfish and their position in the generalist-specialist feeding continuum is of utmost importance for predicting their impact on food web structure, and will help explain their incredible success in the Chesapeake Bay region.

Research Gaps

Previous studies have provided valuable insight in the feeding ecology of Blue Catfish in the Chesapeake Bay, yet have been unable to capture a thorough understanding of how Blue Catfish diet changes with fish size, time of year, and spatial location. This will be important for assessing the trophic impact of this species, as Blue Catfish are known to exhibit ontogenetic diet shifts (Edds et al. 2002), and fish assemblages are known to change temporally and spatially within the Chesapeake Bay (Wagner 1999; Jung and Houde 2003). To date, no studies have explored Blue Catfish diet across broad spatiotemporal scales within the Chesapeake Bay. MacAvoy et al. (2000) used stable isotope analysis to ascertain that Blue Catfish may be preying upon alosine species, yet this study was limited by a small sample ($N=22$) from one stretch of the Rappahannock River and prey items were not identified to species. Schloesser et al. (2011) provides a more thorough description of the food habits of Blue Catfish in Virginia's tidal rivers, though specimens were only captured in mesohaline portions of the James, Rappahannock, and York drainages, which is problematic because Blue Catfish inhabit freshwater, tidal freshwater, and oligohaline portions of these rivers (Greenlee and Lim 2011). Because fish were captured via trawl, the Schloesser et al. (2011) study included only small fish (<590 mm FL), which is problematic because Blue Catfish regularly exceed 1000 mm FL. Given these knowledge gaps,

there is still a need to assess spatiotemporal and size-based differences in the food habits of Blue Catfish in Chesapeake Bay tributaries.

Objectives and Products

The current study has provided four major pieces of information. First, we quantified predation and prey selectivity by Blue Catfish and Flathead Catfish on *Alosa* species during the spring spawning migration (Chapter 2). This is important as American Shad, Blueback Herring, and Alewife once supported major fisheries along the Atlantic coast, yet have reached historic lows (Limburg and Waldman 2009). Predation has been implicated in contributing to these declines (Savoy and Crecco 2004; Hasselman and Limburg 2012), and stable isotope analysis suggested that Blue Catfish were feeding heavily on them (MacAvoy 2000). Next, we described the diet of Blue Catfish across broad spatiotemporal scales and quantified how Blue Catfish diet varies with season, salinity, and fish size (Chapter 3). We also estimated the trophic position, diet breadth, and feeding strategy of Blue Catfish in the Chesapeake Bay using trophic level estimates, omnivory indices, diet breadth indices, and predator feeding strategy diagrams. In addition to providing valuable information about the feeding ecology of these fish, it provides an understanding of where this species resides along the generalist-specialist continuum, and may provide insight into their remarkable success in the Chesapeake Bay. Next, we constructed statistical models to explore the major drivers of Blue Catfish diet and quantify predation of species of concern, including alosines, blue crab, and American Eel, which are species of management concern (Chapter 4). Finally, we quantified Blue Catfish consumption rates using a combination of field experiments, laboratory experiments, and regression models (Chapter 5). These estimates have been integrated with diet information and biomass estimates to quantify predation ($\text{kg}^*\text{yr}^{-1}$) of imperiled or commercially-valuable species (Orth et al. 2017).

Methods Overview

- 1) Chapter 2: Predation and prey selectivity by non-native catfish on migrating alosines in an Atlantic slope estuary
 - a. Quantify predation of river herring and American Shad by non-native Blue Catfish and Flathead Catfish during March, April, and May within freshwater, tidal freshwater, oligohaline, and mesohaline sections of the James River.
 - b. Use cumulative prey curves to assess sample size sufficiency.
 - c. Use advanced molecular techniques (DNA barcoding) to increase the taxonomic resolution of unidentifiable, digested fish prey.
 - d. Quantify prey selectivity by Blue and Flathead Catfish by comparing the percent occurrence of fish prey in stomachs to the relative abundance of fish prey within the river.
 - e. Use logistic regression analysis to predict occurrence of *Alosa* species in the diet as it varies by month and spatial location.
- 2) Chapter 3: Feeding Ecology of Generalist Consumers: a Case Study of Invasive Blue Catfish *Ictalurus furcatus* in the Chesapeake Bay, Virginia, USA
 - a. Employ a stratified random sampling design to explore patterns of prey consumption across broad spatiotemporal scales within the James, Pamunkey, Mattaponi, and Rappahannock Rivers.
 - b. Develop cumulative prey curves to assess sample size sufficiency.
 - c. Use DNA barcoding to increase the taxonomic resolution for unidentifiable fish prey
 - d. Use logistic regression analysis to identify ontogenetic shifts to piscivory by comparing the binary occurrence of fish in the diet versus fish total length for each river.
 - e. Estimate diet breadth, trophic level, omnivory index for Blue Catfish in each of Virginia's tidal rivers as it varies with fish total length.
- 3) Chapter 4: Modeling the Predation Dynamics of Invasive Blue Catfish in the Chesapeake Bay: A Special Focus on Imperiled and Commercially-Valuable Native Biota
 - a. Use multivariate ordination to assess the major drivers of variation in Blue Catfish diet (CCA) in Virginia's tidal rivers
 - b. Develop statistical models to better understand factors contributing to the consumption of "species of concern", which include American Shad, river herring, American Eel, and blue crab (Generalized Additive Models).

- 4) Chapter 5: Multiple approaches used to estimate daily ration and food consumption rates for invasive Blue Catfish *Ictalurus furcatus* in Atlantic Slope tributaries
- a. Use field methods (diel feeding chronologies) to estimate daily ration (C_{24}) and maximum daily ration (C_{\max}) for Blue Catfish within the James, Pamunkey, Mattaponi, and Rappahannock rivers.
 - b. Use a series of laboratory experiments to quantify how C_{\max} varies with temperature, fish size, and prey type.
 - c. Use an empirical regression model (Palomares and Pauly 1998) to estimate consumption to biomass ratios (Q/B) for Blue Catfish based on mean annual water temperatures, growth, mortality, and aspect ratio of the caudal fin.

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Chapter 2: Predation and Prey Selectivity by Nonnative Catfish on Migrating Alosines in an Atlantic Slope Estuary

Introduction

Introduced species are a growing concern for fisheries managers as they can suppress native species, alter food web dynamics, and threaten biodiversity (Moyle and Light 1996; Jelks et al. 2008). Many introduced species cause serious declines in the abundance or diversity of native species, and may cause substantial economic harm (Folkerts 1999). Habitat degradation and introduced species are major drivers of ecosystem change, yet high correlation between the two makes it difficult to distinguish which is causing the observed changes (Macdougall and Turkington 2005; Light and Marchetti 2007). The question often remains whether an invasive species was the driver of change, or merely the passenger of human-mediated changes such as pollution, habitat degradation and fragmentation, and/or climate change (Macdougall and Turkington 2005; Light and Marchetti 2007).

Blue Catfish *Ictalurus furcatus* and Flathead Catfish *Pylodictis olivaris* are both large, long-lived species that can weigh in excess of 50 kg and can live for over 25 years (Graham 1999; Jackson 1999). Blue Catfish are native to the Mississippi drainage with populations extending southward into Mexico and Central America (Graham 1999). Flathead Catfish are native to the Mississippi, Rio Grande, and Mobile drainages with native populations also found in northeastern Mexico and the Great Lakes region (Jackson 1999). Both catfish species have been widely introduced outside of their native range, and are now found in several Atlantic and Pacific drainages (Graham 1999; Jackson 1999).

Blue Catfish were introduced into Virginia tributaries of the Chesapeake Bay during the 1970s and 1980s (Jenkins and Burkhead 1994), a time when many fisheries had collapsed or were on the brink of collapse (Smith 1985; Rothschild et al. 1994; Richards and Rago 1999). Blue Catfish populations have since expanded, and the species now dominates the ichthyofaunal biomass in certain areas (Greenlee and Lim 2011). They are now found within every major tributary of the Chesapeake Bay, and have been captured in salinities as high as 14.7 ppt (Schloesser et al. 2011). Their ability to thrive in brackish habitats has allowed Blue Catfish to spread downriver into oligohaline and mesohaline areas (Schloesser et al. 2011) where electrofishing capture rates have been as high as 6,000 fish/hr (Greenlee and Lim 2011).

Flathead Catfish were originally introduced to the James River, but are now established in the James, Potomac, and Susquehanna drainages (Jenkins and Burkhead 1994; Brown et al. 2005; Orrell and Weigt 2005). We have also captured several juvenile and mature individuals (N=22) from the York River, where Flathead Catfish had previously been undocumented (*personal observation*). Both catfish species are accustomed to foraging in the muddy rivers of their native range, and are well-adapted to life in the present day Chesapeake Bay, which has been transformed into a turbid, nutrient-rich system by agricultural runoff and other anthropogenic disturbances (Boesch et al. 2001).

Blue Catfish are omnivorous, often consuming vegetation, mollusks, insects, and crustaceans, with larger individuals shifting to piscivory (Edds et al. 2002; Eggleton and Schramm 2004). Conversely, Flathead Catfish are almost exclusively piscivorous, even at small sizes (Jackson

1999; Herndon and Waters 2002; Pine et al. 2005). Flathead Catfish have earned respect and admiration from anglers and biologists, mostly for their size, strength, and predatory aggressiveness (Jackson 1999). Their piscivorous nature has also earned them a reputation as a dangerous invasive (Fuller et al. 1999) and food-web simulation models have projected up to 50% declines in native fish biomass after Flathead Catfish are established (Pine et al. 2007). Both catfish species can inhabit brackish waters, though Flathead Catfish seem to prefer lower salinity areas, while Blue Catfish routinely inhabit estuarine waters (Perry 1969; Bringolf et al. 2005; Schloesser et al. 2011). The diverse food habits of these two non-native catfishes have the potential to impact a multitude of imperiled or commercially-valuable native species including American Shad *Alosa sapidissima*, Alewife *A. pseudoharengus*, Blueback Herring *A. aestivalis*, Blue Crab *Callinectes sapidus*, and American Eel *Anguilla rostrata* (Haro et al. 2000; Lipcius and Stockhausen 2002; Limburg and Waldmen 2009).

A major question has been whether introduced catfish are preying heavily upon depleted anadromous clupeids including river herring (Blueback Herring and Alewife) and American Shad, which once comprised major fisheries along the Atlantic coast (Hall et al. 2012; Bethoney et al. 2013). These anadromous clupeids, collectively known as alosines, spend much of their life at sea, but return to freshwater portions of Virginia's tidal rivers every spring to spawn (Garman 1992). The dramatic declines in the abundance of these species has been observed over recent years (Limburg and Waldman 2009), and, despite ongoing restoration efforts, these species have declined to all-time lows across much of their range (Hasselman and Limburg 2012). Several possible causes have been implicated for observed stock declines, including overfishing, habitat loss, climate change, barriers to migration, and predation (Hall et al. 2012; Bethoney et al. 2013;

Brown et al. 2013). While predation is likely only a part of a bigger problem, the presence of introduced catfish within key migratory pathways may hinder alosine restoration efforts.

Previous studies have provided valuable insight into the feeding ecology of Blue Catfish within the Chesapeake Bay, yet have been unable to quantify predation of alosines by introduced catfish. Stable isotope analysis (MacAvoy et al. 2000) suggested that marine-derived nutrients contribute to the diet of Blue Catfish, yet this study was limited by a very small sample from one location on the Rappahannock River ($N = 22$). Schloesser et al. (2011) provides a more thorough description of the food habits of Blue Catfish in Virginia's tidal rivers, though this study was limited to oligohaline and mesohaline portions of Virginia's tidal rivers and captured primarily small fish (≤ 600 mm fork length [FL]). This is problematic because Blue Catfish regularly grow much larger (> 1000 mm FL), and larger fish are more likely to be piscivorous (Edds et al. 2002). Information on Flathead Catfish is scarce within the scientific literature, and there are no published diet descriptions for this species within the Chesapeake Bay. Moreover, there have been no targeted efforts to quantify Blue Catfish or Flathead Catfish predation of *Alosa* species during their spring spawning migration in any Atlantic slope drainage.

We focused our research to answer the following specific questions: First, what are Blue Catfish and Flathead Catfish eating during the spring; do alosines contribute to their diet? Second, are these non-native catfish selectively feeding on alosines or are they preying on them in proportion to their relative abundance in the environment? Third, how does alosine predation vary spatially and temporally during the spring?

Methods

Sampling efforts were focused within the James River because it supports dense populations of large Blue Catfish and Flathead Catfish (Harris and Jones 2008; Greenlee and Lim 2011) and once supported large *Alosa* migrations (Aunins and Olney 2009; Hilton et al. 2011). Blue Catfish and Flathead Catfish were collected in the James River from March – May, as these months correspond with the spring spawning movements of Blueback Herring, Alewife, and American Shad within the Chesapeake Bay (Garman and Nielsen 1992; Hewitt et al. 2009; Hilton et al. 2011). The majority of sampling was conducted in 2015, though some fish were collected during the spring of 2014.

Collection of specimens.— Electrofishing was used to collect catfish, as it collects both active and inactive fish (Bowen 1996). Low-frequency electrofishing is the preferred method for sampling Blue Catfish, yet it is ineffective until waters warm to 18° C and becomes optimal at temperatures > 22° C (Justus 1994; Bodine and Shoup 2010). Water temperatures did not reach 18° C until late May, so high frequency electrofishing (60 hz; 325 volts; 12 amps) was used to collect catfish during March, April, and most of May. High frequency electrofishing is limited to shallow water habitat and is much more time intensive than low frequency electrofishing. Given this constraint, early spring sampling efforts focused on areas shallow enough for the gear to work, typically < 2 m deep (Justus 1994). Sampling was slow, and usually only one or two fish were collected up at a time, often hundreds of meters apart. Sampling during these months occurred in several areas known to contain alosines during their spawning migration. Hundreds of sites were sampled in non-tidal freshwater (tailwaters of Bosher Dam and the area near the Manchester Bridge), tidal freshwater, and three tidal estuarine creeks (Figure 1). The primary

sampling stretch, where most sampling occurred, extended from the bottom of the fall line in Richmond to the Dutch Gap Conservation Area, as *Alosa* species are known to congregate in this stretch during the spring. This primary sampling stretch was divided into 500 m sections, numbered, and a random number generator was used to select sampling locations. Additional sites were located in brackish tributaries of the James River (Herring Creek, Wards Creek, and Gordon Creek), which are also known to contain alosines during the spring (Figure 1). Herring Creek, Wards Creek, and Gordon Creek are all either oligohaline or mesohaline, with recorded salinities ranging from 1.0 ppt – 10.0 ppt. Each major sampling area was sampled, at a minimum, once per week from March 1st through May 31st.

Low-frequency electrofishing was used once water temperatures warmed to 18° C (late May), allowing us to sample fish in deeper water (> 3 m); however, very few fish were encountered in deep water and none had prey items present in their stomachs. Upon capture, diet contents were extracted by sacrificing the fish or with pulsed gastric lavage, which has been demonstrated to be very effective for extracting diet contents from Blue Catfish and Flathead Catfish (Waters et al. 2004). Stomach contents were extracted within 30 minutes of capture, and time, water temperature, tide phase, and coordinates were recorded for each sampling event. Fish total weight and length were also recorded and diet contents were placed on ice and later frozen. In the laboratory, prey items were thawed, weighed, counted, and identified to the lowest possible taxon.

Molecular identification of fish prey.— Partially-digested fish prey that are unrecognizable by gross morphology represent a major obstacle for diet studies, often resulting in the loss of

important information (Dunn et al. 2010; Carreon-Martinez et al. 2011). Previous studies have demonstrated that empty stomachs are common and fish prey are rare within Blue Catfish stomachs (Schloesser et al. 2011), emphasizing the importance of properly identifying fish remains when trying to quantify predation of rare species. Further, some species digest at a quicker pace than others, which can lead to erroneous conclusions about the relative importance of these prey items when digestion has rendered them unidentifiable (Hyslop 1980). Known as differential digestion, this phenomenon has also been demonstrated to impact conclusions pertaining to selectivity and electivity (Ivlev 1961). To mediate this potential bias, we utilized advanced molecular techniques to identify partially digested fish using the methods described in Moran et al. (2015).

Prior to lysis, samples were defrosted and rinsed with ethanol. Utensils were sterilized using 10% bleach mixture then rinsed with autoclaved deionized water and allowed to dry. A 10 mm x 10 mm piece of tissue was excised and transferred to a sterilized microcentrifuge tube using sterilized utensils. Next, 180 µL of digestive solution was transferred to each microcentrifuge tube along with 20 µL of Proteinase K. Samples were then incubated at 56° C to allow for proper lysis. Manual extraction was conducted using protocols listed in a DNeasy blood & tissue kit (Qiagen, Hilden, Germany).

Blue and Flathead Catfish prey upon many species of fish, so universal CO1 primers were selected that would amplify DNA for all fish within the Chesapeake Bay. DNA sequences for the mitochondrial CO1 gene were amplified using a cocktail of four fish primers (FishF2_t1, FishR2_t1, VF2_t1, and FR1d_t1) developed for the CO1-3 region (Ivanova et al. 2007).

Polymerase chain reaction (PCR) amplifications also followed the protocol of Ivanova et al. (2007), with minor modifications. PCR had a total volume of 12.5 µL, which included 6.25 µL of 10% trehalose, 2.00 µL of ultrapure water, 1.25 µL 10 x PCR buffer (10 mM KCl, 10 nM (NH₄)₂SO₄, 20 mM Tris-HCl (ph 8.8), 2 mM MgSO₄, and 0.1% Triton X-100), 0.625 µL MgCl₂ (50 mM), 0.125 µL of each primer (0.01 mM), 0.0625 µL of each dNTP (10 mM), 0.0625 µL of Taq DNA Polymerase (New England Biolabs, Ipswich, Massachusetts) and 2.0 µL of DNA template (mean conc. 74 µg/mL). PCR was conducted on a BIO-RAD MyCycler with the following thermocycline conditions: initial denaturation at 94° C for 2 min, followed by 35 cycles of 94° C for 30 s, 52° C annealing temperature for 40s, 72° C for 1 min, with a final extension step at 72° C for 10 min. PCR reaction products were sequenced using BigDye Terminator Cycle Sequencing Kit v 3.1 on an ABI3730 DNA sequencer. Sequencing reactions were initiated using the C_FishF1t1 or C_FishR1t1 primers of Ivanova et al. (2007) and sequenced samples were analyzed using Bioedit and raw sequences edited in Sequencher v4.5 (Gene Codes Corporation, Ann Arbor, Michigan). Edited samples were then identified using the Basic Local Alignment Search Tool (BLAST) from the National Center for Biotechnology Information website. Possible species were determined based on high quintile scores from % identification, % query cover, and maximum identification score as references.

Selectivity of fish prey.— Selectivity indices compare the relative abundance of prey in the environment to the frequency of occurrence in the diet (Chipps and Garvey 2007). Relative fish prey abundance was assessed on the James River during April and May of 2015, using high-frequency, pulsed DC electrofishing (60 hz; 30% duty cycle; ≈300 volts). Relative prey abundance was estimated at 60 randomly selected locations (30 per month) within the primary

sampling stretch (see above), utilizing three 120 s electrofishing passes at each site. Many selectivity studies have used depletion methods to estimate population sizes for prey species, yet these methods can be inherently biased, often leading to erroneous conclusions (Peterson et al. 2004). A simpler approach is to estimate the relative abundance of each prey species, which is often more pragmatic (Link 2004). These methods still assume equal capture probabilities for the different prey species. This assumption is reasonable as electrofishing has been demonstrated to be effective for estimating multispecies relative abundance in lotic habitats (Edwards et al. 2003).

Data analysis

Sample size sufficiency.— Cumulative prey curves, or rarefaction curves, were used to assess whether our sample size was sufficient to describe the food habits of Blue and Flathead Catfish during the spring. Cumulative prey curves plot the total number of unique taxa in the diet vs. the total number of stomachs analyzed, and sample size is considered sufficient once the curve reaches an asymptote (Ferry and Cailliet 1996). We computed rarefaction curves and associated 95% confidence intervals with EstimateS (version 9.1, R. K. Colwell, Boulder, Colorado), where the cumulative number of unique prey taxa were plotted against the randomly pooled samples. This random process was repeated 500 times to generate means and associated confidence intervals. We used the slope (B) of the last four subsamples (linear regression) as an objective criterion for sample size sufficiency, where sample size is considered sufficient when $B \leq 0.05$ (Bizzarro et al. 2009; Brown et al. 2012).

Ontogenetic diet shifts.— Blue Catfish often exhibit dietary ontogenies, shifting from omnivory to piscivory as they grow (Edds et al. 2002; Eggleton and Schramm 2004). Understanding the size at which this switch occurs in the James River is important, as smaller fish are unlikely to

prey upon native fish species. To assess ontogenetic shifts in the diet of Blue Catfish, prey items were placed into logical ecological groupings (vegetation, invertebrates, mollusks, crustaceans, fish, and miscellaneous) and catfish were grouped by 100 mm length class. Percent weight indices were used to determine the length at which Blue Catfish switch to piscivory. Logit and arcsine transformations of %W data failed to satisfy parametric assumptions, so transformations were abandoned and nonparametric methods were used (Cortes 1997; Zar 1999; Warton and Hui 2011). Kruskal-Wallis analysis of variance (ANOVA) tests were used to determine if predator length significantly influenced the percent weight of the major prey categories (Zar 1999). If significant differences were detected, *post hoc* Tukey's multiple comparisons on ranks were used to determine the length(s) at which diet shifts occurred (Conover and Iman 1981). Statistical significance was evaluated at the 95% level ($\alpha = 0.05$).

Diet composition.— Prey importance was assessed using both single and compound indices. Gravimetric percent by weight (%W) indices were used to determine which prey items were nutritionally valuable while percent occurrence (%O) indices were used to determine which prey items were routinely utilized at the population level (MacDonald and Green 1983). Compound indices were also used as they provide a more balanced understanding of the dietary importance of different prey (Pinkas et al. 1971; Bigg and Perez 1985; Cortes 1997; Brown et al. 2012). The traditionally used Index of Relative Importance (IRI) is inherently flawed, as it combines mathematically dependent measures (Ortaz et al. 2006). Because of this, frequently occurring prey items are overemphasized while rare prey items are underemphasized (Brown et al. 2012). Given these concerns, we decided to use the prey-specific index of relative importance (PSIRI;

Brown et al. 2012). Percent PSIRI values were used to estimate the difference in the importance of different food sources. Percent PSIRI is defined as:

$$\%PSIRI_i = \frac{\%FO_i \times (\%PN_i + \%PW_i)}{2}$$

Where %FO_i is the frequency of occurrence for prey type “i”, %PN_i is the percent by number of prey type “i” in all stomachs containing prey type “i”, and %PW_i is the percent by weight of prey type “i” in all stomachs containing prey type “i”.

Spatiotemporal effects.— Understanding the spatial variability in predation of *Alosa* species will be important for future control strategies of non-native catfish, so logistic regression analysis was used to determine whether sampling location or month could predict the occurrence of American Shad, Blueback Herring, or Alewife in the diet. Logistic regression was used as it does not have assumptions of normality or homoscedasticity; furthermore, it is useful for describing relationships between a dichotomous outcome variable and one or more categorical descriptor variables (Peng et al. 2002). Logistic regression was performed using a Generalized Linear Model with a logit link function and a binary error distribution (Goodnight 1982) which took the general form of:

$$\text{logit}(p_{Alosa}) = \log\left(\frac{p_{Alosa}}{1-p_{Alosa}}\right) = \beta_0 + \beta_1 X_1 + \dots + \beta_j X_j$$

Where p_{Alosa} is the probability of that an individual has an alosine in their stomach, β₀ is the intercept, β₁, β₂, ... β_j are coefficients of spatiotemporal factors (month, spatial location) and X₁, X₂, ... X_j are the variables of spatiotemporal factors. Statistical significance was evaluated at the 95% level ($\alpha=0.05$).

Prey selectivity.— Many different selectivity indices exist, none of which satisfy all statistical criteria (Chipps and Garvey 2007). We used Chesson's index, as it is recommended for most situations and has previously been used to describe feeding selectivity of non-native Flathead Catfish in North Carolina (Baumann and Kwak 2011). Chesson's α was determined for separately for Blue and Flathead Catfish during April and May, and was calculated for individual prey species as:

$$\alpha_i = \frac{r_i / p_i}{\sum_{j=1}^m (r_j / p_j)},$$

where r_i is the percent occurrence of a fish species in the diet, p_i is the proportion of that fish species available in the system, while r_j and p_j are those values for all fish species, and m is the number of fish taxa available in the system, based on relative abundance sampling. Percent occurrence was calculated as the number of Blue Catfish with a given fish taxa in the stomach divided by the total number of stomachs containing fish. Relative prey abundance, or the proportion of the available prey field, was calculated as the mean proportion of a fish species per sampling event (Juanes et al. 2001; Link 2004). Selectivity values were calculated for individual prey species using stomachs from catfish captured within the same sampling stretch during the same time (April and May). The index ranges from 0 to 1, with completely random feeding occurring at $1/m$, where m is the total number of prey types found during sampling. Prey items with Chesson's α values greater than the random feeding value were “selected”, while prey items with Chesson's α values that were less than random feeding were “not selected” (Chesson 1978). Our selectivity analysis focused on *Alosa* species and those species that were consumed by catfish and were found during relative abundance sampling. Only species found in multiple

stomachs ($N > 1$) were analyzed, as inclusion of rare prey can be problematic (Confer and Moore 1987).

Results

Stomach contents were extracted from a total of 2,495 catfish during March, April, and May. Blue Catfish ($N=2,164$) were more commonly encountered than Flathead Catfish ($N=331$), though Flathead Catfish had a larger average size (Figure 2). High frequency electrofishing enabled the capture of many larger fish, with 30.41% of Blue Catfish ($N= 658$) and 87.31% of Flathead Catfish ($N= 289$) exceeding 600 mm TL. Of the catfish collected, prey items were found in 1,539 Blue Catfish stomachs (71.12%) and 204 Flathead Catfish stomachs (61.63%).

Sample size sufficiency.— Cumulative prey curves for both Blue Catfish and Flathead Catfish achieved slopes (B) of less than 0.05 ($B= 0.02$ and $B=0.01$, respectively), indicating adequate sample size for diet description (Brown et al. 2012; Figure 3). Sample size requirements were much greater for Blue Catfish, as they ate a broader array of prey species than Flathead Catfish (approximately 50 prey taxa vs. 20 prey taxa), and the Blue Catfish prey curve required over 1,000 stomachs to reach a sufficient asymptote.

Ontogenetic shifts —. Flathead Catfish were exclusively piscivorous, so ontogenetic shifts were not analyzed. Smaller Blue Catfish relied heavily on vegetation, mollusks, and invertebrates, while larger fish began to include more fish in their diet (Figure 4). Length-specific analysis indicated a significant ontogenetic shift (K-W test; $P < 0.01$), and *post hoc* testing indicated a significant increase in piscivory at 500 mm TL (Tukey's HSD on ranks; $P < 0.01$; Figure 4).

Diet composition. — Blue Catfish exhibited a broad diet consisting of insects, vegetation, mollusks, crustaceans, reptiles, amphibians, fish, birds, mammals, cnidarians, and anthropogenic debris (Table 1). Smaller Blue Catfish mostly consume vegetation, detritus, mollusks, and other invertebrates. Blue Catfish > 500 mm TL become more piscivorous, but still feed on crustaceans, mollusks, and vegetation (Figure 4). It is important to note that while Blue Catfish were far more abundant than Flathead Catfish, the Blue Catfish population is largely comprised of small individuals (\leq 500 mm TL), and the difference in the relative abundance of Flathead Catfish versus larger, piscivorous Blue Catfish (>500 mm TL) was less substantial (Figure 2).

Many species of fish were consumed by Blue Catfish (Table 2), yet only a few species were consumed regularly. When looking at the population as a whole, Gizzard Shad *Dorosoma cepedianum* were the dominant fish prey consumed by Blue Catfish in terms of %W and %O (Figure 5). Alosines were found in 4.46% of Blue Catfish stomachs during the spring; however, this was mostly Hickory Shad *Alosa mediocris*, which was found in 1.17% of Blue Catfish stomachs. American Shad, Alewife, and Blueback Herring were all found in less than 1% of Blue Catfish stomachs. Blue Catfish also preyed upon American Eel, White Perch *Morone americana*, *Lepomis* species, and members of Cyprinidae and Ictaluridae (Figure 5). While DNA barcoding did enable us to identify some 27 species of fish consumed by Blue Catfish (Table 2), unidentifiable fish bones were still routinely encountered in catfish stomachs during the spring (Figure 4). When looking at larger, piscivorous Blue Catfish (>500 mm TL), fish were consumed more frequently, and Gizzard Shad (33.92%) and White Perch (7.73%) were the dominant prey consumed in terms of percent occurrence (Table 2). Hickory Shad were the most

commonly consumed *Alosa* species for large Blue Catfish in terms of percent occurrence (4.99%), followed by Blueback Herring (2.99%), Alewife (2.49%) and American Shad (0.35%; Table 2).

Unlike Blue Catfish, even small Flathead Catfish were exclusively piscivorous, feeding on several species of fish (Table 3). Flathead Catfish preyed heavily on Gizzard Shad, White Perch, and alosines, which were found in 16.67% of stomachs (Figure 5). While Blue Catfish consumed mostly Hickory Shad, Flathead Catfish consumed mostly Blueback Herring, which were found in 9.31% of stomachs (Figure 4). American Shad and Alewife were found in 1.47% and 2.94% of Flathead Catfish stomachs, respectively.

In terms of relative importance, fish prey were generally more important to Flathead Catfish than to Blue Catfish (Figure 6). Here, we compared piscivorous Blue Catfish (>500 mm TL), to Flathead Catfish, which were exclusively piscivorous. For Blue Catfish, Gizzard Shad were the most important fish prey consumed (PSIRI= 10.19%), while Flathead Catfish relied on Gizzard Shad, White Perch, and *Alosa* species; primarily Blueback Herring. Percent relative importance for all four alosine species was 13.46% for Flathead Catfish and only 0.56% for Blue Catfish (Figure 6), further indicating major differences in the utilization of alosine prey by Blue Catfish versus Flathead Catfish.

Spatiotemporal analysis.— Blue Catfish were sampled at hundreds of sites within five distinct sampling areas: non-tidal freshwater, tidal freshwater, Herring Creek, Wards Creek, and Gordon Creek. Due to numerous rapids and hazardous river conditions, fish from non-tidal freshwater

locations were sampled at dozens of sites in the pool below Bosher Dam and the pool near the Manchester Bridge (Figure 1). Spatial analysis showed a significantly higher occurrence of *Alosa* predation ($\approx 10\%$ occurrence) in these areas, with the majority of these samples coming from the tailwaters of Bosher Dam ($P<0.01$; Figure 7). Occurrence of *Alosa* species in the diets of Blue Catfish within Herring Creek, Wards Creek, Gordon Creek, and tidal fresh areas was generally less than 5% (Figure 7). Temporally, *Alosa* predation was not observed in March, peaked in April, and declined in May. This likely corresponded with the pulse of *Alosa* species through our sample locations, which is driven by a variety of abiotic factors (Tyus 1974; Kissil 1974). Flathead Catfish were only regularly encountered in tidal freshwater and non-tidal freshwater areas and, while more *Alosa* predation (31.82% vs 15.93%) occurred in non-tidal freshwater than in tidal freshwater, the difference was not significant ($P=0.08$; Figure 7). While a few Flathead Catfish ($N=3$) were encountered in oligohaline creeks (Herring Creek and Wards Creek), none of these fish preyed on alosines.

Temporal analysis revealed significant differences in *Alosa* predation during the spring (Figure 8). *Alosa* predation peaked in April and continued into May, while no *Alosa* predation was observed in March. This trend generally corresponded with the relative abundance of *Alosa* species in the environment, which was highly variable, but peaked at $\approx 20\%$ during April (Figure 8).

Selectivity of Fish Prey.— In April, no conclusive selectivity patterns for Blue Catfish were detected (Figure 9). There was positive selectivity of cyprinids and White perch, though 95% confidence intervals overlapped with neutral feeding. In May, Blue Catfish selectively fed on

Hickory Shad, which were commonly encountered during our relative abundance sampling (Figure 9). Blue Catfish also showed selective feeding patterns for *Alosa spp.* (all four species pooled), river herring, and White Perch, but these patterns were inconclusive as 95% confidence intervals overlapped with neutral feeding. Selectivity of American Shad by Blue Catfish was not assessed, as American Shad were only found in one Blue Catfish stomach, and inclusion of extremely rare prey can be problematic in selectivity studies (Confer and Moore 1987).

In April, Flathead Catfish selectively preyed on American Shad (Figure 9). Flathead Catfish also demonstrated inconclusive selective feeding of White Perch, as 95% confidence intervals overlapped with neutral feeding (Figure 9). In May, Flathead Catfish selectively preyed on *Alosa* species, Channel Catfish, Cyprinids, and American Shad (Figure 9). There was inconclusive selectivity of river herring and White Perch, as, again, 95% confidence intervals overlapped with neutral feeding (Figure 9).

Discussion

Blue Catfish and Flathead Catfish had differing food habits during the spring. Blue Catfish had diverse, omnivorous diets indicative of a generalist feeding strategy, while Flathead Catfish fed solely on piscine prey. Differences in food habits were further emphasized by the results from our cumulative prey curve analysis. While cumulative prey curves for both species reached sufficient asymptotes ($B<0.05$), sample size requirements for Blue Catfish were much greater, and the curve did not reach an asymptote until nearly 1,000 stomachs. It is logical that an opportunistic omnivore would have greater sample size requirements than a piscivore, as they consume a much broader array of prey species. While studies on Blue Catfish diet have been published with extremely limited replication (e.g. MacAvoy et al. 2000; N=22), we recommend

the inclusion of cumulative prey curves to assess sample size sufficiency, as inadequate replication can lead to erroneous conclusions (Ferry and Cailliet 1996).

Predation of alosines by Flathead Catfish was concerning, as *Alosa* species were found in up to 30% of stomachs in certain areas. The primary *Alosa* species consumed by Flathead Catfish was Blueback Herring, which were found in nearly 10% of stomachs, and they also consumed American Shad and Alewife, to a lesser degree. Even small Flathead Catfish were piscivorous; this is likely mediated by their huge gape, which is one of the largest of any North American freshwater species (Slaughter and Jacobsen 2008). Because of their voracious feeding habits, Flathead Catfish are already considered to be one of the most ecologically harmful introduced species in the United States (Fuller et al. 1999), and several studies have empirically demonstrated declines in native fish populations following Flathead Catfish introduction (Guier et al. 1984, Ashley and Buff 1988, Thomas 1995, Kwak et al. 2006).

Alternatively, Blue Catfish consumed invertebrates, mollusks, crustaceans, amphibians, reptiles, birds, mammals, anthropogenic waste (including condoms, feminine products, and raw sewage), and nearly 30 taxa of fish. *Alosa* species were only occasionally encountered in Blue Catfish stomachs, and these were primarily Hickory Shad, which are common in Virginia's tidal rivers. Blue Catfish dietary ontogenies revealed a significant shift to piscivory at 500 mm TL, yet even large Blue Catfish rarely consumed alosines. Alewife and Blueback Herring were found in less than 3% of "piscivorous" (>500 mm TL) Blue Catfish stomachs, while American Shad were found in less than 0.50% of stomachs. Blue Catfish have incredibly diverse diets and few selective feeding patterns emerged, thus we would classify them as opportunistic omnivores.

This hypothesis could explain the low occurrence of depleted alosines in Blue Catfish stomachs. If this is the case, future *Alosa* predation by Blue Catfish could still be a problem, as it is likely to increase if alosines begin to recover.

High site-specific variability in the relative abundance of prey yielded broad 95% confidence limits, so few conclusive selectivity patterns emerged. Blue Catfish exhibited no selectivity patterns in April, yet began to selectively feed on Hickory Shad in May. The Hickory Shad we observed in May had already spawned and may have been weakened from rigors of reproduction. While other *Alosa* species would be weakened by the spawn as well, Hickory Shad were the most abundant alosine encountered, which further supports the hypothesis that Blue Catfish are opportunistic feeders. Moreover, observed predation of Hickory Shad may actually be scavenging, as *Alosa* species are susceptible to high levels of post-spawn mortality (Durbin et al. 1979) and Blue Catfish are known to scavenge (Graham 1999).

Flathead Catfish displayed several selectivity patterns. Flathead Catfish selectively consumed American Shad during April and May, though, again, we were unable to discern predation events from scavenging events. It is well known; however, that Flathead Catfish prefer live prey and are less prone to scavenging than other North American Ictalurids (Jackson 1999), thus scavenging is unlikely. We encountered several American Shad in the stomachs of Flathead Catfish, while American Shad were rarely encountered during our relative abundance sampling. Our selectivity analysis assumes equal capture probability for each prey species, which could be problematic, as American Shad are large-bodied, strong swimming fish that generally swim deeper in the water column than other *Alosa* species (Waldman 2013), which may make them less susceptible to

electrofishing gear. If this is the case, selectivity of American Shad by Flathead Catfish may be overstated, yet Flathead Catfish still consumed American Shad more frequently than Blue Catfish. Flathead Catfish also selectively preyed on Cyprinids, mostly Common Carp, and Channel Catfish, neither of which are native to the James River (Jenkins and Burkhead 1994).

Consumption of alosines was rare in estuarine creeks, but increased further upstream in tidal freshwater and non-tidal freshwater areas. The James River from Bosher Dam to the bottom of fall line is full of boulders, rapids, and remnants of old bridges and dams. This complex structure offers numerous ambush points for catfish, and alosine predation was significantly higher here. Alosine predation was particularly high in the tailwaters of Bosher Dam. A lowhead dam originally constructed in 1823, Bosher Dam is found just west of Richmond, VA, and currently serves no major purpose. While a vertical slot fishway was constructed in 1999, it appears that this dam is may be an obstacle to anadromous fish passage, as alosines were consumed more often here, and were found in approximately 10% of Blue Catfish stomachs and 32% of Flathead Catfish stomachs. Seasonally, *Alosa* predation peaked in April and declined in May, while no *Alosa* predation was observed in March. Given this evidence, targeted removal efforts should be focused during early April through the end of May. While removal of non-indigenous catfish from big rivers is probably futile for population control (Bonvechio et al. 2011) and is likely to be met with opposition from special interest groups (Weller and Geihlsler 1999), it could still help mitigate alosine predation in areas that “trap” migrating alosines. If attempted, mitigation efforts should focus on structures that act as barriers to alosine migration, as *Alosa* predation was highest in these areas. We realize that “barriers to migration” is a vague descriptor; therefore,

more research will be necessary to identify these critical areas within the Chesapeake Bay if removal programs are to be attempted.

While Blue Catfish do not appear to be “apex predators” as previously suggested (MacAvoy et al. 2000), introduced generalists are quite capable of replacing native species through biotic homogenization, a process that can cause major changes in community structure and ecosystem function (Olden et al. 2004). Generalists are so capable of replacing natives, in fact, that ecologists often call them “winner” species (Layman and Allgeier 2011), and this recognition has sparked renewed interest in the characterization of generalist species worldwide (Araújo et al. 2011, Bolnick et al. 2011, Clavel et al. 2011, Loxdale et al. 2011). Ecological resistance to invasion is often directly proportional to native species richness, as more native species reduce the available niche space through competition (Lockwood et al. 2013). The incredibly omnivorous nature of Blue Catfish may make them immune to competition, as they can survive on abundant resources (e.g. detritus or vegetation). Flathead Catfish don’t appear to have much competition either, as Virginia’s tidal rivers lack native, large-bodied competitor species, with the exception of the Bowfin *Amia calva* and Longnose Gar *Lepisosteus osseus*. Striped Bass *Morone saxatilis* may also compete with non-native catfish, although the majority of the population is only present in the tidal freshwater portions of Virginia’s rivers during the spring, thus limiting the temporal overlap between these species (Walter and Austin 2003). Neither bowfin nor longnose gar offer much competition for invading catfish. Bowfin specialize in swampy, backwater habitat and only rarely occupy brackish waters (Jenkins and Burkhead 1994), while longnose gar feed on smaller fish like silversides (Atherinopsidae) and are generally unable to prey on fish that exceed 200 mm TL (Tyler et al. 1994). This means that

large non-native catfish are likely the only resident fish capable of consuming 300-400 mm adult Gizzard Shad that dominate the biomass of the James River (Garman and Mitchell 1989).

Predation can also limit the success of invasives (Lockwood et al. 2013), but native fish species are unable to prey on anything but the smallest Blue Catfish or Flathead Catfish, though these catfish are susceptible to avian predation (Glass and Watts 2009). Further, both catfish species have locking defensive pectoral and dorsal spines, and defensive spines have been demonstrated to prevent ingestion of catfish by predators (Bosher et al. 2006). These factors, along with others, have likely played a role in the success of non-native catfish in Virginia's tidal rivers.

While the problems associated with introduced species are well documented, many freshwater fish introductions have minimal ecological impacts with great societal benefits (Gozlan 2008). The attention Blue Catfish have received as an “invasive” species in Virginia waters has been the center of much controversy, as the James River now supports a nationally-recognized trophy fishery which financially supports numerous local guides and tackle shops. In addition, Blue Catfish support viable commercial fisheries in several of Virginia's tidal rivers and harvest has been increasing steadily since the early 2000's (Schloesser et al. 2011). The success of Blue Catfish in Virginia's tidal rivers has had a polarizing effect and has resulted in disagreement, as some detest the fish, citing ecosystem changes since introduction, while others rely on this resource for their livelihood. While some argue that all fish introductions should be considered “guilty until proven innocent” (Simberloff 2007), others insist that conclusions about the impact of non-natives should be based on “quantifiable empirical evidence and not *a priori* statements” (Gozlan 2008). While we have shown that Blue Catfish do not routinely consume migrating adult alosines during the spring, there are still concerns about the predation of juveniles as they

emigrate out of the rivers in the fall. Moreover, there are still concerns about impacts on native White Catfish *Ameiurus catus*, which have declined substantially since the introduction of Blue Catfish (Tuckey and Fabrizio 2010) and Blue Crab, which are one of the most commercially valuable species in the Chesapeake Bay (Sharov et al. 2003).

Many factors have been implicated in the decline of *Alosa* species along the Atlantic coast (Bethoney et al. 2013), but can predation really play a role? While correlation doesn't equate to causality, there was a significant statistical relationship between Striped Bass relative abundance and increasing mortality of Blueback Herring and American Shad in the Connecticut River, causing scientists to suspect that predation was a major driver of observed declines (Savoy and Crecco 2004). Striped Bass, a large piscivore that is sympatric with Alewife, Blueback Herring, and American Shad, is known to travel well above the salt wedge in large rivers to gorge on these species during the spring (Savoy and Crecco 2004; Davis and Schultz 2009). Moreover, the Atlantic population of Striped Bass population has recovered to near historic levels (Hartman and Margraf 2003), and has been implicated in contributing to coast-wide alosine declines (Davis and Schultz 2009). Our results demonstrate that Flathead Catfish routinely consume American Shad and Blueback Herring; therefore, the combined predation pressure of Flathead Catfish and Striped Bass may have a significant impact on migrating alosines in rivers where they co-occur. Interestingly, *Alosa* species were found in 16-32% Flathead Catfish stomachs, which is similar to percent occurrence of river herring in the spring diets of Striped Bass in tidal freshwater portions of the Chesapeake Bay ($\approx 29\%$; Walter and Austin 2003).

While this study demonstrates that Flathead Catfish have are likely to have a greater per capita impact on alosines than Blue Catfish, Blue Catfish may exert a greater overall effect due to larger population sizes, though population estimates will be needed for these comparisons to be made. Blue Catfish are generally more abundant than Flathead Catfish, though the Blue Catfish population is largely comprised of small, non-piscivorous individuals. Length-frequency histograms from this study indicate that differences in the relative abundance of Flathead Catfish, which are piscivorous at small sizes, versus “piscivorous” Blue Catfish are considerably less substantial. This may mean that Flathead Catfish, at least within the freshwater and tidal freshwater portions of the James River, are having a greater impact on native fish species than previously anticipated.

Alosine populations crashed long before catfish became established in Virginia’s tidal rivers (Bethoney et al. 2013), thus it is unlikely that catfish are major contributors to these declines. Virginia’s tidal rivers is likely driven by a combination of several problems including degraded spawning habit, obstacles to fish passage, and increasing predation by piscivores (ASMFC 2012; Brown et al. 2013; Bethoney et al. 2014). Moreover, bycatch of river herring and American Shad within offshore fisheries may be extreme, and is believed to be hindering restoration efforts for these species (Bethoney et al. 2013; Hasselman et al. 2016). Striped Bass stocks have also increased substantially since the 1980s (Richards and Rago 1999); therefore, we also recommend revisiting the spring diets of striped bass in Virginia’s tidal rivers, as declining alosine abundance may be driven by the composite effect of increasing native and non-native predator biomass.

While this study provides valuable insight into interactions between introduced catfish and *Alosa* species, there is still a need to describe the diets of Blue and Flathead Catfish across broad spatiotemporal scales within the Chesapeake Bay. Further, we cannot quantify population-level consumption without credible estimates of population size and length structure for both catfish species, though estimates of Blue Catfish density (number/hectare) have been made in Powell Creek, an oligohaline tributary of the James River (*personal communication*, Aaron Bunch, Virginia Department of Game and Inland Fisheries). Further, Flathead Catfish density estimates have been made within the tidal freshwater portion of the James River (*personal communication*, Jason Emmel, Virginia Tech). Flathead Catfish populations should be monitored closely, as future expansion is inevitable within the York River, and piscivorous Flathead Catfish are known to cause major declines in native fish biomass.

This study provides the first published diet description for introduced Flathead Catfish within the Chesapeake Bay; this is particularly important as Flathead Catfish are well-known as a dangerous invaders (Fuller et al. 1999) and future expansion of the species is likely (Brown et al. 2005). This study also represents the first focused description of alosine predation by non-native catfish during the spring, a time during which marine nutrient input from *Alosa* species restructures the food web within Virginia's tidal rivers (MacAvoy et al. 2000). Our estimates of alosine predation have widespread implications, as Blue and Flathead Catfish have been introduced into many Atlantic slope drainages from Pennsylvania to Florida (Graham 1999; Jackson 1999), and many of these rivers support spawning populations of alosines (Schmidt et al. 2003; Ray and Robbins 2016). While river-specific estimates of alosine predation by introduced catfish will be useful in the future, estimates from this study can be applied to other Atlantic

slope rivers in the interim. Findings from this study will be useful in the construction of ecosystem models and subsequent ecosystem-based management recommendations (Pauly et al. 2000; Harvey et al. 2003), which will be useful for the future management of non-indigenous Blue and Flathead Catfish in Atlantic drainages.

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Tables and Figures

Table 1. Percent by number, percent by weight, and percent occurrence for prey consumed by Blue Catfish (N= 1,539) from the James River during March, April, and May.

Prey	%N	%W	%O
Amphibia			
Ranidae			
<i>Rana</i> spp.	0.08%	<0.01%	0.08%
Amphipoda			
<i>Leptocheirus plumulosus</i>	2.91%	<0.01%	0.25%
Gammaridae	3.49%	0.13%	2.01%
Annelida	0.37%	<0.01%	0.21%
Anthropogenic Debris ¹	1.89%	0.63%	1.48%
Aquatic Vegetation	16.53%	4.69%	16.53%
Aves			
Unidentified bird remains	0.12%	0.04%	0.12%
Cnidaria			
Ulmariidae			
<i>Aurelia auris</i>	0.08%	0.02%	0.08%
Decapoda			
Panopeidae			
<i>Panopeus herbstii</i>	0.86%	0.01%	0.21%
<i>Rithropanopeus harrisii</i>	2.95%	0.07%	0.57%
Cambaridae			
<i>Orconectes limosus</i>	1.76%	0.11%	0.70%
<i>Procambarus</i> spp.	0.78%	0.23%	0.70%
Palaemonidae			
<i>Palaemonetes pugio</i>	0.04%	<0.01%	0.04%
Portunidae			
<i>Callinectes sapidus</i>	1.56%	0.33%	1.48%

Diplopoda		0.12%	<0.01%	0.04%
Fish*		30.11%	92.05%	23.34%
Insecta				
Coleoptera		0.33%	<0.01%	0.33%
Hemiptera		0.08%	<0.01%	0.08%
Megaloptera		0.29%	0.01%	0.16%
Trichoptera		0.37%	<0.01%	0.12%
Odonata		2.50%	0.03%	0.94%
Ephemeroptera		0.08%	<0.01%	0.04%
Plecoptera		0.98%	<0.01%	0.29%
Isopoda				
<i>Cyathura polita</i>		1.07%	<0.01%	0.16%
Mammalia				
Cricetidae				
<i>Ondatra zibethicus</i>		0.04%	0.10%	0.04%
Unidentified mammal remains		0.25%	0.05%	0.25%
Mollusca				
Unionidae				
<i>Anodonta</i> spp.		0.25%	0.03%	0.04%
Unionid mussel		5.82%	0.04%	0.57%
Cyrenidae				
<i>Corbicula fluminea</i>		11.28%	0.34%	3.08%
Mactridae				
<i>Rangia</i> spp.		0.21%	<0.01%	0.12%
Dreissenidae				
<i>Mytilopsis leucophaeata</i>		1.93%	0.01%	0.29%
Unidentified Dreissenid		0.08%	<0.01%	0.04%
Tellinidae				
<i>Macoma</i> spp.		0.49%	0.01%	0.16%

Sphaeriidae	0.66%	0.01%	0.25%
Viviparidae	0.12%	<0.01%	0.08%
Balanidae			
<i>Balanus</i> spp.	1.35%	0.01%	0.08%
Sediment and Detritus	8.08%	1.07%	3.53%

¹Anthropogenic debris included fish hooks, plastic worms, candy, chicken bones, corn, peanuts, condoms, feminine products, and raw sewage.

*See Table 2.

Table 2. Percent by number, percent by weight, and percent occurrence for fish prey consumed by Blue Catfish (N=1,539) from the James River during March, April, and May.

Prey		%N	%W	%O
Achiridae				
	<i>Trinectes maculatus</i>	0.27%	0.02%	0.18%
Anguillidae				
	<i>Anguilla rostrata</i>	6.68%	0.42%	6.33%
Atherinopsidae				
	<i>Menidia menidia</i>	0.41%	0.02%	0.18%
Catostomidae				
	<i>Moxostoma</i> spp.	0.14%	0.16%	0.18%
Centrarchidae				
	<i>Lepomis macrochirus</i>	0.27%	0.12%	0.35%
	<i>Lepomis gibbosus</i>	0.27%	0.15%	0.35%
	<i>Lepomis microlophus</i>	0.27%	0.23%	0.35%
	<i>Lepomis</i> spp.	1.50%	0.44%	1.41%
Clupeidae				
	All <i>Alosa</i>	9.54%	15.37%	10.37%
	<i>Alosa aestivalis</i>	3.13%	2.78%	2.99%
	<i>Alosa medocris</i>	2.72%	8.29%	4.99%
	<i>Alosa pseudoharengus</i>	2.04%	2.25%	2.46%
	<i>Alosa sapidissima</i>	0.27%	0.48%	0.35%
	<i>Dorosoma cepedianum</i>	34.88%	66.95%	33.92%
Cyprinidae				
	<i>Cyprinus carpio</i>	0.54%	2.52%	0.70%
	<i>Hybognathus regius</i>	2.86%	0.12%	1.58%
	<i>Nocomis micropogon</i>	0.14%	0.02%	0.18%
	<i>Notropis hudsonius</i>	0.95%	0.10%	1.05%
	<i>Cyprinus</i> spp.	3.41%	0.11%	0.70%
Ictaluridae				
	<i>Pylodictis olivaris</i>	0.14%	0.00%	0.18%
	<i>Ictalurus punctatus</i>	0.14%	0.03%	0.18%
	<i>Ictalurus furcatus</i>	2.04%	2.11%	2.64%
	<i>Ameiurus catus</i>	0.27%	0.19%	0.35%
Lepisosteidae				
	<i>Lepisosteus osseus</i>	0.14%	0.56%	0.18%
Moronidae				
	<i>Morone saxatilis</i>	0.14%	0.05%	0.18%
	<i>Morone americana</i>	7.77%	3.62%	7.73%
Percidae				
	<i>Etheostoma flabellare</i>	0.41%	0.00%	0.18%
	<i>Etheostoma olmstedi</i>	0.41%	0.10%	0.53%
	<i>Perca flavescens</i>	0.41%	0.05%	0.35%
Petromyzontidae				
	<i>Petromyzon marinus</i>	0.14%	0.43%	0.18%

Table 3. Percent by number, percent by weight, and percent occurrence for prey consumed by Flathead Catfish from the James River during March, April, and May (N=204).

Prey	%N	%W	%O
Anguillidae			
<i>Anguilla rostrata</i>	0.31%	0.09%	0.49%
Clupeidae			
All <i>Alosa</i>	24.00%	23.55%	16.67%
<i>Alosa aestivalis</i>	15.08%	10.58%	9.31%
<i>Alosa medocris</i>	0.31%	1.13%	0.49%
<i>Alosa pseudoharengus</i>	2.77%	3.05%	2.94%
<i>Alosa sapidissima</i>	0.92%	3.86%	1.47%
<i>Dorosoma cepedianum</i>	24.92%	48.80%	32.84%
Cyprinidae			
<i>Cyprinus carpio</i>	0.62%	6.51%	0.98%
<i>Cyprinus</i> spp.	11.38%	0.70%	4.90%
Percidae			
<i>Etheostoma flabellare</i>	2.15%	0.07%	0.49%
Ictaluridae			
<i>Pylodictis olivaris</i>	0.31%	0.82%	0.49%
<i>Ictalurus punctatus</i>	1.23%	1.65%	0.98%
Centrarchidae			
<i>Lepomis</i> spp.	0.92%	0.33%	1.47%
Moronidae			
<i>Morone saxatilis</i>	0.62%	1.55%	0.98%
<i>Morone americana</i>	9.54%	2.35%	26.47%

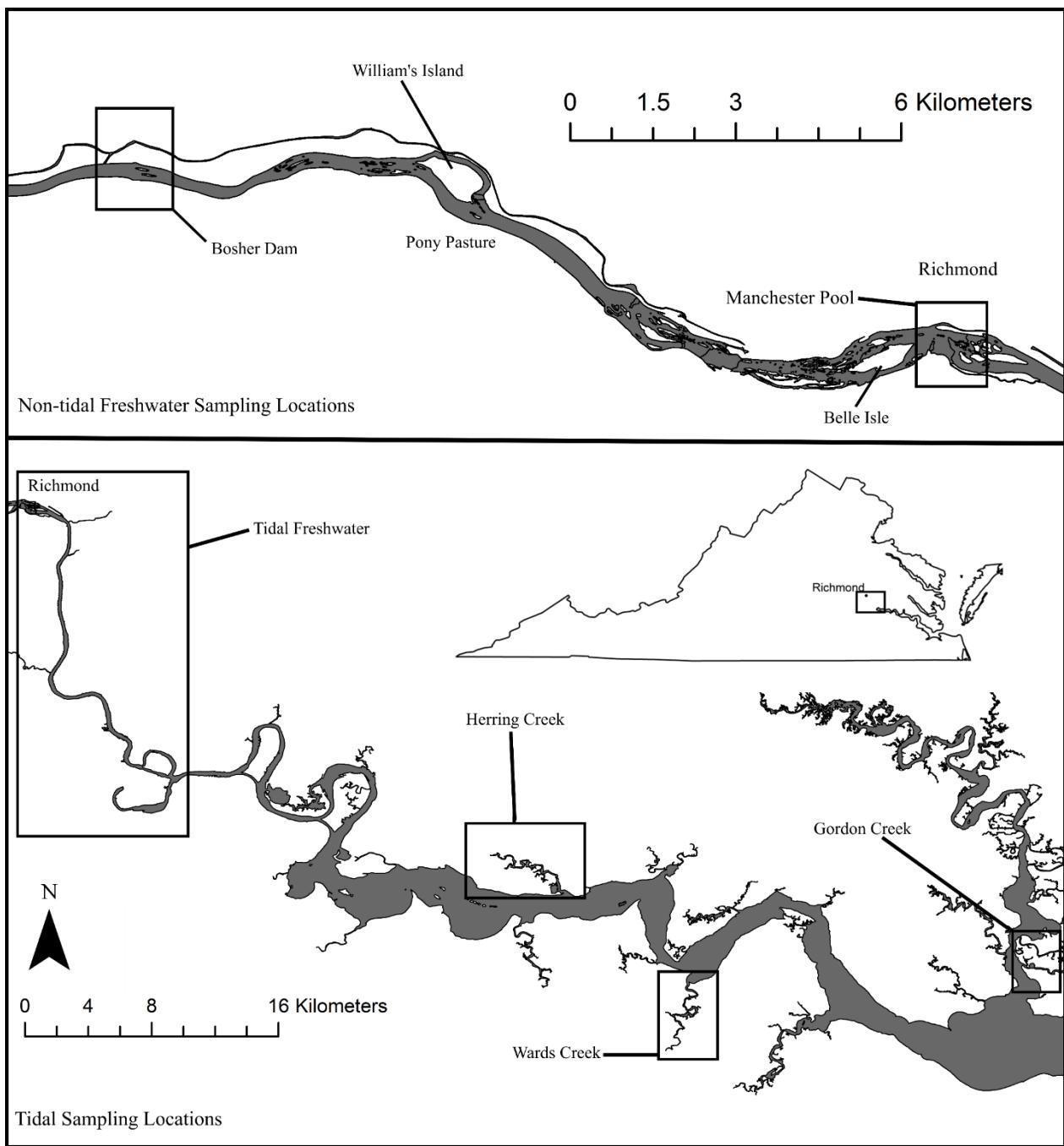


Figure 1. Map of major sampling areas (within rectangles) from the James River near Richmond, Virginia. The top panel includes non-tidal freshwater sampling areas just west of Richmond: Bosher Dam and Manchester Pool. The bottom panel includes tidal sampling areas southeast of Richmond: tidal freshwater (primary sampling area), Herring Creek, Wards Creek, and Gordon Creek.

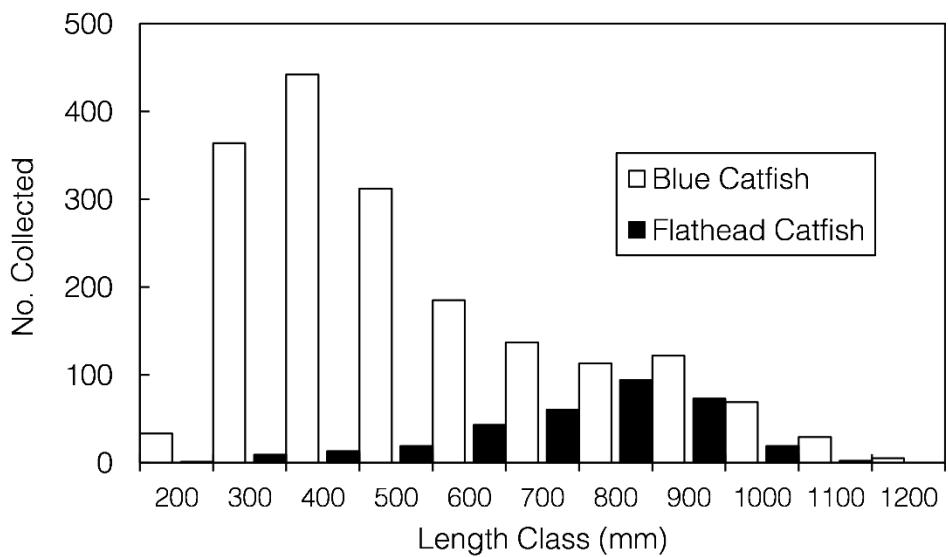


Figure 2. Length frequency distribution for the 2,495 catfish that were collected from the James River during March, April, and May. This included 2,164 Blue Catfish and 331 Flathead Catfish.

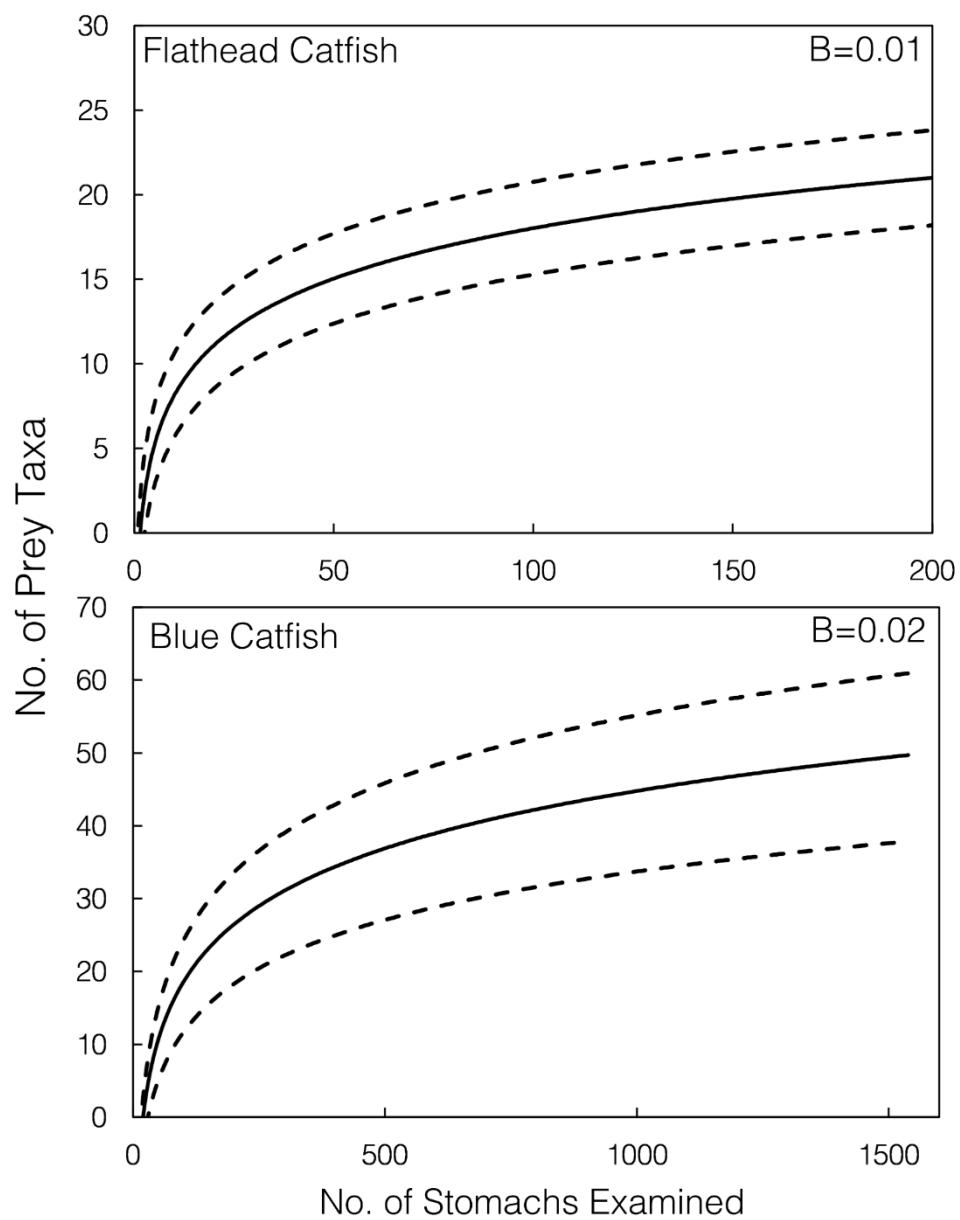


Figure 3. Cumulative prey curves and associated 95% confidence intervals based on stomach data from Flathead Catfish ($N= 204$; top panel) and Blue Catfish ($N=1,539$; bottom panel) collected from the James River during March, April, and May. The last four endpoints for both slopes (B) reached asymptotes indicating sufficient sampling for diet description ($B<0.05$).

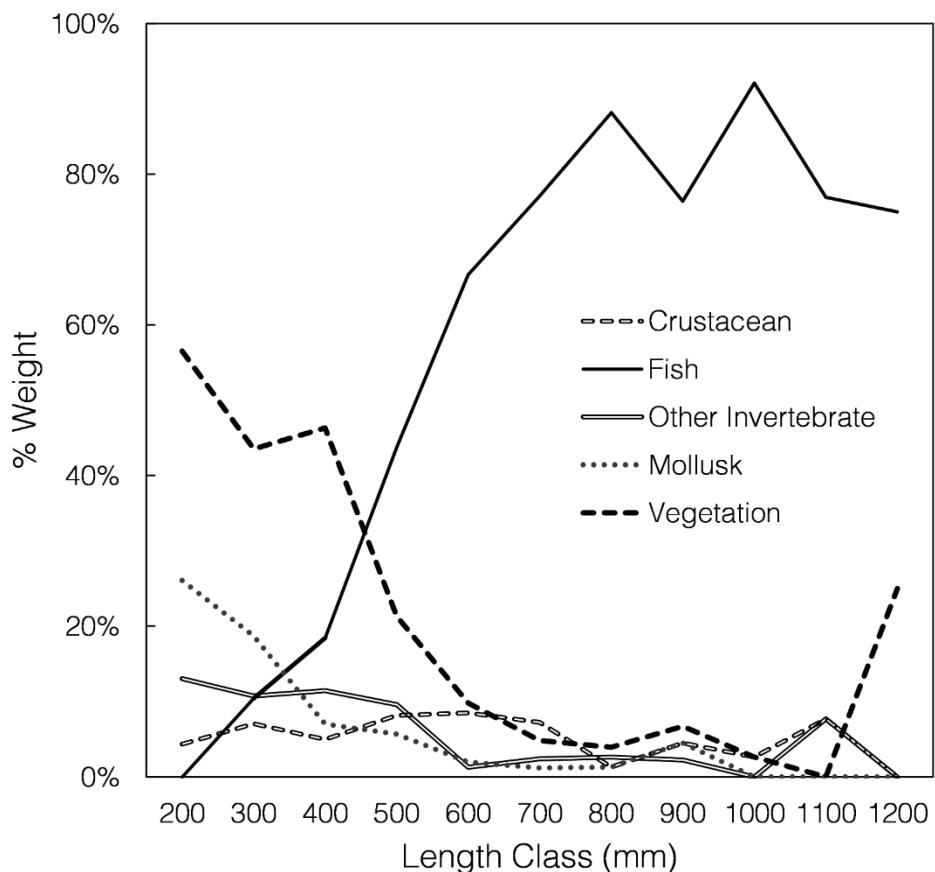


Figure 4. Percent by weight of the major prey groups by 100 mm length class for Blue Catfish collected in the James River during March, April, and May. Blue Catfish begin to include significantly more fish in their diet at 500 mm TL (Tukey's HSD on ranks; $P<0.01$).

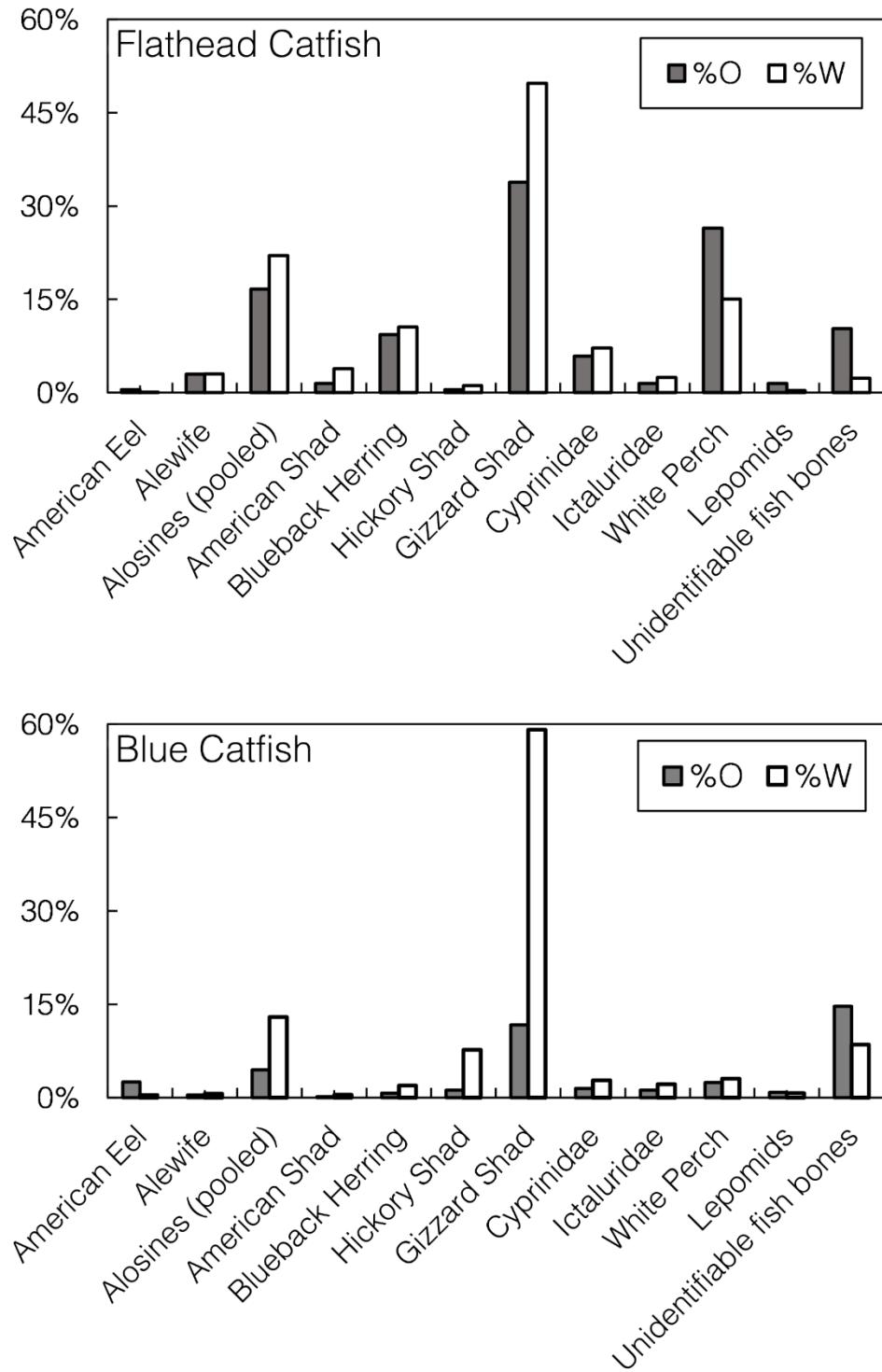


Figure 5. Percent weight (%W) and percent occurrence (%O) for fish prey consumed by Flathead Catfish (top panel) and “piscivorous” Blue Catfish (> 500 mm TL; bottom panel) from the James River, VA, during March, April, and May. “Alosines” includes Alewife, American Shad, Blueback Herring, and Hickory Shad grouped together into a single category.

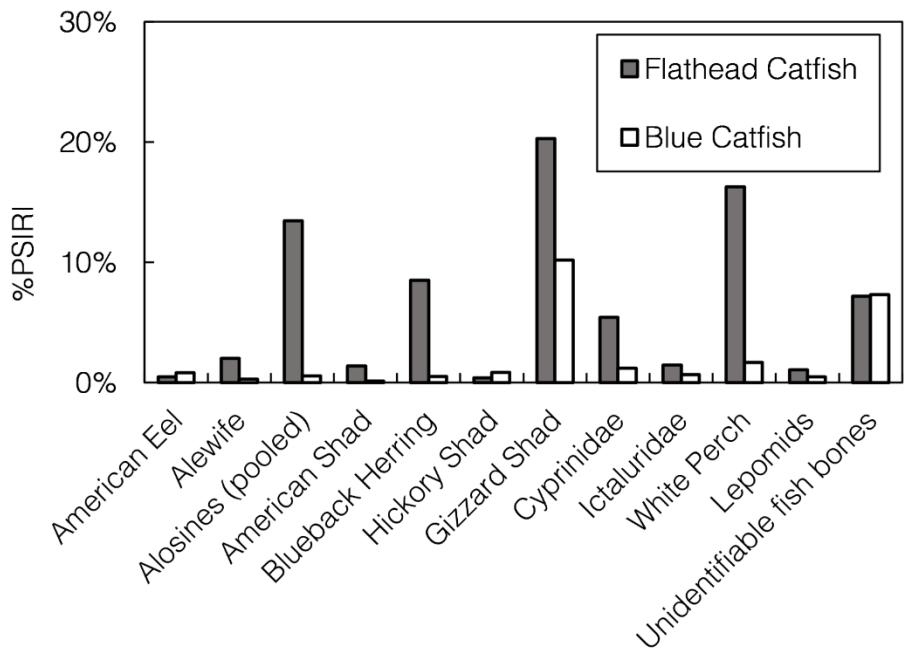


Figure 6. Relative Importance (%PSIRI) of fish prey consumed by Blue Catfish and Flathead Catfish in the James River during March, April, and May. “Alosines” includes Alewife, American Shad, Blueback Herring, and Hickory Shad grouped together into a single category.

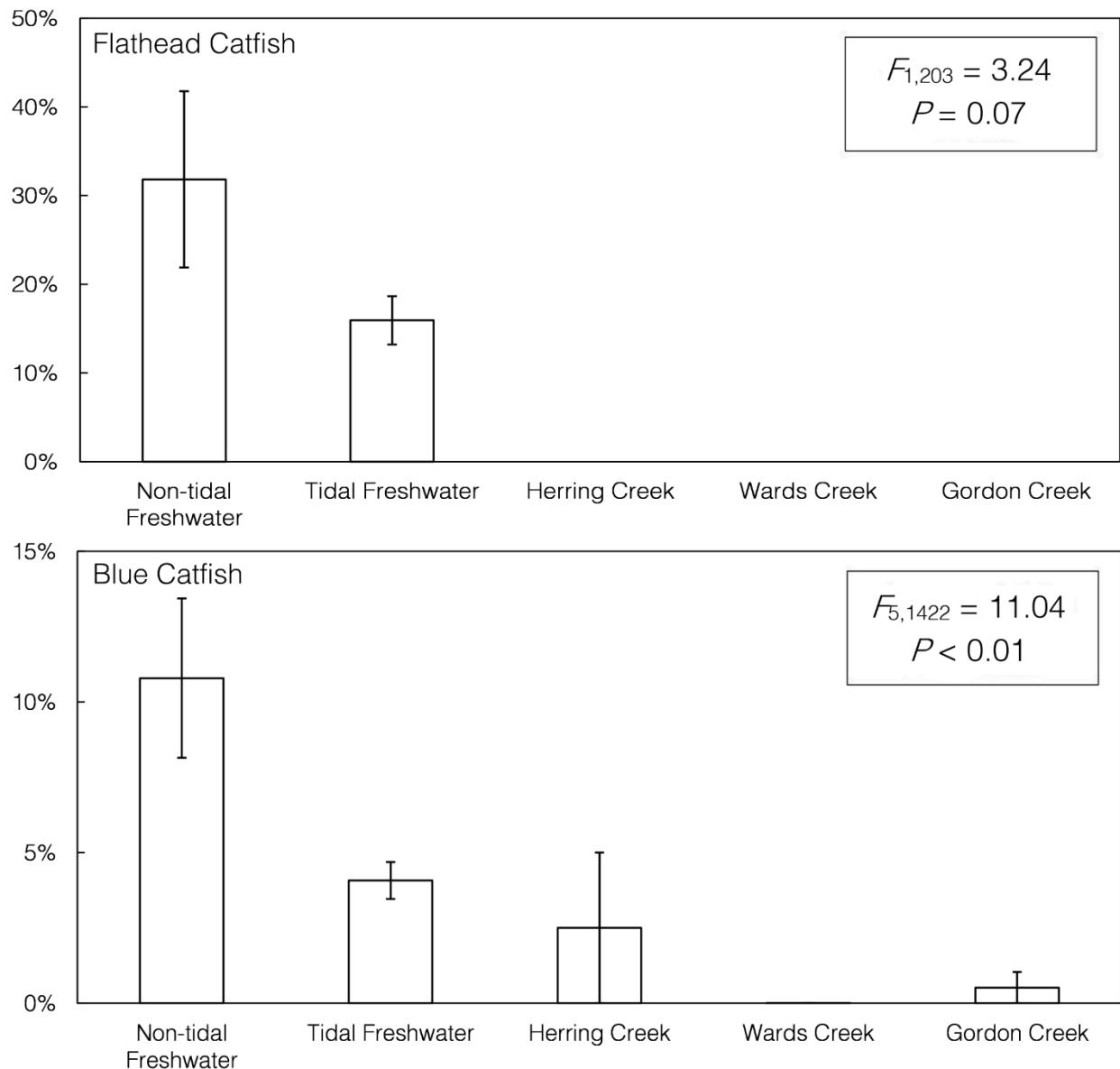


Figure 7. Logistic regression was used to analyze binary differences in *Alosa* predation (1=present, 0=absent) in the spring diet of Flathead Catfish (top) and Blue Catfish (bottom) by sampling area (please note different scales on Y axes). A significant difference was detected for Blue Catfish, and *post hoc* testing revealed that Blue Catfish *Alosa* predation was significantly higher in non-tidal freshwater areas (Tukey's HSD; $P < 0.01$). Error bars represent standard error.

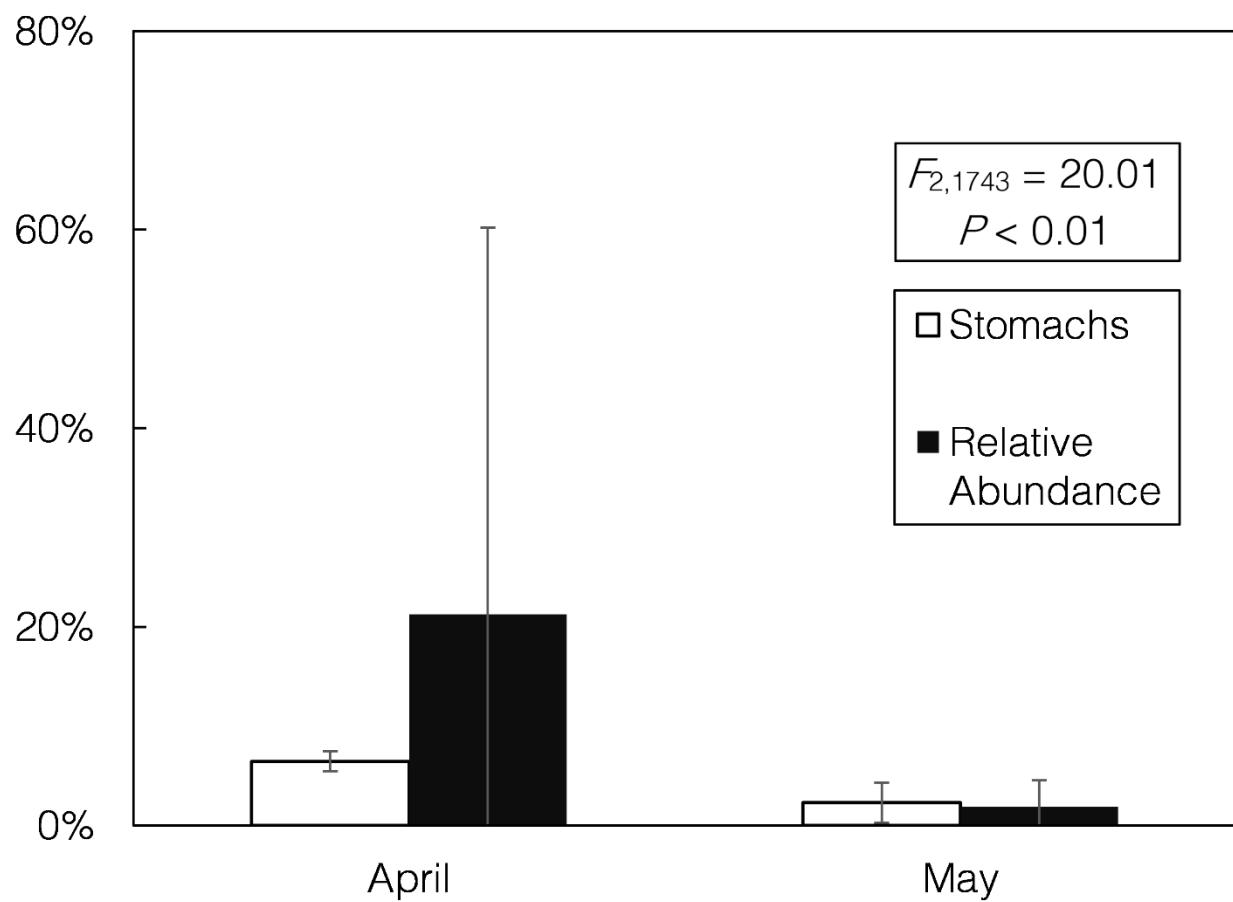


Figure 8. Monthly percent occurrence (%O) of *Alosa* species in the diet of non-native catfish from the James River (stomachs) and percentage of *Alosa* species during prey abundance sampling (relative abundance). The occurrence of alosines in the diet of non-native catfish was significantly higher in April than in May; March was omitted from graph as no *Alosa* predation was observed (logistic regression; $P < 0.001$). Error bars represent standard error.

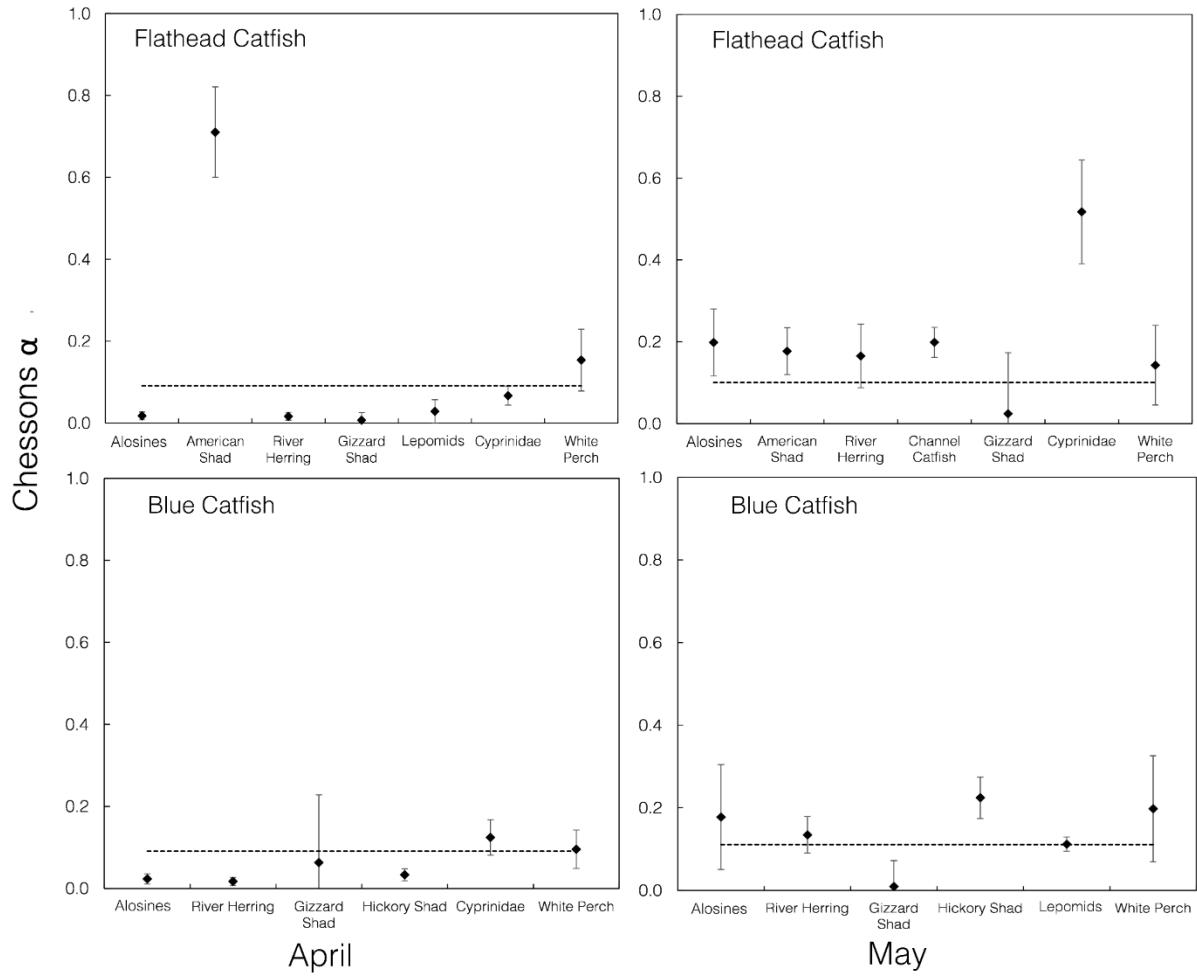


Figure 9. Prey selectivity for Flathead Catfish (top) and Blue Catfish (bottom) during the month of April (left column) and May (right column) collected from the James River, VA. The dotted line equals $1/m$, or neutral selectivity; prey above the dotted line are selected, prey below are not. “Alosines” includes all four *Alosa* species pooled into one group. Error bars represent 95% confidence intervals.

Chapter 3: Feeding Ecology of Generalist Consumers: A Case Study of Invasive Blue Catfish *Ictalurus furcatus* in Chesapeake Bay, Virginia, USA

Introduction

Invasive species can cause population declines and extinction of native species (Mills et al. 2004), and are a major threat to biodiversity (Lockwood et al. 2013). Globally, specialist taxa are being replaced by invasive generalists with broad ecological niches, a trend known as biotic homogenization (McKinney and Lockwood 1999; Clavel et al. 2010). Many generalist species have a competitive advantage due to their ability to thrive in degraded habitats, which has sparked a renewed interest in the characterization of generalist consumers worldwide (McKinney and Lockwood 1999; Layman and Allgeier 2012). Some of the most successful invasives consume a broad array of food items, with diets comprised of both plant and animal material (Twardochleb et al. 2013; Jackson et al. 2017). These omnivorous food habits place them in the middle of the food web, with direct consumptive links to multiple trophic levels; this helps them endure adverse conditions and changes in prey availability (Layman and Allgeier 2012; Jackson et al. 2017). Despite the considerable attention that invasive species receive, little is known about the life history and feeding ecology of many of these organisms, and more observational and experimental studies are urgently needed (Garcia-Berthou 2007; Brandner et al. 2013; Layman and Allgeier 2012).

Once established, novel generalist consumers can drastically alter invaded ecosystems. Food webs are restructured, which can lead to changes in ecosystem function, productivity, and the deterioration of ecosystem goods and services (Mack et al. 2000; Clavel et al. 2010). Populations of invasive generalists can reach densities that are orders of magnitude greater than similar native species, and, because they are linked to multiple trophic levels, result in widespread impacts on

invaded communities (Snyder and Evans 2006). Feeding ecology studies are of particular importance, as diet is a primary determinant for predicting how invasive species will affect food webs of receiving systems (Brandner et al. 2013; Garvey and Whiles 2017). Moreover, the classification of a novel species along the generalist-specialist feeding continuum has significant implications for their long-term success after establishment (Moyle and Light 1996), and the precise ecological impact of an introduced species depends largely on its trophic position within the food web (McKnight et al. 2016).

Native to tributaries of the Mississippi River, the blue catfish *Ictalurus furcatus* is a large catfish species that has been widely introduced into Atlantic and Pacific drainages in the U.S. (Graham 1999; Eggleton and Schramm 2004). This species can weigh in excess of 50 kg, reaches high population densities, and may be a dangerous invader (Graham 1999; Greenlee and Lim 2011; Howeth et al. 2016). Even so, there is a general paucity of information on this species (Graham 1999) and little is known about the feeding ecology of this species outside of its native range (Schmitt et al. 2017). Blue catfish were stocked in tidal freshwater portions of the Chesapeake Bay from 1973-1985 to create new recreational fisheries (Greenlee and Lim 2011). Blue catfish populations have since expanded to occupy all major tributaries of the Chesapeake Bay, and are now considered invasive (Fabrizio et al. 2017). Blue catfish have expanded to brackish portions of the estuary, and have been captured in salinities as high as 21.5 ppt (Fabrizio et al. 2017). Blue catfish dominate the fish biomass in some locales, which has caused concern about their potential interactions with native species (Greenlee and Lim 2011; Schloesser et al. 2011), and prompted the Chesapeake Bay Program (CBP) to develop an “invasive catfish policy”, which calls for more research on the life history and ecological role of this species (CBP 2012).

Previous diet studies of blue catfish in the Chesapeake Bay are limited by sample size, spatiotemporal scope, or include only small individuals (Schmitt et al. 2017). This is problematic because prey assemblages vary seasonally and spatially in the Chesapeake Bay (Jung and Houde 2003) and blue catfish regularly exceed 40 kg in Virginia's tidal rivers (Greenlee and Lim 2011). Only one study has assessed sample size sufficiency for blue catfish, and found that large numbers of stomachs (\approx 1500) were needed for diet description due to the diversity of resources consumed (Schmitt et al. 2017). Considering this, the authors concluded that most of the previous diet work in Chesapeake Bay is unlikely to provide a realistic picture of the full dietary breadth of this species. To date, no studies have assessed trophic position, individual diet specialization, or diet breadth for blue catfish, all of which relate to potential impacts in novel environments (Layman and Allegeier 2012; Garvey and Whiles 2017).

The current study will provide several valuable pieces of information. First, it provides another example of an opportunistic generalist species taking over a degraded ecosystem, a trend that continues to gain attention globally and has serious ecological consequences (McKinney and Lockwood 1999; Layman and Allegeier 2012). Second, the current study will fully characterize spatiotemporal variability in blue catfish diet for three large subestuaries of the Chesapeake Bay, which will help fisheries managers make decisions moving forward. Management of blue catfish will be complicated, as blue catfish support recreational fisheries and expanding commercial fisheries, yet potentially threaten important native resources including blue crab *Callinectes sapidus*, American shad *Alosa sapidissima*, alewife *A. pseudoharengus*, blueback herring *A. aestivalis*, and American eel *Anguilla rostrata* (Schmitt et al. 2017).

Considering this, our specific research objectives were to: 1) characterize the feeding ecology of blue catfish by determining individual diet specialization, trophic position, and generalist versus

specialist feeding strategies; 2) explore spatiotemporal patterns in prey consumption, size-based variation in diet, and assess sample size sufficiency to ensure a robust diet characterization; 3) collect blue catfish stomachs across broad spatiotemporal scales in three large subestuaries of the Chesapeake Bay, so that inference can be drawn for this region as a whole.

Methods

Study area.—The Chesapeake Bay is the largest estuary in the United States, with a surface area of $1.15 \times 10^4 \text{ km}^2$ and a total volume of 70 km^3 (Shiah and Ducklow 1994). The Chesapeake Bay is a shallow, partially-mixed system that receives about 50% of its water from the Atlantic Ocean and the other 50% from freshwater tributaries (Jung and Houde 2004). The Chesapeake Bay watershed is far from pristine, and anthropogenic eutrophication has resulted in major ecological changes within the estuary (Kemp et al. 2005). It is highly productive when compared to other brackish systems (Nixon 1988), and has supported commercial fisheries since the late 1700s (Jung and Houde 2004). This study was conducted in Virginia's tidal rivers—the James, Pamunkey, Mattaponi, and Rappahannock rivers. Blue catfish were originally stocked in these rivers during the 1970s and 1980s, and now occur at high densities (Greenlee and Lim 2011). Virginia's tidal rivers contribute nearly 20% of the total freshwater input for the Chesapeake Bay (Schubel and Pritchard 1987; Figure 1), and support a diverse array of freshwater and marine organisms (Murdy et al. 1997; Schloesser et al. 2011).

Field methods.—From 2013 - 2016, blue catfish were collected using stratified random sampling between April 1 and October 31st, as the potential for interaction with imperiled *Alosa* species is most likely during these periods (Hoffman et al. 2008; Waldman 2013). All four rivers were divided into three strata according to average fall surface salinities available through the Chesapeake Bay Program's website, as salinities are relatively uniform throughout the water

column during the autumn months (Shia and Ducklow 1994). Each river was stratified into freshwater sections (0 – 0.5 ppt), oligohaline sections (>0.5 – 5 ppt), and mesohaline sections (>5 – 18 ppt). Furthermore, each stratum was divided into 2-km reaches which were then randomly sampled. Individuals were collected monthly within each stratum of each river at a minimum of two randomly selected reaches, with a minimum of five sites sampled within each reach. We sampled both nearshore and main channel habitats at each site, and recorded time of day, water temperature, salinity, geographic coordinates, and tide phase at each sample location. When possible, we attempted to collect a minimum of 100 catfish within each reach, and we tried to collect fish of all sizes. Blue catfish were collected using low-frequency, pulsed-DC electrofishing (15 pulses per second; 200 – 300 volts) using a 7.5 kW boat-mounted electrofishing system (Midwest Lake Electrofishing Systems, Polo, MO) and a 50' single dropper anode with 1 m of cable exposed at the terminal end. Low-frequency electrofishing is extremely effective for capturing blue catfish (Bodine and Shoup 2010), particularly in Virginia's tidal rivers (Greenlee and Lim 2011).

We also examined winter (November-March) diets of blue catfish because previous research has shown them to be more piscivorous during this time period (Edds et al. 2002). Because low-frequency electrofishing is only effective at water temperatures greater than 18° C, we used other methods to collect winter diets (Bodine and Shoup 2010). Most fish were collected via high-frequency electrofishing (60 pulses per second; 200 – 300 volts) though we occasionally used trotlines to target larger fish. High-frequency electrofishing is a laborious and time-intensive method for collecting blue catfish (Schmitt et al. 2017), therefore winter samples were only collected from the James and Pamunkey rivers.

Stomach processing.—Stomach contents were extracted by either sacrificing the fish or with pulsed gastric lavage, which has been demonstrated to be effective for extracting diets from blue catfish (Waters et al. 2004). Stomachs were extracted within 30 minutes of capture to minimize losses from regurgitation, and contents were placed on ice and later frozen (Schmitt et al. 2017). In the laboratory, prey items were thawed, blotted dry with paper towels, weighed, counted, and identified to the lowest possible taxon. Unidentifiable fish remains were identified using DNA barcoding methods as described by Moran et al. (2016) and Schmitt et al. (2017). These methods enabled us to identify an additional 70% - 80% of fish prey that were unidentifiable by gross morphology, excluding instances where only bones and/or scales remained.

Sample size sufficiency.—Gathering enough stomachs to adequately characterize the diet of a species is an important step that is overlooked in many studies (Ferry and Cailliet 1996), and large samples are often required to accurately describe the diet of an opportunistic, omnivorous species like blue catfish (Schmitt et al. 2017). Considering this, sample size sufficiency was assessed for each river using rarefaction curves, where the cumulative mean number of unique taxa are plotted against the number of stomachs examined. Sample size is considered sufficient if the slope reaches an asymptote (Ferry and Cailliet 1996; Bizzarro et al. 2009). Rarefaction curves and associated 95% confidence intervals were calculated with EstimateS (version 9.1, R. K. Colwell), where the cumulative number of unique prey taxa were plotted against the randomly pooled samples. This process was bootstrapped 1000 times to generate means and associated confidence intervals. We used the mean slope (B) of the last five subsamples (linear regression) as an objective criterion for sample size sufficiency, where sample size is considered sufficient when $B \leq 0.05$ (Bizzarro et al. 2009; Brown et al. 2012).

Ontogenetic diet shifts.—Blue catfish are known to make dietary shifts as they grow; in general, smaller individuals are highly omnivorous, while larger individuals become more piscivorous (Edds et al. 2002; Eggleton and Schramm 2004; Schmitt et al. 2017). To determine the lengths at which this shift to piscivory occurs, we modeled the binary occurrence of fish in the diet as a function of fish total length using logistic regression. Although many studies use the gravimetric contribution (%W) of prey items to evaluate ontogenetic shifts, we used the binary occurrence of fish in the diet, as occurrence best describes population-level feeding patterns and avoids some of the biases associated with gravimetric methods (Hyslop 1980; MacDonald and Green 1983; Baker et al. 2014). Ontogenetic diet shifts to piscivory were analyzed separately by river, and statistical significance was assessed at the 95% level ($\alpha=0.05$). For simplicity, ontogenetic shifts to piscivory were based on model predictions and were determined as the length at which fish prey were predicted to occur $\geq 50\%$ of blue catfish stomachs, rounded to the nearest 100 mm.

Diet composition and spatiotemporal patterns.—In summarizing blue catfish diet, percent occurrence (%O) was used to identify routinely-utilized prey resources, percent by weight (%W) was used to identify energetically-important prey resources (MacDonald and Green 1983), and the prey-specific index of relative importance (%PSIRI) was used to characterize the overall importance of diet items (Brown et al. 2012). As a compound index, %PSIRI provides a more balanced understanding of the dietary importance of different prey, since it combines multiple metrics into a single estimate of overall importance (Pinkas et al. 1971; Bigg and Perez 1985; Cortes 1997). Percent PSIRI is defined as:

$$\%PSIRI_i = \frac{\%FO_i \times (\%PN_i + \%PW_i)}{2}$$

Where %FO_i is the frequency of occurrence for prey type “i”, %PN_i is the percent by number of prey type “i” in all stomachs containing prey type “i”, and %PW_i is the percent by weight of prey type “i” in all stomachs containing prey type “i”.

Prey assemblages vary seasonally and spatially within the Chesapeake Bay (Jung and Houde 2003), thus we expected blue catfish diets to vary accordingly. To explore these patterns, the percent occurrence of prey in the diet was plotted by season and salinity zone. Season was classified as spring (March - May), summer (June-August), fall (September – November), or winter (December– February). Salinity zone was classified as explained above, and was based on the salinity recorded at capture location.

Predator feeding strategy diagrams were constructed separately for each river, but provide little information (Costello 1990; Amundsen 1996). Predator feeding strategy diagrams were constructed by plotting prey-specific percent by weight (%PW) by percent occurrence (Amundsen 1996). This method provides a visualization of the generalist-specialist feeding dichotomy, as well as individual diet specialization, which are major components of niche theory (Pianka 1988). A population with a narrow niche width is comprised of specialized individuals, but a population with a broad niche can be comprised of individuals with narrow or broad niches (Amundsen 1996). While blue catfish as a species have been demonstrated to have broad diets (Edds et al. 2002; Eggleton and Schramm 2004; Schmitt et al. 2017), individual diet specialization has not yet been assessed for this species.

Trophic characteristics.—Trophic level (TL) estimates provide an approximation of trophic position within complex food webs, and are useful for comparing ecological roles of different species within a given system (Cortes 1999; Ebert and Bizzarro 2007). Trophic level calculations

can help researchers identify which species may be structuring ecosystems through top-down control, bottom-up control, or a combination of the two (Cortes 1999). Trophic level and omnivory indices were calculated for blue catfish in the James, Pamunkey, Mattaponi, and Rappahannock rivers. In addition, we used the results of the preceding ontogenetic diet shift analyses to inform thresholds for calculating respective trophic levels of smaller omnivorous and larger piscivorous blue catfish. Trophic level calculations were based on all stomach contents collected from each river, and TL was calculated as:

where “ DC_{ij} ” is the proportion of prey “j” in the diet of the consumer “i”, “ $TROPH_j$ ” is the trophic level of prey “j”, and “G” is the number of groups in the diet of “i” (Rodriguez-Preciado et al. 2014). Proportion in the diet was calculated as percent occurrence, as this index best represents population-level feeding patterns (MacDonald and Green 1983). Trophic levels for several species of fish were available via FishBase (Froese and Pauly 2016), but species of unknown trophic level were estimated using the mean trophic level of species within that family (Cortes 1999). Trophic levels for non-fish prey (various invertebrates, amphipods, mollusks, and crustaceans) were taken from standardized values published by Ebert and Bizzaro (2007). The trophic level for vegetation was set at 1.0 (Rodriguez-Preciado et al. 2014). Partially-digested fish prey that were unrecognizable morphologically were given the average trophic level for all identified fish taxa from that river. Detritus, debris, and diet items of anthropogenic origin were excluded from these calculations.

We also calculated a dimensionless omnivory index for blue catfish, as it provides valuable information on diet specialization (Christensen and Walters 2004; Pauly and Watson 2005;

Rodrigues-Preciado et al. 2014). Omnivory index (OI) estimates were calculated using the formula:

$$OI_i = \sum_{j=1}^n [TL_j - (TL_i - 1)]^2 \cdot DC_{ij}$$

where “TL_j” is the trophic level of prey “j”, “TL_i” is the trophic level of predator “i”, and “DC_{ij}” is the proportion of prey “j” in the diet of predator “i”. Again, proportion in the diet was calculated as percent occurrence, which best represents population-level feeding patterns and avoids biases associated with differential digestion of different prey (Hyslop 1980; MacDonald and Green 1983). When the omnivory index = 0, the consumer is specialized and only feeds on one trophic level; conversely, a value greater than 0.5 would indicate non-specialization and feeding on many trophic levels (Christensen and Walters 2004; Pauly and Watson 2005). The square root of a consumer’s OI is the standard error of its trophic level (Pauly and Watson 2005).

Diet breadth was estimated for each river using Levin’s standardized index (Krebs 1989; Labropoulou and Papadoulou-Smith 1999; Hajisamae et al. 2003; Akin and Winemiller 2006). Diet breadth (B), was calculated as:

$$B_i = \left(\frac{1}{n-1} \right) \left(\left(\frac{1}{\sum_{i,j=1}^n P_{ij}^2} \right) - 1 \right)$$

Where B_i is the Levin’s standardized index for predator ‘ i ’, P_{ij} is the proportion of the diet represented by item j , and n is the number of prey categories. Here proportion will be defined as percent occurrence, or the percentage of fish that had a given prey item present in their stomach. Our diet breadth calculations, like our omnivory index, will also provide an estimate of how omnivorous blue catfish are, yet differs as it is based on the proportion of different taxa consumed, not the number of trophic levels. Levin’s standardized index ranges from 0 to 1;

values closer to zero have limited dietary breadth, whereas values closer to 1 have greater diet breadth. Proportional diet breadth was estimated separately for each river and was calculated separately for smaller, omnivorous catfish and larger, piscivorous catfish based on results from ontogenetic diet shift analyses. Debris and items of anthropogenic origin were excluded from diet breadth calculations.

Results

Stomach contents were extracted from a total of 16,110 blue catfish at 698 sites on the James, Pamunkey, Mattaponi, and Rappahannock rivers (Figure 1). Of the 16,110 stomachs sampled, 9,823 contained prey (60.38%). Stomachs were collected from blue catfish ranging in size from 206 mm – 1343 mm total length (TL), with 2,440 blue catfish collected in the 600 – 1200 mm TL range, many from the James River (Figure 2). Rarefaction curves reached asymptotes ($B \leq 0.05$) for all four rivers, indicating sufficient sample size for diet description (Figure 3; Bizzarro et al. 2009). Interestingly, numbers of different prey taxa consumed were similar for the Pamunkey River, Mattaponi River, and Rappahannock River (40 – 45 taxa), whereas blue catfish from the James River consumed a more diverse array of taxa (≈ 80 taxa; Tables 1 and 2).

Ontogenetic diet shifts.—Blue catfish in all rivers underwent significant shifts to piscivory ($P < 0.001$), though the length at which these shifts occurred varied by river (500-900 mm TL; Figure 4). Blue catfish from the James River shifted to a fish-based diet at small sizes (piscivorous by 500 mm TL), followed by blue catfish from the Rappahannock River (piscivorous by 700 mm TL). Blue catfish from the Mattaponi River switched to a fish-based diet by 800 mm TL, while fish from the Pamunkey River switched to piscivory by 900 mm TL.

Diet composition.—Blue catfish had a broad diet consisting of mollusks, vegetation, crustaceans, insects, muskrats, frogs, snakes, turtles, birds, jellyfish, worms, various berries, a myriad of fish species, and numerous items of anthropogenic origin (Tables 1 – 2). Some of the more interesting anthropogenic items include a condom, a maxi pad, plastic worms, beer bottle caps, hooks, peanuts, chicken wings, butcher scraps (pig anus), and a Werther’s original candy (in wrapper).

Pooled across seasons, vegetation was the dominant item consumed in all four rivers in terms of gravimetric contribution, frequency of occurrence, and relative importance, with the exception of the James River and Rappahannock River, where gizzard shad *Dorosoma cepedianum* was the dominant prey by weight (Table 1). It is important to note that %W indices are inherently biased by the heavier prey consumed by larger fish, and also over-represent slow to digest diet items such as mollusks and crustaceans (MacDonald and Green 1983; Baker et al. 2014). Considering this, %W index should be considered with caution, while %O indices are the most robust and interpretable measure of diet composition (Baker et al. 2014). The vegetation consumed was primarily Brazilian waterweed *Egeria densa*, common waterweed *Elodea canadensis*, and *Hydrilla verticillata* (hereafter “hydrilla”). Invasive Asian clams *Corbicula fluminea* were another dominant prey item in all four rivers in terms of %O, %W, and %PSIRI. The commercially-valuable blue crab *Callinectes sapidus* was routinely consumed in the James River, Pamunkey River, Mattaponi River, but not in the Rappahannock River (Table 1). Other routinely consumed prey items include white perch *Morone americana*, gammarid amphipods, estuarine mud crabs (*Rithropanopeus harrisii* and *Panopeus herbstii*), macoma clams, cerith snails, and mayflies (Tables 1 and 2).

Spatiotemporal patterns in diet.—Vegetation was the primary diet item consumed during the spring in all salinity zones (Figure 4). Asian clams were dominant in freshwater and oligohaline areas (13-18% occurrence), whereas estuarine mud crabs were dominant in mesohaline areas (20% occurrence). Other important prey included *Dorosoma spp.* (primarily gizzard shad; threadfin shad *Dorosoma petense*) were only found in stomachs from the James River), native mollusks, and blue crab (Figure 5). It is important to note that imperiled *Alosa* species (blueback herring, alewife, and American shad) were found in less than 2% of blue catfish stomachs during the spring when pooled across all rivers, which is lower than estimates from the James River, where imperiled *Alosa* species were found in 4.46% of blue catfish stomachs during the spring (Schmitt et al. 2017).

Similar patterns emerged during the summer months. Vegetation was the primary diet item in all salinity zones, Asian clams were consumed frequently in freshwater and oligohaline areas, and estuarine mud crabs were consumed frequently in mesohaline areas (Figure 5). Amphipods (21% occurrence) and blue crab (7% occurrence) were consumed regularly in mesohaline areas during the summer. Detritus (6% occurrence) and native mollusks (5-6% occurrence) were also consumed during the summer, though detritus was mostly consumed in tidal freshwater areas (Figure 5).

In the fall, blue catfish began to gorge on *Dorosoma spp.* (mostly gizzard shad; 42% occurrence) and Asian clams (32% occurrence) in tidal freshwater areas, while vegetation (21% occurrence) was still routinely consumed (Figure 5). Vegetation was still the dominant food item in oligohaline and mesohaline areas (45-47% occurrence). Blue crabs were consumed routinely during the fall in mesohaline areas (15% occurrence). Other routinely consumed foods include native mollusks (mostly macoma clams) and menhaden *Brevoortia tyrannus* (Figure 5).

Winter data was limited to blue catfish collected from the James and York rivers ($N = 668$). In tidal freshwater areas, blue catfish fed heavily on *Dorosoma spp.* (31% occurrence), crayfish (17% occurrence), and Asian clams (10% occurrence; Figure 5). In oligohaline areas, blue catfish consumed *Dorosoma spp.* (21% occurrence), vegetation (21% occurrence), blue crab (10% occurrence), and detritus (9% occurrence; Figure 5). In mesohaline areas, blue catfish consumed white perch most frequently (58% occurrence), followed by blue crab (33% occurrence), estuarine mud crabs (26% occurrence), and grass shrimp (17% occurrence; Figure 5).

Feeding strategy diagrams.—Vegetation and Asian clams were consumed most frequently in all rivers, but several river-specific patterns did emerge (Figure 6). In the James River, the clustering of several prey (gizzard shad, threadfin shad, and blue catfish) in the top left corner of the graph indicates individual specialization on these food items (Amundsen et al. 1996). In the Mattaponi River, individuals specialized on menhaden, while Pamunkey River blue catfish specialized on gizzard shad (Figure 8). In the Rappahannock River, individual blue catfish specialized on gizzard shad, white perch, other blue catfish, and mayflies (Figure 6).

Trophic niche metrics.—Trophic calculations suggest that the blue catfish is an omnivore-generalist that feeds on many trophic levels (Rodríguez-Preciado et al. 2014). TL values varied by river and blue catfish size, with a range of 2.72 – 3.55, and a mean TL = 2.90 (Table 3). Omnivory index (OI) values indicated that blue catfish consumed a variety of trophic levels, though they varied by river and fish size, with a range of 0.58 – 0.93, and a mean of 0.73 (Table 3). Diet breadth (B) values ranged from 0.10 – 0.90, with a mean of 0.63. While OI values are based on the range of trophic levels consumed, diet breadth values are based on the diversity of taxa and the %O of those prey in the diet. Smaller, non-piscivorous blue catfish (based on

ontogenetic shift analysis) had broader diets (0.49 – 0.90), but diet breadth values decreased (< 0.40) for larger, more piscivorous individuals. This may relate to individual diet specialization at larger sizes, as big fish fed primarily on gizzard shad and smaller blue catfish. While larger catfish still feed on multiple trophic levels (OI values > 0.50), their diet is dominated by a limited number of taxa (diet breadth 0.10 – 0.33).

Discussion

Blue catfish in the Chesapeake Bay are opportunistic generalists, with broad diets that reflect the seasonal and spatial variation in prey availability throughout the estuary. Diets were comprised largely of invasive aquatic vegetation and Asian clams in freshwater and oligohaline areas, while blue catfish in mesohaline areas consumed mostly mud crabs, gammarid amphipods, blue crab, and white perch. Blue catfish are typically non-selective and feed on the most abundant resources (Eggleton and Schramm 2004; Schmitt et al. 2017). The current study adheres to this pattern, as blue catfish primarily feed on abundant resources including other invasive species (see Diaz 1974; Dennison et al. 1993; Posey et al. 1993; Gillet and Schaffner 2009; Freedman 2013). Opportunism has been linked to invasion success in many other organisms (Kostrzewska and Grabowski 2003; Gherardi and Barbaresi 2008; Drown et al. 2011), and may explain the high densities of blue catfish observed in Chesapeake Bay tributaries.

Diet characterization

With over 16,000 stomachs collected, the current study is the largest and most comprehensive diet study on blue catfish to date. This amount of effort was not excessive; however, as our cumulative prey curves revealed that many stomachs were needed to adequately characterize the diet of this broadly distributed, opportunistic feeder. Most prey curves did not reach asymptotes

until 1,000 – 1,500 stomachs, and only 50 – 60% of the blue catfish stomachs contained prey, therefore as many as 3,000 individual fish would need to be collected to adequately characterize the diet of these fish in any given tidal river system. Moreover, ontogenetic diet shift analyses revealed high variation in shifts among rivers, emphasizing the importance of capturing fish of all sizes. Considering this, much of the previous work on blue catfish in the Chesapeake Bay may inadequately characterize the true diet breadth of this species. Schloesser et al. (2011) was the most comprehensive blue catfish diet study prior to this study, yet only a few hundred catfish were collected per river and all catfish were less than 600 mm fork length (FL). We highly recommend the use of cumulative prey curves to assess sample size sufficiency, especially when describing the food habits of a broadly-distributed omnivore.

Our results demonstrate that most of the blue catfish in Chesapeake Bay subestuaries are generalist mesopredators that primarily eat vegetation and invertebrates. This contradicts a previous study that labeled blue catfish as “apex predators” (MacAvoy et al. 2000), though this study had limited sampling (N=22) and no actual estimate of trophic level was made. Blue catfish are herbivore-omnivores at small sizes, and switch to piscivory at larger sizes. Throughout most of the year, blue catfish diet is dominated by vegetation and Asian clams in all four rivers. Hydrilla, Brazilian waterweed, and common waterweed were the primary vegetation species consumed, and vegetation was found in 32.93 – 51.38% of catfish stomachs. These findings are not particularly surprising, as blue catfish in their native range have broad, omnivorous diets and regularly consume aquatic macrophytes (Edds et al. 2002; Eggleton and Schramm 2004).

Blue catfish are also known to consume Asian clams regularly. In Sooner Lake, Oklahoma, blue catfish stomachs commonly contained Asian clams and zebra mussels, *Dreissena polymorpha*,

both of which are invasive in the United States (Gatlin et al. 2013). In Lake Norman, North Carolina, Asian clams comprised up to 87% of blue catfish diets by weight (Grist 2002). Gizzard shad and threadfin shad *Dorosoma petense* are the primary forage of piscivorous length groupings in both native and introduced ranges (Edds et al. 2002; Eggleton and Schramm 2004; Schmitt et al. 2017), a pattern which was also evident in the current study, where *Dorosoma spp.* were the dominant fish species consumed in terms of gravimetric contribution to the diet.

Management concerns

Predation by blue catfish on imperiled or commercially-valuable native species has been a topic of major concern within the region (CBP 2012), yet we were surprised to find that the most frequently consumed diet items are invasive to the Chesapeake Bay, primarily hydrilla, Brazilian waterweed, and Asian clams. When combined, these invasive species were found in over 60% of blue catfish stomachs across all rivers, seasons, and salinity regimes. This is probably just another example of opportunistic feeding by blue catfish, which often feed non-selectively on whatever is most abundant in the environment (Schmitt et al. 2017). Schmitt et al. (2017) expressed concerns about blue catfish predation of juvenile *Alosa* species as they migrate downriver in the fall, namely blueback herring, alewife, and American shad. These imperiled *Alosa* species were found in a maximum of 2% of stomachs during the spring (tidal freshwater areas) and in less than 1% of stomachs during the fall, which is much lower than predation by invasive flathead catfish *Pylodictus olivarus*, where *Alosa* species were found in approximately 17% of stomachs during the spring, respectively (Schmitt et al. 2017). Interestingly, predation of alewife and blueback herring by striped bass also peaked during the spring in freshwater areas (Walter and Austin 2003).

Although predation of imperiled native fish is uncommon, blue crabs were an important diet item in all rivers except the Rappahannock River. Not surprisingly, predation of blue crab was greatest in mesohaline areas, and increased during the fall and winter months, which corresponds with reduced freshwater inflow and higher salinities in tidal subestuaries of the Chesapeake Bay (Schubel and Pritchard 1987). The upriver advancement of the salt wedge is likely to increase spatial overlap between blue crabs and blue catfish, thereby increasing predation opportunities. Moreover, mature female blue crabs migrate downriver during the fall months (Aguilar et al. 2005), which may also make them more susceptible to predation. While blue crabs were typically found in less than 5% of blue catfish stomachs, percent occurrence was as high as 15–32% in mesohaline areas. Predation of blue crabs by blue catfish is not uncommon, as these species naturally overlap in the estuarine portion of the Mississippi River. In Louisiana, blue crabs were found in 21 – 50% of blue catfish stomachs collected in brackish canals (Perry 1969), while blue crabs were found in less than 5% of blue catfish stomachs from Lake Ponchartrain, a brackish estuary (Darnell 1958). These maximal values are similar to literature values for juvenile red drum *Sciaenops ocellatus*, where blue crab were found in up to 36% of stomachs in a nearby estuary (Facendola and Scharf 2012), yet are much lower when compared to another seasonal resident of the Chesapeake Bay, the Cobia *Rachycentron canadum*, where blue crabs occur in 59% of stomachs (Arendt et al. 2001). Blue crabs support the highest value fisheries in Delaware, Maryland, and Virginia (Kahn and Hessler 2005), therefore blue crab predation by invasive catfish will continue to be a topic of management concern. It is important to note; however, that the abundance of mature female blue crabs in the Chesapeake Bay continues to improve since population declines in the late 1990s (CBSAC 2016), despite increasing blue catfish abundance in tidal tributaries (Greenlee and Lim 2011).

Trophic characteristics

News sources and media outlets in the Chesapeake Bay region often portray blue catfish as “apex predators” that threaten commercially-important and imperiled native species via intense predation (e.g. Wolf 2014; Blankenship 2015; Taylor 2015; Springston 2015). These assertions were mere anecdotes; however, as no comprehensive analysis of diet or trophic position for blue catfish had been completed for Chesapeake Bay subestuaries prior to this study. In fact, all of the previous diet work for blue catfish in the Chesapeake Bay were limited to small catfish, had limited numbers of catfish, or were limited in terms of spatiotemporal scope (see MacAvoy et al. 2000; Schloesser et al. 2011; Aguilar et al. 2017; Schmitt et al. 2017).

The current study demonstrates that blue catfish occupy much lower trophic levels than has been suggested. The majority of blue catfish are primary/secondary consumers (average TL=2.90) and occupy lower trophic positions than true apex predators in the Chesapeake Bay, such as striped bass (TL= 4.70; Froese and Pauly 2016) and Flathead Catfish (TL=4.21; J. Emmel, unpublished data). Blue catfish in the Chesapeake Bay occupy a similar trophic position (average TL = 2.90) as another invasive in the region, the common carp *Cyprinus carpio* (TL = 2.96), which is an herbivore/benthic invertivore (Garcia-Berthou 2001). While larger catfish do become more piscivorous, these piscivorous length groupings only represented 20% of our sample from the James River, less than 4% of our sample from the Rappahannock River, and less than 2% of our sample from the Pamunkey and Mattaponi Rivers. Furthermore, our data is likely to overestimate proportions of piscivorous fish, as we actively targeted larger fish during our sampling due to their low abundance. The diet of these larger catfish is mostly comprised of gizzard shad, threadfin shad, and white perch, all of which are abundant species of little conservation concern in Chesapeake Bay.

Omnivory and diet breadth indices revealed that smaller catfish are highly omnivorous and opportunistic, and, while larger catfish are still omnivorous, they consume a smaller pool of resources. Blue catfish have remarkable diet plasticity, with high diet breadth averaged across all rivers ($B=0.63$). While many estuarine fish are omnivorous and capable of shifting diets to exploit temporary peaks in prey abundance (Ley et al. 1994), diet breadth values for blue catfish in the Chesapeake Bay were consistently higher than those estimated for other estuarine fishes. Akin and Winemiller (2006) calculated diet breadth for 27 fish species in Matagorda Bay, an estuary in south-central Texas. Only three species had diet breadths > 0.50 , and the highest diet breadth observed was from the clown goby *Microgobius gulosus*, which had the same diet breadth as the overall mean for blue catfish ($B=0.63$). Hajisamae et al. (2003) calculated the diet breadth for 32 fish species in the Johor Strait, which is a major estuary in southern Malaysia. Only three species had diet breadth values > 0.50 , and the highest observed came from species of grunt *Pomadasys sp.* ($B=0.68$). Blue catfish from the Rappahannock River had the impressive diet breadth ($B=0.90$), which is markedly higher than any diet breadths calculated in the aforementioned studies (Hajisamae et al. 2003; Akin and Winemiller 2006). Interestingly, blue catfish population densities appear to be highest in the Rappahannock River (Greenlee and Lim 2011), and it is possible that greater intraspecific competition has forced blue catfish to diversify their diet, a phenomenon that has been documented in other fish species (Svanbäck and Bolnick 2007).

Individual specialization

Our predator feeding strategy diagrams revealed several interesting river-specific diet specialization patterns. Large blue catfish specialized on *Dorosoma* species in the Pamunkey, James, and Rappahannock Rivers, while they specialized on menhaden in the Mattaponi River.

There was also evidence of diet specialization on detritus in the James River and mayflies in the Rappahannock River. Blue catfish were cannibalistic in all rivers, but there was evidence of cannibalistic specialization in the James and Rappahannock rivers, both of which support dense blue catfish populations (Greenlee and Lim 2011). We hypothesize that cannibalism is a density-dependent function for blue catfish, though more research would be necessary to confirm this. It is also possible that individual diet specialization in these rivers is driven by intraspecific competition (Araújo et al. 2011). In fact, previous studies have demonstrated that increases in population density, a proxy for intraspecific competition, is likely to result in increases in individual diet specialization (Svanbäck and Persson 2004; Svanbäck and Bolnick 2005; Tinker et al. 2008). Blue catfish population densities appear to be greatest in the Rappahannock River (Greenlee and Lim 2011), which is also where the highest diet breadth values were observed. It is also plausible that high variation in blue catfish growth rates is driven by individual diet specialization, as piscine specialists are likely to grow faster than detritus or vegetation specialists. Highly variable growth rates have been observed in the Chesapeake Bay (Greenlee and Lim 2011; Hilling et al. 2018) and in reservoirs in Oklahoma (Boxrucker and Kuklinski 2006), therefore individual diet specialization may be a universal life history strategy for this species, and warrants further investigation. Admittedly, predator feeding strategy diagrams are a primitive method for examining diet specialization as they provide a limited temporal scope. Future studies should utilize more advanced methods (*e.g.* stable isotope analysis) for assessing individual diet specialization of blue catfish (see Bolnick et al. 2002; Araújo et al. 2007; Vander Zanden et al. 2010; Matich et al. 2011).

Conclusions

While some argue that all non-native fish introductions should be considered “guilty until proven innocent” (Simberloff 2007), others insist that conclusions about non-native species should be based on “quantifiable empirical evidence and not a priori statements” (Gozlan 2008). Jumping to conclusions without supporting evidence is the antithesis of the scientific process, and should be avoided. Here we demonstrate that the popular narrative surrounding blue catfish is flawed, though several concerns remain. While we have demonstrated that most blue catfish are not apex predators as has been suggested by others, their incredible success is alarming for other reasons. The rapid expansion and growth of the blue catfish population in the Chesapeake Bay may be linked to opportunistic life history strategies, as blue catfish are generalists with respect to both diet and habitat. Blue catfish, like many other successful invaders (Twardochleb et al. 2013; Jackson et al. 2017), feed on multiple trophic levels with diets comprised of both plant and animal material. These omnivorous food habits place them in the middle of the food web, with direct consumptive links to a multitude of species. While much of the attention this species has received has focused on top down effects and direct predation on important resources (MacAvoy et al. 2000; Schmitt et al. 2017), we suggest that future work focus on competitive interactions and other indirect effects, as the decline in native white catfish *Ameiurus catus* is the only major ecological change that has been directly observed since the blue catfish population explosion (Schloesser et al. 2011). Moreover, it is quite possible that the remarkable abundance of blue catfish in the Chesapeake Bay is an indicator of major underlying issues with ecosystem health (MacDougall and Turkington 2005). The success of novel generalists has largely been attributed to their ability to thrive in highly altered or degraded habitats (Clavel et al. 2010). This is particularly worrying because the Chesapeake Bay is far from pristine, and human activities have resulted in widespread ecosystem changes (Boesch et al. 2001; Kemp et al. 2005; Orth et al.

2006). In essence, anthropogenic eutrophication has been linked to a major ecological shift from benthic diatom production to pelagic phytoplankton production (Kemp et al. 2005). This has been associated with substantial declines in submerged aquatic vegetation, has created anoxic and hypoxic dead zones within the estuary, and has resulted in widespread community changes (Kemp et al. 2005; Diaz and Rosenberg 2008). While nutrient loading can enhance fisheries yields to a point (Nixon and Buckley 2002), it tends to favor benthic organisms with opportunistic life histories (Diaz and Rosenberg 1995). The relationship between eutrophication and blue catfish population density should be explored on a river-specific basis, as it is quite possible that blue catfish abundance is driven by anthropogenic eutrophication. If this is the case, it may be prudent to address the underlying causes, rather than simply trying to eradicate or control the species (Didham 2007).

While blue catfish do not routinely consume imperiled fish species, their predatory impact cannot be assessed without credible estimates of population biomass and size structure (Schmitt et al. 2017), and a population estimate was recently completed for a brackish segment of the James River (Fabrizio et al. 2017). Blue catfish population densities appear to be substantially higher in the Chesapeake Bay than in the native range. Electrofishing capture rates in the Rappahannock River can exceed 6,000 fish/hr (Greenlee and Lim 2011), while capture rates using the same methods in Oklahoma peaked at approximately 700 fish/hr (Boxrucker and Kuklinski et al. 2006). At high enough densities, blue catfish could still exert sizable predatory impacts on imperiled fish species, even at low predation rates.

Considering this, future research should explore spatiotemporal patterns in the predation of species of concern, including American shad, river herring, blue crab, and American eel. Furthermore, in situ estimates of blue catfish maximum daily ration are still needed for the

Chesapeake Bay region, as many introduced species have elevated consumption rates when introduced into a new environment (McKnight et al. 2016). Population estimates (like Fabrizio et al. 2017), consumption estimates, and diet information can then be integrated to quantify predatory impacts on species of concern, which will be necessary for the future management of blue catfish in the Chesapeake Bay.

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Tables and Figures

Table 1. Percent occurrence (%O), percent by weight (%W), and prey-specific index of relative importance (%PSIRI) for nonfish diet items found in blue catfish stomachs (N=9,823) collected from the James, Pamunkey, Mattaponi, and Rappahannock Rivers in eastern Virginia, USA.

Prey	James River			Pamunkey River			Mattaponi River			Rappahannock River		
	%O	%W	%PSIRI	%O	%W	%PSIRI	%O	%W	%PSIRI	%O	%W	%PSIRI
Amphibia												
Ranidae												
<i>Rana spp.</i>	0.22%	<0.10%	<1.00%	0.17%	<0.10%	<1.00%	0.23%	0.13%	<1.00%	0.45%	0.29%	<1.00%
<i>Rana clamitans</i>	<0.10%	<0.10%	<1.00%	-	-	-	-	-	-	-	-	-
Amphipoda												
Corophiidae	-	-	-	0.80%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%	-	-	-
<i>Leptocheirus plumulosus</i>	0.22%	<0.10%	<1.00%	0.10%	<0.10%	<1.00%	0.18%	<0.10%	<1.00%	-	-	-
Gammaidae	2.58%	0.12%	<1.00%	6.37%	0.75%	4.45%	5.60%	0.91%	4.16%	3.44%	0.41%	2.18%
Annelida												
Hirudinea	<0.10%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%	-	-	-	<0.10%	<0.10%	<1.00%
unidentified annelid	0.18%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%	0.10%	<0.10%	<1.00%	0.19%	<0.10%	<1.00%
Anthropogenic debris												
carrots	<0.10%	<0.10%	<1.00%	-	-	-	-	-	-	-	-	-
condom	<0.10%	<0.10%	<1.00%	-	-	-	-	-	-	-	-	-
corn	0.21%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%	-	-	-	-	-	-
chewing gum	<0.10%	<0.10%	<1.00%	-	-	-	-	-	-	-	-	-
chicken bones	0.18%	<0.10%	<1.00%	-	-	-	0.10%	<0.10%	<1.00%	-	-	-
cut bait	<0.10%	0.15%	<1.00%	-	-	-	-	-	-	-	-	-
fishing hook	0.37%	<0.10%	<1.00%	-	-	-	0.10%	<0.10%	<1.00%	0.19%	<0.10%	<1.00%
fishing sinker	<0.10%	<0.10%	<1.00%	-	-	-	-	-	-	-	-	-
hot dog	<0.10%	<0.10%	<1.00%	-	-	-	-	-	-	-	-	-
maxi pad	<0.10%	<0.10%	<1.00%	-	-	-	-	-	-	-	-	-
plastic waste	0.44%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%	-	-	-	0.26%	0.02%	<1.00%
plastic worm	-	-	-	<0.10%	<0.10%	<1.00%	-	-	-	-	-	-
peanuts	0.15%	<0.10%	<1.00%	-	-	-	-	-	-	-	-	-
Aquatic vegetation				32.93%	6.60%	18.27%	51.38%	44.76%	42.32%	40.78%	29.47%	33.22%
Aves												
unidentified bird remains	0.15%	<0.10%	<1.00%	-	-	-	-	-	-	-	-	-
Cnidaria												
Ulmariidae												

	<i>Aurelia aurita</i>	0.18%	<0.10%	<1.00%	-	-	-	-	-	-	<0.10%	<0.10%	<1.00%
Decapoda													
	Cambaridae												
	<i>Orconectes limosus</i>	1.22%	0.24%	<1.00%	0.93%	0.91%	<1.00%	1.15%	1.32%	<1.00%	0.78%	0.63%	<1.00%
	<i>Procambarus spp.</i>	<0.10%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%	0.13%	<0.10%	<1.00%
	Palaemonidae												
	<i>Palaemonetes pugio</i>	<0.10%	<0.10%	<1.00%	0.17%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%	-	-	-
	Panopeidae												
	<i>Dyspanopues sayi</i>	<0.10%	<0.10%	<1.00%	-	-	-	-	-	-	-	-	-
	<i>Panopeus herbstii</i>	0.52%	<0.10%	<1.00%	1.87%	0.53%	<1.00%	4.72%	1.42%	2.55%	0.13%	<0.10%	<1.00%
	<i>Rithropanopeus harrisii</i>	1.07%	0.08%	<1.00%	6.06%	1.66%	3.31%	6.56%	2.37%	4.75%	0.13%	<0.10%	<1.00%
	<i>Hexapanopeus sp</i>	-	-	-	<0.10%	<0.10%	<1.00%	-	-	-	-	-	-
	Portunidae												
	<i>Callinectes sapidus</i>	6.23%	2.78%	3.44%	4.10%	5.50%	2.78%	3.26%	5.98%	2.43%	0.78%	1.21%	<1.00%
	Ucinae												
Diplopoda													
	<i>Uca minax</i>	<0.10%	<0.10%	<1.00%	0.48%	0.26%	<1.00%	<0.10%	1.20%	<1.00%	-	-	-
Emydidae													
	<i>Trachemys scripta elegans</i>	<0.10%	<0.10%	<1.00%	-	-	-	-	-	-	-	-	-
Insecta													
	Coleoptera	0.37%	<0.10%	<1.00%	0.21%	<0.10%	<1.00%	0.37%	0.10%	<1.00%	0.71%	<0.10%	<1.00%
	Diptera	<0.10%	<0.10%	<1.00%	0.28%	<0.10%	<1.00%	0.18%	<0.10%	<1.00%	4.22%	0.32%	<1.00%
	Ephemeroptera	<0.10%	<0.10%	<1.00%	0.55%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%	2.40%	0.33%	2.12%
	Hemiptera	0.12%	<0.10%	<1.00%	-	-	-	0.23%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%
	Hymenoptera	<0.10%	<0.10%	<1.00%	-	-	-	-	-	-	-	-	-
	Megaloptera	0.11%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%	0.58%	<0.10%	<1.00%
	Odonata	0.81%	<0.10%	<1.00%	0.10%	<0.10%	<1.00%	0.60%	0.15%	<1.00%	0.84%	<0.10%	<1.00%
	Plecoptera	0.11%	<0.10%	<1.00%	-	-	-	-	-	-	-	-	-
	Trichoptera	0.11%	<0.10%	<1.00%	-	-	-	-	-	-	0.19%	<0.10%	<1.00%
Isopoda													
	<i>Cyathura polita</i>	0.18%	<0.10%	<1.00%	0.38%	<0.10%	<1.00%	1.38%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%
	Cymothoidae	-	-	-	<0.10%	<0.10%	<1.00%	-	-	-	-	-	-
Mammalia													
	Cricetidae												
	<i>Ondatra zibethicus</i>	<0.10%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%	-	-	-	<0.10%	0.12%	<1.00%
	unidentified mammal remains	0.26%	0.11%	<1.00%	-	-	-	<0.10%	<0.10%	<1.00%	-	-	-
Mollusca													
	Acteonidae												
	<i>Rictaxis punctostriatus</i>	-	-	-	-	-	-	<0.10%	<0.10%	<1.00%	-	-	-
	Balanidae												

	<i>Balanus spp.</i>	<0.10%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%	-	-	-
Cerithiidae	<i>Bittium varium</i>	0.66%	<0.10%	<1.00%	-	-	-	-	-	-	2.73%	1.34%	2.24%
Cyrenidae	<i>Corbicula fluminea</i>	6.08%	0.68%	3.98%	13.39%	9.58%	9.55%	13.90%	17.72%	11.06%	16.18%	5.07%	12.00%
Dreissenidae	<i>Mytilopsis leucophaeata</i>	1.07%	<0.10%	<1.00%	0.17%	<0.10%	<1.00%	0.32%	<0.10%	<1.00%	-	-	-
	unidentified Dreissenid	<0.10%	<0.10%	<1.00%	-	-	-	-	-	-	-	-	-
Hydrobiidae	<i>Hydrobia spp.</i>	<0.10%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%	-	-	-	-	-	-
Lymnaeidae		0.33%	0.11%	<1.00%	<0.10%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%	2.34%	0.70%	1.93%
Mactridae													
Mytilidae	<i>Rangia spp.</i>	0.18%	<0.10%	<1.00%	<0.10%	0.21%	<1.00%	0.18%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%
	<i>Geukensia demissa</i>	<0.10%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%	-	-	-
Planorbidae		<0.10%	<0.10%	<1.00%	0.87%	<0.10%	<1.00%	-	-	-	0.13%	<0.10%	<1.00%
Solecurtidae		<0.10%	<0.10%	<1.00%	-	-	-	-	-	-	0.13%	<0.10%	<1.00%
Sphaeriidae		0.22%	<0.10%	<1.00%	0.42%	<0.10%	<1.00%	0.14%	0.21%	<1.00%	0.19%	<0.10%	<1.00%
Tellinidae													
Unionidae	<i>Macoma spp.</i>	0.66%	<0.10%	<1.00%	0.17%	<0.10%	<1.00%	5.09%	1.75%	<1.00%	1.17%	0.15%	<1.00%
	<i>Anodonta spp.</i>	<0.10%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%	0.32%	0.17%	<1.00%	0.71%	<0.10%	<1.00%
	<i>Lampsilis sp.</i>	0.67%	<0.10%	<1.00%	0.28%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%
Viviparidae		<0.10%	<0.10%	<1.00%	0.17%	<0.10%	<1.00%	-	-	-	0.52%	0.23%	<1.00%
	unidentified bivalve	<0.10%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%	-	-	-
Detritus		4.35%	1.09%	3.26%	0.66%	0.24%	<1.00%	2.57%	0.65%	1.37%	5.78%	0.83%	1.90%
Serpentes	unidentified snake	<0.10%	<0.10%	<1.00%	-	-	-	-	-	-	-	-	-

Table 2. Percent occurrence (%O), percent by weight (%W), and prey-specific index of relative importance (%PSIRI) for fish prey found in blue catfish stomachs (N=9,823) collected from the James, Pamunkey, Mattaponi, and Rappahannock Rivers in eastern Virginia, USA.

Prey	James River			Pamunkey River			Mattaponi River			Rappahannock River		
	%O	%W	%PSIRI	%O	%W	%PSIRI	%O	%W	%PSIRI	%O	%W	%PSIRI
Actinopterygii												
Achiridae												
<i>Trinectes maculatus</i>	0.15%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%	<0.10%	0.16%	<1.00%	0.13%	0.35%	<1.00%
Anguillidae												
<i>Anguilla rostrata</i>	1.73%	0.56%	<1.00%	0.17%	0.56%	<1.00%	0.23%	0.46%	<1.00%	0.26%	0.63%	<1.00%
Atherinopsidae												
<i>Menidia menidia</i>	<0.10%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%	-	-	-	-	-	-
Catostomidae												
<i>Moxostoma macrolepidotum</i>	<0.10%	<0.10%	<1.00%	-	-	-	-	-	-	-	-	-
Centrarchidae												
<i>Lepomis gibbosus</i>	<0.10%	<0.10%	<1.00%	-	-	-	-	-	-	-	-	-
<i>Lepomis macrochirus</i>	0.11%	0.26%	<1.00%	-	-	-	-	-	-	-	-	-
<i>Lepomis microlophus</i>	<0.10%	<0.10%	<1.00%	-	-	-	-	-	-	-	-	-
<i>Lepomis spp.</i>	<0.10%	0.14%	<1.00%	<0.10%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%	<0.10%	0.18%	<1.00%
<i>Micropterus salmoides</i>	<0.10%	<0.10%	<1.00%	-	-	-	-	-	-	0.13%	<0.10%	<1.00%
Clupeidae												
<i>Alosa spp.</i>	0.22%	1.15%	<1.00%	-	-	-	<0.10%	<0.10%	<1.00%	-	-	-
<i>Alosa aestivalis</i>	0.59%	1.45%	<1.00%	<0.10%	0.10%	<1.00%	<0.10%	0.10%	<1.00%	<0.10%	0.10%	<1.00%
<i>Alosa medocris</i>	0.37%	3.83%	<1.00%	<0.10%	0.74%	<1.00%	-	-	-	-	-	-
<i>Alosa pseudoharengus</i>	0.63%	1.28%	<1.00%	<0.10%	<0.10%	<1.00%	<0.10%	0.22%	<1.00%	0.45%	0.87%	<1.00%
<i>Alosa sapidissima</i>	<0.10%	0.56%	<1.00%	<0.10%	6.59%	<1.00%	<0.10%	3.54%	<1.00%	0.19%	6.16%	<1.00%
<i>Brevoortia tyrannus</i>	1.00%	0.42%	1.01%	0.97%	3.45%	<1.00%	1.38%	5.00%	1.26%	0.19%	1.12%	<1.00%
<i>Dorosoma cepedianum</i>	7.96%	52.20%	7.32%	1.42%	13.08%	1.19%	1.15%	15.78%	1.82%	1.88%	48.77%	1.64%
<i>Dorosoma pretense</i>	1.70%	2.15%	1.57%	-	-	-	-	-	-	-	-	-
<i>Dorosoma spp.</i>	1.11%	1.20%	1.04%	-	-	-	-	-	-	-	-	-
Cyprinidae												
<i>Carpoides cyprinus</i>	<0.10%	<0.10%	<1.00%	-	-	-	-	-	-	-	-	-
<i>Cyprinus carpio</i>	0.11%	0.89%	<1.00%	-	-	-	-	-	-	-	-	-
<i>Unidentified cyprinid</i>	0.22%	2.20%	<1.00%	<0.10%	<0.10%	<1.00%	-	-	-	-	-	-
<i>Hybognathus regius</i>	0.18%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%	0.14%	0.20%	<1.00%	<0.10%	<0.10%	<1.00%
<i>Notropis hudsonius</i>	0.26%	<0.10%	<1.00%	-	-	-	<0.10%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%
Ictaluridae												
<i>Ameiurus catus</i>	<0.10%	<0.10%	<1.00%	-	-	-	-	-	-	-	-	-
<i>Ameiurus nebulosus</i>	-	-	-	<0.10%	0.16%	<1.00%	-	-	-	-	-	-
<i>Ictalurus furcatus</i>	1.44%	6.12%	1.26%	0.38%	6.02%	<1.00%	0.46%	2.80%	<1.00%	1.17%	5.24%	1.00%
<i>Ictalurus punctatus</i>	<0.10%	0.63%	<1.00%	-	-	-	-	-	<0.10%	0.48%	<1.00%	-

	<i>Ictalurus spp.</i>	0.70%	0.74%	<1.00%	0.21%	0.06%	<1.00%	-	-	-	-	-	-	-
	<i>Noturus gyrinus</i>	-	-	-	-	-	-	-	-	-	<0.10%	<0.10%	<0.10%	<1.00%
	<i>Pylodictis olivaris</i>	<0.10%	<0.10%	<1.00%	-	-	-	<0.10%	<0.10%	<1.00%	-	-	-	-
Lepisosteidae	<i>Lepisosteus osseus</i>	<0.10%	0.41%	<1.00%	<0.10%	0.21%	<1.00%	<0.10%	0.35%	<1.00%	0.26%	0.56%	<1.00%	
Moronidae	<i>Morone americana</i>	7.07%	4.94%	5.74%	0.69%	2.16%	<1.00%	0.64%	1.63%	<1.00%	1.49%	2.15%	1.29%	
	<i>Morone saxatilis</i>	<0.10%	0.31%	<1.00%	-	-	-	<0.10%	2.33%	<1.00%	<0.10%	<0.10%	<1.00%	
Percidae	<i>Etheostoma flabellare</i>	<0.10%	<0.10%	<1.00%	-	-	-	-	-	-	-	-	-	-
	<i>Etheostoma olmstedi</i>	0.22%	<0.10%	<1.00%	-	-	-	-	-	-	-	-	-	-
	<i>Etheostoma spp.</i>	<0.10%	<0.10%	<1.00%	-	-	-	-	-	-	<0.10%	<0.10%	<1.00%	
	<i>Perca flavescens</i>	0.11%	<0.10%	<1.00%	-	-	-	-	-	-	-	-	-	-
Sciaenidae	<i>Leiostomus xanthurus</i>	<0.10%	<0.10%	<1.00%	-	-	-	<0.10%	<0.10%	<1.00%	-	-	-	-
	<i>Micropogonias undulatus</i>	-	-	-	-	-	-	<0.10%	<0.10%	<1.00%	-	-	-	-
	unidentified ray-finned fish	11.98%	4.72%	7.08%	4.46%	1.78%	2.49%	5.18%	1.67%	3.31%	5.26%	2.61%	3.99%	
Petromyzontida	Petromyzontidae													
	<i>Petromyzon marinus</i>	0.11%	0.33%	<1.00%	-	-	-	-	-	-	-	-	-	-

Table 3. Trophic level, standard error, omnivory index, and diet breadth values for piscivorous and non-piscivorous blue catfish collected from the James, Pamunkey, Mattaponi, and Rappahannock Rivers in eastern Virginia, USA.

River	Length	Trophic Level	Standard Error	Omnivory Index	Diet Breadth
James					
	All	3.152	0.965	0.932	0.582
	<500 mm	2.872	0.932	0.869	0.634
	>500 mm	3.552	0.866	0.749	0.105
Pamunkey					
	All	2.736	0.823	0.678	0.388
	<900 mm	2.717	0.817	0.667	0.474
	>900 mm	3.027	0.865	0.749	0.195
Mattaponi					
	All	2.887	0.810	0.656	0.636
	<900 mm	2.863	0.807	0.651	0.643
	>900 mm	3.277	0.759	0.575	0.325
Rappahannock					
	All	2.841	0.800	0.640	0.896
	<600 mm	2.784	0.777	0.603	0.898
	>600 mm	3.444	0.796	0.634	0.194

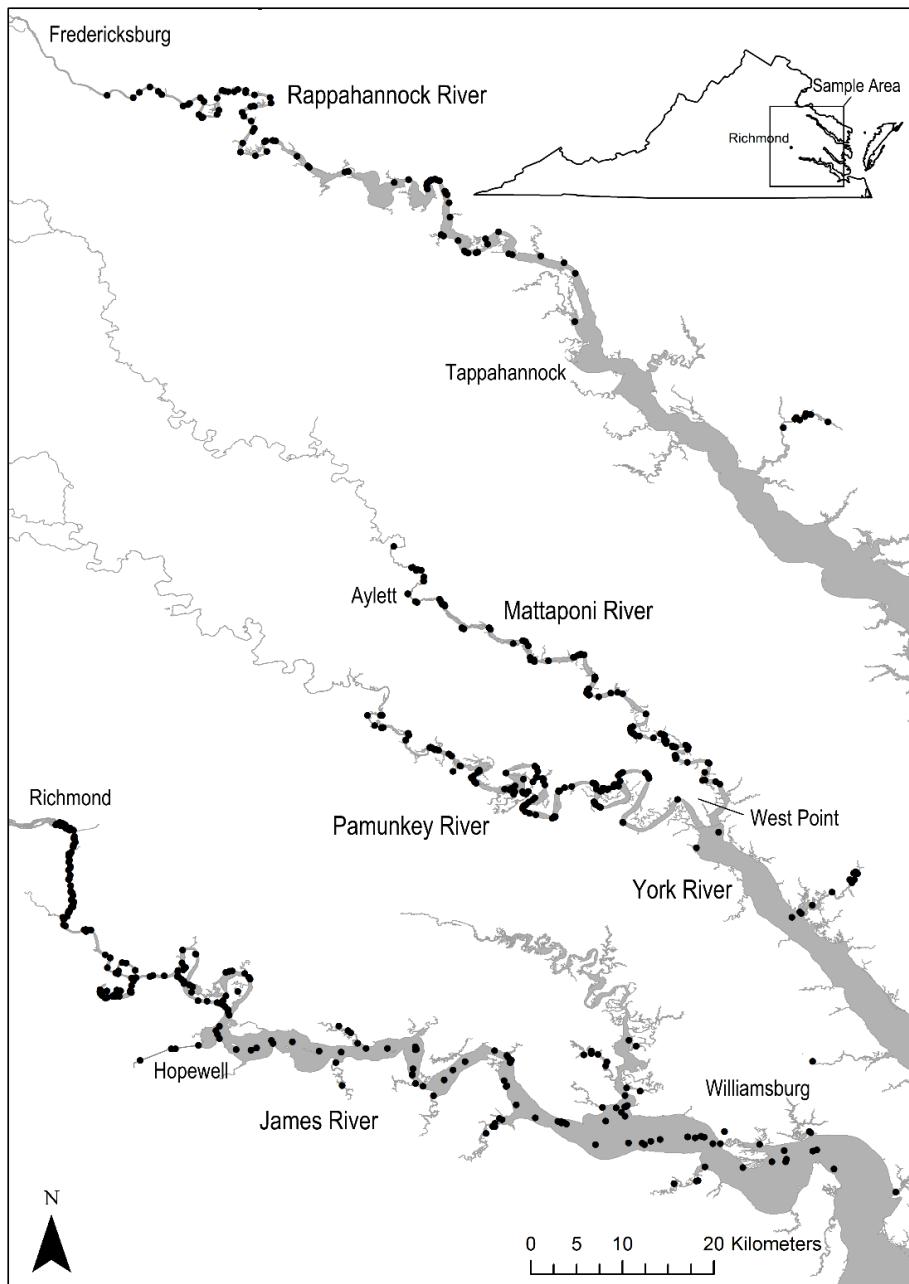


Figure 1. Blue catfish ($N=16,110$) were captured at 698 sites on the James River, Pamunkey River, Mattaponi River, and Rappahannock River in eastern Virginia, USA. Dots represent capture locations. Fish were sampled throughout the year and throughout all salinity zones using a stratified random sampling design.

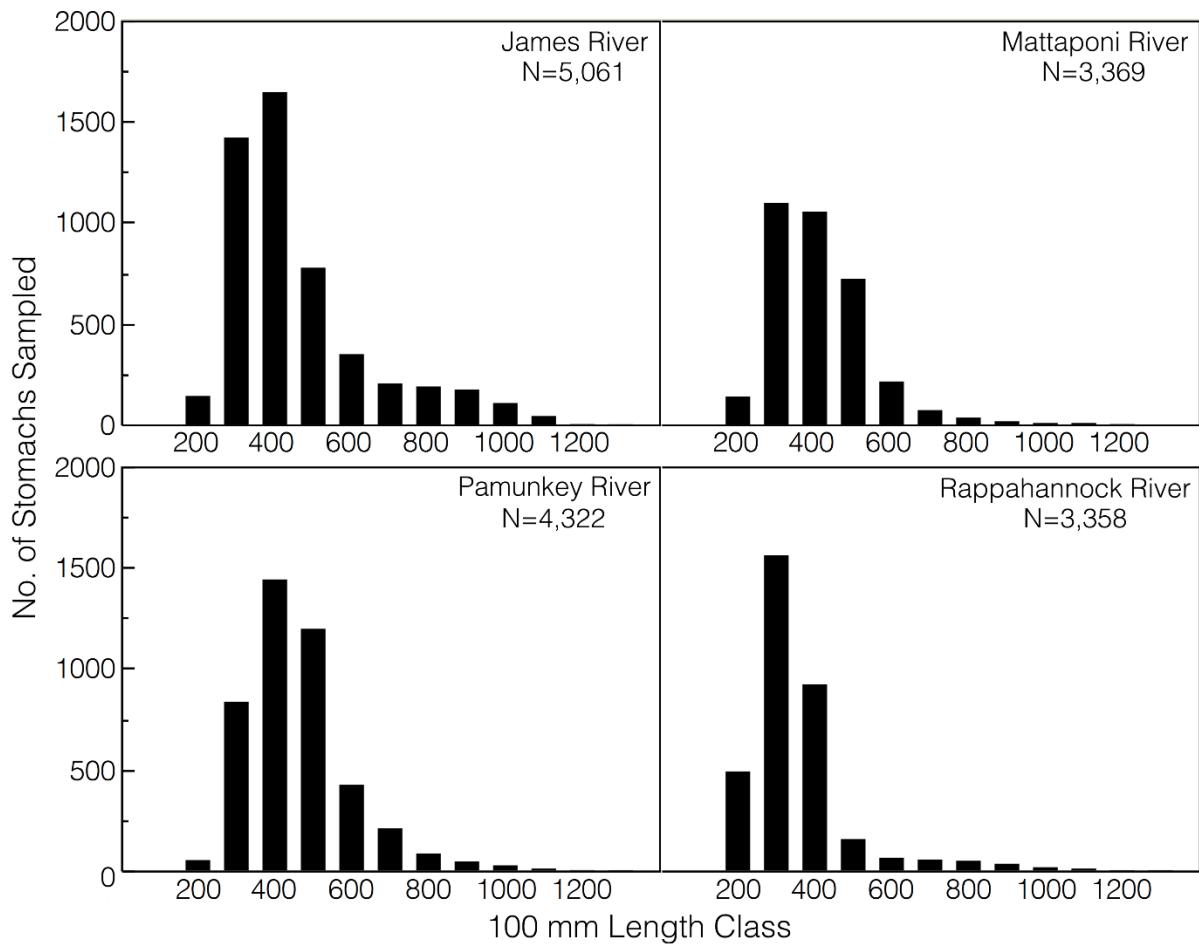


Figure 2. Length frequency histograms for blue catfish (N=16,110) captured in the James River, Pamunkey River, Mattaponi River, and Rappahannock River in eastern Virginia, USA. Blue catfish ranged in size from 206 – 1343 mm total length.

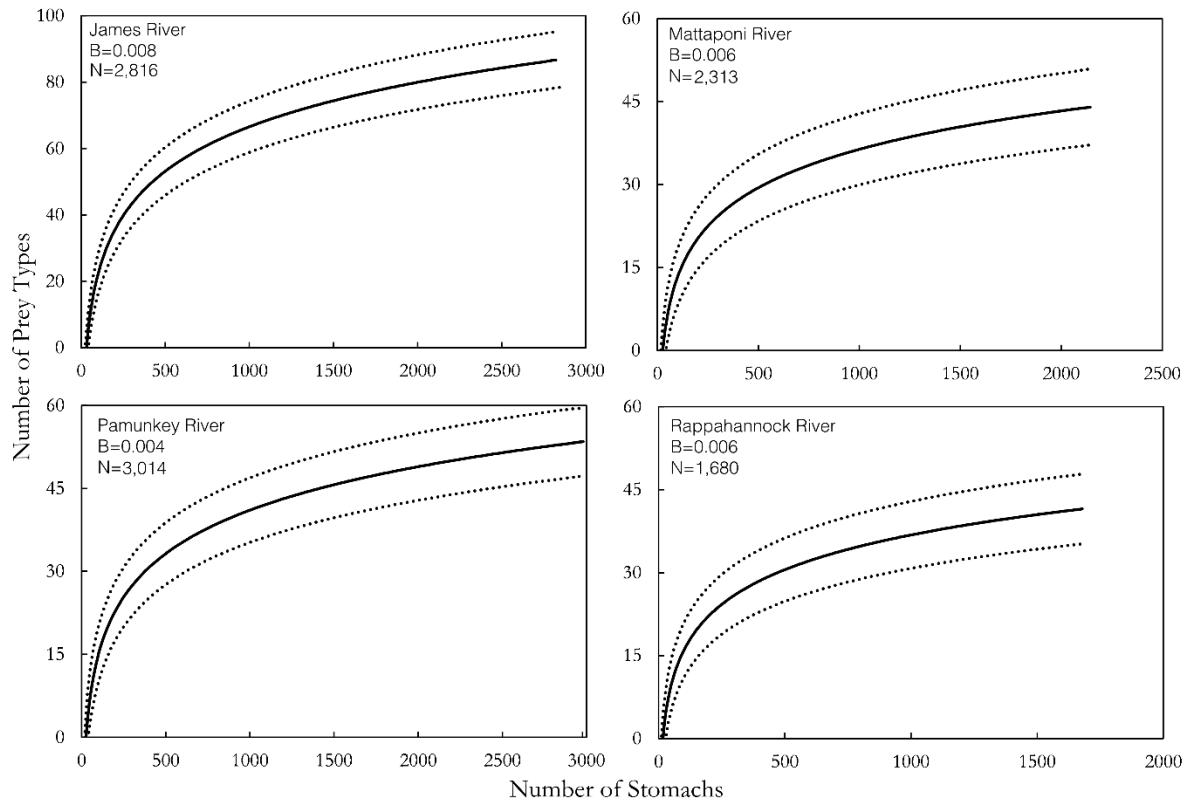


Figure 3. Cumulative prey curves (solid lines) and 95% confidence intervals (dashed lines) based on stomach content data from blue catfish ($N=9,823$) collected from the James, Pamunkey, Mattaponi, and Rappahannock Rivers. All slopes (B) reached asymptotes, indicating that sampling was sufficient for diet description ($B < 0.05$).

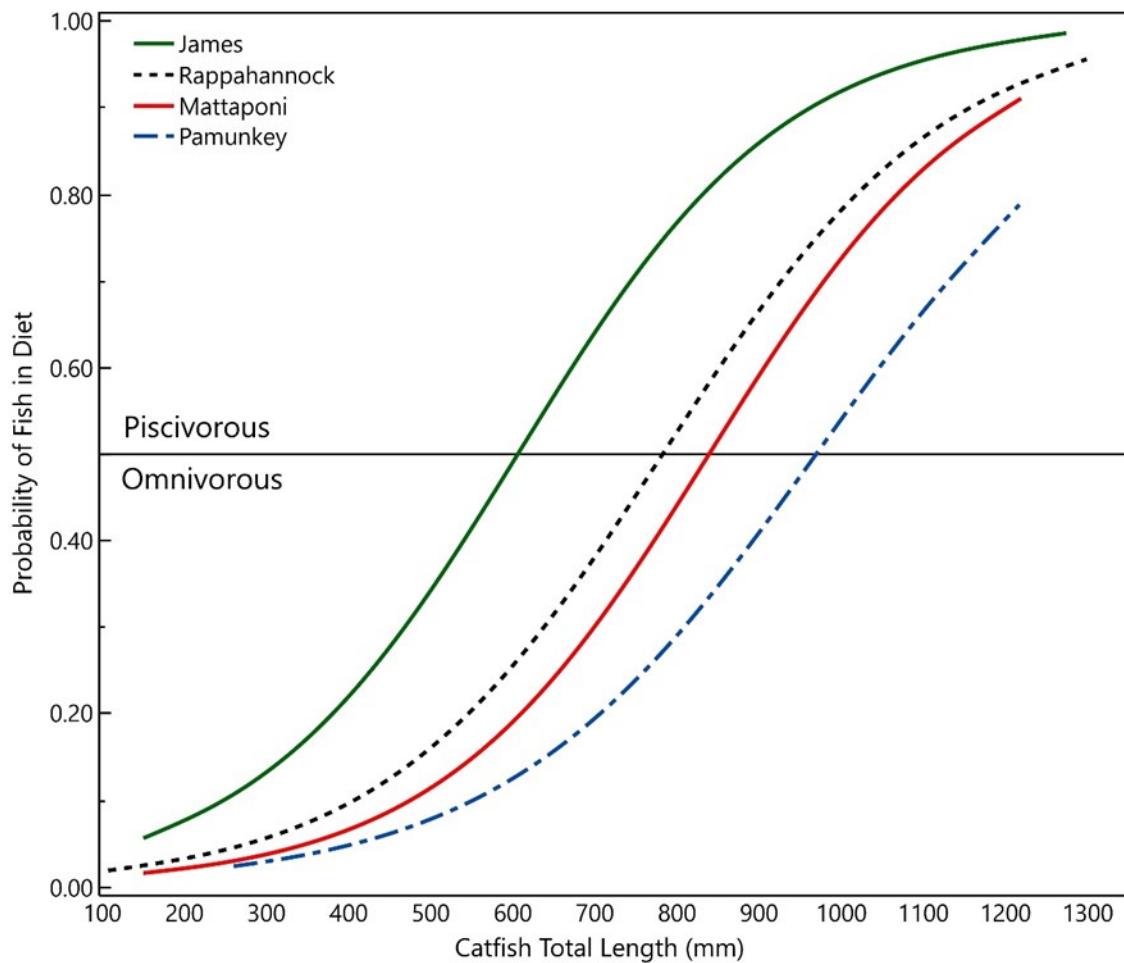


Figure 4. Logistic regression was used to model the binary occurrence of fish in the diet (1=present, 0=absent) versus the total length of the catfish (mm). Blue catfish underwent significant diet shifts to piscivory in all rivers ($P<0.01$), though the length at which fish became piscivorous varied by river. For simplicity, we define “piscivorous” as the length at which fish prey are predicted to occur in $\geq 50\%$ of blue catfish stomachs, rounded to the nearest 100 mm. Based on this criteria, blue catfish became piscivorous at 500 mm TL in the James River, 700 mm TL in Rappahannock River, 800 mm TL in the Mattaponi River, and 900 mm TL in the Pamunkey River.

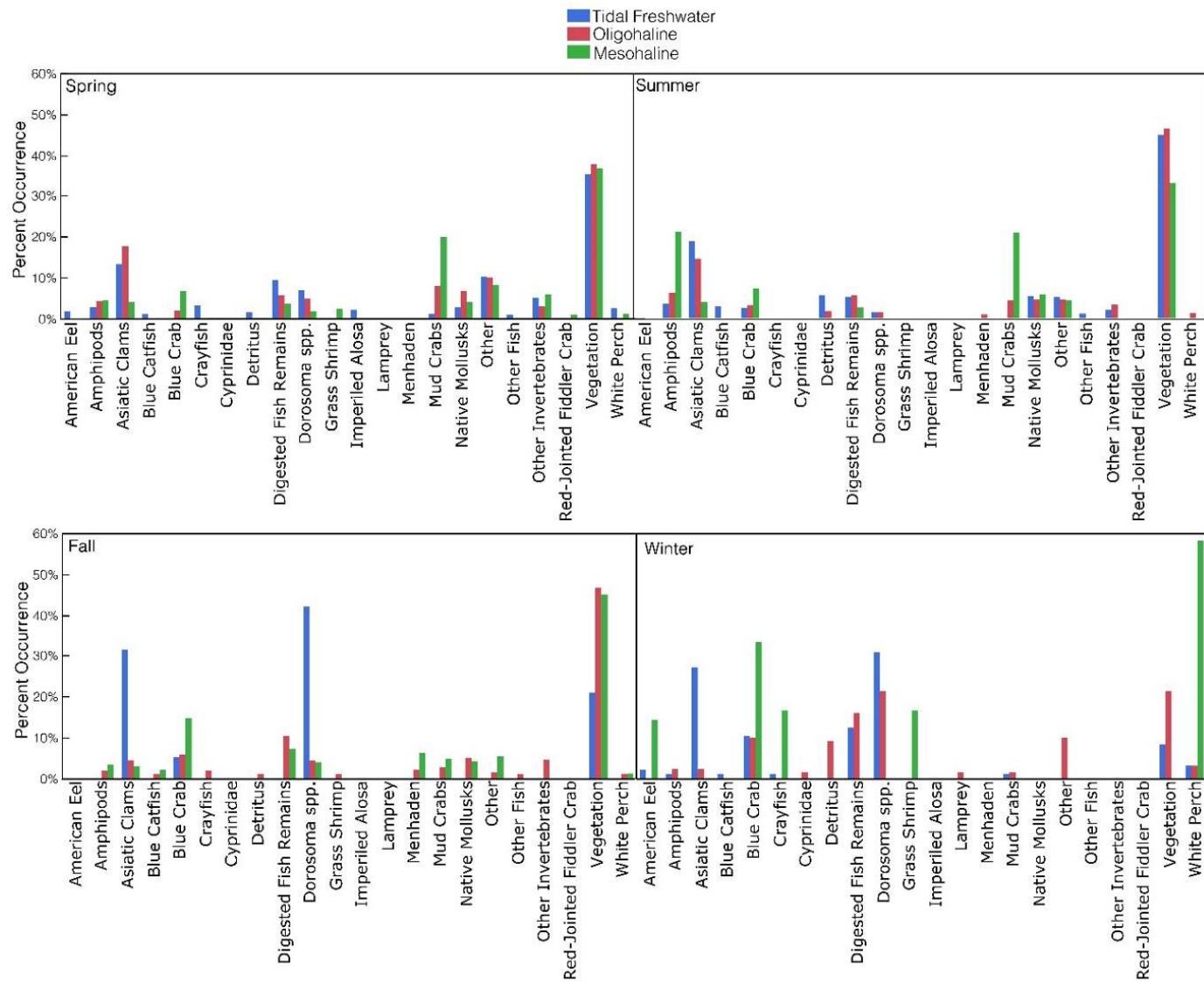


Figure 5. Diets of 9,823 blue catfish by season and salinity regime. Food types that occurred in >1% of stomachs by season or salinity zone have their own category, while all rare prey (<1%) were combined into a single category ("Other"). "Spring" includes stomachs from March – May, "Summer" includes stomachs from June – August, "Fall" includes stomachs from September – November, and "Winter" included stomachs from December – February. Stomachs were collected from the James, Pamunkey, Mattaponi, and Rappahannock Rivers in eastern Virginia, USA.

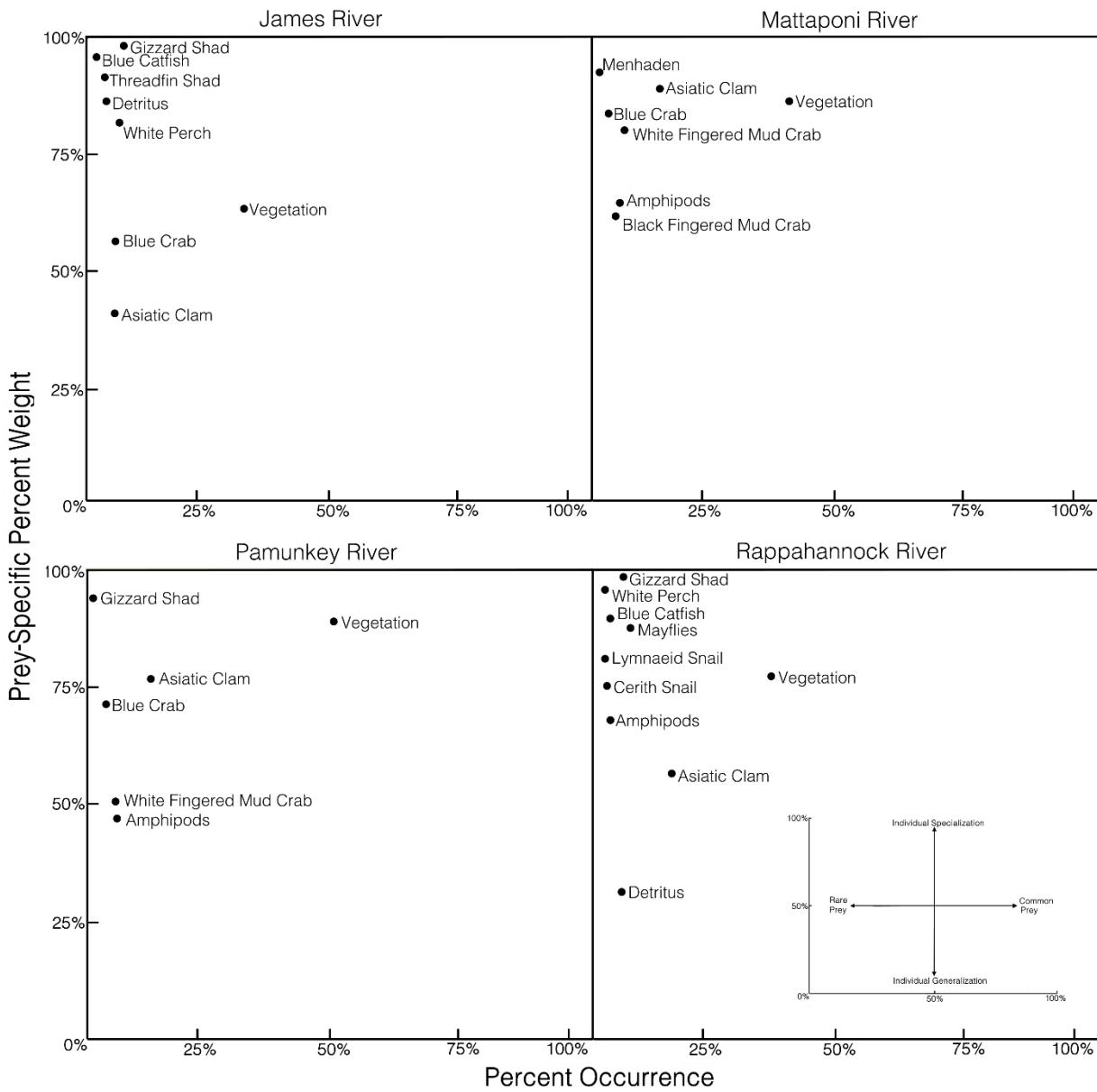


Figure 6. Predator feeding strategy diagrams (Amundsen 1996) for blue catfish collected from the James, Pamunkey, Mattaponi, and Rappahannock Rivers in eastern Virginia, USA. Prey-specific percent weight is defined as the percent weight of item “j” in all stomachs containing item “j”. Feeding strategy interpretation guide included in bottom right panel.

Chapter 4: Modeling the Predation Dynamics of Invasive Blue Catfish in the Chesapeake Bay: A Special Focus on Imperiled and Commercially-Valuable Native Biota

Introduction

The introduction and establishment of invasive species are central to the global biodiversity crisis (Vitousek et al. 1997; Mack et al. 2000; Davis 2011). Invasive species cause billions in economic damages annually, and can result in native species declines and extinctions in recipient ecosystems (Lockwood et al. 2011). Some introduced fishes have remarkable ecological impacts, restructuring native communities through competitive interactions or direct predation (Helfman 2007; Albins and Hixon 2008). Because of this, feeding ecology is a primary determinant for predicting how invasive species will affect receiving ecosystems (Brandner et al. 2013; Dick et al. 2014; Garvey and Whiles 2016).

The blue catfish *Ictalurus furcatus* is the largest North American catfish (Ictaluridae) species, and is one of the most prolific invasive fishes in southeastern Atlantic slope (USA) drainages (Schmitt et al. 2017). The blue catfish has been widely stocked outside of its native range (Mississippi River basin) for recreational fishing purposes (Graham 1999), and were introduced to Virginia tidal rivers during the 1970s (Greenlee and Lim 2011). Blue catfish populations expanded rapidly during the late 1990s, prompting concern and subsequent management action (Fabrizio et al. 2017). Blue catfish populations have expanded from tidal freshwater areas into oligohaline and mesohaline portions of the estuary (Greenlee and Lim 2011), which may be problematic since these brackish areas serve as spawning and nursery habitat for many anthropogenically important marine and estuarine species (MacAvoy et al. 2009; Magoro et al. 2015).

In recent decades, populations of several key native fish species have declined in the Chesapeake Bay, including Atlantic sturgeon *Acipenser oxyrinchus*, American shad *Alosa sapidissima*, river herring (*A. aestivalis* and *A. pseudoharengus*), and America eel *Anguilla rostrata* (Haro et al. 2000; Niklitschek et al. 2005; Limburg and Waldmen 2009). The Chesapeake Bay is far from pristine, and anthropogenic activities have resulted in major ecological changes including the widespread loss of aquatic macrophytes, increased turbidity, and frequent hypoxic and anoxic events (Kemp et al. 2005). However, managers are concerned that predation by invasive blue catfish may result in further declines. While not a rare species, there is also concern about predation of blue crab *Callinectes sapidus*, which support lucrative commercial fisheries in Virginia, Maryland, and Delaware (Paolisso 2002). Other studies have shown that blue catfish are consuming these species, with the exception of Atlantic sturgeon (Schmitt et al. 2017; Schmitt et al. 2018, *in press*). While blue catfish in the Chesapeake Bay have remarkably broad diets that include vegetation, fish, mollusks, crustaceans, birds, terrestrial mammals, reptiles, amphibians, and various invertebrates, the factors that drive dietary variation have not yet been identified (Schmitt et al. 2017). Furthermore, blue catfish predation dynamics of imperiled species like American shad and American eel are not well understood.

While a substantial body of literature is dedicated to factors that drive invasion success (Catford et al. 2009; Blackburn et al. 2011), less work has focused on the impact phase of invasion (Fei et al. 2016) and most studies produce speculative results (Simberloff et al. 2013). This is especially the case for aquatic invasives, where more observational and experimental studies are urgently needed (Garcia-Berthou 2007; Layman and Allgeier 2012; Brandner et al. 2013). While diet studies are not necessarily direct measures of impact, they are commonly used to determine which biota are likely to be affected by an introduced predator (Caut et al. 2007; Layman and

Allgeier 2012). Considering this, the primary objectives of this study were twofold. First, we used multivariate approaches to describe the magnitude and relative influence of various factors (season, salinity, and catfish size) on blue catfish diet, based on previous work. Because blue catfish are opportunistic, non-selective feeders at adult life stages (Schmitt et al. 2017), we expected diet to vary with season and salinity, which influence the relative abundance of organisms in the estuary (Wagner 1999; Jung and Houde 2003). Furthermore, other studies have

demonstrated that blue catfish undergo ontogenetic diet shifts to piscivory (Schmitt et al. 2017; Schmitt et al. 2018, *in press*); therefore, we anticipated that diet would change with catfish size. Second, we incorporated these factors into statistical models quantifying blue catfish predation on species of concern, including American shad, American eel, alewife, blueback herring, and blue crab, all of which are imperiled or commercially-valuable species in Chesapeake Bay.

Methods

Study area.—The Chesapeake Bay is the largest estuary in the United States with a surface area of $1.15 \times 10^4 \text{ km}^2$ and a total volume of 70 km^3 (Shiah and Ducklow 1994). While blue catfish are now found in all tributaries major tributaries of the Chesapeake Bay (Schloesser et al. 2011), many populations are still in the early stages of establishment and support low densities of fish (Aquila et al. 2017). Considering this, we focused our efforts on the James, Pamunkey, Mattaponi, and Rappahannock Rivers in eastern Virginia (Figure 1). These rivers were stocked with hundreds of thousands of blue catfish from 1973-1985, and now contain well-established populations that include mature individuals (Greenlee and Lim 2011).

Field methods.—Each river was divided into three strata according to average fall surface salinities from 1985 – 2016 (CBP 2016), including tidal freshwater stretches (0 – 0.5 practical salinity units, PSU), oligohaline stretches (0.6 – 5 PSU), and mesohaline stretches (5 – 18 PSU). We stratified by fall salinities since density stratification is common during the spring and summer months, yet is more stable during the fall (Shiah and Ducklow 1994). Each stratum was divided into 2-km sections, which were numbered, and then a random number generator was used to select each sampling location. From April - October, a minimum of two randomly selected sections were sampled monthly within each stratum for all four rivers, with near-shore and main channel sampling occurring at each site. Blue catfish were sampled using low-frequency, pulsed-DC electrofishing (5 – 25 hz; 100 – 400 volts), as it captures blue catfish of all sizes (Bodine and Shoup 2010) and is extremely effective in Virginia’s tidal rivers (Greenlee and Lim 2011; Schmitt and Orth 2015).

Upon capture, fish were immediately placed in a 150 gallon aerated livewell, and stomach contents were extracted within 30 minutes of capture to prevent regurgitation (Garvey and Chipps 2012). Diet contents were extracted by either excising the stomachs or with pulsed gastric lavage, which has been demonstrated to be highly effective for extracting diet contents from blue catfish (Waters et al. 2004). Date, time, water temperature, salinity, and coordinates are recorded for each sampling event. Fish total weight and length were also recorded and diet contents are placed on ice and later frozen.

Lab methods.—In the laboratory, stomachs were thawed, and stomach contents were blotted dry with a paper towel (Schmitt et al. 2017). Prey items were then weighed, counted, and identified to the lowest possible taxon. Digested fish remains that lacked morphological distinctiveness were identified using DNA barcoding techniques. This enabled us to identify 70% - 80% of fish

prey that were unidentifiable by gross morphology, excluding instances where only bones or scales remained. Our DNA barcoding methods are fully described in Moran et al. (2015) and Schmitt et al. (2017).

Modeling factors that influence blue catfish diet.—Blue catfish populations extend from tidal freshwater into mesohaline waters in the Chesapeake Bay, where species assemblages change along the salinity gradient (Wagner 1999; Jung and Houde 2003). Seasonality affects the availability of some prey resources, such as *Alosa* species, which swim into tidal rivers during the spring to spawn (Waldman 2013), or blue crab *Callinectes sapidus*, which undergo seasonal migrations (Aguilar et al. 2005). Moreover, blue catfish exhibit ontogenetic trophic niche shifts, with different sized fish utilizing different prey resources (Schmitt et al. 2017). Considering this, we anticipated that blue catfish diet would vary with season, salinity, and fish size.

We analyzed overall patterns in blue catfish diet using canonical correspondence analysis (CCA; ter Braak 1986). CCA is a form of multivariate ordination in which a matrix of response variables is ‘regressed’ (constrained) on a matrix of independent variables; it is the multivariate analog of multiple linear regression. CCA is often used for analyzing relationships between species assemblages and multidimensional environmental data (ter Braak and Verdonschot 1995), but has also been used to assess feeding patterns (Clifton and Motta 1998; Jaworski and Ragnarsson 2006). Because we were interested in general diet patterns, we first grouped all diet items into six broader categories: fish, mollusks, crustaceans, other invertebrates, vegetation, and ‘other’ (e.g. anthropogenic debris, terrestrial mammals, birds, and other rare items). See Schmitt et al. (2018, *in press*) for further diet description and methodology. We then coarsened the data to the presence-absence of diet items, since the binary occurrence of prey in the diet is more reliable and less biased than other diet measures (Baker et al. 2014). Predictor variables included

salinity zone, total length (truncated to the nearest 100 cm), and season (also coded as three dummy variables). We assessed whole-model and variable-wise statistical significance with F -tests. Magnitude of relationships groupings of individual fish and constraining variables or diet items were assessed based on loading scores (an analog of correlation coefficients, centered at 0 and ranging from -1 to 1). Because preliminary analyses show river-specific variability in diet, dietary ontogenies, growth, and population structure, we conducted separate CCAs for each river (Hilling et al. 2018; Schmitt et al. 2018, *in press*). All ordination analyses were performed using the Community Ecology Package “vegan” written by Oksanen (2017), which is an extension to the statistical package R version 3.4.3 (R Development Core Team 2018).

Predation models for species of concern.—We used binomial generalized additive models (GAMs), which are semi-parametric generalizations of logistic regression (Hastie and Tibshirani 1990), to examine relationships between the binary occurrence of imperiled alosines (American shad and river herring), blue crab, and American eel in the diet by several predictor variables. We based our analysis on frequency of occurrence since it is the least biased metric for diet description (Baker et al. 2014). GAMs also offer numerous advantages when compared to other common binomial modeling approaches. Split-sample validation exercises have demonstrated that GAMs outperform classification and regression trees, are have fewer data restrictions than logistic regression, and are comparable to multivariate adaptive regression splines for describing non-linear relationships (Beck and Jackman 1998; Austin 2007).

GAMs only assume that functions are additive and relationships are smooth, thus are very flexible (Guisan et al. 2002). A GAM, like a generalized linear model, uses a link function to establish a relationship between the mean of the response variable and a “smoothed” function of the explanatory variables, which makes it robust to overdispersed or correlated data (Lin and

Zhang 1999). Separate GAMs were constructed for American eel, imperiled *Alosa* species (American shad and river herring), and blue crab, and each included smoothing functions for ‘predator length’, ‘salinity’, and ‘month’, while ‘river’ was treated as a categorical covariate (Weltz et al. 2013). Each model was constructed as:

$$\text{logit}(p) = \beta_0 + f_1(\text{predator length}) + f_2(\text{salinity}) + f_3(\text{month}) + \text{river}$$

where “logit” is the binomial link function, p is the probability of a species being consumed, and f_1-f_3 are smoothing functions realized by thin plate regression splines (Wood 2006). Individual F tests were then used to determine which predictor variables contribute significantly to the deviance explained, and only significant covariates were included in the final models (Wood 2006). The probability of encountering each species in blue catfish stomachs was then predicted separately by river to elucidate the circumstances that lead to higher predation rates for these species. Overall predictive performance was assessed using the area under the receiver operating curve (auROC). An auROC value of 0.5 is equivalent to a random guess, a value of 1.0 indicates perfect model performance, and a value of 0.7 indicates adequate model performance (Bewick et al. 2004; Austin 2007; Brenning 2008). All GAMs were constructed using the R (R Core Development Team 2018) package ‘mgcv’ (Wood 2017).

Results

Data collection.—From 2013-2016, we collected a total a total of 14,488 blue catfish stomachs at 554 sites on the James, Pamunkey, Mattaponi, and Rappahannock Rivers in eastern Virginia, USA (Figure 1). Of the stomachs collected, a total of 7,302 contained prey items (50.40%). While stomachs (N=16,110) were collected year round (Schmitt et al. 2018, *in press*), we limited

the current study to stomachs that were collected using low-frequency electrofishing following a stratified random sampling protocol (April–October).

Major drivers of blue catfish diet.—Blue catfish diets varied by river, salinity, season, and fish total length, and all constraining variables were statistically significant in the CCA ($P<0.0001$, Table 1). For each river, the first two CCA axes accounted for a considerable amount of variation in blue catfish diet: 80% in the James, 85% in the Rappahannock, 97.4% in the Pamunkey, and 93.3% in the Mattaponi. Global F tests on CCAs for each river were highly significant ($P<0.0001$ for all), and nearly all constraining variables significantly affected blue catfish diet in each river ($P<0.0001$), with the exception of salinity zone in the Mattaponi ($P=0.0806$; Figure 2; Table 1).

CCA results suggest several key patterns in blue catfish diet. First, there were consistent, length-mediated (*i.e.* ontogenetic) shifts from omnivory to predation. Second, predatory blue catfish fed more on invertebrates or crustaceans in the spring, and began to consume more fish as the seasons progressed. Third, the predation of various invertebrates is generally associated with lower salinities, while blue catfish shifted towards piscivory in higher salinity areas, especially in the James and Pamunkey Rivers (Figure 2). Not surprisingly, herbivory was strongly associated with spring and summer in all rivers.

Perhaps most importantly, patterns were not consistent among rivers. For example, herbivory was strongly associated with summer in all rivers except the Rappahannock, where it was more prevalent in the spring. Moreover, blue catfish diets exhibited quite distinct length- and season-mediated breaks in individuals from some rivers (*e.g.* the Mattaponi), but exhibited much more overlap in other rivers (*e.g.* the James; Figure 2). All CCA axis loadings of diet items and constraining variables are presented in Table 2.

Predation models for species of concern.—Our GAMs demonstrate that blue catfish predation of species of concern varies by river, salinity, month, and catfish total length (Figures 3–5). All GAMs were globally significant ($P < 0.001$), and all predictors were significant ($P < 0.05$), with the exception of salinity in model of American eel predation (Table 3). All models had adequate predictive performance, with auROC values ranging from 0.84 – 0.86 (Table 2; Pearce and Ferrier 2000).

Imperiled alosines (American shad and river herring) were most susceptible to predation by blue catfish in tidal freshwater areas. As many as 4% of catfish stomachs are expected to contain these species in certain areas (e.g. tidal freshwater stretches of the James River; Figure 3). Our model also suggests that large catfish are most likely to consume these alosines, with a predicted percent occurrence is as high as 8% for 700 – 1000 mm catfish in the James River. Seasonally, the probability of predation for imperiled *Alosa* species is greatest in April, with another increase in predation during October. Overall, predation of alosines was highest in the James and Rappahannock Rivers. River herring were the most commonly consumed species group in both rivers, though American shad were found in more stomachs in the Rappahannock than the James River (Schmitt et al. 2018, *in press*).

Our model suggests that blue crabs become more susceptible to predation with increasing salinity. Nearly 30% of blue catfish stomachs were predicted to contain blue crabs in salinities greater than 8 ppt in the James River, while predicted occurrence is typically less than 5% in the other rivers. Large catfish ate blue crabs more frequently, and model predictions suggest that catfish in the 600 – 900 mm TL range ate the most crabs (Figure 4). Model predictions suggest that blue crab predation is greatest during the late summer and into the fall (August – October).

Model predictions suggested low predation rates for American eel, with predicted occurrence <5% in all modeled scenarios (Figure 5). Salinity did not significantly influence predation of American eel ($P>0.05$), though catfish size and month did ($P<0.02$). Model predictions suggest that medium and large catfish (500 – 900 mm TL) are the most likely to consume American eel. Seasonally, predicted occurrence was highest during spring and fall, particularly April and October (Figure 5).

Discussion

Blue catfish diet in all rivers was driven primarily by season and/or salinity. These two factors have been demonstrated to drive organismal assemblages in the Chesapeake Bay (Wagner 1999; Jung and Houde 2003; Lippson and Lippson 2006). Species assemblages vary drastically along the salinity gradient and some species are only available seasonally (Wagner 1999; Jung and Houde 2003; King et al. 2005). For example, aquatic macrophytes, which are commonly found in blue catfish stomachs (Schmitt et al. 2018, *in press*), are generally only available during the warmer months (Moore et al. 2000). Other seasonal resources in Chesapeake tributaries include adult American shad, hickory shad *Alosa mediocris*, and river herring which make upstream spawning migrations during the spring (Garman and Nielsen 1992; Schmitt et al. 2017), while juveniles emigrate from these rivers during the late summer and autumn months (Hoffman et al. 2008). Blue crabs and American eels also make seasonal movements in and out of these rivers (Wenner and Musick 1974; Aguilar et al. 2005), and our models suggest increased predation during these movements.

Multivariate analyses identified consistent, length-mediated shifts from omnivory to piscivory. In general, small blue catfish are herbivore/benthic-invertivores while large blue catfish become more piscivorous (Schmitt et al. 2018, *in press*). The length at which these shifts occur vary by

river (500 – 700 mm TL) and may be driven by the relative abundance of small-bodied fish prey in the environment (Schmitt et al. 2018, *in press*). While large, piscivorous catfish comprise a small fraction of each population, they still have the potential to have deleterious impacts on important native species like American shad, river herring, and American eel. There is ample evidence to suggest that blue catfish feed on locally-abundant resources, since blue catfish are non-selective, opportunistic feeders (Eggleton and Schramm 2004; Schmitt et al. 2017). These life history traits have been documented in many other estuarine and marine fishes, where diets are a reflection of the variability of resources available in the environment (Beumer, 1978; Livingston, 1984; Ley et al. 1994; Jaworski and Ragnarsson 2006).

Our GAMs revealed the circumstances that lead to greater predation of species of concern by invasive blue catfish. For American shad and river herring, maximal predation occurs in freshwater areas, which corresponds with Schmitt et al. (2017), where predation of imperiled alosines peaked in both tidal and non-tidal freshwater segments of the James River. For all rivers, the highest predation rates occur in April, which agrees with previous work from the James River (Schmitt et al. 2017). The GAM for American shad and river herring also revealed a small increase in predation during September and October, which may be associated with the downstream migration of juveniles into the estuary (Loesch and Lund 1977; Hoffman et al. 2008; Palkovacs et al. 2014). It is important to note that small-bodied juvenile fish digest more rapidly than adults (Bromley 1994), thus we may have underestimated predation rates on juvenile fish prey. Predation of American shad and river herring is highest for blue catfish ranging from 600 – 900 mm TL, though predation probabilities decrease for trophy-sized catfish (> 1072 mm TL; Gabelhouse 1984). This could be explained by individual diet specialization observed in trophy fish, many of which are cannibalistic or specialize on gizzard shad *Dorosoma*

cepedianum (Schmitt et al. 2018, *in press*). The predicted percent occurrence of alosines in the diet is relatively low in all circumstances (<8% occurrence). It is also important to note that blue catfish are known scavengers (Schmitt et al. 2018, *in press*) and *Alosa* species often experience high mortality after spawning (Glebe and Leggett 1981), therefore much of the “predation” we observed may actually be scavenging.

River herring and American shad declines along the Atlantic coast began before the establishment of blue catfish (Limburg and Waldman 2009) and must have been initiated by other casual factors. Alosines face many challenges, including habitat loss, overharvest, poor water quality, climate change, bycatch from coastal intercept fisheries, and dams that block migratory corridors (Limburg and Waldmen 2009; Bethoney et al. 2013; Raabe and Hightower 2014; Hasselman et al. 2016). Nonetheless, predation by invasive catfish could further destabilize the species, especially if predation rates increase at low prey densities (Dick et al. 2014). Interestingly, American shad have shown some signs of recovery in the Rappahannock and Potomac rivers (Cummins 2016; Hilton et al. 2016). Because these rivers support dense populations of catfish, the apparent recovery of American shad may suggest that blue catfish play a reduced role in the population dynamics of this species.

Predation of blue crab by blue catfish increases with salinity. This is likely driven by the relative density and spatial dynamics of the blue crab population. Blue crab abundance was positively correlated with salinity in Chesapeake Bay subestuaries (King et al. 2005), and low salinity areas are typically dominated by adult male crabs, which are less susceptible to predation, while juvenile and female crabs become more abundant in brackish areas (Hines et al. 1987). Most blue crabs we encountered in stomachs were immature, which could explain observed predation patterns. Blue crab predation rates were highest for blue catfish around 800 mm TL, and declined

in larger blue catfish. Maximal predation rates occur during the autumn months in all rivers, though there was an increase in blue crab predation in the spring in the Mattaponi River. The autumn months are typically associated with reduced freshwater inflow, which often results in the upriver advancement of the salt wedge (Schubel and Pritchard 1986). This could also result in greater spatial overlap between blue catfish and blue crab (King et al. 2005). In the James River, we often observed blue crabs at high densities at the lower edge of the fall line during the autumn. This area is usually home to freshwater species like smallmouth bass *Micropterus dolomieu* and various sunfishes (*Lepomis spp.*), but the upriver advancement of the salt wedge may cause blue crabs to colonize the area during extended dry periods.

Blue crabs naturally co-occur with blue catfish in estuaries in Louisiana (Baltz and Jones 2003), and are consumed at higher rates than observed in Virginia's tidal rivers (up to 50% of stomachs; Perry 1969). In spite of high predation rates, Louisiana continues to sustain valuable blue crab fisheries, and annual harvests exceeding both Virginia and Maryland (National Marine Fisheries Service 2017). This is not surprising, as blue crabs have complex life histories (Hines et al. 2010), and population dynamics appear to be strongly influenced by abiotic factors (Bauer and Miller 2010; Colton et al. 2016). Nonetheless, predation of blue crabs by blue catfish should be considered in future population models, since the predicted percent occurrence of blue crabs in blue catfish stomachs can be quite high (up to 28% in certain situations).

For American eel, salinity did not significantly affect predation rates, which makes sense since eels readily colonize freshwater, estuarine, and marine habitats and move freely between them (Feunteun et al. 2003, Daverat et al. 2004). Catfish size significantly affected predation rates of American eels, and maximal predation rates were observed for blue catfish ranging from 600 – 800 mm TL. Most of the eels consumed were yellow phase, though phase determination was

often difficult due to tissue breakdown from digestion. Month was a significant covariate in the American eel model, and maximal predation rates occur during the spring and the fall, especially April and October. This may be related to eel migration patterns driven by seasonal changes in temperature (Welsh et al. 2015; Adlinger and Welsh 2017). For example, silver eels make long spawning migrations in the autumn, while yellow eels are known to make punctuated upstream movements as waters warm in the spring (Welsh and Liller 2013). Overall, blue catfish predation of American eel was rare (predicted percent occurrence <5% in all circumstances).

Eel populations (including American eel) have declined across the northern hemisphere (Bonhommeau et al. 2008), thus blue catfish are unlikely to be drivers of these declines. Population declines may be attributed to many factors, though climate change and the proliferation of an invasive parasitic nematode (*Anguillicoloides crassus*) are most likely driving observed changes (Shepherd 2015). Climate change may impact American eel spawning and recruitment success due to the complex life history of these animals (Knights 2003). Silver eels undergo long spawning migrations to the Sargasso Sea, after which larvae are transported to continental rearing habitats by ocean currents (Wang and Tzeng 2000). Warming temperatures have been associated with changes in physical oceanographic processes in the North Atlantic, which may negatively affect the survival and transport of eel larvae (Knights 2003). Making matters worse, the exotic parasite *Anguillicoloides crassus* has expanded its distribution in the western Atlantic. While this parasite does not cause immediate mortality, it causes damage to the swimbladder, and may increase mortality rates as silver eels undergo long-distance spawning migrations (Fazio et al. 2012; Barry et al. 2014).

Large blue catfish, particularly fish ranging from 500 – 1000 mm TL (20”– 40”), consume disproportionately more American shad, American eel, river herring, and blue crab. This may

explain why our models show higher overall predation in the James River, where large catfish are most abundant (Greenlee and Lim 2011; Hilling et al. 2018). Predation of these species declines as blue catfish approach trophy size (1072 mm; Gabelhouse 1984), and previous work indicates that many trophy blue catfish are cannibalistic or feed on gizzard shad *Dorosoma cepedianum* (Schmitt et al. 2018, *in press*). Understanding the size(s) of catfish that are likely to inflict the greatest damage to valuable or imperiled native resources may help inform future management strategies in the region.

Eradication programs for invasive species often fail in large, open systems (Mueller et al. 2005; Britton et al. 2010; Franssen et al. 2014), and are unlikely to succeed for blue catfish in the Chesapeake Bay region (Orth et al. 2017). Nonetheless, targeted removals of large fish (20" – 40") could reduce predation of imperiled alosines, American eel, and blue crab. In the James and Rappahannock Rivers, blue catfish size structure is already shifting this direction, as growth rates are declining and large fish are becoming rarer (Hilling et al. 2018). Currently, Virginia Department of Game and Inland Fisheries only allows the harvest of one blue catfish over 813 mm (32") per angler, per day. There are consumption advisories for blue catfish due to contamination, and the current regulation exists because large fish carry greater contaminant loads (Hale et al. 2016). It may be time to implement non-consumptive harvest strategies for large fish, since our models demonstrate that catfish in the 20" – 40" range consume disproportionately more species of concern than other size catfish. Non-consumptive harvest options include use for pet foods, fertilizers, and biosolid products (Orth et al. 2017).

Another intriguing option is the removal and transport of large blue catfish to native drainages such as the Ohio and Tennessee River systems (Orth et al. 2017). Trophy-sized blue catfish could provide socioeconomic benefits, as they are exceptionally rare in native populations

(Boxrucker and Kuklinski 2006), yet are very desirable to anglers (Hutt et al. 2013). The relocation of trophy blue catfish could also provide ecological benefits. Large blue catfish are one the few native predators capable of consuming adult bighead carp *Hypophthalmichthys nobilis* and sliver carp *H. molitrix* (O’Keefe 2015), which are dangerous invaders throughout much of the central U.S. (Phelps et al. 2017). Restoring healthy populations of blue catfish and other large native predators (*e.g.* flathead catfish *Pylodictus olivarus*) may be one of the best approaches for slowing the spread and minimizing the ecological impacts of these dangerous invaders. While live transport may seem logistically challenging, blue catfish are a hardy fish, and large fish are especially resilient (Schmitt and Shoup 2013).

Animal relocation is highly controversial (Minter and Collins 2010), and there can be unintended consequences like outbreeding depression and hybridization if new genetics are introduced to a native population (Ricciardi and Simberloff 2009). Blue catfish that were stocked in Chesapeake Bay were originally from river/reservoir systems in Texas (B. Greenlee, *personal communication*), thus genetic “contamination” may not be an issue. Native riverine blue catfish populations were highly migratory and could move freely from river to river prior to the construction of dams (Graham 1999), thus it is doubtful that local endemic processes shaped the genetic structure of these populations prior to human disturbance (*e.g.* the Ohio, Missouri, and Mississippi Rivers were all connected). It is unlikely that selective pressures in the Chesapeake Bay have altered blue catfish genetics, since trophy catfish (> 1072 mm) are at most a few generations old due to slow growth (Greenlee and Lim 2011). These factors could minimize the risk of relocating large Chesapeake catfish to native rivers, and new fish could actually benefit populations that have been forced into reproductive isolation through the construction of dams

(Yamamoto et al. 2004). Other concerns like the introduction of novel diseases and parasites can largely be avoided through proper treatment prior to transport (Cowx 1998).

There are limitations to the current study. First, winter diet information was not included in these modelling exercises because it was not collected in a randomized manner. This is problematic because blue catfish predation of blue crab can be substantial during the winter months, and blue catfish are generally more piscivorous in the winter (Schmitt et al. 2018, *in press*). Second, we had limited success capturing blue catfish using low-frequency electrofishing in brackish areas (>10 ppt), though blue catfish have been captured in salinities as high as 21.5 ppt (unpublished data, cited in Fabrizio et al. 2017). This is simply an artifact of electrofishing, as it becomes ineffective at higher salinities (Bringolf et al. 2005). Predation of blue crab increases with salinity, thus we may be underestimating blue catfish predation of this commercially-valuable species. Future studies in the region should focus on blue catfish diet during the winter and in mesohaline areas.

While the current study focuses on invasive blue catfish in the Chesapeake Bay, the development of similar models could be useful for other invasives, especially if the goal is to minimize predation of specific organisms. While predation does not translate directly to impact (Ney 1990), predation has been identified as a major driver in the decline of native species richness at the global scale (Mollot et al. 2017). Predation is particularly dangerous for imperiled biota, as it can result in population recovery and even drive organisms to extinction. While there is no conclusive evidence suggesting this is happening with alewives and blue catfish (*e.g.* American shad populations have shown some signs of recovery), this has happened with other invasive predators (Spencer et al. 2016). In these cases, the best approach may be to determine the factors that lead to greater predation of certain organisms. Once determined, this information

can provide directive guidance for targeted removals or additional harvest of the invader (Schmitt et al. 2017). Predation models of imperiled species would be especially useful for invasive predators in large, open systems where eradication is not a viable option (Franssen et al. 2014; Thresher et al. 2014). In these circumstances, the best approach may be targeted removals with the goal of “suppress[ing] invasive populations below levels predicted to cause undesirable ecological change” (Green et al. 2014).

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Tables and Figures

Table 1. Whole model and variable-wise statistical significance from our CCA analysis can be seen below. Separate models were developed for each river, and statistical significance was evaluated using *F* tests.

	James			Rappahannock			Pamunkey			Mattaponi		
	<i>df</i>	<i>F</i>	p	<i>df</i>	<i>F</i>	p	<i>df</i>	<i>F</i>	p	<i>df</i>	<i>F</i>	p
Global model	4	17.9	<0.001	4	21.6	<0.001	4	21.7	<0.001	4	14.9	<0.001
Salinity zone	1	32.7	<0.001	1	11.8	<0.001	1	46.7	<0.001	1	1.9	0.081
Season	2	21.6	<0.001	2	49.2	<0.001	2	13.3	<0.001	2	43.1	<0.001
Length category	1	8.9	<0.001	1	7.6	<0.001	1	7.8	<0.001	1	11.3	<0.001

Table 2. Axis loadings for each CCA model shown below. Separate CCA's were constructed for each river (“James”= James River, “Pam”= Pamunkey River, “Matt” = Mattaponi River, “Rapp” = Rappahannock River).

	James		Pam		Matt		Rapp	
	CCA1	CCA2	CCA1	CCA2	CCA1	CCA2	CCA1	CCA2
Salinity	-0.624	0.303	0.816	-0.312	0.150	0.013	0.284	0.105
Spring	0.720	0.574	-0.482	0.759	-0.415	-0.868	-0.665	0.702
Summer	-0.036	-0.756	-0.420	-0.870	-0.092	0.898	0.029	-0.973
Length	-0.050	0.530	0.286	-0.289	-0.194	0.391	-0.041	-0.078

Table 3. Summary statistics for each GAM including significance of each predictor (based on *F* tests) and overall model performance based on deviance explained and Area Under the ROC Curve (auROC).

Predictor	American Eel	Imperiled Alosines	Blue Crab
River	<i>P</i> <0.001	<i>P</i> =0.009	<i>P</i> <0.001
Month	<i>P</i> <0.001	<i>P</i> =0.019	<i>P</i> =0.017
Salinity	<i>P</i> =0.063	<i>P</i> <0.001	<i>P</i> <0.001
Length	<i>P</i> =0.023	<i>P</i> <0.001	<i>P</i> <0.001
Model Fit			
Global Model	<i>P</i> <0.001	<i>P</i> <0.001	<i>P</i> <0.001
auROC	0.859	0.874	0.843
Null Deviance	651.305	698.980	2032.733
Residual Deviance	137.875	151.977	440.578
Deviance Explained	78.84%	78.26%	78.33%

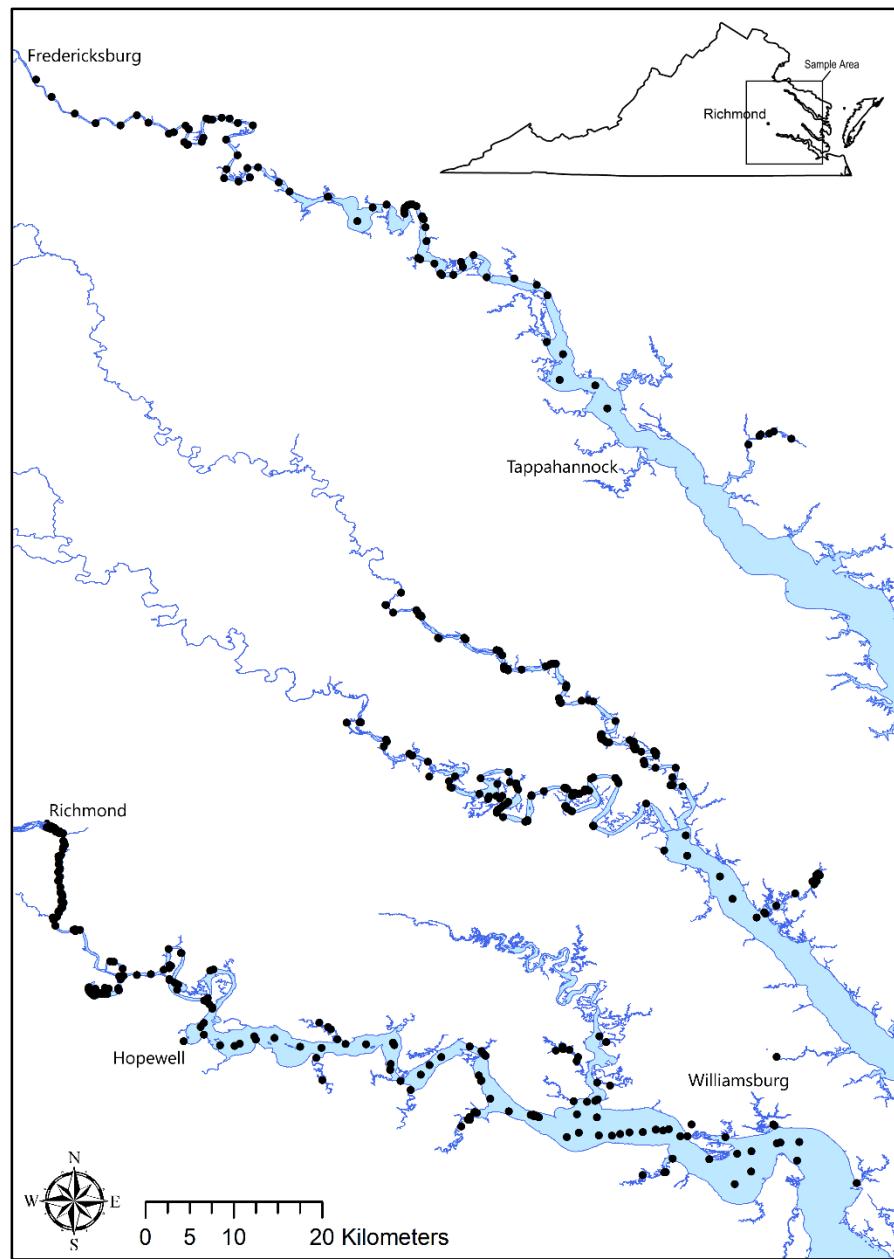


Figure 1. Stomachs were collected from 14,488 blue catfish at 552 locations (dots) in Chesapeake Bay subestuaries in eastern Virginia, USA. Samples were collected in the Rappahannock River (north), York River (central), and James River (south). The York River is formed at the confluence of the Pamunkey River (south) and Mattaponi River (north).

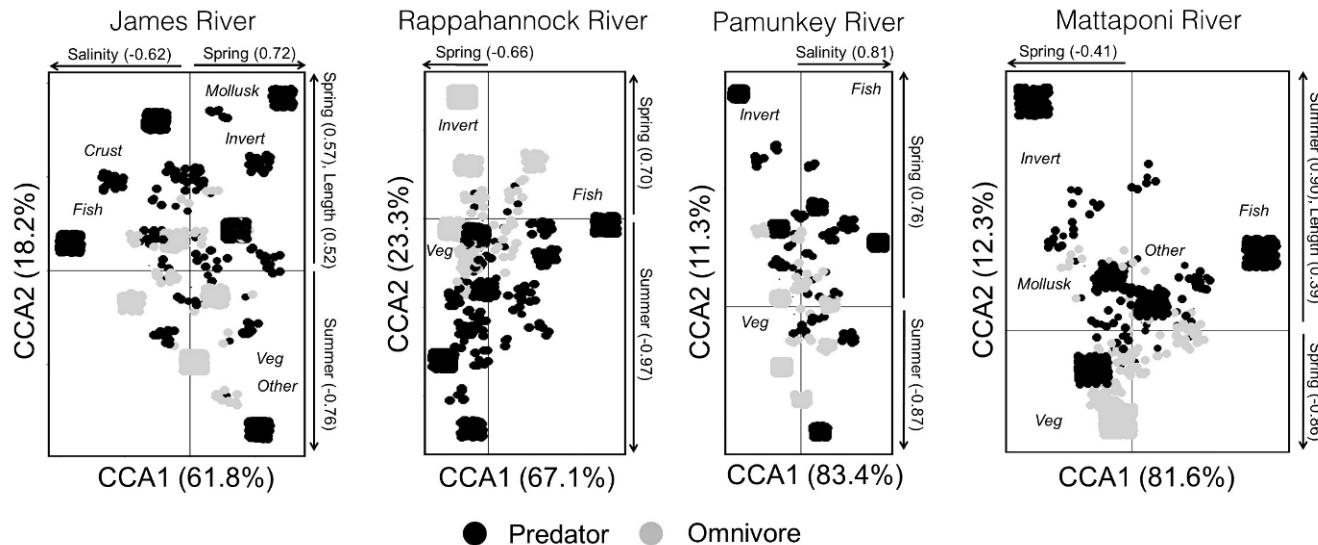


Figure 2. Canonical correspondence analyses (CCAs) of Blue Catfish diet in four tributaries to the Chesapeake Bay, Virginia, from 2012-2015. Points represent individual fish, and have been jittered to reduce overlap of individuals with the same combinations of diet items. Gray points represent individuals containing vegetation in their stomachs (i.e. omnivores); black points represent predatory fish. The amounts of variation in multivariate diet responses described by each axis are reported on axis labels. Loading scores of independent constraining variables (season, salinity zone, and fish total length) are presented on outsides of plots, instead of traditional arrowed vectors within plots. Since scores are centered at 0,0 (represented by solid lines), constraining variable loading scores on a given axis should be interpreted as directional within plot halves. For example, points associated with spring samples occur on the right side of the plot for the James River. For brevity, only loading scores greater than 0.4 are presented (all axis loading scores included in Table 2). Loading scores of diet items are represented by text within plots ('*Invert*'= other invertebrates, '*Crust*'=crustacean, and '*Veg*'=vegetation, etc.). For easier interpretation, diet scores have been jittered to avoid overlap with points; however, they are in correct quadrants as close as possible to original coordinates.

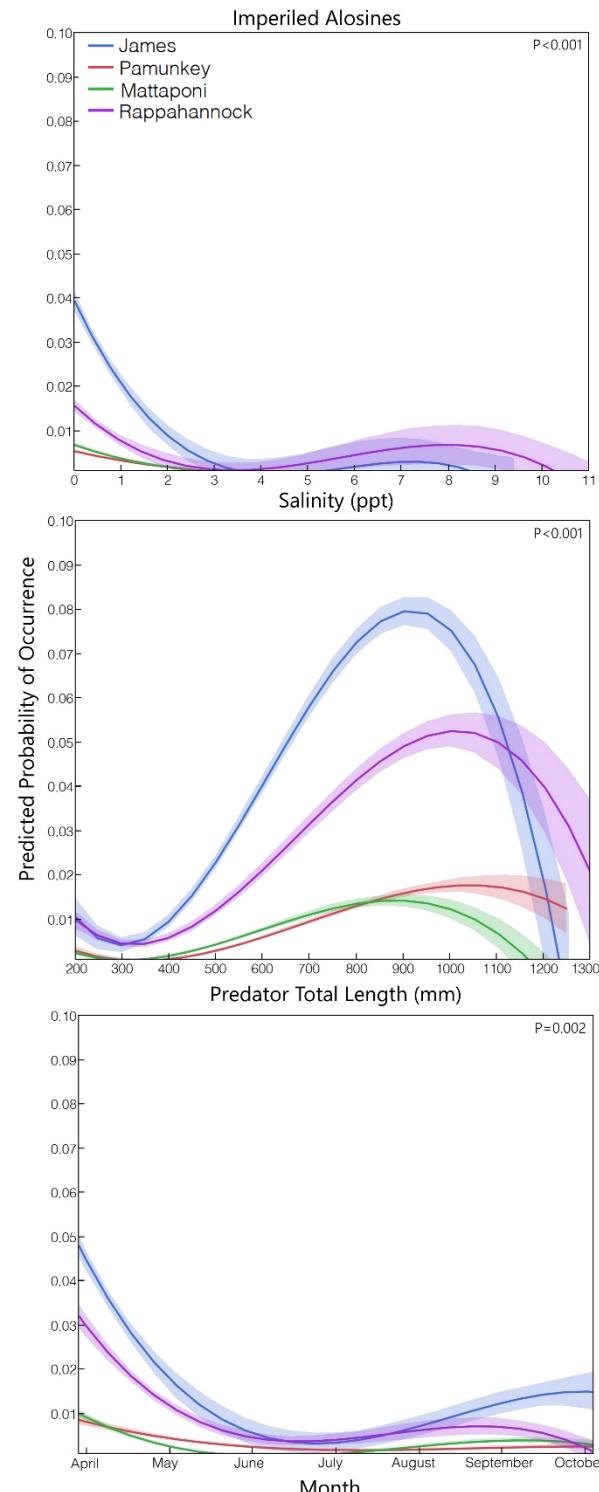


Figure 3. GAM model predictions for imperiled alosine predation (probability of occurrence in a catfish stomach) as it varies by salinity, predator length, and month. Separate curves were plotted for each river. All predictive factors were significant ($P<0.05$). “Imperiled alosines” include blueback herring, American shad, and alewife.

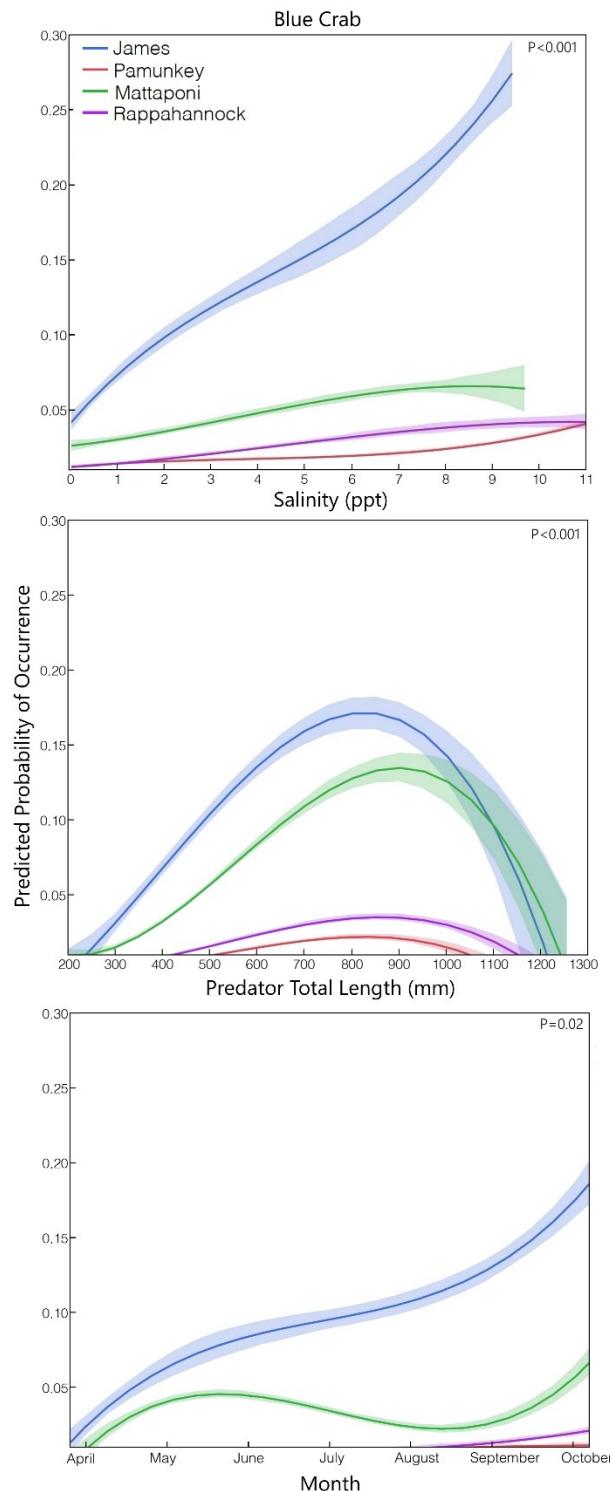


Figure 4. GAM model predictions for blue crab predation (probability of occurrence in a catfish stomach) as it varies by salinity, predator length, month. Separate curves were plotted for each river. All predictive factors were significant ($P<0.05$).

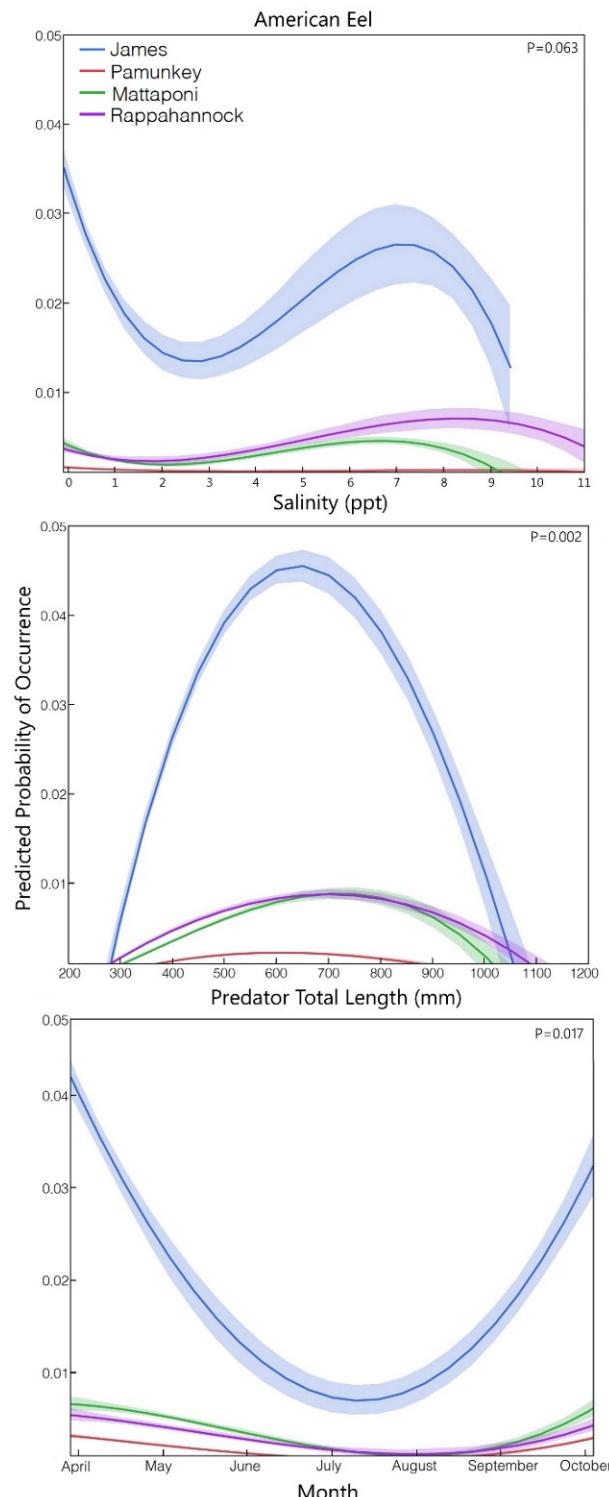


Figure 5. GAM model predictions for American eel predation (probability of occurrence in a catfish stomach) as it varies by salinity, predator length, and month. Separate curves were plotted for each river. All predictive factors were significant ($P<0.05$), with the exception of salinity ($P=0.06$).

Chapter 5: Estimates of Food Consumption Rates for Invasive Blue Catfish *Ictalurus furcatus* in Atlantic Slope Subestuaries

Introduction

Invasive species are a threat to global biodiversity (Lockwood et al. 2013), and are drivers of global change (Garcia-Berthou 2007). Invasive species can impact native biota through predation, competition, or indirectly through the spread of novel diseases and parasites. Because of this, invasions can cause changes in food web structure, which can alter ecosystem function (Mack et al. 2000; Clavel et al. 2011). Freshwater habitats are some of the most invaded ecosystems on earth (Clavero and Garcia-Berthou 2006), and descriptive studies on the biology and life history of invasive freshwater fishes are “urgently needed” (Garcia-Berthou 2007).

The Blue Catfish *Ictalurus furcatus* is a large catfish that is indigenous to the Mississippi River basin and has native populations that extend into Central America (Graham 1999), and is now invasive in several tidal rivers in the eastern United States (Schmitt et al. 2017). Blue Catfish have been widely stocked as a sport and food fish, and non-indigenous populations now occur from Delaware to Georgia (Moser and Roberts 1999; Schloesser et al. 2011; Bonvechio et al. 2012; Fabrizio et al. 2017). Populations are dense in some Chesapeake Bay subestuaries, and there are an estimated 544 Blue Catfish per hectare within a 12-km segment of the James River in eastern Virginia (Fabrizio et al. 2017). Due to rapid population expansion, high population densities, and their potential to impact native biota, Blue Catfish are now considered invasive in Chesapeake Bay and further range expansion is likely (Schmitt et al. 2017). This has resulted in concern that these catfish are consuming species that are in decline, such as American Shad *Alosa sapidissima*, river herring (*A. aestivalis* and *A. pseudoharengus*), and American Eel *Anguilla rostrata* (Schmitt et al. 2018, *in press*). While several studies have described the diet of Blue

Catfish in Chesapeake Bay (Schloesser et al. 2011; Schmitt et al. 2017; Schmitt et al. 2018 *in press*), total annual ingestion of native biota cannot be quantified without consumption rate estimates (Mikkelsen and Pedersen 2012).

Consumption estimates are important for understanding fish foraging rates and community dynamics (Vigg et al. 1991), and are essential for the construction of ecosystem models (Christensen and Walters 2004) and bioenergetics models (Deslauriers et al. 2017). Ecosystem models like Ecopath or Atlantis are excellent tools for exploring complex food web dynamics (Heymans et al. 2016), and are becoming increasingly important as fisheries managers continue to shift towards ecosystem-based management approaches (Long et al. 2015). Determination of consumption rate is especially important for invasive species, as estimates of population biomass, consumption rates, and food habits can be integrated to quantify total annual predation of native biota (Mikkelsen and Pedersen 2012; Cerino et al. 2013).

There is a general paucity of information on Blue Catfish, and no consumption estimates have been published for this species, despite its broad geographic distribution in North and Central America (Graham 1999). Considering this, the major objective of this study was to provide robust estimates of daily ration, maximum daily ration, and consumption per unit biomass for Blue Catfish using a combination of field experiments, lab experiments, and empirical regression models. Lab and field studies will be used to provide multiple estimates of daily ration, while empirical regression models will help determine annual consumption rates per unit biomass (Q/B). While beyond the scope of this paper, the consumption rate information provided here can be integrated with biomass estimates (Fabrizio et al. 2017; Bunch et al. 2018, *in press*) and diet information (Schmitt et al. 2018, *in press*) to calculate total annual consumption (kg/yr) of important native species such as American Shad and blue crab *Callinectes sapidus*.

Methods

Laboratory experiments.—Fifteen Blue Catfish ranging from 332 mm – 878 mm total length (TL) were collected from the Rappahannock River in October of 2015 using high frequency electrofishing (60 hz). Most catfish ranged from 300 – 499 mm TL (N=11), though four large (>500 mm TL) fish were also collected. Fish were transported to Virginia Tech in a cool, aerated livewell and were placed in two aquaria with shared biofiltration and digital temperature control systems. The first tank was 167 cm long by 167 cm wide by 102 cm deep and held approximately 2,800 liters of water. This tank was used for large catfish (> 500 mm TL). A second tank was used for smaller individuals (< 500 mm TL) with a diameter of 107 cm and a height of 107 cm. This tank held approximately 950 liters of water. Salinity within the recirculating aquaculture system (RAS) was kept within ± 0.5 ppt of the salinity recorded at the time of capture using evaporated solar salt (3.0 ppt). Fish were allowed to acclimate for 4 weeks prior to any experimentation (Bourret et al. 2008), and acclimation conditions included 14-hour light: 10-hour dark photoperiod, a constant water temperature of 13° C, and bi-weekly rations of either fresh or frozen Gizzard Shad *Dorosoma cepedianum*.

Fish size, prey type, and water temperature have been demonstrated to be the major drivers of fish daily consumption, while other factors such as salinity have little impact on consumption (Bromley 1990; Temming and Andersen 1992). Given this, maximum daily ration (C_{max}) was estimated at three temperatures (5°, 15°, and 25° C) using two prey types (Gizzard Shad and blue crab *Callinectes sapidus*). The temperature range chosen was very close to the range of water temperatures regularly observed in the Chesapeake Bay (4° C to 28° C; Shiah and Ducklow 1994). Partitions were installed in each tank so that fish had their own enclosure, and fish were allowed to acclimate to each experimental temperature for 21 d. Temperature adjustments

between experiments did not exceed 2° C per day (Hayward and Arnold 1996). Prior to trials, catfish were starved for 72 h to ensure empty stomachs (Amundsen and Klemetsen 1988).

To determine C_{max} , Blue Catfish were fed *ad libitum* rations of Gizzard Shad or blue crab for 24 h with old food being removed and new food added every 3 h, while weights were recorded for each food item that was added or removed (Bourret et al. 2008). Prey items were either fresh or frozen, as freezing prey does not significantly alter evacuation rates; however, shad were kept on ice and frozen promptly after capture to prevent degradation (Andersen 2012). Fish were kept within individual enclosures, so maximum daily consumption was estimated by subtracting the weight of uneaten food from the total weight of food given to each individual catfish. All catfish were weighed at the beginning and end of each experimental test period (Bourret et al. 2008), and three replicates were conducted for each treatment combination.

Data analysis.— Because Blue Catfish varied in weight over the course of the experiment due to *ad libitum* feeding, we used a weight-standardized approach to correct for variation in body size (Hayward and Arnold 1996; Zwiefel et al. 1999). For each individual fish, maximum daily consumption was adjusted to a standardized body weight of 3455 g, which is the mean body weight recorded for all fish throughout the experiment (Hayward and Arnold 1996; Zweifel et al. 1999). To weight-standardize daily consumption rates, the allometric equation $C_{max} = aW^b$ was used to calculate weight-specific maximum daily ration where W is body weight (g) of fish and a and b are regression constants. A value of -0.31 was used for b (Hewitt and Johnson 1992; Hansen et al. 1997), while the dummy value of 1 was used for a (Zwiefel et al. 1999). The mean weight for each fish within each experimental trial was added to the allometric equation, and the resulting C_{max} was divided by the C_{max} value for the grand mean of all fish weights (3455 g; Bourret et al. 2008). All prey and temperature-specific consumption values (g/d) were adjusted

to body weight using the above weight-standardized quotient; further, all data were log-transformed to meet normality and variance assumptions prior to analysis (Bourret et al. 2008).

Differences in weight-adjusted daily consumption among temperatures, prey types, fish lengths, and all interactions were tested using factorial analysis of variance (ANOVA). Significance was evaluated with an effective alpha (α) = 0.05. When significant effects were detected, *post hoc* Tukey's multiple comparisons were used to further explore pairwise differences in consumption rate (Bourret et al. 2008).

Diel feeding chronologies and field estimates of daily ration.—Fish feeding behavior can be highly-structured by the diel cycle (Johnson and Dropkin 1993) and many species of fish exhibit clear diurnal behavioral patterns (Helfman 1993). We conducted 24 h feeding chronologies with 3 h sampling intervals during the summers of 2013, 2014, and 2015 to determine diel variation in Blue Catfish feeding patterns. Diel feeding patterns were determined for each river during the summer months, as low-frequency electrofishing for Blue Catfish works best at water temperatures $> 18^\circ \text{ C}$ (Bodine and Shoup 2010).

In addition to improving our understanding of Blue Catfish feeding patterns, diel feeding chronologies will help future researchers maximize the amount of information gained per fish collected, as they can sample during times when stomachs are fullest. Admittedly, this will only work if fish exhibit clear diel feeding patterns (Bowen 1996).

Field data collected from our diel feeding chronologies was also used to estimate gastric evacuation rates, daily ration, and maximum daily ration. Field estimation of daily ration is preferred, as fish are subject to natural conditions (Jarre et al. 1991; Bromley 1994; Grant and Kott 1999). Daily ration and maximum daily ration were estimated using the model developed by Elliot

and Persson (1978), as this approach has been used for Ictalurid catfishes (Baumann and Kwak 2011). While this model may not be the best choice for exclusively piscivorous fish (Héroux and Magnan 1996), Blue Catfish in Virginia's tidal rivers exhibit a broad, omnivorous diet (Schmitt et al. 2017). Additionally, the Elliot and Persson model (1978) is most effective in the field when sample intervals are 3 hours or less (Cochran and Adelman 1982; Kwak et al. 1992). Fish were sampled at 3 h intervals over a 24 h period from the James, Pamunkey, Mattaponi, and Rappahannock rivers, and diet contents were extracted immediately using pulsed gastric lavage. Gut fullness was calculated for each fish as the wet weight of the stomach contents divided by the wet weight of the fish (Hyslop 1980). Gut fullness was logit transformed prior to estimating daily ration, as it helps stabilize error variance (Warton and Hui 2011).

Daily ration (C_{24}) was calculated as,

$$C_{24} = \sum_{t=1}^p \frac{(F_{t+1} - F_t e^{-Rt})RT}{(1 - e^{-RT})}$$

where F_t is mean stomach fullness at time t , F_{t+1} is stomach fullness at time $t+1$, R is gastric evacuation rate for each interval, T is time interval between samples (3 h), and p is the number of sampling intervals in a 24-h period (12). The gastric evacuation rate (R) was first calculated for each 3-h time interval using the slope of stomach fullness (F_t) plotted against time,

$$R = \frac{\log_e F_{(t+1)} - \log_e F_{(t)}}{T}$$

where $F_{(t)}$ and $F_{(t+1)}$ are mean stomach fullness at the beginning and end of each interval, respectively (Boisclair and Leggett 1988; Héroux and Magnan 1996). The gastric evacuation rate

(R) with the steepest slope was used for modeling maximum daily ration (C_{\max}), where this maximal value of R is applied to all intervals (C_{\max} ; Boisclair and Leggett 1988; Héroux and Magnan 1996). Conversely, daily ration (C_{24}) was estimated using the average value of R calculated from all sampling intervals.

Empirical estimates of consumption to biomass ratios (Q/B).—Consumption to biomass estimates (Q/B) provide a measure of food ingested (Q) per biomass of a population (B) over a period of time, usually one year (Palomares and Pauly 1998; Christensen et al. 2005). We constructed an empirical regression model developed by Palomares and Pauly (1998) to estimate Q/B for rates for Blue Catfish in Virginia's tidal rivers. This regression model was based on lab and field-based estimates of consumption for 108 fish populations, including 38 different species and several catfishes (Palomares and Pauly 1998). The following model was used to estimate Q/B :

$$\text{Log}_{10}(Q/B) = 7.964 + 0.204 (\log W_{\infty}) - 1.965(T') + 0.083(A) + 0.532(h) + 0.398(d)$$

Where W_{∞} is asymptotic weight (g), T' is mean annual water temperature (expressed as $1000/\text{ }^{\circ}\text{K}$), A is the aspect ratio of the caudal fin, h is a dummy variable explaining food type (1 = herbivore, 0 = for non-herbivores), and d is a dummy variable also explaining food type (1=detritivores, 0 = non-detritivores; Palomares and Pauly 1998). Q/B estimates were calculated separately for smaller, omnivorous fish and larger, piscivorous fish in each river by including or excluding h and d terms (note: “d” term was only applied to small fish from the James and Rappahannock Rivers, where detritus was commonly found in stomachs; Schmitt et al. 2018, *in press*). Herbivory and detritivory terms were dropped for piscivorous sized of Blue Catfish based on the results of previous diet studies (Schmitt et al. 2018, *in press*).

Model parameters.—River-specific estimates of W_{∞} were used within each Q/B estimator based on von Bertalanffy growth curves (Orth et al. 2017; Hilling et al. 2018). Estimated W_{∞} values were converted from kg to g and log₁₀-transformed for use in each model. Mean annual water temperature (T') was calculated for all segments (tidal fresh, oligohaline, and mesohaline) of the James, Pamunkey, Mattaponi, and Rappahannock Rivers using Chesapeake Bay Program water data for 2010–2016. Monthly water temperatures were averaged for each year, and then these values were averaged across all years.

Aspect ratios were determined by (1) removing caudal fins from 27 Blue Catfish ranging from 314 mm TL – 887 mm TL, (2) tracing those caudal fins onto paper, and (3) scanning them into a digital database. Features were then analyzed using TpsDig 2.32, which is freeware specifically developed for geometric morphometric analysis (Rohlf 2016). The mean aspect ratio of the caudal fin was incorporated into all Q/B estimates.

Results

Laboratory experiments.—Blue Catfish consumption rates varied significantly with temperature, prey type, and fish size. Maximum daily ration (C_{\max}) varied from 4% to 21% of their body weight per 24 hours (bw/24 h), with a grand mean of 9.56% bw/24 h. C_{\max} varied significantly with temperature, prey type, and fish total length, though interactions were insignificant (Table 1). On average, Blue Catfish can consume significantly more Gizzard Shad than blue crab in a 24 h period (Figure 1). Consumption rates increase with temperature from 5° to 15° C, though consumption rates did not differ significantly from 15° C to 25° C (Tukey's HSD; $P>0.05$). Mean C_{\max} was 7.53% bw/24 h consumed at 5° C, 10.66% bw/24 h at 15° C, and 10.55% bw/24 h at 25° C. Consumption rates also changed with significantly with fish size, and intermediate sized catfish (500 – 600 mm TL) consumed the most food over a 24 h period (Figure 2). This

may be a result of individual feeding behavior due to only one representative fish per length class for fish >500 mm TL, which is discussed below.

Diel feeding chronologies and field estimates of daily ration.—Stomach contents were extracted from 1,226 Blue Catfish on the James, Pamunkey, Mattaponi, and Rappahannock Rivers. All diel feeding chronologies were completed in August, and water temps at all sites ranged from 22.3 ° C to 29.6 ° C, which should correspond with maximal, asymptotic consumption rates based results from the laboratory study. Time of peak feeding varied by river (Figure 3). Peak feeding occurred at 15:00 for the James River, at 9:00 for the Pamunkey River, and at 12:00 for the Rappahannock and Mattaponi Rivers (Figure 3). Field estimates of C_{max} varied by river, ranging from 4.34% bw/24 h in the Mattaponi River to 15.00% bw/ 24 h in the Pamunkey River (Table 2). Similar patterns were observed for daily ration, where C_{24} ranged from 2.27% in the Mattaponi River to 5.22% in the Pamunkey River (Table 2). Estimates of C_{max} from lab experiments (9.56% bw/24 h) versus the field experiments (8.76% bw/24 h) were remarkably close and did not differ significantly (ANOVA; Figure 4).

Empirical estimates of consumption to biomass ratios (Q/B).—Consumption to biomass ratios ranged from 2.42 for large fish in the Mattaponi River to 3.39 for small fish in the James River (Table 3). Small omnivorous fish had the highest Q/B values, particularly fish from the James and Rappahannock Rivers. This can be explained by the inclusion of a detritory term (d) in both of these models since Blue Catfish stomachs regularly contain detritus in these rivers (Schmitt et al. 2018, *in press*). Q/B estimates for Blue Catfish are within the normal range observed in many freshwater and marine benthic fishes (Palomares and Pauly 1998).

Discussion

The current study provides the first estimates of daily ration and total annual consumption for Blue Catfish, information that is critically important for quantifying its predatory impact on native biota in Chesapeake Bay tributaries. Not surprisingly, maximum daily ration varies significantly with temperature, prey type, and fish size. Blue Catfish can consume more Gizzard Shad than blue crab in a 24 h period, which is intuitive since the presence of an exoskeleton slows digestion (Bromley 1994). Blue Catfish maximum daily ration increased with temperature up to 15° C, though it does not increase significantly above 15° C. Fish consumption rates generally increase with temperature, often reaching an asymptote at higher temperatures (Bromley 1994). Maximum daily ration also varied with fish size, yet there is a strong possibility that this is due to individual behavior, as we only had single representative fish within the larger length classes. Two Blue Catfish (500 and 600 mm TL) would gorge themselves to the point where they could no longer maintain vertical orientation and would lay motionless on the bottom of the tank while they digested their meal. These fish exhibited higher consumption rates than the other fish, though it is uncertain whether this is a length-based phenomenon or just individual feeding behavior. Interestingly, previous studies have shown that Blue Catfish begin to shift to piscivory at 500-600 mm TL in the Rappahannock River (Schmitt et al. 2018, *in press*). It is possible that Blue Catfish consume more when making this transition, though more testing would be necessary to confirm this hypothesis. We were only able to house a small number of fish due to the space constraints within our RAS, but it would be interesting to explore this hypothesis in larger aquaria.

Field estimates of maximum daily ration did not differ significantly from lab estimates. Both lab and field experiments demonstrate that in situations of unlimited food, mean consumption rates

are approximately 8-9% of bodyweight per day at optimal water temperatures ($>15^{\circ}\text{ C}$). These results should be interpreted as maximum feeding rates during the summer months, as it is doubtful that Blue Catfish can sustain these feeding rates for extended periods of time. It is important to remember that Blue Catfish were starved for 72 h prior to each feeding trial, and that each feeding trial only lasted 24 h. Our field estimates of daily ration provide a better estimate of sustainable consumption rates, as fish are subject to more natural conditions (Jarre et al. 1991). Our calculations of maximum daily ration are still useful, and would complement field information on peak feeding (e.g. vacuity indices/gut fullness indices) quite well. These maximal values could be applied to consumption models as an upper bound during times when high feeding intensity is observed in the field. Field estimates of daily ration were considerably lower, and these estimates are more reflective of sustainable feeding rates (Bromley 1994).

Our estimates of daily ration are remarkably similar to estimates for Channel Catfish *Ictalurus punctatus*. Growth of Channel Catfish in aquaria occurs at 2-6% bw/day (Andrews and Stickney 1972), which is very similar to our field estimates of Blue Catfish daily ration (2-5% bw/day). Field studies for Channel Catfish have also produced similar estimates of daily ration (2-8% bw/day), though these rates decline to 1.23% bw/day at temperatures $< 15^{\circ}\text{ C}$ (Kwak et al. 1992). We would anticipate a similar decline for Blue Catfish, though more research would be necessary to confirm this. It's important to remember that our field studies were conducted at warm temperatures ($>22^{\circ}\text{ C}$), thus we would expect feeding rates at cooler temperatures ($<15^{\circ}\text{ C}$) to decline significantly based on both our aquaria study and previous Channel Catfish studies (Kwak et al. 1992; Silverstein et al. 2001). These estimates of daily ration and maximum daily ration could be useful for the construction of a Blue Catfish bioenergetics model, which does not currently exist in the scientific literature (Deslauriers et al. 2017).

For the field experiments, consistent diel feeding patterns were not apparent across all rivers. This is may be because much of the Blue Catfish population feeds on rooted macrophytes and sessile bivalves like Asian clams *Corbicula fluminea*, which should be accessible regardless of time of day (Schmitt et al. 2018, *in press*). Increases in feeding may be associated with tidal cycles, as fish may wait for ideal flow conditions to leave resting locations to feed (Stoner 2004). There was some evidence of this, as peak feeding occurred during the end of outgoing tide cycles for Blue Catfish in the James, Pamunkey, and Rappahannock Rivers. The exception to this was the Mattaponi River, where peak feeding occurred towards the end of an incoming tide. It is important to note that low stomach fullness was observed throughout the Mattaponi River diel feeding chronology, and this general lack of activity may explain observed differences. Based on these findings, it seems that Blue Catfish prefer to feed past the midpoint of an outgoing tide cycle. Time of day varied and may be less important, though peak stomach fullness occurred between 9:00 and 15:00 for all four rivers. Blue Catfish congregate in deep, outside bends during late summer (*personal observation*) and light penetration is generally limited to the top 1-2 m of the water column in Chesapeake Bay (Dennison et al. 1993). Considering this, we hypothesize that Blue Catfish spend most of their time in the dark during the summer, thus feeding may be unaffected by time of day, though more research would be necessary to confirm this. Field estimates of maximum daily ration did not differ significantly from estimates obtained in the lab, and similarity across independent observations usually implies some degree of accuracy (Rice and Cochran 1984).

Consumption to biomass estimates were greater for small fish versus large fish, which is intuitive. Small fish consume low energy foods like vegetation and detritus, while large fish are more piscivorous (Schmitt et al. 2018, *in press*). These differences in food habits require the

inclusion of herbivory and detritivory terms in the model, which results in an increase in Q/B ratios for small fish. Logically, fish that eat low caloric value foods will have greater consumption requirements than fish that are consuming prey with higher energy densities (Gerking 1994). Blue Catfish Q/B estimates ranged from 2.43 – 3.39, which are similar to estimates for other benthic generalists like common roach *Rutilus rutilus* ($Q/B=2.68$), Atlantic cod *Gadus morhua* ($Q/B=2.59$), yellow perch *Perca flavescens* ($Q/B= 2.79$), and common dab *Limanda limanda* ($Q/B=3.69$; Palomares and Pauly 1998). Q/B estimates for other catfishes vary broadly, and are as low as 1.32 for African sharptoothed catfish *Clarias gariepinus* or as high as 22.07 for *Bagrus docmak*, which is a large, fast-growing catfish species native to central Africa (Palomares and Pauly 1998).

Studies on the impacts of invasive freshwater fish are rare (Garcia-Berthou 2007), and predatory impact can only be assessed once estimates of diet, consumption rates, and predator biomass are available (Ney 1990). The current study provides several estimates of Blue Catfish consumption rate, which will be critical for assessing ecological impacts of invasive Blue Catfish in Chesapeake Bay (Schmitt et al. 2017). Consumption rate information can also be used for the construction of ecopath models (Christensen et al. 2004) or for the development of a Blue Catfish bioenergetics model, which does not currently exist (Deslauriers et al. 2017). Blue Catfish are generalists in regard to both habitat and diet (Schmitt et al. 2018, *in press*), thus further range expansion along the Atlantic slope is likely. Moreover, Blue Catfish have been identified as potential invaders of the Laurentian Great Lakes, where impacts could be substantial (Howeth et al. 2016). Estimates of Blue Catfish consumption rates are a timely addition to the scientific literature, as further range expansion is likely along the Atlantic coast (Bonvechio et al. 2011; Tuckey et al. 2017).

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Tables and Figures

Table 1. For laboratory experiments, factorial ANOVA was used to test for the effects of temperature, prey type, fish length, and interactions on the consumption rates of blue catfish (% bodyweight per 24 h). Summary statistics are presented below.

Factors	DF	F	P
global model	35	42.22	<0.01
temperature	2	8.80	<0.01
prey type	1	11.06	<0.01
length	5	36.78	<0.01
all interactions	N/A	N/A	>0.05

Table 2. Calculations of daily ration (C_{24}), maximum daily ration (C_{max}), and gastric evacuation rates (R) based on 1,226 blue catfish stomachs collected during 24 h feeding chronologies on the James, Pamunkey, Mattaponi, and Rappahannock Rivers in eastern Virginia.

River	C_{24}	C_{max}	R(average)	R max
James	3.52%	10.32%	0.16	0.39
Mattaponi	2.27%	4.34%	0.06	0.08
Pamunkey	5.22%	15.00%	0.20	0.30
Rappahannock	3.39%	5.37%	0.13	0.15
all rivers	3.60%	8.76%	0.14	0.23

Table 3. Consumption to biomass ratios (Q/B) were estimated for blue catfish in each of Virginia's major tidal rivers based on the aspect ratio (A) of the caudal fin, mean annual water temperature (T), asymptotic weight (W_∞), and herbivory and detritivory dummy variables (h and d , respectively). Q/B estimates were calculated separately for different size groups of catfish based river-specific shifts from omnivory to piscivory (Schmitt et al. 2018, *in press*).

River	Total Length (mm)	<i>A</i>	<i>T</i> (°C)	<i>h</i>	<i>d</i>	<i>W</i> _∞ (kg)	<i>Q/B</i>
James	All	3.74	17.23	1	1	46.77	3.39
	<500	3.74	17.23	1	1	46.77	3.39
	>500	3.74	17.23	0	0	46.77	2.46
Pamunkey	All	3.74	17.41	1	0	30.11	2.96
	<900	3.74	17.41	1	0	30.11	2.96
	>900	3.74	17.41	0	0	30.11	2.43
Mattaponi	All	3.74	17.11	1	0	30.11	2.95
	<800	3.74	17.11	1	0	30.11	2.95
	>800	3.74	17.11	0	0	30.11	2.42
Rappahannock	All	3.74	16.89	1	1	36.09	3.36
	<700	3.74	16.89	1	1	36.09	3.36
	>700	3.74	16.89	0	0	36.09	2.43

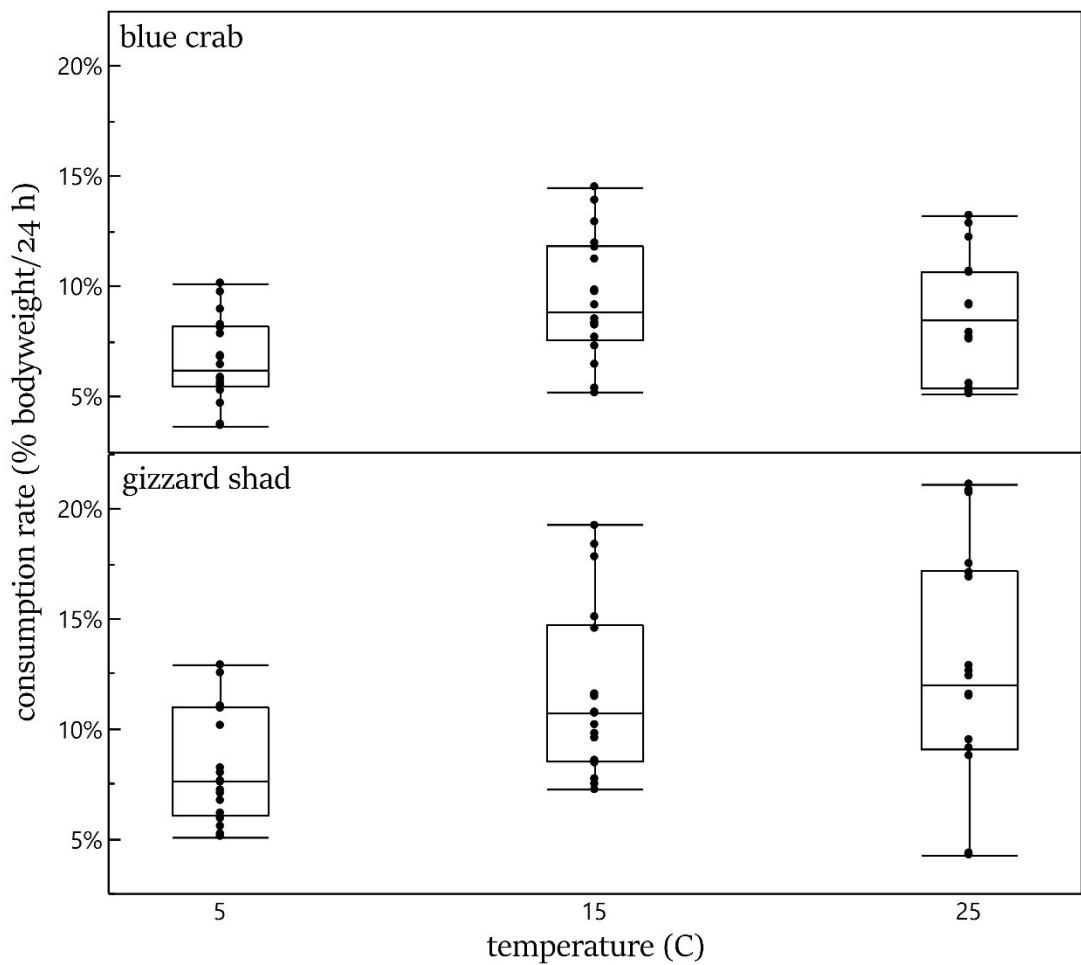


Figure 1. Lab estimates of maximum daily ration (expressed as % bodyweight per 24 h) for blue catfish as it varies by temperature and prey type. Temperature and prey type significantly influenced maximum daily ration ($P<0.01$). In general, blue catfish ate less blue crab than gizzard shad in a 24 h period, and consumption rates increased significantly from 5° to 15° C, with non-significant increases occurring from 15° to 25° C.

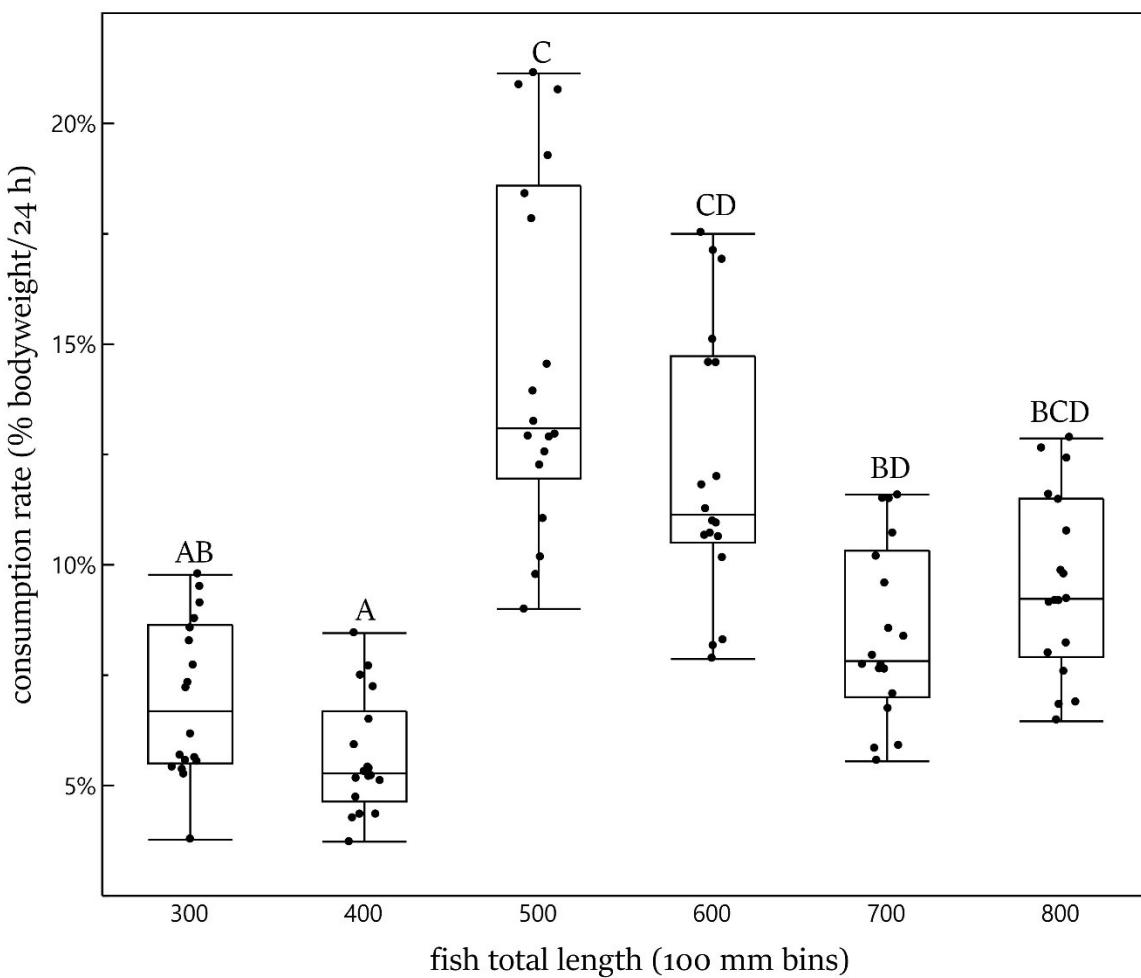


Figure 2. Lab estimates of maximum daily ration (expressed as % bodyweight per 24 h) for blue catfish as it varies by fish total length (mm). Estimates that do not share the same letter (A-D) differ significantly (*Tukey's HSD*; $P < 0.05$)

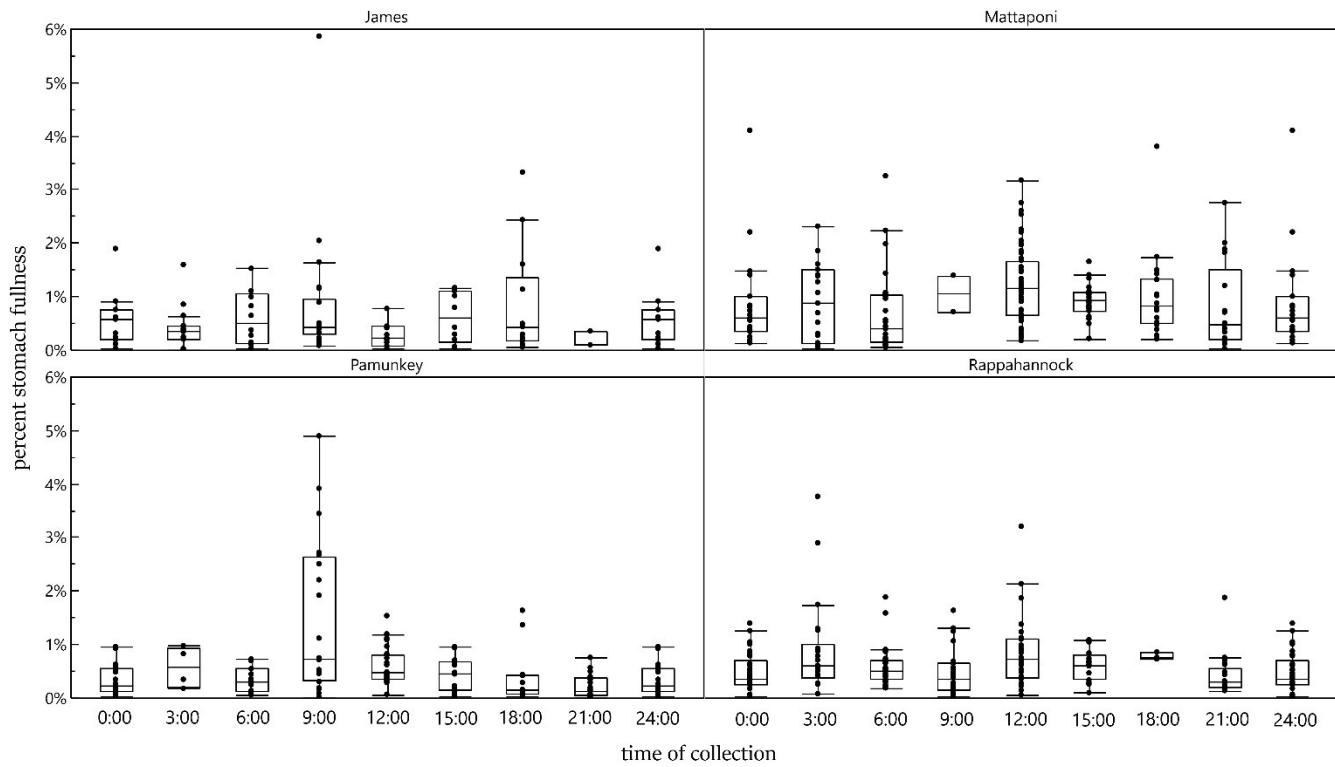


Figure 3. Stomach percent fullness throughout a 24 h period for 1,226 blue catfish captured on the James, Mattaponi, Pamunkey, and Rappahannock Rivers in eastern VA. All diel feeding chronologies were completed during the month of August, and water temperatures ranged from 22.3° C to 29.6° C.

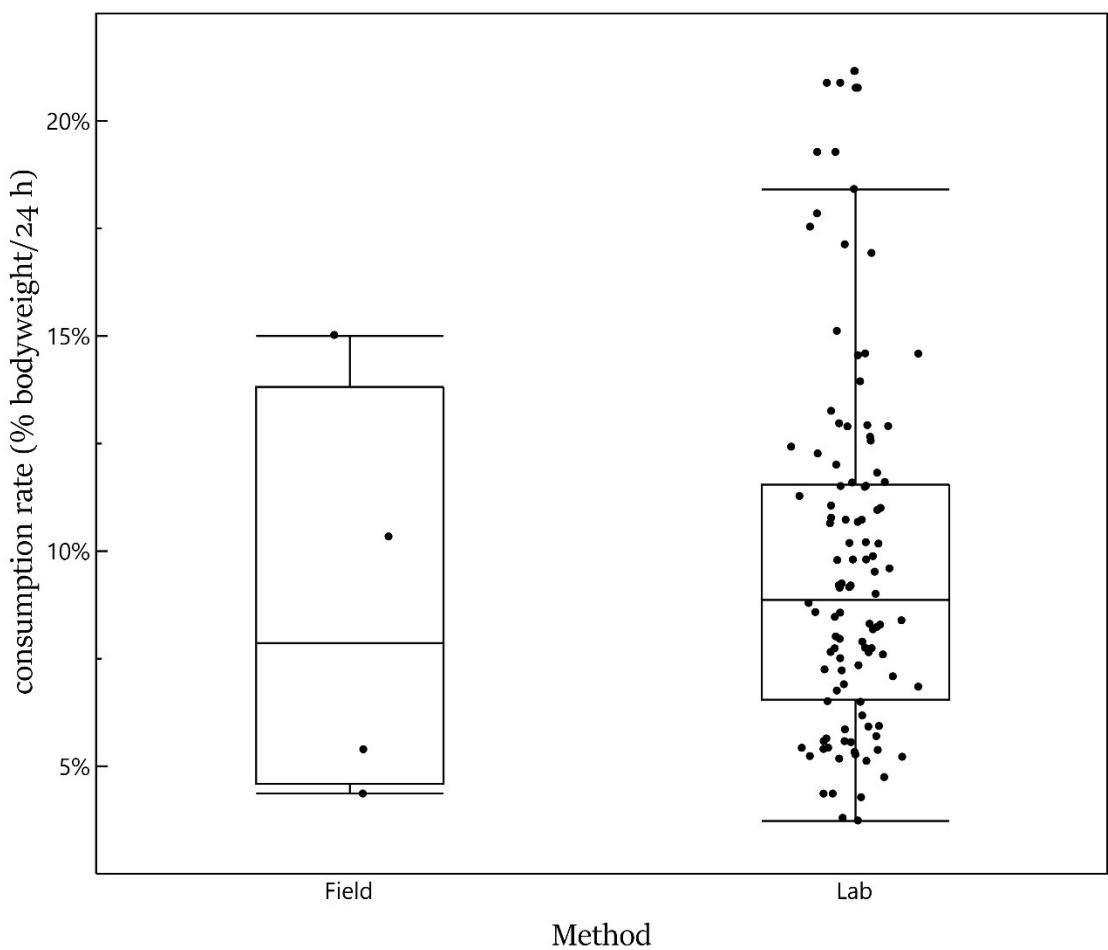


Figure 4. Maximum daily ration estimates (expressed as % bodyweight per 24 h) from field experiments and lab experiments did not differ significantly (ANOVA; $P=0.63$).

Chapter 6: Summary, Conclusions, and Closing Thoughts

Summary

Feeding ecology

Blue Catfish can best be described as opportunistic omnivores regardless of season or spatial location. Blue Catfish have broad, omnivorous diets consisting of vegetation, detritus, mammals, birds, reptiles, amphibians, fish, crustaceans, mollusks, and various other invertebrates. Primary foods included vegetation (common waterweed, *Hydrilla*, etc), Asian clams, estuarine mud crabs, and Gizzard Shad. Blue Catfish occupy lower trophic levels than Flathead Catfish and Striped Bass, which is partially driven by the high occurrence of various plants in their diet. A close comparison to Blue Catfish is common carp, which is another herbivore-benthic invertivore (Berthou-Garcia 2007).

Blue Catfish have high diet breadth, especially small fish in the Rappahannock River. In fact, diet breadth estimates for Blue Catfish in the Rappahannock River were considerably higher than published values for over 50 other estuarine fish species (Hajisamae et al. 2003; Akin and Winemiller 2006). Our omnivory indices further validated that Blue Catfish are opportunistic generalists that feed on multiple trophic levels. Blue Catfish shift from omnivory to piscivory as they grow, though shifts vary by river system. Catfish become more piscivorous in the James and Rappahannock at 500 mm TL, while they become more piscivorous in the York River at 600-700 mm TL. We hypothesize that this may be due to the relative abundance of smaller prey fish. During our sampling we routinely saw juvenile Gizzard Shad in the James River and Rappahannock River. This was not the case in York River tributaries, where Gizzard Shad densities were lower and juveniles were rarely encountered. Omnivory and diet breadth values

generally declined with increases in fish total length, which is presumably caused by ontogenetic shifts from omnivory to piscivory.

In summary, the feeding ecology of Blue Catfish (BCF) in Chesapeake subestuaries can be characterized with the following bullet points:

- BCF are opportunistic generalists that feed on a wide array of plant and animal material
- BCF are highly herbivorous and occupy lower trophic levels than anticipated
- BCF undergo ontogenetic shifts in diet. Small fish are herbivore-benthic invertivores, while large fish become more piscivorous. The size at which shifts occur vary by river.
- BCF feed non-selectively on locally-abundant organisms
- BCF have impressive diet plasticity and feed on multiple trophic levels
- BCF are resilient and appear capable of surviving on diets of vegetation and detritus

Blue Catfish showed some signs of individual diet specialization, which may help explain why growth rates are highly variable for this species (Greenlee and Lim 2011). Logically, a Gizzard Shad specialist should grow faster than a detritus specialist. While primitive, our predator feeding strategy diagrams reveal that large fish often specialize on other Blue Catfish, White Perch, and Gizzard Shad. Small fish often specialize on detritus, mayflies (Rappahannock River), various snails, and estuarine mud crabs. These patterns of individual diet specialization are intriguing and should be explored further using more advanced methods as suggested by Bolnick et al. (2002) and Zaccarelli et al. (2013).

Predation of species of concern

Our spring selectivity analysis revealed that piscivorous Blue Catfish do not selectively prey on alosines; rather, they feed on whatever fish are locally abundant (primarily Gizzard Shad, White Perch, and Hickory Shad; Schmitt et al. 2017). American Shad were rarely consumed by Blue Catfish, but this makes sense since American Shad are uncommon (*e.g.* we only captured two during our prey fish relative abundance sampling during the spring). River herring were also rare in Blue Catfish stomachs, though were more commonly encountered during relative prey abundance sampling.

According to our GAMs, predation of alosines is greatest among large fish (600 – 1000 mm TL), during April in the James River. Fish size and river-based effects may be autocorrelated since the James River population is the only river that *has* a substantial number of large fish. Declines in American Shad and river herring have been coast-wide and appear to be driven by offshore bycatch (Bethoney et al. 2013), though habitat fragmentation, water quality degradation, and predation may also play a role. Alosine declines have also occurred in rivers that do not have invasive catfish (*e.g.* Connecticut River and Hudson River; Limburg and Waldman 2009), and declines in the Chesapeake Bay began before the establishment of these catfish. Logically, one can conclude that *Alosa* declines were initiated by something other than catfish. However, because Blue Catfish are opportunistic, we anticipate that predation could increase if American Shad become more abundant in these rivers, since Blue Catfish feed on locally-abundant resources. This additional predation by Blue Catfish could still impede recovery, especially if Blue Catfish exhibit a Type II functional response curve, where more imperiled alosines are consumed as prey densities decrease (Dick et al. 2014). Our prey selectivity analysis from the spring demonstrates that this is highly unlikely for Blue Catfish, as they feed on whatever fish are locally abundant. Furthermore, American Shad have recently shown some signs of recovery

in the Rappahannock and Potomac Rivers (Cummins 2016; Hilton et al. 2016), and both rivers support dense populations of Blue Catfish. It will be interesting to see if these American Shad populations continue to recover. If further recovery is observed, it is unlikely that Blue Catfish are a key player in the population dynamics of American Shad in these rivers.

Blue crabs are regularly eaten by Blue Catfish. Blue crab predation is highest in September and October in mesohaline areas, and the predicted percent occurrence is as high as 28%. These patterns are likely driven by the spatial dynamics of the blue crab population, which generally form denser populations at higher salinities (King et al. 2005). Larger catfish (500 – 800 mm TL) eat the most blue crab, and predation is highest in the James River. While predation of blue crab may be high, it could be inconsequential since mechanisms other than predation are expected to control blue crab population trajectories (Bauer and Miller 2010; Colton et al. 2014). Nonetheless, predation by Blue Catfish should be considered in future blue crab population models.

American Eel predation peaks during the spring and the fall, and may be related to seasonal movements. Salinity did not significantly influence American Eel predation, which is intuitive since eels readily colonize marine, estuarine, and freshwater habitats and often move freely between them (Feunteun et al. 2003, Daverat et al. 2004). While large catfish (400-800 mm TL) eat more eels, they were still rare and stomachs, and the probability of predation was less than 4% in all circumstances.

Blue Catfish probably eat more blue crab (in terms of kg/year) than any other “species of concern” (Orth et atl. 2017). Nonetheless, the relative impact of Blue Catfish may be more substantial for the other species (especially American Shad), since they are rare and any additional “losses” could impede recovery. It is important to remember that Blue Catfish are the

second nonindigenous catfish as Channel Catfish were stocked in these rivers during the 1800s (Jenkins and Burkhead 1994). While historic information is limited, Channel Catfish were once highly abundant and also ate “species of concern”, including river herring and Blue Crab (Menzel 1945). It is quite possible that Blue Catfish biomass has simply replaced Channel Catfish biomass over the last 40 years, and the net impact of invasive Blue Catfish is minimal (e.g. predator to prey biomass may remain unchanged; see Lauber et al. 2016).

Consumption rates

We used three different approaches to estimate daily consumption by Blue Catfish, including lab experiments, field experiments, and empirical models. Maximum daily ration is strongly influenced by temperature, prey type, and fish size, though the effect of size may be a result of individual feeding behavior. Average estimates of maximum daily ration from the field and lab did not differ significant. Based on these estimates, Blue Catfish can consume a maximum of 8-10% of their bodyweight per 24 h. Field estimates of daily ration range from 2-5% bodyweight per 24 h and are a better reflection of how much Blue Catfish can eat over longer periods of time. In general, Blue Catfish consumption rates are almost identical to the range of consumption rates of Channel Catfish (1 – 8% bw/day Andrews and Stickney 1972; Vigg et al. 1991; Kwak et al. 1992). Field studies were completed during warmer water temperatures ($>22^{\circ}\text{C}$), and based on results from Channel Catfish studies (Kwak et al. 1992), we predict that daily ration would drop to below 1.5% bodyweight per 24 h at water temperatures $<15^{\circ}\text{C}$. Empirical estimates of consumption to biomass ratio (Q/B) were greatest for small, omnivorous Blue Catfish, as they eat food of low nutritional value like vegetation and detritus, while Q/B estimates were lower for large Blue Catfish since they are more piscivorous. Compared to other species, Q/B estimates for

Blue Catfish are similar to estimates for Atlantic Cod *Gadus morhua*, Yellow Perch *Perca flavescens*, and Common Dab *Limanda limanda* (Palomares and Pauly 1998).

Blue Catfish population dynamics are changing in Virginia's tidal rivers. Large fish are becoming less common, growth rates are slowing down, and populations appear to be in decline; presumably due to increased harvest and natural population stabilization processes (Hilling et al. 2018; Bunch et al. 2018, *in press*). Many invasions follow a similar progression. After introduction there is often a lag phase, followed by a population boom, followed by a decline as the population reaches equilibrium (Strayer et al. 2017). There is sufficient evidence to suggest that populations in the James and the Rappahannock Rivers are in the “decline” phase of the invasion process. The York River was stocked about a decade after the James and Rappahannock Rivers, therefore these declines are not yet evident (Hilling et al. 2018). Ultimately, large catfish have the greatest predatory impact on species of concern, therefore relative impact should decrease as Blue Catfish populations reach equilibrium and shift towards fewer and smaller individuals.

Discussion and Conclusions

The advantages of generalism

The rapid expansion and growth of the Blue Catfish population in the Chesapeake Bay may be linked to opportunistic life history strategies, as Blue Catfish are generalists with respect to both diet and habitat (Schmitt et al. 2018, *in press*). Globally, specialist taxa are being replaced by invasive generalists with broad ecological niches, a trend known as biotic homogenization (McKinney and Lockwood 1999; Clavel et al. 2011). Many successful generalists outcompete more specialized ones due to their ability to thrive in altered or degraded habitats, which has sparked a renewed interest in the characterization of generalist species worldwide (McKinney

and Lockwood 1999; Layman and Allgeier 2012). Moreover, dietary plasticity helps an organism endure stochastic fluctuations in prey availability, which often provides a competitive advantage in degraded systems (Layman and Allgeier 2012). These traits may explain the success of Blue Catfish in the Chesapeake Bay, as anthropogenic activities have resulted in widespread habitat degradation and major ecological changes over the last 50 years (Kemp et al. 2005).

Why are population densities so high?

Hypothesis development and testing to explain why some nonnatives succeed while others don't often produces speculative and contradictory results (Lockwood et al. 2013). Propagule pressure, which refers to the number of animals introduced and the number of introduction events, is the only theory that has been consistently validated with empirical data (Jeschke 2014). Logically, a greater number of animals per event and a greater number of introduction events leads to a greater probability of invasion success (Jeschke 2014). Time since introduction can also influence invasion success, where more time increases the chance of invasiveness (Peoples and Goforth 2017). As an intentional introduction, propagule pressure for Blue Catfish in Virginia's tidal rivers was high, and hundreds of thousands of catfish were stocked over many years with many different introduction events (Jenkins and Burkhead 1994). Moreover, Blue Catfish populations didn't really "boom" until the early 2000s, which was nearly 30 years after their initial introduction (Greenlee and Lim 2011). Considering these factors, the proliferation of Blue Catfish in Chesapeake Bay subestuaries during the early 2000s was likely due to 1) high propagule pressure in terms of numbers of individuals and numbers of introduction events, and 2) the length of time since introduction (*e.g.* 15 – 30 years).

Blue Catfish success in Atlantic slope drainages may partially be explained by the biotic resistance hypothesis, where a species that is transplanted from an area higher biodiversity to an

area of lower biodiversity will have a competitive advantage in its new environment (Fitzgerald et al. 2016). Blue Catfish would have an advantage in Virginia's tidal rivers, since these drainages have simpler native fish communities than where Blue Catfish evolved, *e.g.* the Mississippi River and its tributaries. The Mississippi River basin is home to over 400 native fish species (Muneeperakul et al. 2008), while tidal rivers like the James, York, and Rappahannock only support about 40 – 50 native fish species (Jenkins and Burkhead 1994). Moreover, our highest captured rates for Blue Catfish were in oligohaline sections of these rivers, and these areas have been documented to have high densities of catfish by others (Fabrizio et al. 2017; Bunch et al. 2018, *in press*). This pattern could further support the biotic resistance hypothesis, as fish biodiversity declines precipitously at the freshwater/saltwater interface (oligohaline and mesohaline zones; Wagner 1999). If the biotic resistance hypothesis is valid, Blue Catfish would have a competitive advantage in all Atlantic slope drainages. Moreover, Blue Catfish would be expected to be most abundant at the species minimum, which occurs at salinities of approximately 9 ppt (Wagner 1999).

Another possible explanation for the incredible success of Blue Catfish in Virginia's tidal rivers is the climate match hypothesis, which states that a nonnative fish is more likely to become invasive if the climate (specifically temperature and precipitation) in the recipient basin is similar to that of the donor basin (Bomford et al. 2010). The climate match hypothesis could explain the success of Blue Catfish in Virginia's tidal rivers, since temperature and rainfall extremes in Virginia should fall within the minima and maxima that occur in the native range. Remember that native Blue Catfish populations stretch from South Dakota to Central America (Graham 1999), which means that Blue Catfish are adapted to diverse thermal and precipitation regimes. While hurricanes can result in extreme precipitation events in Virginia's tidal rivers (Franklin et

al. 2004), Blue Catfish are native to the estuarine portions of the Mississippi River which are also regularly impacted by hurricanes. Blue Catfish are well-adapted to life in the Chesapeake Bay, and many other rivers along the Atlantic coast would be susceptible to invasion under this hypothesis. If either of these hypotheses are valid (biotic resistance and climate match), I would anticipate further range expansion in and among Atlantic coastal rivers. To further support these hypotheses, established and expanding populations of Blue Catfish now occur in coastal rivers in Georgia, South Carolina, North Carolina, Maryland, and Delaware (Moser and Roberts 1999; Upchurch and Wenner 2008; Schloesser et al. 2011; Bonvechio et al. 2012).

The success of Blue Catfish in the region could also be explained, at least partially, by a variant of the vacant niche hypothesis (*sensu* Cizek et al. 2003). In this variant, the nonnative species is at an advantage if it can utilize resources that are either unutilized or underutilized by native biota (Garcia-Berthou 2007). Virginia's tidal rivers support impressive populations of both juvenile and adult Gizzard Shad *Dorosoma cepedianum*, and many adults range between 300 and 400 mm TL (Schmitt, *unpublished data*). These large shad are inaccessible to native predators such as Longnose Gar and Bowfin due to gape limitations (see Schmitt et al. 2017), and would be unavailable to most largemouth bass *Micropterus salmoides* (DiCenzo et al. 1996).

Piscivorous Blue Catfish and Flathead Catfish have taken advantage of this, and Gizzard Shad comprise over 50% of their diet by weight (Schmitt et al. 2017). Other invasive species, such as *Hydrilla* and Asian clams, are found in over 50% of smaller Blue Catfish stomachs. While it's possible that *Hydrilla* and Asian clams are utilized by other biota, they likely still serve as a "vacant niche" since they exist at such high densities in Virginia's tidal rivers (Posey et al. 1993; Phelps 1994). Blue Catfish, particularly in the James River near Richmond, also feed heavily on detritus. We believe that this detritus forms as a result of raw sewage being discharged into the

river during combined sewer overflow events, which is a common occurrence in Richmond during the spring. It is unlikely that this detritus is a limited resource, and it could serve as another “vacant niche” for Blue Catfish. As nonselective generalists that use many different feeding strategies (*e.g.* herbivory, detritivory, piscivory, and omnivory; Schmitt et al. 2017; Schmitt et al. 2018, *in press*), Blue Catfish success is definitely driven, to some degree, by their ability to exploit all available resources.

The magnitude of these “vacant niches”, especially Gizzard Shad and detritus, is likely driven by an excess of nutrients in these tidal rivers (DiCenzo et al. 1996; Kemp et al. 2005). While modest nutrient reductions have occurred since the 1980s in the Chesapeake Bay (Harding et al. 2016), elevated levels of nitrogen and phosphorous are still problematic in many subestuaries (Jordan et al. 2017). This eutrophication has resulted in a major regime shift from benthic diatom production to pelagic phytoplankton production, resulting in widespread ecological changes (Kemp et al. 2005). Phytoplankton blooms have been a frequent problem, as they block sunlight and have resulted in massive losses of submerged aquatic vegetation (SAV; Orth et al. 2006). The loss of SAV has turned these Chesapeake subestuaries into turbid, nutrient-rich systems that resemble the rivers of the Blue Catfish’s native range. Blue Catfish are well-adapted to foraging in murky waters, as catfish possess incredible olfactory, gustatory, and mechanoreceptory abilities (Pohlmann et al. 2004).

Increases in system productivity have probably caused increases in Gizzard Shad populations (Michaletz 1998), which are the preferred prey of large Blue Catfish in both their native and introduced ranges (Edds et al. 2002; Eggleton and Schramm 2004; Schmitt et al. 2018, *in press*). While rare, large catfish likely drive population dynamics for this species in these rivers. This is partially because large female fish have been documented to produce more eggs, bigger eggs,

and contribute substantially more reproductive output than an equivalent biomass of younger, smaller individuals (Hixon et al. 2014). Moreover, for other nest-guarding Siluriformes, large male catfish were more desirable to females and had higher brood survival rates (Bisazza and Marcanato 1988). Thus, large individual catfish of both sexes are likely to contribute substantially more reproductive output than smaller, younger fish.

The second “invasive” catfish

While we've demonstrated that Blue Catfish consume imerpiled alosines, blue crab, and American Eel, any speculation as to “impact” on these resources may be misleading. It is important to remember that nonindigenous Channel Catfish *Ictalurus punctatus* were stocked in these tidal rivers during the 1800s (Jenkins and Burkhead 1994). Channel Catfish were the dominant catfish species in these tidal rivers until the mid-1990s, after which Blue Catfish became dominant (R. Greenlee, *personal communication*). It is very possible that Blue Catfish biomass has simply replaced Channel Catfish biomass to some degree, thus ecological “impact” may be negligible. Blue Catfish and Channel Catfish have many similarities and even hybridize naturally in some systems (Tyus and Nikirk 1990; Graham 1999). Like Blue Catfish, Channel Catfish consumed blue crab and river herring prior to the Blue Catfish introduction, and these species of concern were found in up to 50% of Channel Catfish stomachs (Menzel 1945). Two differences between the species are that 1) Blue Catfish can grow considerably larger and 2) Blue Catfish appear to have expanded further into brackish areas, though we do not know the historic distribution of Channel Catfish. Large Blue Catfish are rare, yet their large gape allows them to consume prey like American Shad and Hickory Shad that were likely inaccessible to Channel Catfish. While American Shad are not found in many Blue Catfish stomachs (<1%

occurrence), this may be one of the only “net” differences between the two catfish species in terms of impact to species of concern.

The only detectable ecological change since the Blue Catfish introduction is a marked reduction in the relative abundance of White Catfish (Tukey and Fabrizio 2010). This is probably not driven by direct predation, since White Catfish are rarely found in Blue Catfish stomachs, but is more likely to be due to competition for spawning habitat (*personal observation*). We documented both species forming spawning aggregations in the same areas at the same time; usually deep, undercut clay banks in large tributaries out of the main current. Spawning generally took place in late May (the biggest catfish spawn first) and continued through the entire month of June. Both species are cavity spawners and males actively defend the nest (Graham 1999).

Without a doubt, a 25 kg Blue Catfish has a substantial advantage over a 2 kg White Catfish. We documented many male White Catfish with large bite marks on their bodies during the spawn, and we hypothesize that larger Blue Catfish were forcibly removing White Catfish from prime spawning locations. Having shocked catfish at hundreds of sites in these rivers, I can say with certainty that spawning habitat is fairly limited, especially in York River system. I suspect this to be the primary reason for White Catfish declines in these systems, though competition for food could also play a role. It is important to note; however, that resources are likely not limited in highly eutrophic systems like the James and Rappahannock Rivers.

Gaps and future research

With over 16,000 Blue Catfish stomachs collected, the current study is the largest diet study ever completed for this species. Cumulative prey curves revealed that samples sizes were adequate for all rivers, yet, there are still several limitations to the study. First, Blue Catfish sampling during the winter months was limited to the James and Pamunkey Rivers since low-frequency

electrofishing does not work in cold water (Bodine and Shoup 2010), and high-frequency electrofishing is a laborious sampling method for this species (Schmitt et al. 2017). This knowledge gap is concerning since our diet data indicates that Blue Catfish are more piscivorous and eat more blue crabs during the winter (Schmitt et al. 2018, *in press*). While consumption rates in the winter are probably much lower (based on our aquaria study), it still warrants further investigation. Second, our sampling was limited to salinities <10 ppt, and the majority of our fish came from salinities <7 ppt. This is problematic because Blue Catfish have been captured in salinities as high as 21.5 ppt (*unpublished data*, cited in Fabrizio et al. 2017) and our GAMs demonstrate that predation of blue crabs increases with salinity. Considering this, we may be underestimating predation of Blue Crab since we have little diet information for Blue Catfish in salinities of 10-20 ppt. Finally, while Blue Catfish consume blue crab, river herring, and American Shad, we have no way of determining what percentage of these are scavenging events. Unlike Flathead Catfish, Blue Catfish are known scavengers (Graham 1999), and we found evidence of this in several stomachs (e.g. chicken bones, cut bait). It is nearly impossible to determine if the American Shad and river herring we found in catfish stomachs during the spring truly represent predation events. It's also possible that Blue Catfish simply picked them up off the bottom, as mortality of alosines can be high following the spawn (Glebe and Leggett 1981).

Potential management strategies

Several potential management strategies were suggested by Orth et al. (2017), including “invasivorism”, nutrient reduction strategies, and targeted removal at specific life history stages. The current management approach in the Chesapeake Bay is “invasivorism”, which essentially means you eat your way out of the problem. Commercial harvest of Blue Catfish has increased steadily since the early 2000s (Schloesser et al. 2011) and electrofishing is currently being used

to harvest this species (Trice and Balazik 2015). Low frequency electrofishing works best during the summer months (Bodine and Shoup 2010), which can result in oversupply and drive prices down during this short time frame. Moreover, traditional harvesters fervently believe that electrofishing interferes with their harvest methods (typically pots, pound nets, and gillnets). Considering this, it may be best to limit harvest to traditional gears (Orth et al. 2017). Some catfish (particularly large fish) are unfit for human consumption due to contaminants (Hale et al. 2016) so managers may want to consider the organic feed market, where Blue Catfish can be turned into pet food (*e.g.* EcoCarp) or plant food (*e.g.* SF Organics; Orth et al. 2017).

Another policy option is a more holistic approach which encourages efforts to reduce nutrient loads while simultaneously harvesting Blue Catfish for multiple markets. These actions are logically coupled, since nutrient inputs likely drive the abundance of Gizzard Shad (DiCenzo et al. 1996), which are the dominant prey of large invasive catfishes (Schmitt et al. 2017; Schmitt et al. 2018, *in press*). It stands to reason that reductions in nutrients could yield reductions in Gizzard Shad, which could result in diminished biomass of large catfish. This, in turn, could reduce population densities since large fish are known to contribute disproportionately more offspring than smaller fish (Hixon et al. 2014). Gizzard Shad and Blue Catfish likely act as major nutrient “sinks”, thus the removal of these fishes from the system may help managers achieve TMDL goals. While modest reductions in nutrient levels have been achieved since the 1980s (Beegle 2013), forecasts show an increase in nitrogen loading in the future (Sinha et al. 2017). Solutions for this issue may reside in the local development of nutrient markets and nutrient trading credits (Miller and Duke 2013). While nutrient markets are largely restricted to agriculture, there is no reason that this cannot market cannot be expanded to fish. Furthermore,

the levels of nitrogen and phosphorous removed per biomass of fish is easily calculated (Orth et al. 2017).

Finally, if managers want to reduce the impacts of Blue Catfish on specific biota, our predation models can provide directive guidance for removal efforts. Potential benefits for Blue Catfish control will vary by river, and our models can help managers decide when and where to allocate resources for control strategies (Januchowski-Hartley et al. 2017). In general, large catfish eat the most “species of concern”, while seasonality and salinity also influences predation rates. If attempted, managers can focus removals to focus on certain seasons and locations, and can direct their efforts towards large individuals. While eradication is not a viable option at this point, targeted removals in certain locations at certain times (*e.g.* the fall line stretch in Richmond in the spring) may have positive impacts on species like American Shad, Alewife, and Blueback Herring (Schmitt et al. 2017). While removals are most likely to benefit White Catfish, other expected benefits should be monitored closely to gauge responses (Orth et al. 2017). Changes in alewife populations may not be detectable since declines are occurring coast wide and may be caused by bycatch in coastal intercept fisheries (Bethoney et al. 2013). If managers decide targeted removals are cost-prohibitive, it is still likely that “impact” to these resources will decline due to shifting size structure in these rivers (Hilling et al. 2018).

Closing thoughts

The Blue Catfish narrative in Chesapeake Bay has primarily focused on top-down impacts, and has neglected competitive interactions and other indirect effects. Journalists and scientists have called these catfish “Bengal tigers of the Chesapeake” and “apex predators”, which is not exactly true and may distract us from more pressing matters. I urge scientists and the media to shift the narrative back towards the truth, and start considering the other threats this species may pose.

Future research should focus on competitive interactions between Blue Catfish and other benthic fishes that utilize the same resources. We have already collected several hundred stomachs from White Catfish *Ameirus catus*, and diet overlap between these two catfish species appears to be high (*unpublished data*). I also have concerns about Blue Catfish forcing White Catfish out of prime spawning habitat based on multiple field observations. This should be explored further. Finally, Blue Catfish in brackish areas may be competing with native benthic invertivores like Atlantic Croaker *Micropogonias undulatus*, which have declined (Nye et al. 2011), and Spot *Leiostomus xanthurus*, which support commercial fisheries in the Chesapeake Bay (Hines et al. 1990). These questions are difficult to explore with our data, as electrofishing efficiency is limited at higher salinities.

Fisheries conflict can manifest itself in many ways (Arlinghaus 2005). For Blue Catfish in Chesapeake Bay subestuaries, conflicting opinions exist between stakeholder groups (e.g. trophy anglers vs. commercial waterman), between agencies (e.g. VDGIF and MDDNR), and within stakeholder groups (e.g. traditional commercial harvesters vs. electrofishing harvester). These conflicts make management complicated going forward (Orth et al. 2017). While it is impossible to please everyone, managers may benefit from incorporating a structured, participatory approach within an adaptive management framework for dealing with these conflicts (Bunnefeld et al. 2017). Because many invasions are a social process, we suggest that managers direct more attention to the sociopolitical contexts of management. Moreover, inclusive public engagement and open communication strategies are imperative to success (Crowley et al. 2017). Open dialogue and collaborative problem solving may be our only approach for dealing with this issue in the Chesapeake Bay. While eradication is not feasible at this point, targeted removals and

increased commercial and recreational harvest have the potential to limit the impact and future range expansion of Blue Catfish in Chesapeake Bay.

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