Summer 2020

A Mechanistic Understanding of Range Expansion of Invasive Blue Catfish in the Chesapeake Bay Region

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Recommended Citation

Nepal, Vaskar, "A Mechanistic Understanding of Range Expansion of Invasive Blue Catfish in the Chesapeake Bay Region" (2020). *Dissertations, Theses, and Masters Projects.* William & Mary. Paper 1681950279.
https://scholarworks.wm.edu/etd/1681950279

A Mechanistic Understanding of Range Expansion of Invasive Blue Catfish in the Chesapeake Bay Region

A Dissertation
Presented to
The Faculty of the School of Marine Science
The College of William & Mary

In Partial Fulfillment
of the Requirements for the Degree of
Doctor of Philosophy

by
Vaskar Nepal
August 2020

APPROVAL PAGE

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

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Approved by the Committee, August 2020

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ACKNOWLEDGMENTS

I thank my advisor, Mary Fabrizio, for her guidance, support and encouragement over the past six years. She was always available to discuss my progress and plans, to reel me in when my research ideas went into fantasy lands and to nudge me ahead when I stagnated. She went out of her way to help me succeed in my endeavors and achieve my dreams, one being that of conducting research in Nepal. And, importantly, she ensured that I knew I did not have to worry about funds for my research, stipend or tuition. A role model. She deserves her own paragraph.

I also thank my committee members for their help in completing this dissertation. Rich Brill and Wolf Vogelbein contributed greatly to my understanding of how a fish works, and were instrumental in helping me complete my experiments in Seawater Research Laboratory. Roger Mann helped me see the ecological forest for my blue catfish trees. Jaap van der Meer helped with the design of laboratory experiments and with the formulation of the dynamic energy budget (DEB) model. Finally, despite a short notice, Donna Bilkovic agreed to serve as a reader for my dissertation and provided valuable suggestions. I must also thank Romain Lavaud, who, though not a committee member, was instrumental in helping me finish the DEB chapter. Thank goodness for Romain!

Jack Buchanan was the workhorse for many chapters of the dissertation. He was knowledgeable, dependable and fun to be around. Jack, I hope you understand how much I appreciate and value your help and friendship. Patrick Kilduff (aka Mr. Awesome), Ben Marcek and Rachel Dixon were fantastic office mates (though they may not have felt as enthusiastic about me, sorry). Thanks are also due to Jim Brister and Jingwei Song for their help in SRL, and to George Trice, Aaron Bunch and Pat McGrath for helping me collect valuable samples. I also thank Jenny Dreyer for her friendship and for allowing me to use her lab space and equipment.

I want to thank all the past and present members of the recruitment surveys lab group (Wendy Lowery, Matt Oliver, Emily Loose, Brian Gallagher, Jillian Swinford, Aimee Comer, Voight “Bubba” Hogge, Shannon Smith and many others). I want to single out Troy Tuckey, who was absolutely amazing. Accommodating. Resourceful. Witty. This is a person I would always want on my side. Numerous volunteers, interns and summer hires also suffered for this research; I thank them for their help.

This work was supported by funds from many sources including the Virginia Sea Grant Graduate Fellowship Program, Virginia Sea Grant Project Development Fund, Virginia Institute of Marine Science, the Virginia Institute of Marine Science Foundation and the Virginia Marine Resources Commission. Numerous travel grants allowed me to present the research at different venues. I thank everyone that processed the mountain of paperwork that went into these travel- or grant-related efforts.

Finally, I want to thank my family for their steadfast support. My parents and my brother let me believe that my being in school all these years is quite natural. Their greatest sacrifice was perhaps that we lived in different continents and were able to meet only once every few years. I thank my daughter Bhumika for bringing cheer to my life like nobody else could. But, I reserve my sincerest, deepest thanks for my wife Manisha for her unwavering support over the past decade. She was quite an academic partner, helping me through all parts of my research, from processing tissues to reading drafts of chapters. But importantly, she ran our home when I was consumed with research; she anchored me to the real world. I have been truly lucky to have you in my life.

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ABSTRACT

Blue catfish *Ictalurus furcatus* is an invasive species of great concern in coastal habitats throughout the eastern United States, inclulding the Chesapeake Bay and its tributaries. In this dissertation, I use field surveys, laboratory experiments and quantitative modeling to provide insights into several aspects of blue catfish biology at the individual level. In chapter 1, I characterize and compare patterns in growth and body condition in blue catfish populations in the James and York river subestuaries during two stages of invasion. Both the mean growth rate and mean body condition of blue catfish declined in the recent period in response to increases in population abundance. In chapter 2, I uncover life-history plasticity in the reproductive biology of the species: blue catfish in the James River mature at a smaller mean size but provision a greater amount of energy into reproduction than York River fish, which exhibit lower densities than James River fish. In chapter 3, I assess the food demands of blue catfish in a laboratory experiment. I demonstrate that blue catfish have low metabolic demands, as expected for a relatively sedentary benthic fish. Importantly, blue catfish had high survival and significant growth at food levels as low as one third of the maximum, suggesting that the species has a high tolerance of starvation and that individuals may be able to invade and establish in low food habitats in coastal waters. In chapters 4 and 5, I report the results of two laboratory experiments studying the effects of increased salinity on survival, growth and body condition of blue catfish. Blue catfish, typically considered a freshwater species, was found to have a higher salinity tolerance (72-hour LC_{50} = 15.7 psu) than many freshwater fishes, suggesting the potential of the species to expand its range into most subestuaries of the Chesapeake Bay particularly during wet seasons. Habitats with salinities around 4 psu seemed particularly suitable for blue catfish as growth and body condition were maximized at this salinity despite the lower mean ingestion rates than fish maintained in freshwater. Finally, in chapter 6, I parameterize a full life-cycle bioenergetics model for female blue catfish using data from the literature and from the other chapters of this dissertation. The model supported the implications from other chapters that blue catfish have low maintenance costs, relatively high resistance to starvation and a plastic ability to fuel reproduction even in environments with low food availability. The model, together with results from other chapters, also opened up avenues for further research on characterization of the energetic basis for the observed phenotypic plasticity, identification of physiological modes of action by which salinity might limit survival, growth and reproduction of blue catfish, and ultimately the identification of coastal habitats that might support self-sustaining populations of this invasive fish. This research highlights the need for management efforts to control blue catfish populations in subestuaries where they are already established and to limit the range expansion into novel habitats. Towards this end, this dissertation provides important information on vital rates of blue catfish needed for population models that can be used for management strategy evaluations.

"An ounce of prevention is worth a pound of cure."

- Benjamin Franklin

AUTHOR’S NOTE

With the exception of the Introduction and the Conclusion sections, the chapters in this dissertation were written with the goal of publication in peer-reviewed scientific journals. Chapters contain redundancies, especially in the introduction section of each chapter, because of the formatting as stand-alone manuscripts. I use plural pronouns in all chapters to reflect the contributions of my co-authors. The citation and reporting styles also vary among the chapters so as to meet specific journal guidelines. The chapters and their citations are:

Introduction

Chapter 1: Nepal V., M.C. Fabrizio and W.J. Connelly (In press). Phenotypic plasticity in life-history characteristics of invasive blue catfish, *Ictalurus furcatus*. Fisheries Research

Chapter 2: Nepal V. and M.C. Fabrizio (In review). Reproductive and life-history traits of invasive blue catfish: novel tactics in novel environments. North American Journal of Fisheries Management.

Chapter 3: Nepal, V., R.W. Brill and M.C. Fabrizio (In preparation). The effect of food limitation on non-native blue catfish from a mid-Atlantic estuary. Environmental Biology of Fishes.

Chapter 4: Nepal, V., and M.C. Fabrizio (2019). High salinity tolerance of invasive blue catfish suggests potential for further range expansion in the Chesapeake Bay region. PLOS ONE 14(11): e0224770

Chapter 5: Nepal, V., and M.C. Fabrizio (In preparation). Sublethal effects of salinity and temperature on non-native blue catfish: implications for establishment in Atlantic Slope drainages. Environmental Biology of Fishes.

Chapter 6: Nepal, V., M.C. Fabrizio, R. Lavaud, and J. van der Meer (In preparation). A full life-cycle bioenergetics model for an invasive population of blue catfish. Ecological Modeling.

Conclusions

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INTRODUCTION

Setting the Stage: An Example of Nile Perch in Lake Victoria

Lake Victoria became famous among evolutionary biologists when it was discovered that this African lake, only 12,000 years old, supported the evolution of over 500 unique haplochromine cichlid fishes (Goudswaard et al. 2002). These endemic fishes sustained an artisanal fishery, but as harvests increased, stocks were rapidly depleted in some areas. Four exotic tilapiine species were introduced during 1951-1954 to augment the fishery (Welcomme 1967), but only one of them, the Nile perch *Lates niloticus*, became important in the fishery.

Following a lag period of nearly three decades, the population of Nile perch exploded. Concurrently, nearly 200 species of native cichlids were extirpated (Witte et al. 1992), primarily due to predation by Nile perch (Marshall 2018). Concerns regarding the negative impacts of Nile perch on native fishes were somewhat countered by the economic benefits associated with the non-native Nile perch: a substantial, export-oriented, commercial fishery for the species had developed in the neighboring countries resulting in a 10-fold increase in fisheries productivity (Taabu-Munyaho et al. 2016). Nile perch had slowly become a part of the livelihood of the local people.

In recent decades, intensive fishing for Nile perch (as well as changes in key environmental variables) has greatly decreased both the population size and mean size of the species (Marshall 2018). Because smaller fish rarely prey on haplochromines

(Wanink et al. 2008), predation pressure declined, allowing some of these native fishes to recover (Kishe-Machumu et al. 2015). The decline in abundance of Nile perch, though welcome news to conservationists, had some negative impacts on the local economy. Many processing plants closed, and revenues from fish exports declined. Regional governments, as well as international agencies such as the Food and Agricultural Agency of the United Nations, are now interested in identifying management scenarios that can recover the biomass of Nile perch and meet the goal of sustainable and equitable fisheries (FMP 2016).

Nile perch in Lake Victoria is “the quintessential invasive species” (Marshall 2018) and considered by the World Conservation Union's Invasive Species Specialist Group to be one of the world’s 100 worst invasive species (ISSP 2014). Yet, contrary to the negative connotation associated with its status as an “invasive species”, Nile perch has a complex role in Lake Victoria. Any account of the species must consider both the socio-economic and the biological impacts of the fish. In fact, such is the case with many non-native species in novel ecosystems, including the blue catfish *Ictalurus furcatus* in the Chesapeake Bay.

Biological Invasions

For the purposes of this dissertation, I define “invasive species” as those introduced to a new location, where they form self-sustaining populations, spread beyond the point of introduction and cause demonstrable ecological, economic or medical harm (Lockwood et al. 2013). This definition is more restrictive than that commonly used by biologists because it requires demonstrable negative impacts (Simberloff 2013). In this sense, all invasive species are necessarily also “non-native” species. “Non-native”, “alien”, “exotic” and “introduced” are four terms used equivalently in this dissertation, and refer to any species not native to a particular location regardless of the ability to form self-replicating populations or of their impacts in the non-native region. Though the definition of invasive species as used here is subjective and clearly anthropocentric, it is in general agreement with federal government policies, such as President Bill Clinton’s Executive Order 13112 of 1999 (Federal Register 64:6183-6186), and with the criteria used to define invasive species by the International Union for Conservation of Nature (IUCN), the Convention on Biological Diversity and the World Trade Organization.

Invasive species are often considered one of the greatest threats to the diversity of global ecosystems (Mack et al. 2000; Sakai et al. 2001; Simberloff 2013). Together with the loss of native populations through local extirpations, the establishment and spread of non-native species is causing a dramatic reconfiguration of current biodiversity (Olden et al. 2004). This reconfiguration has caused substantial health and economic harm to human societies and will affect current and future ecological and evolutionary dynamics (Sakai et al. 2001; Mooney and Cleland 2001; Pimentel 2011; Lockwood et al. 2013). The potential impacts of non-native species on ecosystems are numerous and include habitat modification, biodiversity loss due to predation and competition, homogenization and differentiation of biological communities, introduction of disease, and hybridization (Moyle and Light 1996; Mckinney and Lockwood 1999; Sakai et al. 2001; Mooney and Cleland 2001; Olden et al. 2004; Gozlan et al. 2005; Lovell et al. 2006; Wallentinus and Nyberg 2007; Simberloff 2013; Hulme 2014; Gallardo et al. 2016). Biological invasions can also have severe economic costs. For example, damages due to invasive species are evaluated at 1.7 billion pounds for Great Britain (Williams et al. 2010) and 120 billion dollars per year for the United States (Pimentel 2011). Global damages are estimated to be over 1 trillion dollars per year (Pimentel 2011). Given the severe negative impacts that invasive species can have on recipient ecosystems, as highlighted above for Nile perch, it is crucial to understand, predict and minimize the spread and impacts of invasive species.

Humans have contributed greatly to species introductions through both unintentional transport (e.g., via ship ballast) and intentional transport (e.g., for food, recreation, scientific studies, biocontrol, etc.). The number of established non-native species has strongly increased worldwide during the past few centuries (Seebens et al. 2017), an observation attributed largely to an increase in human mobility, expanding trade networks (Hulme 2009), and rising establishment rates due to habitat degradation (Pauchard and Alaback 2004). Such trends in numbers of non-native species are expected to continue to increase during the next century (Essl et al. 2011; Seebens et al. 2018). Climate change is also expected to influence the numbers of invasive species and the invasion process in many ways such as offering new opportunities for introductions, facilitating colonization and successful reproduction, and enabling population persistence and spread (Rahel and Olden 2008; Cheung et al. 2009; Walther et al. 2009; Britton et al. 2010). Eradication and suppression efforts have increased in frequency and scale in recent years, perhaps as an indication of both the increasing numbers of invasive species and the increasing recognition of the negative impacts of invasive species (Britton et al. 2011).

A key goal in invasion biology is to understand how and why introduced species become successful invaders. Several life history, genetic and other biological traits are believed to facilitate and promote invasion success (Tilman 1982; Sakai et al. 2001; Lockwood et al. 2013; Dick et al. 2017; Lagos et al. 2017). Yet, the complex and "causally heterogeneous" nature of species invasions hinder successful quantitative predictions (Elliott-Graves 2016). Detailed studies of species invasions are therefore required to understand and predict the niche and invasion timelines of a species. In addition, as highlighted by the Nile perch example, the nature of an invader's full impact in a novel ecosystem can take years to develop. A longer-term perspective is therefore required to understand the impact of invasive species (Strayer et al. 2006).

Management actions are often necessary to curtail the expansion of invasive species. Simulation modeling of the effects of management actions can greatly aid predictions of population trajectories and efficacy of management efforts. Models, however, can only be as good as the available data. Biological information about the species from the invaded range is usually limited, especially during the early stages of invasion. For modeling purposes, vital demographic rates are often borrowed from observations made from the species' native range (e.g., northern snakehead *Channa argus*, Jiao et al. 2009; Pacific lionfish *Pterois* spp., Morris Jr. et al. 2011; lake trout *Salvelinus namaycush*, Syslo et al. 2011), even though demographic rates such as mortality and growth can differ greatly between native and non-native populations, and indeed among the multiple stages of invasion (Bøhn et al. 2004; Syslo et al. 2020). The assumption of equal demographic rates for native and non-native populations may result in considerably different recommendations for management actions (Syslo et al. 2020). Population modeling of invasive species therefore requires quantification of vital rates from the non-native populations of interest. Successful population models should also invariably include feed-back loops that derive from intraspecific interactions such as density-dependent competition and cannibalism.

Species Distributions and Niche

Understanding the factors that limit the geographical range of a species is a fundamental goal in ecology (Andrewartha and Birch 1954). Organisms do not passively experience their environments but actively select and even modify them, based on their physiological tolerance limits and energetic or reproductive needs (i.e., autecology; Odling-Smee et al. 2003). The autecology of a species then contributes to population biology and dynamics via density-dependence, and to community ecology via inter-specific interactions. The bridge between autecology (i.e., individual level) and higher levels of organization (e.g., population, community) is provided by the concept of niche. The most common definition of niche used by modern ecologists comes from Hutchinson (1957), who defined an organism’s niche as a multidimensional hypervolume where each dimension corresponds to an environmental factor affecting the survival of the organism. In other words, the niche of an organism is the set of environmental conditions that allows the organism to complete its life cycle and have positive fitness (i.e., successful reproduction; Kearney 2006). The habitat of an organism is simply the geographic projection of its niche.

The concept of niche emphasizes the individual instead of the population or species as the most relevant level of biological organization. The benefits of using individuals in studying population-level processes are two-fold. First, individuals behave as autonomous entities according to behavioral rules, responding to the environment in an integrated manner, with an aim at maintaining homeostasis (Kearney 2019). Inter-individual differences, combined with natural selection, result in evolution: individuals are the “survival machines of life” (Kooijman 2010). Second, from a thermodynamic standpoint, individuals provide a natural boundary to measure, model and balance the flow of mass and energy. The direct estimation of mass and energy balances at higher levels of organization would be far more difficult.

Ecologists have partitioned the niche into the fundamental niche, which is defined by physiological tolerances and energetic needs of the organism, and the realized niche, which is a subset of the fundamental niche as constrained by the limiting effects of biotic interactions and dispersal barriers (Chase and Leibold 2003). The realized niche appears to be of utmost practical use in studying the distribution of a species. Why then would the fundamental niche, and hence the *potential* range and distribution of a species, be of interest? Kearney’s (2013) metaphor of a jigsaw puzzle answers this question well. The task of defining an organism’s niche can be thought of as solving a jigsaw puzzle, the edge pieces of which provide the thermodynamic boundary for the organism to complete its life cycle (i.e., define its fundamental niche; Kearney 2013). These boundaries allow quantification of population-level characteristics of interest, such as the intrinsic rate of increase and dispersal potential. It seems natural, therefore, that an ecologist starts with the fundamental niche of an organism just as a puzzle-solver starts with the edge pieces of the jigsaw puzzle. This metaphor also illustrates why the fundamental niche is of particular relevance in studying populations of an invasive species undergoing range expansion, and potential range is obviously of interest to managers.

Niche Projections and Physiology

Standard approaches to predicting the niche, and hence the distribution of a species, rely on correlations between observed distributions and environmental conditions (i.e., the realized niche; Elith and Leathwick 2009). These models, generally called species distribution models (SDMs), confound the influences of abiotic and biotic influences on species' ranges, and assume equilibrium between organisms and their environment (i.e., that species occur at all locations where the environmental conditions are favorable; Jeschke and Strayer 2008). The equilibrium assumption is not met by invasive species, which are often limited in their distribution, not because of low habitat quality but because of dispersal limitations (Araújo and Guisan 2006). SDMs cannot therefore be used to make projections beyond the available data, a fact that severely limits the applicability of this approach.

Mechanistic approaches based on physiological processes provide a useful alternative to traditional SDMs (Kearney and Porter 2009; Teal et al. 2018). Physiological processes underpin an organism's response to its environment, and therefore, define the fundamental niche of the organism. Physiology-based models mechanistically link spatial data with physiological responses and constraints of organisms (Kearney and Porter 2009). They thus result in predictions that are supported by underlying causal mechanisms, thereby increasing their reliability, interpretability and robustness to extrapolation (Teal et al. 2018). Most impacts of invasive species are, moreover, likely mediated through physiological mechanisms (e.g., stress responses to perceived predation threats by invasive predators (Preisser and Bolnick 2008)), and therefore physiological stress responses may be noticeable substantially earlier than population responses (Meyerson et al. 2019). For these reasons, there is increasing recognition that physiology-based approaches can support invasive species management and conservation science in general (Lennox et al. 2015; Horodysky et al. 2015; McKenzie et al. 2016; Teal et al. 2018; Meyerson et al. 2019).

I contend that an ideal approach to studying the fundamental niche of an organism would be quantitative, mechanistic, general, flexible and operate at the level of individuals. Such an approach could be based either on *experimental data* or on *first principles*. Experimental data-based approaches rely on data collected from laboratory experiments to derive physiological limits or to establish a relationship between important environmental factors and a physiological performance trait (Peck et al. 2018). Physiological limits can be related to either an acute endpoint such as death or a chronic endpoint such as hindrance of growth, development or reproduction (Teal et al. 2018). Because acute endpoints generally occur at more extreme environmental conditions (or at higher concentrations of toxicants) than chronic endpoints, the two provide complementary information on the impact of stressors on the biology of an organism. For example, Schofield et al. (2011) and Lowe et al. (2012) assessed effects of increased salinity on survival (i.e., acute endpoint), as well as on growth and reproduction (i.e., chronic endpoints) of the non-native freshwater fish Nile tilapia *Oreochromis niloticus*. They identified habitats in coastal Mississippi where the species could survive but not grow or reproduce. High-salinity areas that could be used by Nile tilapia to gain access to other watersheds, termed “salt-bridges”, were also identified (Lowe et al. 2012).

Physiological-limit approaches, as the term suggests, operate at the limits of physiological tolerance, and as such, cannot reveal subtle differences in overall performance of a physiological trait of a species at conditions that support survival, development, growth and reproduction. These differences determine the optimal or physiologically preferred environmental conditions, and could therefore characterize differences in densities across a species' geographic range. A common approach relating the environment to the performance of a fish is based on the concept of aerobic scope (AS; Fry 1971). AS is quantified as the difference between the maximum rate of aerobic metabolism (MMR) and standard rate of aerobic metabolism (SMR), the latter representing the minimum energy required to maintain homeostasis. AS therefore measures the metabolic confines within which all aerobic activities must be carried out (Claireaux and Lagardère 1999). At optimal conditions, the AS is maximized. Deviations in AS across the range of an environmental variable (i.e., a stressor) can, therefore, be used to predict the distribution and density of a species in novel habitats. Although temperature is the most commonly used stressor in AS studies, the approach can also be useful when considering other stressors. For example, Behrens et al. (2017) used AS measurements across a salinity range to predict the dispersal potential of invasive round goby *Neogobius melanostomus* through the Baltic Sea-North Sea salinity transition zone.

Experimental approaches are not practical for all species (Araújo and Peterson 2012; Lawson et al. 2019). For example, the heaviest elasmobranch for which metabolic rates have been measured in the laboratory is 47.7 kg, even though many species weigh more than 1,000 kg (Lawson et al. 2019). In general, when limited experimental data are available, a first principles approach may provide a useful alternative. Bioenergetics or biophysical models fall under this umbrella. These quantitative models are based on foundational thermodynamic principles and aim to provide a general theoretical framework to describe the empirical patterns found consistently across the animal kingdom (Hou et al. 2008; Kearney and Porter 2009; Kooijman 2010). An example of a first principles approach is the Dynamic Energy Budget (DEB) model (Kooijman 2010). Building on the laws of thermodynamics and several simplifying assumptions of homeostasis, DEB models describe the energy and mass balance of an individual throughout its life cycle (van der Meer 2006; Kooijman 2010). The processes whereby environmental variables exert an influence on the energy balance of an organism can then be generalized to all animals; species differ based on species-specific parameters.

The flexibility of first-principles approaches comes from the fact that such approaches can be informed by experiments or empirical observations. In a recent application of DEB theory, Augustine et al. (2017) assessed the life-history traits of Greenland shark *Somniosus microcephalus*, a large, long-lived species for which only limited field-collected data were available from the wild; no data from the lab existed. First-principles approaches can also be combined with correlative approaches to obtain reliable and accurate projections of the fundamental and realized niche of invasive species (e.g., Tingley et al. 2014).

In this dissertation, I use a combination of empirical observations from the wild, data from physiological limit experiments, data from an AS experiment and a first-principles approach to elucidate the life-history characteristics of the invasive blue catfish in the eastern United States. Specifically, I aim to increase our understanding of blue catfish biology, to predict the fundamental niche of the species with regard to important forcing variables, and to support management strategies relating to this fish. The next section details the biology and invasion of blue catfish in the Chesapeake Bay. Many parallels between blue catfish invasion in the Chesapeake Bay and Nile perch in Lake Victoria become evident. These parallels include transport vectors, lag periods, ecological impacts and socio-economic roles of these species in introduced habitats.

Blue Catfish in the Chesapeake Bay

Blue catfish, a primarily freshwater fish, is native to large rivers in the Midwestern and Southern United States (Fuller and Neilson 2020). They are long-lived (>30 years) and reach body masses >50 kg. In their native range, they inhabit deep, fast-flowing areas and are considered to be the most migratory of the ictalurids (Graham 1999). Movement rates in the wild do not exhibit diel patterns (Hunter et al. 2009; Gerber et al. 2019), although laboratory studies suggest that blue catfish rarely feed during daytime and are more likely to disperse throughout the water column during nighttime (Tyler and Kilambi 1973; V. Nepal, *pers. obs.*). Adult blue catfish exhibit seasonal movements (Grist 2002; Buckmeier and Schlechte 2009; Gerber et al. 2019) with many individuals moving great distances in search of spawning habitats. Like other catfishes, the males build nests and protect the eggs and larvae (Graham 1999).

Blue catfish is also targeted by recreational and commercial fishers in their native range. Blue catfish, therefore, must have seemed a natural choice when the Virginia Department of Game and Inland Fisheries (VDGIF) and the US Fish and Wildlife Service sought to introduce a novel fish species into tidal rivers of Virginia to create a trophy fishery and to enhance recreational fishing opportunities for non-trophy fish (Higgins 2006). Indeed, blue catfish was one of several fish species that were introduced to the Chesapeake Bay watershed during the 1970s and 1980s. The James, York and

Rappahannock rivers received >130,000 blue catfish fingerlings between 1974 and 1989, and seventy impoundments and reservoirs throughout the state of Virginia received >330,000 fingerlings between 1981 and 1989 (Higgins 2006). A characteristic lag period of one or two decades followed, when individuals were encountered in low frequency and only from the systems where they were introduced. Since the 1990s, however, encounter rates and numbers have increased considerably in all three rivers (Schloesser et al. 2011; Tuckey and Fabrizio 2018). In addition, spawning populations of blue catfish have been observed in all major tributaries in the Virginia portion of Chesapeake Bay, and in many tributaries in Maryland (Schloesser et al. 2011; Nepal and Fabrizio 2019).

In addition to the spatial expansion of its range in these tributaries, the abundance of blue catfish has increased such that in some areas, blue catfish dominate survey catches (Schloesser et al. 2011). Two recent mark-recapture studies in the James River estimated the absolute density of blue catfish to be between 239 and 708 fish/ha (Bunch et al. 2018) and 522 fish/ha (Fabrizio et al. 2018). These estimates are higher than many native populations of blue catfish and invasive populations of fishes in general (Fabrizio et al. in review). As an abundant omnivore in the Chesapeake Bay region, blue catfish prey on a variety of organisms, including fishes, freshwater mussels and blue crabs *Callinectes sapidus*. Their predation on American shad *Alosa sapidissima*, river herring *Alosa* spp., and menhaden *Brevoortia tyrannus* (Chandler 1998; MacAvoy et al. 2009; Schmitt et al. 2017) may be negatively affecting species abundance. Some of these species are of management and conservation concern. Blue catfish may also compete with native predators, such as white catfish *I. catus*, relative densities of which have decreased precipitously in the James, York and Rappahannock rivers during the 1990s and 2000s concurrent with the increase in densities and occupied habitats of blue catfish in these rivers (Schloesser et al. 2011).

A management strategy to minimize the potential for ecological and economic harm of blue catfish is currently under development in the Chesapeake Bay region (Fabrizio et al. in review). One management goal is to reduce high densities and decrease the spread of blue catfish (ICTF 2014). As such, the Virginia Marine Resources Commission (VMRC) has explored ways to develop additional markets for blue catfish that are harvested from the Chesapeake Bay region. VMRC also supported a feasibility study of electrofishing as a commercial gear. Yet, total harvests remain low primarily due to two reasons: (1) the 2016 federal regulation that assigned responsibility for the inspection of catfishes to the Food Safety and Inspection Service of the U.S. Department of Agriculture (USDA) makes it less cost-effective for seafood processors to handle wild blue catfish catches, and (2) the market demand for blue catfish, though increasing in recent years, remains low (Fabrizio et al. in review). As such, additional strategies to control the abundance of blue catfish are desired.

Management of blue catfish in Virginia’s coastal rivers is complicated by various factors. First, blue catfish support a nationally-acclaimed trophy fishery in Virginia. But a desire to sustain this fishery conflicts with the objectives to maximize commercial fishery harvests and reduce population size (Pasko and Goldberg 2014). Second, and somewhat surprisingly, little is known about the biology of blue catfish, even in their native range; blue catfish is considered the least studied of the ictalurids in North America (Boxrucker 2007). Yet, identification of effective management strategies requires knowledge of the biological and ecological factors that facilitate production and range expansion (Bilkovic and Ihde 2014), particularly demographic characteristics such as growth, longevity, reproductive potential, physiological tolerances and energetic requirements (Lockwood et al. 2013).

Studies of the trophic ecology (Schmitt et al. 2019), population size (Bunch et al. 2018; Fabrizio et al. 2018), and growth (Greenlee and Lim 2011; Latour et al. 2013; Hilling et al. 2018) of blue catfish were recently published, but other processes critical to invasion success such as the reproductive biology, energetic requirements, and physiological tolerances (Lockwood et al. 2005, 2013; Bringolf et al. 2005) remain unknown. My dissertation research expands our current knowledge of blue catfish biology by elucidating critical life-history characteristics that affect the ability of this species to invade new environments. In particular, I aim to provide information on the reproductive potential of individuals, ecological constraints on growth and survival, and bioenergetic demands of individuals, all of which have been recognized as important to the development of population and ecosystem-based models in support of management (Bilkovic and Ihde 2014). I will combine this information with observations from the literature to build a model that characterizes blue catfish life-history using a full life-cycle energy-balance approach. This bioenergetics model can be extended to include the effects of important stressors such as temperature and salinity on the fundamental niche of blue catfish in the Chesapeake Bay.

Specifically, the objectives of my research on blue catfish are to:

1) assess the phenotypic plasticity in life-history characteristics, and relate this to invasion history,
2) describe the reproductive biology of females,

3) estimate metabolic and growth rates relative to ration size,

4) determine the acute effects of elevated salinity,

5) determine the sublethal effects of elevated salinity, and

6) examine their bioenergetic strategy

Each of these objectives corresponds with a chapter of my dissertation.

For the purposes of this dissertation, I focus mostly on the non-native blue catfish populations in the Chesapeake Bay, with data collected from Virginia tributaries of the Bay. It is worth noting that non-native populations of blue catfish exist in estuarine and inland waters in the Atlantic coastal plain of the US (Fuller and Neilson 2020). Indeed, non-native populations of two other ictalurid catfishes, the flathead catfish *Pylodictis olivaris* and the channel catfish *Ictalurus furcatus*, also exist in many states in the region. I will likewise limit the dissertation to the eco-physiological and life-history aspects of the blue catfish, and will not delve into the economic impacts of the species or their fisheries. Instead, I refer the reader to Fabrizio et al. (in review) and Orth et al. (in press) for detailed description of the status, conflicts and outlook on blue catfish in the Chesapeake Bay region.

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CHAPTER 1: Phenotypic Plasticity in Life-History Characteristics of Invasive Blue Catfish, *Ictalurus furcatus*

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Abstract

Blue catfish, *Ictalurus furcatus*, are an invasive species in the Chesapeake Bay region, where they negatively impact native species of ecological, economic and cultural value. Management of blue catfish is, however, hindered by a lack of information on their population dynamics. We studied decadal changes in growth and body condition and made inferences about maturity schedules of blue catfish in two Chesapeake Bay subestuaries (James and York rivers). Specifically, we quantified the dynamic responses of these populations to biotic and abiotic characteristics experienced by fish during two stages of invasion (1998-2000 or “early” period and 2015-2017 or “recent” period). In general, somatic growth rate, body condition and reproductive allocation were greater in the early, less dense populations, which also exhibited larger mean size-at-maturity. We observed sexual dimorphism in growth patterns where males reached larger asymptotic sizes than females in both rivers. Such sex-specific and density-dependent responses in life-history characteristics provide information critical for the development of quantitative models and deployment of effective management plans. Our results highlight the need for management plans to consider dynamic feedback mechanisms: efforts to decrease population density may diminish the negative impacts of blue catfish on native species, but this will be offset by increased growth rates and higher reproductive output.

Keywords: Blue catfish; Invasive species; Phenotypic plasticity; Growth dynamics; Body condition

1. Introduction

Fisheries managers directly rely on population metrics such as length-at-age, age-at-maturity and body condition to optimize management strategies (Hilborn and Walters 1992). Traditional fisheries management approaches consider these metrics as time-invariant; but there is increasing recognition that spatiotemporal differences in these characteristics can be substantial (Lorenzen 2016). Changes in resource availability, temperature or density often engender concomitant changes in growth rates and maturation schedules of fishes (Enberg et al. 2012; Masson et al. 2016). Such changes are particularly relevant for non-native species because they experience novel and dynamic environmental conditions as they pass through different stages of invasion.

During establishment, an opportunistic life-history strategy (*sensu* Winemiller and Rose 1992) promotes the survival of an invasive species (Hutchings 1993; Olden et al. 2006; Fox et al. 2007). An opportunistic life-history strategy is characterized by rapid growth (especially in juveniles), early maturation and a high reproductive investment. As the invasive species establishes, resources may become limiting due to an increase in inter- and intra-specific competition. Under such conditions of density dependence, the traits most favorable for survival include slow growth, late maturation and low reproductive investment that are typical of the equilibrium life-history strategy (Winemiller and Rose 1992; Hutchings 1993; Fox et al. 2007). The ability of an organism to adapt its life-history characteristics in response to environmental conditions such as food supply, temperature and population density is termed phenotypic plasticity (Lorenzen 2016). High levels of phenotypic plasticity of life-history traits enable invasive species to maximize their fitness in new habitats (Sakai et al. 2001). Potentially high phenotypic plasticity in invasive species necessitates that management plans for such species consider plasticity in key life-history characteristics for optimal and adaptive management of these fishes.

Management of invasive blue catfish, *Ictalurus furcatus*, in Chesapeake Bay could greatly benefit from knowledge of spatiotemporal differences in growth and condition dynamics of the fish. Blue catfish is a freshwater fish native to the Mississippi, Missouri and Ohio river basins throughout the central and southern United States (Graham 1999). Because of their fame as a recreationally and commercially important species in their native range, blue catfish have been introduced into river systems throughout the United States. During the 1970s and 1980s, blue catfish were introduced into the tidal freshwater regions of the Rappahannock, York and James rivers in the Chesapeake Bay (Schloesser et al. 2011). Since then, blue catfish population densities and range have increased throughout the riverine and estuarine areas of the Chesapeake Bay (Schloesser et al. 2011; Fabrizio et al. 2018; Nepal and Fabrizio 2019). Blue catfish have now been reported from all major Chesapeake Bay subestuaries (Nepal and Fabrizio 2019) from salinities as high as 21.8 practical salinity units (psu; Fabrizio et al. 2018). Blue catfish support a nationally-acclaimed trophy fishery as well as a burgeoning commercial fishery in the region; resource managers are, however, concerned about the negative impacts of blue catfish on species such as blue crab, *Callinectes sapidus*, river herring, *Alosa* sp., American eel, *Anguilla rostrata* and Atlantic sturgeon, *Acipenser oxyrinchus oxyrinchus* (Schloesser et al. 2011; ICTF 2014; Schmitt et al. 2019). Blue catfish are now considered an invasive species in the Chesapeake Bay region, and coordinated management will be undoubtedly necessary to minimize their ecological and economic harm (Fabrizio et al. In review; ICTF 2014). The development of management plans has, however, been hindered by a poor understanding of their population dynamics.

Biological data on length, weight and age are key components of population and ecosystem models that inform management of fish stocks. Many researchers have studied growth of blue catfish in both the native and non-native ranges, but most of these studies are based on a narrow range of ages (e.g., Connelly 2001; Greenlee and Lim 2011; Latour et al. 2013) and lack information on sex-specific differences (e.g., Hilling et al. 2018). Information regarding body condition and estimated time to sexual maturity is limited. Yet, these population characteristics directly contribute to the relative abundance, distribution and ecological impacts of the fish. For example, larger and more robust (i.e., higher body condition) individuals of blue catfish have a greater salinity tolerance than smaller, less robust fish (Nepal and Fabrizio 2019). Individuals with rapid growth rates will therefore contribute disproportionately to dispersal, colonization and range expansion of the species. The situation is analogous to that of European anchovy, *Engraulis encrasicolus,* where individuals with higher body conditions are better prepared for migration and better able to migrate to more suitable winter habitats (Shulman 2002).

Our objective was to assess plasticity in life-history traits of blue catfish across two stages of invasion in two tidal rivers of Virginia, United States. Blue catfish populations in the James and York rivers differ in several ways (Table 1). For example, blue catfish were introduced earlier into the James River (1973-1977) than the York River (1985) at different stocking densities (Higgins 2006). The relative abundance and recruitment of blue catfish remain greater in the James River (Greenlee and Lim 2011;

Tuckey and Fabrizio 2018), potentially due to inter-population differences in growth rates, body condition, and time to maturity. We examined the variability in growth patterns and life-history traits during two decades in the James and York rivers. We hypothesized that older, established populations will have lower mean somatic condition and growth rate, but greater age-at-maturity owing to higher density and intra-specific competition compared with the more recently established populations (Masson et al. 2016). We thus, sought to provide critical information for the formulation of population and ecosystem models needed to develop management strategies for blue catfish in the Chesapeake Bay region.

2. Methods

2.1 Specimen collection

We examined blue catfish from the James and York rivers (Fig. 1) and from two periods (1998-2000 or "early" period and 2015-2017 or "recent" period). These two periods were chosen because they represent different stages of blue catfish invasion and because relevant data were available from these periods. Fish from the early period provided data on sex, fork length (FL), weight and age of fish. During the early period, 364 blue catfish (290 from the James and 74 from the York) were collected using Virginia Institute of Marine Science Juvenile Fish Trawl Survey (hereafter, "VIMS Trawl Survey"). We also collected samples opportunistically from the VIMS Striped Bass Seine Survey, anchor gillnets, and the Virginia Department of Game and Inland Fisheries (VDGIF) Electrofishing Survey (Connelly 2001).

In the recent period, we collected data from 1,726 blue catfish from the James and York rivers. Most fish were collected with the help of a commercial fisher using low frequency DC electrofishing technique at salinities <5 psu. We also obtained fish from the VDGIF Electrofishing Survey and VIMS Trawl Survey during April and May when the commercial fisher did not operate. Our goal was to obtain random samples of blue catfish from the James and York rivers. We measured fork lengths (FL) to the nearest mm and fish mass to the nearest 0.1 g. We identified sex of each fish by macroscopic examination of the gonads, although sex could not be determined or was not recorded for 16.6% of the fish. All collection, fish handling, and euthanasia procedures followed institution-approved protocols. During the recent period, we followed William & Mary Institutional Animal Care and Use Committee (IACUC) protocol # IACUC-2015-06-15-10382-mcfabr; the IACUC did not exist at William & Mary during the early period.

2.2 Age estimation

We removed lapillus otoliths, which were then dried and stored in labelled plastic vials. We sectioned the left otolith perpendicular to the longitudinal axis to obtain a thin (~0.5 mm) section through the nucleus. These were mounted on a glass slide using CrystalBond^{TM}, and sanded on 320-grit sandpaper until the annuli were clearly visible (Latour et al. 2013). The section was then covered with a thin layer of CrystalBond^{TM} to further increase clarity. Processed lapilli were read independently by two readers using a stereomicroscope. The total number of dark bands (annuli) represented the estimated age (in years) of each individual. Because annuli form during May-July in blue catfish (Connelly 2001), we adjusted the age of the fish based on the date of capture. For instance, if we captured the fish between July and December, we assigned an age equal to the number of dark bands. But if we captured the fish between January and June, we assigned an age equal to the number of bands if the edge of the otolith was dark (i.e., annulus for that year was forming or had formed by the time of capture), or the number of bands plus one if a dark band was absent from the edge (i.e., the specimen was captured prior to annulus formation for that year). If the two readers did not agree on the age of an individual, the readers aged the otolith together to arrive at a consensus. Otoliths were discarded if the readers could not reach a consensus (6.06% of the total cases). Our age estimation protocol was consistent between the two periods.

We checked for systematic differences in assigned ages between the two readers using a modified age-bias plot (Ogle et al. 2019) and the McNemar test of symmetry (Hoenig et al. 1995). We assessed the precision of the ages between the readers using the average coefficient of variation (ACV, Chang 1982).

$$ACV = \frac{\sum_{j=1}^{n} \frac{s_j}{\bar{x}_j}}{n} \times 100 \qquad (1)$$

where s_j is the standard deviation of the age estimates for the jth fish, $\bar{x}_j$ is the mean age for the jth fish, and n is the number of aged fish in the sample. We considered an ACV < 5% to be acceptable.

2.3 Size- and age-at-maturity

To estimate the size- and age-at-maturity from the length-at-age data, we used Lester's biphasic growth model (LM, Lester et al. 2004; Quince et al. 2008). The basic form of the LM assumes that immature growth is linear because surplus energy (i.e., the energy beyond that needed for homeostasis) is invested solely in somatic growth. Mature growth is assumed to be asymptotic because energy is invested in both somatic growth and reproduction. We contend that LM is suitable for addressing questions related to life-history strategies and phenotypic plasticity because it is grounded in life-history theory. It also allows estimation of life-history traits such as juvenile growth rate, length-at-maturity, asymptotic length, natural mortality rate and the cost to somatic growth of maturity (Quince et al. 2008).

In LM, the length at age t (l_t) is given by

$$l_t = l_0 + ht, t \leq T \text{ for juveniles} \quad (2)$$

$$l_t = l_\infty\left(1 - \mathrm{e}^{-k(t-t_0)}\right), t > T \text{ for adults} \quad (3)$$

where l_0 is the theoretical length at age 0 (mm), h is the somatic growth rate (mm y^{-1}), T is the LM parameter for age at maturity (y), l_∞ is the asymptotic length (mm), k is the von Bertalanffy (VB) growth coefficient (y^{-1}), and t_0 is the hypothetical age at length 0 based on the VB growth curve for adults (y). These quantities are related to t_1, the hypothetical age at length 0 for immature fish (y), and g (the cost to somatic growth of maturity) as:

$$h = -\frac{l_0}{t_1} = \frac{g l_\infty}{3} \quad (4)$$

$$k = \ln\left(1 + \frac{g}{3}\right) \quad (5)$$

$$t_0 = T + \ln\left(1 - \frac{g(T-t_1)}{3}\right) / \ln\left(1 + \frac{g}{3}\right) \quad (6)$$

We used a likelihood-based approach to infer age- and length-at-maturity from LM for blue catfish following Honsey et al. (2017). In brief, we fitted LM on length-at-age data with age-at-maturity (T) allowed to vary between two and 10 years in increments of 0.1 year (i.e., 81 models corresponding to 81 potential values of T for each population). For each of the 81 models, we maximized the model likelihood using the optim function in R version 3.6.0 (R Core Team 2019). For each river, we selected the most parsimonious model, which was the one that resulted in the highest maximum likelihood among the 81 alternative models. LM parameter estimates for each river were based on the final (selected) model. Following Honsey et al. (2017), we assessed the goodness of model fit based on the shape of the likelihood profile: a good fit has a single likelihood peak and a likelihood interval ≤2 y. We also calculated precision in length at age for each population because precision can affect the goodness of fit of the LM models (Honsey et al. 2017). Precision was calculated as the average of the inverse of the coefficient of variation in length at each age across all ages, weighted by sample size at age.

We used bootstrap techniques to estimate 95% confidence intervals for each parameter (Efron and Tibshirani 1993). Specifically, we obtained 1,000 bootstrap resamples, and estimated LM parameters for each resample. Lower and upper confidence limits for each parameter were estimated as the 2.5th and 97.5th percentile of the 1,000 estimates for the parameter. We calculated bootstrap-based two-tailed *p*-values to compare statistically the parameter estimates between populations (Efron and Tibshirani 1993). We followed the standard approach of fitting LM only on female blue catfish because increased investment of energy into reproduction after maturity is reasonable for females but not for males (Ward et al. 2017; Honsey et al. 2017). In addition, the “early” period had a low sample size and the model did not fit well. We therefore fit the LM only for observations from the “recent” period.

Model fit was validated by comparing LM model estimates with empirical estimates based on observation of gonads by Perry and Carver (1977), who report the maturity status (mature or immature) along with the size bins of fish (bin width = 50 mm total length (TL)) for female blue catfish in southwest Louisiana. We modeled the effect of size on maturity status of the fish using a logistic regression:

$$\ln\left(\frac{p_i}{1-p_i}\right) = \mu + \beta TL \tag{7}$$

where p_i is the probability of fish *i* being mature, $\ln\left(\frac{p_i}{1-p_i}\right)$ is the log-odds of being mature, μ is the overall mean log-odds of being mature, β is the regression coefficient, and *TL* is the mean of the corresponding length class. We used the logistic regression model to estimate the mean size-at-maturity (l_{50}) for the population. For accurate comparison with the l_{50} estimate from the LM model, we converted the l_{50} estimate from the logistic regression from TL to FL using the equation FL = -3.944 + 0.862×TL + $7.933\times10^{-5}\times\mathrm{TL}^2$. This equation was based on FL and TL data from 659 blue catfish collected from Chesapeake Bay during 2015-2017 (Nepal and Fabrizio, unpublished data). Perry and Carver (1977) did not age the fish used for maturity analysis, but estimated the age-at-maturity for female blue catfish to be ~5 y based on visual examination of length frequency distributions. Maturation schedules of blue catfish are not yet available from the James and York rivers.

2.4 Growth in the recent period (2015-2017)

Most published reports on growth of blue catfish (and other fishes, in general) use VB growth function to characterize length-at-age throughout the observed age range (e.g., Marshall et al. 2009; Hilling et al. 2018). In contrast, the LM we described in the previous section considers VB growth only for mature female fish. We also modeled length-at-age during the recent period with the VB model to allow direct comparisons with previous studies and to explicitly characterize sexual dimorphism in growth of blue catfish. We did not fit the VB growth model to observations from the early period because of poor model fit, stemming from the fact that few individuals were greater than 12 years old (Connelly 2001). As a result, we could not estimate l_∞ or k.

The basic formulation of the VB growth equation, presented in eq. (3), was modified in two ways. First, we applied eq. 3 to the entire age range for both sexes, instead of just the mature female fish. Second, we used a multiplicative error structure to account for higher variation in FL at older ages and to aid model fitting (Kimura 2008). We used non-linear regression with river (York and James) and sex (male and female) as covariates in the VB growth model following the approach outlined by Kimura (2008). The length-at-age model included two dummy variables, s_i and r_i, indicating sex and river of origin of fish i:

$$l_{ti} = (\beta_{0l_\infty} + s_i\beta_{1l_\infty} + r_i\beta_{2l_\infty})\left(1 - e^{-(\beta_{0k}+s_i\beta_{1k}+r_i\beta_{2k})\left(t_i-(\beta_{0t_0}+s_i\beta_{1t_0}+r_i\beta_{2t_0})\right)}\right) \quad (8)$$

where $s_i = 0$ for females and $s_i = 1$ for males, and $r_i = 0$ for James River and $r_i = 1$ for York River. We estimated the 95% confidence interval for all model parameters by bootstrapping the residuals 1,000 times (Efron and Tibshirani 1993). River- and sex-specific differences in VB parameters were assessed by calculating bootstrap-based p-values as described previously.

2.5 Immature growth rate

To assess spatiotemporal differences in the growth rates of blue catfish, we compared growth of immature blue catfish between the two rivers and the two periods using a growing degree-day (GDD) model because river- and period-specific differences in growth rate may be influenced by differences in temperature (Nepal and Fabrizio 2020). We controlled for the effects of temperature on the size of immature blue catfish (≤ 4 y old; see results below) using the GDD approach, which is based on the idea that temperatures above a minimum threshold are conducive to growth of ectotherms, including fishes (Neuheimer and Taggart 2007). As an index of thermal energy, GDD is known to influence growth rates in fishes (Neuheimer and Taggart 2007; Venturelli et al. 2010). Note from section 2.3 that LM yielded immature growth rates for blue catfish during the recent period only, and from section 2.4 that the growth coefficient k in the VB growth models does not represent the growth rate, but rather the rate of approaching l_∞ (Hilborn and Walters 1992). We used June 1 of the first year of life as the first day of GDD accumulation for all individuals because of the absence of hatch-date information and because June 1 is the peak of blue catfish spawning in Virginia waters (Nepal and Fabrizio, unpublished data). Because GDD represents the cumulative thermal energy experienced by an individual over its lifetime, GDD was calculated up to the day of capture for each fish. Therefore, number of GDDs accumulated by fish i was calculated as:

$$GDD_i = \sum_{t=1}^{N} \bar{T}_{ti} - T_b \, , \bar{T}_{ti} > T_b \qquad (9)$$

where N is the number of days between June 1 of first year of life (t = 1) and the day of capture for fish i, $\bar{T}_{ti}$ is the mean temperature experienced by fish i on day t, and T_b is the base temperature below which growth ceases. We used T_b of 9°C as reported for blue catfish in the Chesapeake Bay region (Nepal and Fabrizio 2020).

We compared the immature growth rate of blue catfish during the two periods using a generalized least squares model of the form

$$L_{irp} = \mu + River_r + Period_p + \beta GDD + \varepsilon_{irp} \tag{10}$$

where L_{irp} is the FL of fish *i* in river *r* during period p, μ is the overall mean FL, $River_r$ and $Period_p$ are the fixed effects of river and period respectively, β is the regression coefficient for GDD, and ε_{irp} is the random unexplained error. We also included two-way interactions of GDD with river and period in the model. We did not include sex of the fish in the model because (1) we did not have this information for many fish, and (2) graphical analysis showed that growth rates of immature males and immature females were similar. For immature fish, all energy in excess of that needed for homeostasis is channeled into growth, not reproduction, regardless of the sex of the fish (Lester et al. 2004). We initially considered including an index of relative abundance as a covariate to assess the effect of conspecific density on growth of blue catfish. We could not, however, include this variable in the model because relative abundance was confounded with period and river (Table 1). Graphical analysis showed increasing variance in FL (i.e., heteroscedasticity) with GDD. In addition, the heteroscedasticity was greater in the York River compared with the James River. We therefore explicitly modeled the heteroscedasticity in FL using a variance function of the type "constant plus power," which allows variance in each river to increase as a power function of the covariate GDD (Pinheiro and Bates 2000). Analysis of residuals showed that this variance function was appropriate.

2.6 Body condition

We used fish body condition to assess spatiotemporal differences in health of individual blue catfish in the Chesapeake Bay region. Specifically, we calculated the scaled mass index (SMI; Peig and Green 2009) as a morphometric index of body condition. We chose SMI as the measure of body condition for two reasons. First, SMI has been shown to be one of the most accurate morphometric indices of body condition in fishes (Wuenschel et al. 2018). Second, unlike most morphometric indices of body condition, the scaling relationship used in the SMI approach acknowledges that natural variability due to growth affects both weight and length. It thus acknowledges that there may be measurement error not only in weight but also in length (Peig and Green 2009).

SMI of fish *i* was calculated as

$$\widehat{SMI}_i = M_i \left[\frac{L_0}{L_i}\right]^{b_{SMA}} \qquad (11)$$

where M_i and L_i are respectively the body mass and FL of fish i; b_{SMA} is the scaling exponent estimated by the standardized major axis (SMA) regression of *M* on *L*; L_0 is an arbitrary *L* to which all individuals of blue catfish are standardized; and $\widehat{SMI}_i$ is the predicted eviscerated body mass for individual i when FL is standardized to L_0. We used median FL (420 mm) as L_0, and report this value to allow comparison among studies. We used the two-step procedure suggested by Peig and Green (2009) to compute b_{SMA}. First, we identified and subsequently removed strong outliers based on a bivariate plot of *M* and *L* ($n = 6$; 0.3% of the total observations). Second, we fit an SMA regression to log-transformed *M* and *L* values to obtain b_{SMA}, which is the slope of the regression. The SMA regression approach acknowledges the natural and measurement variability in both *M* and *L*, and is therefore preferred over ordinary least-squares approaches (Peig and Green 2009). Because the size range of fish differed between periods, we restricted SMI calculation to fish between 110 and 765 mm to allow comparisons between periods.

We modeled the effects of river, sampling period and sex of fish on mean SMI using a linear mixed model:

$$SMI_{irpsm} = \mu + River_r + Period_p + Sex_s + s(FL) + Month_m + \varepsilon_{irpsm} \qquad (12)$$

where SMI_{irpsm} is the SMI of the *i*th blue catfish from the *r*th river, *p*th period, *s*th sex and *m*th month, μ is the overall population mean of the response variable SMI, $River_r$, $Period_p$ and Sex_s are the fixed effects of river, period and sex respectively, $Month_m$ is the random effect of month, and ε_{irpsm} is the random unexplained error. Preliminary graphical analysis showed that SMI changed in a slightly non-linear fashion with FL. This violates a key requirement for a condition index, that a condition index should not covary with body size (Peig and Green 2009). We therefore detrended SMI across FL to control for the effect of period-specific differences in FL distributions. As such, our model included FL as a cubic B-spline function with three degrees of freedom, represented as $s(FL)$ in eq. 12. Graphical analyses showed that the spline function was adequate in detrending SMI across the FL distribution. We included the random effect of month in the model to account for potential seasonal differences in body condition, particularly for females as a result of gonadal development during spring and summer in preparation for spawning. We also considered two- and three-way interactions among river, period and sex in the model. To assess whether the random effect of month was important in the model, we compared the mixed model (eq. 12) with a reduced linear model without the random effect using a simulation-based likelihood ratio test. As with the model for immature growth rates (eq. 10), we did not include mean annual abundance index as a predictor variable because abundance indices were confounded with river and period. We did, however, calculate Pearson’s correlation between the predicted mean SMI and abundance index based on the VIMS Trawl Survey to assess whether mean SMI was lower in rivers or periods with higher blue catfish densities.

We performed all statistical analyses in R version 3.6.0 using packages FSA version 0.8.4 for ageing bias and precision analysis (Ogle et al. 2019), nlme version 3.1-137 for generalized least squares model (Pinheiro and Bates 2000), smatr version 3.4-8 for SMA regression (Warton et al. 2012) and lme4 version 1.1-21 for linear mixed-effects models (Bates et al. 2015). Generalized least squares models and linear mixed-effects models were fitted using the restricted maximum likelihood approach.

3. Results

3.1 Sample characteristics

During the early period, blue catfish FL ranged between 28 and 938 mm, body mass between 78.6 and 19,750 g and age estimates between 0 and 15 y. In contrast, in the recent period, blue catfish were slightly larger (35 and 1,125 mm FL), had a more variable body mass (15.9 and 29,610 g) and attained older ages (0 and 29 y). Of the 1,726 blue catfish from the recent period that were aged by two readers, 87.6% (n = 1,512) of the otolith readings agreed, and an additional 11.0% (n = 189) agreed within one year (Fig. 2). The ACV was 1.2%, and there was no systematic bias in ageing between the two readers (McNemar's χ_1^2 = 0.92; p = 0.34). Graphical analysis also showed that the coefficient of variation was consistently less than 3.5% throughout the age or FL ranges.

3.2 Size- and age-at-maturity in the recent period

During the recent period, immature female blue catfish in the York River grew significantly faster (h = 51.8 mm y^{-1}; 95% Confidence Limits [CI]: 45.8 and 58.8) than those in the James River (h = 39.9 mm y^{-1}; CI: 34.3 and 45.5; p = 0.002; Table 2). Fish in the York River also began allocating energy towards reproduction at a larger mean size (l_{50} = 350 mm FL; CI: 317 and 403) and greater mean age (T = 5.2 y; CI: 4.3 and 6.3) compared with those in the James River (l_{50} = 255 mm; CI: 228 and 278; $p < 0.001$; T = 3.6 y; CI: 3.0 and 4.1; p = 0.002; Table 2; Fig. 3). Note that these l_{50} estimates are lower than those reported for a Louisiana population (l_{50} = 518 mm FL; CI: 491 and 540); T estimate for the Louisiana population (5 y) is greater than that for James, but comparable to that for York river (Fig. 3). Further, fish in the York River allocated a marginally larger fraction of energy towards reproduction (g_{York} = 0.17; CI_{York}: 0.11 and 0.23; g_{James} = 0.10; CI_{James}: 0.04 and 0.15; p = 0.08) but attained a mean asymptotic size ($l_{\infty\text{York}}$ = 924 mm; CI_{York}: 756 and 1267; $l_{\infty\text{James}}$ = 1210 mm; CI_{James}: 885 and 2440; p = 0.23) comparable to fish from the James River. Model fit was excellent for York River fish with a single likelihood peak that spanned <2 y. The fit for James river fish was poorer with a single likelihood peak, but spanning 5 y. Precision estimates for length at age for the James and York River blue catfish were respectively 8.8 and 9.6.

3.3 Growth in the recent period

Blue catfish growth during 2015-2017 was characterized by the following equations:

$FL = 990.7\left(1 - e^{-0.049(t+2.6)}\right)$ for males in the James River

$FL = 918.2\left(1 - e^{-0.050(t+3.0)}\right)$ for females in the James River

$FL = 821.5\left(1 - e^{-0.093(t+0.9)}\right)$ for males in the York River

$FL = 750.0\left(1 - e^{-0.093(t+1.2)}\right)$ for females in the York River

Female asymptotic sizes were significantly smaller than those of males in both the James and York rivers ($p_{\text{James}} = 0.002$; $p_{\text{York}} = 0.002$) but females and males approached asymptotic sizes at comparable rates ($p_{\text{James}} = 0.411$; $p_{\text{York}} = 0.397$; Table 3). When comparing the blue catfish populations in the two rivers, fish in the York River reached smaller mean asymptotic sizes ($p_{\text{Male}} = 0.036$; $p_{\text{Female}} = 0.036$) but approached the asymptotic sizes significantly faster than those in the James River ($p_{\text{Male}} < 0.001$; $p_{\text{Female}} < 0.001$; Table 3; Fig. 4). Blue catfish growth in the Chesapeake Bay region is lower than those of most native and non-native populations examined to date (Fig. 5).

3.4 Immature growth

Immature blue catfish (estimated age ≤ 4 y) grew linearly with accumulation of GDD, but demonstrated period- and river-specific differences in growth rates (Fig. 6). During both periods, the mean size of newly hatched blue catfish in the James River (i.e., the intercept) was higher than that in the York River ($p < 0.05$; Fig. 6), in agreement with our LM results (Fig. 3). Immature blue catfish grew faster in the York River compared with the James River (GDD×River: Wald $\chi^2_1 = 41.6$; $p < 0.001$). Within river, immature blue catfish grew faster during the early period than during the recent period (GDD×Period: Wald $\chi^2_1 = 17.6$; $p < 0.001$; Fig. 6).

3.5 Body condition

SMI was highly variable and ranged between 618.2 and 1,652.5 g for a 420 mm fish. Sex, river and period had interactive effects on mean SMI of blue catfish (Sex×River×Period: $F_{1,1742.55} = 5.06$; $p = 0.025$). In general, fish in the recent period had lower mean body condition (i.e., lower SMI) compared with the early period. The decline in body condition through time was, however, particularly evident for male blue catfish in the York River (Figure 7). Interestingly, mean SMIs were similar for males and females in both rivers during both periods, except for the York River during the early period, when females had considerably lower mean SMI compared with males (Figure 7). The likelihood ratio test comparing the mixed model with a reduced fixed-effect model was significant (χ^2 likelihood ratio = 65.86; $p < 0.001$), suggesting considerable intra-annual variation in SMI: mean SMI was higher than average during May and June, and lowest during February (Figure 8). Mean SMI was negatively correlated with the relative abundance index, but the relationship was weak and not significant ($r = -0.37$; $t_{10} = -1.24$; $p = 0.24$).

4. Discussion

Invasive populations of blue catfish in the James and York rivers demonstrated considerable plasticity in life-history characteristics during two decades. Populations established for longer periods (i.e., recent period and James River) generally exhibited higher densities, smaller size-at-maturity, slower growth rates and lower body condition. These results showcase the expected changes in vital rates that characterize the population dynamics of an invasive species during two stages of invasion (Bøhn et al. 2004; Masson et al. 2016). As such, they emphasize the need to consider sex-, population- and period-specific rates in the development of management strategies for invasive species (Lorenzen 2016).

We observed a greater number (and proportion) of older fish in the recent period compared with the early period. Indeed, the maximum ages observed for blue catfish populations in the James and York rivers are higher than those reported for many other populations (Graham 1999; Stewart et al. 2016). The presence of older fish allowed us to use the VB model as an appropriate representation of blue catfish growth in the Chesapeake Bay. Connelly (2001), Greenlee and Lim (2011) and Latour et al. (2013) fit linear growth models due to lack of older (>15 y) individuals in their samples. Elsewhere, Homer et al. (2015) could not fit VB model for a non-native population of blue catfish in Georgia because the population lacked older, larger fish. Recently, Hilling et al. (2018) fit VB growth models to blue catfish populations in Virginia. Compared to the estimates by Hilling et al. (2018), who based their model on composite data collected between 2002-2016, our temporally explicit approach shows generally faster growth during the early period and slower growth in the recent period. Fish in the recent period also achieved smaller asymptotic sizes, further highlighting the need to consider plastic changes in growth dynamics when modeling this species. The growth patterns and VB growth parameters in our model were within the range reported from other populations throughout the native and non-native ranges (Graham 1999; Stewart et al. 2016; Hilling et al. 2018). In general, the growth rates and mean asymptotic sizes of blue catfish from the James and York rivers during 2015-2017 are lower than many native populations, including that studied by Perry and Carver (1977), likely due to higher density dependence in the James and York rivers.

We observed a shift in life-history strategy from “opportunistic” to “equilibrium” (Winemiller and Rose 1992), as blue catfish populations progressed through stages of invasion. Our findings are consistent with the predictions of life-history theory where individuals in established, more dense populations grow more slowly, mature at a smaller size, and allocate more energy towards reproduction (Bowen et al. 1991; Walters and Post 1993). Similar results have been reported for other invasive fishes such as round goby, *Neogobius melanostomus* (Masson et al. 2016), vendace, *Coregonus albula* (Bøhn et al. 2004) and white perch, *Morone americana* (Feiner et al. 2012). Individuals in established populations would also be expected to mature later (e.g., Feiner et al. 2012; Masson et al. 2016), although we did not observe this. A reason for this might come from the relatively poor LM fit for the James River population. Somewhat low precision in length-at-age and low reproductive allocation for James River fish resulted in poorer model fits, as evidenced by large confidence intervals for the g and l_∞ parameters of the model. Honsey et al. (2017) found that their implementation of LM was less accurate in predicting maturity in such scenarios. Gear selectivity is also likely to affect LM estimates, though the precise nature of the effects is not yet clear. We did not consider gear selectivity in our model, but future implementations of LM might benefit from incorporating gear selectivity.

Observed decreases in growth rates and body condition in the recent period reflect resource limitations and density-dependent effects. Similar results have been observed in invasive bigheaded carp, *Hypophthalmicthys* sp. (Coulter et al. 2018) and Indo-Pacific red lionfish, *Pterois volitans* (Dahl et al. 2019). Many other river-specific factors likely contributed to the observed plasticity in growth rates, maturation rates and body condition of blue catfish. Despite the higher primary productivity and low inbreeding in the James River population, fish grew slower than those in the York River. Moreover, the discrepancy in length-at-maturity between the Chesapeake Bay populations and the Louisiana population likely results from higher water temperature, lower density and considerably faster growth in the latter. This suggests that several spatiotemporally variable biotic and abiotic factors act together to determine the growth dynamics of fish; quantification of such dynamics for population assessment purposes needs to consider these plastic changes.

Declines in growth rate and body condition has mixed implications for management. The negative impacts on native fishes due to predation are likely to decrease because smaller blue catfish are less likely to prey upon other fishes (Schmitt et al. 2019). Further, smaller and less robust (i.e., lower body condition) individuals are less tolerant of elevated salinities than larger, more robust individuals (Nepal and Fabrizio 2019). Therefore, dispersal, colonization and range expansion into high salinity habitats may decrease. Slower growth rates imply, however, that small individuals may accumulate higher concentrations of contaminants such as mercury and polychlorinated biphenyl (PCB; Luellen et al. 2018). High contaminant loads in small, but older fish will negatively impact raptors that prey on blue catfish, such as bald eagle, *Haliaeetus leucocephalus*, and osprey, *Pandion haliaetus*, (Viverette et al. 2007). High contaminant loads also have implications for the safe human consumption of blue catfish. Because smaller blue catfish feed at lower trophic levels (Schmitt et al. 2019), negative impacts due to competition may increase on some fishes (such as juvenile striped bass, *Morone* *saxatilis*, and Atlantic croaker, *Micropogonias undulatus*) and invertebrates (such as freshwater mussels and blue crabs).

Recreational and commercial harvests have been suggested as a management measure to ameliorate the negative impacts of blue catfish (Fabrizio et al. 2018). Our results show, however, that such declines may release the remaining individuals from density-dependent mechanisms currently suppressing individual growth rates. This will, in turn, cause compensatory changes in demographic characteristics including mean growth rates, body condition and age-at-maturity. These effects have been observed in other teleost fishes, but are most common among long-lived fishes with high fecundity (Rose et al. 2001). We argue that blue catfish will demonstrate such compensatory mechanisms because they are long-lived (maximum age >25 y) and have relatively high fecundity for a nest-guarding species (>40,000 eggs per fish for large individuals, Nepal and Fabrizio in review). Increased growth rates would also increase predation on native fishes because large blue catfish consume a high proportion of fishes (Schmitt et al. 2019). Our conclusions are bolstered by the observations of higher recruitment and earlier maturation in response to increased exploitation in flathead catfish, *Pylodictis olivaris* (Bonvechio et al. 2011), another non-native ictalurid catfish now present in the Chesapeake Bay region. These findings are also consistent with predictions from life-history theory that an increase in adult mortality rate due to exploitation will select for earlier age at maturity and higher reproductive investment (Lester et al. 2014).

Blue catfish from the James and York rivers show sexually dimorphic growth, where males grow faster and attain larger sizes, a pattern consistent with observations in a native population in Alabama (Marshall et al. 2009). Because male blue catfish exhibit nest guarding behavior and provide parental care for eggs and fry (Graham 1999), larger males have a reproductive advantage in aggressive confrontations. There would thus be a positive selection pressure towards larger males (Parker 1992). Sexual dimorphism in growth of blue catfish has important management implications. Because harvest efforts typically remove larger individuals (>500 mm), a larger proportion of males will be removed, thus allowing a large proportion of females to continue reproduction. Harvesting strategies that differentially remove larger male fish may enhance recruitment, at least until males become limiting. Management actions to successfully curtail the reproductive output of blue catfish will, therefore, need to ensure removal of a sufficient number of large females.

Our findings also bring to light avenues for future research. First, we assessed plasticity in age- and size-at-maturity based on Lester's model fitted to length-at-age data for female blue catfish. For increased accuracy and a more complete treatment, however, maturity schedules should be based on examination of gonads. Second, we did not explicitly study the size-at-age of blue catfish at different densities observed throughout the invasion history. A more thorough analysis should relate year-specific density to corresponding incremental growth of blue catfish during that year via mark-recapture techniques or otolith increment analysis (Lorenzen 2016). Finally, future studies should expand the spatiotemporal domain of study; we focused on two subestuaries in two periods, the earlier of which encompassed a period 15-25 y after introduction. With documented range expansion of blue catfish throughout the Chesapeake Bay watershed (Nepal and Fabrizio 2019), managers and conservation biologists would benefit from knowing the likely colonization pathways and characteristics of populations in newly invaded tributaries. Range expansions during wet seasons may lead to periodic supply of propagules and potentially the development of metapopulations, inducing novel spatiotemporal differences in population dynamics of invasive blue catfish populations in the Chesapeake Bay region.

Management plans for invasive species need to consider the sex-and population-specific life-history traits in a dynamic context. In other words, management plans need to take into account the phenotypic plasticity and compensatory feedbacks that are likely to occur in response to management actions. Towards this end, our findings provide baseline information needed for the development of management plans for blue catfish. Our findings also provide a template for expected changes in life-history strategies of blue catfish populations in more recently invaded systems in the Chesapeake Bay region (e.g., Nanticoke River) and elsewhere in the tidal rivers in Maryland, Pennsylvania and Delaware. With the expected range expansion of blue catfish in the Chesapeake Bay region over the next decades (Nepal and Fabrizio 2019), vigilant monitoring and proactive management plans are crucial in determining the status and ultimately the impacts of this invasive species on the ecology of this region.

Author Contributions

V. Nepal: Conceptualization; Data collection, curation, analysis and visualization; Writing – original draft preparation; Funding acquisition; **M. Fabrizio:** Conceptualization; Supervision; Writing – Reviewing and editing; Funding acquisition; Resources; **W. Connelly:** Data collection, curation and analysis.

Acknowledgments

We thank commercial fisher G. Trice, VDGIF biologist Aaron Bunch, members of the American Shad and River Herring Monitoring Program and VIMS Trawl Survey crew for assistance with collection of fish. We also appreciate the volunteers, technicians and interns, who assisted with processing of the fish samples. Special thanks to Jack Buchanan, Manisha Pant and Jameson Gregg for assistance with the preparation and ageing of otoliths. Comments from two anonymous reviewers improved the manuscript. V. Nepal was supported by graduate fellowships from VIMS Office of Academic Studies and a graduate research fellowship from Virginia Sea Grant. The views expressed in the manuscript do not necessarily represent the views of the Federal Energy Regulatory Commission or the United States.

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Tables

Table 1: Period-specific characteristics of James and York rivers, demonstrating the history of blue catfish introduction and relevant environmental conditions. For characteristics that do not change between the periods, values are provided in only one column. USGS NWIS = United Stated Geological Survey National Water Information System; VECOS = Virginia Estuarine and Coastal Observing System

	Early (1998-2000)		Recent (2015-2017)		Source
	James	York	James	York	
Founder population size	115,614	1,850			Table 1 in Higgins (2006)
Inbreeding coefficient F	0.22	0.27			Table 4 in Higgins (2006)
Mean annual discharge (m^3s^{-1})	193.5	30.7			Data from USGS NWIS website
Years since initial introduction	23-25	13-15	40-43	30-33	Table 1 in Higgins (2006)
Mean chlorophyll a ($\mu g\ l^{-1}$)	21.7	6.5	16.1	5.5	Annual mean, data from VECOS
Mean relative density	23.8	0.01	43.4	4.4	Random Stratified Index; data from Tuckey and Fabrizio (2018)

Table 2: Primary and derived parameter estimates for Lester's biphasic growth model fitted on length-at-age data on female blue catfish in the James and York rivers during 2015-2017. Two-tailed *p*-values for difference in parameter estimates between York and James rivers are also provided.

Parameter	York	James	p
g	0.168	0.099	0.080
h	51.8	39.9	0.002
T	5.2	3.6	0.002
l_0	80.6	111.5	0.006
t_1	-1.6	-2.8	0.002
l_∞	924.1	1210.2	0.228
k	0.055	0.032	0.074
t_0	-3.5	-3.7	0.746
L_{50}	349.9	255.2	<0.001

Table 3: Parameter estimates for sex-specific von Bertalanffy growth curves for non-native blue catfish from two Virginia rivers during 2015-2017. For each parameter, p values for river-specific differences for each sex are given in the right column (p_{River}) and those for sex-specific differences within each river are given below the parameter estimates (p_{sex}).

Parameter	Sex	York	James	p_{River}
l_∞	Male	821.5	990.7	0.036
	Female	750.0	918.2	0.036
		p_{sex} = 0.002	p_{sex} = 0.002	
k	Male	0.092	0.049	<0.001
	Female	0.093	0.05	<0.001
		p_{sex} = 0.397	p_{sex} = 0.411	
t_0	Male	-0.9	-2.6	<0.001
	Female	-1.2	-3.0	<0.001
		p_{sex} = 0.002	p_{sex} = 0.002	

Figures

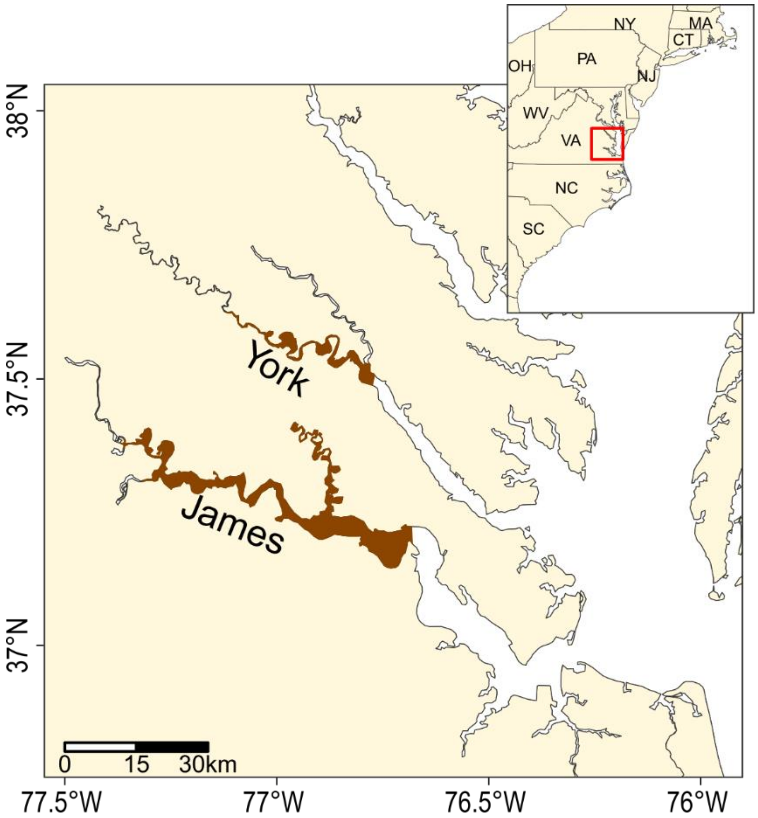

Figure 1: Map of blue catfish collection locations (dark shaded region) in the tidal James and York rivers during early (1998-2000) and recent (2015-2017) periods.

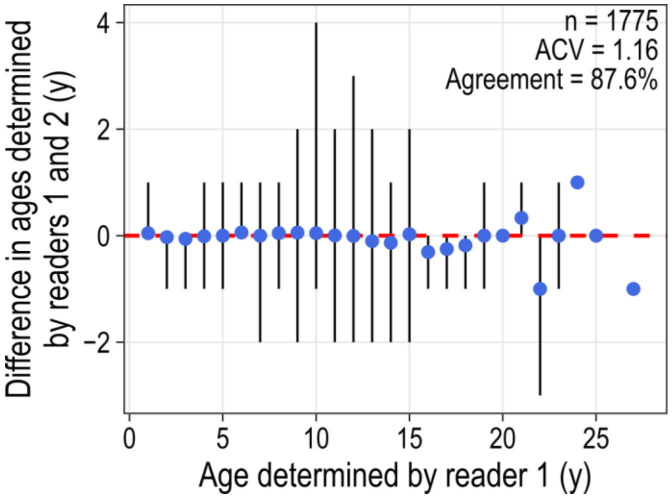

Figure 2: A modified age-bias plot for blue catfish aged blindly by two readers. The dot indicates the mean difference in age estimates of the two readers, and the vertical line indicates the range of discrepancies. ACV is the average coefficient of variation.

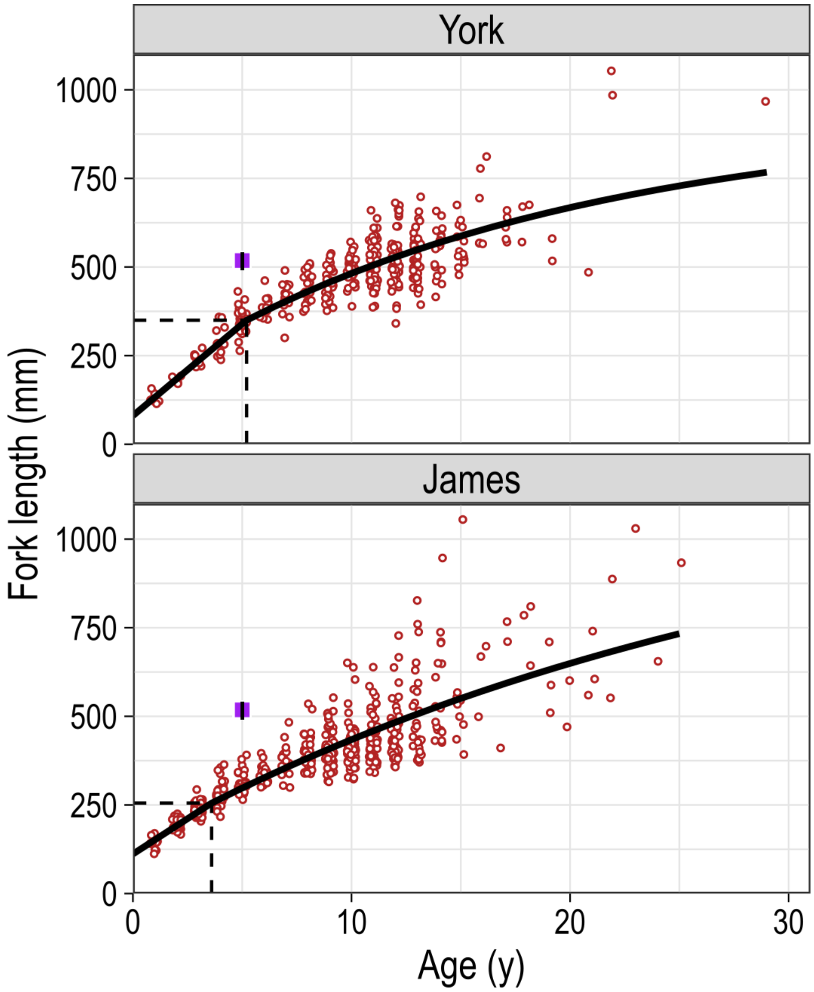

Figure 3: Growth of female blue catfish from the James and York rivers, 2015-2017, based on Lester’s biphasic growth model. Maturity occurs at the point of inflection, where the growth changes from linear to von Bertalanffy; the two stages are delineated in the graph by the horizontal and vertical dashed lines. Points are jittered to show detail. Purple square with the error bar shows the estimated mean length at maturity and corresponding 95% confidence interval for female blue catfish based on data from Perry and Carver (1977).

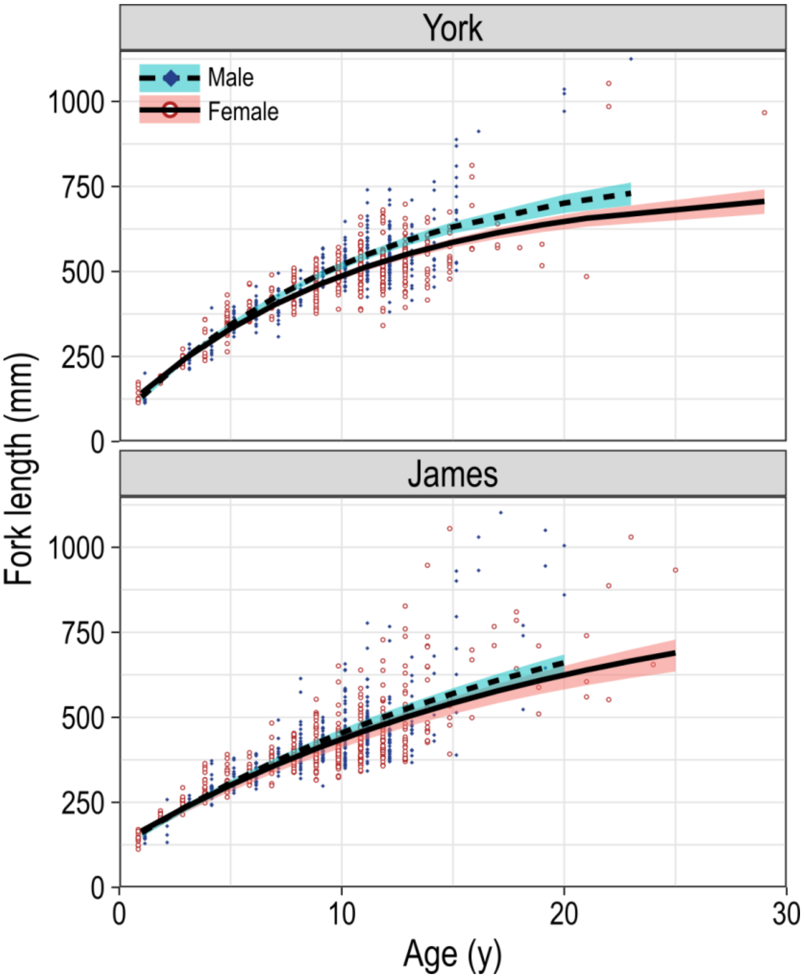

Figure 4: von Bertalanffy growth curves for blue catfish from the James and York rivers, 2015-2017. Males are represented by blue diamonds and dashed lines, and females by empty red circles and solid lines. Shaded polygons around the predicted von Bertalanffy curves represent the 95% confidence bands. Points are slightly offset to show detail. Figure available in color online.

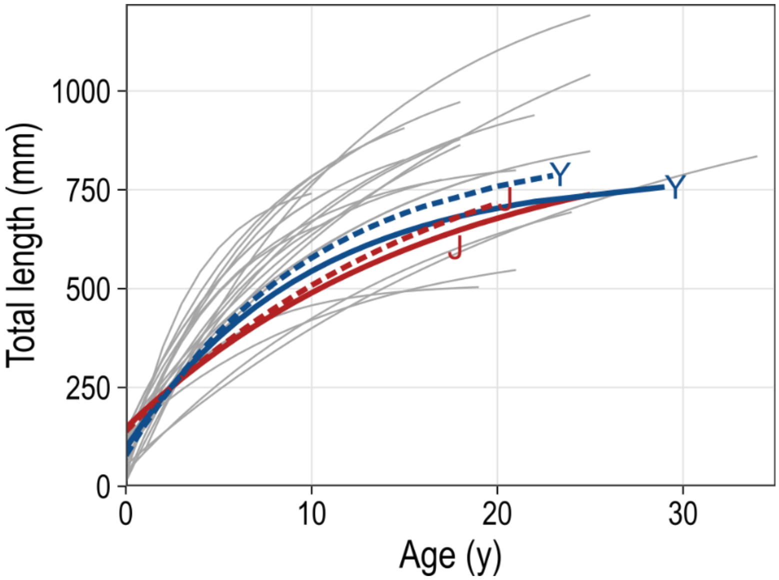

Figure 5: von Bertalanffy growth curves for 19 blue catfish populations from native and non-native ranges (thin grey lines). Thicker lines show corresponding curves for male (dashed lines) and female (solid lines) blue catfish from the James (marked with “J”, red) and York (marked with “Y”, blue) rivers collected during 2015-2017. To allow valid comparisons with other populations, we show von Bertalanffy growth curves for James and York rivers based on total length (estimated based on fork length: TL = 2.477 + 1.169×FL - 0.00012×FL^2). Note, however, that the curves for the total length-age relationships provided here are for illustration purposes only and do not depict the equations given in the text, which are based on fork length. Figure available in color online.

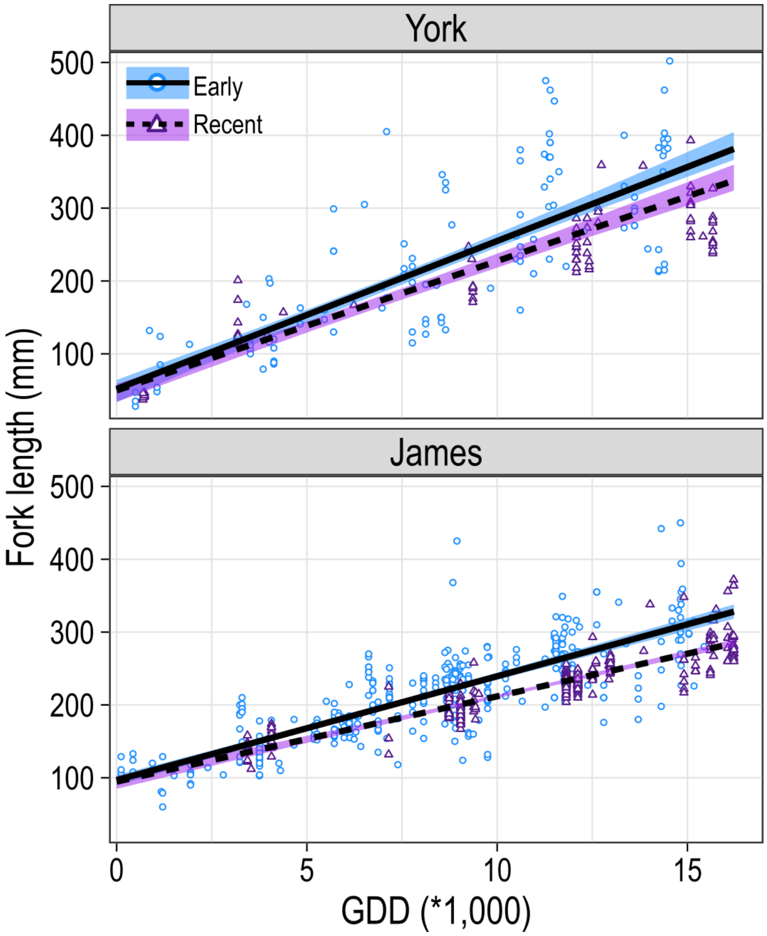

Figure 6: Fork length as a function of cumulative growing degree days (GDD) for immature blue catfish (≤4 y) collected from the James and York rivers during early (blue circles and solid lines; 1998-2000) and recent (purple triangles and dashed lines; 2015-2017) periods. The lines and surrounding shaded polygons represent the model-predicted values and the corresponding 95% confidence bands respectively. Figure available in color online.

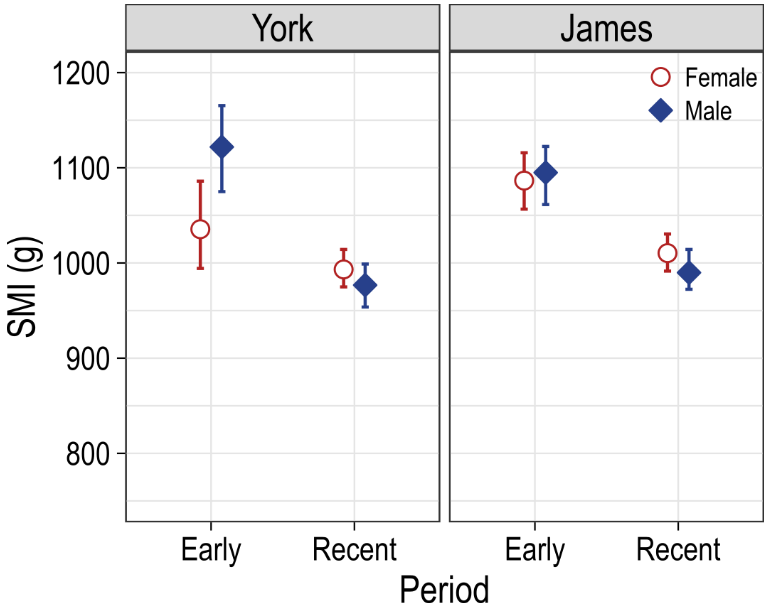

Figure 7: Marginal mean scaled mass index (SMI, g) for a 420 mm FL blue catfish collected during early (1998-2000) and recent (2015-2017) periods from the James and York rivers. Females are represented by open red circles, and males by filled blue diamonds. Error bars represent 95% confidence intervals for the predicted SMI. Figure available in color online.

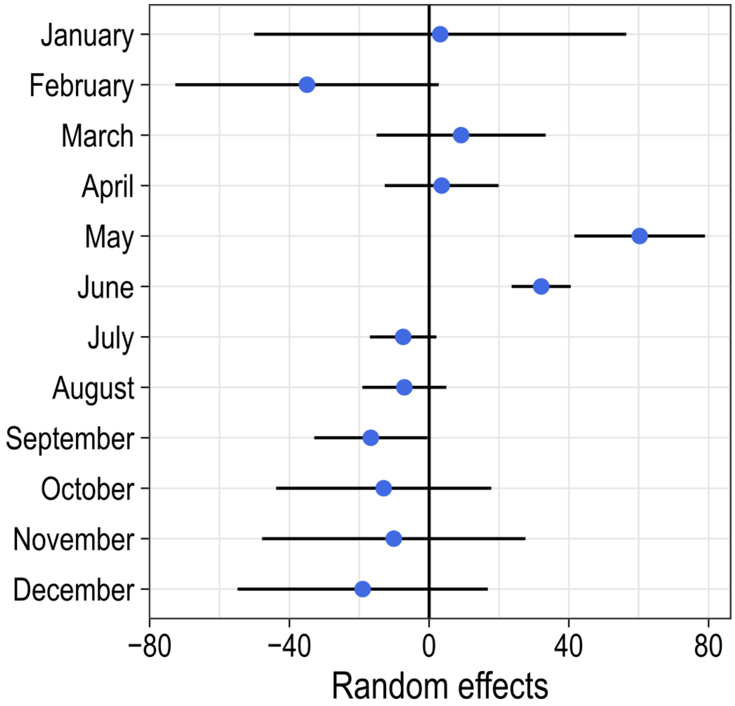

Figure 8: Conditional modes and the corresponding 95% confidence intervals for the random effect of month in the linear mixed-effects model on scaled mass index of blue catfish in two rivers.

CHAPTER 2: Reproductive and Life-History Traits of Invasive Blue Catfish: Novel Tactics in Novel Environments

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Abstract

The management of invasive Blue Catfish *Ictalurus furcatus* in Chesapeake Bay tributaries is hindered by the lack of information on this species' reproductive biology, a key component of population models used to forecast abundance. We quantified and compared the reproductive traits of female Blue Catfish from two populations, the tidal reaches of the James and York river subestuaries, during 2015-2017. Blue Catfish in the more densely populated James River matured at a marginally older age, but significantly smaller size than fish in the York River. The smaller size-at-maturity and lower fecundity-at-age of fish in the James River results in more energy being allocated to reproduction thereby potentially increasing survival rate of their offspring. This, in turn results in a Blue Catfish in the more densely populated James River having a lifetime fecundity and fitness comparable to the fish in the York River. Fish in the James River also had greater mean gonadosomatic indices, fecundity at mean size, egg organic content and proportion of organic content in the eggs. These observations from James River fish contrast with general predictions from life-history theory, which suggest that individuals from populations with greater densities tend to allocate a smaller proportion of energy into reproductive tissues. Blue Catfish in the Chesapeake Bay region appear to be using a different tactic in novel ecosystems to maximize their fitness. Models that incorporate the reproductive rate of invasive Blue Catfish must reflect the variations in reproductive traits observed among populations in the Chesapeake Bay region.

Introduction

The reproductive strategy and potential of a fish are important factors that influence the success of a species in a novel environment (Winemiller 2005; García-Berthou 2007). In such environments, the quantity and quality of propagules (i.e., eggs) may affect the dispersal and range expansion of species (Winemiller 2005). For example, fish egg size and quality are often positively related to survival of the offspring (Moran and McAlister 2009). Parental care of eggs and larvae also increase the probability of offspring survival (Stearns 1992; Winemiller and Rose 1992; Jørgensen et al. 2011). Similarly, characteristics such as early maturation, high fecundity, long spawning season and long reproductive lifespan increase lifetime fecundity, thus increasing the potential individual fitness (Wootton and Smith 2015). Species that possess these characteristics are likely to be more successful invaders (Morris and Whitfield 2009; Lockwood et al. 2013).

It is not surprising therefore that Blue Catfish *Ictalurus furcatus*, a species with male nest-guarding behavior, have become a highly successful invasive species in the Chesapeake Bay region (Fabrizio et al. this issue). Native to large rivers in the midwestern United States, Blue Catfish is a large (>50 kg), long-lived (>25 years) freshwater fish that was introduced in Virginia tidal rivers of Chesapeake Bay during the 1970s and 1980s to create a recreational fishery. Since then, the species range has expanded and Blue Catfish now occupy many subestuaries of the Chesapeake Bay (Schloesser et al. 2011; Nepal and Fabrizio 2019). Populations in the Virginia tributaries such as the James and York rivers remain genetically distinct stocks with little mixing (Higgins 2006). Blue Catfish densities have also increased greatly in many systems throughout the Chesapeake Bay region, such that this species now supports commercial, recreational and nationally-recognized trophy fisheries in some subestuaries (Fabrizio et al. this issue). Yet, due to the potential negative impacts of competition and predation on native species such as White Catfish *Ameiurus catus*, river herring *Alosa* sp., blue crab *Callinectes sapidus* and native mussels (Schloesser et al. 2011; Schmitt et al. 2019), Blue Catfish has become a significant nuisance species in many Atlantic slope estuaries. Management goals currently focus on reducing population size and limiting range expansion, but development of management plans is hindered by the lack of information on key biological characteristics such as growth, reproductive biology, physiological tolerances and energetic demands (ICTF 2014).

Knowledge of the reproductive biology of Blue Catfish will inform development of full life-cycle bioenergetics models (e.g., dynamic energy budget models; Kooijman 2010) as well as stock assessments and spawner-recruit models to support better management of this species (Hilborn and Walters 1992). Models that incorporate reproductive rates of fishes are required to forecast population growth and to design harvest regulations. Fecundity and egg characteristics of Blue Catfish are, however, unknown from both their native range and the Chesapeake Bay region, and maturity schedules are poorly known from their native range (Graham 1999).

In addition, if the reproductive biology varies among populations, then population models for Blue Catfish must reflect these differences. Populations of a given species may express different reproductive traits in different environmental conditions (Green 2008). Many fishes demonstrate plastic responses in novel ecosystems, for example, by allocating more energy towards reproduction and producing more numerous but smaller eggs during the early phase of establishment (Olden et al. 2006; Fox et al. 2007). Such plasticity is often a response to environmental stability or to minimal inter- and intra-specific competition observed in novel environments during early establishment (Winemiller and Rose 1992). In tidal rivers of Virginia, Blue Catfish demonstrate density-dependent growth, likely as a result of high intra-specific competition for food resources (Nepal and Fabrizio 2020; Nepal et al. 2020). Density-dependent growth can affect lifetime fecundity via alterations in age- and size-at-maturity, or by modifying the proportion of energy allocated to reproduction (Winemiller 2005). This adaptive response to intraspecific competition may also extend to maturity schedules and energy allocation rules of fish (Nepal et al. 2020). Reproductive plasticity must, therefore, be considered in population models if such models are to predict population growth accurately.

In this paper, we provide a quantitative evaluation of reproductive potential and characteristics for Blue Catfish in the James and York River subestuaries to enhance understanding of the contribution of reproduction to the persistence of this invader in the Chesapeake Bay region. We, therefore, specifically quantified maturation rates and reproductive allocation in females by examining egg characteristics and the gonadosomatic index (GSI = ovary weight/fish weight × 100). The gonadosomatic index can be used to infer accurately both size-at-maturity and spawning season (Schemmel et al. 2016). Egg characteristics such as size (egg diameter and ash-free dry weight [AFDW]) and composition (the relative proportion of ash weight and AFDW in the egg) influence the probability of fertilization and viabilities of the embryo and larva. AFDW, which corresponds to the organic content in the egg, is an excellent surrogate for energy density across taxa (Weil et al. 2019). High quality eggs are marked by higher AFDWs and higher AFDW proportions. These key metrics (egg diameter, AFDW and AFDW proportion) provide crucial insights on reproductive tactics used by fishes under varying conditions.

As a nest-guarding species, Blue Catfish is expected to have large (>3 mm), well-provisioned eggs and a relatively low individual fecundity (<25,000 eggs; Winemiller and Rose 1992). Based on the predictions of life-history theory (Stearns 1992), however, we also expect plasticity in reproductive traits. We therefore hypothesized that fish from the more densely populated James River will exhibit higher age-at-maturity, lower size-at-maturity and a lower investment in reproductive tissues relative to fish from the York River. These variations in reproductive characteristics will ultimately affect the productivity of these two populations.

Methods

Sample collection and processing.— All animal capture, handling and experimental procedures were approved by Institutional Animal Care and Use Committee (protocols IACUC-2015-06-15-10382-mcfabr and IACUC-2017-05-22-12111-tdtuck). Blue Catfish were captured from the tidal portions of the James and York rivers in habitats that ranged in salinity between 0 and 5 ppt (parts per thousand) and during February-August 2015-2017. These months were expected to encompass the pre-spawning and spawning seasons in these subestuaries (Graham 1999). The majority of fish was captured by a commercial fisher using a low-frequency direct current (DC) electrofishing system. Because the commercial fisher did not operate before June of each year, we supplemented our samples during April and May with fish collected by the Virginia Department of Game and Inland Fisheries Electrofishing Survey and the Virginia Institute of Marine Science Juvenile Fish and Blue Crab Trawl Survey (hereafter, VIMS Trawl Survey). We took care to ensure random sampling of Blue Catfish across broad spatial areas throughout the tidal James and York rivers (Figure 1). Fish were usually collected weekly, returned to VIMS on ice, and processed on the day of capture.

Blue Catfish were measured (mm FL) and weighed (g) individually. We also collected lapillus otoliths for ageing, and processed the left otolith to obtain a thin (~0.5 mm) section through the nucleus. The processed otoliths were read independently by two readers using methods described in Nepal et al. (2020). The number of dark bands (annuli) was recorded as the age (years) of the fish. If the readers did not agree on the age of a fish, the final age was determined by consensus. We disregarded samples for which consensus could not be reached.

We were able to determine sex of the fish by gross examination of the gonads, as testes are thin and tubular in small males and lobate in larger males (Sneed and Clemens 1963), whereas paired ovaries are saccular (V. Nepal, *pers. obs.*). To increase the sample size of females in 2017, we opportunistically obtained gonadal biopsy samples (needle diameter of 5 mm) and identified gravid females as those with egg diameters >2 mm.

Gonadosomatic index.— We removed both ovaries from all females and weighed them together (to the nearest 0.01 g) to calculate GSI. We assessed size- and age-specific differences in mean GSI of Blue Catfish among months and between populations using generalized least squares models (GLS, Zuur et al. 2009; Harrell 2015). We modeled GSI as a function of month, population and either FL or age. To determine if the effect of size or age on GSI varied within the spawning season, we also included FL×month or age×month interactions in the model (models 1 and 2 in Table 1). We used fish collected during June and July, as these were the only months when sufficient numbers of gravid females of comparable size and age ranges were available. Because preliminary graphical analysis of GSI data indicated that the variance differed between populations, we configured the GLS models to estimate population-specific GSI variances (Zuur et al. 2009).

Maturation rates.—We used the GSI approach developed by Fontoura et al. (2009) to assess maturity status. In this approach, females with a GSI greater than 5% of the maximum GSI are considered mature (Fontoura et al. 2009). When identifying mature females, care was taken to include only females captured between April 1 and June 1, because mature active females during this period had high GSI values (see results below). After spawning starts in late May, the GSI of some of the mature females declines due to egg deposition and thus, these females may be categorized incorrectly as immature (Fontoura et al. 2009). To evaluate the effect of designating the end of the pre-spawning season as June 1, we reclassified fish using May 20th or June 10th as the end date. Because the results for these alternative dates were qualitatively similar to those using the original June 1 date, we used June 1 as the end of the pre-spawning period for subsequent analyses.

We used logistic regression to develop maturity ogives for Blue Catfish from the James and York subestuaries. Maturity status (mature or immature) based on GSI was modeled as a function of population and FL or age using the binomial distribution and the logit link (Table 1, models 3 and 4). We estimated the 95% confidence limits (CL) for mean length-at-maturity and mean age-at-maturity using the bootstrap percentile method (2,000 bootstraps; Efron and Tibshirani 1993). We subsequently calculated the two-tailed *P*-value for the difference in mean length-at-maturity for the two populations as twice the proportion of instances when the length-at-maturity for York River fish was greater than that for James River fish (Efron and Tibshirani 1993). *P*-value for the difference in mean age-at-maturity was similarly calculated as twice the proportion of instances when the age-at-maturity for James River fish was greater than that for the York River fish. We did not model age- or size-at-maturity as functions of fish weight or body condition as these varied at intra-year timescales.

Fecundity and lifetime fecundity modeling.— We estimated fecundity using the standard gravimetric method. We obtained and weighed three systematic subsamples (4 – 50% of total ovary weight) from the right ovary of gravid females sampled in 2015-2016. We used subsampling because ova size and density can vary within an ovary (West 1990). For fish collected in 2017, we subsampled only the middle portion of the right ovary. Ovarian sections were fixed in 10% buffered formalin for at least 72 hours and transferred to 70% ethanol. To estimate annual fecundity, we counted the number of eggs in each subsample and scaled up the number by the total weight of both ovaries:

$$\text{Fecundity} = \frac{\sum_i \left(\frac{o_i}{w_i}\right)}{n} \times W \tag{1}$$

where o_i is the number of eggs in subsample i, w_i is the weight of subsample i, n is the number of subsamples, and W is the weight of both ovaries.

We compared mean egg size from the anterior, middle and posterior sections of the ovary to determine if the number of eggs per gram of ovary varied among the three sections. We used a GLS model with mean egg diameter (mm) as the response, and ovary section as the independent factor (Table 1, model 7). Because we measured egg size multiple times from the same fish, we fitted a model with a compound symmetric correlation structure among the three measurements – anterior, middle and posterior (Zuur et al. 2009). In subsequent analyses of population-, age- and size-specific effects on fecundity, we used mean egg diameters from the middle section of the ovary because we did not detect a statistical difference in mean egg diameters among the ovarian sections (see results below). Fecundity was modeled as an additive function of population and either FL or age using generalized linear models with a gamma distribution and a log link (Table 1, models 5 and 6; Zuur et al. 2009).

We developed a simple quantitative model to assess the effects of population and fish size on the lifetime fecundity of female Blue Catfish. To do this, we chose to use the fecundity-FL relationship (model 5) instead of the fecundity-age relationship (model 6) because the former relationship was more precise (as described below). Nonetheless, we estimated fecundity for ages 1 to 25 using predicted mean lengths-at-age from von Bertalanffy growth curves (Nepal et al. 2020) and the fecundity-FL relationship we describe here (Table 1, model 5). Growth models for female Blue Catfish from the James and York rivers (respectively) in 2015-2017 from (Nepal et al. 2020) are:

$$\mathrm{FL} = 918.2 \times (1 - e^{-0.050 \times (\mathrm{age} - 3.0)}) \tag{2}$$

$$\mathrm{FL} = 750.0 \times (1 - e^{-0.093 \times (\mathrm{age} + 1.2)}) \tag{3}$$

We assumed a fecundity of zero for ages below the predicted age at maturity for each population. Finally, we calculated the cumulative fecundity over the lifetime of each female, assuming successful spawning each year.

Egg characteristics.— We assessed three egg characteristics from Blue Catfish: (1) mean oocyte diameter, (2) AFDW and (3) proportion of ash. To determine mean oocyte size, oocytes from preserved egg samples were teased apart, and the diameters of at least 10 oocytes were measured under a stereomicroscope using imaging software. In addition, we obtained mean fresh oocyte diameters from 144 spawning-capable fish both immediately after dissection and after preservation to assess the effect of preservation on egg size. The relationship between mean fresh and preserved oocyte diameters for the 144 fish was given by:

$$\text{Fresh diameter} = 1.937\times(\text{Preserved diameter})^{0.461} \qquad (4)$$

We used this relationship to correct the mean oocyte diameter of preserved samples for shrinkage due to preservation. Subsequently, we tested for the effects of FL, age, sampling month and population on mean egg diameter determined from the middle section of the ovary using multiple regression models (Table 1, models 8 and 9).

We measured AFDW of egg samples as an index of energy content in the eggs. Egg samples from spawning-capable fish were stored in individual 20-ml scintillation vials at -80°C. From each vial, we obtained three 20-egg subsamples, which we dried at 60°C for 72 hours. These were weighed prior to combustion in a muffle furnace. We thus obtained ash weight from each sample, and calculated AFDW as the difference between ash weight and dry weight. We determined the mean AFDW of a single egg by dividing the total AFDW by 20. To ascertain if mean egg quality varied between populations, we calculated the mean proportion of ash in the eggs by dividing the ash weight by the dry weight of each sample. Eggs of higher quality are expected to have a lower proportion of ash, hence a greater proportion of organic matter.

We modeled mean AFDW as the dependent variable using a GLS model with population and either age or FL as the independent variables. A compound symmetric correlation structure was used to account for multiple measurements (i.e., three subsamples) from the same individual. FL was linearly related to egg AFDW, but age had a nonlinear relationship with AFDW. We therefore modeled the relationship between AFDW and age using a restricted cubic spline with 4 internal knots (Harrell 2015; model 11 in Table 1). Finally, we assessed potential population-, size- and age-specific variation in the proportion of ash in the dry mass of eggs using GLS models with a compound symmetric correlation structure and separate variance estimates for each population, as described above (Table 1, models 12 and 13).

Statistical analyses were conducted in R version 3.6.0 using packages “nlme” (version 3.1-139) and “stats” with a significance level (α) of 0.05. We included only those sizes, ages and months for which observations were available from both populations.

Results

We assessed 875 Blue Catfish from the James River (382 males and 493 females) and 765 Blue Catfish from the York River (438 males and 327 females). Females ranged from 112 to 1055 mm in FL, and 1 to 29 years in age.

Gonadosomatic index

The GSI of female Blue Catfish ranged from 0.04 – 21.83%, and varied with fish size and season (Figure 2). In general, mean GSI was lowest in fall and winter, and highest in May–July, suggesting spawning occurs during May-July. Larger Blue Catfish (>600 mm FL) achieved peak GSI values earlier in the spawning season than smaller fish (<400 mm; Figure 2). Similar relationships occurred with fish age, such that GSI peaked during May for older females. Mean GSI of ovigerous females also varied with fish size, age and population (Figure 3). Mean GSI decreased significantly with FL (χ_1^2 = 24.58, $P < 0.001$), but was not significantly different in June versus July (i.e., months during which ovigerous females were collected from both populations; χ_1^2 = 1.25, P = 0.26). The mean GSI for the average-sized fish (mean FL = 486 mm) was significantly greater in the James River (mean GSI = 13.8%; CL = 13.2 and 14.5%) compared with the York River (mean GSI = 12.6%; CL = 11.9 and 13.3%; χ_1^2 = 9.21, P = 0.002; Figure 3). Age, month and age×month did not have significant effects on mean GSI (F_{age} = 0.19; F_{month} = 0.43; $F_{\text{age×month}}$ = 0.90; $P > 0.05$). At the mean age (11.4 y), however, mean GSI was significantly greater in the fish from James River (mean = 14.2%; CL = 13.5 and 14.9%) compared with the fish from York River (mean = 12.4%; CL = 11.6 and 13.2%; χ_1^2 = 19.181, $P < 0.001$; Figure 3).

Maturity schedules

The mean length-at-maturity was significantly lower for the fish from the James River (mean = 343 mm FL; CL = 334 and 352 mm) compared with those from the York

River (mean = 382 mm; CL = 367 and 396 mm; bootstrap P = 0.001; Figure 4). In contrast, the mean age-at-maturity was marginally higher for the James River population (mean = 7.7; CL = 7.3 and 8.0 y) compared with the York River population (mean = 7.0 y; CL = 6.5 and 7.6 y; bootstrap P = 0.058; Figure 4). These differences in size- and age-at-maturity reflect variation in reproductive characteristics of these populations.

Fecundity and lifetime fecundity modeling

Fecundity varied between 2,613 and 68,356 eggs/fish (grand mean = 15,060). Fecundity increased significantly with FL (R^2 = 0.77; χ_1^2 = 980.42, P < 0.001). At mean FL, fecundity was greater for fish from the James River (mean = 14,377; CL = 13,775 and 15,014) compared with those from the York River (mean = 12,568; CL = 12,036 and 13,131; χ_1^2 = 17.21, P < 0.001; Figure 5). Similar to FL, fecundity increased significantly with fish age (χ_1^2 = 77.22, P < 0.001), though the fit was characterized by greater uncertainty (R^2 = 0.41; Figure 5) compared with the fecundity-fish size relationship. At mean age, however, fecundity was marginally lower for the fish from the James River (mean = 13,660; CL = 12,604 and 14,839) compared with those from the York River (mean = 15,326; CL = 14,132 and 16,657; χ_1^2 = 3.75, P = 0.053; Figure 5).

At any given size, Blue Catfish from the James River had greater fecundity compared with those from the York River, but owing to faster growth rates and earlier maturation, the latter had higher annual fecundity until age 19 (Figure 6). Mean cumulative fecundity increased at different rates for fish from the two populations, with fish from the James River population exhibiting higher cumulative fecundity-at-size until age 24 but lower fecundity-at-age until age 25 (Figure 6). A 25-year old female Blue

Catfish from the James and York rivers could potentially produce 446,000 and 444,000 eggs (respectively) over their lifetime (Figure 6).

Egg characteristics

Mean fresh egg diameter ranged from 1.57 to 4.03 mm (mean 3.14 mm), and did not differ significantly among the anterior, middle and posterior sections of the ovary (χ^2_2 = 1.52; P = 0.47). We observed similar results for preserved egg diameters (χ^2_2 = 1.51; P = 0.47). Subsequent assessment of mean egg diameters from the middle section of the right ovary revealed no significant differences across the range of fish lengths (Model 8: $F_{1,303}$ = 0.52; P = 0.47) or ages (Model 9: $F_{1,299}$ = 0.48; P = 0.49) considered. We did not detect significant differences in mean egg diameters between months (Model 8: $F_{2,303}$ = 1.82; P = 0.17; Model 9: $F_{2,303}$ = 2.18; P = 0.12) or between populations (Model 8: $F_{1,303}$ = 0.36; P = 0.55; Model 9: $F_{1,303}$ = 0.22; P = 0.64) when size or age was included in the model.

Mean egg AFDW ranged from 2.18 to 12.94 mg/egg (mean 6.60 mg/egg), and did not vary with fish size for fish from either the James River or the York River (Model 10: χ^2_1 = 2.52, P = 0.11). The relationship of egg AFDW to fish age was non-linear such that AFDW increased during the first few years after maturity, before stabilizing at older ages (χ^2_1 = 16.23, P = 0.001; Figure 7). Post-hoc contrasts indicated that after age 10, mean age-specific AFDW was not significantly different among ages (P > 0.05). Mean egg AFDW was significantly greater for fish from the James River fish (mean = 6.87 mg/egg) than for the fish from the York River (mean = 6.27 mg/egg; χ^2_1 = 3.91, P = 0.048; Figure 7).

Across all samples, ash comprised 1.6 – 8.5% of egg dry mass. The proportion of ash in eggs did not vary with fish length (Model 12: χ^2_1 = 0.08, P = 0.78) or age (Model 13: χ^2_1 = 0.34, P = 0.56), but was significantly greater for the fish from the York River (mean = 5.1%) compared with those from the James River (mean = 4.1%; Model 12: χ^2_1 = 46.55, P < 0.001; Model 13: χ^2_1 = 48.20, P < 0.001).

Discussion

To our knowledge, our study is one of the first to quantify the reproductive biology of wild Blue Catfish. A long reproductive lifespan, combined with large egg size and a relatively small number of eggs per batch that are guarded by males, suggest that the Blue Catfish is an equilibrium strategist (*sensu* Winemiller and Rose 1992), with reproductive traits that are conducive to invasion in novel habitats (Olden et al. 2006; Fox et al. 2007; Morris and Whitfield 2009; Lockwood et al. 2013). Reproductive characteristics of Blue Catfish varied substantially between populations, and among size and age groups. As such, population differences for invasive Blue Catfish extend beyond growth dynamics and maturation rates, and include the proportional allocation of energy to reproductive tissues (as evidenced by GSIs) as well as egg characteristics (number, size and quality).

Maturation rates

Blue Catfish in the more densely populated James River (Fabrizio et al. this issue) matured at a smaller size but older age compared with those in the York River. Maturity at smaller sizes and older ages at high population densities has been reported in other fishes including Vendace *Coregonus albula* (Karjalainen et al. 2016), Rainbow Trout *Oncorhynchus mykiss* (Ward et al. 2017), Walleye *Sander vitreus* (Venturelli 2009) and Trinidadian Guppy *Poecilia reticulata* (Auer 2010). Our observations for Blue Catfish are in line with predictions from life-history theory (Stearns 1992; Winemiller and Rose 1992), and are likely linked to growth dynamics in these systems (Nepal et al. 2020). In newly established populations, relative densities and intraspecific competition are low, resulting in low mortality and rapid somatic growth (Lockwood et al. 2013). Under these conditions, individual fitness is maximized by achieving maturity at large sizes and young ages (Fox 1994; Masson et al. 2016). As population densities increase, however, individual fecundity increases because fish mature at larger body sizes (Stearns 1992). In other words, fish remain immature for longer. Mortality constraints often dictate that lifetime reproductive output will be maximized when maturity occurs at a suboptimal size, and this appears to describe the different maturation tactics of female Blue Catfish in the James and York rivers.

Our study, based on macroscopic evaluation of gonads, confirms a previous study (Nepal et al. 2020) that suggested that female Blue Catfish in the James River matured at a smaller size than females from the York River. Nepal et al. used a growth model that incorporated the cost of reproduction (Ward et al. 2017) to identify size at maturity. Both studies used fish from the same time period and thus, provide independent lines of evidence for variation in maturity schedules for invasive Blue Catfish.

Blue Catfish from the James and York rivers mature at an older age and smaller size compared with conspecifics from their native range, where population densities tend to be lower. The relatively high densities of Blue Catfish in Chesapeake Bay waters

(Fabrizio et al. 2018) accounts for some of the differences in maturity schedules of fish from native and nonnative waters. Specifically, the size-at-maturity of individuals from the James and York rivers (mean 343 – 382 mm FL) are at the lower end of the range reported for native populations (350 – 722 mm; Perry and Carver 1973; Hale and Timmons 1989). Conversely, the age-at-maturity of Blue Catfish from the tributaries of the Chesapeake Bay (mean 7 – 7.7 y) is closer to the upper range for fish from native waters (4 – 7 y; Graham 1999). A potential reason of the discrepancy may be methodological, however. The age-at-maturity for native Blue Catfish populations was determined from ages inferred from length-frequency distributions and not otoliths, as we did here. Thus, the results reported by Graham (1999) are likely less reliable than what we report.

Life-history tactics

The delayed maturation and smaller size-at-maturity observed for Blue Catfish from the James River may have negative consequences on fitness. Delayed maturation results in a longer generation time, lower survival to maturity and a shorter reproductive lifespan; smaller size-at-maturity results in lower age-specific fecundity and higher mortality rates (Stearns 1992). Fishes that mature later and at smaller sizes may, however, compensate for these losses by changing their life-history tactics. For example, late maturing Trinidadian Guppies allocated less energy towards reproduction and a larger fraction towards somatic growth in the first few spawning events, allowing fish to attain large sizes (Auer 2010). As the fish aged, an increasing fraction of energy was allocated towards reproduction. Increasing numbers of offspring were produced, eventually matching the lifetime cumulative fecundity of conspecifics with earlier age-at-maturity (Auer 2010). Blue Catfish from the James River employ a different tactic, allocating relatively more energy into reproductive tissue after maturation, and producing more eggs of higher quality. Specifically, they require 25 y to match the cumulative fecundity of fish from the York River, though few fish survive to age 25 in these rivers. Blue Catfish from the James River however produced eggs of higher quality (i.e., greater organic content and lower proportion of ash), than the fish from the York River; higher quality eggs generally confer greater survivability to the larval stage (Johnston 1997). Finally, the reported lower rate of inbreeding in the James River Blue Catfish population (Higgins 2006) may result in higher survival of eggs because hatchability of eggs is negatively affected by inbreeding depression in fishes (e.g., Rainbow Trout; Su et al. 1996). Together, these factors suggest that the production of juvenile Blue Catfish from the York River may be lower than expected, and thus lifetime fitness of fish from the two populations may be similar, even though egg quality and cumulative fecundity differ. Additional research on the effect of egg quality on survival of young stages is necessary to understand realized lifetime fitness for these two populations.

Given the earlier maturity of Blue Catfish in the York River, we may expect to observe larger adult fish in the York River compared with the James River. This is not the case, however. We contend that Blue Catfish from the James River have low selection pressure to grow large before maturation. Although large individuals are less prone to predation (Stearns 1992), Blue Catfish have few predators in Chesapeake Bay waters. Large individuals also tend to have greater fecundity, but for a given size, Blue Catfish from the James River produce more and higher-quality eggs compared with those from the York River. Indeed, the growth rate of adult Blue Catfish is lower in the James River, such that the mean FL of a 12 y old fish was 456 mm in the James River and 517 mm in the York River (Nepal et al. 2020). Furthermore, fish length can underestimate the energy available for reproduction. For example, non-reproductive Trinidadian Guppies store energy in fat tissues for future reproduction rather than redirecting it to somatic growth (Reznick 1983). As such, the smaller body size of mature Blue Catfish from the James River does not necessarily imply lower energy availability for reproduction.

Together with previous work, our study demonstrates the diversity and context-dependence of tactics used by fishes to maximize fitness in competitive environments. Some species demonstrate greater plasticity in age-at-maturity than in size-at-maturity when exposed to varying competitive environments (e.g., Amur sleeper *Percottus glenii*, Joanna et al. 2011; Walleye, Venturelli 2009). Likewise, Pumpkinseed *Lepomis gibbosus*, matured earlier and invested a greater amount of energy into reproduction at high densities (Fox 1994). Yet, some species, such as Trinidadian Guppies, exhibited expected trends of late maturity and smaller size-at-maturity during food limitation, but progressively increased their size-specific investment in reproduction (Auer 2010). We can, therefore, conclude that various factors such as species identity, individual identity, intra- and inter-specific competition and many environmental variables are likely to interact to determine the lifetime fecundity of fishes (Stearns 1992; Green 2008; Jørgensen et al. 2011).

Size and age effects

Larger Blue Catfish spawned earlier during the spawning season, as reported for many fish species (e.g., Hixon et al. 2014). Size and age had strong positive effects on the number of eggs produced, though the former had a greater influence. This information can be used to identify the optimal harvest seasons for Blue Catfish in systems where managers wish to support a trophy fishery. For example, regulations that protect large individuals, particularly during the early part of the spawning season, would maintain the trophy fishery for Blue Catfish and achieve high reproductive rates to sustain recruitment. This management strategy would also permit substantial harvests of medium-sized or medium-aged fish and, thereby reduce overall population abundance (Ng et al. 2016).

Fecundity of Blue Catfish was more strongly correlated with FL than age, in agreement with observations in other fishes (reviewed in Green 2008). Fecundity was higher in large younger fish than in small older fish. Similar results were observed in Bullhead *Cottus gobio* (Abdoli et al. 2005) and Northeast Atlantic Cod *Gadus morhua* (Folkvord et al. 2014). This suggests that, within the same population, faster immature growth, coupled with larger size-at-maturity, may result in greater female fitness. Access to optimal nursery habitats with high availability of food during juvenile stages may, therefore, greatly affect the immature growth rate, size-at-maturity and ultimately the lifetime reproductive output of an individual fish.

Contrary to our observations for Blue Catfish, fish size also positively affects GSI, egg diameter and egg weight in many fish species (Green 2008; Hixon et al. 2014). We note, however, that other catfish species exhibit deviations similar to what we report for Blue Catfish. For instance, GSI and egg diameter of Bullhead exhibit an initial increase followed by a decrease with length and age of females (Abdoli et al. 2005). GSI was not related to fish size or age of Channel Catfish *Ictalurus punctatus*, a Blue Catfish congener that also provides parental care (Brauhn and McCraren 1975). For Blue Catfish, a significant increasing trend with fish age in egg organic mass in young mature females (age 6 – 10 years) highlights the importance of spawning experience in females. Physiological machinery for reproduction may not be well-developed in first-time spawners (likely 6 – 7 y old), resulting in fewer eggs or eggs of lesser quality than repeat spawners (> 10 y old; Green 2008).

Future directions

Our study suggests a few avenues for future research. First, we studied mean age- and size-at-maturity at the population level. Knowledge of these metrics at the level of individual fish would, however, allow direct assessment of the effects of biotic (e.g., population density) and abiotic (e.g., temperature, salinity, etc.) factors on growth trajectories and reproductive output at the individual as well as population level. Second, histological analyses may increase the accuracy of maturity designations and allow study of the presence and effects of seasonal atresia and skipped spawning on growth and fecundity dynamics (Lowerre-Barbieri et al. 2011). Atresia and skipped spawning may affect both the age-specific and lifetime reproductive output of fish. Third, the effects of salinity on spawning and the reproductive biology of Blue Catfish need to be evaluated. Although traditionally considered a freshwater fish, Blue Catfish have been collected from salinities up to 21.8 ppt in the Chesapeake Bay (Fabrizio et al. 2018). Blue Catfish are unlikely to survive at salinities >15 ppt for extended periods (Nepal and Fabrizio 2019), but sublethal effects on growth and reproduction have not been measured.

Reproduction has been hypothesized not to occur at salinities >2 ppt (Perry 1973), but this has not been confirmed. At least one freshwater fish species, Eurasian Minnow *Phoxinus phoxinus,* is known to spawn in brackish waters up to 6 ppt in the Baltic Sea, where this species is invasive (Svirgsden et al. 2018). Finally, the carry-over effects of parental experience in brackish waters on reproduction and viability of eggs also have not been studied, but could be instrumental in determining population size and potential range expansion of Blue Catfish throughout the Chesapeake Bay region.

As an equilibrium life-history strategist, the Blue Catfish has characteristics supportive of successful invasion: parental care, large eggs, long reproductive lifespan and large size. In the James and York rivers, this species demonstrated considerable flexibility in reproductive tactics. Their reproductive and growth characteristics conform to some, but not all, of the predictions of life-history theory or the general observations concerning allometric scaling. Yet, despite population-specific differences, female Blue Catfish in the James and York rivers may have similar lifetime fitness, depending on mortality and recruitment rates in these systems. Our findings provide quantitative information applicable to managers both directly (e.g., through regulating seasonal harvest) and indirectly (through inputs to stock assessment models), and suggest the need to consider plasticity at population levels when developing management strategies.

Acknowledgments

We thank commercial fisher G. Trice, VDGIF biologist Aaron Bunch, members of the American Shad and River Herring Monitoring Program, and past and present members of the VIMS Trawl Survey crew for assistance with collection of Blue Catfish for this study. We also appreciate the volunteers, technicians and interns, who helped process the fish samples. This manuscript benefitted from discussions with and comments from R. Brill, W. Vogelbein and R. Mann. V. Nepal was supported by graduate fellowships from VIMS Office of Academic Studies and a graduate research fellowship from Virginia Sea Grant; the trawl survey was funded by the Virginia Marine Resources Commission and the U.S. Fish and Wildlife Service.

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Tables

Table1: Statistical models used to examine the reproductive biology of Blue Catfish collected from the James and York rivers during 2015-2017. All independent variables have linear relationships with the corresponding response, except for s(Age) which represents a 3-degree restricted cubic spline relationship. GSI = Gonadosomatic index; GLS = generalized Least-Squares; GzLM = Generalized linear model; FL = Fork Length; AFDW = Ash-free dry weight

Model	Response	Response data type	Model type	Independent variables	Comments
1	Maturity	Binomial (mature/immature)	Logistic regression	FL, Population	Fixed effect of population on each parameter
2				Age, Population	Fixed effect of population on each parameter
3	GSI	Continuous, positive proportion	GLS model	FL, Population, Month, FL×Month	Response exponentiated to meet the normality assumption; separate variance estimates for each population
4				Age, Population, Month, Age×Month	Response exponentiated to meet the normality assumption; separate variance estimates for each population
5	Fecundity	Discrete, positive	Gamma GzLM with log link	FL, Population	FL mean-centered for better interpretability of the model
6				Age, Population	Age mean-centered for better interpretability of the model
7	Mean egg diameter	Continuous, positive	GLS model	section	Compound symmetric correlation structure to account for multiple observations from a single fish

8	Mean egg diameter	Continuous, positive	Linear regression	Age, Month, Population	Using middle section of the ovary
9				FL, Month, Population	Using middle section of the ovary
10	Mean AFDW	Continuous, positive	GLS model	FL, Population	Compound symmetry
11				s(Age), Population	Compound symmetry
12	Mean egg ash proportion	Continuous, positive proportion	GLS model	FL, Population	Compound symmetry; separate variance estimates for each population
13				Age, Population	Compound symmetry; separate variance estimates for each population

Table 2: Type III analysis of variance or analysis of deviance results for models assessing reproductive characteristics of invasive Blue Catfish in Chesapeake Bay subestuaries. Model numbers and abbreviations are given in Table 1. N is sample size for each model; ϕ is the dispersion parameter for the gamma GLM, and ρ is the correlation coefficient for the compound symmetric correlation structure.

Model	Response	N	Parameter	Statistic	df	P	Comments
1	Maturity	728	FL	$\chi^2 = 483.6$	1	<0.001	
1			Population	$\chi^2 = 18.4$	1	<0.001	
2	Maturity	698	Age	$\chi^2 = 600.9$	1	<0.001	
2			Population	$\chi^2 = 3.70$	1	0.055	
3	GSI	261	FL	$\chi^2 = 24.58$	1	<0.001	
3			Month	$\chi^2 = 2.14$	1	0.143	
3			Population	$\chi^2 = 9.21$	1	0.002	$SD_{York} = 0.036$; $SD_{James} = 0.033$
3			FL×Month	$\chi^2 = 1.25$	1	0.263	
4	GSI	260	Age	$\chi^2 = 0.19$	1	0.665	
4			Month	$\chi^2 = 0.43$	1	0.514	
4			Population	$\chi^2 = 19.18$	1	<0.001	$SD_{York} = 0.039$; $SD_{James} = 0.033$
4			Age×Month	$\chi^2 = 0.90$	1	0.342	
5	Fecundity	299	FL	$\chi^2 = 980.42$	1	<0.001	$\phi = 0.07$
5			Population	$\chi^2 = 17.21$	1	<0.001	
6	Fecundity	299	Age	$\chi^2 = 77.22$	1	<0.001	$\phi = 0.21$
6			Population	$\chi^2 = 3.75$	1	0.053	
7	Mean egg diameter	159	Intercept	$\chi^2 = 47730.3$	1	<0.001	$\rho = 0.55$
7			portion	$\chi^2 = 1.52$	2	0.468	
8	Mean egg diameter	308	Intercept	$F = 2575.21$	1	<0.001	
8			FL	$F = 0.52$	1	0.470	
8			Month	$F = 1.82$	2	0.165	

8			Population	$F = 0.36$	1	0.551	
8			Residuals		303		
9	Mean egg diameter	304	Intercept	$F = 3586.79$	1	<0.001	
9			Age	$F = 0.48$	1	0.490	
9			Month	$F = 2.18$	2	0.115	
9			Population	$F = 0.22$	1	0.639	
9			Residuals		299		
10	Mean egg AFDW	324	Intercept	$\chi^2 = 33.73$	1	<0.001	$\rho = 0.699$
10			FL	$\chi^2 = 2.52$	1	0.113	
10			Population	$\chi^2 = 3.96$	1	0.046	
11	Mean egg AFDW	324	s(Age)	$\chi^2 = 16.23$	3	0.001	$\rho = 0.674$
11			Population	$\chi^2 = 3.91$	1	0.048	
12	Egg ash proportion	324	FL	$\chi^2 = 0.08$	1	0.782	$\rho = 0.613$
12			Population	$\chi^2 = 46.55$	1	<0.001	$SD_{York} = 0.009$; $SD_{James} = 0.007$
13	Egg ash proportion	324	Age	$\chi^2 = 0.34$	1	0.559	$\rho = 0.613$
13			Population	$\chi^2 = 48.20$	1	<0.001	$SD_{York} = 0.009$; $SD_{James} = 0.007$

Figures

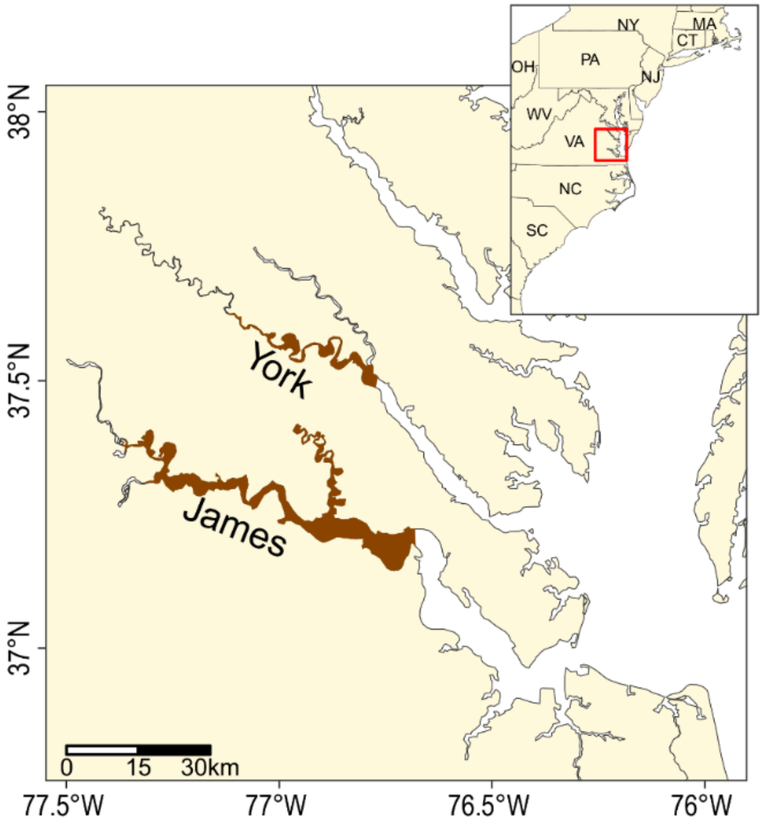

Figure 1: Sampling locations for Blue Catfish from the James and York river subestuaries in Chesapeake Bay. Brown polygons correspond to Blue Catfish capture locations during 2015-2017.

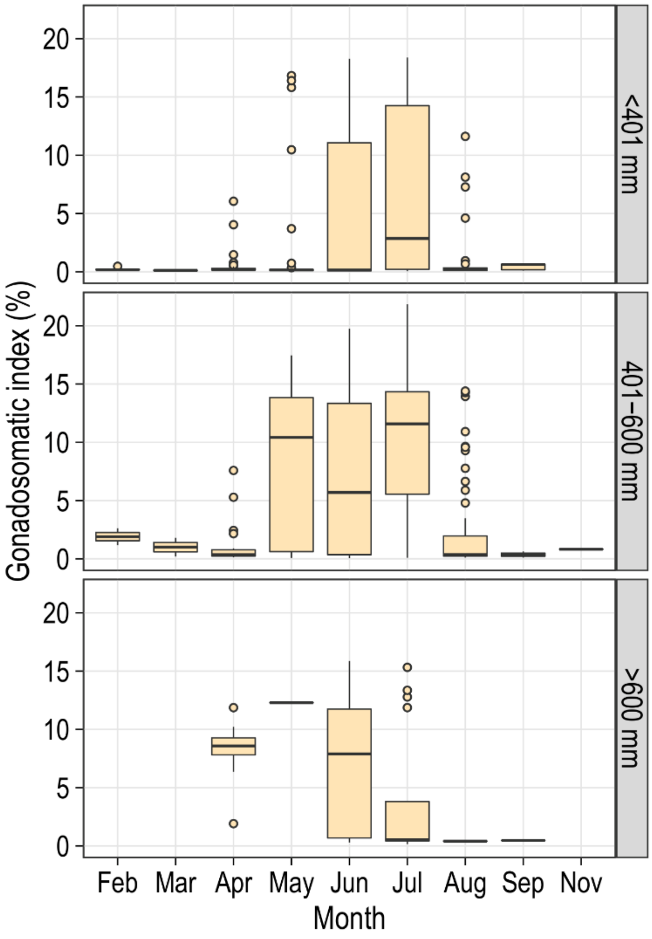

Figure 2: Box-plots of monthly gonadosomatic indices of female Blue Catfish for three size groups collected from the James and York rivers during 2015-2017.

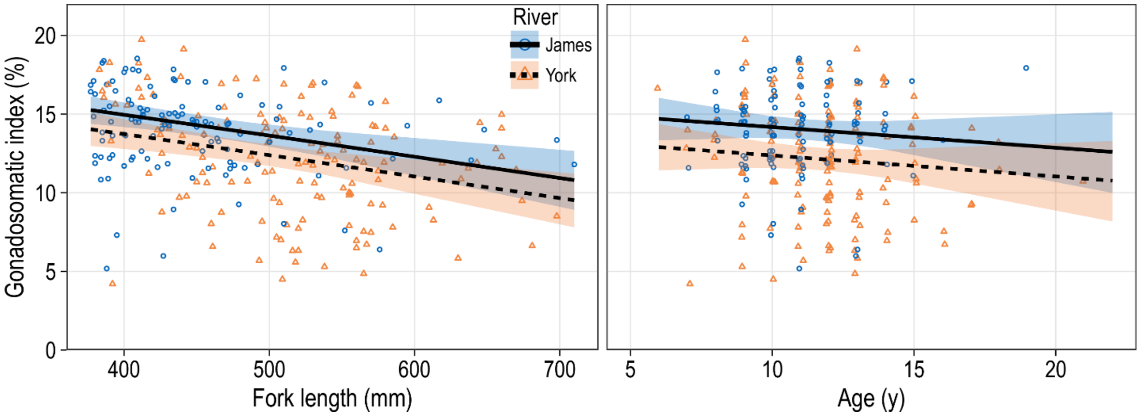

Figure 3: Relationships between the gonadosomatic index and fork length or age of Blue Catfish collected from the James (blue circles) and York (orange triangles) rivers during 2015-2017. The lines and surrounding shaded polygons represent the model-predicted values and the corresponding 95% confidence bands respectively. Figure available in color online.

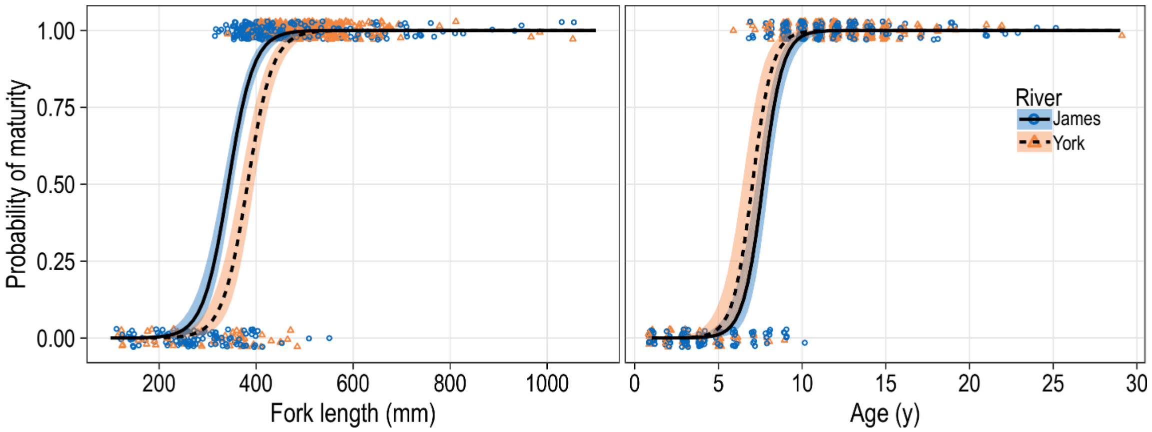

Figure 4: Maturity ogives for female Blue Catfish collected from the James (blue circles, *n* = 493) and York (orange triangles, *n* = 438) rivers during 2015-2017. The lines and surrounding shaded polygons represent the model-predicted values and the corresponding 95% confidence bands. Raw data are jittered to improve visibility. Figure available in color online.

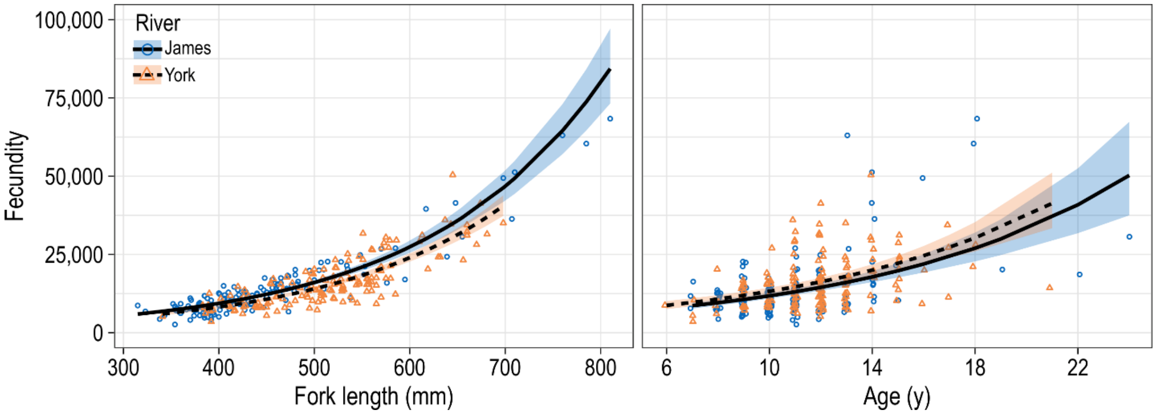

Figure 5: Relationships between the fecundity and fork length or age of Blue Catfish collected from the James (blue circles) and York (orange triangles) rivers during 2015-2017. The lines and surrounding shaded polygons represent the model-predicted values and the corresponding 95% confidence bands respectively. Figure available in color online.

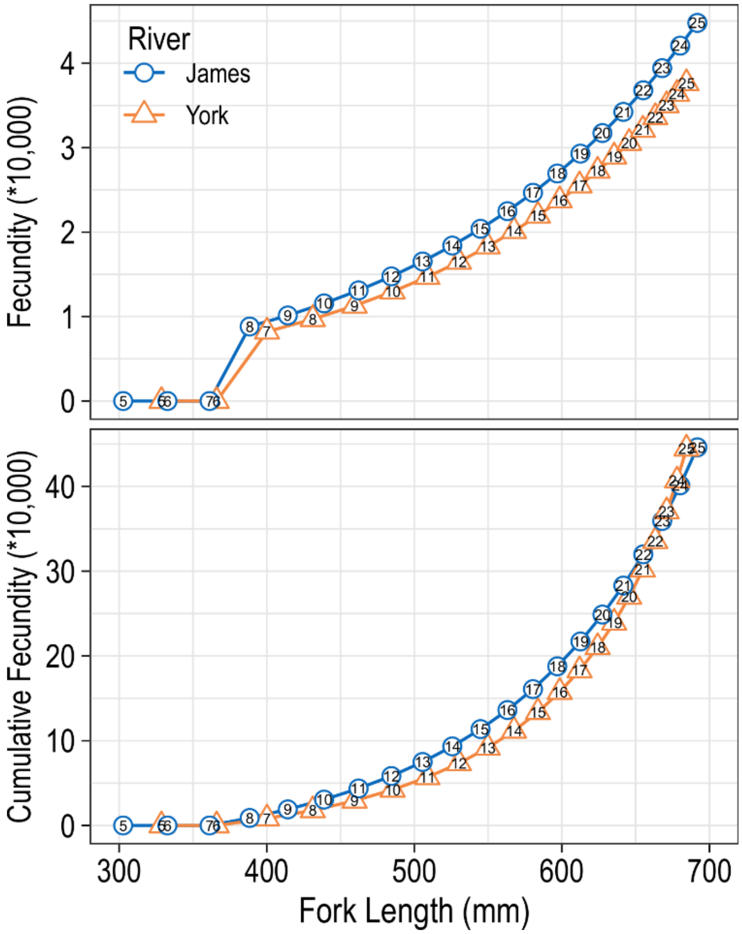

Figure 6: Predicted fecundity and cumulative lifetime fecundity for female Blue Catfish at ages 5-25 y from the James (blue circles) and York (orange triangles) rivers. Numbers within the symbols represent the age (years) of Blue Catfish.

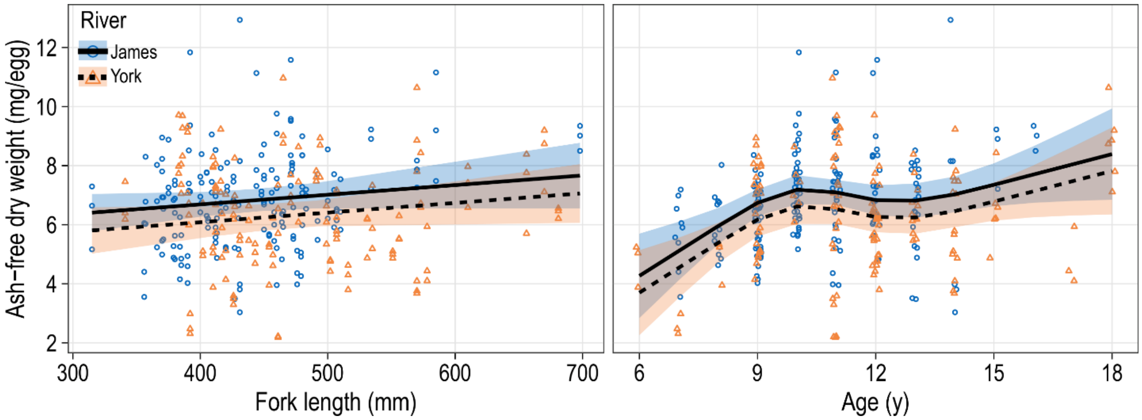

Figure 7: Relationships between the mean ash-free dry weight of eggs and fork length or age of Blue Catfish collected from the James (blue circles) and York (orange triangles) rivers during 2015-2017. The lines and surrounding shaded polygons represent the model-predicted values and the corresponding 95% confidence bands respectively. Figure available in color online.

CHAPTER 3: The Effect of Food Limitation on Non-Native Blue Catfish from a Mid-Atlantic Estuary

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Abstract

Blue catfish *Ictalurus furcatus* is an invasive species of management concern in many lakes, coastal rivers and estuaries throughout the Atlantic coastal plain of the United States. Further range expansion and establishment of this species depend on food availability in these habitats and the energetic requirements of the fish. Knowledge of growth and metabolic rates at various food levels is particularly critical to inform models that assess the ability of this species to establish populations in new environments. We compared growth rates, body condition, and metabolic rates of juvenile blue catfish at three ration levels (*ad libitum*, two-thirds *ad libitum* and one-third *ad libitum*) for four months. All fish survived the entire duration of the experiment regardless of ration level. Similar to other benthic fishes, blue catfish exhibited a relatively low routine metabolic rate. Mean growth rates were lower for fish at reduced ration levels, but we found no evidence that body condition and metabolic rates differed among the various ration levels. Blue catfish therefore appear to have mechanisms which enable them to survive low rates of food intake for long periods, indicating the potential of the fish to become established in novel habitats with low prey availability.

Keywords: Chesapeake Bay, invasive species, food limitation, metabolic rate, blue catfish

Introduction

Blue catfish *Ictalurus furcatus*, a primarily freshwater fish native to large rivers in the Midwestern United States, has been introduced throughout North America to promote recreational fisheries (Fuller and Neilson 2020). During the 1970s and 1980s, blue catfish were stocked in the tidal freshwater regions of three rivers in Virginia, but have since become established in all major tributaries of the Chesapeake Bay (Fabrizio et al. In review; Schloesser et al. 2011). Owing to the range expansion, increase in relative density and abundance, and potential negative effects on native fish and shellfish resources, blue catfish are now considered an invasive species in the region (Fabrizio et al. 2018; Schmitt et al. 2019; Nepal and Fabrizio 2019, 2020). Blue catfish are also of concern in coastal rivers and lakes in other states throughout the Eastern United States, including Delaware, North Carolina and Georgia (Homer and Jennings 2011; Bonvechio et al. 2012). As such, resource managers seek to limit the dispersal, population size and potential trophic impacts of blue catfish in these systems (Fabrizio et al. In review).

The establishment and trophic impacts of blue catfish in novel habitats will be determined, in part, by their energetic requirements and responses to variable food regimes. Because food is a driving force governing the growth and metabolism of fishes (Brett and Groves 1979), a mismatch between the demand for and availability of food resources may impede establishment of blue catfish in novel habitats. In addition, the role and impacts of the fish in established habitats would also depend largely on its consumptive demands and competitive abilities. In a community where multiple species compete for limited resources, the resource-ratio hypothesis predicts that the species with the lowest resource requirements (i.e., R*) will outcompete other species when resources are drawn below levels that other species can tolerate (Tilman 1982). For example, invasive bighead carp *Hypophthalmichthys molitrix* were able to outcompete native paddlefish *Polyodon spathula* in mesocosms through low metabolic demands and superior feeding efficiency (Schrank et al. 2003). If blue catfish have lower food requirements than native species, and if blue catfish can persist under low food levels, then they may become established in low food environments throughout Eastern United States, where they may negatively impact the diversity, density and health of native species through exploitative competition (Hart and Marshall 2012). On the other hand, if blue catfish have high energetic requirements, they may still be successful in a novel ecosystem if they are able to efficiently seize resources from established native residents via interference competition (Hart and Marshall 2012). The resource needs of blue catfish, though clearly important in understanding their invasion and establishment success, are currently unknown.

Characterization of the consumptive demand of blue catfish and of the response of the fish to limited food can inform population and bioenergetics models that can shed light on trophic impacts and potential dynamics of the fish in novel ecosystems. For example, Cooke and Hill (2010) developed a bioenergetics model for invasive Asian carp *Hypophthalmichthys* spp. to identify both the environmental conditions and specific basins in the Laurentian Great Lakes that may be susceptible to invasion due to the low metabolism and low consumptive demands of the fish. Similarly, a full life-cycle bioenergetics model for the purple mauve stinger *Pelagia noctiluca*, an invasive holoplanktonic cnidarian in the Mediterranean Sea, revealed that an individual could mature and reproduce even at ingestion levels as low as 14% of maximum (Augustine et al. 2014). Bioenergetics models such as these, however, rely on information on the biological characteristics of the species of interest under different food levels. In particular, knowledge of growth, body condition and metabolism at specific food densities can inform bioenergetics models and provide insights on growth and feeding rates observed in the wild (Kooijman 2010). An ability to grow and maintain good body condition in restricted food environments would be beneficial for an invading organism.

The energetic and metabolic needs of wild blue catfish are not well-studied. Schmitt (2018) estimated the maximum consumption rates of wild blue catfish from the Chesapeake Bay region to be about 9% body weight per day, but the impacts of reduced ration on blue catfish biology are not known. Estimates of metabolic rates of blue catfish can also inform growth dynamics (van Poorten and Walters 2016), elucidate ecological traits (Killen et al. 2016), and support development of bioenergetics models for this species (Kooijman 2010; Cooke and Hill 2010). Species with low maintenance costs and metabolic demands, as measured by standard metabolic rate (SMR) in fish, are more likely to succeed in coping with harsh, patchy or unpredictable environmental conditions that invading species may experience in novel ecosystems (Tilman 1982; Reid et al. 2012). Additionally, a high maximum capacity to mobilize energy (maximum metabolic rate, MMR) may increase foraging rates and behavioral dominance (Metcalfe et al. 2016). Finally, a change in the relative ability of an organism to expend energy beyond that required for homeostasis (i.e., the factorial scope, FS = MMR/SMR) under restricted food conditions could provide a holistic indicator of fish health. Bringing these ideas together, the “compensation hypothesis” predicts that a lower SMR allows for the allocation of more energy to growth and reproduction (Deerenberg et al. 1998), two processes that facilitate invasion. As observed in many fish species, the ability to decrease maintenance costs (and hence, SMR) during restricted food conditions (e.g., Van Leeuwen et al. 2012; Auer et al. 2016; Liu and Fu 2017), may offer a competitive advantage for colonization of and establishment in novel habitats.

We quantified the effects of food limitation on growth, condition and metabolic rates of invasive blue catfish. Specifically, we monitored body length, condition and metabolic rate indices (MMR, SMR and FS) of blue catfish subjected to one of three ration sizes for four months. Our main objective was to understand the food and energetic requirements of blue catfish (1) to characterize the role of this invasive species in non-native habitats throughout the Eastern United States and (2) to inform bioenergetic and population models that examine the future distribution, dynamics, and impacts of this species.

Methods

All animal capture, handling and experimental procedures followed approved Institutional Animal Care and Use Committee protocols (IACUC-2015-06-30-10455-mcfabr and IACUC-2017-05-22-12111-tdtuck) and all applicable U.S. guidelines.

Experimental system

We assessed the effects of reduced ration size on growth, body condition and metabolic rates of juvenile blue catfish because growth is fastest in young fish. We captured fish using a 9.14-m otter trawl from the James River subestuary following sampling protocols of the Virginia Institute Marine Science (VIMS) Juvenile Fish Trawl

Survey. Fish were brought to the VIMS Seawater Research Laboratory, anesthetized using clove oil (50 mg/L concentration), weighed, and tagged with unique 8.4 mm Passive Integrated Transponder (PIT) tags using a sterile syringe injector. Before the start of the experiment, fish were held in 500-L cylindrical tanks at 20°C and 1.5 psu (practical salinity units) for at least two weeks, during which time they were fed commercial slow-sinking catfish pellets *ad libitum* three times per week. The 3-mm pellets were fishmeal-based and contained 40% protein and 10% fat (Zeigler Bros, Inc.).

The experiment used a randomized nested design with five blocks and three treatment levels. Blocks were represented by five recirculating aquaculture systems (RAS), each of which contained three 270-L cylindrical aquaria supplied with mechanical and biological filtration devices. The 5 RAS ensured uniformity of temperature conditions among the three aquaria within each RAS, and among the RAS. Individuals were sorted by size (fork length [FL]) and randomly assigned to one of the five RAS (one of five blocks), such that each aquarium within an RAS received two fish of similar size. We held two fish in each aquarium because feeding declined considerably when only one individual was placed in each aquarium. We did not know the sex of the fish at the start of the experiment. Each aquarium within an RAS was randomly assigned to one of three ration size treatment levels: *ad libitum*, two-thirds of *ad libitum* ("two-thirds" hereafter) and one-third of *ad libitum* ("one-third" hereafter).

To estimate the *ad libitum* ration size, we added fixed amounts of food, either 2.0, 2.5, 3.0, 3.5, 4, 4.5, 5, 5.5 or 6.0% of the total fish biomass, to each aquarium. These pre-trials were conducted 3 times with 48-hour intervals between trials. Fish were starved for 34 hours between each trial. The greatest mean ration size that was fully consumed overnight (14 hours) by fish (3.5% of total fish biomass) was chosen as the *ad libitum* ration size. Ration size based on proportion of fish weight results in a fish with lower body condition (lower body mass for its length) receiving smaller rations than another fish of the same length but with higher body condition, potentially resulting in further loss of body mass over time for the lower conditioned fish. To avoid this, we estimated ration size for each fish using the relationship between ration and fish length, rather than fish weight. We fit a linear regression between mass-based ration size (g) for each fish and the square of fork length (FL^2) of the fish; FL^2 was chosen because bioenergetics theory suggests that consumption rates in fish are proportional to $mass^{2/3}$ (Kooijman 2010; van Poorten and Walters 2016), which is equivalent to $length^2$ for a fish growing isometrically. We used the linear regression model ($ration = 0.0114 \times FL^2 - 1.7257$; $R^2 = 0.85$; $n = 30$) to calculate mean ration size (g) for each fish based on its length. Total allotted ration size for each pair of fish in a given aquarium was the sum of the estimated ration sizes for the two fish.

We adjusted ration size for each pair of fish using the above ration-FL^2 relationship at one-month intervals to account for changes in FL over time. Fish assigned to *ad libitum* rations were fed daily and those assigned to one-third ration size were fed full rations every third day; fish in the two-thirds ration size were fed a full ration two consecutive days but not on the third day. Fish were fed between 4:30 and 8:00 PM, and excess food was siphoned from each aquarium the next morning. We monitored water quality (dO_2, salinity, NH_3, NO_3^-, and NO_2^-) twice per week, and performed water changes as necessary to maintain water quality. All systems were maintained at 20°C (range 18.6 – 21.1°C) and 1.5 psu (range 1.3–1.7 psu) to prevent parasitic infestations that we commonly observed at lower salinities.

At the start of the experiment, we estimated metabolic rates of each fish using intermittent-flow respirometry protocols as described below. Following the respirometry trial, fish were returned to their respective aquaria. We performed respirometry trials on each individual five times with a one-month interval between trials. To ensure that the time interval between two monthly measurements was similar for all individuals, we exposed fish to the respirometry trials in the same order each month; the order during the first month was random. Condition of the fish was calculated for each month as Fulton's condition factor (*K*):

$$K = 100{,}000 \times W \times FL^{-3} \tag{1}$$

where *W* is the weight of the fish.

During the third measurement period, four fish died due to the malfunction of the respirometry system. These fish were replaced with newly collected individuals from the James River that were allowed to acclimate to laboratory conditions for 7 days prior to tagging and obtaining length and weight measurements. At the conclusion of the experiment (4 months), we euthanized all fish by immersion in an ice slurry, and subsequently determined the sex of each fish using macroscopic examination of the gonads.

Measurement of metabolic rates

We used intermittent-flow respirometry (Svendsen et al. 2016b) to determine the standard metabolic rate (SMR) and maximum metabolic rate (MMR) of blue catfish (n =

10 from each ration size, total = 30) at 20°C and 1.5 psu. Respirometry trials were conducted in 4-L cylindrical respirometry chambers (Loligo Systems, Viborg, Denmark). To ensure that chamber volume was no more than 50 times the volume of the fish (Svendsen et al. 2016a), we reduced the volume of the chamber by inserting a glass flask of known volume into the chamber. The flasks did not hinder the mixing of water during flushing, and were impermeable to oxygen.

Metabolic rates of each blue catfish were measured in independent respirometry chambers (one fish per chamber), submersed in an individual temperature-controlled water bath bubbled with air to maintain normoxic conditions. We placed an opaque cover over the water bath and respirometry chamber to minimize visual disturbance. The oxygen saturation (%) of the water in the chamber was measured every second by a pre-calibrated FireSting fiber-optic oxygen meter (Pyro-science, Aachen, Germany), the sensor of which was inserted in the water circulation tubing. We converted oxygen saturation to oxygen concentration ($[O_2]$, mg O_2 L^{-1}) using standard equations based on temperature, salinity and partial pressure. The mean oxygen consumption rate ($\Delta[\dot{O_2}]$, mg O_2 L^{-1} h^{-1}) during each cycle was calculated as the slope of a linear regression of recorded oxygen concentrations against elapsed time, and was subsequently converted to mass-corrected oxygen consumption rates ($\dot{M}O_2$, mg O_2 kg^{-1} h^{-1}) using the relationship:

$$\dot{M}O_2 = \Delta[\dot{O_2}] \times V \times W^{-1} \qquad (2)$$

where *V* is the volume of the respirometry chamber (L) corrected for fish and flask volume, and *W* is the weight of the fish (kg) at the time of the respirometry trial. Each trial was automated by controlling the pumps using the open-source software program

AquaResp (www.AquaResp.com). For each trial, we used flush, wait and measure periods of 3 min, 1 min and 7 min, respectively.

For each respirometry chamber, background respiration due to bacteria (i.e., the rate of oxygen depletion in the respirometry chamber without a fish) was measured at the start and end of each week. We measured background respiration over 24-hours using measurement periods of 1 h. Background respiration ranged between 0 and 17.3% of the fish oxygen consumption, with a median of 0.3% and 95th percentile of 8.3%. Assuming a linear relationship between background respiration at the start and the end of the week, we estimated background respiration rate throughout the week. Oxygen consumption rate for each fish was subsequently corrected for background respiration by subtracting the estimated background respiration on the day of the trial (Svendsen et al. 2016b). We did not use parallel chambers to measure background respiration because preliminary trials showed that most of the variation in background respiration was chamber-specific but highly repeatable for each chamber. To minimize background respiration, all chambers, tubing and flasks were cleaned in a 10% bleach solution at the start of each week.

We starved fish for a minimum of 40 h before the respirometry trials to ensure post-absorptive state prior to measuring oxygen consumption rates. Fish were exercised to exhaustion (the point at which they no longer elicited an escape response to handling) in a water flume, and subjected to a brief period (~1 min) of air exposure. This protocol is suited for eliciting MMR in benthic fish species that do not regularly exhibit prolonged swimming (Killen et al. 2017). Fish length and weight were recorded immediately prior to the fish being placed into the respirometry chamber, whereafter they remained for 21-29 h. We determined MMR of each fish as the highest recorded $\dot{M}O_2$ and SMR as the

20th percentile of $\dot{M}O_2$, excluding the first 10 hours after introduction (Chabot et al. 2016). Factorial scope (FS) was calculated as the ratio of MMR to SMR of each fish.

Statistical analysis

We first assessed the correlations among the response variables (FL, K, SMR, MMR and FS) using pairwise Pearson's correlations. We considered two variables with a correlation coefficient (r) less than 0.3 to be weakly correlated and those with r greater than 0.6 to be strongly correlated. Strong correlation between two response variables suggest mutual dependence and correlated errors, thus requiring a joint modeling approach. Correlations among the variables were generally weak, however, allowing us to model and examine each response variable independently.

We assessed the effects of ration size and sex of fish on body length, body condition and metabolic rates of blue catfish using a mixed-effects repeated measures modeling approach. Specifically, we fitted separate linear mixed effects models for each response variable. The model for FL took the form:

$$FL_{ijkl} = \mu + S_i + R_j + D + B_k + R_j \times D + I_{k(l)} + \varepsilon_{ijkl} \qquad (3)$$

where μ is the overall mean response, S_i is the effect of sex i, R_j is the effect of ration size j, D is the number of days since the start of the experiment, B_k is the baseline or initial FL of fish k (i.e., FL observed on the start date of the experiment), $R_j \times D$ is the interaction between ration size and number of days since the start of the experiment, $I_{k(l)}$ is the random effect of fish k nested within RAS l, and ε_{ijkl} is the unexplained random variation.

We included fish weight at the time of monthly measurement as a covariate in mixed models for K, SMR, MMR and FS, because body mass affects Fulton's body condition (Froese 2006) as well as metabolic rates of fish (Schmidt-Nielsen 1984; Killen et al. 2016):

$$Y_{ijkl} = \mu + S_i + R_j + D + B_k + R_j \times D + I_{k(l)} + W_k + \varepsilon_{ijkl} \qquad (4)$$

where Y_{ijkl} is the response and W_k is the effect of wet weight of fish k, and other symbols are as previously defined. We note that even though metabolic rate indices have been shown to decline exponentially with weight of fish (Killen et al. 2016), such decline is approximated well by a linear relationship when a narrow range of fish weights is considered, as was the case in our study. For each model, our primary interest was in the ration size-by-time interaction $R_j \times D$, which, if significant, would indicate variable effects of time on the observed response (length, condition, or metabolic rates of blue catfish) depending on ration size. We did not include other interaction terms because preliminary graphical analysis indicated no interactions.

We assessed various covariance structures to account for potential autocorrelations in repeated measurements of each response. Specifically, we considered unstructured, first order autoregressive (ar1), Toeplitz and spatial power covariance structures to model autocorrelations in response variables over time (Littell et al. 2006). We note that autoregressive and Toeplitz covariance structures assume equally spaced time intervals between repeated measurements (Littell et al. 2006), even though in our experiment, the time intervals among individual measurements ranged from 28 and 35 days. By fitting these covariance structures, we therefore assumed that intervals of 28 to 35 days were equivalent. Covariance structures with heterogeneous variances, such as heterogeneous autoregressive and heterogeneous Toeplitz were also considered (Littell et al. 2006). Models with these alternative covariance structures were fitted using restricted maximum likelihood (Littell et al. 2006) and compared using Akaike Information Criterion corrected for small sample sizes (AICc; Burnham and Anderson 2002). For each response variable, the most parsimonious model of the covariance structure, defined as the one with the lowest AICc value, was refitted with maximum likelihood to obtain unbiased parameter estimates for the fixed effects (Littell et al. 2006).

We mean-centered some of the predictor variables to aid computations and suppressed the intercept to aid model interpretation. Assumptions of homogeneity of variance and normality were assessed using diagnostic plots. We conducted all statistical analyses in SAS version 9.4 (SAS Institute, Cary, NC) following procedures outlined in Littell et al. (2006). Statistical significance was set at $\alpha = 0.05$.

Results

Mean FL was 207 mm (range 188-241 mm) and mean wet weight was 114 g (range 73.5-170.5 g) at the beginning of the experiment. We found a weak positive correlation between FL and K ($r = 0.26$; $P = 0.001$; Fig. 1). MMR and SMR were also positively correlated with each other ($r = 0.40$; $P < 0.001$). Factorial Scope had a relatively strong positive correlation with MMR ($r = 0.70$; $P < 0.001$), but a weak negative correlation with SMR ($r = -0.37$; $P < 0.001$; Fig 1). SMR and MMR were weakly correlated with FL ($|r| \leq 0.29$; $P < 0.05$). None of the metabolic rate indices were correlated with body condition ($|r| \leq 0.13$; $P > 0.05$).

Mass-corrected MMR of juvenile blue catfish at 20°C ranged between 173.6 and 430.7 mg O_2 kg^{-1} h^{-1}; the mean MMR of blue catfish (283.8 mg O_2 kg^{-1} h^{-1}) was greater than that of 35.4% of the fish species with published MMR values at 20°C (Fig. 2). SMR ranged between 48.6 and 89.9 mg O_2 kg^{-1} h^{-1}, with the mean SMR (67.6 mg O_2 kg^{-1} h^{-1}) greater than that of 38.4% of the fish species with published SMR values (Fig. 2).

First-order autoregressive covariance structure (ar1) was chosen as the most parsimonious structure for the models describing variation in MMR and FS, suggesting that early measurements of these variables affected subsequent measurements, and that the correlations declined exponentially with time (Table 1). The most parsimonious structure for models describing the variation in FL and SMR was the heterogeneous ar1 structure, suggesting that adjacent measurements were more highly correlated than measurements farther apart in time (similar to ar1), but that the variance (and hence, covariances) in FL and SMR differed among measurement periods (different from ar1; Table 1, 2). Finally, the spatial power structure was chosen for the models describing variation in K suggesting that adjacent measurements were more highly correlated than measurements farther apart in time (similar to ar1), but that the number of days between measurements was also important to consider (Table 1).

As expected, ration size had a significant positive effect on the mean growth rate (change in FL per unit time) of juvenile blue catfish ($F_{2,\,77.9} = 4.16$; $P = 0.019$; Table 3). Blue catfish that were fed one-third ration size grew slowest (mean=0.014 mm/d), and those that were fed *ad libitum* grew at significantly faster (mean = 0.080 mm/d) than those fed one-third ration size ($t_{79.8} = 2.84$; $P = 0.006$; Fig. 3). Fish fed two-thirds ration size grew at an intermediate rate (mean=0.056 mm/d), which was marginally lower from fish fed *ad libitum* ($t_{77.5} = 1.93$; $P = 0.057$), but not different from fish fed one-third ration size ($t_{76.5} = -0.95$; $P = 0.35$). Ration size did not have significant effects on K, SMR, MMR and FS, or on the rate of change in these variables during the experiment ($P >$

0.05; Table 3). All responses were positively affected by their baseline values (i.e., the values of the response before the start of the experiment). For example, fish with a higher baseline FL also had a greater FL at the end of the experiment, regardless of ration size ($F_{1, 32.1} = 2115.66$; $P < 0.001$; Table 3). Finally, weight of the fish during the trials had a significant positive effect on body condition ($F_{1, 43} = 43.12$; $P < 0.001$), marginal negative effect on MMR ($F_{1, 43.4} = 3.14$; $P = 0.083$) and significant negative effect on SMR ($F_{1, 38.4} = 8.83$; $P = 0.005$), but no effect on FS ($F_{1, 48.1} < 0.01$; $P > 0.999$; Table 3; Fig. 4).

Discussion

Blue catfish exhibited relatively low metabolic rates in comparison to most fish species (Killen et al. 2016, 2017). A reduction in ration to as low as one-third of *ad libitum* ration size had little negative impacts on the mean body condition and mean metabolic rates of blue catfish, although a small but significant negative effect on mean growth rates was observed. Together, these observations suggest that blue catfish may be able to survive and subsequently to maintain sustainable populations in low food environments.

Mean SMR and MMR of blue catfish were less than those observed in about two-thirds of fish species, likely owing to the benthic lifestyle and feeding strategy of this species. Benthic fishes tend to be sluggish and many employ slow foraging strategies. Because of the low energetic investment required to maintain homeostasis and to search for and consume food, many benthic fishes have evolved to have low metabolic demands as characterized by low SMR and MMR (Killen et al. 2016, 2017). Low metabolic rates allow blue catfish to tolerate environments or periods with low or patchy resources at the expense of slower growth rates (Killen et al. 2016). In Chesapeake Bay, pelagic fishes such as bluefish *Pomatomus saltatrix* and benthopelagic fishes such as spot *Leiostomus xanthurus* have higher metabolic rates compared with blue catfish (Freadman 1981; Marcek et al. 2019). Species with high metabolic demands may not survive or thrive in low food habitats in coastal rivers in the Eastern United States as well as blue catfish can, as predicted by the resource-ratio hypothesis (Tilman 1982). In addition, blue catfish are generalist omnivores that have a particularly high diet breadth compared with other estuarine fishes (Schmitt et al. 2019). The competitive advantage conferred by these characteristics suggests that blue catfish may outcompete native species and result in declines of outcompeted species via suppression or displacement. Indeed, declines in relative abundance of the congeneric native white catfish *Ameiurus catus* in Chesapeake Bay subestuaries during the past few decades may have resulted from exploitative competition with blue catfish (Fabrizio et al. in review; Schloesser et al. 2011).

Blue catfish from all ration treatments grew in length, consistent with life-history trade-off mechanisms: when food is limited, juvenile fish may allocate more energy to growth as measured by an increase in length (Garvey and Marschall 2003). Length increases are prioritized over gonadal development or storage (increases in weight) because growth that leads to a larger eventual body size allows for greater future reproductive output (Stearns 1992). If instead, a fish invests energy towards reproduction when it is young, its growth rate would decline, thereby permanently reducing the likelihood of a high lifetime reproductive output.

Mean body condition of blue catfish was generally stable over the four-month experimental period and indistinguishable among fish from the different ration treatment groups. This could be because the increase in food conversion efficiency at lower ration sizes (Abbas and Siddiqui 2009; Liu and Fu 2017) may result in relatively stable body weights and hence, stable body condition when ration size is reduced. Also, the loss of body mass at reduced ration sizes is often partially offset by an increase in the proportion of water, resulting in relatively low declines in overall wet weight of fish (Brett et al. 1969; Abbas and Siddiqui 2009; McCue 2010).

Reduced ration size did not have a significant effect on mean SMR, MMR and FS of blue catfish. Previous research shows that even after accounting for the energy costs associated with the burst of protein synthesis following feeding (i.e., specific dynamic action), well-fed fish tend to have higher SMR compared with starved fish (Van Leeuwen et al. 2011, 2012; Auer et al. 2016; Liu and Fu 2017). This is because low rates of feeding induce plastic decreases in the size of the digestive tract resulting in lower maintenance rates (i.e., lower SMR; Shoemaker et al. 2003; Abbas and Siddiqui 2009; Armstrong and Bond 2013). Fishes with low SMR, however, generally lack this plastic ability to regulate metabolism. For example, salamanderfish *Lepidogalaxias salamandroides* (mean SMR = 50 ml O_2 kg^{-1} h^{-1}) and traíra *Hoplias malabaricus* (mean SMR = 42 ml O_2 kg^{-1} h^{-1}), two species with low metabolic rates under *ad libitum* or normal feeding conditions, did not demonstrate declines in SMR despite 40 and 180 days of starvation respectively (Pusey 1986; Rios et al. 2002). For such species, further reduction in metabolic expenditures might compromise normal physiological function (Pusey 1986; Rios et al. 2002). This might be the reason we did not observe declines in SMR in blue catfish even at low ration size. Few researchers have studied the effects of food reduction on MMR, and those that have suggest that the nutritional state of a fish may not greatly influence its MMR (Van Leeuwen et al. 2011; Auer et al. 2016). Finally, change in FS depends on the response of SMR and MMR. Because we did not observe differences in SMR and MMR during the experimental period, it is not surprising that FS did not change with ration level. Overall, the metabolism of invasive blue catfish in established habitats does not seem to change in response to food availability.

Food restriction may have affected other aspects of blue catfish biology that were not studied here. During starvation, fishes can use endogenous reserves to maintain homeostasis, grow and even reproduce (Kooijman 2010; McBride et al. 2015), thereby changing their energy density and body composition. For example, total energy content of largemouth bass *Micropterus salmoides* declined under food restriction (Garvey et al. 1998), and starved sockeye salmon *Oncorhynchus nerka* had a lower proportion of fat than well-fed fish (Brett et al. 1969). Similar results were reported for channel catfish under food restriction (Shoemaker et al. 2003). Differential utilization of metabolic compounds (i.e., lipids versus proteins) during starvation can also affect the weight and body condition of a fish (McCue 2010). Because lipids are more energy-dense (9 calories/g) than proteins (4 calories/g), prioritized use of reserve lipids would result in lower weight loss. Studies on body composition and hormonal changes during starvation would be useful in uncovering such patterns.

Finally, our results do not account for the developmental and environmental histories of fish. Recent studies suggest that pre-exposure to starvation events often induces adaptive responses such as reduced rates of mass loss, reduced metabolic rates and lower costs of digestion during subsequent starvation events (reviewed in McCue et al. 2017). In tidal tributaries of the Chesapeake Bay, and more specifically in the James River from where the experimental fish were collected, the densities of the fish are high (Fabrizio et al. In review, 2018; Nepal and Fabrizio 2020), and thus fish may have experienced starvation prior to capture. Importantly, these observations suggest that metabolic rates and the response of blue catfish to reduced food availability have likely changed since the introduction of the species into the region. Further, fish on the leading edge of the range or in newly invaded rivers may have higher metabolic rates, which can confer a competitive advantage by increasing aggressiveness and growth rates (Myles-Gonzalez et al. 2015). It may also, in part, explain why blue catfish growth rates were higher during the early years of invasion (Nepal et al. in press; Nepal and Fabrizio 2020).

The observed lack of negative impacts of reduced rations could also result from ration sizes that were too large, regardless of treatment level. If the *ad libitum* ration size we used in this experiment (roughly 3.5% of fish biomass per day) was much higher than the actual *ad libitum* ration size, the lower ration sizes would have been sufficient to avoid negative impacts on condition and metabolic rates. Indeed, we noted uneaten food in several aquaria, though the frequency of such occurrences was lower in the reduced ration treatments. Studies support that the ration size used in our experiment reflected true feeding rates of juvenile blue catfish. Blue catfish from the same population as our study (tidal James River) have maximum daily consumption rates of ~9% body mass per day when starved for 72 hours (Schmitt 2018). Likewise, channel catfish, a blue catfish congener, consumes about 3.4% of fish biomass per day (Green and Rawles 2010). It therefore seems unlikely that our *ad libitum* or reduced ration sizes were too high. The energy density of the catfish pellets used in this study, however, may be greater than that of the food consumed by blue catfish in the wild. Energy density and proximate composition of the food can affect the energy absorption efficiency (Targett and Targett 1990) and energy allocation (Garvey et al. 1998) in fish.

Our findings highlight the concern about further range expansion and potential negative impacts of blue catfish in non-native environments such as the Chesapeake Bay and Atlantic slope rivers of the eastern US. Range expansion and impacts of blue catfish in Chesapeake Bay waters may not be hindered by the estuarine salinity gradient (Nepal and Fabrizio 2019) or global warming (Nepal and Fabrizio 2020). Here we report that blue catfish had low energetic demands and were able to maintain positive growth in low food environments. Blue catfish may survive food limitations for up to four months without reduction in maintenance metabolism (SMR) or in the relative ability to respond to challenges (FS). Together, these results suggest that blue catfish may have low somatic maintenance and high reserve capacity (*sensu* Kooijman 2010), and that severe and long periods (> 4 months) of food shortages are needed to hamper growth and reproduction. Such conditions are likely not commonly encountered by blue catfish in most estuarine habitats today, particularly given their omnivorous feeding behavior. Blue catfish, therefore, have the potential to disperse to and establish in low food habitats in estuarine systems. Importantly, blue catfish can also use these low food habitats as a “stepping-stone” to disperse to more suitable and energetically rich habitats. Metabolic characteristics of blue catfish, therefore, seem conducive to establishment and range expansion in novel habitats with low or patchy food availability.

Resource managers and conservationists should be concerned about the potential for blue catfish to continue their range expansion and establishment in mid-Atlantic estuaries and to negatively impact native resources of economic, cultural or conservation value. It appears that food availability will not be a limiting factor in their potential range expansion. This non-native species may alter estuarine ecosystem structure and function, and potentially result in the loss of ecosystem services. In particular, with rising temperatures, feeding rates of blue catfish are likely to increase (Brett et al. 1969), exacerbating negative impacts on native organisms. Resource managers should, therefore, strive to prevent further expansion of blue catfish into novel areas through vigilant monitoring and targeted removals.

Acknowledgments

We thank the staff of the Juvenile Fish Trawl Survey at the Virginia Institute of Marine Science for help with the collection of blue catfish for this experiment, particularly Troy Tuckey and Wendy Lowery. We also thank Wolfgang Vogelbein, Jack Buchanan, Ben Marcek and Jingwei Song for guidance and assistance with laboratory techniques and animal husbandry. The experimental design benefitted from discussions with Jaap van der Meer. Funding for this study was provided by Virginia Sea Grant (VN), the Office of Academic Studies at the Virginia Institute of Marine Science (VN), Virginia Marine Resources Commission (MCF), and Fish and Wildlife Service (MCF).

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Tables

Table 1: Akaike's Information Criterion adjusted for small sample size (AICc) for different covariance structures applied to repeated measures mixed-effects models for various response variables. For each response variable, the most parsimonious model was identified as the model with lowest AICc value, highlighted here in bold. FL = Fork length; K = Fulton's body condition; SMR = Standard Metabolic Rate; MMR = Maximum Metabolic Rate; FS = Factorial Scope

Response	Unstructured	Autoregressive (1)	Heterogeneous Autoregressive (1)	Toeplitz	Heterogeneous Toeplitz	Spatial Power
FL	452.3	488.5	**450.3**	486.3	454.2	487.3
K	597.9	597.2	597.6	598.8	598	**593.9**
MMR	1120.8	**1104.3**	1110.4	1107.6	1114	1106.9
SMR	776.9	768.8	**766.7**	772.8	770.8	767.4
FS	266.4	**250.9**	257	253.1	259.5	252.5

Table 2: Random effects parameter estimates for repeated measures mixed-effects models for fork length (FL), Fulton's body condition (K), maximum metabolic rate (MMR), standard metabolic rate (SMR) and factorial scope (FS). σ^2 = random unexplained variance; ρ = correlation. Subscripts for variances correspond to specific measurement period; see table 1 and text for model details.

Parameter	Estimate for FL	Estimate for *K*	Estimate for MMR	Estimate for SMR	Estimate for FS
ρ	0.80	0.98	0.29	0.22	0.11
σ^2		0.001	1324.17		0.32
$\sigma^2_{\text{week 4}}$	1.83			78.57	
$\sigma^2_{\text{week 8}}$	3.10			32.00	
$\sigma^2_{\text{week 12}}$	5.30			29.37	
$\sigma^2_{\text{week 16}}$	14.50			55.87	

Table 3: Results of the hypotheses tests for the significance of each of the fixed effects on various response variables. For each response, the effects that are significant at α = 0.05 are highlighted in bold. However, the main effect is not directly interpretable if it has a significant interaction with another effect; such main effects are not presented in bold. FL = Fork length; K = Fulton's body condition; MMR = Maximum Metabolic Rate; SMR = Standard Metabolic Rate; FS = Factorial Scope

Response	Effect	Num DF	Den DF	*F*	*P*
FL	Sex	1	32.4	0.01	0.919
	Ration	2	33.9	0.84	0.439
	Days	1	76.8	136.28	<0.001
	Baseline FL	1	32.1	2115.66	**<0.001**
	Days×Ration	2	77.9	4.16	**0.019**
K	Sex	1	34.1	3.28	0.079
	Ration	2	86.9	1.89	0.158
	Days	1	112	0.15	0.700
	Baseline K	1	32.5	98.70	**<0.001**
	Days×Ration	2	116	0.71	0.495
	Weight	1	43	43.12	**<0.001**
MMR	Sex	1	38.7	2.18	0.148
	Ration	2	89.9	2.48	0.089
	Days	1	103	5.26	**0.024**
	Baseline MMR	1	38.5	9.12	**0.005**
	Days×Ration	2	106	0.87	0.422
	Weight	1	43.4	3.14	0.083
SMR	Sex	1	35.1	0.01	0.933
	Ration	2	55.5	0.06	0.942
	Days	1	69	3.06	0.085
	Baseline SMR	1	35.1	8.52	**0.006**
	Days×Ration	2	68.1	0.16	0.854
	Weight	1	38.4	8.83	**0.005**
FS	Sex	1	44.3	2.60	0.114
	Ration	2	89.9	2.74	0.070
	Days	1	98.6	0.28	0.595
	Baseline FS	1	45.2	12.78	**0.001**
	Days×Ration	2	101	1.18	0.310
	Weight	1	48.1	<0.01	>0.999

Figures

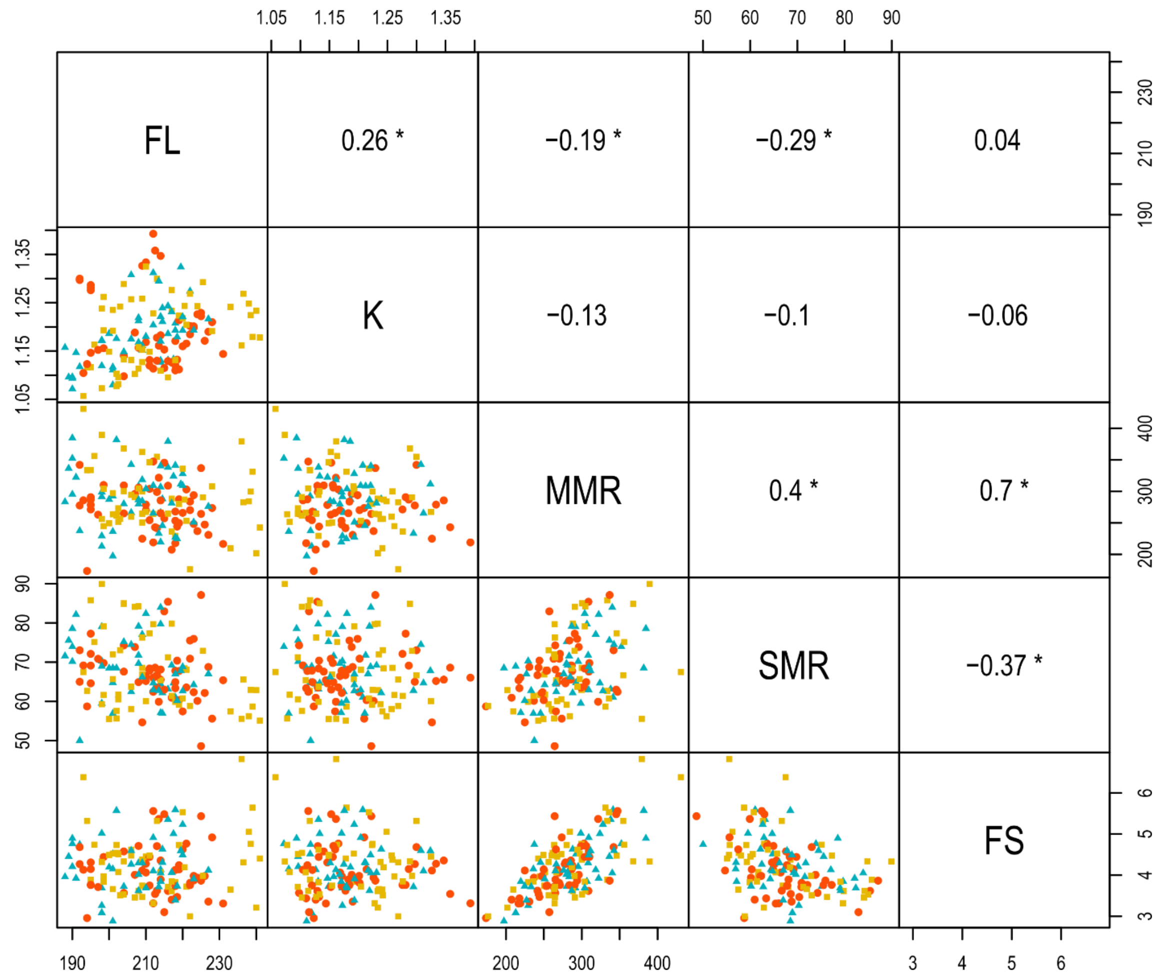

Figure 1: Scatterplot matrix of fork length (FL), Fulton’s body condition (K), standard metabolic rate (SMR), maximum metabolic rate (MMR) and factorial scope (FS) of juvenile blue catfish under *ad libitum* (▲), two-thirds of *ad libitum* (●) and one-third of *ad libitum* (■) ration size. Upper panels show the pairwise Pearson’s correlation coefficients, which are significant at α = 0.05 if accompanied by an asterisk (*). See text for details on units of each variable. Figure available in color online.

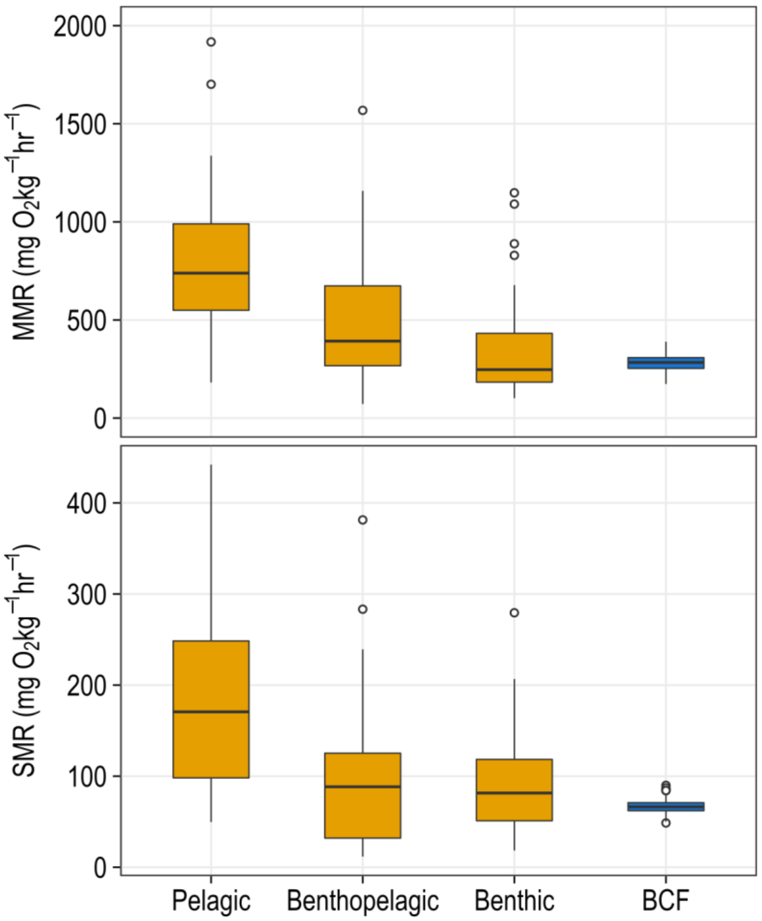

Figure 2: Comparison of the maximum metabolic rate (MMR) and standard metabolic rate (SMR) of juvenile blue catfish (BCF) with other pelagic, benthopelagic and benthic fishes. All data are standardized to 1 kg and 20°C. Data for MMR (n = 121) and SMR (n = 112) were obtained from supplementary documents in Killen et al. (2017) and Killen et al. (2016) respectively.

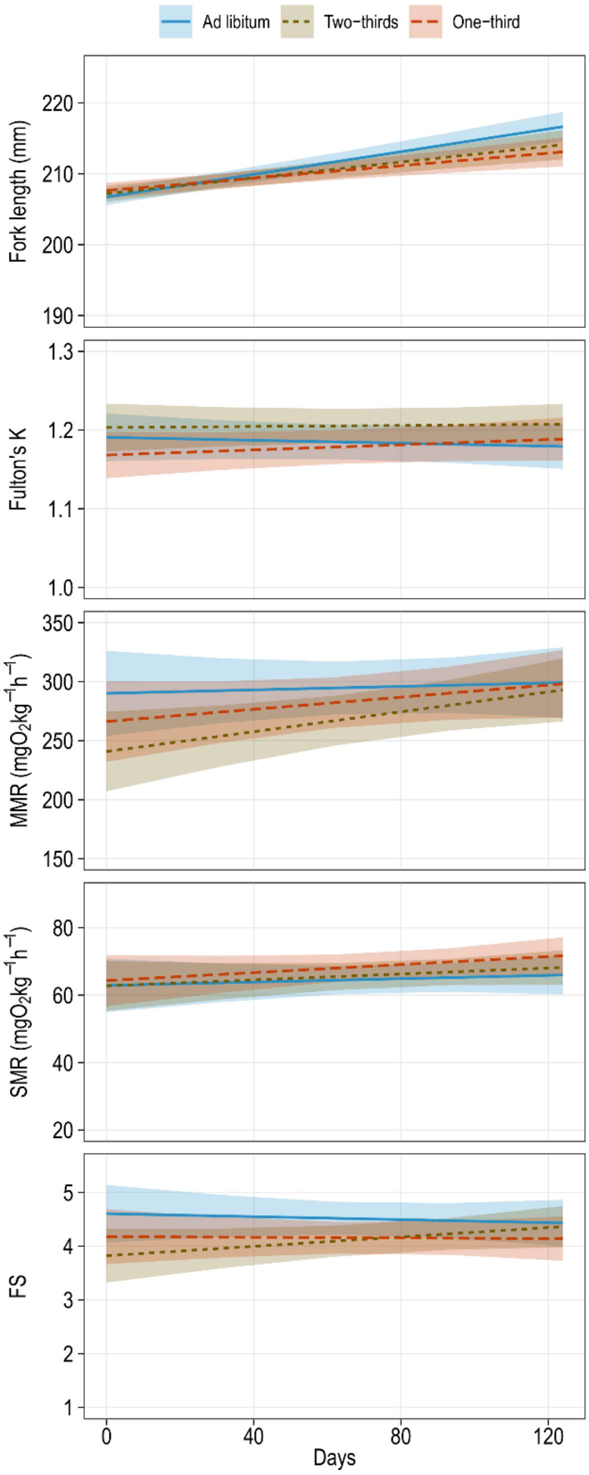

Figure 3: Predicted mean fork length (FL), Fulton’s body condition (K), maximum metabolic rate (MMR), standard metabolic rate (SMR) and factorial scope (FS) of juvenile blue catfish fed *ad libitum*, two-thirds of *ad libitum* or one-third of *ad libitum* ration size for 124 days. Polygons around each line denote the corresponding 95% confidence bands. Y-axis scales differ among panels. Figure available in color online.

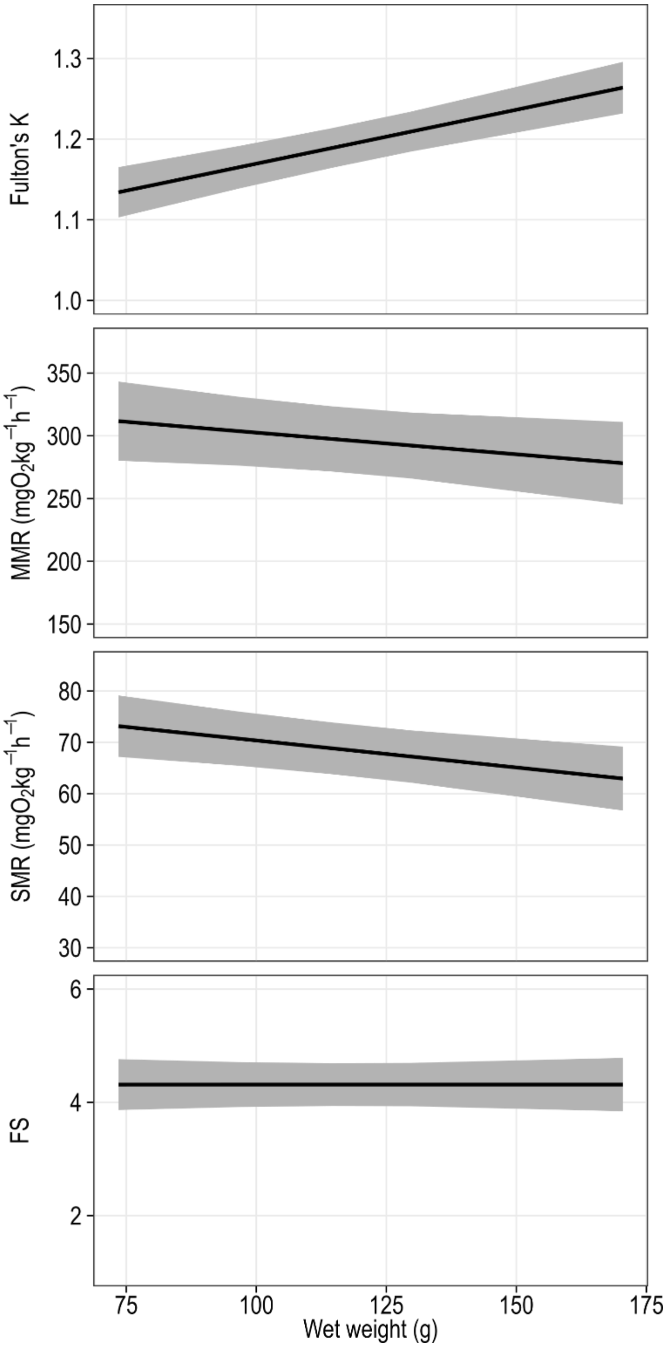

Figure 4: Effect of fish wet weight on predicted mean Fulton's body condition (K), maximum metabolic rate (MMR), standard metabolic rate (SMR) and factorial scope (FS) of juvenile blue catfish. Polygons around each line denote the corresponding 95% confidence bands. Y-axis scales differ among panels.

CHAPTER 4: High Salinity Tolerance of Invasive Blue Catfish Suggests Potential for Further Range Expansion in the Chesapeake Bay Region

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Abstract

In estuaries, salinity is believed to limit the colonization of brackish water habitats by freshwater species. Blue catfish *Ictalurus furcatus*, recognized as a freshwater species, is an invasive species in tidal rivers of the Chesapeake Bay. Salinity tolerance of this species, though likely to determine its potential range expansion and dispersal in estuarine habitats, is not well-known. To address this issue, we subjected blue catfish to a short-term salinity tolerance experiment and found that this species tolerates salinities higher than most freshwater fishes and that larger blue catfish tolerate elevated salinities for longer periods compared with smaller individuals. Our results are supported by spatially extensive, long-term fisheries surveys in the Chesapeake Bay region, which revealed a gradual (1975-2017) down-estuary range expansion of blue catfish from tidal freshwater areas to habitats exceeding 10 psu [practical salinity units] and that large blue catfish (> 200 mm fork length) occur in salinities greater than 10 psu in Chesapeake Bay tributaries. Habitat suitability predictions based on our laboratory results indicate that blue catfish can use brackish habitats to colonize new river systems, particularly during wet months when salinity decreases throughout the tidal rivers of the Chesapeake Bay.

Introduction

Salinity tolerance is an important determinant of the survival, growth, reproduction and, ultimately, spatial distribution of animals in estuaries [1,2]. Tolerance of salt concentrations greater than those of its tissues depends on an organism's ability to maintain its internal ionic concentration and to compensate for the loss of water from tissues [3,4]. However, freshwater fishes vary in their salinity tolerances; some are stenohaline and do not survive in salinities > 5 psu [practical salinity units]), whereas other species are euryhaline and can survive in salinities in excess of full-strength seawater (34 psu; [5]). Understanding the salinity tolerance of freshwater fishes introduced in estuarine or coastal systems is crucial to determine their potential expansion and dispersal into novel estuarine habitats. For example, Prussian carp (*Carassius gibelio*), believed to be stenohaline, were introduced into small lakes in Estonia but subsequently spread along the entire Estonian Baltic coastline [6].

Blue catfish (*Ictalurus furcatus*), a freshwater species native to the Mississippi, Missouri and Ohio River basins, have been introduced throughout North America due to their appeal to recreational fishers [7]. This includes the introduction to tidal freshwater regions of the Rappahannock, York and James rivers (subestuaries of the Chesapeake Bay) during the 1970s and 1980s, with a goal of enhancing recreational fisheries [8]. Blue catfish abundance subsequently increased and there are now an estimated 544 fish/ha, with an estimated population size of 1.6 million fish in a 12-km stretch of the James River [9]. Blue catfish have also expanded into tidal oligohaline (salinity < 5 psu) and mesohaline (5-18 psu) habitats throughout Chesapeake Bay [8,10; Fig 1] where they feed on vegetation, molluscs, and fishes [11]. They also compete with native species, such as white catfish (*Ameiurus catus*), whose population densities have declined concurrent with the increase in abundance of blue catfish [8].

The expansion and ultimate geographic range of blue catfish in the Chesapeake Bay region may be limited by their salinity tolerance. Salinities below 9 psu are not likely to affect the homeostasis of freshwater fishes like blue catfish because osmolality of the extracellular body fluids in freshwater teleost fishes is ~300 mOsm kg^{-1}, which is isosmotic to this salinity [12]. If blue catfish are, however, able to tolerate salinities > 9 psu, then they have the potential to occupy and exploit a large fraction of habitats in Chesapeake Bay subestuaries, and thus, to negatively affect the ecological integrity of this estuary. A broad salinity tolerance presents an evolutionary advantage favoring spatial expansion in a climate of rapidly fluctuating salinity [12], as predicted for the Chesapeake Bay region in the coming century [13]. Current projections of the potential distribution of blue catfish in this region use a 14 psu tolerance threshold [10], which is the threshold reported for hatchery-reared blue catfish in their native range [14]. Yet, wild blue catfish have been observed in nearshore coastal waters of the southeastern U.S. (P. Fuller, USGS, *pers. comm.*) and in salinities up to 21.8 psu in the Chesapeake Bay [9]. Salinity in the mainstem of Chesapeake Bay varies seasonally and spatially from 0 to 28 psu due to > 5-fold differences in river discharge between dry and wet months (Fig 2; [15,16]). This might allow continued range expansion of blue catfish throughout the Maryland and Virginia portions of the Chesapeake Bay. In particular, the Chesapeake and Delaware Canal (“the Canal” hereafter) connects the upper Chesapeake Bay with Delaware Bay. If blue catfish are able to exploit the salinities in the Canal, they may also colonize Delaware Bay, potentially leading to negative impacts on estuarine resources and function in Delaware Bay.

Fisheries surveys and field measurements can indicate the salinity tolerance of blue catfish in the wild [17], though they cannot provide a causal link [18]. Observation of a species at a particular salinity implies that the species can survive at that salinity, at least for a short time, and information on the size, sex and other individual characteristics of the fish may be helpful in understanding differential tolerances of the species. However, the estimated salinity tolerance based on survey data may be biased because of a spatial and/or temporal mismatch of survey effort and fish distribution [17]. Particularly, for a range-expanding non-native species, the maximum field salinity where a fish is captured may be lower than the potential maximum, which may not have been realized. We contend, therefore, that laboratory experiments are needed to obtain a comprehensive and accurate characterization of salinity tolerance of blue catfish.

A robust measure of salinity tolerance using standardized laboratory methods has yet to be reported for blue catfish. Salinity tolerance may be assessed by exposing fish to increased salinities and recording the median lethal concentration (LC_{50}, the concentration at which 50% of the individuals die within the specified period of time). It is, however, useful to understand how long a fish can survive at a given salinity, as quantified by time-to-death or survival models. These models, in turn, allow testing of the hypothesis that blue catfish can survive in mesohaline habitats long enough to allow movement between lower salinity environments. On the other hand, understanding how long a blue catfish can survive at a given salinity allows inferences as to whether this fish can use estuarine corridors as “saline bridges” to colonize rivers other than the ones into which they were originally stocked [19].

We assessed the salinity tolerance of blue catfish in a 72-hour laboratory experiment and compared the results with monthly survey data (collected over a 40-year period) from the Rappahannock, York and James rivers. We hypothesized that blue catfish will exhibit a relatively high salinity tolerance, allowing the species to expand in range throughout the Chesapeake Bay region. Our aim was to predict the suitability of different Chesapeake Bay habitats to illustrate potential colonization routes of blue catfish.

Methods

All animal capture, handling, and experimental procedures were approved by the College of William & Mary Institutional Animal Care and Use Committee (protocols: IACUC-2017-05-22-12111-tdtuck and IACUC-2016-08-19-11376-mcfabr) and followed all applicable U.S. laws and regulations.

Distribution of blue catfish in Chesapeake Bay subestuaries

To monitor the distribution of invasive blue catfish throughout its invasion history in the Rappahannock, York and James rivers, we used catch records covering 1975-2017 from the Virginia Institute of Marine Science (VIMS) juvenile fish trawl survey (conducted using a 9.14-m otter trawl towed along the bottom for five minutes). Temperature and salinity data (measured 1 m from the sea floor) were also collected. The juvenile fish trawl survey uses a stratified random sampling design between river kilometer (rkm) 64.4 and the mouth (rkm 0) of the Rappahannock, York and James rivers [16]. Survey stratification is based on depth and longitudinal region to ensure broad spatial coverage. As such, each subestuary is partitioned along its axis into four regions of ~10 longitudinal minutes and into four depth strata in each region (1.2–3.7 m, 3.7–9.1 m, 9.1–12.8 m, and >12.8 m). These areas are characterized by a gradient in salinity, which varies at both tidal and seasonal time scales [15,16]. In addition, salinity in the Rappahannock River is generally lower than that in the James and York rivers [16]. At each sampling location, all blue catfish were counted and a representative sample was measured (to the nearest mm). The gear used for the trawl survey is effective at capturing blue catfish ranging from 70 mm to 300 mm fork length (FL), although fish as large as 1000 mm have been captured [16].

To characterize changes in size structure of blue catfish along the salinity gradient, we used quantile regression [20], which better reflects salinity limitations on blue catfish than does mean regression [21]. The quantile regression approach also allowed for unequal variance in size of fish; such variance may arise from complex interactions of physiological limits and the invasion history of blue catfish. To characterize the effects of salinity on the minimum size of blue catfish captured in these subestuaries, we used piecewise quantile regression splines with conditional quantiles, τ, at 0.1 and 0.01. The quantile regression splines at conditional quantile τ = 0.1 and τ = 0.01 mean that about 10% and 1%, respectively, of the captured blue catfish were less than a given size at a given salinity. In addition, we fit regression splines with the 0.50 conditional quantile ($\tau = 0.5$) to assess consistency in observed patterns for fish of median size as well. The salinities at which major changes in size structure of blue catfish occur can be identified using break-points (knots), which are values of the predictor variable (in this case, salinity) at which the adjacent polynomial splines are joined [20]. Two break-points were chosen for each subestuary based on the analysis of residuals. Quantile regression splines were fit in the statistical software R 3.5.1 using the package 'quantreg' version 5.38.

Salinity tolerance experiments

Blue catfish were captured from the tidal portion of the James River (coordinates 37°14'N 76°52'W; salinity < 2 psu), and individuals between 165 mm and 265 mm FL were transported to the VIMS Seawater Research Laboratory. We selected fish between 165 mm and 265 mm FL for this study because these individuals are abundant in Chesapeake Bay subestuaries, and are readily captured by the trawl survey. At this size range, there is little sexual dimorphism in size-at-age of blue catfish such that both male and female blue catfish are between 1 and 3 years old (V. Nepal, unpublished data). Further, young of the year blue catfish (< 165 mm FL) are not likely to contribute to dispersal and range expansion of this population [9]. Fish were held for two weeks at 22°C at 2 psu salinity prior to use in an experiment. We used 2 psu for acclimation because preliminary experiments showed that blue catfish held in freshwater (0 psu) exhibited low survival rates and disease.

Based on a pre-trial study (see below), we chose 0 (control), 10, 13, 16 and 19 psu as the salinity treatment levels for the salinity trials, with 3 experimental aquaria (replicates) for each salinity level and 10 fish per replicate (total 150 fish). We used a gradual acclimation scheme (as opposed to a direct transfer of blue catfish to the target salinity) because the gradual acclimation resembles what blue catfish experience in the wild and has been reported to yield better estimates of field salinity distribution [17]. Ten random blue catfish were placed in each of the eighteen 340-liter circular experimental aquaria containing water at 0.1 psu and fitted with an air bubbler. All experimental aquaria were partially covered to reduce distress on the fish; the experiment was conducted using a natural dark/light cycle. Salinity was gradually increased by adding brine solution (55 psu) created by mixing Instant Ocean® (Spectrum Brands, Blacksburg, Virginia) with filtered York River water (~18 psu) at rates such that the target salinity was reached in seven hours. The rate of increase in salinity we employed reflects that occurring due to tidal cycles in the section of the James River where the experimental fish were collected. All experimental aquaria were supplied water from the same brine solution mixed with de-chlorinated municipal water. Once the target salinity was reached, we monitored fish mortality by assessing reflex impairment every hour for the first four hours, then every four hours thereafter. Specifically, if a fish was unable to maintain equilibrium when handled, and exhibited reduced swimming ability or mouth gaping, the fish was considered moribund [22]. Moribund fish were immediately removed from the trial and euthanized by immersion in an ice slurry as recommended by Blessing et al. [23]. Five blue catfish died before meeting the above criteria for euthanasia (i.e. they had died during the periods between the four-hour monitoring checks). An additional fish that had jumped out of the tank at an unknown time was discovered dead later on. This individual was not used in the statistical analysis. The trials ran for 72 hours after the target salinities were reached. All fish that were alive at the end of the trials (n = 111) were euthanized.

To identify informative salinity levels for the salinity tolerance experiment, we performed a 72-hr pre-trial study, in which 10 fish were exposed to 7, 17 and 27 psu (total of 3 aquaria and 30 fish) at 22°C using the protocol described above. Fish were randomly assigned to treatment aquaria, though care was taken to ensure that the length ranges of fish were similar in all experimental aquaria. All individuals at 7 psu survived until the end of the experiment (72 hours), and all individuals at 27 psu died within 4 hours of reaching the target salinity (Fig 3). Mortality in the 17 psu treatment was first observed 40 hours after the target salinity was reached, and the last individual died was found dead 72 hours after the target salinity was reached (Fig 3). Hence, we chose 0, 10, 13, 16 and 19 psu as the salinity treatments for the main experiment.

To reduce the production of nitrogenous wastes, fish were not fed during the salinity trials. Water temperature, dissolved oxygen (DO), pH and ammonia concentration were measured daily, and 40% of the water was changed in each aquarium daily to maintain water quality. Water temperature ranged between 21.3 to 23.1°C (grand mean for initial and main trials = 21.9, S.E. = 0.1); DO ranged between 7.0 and 11.2 mgL^{-1} (grand mean = 9.1, S.E. = 0.2). Similarly, pH ranged between 7.6 and 8.2 mgL^{-1} (grand mean = 8.0, S.E. < 0.1), and ammonia ranged between 0.15 and 0.5 mgL^{-1} (grand mean = 0.35, S.E. < 0.1). Salinity was monitored to the nearest 0.1 psu using a handheld meter every hour during the 7-hour salinity increase period and twice a day thereafter. At the end of the experiment or upon death, fish were measured (mm FL) and dissected to obtain eviscerated weight (g). We subsequently calculated Fulton's K as an index of body condition:

$$K = W \times L^{-3} \times 10^{5} \qquad (1)$$

where W is eviscerated weight and L is the length of the fish. Sex of each blue catfish was assessed by macroscopic examination of the gonads.

To compare whether mean size and body condition of blue catfish were significantly different among the different salinity treatments, we combined observations from the pre-trial and the salinity experiment and fit linear mixed-effects models that modeled FL and body condition as a function of salinity and aquarium. The model took the form

$$y_{ij} = \mu + \beta Salinity + Aquarium_j + \varepsilon_{ij} \tag{2}$$

where y_{ij} is the response variable (FL or body condition) for fish i in aquarium j, μ is the overall mean FL or body condition, β is the rate of change in y with respect to salinity, $Aquarium_j$ refers to the random effect of aquarium, accounting for potential similarities in observations among multiple blue catfish from a given aquarium (i.e., accounting for pseudoreplication), and ε_{ij} is the unexplained random variance in y. For each response variable, we fit a null model without salinity, and compared the likelihoods of the full and null models using Bayesian Information Criterion (BIC, [24]) calculated for each model as $BIC = -2 * \ln(likelihood) + p * ln(n)$, where p is the number of parameters in the fitted model and n is the sample size. In this approach, models with lower BIC values or with higher BIC weights represent the more parsimonious fit to the data [24].

Next, we modeled the effects of salinity, FL, sex, and condition on two responses: time-to-death and fate of the fish (i.e., whether it survived to the end of the experiment or not). We used a Cox proportional hazards model [25] to analyze the time-to-death and identify factors associated with changes in the risk of death. Potential predictors in the model included salinity, FL, body condition and sex.

$$h(t,X) = h_0(t)e^{\beta_1 Salinity + \beta_2 FL + \beta_3 K} \quad (3)$$

where $h(t,X)$ is the hazard rate at time t with covariates X (salinity, FL, condition [K] and sex of the fish), $h_0(t)$ is the baseline hazard function describing the change in risk of death per unit time at the baseline level of covariates (i.e., set at zero), and the βs correspond to the log-hazard ratio for the effect of each covariate on survival, adjusting for the other covariates in the model. Preliminary analysis indicated that stratification by sex was necessary to address the difference in baseline hazard rates between the male and female blue catfish (i.e., to address the violation of the proportional hazards assumption of the Cox model by the variable sex). Therefore, we obtained two baseline hazard functions—one for each sex [$h_{0female}(t) and\ h_{0male}(t)$]. For the Cox model, we estimated robust standard errors for each parameter following Lin and Wei [26]; this approach accounts for potential similarities among individuals within each aquarium.

The fate of each fish (dead/alive) was modeled using a logistic regression model, with salinity, FL, body condition and sex as potential predictors.

$$ln\left(\frac{p_i}{1-p_i}\right) = \mu + \beta_1 Salinity + \beta_2 FL + \beta_3 K + \beta_4 Sex \quad (4)$$

where p_i is the probability of death for fish i, $ln\left(\frac{p_i}{1-p_i}\right)$ is the log-odds of death, μ is the overall mean log-odds of death, and βs are partial regression coefficients. Collinearity among predictors was checked graphically, and found to be absent (i.e., we found no evidence for linear relationships among pairs of predictors). Salinity was highly predictive such that all individuals exposed to salinities ≥ 17 psu died and all individuals exposed to salinities ≤ 13 psu survived. To avoid biases in parameter estimates and their standard errors caused by such quasi-complete separation, we used Firth's penalized-likelihood logistic regression [27]. Currently, Firth's logistic regression approach is limited to fixed effects, and thus, we included aquarium as a fixed effect in the model. As before, we calculated BIC and BIC weights for competing models and compared these metrics to inform model selection. Models within 2 BIC units of the best model were averaged using model weights [24], and the averaged model was used to estimate the 72-hour LC_{50} (salinity at which 50% of the individuals die within 72 hours). To permit comparison with previous studies, we also calculated LC_{50} using the modified Spearman-Karber method [28]. These calculations used the log of the doses, and as recommended by Hamilton et al. [28], 10% of the extreme observations were trimmed from each end of the response. We used R packages 'lme4' version 1.1-21 to fit linear mixed effects models, 'survival' version 2.43-3 to fit time-to-death models, 'brglm' version 0.6.2 to fit Firth's logistic regression, and 'drc' version 3.0-1 for trimmed Spearman-Karber LC_{50}.

Spatially-explicit habitat suitability in the Chesapeake Bay

Model-averaged parameters from the logistic regression analysis were used to estimate the 72-hour survival probability of a blue catfish of size 224 mm FL for salinities between 0 and 32 psu. We selected 224 mm FL because this was the median length of blue catfish used in the salinity trials. Salinity conditions were based on the model by Du and Shen [15], which provides monthly mean salinity profiles (from surface to bottom) throughout tidal waters of the Chesapeake Bay and its tributaries. Visual inspection of the maps produced by the Du and Shen model implied that salinity in some subestuaries was not well characterized by the model (e.g., the model predicted unexpectedly high salinity in the central portion of a subestuary). These cases were replaced with values obtained by linear interpolation between adjacent values. For simplicity, we first used depth-averaged mean salinity at each location. However, vertical salinity profiles in Chesapeake Bay are tidally and seasonally stratified with heavier, saltier waters near the bottom, and lighter, fresher water near the surface. Therefore, we also used surface salinity to predict habitat suitability at each location throughout the Chesapeake Bay. Surface salinity was defined as the mean of the predicted salinities in the top 1 m of the water column in each location; when salinity predictions were not available for the top 1 m, we used the predicted salinity of the topmost layer as the surface layer (0.002% of the cases; in these cases, the maximum depth of the topmost layer was 1.8 m). The predicted survival probability was mapped to mean or surface salinity conditions of Chesapeake Bay to obtain spatially-explicit, but static, representations of habitat suitability for blue catfish throughout the Chesapeake Bay and its subestuaries during spring (April) and fall (October) in years with average (2012), above average (2011) and below average (2009) freshwater discharge rates ("average", "wet" and "dry" years, respectively). For comparison, the annual mean freshwater discharge rates into the Chesapeake Bay during 2009, 2011 and 2012 are estimated to be 1795, 3200 and 2265 m^3s^{-1} respectively; the mean freshwater discharge rates during dry fall (October 2009) and wet spring (April 2011) were respectively 1418 and 7419 $m^{-3}s^{-1}$; a 5.2-fold difference in discharge rates (data from https://md.water.usgs.gov/waterdata/chesinflow/wy/).

Results

Distribution of blue catfish in Chesapeake Bay subestuaries

A total of 178,611 blue catfish was collected from the Rappahannock (*n* = 76,322), York (*n* = 10,536) and James (*n* = 91,753) river subestuaries between 1975 and 2017. Overall, 31.7% of blue catfish were collected from waters with salinity < 1 psu, and 98.6% were collected from waters with salinity < 10 psu, although subestuary-specific differences occurred (Fig 4). The highest salinity where blue catfish were collected was 21.8 psu in the James River. Quantile regression splines for each subestuary indicated an increase in size of fish with increasing salinity, such that individuals < 200 mm FL were primarily limited to salinities < 10 psu (Fig 4).

Salinity tolerance

Mean body condition of blue catfish decreased systematically with increasing salinity (BIC for full model = -407.2; BIC for null model = -405.8); more specifically, the predicted mean Fulton's K decreased from 1.06 to 0.98 (fraction change = 7.3%) when salinity increased from 0 psu (freshwater) to 10 psu. In contrast, the mean size of blue catfish did not differ among the salinity levels used in the experiment (BIC for full model = 1645; BIC for null model = 1638.9), suggesting that comparisons among salinity treatments were not biased by size differences.

Salinity had a negative effect on the time-to-death of blue catfish; a 1 psu increase in salinity increased the hazard (risk of death) by a factor of 9 (Table 1; Fig 5). However, the negative effects of salinity were lower for fish that were larger or had better body condition; larger fish with better body condition had a lower risk of dying (Table 1; Fig 5). Males and females had different baseline hazard rates such that the risk of death varied differently over time for male and female blue catfish.

Table 1. Parameter estimates for the stratified Cox proportional hazards model fit to the time-to death data from the toxicity test on blue catfish. CL = 95% confidence limit

Variables	Estimate	Hazard Rate	Lower CL	Upper CL
Salinity	2.20	9.03	6.07	13.43
Fork length	-0.04	0.96	0.95	0.97
Condition	-5.93	0.002	<0.001	0.11

None of the experimental blue catfish died at salinities ≤ 13 psu, and all blue catfish died at salinities ≥ 17 psu. At 16 psu, 11 of 30 experimental blue catfish (36.7%) died before the end of the experiment. The effects of salinity, fish length, condition and sex on whether the fish was alive at the end of 72-hours were analyzed with Firth's logistic regression. The two most parsimonious models, accounting for total BIC weight of 0.89, were averaged to provide model-averaged parameter estimates for the effect of salinity and fish length on fate of the fish (Table 2). The odds of survival decreased by 88% with a 1 psu increase in salinity (odds ratio: 0.12; 95% confidence interval [CI]: 0.03-0.53) but increased by 5% with a 1 mm increase in fork length (odds ratio: 1.05; CI: 1.00-1.09; Table 3). The 72-hour LC_{50} from the averaged model was 15.7 psu (CI: 14.7–16.1; Fig 6). In comparison, the corresponding LC_{50} based on the Spearman-Karber method was 15.2 psu (CI: 14.8–15.7).

Table 2: Bayesian Information Criterion (BIC), ΔBIC, number of parameters and BIC weight for Firth logistic regression models fitted to describe the 72-hour mortality of blue catfish exposed to various salinities. The two most parsimonious models, highlighted in bold, were averaged to determine the final model. FL = Fork length

Variables included	BIC	No. pars.	ΔBIC	Weight
Salinity, FL	**50.8**	**3**	**0**	**0.54**
Salinity	**51.7**	**2**	**0.9**	**0.35**
Salinity, FL, Sex	54.8	4	4	0.07
Salinity, FL, Condition	56.2	4	5.4	0.04
Salinity, FL, Condition, Sex	60	5	9.2	0.01
Salinity, FL, Condition, Sex, Aquarium	147.1	21	96.3	0
Salinity, FL, Sex, Aquarium	144.2	20	93.4	0
Salinity, FL, Condition, Aquarium	144.1	20	93.3	0

Table 3: Parameter estimates for the most parsimonious Firth logistic regression model to describe the 72-hour mortality of blue catfish exposed to various salinities. CL = 95% confidence limit

Parameters	Estimate	Odds Ratio	Lower CL	Upper CL
Intercept	25.02	7.36×10^{10}	1.53	3.5×10^{21}
Salinity	-2.14	0.12	0.03	0.53
Fork length	0.04	1.05	1.00	1.09

Habitat suitability mapping

Static representations of Chesapeake Bay during typical average, dry and wet months show considerable spatial variation in average predicted salinity (Fig 2). In addition to the north-south gradient in the mainstem of Chesapeake Bay and the headwater-mouth gradient in the tributaries, there are also seasonal and inter-annual differences in salinity gradients (Fig 2). Vertically-averaged salinity in spring was lower than that in fall during dry and average precipitation years; in wet years, there was a considerable reduction in salinity during both spring and fall (Fig 2). Vertical, seasonal and annual variability in salinity resulted in marked variation in habitat suitability throughout the Chesapeake Bay. As expected, the proportion of suitable habitat was highest towards the headwater of the tributaries and at the head of the Chesapeake Bay (Figs 7 and 8). In addition, larger areas of Chesapeake Bay became habitable during wet months compared with dry months (Figs 7 and 8). For example, under the vertically-averaged salinity scenario in fall, the predicted probability of survival for a 224 mm FL blue catfish during average conditions exceeded 0.8 in only about 26.7% of Chesapeake Bay habitats, but the proportion of habitable area increased to 65% during wet conditions (Fig 7). Corresponding predicted proportions of habitable areas increased further to 30.2% and 75.5% respectively if only the surface layers are considered (Fig 8). Of note here is that the probability of survival was near 1.0 in the Elk River regardless of the discharge scenario, suggesting that salinity conditions in the Elk River could facilitate blue catfish dispersal into Delaware Bay via the Chesapeake and Delaware Canal (Figs 2, 7 and 8).

Discussion

Blue catfish survived short-term (72-hr) exposure to mesohaline waters (< 15 psu), indicating that this species has the potential to survive in most downstream areas of major rivers entering Chesapeake Bay, and to use the mainstem of the upper Bay for movement into other subestuaries in Maryland and into Delaware Bay. Large (> 200 mm FL) individuals in particular are more tolerant of salinities > 10 psu than smaller, immature fish, and thus have a greater ability to use mesohaline and polyhaline habitats and invade additional areas throughout the Chesapeake Bay. Large individuals during wet months may exhibit jump dispersal, which is characterized by occasional long-distance movements; such movements are likely to increase the rate of spatial expansion [29] and the probability of regional persistence [30] of non-native blue catfish in the Chesapeake Bay region.

The salinity tolerance of blue catfish (LC_{50} = 15.7 psu) was higher than that of many freshwater fishes such as the percichthyid *Nannatherina balstoni* (LC_{50} = 8.2 psu; 72 hrs; [31]), and eastern mosquitofish *Gambusia holbrooki* (11.5 psu; 96 hrs; [32]), including some species of catfishes such as South American sailfin catfish *Pterygoplichthys* spp. (10.6 psu; 96 hrs; [33]) and African sharptooth catfish *Clarias lazera* (10.5 psu; 72 hrs; calculated based on [34]). The observed LC_{50} is, however, comparable to that of other members of the family Ictaluridae: flathead catfish *Pylodictis olivaris* (14.5-15.8 psu [35]); black bullhead *Ameiurus melas* (13.8 psu [36]); white catfish (14.0 psu [37]); channel catfish *Ictalurus punctatus* (12.0-15.5 psu [14,36]). Kendall and Schwartz [37] hypothesized that the relatively less permeable integument of catfishes might allow them to tolerate greater osmotic stress resulting in the somewhat high salinity tolerance of ictalurid catfishes. There is, however, little empirical support for this hypothesis because a majority of the water or ion exchange in fishes occurs across the gills but not the integument [4].

Although our results are consistent with previous studies with other ictalurid fishes, they may have been affected by our experimental procedures. First, the gradual increase in salinity we employed is unlike protocols that include abrupt changes from freshwater to the target salinity, or those that gradually increase salinity over several days [35]. In general, gradual increases in salinity result in estimates of salinity tolerances that are higher than those observed under abrupt changes (e.g., [34,35,38]). Second, the source or type of salt used in salinity tolerance experiments also varies among studies. These have included synthetic sea salt (Instant Ocean®; [35]), sodium chloride solutions (NaCl which comprises about 85% of the salts in seawater; e.g., [35]), diluted seawater (e.g., [37]) and diluted water from brine ponds (e.g., [36]). These differences have been shown to affect the measured salinity tolerances. For example, Bringolf et al. [35] observed that the 72-hr LC_{50} for juvenile flathead catfish was significantly lower when fish were exposed to NaCl solutions (10.0 psu) than when fish were exposed to synthetic seawater (14.5 psu). We used Instant Ocean® because of the compositional resemblance of the resulting solution to natural seawater. Instant Ocean® was supplemented by water from the York River to ensure that any trace elements or compounds not available in Instant Ocean® would be provided by York River water. Third, different life stages and sizes of fish affect the determination of salinity tolerance. As we demonstrate, larger blue catfish have better osmoregulatory abilities compared with smaller individuals. This finding is consistent with studies on a wide range of freshwater fishes [32,39–41]. Such observations might result from size- and age-dependent changes in allometric scaling of body size, and development of endocrine and ionoregulatory pathways [41]. Compared with larger individuals, smaller fish have higher weight-specific aerobic metabolic rates and higher gill surface area to body mass ratios [42]. The result is that smaller individuals have higher rates of passive ion and water exchange per unit body mass which must be compensated by higher rates of active ion exchange in the gill and gut. Finally, the time of removal of moribund fish may also have affected our estimate of time-to-death, which was accurate to ± 4 hours.

The relatively high salinity tolerance we observed in blue catfish may have resulted, at least in part, from the acclimation of fish at 2 psu for 2 weeks. Hyperosmotic abilities may be upregulated after acclimation to low or moderate salinity conditions, as reported for anadromous fishes such as the Gulf sturgeon *Acipenser oxyrhynchus desotoi* [43], white sturgeon *Acipenser transmontanus* [44] and various salmonid species [45]. Such mechanisms may be active in non-anadromous fishes as well, because salinity tolerance is likely a conserved trait [12]. The acclimation protocol we followed with blue catfish may have led to the upregulation of hyperosmotic abilities in these fish, and thus to increased salinity tolerance. In addition, blue catfish in the James River subestuary are regularly exposed to low to moderate salinities. Therefore, osmotic abilities of blue catfish undergoing dispersal events, particularly those at the leading edge of the invasion, would likely be upregulated, and thus, the fish from the James River subestuary may have had an increased physiological ability to use brackish waters. Likewise, the salinity tolerance of blue catfish that were hatched in brackish conditions may be higher than that of fish hatched in freshwater, as demonstrated for Nile tilapia *Oreochromis niloticus* [46]. Such upregulation of salinity tolerance at the egg stage suggests that salinity tolerance of blue catfish may increase as the population expands into estuarine waters; upregulation may allow blue catfish to exploit a large portion of the Chesapeake Bay, possibly even exceeding the exploitable areas predicted here. Further, salinity tolerance of fishes can vary based on their genetic makeup and geographic distribution [40]; therefore, future research should compare salinity tolerance of different blue catfish populations within the Chesapeake Bay region.

Blue catfish exposed to high salinities had the lowest mean body condition indices, suggesting that fish may lose body mass under these conditions. We did not measure weight of fish before the salinity trials commenced but presume that the mean body mass of the blue catfish assigned to different salinity levels were similar because individuals were assigned randomly to salinity treatments. Reduction in body mass has been observed in other fishes such as California halibut *Paralichthys californicus* [47] and shortnose sturgeon *Acipenser brevirostrum* [48] when exposed to elevated salinities. Such decreases in body mass and condition are likely caused by a reduction in muscle water content [48,49]. Loss of muscle water content is often accompanied by increased plasma osmolality and indicates a breakdown of osmoregulatory abilities [49]; a critical level of water loss at high salinities could lead to mortality [48].

Our predictions of suitable habitats for blue catfish in the Chesapeake Bay are likely conservative and may be only relevant for the size range we studied. We gradually increased salinity over seven hours and exposure to the target salinity was 72 hours. In the wild, the rate of increase in salinity could be slower. The effects of temperature on salinity tolerance of blue catfish, though not investigated in this study, could also influence the predictions in this study. For example, when exposed to high salinity conditions, individuals of the tropical freshwater fish oscar *Astronotus ocellatus* survived longer at 28°C than at 18°C [50]. If such patterns hold for blue catfish, then warming water temperatures due to climate change would favor survival and dispersal of this species. This also highlights the potentially counteracting effects of high precipitation and freshwater influx on dispersal of this fish. Whereas high freshwater influx from headwaters into the subestuaries decreases salinity and positively influences the likelihood of dispersal, such events are typically accompanied by cooler temperatures, which somewhat offset the positive effect of lower salinities. However, the positive effect of decreased salinity likely outweighs the negative effects of decreased temperature. Future research should explicitly study the relative influences of temperature and salinity on survival and dispersal of blue catfish. In addition to mortality, high salinities may have sublethal effects on growth [1], reproduction [39] and metabolic rates [1] of fishes. Therefore, salinities > 9 psu may further limit the long-term occupation of estuarine habitats by blue catfish. Sublethal effects may explain why relatively few blue catfish have been consistently captured at salinities > 9 psu in the Rappahannock, York and James rivers. Sublethal effects of increased salinity should be investigated to obtain better predictions of blue catfish range expansion in the Chesapeake Bay.

The ability of blue catfish to use estuarine waters to expand in range and colonize novel habitats throughout the Chesapeake Bay region is aided by the most energetically efficient mode of transportation available to animals, swimming [4]. With a sustained swimming speed of 30 cm s^{-1} [51], in 72 hours a 250 mm blue catfish would be able to move 77.8 km, which is greater than the maximum width of Chesapeake Bay (48 km). A mark-recapture study on blue catfish in the Potomac River in the Chesapeake Bay has shown that blue catfish are capable of such long-distance movements [52]. Telemetry tracking of this species using acoustic tags equipped with depth sensors is needed to elucidate the effects of seasonal distribution and vertical stratification in salinity on size-specific habitat use and dispersal of blue catfish. To this end, we showed that low salinity surface waters can provide suitable habitats for blue catfish dispersal. Such behavior has been observed in the freshwater pikeperch *Sander lucioperca,* which exhibits increased swimming and vertical movement within the water column at salinities greater than 12.5 psu [19]. Overall, we conclude that blue catfish have the potential to expand to most subestuaries on both sides of the Chesapeake Bay, and also to the Delaware Bay via the Chesapeake and Delaware Canal. The role of the Canal as a two-way bridge for exchange of fishes between the Chesapeake and Delaware bays was highlighted by Brown et al. [19], who proposed that flathead catfish—another introduced ictalurid catfish—may have dispersed from the Delaware Bay (where they were introduced) into the Susquehanna River (a river entering the northern end of Chesapeake Bay, see Fig 1) drainage via this route. We postulate that some subestuaries in the Chesapeake Bay region are less likely to supply fish for cross-estuary movements. In particular, blue catfish in the James and York river subestuaries are less likely than those from other tributaries to disperse and colonize adjacent systems because of the considerably high salinities at the mouths of these subestuaries.

Despite their presence in the Chesapeake Bay region since the 1970s, blue catfish have not yet invaded some of the Chesapeake Bay subestuaries or the Delaware Bay. We postulate that this is because dispersal of blue catfish from one subestuary to another is largely restricted by salinity conditions in the Chesapeake Bay, and most of the inter-subestuary dispersal occurs only during high precipitation events when salinity declines. In the future, the frequency of extreme wet events is expected to increase, resulting in fluctuating salinity distributions throughout the Chesapeake Bay [13]. Such events will likely facilitate dispersal of blue catfish in the Chesapeake Bay. Tropical storms may also affect the dispersal of blue catfish. The short-term pulse in salinity (maximum of 10-15 psu for 12-36 hours) at oligohaline reaches of Chesapeake Bay during tropical storm events [53] is likely insufficient to cause mass mortality of blue catfish. However, the inundation of coastal lands during such storms and the subsequent declines in salinity throughout the lower portions of the Bay could provide opportunities for further range expansion. Such conditions were observed during tropical cyclone Isabel in 2003 [53].

Our findings highlight that resource managers and conservationists should be concerned about the potential for blue catfish to continue their range expansion in the rivers draining into the Chesapeake Bay and to impact negatively the native invertebrate and fish species of commercial, recreational and cultural value such as the blue crab *Callinectes sapidus* and Atlantic menhaden *Brevoortia tyrannus*, as well as species of conservation concern such as the catadromous American eel *Anguilla rostrata* and anadromous Atlantic sturgeon *Acipenser oxyrhynchus oxyrhynchus* [8,11, J. Watterson, *pers. comm*., Naval Facilities Engineering Command Atlantic]. Although diet studies of blue catfish in oligohaline habitats of Chesapeake Bay suggest relatively low predation rates on such species [11], similar studies have not been conducted in the mesohaline habitats. Because of the high population densities [9,54] and relatively large sizes of blue catfish in mesohaline areas, their overall impact on native species is likely to be substantial. More importantly, their expansion into the Delaware Bay would have a similar impact.

The development of spatio-temporally explicit management plans may assist in the management of blue catfish by limiting the range expansion of this species in the region. Because range expansion potential is maximized during wet months and years, increased monitoring of likely dispersal corridors during these periods may allow selective removal of blue catfish, and disruption of dispersal processes. Proactive prevention and early eradication of blue catfish in novel habitats is likely to be the best approach to minimizing the negative impacts of this invasive species.

Acknowledgments

We thank Jack Buchanan, Emily Loose, Wendy Lowery, Jillian Swinford and Ben Szykman for assistance in collecting the fish and in conducting the experiment. We also thank Jiabi Du and Jian Shen for Chesapeake Bay salinity predictions, Jim Gartland for survey data from the mainstem of the Chesapeake Bay during 2018 and 2019, and Richard Brill, Brian Gallagher, Roger Mann, Manisha Pant, Troy Tuckey and Bruce Vogt for helpful comments and discussions. The manuscript also benefitted from the comments from two anonymous reviewers.

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Figures

Fig 1: Stocking locations (green triangles, ▲) and current distribution of non-native blue catfish in Chesapeake Bay. Blue dots (●) correspond to additional locations where blue catfish were collected from the mainstem of the Chesapeake Bay during 2018 and 2019 (total fish collected = 63). The Chesapeake and Delaware Canal (C&D Canal) connecting the Chesapeake Bay with the Delaware Bay is also shown. Note that blue catfish have not been recorded from the Delaware Bay yet. Inset shows the location of the Chesapeake Bay in relation to Virginia (VA) and Maryland (MD). Figure available in color online.

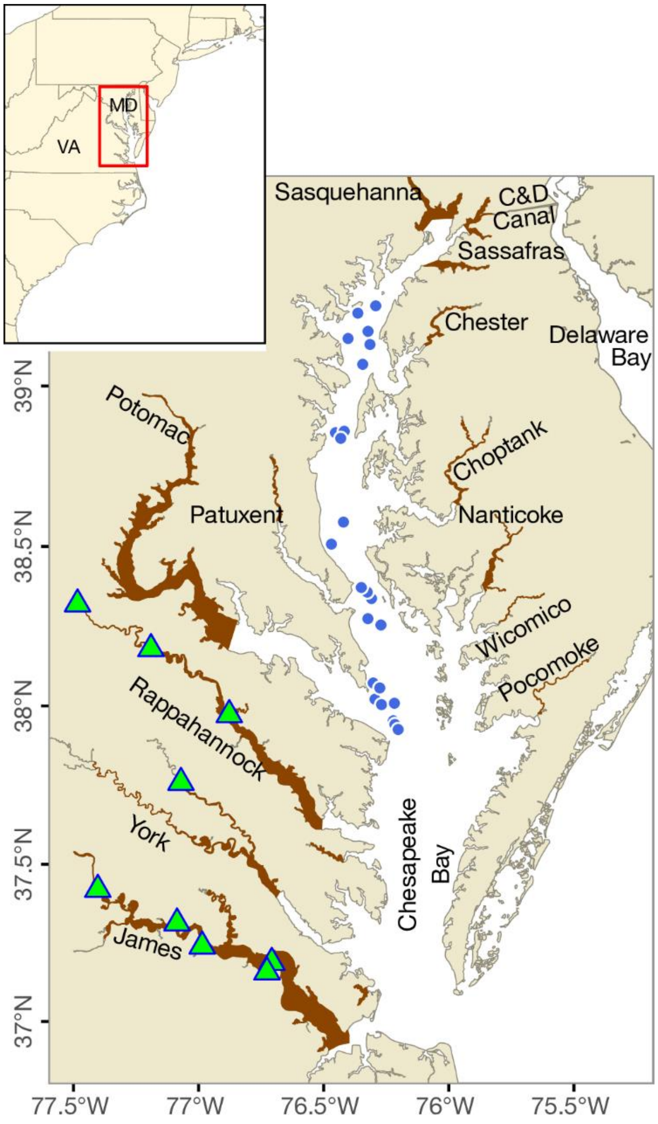


Fig 2: Vertically-averaged salinity (in psu) in the Chesapeake Bay typically encountered in spring (April) and fall (October) during average (2012), dry (2009) and wet (2011) years. Maps are based on the model developed by Du and Shen (2015).

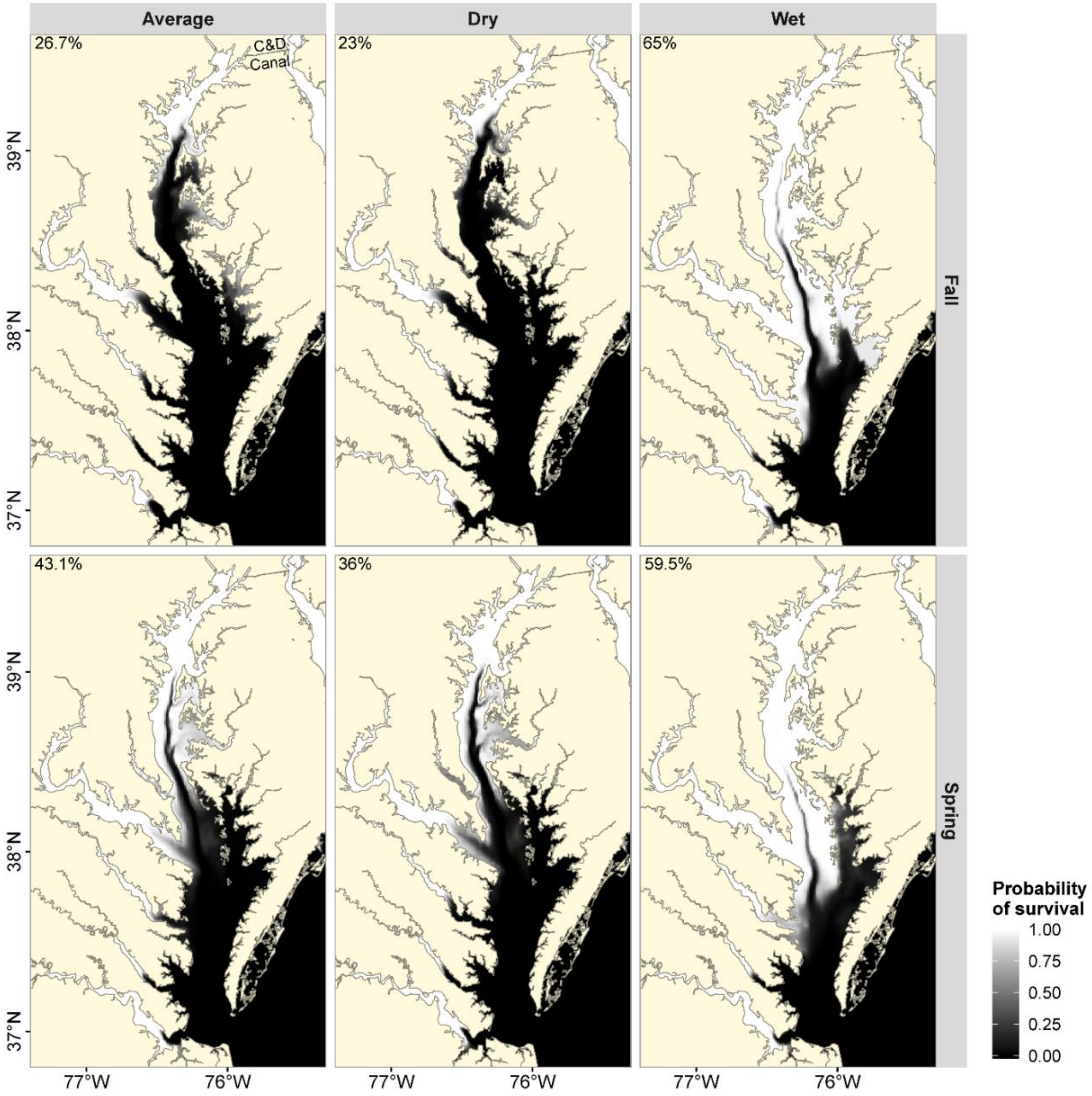


Fig 3: Survival of blue catfish over time after gradual transfer from freshwater to one of three salinity treatments during the pilot experiment. Figure available in color online.

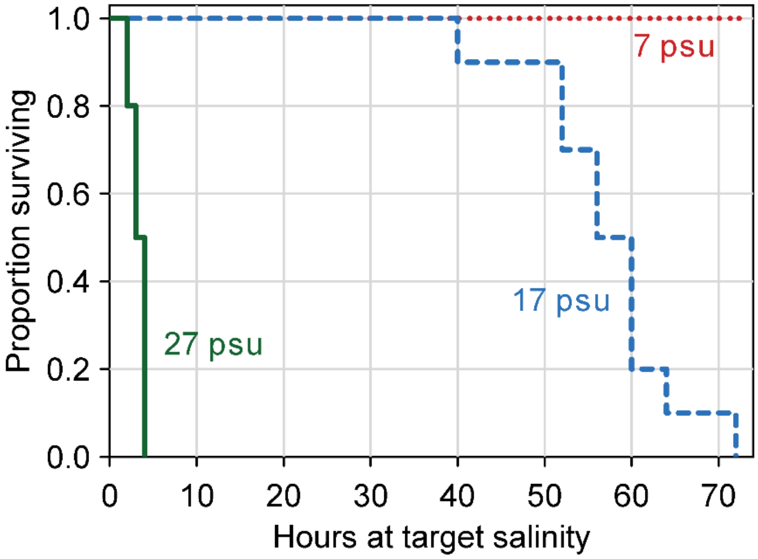


Fig 4: Bottom salinity and fork length of invasive blue catfish captured from the Rappahannock, York and James river subestuaries of the Chesapeake Bay during 1975-2017 by the VIMS juvenile fish trawl survey. The quantile regression splines for salinity ≤ 15 psu are shown for three quantiles ($\tau = \{0.01, 0.1, 0.5\}$). Note that the y axis of the histogram is truncated for the York and James rivers; the percent of blue catfish captured at salinities < 1 psu in the York (47.8%) and James (46.1%) rivers are indicated in the figure.

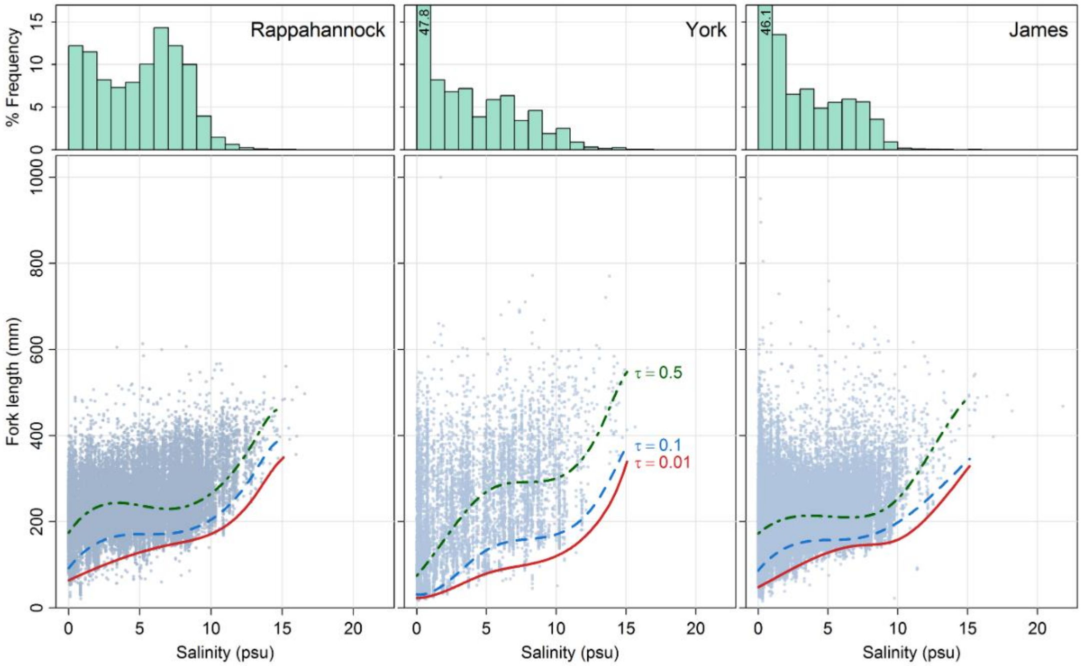


Fig 5: Median time-to-death (h) for male and female blue catfish at various salinities predicted by the stratified Cox proportional hazards model. Numbers at the end of the lines represent salinities in practical salinity units (psu). Figure available in color online.

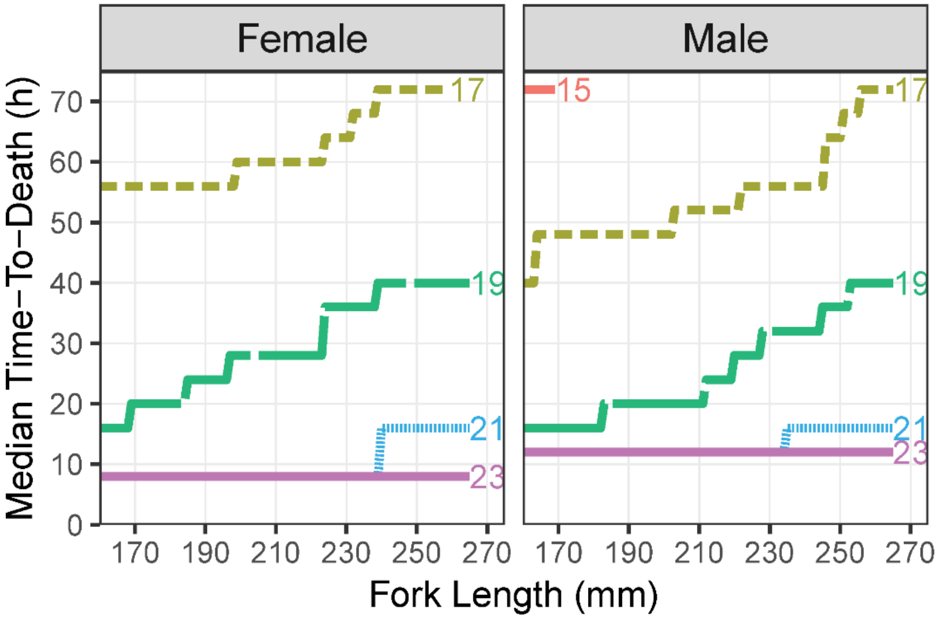


Fig 6: Predicted survival of blue catfish based on Firth Logistic regression fit to data from the 72-hour salinity tolerance experiment. The point and the bar correspond to the predicted salinity at 50% mortality (LC_{50}) and the corresponding 95% confidence interval based on the logistic regression. Numbers along the line represent the minimum, median and maximum length (mm) of blue catfish used in this study.

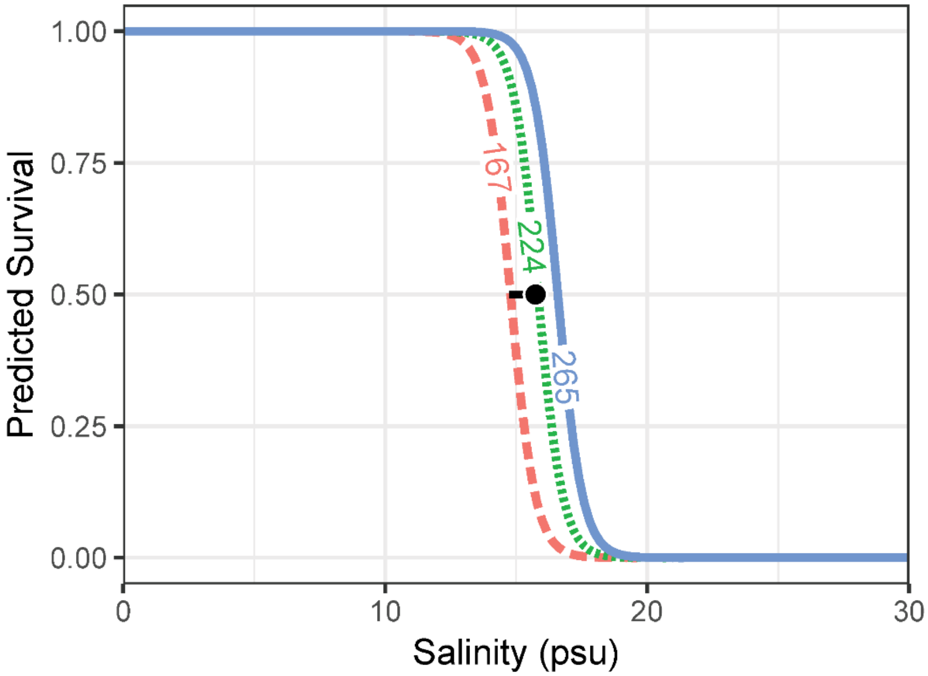


Fig 7: Spatially explicit probabilities of survival (72-hour) for a 224 mm blue catfish (median length in the salinity tolerance experiment) throughout the Chesapeake Bay based on vertically-averaged salinities in spring (April) and fall (October) during average (2012), dry (2009) and wet (2011) years. Number at the top left corner of each panel denotes the percent area of the Chesapeake Bay where predicted probability of survival for blue catfish was greater than 0.8. Note that the probability of survival was nearly 1 in the Chesapeake and Delaware Canal (C&D Canal).

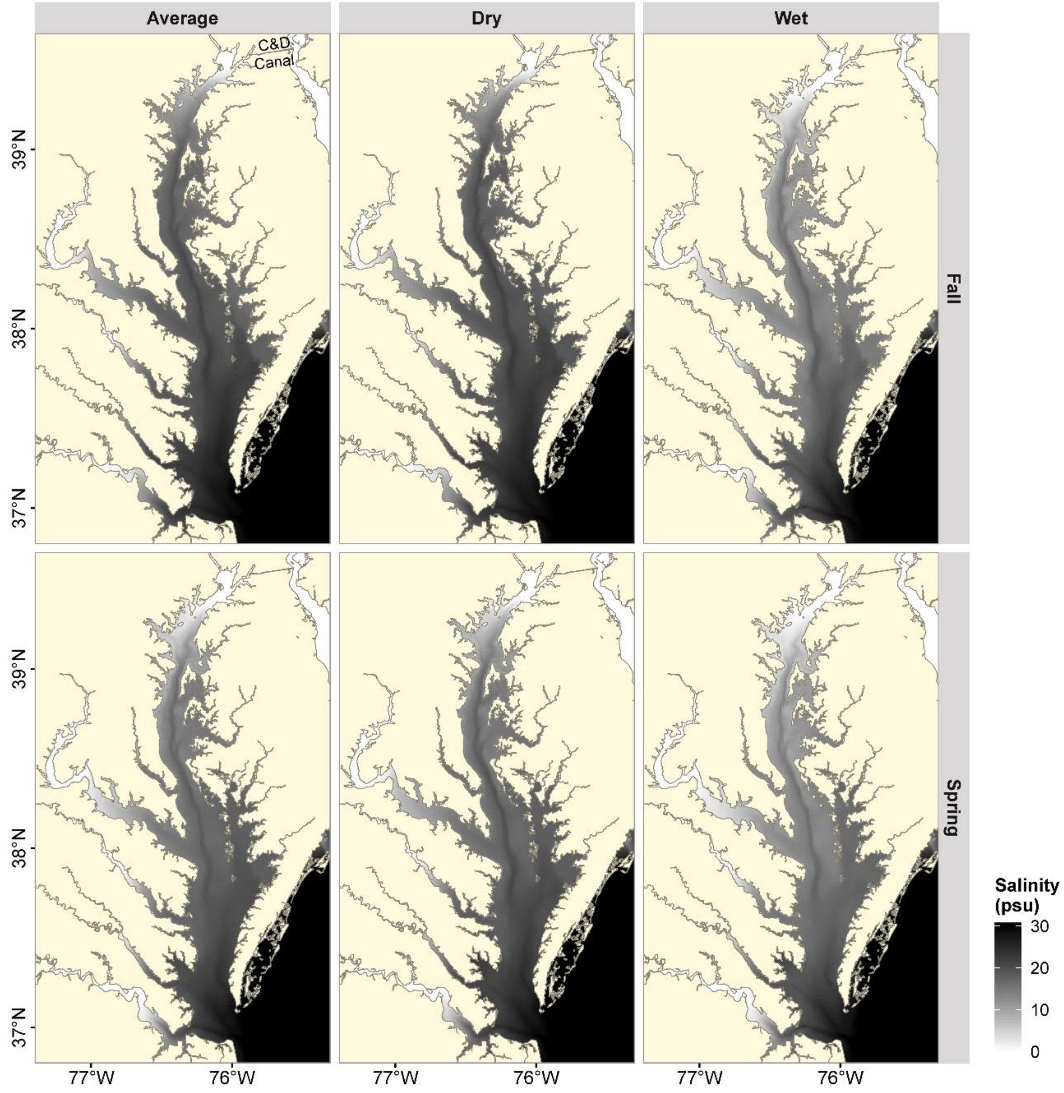
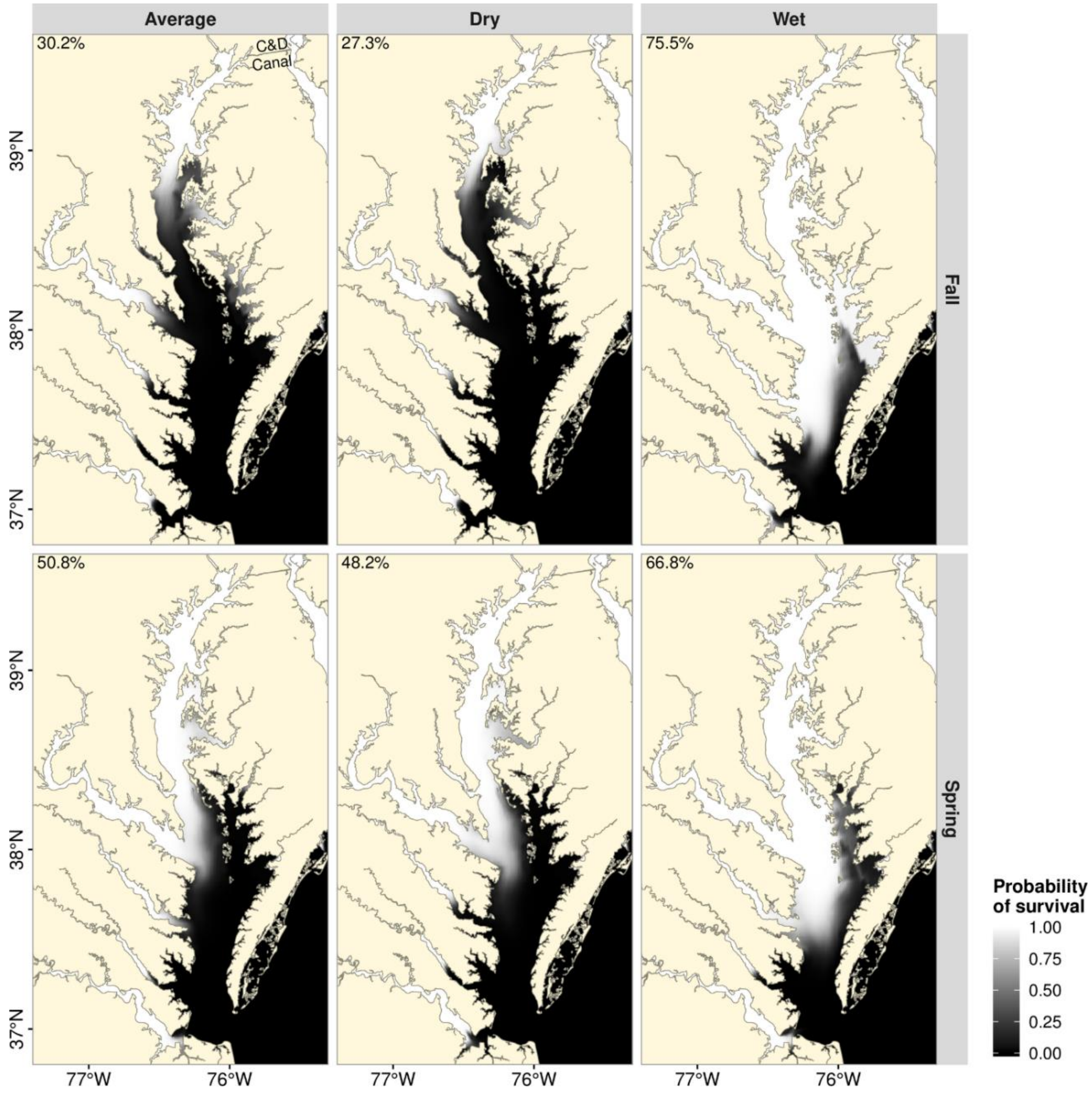


Fig 8: Spatially explicit probabilities of survival for a 224 mm blue catfish throughout the Chesapeake Bay based on surface salinities. See Fig 7 for additional details.



CHAPTER 5: Sublethal Effects of Salinity and Temperature on Non-native Blue Catfish: Implications for Establishment in Atlantic Slope Drainages

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Abstract

The distribution and further range expansion of non-native blue catfish *Ictalurus furcatus* in coastal waters throughout the United States Atlantic slope depend, in part, on the salinity tolerance of the fish. Temperature-mediated sublethal effects of increased salinities on blue catfish biology are not yet known, however. We assessed the effects of salinity and temperature on growth, body condition, body composition and food consumption of juvenile blue catfish in a controlled laboratory experiment. Temperature and salinity had an interactive effect on blue catfish biology, although most fish survived 112 days in salinities up to 10 psu. At salinities ≤7 psu, mean growth rate, body condition and consumption rates were higher at 22°C than at 12°C. Mean consumption rates declined significantly with increasing salinities, yet, salinities ≤7 psu were conducive to rapid growth and high body condition, with highest growth and body condition at 4 psu. Fish at 10 psu exhibited low consumption rates, slow growth, low body condition and lower proportions of lipids. Habitats with hyperosmotic salinities (>9 psu) likely will not support the full lifecycle of blue catfish, but the fish may use salinities up to 10 psu for foraging, dispersal and even growth. Many oligohaline and mesohaline habitats in U.S. Atlantic slope drainages may thus be vulnerable to establishment of invasive blue catfish, particularly given the increasing temperatures as a result of climate warming.

Introduction

Biological invasions can cause major conservation, economic and human health issues in recipient ecosystems (Lockwood et al. 2013). A classic example is Nile perch *Lates niloticus,* which contributed to the extinction of over 200 species of endemic cichlid fishes from Lake Victoria, after it was introduced into the lake to create a novel fishery (Goudswaard et al. 2002). Unsurprisingly, prevention of such catastrophic impacts due to invasive species is a priority for governments throughout the world, prompting policies to prevent the introduction of non-native species, to manage existing invasive species, and to minimize overall negative impacts of invasive species. An invasive species of increasing concern in Atlantic slope rivers of the United States is the blue catfish *Ictalurus furcatus* (Fabrizio et al., in review). This freshwater fish, native to large Midwestern rivers, was introduced in tidal freshwater portions of the James, York and Rappahannock rivers in the Chesapeake Bay region during the 1970s and 1980s to create a recreational fishery (Schloesser et al. 2011). Since then, the fish has expanded in range both within the tidal rivers where they were introduced and into most other tidal rivers throughout the Chesapeake Bay (Schloesser et al. 2011; Nepal and Fabrizio 2019). Similar introductions have resulted in the establishment of non-native blue catfish populations in many tidal rivers along the Atlantic coast between Georgia and Delaware and in the Gulf of Mexico drainage in Florida (Fuller and Neilson 2020). In some of these systems, blue catfish densities are high, and this species may be numerically dominant in the catch of fisheries-independent surveys (Tuckey and Fabrizio 2019). In addition, the generalist, opportunistic feeding behavior of blue catfish is likely resulting in negative impacts on native species via competition and predation (Schloesser et al. 2011; Schmitt et al. 2019). As such, resource managers in the Chesapeake Bay region are interested in managing blue catfish populations to limit further range expansion of the species and to decrease its negative impacts on native ecosystems (Fabrizio et al. in review).

The potential distribution of a species is determined by the species' physiological constraints, which define its fundamental niche (Hutchinson 1957). For blue catfish in the coastal rivers of the eastern U.S., salinity tolerance may limit its range expansion. Most freshwater fishes are unable to penetrate oligohaline (0–5 psu [practical salinity units] salinity) and mesohaline (5–18 psu salinity) environments in estuaries due to low physiological tolerance to elevated salinities or to biotic interactions such as competition with or predation from marine species (Whitfield 2015). Fishes in freshwaters maintain the Na^+ and Cl^- levels in their body at a higher concentration than those of the surrounding water by active uptake of the salts and excretion of large volumes of dilute urine (Marshall and Grosell 2006). The osmotic pressure inside and outside the fish body is balanced at ~9 psu (i.e., isosmotic concentration), beyond which the osmoregulatory process reverses: fish drink copious amounts of water and excrete very small amounts of concentrated urine to balance the salts in the body (Marshall and Grosell 2006; Kültz 2015). Such hyperosmotic salinities are expected to be uninhabitable by freshwater fishes due to the inability to rearrange their osmoregulatory processes. Yet, blue catfish, primarily considered a freshwater species, has native populations in oligohaline and mesohaline regions of coastal rivers in the Southern United States. Perry (1968) captured blue catfish at salinities up to 11.4 psu, though most frequently at salinities <3.7 psu. In the non-native systems in Atlantic slope rivers, however, blue catfish have been captured at salinities as high as 21.8 psu (Fabrizio et al. 2018).

The long-term effects of increased salinity on blue catfish biology are not clear. A recent study assessing lethal effects of increased salinity on wild-caught blue catfish found that juvenile blue catfish have a relatively high salinity tolerance, which might allow this invasive fish to exploit mesohaline environments for dispersal and range expansion throughout the Chesapeake Bay and into the Delaware Bay watershed (Nepal and Fabrizio 2019). Abass et al. (2017) reported maximum survival and growth of hatchery-spawned larval blue catfish at 3 ppt (parts per thousand), but 100% mortalities at salinities ≥6 ppt. These results, though useful as a general indication of the salinity tolerance of blue catfish, may not be readily applicable to individuals in the wild. First, older, larger and pre-acclimated fish, which we contend are more likely to participate in dispersal and range expansion than larvae, tend to tolerate salinity better than their younger, smaller conspecifics (Nepal and Fabrizio 2019). Second, Abass et al. (2017) used sodium chloride solutions to represent different salinities, but salinity tolerance of fish tends to be lower for sodium chloride solutions than for solutions obtained from natural seawater (Bringolf et al. 2005). Accurate projections of estuarine habitat use by blue catfish, therefore, need further information on sublethal impacts of salinity conditions on vital rates.

In temperate estuaries such as Chesapeake Bay, salinity and temperature are dynamic, varying annually and seasonally. Because the effects of stressors such as salinity on physiological processes may vary with temperature (Hill et al. 2008), optimal habitats for a fish are likely to change seasonally and annually depending on the prevailing salinity-temperature combinations. For example, during late spring, juvenile weakfish *Cynoscion regalis* have higher consumption rates and growth rates in oligohaline areas, but by late summer, mesohaline areas are more conducive to higher growth rates (Lankford and Targett 1994). The effects of temperature and salinity on blue catfish, therefore, must be studied together. Though observations of wild fish can inform our understanding of these effects (e.g., Akin et al. 2005; Buchheister et al. 2013; Schloesser and Fabrizio 2019), an approach based on controlled experiments can reveal general patterns and provide information to allow more robust projections of the future distributions of invasive species (Tingley et al. 2014; Evans et al. 2015).

Growth rates, body condition and energy reserves of a fish at a particular environment condition indicate the quality of the environment to the fish. Fishes in suboptimal environments (in terms of habitat, prey availability or abiotic factors) grow slowly and have low body condition and energy reserves, which together signify poor health (Lloret et al. 2013). Effects of increased salinity on the general health and well-being of blue catfish could therefore be assessed using growth and body condition indicators. An accurate characterization of the health, and hence the niche width, of a fish requires estimation of multiple metrics. For example, juvenile largemouth bass *Micropterus salmoides* prioritize growth in length over maintenance of body condition in suboptimal conditions (Garvey and Marschall 2003). In turn, body condition, as quantified using morphometric indicators, may not accurately represent the available energy content in a fish (Lloret et al. 2013; Schloesser and Fabrizio 2017).

We studied the sublethal effects of increased salinity at two temperatures to further constrain the predicted niche of non-native blue catfish in coastal rivers of Eastern US. Specifically, we assessed differences in growth rates, body condition, consumption rates and proximate body composition—the relative proportions of water, lipids, protein and ash—of juvenile blue catfish exposed to one of four salinity treatments (1, 4, 7 or 10 psu) at either 12 or 22°C for 16 weeks. Any observed effects of salinity and temperature on growth, body condition and body composition could, however, result from one or more physiological modes of action, including changes in consumption rate, assimilation rate or energy allocation rules (Wang et al. 1997; Garvey and Marschall 2003; Hill et al. 2008; Kooijman 2010). To help differentiate among these potential processes, we also quantified consumption rates of blue catfish at different temperatures and salinities. Based on bioenergetics and osmoregulation theory, we hypothesized that fish growth, body condition and consumption rates would be maximized at 7 psu and 22°C. We also expected salinities of 1 and 4 psu and temperature of 22°C to have positive effects on blue catfish growth and condition. Salinity of 10 psu, however, was hypothesized to adversely impact blue catfish because of the need to adjust osmoregulatory strategies at this hyperosmotic salinity.

Methods

All animal capture, handling and experimental procedures followed approved Institutional Animal Care and Use Committee protocols (IACUC-2016-08-19-11376-mcfabr and IACUC-2017-05-22-12111-tdtuck) and all applicable U.S. guidelines.

Fish collections

Blue catfish (168–234 mm fork length [FL]) were captured from the tidal James River using a 9.14-m otter trawl following protocols of the Virginia Institute of Marine Science (VIMS) Juvenile Fish Trawl Survey; Tuckey and Fabrizio (2019) provide details of the sampling design and protocols of this survey. Fish were collected from only the oligohaline reaches with salinity <2 psu. Blue catfish were brought to the VIMS Seawater Research Laboratory and treated prophylactically for potential parasites with a formalin bath and a saltwater dip using standard protocols (Noga 2011). To allow identification of individual fish, each fish was subsequently tagged with a unique 12.5 mm Passive Integrated Transponder (PIT) tag. After a three-day recovery period, blue catfish were randomly assigned to either the 12 or 22°C treatment group, and were acclimated at the corresponding temperature for 3 weeks. During acclimation, salinity was 2 psu because preliminary trials showed high mortality of blue catfish at salinity ≤1 psu due to freshwater ich—a parasitic infection common to freshwater catfish species; ich infestations are impeded by chronic exposure to salinity >1 psu (Noga 2011).

Experimental setup

To study the combined effects of salinity and temperature, we used a 4×2 factorial design with four levels of salinity (1, 4, 7 and 10 psu) and two levels of temperature (12°C and 22°C); two replicate aquaria were maintained for each salinity-temperature treatment combination. For each temperature treatment level, we constructed two water baths, inside of which four identical 270-L cylindrical aquaria, corresponding to the four salinity levels, were randomly placed. The experimental aquaria and the water bath exchanged heat but not water. The temperature of the water bath was controlled with an automated heater or chiller, and this controlled the temperature in the experimental aquaria. We supplied each experimental aquarium with mechanical and biological filters and an aerator to maintain adequate dissolved oxygen concentrations. To obtain the desired salinity levels, we diluted filtered York River water (mean salinity: 12.1 psu; range: 10.4–16.3 psu) with deionized water. Fish were fed commercial fish food (3 mm slow-sinking Finfish Silver; Zeigler Bros, Inc.) every other day *ad libitum* during the acclimation period and throughout the experiment; excess food and wastes were removed the next day. We monitored water quality (dO_2, salinity, pH, NH_3, NO_3^-, and NO_2^-) twice per week, and performed water changes as necessary to maintain water quality. Light schedule was computer-controlled to simulate natural photoperiod regimes, and all aquaria were partially covered to provide darkened areas for refuge.

We chose the salinity and temperature levels for the experiment based on a literature review. As the lowest salinity to be used for the experiment, we chose 1 psu to prevent ich infestations, as stated earlier. We chose 10 psu as the highest salinity treatment level because we assumed that long-term exposure to salinities much higher than 9 psu (isosmotic salinity) would be energetically and osmotically too costly for fish and may lead to mortality (Kültz 2015). We suspected that a salinity of 10 psu may lead to some osmotic stress but not mortality (Nepal and Fabrizio 2019). Blue catfish growth is maximized at 24°C (Collins 1988), and temperatures below 9°C was assumed to lead to cessation of growth (Nepal and Fabrizio 2020). We therefore chose 12 and 22°C as temperatures typical of areas of the Chesapeake Bay region occupied by blue catfish during the winter and spring (V. Nepal, *pers. obs.*).

The experiment was performed by exposing fish to 1 psu and subsequently increasing the salinity of the experimental aquaria at a fixed rate of 3 psu per day until target salinities were reached (n = 10 fish per aquarium). We held multiple fish in each aquarium because feeding declined considerably when only one individual was present (V. Nepal, *pers. obs.*). Fish were held in the aquaria for 16 weeks; dead fish were removed as they succumbed and frozen for later analysis. All surviving fish were euthanized at the end of the experiment by immersion in an ice slurry and frozen. Wet weights of all fish were recorded before freezing. At a later date, all frozen fish were processed to determine sex and obtain samples for subsequent analysis of proximate composition.

On day 71, all fish from two aquaria (salinity 10 psu, temperature 22°C, replicate 1, n = 10 fish; and salinity 1 psu, temperature 22°C, replicate 2, n = 10 fish) died of unknown causes. Water quality analyses and gross inspection of the dead fish revealed no abnormalities. These 20 fish were not included in mortality rate calculations, and were replaced with wild fish that had been maintained at 2 psu and 22°C and used for the remaining duration of the experiment. Fish were abruptly transferred to 1 psu, but salinity of the experimental aquarium at 10 psu was increased at the rate of 3 psu per day, as described above for other fish in this treatment group.

Body size and condition

We recorded fork length (mm) and weight (0.1 g) of each fish at the beginning of the experiment and once every four weeks. Fish were not fed for 48 hours before length and weight measurements were recorded. As an index of body condition, we calculated relative condition factor (K_n, Le Cren 1951). To calculate K_n, we first fit an allometric length-weight regression to the observations collected from all fish in the experiment, and used the regression to calculate the predicted weight of each fish given the fork length of the fish. Relative condition factor of fish i was defined as

$$K_{ni} = W_{oi}/W_{pi} \tag{1}$$

where W_{oi} is the observed weight of fish i, and W_{pi} is the predicted weight of fish i based on the length-weight regression. $K_n > 1$ implies higher condition than the average fish in the experiment, and $K_n < 1$ implies lower condition than the average fish in the experiment (Le Cren 1951). Sex of each blue catfish (male or female) was assessed at the end of the experiment by macroscopic examination of the gonads.

Changes in FL and K_n were analyzed using separate repeated measures analysis of variance models in the linear mixed-effects modeling framework. The models took the form:

$$Y_{ijklmn} = \mu + T_j + S_k + P_l + M_m + \beta B + a_n + f_{i(n)} + \varepsilon_{ijklmn} \qquad (2)$$

where Y_{ijklmn} is the response variable (either FL or K_n) for fish i (i.e., PIT tag i) from aquarium n in the temperature treatment j (12°C or 22°C), salinity treatment k (1, 4, 7 or 10 psu), measurement period l (4, 8, 12 or 16 weeks) and sex m; μ is the overall mean of the response Y; T_j, S_k, P_l and M_m are the fixed effects of temperature, salinity, measurement period and sex respectively; β is the regression coefficient for the effect of the baseline value of the response B (i.e., FL or K_n at the start of the experiment); ε_{ijklmn} is the unexplained random error assumed to have a normal distribution. The term a_n denotes the random effect of aquarium n, accounting for the potential pseudoreplication among observations from multiple individuals from a single aquarium. Similarly, $f_{i(n)}$ denotes the random effect of fish i nested in aquarium n, accounting for the repeated measurements on each fish. We also included two- and three-way interactions among temperature, salinity and period. Our primary interest was in the interaction terms, which, if significant, would indicate significant diversions over time in FL or K_n at different temperatures ($T \times P$), salinities ($S \times P$) or both ($T \times S \times P$). The FL model included a two-way interaction between sex of the fish and time ($M \times P$) to examine growth differences between males and females. Other interaction terms were not considered because preliminary graphical analysis indicated lack of strong interactions. We used a first-order autoregressive (ar1) variance-covariance structure to account for the temporal autocorrelation in the response for each fish. Specifically, we used the heterogeneous version of the ar1 structure because the variance increased over the measurement period. The Kenward-Roger method was used to calculate the degrees of freedom for the approximate *F*-tests.

Because change in FL over time (i.e., growth rate) was linear (see results below), we refit equation 2 for FL with period as a continuous predictor, and calculated Q_{10} for each salinity level to allow us to compare growth rates of blue catfish at different temperatures. Q_{10} represents the factor by which growth rate changes over a 10°C change in temperature (Hill et al. 2008), and was calculated as:

$$Q_{10k} = \frac{\beta_{22^{\circ}\mathrm{C}k}}{\beta_{12^{\circ}\mathrm{C}k}} \tag{3}$$

where Q_{10k} is the Q_{10} for salinity *k*, and $\beta_{22^{\circ}\mathrm{C}k}$ and $\beta_{12^{\circ}\mathrm{C}k}$ are respectively the salinity-specific growth rates (i.e., slopes) at 22°C and 12°C respectively. We subsequently compared growth rates between temperatures and among salinities using bootstrap hypothesis tests (Efron and Tibshirani 1993). Statistical analyses were conducted in SAS version 9.4 (SAS Institute, Cary, NC) following procedures in Littell et al. (2006).

Body composition

We homogenized all blue catfish in an electric blender at the end of the experiment to assess differences in composition at different temperature-salinity combinations. Samples were dried at 60°C in a drying oven for several weeks. Once the sample had dried to constant weight, the tissue was homogenized further in a mortar and pestle and subsequently dried for another 48 hours. We calculated water content in each fish by subtracting the dry weight from the wet weight. Dry tissue samples were analyzed at the Aquaculture Laboratory in Southern Illinois University, Carbondale, Illinois, for proximate body composition. Fish dry tissues were separated into three components, namely lipids, protein and ash; carbohydrates were ignored because they form a minor constituent of fish tissues (Hill et al. 2008). We report proximate body composition as fractional composition data where the four components (water, lipids, protein and ash) add up to 1. We were primarily interested in the relative ratios of components (e.g., lipid to ash ratio).

The components of compositional data such as ours must add to a constant, a condition called the constant-sum constraint, making traditional univariate or multivariate tests inappropriate (Aitchison 1986). We therefore analyzed the body composition data using Aitchison's log-ratio approach (Aitchison 1986). Specifically, we transformed the four-part proximate body composition data into three transformed variables using the isometric log-ratio (ilr) transformation, which allows analysis of the transformed variables using classical statistical techniques (Egozcue et al. 2003). The three transformed variables z_{water}, $z_{protein}$ and z_{lipids}, called balances, were calculated as

$$z_{water} = \sqrt{\frac{3}{4}} \times \log \frac{water}{\sqrt[3]{protein \times lipids \times ash}} \tag{4}$$

$$z_{protein} = \sqrt{\frac{2}{3}} \times \log \frac{protein}{\sqrt{lipids \times ash}} \tag{5}$$

$$z_{lipids} = \sqrt{\frac{1}{2}} \times \log \frac{lipids}{ash} \tag{6}$$

These ilr balances correspond to the ratio of water to all other components (z_{water}), protein to the remaining components ($z_{protein}$), and lipids to ash (z_{lipids}), and can be back-transformed to proximate compositions to allow easy interpretation (Egozcue et al. 2003). We modeled the ilr balances jointly using a multivariate linear mixed-effects model (LMM) of the form:

$$z_{cijkmn} = \mu + T_j + S_k + T_j \times S_k + M_m + \beta\log(W) + a_n + \varepsilon_{ijkmn} \qquad (7)$$

where z_{cijkmn} is the c^{th} ilr balance for fish i from aquarium n in temperature treatment j, salinity treatment k and sex m; β is the regression coefficient for the effect of natural log of fish weight $\log(W)$, and all other symbols are as described previously. We used $\log(W)$ instead of W because the former resulted in a better fit.

To ease interpretation, we obtained estimated marginal means for each balance at each salinity-treatment composition, and back-transformed the marginal means to the four components (percent water, lipids, protein, and ash). We tested hypotheses of pairwise differences in mean proportions of each component among the salinity and temperature treatments using bootstrap techniques (Efron and Tibshirani 1993). Specifically, we obtained 1,000 bootstrap resample datasets of ilr balances, with size of each bootstrap resample equal to the original sample size. We then fitted multivariate LMMs on each resample dataset and obtained the marginal means for each salinity-temperature treatment. Finally, we calculated bootstrap-based two-tailed P-values to compare statistically the estimated marginal means at different temperatures and salinities (Efron and Tibshirani 1993).

Treatment-specific differences in proximate body composition of blue catfish at the end of the experiment may result from differences that were present at the start of the experiment. To check for this potential confounding effect, we examined differences in proximate body composition of fish and wet weight of fish at the start of the experiment and between temperature treatments (12 or 22°C). To do this, we euthanized 30 randomly selected fish (*n* = 15 for each temperature level) before the start of experimental trials and obtained proximate body composition of these fish as stated above. We subsequently tested for the effects of fish weight and water temperature on mean body composition of these blue catfish using multivariate LMM of the form:

$$z_{cijm} = \mu + T_j + M_m + \beta \log(W) + \varepsilon_{ijm} \qquad (8)$$

where z_{cijm} is the c^{th} ilr balance for fish *i* of sex *m* held at temperature *j*; all other variables are as described above.

We used the package robCompositions version 1.3.3 (Templ et al. 2011) in R version 3.6.1 (R Core Team, Vienna) for ilr transformation and back-transformation, and proc mixed in SAS to fit the multivariate LMM (Gao et al. 2006). Assumptions of homogeneity of variance and normality of residuals were assessed using diagnostic plots.

Consumption rate

In each experimental aquarium, we conducted feeding trials to determine the consumption rate of blue catfish at different salinities and temperatures. Due to logistical difficulties, we could not measure consumption rates of individual blue catfish, instead we measured the cumulative consumption rate for all (up to 10) blue catfish in each experimental aquarium. Fish were not fed for 48 hours before the consumption trials. A measured quantity of commercial fish feed was introduced to each experimental aquarium at 1700 hours, before the lights turned off. The fish were left undisturbed to allow feeding for the next 3 hours. We chose a relatively short period of 3 hours to minimize the accumulation of waste from egestion, while ensuring that blue catfish had enough time to consume the food. At 2000 hours, we pumped the uneaten food into a 200 µm mesh bag, and subsequently transferred the food into pre-weighed aluminum pans. The aluminum pan containing the food was dried at 60°C for 96 hours when constant weight was observed. The weight of the uneaten food was obtained by subtracting the weight of the aluminum pan from the total weight, and the amount consumed (C_F, g of food) was calculated by subtracting the weight of uneaten food from the weight of the food introduced in the corresponding aquarium. Consumption rate trials were conducted twice for each aquarium.

Disintegration of food in the experimental aquaria during the trial period (3 hours) could bias the measured consumption rates. To adjust for this effect, we conducted food disintegration trials in the experimental aquaria after the termination of the experiment when blue catfish were removed from the aquaria. We calculated the weight of food lost to disintegration (C_0) after 3 h in each aquarium by subtracting the dry weight of remaining food from the weight of the food introduced in the aquarium. These amounts were calculated for each aquarium in the experiment and represented as C_{0i}, or the amount of food lost to disintegration in aquarium i. The mass-specific consumption rates (CR, mg food per g fish) for each aquarium were subsequently calculated as:

$$CR_{ij} = \frac{C_{Fij} - C_{0i}}{\Sigma W_i} \tag{9}$$

where CR_{ij} is the mass-specific consumption rate for all blue catfish in aquarium i during event j, C_{Fij} is the amount of food consumed by blue catfish in aquarium i during event j, and ΣW_i is the total wet weight of blue catfish in aquarium i.

Effect of water temperature and salinity on the consumption rate of blue catfish was assessed using a generalized LMM of the form:

$$\log(\lambda_{jkn}) = \mu + T_j + S_k + a_n + \varepsilon_{jkn} \tag{10}$$

where $\log(\lambda_{jkn})$ is the natural log of mean CR (λ) of all fish in aquarium *n* at temperature *j* and salinity *k*. Other variables are as before. Here, we used a gamma distribution with a log link, and fit the model using proc glimmix in SAS (Littell et al. 2006).

Some predictor variables were scaled to aid model fitting, and the intercept (μ) was suppressed to aid model interpretation. We report 95% confidence intervals (CI) for all predicted means and model parameters. Assumptions of homogeneity of variance and normality of residuals were assessed using diagnostic plots.

Results

Water quality

Water temperature and salinity were fairly stable during the experiment. Mean ammonia concentrations were higher during the first few weeks of the experiment, but decreased to acceptable low levels thereafter (Table 1). Dissolved oxygen concentrations remained consistently high (> 5.0 mgL^{-1}) in all aquaria, though values were lower for aquaria at 22°C (mean 7.4 mgL^{-1}) than at 12°C (mean 10.8 mgL^{-1}; Table 1) due in part to reductions in oxygen solubility at higher temperatures. Mean pH of all aquaria was 7.4 with little fluctuation (Table 1).

Survival, body size and condition

Of the 160 experimental fish, 154 (96.25%) survived to the end of the experiment. Six fish that died during the experiment were in the 22°C treatments: four fish died at 10 psu (20% mortality rate), and one fish died in each of the 7 and 4 psu treatments (5% mortality rate; Figure 1).

Temperature had a positive effect on growth rate of juvenile blue catfish: growth rates were faster at 22°C than at 12°C ($P < 0.05$; Table 2; Figure 2). There was, however, an interactive effect of time with temperature and salinity ($F_{3,198} = 11.1$; $P < 0.001$) reflecting differences in growth patterns among the treatment groups. Pairwise comparisons revealed that growth rates at 12°C were similar across salinity levels ($P > 0.999$), but at 22°C, considerable differences existed such that fish grew fastest at 4 psu and slowest at 10 psu (Figure 2, Table 3). Variance in FL measurements increased over time, and proximal FL measurements on the same fish were more correlated than measurements further apart in time (Table 4). Q_{10}'s at 1, 4, 7 and 10 psu were 6.8, 6.0, 5.1 and 3.2, respectively, implying that increased temperature had the greatest positive impact on blue catfish at 1 psu and smallest positive impact on fish at 10 psu (Figure 2). Unsurprisingly, initial size of the fish was highly predictive of subsequent FL measurements ($F_{1,144} = 26663.6$, $P < 0.001$), indicating that through time, larger fish continued to be larger than their smaller counterparts. Furthermore, we found no evidence for sexual dimorphism in growth rates of blue catfish ($F_{1,186} = 0.09$; $P = 0.763$).

Mean body condition exhibited a significant interaction among time, temperature and salinity ($F_{9,308} = 7.25$; $P < 0.001$), however, at salinities of 7 or less, temperature had a largely positive effect on mean body condition with significantly higher K_n at 22°C than at 12°C (Figure 3). At 12°C, mean K_n at 1, 4 or 7 psu was fairly stable through time, fluctuating around the mean of 1.0; at 22°C, mean K_n increased through time for fish in the 1, 4 and 7 psu treatment levels. These patterns were different for fish held at 10 psu:

mean body condition declined for fish at both 12 and 22°C, with the most severe declines observed at 22°C (Figure 3). Repeated measurements of the same fish revealed that fish at 10 psu, and in particular those at the 10 psu-22°C treatment, were also less able to heal skin abrasions. Similar to FL, variance in K_n measurements increased over time, and proximal K_n measurements on the same fish were more correlated than the measurements taken further apart in time (Table 4). In general, fish with high mean initial K_n continued to exhibit high mean K_n throughout the experiment ($F_{1,138} = 430.3$; $P < 0.001$); sex did not affect the K_n ($F_{1,138} = 0.82$; $P = 0.37$).

Body composition

On average, water, protein, lipids and ash comprised 74.5%, 14.8%, 7.2% and 3.6% of the wet weight. However, mean relative proportions of these components differed considerably among treatment levels and between the initial and post-experimental period. Blue catfish at 12°C that were sacrificed before the start of the experiment had significantly different mean body compositions than fish at 22°C ($F_{3,30} = 6.3$; $P = 0.002$). Specifically, compared with the fish at 12°C, fish at 22°C had a significantly greater mean proportion of protein (bootstrap $P < 0.001$), but a significantly lower mean proportion of lipids (bootstrap $P = 0.036$); mean proportions of water and ash did not differ significantly between fish from the two temperatures (Figure 4). Mean body compositions were not significantly affected by initial wet weight ($F_{3,30} = 2.15$; $P = 0.115$) or sex ($F_{3,30} = 1.19$; $P = 0.331$).

Mean body composition of fish differed significantly with temperature ($F_{3,424} = 7.5$; $P < 0.001$) and salinity ($F_{9,424} = 3.4$; $P < 0.001$), and the interaction between temperature and salinity was not significant ($F_{9,424} = 1.45$; $P = 0.163$). Bootstrap analysis revealed that the mean proportion of water was significantly higher for fish at 12℃ than at 22℃ at 1 ($P = 0.008$), 4 ($P < 0.001$) and 7 psu ($P = 0.014$; Table 2; Figure 4). Within the 12℃ treatment, mean proportion of protein was significantly lower for blue catfish held at 10 psu compared with fish in lower salinities ($P < 0.05$; Table 3; Figure 4). Most other components did not differ significantly among the salinity treatment levels. Similarly, at 22℃, the primary differences were observed between fish at 10 psu and those in lower salinities: fish at 10 psu had significantly higher mean proportions of water and lower mean proportions of lipids than those at 1, 4 or 7 psu ($P < 0.05$; Table 3; Figure 4). Mean body compositions were similar for males and females ($F_{3,424} = 1.4$; $P = 0.242$) but differed significantly with fish weight ($F_{3,424} = 7.5$; $P < 0.001$). As fish increased in length, the mean proportion of water decreased and the mean proportion of lipids increased, but the mean proportions of protein and ash remained stable (Figure 5).

Consumption rate

Consumption rates of blue catfish ranged between 3.5 and 35.0 g/kg of fish body weight and varied considerably within aquaria (intraclass correlation = 0.12). Mean consumption rates were highest at 1 psu and 22°C (23.4 g/kg of the fish body weight) and lowest at 10 psu and 12°C (6.1 g/kg of the fish body weight). Temperature had a significant positive effect on consumption rates ($F_{1,16} = 17.2$; $P < 0.001$; Figure 6), though these differences were significant only at 7 ($t_{16} = 2.6$; $P = 0.022$) and 10 psu ($t_{16} = 2.2$; $P = 0.046$; Table 2). Increased salinity negatively influenced mean consumption rates

($F_{3,16} = 5.2$; $P = 0.011$; Figure 6), however, pairwise comparisons did not reveal significant differences among salinities within a temperature (Table 3).

Discussion

Most juvenile blue catfish in the Chesapeake Bay region can survive in salinities up to 10 psu for 112 days. Salinities up to 7 psu seemed to have little negative impact on growth, body condition and compositions. Together with previous research that demonstrated high short-term tolerance of blue catfish to acute changes in salinity (Nepal and Fabrizio 2019), these findings suggest that US Atlantic coast habitats with salinities ≤10 psu are vulnerable to establishment of blue catfish populations. Further, higher temperature had positive effect on blue catfish at salinities ≤7 psu. As such, increase in winter and spring water temperatures due to global warming may foster establishment in brackish water habitats.

Salinity and temperature had an interactive effect on blue catfish biology, in agreement with reports for other species (e.g., grass carp *Ctenopharyngodon idella,* Kilambi and Zdinak 1980; Watanabe et al. 1993; Atlantic cod *Gadus morhua*, Lambert et al. 1994; Nile tilapia *Oreochromis niloticus*, Schofield et al. 2011). In general, blue catfish had higher consumption rates, faster growth, better body condition, and a greater proportion of lipids at 22°C than at 12°C. Higher consumption and growth rates of animals at higher temperatures is a well-known tenet in physiology (e.g., Hill et al. 2008). Further, the greater proportion of lipids and lower proportion of water and ash in fish held at high temperatures likely indicate faster short-term growth (Holdway and Beamish 1984).

Positive effects of temperature at salinities ≤7 psu did not extend to 10 psu, where mean growth rates and body conditions declined significantly. In particular, fish at the 10 psu-22°C treatment were emaciated (i.e., low K_n), less able to heal abrasions and had lower mean proportions of lipids compared with fish from other treatments. These results conform to expectations from osmoregulatory physiology, emphasizing that the physiological mechanisms in freshwater fish are unable to maintain homeostasis in hyperosmotic environments (i.e., >9 psu; Bœuf and Payan 2001; Kültz 2015). As such, these fish allocated less energy to growth (both in terms of length and mass) and have low lipid reserves. Many other studies have reported similar results where growth rates and body condition of freshwater fish decline starkly at salinities greater than ~9 psu (e.g., channel catfish *Ictalurus punctatus*, Allen and Avault 1969, goldfish *Carassius auratus*, Altinok and Grizzle 2001; feral catfish *Heterobranchus bidorsalis*, Fagbenro et al. 1993; Asian swamp eel *Monopterus albus*, Pedersen et al. 2014).

The optimal salinity for juvenile blue catfish appears to be around 4 psu as indicated by fastest growth and good body condition despite relatively low mean consumption rates. These results are in general agreement with the previous study on larval blue catfish which reported the highest survival and growth at 3 psu (Abass et al. 2017) and with other studies of freshwater species. For example, freshwater snakehead *Channa punctata* grew faster at 5 psu than at 0 or 10 psu (Dubey et al. 2016), and Asian swamp eel grew fastest at 3 psu (Pedersen et al. 2014). Yet, others have found contrasting results for freshwater fish with fastest growth in freshwater (e.g., common carp, Wang et al. 1997; goldfish, Altinok and Grizzle 2001), or similar growth rates up to the isosmotic salinity (e.g., channel catfish, Allen and Avault 1969; feral catfish, Fagbenro et al. 1993).

Change in consumption rate with salinity is also species-specific and can increase with salinity (e.g., striped dwarf catfish *Mystus vittatus*, Arunachalam and Reddy 1979), decrease with salinity (e.g., walking catfish *Clarias batrachus*, Sahoo et al. 2003) or maximize at intermediate salinities (e.g., Nile tilapia, Herath et al. 2018). Taken together, the effects of salinity on food intake, food conversion efficiency and ultimately growth rate of freshwater fishes seem species-specific, and likely to be mediated interactively by temperature. In general, however, freshwater fish growth seems to be maximized either in freshwater or at salinities around 3-6 psu. This result may be because the osmotic gradient is lower at these salinities, and hence smaller amounts of energy are spent on osmoregulation, leaving a larger fraction of energy for growth (Bœuf and Payan 2001; Kültz 2015).

The observed effects of salinity and temperature may result from any of several proximate physiological modes of action, including changes in consumption rate (i.e., food detection ability or appetite), assimilation rate, or the partition of assimilated energy to various life processes such as maintenance of homeostasis, activity, and somatic or gonadal growth (Kooijman 2010). In particular, decrease in consumption rate in brackish waters may be a result of reduced prey detection ability due to diminished electroreceptory ability of blue catfish in brackish waters. Catfishes of the order siluriformes are electroreceptive, and can use electroreception for prey detection (New 1999). Electroreceptory organs in freshwater fishes, however, are anatomically different from those in saltwater species, and thus, do not function in brackish and marine waters (New 1999). It seems likely, therefore, that blue catfish may not be able to detect prey as well in brackish waters, leading to lower consumption rates. We cannot, however, rule out other potential modes of action, particularly because multiple modes of action likely act concurrently. For example, compared with fish at 1 psu, fish at 4 psu may feed less, and have a lower assimilation rate, but still maintain high growth by allocating a smaller fraction of energy to maintenance of osmoregulatory homeostasis. The specific combinations of these modes of action that lead to specific response of fishes to changing salinity are likely to depend on the evolutionary history and life-history adaptations of the species. This is evidenced by the observation that even though most freshwater fishes are relatively uncommon in estuaries, some groups of freshwater fishes, such as members of the family Cichlidae, have unusually high salinity tolerance and occupy a wide range of estuarine and marine environments (Whitfield 2015).

Future research should attempt to identify the combination of modes of action that lead to the observed results, though bioenergetics modeling may also reveal likely processes (Kooijman 2010). Towards this end, our results provide important inputs for the parameterization of a bioenergetics model that accounts for the effect of salinity and temperature on vital rates of blue catfish in coastal rivers. The inferences from our study and their use in bioenergetics modeling would have benefitted from measurement of consumption rate, egestion rate and energy assimilation rate at the level of individual fish. Measurement of these rates at finer resolutions of temperature, and especially salinity, could also help obtain a better understanding of the effects of temperature and salinity on blue catfish.

Despite the suggestion from our results that brackish water habitats with salinities ~4 psu provide the most energetically optimal environments for blue catfish, >45% of blue catfish captured from the tidal James and York rivers in the Chesapeake Bay by a fishery-independent trawl survey (VIMS trawl survey) occurred at salinities ≤1 psu (Nepal and Fabrizio 2019). This discrepancy suggests that salinities >1 psu may have negative impacts on other aspects of blue catfish biology not studied here. For example, Perry (1973) suggested that reproduction of blue catfish may be curtailed at salinity >2 psu, though it is not clear whether this is caused by hinderance in development of oocytes or mortality of eggs and larvae. Maternal effects (e.g., increased salinity tolerance of the offspring from mothers pre-exposed to increased salinities; Shikano and Fujio 1998) and behavioral effects (e.g., decreased parental care of eggs from fathers under high salinity conditions; St Mary et al. 2001) may also play important roles, but have not been studied. Research is needed to estimate sublethal effects on the reproductive biology of blue catfish. It should be noted that the reproductive biology of blue catfish has been described in two invasive populations (Nepal and Fabrizio in review), and that because these systems are tidally influenced, an individual fish can potentially use salinities >2 psu for foraging and dispersal or to offload parasitic infestations yet return to freshwater habitats for spawning.

Our study provides an indication of the fundamental niche of blue catfish in relation to the salinity and temperature axes (*sensu* Hutchinson 1957) and provides crucial information towards development of a mechanistic species distribution model (Kearney and Porter 2009) for blue catfish throughout tidal rivers and estuaries of the U.S. Atlantic slope. The results also emphasize the need to consider multiple biological end-points (e.g., growth, body condition, body composition) and to consider important environmental variables together when studying their effects on fish biology as experiments that incorporate factorial designs are likely to yield more realistic predictions than more simplistic experiments that focus on a single variable. Overall, our results indicate that estuarine habitats throughout the Eastern U.S. with salinities ≤7 psu may be highly vulnerable to blue catfish establishment, and thus critical habitats at these salinities (e.g., areas that provide nursery habitats for species of conservation concern) should be prioritized for protection by state and regional management agencies. The overall negative impacts of individual blue catfish on local fauna at salinities >2 psu may not be high because of relatively lower consumption rates in brackish environments compared with freshwater environments. Yet, if the population size of the fish at these salinities increases, the total impacts may be high. Even though such areas are not likely to support reproduction, they are likely to support foraging and dispersal. Down-estuary shift of salinity gradients during wet years or increased water temperatures due to global warming are likely to increase the chances of dispersal, range expansion (Nepal and Fabrizio 2019), and establishment of blue catfish, and hence the severity of its impacts in brackish-water habitats. On the other hand, salinity intrusion with sea level rise, as predicted to occur in coastal and estuarine waters in future, may serve to limit the dispersal pathways and lead to formation of discrete subpopulations of blue catfish that are intermittently connected during periods of high flow.

Acknowledgments

We thank the members of VIMS juvenile trawl survey for help with collection of fish for the experiment, and Jaap van der Meer, Richard Brill, Wolfgang Vogelbein and Manisha Pant for assistance and suggestions throughout the various aspects of the study. We also thank Jack Buchanan, Grace Breitenbeck, Matthew Oliver, Brian Gallagher and

Shannon Smith for help conducting the experiment and processing the fish samples. Funding for this research came from a VIMS student research grant and Virginia Sea Grant graduate fellowship to V. Nepal. The trawl survey was funded by the Virginia Marine Resources Commission and the U.S. Fish and Wildlife Service.

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Tables

Table 1: Water quality variables measured in the experimental aquaria where blue catfish were exposed to one of four salinities at either 12 or 22°C for a period of 16 weeks. Values of the water quality represent the mean ± SEM. psu = practical salinity units; dO_2 = Dissolved Oxygen

Temperature (°C)	Salinity (psu)	Ammonia (mg/L)	dO_2 (mg/L)	pH
12	1	0.3±0.1	10.9±0.3	7.2±0.1
12	4	0.5±0.2	10.2±0.3	7.2±0.1
12	7	0.6±0.2	10.8±0.2	7.3±0.1
12	10	0.5±0.2	10.9±0.1	7.4±0.1
22	1	0.8±0.3	7.7±0.2	7.4±0.1
22	4	0.2±0.1	7.7±0.2	7.4±0.1
22	7	0.2±0.1	7.0±0.1	7.5±0.0
22	10	0.5±0.1	7.2±0.1	7.4±0.1

Table 2: Bootstrap-based *P*-values comparing growth rate (change in FL/day), proportions of water, protein, lipids and ash, and consumption rates of juvenile blue catfish at 12 versus 22°C at 1, 4, 7 or 10 psu. *P*-values < 0.05 are shown in bold.

Salinity (psu)	Growth rate	Prop. water	Prop. protein	Prop. lipids	Prop. ash	Consumption rate
1 psu	**<0.001**	**0.008**	0.730	**0.048**	0.922	0.074
4 psu	**<0.001**	**<0.001**	0.188	0.172	**0.004**	0.121
7 psu	**<0.001**	**0.014**	0.738	0.110	0.364	**0.022**
10 psu	**0.050**	0.652	0.362	0.326	0.610	**0.046**

Table 3: Bootstrap-based *P*-values comparing pairwise differences in growth rate (change in FL/day), proportions of water, protein, lipids and ash, and consumption rates of juvenile blue catfish at 1, 4, 7 or 10 psu at 12 or 22°C. *P*-values < 0.05 are shown in bold.

Temperature	Comparison	Growth rate	Prop. water	Prop. protein	Prop. lipids	Prop. ash	Consumption rate
12°C	1 psu v 4 psu	>0.999	0.716	0.546	0.494	0.56	>0.999
	1 psu v 7 psu	>0.999	0.444	0.338	0.294	0.842	0.680
	1 psu v 10 psu	>0.999	0.682	**0.038**	0.144	0.532	0.064
	4 psu v 7 psu	>0.999	0.636	0.592	0.592	0.448	>0.999
	4 psu v 10 psu	>0.999	0.470	**0.002**	0.054	0.870	0.479
	7 psu v 10 psu	>0.999	0.268	**0.006**	**0.014**	0.436	>0.999
22°C	1 psu v 4 psu	0.121	0.110	0.618	0.720	**0.014**	>0.999
	1 psu v 7 psu	**<0.001**	0.396	0.290	0.268	0.252	>0.999
	1 psu v 10 psu	**<0.001**	**<0.001**	**0.040**	**<0.001**	0.280	0.091
	4 psu v 7 psu	**<0.001**	0.424	0.186	0.654	0.110	>0.999
	4 psu v 10 psu	**<0.001**	**<0.001**	0.232	**<0.001**	**<0.001**	>0.999
	7 psu v 10 psu	**<0.001**	**<0.001**	**0.002**	**<0.001**	0.052	0.777

Table 4: Random effects parameter estimates for mixed effects models fitted on fork length (FL) or body condition (*K*_{*n*}) of blue catfish exposed to increased salinity at 12 or 22°C. σ^2 = variance; ρ = correlation

Parameter	Estimate for FL	Estimate for K_n
$\sigma^2_{\text{week 4}}$	1.48	0.0013
$\sigma^2_{\text{week 8}}$	4.97	0.0031
$\sigma^2_{\text{week 12}}$	9.85	0.0033
$\sigma^2_{\text{week 16}}$	11.3	0.0038
ρ	0.84	0.6993

Figures

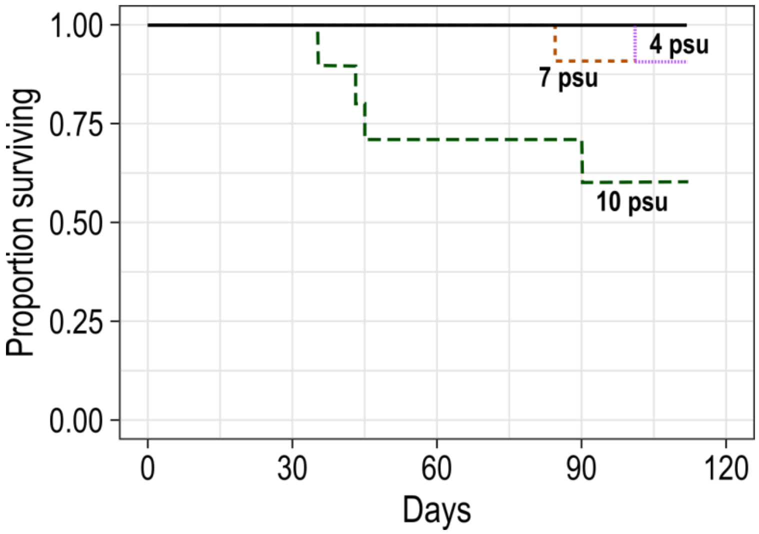

Figure 1: Survival of blue catfish over time in various salinity treatments at 12 and 22°C for 112 days. Each line represents one aquarium with 10 blue catfish; black solid line includes multiple overlapping lines. All mortalities occurred in 22°C treatments.

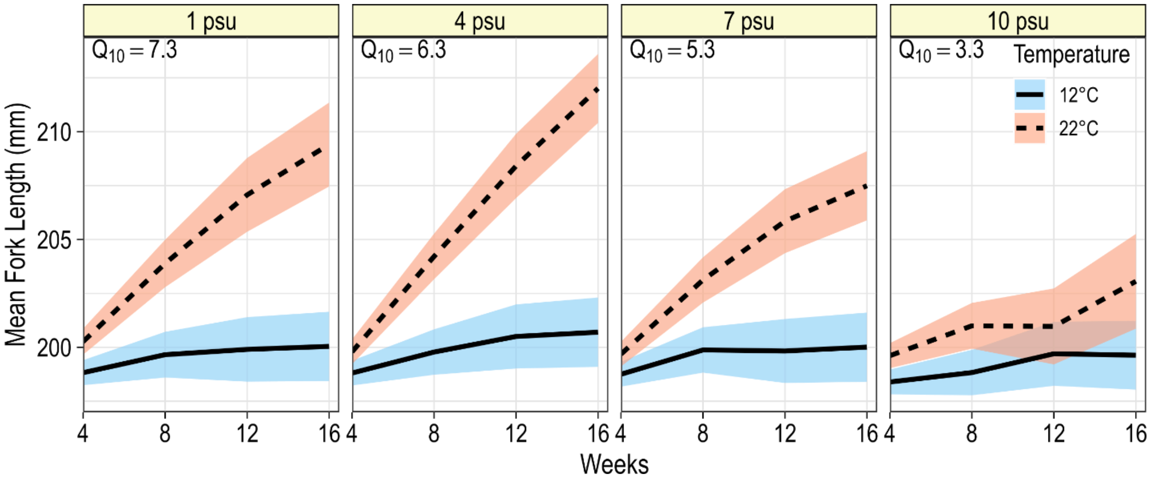

Figure 2: Mean fork length of juvenile blue catfish during a 16-week period at two temperatures and four salinities. Ribbons represent 95% confidence bands around the predicted mean fork lengths. Predictions are for a fish that was 198 mm at the start of the experiment (i.e., at week 0). For each salinity, Q_{10} estimates, assuming linear growth, are provided at the top left corner of each panel.

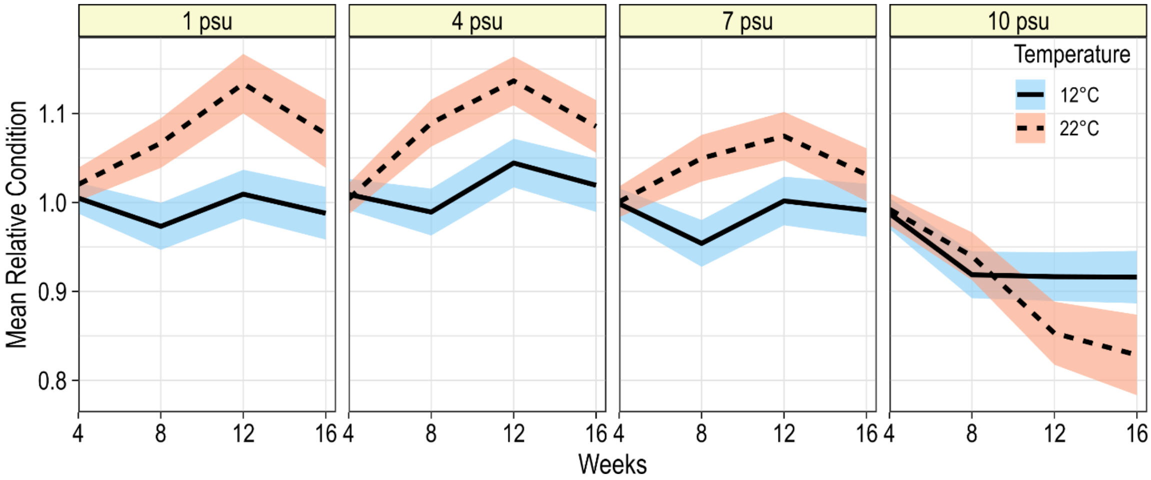

Figure 3: Mean relative condition factor (K_n) of juvenile blue catfish during a 16-week period at two temperatures and four salinities. Ribbons correspond to 95% confidence bands around the predicted mean condition factors. Predictions are for a fish that had a K_n of 1.02 at the start of the experiment (i.e., at week 0).

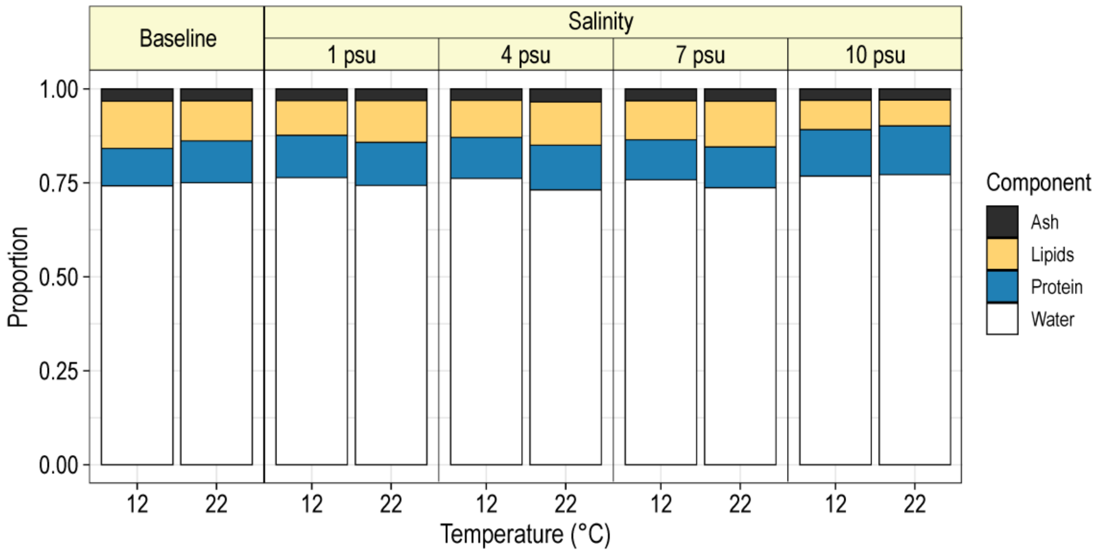

Figure 4: Mean body composition of juvenile blue catfish subjected to one of four salinities at 12 or 22°C for 16 weeks. Baseline refers to mean body composition of blue catfish prior to exposure to salinity treatments. Predictions are for a fish with wet weight of 96.5 g (average weight of fish in the analysis).

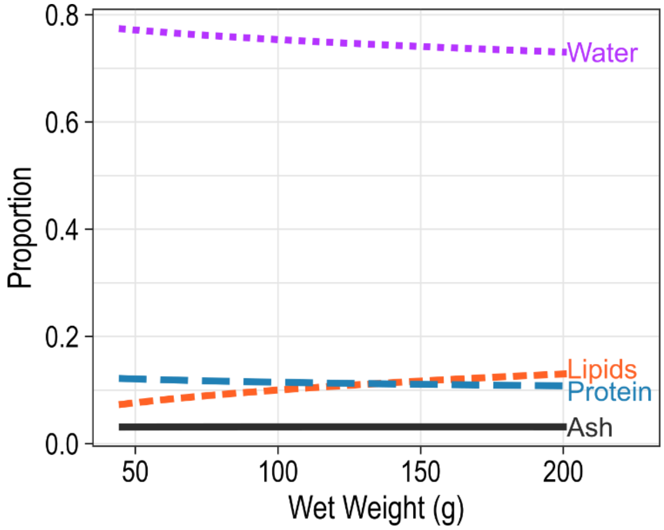

Figure 5: Mean body composition of juvenile blue catfish as a function of wet weight of the fish.

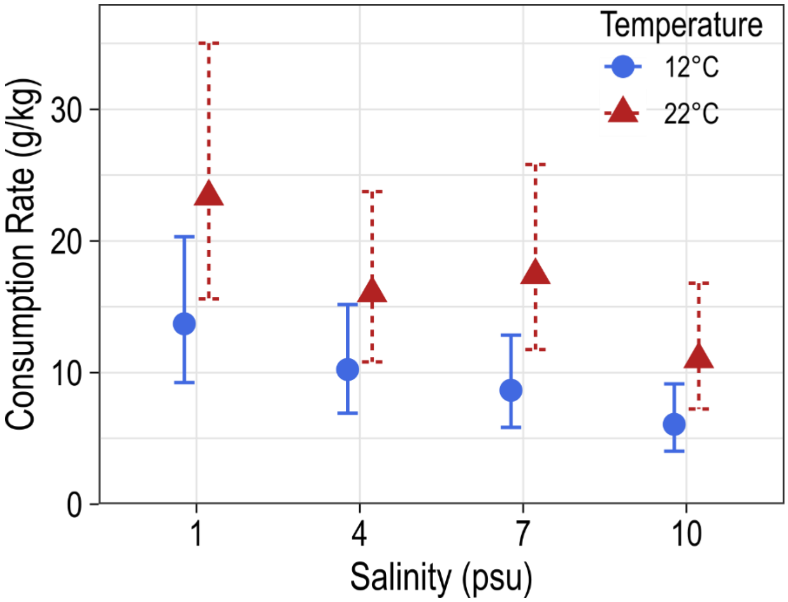

Figure 6: Mean consumption rates (g/kg) of juvenile blue catfish at two temperatures and four salinities. Error bars correspond to 95% confidence bands around the predicted consumption rates.

CHAPTER 6: A Full Life-Cycle Bioenergetics Model for an Invasive Population of Blue Catfish

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Abstract

Blue catfish *Ictalurus furcatus* is an invasive species in lakes and coastal rivers throughout the eastern United States. Due to high population densities and negative effects on native species, the potential for blue catfish to invade and colonize aquatic ecosystems is a key management concern. Identification of the eco-physiological mechanisms and strategies of this species is necessary to determine its potential range. To aid this, we developed a mechanistic, full life-cycle bioenergetics model based on Dynamic Energy Budget (DEB) theory for an invasive population of blue catfish. The DEB model suggested that blue catfish have low maintenance costs but relatively high reserve capacity. The species is well adapted for life in low food conditions, such that individuals can mature and reproduce even when food levels are as low as 17.3% of maximum. Blue catfish may thus outcompete native species in novel habitats. Moreover, blue catfish allocate a large fraction (55%) of assimilated energy towards reproductive processes, and the reproductive output of large individuals is relatively insensitive to food availability during the spawning season. Because smaller fish cannot tolerate starvation as well as larger fish, population density and reproductive output of blue catfish may be controlled by focusing efforts on the disruption of survival and growth of juveniles.

Keywords: Dynamic Energy Budget (DEB) theory; invasive species; blue catfish; metabolic demands; bioenergetics

1. Introduction

Projection of a species' ability to shift or expand its range and distribution is an important consideration for management of invasive species (Lockwood et al., 2013). When combined with information on the ecological role of the species, such projections may provide insight on the arrival time and, thus, likely impacts of invasive species in particular habitats. Predictive models of range expansion allow managers to identify and conduct targeted actions, and thus, decrease the rate of spread of invasive species (Guisan et al., 2013; Simberloff and Gibbons, 2004). Commonly used approaches for projections of range expansion, such as species distribution models (Elith and Leathwick, 2009), are correlative by nature, and thus, such projections cannot be extrapolated beyond the spatial or temporal range of the data used to develop the model (Torres et al., 2015). Mechanistic approaches based on physiological processes are, therefore, better suited to assess the fundamental niche, and hence the habitat suitability and potential distribution and establishment of non-native species in novel habitats.

The Dynamic Energy Budget (DEB) theory (Kooijman, 2010a) provides a mechanistic, first-principles framework to assess the fundamental niche of a species. DEB models quantify changes in energy flow at the organism level by explicitly allocating energy to growth, reproduction, and maintenance. Environmental conditions that affect energy acquisition and use by an individual can therefore be investigated using DEB models. By mathematically linking individual physiology and life-history traits to environmental conditions, DEB theory provides a comprehensive framework for investigating the consequences of environmental factors on growth and reproduction (Martin et al., 2012). For example, Teal et al. (2012) combined DEB-model results with spatiotemporal observations of environmental conditions to map optimal habitats for growth of marine flatfishes and to explore the effect of climate-driven warming on such habitats. Similarly, DEB models were used to predict range expansion of an invasive mussel in the Mediterranean Sea (Sarà et al., 2013).

We developed a DEB model for blue catfish *Ictalurus furcatus* as a first step towards identification of environmental conditions that support movement and occupancy of the species in coastal rivers of the eastern United States. Blue catfish is an invasive species of management concern in tidal rivers and estuaries along the Atlantic coastal plain of the United States (Fabrizio et al., in review; Schloesser et al., 2011). Owing to large population size and densities (Bunch et al., 2018; Fabrizio et al., 2018), opportunistic feeding behavior, broad diet breadth (Schloesser et al., 2011; Schmitt et al., 2019), and increasing ranges (Nepal and Fabrizio, 2019), blue catfish may negatively impact the structure and function of novel ecosystems through competition with, and predation on, native species. Managers are therefore interested in predicting the potential distribution and range expansion of this species in non-native ranges throughout the eastern U.S. (Fabrizio et al., in review).

Identification of food densities that allow blue catfish to survive, grow or reproduce can be important in understanding the potential range of the fish (Tilman, 1982): if blue catfish can survive in low food conditions, they may outcompete native species, and establish populations even in marginal habitats. In addition, temperature affects the rate of growth, maturation and senescence via effects on ingestion and metabolic costs (Brett and Groves, 1979; Kooijman, 2010a). Blue catfish have low metabolic rates and can survive for extended periods even at low food conditions (chapter

3). The combined effects of food availability and temperature on the energetic requirements of this species are, however, not known. Yet, in temperate lakes, rivers and estuaries, which are characterized by considerable spatiotemporal variability in environmental conditions, an organism faces dynamic changes in food and temperature. It is therefore crucial to incorporate the effects of both forcing variables on the energetics of blue catfish to obtain ecologically meaningful estimates of its fundamental niche. In the blue catfish DEB model developed here, we used food level and temperature as the forcing variables that govern growth and metabolism.

We used information from the first three chapters, together with observations from the literature, to parameterize a DEB model for the non-native population of blue catfish in the tidal James River, Virginia. This river is a subestuary of Chesapeake Bay. Our aim was to identify the energetic mechanisms that allowed blue catfish to establish and expand into non-native habitats, and to provide a template for the development of predictive models of blue catfish range expansion throughout the eastern United States.

2. Methods

Description of DEB model: DEB theory is an efficient, general and thermodynamically formalized framework for modeling the energetics of an organism throughout its entire life cycle (Kooijman, 2010a; van der Meer, 2006). DEB models, rooted in biochemical and thermodynamic principles, comprise quantitative descriptions of the macro-physiological processes affecting energy use of organisms, and the outcome of such processes on life-history parameters and events. Animals modeled in the DEB framework also follow several homeostasis and allocation rules and metabolic scaling assumptions as described in detail elsewhere (Kooijman, 2010a).

In the DEB model, an individual blue catfish is described by four state variables: structure V (volume in cm^3), reserves E (energy in joules, J), maturity E_H (J) and reproduction buffer E_R (J). Dynamics of the state variables are quantitatively defined by eight energy fluxes: ingestion, assimilation, mobilization, growth, somatic maintenance, maturity, maturity maintenance and reproduction (Figure 1a, Table 1). Food ingested by an animal is assimilated into the body in the form of reserves, which is mobilized to fuel all activities of the organism such as swimming, respiration, digestion, and so forth. The assimilation flux $\dot{p}_A$ is given as:

$$\dot{p}_A = f\{\dot{p}_{Am}\}V^{\frac{2}{3}} \tag{1}$$

where the scaled functional response f ranges between 0 (no food) and 1 (maximum amount of food ingested by an animal with structural volume V). $\{\dot{p}_{Am}\}$ (J d^{-1} cm^{-2}) is the maximum surface-area specific assimilation rate, and $V^{2/3}$ is the structural surface area.

The assimilated energy is mobilized using the so-called κ rule, which is a central tenet in DEB theory (Kooijman, 2010a). A constant fraction κ is allocated to growth and somatic maintenance (soma) and the remainder (i.e., 1 – κ) to maturation, maturity maintenance and reproduction (Figure 1a). Growth, defined as the synthesis of structure from the reserve, requires energy to combine the building blocks into biomass. This process has some overhead costs (i.e., energy) to account for inefficiency in conversion of reserve into mass. Structure also requires energy for maintenance, the cost of which is proportional to the size of structure. The $1 - \kappa$ fraction of mobilized energy initially goes towards maturation, which is the process of increasing complexity in the organism as it develops. Maturity is therefore quantified as the cumulative amount of energy invested into the process of maturation. Unlike most fisheries literature where the term “maturity” refers to the attainment of the capacity to reproduce, DEB theory uses the term to refer to the status of the organism throughout its life; the transition into the stage capable of reproduction is termed “puberty” in DEB theory (Kooijman, 2010a). Energy invested in maturation is assumed to be lost into the environment in the form of heat and metabolites and thus, does not contribute to the weight of the fish (Kooijman, 2010a). Similar to structure, maturity also requires maintenance, proportional in size to the maturity status of the fish. After puberty, the energy allocated to maturation is diverted to a reproduction buffer E_R, which is utilized to produce gametes. DEB theory dictates that somatic maintenance is prioritized over growth, and maturity maintenance is prioritized over maturation and reproduction. Sets of equations for energy fluxes and dynamics of state variables together fully describe the energy budget of an animal (Table 1).

Life-stage transitions occur at specific maturity thresholds. The standard DEB model predicts that post-embryonic growth in constant environments is described by the von Bertalanffy growth model, and this prediction supports the widespread characterization of fish growth with the von Bertalanffy model. Most fishes are modeled with an ‘abj’-type model because larvae undergo metabolic acceleration such that growth before and after metamorphosis follows different patterns, viz. an upcurving, exponential growth curve between birth and metamorphosis and a von Bertalanffy-type curve after metamorphosis (Kooijman et al., 2011). Ictalurid catfishes, such as blue catfish do not undergo such metamorphosis however, because in this species, individuals that have used their yolk-sac resemble adults (Cloutman, 1979). Early growth of blue catfish does not, therefore, exhibit an “upcurving” shape. We therefore used the “std”-DEB model for blue catfish, thereby assuming four life stages: eggs, yolk-sac larvae, juveniles and adults (Figure 1b). At conception, an animal has a maturation energy of zero ($E_H = 0$ J). Eggs and yolk-sac larvae do not feed and thus depend on reserves for survival and growth. Juveniles start exogenous feeding at maturity level $E_H = E_H^b$, an event considered “birth” in DEB theory (Kooijman, 2010a). After puberty ($E_H = E_H^p$; i.e. the adult stage), allocation of energy towards maturation stops and allocation of energy towards reproduction starts. Because in general a critical amount of energy has to be invested into gonads before successful reproduction can occur, the age at puberty in DEB theory corresponds to an age earlier than the age at first spawning. Fish growth is assumed to follow isomorphy (i.e., the animal’s shape does not change with growth), and the ratio between surface area and volume remains constant during ontogeny (Kooijman, 2010a).

The state variables, structure and reserve, are abstract quantities and do not directly link to specific chemical compounds in the organism. These variables, however, can be converted to commonly measured quantities such as length and mass using conversion factors. Fish length (L_w) is related to structural length ($L \equiv V^{1/3}$) as

$$L_w = L/\delta_M \qquad (2)$$

where δ_M is the shape factor. Dry body mass W_d of an individual is composed of structure, reserve and reproduction buffer:

$$W_d = d_{Vd}V + E\frac{w_E}{\mu_E} + E_R\frac{w_E}{\mu_E} \qquad (3)$$

where d_{Vd} is the specific density of dry structure (g cm^{-3}), w_E is the molecular weight of reserve (g mol^{-1}) and μ_E is the chemical potential of the reserve (J mol^{-1}). Assuming that reserves do not contain water and that specific density of fish wet structure d_{Vw} is 1 g cm^{-3}, wet body mass W_w of fish can be given as:

$$W_w = d_{Vw}V + E\frac{w_E}{\mu_E} + E_R\frac{w_E}{\mu_E} \tag{4}$$

Mass fluxes of organic (food X, feces P, reserve E and structure V) and mineral (CO_2, O_2, H_2O and NH_3) compounds can be calculated based on mass balance equations as a weighted sum of assimilation, dissipation and growth fluxes ($\dot{p}_A$, $\dot{p}_D$ and $\dot{p}_G$). Conversion of oxygen flux to state variables requires mass-energy couplers η for conversion of mineral flux to energy flux. Table 1 and Kooijman (2010a) provide details on full model specification. Because oxygen consumption rates of fish used in this study were estimated from individuals that had not been fed for at least 40 hours, we set the assimilation flux $\dot{p}_A$ to zero.

Data and parameter estimation: We used a combination of field and laboratory data to parameterize the DEB model. We restricted the DEB model to female blue catfish because we had the most relevant data for females. Blue catfish show sexual dimorphism in growth and potentially other life-history characteristics (Nepal et al., 2020); from a bioenergetics perspective, males are likely to have different DEB parameter sets compared with females. Future versions of the DEB model for blue catfish may incorporate male fish. Whenever possible, model input data were obtained from the James river population of blue catfish, but additional inputs were obtained from the literature.

Zero-variate data (i.e., scalar data) included age at birth (d), total length (TL) at birth (cm), egg diameter (cm), ash-free dry mass of an individual egg (µg egg^{-1}), TL at puberty (cm), total wet weight at puberty (g), maximum life span (d) and maximum wet weight for the James River population (g, estimated as the mean of the largest five female blue catfish in our samples). Univariate data (i.e., a list of two paired vectors corresponding to an independent and a dependent variable) included TL at age for female blue catfish collected from James River during two time periods (1998-2000 [“early”; Connelly, 2001], and 2015-2017 [“recent”; Nepal et al., 2020]), fecundity at length from the recent period, 2015-2017 (chapter 2), and mass-specific oxygen consumption rates for fish of varying size (chapter 3). The early and recent populations were assumed to differ by their consumption rates which reflected density-dependent processes: relative density of blue catfish was substantially lower during the early period compared with the recent population (Chapter 1). This difference was modeled by allowing the functional response f to vary between the two stages (i.e., one constant f for each population). The most likely f values for each stage that resulted in the observed growth patterns were identified in the estimation procedure by optimization (see below).

The specific density of dry structure d_{Vd} was fixed to 0.26 g cm^{-3} based on data collected from wild-captured blue catfish during 2018. Specifically, we calculated d_{Vd} as the mean of the ratio of dry weight to wet weight of blue catfish (15-128 g wet weight; n = 30). Specific density of dry reserves d_{Ed} was set equal to d_{Vd} following the general convention (Kooijman, 2010b). A constant d_{Vd} as used here assumes that the proportion of water does not change over the lifetime of a fish; in reality, however, the proportion of water decreases with size (chapter 5).

We used TL as the length measure in the DEB model. For length data that were available only as fork length (FL), we converted FL to TL using the relationship:

$$TL = 2.477 + 1.169 \times FL - 0.00012 \times FL^2 \qquad (5)$$

where TL and FL are both measured in mm. We developed this relationship from 1,308 blue catfish (TL 108-1,131 mm) captured from the James and York rivers during 2015-2017 ($R^2 = 0.99$).

We used a single shape factor δ_M for both larvae and adults, thus assuming that the shape of the fish does not change with ontogeny. We included another shape factor δ_{Me} to convert between the measured diameter and the structural diameter of the egg. For simplicity, spawning and egg production of blue catfish were modeled on a continuous basis throughout the year (eggs day^{-1}) even though spawning mostly occurs during spring and summer (Graham, 1999; chapter 2). Seasonal reproduction can, however, be simulated in the DEB model by allowing the reproduction buffer to accumulate energy throughout the year, but to produce eggs, the reproduction reserve is drawn upon only between the egg development and spawning periods (Pecquerie et al., 2009).

In addition to food, temperature was also treated as a forcing variable as it affects metabolic rates, and thus consumption rates and growth of an organism. In the DEB model, the effect of temperature on physiological processes is characterized by its Arrhenius temperature T_A (K):

$$\dot{k}(T) = \dot{k}_1 \exp\left(\frac{T_A}{T_{ref}} - \frac{T_A}{T}\right) \qquad (6)$$

where $\dot{k}(T)$ is the physiological rate at temperature T (K), and $\dot{k}_1$ is the physiological rate at the chosen temperature T_{ref} (Kooijman, 2010b). For this study, we chose a reference temperature T_{ref} of 293.15 K (i.e., 20°C). Estimation of T_A requires measurements of physiological rates at multiple temperatures; such data were not available for blue catfish. We, therefore, used data on the mean oxygen consumption rates of flathead catfish

Pylodictis olivaris between 3°C and 32°C (Bourret et al., 2008). By regressing the natural log of oxygen consumption rates against 1/T, we obtained the value of T_A = 5000 K, the slope of the linear regression (see Appendix B). Measured physiological rates at specific temperatures were subsequently converted to those at T_{ref} = 20°C by multiplying by the Arrhenius correction factor (Kooijman, 2010a; van der Meer, 2006).

Lack of data precluded us from estimating some of the DEB parameters, which were replaced with values of the generalized animal (Kooijman, 2010b). These fixed parameters included maximum surface area-specific searching rate $\{F_m\}$ = 6.5 cm^{-2} d^{-1}, defecation efficiency κ_P = 0.1, reproduction efficiency κ_R = 0.95, Gompertz stress coefficient s_G = 0.0001, the chemical potential parameters (μ_V= 500 kJ mol^{-1}, μ_E = 550 kJ mol^{-1}, μ_X = 525 kJ mol^{-1} and μ_P = 480 kJ mol^{-1}) and the molecular weights of food w_{Xd}, structure w_{Vd} and reserve w_{Ed} ($w_{Xd} = w_{Vd} = w_{Ed}$ = 23.9 g mol^{-1}). Surface area-specific somatic maintenance rate $\{\dot{p}_T\}$, which accounts for osmotic work, was also fixed to zero, as is typically done for fishes when relevant data are not available (Kooijman, 2010a).

Initial model runs suggested substantially lower volume-specific somatic maintenance compared to most animals in the Add-my-Pet (AmP) library (https://www.bio.vu.nl/thb/deb/deblab/add_my_pet/index.html). Therefore, we replaced the pseudo-data point $\dot{k}_J$ with maintenance ratio k ($\equiv \dot{k}_J/\dot{k}_M$); the initial value of k was set to 0.3 with a low weighting factor of 0.1. A maintenance ratio of k < 1 suggests that well-fed fish reach puberty at a larger size but younger age compared with less well-fed fish (Kooijman, 2010a). This agrees with our observations for blue catfish from the James and York rivers (Nepal et al., 2020; chapter 1, 2). Moreover, the volume-specific cost of structure $[E_G] = \frac{\mu_V d_{Vd}}{\kappa_G w_{Vd}}$ was fixed to the value of 6.8 kJ cm^{-3}, assuming growth efficiency κ_G = 0.8. Assimilation efficiency (i.e., from food to reserve) was fixed to the value of $\kappa_X = 0.7$, as opposed to the typical value of 0.8 used for the generalized animal (Kooijman, 2010b). We opted for the lower value of 0.7 because wild blue catfish, such as those used in this study, feed on diverse prey items including vegetation, polychaetes, bivalves and fishes (Schloesser et al., 2011; Schmitt et al., 2019); assimilation efficiency depends on food type and is generally lower for vegetation (<0.4) and higher for animal prey (0.7-0.9%; Castro et al., 1989).

The parameters of the Chesapeake Bay blue catfish DEB model were estimated through the AmP procedure (Marques et al., 2018) using the Matlab package DEBtool (downloaded on 02/17/2020 from https://github.com/add-my-pet/DEBtool_M/). In essence, the AmP procedure attempts to identify parameters which result in predictions as close to inputs as possible. In this regard, predictions are obtained for each input data point or data set, but additional predictions and implied properties (see below) can be obtained based on DEB theory. Parameters were estimated simultaneously from the datasets by minimizing the bounded loss function F:

$$F = \sum_{i=1}^{n} \sum_{j=1}^{n_i} \frac{w_{ij}(d_{ij} - p_{ij})^2}{d_i^2 + p_i^2} \qquad (7)$$

where n is the number of different data sets, n_i is the number of datapoints in data set i, w_{ij}'s are weight coefficients, d_{ij}'s are data points, p_{ij}'s are the predicted values, d_i is the mean value for dataset i:

$$d_i = 1/n_i \sum_{j=1}^{n_i} d_{ij} \qquad (8)$$

and p_i is the mean predicted value for dataset i:

$$p_i = 1/n_i \sum_{j=1}^{n_i} p_{ij} \quad (9)$$

The minimum is found using the Nelder-Mead simplex method. Marques et al. (2018) and the online AmP manual (http://www.debtheory.org/wiki/) provide details on the estimation procedure.

We assessed goodness of fit of the DEB model by calculating the relative error of the model for each data set. Mean relative error (MRE) quantifies the overall goodness of fit of the model (Marques et al., 2018). Relative error and MRE range between [0, ∞] with lower values representing model predictions close to the data; an MRE of 0 means predictions match the data exactly.

Implied properties and predictions: The DEB parameters allowed us to infer additional bioenergetic characteristics of female blue catfish. Specifically, we report the age at puberty, maximum reserve capacity, von Bertalanffy growth coefficient, maximum length and weight, and the minimum food density that would allow puberty to occur. See Kooijman (2010b) for details on the calculation of these metrics. Important primary parameters and implied properties of blue catfish were compared with those for other bony fishes (class Actinopterygii) in the AmP library (*n* = 502 species; accessed on February 16, 2020).

The DEB parameters obtained for blue catfish were used to predict the scaled functional responses for blue catfish fed three ration sizes (chapter 3). Juvenile fish were fed either *ad libitum* (a ration size of about ~3.5% of fish body mass), two-thirds of *ad libitum* or one-third of *ad libitum* ration size (*n* = 10 for each ration-size treatment level). Total length was measured every 4 weeks for 16 weeks, though we only use the initial and final lengths for each fish here. Growth was observed in fish from all three ration-size treatment groups. The mean growth rate (mm d^{-1}) was significantly higher for the *ad libitum* ration size, but fish from the two reduced ration sizes did not exhibit significant differences in mean growth rates. Body condition indices did not differ significantly among the three treatments. See chapter 3 for details on the experimental protocol and results.

A possible concern with the results reported in chapter 3 was that ration sizes may have been too high for all treatment levels, especially given the generally good water quality conditions in all three treatment groups. We wanted to test this hypothesis by estimating the functional response f for each treatment level; f values above 1 suggest that ration size was higher than needed. To estimate f for each ration-size treatment level, we set the DEB parameters constant at those obtained above in the estimation step. These DEB parameters were then used in the AmP procedure to identify the f values that resulted in the observed changes in length of fish.

3. Results

The DEB parameters for blue catfish were estimated from wild-captured fish and eco-physiological experiments conducted on fish from the James River. The parameter estimation resulted in an MRE of 0.145, suggesting a good match between predictions and observations (Figure 2; Table 2). For age and length at birth, we used an f of 1 (i.e., *ad libitum* feeding) and assumed that the observations apply to females, even though the sex of the fish was not reported in the source (Simon and Wallus, 2003). For the James River population, f for the early and recent stages were estimated to be 1 and 0.82

respectively; these values represent the average feeding conditions experienced by blue catfish during the two stages of invasion. However, we detected systematic biases in the length-weight relationship predicted by the DEB model for the individual datasets. In particular, weight was predicted to be consistently higher than that observed for most lengths, with relative errors of 0.41 and 0.33 respectively for the early and recent stages (Figure 2b; Table 2). The bias in the length-weight relationship was also evident in the prediction of length and weight at puberty, such that weight at puberty was predicted to be higher than that observed even though TL at puberty was predicted to be slightly lower than observed (Table 2). In contrast, fecundity-at-size and oxygen consumption rate-at-size relationships were relatively well-predicted (Figure 2c, 2d; Table 2).

The DEB parameter estimates, presented in table 3, suggested that blue catfish allocate about 55% of assimilated energy towards reproductive and immune processes ($\kappa = 0.45$). The maximum reserve capacity $[E_m]$ of blue catfish was 6.14 kJ cm^{-3}, a value at the 59th percentile for all bony fishes in AmP library. Together, these parameters suggest that reserve mass is roughly equal to structural mass for adult fish (i.e., after puberty; structural mass : reserve mass = 0.97). The specific somatic maintenance for blue catfish $[\dot{p}_M]$ = 6.76 J d^{-1} cm^{-3} was lower than that for 98% of all bony fishes in the AmP library. The estimated parameters imply that female blue catfish from the James river can attain a maximum TL of 138 cm and wet weight of 41.2 kg under *ad libitum* food throughout the life (i.e., f = 1). An individual would approach these sizes at the rate of 0.086 y^{-1} (von Bertalanffy growth coefficient) assuming a constant temperature of 20°C. Age at puberty was estimated at 3.15 y at 20°C and an f of 1. The minimum f that would allow a fish to reach puberty was estimated at 17.3% of the maximum food level. Finally, estimated

DEB parameters for blue catfish resulted in a value of f of 0.41, 0.37 and 0.35 for the fish fed *ad libitum*, two-thirds *ad libitum* and one-thirds of *ad libitum* respectively (Figure 3; chapter 4).

4. Discussion

DEB parameters and implications: The standard DEB model has been applied to many species of animals, but to the best of our knowledge, this is the first published model for an invasive fish species. The DEB framework allowed us to quantify key eco-physiological and life-history processes of interest to invasion biologists and regional fisheries managers. A single set of DEB parameters captured the biology of blue catfish at two stages of invasion, and allowed testing of important hypothesis about the effect of ration size on growth of juvenile blue catfish. Our DEB model suggested that blue catfish have a relatively slow, “supply-driven” physiology (Lika et al., 2014), characterized by low metabolic demands and a relatively high ability to survive in low or variable food conditions. These results are supported by previous observations on the plasticity in growth and body condition (chapter 1), maturation schedules and reproductive output (chapter 2) and low metabolic rates (chapter 3) of blue catfish.

Blue catfish allocate a smaller fraction of assimilated energy towards somatic processes (κ = 0.45) than 95.2% of bony fishes in the AmP library. This value, though low, is comparable to that for other invasive species such as the mussel *Mytilus galloprovincialis* (κ = 0.47; Monaco and McQuaid, 2018) and the cnidarian *Pelagia noctiluca* (κ = 0.37; Augustine et al., 2014). Despite the low allocation to soma, blue catfish are still able to grow to relatively large sizes (>20 kg) because a comparatively small amount of energy is spent on maintenance of somatic tissues (i.e., low $[\dot{p}_M]$ and low specific oxygen-consumption rates). Because $[\dot{p}_M]$ includes movement and activity costs (Kooijman, 2010a), low $[\dot{p}_M]$ likely also reflects the benthic, sluggish lifestyle of blue catfish. Further, the above-average maximum reserve capacity $[E_m]$ suggests that blue catfish are able to survive relatively long periods of starvation. Together with a low value of κ, the above-average $[E_m]$ suggests that reproductive output is likely to be strongly influenced by fish size and thus food levels during the early stages of life, but reproductive output is likely to remain comparatively insensitive to food intake of mature fish (Augustine et al., 2014).

Habitats where organisms experience reproductive failure often act as barriers to the distribution of invasive species (Petes et al., 2007) and can be used to explore the potential for spatial expansion of blue catfish in rivers of the Atlantic coastal plain (e.g., Sarà et al., 2013). Unfortunately, few coastal habitats in the eastern United States are likely to have food levels low enough to limit establishment and reproduction of blue catfish. The DEB parameter set for blue catfish implies that ingestion levels as low as 17.3% of the maximum for a given size would still allow a fish to mature and reproduce. The key implication is that large fractions of non-native habitats are vulnerable to blue catfish invasion, particularly given the omnivorous, opportunistic feeding behavior of the fish (Schmitt et al., 2019). Categorization of specific habitats into suitable and unsuitable for blue catfish will, however, require information on food, temperature and oxygen levels throughout the area of interest.

Well-fed fish mature at a larger size and younger age than less well-fed fish as implied by the maintenance ratio $k < 1$. This means that fish in the early stage of invasion likely matured at an earlier age and larger size than those at the recent stage of invasion because the higher density in the recent stage is likely to exert density-dependent food limitation (Nepal et al., 2020; Nepal and Fabrizio, 2020). Assuming that k is similarly less than 1 for the York river population, one would expect the fish from the York River to mature at a younger mean age and larger mean size than the fish from the James River because relative density of blue catfish is lower in the York River than in the James River (Tuckey and Fabrizio, 2018). These expectations are supported by the observation that fish in the early period grew faster than those in the recent period in both the James and York rivers (Nepal et al., 2020; chapter 1), and fish from the York River grew faster and reached maturity at a larger size but younger age than those from the James River (chapter 2). Similar results with maturation at an earlier age but larger size during early stages of invasion have been observed in other fishes such as round goby *Neogobius melanostomus* (Masson et al., 2016) and white perch *Morone americana* (Feiner et al., 2012). The James and York river populations of blue catfish also differ in fecundity rates, egg sizes and egg densities. Such differences in life-history characteristics cannot be captured by the present model, however. Future versions of the blue catfish DEB model will need to allow for variability in some DEB parameters to accurately characterize these differences.

Given that trophy and commercial fishers frequently catch fish larger than those used to develop our model, the ultimate TL of 138 cm and wet weight of 41.2 kg at maximum food levels are reasonable. The largest, verified blue catfish from the Chesapeake Bay region was 64.9 kg (VDGIF, 2020), though the sex of the individual is not known. Because male blue catfish grow larger than females (Nepal et al., 2020;

chapter 1), it is possible that the 64.9 kg fish was a male. Modification of the presented blue catfish DEB model to include life-history characteristics of males would provide a better indication of ultimate size for blue catfish as a species. The von Bertalanffy growth coefficient ($\dot{r}_B$ in DEB terminology) at 20°C predicted by the DEB model (0.086 y^{-1}) also seems reasonable given that $\dot{r}_B$ was 0.06 for female blue catfish from the James River (mean temperature 17.3°C) during the recent period (Nepal et al., 2020). Estimated age-at-puberty of 3.15 y is substantially lower than the mean age at maturity observed based on assessment of gonads (7.7 y; chapter 2), but comparable to the 3.6 y estimated by Lester's biphasic growth model (Lester et al., 2004; Nepal et al., 2020). Note that in both Lester's biphasic model and the DEB model, age at puberty represents the mean age at which a fish starts allocating energy towards production of gametes. This age is substantially earlier than the actual age at first spawning.

The DEB parameters suggested that ration sizes for the three treatments discussed in chapter 3 were indeed not higher than the maximum food level. In fact, the ration sizes were likely limiting ($f \leq 0.41$), despite our observation that some food was left uneaten in the aquaria in each of the treatment levels (chapter 3). This suggests that fish growth was hindered by other factors such as water quality, light regimes, food palatability, or stress. Given that water quality and light regimes were conducive to fish growth, we hypothesize that social, behavioral or immune system issues resulted in the observed slow growth and lack of differences in body condition indices among the treatment levels. Blue catfish are greatly susceptible to parasitic infestations (e.g., freshwater ich *Ichthyophthirius multifiliis*), and do not tolerate handling stress well (Dunham et al., 1994; V. Nepal *pers. obs.*). Juvenile blue catfish in aquaria also do not feed well when fish density is low (V.

Nepal, *pers. obs*.). The appetite of fish might have been lower in the experiment than in the wild. Slow growth in laboratory conditions for larval and early juvenile stages of blue catfish was also reported by Sakaris et al. (2011).

Future model developments: The DEB model developed here provides the framework required to predict the range of blue catfish in non-native habitats throughout the eastern United States. Such an analysis requires quantification and simulation of the evolution of energy fluxes throughout the life cycle of an individual based on spatiotemporally explicit observations on food availability, ingestion rates and temperature in non-native habitats (Lavaud et al., 2019; Sarà et al., 2013). These environmental data can also be used to validate the DEB model. Finally, the DEB model developed here for a generalized individual can be used to explore, understand and predict inter-individual differences and population dynamics of blue catfish in novel habitats by incorporating behavioral rules, stochasticity in parameter estimates, and variation in resource density in the environment (Koch and De Schamphelaere, 2020; Martin et al., 2012; van der Meer et al., 2011).

We assumed constant f for the two population stages in the James River (i.e., early and recent stages). This assumption may not hold because of (1) spatiotemporal differences in densities and distribution of blue catfish, and (2) ontogenetic changes in diet. In particular, ontogenetic changes in diet constrain f on the availability and abundance of different prey items at different locations and periods. Seasonal and ontogenetic diet changes also suggest that assimilation efficiency κ_X likely differed with fish size and season. Such differences in κ_X have downstream effects on energy fluxes such as the assimilation rate $\dot{p}_A$. Future work would benefit from quantifying the amounts and assimilation efficiencies for different kinds of prey items consumed by blue catfish during different seasons and stages of life.

The DEB model for female blue catfish from the James River requires modification prior to application to male fish or to other populations of blue catfish. This is because different sexes and different populations likely have substantially different energetic strategies that reflect genetic and environmental pressures. For example, Kearney (2012) used a DEB model to study life-history variation and geographic range limits in the eastern fence lizard *Sceloporus undulatus*, and was able to explain inter-population differences in life-history traits, specifically size at maturity, maximum size, reproductive output and length-mass allometry, by changing a single DEB parameter: the zoom factor *z*. Other parameters such as κ and E_H^p may also be varied to gain insight on life-history strategies (Lika and Kooijman, 2003). Such an analysis would greatly complement our current knowledge of life-history differences between the James and York River populations of blue catfish (Nepal et al., 2020; chapter 2), providing an energetic basis for the observed differences.

Future work should also consider applying the blue catfish DEB model to study the effects of increased salinity on energetics and life-history characteristics of blue catfish. Blue catfish have traditionally been considered a freshwater fish, but have invaded increasingly saline waters in coastal rivers of the eastern United States (Nepal and Fabrizio, 2019). The mechanisms that allow the fish to exploit these estuarine waters and the effects of such conditions on the energetics of blue catfish can be quantified using DEB models. For example, Lavaud et al. (2019) parameterized a DEB model to study the effects of hypoxia (low dissolved oxygen concentration) on Atlantic cod *Gadus morhua*, and predicted reduced growth, biomass and reproductive capacity at reduced dissolved oxygen conditions. Similarly, Maar et al., (2015) and Lavaud et al. (2017) studied the effects of reduced salinity on growth potential and energetics of mussel species. Inclusion of salinity as a forcing variable in the blue catfish DEB model would allow accurate predictions of salinity conditions that would allow establishment, reproduction, and exploitation of specific habitats in Chesapeake Bay as well as other coastal rivers and lakes in the U.S. mid-Atlantic region. Finally, future DEB models would provide a useful first-approximation of exploitable habitats for other invasive fishes in the region, such as the flathead catfish *Pylodictis olivaris,* which has an acute salinity tolerance similar to that of blue catfish (Bringolf et al., 2005; Nepal and Fabrizio, 2019).

Development of DEB models for other native (i.e., white catfish *Ameiurus catus*) and non-native catfish species (flathead catfish and channel catfish *Ictalurus punctatus*) would allow interspecific comparison of bioenergetic strategies of the different species. A key puzzle in catfish invasion in the Chesapeake Bay is why the four catfish species show different levels of success in this region. Channel catfish were introduced to Chesapeake Bay tributaries nearly a century earlier than the blue catfish and are believed to have supported a substantial commercial fishery. Over the past few decades, the relative densities of this species have declined in the Rappahannock, York and James rivers (Tuckey and Fabrizio, 2018). Flathead catfish were introduced to Chesapeake Bay waters during the 1960s and 1970s, and have become a notable invasive species. Yet, the distribution of flathead catfish is patchy, with few individuals captured from oligohaline or mesohaline waters. Finally, the white catfish populations have declined in many

Chesapeake Bay subestuaries (Schloesser et al., 2011). The biological and ecological reasons for these differences in success are not clear, particularly given that the salinity tolerances of these species are similar (Allen and Avault, 1969; Bringolf et al., 2005; Kendall and Schwartz, 1968; Nepal and Fabrizio, 2019). Some competing hypotheses include differences in diet characteristics (e.g., diet breadth, preferences, etc.), in levels of phenotypic plasticity in life-history characteristics, in competitive ability (e.g., aggression) and in metabolic demands. Experimental approaches and evaluation of life-history strategies for each of these species, as outlined for blue catfish in this dissertation, can be helpful in identifying the most likely reason. Development of DEB models for each of these species, based on currently available data, can also aid in this effort by identifying differences in the bioenergetic strategies of these species.

Conclusions: The DEB model for female blue catfish from the James River suggests that blue catfish have low resource requirements and relatively flexible metabolic characteristics allowing survival in resource-limited environments. Such characteristics are conducive to establishment success in novel habitats where this species may be able to survive with a lower amount of resources than that required by other species (Tilman, 1982). Because blue catfish grow large and have few predators in novel habitats, they are able to allocate a large fraction of energy into reproductive processes, producing numerous, large eggs (chapter 2). Importantly, the reproductive output of a blue catfish depends on the size, and not so much on the condition, of the mature fish. Early growth is, therefore, a key factor determining the fitness and overall success of blue catfish in novel habitats. Managers should aim to curtail the growth and survival of early-life stages of blue catfish by disruption of nests and targeted removal of juvenile blue catfish from nursery habitats. Relatively frequent disruption of resource acquisition by juvenile fish may prove to be particularly useful because young, small fish have smaller absolute amounts of reserve than larger fish, and therefore are not able to tolerate starvation as well as larger fish (Kooijman, 2010a). Such management actions must, however, consider the potential harm of these techniques on native species, including the native white catfish, which may be sympatric with blue catfish and use the same habitats for foraging, nursery or spawning.

Author contributions

VN and MCF conceived the idea; VN, MCF and JvdM designed the experiments; VN fitted the DEB model to the data with the help of JvdM and RL; VN led the writing and all authors contributed to the drafts.

Acknowledgments

We thank W. Connelly for providing the growth data for blue catfish from 1998-2000. Funding for this study was provided by Virginia Sea Grant (VN), the Office of Academic Studies at the Virginia Institute of Marine Science (VN), Virginia Marine Resources Commission (MCF) and the US Fish & Wildlife Service (MCF).

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Tables

Table 1: Energy fluxes linked to metabolic processes, state variables, and dynamics of the standard DEB model. Quantities in brackets [ ] are expressed per unit of structural volume, and those in braces {} are expressed per unit of structural surface area. Of the several mineral fluxes considered in DEB, only oxygen consumption flux is shown here.

Energy fluxes	
Ingestion	$\dot{p}_X = \{\dot{p}_{Xm}\} f V^{\frac{2}{3}}$
Assimilation	$\dot{p}_A = \kappa_X \dot{p}_X = \{\dot{p}_{Am}\} f V^{\frac{2}{3}}$
Mobilization	$\dot{p}_C = E \frac{[E_G]\dot{v}V^{\frac{2}{3}} + \dot{p}_S}{\kappa E + [E_G]V}$
Somatic maintenance	$\dot{p}_S = [\dot{p}_M]V + \{\dot{p}_T\}V^{\frac{2}{3}}$, with $\dot{p}_T$ fixed at 0
Growth	$\dot{p}_G = \kappa \dot{p}_C - \dot{p}_S$
Maturity maintenance	$\dot{p}_J = \dot{k}_j E_H$
Maturity	$\dot{p}_H = (1-\kappa)\dot{p}_C - \dot{p}_J$
Reproduction	$\dot{p}_R = (1-\kappa)\dot{p}_C - \dot{p}_J$
Dissipation	$\dot{p}_D = \dot{p}_M + (1-\kappa)\dot{p}_C$ if $E_H < E_H^p$, else $\dot{p}_D = \dot{p}_M + (1-\kappa_R)\dot{p}_R + \dot{p}_J$

Dynamics of state variables	
Reserve	$\frac{dE}{dt} = \dot{p}_A - \dot{p}_C$
Structure	$\frac{dV}{dt} = \frac{\dot{p}_G}{[E_G]}$
Maturity	$\frac{dE_H}{dt} = \dot{p}_R$ if $E_H < E_H^p$, else $\frac{dE_H}{dt} = 0$
Allocation to reproduction	$\frac{dE_R}{dt} = \kappa_R \dot{p}_R$ if $E_H = E_H^p$, else $\frac{dE_R}{dt} = 0$

Mineral flux	
Oxygen consumption	$\dot{J}_O = \eta_{OA}\dot{p}_A + \eta_{OD}\dot{p}_D + \eta_{OG}\dot{p}_G$

Table 2: Inputs used to estimate the DEB parameters for female blue catfish in the James River. See figure 2 for the observations and predictions for univariate data. RE = Relative error

Description	Symbol	Unit	Observed	Predicted	RE	Reference and comments
Egg diameter	L_{w0}	cm	0.314	0.314	<0.001	Chapter 2
Egg organic content	W_{C0}	mg	6.87	6.712	0.023	Chapter 2
Age at birth	a_b	d	9	9.945	0.105	Simon and Wallus 2003; sex unknown
Life span	a_m	d	9125	9125	<0.001	Chapter 1
Length at birth	L_b	cm	1.6	1.25	0.219	Simon and Wallus 2003; sex unknown
Length at puberty	L_p	cm	36	33.06	0.082	Chapter 2
Wet weight at puberty	W_{wp}	g	501	516.1	0.030	Chapter 2
Ultimate wet weight (James River)	W_{wi}	g	22120	20950	0.053	Chapter 1; mean of the largest 5 females
Age since birth vs total length	$t - L_w$	d-cm			0.159	Connelly 2001; collected during 1998-2000
Age since birth vs total length	$t - L_w$	d-cm			0.303	Chapter 1; collected during 2015-2017
Total length vs wet weight	$L_w - W_w$	cm-g			0.414	Connelly 2001; collected during 1998-2002
Total length vs wet weight	$L_w - W_w$	cm-g			0.330	Chapter 1; collected during 2015-2017
Total length vs fecundity	$L_w - N$	cm-#			0.227	Chapter 2
Wet weight vs oxygen consumption	$W_w - JO$	g-mg/kg/hr			0.082	Chapter 3; sex unknown

Table 3: DEB parameter estimates for James River blue catfish, corrected for the reference temperature of 20°C. Quantities in brackets [ ] are expressed per unit of structural volume and those in braces {} are expressed per unit of structural surface area. Symbols with a dot are rates. Free = 1 indicates that a parameter was estimated in the model; Free = 0 indicates that a parameter was fixed during estimation.

Symbol	Units	Value	Free	Interpretation
T_A	K	5000	0	Arrhenius temperature
z		27.3	1	zoom factor
F_m	d^{-1} cm^{-2}	6.5	0	Maximum surface area-specific searching rate
κ_X		0.7	0	Digestion efficiency of food to reserve
κ_P		0.1	0	Faecation efficiency of food to faeces
v	cm d^{-1}	0.06722	1	Energy conductance
κ		0.4476	1	Allocation fraction to soma
κ_R		0.95	0	Reproduction efficiency
$[\dot{p}_M]$	J d^{-1} cm^{-3}	6.765	1	Volume-specific somatic maintenance rate
$\{\dot{p}_T\}$	J d^{-1} cm^{-2}	0	0	Surface-specific somatic maintenance rate
$\dot{k}_J$	d^{-1}	0.0003022	1	Maturity maintenance rate coefficient
$[E_G]$	J cm^{-3}	6800	0	Specific cost for structure
$[E_b^H]$	J	127.5	1	Maturity at birth
$[E_p^H]$	J	2.918e+06	1	Maturity at puberty
$\dot{h}_a$	d^{-2}	3.674e-09	1	Weibull aging acceleration
s_G		0.0001	0	Gompertz stress coefficient
δ_M		0.1978	1	Shape coefficient for larvae and adults
δ_{Me}		1.184	1	Shape coefficient for egg diameter
f		1	0	Scaled functional response for 0-var data
f_1		1	1	Scaled functional response for early period
f_2		0.8233	1	Scaled functional response for recent period

Figures

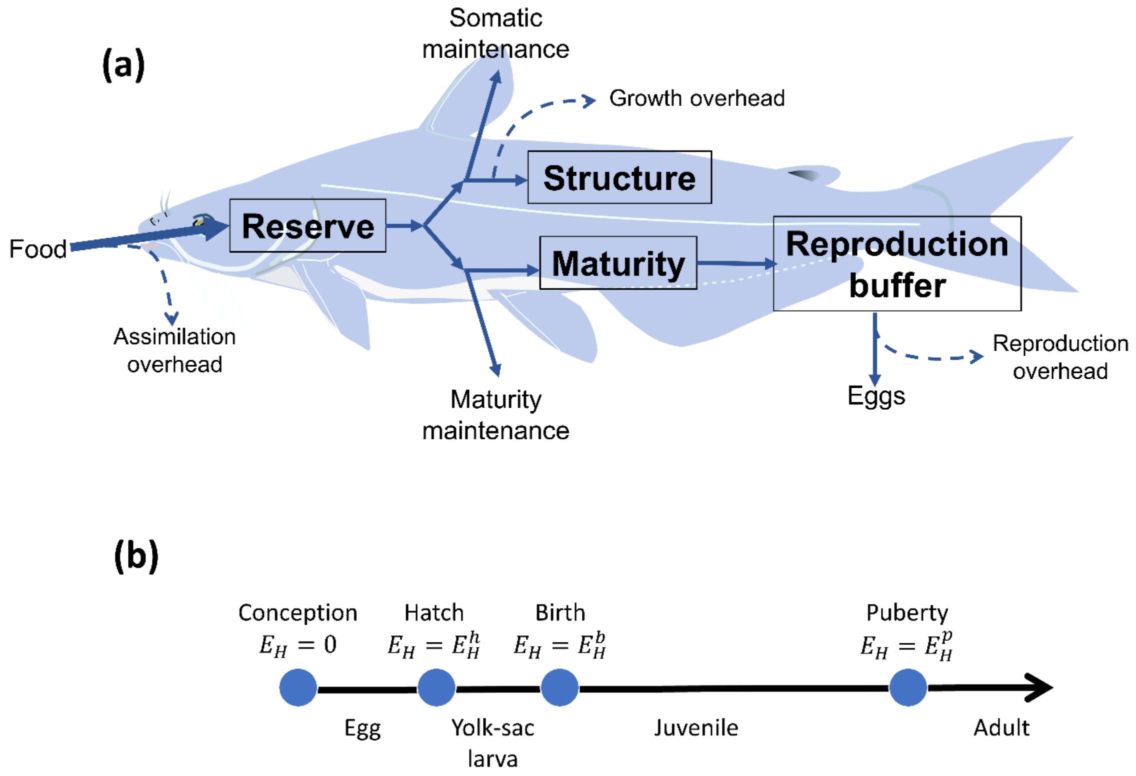

Figure 1: (a) Schematic view of the standard DEB model for female blue catfish. Energy fluxes are defined in Table 1. (b) Schematic of life stages in the DEB model. Each filled circle corresponds to a switch in life stage, from egg to yolk-sac larva at $E_H = E_H^h$, larva to juvenile at $E_H = E_H^b$, and juvenile to adult at $E_H = E_H^p$. At puberty, allocation towards maturation stops, and allocation towards reproduction starts. See text for details.

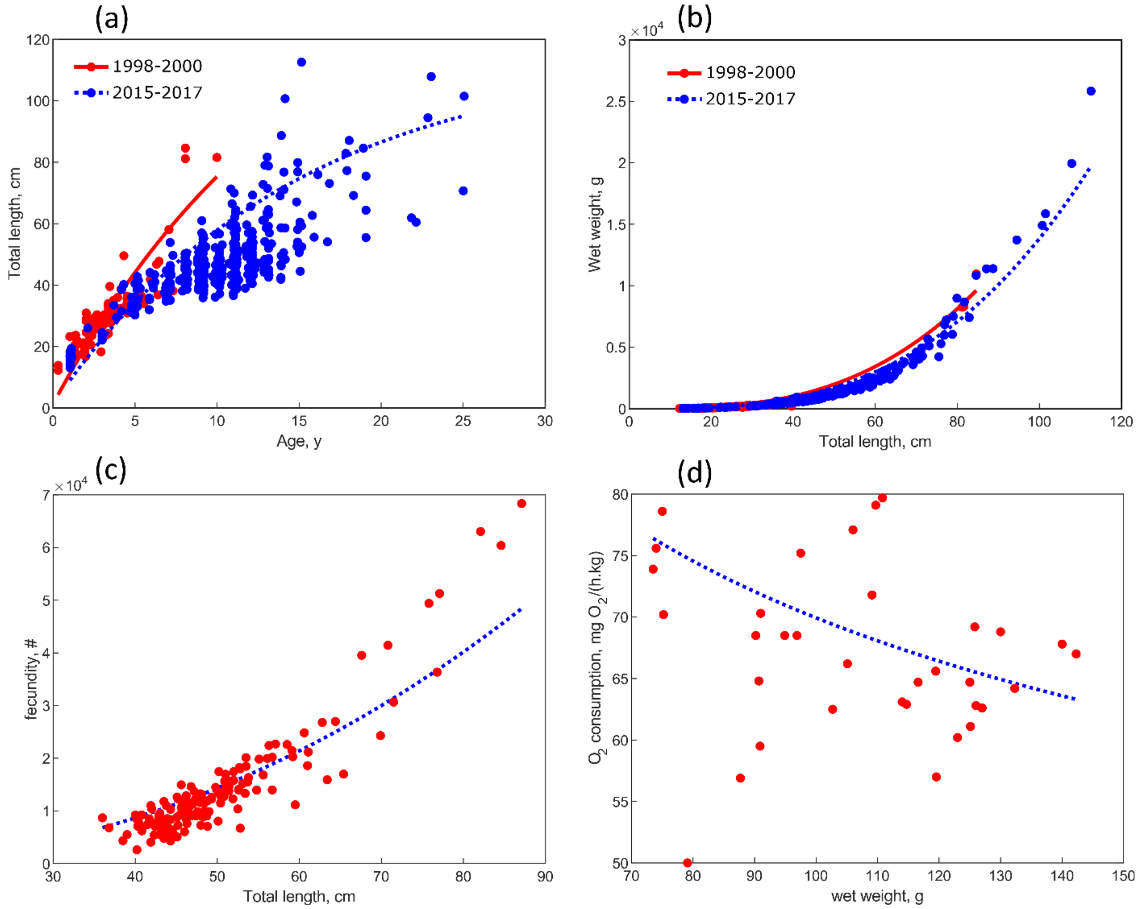

Figure 2: Model fit for the univariate data in the DEB model for female blue catfish from the James River. Points correspond to the observed data and lines indicate model predictions. (a) Total length at age for early (1998-2000; solid red line) and recent (2015-2017; dashed blue line) sampling periods. (b) Wet weight as a function of total length. (c) Fecundity as a function of length for the recent period. (d) Mass-specific oxygen consumption rate for different sizes of fish collected during the recent period.

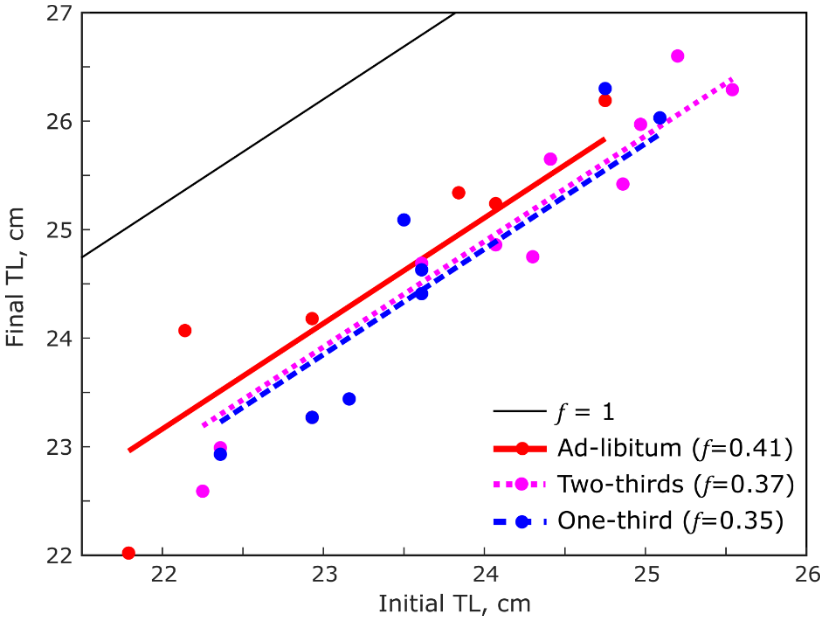

Figure 3: Predicted final total lengths (TL) and scaled functional responses (f) for experimental blue catfish fed either *ad libitum* (solid, red), two-thirds of *ad libitum* (dotted, pink) or one-third of *ad libitum* (dashed, blue) ration size. The predicted length trajectory for maximum food level ($f = 1$, solid black line) is shown also shown for reference.

Appendix

Appendix A

Bourret et al. (2008) report the mean specific daily metabolic demand of flathead catfish *Pylodictis olivaris* at temperatures ranging between 3 and 32°C. We extracted the values from the figure using PlotReader (https://jornbr.home.xs4all.nl/plotreader/). Using the description in Bourret et al. (2008), we converted daily metabolic demand (MET, % body weight d^{-1}) to mass-specific oxygen consumption rates ($\dot{M}O_2, mg\ O_2\ kg^{-1}h^{-1}$):

$$\dot{M}O_2 = MET \times \frac{706 \times 1000 \times 24}{100 \times 3280}$$

We subsequently fitted a linear regression model between $\ln(\dot{M}O_2)$ and $1/T$ where temperature T is in Kelvin. The regression was restricted to temperatures between 10 and 30°C, corresponding to the normal temperature range of flathead catfish activity (i.e., between the lower and upper pejus temperatures). The slope of the regression, which represents the Arrhenius temperature T_A, was -5020. We therefore chose 5000 K as the T_A for the blue catfish DEB model. Inclusion of the measurement at 5°C changed T_A to 4300 K, but this had negligible effect on DEB parameter estimates.

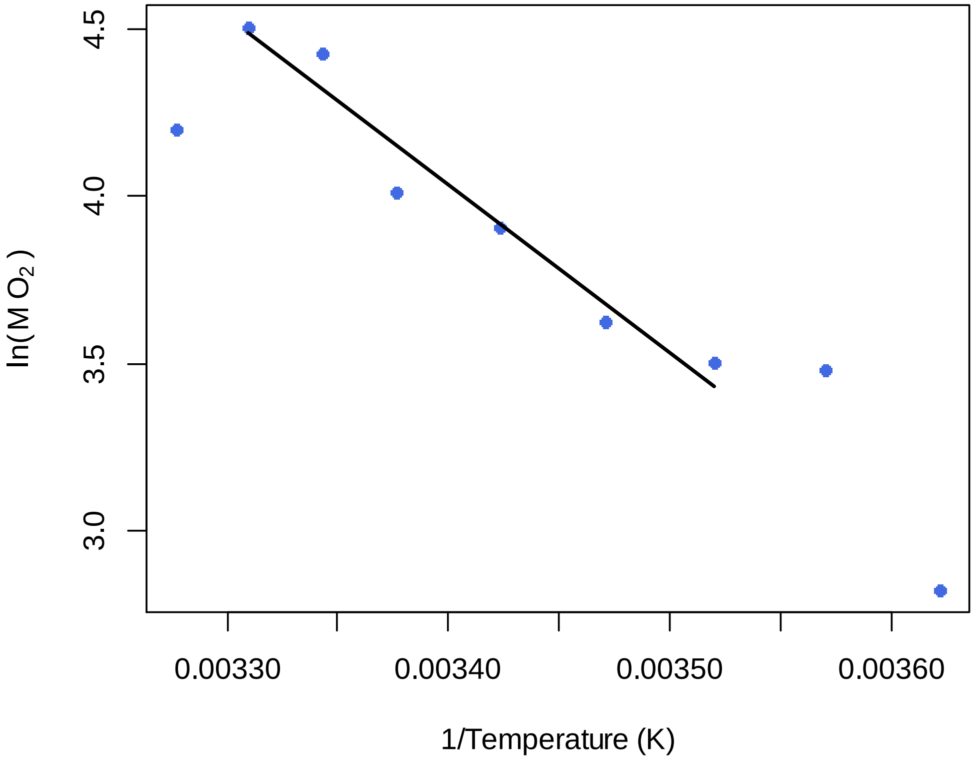

Figure A1: Arrhenius plot for the natural log of mass-specific oxygen consumption rates ($\ln(\dot{M}O_2)$) of flathead catfish resulting in an Arrhenius temperature T_A of 5000 K. The data are based on Bourret et al. (2008); the solid blue line corresponds to the best fit line, the slope of which corresponds to the Arrhenius temperature (-5020 K).

CONCLUSIONS

Blue catfish have many biological traits that seem to support invasion success. These traits include large body size, long lifespan, high phenotypic plasticity (chapter 1), high reproductive output and parental care (chapter 2), low energetic demands (chapter 3), high salinity tolerance (chapters 4 and 5), and relatively high tolerance to starvation (chapter 6). Blue catfish may therefore be able to survive and reproduce in conditions that may be poor or inhospitable for native species. In this regard, blue catfish have the ability to outcompete and hence displace or replace native species through exploitative competition (Tilman 1982; Al-Chokhachy et al. 2016). Predation impacts may also be important because blue catfish have a generalist, opportunistic feeding behavior, with larger individuals specializing on fishes (Schloesser et al. 2011; Schmitt et al. 2017, 2019). Combined with higher mobility of blue catfish compared with other ictalurids (Graham 1999), these characteristics suggest that blue catfish can invade most subestuaries and tidal rivers in Chesapeake Bay and other areas throughout the Atlantic coast of the US.

From a conservationist’s perspective, a key management goal should be the reduction of the population size of blue catfish. Increasing harvest of blue catfish, though not entirely without controversy (see Fabrizio et al., in review), has the two-fold benefit of decreasing the population size of blue catfish and increasing revenue for commercial fishers. The dynamic energy budget (DEB, Kooijman 2010) model for blue catfish (chapter 6) suggested that disruption of spawning and removal of juveniles are likely to be particularly effective because juveniles have a lower tolerance to starvation than adults. Yet, small blue catfish (<250 g) are of little interest to commercials fishers (G. Trice, *pers. comm*.) and are not handled by fish processors. Additionally, larger fish have a disproportionately high contribution to predatory effects on native fishes (Schmitt et al. 2019) and on range expansion and recruitment of blue catfish (chapters 2, 3). Removal of larger individuals may therefore be a more efficient approach to population control. Yet, due to high contaminant loads in large fishes (Luellen et al. 2018) and the value of large fishes in the trophy fishery, harvests of such individuals are not without human health risks and stakeholder conflicts. Regardless, the harvest of blue catfish in Chesapeake Bay habitats is currently limited, among other things, by market size (Fabrizio et al. In review). A key focus must therefore be on increasing market demand for Chesapeake Bay blue catfish.

A key objective of my dissertation was to provide managers with information required for “proactive” management of blue catfish in the Chesapeake Bay. Towards this end, I provided information on important life-history characteristics that drive population models. Proactive management is particularly important in the case of invasive species such as blue catfish: the immense and irrevocable negative impacts that an invasive species can have in novel ecosystems mean that management efforts should start as early as possible (Simberloff 2003). The differences in life-history characteristics of blue catfish in the James and York rivers (chapters 1, 2) also highlight the need for “reactive” management. Because blue catfish populations at different stages or under different fishing pressures demonstrate plasticity in life-history characteristics, population models and management strategies should consider feedback loops and compensation. Continuous monitoring of blue catfish populations is therefore important for proper management of this species.

First-principle approaches can guide management of invasive species. The blue catfish DEB model identified bioenergetic strategies of this species and cleared the path for identification of the physiological mode of action (PMoA) by which high salinity inhibits survival and growth of blue catfish (chapter 3, 4). Common PMoAs include a decrease in assimilation, an increase in the costs for maintenance, growth or reproduction, and a direct hazard to the embryo (Kooijman 2010). Identification of specific PMoAs is important because different PMoAs that lead to the same outcome at the individual level (e.g., reduction in fecundity) may have drastically different effects on populations (e.g., negligible decline in biomass or population extinction) when consumer-resource interactions are considered (Martin et al. 2014). Ultimately, the combination of the blue catfish DEB model with spatio-temporally explicit data on forcing variables (food, temperature and salinity) will allow mechanistic predictions of the fundamental niche of blue catfish in the Chesapeake Bay.

Avenues for future research

The current status and outlook of Chesapeake Bay blue catfish are described in detail in Fabrizio et al. (in review). For the sake of completeness, here I provide some avenues for future research that arise from this dissertation, even if it is somewhat repetitive with Fabrizio et al. (in review). These research avenues come from an academic’s perspective, and ought to be updated in collaboration with managers to enhance their usefulness and value (Funk et al. 2020). Identification of appropriate spatial and temporal scales, and of non-traditional funding and labor sources for long-term monitoring will be crucial towards effective management of this invasive species (Funk et al. 2020).

1. **Connectivity:** A key unknown for blue catfish in the Chesapeake Bay region is the role of connectivity in completion of the life-cycle and in population regulation. Role of high salinity habitats in foraging or range expansion of blue catfish has not yet been studied rigorously. Diel or seasonal activity budgets of blue catfish in the main river channel, river tributaries and shallow, marginal habitats of the rivers are also not known. Finally, the movement of blue catfish among subestuaries, which, if present, would imply existence of blue catfish metapopulations, has not been studied. The inter-subestuary movement and formation of metapopulations are particularly important in the Maryland portion of the Chesapeake Bay, where the salinities are typically low and may be conducive to widespread movement. Seasonal movements and metapopulation dynamics directly influence the population size estimates of, and hence the management strategies for, blue catfish; metapopulations are much harder to extirpate than individual populations (Gotelli 2008; Weber et al. 2016). Otolith microchemistry and acoustic telemetry techniques may provide important insights on the connectivity of blue catfish populations (Möller et al. 2019; Roloson et al. 2020). Role of high salinity habitats in energy balance of blue catfish could also be studied more directly using diet studies; such a study is currently in progress in the James River subestuary (M. Fabrizio, *pers. comm.*).

2. **Physiological traits that facilitate invasion:** Invasive species are often generalists with broad physiological tolerance and low energetic needs, as was observed for blue catfish. Other aspects of blue catfish biology may also affect the success of the species in the Chesapeake Bay region and other estuarine habitats throughout the Eastern United States. First, as the R* hypothesis suggests, ability to survive under low resource conditions and draw down resources to levels below that needed by other species for survival will allow a species such as blue catfish to competitively exclude native species from a location (Tilman 1982). I addressed this idea in terms of standard metabolic rate and growth at low food conditions for blue catfish in laboratory conditions. Yet, food is just one dimension of an organism's niche; the tolerance levels of blue catfish to other conditions are not known. For example, Lagos et al. (2017) reported that invasive marine invertebrates have lower oxygen needs than their native counterparts, suggesting that species with greater hypoxia tolerance are likely to outcompete native species in disturbed, manmade habitats such as marinas. It would therefore be worthwhile to assess the hypoxia tolerance of blue catfish, especially as hypoxic zones are increasing in Chesapeake Bay and its tributaries (Boesch et al. 2007). Such a study would be particularly revealing if comparisons can be made with native species of interest such as white catfish *Ameiurus catus*.

   The ability of blue catfish to invade high salinity waters will depend on the ability of individuals to find food in these environments. Because catfishes rely on electroreception to sense food and the electroreceptory ability of freshwater fishes is likely to be diminished in high salinity environments (New 1999), blue catfish may not be able to sense food in such environments. A confirmation of this hypothesis is needed. Finally, measurement of metabolic rates at different salinities and temperatures would also help predict the suitability of high salinity waters for blue catfish, especially considering the temperature increases and saltwater intrusions expected due to climate change (Claireaux and Lagardère 1999; Rahel and Olden 2008; Ern et al. 2014).

3. **Socioeconomic role of blue catfish:** Blue catfish support a burgeoning commercial fishery as well as well-established recreational and trophy fisheries in many Chesapeake Bay subestuaries. As such, management decisions regarding the reduction of blue catfish population sizes should consider the socioeconomic ramifications of such policies (Pasko and Goldberg 2014). Identification of the best policy under conflicting socioeconomic and conservation interests is difficult and needs to consider human psychology as much as biological reality. The first step towards this might be the economic valuation of blue catfish fishery (commercial, recreational and trophy) in specific rivers and throughout the Chesapeake Bay. Creel surveys and quantitative modeling would benefit this effort. Such data can then be used to support a comprehensive cost-benefit analysis of different management options. For example, an optimal management policy must weigh the benefits of trophy fishery against the adverse ecological and economic impacts from the presence of the non-native blue catfish (and indeed, the flathead catfish *Pylodictis olivaris*).
4. **Simulation modeling of removals:** Hilling (2020) constructed a stock assessment model for blue catfish in the James River and simulated the effects of various harvest strategies on blue catfish size structure and population size, and on the predation

pressure from blue catfish on native species. The model, however, did not include compensatory feedback mechanisms and potential metapopulation dynamics. Currently, it seems that blue catfish populations have reached equilibrium in some rivers (e.g., James and Rappahannock rivers), with decreased growth rates and potentially stabilizing population sizes (Bunch et al. 2018; Hilling 2020; Nepal et al. 2020). Increasing removals will likely engender feedback mechanisms resulting in increased growth rates, increased recruitment and a greater proportion of larger, piscivorous fishes in the population (Nepal and Fabrizio 2020; Nepal et al. 2020). This plastic response is likely to negate the benefits of removals (Bonvechio et al. 2011). Fishing-induced evolution could also be an important aspect to consider (Enberg et al. 2012). The magnitude of plastic and evolutionary feedbacks, though important in calibrating harvest models, is not known. Future management strategy evaluations should attempt to include such feedback loops.

5. **Alternative strategies to population control:** Eradication of blue catfish from the Chesapeake Bay region is neither possible nor of general management interest. As such, alternative approaches to population control need to be developed. For other invasive species, researchers have identified and successfully used various techniques such as disruption of reproductive ability via introduction of sterile males (Twohey et al. 2003) or application of pheromones to induce behavioral changes (Sorensen and Hoye 2007). Development of such techniques for blue catfish would be of practical use for managers of blue catfish. The greatest benefit of these approaches is that the effect on blue catfish populations is gradual, allowing fishers dependent on blue

catfish as a resource to gradually shift efforts towards other fishes and fisheries (Pasko and Goldberg 2014).

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