

Feeding ecology of generalist consumers: a case study of invasive blue catfish *Ictalurus furcatus* in Chesapeake Bay, Virginia, USA

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Abstract Globally, invasive species cause extensive economic damage and are a major threat to biodiversity. Generalist species are particularly dangerous invaders, as they can thrive in degraded habitats and endure environmental stochasticity, often outcompeting more specialized native taxa. Blue catfish *Ictalurus furcatus* were first introduced into the Chesapeake Bay during the 1970s, and now form dense populations in several tidal rivers. Despite being labeled as a dangerous invasive, the feeding ecology of this species is largely unknown. We used a stratified random design to collect stomachs from 16,110 blue catfish in tidal freshwater, oligohaline, and mesohaline segments of the James, Pamunkey, Mattaponi, and Rappahannock Rivers. Indices of diet breadth and omnivory reveal that blue catfish are generalist omnivores with some of the highest diet breadths ever observed in an estuarine fish species, while trophic level calculations demonstrate that blue catfish are a mesopredator occupying lower trophic levels than previously claimed. Cumulative prey curves revealed that large numbers of stomachs are necessary to adequately characterize the diet of blue catfish, thus previous diet descriptions of this species should be

considered with caution. Blue catfish feed primarily on invasive aquatic vegetation and Asian clams, though the economically-valuable blue crab *Callinectes sapidus* is also consumed regularly. While the per capita impact of blue catfish on imperiled native species appears to be low, this impact could still be substantial due to high population densities.

Keywords Invasive species · Food habits · DNA barcoding · Diet · Generalist invaders · Biotic homogenization · Feeding ecology · Blue catfish · Diet breadth · Trophic level · Omnivory index · Ontogenetic shifts · Predator-prey interactions

Introduction

Invasive species can cause population declines and extinction of native species (Mills et al. 2004), and are a major threat to biodiversity (Lockwood et al. 2013). Globally, specialist taxa are being replaced by invasive generalists with broad ecological niches, a trend known as biotic homogenization (McKinney and Lockwood 1999; Clavel et al. 2010). Many generalist species have a competitive advantage due to their ability to thrive in degraded habitats, which has sparked a renewed interest in the characterization of generalist consumers worldwide (McKinney and Lockwood 1999; Layman and Allgeier 2012). Some of the most successful invasives consume a broad array of food items, with diets comprised of both plant and animal material (Twardochleb et al. 2013; Jackson et al. 2017). These omnivorous food

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habits place them in the middle of the food web, with direct consumptive links to multiple trophic levels; this helps them endure adverse conditions and changes in prey availability (Layman and Allgeier 2012; Jackson et al. 2017). Despite the considerable attention that invasive species receive, little is known about the life history and feeding ecology of many of these organisms, and more observational and experimental studies are urgently needed (García-Berthou 2007; Layman and Allgeier 2012; Brandner et al. 2013).

Once established, novel generalist consumers can drastically alter invaded ecosystems. Food webs are restructured, which can lead to changes in ecosystem function, productivity, and the deterioration of ecosystem goods and services (Mack et al. 2000; Clavel et al. 2010). Populations of invasive generalists can reach densities that are orders of magnitude greater than similar native species, and, because they are linked to multiple trophic levels, result in widespread impacts on invaded communities (Snyder and Evans 2006). Feeding ecology studies are of particular importance, as diet is a primary determinant for predicting how invasive species will affect food webs of receiving systems (Brandner et al. 2013; Garvey and Whiles 2017). Moreover, the classification of a novel species along the generalist-specialist feeding continuum has significant implications for their long-term success after establishment (Moyle and Light 1996), and the precise ecological impact of an introduced species depends largely on its trophic position within the food web (McKnight et al. 2016).

Native to tributaries of the Mississippi River, the blue catfish *Ictalurus furcatus* is a large catfish species that has been widely introduced into Atlantic and Pacific drainages in the U.S. (Graham 1999; Eggleton and Schramm Jr 2004). This species can weigh in excess of 50 kg, reaches high population densities, and may be a dangerous invader (Graham 1999; Greenlee and Lim 2011; Howeth et al. 2016). Even so, there is a general paucity of information on this species (Graham 1999) and little is known about the feeding ecology of this species outside of its native range (Schmitt et al. 2017). Blue catfish were stocked in tidal freshwater portions of the Chesapeake Bay from 1973 to 1985 to create new recreational fisheries (Greenlee and Lim 2011). Blue catfish populations have since expanded to occupy all major tributaries of the Chesapeake Bay, and are now considered invasive (Fabrizio et al. 2017). Blue catfish have expanded to brackish portions of the estuary, and

have been captured in salinities as high as 21.5 ppt (Fabrizio et al. 2017). Blue catfish dominate the fish biomass in some locales, which has caused concern about their potential interactions with native species (Greenlee and Lim 2011; Schloesser et al. 2011), and prompted the Chesapeake Bay Program (CBP) to develop an “invasive catfish policy”, which calls for more research on the life history and ecological role of this species (CBP 2012).

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

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

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

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

Methods

Study area

The Chesapeake Bay is the largest estuary in the United States, with a surface area of 1.15×10^4 km² and a total volume of 70 km³ (Shiah and Ducklow 1994). The Chesapeake Bay is a shallow, partially-mixed system that receives about 50% of its water from the Atlantic Ocean and the other 50% from freshwater tributaries (Jung and Houde 2003). The Chesapeake Bay watershed is far from pristine, and anthropogenic eutrophication has resulted in major ecological changes within the estuary (Kemp et al. 2005). It is highly productive when compared to other brackish systems (Nixon 1988), and has supported commercial fisheries since the late 1700s (Jung and Houde 2003). This study was conducted in Virginia's tidal rivers—the James, Pamunkey, Mattaponi, and Rappahannock rivers. Blue catfish were originally stocked in these rivers during the 1970s and 1980s, and now occur at high densities (Greenlee and Lim 2011). Virginia tidal rivers contribute nearly 20% of the total freshwater input for the Chesapeake Bay (Schubel and Pritchard 1987; Fig. 1), and support a diverse array of freshwater and marine organisms (Murdy et al. 1997; Schloesser et al. 2011).

Field methods

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

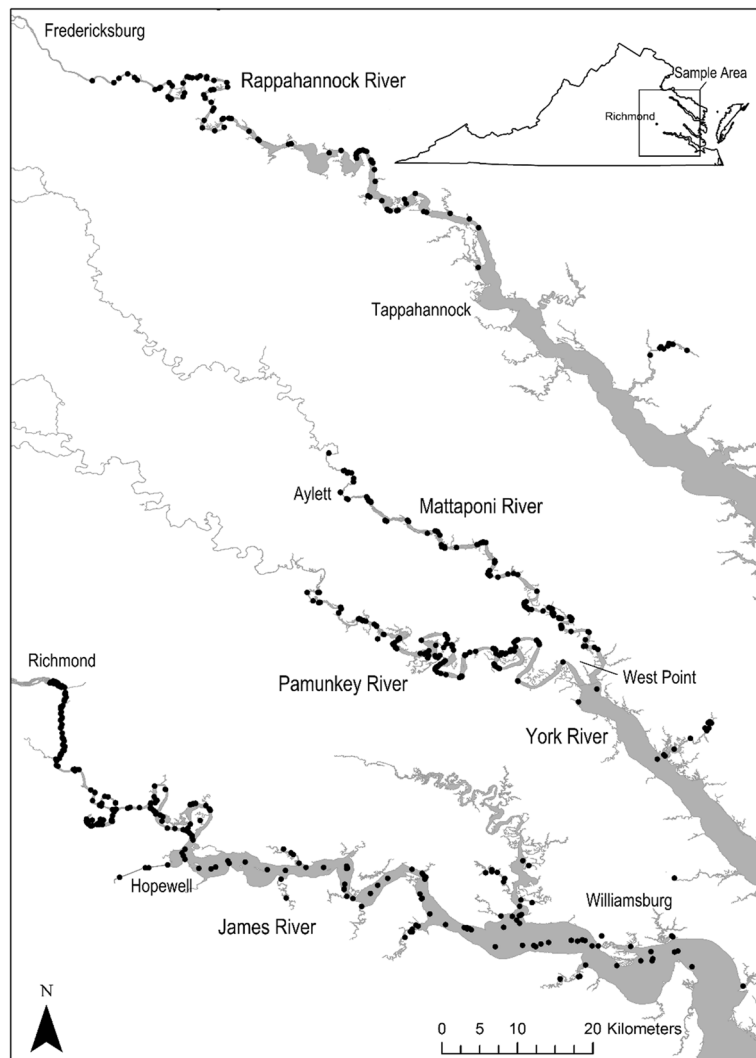
(Shiah and Ducklow 1994). Each river was stratified into freshwater sections (0–0.5 ppt), oligohaline sections (>0.5–5 ppt), and mesohaline sections (>5–18 ppt). Furthermore, each stratum was divided into 2-km reaches which were then randomly sampled. Individuals were collected monthly within each stratum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

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

Stomach processing

Stomach contents were extracted by either sacrificing the fish or with pulsed gastric lavage, which has been demonstrated to be effective for extracting diets from blue catfish (Waters et al. 2004). Stomachs were extracted within 30 min of capture to minimize losses from regurgitation, and contents were placed on ice and later frozen (Schmitt et al. 2017). In the laboratory, prey items were thawed, blotted dry with paper towels, weighed, counted, and identified to the lowest possible taxon.

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



Unidentifiable fish remains were identified using DNA barcoding methods as described by Moran et al. (2016); Schmitt et al. (2017). These methods enabled us to identify an additional 70% - 80% of fish prey that were unidentifiable by gross morphology, excluding instances where only bones and/or scales remained.

Sample size sufficiency

Gathering enough stomachs to adequately characterize the diet of a species is an important step that is overlooked in many studies (Ferry and Cailliet 1996), and large samples are often required to accurately describe the diet of an opportunistic, omnivorous species like blue catfish (Schmitt et al. 2017). Considering this,

sample size sufficiency was assessed for each river using rarefaction curves, where the cumulative mean number of unique taxa are plotted against the number of stomachs examined. Sample size is considered sufficient if the slope reaches an asymptote (Ferry and Cailliet 1996; Bizzarro et al. 2009). Rarefaction curves and associated 95% confidence intervals were calculated with EstimateS (version 9.1, R. K. Colwell), where the cumulative number of unique prey taxa were plotted against the randomly pooled samples. This process was bootstrapped 1000 times to generate means and associated confidence intervals. We used the mean slope (B) of the last five subsamples (linear regression) as an objective criterion for sample size sufficiency, where sample size is considered sufficient when $B \leq 0.05$ (Bizzarro et al. 2009; Brown et al. 2012).

Ontogenetic diet shifts

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

Diet composition and spatiotemporal patterns

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

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

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

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

Predator feeding strategy diagrams

Predator feeding strategy diagrams were constructed separately for each river, but only prey items with $\geq 1\%$ PSIRI were included, as rare diet items provide little information (Amundsen 1996; Costello 1990). Predator feeding strategy diagrams were constructed by plotting prey-specific percent by weight (%PW) by percent occurrence (Amundsen et al. 1996). This method provides a visualization of the generalist-specialist feeding dichotomy, as well as individual diet specialization, which are major components of niche theory (Pianka 1988). A population with a narrow niche width is comprised of specialized individuals, but a population with a broad niche can be comprised of individuals with narrow or broad niches (Amundsen et al. 1996). While blue catfish as a species have been demonstrated to have broad diets (Edds et al. 2002; Eggleton and Schramm Jr 2004; Schmitt et al. 2017), individual diet specialization has not yet been assessed for this species.

Trophic characteristics

Trophic level (TL) estimates provide an approximation of trophic position within complex food webs, and are useful for comparing ecological roles of different species within a given system (Cortés 1999; Ebert and Bizzarro 2007). Trophic level calculations can help researchers identify which species may be structuring ecosystems through top-down control, bottom-up control, or a combination of the two (Cortés 1999). Trophic level and omnivory indices were calculated for blue catfish in the James, Pamunkey, Mattaponi, and Rappahannock rivers. In addition, we used the results of the preceding ontogenetic diet shift analyses to inform thresholds for calculating respective trophic levels of smaller omnivorous and larger piscivorous blue catfish. Trophic

level calculations were based on all stomach contents collected from each river, and TL was calculated as:

$$\text{TROPH}_i = 1 + \sum_{j=1}^G \text{DC}_{ij} \times \text{TROPH}_j$$

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

We also calculated a dimensionless omnivory index for blue catfish, as it provides valuable information on diet specialization (Christensen and Walters 2004; Pauly and Watson 2005; Rodríguez-Preciado et al. 2014). Omnivory index (OI) estimates were calculated using the formula:

$$\text{OI}_i = \sum_{j=1}^n [\text{TL}_j - (\text{TL}_i - 1)]^2 \cdot \text{DC}_{ij}$$

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

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

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

where *B_i* is the Levin’s standardized index for predator ‘i’, *P_{ij}* is the proportion of the diet represented by item *j*, and *n* is the number of prey categories. Here proportion will be defined as percent occurrence, or the percentage of fish that had a given prey item present in their stomach. Our diet breadth calculations, like our omnivory index, will also provide an estimate of how omnivorous blue catfish are, yet differs as it is based on the proportion of different taxa consumed, not the number of trophic levels. Levin’s standardized index ranges from 0 to 1; values closer to zero have limited dietary breadth, whereas values closer to 1 have greater diet breadth. Proportional diet breadth was estimated separately for each river and was calculated separately for smaller, omnivorous catfish and larger, piscivorous catfish based on results from ontogenetic diet shift analyses. Debris and items of anthropogenic origin were excluded from diet breadth calculations.

Results

Stomach contents were extracted from a total of 16,110 blue catfish at 698 sites on the James, Pamunkey, Mattaponi, and Rappahannock rivers (Fig. 1). Of the 16,110 stomachs sampled, 9823 contained prey (60.38%). Stomachs were collected from blue catfish ranging in size from 206 mm – 1343 mm total length (TL), with 2440 blue catfish collected in the 600–1300 mm TL range, many from the James River (Fig. 2). Rarefaction curves reached asymptotes (*B* ≤ 0.05) for all four rivers, indicating sufficient sample size for diet description (Fig. 3; Bizzarro et al. 2009). Interestingly, numbers of different prey taxa consumed were similar for the Pamunkey River, Mattaponi River, and Rappahannock River (40–45 taxa), whereas blue catfish from the James River consumed a more diverse array of taxa (≈ 80 taxa; Tables 1 and 2).

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

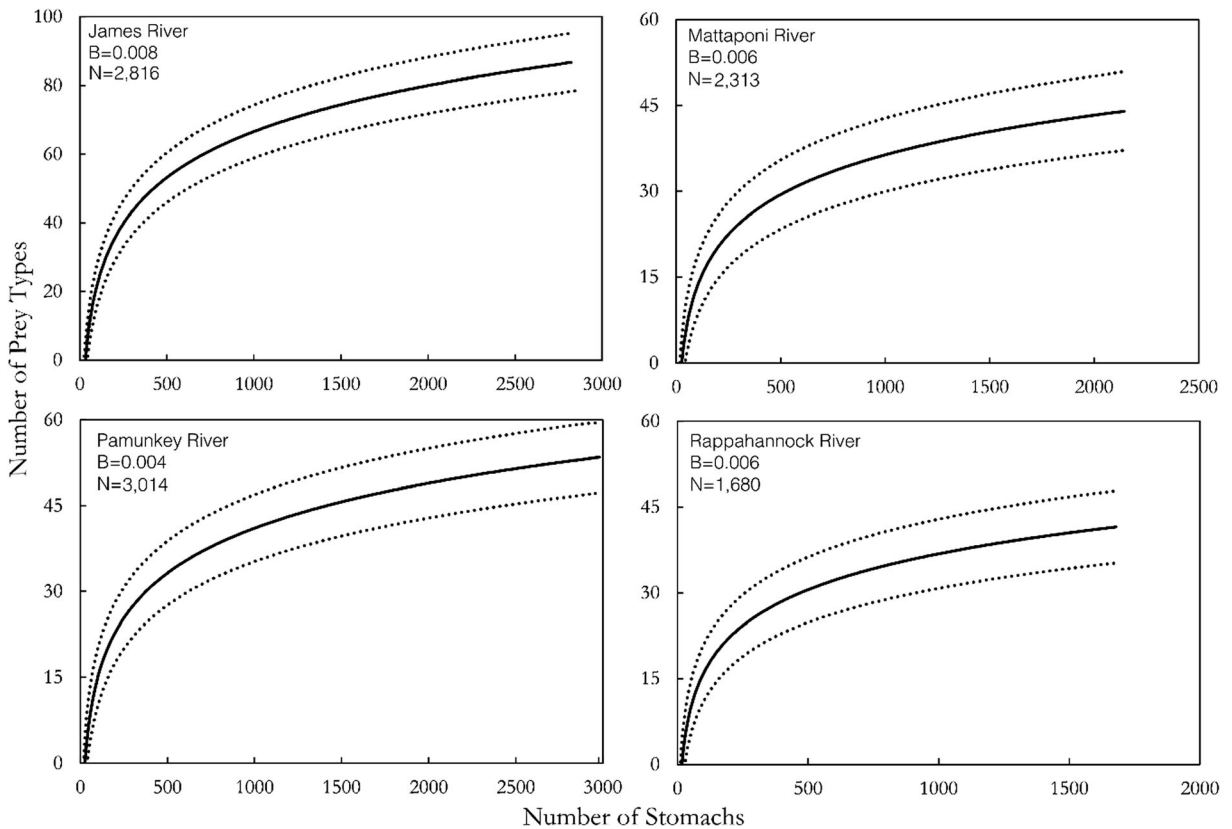
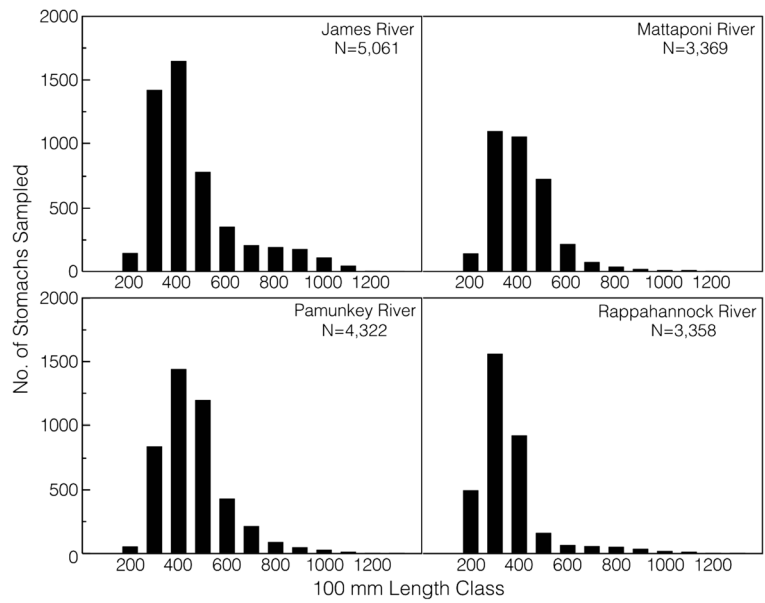


Fig. 3 Cumulative prey curves (solid lines) and 95% confidence intervals (dashed lines) based on stomach content data from blue catfish ($N = 9823$) collected from the James, Pamunkey,

Mattaponi, and Rappahannock Rivers. All slopes (B) reached asymptotes, indicating that sampling was sufficient for diet description ($B < 0.05$)

Table 1 Percent occurrence (%O), percent by weight (%W), and prey-specific index of relative importance (%PSIRI) for nonfish diet items found in blue catfish stomachs (N = 9823) collected from the James, Pamunkey, Mattaponi, and Rappahannock Rivers in eastern Virginia, USA

Prey	James River			Pamunkey River			Mattaponi River			Rappahannock River		
	%O	%W	%PSIRI	%O	%W	%PSIRI	%O	%W	%PSIRI	%O	%W	%PSIRI
Amphibia												
Ranidae												
<i>Rana spp.</i>	0.22%	<0.10%	<1.00%	0.17%	<0.10%	<1.00%	0.23%	0.13%	<1.00%	0.45%	0.29%	<1.00%
<i>Rana clamitans</i>	<0.10%	<0.10%	<1.00%	-	-	-	-	-	-	-	-	-
Amphipoda												
<i>Corophiidae</i>	-	-	-	0.80%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%	-	-	-
<i>Leptocheirus plumulosus</i>	0.22%	<0.10%	<1.00%	0.10%	<0.10%	<1.00%	0.18%	<0.10%	<1.00%	-	-	-
<i>Gammaridae</i>	2.58%	0.12%	<1.00%	6.37%	0.75%	4.45%	5.60%	0.91%	4.16%	3.44%	0.41%	2.18%
Annelida												
Hirudinea	<0.10%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%
unidentified annelid	0.18%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%	0.10%	<0.10%	<1.00%	0.19%	<0.10%	<1.00%
Anthropogenic debris												
carrots	<0.10%	<0.10%	<1.00%	-	-	-	-	-	-	-	-	-
condom	<0.10%	<0.10%	<1.00%	-	-	-	-	-	-	-	-	-
com	0.21%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%	-	-	-	-	-	-
chewing gum	<0.10%	<0.10%	<1.00%	-	-	-	-	-	-	-	-	-
chicken bones	0.18%	<0.10%	<1.00%	-	-	-	0.10%	<0.10%	<1.00%	-	-	-
cut bait	<0.10%	0.15%	<1.00%	-	-	-	-	-	-	-	-	-
fishing hook	0.37%	<0.10%	<1.00%	-	-	-	0.10%	<0.10%	<1.00%	0.19%	<0.10%	<1.00%
fishing sinker	<0.10%	<0.10%	<1.00%	-	-	-	-	-	-	-	-	-
hot dog	<0.10%	<0.10%	<1.00%	-	-	-	-	-	-	-	-	-
maxi pad	<0.10%	<0.10%	<1.00%	-	-	-	-	-	-	-	-	-
plastic waste	0.44%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%	-	-	-	0.26%	0.02%	<1.00%
plastic worm	-	-	-	<0.10%	<0.10%	<1.00%	-	-	-	-	-	-
peanuts	0.15%	<0.10%	<1.00%	-	-	-	-	-	-	-	-	-
Aquatic vegetation	32.93%	6.60%	18.27%	51.38%	44.76%	42.32%	40.78%	29.47%	33.22%	36.84%	17.55%	26.93%
Aves												
unidentified bird remains	0.15%	<0.10%	<1.00%	-	-	-	-	-	-	-	-	-
Cnidaria												
Ulmaridae												
<i>Aurelia aurita</i>	0.18%	<0.10%	<1.00%	-	-	-	-	-	-	<0.10%	<0.10%	<1.00%
Decapoda												
Cambaridae												
<i>Orconectes limosus</i>	1.22%	0.24%	<1.00%	0.93%	0.91%	<1.00%	1.15%	1.32%	<1.00%	0.78%	0.63%	<1.00%

Table 1 (continued)

Prey	James River			Pamunkey River			Mattaponi River			Rappahannock River		
	%O	%W	%PSIRI	%O	%W	%PSIRI	%O	%W	%PSIRI	%O	%W	%PSIRI
<i>Procambarus</i> spp.	<0.10%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%	0.13%	<0.10%	<1.00%
Palaemonidae												
<i>Palaemonetes pugio</i>	<0.10%	<0.10%	<1.00%	0.17%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%	-	-	-
Panopeidae												
<i>Dyspanopus sayi</i>	<0.10%	<0.10%	<1.00%	-	-	-	-	-	-	-	-	-
<i>Panopeus herbstii</i>	0.52%	<0.10%	<1.00%	1.87%	0.53%	<1.00%	4.72%	1.42%	2.55%	0.13%	<0.10%	<1.00%
<i>Rithropanopeus harrisi</i>	1.07%	0.08%	<1.00%	6.06%	1.66%	3.31%	6.56%	2.37%	4.75%	0.13%	<0.10%	<1.00%
<i>Hexapanopeus</i> sp	-	-	-	<0.10%	<0.10%	<1.00%	-	-	-	-	-	-
Portunidae												
<i>Callinectes sapidus</i>	6.23%	2.78%	3.44%	4.10%	5.50%	2.78%	3.26%	5.98%	2.43%	0.78%	1.21%	<1.00%
Ucainae												
<i>Uca minax</i>	<0.10%	<0.10%	<1.00%	0.48%	0.26%	<1.00%	<0.10%	1.20%	<1.00%	-	-	-
Diplopoda	<0.10%	<0.10%	<1.00%	-	-	-	-	-	-	-	-	-
Emydidae												
<i>Trachemys scripta elegans</i>	<0.10%	<0.10%	<1.00%	-	-	-	-	-	-	-	-	-
Insecta												
Coleoptera	0.37%	<0.10%	<1.00%	0.21%	<0.10%	<1.00%	0.37%	0.10%	<1.00%	0.71%	<0.10%	<1.00%
Diptera	<0.10%	<0.10%	<1.00%	0.28%	<0.10%	<1.00%	0.18%	<0.10%	<1.00%	4.22%	0.32%	<1.00%
Ephemeroptera	<0.10%	<0.10%	<1.00%	0.55%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%	2.40%	0.33%	2.12%
Hemiptera	0.12%	<0.10%	<1.00%	-	-	-	0.23%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%
Hymenoptera	<0.10%	<0.10%	<1.00%	-	-	-	-	-	-	-	-	-
Megaloptera	0.11%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%	0.58%	<0.10%	<1.00%
Odonata	0.81%	<0.10%	<1.00%	0.10%	<0.10%	<1.00%	0.60%	0.15%	<1.00%	0.84%	<0.10%	<1.00%
Plecoptera	0.11%	<0.10%	<1.00%	-	-	-	-	-	-	-	-	-
Trichoptera	0.11%	<0.10%	<1.00%	-	-	-	-	-	-	0.19%	<0.10%	<1.00%
Isopoda												
<i>Cyathura polita</i>	0.18%	<0.10%	<1.00%	0.38%	<0.10%	<1.00%	1.38%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%
Cymothoidae												
Mammalia												
Cricetidae												
<i>Ondatra zibethicus</i>	<0.10%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%	-	-	-	<0.10%	0.12%	<1.00%
unidentified mammal remains	0.26%	0.11%	<1.00%	-	-	-	<0.10%	<0.10%	<1.00%	-	-	-
Mollusca												
Acteonidae												
<i>Rictaxis punctostriatus</i>	-	-	-	-	-	-	<0.10%	<0.10%	<1.00%	-	-	-

Table 1 (continued)

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

Table 2 Percent occurrence (%O), percent by weight (%W), and prey-specific index of relative importance (%PSIRI) for fish prey found in blue catfish stomachs (N = 9823) collected from the James, Pamunkey, Mattaponi, and Rappahannock Rivers in eastern Virginia, USA

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

Table 2 (continued)

Prey	James River			Pamunkey River			Mattaponi River			Rappahannock River		
	%O	%W	%PSIRI	%O	%W	%PSIRI	%O	%W	%PSIRI	%O	%W	%PSIRI
<i>Hybognathus regius</i>	0.18%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%	0.14%	0.20%	<1.00%	<0.10%	<0.10%	<1.00%
<i>Notropis hudsonius</i>	0.26%	<0.10%	<1.00%	-	-	-	<0.10%	<0.10%	<1.00%	<0.10%	<0.10%	<1.00%
Ictaluridae												
<i>Ameiurus catus</i>	<0.10%	<0.10%	<1.00%	-	-	-	-	-	-	-	-	-
<i>Ameiurus nebulosus</i>	-	-	-	<0.10%	0.16%	<1.00%	-	-	-	-	-	-
<i>Ictalurus furcatus</i>	1.44%	6.12%	1.26%	0.38%	6.02%	<1.00%	0.46%	2.80%	<1.00%	1.17%	5.24%	1.00%
<i>Ictalurus punctatus</i>	<0.10%	0.63%	<1.00%	-	-	-	<0.10%	<0.10%	<1.00%	<0.10%	0.48%	<1.00%
<i>Ictalurus spp.</i>	0.70%	0.74%	<1.00%	0.21%	0.06%	<1.00%	-	-	-	-	-	-
<i>Noturus gyrinus</i>	-	-	-	-	-	-	-	-	-	<0.10%	<0.10%	<1.00%
<i>Pylodictis olivaris</i>	<0.10%	<0.10%	<1.00%	-	-	-	<0.10%	<0.10%	<1.00%	-	-	-
Lepisosteidae												
<i>Lepisosteus osseus</i>	<0.10%	0.41%	<1.00%	<0.10%	0.21%	<1.00%	<0.10%	0.35%	<1.00%	0.26%	0.56%	<1.00%
Moronidae												
<i>Morone americana</i>	7.07%	4.94%	5.74%	0.69%	2.16%	<1.00%	0.64%	1.63%	<1.00%	1.49%	2.15%	1.29%
<i>Morone saxatilis</i>	<0.10%	0.31%	<1.00%	-	-	-	<0.10%	2.33%	<1.00%	<0.10%	<0.10%	<1.00%
Percidae												
<i>Etheostoma flabellare</i>	<0.10%	<0.10%	<1.00%	-	-	-	-	-	-	-	-	-
<i>Etheostoma olmstedti</i>	0.22%	<0.10%	<1.00%	-	-	-	-	-	-	-	-	-
<i>Etheostoma spp.</i>	<0.10%	<0.10%	<1.00%	-	-	-	-	-	-	<0.10%	<0.10%	<1.00%
<i>Percia flavescens</i>	0.11%	<0.10%	<1.00%	-	-	-	-	-	-	-	-	-
Sciaenidae												
<i>Leiostomus xanthurus</i>	<0.10%	<0.10%	<1.00%	-	-	-	<0.10%	<0.10%	<1.00%	-	-	-
<i>Micropogonias undulatus</i>	-	-	-	-	-	-	<0.10%	<0.10%	<1.00%	-	-	-
unidentified ray-finned fish	11.98%	4.72%	7.08%	4.46%	1.78%	2.49%	5.18%	1.67%	3.31%	5.26%	2.61%	3.99%
Petromyzontida												
Petromyzontidae												
<i>Petromyzon marinus</i>	0.11%	0.33%	<1.00%	-	-	-	-	-	-	-	-	-

Ontogenetic diet shifts

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

Diet composition

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

Pooled across seasons, vegetation was the dominant item consumed in all four rivers in terms of gravimetric contribution, frequency of occurrence, and relative importance, with the exception of the James River and Rappahannock River, where gizzard shad *Dorosoma cepedianum* was the dominant prey by weight (Table 1). It is important to note that %W indices are inherently biased by the heavier prey consumed by larger fish, and also over-represent slow to digest diet items such as mollusks and crustaceans (MacDonald and Green 1983; Baker et al. 2014). Considering this, %W index should be considered with caution, while %O indices are the most robust and interpretable measure of diet composition (Baker et al. 2014). The vegetation consumed was primarily *Hydrilla verticillata* (hereafter "hydrilla"), common waterweed *Elodea canadensis*, and also Brazilian waterweed *Egeria densa* in some sections of the James River. Invasive Asian clams *Corbicula fluminea* were another dominant prey item in all four rivers in terms of %O, %W, and %PSIRI. The commercially-valuable blue crab *Callinectes sapidus* was routinely consumed in the James River, Pamunkey River, Mattaponi River, but

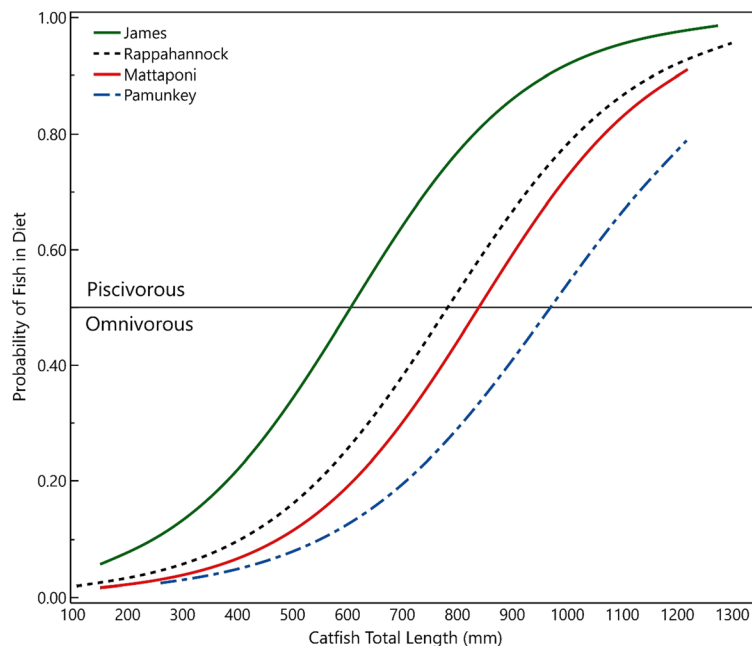


Fig. 4 Logistic regression was used to model the binary occurrence of fish in the diet (1 = present, 0 = absent) versus the total length of the catfish (mm). Blue catfish underwent significant diet shifts to piscivory in all rivers ($P < 0.01$), though the length at which fish became piscivorous varied by river. For simplicity, we

define “piscivorous” as the length at which fish prey are predicted to occur in $\geq 50\%$ of blue catfish stomachs, rounded to the nearest 100 mm. Blue catfish became piscivorous at 500 mm TL in the James River, 700 mm TL in Rappahannock River, 800 mm TL in the Mattaponi River, and 900 mm TL in the Pamunkey River

not in the Rappahannock River (Table 1). Other routinely consumed prey items include white perch *Morone americana*, gammarid amphipods, estuarine mud crabs (*Rithropanopeus harrisi* and *Panopeus herbstii*), macoma clams, cerith snails, and mayflies (Tables 1 and 2).

Spatiotemporal patterns in diet

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

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

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

Winter data was limited to blue catfish collected from the James and York rivers ($N = 668$). In tidal freshwater areas, blue catfish fed heavily on *Dorosoma spp.* (31%

occurrence), crayfish (17% occurrence), and Asian clams (10% occurrence; Fig. 5). In oligohaline areas, blue catfish consumed *Dorosoma spp.* (21% occurrence), vegetation (21% occurrence), blue crab (10% occurrence), and detritus (9% occurrence; Fig. 5). In mesohaline areas, blue catfish consumed white perch most frequently (58% occurrence), followed by blue crab (33% occurrence), estuarine mud crabs (26% occurrence), and grass shrimp (17% occurrence; Fig. 5).

Feeding strategy diagrams

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

Trophic niche metrics

Trophic calculations suggest that the blue catfish is an omnivore-generalist that feeds on many trophic levels (Rodríguez-Preciado et al. 2014). TL values varied by river and blue catfish size, with a range of 2.72–3.55, and a mean TL = 2.90 (Table 3). Omnivory index (OI) values indicated that blue catfish consumed a variety of trophic levels, though they varied by river and fish size, with a range of 0.58–0.93, and a mean of 0.73 (Table 3). Diet breadth (B) values ranged from 0.10–0.90, with a mean of 0.63. While OI values are based on the range of trophic levels consumed, diet breadth values are based on the diversity of taxa and the %O of those prey in the diet. Smaller, non-piscivorous blue catfish (based on ontogenetic shift analysis) had broader diets (0.49–0.90), but diet breadth values decreased (< 0.40) for larger, more piscivorous individuals. This may relate to individual diet specialization at larger sizes, as big fish fed primarily on gizzard shad and smaller blue catfish. While larger catfish still feed on multiple trophic levels (OI values > 0.50), their diet is dominated by a limited number of taxa (diet breadth 0.10–0.33).

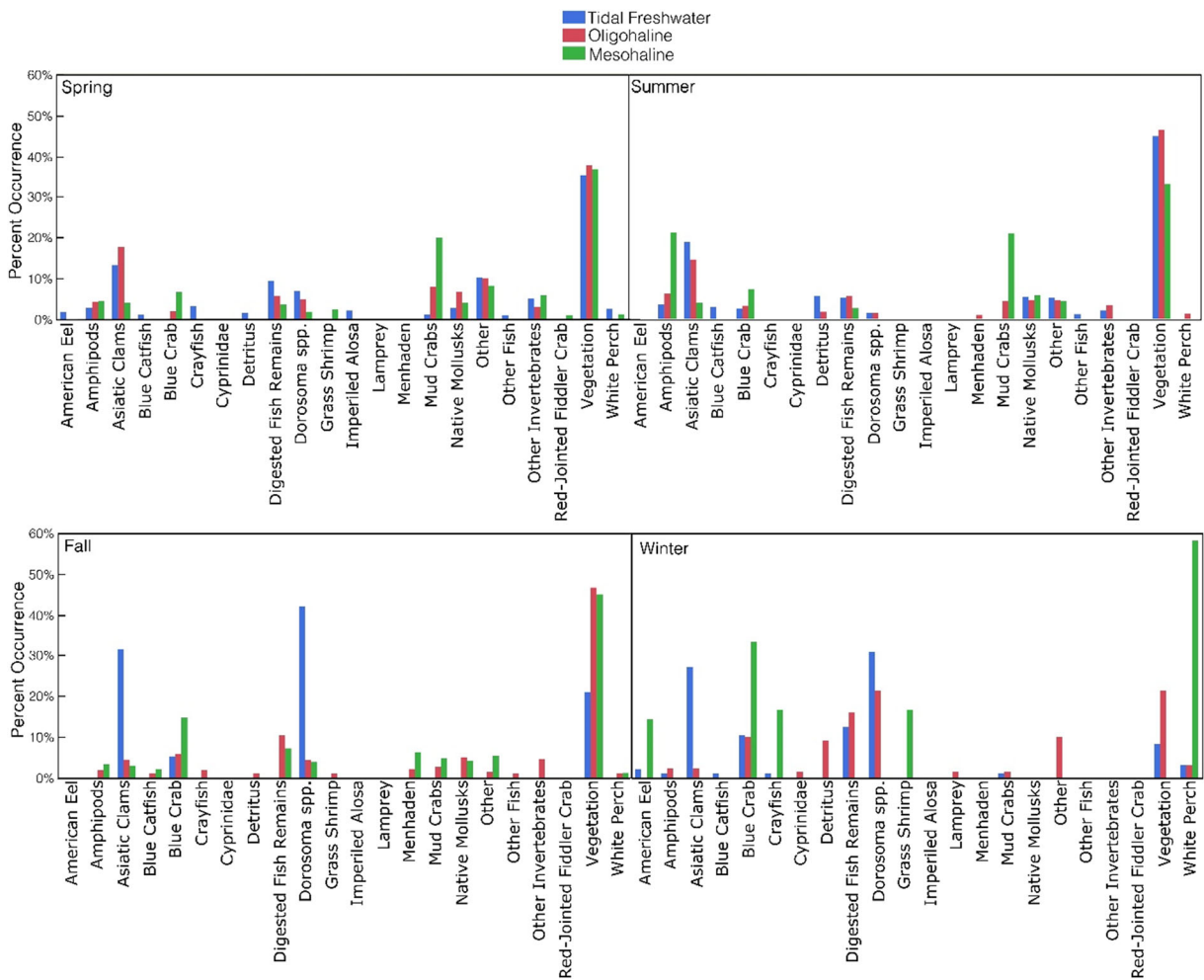


Fig. 5 Percent occurrence of prey in the diets of 9823 blue catfish as it varies by season and salinity regime. Food types that occurred in >1% of stomachs by season or salinity zone have their own category, while all rare prey (<1%) were combined into a single category (“Other”). “Spring” includes stomachs from March –

May, “Summer” includes stomachs from June – August, “Fall” includes stomachs from September – November, and “Winter” included stomachs from December – February. Stomachs were collected from the James, Pamunkey, Mattaponi, and Rappahannock Rivers in eastern Virginia, USA

Discussion

Blue catfish in the Chesapeake Bay are opportunistic generalists, with broad diets that reflect the seasonal and spatial variation in prey availability throughout the estuary. Diets were comprised largely of invasive aquatic vegetation and Asian clams in freshwater and oligohaline areas, while blue catfish in mesohaline areas consumed mostly mud crabs, gammarid amphipods, blue crab, and white perch. Blue catfish are typically non-selective and feed on the most abundant resources (Eggleton and Schramm Jr 2004; Schmitt et al. 2017). The current study adheres to this pattern, as blue catfish primarily feed on abundant resources including other

invasive species (see Diaz 1974; Dennison et al. 1993; Posey et al. 1993; Gillett and Schaffner 2009; Freedman 2013). Opportunism has been linked to invasion success in many other organisms, and may explain the high densities of blue catfish observed in Chesapeake Bay tributaries (Kostrzewa and Grabowski 2003; Gherardi and Barbaresi 2008; Drown et al. 2011).

Diet characterization

With over 16,000 stomachs collected, the current study is the largest and most comprehensive diet study on blue catfish to date. This amount of effort was not excessive; however, as our cumulative prey curves revealed that

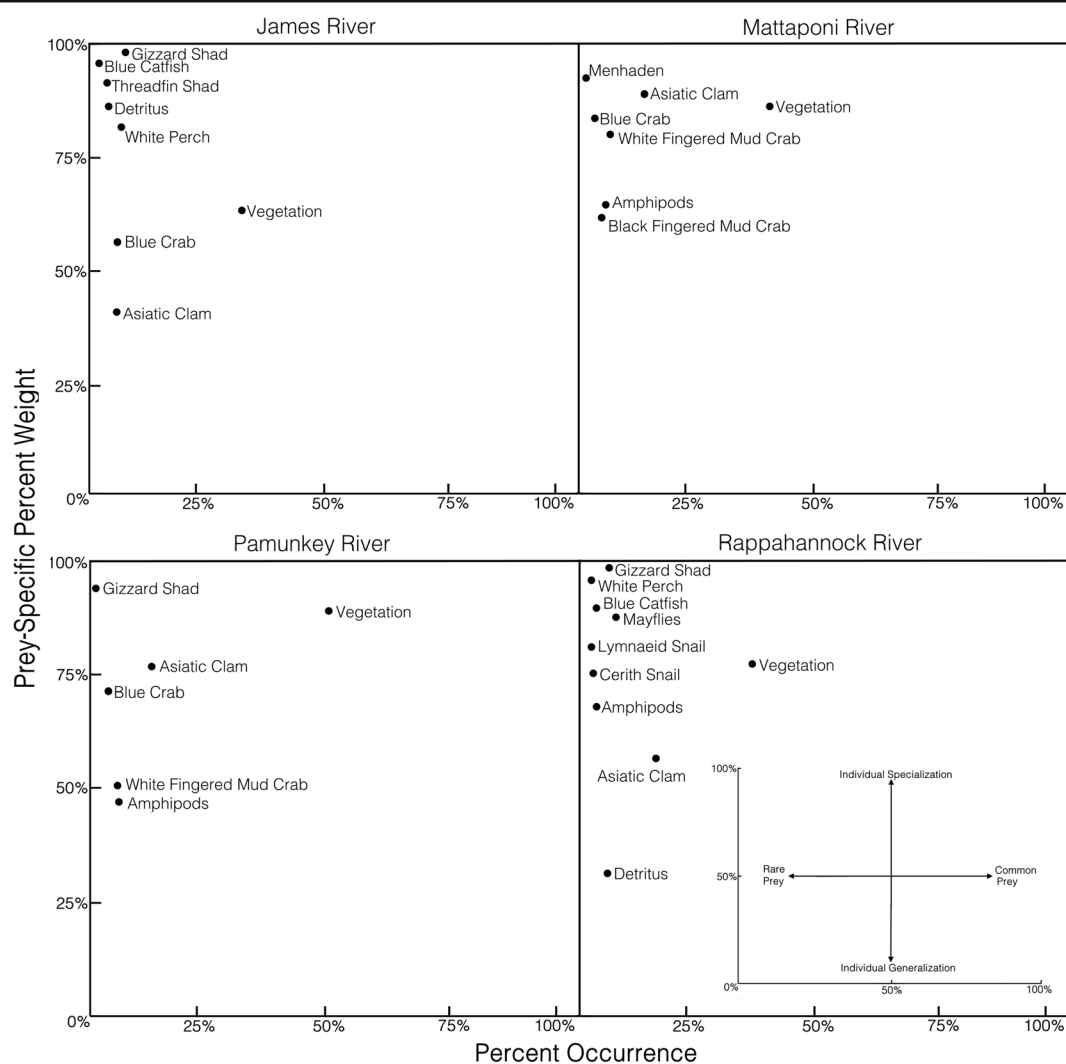


Fig. 6 Predator feeding strategy diagrams (Amundsen et al. 1996) for blue catfish collected from the James, Pamunkey, Mattaponi, and Rappahannock Rivers in eastern Virginia, USA. Prey-specific

percent weight is defined as the percent weight of item “j” in all stomachs containing item “j”. Feeding strategy interpretation guide included in bottom right panel

many stomachs were needed to adequately characterize the diet of this broadly distributed, opportunistic feeder. Most prey curves did not reach asymptotes until 1000–1500 stomachs, and only 50–60% of the blue catfish stomachs contained prey, therefore as many as 3000 individual fish would need to be collected to adequately characterize the diet of these fish in any given tidal river system. Moreover, ontogenetic diet shift analyses revealed high variation in shifts among rivers, emphasizing the importance of capturing fish of all sizes. Considering this, much of the previous work on blue catfish in the Chesapeake Bay may inadequately characterize the true diet breadth of this species. Schloesser et al.

(2011) was the most comprehensive blue catfish diet study prior to this study, yet only a few hundred catfish were collected per river and all catfish were less than 600 mm fork length (FL). We highly recommend the use of cumulative prey curves to assess sample size sufficiency, especially when describing the food habits of a broadly-distributed omnivore.

Our results demonstrate that most of the blue catfish in Chesapeake Bay subestuaries are generalist mesopredators that primarily eat vegetation and invertebrates. This contradicts a previous study that labeled blue catfish as “apex predators” (MacAvoy et al. 2000), though this study had limited sampling

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

River	Length	Trophic Level	Standard Error	Omnivory Index	Diet Breadth
James					
	All	3.152	0.965	0.932	0.582
	<500 mm	2.872	0.932	0.869	0.634
	>500 mm	3.552	0.866	0.749	0.105
Pamunkey					
	All	2.736	0.823	0.678	0.388
	<900 mm	2.717	0.817	0.667	0.474
	>900 mm	3.027	0.865	0.749	0.195
Mattaponi					
	All	2.887	0.810	0.656	0.636
	<800 mm	2.863	0.807	0.651	0.643
	>800 mm	3.290	0.759	0.575	0.325
Rappahannock					
	All	2.841	0.800	0.640	0.896
	<700 mm	2.784	0.777	0.603	0.898
	>700 mm	3.544	0.796	0.634	0.194

($N = 22$) and no actual estimate of trophic level was made. Blue catfish are herbivore-omnivores at small sizes, and switch to piscivory at larger sizes. Throughout most of the year, blue catfish diet is dominated by vegetation and Asian clams in all four rivers. Hydrilla and common waterweed were the primary vegetation species consumed, and vegetation was found in 32.93–51.38% of catfish stomachs. These findings are not particularly surprising, as blue catfish in their native range have broad, omnivorous diets and regularly consume aquatic macrophytes (Edds et al. 2002; Eggleton and Schramm Jr 2004).

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

Management concerns

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

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

Trophic characteristics

News sources and media outlets in the Chesapeake Bay region often portray blue catfish as “apex predators” that threaten commercially-important and imperiled native species via intense predation (e.g., Wolf 2014; Blankenship 2015; Taylor 2015; Springston 2015). These assertions were mere anecdotes; however, as no

comprehensive analysis of diet or trophic position for blue catfish had been completed for Chesapeake Bay subestuaries prior to this study. In fact, all of the previous diet work for blue catfish in the Chesapeake Bay were limited to small catfish, had limited numbers of catfish, or were limited in terms of spatiotemporal scope (see MacAvoy et al. 2000; Schloesser et al. 2011; Aguilar et al. 2017; Schmitt et al. 2017).

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

Omnivory and diet breadth indices revealed that smaller catfish are highly omnivorous and opportunistic, and, while larger catfish are still omnivorous, they consume a smaller pool of resources. Blue catfish have remarkable diet plasticity, with high diet breadth averaged across all rivers ($B = 0.63$). While many estuarine fish are omnivorous and capable of shifting diets to exploit temporary peaks in prey abundance (Ley et al. 1994), diet breadth values for blue catfish in the Chesapeake Bay were consistently higher than those estimated for other estuarine fishes. Akin and Winemiller (2006) calculated diet breadth for 27 fish species in Matagorda Bay, an estuary in south-central Texas. Only three species had diet breadths >0.50 , and the highest diet breadth observed was from the clown goby *Microgobius gulosus*, which had the same diet breadth as the overall mean for blue catfish ($B = 0.63$).

Hajisamae et al. (2003) calculated the diet breadth for 32 fish species in the Johor Strait, which is a major estuary in southern Malaysia. Only three species had diet breadth values >0.50 , and the highest observed came from species of grunt *Pomadasyss sp.* ($B = 0.68$). Blue catfish from the Rappahannock River had the impressive diet breadth ($B = 0.90$), which is markedly higher than any diet breadths calculated in the aforementioned studies (Hajisamae et al. 2003; Akin and Winemiller 2006). Interestingly, blue catfish population densities appear to be highest in the Rappahannock River (Greenlee and Lim 2011), and it is possible that greater intraspecific competition has forced blue catfish to diversify their diet, a phenomenon that has been documented in other fish species (Svanbäck and Bolnick 2007).

Individual specialization

Our predator feeding strategy diagrams revealed several interesting river-specific diet specialization patterns. Large blue catfish specialized on *Dorosoma* species in the Pamunkey, James, and Rappahannock Rivers, while they specialized on menhaden in the Mattaponi River. There was also evidence of diet specialization on detritus in the James River and mayflies in the Rappahannock River. Blue catfish were cannibalistic in all rivers, but there was evidence of cannibalistic specialization in the James and Rappahannock rivers, both of which support dense blue catfish populations (Greenlee and Lim 2011). We hypothesize that cannibalism is a density-dependent function for blue catfish, though more research would be necessary to confirm this. It is also possible that individual diet specialization in these rivers is driven by intraspecific competition (Araújo et al. 2011). In fact, previous studies have demonstrated that increases in population density, a proxy for intraspecific competition, is likely to result in increases in individual diet specialization (Svanbäck and Persson 2004; Svanbäck and Bolnick 2007; Tinker et al. 2008). Blue catfish population densities appear to be greatest in the Rappahannock River (Greenlee and Lim 2011), which is also where the highest diet breadth values were observed. It is also plausible that high variation in blue catfish growth rates is driven by individual diet specialization, as piscine specialists are likely to grow faster than detritus or vegetation specialists. Highly variable growth rates have been observed in the Chesapeake Bay (Greenlee and Lim 2011; Hilling et al. 2018) and in

reservoirs in Oklahoma (Boxrucker and Kuklinski 2006), therefore individual diet specialization may be a universal life history strategy for this species, and warrants further investigation. Admittedly, predator feeding strategy diagrams are a primitive method for examining diet specialization as they provide a limited temporal scope. Future studies should utilize more advanced methods (e.g., stable isotope analysis) for assessing individual diet specialization of blue catfish (see Bolnick et al. 2002; Araújo et al. 2007; Vander Zanden et al. 2010; Matich et al. 2011).

Conclusions

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

Turkington 2005). The success of novel generalists has largely been attributed to their ability to thrive in highly altered or degraded habitats (Clavel et al. 2010). This is particularly worrying because the Chesapeake Bay is far from pristine, and human activities have resulted in widespread ecosystem changes (Boesch et al. 2001; Kemp et al. 2005; Orth et al. 2006). In essence, anthropogenic eutrophication has been linked to a major ecological shift from benthic diatom production to pelagic phytoplankton production (Kemp et al. 2005). This has been associated with substantial declines in submerged aquatic vegetation, has created anoxic and hypoxic dead zones within the estuary, and has resulted in widespread community changes (Kemp et al. 2005; Diaz and Rosenberg 2008). While nutrient loading can enhance fisheries yields to a point (Nixon and Buckley 2002), it tends to favor benthic organisms with opportunistic life histories (Diaz and Rosenberg 1995). The relationship between eutrophication and blue catfish population density should be explored on a river-specific basis, as it is quite possible that blue catfish abundance is driven by anthropogenic eutrophication. If this is this case, it may be prudent to address the underlying causes, rather than simply trying to eradicate or control the species (Didham et al. 2007).

While blue catfish do not routinely consume imperiled fish species, their predatory impact cannot be assessed without credible estimates of population biomass and size structure (Schmitt et al. 2017), and a population estimate was recently completed for a brackish segment of the James River (Fabrizio et al. 2017). Blue catfish population densities appear to be substantially higher in the Chesapeake Bay than in the native range. Electrofishing capture rates in the Rappahannock River can exceed 6000 fish/h (Greenlee and Lim 2011), while capture rates using the same methods in Oklahoma peaked at approximately 700 fish/h (Boxrucker and Kuklinski 2006). At high enough densities, blue catfish could still exert sizable predatory impacts on imperiled fish species, even at low predation rates.

Considering this, future research should explore spatiotemporal patterns in the predation of species of concern, including American shad, river herring, blue crab, and American eel. Furthermore, in situ estimates of blue catfish maximum daily ration are still needed for the Chesapeake Bay region, as many introduced species have elevated consumption rates when introduced into a new environment (McKnight et al. 2016). Population estimates (like Fabrizio et al. 2017), consumption

estimates, and diet information can then be integrated to quantify predatory impacts on species of concern, which will be necessary for the future management of blue catfish in the Chesapeake Bay.

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