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ARTICLE

Feeding Ecology and Distribution of an Invasive Apex Predator: Flathead Catfish in Subestuaries of the Chesapeake Bay, Virginia

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Abstract
Native to the central United States, Flathead Catfish *Pylodictus olivaris* have invaded Atlantic coast rivers from Florida to Pennsylvania. They are now invasive in several subestuaries of the Chesapeake Bay, yet contemporary accounts of their distribution do not exist. Due to their piscivorous nature, Flathead Catfish could have deleterious impacts on native ichthyofauna, yet their feeding ecology has not been well described in these systems. We used a large-scale, stratified random sampling effort to describe the current distribution and feeding ecology of Flathead Catfish in Virginia tidal rivers. Low-frequency electrofishing was conducted at more than 1,500 sites in the James, Pamunkey, Mattaponi, and Rappahannock rivers in eastern Virginia, resulting in 766 Flathead Catfish being captured in the James, Pamunkey, and Mattaponi rivers. Flathead Catfish are abundant in the tidal James River from Richmond, Virginia, to the confluence of the Chickahominy River. A relatively new but established population was also observed in the Pamunkey River, where the highest observed densities of Flathead Catfish occurred near Williams Landing (37°36′21.49″N, 77°5′33.42″W) in New Kent County, Virginia. Stomachs collected from 731 Flathead Catfish revealed that they are piscivores that feed heavily on Gizzard Shad *Dorosoma cepedianum*, White Perch *Morone americana*, and various *Alosa* species. Analysis of trophic level, diet breadth, and feeding strategy demonstrated that Flathead Catfish are piscine specialists that occupy trophic positions indicative of an apex predator. Our results show that Flathead Catfish could have substantial per capita impacts on at-risk native species including American Shad *Alosa sapidissima*, Blueback Herring *A. aestivalis*, and Alewife *A. pseudoharengus* as they make seasonal migrations in and out of these river systems. Moreover, future range expansion of Flathead Catfish into the Rappahannock River is plausible, as established populations now exist in adjacent tributaries.

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Globally, invasive fishes have caused substantial ecological damage through predation, competition, and the introduction of novel diseases and parasites (García-Berthou 2007; Cucherousset and Olden 2011; Villizzi et al. 2015). Nonetheless, the impact phase of fish invasions has not been well studied (García-Berthou 2007), and most studies have focused on centrarchids, cyprinids, salmonids, and cichlids (Cucherousset and Olden 2011). In the Chesapeake Bay, Flathead Catfish *Pylodictis olivaris* were first detected in the upper James River during the 1980s, though anecdotal accounts also state that Flathead Catfish were captured farther downriver near Hog Island (37°11′41.48″N, 76°41′12.47″W) in the 1960s (Jenkins and Burkhead 1994). They have since established nonindigenous populations in the Potomac and Susquehanna River tributaries (Brown et al. 2005; Orrell and Weigt 2005). Flathead Catfish are tolerant of high salinities (Bringolf et al. 2005); therefore, Flathead Catfish may already be present in other tributaries, and further range expansion is likely.

Flathead Catfish are native to the Mississippi, Mobile, and Rio Grande River drainages in the central United States and are believed to be native to portions of Mexico and the Laurentian Great Lakes region (Jackson 1999), though the latter has recently been questioned (Fuller and Whelan 2018). Flathead Catfish thrive in many habitats, and have invaded estuaries, rivers, reservoirs, and natural lakes across North America (Guier et al. 1984; Weller and Robbins 1999; Syväranta et al. 2009; Dobbins et al. 2012; Schmitt et al. 2017; Fuller and Whelan 2018; Massie et al. 2018). Flathead Catfish are the most carnivorous of the North American catfishes and become almost exclusively piscivorous at small sizes (Jackson 1999; Herndon and Waters 2002; Pine et al. 2005). This is likely due to their gape size, which is the one of the largest of any freshwater species in North America (Slaughter and Jacobson 2008). Their potential to reach large sizes (>50 kg) and their carnivorous food habits have led to concerns about the spread of Flathead Catfish outside of its native range (Fuller et al. 1999; Kwak et al. 2006), and food web simulation models in other Atlantic slope drainages have predicted up to a 50% decline in native fish biomass once new populations become established (Pine et al. 2007).

Despite their reputation as voracious predators, little is known about invasive Flathead Catfish in Chesapeake Bay tributaries (Schmitt et al. 2017). Flathead Catfish may have substantial predatory impacts on native species like American Shad *Alosa sapidissima*, river herring (Blueback Herring *A. aestivalis* and Alewife *A. pseudoharengus*), White Perch *Morone americana*, White Catfish *Ameirus catus*, sunfishes *Lepomis* spp., endangered Atlantic Sturgeon *Acipenser oxyrinchus*, and recreationally valuable Largemouth Bass *Micropterus salmoides*. There is only one published diet description for Flathead Catfish in the Chesapeake Bay (Schmitt et al. 2017), which was limited to March–May; therefore diet information for summer and autumn is still needed (Flathead Catfish are generally inactive during the winter months, even in warm climates: Weller and Winter 2001; Daugherty and Sutton 2005). Moreover, better spatial coverage is needed, as the Schmitt et al. (2017) study was limited to freshwater and tidal freshwater portions of the James River. In Virginia tidal rivers, a comprehensive analysis of Flathead Catfish food habits is still needed since fish communities change seasonally and spatially in the Chesapeake Bay (Jung and Houde 2003), and nonindigenous catfish diets often reflect this spatiotemporal variability (Schmitt et al. 2017, 2018). This study provides two valuable pieces of information. First, it describes the feeding ecology of invasive Flathead Catfish in Virginia tidal rivers, and second, it describes the current distribution of Flathead Catfish in these rivers.

METHODS

Study area.— The diet and distribution of Flathead Catfish in Virginia tidal rivers was described across broad spatiotemporal scales in the lower Chesapeake Bay, which included the James, Pamunkey, Mattaponi, and Rappahannock River subestuaries. It is important to note that the Pamunkey and Mattaponi rivers converge at West Point, Virginia, to form the York River (Figure 1). This project employed a stratified, random-sampling design to collect nonindigenous catfishes across broad spatial scales including tidal freshwater, oligohaline, and mesohaline segments of each river, based on mean surface salinities. Each river was divided into 2-km sections, which were enumerated, and then a random number generator was used to select sampling reaches. For the James River, randomized sampling occurred from the fall line in the city of Richmond (37°31′41.88″N, 77°26′7.73″W) to Hog Island (37°11′41.48″N, 76°41′12.47″W). For the Pamunkey River, randomized sampling occurred from near the route 360 bridge (37°41′13.92″N, 77°11′4.72″W) to Croaker Landing on the York River (37°25′41.64″N, 76°43′31.41″W). For the Mattaponi River, randomized sampling occurred from a few river kilometers upriver from Aylett, Virginia (37°48′34.89″N, 77°5′34.97″W), to Poropotank Bay on the York River (37°26′35.75″N, 76°42′16.97″W). For the Rappahannock River, randomized sampling occurred from the Fredericksburg, Virginia, area (38°15′22.68″N, 77°24′58.74″W) to Tappahannock, Virginia (37°55′17.74″N, 76°51′6.34″W). From April to October, each stratum of each river was sampled on a monthly basis at a minimum of two randomly selected reaches, within which multiple sites were sampled. More detailed descriptions of sampling methodologies are provided by Schmitt and Orth (2015), Schmitt et al. (2017, 2018). This stratified, random-sampling approach was used to describe the distribution of a relatively new population in the York River basin

(Pamunkey and Mattaponi rivers), and CPUE data from fixed-site catfish monitoring by the Virginia Department of Game and Inland Fisheries (VDGIF) was used to explore trends in catfish relative abundance through time, which is explained in greater detail below.

Field collections.— Boat-mounted, low-frequency electrofishing (10–30 Hz, 200–500 V) was used to collect Flathead Catfish from 2013 to 2016 via monthly sampling from April to October. Low-frequency electrofishing is the most efficient technique for capturing Blue Catfish *Ictalurus furcatus* and Flathead Catfish across depth strata (Stauffer and Koenen 1999), yet its application is limited to a minimum temperature threshold of 18°C (Bodine et al. 2013) with optimal efficiency occurring at temperatures >22°C (Justus 1994). Within our study area, water temperatures did not reach 18°C until mid-May, but typically remained above this threshold until mid-October. High-frequency electrofishing (60 Hz, 200–500 V) was used to collect additional fish during March, April, and early May but was limited to shallow water habitats near

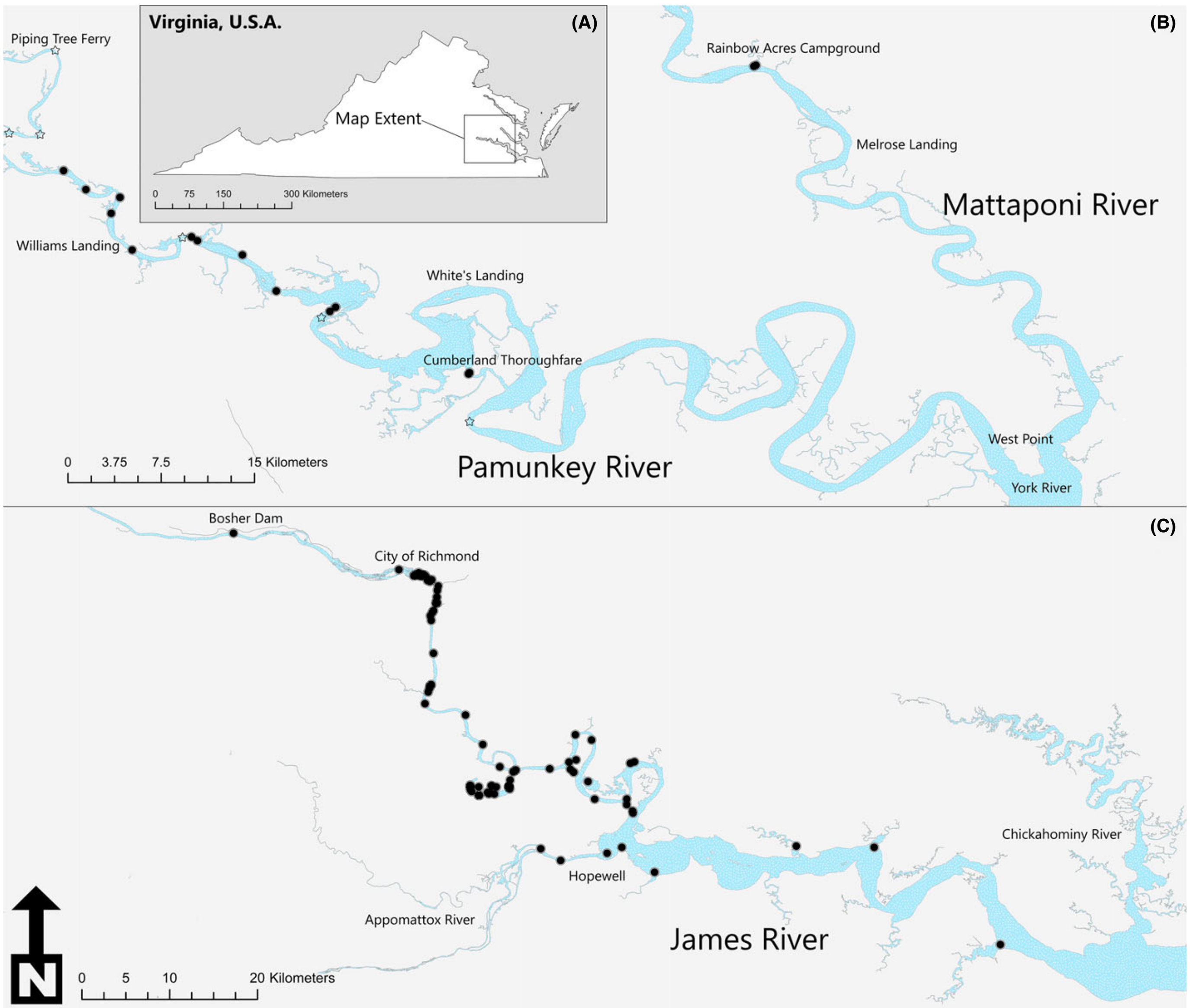

FIGURE 1. Solid circles represent locations where Flathead Catfish (n = 766) were captured during stratified random sampling (**A**) in eastern Virginia between 2013–2016. Zero Flathead Catfish were captured in the Rappahannock River despite extensive sampling; however, Flathead Catfish (n = 35) were captured (**B**) in the Mattaponi and Pamunkey Rivers. Numerous Flathead Catfish (n = 731) were also captured (**C**) in the James River, which has supported a population for several decades. Open stars represent locations where Flathead Catfish were sampled during VDGIF's catfish monitoring on the Pamunkey River, which occurred at 6–11 fixed sites per year between 2002 and 2017. [Color figure can be viewed at afsjournals.org.]

submerged structures, in waters <2 m deep (Schmitt et al. 2017). For the recently established York River population, distribution data was supplemented with density information provided by VDGIF's standardized catfish sampling. Low-frequency electrofishing as described in Greenlee and Lim (2011) was used to selectively sample nonidigenous ictalurids in 2002–2006, 2008, 2010, 2014, and 2016–2017 in the Pamunkey and Mattaponi rivers. An electrofishing boat outfitted with either a 7.5 or 9.0 GPP Smith-Root electrofisher (equipment selection based on river conductivity), gasoline generator, and trailing anode fished for a duration of ~600 s at each of 6–11 fixed sites per year.

Diet analysis.— Stomach contents were collected by excising the stomach or with pulsed gastric lavage, which is highly effective (>95%) for collecting dietary items from Flathead Catfish (Waters et al. 2004). For stomachs that were excised, catfish were humanely euthanized using cervical dislocation. Flathead Catfish that were processed using pulsed gastric lavage were returned to the water unharmed. Fish TL, weight, time of capture, water temperature, salinity, and geographical coordinates were recorded for each individual Flathead Catfish captured. Stomach contents were sealed in individually labeled bags, immediately placed on ice to halt further digestion, and later frozen. In the laboratory, stomach samples were thawed immediately before analysis. All prey items were weighed (blotted wet weight ±0.01 g), enumerated, and identified to the lowest possible taxon based on morphological characteristics (Chipps and Garvey 2007).

Fish prey were routinely encountered in the late stages of digestion, making identification difficult (Chipps and Garvey 2007). Highly degraded prey items present a major hurdle in diet analyses, and loose tissues are often difficult to assign to appropriate prey groups (Baker et al. 2014). Although otoliths or other hard structures such as scales, cleithra, vertebrae, and pharyngeal teeth may be useful for identifying prey, identification is frequently limited to coarse taxonomic resolution. These challenges can be particularly problematic for studies estimating predator consumption of specific taxa and can lead to erroneous conclusions about the relative importance of prey items in the diet (Hyslop 1980). To help mitigate these concerns, we used advanced molecular techniques (DNA barcoding) to identify digested fish prey. This tool allowed us to identify many of our samples that would have otherwise been classified as "unidentifiable" (Moran et al. 2016; Schmitt et al. 2017). There were situations where DNA barcoding was not possible (e.g., only bones or scales remained, or sequencing failed), and these prey were classified as "unidentified fish."

Molecular identification of fish prey.— For each sample of digested fish prey, total DNA was extracted from a ~10-mg tissue plug using a DNeasy Tissue Kit (Qiagen, Hilden, Germany) following the manufacturer's written instructions. Before lysis, each sample was defrosted and rinsed with ethanol to eliminate any chime. Before each tissue plug was extracted, utensils were sterilized by using a 10% bleach solution and then rinsed with autoclaved deionized water and allowed to dry. Freshly sterilized utensils were used for each sample. Each tissue sample was then placed in a sterilized microcentrifuge tube, and 180 μL of digestive solution and 20 μL of Proteinase K were added. Samples were then incubated at 56°C to allow for proper lysis.

Flathead Catfish prey upon many fish species, so universal cytochrome c oxidase subunit I (COI) primers were selected that would amplify DNA for all fish within the Chesapeake Bay. We amplified DNA sequences using a cocktail of four fish primers (FishF2_t1, FishR2_t1, VF2_t1, and FR1d_t1) developed for the COI-III region (Ivanova et al. 2007). Amplifications obtained with PCR also followed the protocol of Ivanova et al. (2007) with minor modifications. Vials for PCR amplification contained a total volume of 12.5 μL, which included 6.25 μL of 10% trehalose, 2.00 μL of ultrapure water, 1.25 μL 10 × PCR buffer (10 mM KCl, 10 nM $[NH_4]_2SO_4$, 20 mM Tris-HCl [pH 8.8], 2 mM $MgSO_4$, and 0.1% Triton X-100), 0.625 μL $MgCl_2$ (50 mM), 0.125 μL of each primer (0.01 mM), 0.0625 μL of each dNTP (10 mM), 0.0625 μL of Taq DNA Polymerase (New England BioLabs), and 2.0 μL of DNA template (mean concentration 74 μg/mL). All PCRs were conducted on a Bio-Rad MyCycler with the following thermocycling conditions: initial denaturation at 94°C for 2 min, followed by 35 cycles of 94°C for 30 s, 52°C annealing temperature for 40 s, 72°C for 1 min, and a final extension step at 72°C for 10 min. Products of PCR reactions were sequenced using BigDye Terminator Cycle Sequencing Kit version 3.1 on an ABI3730 DNA sequencer. Sequencing reactions were initiated using the C_FishF1t1 or C_FishR1t1 primers of Ivanova et al. (2007), and sequenced samples were analyzed using BioEdit and raw sequences edited in Sequencher version 4.5 (Gene Codes Corporation). Edited samples were then identified using the basic local alignment search tool (BLAST) from the National Center for Biotechnology Information Web site. Possible species were determined based on high quintile scores from percent identification, percent query cover, and maximum identification score as references; for more details see Moran et al. (2016).

Sample size sufficiency.— Gathering enough stomach samples to adequately assess the diet of a species is an important step that is overlooked by many diet studies (Ferry and Cailliet 1996). Sample size sufficiency was assessed using rarefaction curves, where the cumulative mean numbers of unique taxa were plotted against the cumulative number of stomachs examined. Sample size is considered sufficient if the slope reaches an asymptote (Ferry and Cailliet 1996; Bizzarro et al. 2007). Rarefaction curves and associated 95% CIs were calculated with EstimateS (version 9.1; Colwell 2013), where the cumulative numbers of unique prey taxa are plotted against the randomly pooled samples. This random process was repeated 500 times to generate means and associated CIs. We considered our sample to be sufficient when the mean slope (*b*) of the last four subsamples was less than 0.05 (Bizzarro et al. 2007; Brown et al. 2012).

Diet composition.— Percent frequency of occurrence (%FO) was used to identify prey resources that are routinely utilized by the population, as percent by weight and percent by number have inherent biases (MacDonald and Green 1983; Baker et al. 2014). We also characterized the relative importance of Flathead Catfish prey using the prey-specific index of relative importance (%PSIRI), which fixes several problems that are inherent in the more traditional index of relative importance (Brown et al. 2012). Percent PSIRI values were calculated for major fish prey and were used to estimate the difference in the importance of different prey resources. Percent PSIRI is defined as

$$\%\text{PSIRI} = \frac{\%\text{FO}_i x(\%\text{PN}_i + \%\text{PW}_i)}{2},$$

where $\%\text{FO}_i$ is the frequency of occurrence for prey type i, $\%\text{PN}_i$ is the percent by number of prey type i in all stomachs containing prey type i, and $\%\text{PW}_i$ is the percent by weight of prey type i in all stomachs containing prey type i. All diet composition analyses were first completed for all stomachs pooled, then analyzed by length bin (<400 mm TL, 400–800 mm TL, >800 mm TL) to better understand how feeding ecology changes with size (Schmitt et al. 2015).

Trophic position and feeding strategy.— Trophic level calculations, diet breadth measures, and omnivory indices were used to describe the trophic position and feeding strategy of Flathead Catfish within Chesapeake subestuaries. Trophic levels (TROPH) were calculated as

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

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 (Williams and Martinez 2004). Proportion in the diet was calculated as percent occurrence, as this index best represents population-level feeding patterns and circumvents biases associated with other indices (MacDonald and Green 1983; Baker et al. 2014). Trophic levels for several species of prey fish were available in the scientific literature (Baird and Ulanowicz 1989) and on the FishBase Web site (Froese and Pauly 2016), but species of unknown trophic level were estimated using the mean trophic level of species within that family (Cortés 1999). We also calculated a dimensionless omnivory index for Flathead Catfish, which provides valuable information on diet specialization (Christensen and Walters 2004; Rodríguez-Preciado et al. 2014). Omnivory indices (OI) were calculated using the formula

$$\text{OI}_i = \textstyle\sum_{i=1}^{n} [\text{TROPH}_j - (\text{TROPH}_i - 1)]^2 \times \text{DC}_{ij},$$

where TROPH_j is the trophic level of prey j, TROPH_i is the trophic level of predator i, and $\text{DC}ij$ 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 (Hyslop 1980; MacDonald and Green 1983). When OI = 0, the consumer is specialized and only feeds on one trophic level; conversely, an OI value > 0.5 would indicate nonspecialization and feeding on many trophic levels (Christensen and Walters 2004; Rodríguez-Preciado et al. 2014). The square root of a consumer's OI is the SE of its trophic level (Rodríguez-Preciado et al. 2014).

Diet breadth was estimated for each river using Levin's standardized index (Krebs 1989; Labropoulou and Papadopoulou-Smith 1999; Hajisamae et al. 2003). Diet breadth (DB), is calculated as

$$\text{DB}_i = \left(\frac{1}{n-1}\right)\left(\left(\frac{1}{\sum_{i,j=1}^{n} p_{ij}^2}\right) - 1\right),$$

where DB_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 was defined as percent occurrence, or the percentage of fish that had a given prey item present in their stomach. Levin's standardized index ranges from 0 to 1; values closer to 0 have limited dietary breadth, whereas values closer to 1 have greater diet breadth. Proportional diet breadth was estimated separately for each river.

Predator feeding strategy diagrams were constructed for major (>5% occurrence) prey groups. Feeding strategy diagrams were constructed by plotting prey-specific percent by number (%PN) by percent occurrence (Amundsen et al. 1996). This graphical method examines the generalist–specialist feeding dichotomy, which is a major component of niche theory (Pianka 1988). It also provides rudimentary information on individual diet specialization. A population with a narrow niche width is composed of specialized individuals; however, a population with a broad niche can be composed of individuals with either narrow or broad niches, or a combination of both (Amundsen et al. 1996). These diagrams provide insight into these patterns and help describe diet specialization and population niche width for Flathead Catfish in Virginia's tidal rivers.

RESULTS

Current Distribution and Relative Abundance Trends

A total of 766 Flathead Catfish were collected from the James, Pamunkey, and Mattaponi rivers, yet none were observed in the Rappahannock River despite extensive sampling (Schmitt and Orth 2015; Orth et al. 2017). Flathead Catfish were routinely captured in the James River from the fall line in Richmond to the confluence of the Appomattox River in Hopewell, Virginia, whereas Flathead Catfish were sparse and limited to smaller tidal creeks between the confluences of the Appomattox River and the Chickahominy River (Figure 1). A total of 731 Flathead Catfish were collected from the James River, which has supported a population since at least the 1960s (Jenkins and Burkhead 1994). While most stomachs were collected from fish in the tidal portion of the James River, additional Flathead Catfish stomachs (n = 37, 21 contained prey) were collected from boat-accessible sites below Bosher Dam, located approximately 13 km upstream from the fall line, and from Manchester Pool located immediately upstream from the fall line in downtown Richmond (Figure 1). Flathead Catfish from the James River ranged in size from 157 to 1,230 mm TL with an average size of 721 mm TL (Figure 2).

Our stratified random sampling revealed a sparse population of Flathead Catfish in the York River drainage; 34 Flathead Catfish were collected from the Pamunkey River, and one Flathead Catfish was observed in the Mattaponi River at Rainbow Acres Campground (37°39′31.30″N, 76°53′5.60″W; Figure 1). Flathead Catfish in the York River ranged in size from 248 to 960 mm TL with an average size of 605 mm TL (Figure 2). In the York River drainage, most Flathead Catfish were captured in the Pamunkey River within a few river miles of William's Landing (37°36′21.49″N, 77°5′33.42″W), which is a private boat landing in New Kent County, Virginia. These distribution patterns were corroborated with VDGIF's catfish monitoring data, where Flathead Catfish were first documented in the Pamunkey River in 2008. Flathead Catfish have been collected from a bend near Piping Tree Ferry Road (37°39′49.60″N, 77°6′41.26″W) all the way downriver to a bend just south of the Cumberland Thoroughfare (37°32′36.19″N, 76°58′34.32″W). The CPUE (fish/h) data from VDGIF's catfish monitoring also suggested that Flathead Catfish abundance has increased over the last decade. Despite wide variability in CPUE due to a high number of zero catches, CPUE generally increased between 2008 and 2014, after which it stabilized at a CPUE of approximately 10 fish/h through 2017 (Figure 3).

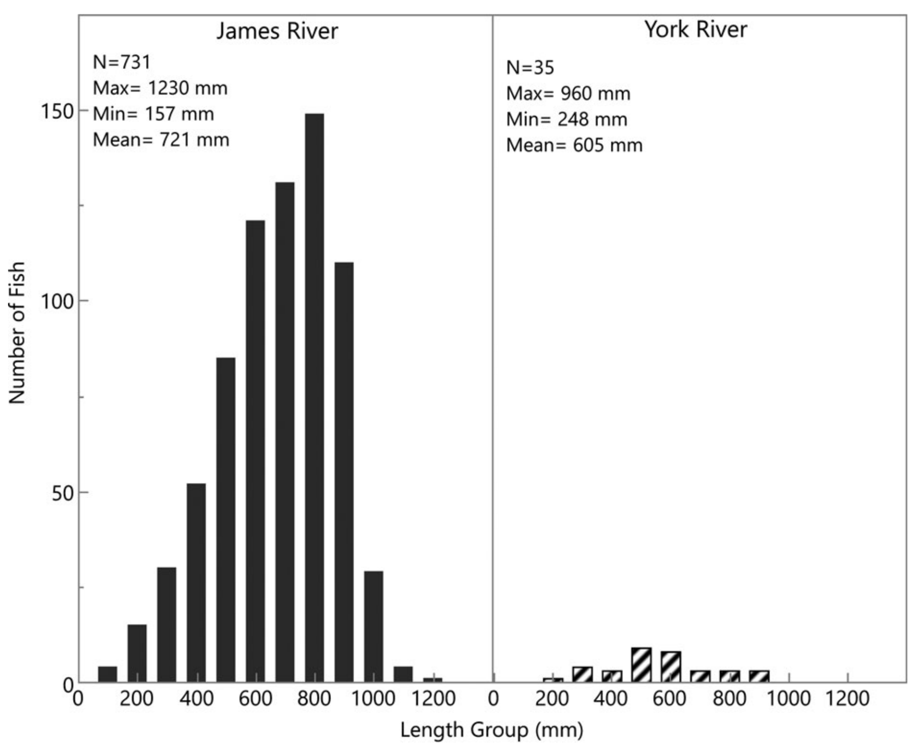

FIGURE 2. Length-frequency histograms for 766 Flathead Catfish captured in the James River (n = 731) and York River (n = 35) in eastern Virginia between 2013 and 2016. Minimum size, maximum size, and mean size are listed in the figure.

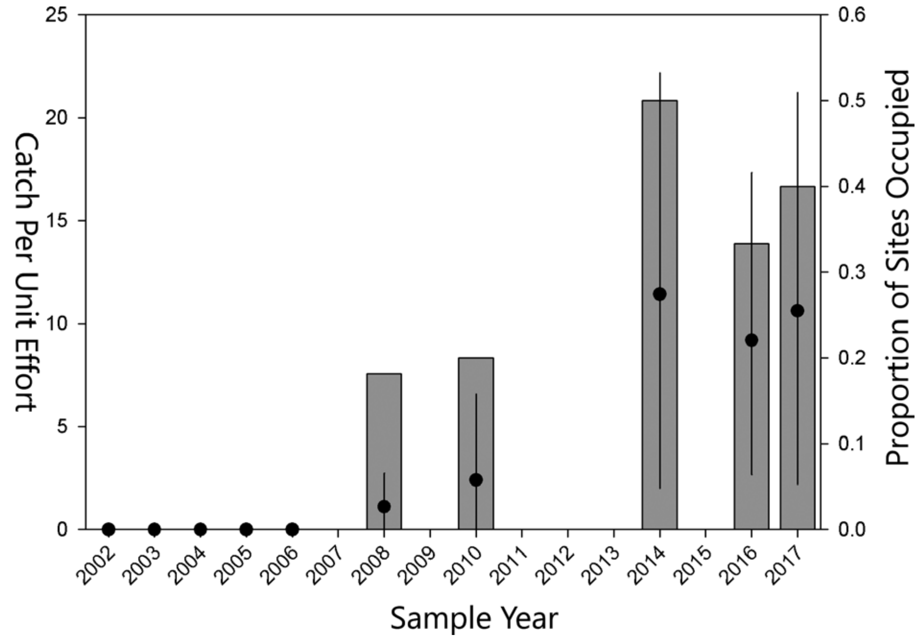

FIGURE 3. The CPUE is expressed as the number of Flathead Catfish caught per hour of low-pulse electrofishing (solid circles) in the Pamunkey River between 2002 and 2017. The 95% CI limits were estimated as the 2.5 and 97.5 percentiles from a 1,000-iteration bootstrap routine. The gray bars indicate the proportion of sites occupied by Flathead Catfish during long-term catfish monitoring completed by VDGIF.

Diet Composition

Flathead Catfish were captured in the Pamunkey and Mattaponi rivers (n = 35); however, most had empty stomachs and only a few contained prey (n = 9). Because diet studies with limited replication often produce speculative and misleading results, we restricted analyses of diet composition to Flathead Catfish collected from the James River basin. A total of 731 stomachs were collected from catfish in the James River subestuary, of which roughly half (47%, n = 343) contained prey items. The cumulative prey diversity curve reached an asymptote (b = 0.02) and displayed little variability at the final five endpoints (CV [100·SD/mean] = 0.09%; Figure 4), indicating sample size was sufficient for overall diet description of Flathead Catfish in the tidal James River. The cumulative prey curve reached a sufficient asymptote at n = 165 stomach samples where the regression line slope (b) was equal to 0.05 (Figure 4).

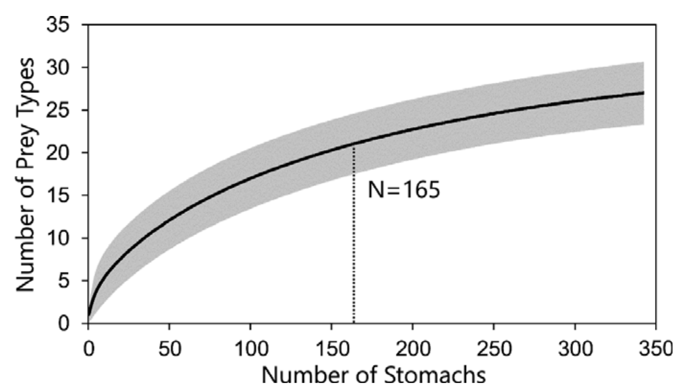

FIGURE 4. Cumulative prey curve (solid line) and 95% CI (shaded area) based on stomach content data from Flathead Catfish collected in the James River in eastern Virginia. The slope reached a sufficient asymptote ($b \leq 0.05$) at n = 165 stomachs, indicating that our sample size was more than sufficient for diet characterization.

Flathead Catfish of all sizes were highly piscivorous with 99% of the %PSIRI consisting of fish prey. The most important prey species by frequency of occurrence (36.2%) and %PSIRI (33.9%) was White Perch. Gizzard Shad *Dorosoma cepedianum* were also highly important with %FO and %PSIRI values ≈ 28% (Table 1). Among higher-order taxonomic groupings, Clupeidae, Moronidae, and unidentified teleosts ranked highest across all metrics, with %PSIRI values of 41.1, 34.5, and 13.5%, respectively. Other prey categories consumed to a lesser degree included Cyprinidae (5.3%), Ictaluridae (2.8%), bivalves of the order Veneroida (<1%), and Centrarchidae, Percidae, Atherinopsidae, Fundulidae, Achiridae, and Anguillidae, each representing <1% of %PSIRI. It is important to note that the observed bivalve predation could be due to what we call a "Matryoshka doll effect," where the bivalves occurred in the stomachs of prey fishes (Blue Catfish and White Perch), but persisted in the stomachs of Flathead Catfish due to differential digestion rates between fish and mollusks (MacDonald and Green 1983; Baker et al. 2014). Small Flathead Catfish (<400 mm TL)

TABLE 1. Diet composition, percentage of empty stomachs, trophic level (TROPH), diet breadth (DB), and omnivory indices (OI) for various sizes (mm TL) of Flathead Catfish (n = 731) collected from the James River near Richmond, Virginia. Diet metrics include percent frequency of occurrence (%FO) and prey-specific indices of relative importance (%PSIRI).

		All sizes n = 731 53.1% empty TROPH = 4.21 DB = 0.12 OI = 0.32		<400 mm TL n = 51 51.0% empty TROPH = 4.23 DB = 0.47 OI = 0.29		400–800 mm TL n = 387 55.0% empty TROPH = 4.27 DB = 0.13 OI = 0.25		>800 mm TL n = 293 50.9% empty TROPH = 4.13 DB = 0.14 OI = 0.39	
Prey family	Species	%FO	%PSIRI	%FO	%PSIRI	%FO	%PSIRI	%FO	%PSIRI
Achiridae	*Trinectes maculatus*	0.3	0.3	4.0	4.0				
Anguillidae	*Anguilla rostrata*	0.3	0.3			0.6	0.6		
Atherinopsidae	*Menidia beryllina*	0.6	0.6			1.1	1.1		
Centrarchidae	*Lepomis* spp.	0.9	0.7			1.7	1.4		
Clupeidae	*Alosa aestivalis*	6.7	6.6			2.9	2.9	12.5	12.2
	Alosa mediocris	0.3	0.3					0.7	0.7
	Alosa pseudoharengus	2.0	1.6			1.7	1.6	2.8	1.9
	Alosa sapidissima	0.6	0.6					1.4	1.4
	Alosa spp.	1.2	0.8					2.8	1.9
	Brevoortia tyrannus	0.3	0.3	4.0	4.0				
	Dorosoma cepedianum	28.3	27.7			12.6	12.3	52.1	51.1
	Dorosoma petenense	1.7	1.7			3.4	3.4		
	Dorosoma spp.	0.6	0.6			1.1	1.1		
Cyprinidae	*Cyprinus carpio*	0.6	0.6			0.6	0.6	0.7	0.7
	Cyprinus spp.	2.0	2.0	16.0	16.0	1.1	1.1	0.7	0.7
	Hybognathus regius	2.9	2.4	16.0	16.0	3.4	2.4		
	Nocomis micropogon	0.3	0.3					0.7	0.7
Fundulidae	*Fundulus heteroclitus*	0.6	0.6	8.0	8.0				
Ictaluridae	*Ictalurus furcatus*	2.0	1.8			2.9	2.4	1.4	1.4
	Ictalurus punctatus	0.9	0.9			1.1	1.1	0.7	0.7
	Pylodictis olivaris	0.3	0.1					0.7	0.3
Moronidae	*Morone americana*	36.2	33.9	36.0	34.2	50.0	48.1	19.4	16.8
	Morone saxatilis	0.6	0.6			0.6	0.6	0.7	0.7
Percidae	*Etheostoma flabellare*	0.9	0.3	4.0	0.8	1.1	0.5		
Unidentified Teleostei	Unidentified fish	15.2	13.5	20.0	17.0	19.0	16.8	9.7	8.9
Veneroida	*Corbicula fluminea*[a]	0.9	0.9			1.7	1.7		
	Unidentified Sphaeriidae[a]	0.3	0.2					0.6	0.3

[a]May have been in the stomachs of piscine prey consumed by Flathead Catfish.

consumed a diverse mixture of smaller fishes, including Hogchoker *Trinectes maculatus*, Eastern Silvery Minnow *Hybognathus regius*, Mummichog *Fundulus heteroclitus*, Fantail Darter *Etheostoma flabellare*, Menhaden *Brevoortia tyrannus*, and White Perch. Medium-sized Flathead Catfish (400–800 mm TL) consumed mostly Gizzard Shad and White Perch. Large Flathead Catfish (>800 mm TL) consumed mostly Gizzard Shad, White Perch, and *Alosa* species (primarily Blueback Herring). In terms of relative dietary importance, *Alosa* spp. represented 4.4%PSIRI in stomachs of Flathead Catfish 401–799 mm TL and 18%PSIRI in stomachs of Flathead Catfish > 800 mm TL. Individuals < 400 mm TL did not consume *Alosa* spp. (Table 1).

Trophic Position and Feeding Strategy

Flathead Catfish occupied high trophic positions (TROPH = 4.13–4.27) that showed little variation across length groupings, which is not surprising as Flathead Catfish become piscivorous at small sizes (Table 1). Omnivory indices were also relatively uniform across length groupings, ranging from 0.25 to

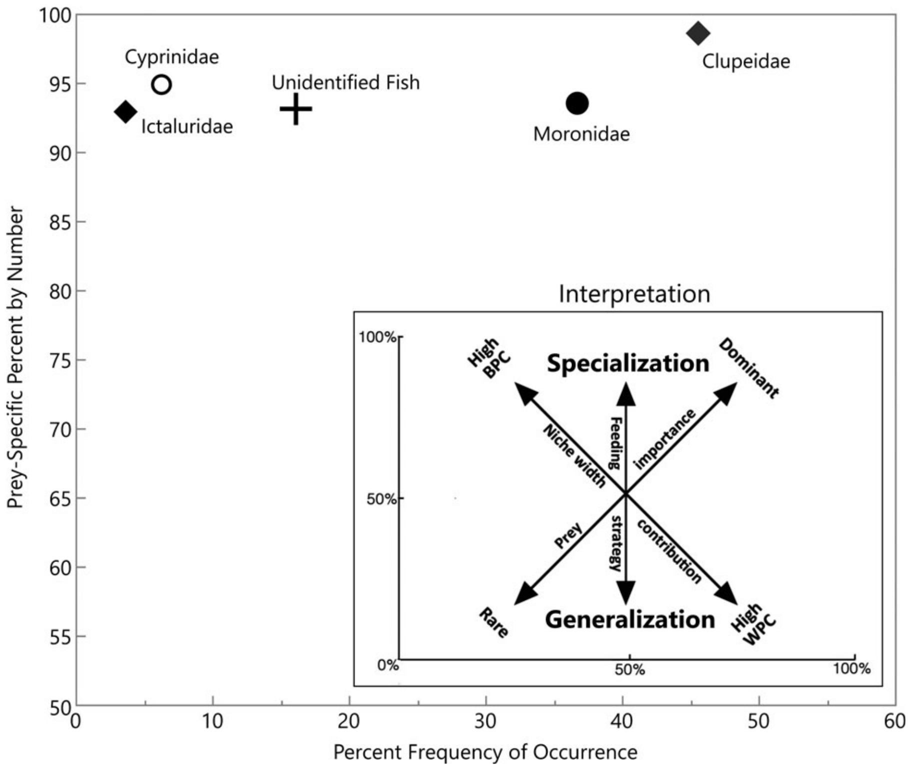

FIGURE 5. Feeding strategy diagram for 731 Flathead Catfish collected from the James River in eastern Virginia. Prey-specific percent by number is defined as the percent number of item *j* in all stomachs containing item *j*; a feeding strategy interpretation guide is included in the lower right panel. The upper half of the graph indicates a specialist feeding strategy, while the lower half indicates a generalist feeding strategy. Prey farther to the right on the *x*-axis are more commonly consumed, while prey farther to the left are rarely consumed. High BPC indicates a high between phenotype component to niche width, while high WPC indicates a high within phenotype component to niche width.

0.39, which is towards the "specialist" end of the generalist–specialist continuum (specialized feeding occurs at values < 0.50: Christensen and Pauly 1992; Christensen and Walters 2004). Diet breadth values were similar for medium and large fish (DB = 0.13 and 0.14, respectively), yet small fish (<400 TL) had higher diet breadth values (DB = 0.47) because they consume a more diverse array of ichthyofauna (Table 1). Our feeding strategy diagrams demonstrate that clupeids (mostly Gizzard Shad and Blueback Herring) and moronids (White Perch) are the most dominant prey species (Figure 5). Because all dietary items were located in the upper portion of the graph (>90% prey-specific percent by number; Figure 5), Flathead Catfish can be classified as piscivores that specialize at the individual level (Amundsen et al. 1996).

DISCUSSION

The current study provides the first comprehensive analysis of diet and trophic position for invasive Flathead Catfish in the Chesapeake Bay region. We demonstrate that Flathead Catfish are apex predators in these systems, with a mean trophic level > 4.0, as estimated trophic level "maximums" in nearby Chesapeake Bay food webs range from 3.0 to 4.9 (Williams and Martinez 2004). Blue Catfish have received more attention as harmful invaders in Chesapeake Bay (Schloesser et al. 2011; Aguilar et al. 2017; Schmitt et al. 2018), while Flathead Catfish have largely gone unnoticed (Schmitt et al. 2017). Whereas Blue Catfish are generalist omnivores that occupy lower trophic levels (Schmitt et al. 2018), the current study has demonstrated that Flathead Catfish are apex predators and piscine specialists. As piscine specialists with large gape sizes (Slaughter and Jacobson 2008), the concern surrounding the predatory impacts of Flathead Catfish on depleted *Alosa* species, Largemouth Bass, White Catfish, and Atlantic Sturgeon was justified, though predation of imperiled *Alosa* species will be the biggest concern moving forward. Predation of alosines was previously documented in the James River during the spring migratory period (Schmitt et al. 2017), a pattern that was also evident in the current study; Blueback Herring were consumed most regularly in both studies. While Schmitt et al. (2017) examined food habits of Flathead Catfish during the spring, the current study has demonstrated that Flathead

Catfish also prey on juvenile alosines as they migrate downriver during autumn, and approximately 5% of the Flathead Catfish stomachs we collected in October contained river herring. Another concern is Flathead Catfish predation on the recreationally and commercially valuable Striped Bass *Morone saxatilis* (Richards and Rago 1999), which were found in two catfish stomachs. While rare, predation of Striped Bass could still be problematic since disease is now threatening the population viability of the Atlantic coastal migratory stock (Hoenig et al. 2017).

Our extensive stratified random sampling provides a thorough description of the current distribution of Flathead Catfish in the tidal portions of the James, York, and Rappahannock rivers, particularly within tidal freshwater and oligohaline segments. It is important to note that all fish were captured using low-frequency electrofishing, which becomes less effective at higher salinities (Schmitt et al. 2018). Considering this, Flathead Catfish may be more abundant in brackish areas than this study indicates. In the tidal James River, Flathead Catfish are common from the fall line in the city of Richmond to the confluence of the Appomattox River near Hopewell, Virginia. Flathead Catfish are also common throughout the entire nontidal James River upriver from Richmond (Virginia Department of Game and Inland Fisheries, unpublished data). Flathead Catfish have been present in the James River for decades (Jenkins and Burkhead 1994) and are tolerant of brackish salinities (Bringolf et al. 2005), yet it is interesting that Flathead Catfish seemingly prefer the freshwater stretch between Richmond and Hopewell. We observed high densities of their preferred forage (e.g., Gizzard Shad and White Perch) farther downriver, yet Flathead Catfish are rarely encountered downriver from Hopewell. It is unclear why Flathead Catfish are less common in these oligohaline segments.

In the York River drainage, there is a relatively new Flathead Catfish population in the tidal Pamunkey River near Williams Landing in New Kent, Virginia. Flathead Catfish are established in the Pamunkey River, as we collected both juveniles (<250 mm TL) and gravid adults >900 mm TL (Brown et al. 2005), and VDGIF's catfish monitoring program first detected Flathead Catfish in the system in 2008. Flathead Catfish may have also emigrated from the Pamunkey River to the Mattaponi River, as we observed one catfish in the Mattaponi River near Rainbow Acres Campground in King and Queen County, though it is uncertain whether the Mattaponi River population is established. No Flathead Catfish were observed in the Rappahannock River, yet there is potential for future invasion. Flathead Catfish now occupy the two largest adjacent watersheds (York and Potomac rivers: Orrell and Weigt 2005) and have high salinity tolerances (Bringolf et al. 2005). Flathead Catfish could plausibly move into the Rappahannock River from either of these drainages, particularly during substantial rain events that push the salt wedge farther downriver. For example, Higgins (2006) hypothesized that invasive Blue Catfish populated the Potomac River basin through similar mechanisms, expanding from the York and Rappahannock rivers during high flow events. It is also plausible that the range of Flathead Catfish will not expand, as the current study demonstrated an apparent preferendum for tidal freshwater areas, at least in these systems.

The relatively new population of Flathead Catfish in the York River drainage could be a result of anglers relocating catfish from the James River. Most Flathead Catfish were captured in the Pamunkey River near Williams Landing, which is a private boat launch that is less than 30 mi (48 km) from the James River. Flathead Catfish are a hardy species (Muoneke 1991), and anglers could have easily transported them in a live well from the James River to the Pamunkey River. There is angler incentive to illegally stock this fish, as Flathead Catfish are a popular game fish in the James River near Richmond, where anglers commonly target the species in the high gradient stretch in between Bosher Dam and the 14th Street Bridge (J. D. Schmitt, personal observation). The phenomenon of illegal fish stocking is not new and is particularly problematic with Flathead Catfish (Bonvechio et al. 2011; Fuller and Whelan 2018). While laws are in place to deter such behaviors, penalties vary broadly by jurisdiction and enforcement is often limited (Johnson et al. 2009).

The Chesapeake Bay has a long history of fish invasions, and 27 fish species have invaded since European colonization in 1608 (Ruiz and Reid 2007). Much of the recent work on nonindigenous fishes in the Chesapeake Bay has focused on Blue Catfish (Fabrizio et al. 2018; Hilling et al. 2018; Schmitt et al. 2018) and Northern Snakehead *Channa argus* (Wegleitner et al. 2016; Resh et al. 2018), while invaders like Flathead Catfish have received little attention. Flathead Catfish occupy higher trophic positions than Blue Catfish (Schmitt et al. 2018) and have a larger average body size (Schmitt et al. 2017). As large-bodied apex predators that feed almost exclusively on fish, their impact on native ichthyofauna could be substantial. Invasive Flathead Catfish have been estimated to cause substantial declines in native fish biomass in other Atlantic slope drainages (Pine et al. 2007) and are considered to be one of the most dangerous freshwater invaders in North America (Fuller et al. 1999). While Blue Catfish have attracted a great deal of attention from the media and the scientific community (Orth et al. 2017), Flathead Catfish will have greater per capita impacts on native fishes, as our data show that Flathead Catfish are piscine specialists, whereas Blue Catfish are primarily herbivores–benthic invertivores (Schmitt et al. 2018).

Despite being in the early stages of the invasion process, it is unlikely that Flathead Catfish in the York River can be eradicated or contained. In Georgia, over 25,000 Flathead Catfish were removed from the Satilla River between 1996 and 2009, which is another Atlantic tributary similar in size to the York River (Bonvechio et al. 2011). This eliminated large fish from the population; however, compensatory responses including increased recruitment, increased growth, and quicker maturation were observed (Bonvechio et al. 2011; Massie et al. 2018). Those authors concluded that eradication or containment of Flathead Catfish in the Satilla River was improbable, though length structure truncation can be achieved as large fish are removed from the population. This suggests that periodic removals could be used to reduce predatory impacts on at-risk species in Virginia's tidal rivers, as we found that large Flathead Catfish (≥800 mm TL) are most likely to consume depleted river herring and American Shad. It is unknown whether this would be an effective expenditure of resources. Bycatch in offshore Atlantic Herring *Clupea harengus* fisheries, poor water quality, and impediments to migration are likely driving observed declines of river herring and American Shad (Limburg and Waldman 2009), and offshore bycatch is especially problematic for populations of mid-Atlantic river herring (Hasselman et al. 2015). It is probable that Flathead Catfish will be permanent members of these riverine fish communities, as the window for effective removal has likely passed. This suggests that public education campaigns, stricter penalties, and more proactive enforcement are needed to curb the illegal spread of nonindigenous fishes (Johnson et al. 2009). This is especially the case for Flathead Catfish, as illegal stocking likely resulted in the establishment of nonindigenous populations in Michigan, Wisconsin, Georgia, Delaware, and Pennsylvania (Brown et al. 2005; Bonvechio et al. 2011; Fuller and Whelan 2018).

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