Abstract—Blue catfish (*Ictalurus furcatus*) have been widely introduced throughout the United States and are invasive in Chesapeake Bay. Despite this proliferation, little is known about the diet of this large, predatory catfish. We used stratified random sampling to collect stomachs from 14,488 blue catfish in Chesapeake Bay. Canonical correspondence analysis (CCA) was used to identify key drivers of the diet of blue catfish, and generalized additive models (GAMs) were used to explore trends in rates of predation by blue catfish on depleted or commercially valuable native species, including American shad (*Alosa sapidissima*), blueback herring (*A. aestivalis*), alewife (*A. pseudoharengus*), American eel (*Anguilla rostrata*), and blue crab (*Callinectes sapidus*). Results of CCA reveal that diets were significantly correlated with season, salinity, and total length (TL) of blue catfish, and those from our GAMs reveal the circumstances associated with greater predation on these species. For example, we found that *Alosa* species were most susceptible to predation by large catfish (>600 mm TL) in freshwater areas during the month of April. This paper describes methods for identifying times, locations, and other circumstances that are associated with maximal predation rates upon certain taxa. The information gained from these approaches can be used to inform management strategies, with the goal of reducing effects of predation on specific organisms.

Modeling the predation dynamics of invasive blue catfish (*Ictalurus furcatus*) in Chesapeake Bay

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Invasive species are key drivers of the global biodiversity crisis (Vitousek et al., 1997; Mack et al., 2000), can cause enormous economic losses (Pimentel, 2011), and can result in native species declines and extinctions (McGee et al., 2015). Invasive fish species have been a chronic problem at the global scale, yet there are considerable knowledge gaps pertaining to their impacts on recipient ecosystems (Cucherousset and Olden, 2011). Some introduced fish species appear to be benign, but others have deleterious ecological effects, restructuring native communities through competitive interactions or direct predation (Helfman, 2007; Albins and Hixon, 2008). Because of these potential impacts, description of the diet is important in understanding how an invader may affect a given ecosystem (Brandner et al., 2013; Dick et al., 2014).

The blue catfish (*Ictalurus furcatus*) is the largest catfish species (Ictaluridae) in North America and is one of the most prolific invasive fish species in Atlantic slope drainages of the southeastern United States (Fuller and Neilson, 2018). Blue catfish have been widely stocked outside of their native range (Mississippi River basin) for recreational fishing purposes (Graham, 1999), and they were introduced to tidal rivers in Virginia during the 1970s (Greenlee and Lim, 2011). Blue catfish populations grew rapidly during the late 1990s, prompting concern and subsequent management action (Fabrizio et al., 2018). Populations of blue catfish have since expanded from tidal freshwater areas into oligohaline and mesohaline portions of several tidal tributaries of Chesapeake Bay (Greenlee and Lim, 2011). This expansion is problematic because these brackish areas serve as spawning and nursery habitat for many native marine and estuarine species (MacAvoy et al., 2009; Magoro et al., 2015).

Over several decades, populations of native fish taxa, including the Atlantic

sturgeon (*Acipenser oxyrinchus*), the American shad (*Alosa sapidissima*), *river herring*, a collective term for the blueback herring (*A. aestivalis*) and the alewife (*A. pseudoharengus*), and the American eel (*Anguilla rostrata*), have declined in Chesapeake Bay (Haro et al., 2000; Niklitshek and Secor, 2005; Limburg and Waldmen, 2009). Chesapeake Bay is far from pristine, and anthropogenic activities have resulted in major ecological changes, including the widespread loss of aquatic macrophytes, increased turbidity, and frequent hypoxic and anoxic events (Kemp et al., 2005). Scientists and fisheries managers are now concerned that predation by invasive blue catfish may lead to further declines of depleted native fish species. Although blue crab (*Callinectes sapidus*) are not rare, there is concern about predation pressure on this species because it supports lucrative commercial fisheries in Virginia, Maryland, and Delaware (Paolisso, 2002). Other studies have shown that blue catfish are consuming the aforementioned fish and crab species, with the exception of Atlantic sturgeon (Schmitt et al., 2017, 2019). Previous research has revealed that blue catfish in Chesapeake Bay have remarkably broad diets that include vegetation, numerous fish species, mollusks, crustaceans, birds, terrestrial mammals, reptiles, amphibians, and various invertebrates, yet the factors that drive dietary variation have not yet been identified (Schmitt et al., 2019). Furthermore, the predation dynamics of blue catfish on depleted species like the American shad and American eel have not been described.

Although a substantial body of literature is dedicated to factors that influence the establishment of invasive species (Catford et al., 2009; Blackburn et al., 2011), fewer works have focused on the impact phase of invasion (Fei et al., 2016), and most studies produce speculative results (Simberloff et al., 2013). This is especially the case for invasive fish species, for which more observational and experimental studies are urgently needed (García-Berthou, 2007; Layman and Allgeier, 2012; Brandner et al., 2013). Diet studies are not necessarily direct measures of impact, but they are useful for determining which organisms are most likely to be affected by an introduced predator (Caut et al., 2008; Layman and Allgeier, 2012). Diet studies can also be used to determine when and where depleted species are most vulnerable to predation by an invader, information that can be used to guide management efforts (Schmitt et al., 2017).

This study fulfilled 2 main objectives. First, we used multivariate modeling to determine the significance and relative influence of several factors that were suspected to influence the food habits of blue catfish. We hypothesized that diets would vary spatiotemporally, as these tidal systems support diverse assemblages that change in space and time due to salinity preference and seasonal migration patterns (Wagner and Austin, 1999; Jung and Houde, 2003). We also expected diets to vary with catfish size, as previous work has demonstrated that blue catfish undergo ontogenetic diet shifts from omnivory to piscivory at larger sizes (500–900 mm total length [TL], depending on the river; Schmitt et al., 2019). Second, we incorporated any significant factors from the first objective into models

of predation on American shad, river herring, American eel, and blue crab. These models were then used to elucidate the circumstances that result in greater predation on these depleted or economically valuable native taxa. This information can be used to direct management efforts, which we discuss later.
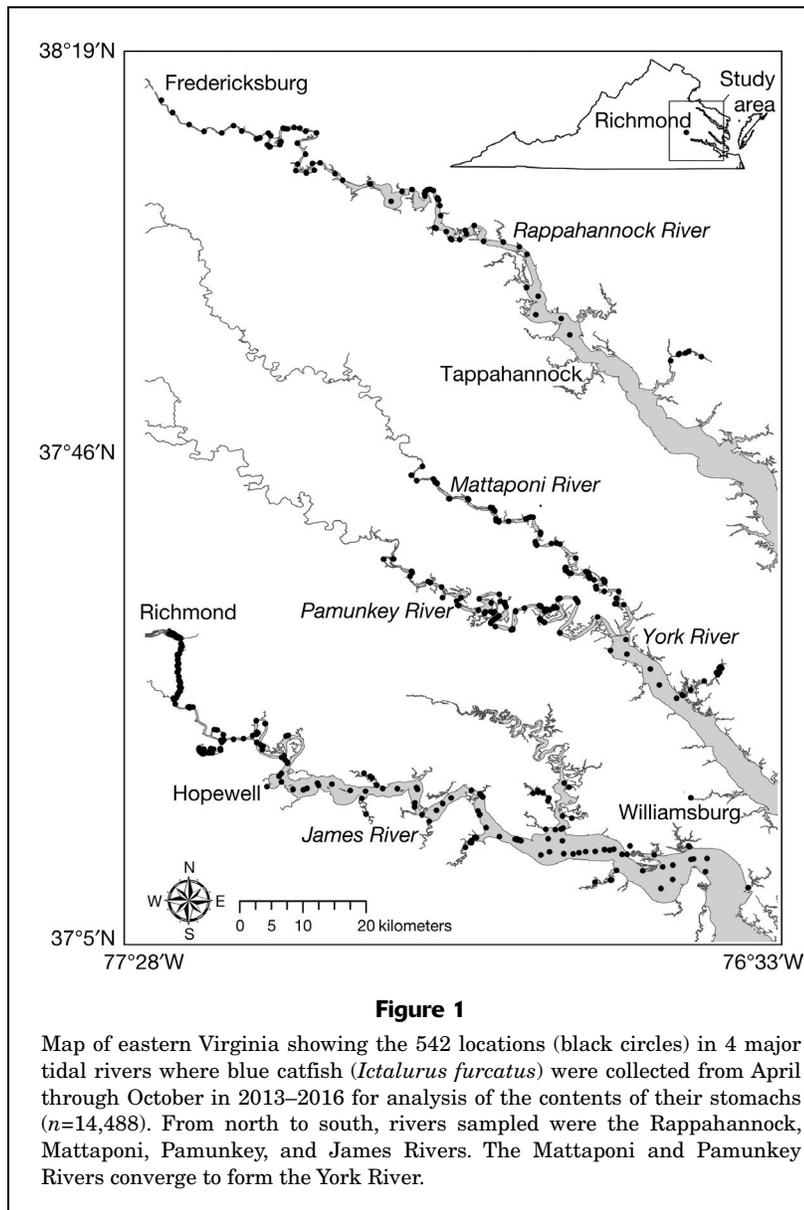
Materials and methods

Study area

Chesapeake Bay is the largest estuary in the continental United States and has a long history of commercial and recreational exploitation (McHugh and Bailey, 1957; Richards and Rago, 1999). Although blue catfish are now found in all major tributaries of Chesapeake Bay (Schloesser et al., 2011), many populations are still in the early stages of establishment and support low densities of fish (Aguilar et al., 2017). We therefore focused our efforts on the James, Pamunkey, Mattaponi, and Rappahannock Rivers in eastern Virginia (Fig. 1). These rivers were stocked with hundreds of thousands of blue catfish between 1973 and 1985 and now contain well-established populations that include mature individuals (Greenlee and Lim, 2011; Bunch et al., 2018).

Field methods

Each river was divided into 3 strata according to average fall surface salinies during 1985–2016 by using data from the Chesapeake Bay Program's Water Quality Database (available from website). The 3 strata included tidal freshwater stretches (Practical Salinity [S_P]: 0.0–0.5), oligohaline stretches (S_P: 0.6–5.0), and mesohaline stretches (S_P: 5.0–18.0). We stratified each river by autumn salinities because density stratification is less problematic during fall (Shiah and Ducklow, 1994). Each stratum was divided into 2-km sections, which were numbered, and then a random number generator was used to select each sampling location. During April–October, a minimum of 2 randomly selected sections were sampled monthly within each stratum for all 4 rivers, with both nearshore and main-channel sampling occurring when possible. Most blue catfish were sampled by using low-frequency, pulsed direct current electrofishing (5–25 Hz, 100–400 V) because it captures blue catfish of all sizes (Bodine and Shoup, 2010) and is extremely effective in Virginia's tidal rivers (Greenlee and Lim, 2011; Schmitt and Orth, 2015). In higher salinities, pulsed alternating current electrofishing was occasionally used, and anode design, voltage, and pulse frequency were adjusted on the basis of water conductivity and other environmental conditions.

Upon capture, fish were immediately placed in a 568-L aerated livewell, and stomach contents were extracted within 30 min of capture to prevent regurgitation (Garvey and Chipps, 2012). Stomach contents were extracted either by excising the stomachs or with pulsed gastric lavage, which is highly effective for extracting stomach contents from blue catfish (Waters et al., 2004). Date, time,

Figure 1

Map of eastern Virginia showing the 542 locations (black circles) in 4 major tidal rivers where blue catfish (*Ictalurus furcatus*) were collected from April through October in 2013–2016 for analysis of the contents of their stomachs (*n*=14,488). From north to south, rivers sampled were the Rappahannock, Mattaponi, Pamunkey, and James Rivers. The Mattaponi and Pamunkey Rivers converge to form the York River.

water temperature, salinity, and coordinates were recorded for each sampling event. Fish weight (in grams) and TL (in millimeters) were also recorded, and stomach contents were placed on ice and later frozen.

Laboratory methods

Prior to examination, stomachs were thawed, and stomach contents were blotted dry with a paper towel (Schmitt et al., 2017). Prey items were then weighed, counted, and identified to the lowest possible taxon. Digested fish remains that lacked morphological distinctiveness were identified by using DNA barcoding techniques. The use of DNA barcoding enabled us to identify 70–80% of fish prey that were unidentifiable by gross morphology, excluding instances in which only bones or scales remained. Our

DNA barcoding methods are described in Moran et al. (2016) and Schmitt et al. (2017, 2019).

Modeling diet drivers for blue catfish

Populations of blue catfish extend from tidal fresh water into mesohaline waters in Chesapeake Bay, where species assemblages change along the salinity gradient (Wagner and Austin, 1999; Jung and Houde, 2003). Seasonality affects the availability of some prey resources, such as adults of *Alosa* species, which enter tidal rivers during spring to spawn (Waldman, 2013), or blue crab, which migrate seasonally (Aguilar et al., 2005). Moreover, blue catfish exhibit ontogenetic trophic niche shifts, with differently sized fish consuming different prey (Schmitt et al., 2017). We therefore hypothesized that the diet of blue catfish would vary with season, salinity, and catfish size.

We explored overall patterns in the diet of blue catfish by using canonical correspondence analysis (CCA; ter Braak, 1986). This analysis is a form of multivariate ordination in which a matrix of response variables is "regressed" (constrained) on a matrix of independent variables; it is the multivariate analog of multiple linear regression. It is often used for analyzing relationships between species assemblages and multidimensional environmental data (ter Braak and Verdonschot, 1995), but CCA has also been used for assessing feeding patterns (Clifton and Motta, 1998; Jaworski and Ragnarsson, 2006). Because we were interested in general diet patterns, we first grouped all diet items into 6 broader categories: fish species, mollusks, crustaceans, other invertebrates, vegetation, and *other* (e.g., anthropogenic debris, terrestrial mammals, birds, and other rare items). Each CCA was based on the binary presence–absence of diet items (i.e., frequency of occurrence) because it is less biased than other diet measures and is preferred for assessing feeding patterns (Baker et al., 2014; Buckland et al., 2017). Predictor variables included salinity zone, TL (rounded to the nearest 100 mm), and season (also coded as 3 dummy variables).

We assessed whole-model and variable-wise statistical significance with *F*-tests, and significance was assessed by using an alpha threshold of 0.05. Magnitude of relationship groupings of individual fish and constraining variables or diet items were assessed on the basis of loading scores (an analog of correlation coefficients, centered at 0 and ranging from −1 to 1). Because previous studies

showed river-specific variability in diet, dietary ontogeny, growth, and population structure, we conducted a separate CCA for each river (Hilling et al., 2018; Schmitt et al., 2019). Each CCA was completed in the package vegan (vers. 2.4-4; Oksanen et al., 2017), which is an extension of the statistical software R, vers. 3.4.3 (R Core Team, 2017).

Predation models for species of concern

We used binomial generalized additive models (GAMs), which are semiparametric generalizations of logistic regression (Hastie and Tibshirani, 1990), to examine relationships between the binary occurrence of depleted alosines (American shad and river herring), blue crab, and American eel in the diet of blue catfish by predictor variables identified in each CCA. This approach was especially useful for identifying when and where predation by blue catfish on these species of concern was most likely. Again, the GAMs were based on occurrence data because it is the best metric for assessing predation and is often more reliable than other diet measures (Baker et al., 2014; Buckland et al., 2017). A GAM is flexible because it assumes only that functions are additive and relationships are smooth (Guisan et al., 2002). A GAM, like a generalized linear model, uses a link function to establish a relationship between the mean of the response variable and a "smoothed" function of the explanatory variables, making it robust to scattered or correlated data (Lin and Zhang, 1999). Separate GAMs were constructed for American eel, depleted *Alosa* species (American shad and river herring), and blue crab. Each GAM included smoothing functions for *predator length* and *salinity*, yet *month* and *river* were treated as categorical factors (Wood, 2006). Although interannual variation is likely an important driver of dietary patterns, stomach contents for each month were pooled across years (e.g., contents for June in 2013, 2014, 2015, and 2016 were combined into the single category for June) to increase sample sizes. This pooling was a necessary step because circumstances that were out of our control (equipment failure and weather) resulted in limited sampling during some combinations of month and year (e.g., June 2014).

Each model was created by using the R package mgcv, vers. 1.8.28 (Wood, 2017), with default values unless otherwise specified. Each model was constructed as follows:

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

where logit = the binomial link function;
P = the probability of a species being consumed;
β_0 = the model intercept; and
f_1–f_2 = the smoothing functions realized by penalized thin plate regression splines (Wood, 2006).

For each covariate, the mgcv package fits a series of penalized regression splines as smoothing functions and supplies degrees of freedom for smooth terms by minimizing generalized cross-validation scores (Wood, 2006). Individual F-tests were then used to determine which predictors contribute significantly to the deviance explained (Wood, 2006). The probability of encountering each species in stomachs of blue catfish was then predicted separately by river to elucidate the conditions that lead to higher predation rates for these species. Overall predictive performance of each model was then assessed by using the area under the receiver operating curve (ROC) in the package ROCR (vers. 1.0-7; Sing et al., 2005) in R. An area under the ROC of 0.5 is equivalent to a random guess, a value of 1.0 indicates perfect model performance, and a value >0.7 indicates adequate model performance (Bewick et al., 2004; Austin, 2007).

Results

Data collection

During 2013–2016, we collected 14,488 blue catfish stomachs at 542 sites on the James, Pamunkey, Mattaponi, and Rappahannock Rivers in eastern Virginia (Fig. 1). In addition, stomachs were collected from several hundred fish that were captured from the York River, which forms at the confluence of the Pamunkey and Mattaponi Rivers near Westpoint, Virginia (Fig. 1). For simplicity, fish captured from the northern half of the York River were allocated to the Mattaponi River sample, and fish captured on the southern half were allocated to the Pamunkey River sample. Of the stomachs collected, 7302 contained food items (50%). Although stomachs (sample size [n]=16,110) were collected year-round (Schmitt et al., 2019), we limited this study to stomachs that were collected by using low-frequency electrofishing following a stratified random sampling protocol (April–October) to avoid spatiotemporal biases.
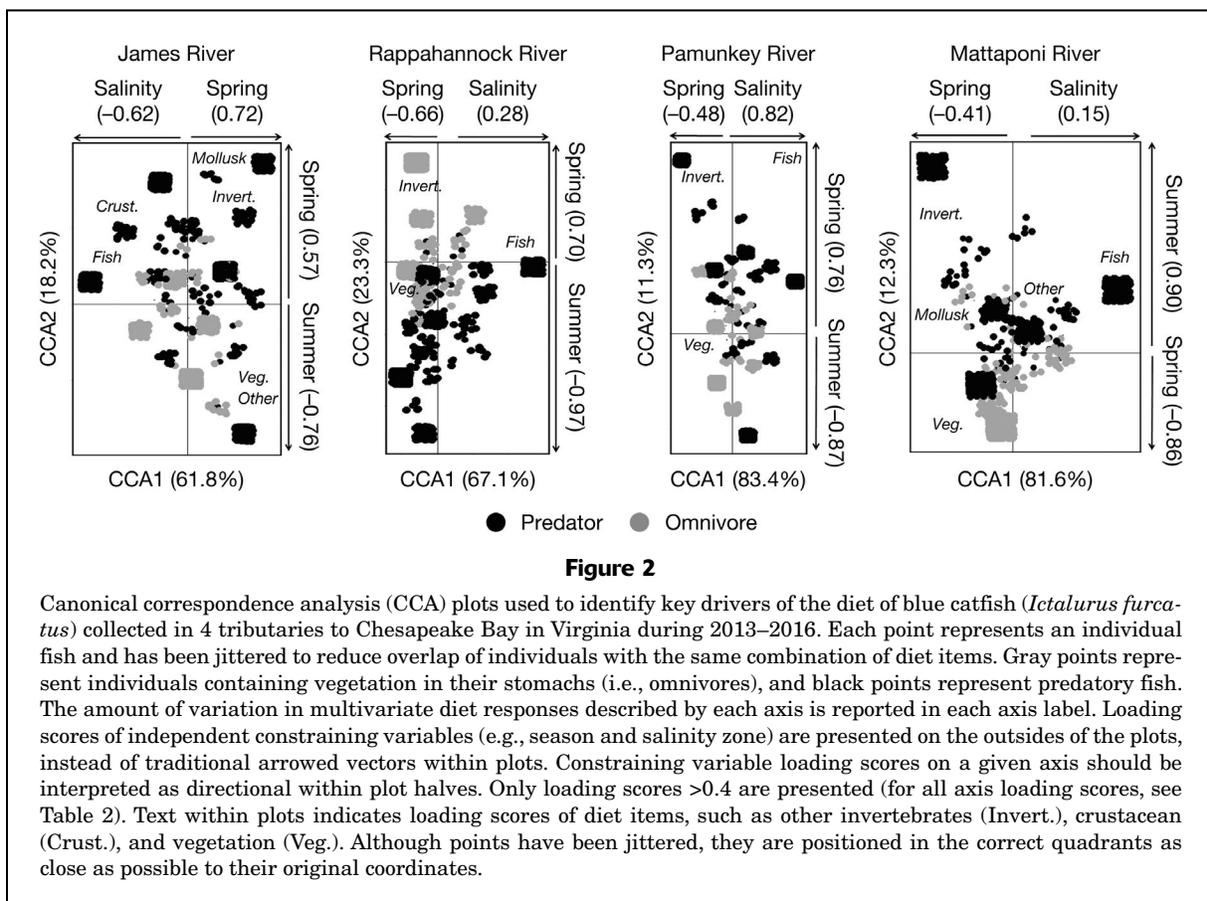
Major diet drivers for blue catfish

Diets of blue catfish varied by river, salinity, season, and predator TL, and all constraining variables were statistically significant in the CCA ($P<0.001$; Table 1). For each river, the first 2 CCA axes accounted for a considerable amount of variation in the diet of blue catfish: 80.0% in the James River, 85.0% in the Rappahannock River, 97.4% in the Pamunkey River, and 93.3% in the Mattaponi River. Global F-tests on each CCA for each river were highly significant ($P<0.001$ for all), and nearly all constraining variables significantly affected the diet of blue catfish in each river ($P<0.001$), with the exception of salinity zone in the Mattaponi River ($P=0.081$; Table 1, Fig. 2).

Results of each CCA indicate several key patterns in the diet of blue catfish. First, there were consistent, length-related (i.e., ontogenetic) shifts from omnivory to piscivory in all rivers. Second, blue catfish more frequently preyed on invertebrates or crustaceans during spring than during other seasons and began to consume more fish as the seasons progressed. Third, the predation of various invertebrates is generally associated with lower salinities,

Table 1

Results of the canonical correspondence analyses used to identify key drivers of the diet of blue catfish (*Ictalurus furcatus*) collected in 4 tributaries to Chesapeake Bay in Virginia during 2013–2016. Whole-model and variable-wise statistical significance (*P*<0.05) were evaluated with *F*-tests. Predictor variables include salinity zone, season, and predator total length. Separate models were developed for each river.

Variable	James River df	James River F	James River P	Rappahannock River df	Rappahannock River F	Rappahannock River P	Pamunkey River df	Pamunkey River F	Pamunkey River P	Mattaponi River df	Mattaponi River F	Mattaponi River P
Whole model	4	17.9	<0.001	4	21.6	<0.001	4	21.7	<0.001	4	14.9	<0.001
Salinity zone	1	32.7	<0.001	1	11.8	<0.001	1	46.7	<0.001	1	1.9	0.081
Season	3	21.6	<0.001	2	49.2	<0.001	2	13.3	<0.001	2	43.1	<0.001
Total length	1	8.9	<0.001	1	7.6	<0.001	1	7.8	<0.001	1	11.3	<0.001

Figure 2

Canonical correspondence analysis (CCA) plots used to identify key drivers of the diet of blue catfish (*Ictalurus furcatus*) collected in 4 tributaries to Chesapeake Bay in Virginia during 2013–2016. Each point represents an individual fish and has been jittered to reduce overlap of individuals with the same combination of diet items. Gray points represent individuals containing vegetation in their stomachs (i.e., omnivores), and black points represent predatory fish. The amount of variation in multivariate diet responses described by each axis is reported in each axis label. Loading scores of independent constraining variables (e.g., season and salinity zone) are presented on the outsides of the plots, instead of traditional arrowed vectors within plots. Constraining variable loading scores on a given axis should be interpreted as directional within plot halves. Only loading scores >0.4 are presented (for all axis loading scores, see Table 2). Text within plots indicates loading scores of diet items, such as other invertebrates (Invert.), crustacean (Crust.), and vegetation (Veg.). Although points have been jittered, they are positioned in the correct quadrants as close as possible to their original coordinates.

but blue catfish shifted toward piscivory in higher salinity areas, especially in the James and Pamunkey Rivers (Fig. 2). Not surprisingly, herbivory was strongly associated with spring and summer in all rivers.

Perhaps most importantly, patterns were not consistent among rivers. For example, herbivory was strongly associated with summer in all rivers except the Rappahannock River, where it was more prevalent in spring. Moreover, distinct length- and season-related breaks were observed in diets of individual blue catfish from some rivers (e.g.,

the Mattaponi River), but much more overlap occurred in other rivers (e.g., the James River; Fig. 2). All CCA axis loadings of diet items and constraining variables are presented in Table 2.

Predation models for species of concern

Our GAMs demonstrate that predation by blue catfish on species of concern varies by river, salinity, month, and predator TL (Figs. 3–5). All GAMs were globally significant

Table 2

All canonical correspondence analysis (CCA) axis loadings (CCA1 and CCA2) of diet items and constraining variables used to identify patterns in the diet of blue catfish (*Ictalurus furcatus*) collected during 2013–2016 in 4 tributaries to Chesapeake Bay in Virginia—the James, Pamunkey, Mattaponi, and Rappahannock Rivers. Variables include salinity zone, season (spring and summer), and predator total length. Separate models were constructed for each river.

Variable	James		Pamunkey		Mattaponi		Rappahannock	
	CCA1	CCA2	CCA1	CCA2	CCA1	CCA2	CCA1	CCA2
Salinity zone	−0.624	0.303	0.816	−0.312	0.150	0.013	0.284	0.105
Spring	0.720	0.574	−0.482	0.759	−0.415	−0.868	−0.665	0.702
Summer	−0.036	−0.756	−0.420	−0.870	−0.092	0.898	0.029	−0.973
Total length	−0.050	0.530	0.286	−0.289	−0.194	0.391	−0.041	−0.078

($P<0.001$), and all predictors were significant ($P<0.05$), with the exception of salinity in the model for predation on American eel (Table 3). All GAMs had acceptable predictive performance, with areas under the ROC of 0.84–0.86 (Table 2; Pearce and Ferrier, 2000).

Our models demonstrate that depleted alosines, American shad and river herring, were most susceptible to predation by blue catfish in tidal freshwater areas. As many as 4% of stomachs from blue catfish were expected to contain these taxa in certain areas (e.g., tidal freshwater stretches of the James River; Fig. 3). Our model also revealed that large blue catfish consumed more alosines, and as many as 8% of stomachs from 700–1000-mm-TL blue catfish were predicted to contain American shad or river herring in the James River. Seasonally, the probability of predation upon depleted *Alosa* species was greatest in April, with another increase in predation during October. Overall, predicted predation on alosines was highest in the James and Rappahannock Rivers. In the imperiled alosine GAM, river herring were the most commonly consumed species group in both rivers, although American shad were found in more stomachs of blue catfish from the Rappahannock River than in those from the James River (Schmitt et al., 2019).

Our model suggests that predation on blue crab increases at higher salinities. Nearly 30% of stomachs from blue catfish were predicted to contain blue crab in S_P levels >8 in the James River, and predicted percent occurrence of blue crab in stomachs was typically less than 5% in the other rivers. Large blue catfish consumed blue crab more frequently, and model predictions indicate that catfish between 600 and 900 mm TL were most likely to consume blue crab (Fig. 4). Model predictions also indicate that predation on blue crab was greatest during the late summer and into fall (August–October).

Predation on American eel was uncommon, and predicted occurrence in stomachs of blue catfish was <5% in all modeled scenarios (Fig. 5). Predation on American eel was not significantly correlated with salinity ($P>0.05$), although it was correlated with predator TL and month ($P<0.02$). Model predictions indicate that medium and large blue catfish (500–900 mm TL) were the most likely

to consume American eel. Seasonally, predicted occurrence was highest during spring and fall, particularly in April and October (Fig. 5).

Discussion

In all rivers, the diet of blue catfish varied with season, salinity, or both. These 2 factors also influence the structure of assemblages of organisms in Chesapeake Bay (Wagner and Austin, 1999; Jung and Houde, 2003; Lippson and Lippson, 2006). These relationships are intuitive because species assemblages vary drastically along the salinity gradient and some species are only available seasonally (Wagner and Austin, 1999; Jung and Houde, 2003; King et al., 2005). For example, aquatic macrophytes, which are commonly found in stomachs of blue catfish (Schmitt et al., 2019), are generally only available during the warmer months (Moore et al., 2000). Other potential prey in tributaries of Chesapeake Bay include adult American shad, hickory shad (*A. mediocris*), and river herring that make upstream spawning migrations during spring (Garman and Nielsen, 1992; Schmitt et al., 2017). Additionally, juveniles of these taxa emigrate from these rivers during the late summer and autumn months (Hoffman et al., 2008). Blue crab and American eel also make seasonal movements in these rivers (Wenner and Musick, 1974; Aguilar et al., 2005), and our models revealed increased predation during these migratory periods. Lastly, although interannual variation is likely an important driver of dietary patterns for blue catfish, stomach contents were pooled across years for each month to increase sample sizes for our study. Other diet studies have reported strong interannual trends that mirror fluctuations in prey abundance (Latour et al., 2008).

Multivariate analyses identified consistent, length-related shifts from omnivory to piscivory, a finding consistent with previous work (Schmitt et al., 2017, 2019). In general, small blue catfish feed primarily on macrophytes and benthic invertebrates, and large blue catfish become more piscivorous (see Schmitt et al., 2019). The size at which this shift to piscivory occurs varies from
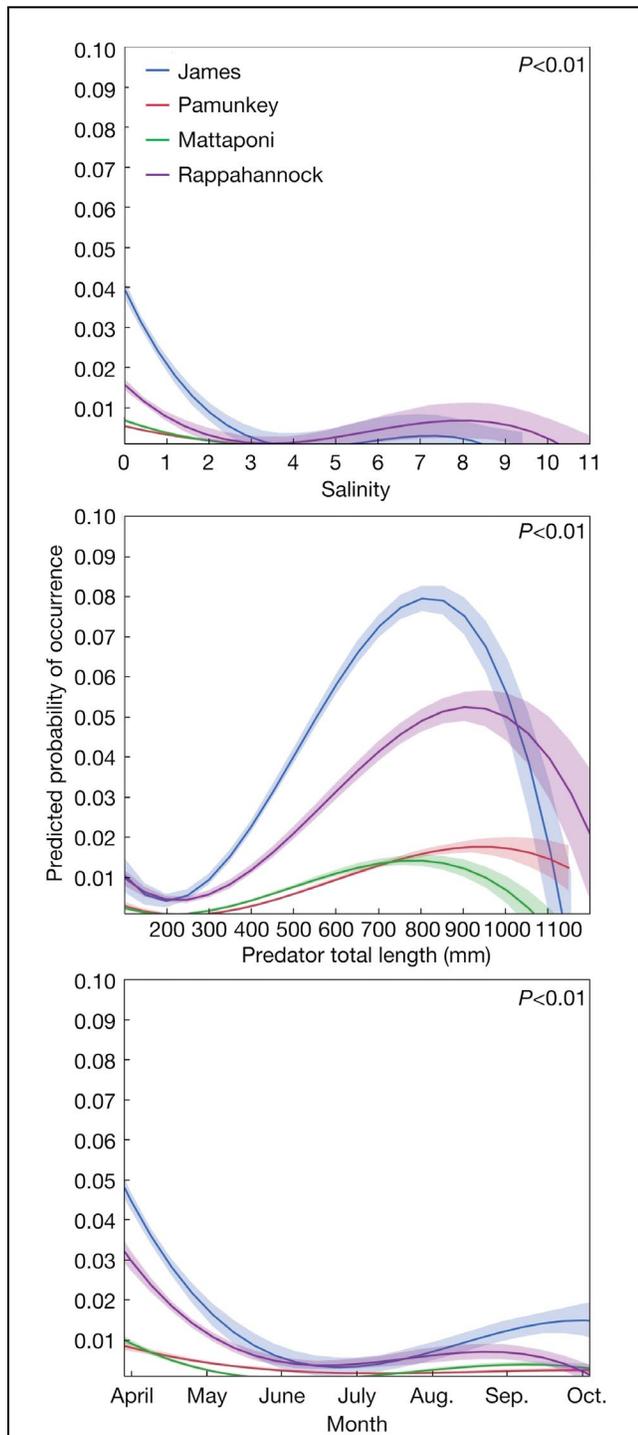
Figure 3

Predictions from the generalized additive model for predation on imperiled alosines by blue catfish (*Ictalurus furcatus*), calculated as probability of occurrence in a catfish stomach, by salinity, predator total length, month, and river. All predictive factors were significant (*P*<0.05). Imperiled alosines include the American shad (*Alosa sapidissima*), blueback herring (*A. aestivalis*), and alewife (*A. pseudoharengus*). Blue catfish were collected in the James, Pamunkey, Mattaponi, and Rappahannock Rivers in eastern Virginia during 2013–2016.
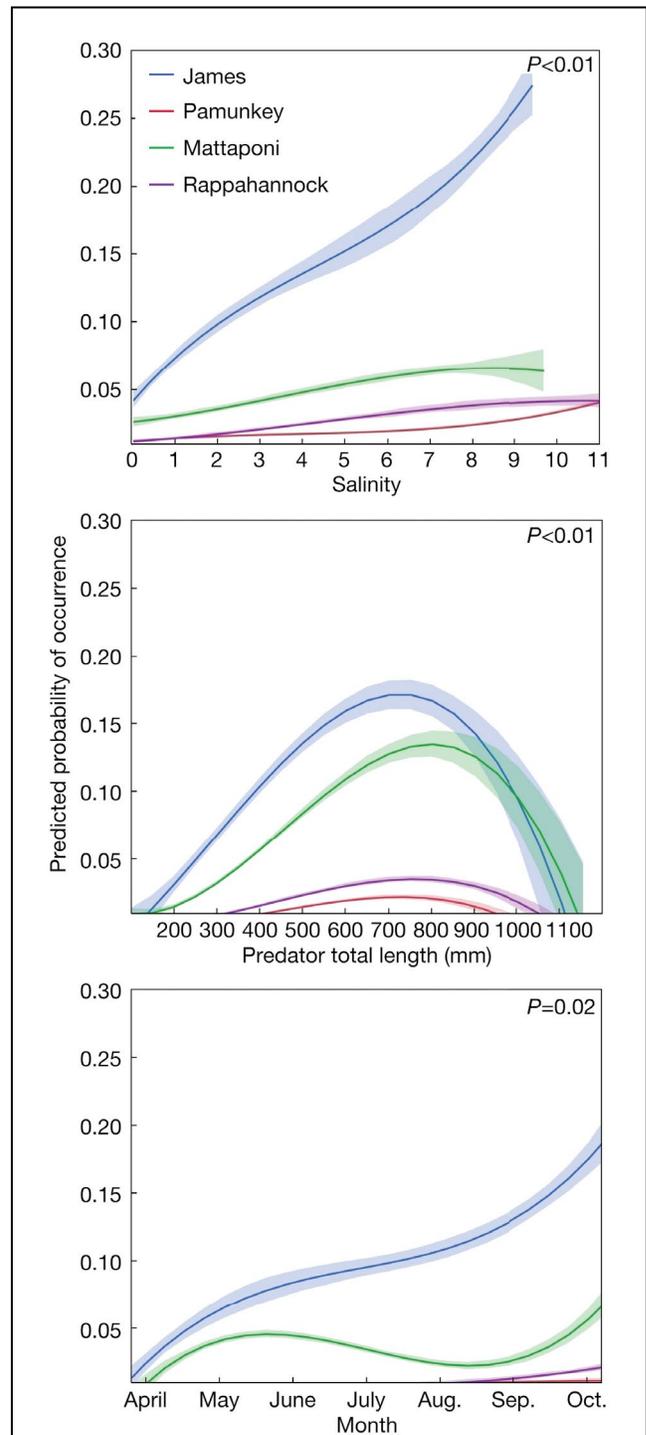
Figure 4

Predictions from the generalized additive model for predation on blue crab (*Callinectes sapidus*) by blue catfish (*Ictalurus furcatus*), calculated as probability of occurrence in a catfish stomach, by salinity, predator total length, month, and river. All predictive factors used in the model were significant (*P*<0.05). Blue catfish were collected in the James, Pamunkey, Mattaponi, and Rappahannock Rivers in eastern Virginia from April through October during 2013–2016.
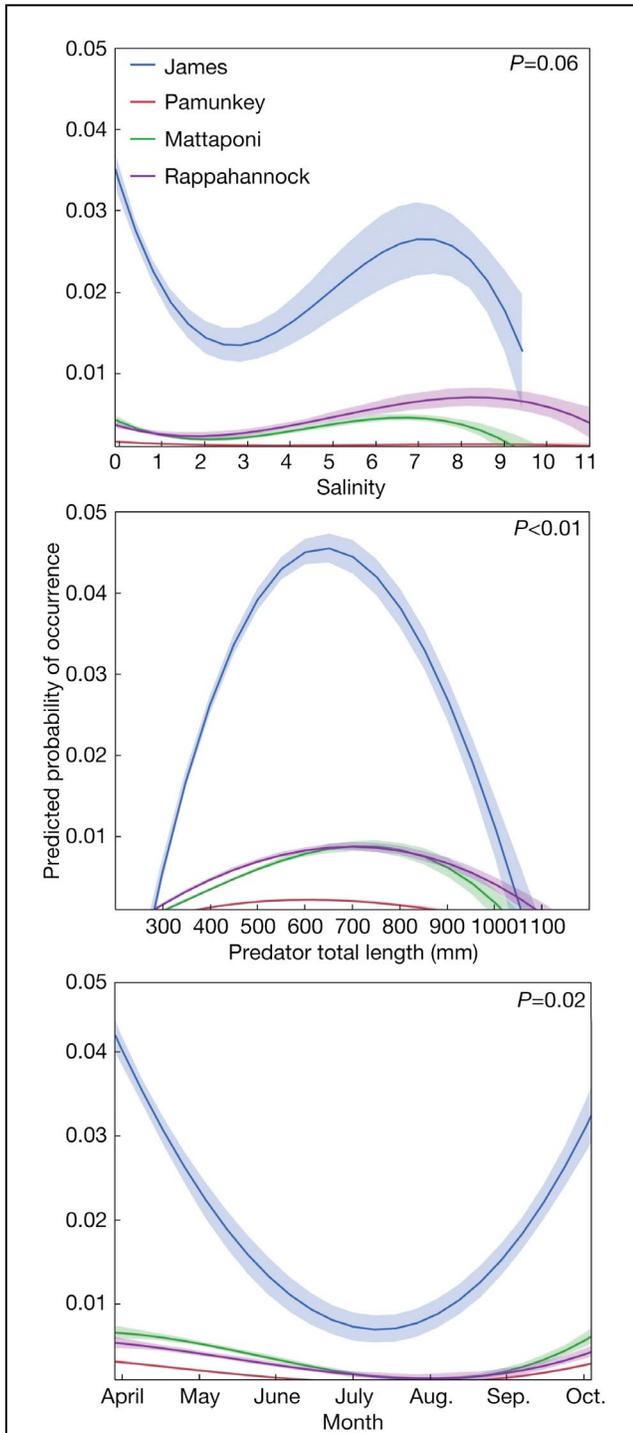
Figure 5

Predictions from the generalized additive model for predation on American eel (*Anguilla rostrata*) by blue catfish (*Ictalurus furcatus*), calculated as probability of occurrence in a catfish stomach, by salinity, predator total length, month, and river. All predictive factors were significant (*P*<0.05), with the exception of salinity (*P*=0.06). Blue catfish were collected in the James, Pamunkey, Mattaponi, and Rappahannock Rivers in eastern Virginia during 2013–2016.

Table 3

Whole-model and variable-wise statistical significance for each generalized additive model (GAM) used to explore trends in rates of predation by blue catfish (*Ictalurus furcatus*) on American eel (*Anguilla rostrata*); imperiled alosines, including American shad (*Alosa sapidissima*), blueback herring (*Alosa aestivalis*), and alewife (*A. pseudoharengus*); and blue crab (*Callinectes sapidus*) in Chesapeake Bay in Virginia during 2013–2016. An asterisk indicates that the value was insignificant (α=0.05). Model performance was evaluated by using area under the receiver operating curve (ROC) and deviance explained.

Predictor	American eel	Imperiled alosines	Blue crab
River	*P*<0.001	*P*=0.009	*P*<0.001
Month	*P*<0.001	*P*=0.019	*P*=0.017
Salinity	*P*=0.063*	*P*<0.001	*P*<0.001
Total length	*P*=0.023	*P*<0.001	*P*<0.001
Model fit			
Area under ROC	0.859	0.874	0.843
Null deviance	651.305	698.980	2032.733
Residual deviance	127.875	151.977	440.578
Deviance explained	523.430	547.003	1592.155

500 mm TL (James River) to 900 mm TL (Pamunkey River) and may be driven by the relative abundance of small fish prey in each river (Schmitt et al., 2019). Although large, piscivorous catfish compose a small fraction of each population, they could still have deleterious effects on important native taxa like American shad, river herring, and American eel. Ample evidence indicates that blue catfish feed on locally abundant prey, as other studies have reported that blue catfish are nonselective, opportunistic feeders (Eggleton and Schramm, 2004; Schmitt et al., 2017). These life history traits have been documented in many other estuarine and marine fish species, for which diets are a reflection of the variability of available prey (Beumer, 1978; Livingston, 1984; Ley et al., 1994; Jaworski and Ragnarsson, 2006).

Our GAMs revealed the circumstances that lead to greater predation on species of concern by invasive blue catfish. For American shad and river herring, maximal predation occurred in freshwater areas, a finding that corresponds with those of Schmitt et al. (2017), who reported that predation on depleted alosines peaked in both tidal and non-tidal freshwater segments of the James River. For simplicity, we pooled imperiled alosines for analysis; however, river herring were consumed more frequently than American shad, which are larger and faster-swimming fish (Waldman, 2013). For more detailed, species-specific data, please see Schmitt et al. (2019). For all rivers, the highest predation rates occurred in April, a result that agrees with previous work from the James River (Schmitt et al., 2017). Although some of the alosine prey items were in the late stages of digestion, all of the discernible

specimens captured during spring were mature, spawning adults. The model for American shad and river herring also revealed a small increase in predation during September and October. All alosines consumed during this period were small, and autumn is associated with the outriver migration of juvenile alosines in Atlantic estuaries (Loesch and Lund, 1977; Hoffman et al., 2008; Palkovacs et al., 2014). Therefore, this migratory behavior may make juvenile alosines more susceptible to predation by blue catfish at this time. It is important to note that small, juvenile fish are digested more rapidly than adults (Bromley, 1994) and that, as a result, we may have underestimated predation on juvenile alosines during autumn.

Predation on American shad and river herring was highest for blue catfish ranging in size from 600 to 900 mm TL, although predation probabilities decrease for trophy-sized catfish (≥1072 mm TL; Gabelhouse, 1984). These feeding patterns may be driven by individual diet specialization, where trophy-sized blue catfish are cannibalistic or specialize on gizzard shad (*Dorosoma cepedianum*) as observed by Schmitt et al. (2019). The predicted percent occurrence of alosines in the diet of blue catfish was relatively low in all circumstances (<8% occurrence). It is also important to note that some *Alosa* species can experience high post-spawning mortality because of energetic demands (Glebe and Leggett, 1981), and the presence of alosines in blue catfish stomachs could be, in part, due to scavenging (Schmitt et al., 2019).

Along the Atlantic coast, declines in populations of river herring and American shad began well before the proliferation of blue catfish and must have been initiated by other mechanisms (e.g., declines in populations of American shad began during the 1800s, and river herring populations declined precipitously in the 1960s; Limburg and Waldman, 2009). Alosines face many challenges, including habitat loss, overharvesting, poor water quality, climate change, and impediments that block migratory corridors (Limburg and Waldmen, 2009; Raabe and Hightower, 2014). Moreover, alosines are frequently taken as bycatch in Atlantic herring (*Clupea harengus*) fisheries (Bethoney et al., 2013; Hasselman et al., 2016). Nonetheless, predation by invasive catfish could further destabilize these species, especially if functional response curves are such that predation rates increase at low prey densities (Dick et al., 2014). Interestingly, some signs of recovery have been observed for populations of American shad in the Rappahannock and Potomac Rivers (Cummins[1]; Hilton et al.[2]). Both of these rivers support dense populations of blue catfish, possibly indicating that blue catfish play an insignificant role in the population dynamics of American shad.

Blue catfish predation on blue crab increased with salinity, and this increase was likely driven by the relative density and spatial dynamics of blue crab populations in the James, York, and Rappahannock Rivers. Previous research has indicated that blue crab abundance (measured as the number of blue crab caught per 24 h in fyke nets) was positively correlated with salinity in tidal tributaries of Chesapeake Bay (King et al., 2005). Moreover, low-salinity areas are typically dominated by adult male crab, which, because of their large size, are less susceptible to predation, yet smaller juvenile and female crab become more abundant at higher salinities (Hines et al., 1987). Many of the blue crab we found in stomachs were immature, a finding that correlates well with the observed relationship between salinity and predation on blue crab. Rates of predation on blue crab were highest for blue catfish around 800 mm TL and declined in larger blue catfish. Maximal predation rates occurred during the autumn months in all rivers, although predation on blue crab increased during spring in the Mattaponi River. The autumn months are typically associated with reduced freshwater inflow, which often results in the upriver advancement of the salt wedge (Schubel and Pritchard, 1986). As the salt wedge advances upriver, we would expect there to be greater spatial overlap between blue catfish and blue crab (King et al., 2005). We directly observed this phenomenon in the James River when we found blue crab at high densities along the lower edge of the fall line during August and September. This area is usually home to freshwater species, like the smallmouth bass (*Micropterus dolomieu*) and various sunfish species (*Lepomis* spp.), but the upriver advancement of the salt wedge enables blue crab to colonize this area during extended dry periods.

Blue crab naturally co-occur with blue catfish in estuaries in Louisiana (Baltz and Jones, 2003) and are consumed at higher rates there (up to 50% of stomachs; Perry, 1969) than those observed in Virginia's tidal rivers. In spite of high predation rates, Louisiana continues to sustain valuable blue crab fisheries, and annual harvests exceed those in both Virginia and Maryland (NMFS[3]). This is not surprising because blue crab have complex life histories (Hines et al., 2010) and population dynamics appear to be strongly influenced by abiotic factors (Bauer and Miller, 2010; Colton et al., 2014). Nonetheless, predation of blue crab by blue catfish should be considered in future population models; after all, the predicted percent occurrence of blue crab in stomachs of blue catfish can be quite high (up to 28% in brackish portions of the James River).

For American eel, salinity did not significantly affect predation rates. This result is intuitive because eels readily colonize freshwater, estuarine, and marine habitats and move freely between them (Feunteun et al., 2003; Daverat et al., 2006). Size of blue catfish significantly affected predation rates on American eel, and maximal predation rates were observed for blue catfish between

[1] Cummins, J. 2016. The return of American shad to the Potomac River: 20 years of restoration. Final Report. Interstate Comm. Potomac River Basin, ICPRB Rep. ICP16-5, 23 p. [Available from website.]

[2] Hilton, E. J., R. Latour, P. E. McGrath, B. Watkins, and A. Magee. 2016. Monitoring relative abundance of American shad and river herring in Virginia rivers 2015 annual report, 98 p. Va. Inst. Mar. Sci., Coll. William Mary, Gloucester, VA. [Available from website.]

[3] NMFS (National Marine Fisheries Service). 2017. Fisheries of the United States 2016. NOAA, Natl. Mar. Fish. Serv., Curr. Fish. Stat. 2016, 147 p. [Available from website.]

600 and 800 mm TL. Most of the American eel consumed were yellow-phase (sexually immature adults), although phase determination was often difficult because of tissue degradation from digestion. Month was a significant factor in the model for American eel, and maximal predation rates occurred during spring and fall, especially in April and October. This observation may be related to eel migration patterns driven by seasonal changes in temperature (Welsh et al., 2016; Aldinger and Welsh, 2017). For example, silver-phase American eel (sexually mature adults) make long spawning migrations in autumn, and yellow-phase American eel are known to make punctuated upstream movements as waters warm in spring (Welsh and Liller, 2013). Overall, predation by blue catfish on American eel was rare (predicted percent occurrence was <5% in all circumstances).

Populations of eel species, including the American eel, have declined across the northern hemisphere (Bonhommeau et al., 2008); therefore, blue catfish are unlikely to be drivers of these declines. Population declines may be attributed to many factors, although climate change and the proliferation of an invasive parasitic nematode are likely culprits (Shepard, 2015). Climate change may affect spawning and recruitment success of American eel because of their complex life history (Knights, 2003). Silver-phase eel undergo long spawning migrations to the Sargasso Sea, after which ocean currents transport larvae to nurseries on the continental slope (Wang and Tzeng, 2000). Warming temperatures have been associated with changes in physical oceanographic processes in the North Atlantic Ocean, changes that may negatively affect the survival and transport of eel larvae (Knights, 2003). Furthermore, an exotic parasitic nematode, *Anguillicoloides crassus*, has expanded its distribution across the western Atlantic Ocean. Although this parasite does not cause immediate mortality, it damages the swim bladder and may increase mortality rates as silver-phase eel undergo long-distance spawning migrations (Fazio et al., 2012; Barry et al., 2014).

Several conclusions can be drawn from the results of this study. First, our models revealed that American shad, river herring, and American eel are rarely consumed by blue catfish; however, large catfish (500–1000 mm TL) consume disproportionately more of these taxa. This may explain why results from all models indicate that overall predation on species of concern is highest in the James River, where large blue catfish are most abundant (Greenlee and Lim, 2011; Hilling et al., 2018). Predation on these taxa declines as blue catfish approach trophy size (≥1072 mm TL; Gabelhouse, 1984), and reports from previous work indicate that many trophy-sized blue catfish are cannibalistic or feed on gizzard shad (Schmitt et al., 2019). Although American shad, river herring, and American eel are rarely consumed, blue crab are frequently consumed by large catfish in brackish areas.

These length-based feeding patterns have important implications for management of blue catfish in Atlantic drainages of the United States. In the James River, fishing for large blue catfish is quite popular (Greenlee and Lim, 2011), and many fishing guide services and tackle

shops rely on this resource. For individuals involved in these businesses, the status of blue catfish as *invasive* is controversial because several other nonindigenous fish species are not considered invasive in this river, for example, the smallmouth bass and muskellunge (*Esox masquinongy*) in the non-tidal James River and the largemouth bass (*Micropterus salmoides*) and channel catfish (*Ictalurus punctatus*) in the tidal James River. This argument is valid; however, these species exist at much lower densities and are far more spatially restricted than blue catfish. Blue catfish have spread to every major tributary of Chesapeake Bay (Schloesser et al., 2011) and are abundant in brackish areas (Fabrizio et al., 2018). Moreover, population densities in the tidal James River have been estimated to be as high as 70,800 blue catfish/km^2 (Bunch et al., 2018).

Although the results of our study indicate that trophy-sized blue catfish (≥1072 mm TL; Gabelhouse, 1984) do not routinely consume imperiled species, it is likely that these large fish produce disproportionately more offspring than smaller fish (Hixon et al., 2014). Therefore, current regulations that require mandatory release of large blue catfish (e.g., in Virginia, anglers can only keep one blue catfish >813 mm TL per day) could potentially contribute to increases in population densities and further range expansion for this species. Mandatory release regulations may not be ideal; however, high contaminant burdens in large blue catfish can render them unfit for human consumption, particularly in the James and Potomac Rivers (Luellen et al., 2018). Ultimately, it is probable that all future management of blue catfish in Chesapeake Bay will be controversial because differing opinions exist among various user groups and management agencies (Orth et al.[4]).

Eradication programs for invasive species often fail in large, open systems (Britton et al., 2011; Franssen et al., 2014) and are unlikely to succeed for blue catfish in the Chesapeake Bay region (Orth et al.[4]). Nonetheless, increased commercial harvest of large blue catfish (500–1000 mm TL) could reduce their predation on depleted alosines, American eel, and blue crab. In the James and Rappahannock Rivers, size structure of blue catfish is already shifting toward smaller sizes, as growth rates decline and large fish become rarer (Hilling et al., 2018). Currently, harvest of large catfish is limited because of concerns about contaminant burdens (Hale et al.[5]); however, it may be time to consider uses other than as human food for the harvest of these large catfish, including uses for pet foods and fertilizers (Orth et al.[4]). Because blue crab are consumed most commonly in brackish segments of these rivers, managers may want to explore options to incentivize more harvest of blue catfish in these areas.

[4] Orth, D. J., Y. Jiao, J. D. Schmitt, C. D. Hilling, J. A. Emmel, and M. C. Fabrizio. 2017. Dynamics and role of non-native blue catfish *Ictalurus furcatus* in Virginia's tidal rivers, 102 p. Final Report. Va. Dep. Game Inland Fish., Henrico, VA.
[5] Hale, R. C., T. D. Tuckey, and M. C. Fabrizio. 2016. Risks of expanding the blue catfish fishery as a population control strategy: influence of ecological factors on fish contaminant burdens, 48 p. [Available from Va. Inst. Mar. Sci., Coll. William Mary, 1375 Great Rd., Gloucester Point, VA 23062.]

This study had limitations. First, winter diet information was not included in our modeling exercises because it was not collected in a randomized manner. This omission is problematic because blue catfish consume blue crab during winter, although the spatiotemporal extent of these data is limited (Schmitt et al., 2019). Second, we had limited success capturing blue catfish when using low-frequency electrofishing in brackish areas ($S_P \geq 10$), although blue catfish have been captured in S_P levels as high as 21.5 (Fabrizio et al., 2018). Our limited success in these locations is simply an artifact of low-frequency electrofishing, which becomes ineffective at higher salinities (Bringolf et al., 2005). Predation on blue crab increases with salinity; therefore, we may be underestimating predation by blue catfish on this commercially valuable species. Future studies in Chesapeake Bay should focus on the diet of blue catfish during winter, particularly in brackish areas with S_P levels ≥ 10.

This study focused on invasive blue catfish in Chesapeake Bay; however, the development of similar models could be useful for other invasive species, especially if the goal is to minimize predation for specific organisms. Although it does not necessarily result in population-level effects (Ney, 1990), predation has been identified as a major driver in the decline of native species richness at the global scale (Mollot et al., 2017). Predation is particularly dangerous for depleted biota because it can impede population recovery and even drive organisms to extinction. No evidence conclusively indicates that blue catfish are driving alosines to extinction (e.g., some signs of recovery have been observed for populations of American shad in the Rappahannock River), yet other invasive predators have driven prey to extinction (Spencer et al., 2016). In these cases, the best approach may be to determine the factors that lead to greater predation on specific biota. This information could also provide guidance for additional harvest of the invader (Schmitt et al., 2017). Models of predation for depleted species could be especially useful for control of invasive predators in large, open systems where eradication is not a viable option (Franssen et al., 2014; Thresher et al., 2014). In these circumstances, targeted harvest may be the best approach, with the goal of "suppress[ing] invasive populations below levels predicted to cause undesirable ecological change" (Green et al., 2014).

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