

ARTICLE

Estimates of Food Consumption Rates for Invasive Blue Catfish

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Abstract

As a prolific invasive species, Blue Catfish *Ictalurus furcatus* threaten native organisms in numerous estuarine and tidal freshwaters along the Atlantic coast of the United States. However, no published estimates of consumption rates are available for Blue Catfish in the scientific literature. This information is critical for development of bioenergetics models or estimation of population-level impacts on native species. Using a combination of field and laboratory studies, we provide the first estimates of daily ration, maximum daily ration, and consumption to biomass ratios for Blue Catfish populations. Ad libitum feeding trials conducted in our laboratory reveal that maximum daily ration in Blue Catfish varies by prey type, temperature, and fish size, with maximal feeding occurring in medium-sized Blue Catfish (500–600 mm total length) and at temperatures $\geq 15^{\circ}\text{C}$. Furthermore, estimates of daily ration were higher for fish prey (Gizzard Shad *Dorosoma cepedianum*) than for crustacean prey (blue crab *Callinectes sapidus*). Diel feeding chronologies based on field-collected diet samples from 1,226 Blue Catfish demonstrated river-specific variability in daily ration and maximum daily ration. Blue Catfish daily ration ranged between 2.27% and 5.22% bodyweight per 24 h, while maximum daily ration ranges between 8.56% and 9.37% bodyweight per 24 h. Estimates of consumption to biomass ratios varied by river and Blue Catfish size groupings but range between 2.42 and 3.39, which is similar to other benthic omnivores. This research will inform the assessment of predatory impacts of invasive Blue Catfish in the Chesapeake Bay and beyond as it will enable researchers to estimate predatory impacts through the coupling of population models, food habit information, and consumption rate information (current study).

Over the past two decades, invasive species have been increasingly recognized as a major threat to global biodiversity (Lockwood et al. 2013) and are major drivers of global change (Garcia-Berthou 2007). Invasive species can impact native biota through predation and competition or indirectly through the spread of novel diseases and parasites. Because of this, invasions can cause changes in food web structure, which can alter ecosystem function (Mack et al. 2000; Clavel et al. 2011).

Freshwater habitats are some of the most invaded ecosystems on earth (Clavero and Garcia-Berthou 2006), and more studies on the biology of invasive freshwater fishes are “urgently needed” (Garcia-Berthou 2007) as it will aid in the development of more effectual management strategies.

Blue Catfish *Ictalurus furcatus* are native to the Mississippi River and several Gulf of Mexico tributaries and are the fourth largest freshwater fish in North America

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(Graham 1999). Blue Catfish have been widely stocked as a sport and food fish, and nonindigenous populations now occur in many Atlantic slope drainages from Maryland to Georgia (Moser and Roberts 1999; Schloesser et al. 2011; Bonvechio et al. 2012). Populations are remarkably dense in Chesapeake Bay tributaries, with tagging studies in relatively small areas estimating densities from 239 to 708 Blue Catfish per hectare (Fabrizio et al. 2017; Bunch et al. 2018). Due to rapid population expansion, high population densities, and their potential to impact native biota, Blue Catfish are now considered invasive along the Atlantic slope (ASMFC 2011), and further range expansion is likely (Nepal and Fabrizio 2019).

One potential mechanism of ecosystem impact by invasive species is through predation on native species. In wild populations, estimation of predatory impacts requires an understanding of consumption rates (Ney 1990; Cerino et al. 2013), and estimates for Blue Catfish do not currently exist in the scientific literature. Consumption estimates are important for understanding fish foraging rates and community dynamics (Vigg et al. 1991) and are essential for the construction of ecosystem models (Christensen and Walters 2004) and bioenergetics models (Deslauriers et al. 2017). Considering this, our major objective was to provide estimates of daily ration, maximum daily ration, and consumption per unit biomass for all sizes of Blue Catfish using a combination of field experiments, lab experiments, and empirical regression models (e.g., Palomares and Pauly 1998).

METHODS

Laboratory estimates of maximum daily ration.—Fifteen Blue Catfish ranging from 332 to 878 mm total length (TL) were collected from the Rappahannock River (38°09'42.4"N, 77°03'48.0"W) in October of 2015 with high-frequency electrofishing (60 Hz) using a 7.5 GPP Midwest Lakes electrofishing system. Most of the Blue Catfish ranged from 332 to 500 mm TL ($N=11$), though four large (>500 mm TL) fish were also collected. Fish were transported to the Virginia Tech Freshwater Mussel Conservation Center in a cool, aerated live well, and upon arrival, they were placed within two aquaria with shared biofiltration and digital temperature control systems. The first tank was 167 cm long × 167 cm wide × 102 cm deep and held approximately 2,800 L of water—this tank was used for the large Blue Catfish (>500 mm TL). A second, round tank was used for smaller individuals (<500 mm TL) and had a diameter of 107 cm and a height of 107 cm. This tank held approximately 950 L of water. Salinity within the recirculating aquaculture system was kept within $\pm 0.5\%$ of the salinity recorded at the time of capture (3.0‰) using evaporated solar salt. Fish were allowed to acclimate for 4 weeks prior to any

experimentation (Bourret et al. 2008), and acclimation conditions included a 14 h light : 10 h dark photoperiod, a constant water temperature of 13°C, and biweekly rations ($\approx 5\%$ of their bodyweight) of fresh Gizzard Shad *Dorosoma cepedianum*.

Fish size, prey type, and water temperature have been demonstrated to be the major drivers of fish daily consumption, while other factors, such as salinity, have little impact on consumption (Bromley and Last 1990; Temming and Andersen 1992). Given this, maximum daily ration was estimated at three temperatures (5, 15, and 25°C) with two prey types (Gizzard Shad and blue crab *Callinectes sapidus*) for Blue Catfish ranging from 332 to 878 mm TL. The temperature range chosen was very close to the range of water temperatures regularly observed in the Chesapeake Bay (4°C to 28°C; Shiah and Ducklow 1994). Partitions were installed in each tank so that each fish had their own enclosure, and fish were allowed to acclimate to each experimental temperature for 14 d. Temperature adjustments between experiments did not exceed 2°C per day (Hayward and Arnold 1996). Prior to trials, Blue Catfish were starved for 72 h to ensure empty stomachs (Amundsen and Klemetsen 1988).

To determine laboratory maximum consumption (C_{Lmax}), Blue Catfish were fed ad libitum rations of Gizzard Shad or blue crab for 24 h, with old food being removed and new food added every 3 h, with weights recorded for each food item that was added or removed (Bourret et al. 2008). Six different combinations of feeding trials were completed: one for each prey type (Gizzard Shad and blue crab) at each temperature (5, 15, and 25°C). Furthermore, a total of three replicates were completed for each treatment combination. Food items were either fresh (within 2 d of capture) or previously frozen, as freezing does not significantly alter evacuation rates (Andersen 2012). However, Gizzard Shad were kept on ice and frozen promptly after capture to prevent degradation. Blue Catfish were kept within individual enclosures, so maximum daily consumption was estimated by subtracting the weight of uneaten food from the total weight of food given to each individual fish. All Blue Catfish were weighed at the beginning and end of each experimental test period (Bourret et al. 2008).

Laboratory analysis.—Blue Catfish varied in weight over the course of the experiment since the same fish were used in multiple trials and substantial weight gain occurred due to ad libitum feeding. To make consumption rates comparable among temperatures and prey types, we used a weight-standardized approach to correct for variation in body size (Hayward and Arnold 1996; Zwiefel et al. 1999). For each individual fish, maximum daily consumption was adjusted to a standardized body weight of 3,455 g, which is the mean body weight recorded for all fish throughout the

experiment (Hayward and Arnold 1996; Zweifel et al. 1999). To weight-standardize daily consumption rates, the allometric equation $C_{Lmax} = aW^b$ was used to calculate weight-specific maximum daily ration, where W is the body weight (g) of the fish and a and b are regression constants. A value of -0.31 was used for b (Hansen et al. 1997), while the dummy value of 1 was used for a (Zwiefel et al. 1999). The mean weight for each fish within each experimental trial was added to the allometric equation, and the resulting C_{Lmax} was divided by the C_{Lmax} value for the grand mean of all fish weights (3,455 g; Bourret et al. 2008). All prey- and temperature-specific consumption values (g/d) were adjusted to body weight using the above weight-standardized quotient (Bourret et al. 2008). Differences in weight-adjusted daily consumption among temperatures, prey types, and fish total length were tested using a univariate, repeated measures analysis of variance (ANOVA) because the same fish were reused in subsequent treatments (Green 1993). Before proceeding with ANOVA, the data were tested for normality (Shapiro–Wilk test), for heteroscedasticity (Levene’s test), and for sphericity (Mauchly’s sphericity test). Normality and equal variance assumptions were not initially met, so a logit transformation was used (Warton and Hui 2011). Subsequent tests revealed that assumptions were satisfied. Significance was evaluated with an effective alpha (α) = 0.05. When significant effects were detected, post hoc Tukey’s multiple comparisons (using a Bonferroni correction) were used to further explore pairwise differences in consumption rate (Bourret et al. 2008). All analyses were performed in the programming language R (R Core Team 2018).

Field estimates of consumption.—Fish feeding behavior can be highly structured by the diel cycle (Johnson and Dropkin 1993), and many species of fish exhibit clear diurnal behavioral patterns (Helfman 1993). We conducted 24-h feeding chronologies with 3-h sampling intervals during the summers of 2013, 2014, and 2015 to determine consumption rates and diel variation in Blue Catfish feeding patterns. Because 24-h feeding chronologies require some degree of operation in complete darkness, we chose areas on the James, Pamunkey, Mattaponi, and Rappahannock rivers (Figure 1) that support high densities of Blue Catfish but have fewer hazards than other areas (e.g., we avoided upstream areas with shallow water and strainers or downstream areas that are more susceptible to wave action). Diel feeding patterns were determined for each river during the summer months as low-frequency electrofishing for Blue Catfish works best at water temperatures $>18^{\circ}\text{C}$ (Bodine and Shoup 2010). In addition to improving our understanding of Blue Catfish feeding patterns, diel feeding chronologies will help future researchers maximize the amount of information gained per fish

collected as they can sample during times when stomachs are fullest (Bowen 1996).

Field data collected from our diel feeding chronologies were also used to estimate gastric evacuation rates, daily ration, and maximum daily ration. Field estimation of daily ration is preferred as fish are subject to natural conditions (Jarre et al. 1991; Bromley 1994; Grant and Kott 1999). Daily ration and maximum daily ration were estimated using the model developed by Elliot and Persson (1978) as this approach has been used for other catfish species (family Ictaluridae; Baumann and Kwak 2011). While this model may not be the best choice for exclusively piscivorous fish (Héroux and Magnan 1996), Blue Catfish in Virginia’s tidal rivers exhibit a broad, omnivorous diet (Schmitt et al. 2017, 2019a, 2019b). Additionally, the Elliot and Persson (1978) model is most effective in the field when sample intervals are 3 h or less (Cochran and Adelman 1982; Kwak et al. 1992). Fish were sampled at 3-h intervals over a 24-h period from the James, Pamunkey, Mattaponi, and Rappahannock rivers, and diet contents were extracted immediately using pulsed gastric lavage. Gut fullness was calculated for each fish as the wet weight of the stomach contents divided by the wet weight of the fish (Hyslop 1980).

Field analysis.—Daily ration (C_{24}) was calculated as

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

where F_t is the mean stomach fullness at time t , F_{t+1} is the stomach fullness at time $t + 1$, R is the gastric evacuation rate for each interval, T is the time interval between samples (3 h), and p is the number of sampling intervals in a 24-h period (8). The gastric evacuation rate (R) was first calculated for each 3-h time interval using the slope of stomach fullness (F_t) plotted against time,

$$R = \frac{\log_e F_{t+1} - \log_e F_t}{T},$$

where F_t and F_{t+1} are the mean stomach fullness at the beginning and end of each interval, respectively (Boisclair and Leggett 1988; Héroux and Magnan 1996). The gastric evacuation rate (R) with the steepest slope was used for modeling maximum daily ration (C_{max}), where this maximal value of R is applied to all intervals (Boisclair and Leggett 1988; Héroux and Magnan 1996). Conversely, daily ration (C_{24}) was estimated using the average gastric evacuation rate calculated from the entire 24-h time series.

Consumption to biomass ratios.—Consumption to biomass (Q/B) estimates provide a measure of food ingested (Q) per biomass of a population (B) over a period of time, usually 1 year (Palomares and Pauly 1998; Christensen et al. 2005). We estimated Q/B rates for Blue

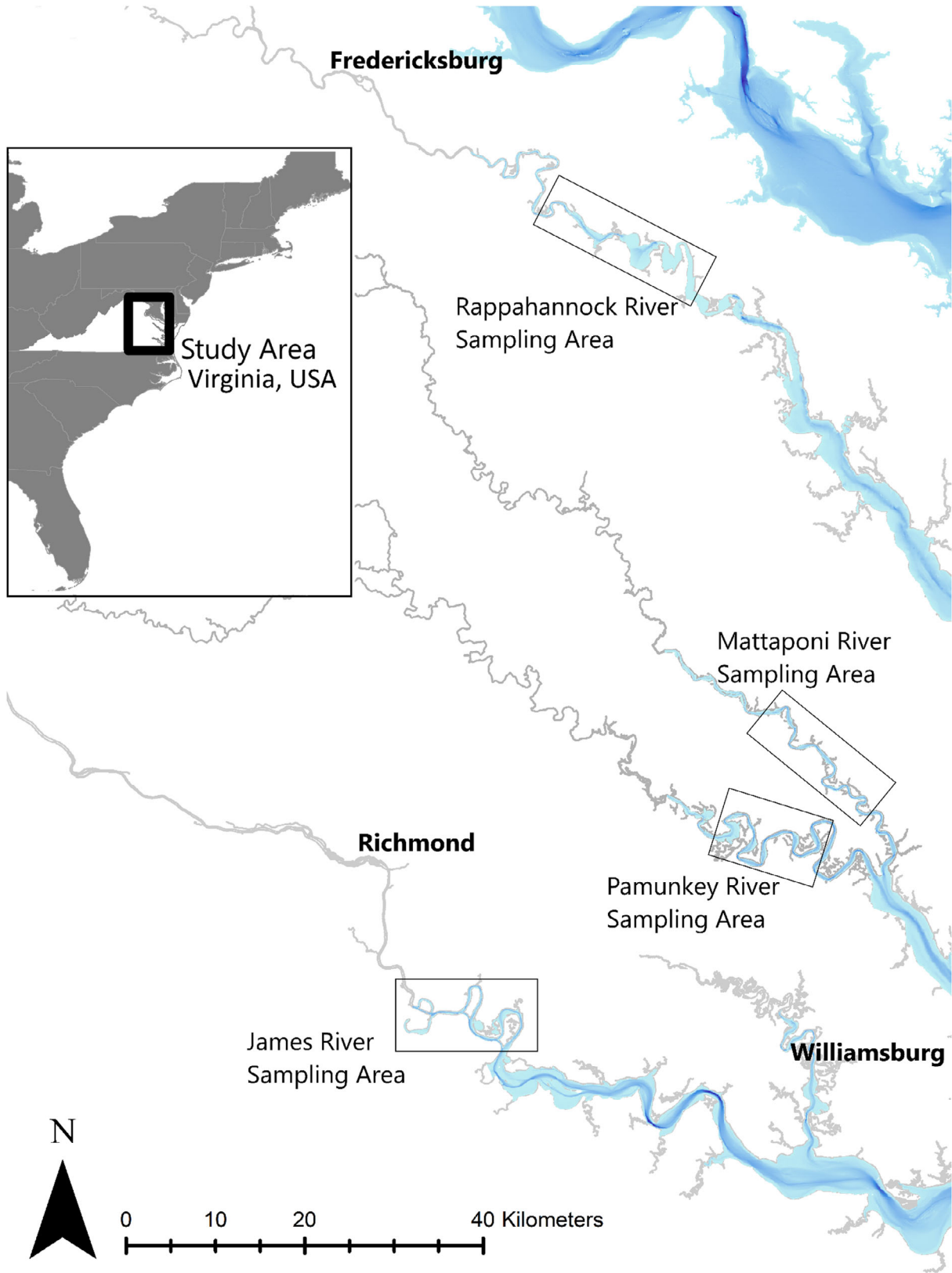


FIGURE 1. Locations for 24-h diel feeding chronology studies to estimate Blue Catfish consumption rates and feeding rhythms in the James, Pamunkey, Mattaponi, and Rappahannock rivers of eastern Virginia. [Color figure can viewed at afs.journals.org.]

Catfish in Virginia's tidal rivers based on an empirical regression model developed by Palomares and Pauly (1998). This regression model was based on lab and field-based estimates of consumption for 108 fish populations, including 38 different species and several catfishes (Palomares and Pauly 1998). The following model was used to estimate Q/B :

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

where W_{∞} is the average maximum weight (g), T' is the mean annual water temperature (expressed as $1,000/^{\circ}\text{K}$), A is the aspect ratio of the caudal fin, h is a dummy variable explaining food type (1 = herbivore, 0 = for nonherbivores), and d is a dummy variable also explaining food type (1 = detritivores, 0 = nondetritivores; Palomares and Pauly 1998). The Q/B estimates were calculated separately for smaller, omnivorous fish and for larger, piscivorous fish in each river by including or excluding h and d terms (note: " d " term was only applied to small fish from the James and Rappahannock rivers, where detritus was commonly found in stomachs; Schmitt et al. 2019b). Herbivory and detritivory terms were dropped for piscivorous sizes of Blue Catfish based on studies that demonstrated ontogenetic shifts from omnivory to piscivory, which occur between 500 and 900 mm TL, depending on river (Schmitt et al. 2019b).

Model parameters.—River-specific estimates for Blue Catfish W_{∞} were used within each Q/B estimator based on von Bertalanffy growth curves (Orth et al. 2017). Mean annual water temperature (T') was calculated for all segments (tidal fresh, oligohaline, and mesohaline) of the James, Pamunkey, Mattaponi, and Rappahannock rivers using Chesapeake Bay Program water data for 2010–2016 (CBP 2017). Temperatures were averaged by month, and then these values were averaged across all years. Aspect ratio, an index of fish activity level, was determined by (1) removing caudal fins from 27 Blue Catfish (captured in the James River) ranging from 314 to 887 mm TL, (2) tracing those caudal fins onto paper, and (3) scanning them into a digital database. Aspect ratio was then calculated using TpsDig 2.32, which is freeware specifically developed for geometric morphometric analysis (Rohlf 2016). The mean caudal fin aspect ratio was incorporated into all Q/B estimates.

RESULTS

Laboratory Estimates of Consumption

Blue Catfish consumption rates varied significantly with temperature, prey type, and fish size ($P < 0.01$). Across all treatment combinations, laboratory estimates of maximum

daily ration ($C_{L\text{max}}$) varied from 4% to 21% of their body weight per 24 h (bw/24 h), with a grand mean of 9.56% bw/24 h. The term " $C_{L\text{max}}$ " varied significantly with temperature, prey type, and fish total length, though interactions were insignificant (Table 1). On average, Blue Catfish can consume significantly more Gizzard Shad than blue crab in a 24-h period (Figure 2). Consumption rates increase with temperature from 5°C to 15°C, though consumption rates did not differ significantly from 15°C to 25°C (Tukey's honestly significant difference: $P > 0.05$). Mean $C_{L\text{max}}$ was 7.53% bw/24 h consumed at 5°C, 10.66% bw/24 h at 15°C, and 10.55% bw/24 h at 25°C. Consumption rates also differed significantly with fish size, and intermediate-sized Blue Catfish (500–600 mm TL) consumed the most food over a 24-h period (Figure 3). This may be a result of individual feeding behavior due to only one representative fish per length-class for fish >500 mm TL, which is discussed below.

Field Estimates of Consumption

Stomach contents were extracted from 1,226 Blue Catfish on the James, Pamunkey, Mattaponi, and Rappahannock rivers. All diel feeding chronologies were completed in August, and water temperature at all sites ranged from 22.3°C to 29.6°C, which should correspond with maximal, asymptotic consumption rates based on the results from our laboratory study. The time of peak feeding varied by river (Figure 4). Peak feeding occurred at 1500 hours for the James River, at 0900 hours for the Pamunkey River, and at 1200 hours for the Rappahannock and Mattaponi rivers (Figure 4). Field estimates of C_{max} varied by river, ranging from 4.34% bw/24 h in the Mattaponi River to 15.00% bw/24 h in the Pamunkey River (Table 2). Similar patterns were observed for daily ration, where C_{24} ranged from 2.27% in the Mattaponi River to 5.22% in the Pamunkey River (Table 2). Estimates of maximum daily ration from lab experiments (9.56% bw/24 h) versus the field experiments (8.76% bw/24 h) were remarkably close and did not differ significantly (ANOVA; Figure 5).

TABLE 1. For laboratory experiments, a univariate, repeated-measures ANOVA was used to test for the effects of temperature, prey type, fish length, and interactions on the consumption rates of Blue Catfish (percent body weight per 24 h), where the individual fish was treated as the subject. Summary statistics are presented in the table, and the adjusted $R^2 = 0.86$.

Factors	df	F	P
Global model	8	44.10	<0.01
Temperature	2	8.80	<0.01
Prey type	1	11.19	<0.01
Length	5	39.78	<0.01
All interactions			>0.05

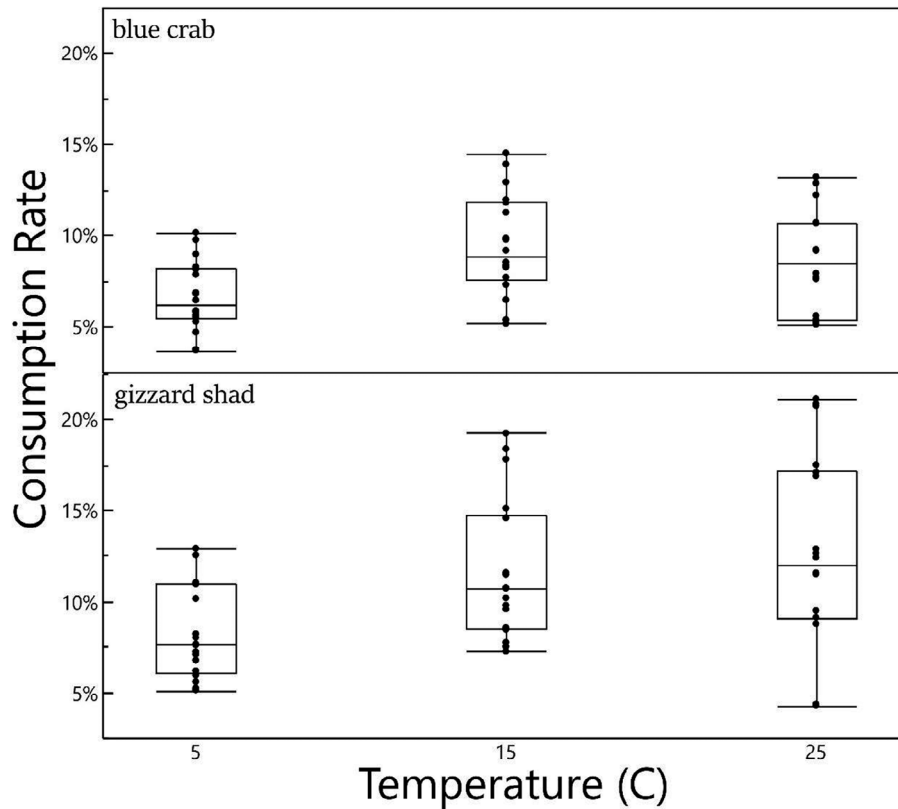


FIGURE 2. Lab estimates of maximum consumption rate (expressed as percent body weight per 24 h) for Blue Catfish as it varies by temperature and prey type. Temperature and prey type significantly influenced maximum daily ration ($P < 0.01$). In general, Blue Catfish ate less blue crab than Gizzard Shad in a 24-h period, and consumption rates increased significantly from 5°C to 15°C, with little change occurring from 15°C to 25°C. For the box plots, the horizontal line in each box indicates the median, the box dimensions indicate the 25th to 75th percentile ranges, the error bars indicate the 5th to 95th percentile ranges, and the black dots are each individual measurement.

Empirical Estimates of Consumption to Biomass Ratios

Mean annual water temperatures varied little by river, ranging from 16.89°C for the Rappahannock River to 17.23°C for the James River. Asymptotic weight (W_{∞}) was more variable, ranging from 30.11 kg for the Pamunkey and Mattaponi rivers to 46.77 kg for the James River. Consumption to biomass ratios ranged from 2.42 for large fish in the Mattaponi River to 3.39 for small fish in the James River (Table 3). Consumption to biomass ratios also varied in each river, depending on the size of the Blue Catfish (Q/B range for James River = 2.46–3.39, Q/B range for Pamunkey River = 2.43–2.96, Q/B range for Mattaponi River = 2.42–2.95, Q/B range for Rappahannock River = 2.43–3.36). Small omnivorous fish had the highest Q/B values, particularly fish from the James and Rappahannock rivers. This was due to the inclusion of both herbivory and detritivory terms in these river-specific models (Table 3), based on evidence that small Blue Catfish in these rivers routinely consume both detritus and vegetation (Schmitt et al. 2019b). For larger, piscivorous Blue Catfish, the Q/B ratios varied little across rivers, ranging from 2.42 in the Mattaponi River to 2.46 in the

James River. This pattern was driven primarily by differences in W_{∞} , though subtle differences in average annual water temperature also played a role (Table 3).

DISCUSSION

Maximum daily ration of Blue Catfish varied significantly with temperature, prey type, and fish size. Blue Catfish consumed more Gizzard Shad than blue crab in a 24-h period, a pattern that has been demonstrated in several other studies, as the presence of an exoskeleton slows digestion (see Bromley 1994). Blue Catfish maximum daily ration increased with temperature up to 15°C yet did not change significantly at 25°C. Fish consumption rates generally increase with temperature, often reaching an asymptote at higher temperatures (Bromley 1994). Maximum daily ration also varied with fish size, yet there is a strong possibility that this is due to individual behavior as we only had single representative fish within the larger length-classes. Two Blue Catfish (500 and 600 mm TL) would gorge themselves to the point at which they could no longer maintain vertical orientation and would lay

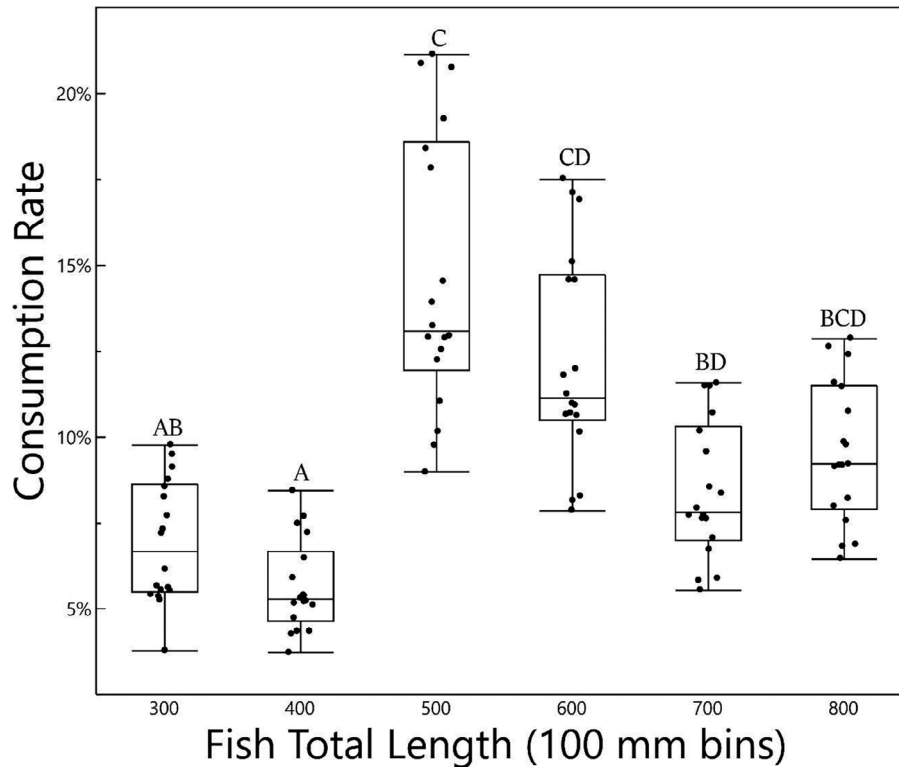


FIGURE 3. Lab estimates of maximum consumption rate (expressed as percent body weight per 24 h) for Blue Catfish as it varies by fish total length (mm). Estimates that do not share a letter (A–D above the boxes) differ significantly (Tukey’s honestly significant difference: $P < 0.05$). See Figure 2 for a description of the box plots.

motionless on the bottom of the tank while they digested their meal. These fish exhibited higher consumption rates than the others, though it is uncertain whether this is a length-based phenomenon or just individual feeding behavior. Interestingly, previous studies have shown that Blue Catfish undergo an ontogenetic shift from omnivory to piscivory near this size in the Rappahannock River (e.g., 500–600 mm TL is the “inflection point” in a logistic regression model of fish prey in the diet; Schmitt et al. 2019b). It is possible that Blue Catfish consume more when making this dietary transition, though more testing would be necessary to confirm this hypothesis.

Field estimates of maximum daily ration did not differ significantly from estimates obtained in the lab, and similarity across independent observations usually implies some degree of accuracy (Rice and Cochran 1984). Both lab and field experiments demonstrate that, in situations of peak feeding (e.g., *maximum* daily ration), consumption rates are approximately 8–9% of body weight per day at warmer water temperatures ($>15^{\circ}\text{C}$). These results should be interpreted as maximal feeding rates during the summer months as it is doubtful that Blue Catfish feed at these rates throughout the year. It is important to remember that Blue Catfish were starved for 72 h prior to each feeding trial and that each feeding trial only lasted 24 h, which

means that the fish really gorged themselves. Our field estimates of daily ration are likely more realistic as fish were subject to natural conditions (Jarre et al. 1991). Nonetheless, laboratory and field-derived estimates of maximum daily ration would complement information on peak feeding (e.g., vacuity indices or gut fullness indices) quite well (Kanou et al. 2005; Vinson and Angradi 2011) and could be applied to consumption models as an upper bound during times when high feeding intensity is observed in the field. Field estimates of daily ration were considerably lower (see below) than both lab and field estimates of maximum daily ration, and these estimates are likely more reflective of long-term, sustainable feeding rates (Bromley 1994).

Our estimates of daily ration are similar to estimates for Channel Catfish *Ictalurus punctatus*. Growth of Channel Catfish in aquaria occurs at 2–6% of body weight per day (bw/d; Andrews and Stickney 1972), which is very similar to our field estimates of Blue Catfish daily ration (2–5% bw/d). Field studies for Channel Catfish have also produced similar estimates of daily ration (2–8% bw/d), though these rates decline to 1.23% bw/d at temperatures $<15^{\circ}\text{C}$ (Kwak et al. 1992). We would anticipate a similar decline in feeding rates for Blue Catfish during the winter months. It is important to remember that our field studies

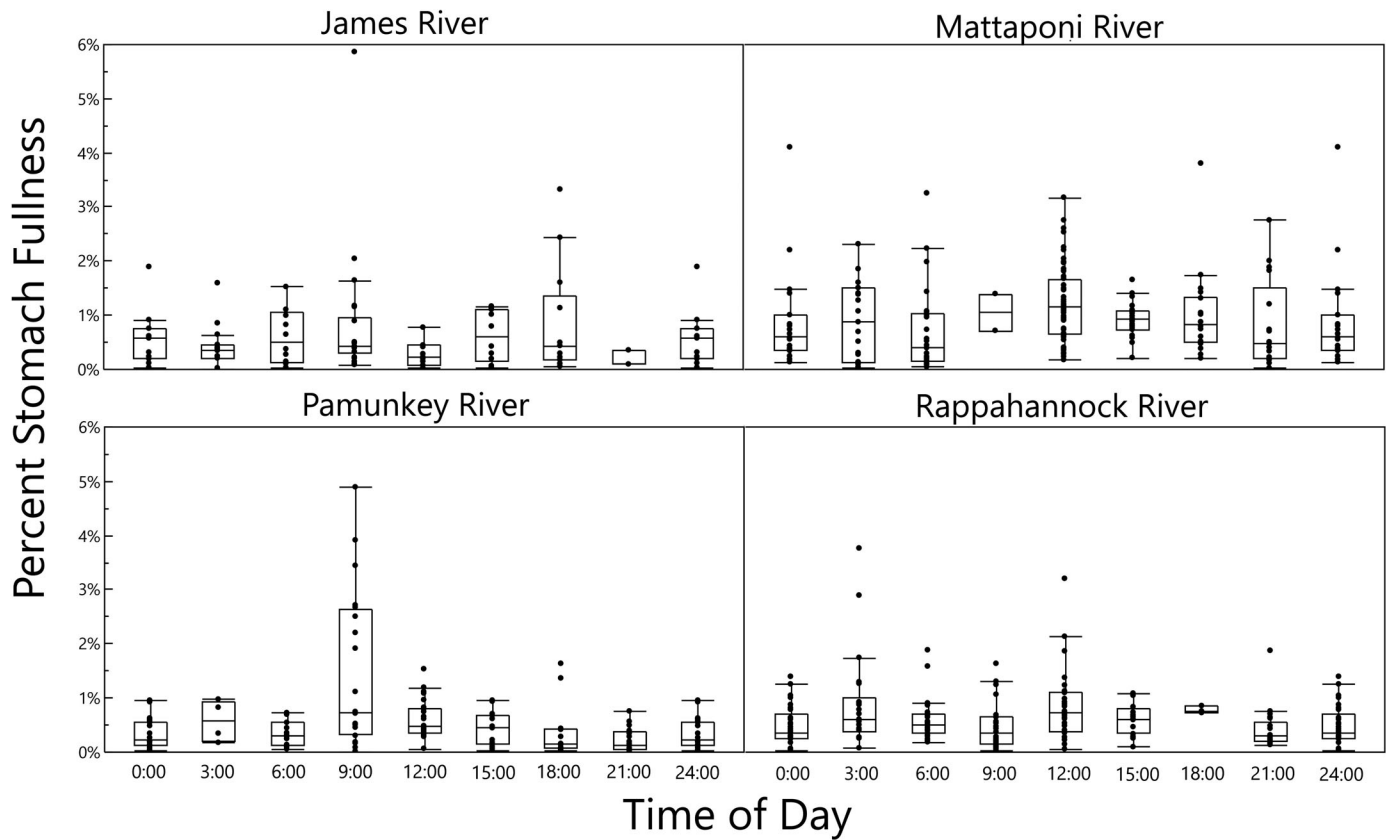


FIGURE 4. Stomach percent fullness (calculated as the wet weight of the stomach contents divided by the wet weight of the fish, times 100) throughout a 24-h period for 1,226 Blue Catfish captured on the James, Mattaponi, Pamunkey, and Rappahannock rivers in eastern Virginia. All diel feeding chronologies were completed during the month of August, and water temperatures ranged from 22.3°C to 29.6°C. See Figure 2 for a description of the box plots.

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

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

were conducted at warm temperatures (>22°C); thus, we would expect that feeding rates at cooler temperatures (<15°C) would decline based on both our aquaria experiments (current study) and previous Channel Catfish studies (Kwak et al. 1992; Silverstein et al. 2001). Field estimates of Blue Catfish daily ration are also quite similar to another common predatory fish in these tidal rivers—

the Largemouth Bass *Micropterus salmoides*. While diel feeding chronologies have never been completed for Largemouth Bass in Chesapeake Bay, studies from other systems have revealed that daily ration varies between 1.19% and 5.58% bw/d (Cochran and Adelman 1982), which is similar to our estimates for Blue Catfish (2–5% bw/d).

In our field experiments, consistent diel feeding patterns were not apparent across all rivers. This is intuitive since much of the Blue Catfish population feeds on macrophytes and sessile bivalves like Asian clams *Corbicula fluminea*, which should be accessible regardless of the time of day (Schmitt et al. 2019a, 2019b). Increases in feeding may be associated with tidal cycles, as fish may wait for ideal flow conditions to leave resting locations to feed (Stoner 2004; Childs et al. 2008). There was some evidence of this as peak feeding occurred during the end of outgoing tide cycles for Blue Catfish in the James, Pamunkey, and Rappahannock rivers. The exception to this was the Mattaponi River, where peak feeding occurred towards the end of an incoming tide. It is important to note that low

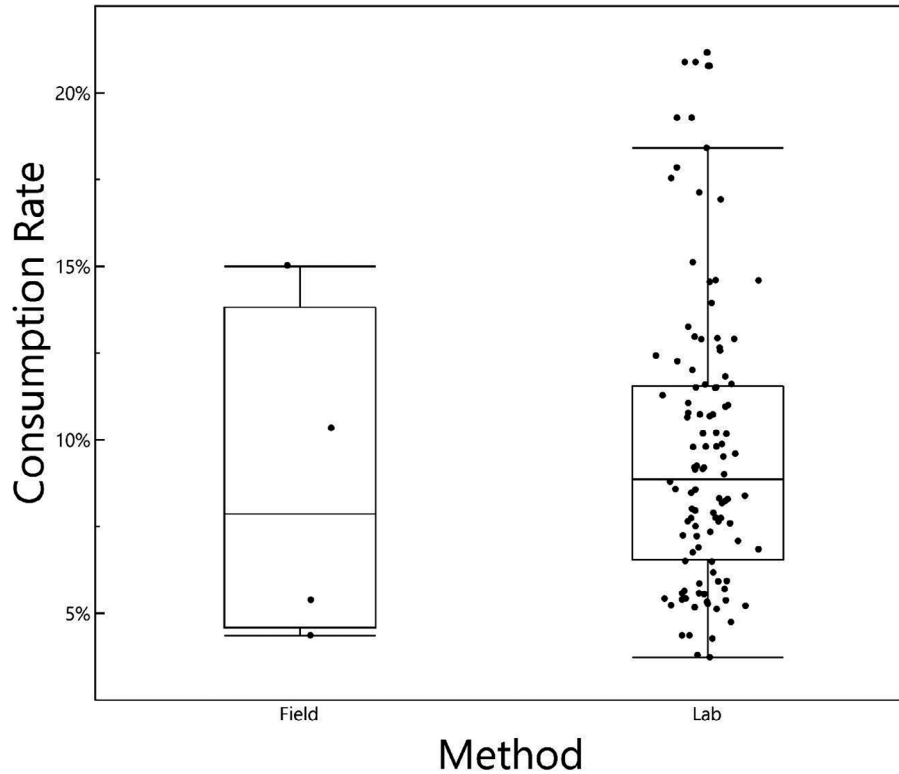


FIGURE 5. Maximum consumption rates (expressed as percent body weight per 24 h [% bw/24 h]) from the field and from the lab did not differ significantly (ANOVA: $P=0.63$). Mean maximum daily ration was 8.76% bw/24 h in the field and 9.56% bw/24 h in the lab. See Figure 2 for a description of the box plots.

stomach fullness was observed during the Mattaponi River diel feeding chronology, and this general lack of activity may explain observed differences. Based on these findings, it appears that Blue Catfish prefer to feed past the midpoint of an outgoing tide cycle, though more research would be needed to assess this. Time of day varied, and may be less important, though peak stomach fullness occurred between 0900 and 1500 hours for all four rivers. Blue Catfish congregate in deep, flowing areas of rivers during late summer (J. D. Schmitt, personal observation), and light penetration is generally limited to the top 1–2 m of the water column in Chesapeake Bay (Dennison et al. 1993). Considering this, we hypothesize that Blue Catfish spend most of their time in darkness and foraging may be more influenced by other environmental factors (e.g., tides) than photoperiod, though more research is needed.

Consumption to biomass estimates were greater for small fish versus large fish, which is intuitive. Small Blue Catfish consume low-energy foods like vegetation and detritus, while large Blue Catfish are more piscivorous (Schmitt et al. 2019b). These differences in food habits require the inclusion of herbivory and detritivory terms in the model, which results in an increase in Q/B ratios for small Blue Catfish. Logically, fish that eat low-energy

foods like detritus will need to consume larger volumes of food than fish that eat energy-rich prey like Gizzard Shad (Gerking 1994). Blue Catfish Q/B estimates ranged from 2.43 to 3.39, which are similar to estimates for other benthic fish like Atlantic Cod *Gadus morhua* ($Q/B=2.59$), Yellow Perch *Perca flavescens* ($Q/B=2.79$), Lake Trout *Salvelinus namaycush* ($Q/B=2.89$), Burbot *Lota lota* ($Q/B=3.29$), and Common Dab *Limanda limanda* ($Q/B=3.69$; Palomares and Pauly 1998; Liao et al. 2005). The Q/B estimates for other catfishes vary broadly and are as low as 1.32 for African Sharptoothed Catfish *Clarias gariepinus* or as high as 22.07 for *Bagrus docmak*, which is a large, fast-growing catfish species native to central Africa (Palomares and Pauly 1998).

Studies on the impacts of invasive freshwater fish are rare (Garcia-Berthou 2007), and predatory impact can only be assessed once estimates of diet, consumption rates, and predator biomass are available (Ney 1990). The current study provides several estimates of Blue Catfish consumption rate, which will be critical for assessing ecological impacts of invasive Blue Catfish in the Chesapeake Bay and beyond (Schmitt and Orth 2015; Schmitt et al. 2017, 2019a, 2019b). The current study indicates that consumption rates vary considerably based on

TABLE 3. Consumption to biomass (Q/B) ratios were estimated for Blue Catfish in each of Virginia's major tidal rivers based on the aspect ratio (A) of the caudal fin, mean annual water temperature (T), average maximum weight (W_{∞}), and herbivory and detritivory dummy variables (h and d , respectively). The Q/B estimates were calculated separately for different size-groups of Blue Catfish based on river-specific shifts from omnivory to piscivory (Schmitt et al. 2019b).

River	Total length (mm)	A	T ($^{\circ}\text{C}$)	h	d	W_{∞} (kg)	Q/B
James	All lengths	3.74	17.23	1	1	46.77	3.39
	<500	3.74	17.23	1	1	46.77	3.39
	>500	3.74	17.23	0	0	46.77	2.46
Pamunkey	All lengths	3.74	17.41	1	0	30.11	2.96
	<900	3.74	17.41	1	0	30.11	2.96
	>900	3.74	17.41	0	0	30.11	2.43
Mattaponi	All lengths	3.74	17.11	1	0	30.11	2.95
	<800	3.74	17.11	1	0	30.11	2.95
	>800	3.74	17.11	0	0	30.11	2.42
Rappahannock	All lengths	3.74	16.89	1	1	36.09	3.36
	<700	3.74	16.89	1	1	36.09	3.36
	>700	3.74	16.89	0	0	36.09	2.43

temperature, size of fish, and river system. Furthermore, dietary patterns of Blue Catfish in these rivers exhibit strong spatiotemporal heterogeneity (Schmitt et al. 2019a, 2019b). Considering this, it is *imperative* that future assessments of predatory impact include variability in diets and consumption rates as extrapolations and sweeping generalizations across broad spatiotemporal scales will introduce error and provide unrealistic estimates. Consumption rate information can also be used for the construction of Ecopath models (Christensen et al. 2004) or for the development of a Blue Catfish bioenergetics model, which does not currently exist (Deslauriers et al. 2017). Blue Catfish are generalists in regard to both habitat and diet (Schmitt et al. 2019b); thus, further range expansion along the Atlantic slope is likely (Nepal and Fabrizio 2019). Moreover, Blue Catfish have been identified as potential invaders of the Laurentian Great Lakes, where impacts could be substantial (Howeth et al. 2016). Considering this, consumption estimates provided by this study are a timely addition to the scientific literature as invasive Blue Catfish will become more problematic in the future.

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