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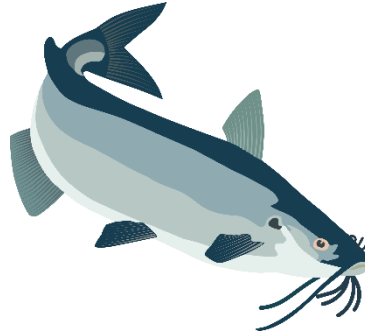
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Predation Impacts of Invasive Blue Catfish on Blue Crabs in Estuarine Environments



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Executive Summary

The frequency of occurrence by number and weight of blue crabs in the diet of blue catfish in the mesohaline (5 – 18 psu) portion of the James River was greater than that previously reported for tidal freshwater reaches of this subestuary. Blue crab predation likelihoods varied spatially, temporally, and with blue catfish size; although blue crabs were consumed throughout the year, we were unable to detect a seasonal signal in blue crab predation. Blue catfish were 1.75 times (95% confidence interval [CI]: 1.25 – 2.45) more likely to consume blue crabs in Burwell Bay than in Hog Island, suggesting that higher salinity reaches are areas of greater predation intensity on blue crabs. Indeed, the likelihood of observing any type of prey in the stomach of blue catfish from Burwell Bay was 2.08 times greater (95% CI: 1.62 – 2.67) than the likelihood of observing prey in the stomach of blue catfish from Hog Island.

Intermediate (301 – 500 mm fork length, FL) and large (≥ 501 mm FL) blue catfish were more likely to consume blue crabs than were small (200 – 300 mm FL) blue catfish. Large blue catfish were 1.68 times (95% CI: 1.37 – 2.04) more likely to consume blue crabs than intermediate sized fish, and 7.65 times (95% CI: 3.32 – 17.66) more likely to consume blue crabs than small blue catfish. Among the blue catfish that consumed crabs, the average number of blue crabs consumed per day by an individual varied between 0.98 and 1.57, depending on fish size, season, and salinity zone (Burwell Bay or Hog Island). Annually, about 2.3 million blue crabs were removed through predation by blue catfish in the study area which comprises 199.2 km² and includes the Burwell Bay and Hog Island areas. The estimated overall predation impact of blue catfish reflected the relative abundance of size classes of blue catfish in the lower James River such that fish of intermediate size (301 – 500 mm FL) removed a greater number of blue crabs through predation because of the relatively greater number of intermediate size blue catfish in the James River population.

Introduction

Blue crab (*Callinectes sapidus*) is an important resource in Chesapeake Bay serving as predator and prey in the estuarine food web and supporting one of the most valuable fisheries in the region with landings in 2019 exceeding 55,501,000 lbs. and valued at more than \$81,465,000 (NOAA Fisheries 2021). Fluctuations in the abundance of blue crabs in the Chesapeake Bay reflect annual changes in recruitment, fishing mortality, and natural mortality (Lipcius and Van Engel 1990). During the 1990s, blue crab abundance in Chesapeake Bay declined markedly (Lipcius and Stockhausen 2002) and management plans were subsequently enacted to rebuild blue crab stocks to former levels of abundance. Such rebuilding plans aim to protect the spawning stock to ensure recruitment and required significant reductions in fishing mortality rates. Recruitment in this stock is closely monitored, and fishing mortality is regulated through area closures, minimum size, and seasonal harvest limits, but natural mortality due to predation is not well known or estimated. Indeed, a comprehensive list of blue crab predators is lacking for Chesapeake Bay (Bromilow and Lipcius 2017). Nonetheless, predation mortality on blue crabs may contribute to notable annual fluctuations in the abundance of juvenile and harvestable blue crabs.

Juvenile blue crabs use the Chesapeake Bay as a nursery area, such that small individuals (<20-30 mm carapace width) occupy primarily vegetated habitats and larger crabs are found in unvegetated areas (Bromilow and Lipcius 2017). Juvenile blue crabs that use unvegetated habitats may be particularly susceptible to predation by fishes; in these habitats, blue crabs escape predation by burrowing in the sediment (Bromilow and Lipcius 2017). This escape response may be effective for avoiding predation by visual predators, but less effective for avoiding predation by predators that use tactile or chemical cues to locate prey. One such tactile predator is the invasive blue catfish *Ictalurus furcatus*; this species uses electroreception as well as its barbels and keen sense of taste to detect prey within the sediment (New 1999). The blue catfish, native to the Missouri and Mississippi River basins, was introduced in Virginia's rivers in the 1970s and 1980s to establish recreational fisheries (Schloesser et al. 2011). Blue catfish is an omnivorous predator that feeds on local native and non-native resources (Moran et al. 2015; Aquilar et al. 2017; Schmitt et al. 2017; Schmitt et al. 2019); the species can achieve large sizes and high densities in subestuaries of the Chesapeake Bay (Schloesser et al. 2011; Fabrizio et al. 2018). Blue crabs and blue catfish are found in estuarine environments, but habitat overlap and the effect of blue catfish predation on blue crabs has not been well studied. Blue catfish are known to consume blue crabs: in a study conducted in the James, York, and Rappahannock rivers, the percent occurrence of blue crabs in the diets of blue catfish from tidal freshwater areas ranged from 15% to 32% (Schmitt et al. 2019). Coupled with the exceedingly high relative abundance of blue catfish in these systems, particularly the James River (Fabrizio et al. 2018), this consumption of blue crab may represent a significant source of mortality for juvenile blue crabs. Thus, additional research on predation effects of blue catfish on blue crabs from estuarine habitats where the two species exhibit spatial overlap is warranted.

The objective of this study was to better understand predation of blue catfish on blue crabs and to quantify predatory impacts in an estuarine environment. To do this, we characterized the seasonal (spring, summer, fall, winter) diets of blue catfish from the lower James River with specific reference to blue crabs during a two-year period from 2018 to 2020. Multi-panel gillnets were used to sample blue catfish from a broad range of sizes, and although passive gear such as gillnets may not be ideal for diet studies, this was the only gear that reliably and efficiently captured large fish throughout the year and from higher salinity reaches of the James River. To allow for comparisons with recent studies on the feeding ecology of invasive blue catfish (e.g., Schmitt et al. 2017), we characterized the diet of blue catfish from the lower James River by examining percent occurrence, percent by weight, the prey-specific index of relative importance, Chesson's selectivity index, and electivity. We also examined diet variability along the salinity gradient of the lower James to determine the relationship between salinity and the extent of blue catfish predation on blue crabs using statistical models. Finally, we estimated the number and weight of blue crab removals due to blue catfish predation in the lower James River using a method developed for observations from a fishery-independent survey (Link et al. 2002).

Methods

Field Collections and Sampling Design: A commercial waterman experienced in harvesting blue catfish with anchored gillnets was contracted to deploy nets in the lower James River from August 2018 to June 2020 (Figure 1). Each gillnet (either 91.4 m X 1 m or 182.9 m X 1 m) comprised 3 panels with mesh sizes 133 mm, 140 mm, and 152 mm arranged in random order to capture a wide size range of blue catfish. We sampled in two regions of the lower James River -- Burwell Bay and Hog Island -- where blue catfish and blue crabs are known to commonly co-occur (Tuckey and Fabrizio 2021; Figure 2). In addition, a multi-year, spatially explicit study indicates that these regions exhibit some of the highest relative abundances of juvenile blue crabs in the James River (for blue crabs between 25 and 90 mm carapace width; Hyman et al. *in prep.*).

Gillnets were deployed using a stratified random sampling design where stratum was either Burwell Bay or Hog Island; due to their relative positions in the James River subestuary, the regions exhibit different salinity conditions. The stratified sampling ensured broad spatial coverage of the lower James River subestuary and allowed us to estimate predation impact in two salinity zones. Each stratum was partitioned into 2 km X 2 km segments and enumerated to permit random selection of segments (sites) for sampling. In each month, 12 gillnets equipped with temperature dataloggers were deployed for about 21 hours (range: 15.0 to 27.0 hours) at randomly selected sites; deployments occurred twice per month with 3 nets set per stratum (6 nets) in the early part of the month, and 3 nets per stratum (6 nets) in the later part of the month (Table 1). During the first two months, we observed low numbers of blue catfish

with prey in their stomachs, therefore, additional nets were subsequently deployed to increase the number of blue catfish sampled. Mean depth of net deployments was 2.7 m (range: 0.61 – 7.92 m) and was similar between strata.

Bottom temperature was obtained from Tidbit dataloggers attached to each gillnet. Temperature was recorded once per minute of the gillnet deployment, and the average bottom water temperature associated with each net was calculated as the mean of the recorded temperatures during the time the net was fishing. Water depth (m) and salinity (psu) at each net location were recorded at the time of deployment using a YSI hand-held meter.

Upon net retrieval, blue catfish were placed on ice and immediately returned to VIMS for processing. If more than 20 individuals were captured per net, we subsampled the catch by size class (200 – 300 mm, 301 – 400 mm, and \geq 401 mm fork length [FL]) to ensure representation of blue catfish across size classes (Chipps and Garvey 2007). We limited collections to 20 fish per net because such samples are considered cluster samples and therefore not independent: fish captured by one net are likely to be more similar (e.g., have similar recent feeding activity) than fish captured in a different net (Buckel et al. 1999).

Laboratory Methods – Diet: In the laboratory, fish size (FL) was recorded to the nearest millimeter, fish weight was recorded to the nearest 0.1 gram, and stomach weight with prey, prey weights, and weight of the stomach without prey were recorded to the nearest 0.001 gram. Individuals with empty stomachs were so noted. Blue catfish stomachs were excised and preserved in normalin for later processing. Due to an equipment malfunction, erroneous weights were recorded for five blue catfish. These individuals were not included in our analyses.

Stomach contents were sorted by prey type – blue crabs, fishes (identified to species whenever possible), and so forth. Because this study focused on blue crabs as prey, we did not identify mollusks, insects, polychaetes, and other invertebrate prey to the species level, instead, these taxa were combined into a single prey category, which we labeled ‘other.’ This approach reduces the difficulty in identifying partially digested items (Schmitt et al. 2017) and eliminates the need for time-consuming and costly DNA analyses of stomach contents. Further, the diet of blue catfish from the tidal freshwater portion of the James River has been well studied (Schmitt et al. 2017; Schmitt et al. 2019), but the relative contribution of blue crabs to the diet of blue catfish in mesohaline (5 – 18 psu) waters is unknown. Each prey type was counted and weighed to permit estimation of the percent of the diet comprised by blue crab in terms of number of prey and weight of prey. When possible, carapace width (CW) was measured from blue crabs obtained from stomachs to characterize the size distribution of blue crabs consumed; this occurred for 254 blue crabs. However, blue crab carapaces were often damaged or observed at various stages of digestion; this occurred in 406 blue catfish stomachs. Therefore, when possible, we followed the linear regression procedure in Scharf and Schlicht (2000) to estimate carapace width using surrogate measures of size (regression parameters provided by F. Scharf). We used the distance between the outer and inner orbital teeth for 97% (75 of the 77) of the

blue crabs with partial carapaces, and the distance between the two frontal teeth for 3% (2 of the 77) of the blue crabs with partial carapaces. Carapace width was therefore measured or estimated for 331 (254 + 77) blue crabs; CW could not be estimated for the remaining blue crabs consumed by blue catfish.

Blue catfish consumed 559 blue crabs or blue crab parts, which we counted directly. In some instances (117 blue catfish stomachs), we were unable to determine the number of blue crabs consumed by an individual fish. For these fish, we estimated the number of blue crabs consumed by dividing the total weight of blue crab tissues in the stomach by the average weight of a single blue crab ($\bar{x} = 7.004$ g) recovered from blue catfish stomachs. Counts were also estimated for fishes (402 times) and for prey in the ‘other’ category (737 times). For fishes, counts were estimated by dividing the total weight of the fishes in the stomach by the average weight of a single fish of that particular species (or group of fishes when species level identification was not possible, e.g., herrings). For ‘other’ prey items, count was estimated by dividing the total weight of the item in the stomach by the average weight of a prey item in the category ‘other’ ($\bar{x} = 0.2014$ g). Counts were not quantifiable for several prey items (e.g., detritus, macroalgae, and vegetation), so we assigned a count of 1 to these prey types. This occurred 345 times.

In instances where a large number of a particular prey occurred in the stomach of a blue catfish, a subsample was used to estimate the total number of that prey item using prey weight. We observed 180 instances of items with no caloric value in the stomachs of blue catfish; this included fishing lures, gravel, trash and plastics, and unidentified material; these non-digestible items and their weights were not included in our analyses. For these instances, the total weight of the blue catfish’s stomach was recalculated to account for the removal of the non-caloric item(s).

Factors Affecting Consumption: To characterize the observed variation in blue catfish consumption, we estimated the probability that blue catfish consumed any prey item (i.e., had a non-empty stomach), and the probability that blue catfish consumed blue crabs. The probability of a blue catfish having a non-empty stomach, π_{fed} , was estimated using a hierarchical logistic regression model with a random gillnet effect to account for the clustering of fish within nets:

$$y_{ij} = \pi_{fed_{ij}} + e_{ij} \quad \text{where}$$

$$\text{Logit}(\pi_{fed_{ij}}) = \alpha + u_j + \beta_1 \text{Size}_{ij} + \beta_2 \text{Mon}_{ij} + \beta_3 \text{Stra}_{ij} + \beta_4 \text{Sal}_{ij} + \beta_5 \text{Temp}_{ij} \quad (1)$$

Here, y_{ij} is a binary variable indicating the presence or absence of prey in the stomach of the i^{th} blue catfish from the j^{th} gillnet, $\pi_{fed_{ij}}$ is the probability that at least one prey item was present in the stomach of the i^{th} blue catfish from the j^{th} gillnet, α is the overall mean logit of the probability of consuming prey, u_j is the random effect associated with gillnet j , β_1 is the fixed effect of size class, Size_{ij} is the size class (1, 2, or 3) of the i^{th} fish from the j^{th} gillnet, β_2 is the

fixed effect of month, Mon_{ij} is the month of capture of the i^{th} fish from the j^{th} gillnet (month=1, 2, 3,...23), β_3 is the fixed effect of stratum, $Stra_{ij}$ is the stratum (Burwell Bay or Hog Island) from which the i^{th} fish from the j^{th} gillnet was captured, β_4 is the fixed effect of salinity, Sal_{ij} is the bottom salinity associated with the i^{th} fish from the j^{th} gillnet, β_5 is the fixed effect of the daily mean bottom temperature, and $Temp_{ij}$ is the daily mean bottom temperature associated with the i^{th} fish from the j^{th} gillnet. In this model, we assumed

$$Y_{ij} | u_j \sim \text{binomial}(n_{ij}, \pi_{fed_{ij}}) \quad (2)$$

That is, the response, Y_{ij} , is conditional on the random effects and is distributed as a binomial random variable with sample size n_{ij} and probability of consumption, $\pi_{fed_{ij}}$. The random gillnet effect, u_j , is a measure of the variation among nets controlling for the other effects in the model; this term allowed us to account for the hierarchical nature of the data, that is, fish captured by a single net are more likely to exhibit similar feeding habits, and these habits are likely to vary among fish captured across multiple nets. The values of u_j were assumed to be normally distributed and independent of the fish-level random errors, e_{ij} (Schabenberger 2005; Dai et al. 2006):

$$u_j \sim \text{iid } N(0, \sigma_u^2). \quad (3)$$

Preliminary analyses indicated that two-way interactions between the fixed effects were not important so they were not considered here. We coded time as month 1, 2, ..., 23 to allow for inter-year differences in temporal effects. Note that size classes for analysis were adjusted to reflect the observed size distribution of blue catfish examined in this study: size class 1 was 200 – 300 mm FL, size class 2 was 301 – 500 mm FL, and size class 3 was ≥ 501 mm FL. The hierarchical logistic model was fit using the GLIMMIX procedure in SAS, specifying the Laplace method of maximum likelihood estimation, the Newton-Raphson optimization method, and the between-within method to calculate the degrees of freedom (Dai et al. 2006; Kiernan 2018). These methods reduce the bias in parameter estimates and the bias of the estimates of the variance components of models with a binary response (Kiernan 2018).

The probability of observing blue crab(s) in the stomach of a blue catfish, π_{crab} , was estimated with a similar hierarchical logistic regression model that accounted for the clustering of fish within nets:

$$y_{ij} = \pi_{crab_{ij}} + e_{ij} \quad \text{where}$$

$$\text{Logit}(\pi_{crab_{ij}}) = \alpha + u_j + \beta_1 \text{Size}_{ij} + \beta_2 \text{Mon}_{ij} + \beta_3 \text{Stra}_{ij} + \beta_4 \text{Sal}_{ij} + \beta_5 \text{Temp}_{ij} \quad (4)$$

Here, y_{ij} is a binary variable indicating the presence or absence of blue crab in the stomach of the i^{th} blue catfish from the j^{th} gillnet, $\pi_{crab_{ij}}$ is the probability that at least one blue crab was observed in the stomach of the i^{th} blue catfish from the j^{th} gillnet, and all other parameters are as described above. As before, we assumed that the response, Y_{ij} , was conditional on the

random effects and was distributed as a binomial random variable. The values of u_j are assumed to be normally distributed and independent of the fish-level random errors, e_{ij} (Schabenberger 2005; Dai et al. 2006). Preliminary analyses indicated that two-way interactions between the fixed effects resulted in models with unestimable parameters so they were not considered here. The hierarchical logistic model was fit using the GLIMMIX procedure in SAS with the same specifications described above.

The average number of blue crabs consumed by an individual blue catfish, μ , was estimated by a Poisson hierarchical model using Generalized Estimating Equations (Højsgaard et al. 2006). Similar to the model used to estimate the probability of observing blue crabs in the stomach, we considered blue catfish size, stratum, season, salinity, and temperature as predictors in the model but used the number of blue crabs consumed as the response variable:

$$y_{ij} = \mu_{ij} + e_{ij}$$

$$\text{Log}(\mu_{ij}) = \alpha + u_j + \beta_1 \text{Size}_{ij} + \beta_2 \text{Mon}_{ij} + \beta_3 \text{Stra}_{ij} + \beta_4 \text{Sal}_{ij} + \beta_5 \text{Temp}_{ij} \quad (5)$$

where μ_{ij} is the number of blue crabs observed in the stomach of an individual blue catfish and other symbols are as previously defined. The model was fit assuming a Poisson distribution for count data with a log link using the “glmtoolbox” package in R. Multiple correlation terms were compared using QAIC_c and compound symmetry (equal variances and equal covariances) was best supported by the data; the model also accounted for the correlation among fish captured in the same gillnet, u_j . From this model we obtained population-level estimates of the average number of crabs in the stomach of a blue catfish for each size class, stratum, and season.

Diet Characterization: The percent of blue catfish with non-empty stomachs was estimated annually and seasonally for each size class, along with the percent of blue catfish that had consumed blue crabs. These metrics were used to estimate the relative importance of blue crabs in the diet of blue catfish as well as the degree to which blue crabs were selected as prey. Using diet analysis methods consistent with recent studies of blue catfish from the James River (Schmitt et al. 2017), we estimated the proportion of blue catfish with blue crab in their stomach, and expressed this as the frequency of prey occurrence, %O. Although the frequency of prey occurrence does not indicate relative importance of the prey item to the diet, %O indicates how often a particular prey was consumed (Chipps and Garvey 2007). Prey type contribution to the diet was also expressed as percent composition by number, %N (i.e., the number of blue crabs relative to the number of all prey items in the stomach) and as percent composition by weight, %W (i.e., the percent of blue crabs by weight relative to the weight of all prey items in the stomach). The relative importance of blue crabs to the diet of blue catfish was estimated with the prey-specific index of relative importance, or PSIRI (Schmitt et al. 2017):

$$PSIRI_i = \%O_i \times \frac{\%N_i + \%W_i}{2} \quad (6)$$

where %O, %N, and %W were as before and i refers to individual prey types (i.e., blue crab, fishes, other). The PSIRI is expressed as a percentage and allows comparison of the relative importance of prey types to the diet. Because we were interested in making comparisons of the PSIRI among seasons and among size classes of blue catfish, we estimated diet metrics from individual fish, prior to averaging for each prey type (Chipps and Garvey 2007). The averaging method we used accounted for the clustered nature of the data.

Diet composition metrics (%O, %N, %W, PSIRI) were estimated in R with data that were reviewed for quality assurance and quality control, and accounting for the clustering of samples (i.e., fish captured by the same net). Preliminary investigations revealed that the probability of consuming crabs and the mean number of crabs consumed per blue catfish varied by fish size class, stratum, and season; therefore, seasonal and stratum-based variations in %O, %N, %W, and PSIRI were examined for three size classes of blue catfish.

Preference for blue crab was determined using Chesson's α , a commonly used selectivity index for fishes (Chesson 1978; Confer and Moore 1987; Chipps and Garvey 2007). The selectivity index is a ratio of the frequency of occurrence of blue crabs in the diet of blue catfish to the relative abundance of blue crabs in the environment. Chesson's selectivity index for prey type i (e.g., blue crabs) is estimated by:

$$\alpha_i = \frac{r_i/n_i}{\sum_{j=1}^m [r_j/n_j]} \quad (7)$$

where r_i is the proportion of prey type i in the predator's diet, r_j is the proportion of prey type j in the diet, n_i is the proportion of prey type i in the environment, n_j is the proportion of prey type j in the environment, and m is the total number of prey types (Chesson 1978). Chesson's selectivity index is normalized so that values of α_i range from 0 to 1, and so that the sum of the α_i 's equals 1. An α_i value greater than $1/m$ indicates preference for prey type i (Chipps and Garvey 2007). In addition to information on diet composition, Chesson's α requires an estimate of the abundance of prey in the environment (the n terms in the equation). Due to lack of information on the relative abundance of 'other' prey types in the lower James River, we focused our analysis of selectivity on two prey types, fishes and blue crabs. We estimated relative abundance of blue crabs and fishes in the lower James River from monthly data collected by the VIMS Juvenile Fish Trawl Survey (Tuckey and Fabrizio 2021) during the 3-year period immediately preceding our study and the 2-year period coincident with our study (Figure 3). Thus, we examined fish and blue crab relative abundance for the period 2016-2020. We used this five-year period because the number of tows during the August 2018 – June 2020 study period was insufficient to provide a reliable estimate of density. The low sample size was a result of cessation of trawl sampling in the James River in April, May, and June of 2020 due to COVID-19 restrictions imposed by the Commonwealth of Virginia and William & Mary.

To estimate the proportion of blue crabs in the environment, we considered individuals larger than 25 mm CW captured by the VIMS Juvenile fish Trawl Survey; blue crabs smaller than this

were not captured consistently or relative to their abundance in the environment (Tuckey and Fabrizio, *pers. obs.*). For fish prey, we considered all fishes larger than 30 mm FL as this is the smallest size reliably sampled by the VIMS Juvenile Fish Trawl Survey (Tuckey and Fabrizio, *pers. obs.*). The maximum size of blue crabs was based on the largest blue crab observed in the stomachs; this blue crab measured 128 mm CW. The maximum size of potential fish prey is limited by gape size and was estimated as 50% of the midpoint of the size class of blue catfish. For example, for size class 2 (301 – 500 mm FL) blue catfish, we used 200 mm as the upper threshold of fish prey size. Gape sizes for each blue catfish size class were based on our observations of fish prey sizes consumed by blue catfish and were consistent with those reported for marine predators (Scharf et al. 2000). These calculations were performed in R. The electivity index was calculated from Chesson's α and ranged between -1 (blue crabs are absent in the diet) to +1 (blue crabs represent 100% of the diet; Ivlev 1961):

$$E = \frac{r_i - n_i}{r_i + n_i} \quad (8)$$

where r_i is the proportion of prey type i in the predator's diet and n_i is the proportion of prey type i in the environment. Chesson's α is not sensitive to changes in the density of prey in the environment and is suitable when the number of prey types is fairly constant (Chesson 1983; Confer and Moore 1987), which is a reasonable assumption for omnivorous blue catfish feeding in the lower James River. Selectivity and electivity were estimated for each fish size class, stratum, and season using R.

Quantifying Predation Impact: The impact of blue catfish predation on blue crabs was assessed by estimating daily consumption and abundance of predators and prey in the environment following methods in Link et al. (2002) but with modifications to accommodate our sampling design (i.e., two strata, one predator, multiple size classes of the predator, and four time periods). Areal estimates of blue crab consumption were scaled to the total area of the lower James River (Burwell Bay and Hog Island) to yield estimates of the total removal of blue crabs (numbers of blue crab) due to predation by blue catfish.

Daily consumption, C_d , was estimated for blue catfish by

$$C_d = 24 \cdot E \cdot \bar{S}^\gamma \quad (9)$$

where 24 is the number of hours per day, E is the instantaneous rate of gastric evacuation (per hr), \bar{S}^γ is the mean weight of stomach contents (g), and γ is a constant assumed to be 1 (Link et al. 2002). E was estimated for three size classes of blue catfish from each stratum and season using an exponential decay function of temperature, T

$$E = \alpha e^{\beta T} \quad (10)$$

where α and β are constants; for these constants we used $\alpha=0.01$ and $\beta=0.0964$ reported by Hedden et al. (2020) for channel catfish because temperature-dependent evacuation rates are

not available for blue catfish. Estimates of α and β derived from channel catfish observations were more likely to represent blue catfish evacuation rates than those reported for marine teleosts (Durbin et al. 1983; Link et al. 2002) or brown trout (He and Wurtsbaugh 1993). Furthermore, the Hedden et al. (2020) estimates were based on observations from channel catfish exposed to temperatures ranging from 8 to 27°C, which was similar to the range of mean temperatures observed in our study. We used the mean bottom water temperature (°C) for a given stratum and season to estimate temperature-dependent evacuation rates for blue catfish without regard to predator size class (Table 2).

The mean weight of the stomach contents, \bar{S} , was estimated for each size class, stratum, and season (for clarity, we omitted subscripts for these groupings) by:

$$\bar{S} = \frac{\sum_{net=1}^N (catfish) \cdot \bar{S}_{net}}{N} \quad (11)$$

where *net* refers to the individual gillnet, *N* is the total number of gillnets, *catfish* is the number of fish in each net, and \bar{S}_{net} is the mean stomach weight for blue catfish in a given net. \bar{S}_{net} was estimated for each net, size class, stratum, and season by

$$\bar{S}_{net} = \frac{\sum_{i=1}^I S_i}{I} \quad (12)$$

where *i* refers to an individual blue catfish, *I* is the total number of blue catfish captured in each net, and *S_i* is the stomach content weight for fish *i*.

To estimate the number of blue crabs that were consumed by blue catfish in the lower James River, we first estimated the total weight of blue crabs consumed (see below) and divided this weight by the average weight of a single blue crab. The average weight of a single blue crab was estimated from the observed CW using the weight-CW relationship (Smith and Chang 2007):

$$W = 0.0003145 \cdot CW^{2.6165} \quad (13)$$

where *W* is the mean weight (g) of a blue crab for a given CW (mm) observed in the diet study.

Removals of blue crabs due to predation by blue catfish were estimated from the diet composition data in a multi-step process that converted weight consumed to numbers consumed. Specifically, to obtain an estimate of the weight of blue crabs consumed each day, we multiplied the weight of all prey consumed by the proportion of prey comprised of blue crab; this was done for each season, stratum, and size class of blue catfish. The weight of blue crabs consumed was then divided by the average weight of a single blue crab, *W*, to obtain an estimate of the number of blue crab consumed per day, *C_d*. Population-level consumption was then estimated for each size class, stratum, and season as the product of the daily consumption (*C_d*), the number of days in each season (*d*), and the estimate of the abundance of blue catfish (\hat{N}) using:

$$C = C_d \cdot d \cdot \hat{N} \quad (14)$$

Mean abundances of blue catfish (\hat{N}) for a given size class, stratum, and season were obtained from catch observations from the VIMS Juvenile Fish Trawl Survey:

$$\hat{N} = \overline{catch/_{km^2}} \cdot A \quad (15)$$

where A is the area of the stratum (in km^2) and $\overline{catch/_{km^2}}$ is the mean density of blue catfish by size class, stratum, and season. Mean density was calculated as:

$$\overline{catch/_{km^2}} = \frac{\sum_{j=1}^J (catch/_{km^2})}{J} \quad (16)$$

where j refers to the trawl tow, J is the total number of tows in a given stratum and season, and $catch$ is the number of blue catfish captured in a tow.

For these density estimates (equation 19), we considered blue catfish greater than or equal to 200 mm FL collected by the VIMS Juvenile Fish Trawl Survey from 2016-2020 (Tuckey and Fabrizio 2021; Figure 3). Mean density estimates were based on completed tows, including those in which no blue catfish were captured. The number of tows completed per season ranged between 29 and 35 in Burwell Bay, and between 87 and 118 in Hog Island. The VIMS Juvenile Fish Trawl Survey is characterized by a greater number of sampling sites in the Hog Island area than in the area around Burwell Bay. Portions of the Burwell Bay stratum could not be sampled with fishing gear due to US military use (US Army Base Fort Eustis; US Navy James River Reserve Fleet).

Results

We deployed 416 gillnets from August 2018 through June 2020 with varying levels of monthly effort (Table 1), and processed 6,388 blue catfish ranging in length from 200 to 1,102 mm FL (Figure 4); mean length was 454.3 mm (standard error [SE] = 1.05). Slightly more than half (54.2% or 3,429) of blue catfish contained prey in their stomachs. The proportion of blue catfish stomachs with prey varied by month with a low of 17.0% in July 2019 to a high of 81.5% in March 2019 (Table 1). Blue crabs were present in the stomachs of blue catfish that ranged in length from 240 to 846 mm FL (mean length = 486.9 mm; SE = 3.36; N = 527; Figure 4).

Seasonal variations in bottom water temperatures and salinities in Burwell Bay and Hog Island reflected the seasonal cycles observed in temperate east coast estuaries (Tables 2 and 3). Mean temperatures during deployments ranged from a low of 4.7 to a high of 32.2°C, capturing nearly the full range of natural variation in this estuarine system. Mean bottom water temperatures were lowest in winter, highest in summer (Figure 5A), and exhibited the greatest

variation in spring and fall (Figure 5B). Bottom salinity was higher in summer and fall, and varied between 0 psu and 17 psu during the study period (Figure 6A). In general, conditions during deployments in Burwell Bay were characterized by slightly lower mean bottom temperatures across all seasons (Table 2; Figure 5B) and higher mean bottom salinities (Table 3; Figure 6) compared with conditions in the Hog Island stratum. Salinity differences between the two strata were more pronounced than bottom temperature differences (compare Figures 5B and 6B).

Air temperatures in the region during 2018, 2019, and 2020 were ‘much above average’ (NOAA statewide data); changes in atmospheric conditions (air temperature and longwave radiation) are the primary driver of changes in water temperature in the Chesapeake Bay region (Hinson et al. 2021). As such, water temperatures in the lower James River during the study period were warmer than average. In terms of precipitation in Virginia, the study years were ‘above average’ (NOAA statewide data); 2018 was the record wettest year, and salinity conditions in Burwell Bay and Hog Island were markedly lower during 2018 than in 2019 or 2020 (Figure 6A).

Factors Affecting Consumption: The probability of observing prey in a catfish stomach, π_{fed} , was estimated with a hierarchical logistic model that considered 6,314 blue catfish captured by 375 gillnets; an additional 16 fish were not considered because bottom salinity or bottom temperature data were unavailable for these fish. Of the 6,314 fish, 3,418 (~54%) had consumed prey. The probability of observing prey in a catfish stomach, π_{fed} , varied with month ($F = 7.17, P < 0.01$) and among strata ($F = 33.16, P < 0.01$), but was not significantly different among blue catfish size classes ($F = 1.11, P = 0.33$). The mean probability of observing prey in the stomach varied between 0.59 for size class 1 (200 – 300 mm FL), and 0.54 for size class 3 (≥ 501 mm FL; Appendix Table A1). An alternate model that considered season instead of month yielded AIC_c values that were 68.3 units higher than the model with month, indicating that temporal effects were best explained by month (Burnham and Anderson 2002). Mean bottom temperature ($F = 6.52, P = 0.01$) was a significant predictor of π_{fed} , but bottom salinity was not ($F = 0.81, P = 0.37$). The hierarchical logistic model provided a good fit to the data according to the Pearson goodness-of-fit criterion (Pearson χ^2 /degrees of freedom = 0.92). Relative to 1.0, which is the expected value of this fit statistic, our data were slightly under-dispersed; in this situation, the outcomes from the model are more conservative. The variation associated with individual gillnets was significant ($\hat{\sigma}_u^2 = 0.352, SE = 0.056$), and implied that π_{fed} values were heterogeneous among blue catfish sampled from the James River, even after accounting for the effects of fish size, stratum, and month. The mean probability of observing prey in the stomach of blue catfish was significantly greater among fish captured from Burwell Bay ($\hat{\pi}_{fed} = 0.65$) than among fish from Hog Island ($\hat{\pi}_{fed} = 0.47; t = 5.76, P < 0.01$; Appendix Table A1; Figure 7). The likelihood of observing prey in the stomach of blue catfish from Burwell Bay was 2.08 (95% confidence interval [CI]: 1.62 – 2.67) times greater than the likelihood of observing prey in the stomach of blue catfish from Hog Island. Variation in $\hat{\pi}_{fed}$ was evident, but the pattern varied among months and years of the study (Appendix Table A1). The probability of observing prey in

the stomach of blue catfish tended to be lowest in December 2018 and 2019, but the highest probabilities were observed in November 2019, suggesting that monthly variability was high (Appendix Table A1). Nonetheless, the probability of observing prey in the stomach of blue catfish increased monotonically in both years from January to April. At mean bottom water temperatures below 18°C, values of $\hat{\pi}_{fed}$ were somewhat stable and relatively high, but these values declined markedly as mean temperatures increased (Figure 8).

The probability that a catfish consumed at least one blue crab, π_{crab} , was estimated with a hierarchical logistic model that considered 6,314 blue catfish captured in 375 gillnets; an additional 16 fish were not considered because bottom temperature data were unavailable for these fish. Of the 6,314 fish, at least one blue crab was observed in 527 (8.35%) blue catfish stomachs. The probability that a catfish consumed at least one blue crab, π_{crab} , varied with time ($F = 2.84$, $P < 0.01$), among strata ($F = 10.85$, $P < 0.01$), and by blue catfish size class ($F = 21.41$, $P < 0.01$). Neither bottom salinity ($F = 0.24$, $P = 0.62$) nor mean bottom temperature ($F = 0.27$, $P = 0.60$) were significant factors in the model suggesting that daily fluctuations in water quality conditions were not necessary to explain the variation in π_{crab} in models that considered stratum and month. An alternate model that considered season instead of month yielded AIC values that were 12.4 units higher than the model with month, indicating that temporal effects were best explained by month (Burnham and Anderson 2002). The hierarchical logistic model provided a good fit to the data (Pearson $\chi^2/\text{degrees of freedom} = 0.86$). As before, the data were slightly under-dispersed, thus model estimates tend to be conservative. The variation associated with individual gillnets was significant ($\hat{\sigma}_u^2 = 0.339$, SE = 0.093), and implied that probabilities of blue crab consumption were heterogeneous among the blue catfish that we examined from the lower James River; this between-net heterogeneity accounted for variation that was not explained by the effects of fish size, stratum, and month. Estimates of π_{crab} indicated that the mean probability of blue crab consumption increased with increasing fish size class ($\hat{\pi}_{crab} = 0.02$ for size class 1, $\hat{\pi}_{crab} = 0.07$ for size class 2, and $\hat{\pi}_{crab} = 0.11$ for size class 3; Appendix Table A2; Figure 9A). Large fish (size class 3) were 1.68 (95% CI: 1.37 – 2.04) times more likely to consume blue crabs than intermediate size fish (size class 2), and 7.65 (95% CI: 3.32 – 17.66) times more likely to consume blue crabs than small fish (size class 1). The mean probability of crab consumption was significantly greater among fish captured from Burwell Bay ($\hat{\pi}_{crab} = 0.06$) than among fish captured from Hog Island ($\hat{\pi}_{crab} = 0.04$; $t = 3.29$, $P < 0.01$; Appendix Table A2; Figure 9B). Blue catfish were 1.75 (95% CI: 1.25 – 2.45) times more likely to consume blue crabs in Burwell Bay than in Hog Island. Monthly variation in π_{crab} was evident, (Figure 9C), with no clear seasonal signal. Contrasts of the mean probabilities across seasons indicated no significant differences in mean π_{crab} in summer versus other seasons (summer vs. spring $t = 0.00$, $P = 0.99$; summer vs. fall $t = -0.42$, $P = 0.68$; summer vs. winter $t = 0.24$, $P = 0.81$). Similarly, we found no significant difference in mean π_{crab} between fish captured in spring and winter ($t = 0.41$, $P = 0.68$); the mean π_{crab} in fall was not significantly different than in winter ($t = 1.54$, $P = 0.12$) or spring ($t = 0.88$, $P = 0.38$). The lack of significant seasonal differences reflected the overall low probabilities of blue crab consumption, and the

imprecision (larger CIs) of the seasonal estimates due to large annual differences (Appendix Table A2).

The number of blue crabs consumed daily by an individual blue catfish, given that blue crabs were consumed, ranged from an average of 0.98 to 1.57 crabs per catfish (Figure 10, Appendix Table A3). On average, small blue catfish (200-300 mm FL) consumed one crab, whereas the number of blue crabs consumed by intermediate and large (≥ 301 mm FL) blue catfish was greater than one.

The average number of blue catfish observed in a single year ($N = 8,202,284$ fish) in the lower James River varied by size class and stratum (Figure 11). The majority of these were small fish between 200 and 300 mm FL ($N = 7,092,960$), followed by intermediate size fish ranging from 301 to 500 mm FL ($N = 1,068,013$ fish). Small (200 – 300 mm FL) blue catfish were found in greater numbers in the Hog Island area than in Burwell Bay, but the numbers of intermediate (300 – 500 mm FL) and large (≥ 501 mm FL) blue catfish were similar across strata (Figure 11).

Blue crabs consumed by blue catfish ranged between 6.2 and 128 mm CW (mean = 45.6 mm, SD = 18.7), and, in general, these crabs were adequately sampled by the VIMS Juvenile Fish Trawl Survey (Figure 12). The trawl net used for this survey effectively captured blue crabs 25 mm CW and larger, but under-sampled smaller blue crabs, thus making comparisons problematic between blue crab abundance and the number of blue crabs consumed by blue catfish in the lower James River.

Diet Characterization: The diet of blue catfish from the mesohaline portion of the James River was diverse, and consisted of fishes, crustaceans, mollusks, vegetation, polychaetes, birds, insects, cnidarians, and anthropogenic debris. The occurrence of blue crabs, fishes, and other prey types in the diets of blue catfish was similar in Burwell Bay and Hog Island but differed among blue catfish size classes (Figure 13). Small blue catfish (200 – 300 mm FL) fed most frequently on 'other' prey items (i.e., vegetation, mollusks, other invertebrates) regardless of season or stratum (Figure 13), and 'other' prey had the largest contribution to the diet of small blue catfish (Figures 14 and 15). Compared with small blue catfish, individuals between 301 and 500 mm FL incorporated a greater proportion of fishes and blue crabs in their diet (Figures 13, 14, and 15). 'Other' prey, however, were more important than fish and blue crabs in terms of frequency of occurrence (%O) and contribution to the diet (%N, and %W) of intermediate size blue catfish (Figures 13, 14, and 15). Large blue catfish (≥ 501 mm FL) generally fed most frequently on fishes (Figure 13). In terms of weight-based contributions to the diet (%W), fishes were the dominant prey for large blue catfish (≥ 501 mm FL), especially in winter (Figure 15). The contribution of blue crab to the diet in terms of numbers and weight were generally lowest in winter and greatest in summer across all size classes of blue catfish in Burwell Bay and Hog Island (Figures 14 and 15).

'Other' prey were most important for small (200 – 300 mm FL) and intermediate size (301 – 500 mm FL) blue catfish, with PSIRI ranging from 76.4 to 100% for small blue catfish, and 42 to

67.4% for intermediate blue catfish (Figure 16; Appendix Table A4). Fishes were the most important prey (PSIRI = 30.1 – 76.6%) for large blue catfish (≥ 501 mm FL), with the exception of Hog Island in summer, when the blue crab index of relative importance (PSIRI_{crab} = 56.6%) exceeded the fish index (PSIRI_{fish} = 30.1%; Figure 16; Appendix Table A4).

In Burwell Bay and Hog Island, intermediate and large blue catfish selected for blue crabs in all seasons according to estimates of Chesson's α (Figure 17, Appendix Table A5). With the exception of blue catfish ≤ 300 mm FL in Burwell Bay in the winter and fall (Figure 17), selection for fishes was low (below 0.5), but we note that these estimates reflect selection of fishes relative to blue crabs, and not other prey, for which we were unable to estimate abundance. Overall, diet characterization was similar using Chesson's selectivity index and the index of electivity. Based on estimates of the electivity index, blue catfish generally selected for blue crabs over fish in Burwell Bay and Hog Island in all seasons (Figure 18, Appendix Table A5). Small blue catfish showed slight selection for fishes over blue crabs in winter and fall in Burwell Bay.

Quantifying Predation Impact: Expanding the total number of blue crabs eaten by blue catfish and accounting for the size of blue catfish, season, and area of each stratum resulted in 2,341,230 blue crabs consumed annually (Table 4; Figure 19). Although we intended to provide a measure of uncertainty for this estimate, and Link et al. (2002) suggest that such estimates are possible, we were unable to find an appropriate method. This estimate of total annual blue crab consumption is likely biased low because consumption estimates were derived from trawl-based estimates of the mean number of blue catfish captured by the trawl and this gear under-sampled large (> 400 mm FL) blue catfish. Length-frequency histograms of blue catfish sampled by the trawl and by gillnets depict the negative bias of the trawl for fish greater than 400 mm FL (Figure 20). However, we note that the range of gillnet selectivity was greater than that of the trawl due to the multiple mesh sizes of gillnets that were deployed, whereas the trawl gear targeted primarily fish less than 400 mm FL. Nevertheless, observed seasonal and size-based patterns in consumption are likely to hold: most blue crabs (86%) were consumed by blue catfish between 301 and 500 mm FL and more crabs (56%) were consumed in the higher salinity waters of Burwell Bay than in Hog Island (Figure 19). Although blue crabs were consumed in all seasons, the greatest number of blue crabs were consumed in summer and fall.

Discussion

The diet of blue catfish from rivers in their native range and from tidal freshwater regions of Chesapeake Bay are known to vary annually and seasonally (Eggleton and Schramm 2004; Schmitt et al. 2019), but ours is the first examination of the diets of invasive blue catfish to focus on seasonal variation that encompasses the entirety of the mesohaline region. Blue catfish in the lower James River consumed blue crabs throughout the year. All size classes of blue catfish consumed blue crabs, but on a population level, the greatest predation impact on

blue crabs was exerted by intermediate size (301 – 500 mm FL) fish. This size class of fish roughly corresponds with the segment of the population represented by 1.6 million fish in a 12-km section of the James River, just upriver of our study site (Fabrizio et al. 2018). Large fish (\geq 501 mm FL) were more likely to consume blue crabs, but because the abundance of large fish was relatively low, predation impact due to large blue catfish was also relatively low.

We observed spatial variation in predation impacts on blue crabs such that predation removals were greater in Burwell Bay than in Hog Island. Blue crabs contributed a greater proportion by number and by weight to the diet of intermediate-sized blue catfish in Burwell Bay compared with those in Hog Island. Because the abundance of the intermediate size group of blue catfish was similar in Burwell Bay and Hog Island, the observed spatial difference in predation impact was not likely due to predator abundance. Instead, the spatial pattern may have resulted from differences in blue crab abundance, availability, or vulnerability in these regions. In general, blue crab abundance in these regions of the lower James River is relatively high, suggesting that spatial variation in availability and vulnerability of blue crabs to predation may have played a role in the greater predation removals observed in Burwell Bay. The relatively higher salinity conditions observed in Burwell Bay (up to 17 psu) did not seem to provide an effective release from blue catfish predation, even though blue catfish generally favor habitats with salinities less than 10 psu (Nepal and Fabrizio 2019). We hypothesize that other habitat factors may have contributed to the increased predation impacts estimated for Burwell Bay. For example, structured habitats in Burwell Bay may attract or aggregate blue crabs and provide efficient feeding opportunities for blue catfish. In particular, we note the greater presence of oyster habitats in Burwell Bay compared with Hog Island (Harding et al. 2008, Mann et al. 2009). Most oyster reefs in the lower James River are located in Burwell Bay (and downriver) with only a small patch extending into the southern end of Hog Island. Because of the complex three-dimensional nature of oyster reefs, these structures offer a refuge from predation for small blue crabs (10 – 50 mm CW; Longmire et al. 2021). Typically, small blue crabs are able to hide among the crevices of the reef and thus avoid detection by visual predators. Blue catfish, however, have well-developed sensory systems (chemoreception and electroreception), which allow them to easily locate prey whether hidden or not (New 1999). Small blue crabs that use oyster habitats as a predation refuge may be more vulnerable to predation by blue catfish than by visual predators. Instead of providing a protective function for blue crabs, oyster reefs may attract blue catfish to concentrated areas of potential prey. Availability and vulnerability of blue crabs to blue catfish predation at the spatial scale of our study have not been examined, but such research could help to understand the observed spatial pattern in predation impact. We note that a field-based study of blue crab predation mortality is currently underway at VIMS (A. Hyman, PhD research under the direction of R. Lipcius), but laboratory experiments are also needed to elucidate the role of structure, particularly oyster reefs and vegetation, as a refuge from blue catfish predation.

Similar to previous studies of fish predation on blue crabs (Scharf and Schlicht 2000), we found that the size range of blue crabs (6 – 128 mm CW) consumed by blue catfish was narrower than

the size range of blue crabs (8 – 192 mm CW) in the environment, suggesting that a size refuge may exist for blue crabs in the lower James River. Although the size range of consumed blue crabs was quite wide, we note that 2.5% of blue crabs were > 90 mm CW, whereas 25.7% of blue crabs in the environment were > 90 mm CW. Red drum predation on blue crabs was restricted to blue crabs less than 85 mm CW (Scharf and Schlicht 2000), and an earlier study suggested that most (78%) blue crabs consumed by red drum are < 50 mm CW (Guillory and Prejean 2001). Blue crab vulnerability to predation decreases almost linearly with increasing blue crab size and blue crabs attain a 95% size refuge from predation around 90 mm CW (Moody 2001). In the Chesapeake Bay, blue crabs reach an average size of 85 mm CW during their first year of growth; this is also the size when blue crabs reach reproductive maturity (Van Engel 1958; Millikin and Williams 1984). Together, these studies and our observations from the lower James River suggest that blue catfish predation has little effect on adult blue crabs, but appears to be significant for juvenile blue crabs. The potential for a size refuge for adult blue crabs may arise because: (1) predation attempts on adult blue crabs incur an injury risk to the predator, (2) the energetic cost of handling large blue crabs is high; or (3), adult blue crabs can effectively evade predation attempts by swimming away. Juvenile blue crabs may bury to escape predation (Bromilow and Lipcius 2017), but this tactic is ineffective against blue catfish predation.

Across all seasons, an average of 54.1% of the blue catfish consumed prey; this is lower than the 71.1% reported by Schmitt et al. (2017) and 60.4% reported by Schmitt et al. (2019), who captured fish using primarily electrofishing. We note, however, that in some months (e.g., March 2019), up to 81.5% of blue catfish had consumed prey in our study, indicating that consumption varied temporally. Some of the blue catfish captured during the early portion of net deployments may have fully or partially digested prey by the time of net retrieval, which was about 21 hours after deployment. This was particularly noticeable in summer, when the proportion of fish with empty stomachs increased markedly, likely reflecting the rapid digestion induced by warm temperatures (> 18°C).

Conclusions drawn from diet studies are contingent upon the assumptions made with regard to study design and data collection. We made a number of assumptions concerning the sampling of blue catfish, the grouping of prey types and characterization of the diet, the estimation of daily consumption rates, and the estimation of the annual mean abundance of blue catfish in the lower James River. Below, we describe these assumptions and explore how violations may have affected the characterization of blue catfish diets and estimates of blue crab removals due to predation.

The partial digestion of prey may have biased estimates of the relative importance of blue crab prey as indicated by diet metrics and the mean probability of observing blue crab in the diet. For example, when fish prey were found in a relatively highly digested state, we estimated the number of fish that had been consumed by using the mean weight of fish observed in the diet. In many cases we were unable to identify fish prey to species, and the average weight for a

group of species or closely related taxa (e.g., herring) was used. Such estimation techniques may work relatively well for fish, but for the prey category we identified as 'other', which included mollusks, vegetation, and polychaetes, the average weight technique may or may not be accurate. These estimates of the numbers of prey were used to calculate percent occurrence by number. In general, we found diet metrics provided rough characterizations of the diet, but were useful in confirming that predator size affected the consumption of specific prey types. Statistical models based on presence/absence of prey were more efficient and provided additional insights.

In addition to the digestion of prey due to extended fishing times, the partial or full regurgitation of stomach contents may have biased our diet study. Some fish regurgitate stomach contents upon capture and this varies by species and with capture method (Bowen 1996). A common assumption of diet studies is that regurgitation does not occur, or if regurgitation occurs, it occurs only rarely. Because we did not capture the fish ourselves, we could not estimate the number of blue catfish that may have regurgitated prey; thus, we assumed that if regurgitation did occur, all stomach contents were expelled and the individual was recorded as having an empty stomach. If the assumption of no or little regurgitation is violated, then a greater number of blue catfish may have had prey in their stomach, including blue crabs. Estimates of %N, %O, %W, PSIRI, and the probability of consuming prey could be biased if regurgitation occurred. In this study, we assumed that the occurrence of regurgitation was randomly distributed across time, strata, and size class and was independent of prey type. Given the large number of samples that we examined (N = 6,314 fish), and the inspection of stomach samples throughout the year, any bias resulting from regurgitation was likely low.

We assumed that a successful blue crab predation event occurred when the stomach contents of blue catfish included any part of a blue crab (e.g., leg, claw). If this assumption did not hold, then we overestimated the number of blue crabs consumed, the blue crab index of relative importance, and the total number of blue crabs removed by predation. Although possible, such a bias is not likely to alter our interpretation of the magnitude of predation mortality on blue crabs; this is because crabs that lose a claw or leg may not survive. For example, injured crabs may attract the attention of other predators. We plan to explore this potential source of bias in a follow-up study.

Other sources of potential bias arose from the clustered or hierarchical nature of sampling multiple blue catfish from a single gillnet. We accounted for this cluster sampling in our estimates of percent occurrence as well as in our statistical models of the probability of observing prey, the probability of observing blue crab in the diet, and the average number of blue crabs consumed by blue catfish. Such clustering was significant in our study suggesting that the distribution of fish is not random with respect to feeding history. This clustering effect is also consistent with the diet specialization reported for individual blue catfish (Schmitt et al. 2019). Regardless of gear type used, the clustered nature of fisheries observations must be

statistically addressed to provide proper estimates of diet composition, the importance of prey, and descriptions of consumption (Buckel et al. 1999).

Our estimates of the frequency of occurrence of blue crabs in the diet of intermediate size (301 – 500 mm FL) blue catfish (%O range: 12.8 to 51.1%) were similar to the 10 to 33% range reported from fish sampled in the oligohaline and mesohaline reaches of the James River using electrofishing and trotlines (Schmitt et al. 2019). Our estimates of the frequency of occurrence of blue crabs in the diet was lower for small blue catfish (200 – 300 mm FL; %O range: 0 to 5.8%) and higher for large blue catfish (≥ 501 mm FL; %O range: 14.0 to 65.6%). Predator sizes as well as temperature and salinity likely contributed to the differences we observed relative to those reported by Schmitt et al. (2019): the frequency of occurrence of blue crabs in the diet of blue catfish was greater in Burwell Bay, which on average exhibited greater salinity than Hog Island. Large blue catfish tolerate higher salinities than small conspecifics and can therefore make use of blue crab resources in these areas, whereas the salinity tolerance of small blue catfish suggests that this size class is less likely to undergo feeding forays into waters greater than 10 psu (Nepal and Fabrizio 2020). In addition, the relative abundance of juvenile blue crabs is lower in upriver, oligohaline (0 – 5 psu) areas than in the mesohaline habitats that we sampled (Hyman et al. *in prep.*), thus lower frequency of occurrences can be expected. Indeed, the frequency of occurrence of blue crabs in the diet of blue catfish from the freshwater reaches of the James River is 1.48% (Schmitt et al. 2017). In the James River, blue crabs are an important component of the diet of blue catfish in fall (15% occurrence) and winter (33% occurrence), particularly in mesohaline habitats (5 – 18 psu; Schmitt et al. 2019). Our study of blue catfish from mesohaline habitats suggested that the frequency of occurrence of blue crabs in the diet varied among seasons, but was generally greater in summer (Figure 13; Appendix Table A4). Mesohaline habitats were probably not well sampled in summer by Schmitt et al. (2019) due to limitations of low-frequency electrofishing; therefore, our collections in summer likely included a greater proportion of blue catfish from salinities exceeding 5 psu and from areas of the James River that likely supported a greater abundance of blue crabs.

The assessment of the impact of predation on blue crabs followed methods previously used to calculate predator consumption from fishery-independent surveys (i.e., Link et al. 2002). This approach, like other approaches, relies on estimates of predator evacuation rates. Due to a lack of studies on the evacuation rate of blue catfish, we used parameter values obtained from a model of temperature-dependent evacuation rates for channel catfish, a closely related species. We believe these are reasonable model parameters for blue catfish because daily rations of blue catfish and channel catfish are similar (Schmitt et al. 2021). Evacuation rates may also be affected by prey type: crabs require longer times to digest than fish (average time to 95% digestion of crabs=21.7 hours versus average time to 95% digestion of fish=17.2 hours at 28°C; Berens and Murie 2008). Similarly, digestion of fish prey requires more time than digestion of small invertebrate prey such as shrimp (Durbin et al. 1983). Evacuation rates for fish are likely greater than those for blue crab because daily ration is greater for fish prey than for blue crab (Schmitt et al. 2021). Because Hedden et al. (2020) used fish as prey, our

estimates of evacuation rates for blue catfish that consumed blue crabs may have been biased high, and hence we may have also overestimated the number of blue crabs consumed. Note, however, that blue catfish are omnivorous and evacuation rates estimated from experiments using a single prey type may not be appropriate for fish that consume a mixed diet. Therefore, we recommend a study of evacuation rates for blue catfish; furthermore, because of the temperature dependence of these rates, a wide range of temperatures, similar to those observed during our study, should be used to provide robust parameter estimates. In addition, multiple prey types could be examined simultaneously, including vegetation, blue crabs, and fish. In addition to temperature and prey type, predator size (Gillum et al. 2012; Hedden et al. 2021) and the degree of armament of the prey (Anderson 2012; Anderson et al. 2016; Schmitt et al. 2021) may contribute to variation in evacuation rates. Such factors warrant investigation for invasive blue catfish.

The scaling of blue crab consumption using areal estimates of stratum size in the lower James River assumed that blue catfish sampling was random over the spatial extent of the study area and that the numbers and size ranges of blue catfish captured in the gillnets were representative of the population in Burwell Bay and Hog Island. Although we implemented a stratified random sampling design, the placement of gillnets was left to the discretion of the waterman. This was due to practical reasons (e.g., the presence of anchored crab pots, active fishing, and so forth) and to the realization that catch rates were significantly improved by sampling near the mouth of creeks and sub-tributaries (Figure 1). When those segments were selected for sampling, gillnets tended to be deployed in the same or similar portion of the segment. This was a compromise to allow us to obtain sufficient numbers of blue catfish with prey in their stomachs. Because of this implementation, we may have overestimated the total consumption of blue crabs if encounter rates between blue catfish and blue crabs were lower in portions of the study site that were not well sampled. We note, however, that blue crabs and blue catfish are widely distributed in this system and on this basis, we expect our estimates of total blue crab consumption to be relatively unbiased.

The trawl net, which was used to estimate the abundance of blue catfish in the lower James River, does not capture all of the fish in the path of the net, and as such, trawl-based estimates of abundance are considered 'minimum' estimates (e.g., Link et al. 2002). The number of blue catfish in Burwell Bay and Hog Island may have been underestimated due to the imperfect efficiency of the net. If blue catfish abundance was underestimated, then we also underestimated total consumption of blue crabs.

The abundance estimates of blue catfish in the lower James River considered fish greater than or equal to 200 mm FL, but the population comprises many smaller fish. Based on the observed low occurrence of blue crabs in the diet of 200-300 mm FL blue catfish, we expect blue crabs to be absent or present in only low numbers in the diet of fish less than 200 mm FL. Thus, the 200 mm FL threshold used for abundance estimation was reasonable and likely did not affect the estimate of predation removals. We did not, however, examine the diet of fish less than 200

mm FL and it is possible that this size class consumes small crabs (< 25 mm CW); these small crabs may be rapidly digested and difficult to detect. Hence, DNA methods (e.g., Aguilar et al. 2017) are needed to assess the presence of blue crab tissues in the stomachs of blue catfish less than 200 mm FL. Even if the occurrence of blue crabs in the stomachs of this size class of blue catfish is low, the high abundance of this size class may result in substantial predation mortality on blue crabs. This phenomenon has been reported for other invasive fish predators: when present in high densities, “a low incidence of prey in the diet scales up to a relatively large number consumed” (Hedden et al. 2020).

The sampling limitations of trawl nets – inefficiency and selection against large (> 400 mm FL) blue catfish – are not unique to this gear. Indeed, these limitations also characterize low-frequency electrofishing: size-frequency distributions of fish captured by electrofishing (see Figure 8 in Greenlee and Lim 2011) are remarkably similar to those from trawl surveys, and not all stunned blue catfish are retrieved by netters, particularly when large numbers of fish are present. Better estimates of the relative abundance of blue catfish > 400 mm FL in the James River are needed to fully assess the predation impact of this segment of the population, particularly because these fish are more likely to consume blue crabs. We recommend implementation of a targeted survey for this size class of blue catfish using gear that can readily yield density estimates. Gillnet surveys are one possibility, but gillnet catch rates cannot be converted readily to densities. A Bayesian method to estimate densities from gillnet catches has been developed by Griffiths et al. (2007), but is yet to be widely implemented. Alternatively, acoustic cameras may be used to assess abundance of large blue catfish, but this method is subject to identification bias, that is, acoustic shadows may be difficult to unequivocally identify as blue catfish. Nevertheless, few other species attain a size of 400 mm, and those that do (e.g., Atlantic sturgeon, striped bass, longnose gar) are morphologically dissimilar to blue catfish. We do not recommend the use of electrofishing surveys because of the size selectivity of the gear, the inability to sample in mesohaline waters and in winter, and the inability to reliably estimate fish densities.

Thermal conditions in the lower James River were above average during our study in 2018, 2019, and 2020. Because elevated temperatures result in increased feeding rates of fish (Brett et al. 1969), the consumption rates of blue catfish during our study were also likely to be elevated. As temperatures continue to rise in the Chesapeake Bay, blue catfish consumption rates may increase further. Our study years were also considered ‘wet years’ and increased precipitation in the watershed reduced salinity in the tributaries thereby facilitating greater spatial overlap between blue crabs and blue catfish (Nepal and Fabrizio 2019). The likely range expansion of blue catfish (Nepal and Fabrizio 2020) coupled with the ability of this species to survive in 15.7 psu (Nepal and Fabrizio 2019) and higher (Tuckey and Fabrizio, *pers. obs.*), suggest that blue catfish predation intensity on blue crabs and other native species is not likely to stabilize or decline.

In summary, the number of blue crabs removed by blue catfish was likely underestimated and the true number of blue crabs consumed each year in the lower James River may be higher than what we reported. We identified a number of assumptions made in the estimation procedures, as well as in the handling of the diet composition data. The assumptions we made were reasonable, given the lack of information and the need to simplify calculations. If some of these assumptions did not hold, then our estimate of predation removals could be biased. In some instances, the direction of the bias was known, but in other cases, the bias could be either positive or negative. In particular, we considered the estimates of the number of blue catfish in the lower James River to be minimal estimates of the true population size; this is due to the inability of the trawl to capture 100% of the fish that are present in the system. For example, blue catfish may be present, but not available to the bottom trawl because they occupy habitats that are too shallow for the vessel to sample. Because the population size of blue catfish in the lower James River is likely to be higher than what we estimated, blue crab removals are likely to also be higher; blue crab removals per season were obtained by multiplying the number of blue catfish present in the system by the estimate of daily consumption of blue crabs and number of days in each season. The average per-fish consumption of blue crabs may have been overestimated because we used evacuation rates reported for another ictalurid that consumed primarily fish. Nevertheless, the component that most influenced the magnitude of blue crab removals was the estimate of the blue catfish population size. Furthermore, we under-sampled large (≥ 501 mm FL) blue catfish and this segment of the population had the highest probability of consuming blue crabs. Taken together, our estimates of blue crab removals due to blue catfish predation are likely conservative.

Acknowledgments

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Table 1. The number of nets fished (Effort), the catch per net (CPUE), and the number of blue catfish processed for stomach contents by month and year. Shown are the number of blue catfish with empty stomachs, the number that contained prey, and the percent with prey. All nets were 182.9 m long, except those deployed in August and September 2018; those nets were 91.4 m long. *Effort and CPUE for August and September 2018 were adjusted to account for the smaller net length in those months.

Year	Month	Effort	CPUE	Stomachs		
				Empty	Contain prey	%
2018	8	6*	11.7	49	21	30.0
	9	8*	19.5	108	48	30.8
	10	24	15.8	233	145	38.4
	11	16	10.3	84	81	49.1
	12	12	11.9	83	60	42.0
2019	1	24	11.8	113	171	60.2
	2	24	10.3	89	159	64.1
	3	24	11.7	52	229	81.5
	4	28	15.0	125	294	70.2
	5	20	15.6	117	195	62.5
	6	16	5.6	51	39	43.3
	7	12	3.9	39	8	17.0
	8	20	2.7	35	19	35.2
	9	16	3.7	39	20	33.9
	10	16	11.8	144	45	23.8
	11	16	12.7	56	147	72.4
	12	16	26.3	264	156	37.1
2020	1	16	24.3	221	168	43.2
	2	16	33.1	201	329	62.1
	3	16	29.1	151	314	67.5
	4	24	31.8	335	428	56.1
	5	16	21.1	165	172	51.0
	6	16	20.5	147	181	55.2

Table 2. Seasonal mean bottom temperature (°C) recorded via Tidbit dataloggers attached to gillnets. Some of the daily values were interpolated; N is the number of gillnets from which temperature was recorded; SE is the standard error of the mean.

Stratum	Season	N	Mean (SE)	Range
Both	Winter	118	8.67 (0.21)	5.17-14.22
	Spring	120	20.24 (0.46)	10.45-28.41
	Summer	76	28.93 (0.16)	25.88-32.17
	Fall	100	15.05 (0.67)	4.66-26.41
Burwell Bay	Winter	60	8.31 (0.28)	5.17-13.63
	Spring	60	19.71 (0.67)	10.45-27.95
	Summer	38	28.40 (0.20)	25.88-30.87
	Fall	50	14.74 (0.96)	5.27-25.36
Hog Island	Winter	58	9.05 (0.29)	5.48-14.22
	Spring	60	20.77 (0.63)	12.31-28.41
	Summer	38	29.46 (0.23)	26.92-32.17
	Fall	50	15.35 (0.94)	4.66-26.41

Table 3. Seasonal mean bottom salinity (psu) recorded with a YSI hand-held meter at the time of gillnet deployment. N is the number of salinity observations recorded (one observation per gillnet deployment); SE is the standard error of the mean.

Stratum	Season	N	Mean (SE)	Range
Both	Winter	119	4.03 (0.42)	0.1-18.1
	Spring	119	4.08 (0.37)	0.1-16.6
	Summer	76	8.36 (0.46)	0.6-15.8
	Fall	100	6.04 (0.54)	0.1-16.9
Burwell Bay	Winter	60	6.02 (0.65)	0.1-18.1
	Spring	59	7.07 (0.49)	0.8-16.6
	Summer	38	11.29 (0.47)	3.1-15.8
	Fall	50	7.85 (0.82)	0.1-16.9
Hog Island	Winter	59	2.01 (0.37)	0.1-9.1
	Spring	60	1.15 (0.15)	0.1-3.8
	Summer	38	5.43 (0.40)	0.6-10.2
	Fall	50	4.23 (0.61)	0.1-11.7

Table 4. Mean number and standard error (SE) of the mean of blue crabs consumed by blue catfish by size class and stratum, from the lower James River from August 2018 to June 2020. Blue catfish size classes are: (1) 200 – 300 mm fork length (FL), (2) 301 – 500 mm FL, and (3) \geq 501 mm FL. The total number of crabs consumed by blue catfish was 2,341,230.

Stratum	Blue catfish size class	Number of crabs	SE
Burwell Bay	1	726	726.0
Burwell Bay	2	1,284,852	444,470.0
Burwell Bay	3	30,172	16,437.7
Hog Island	1	239,277	164,861.2
Hog Island	2	720,852	93,166.6
Hog Island	3	65,351	31,899.8

Figure 1. Gillnet sampling locations (open circles; N = 416) for blue catfish in the Hog Island and Burwell Bay regions in the James River, VA, from August 2018 to June 2020. Division of the study area into two strata is indicated by the red line.

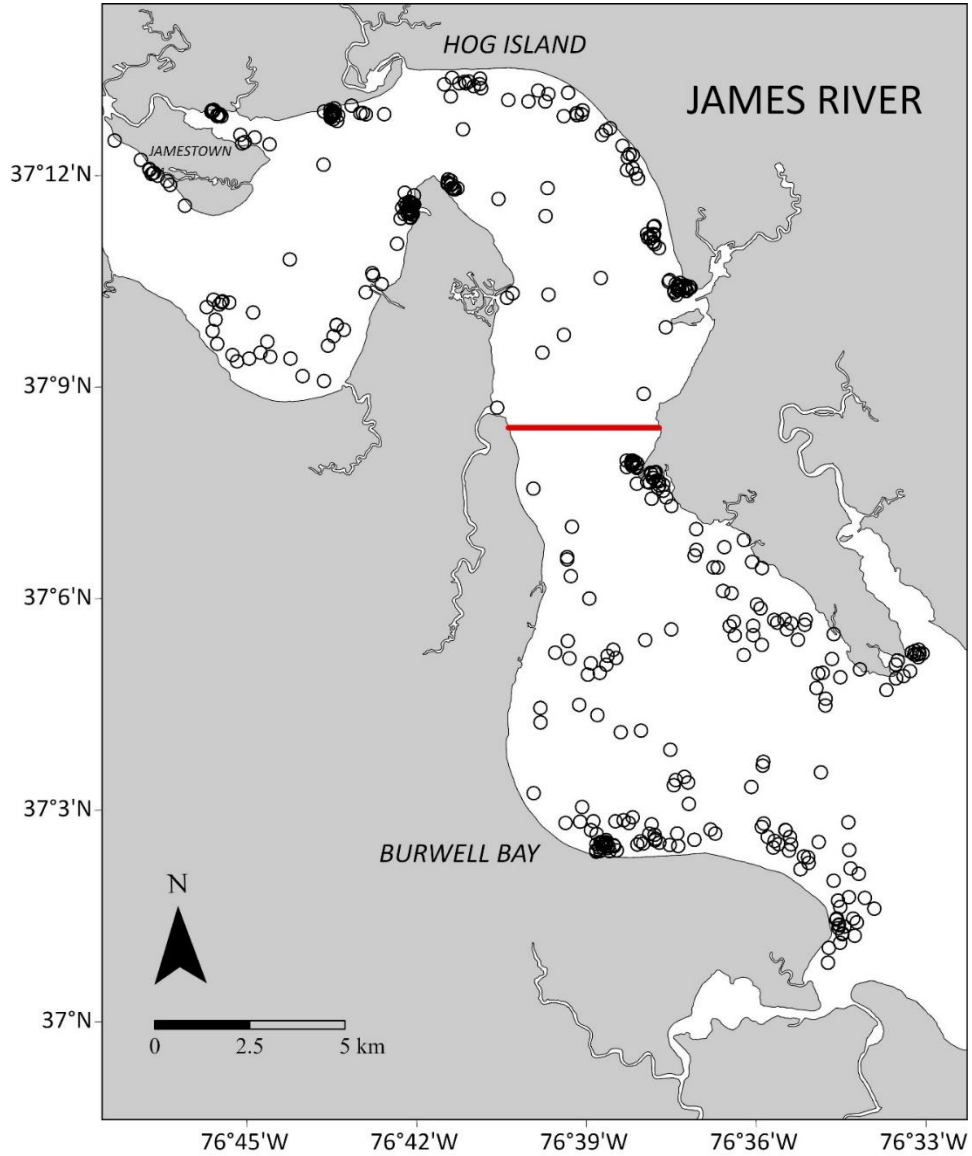


Figure 2. Distribution and occurrence of blue catfish (orange circles) and blue crabs (green triangles) in the lower James River, Virginia. Observations are from bottom trawl samples taken in 2016-2020 by the VIMS Juvenile Fish Trawl Survey in the study area (Burwell Bay and Hog Island). Division of the study area into two strata is indicated by the red line. Note: Only blue crabs with carapace widths between 25 and 128 mm are shown as crabs less than 25 mm are not fully recruited to the trawl gear. Only blue catfish greater than > 200 mm FL are depicted.

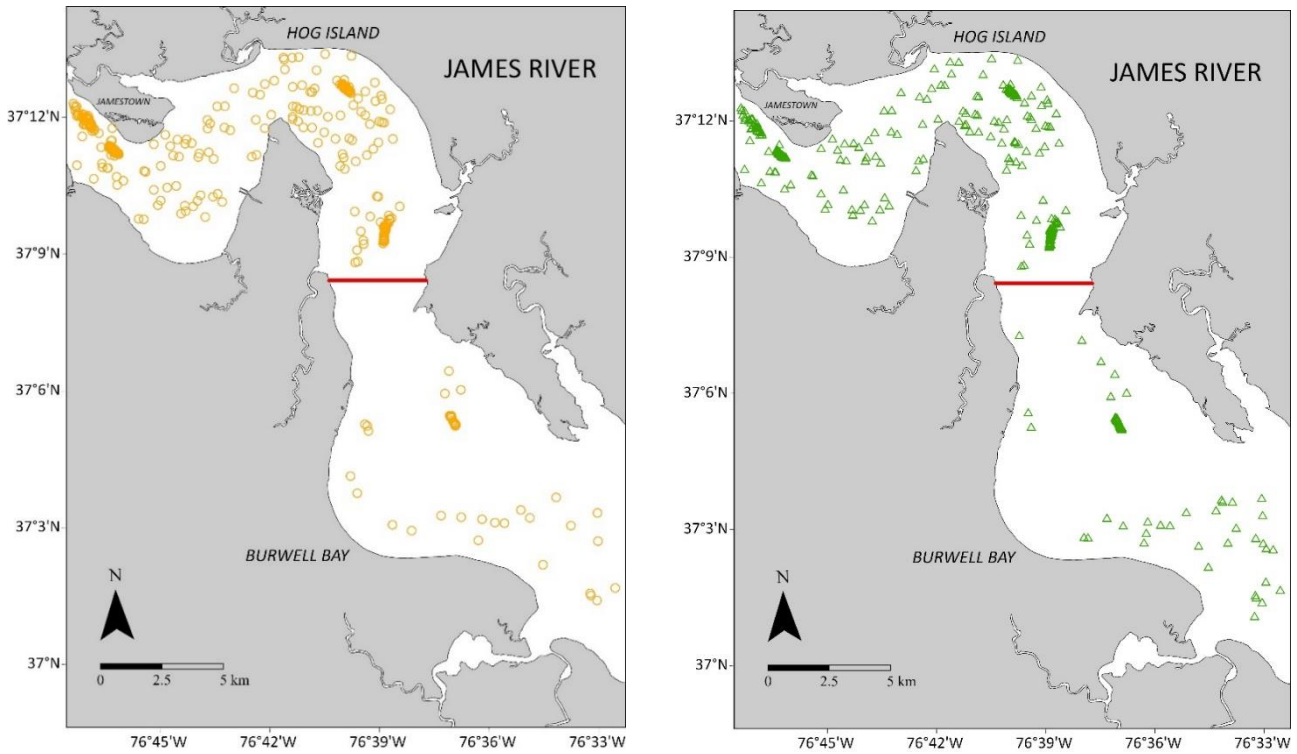


Figure 3. Location of trawl stations (open triangles; N = 522) sampled by the VIMS Juvenile Fish Trawl Survey in Hog Island and Burwell Bay in the lower James River, VA, from 2016 to 2020. Division of the study area intra two strata is indicated by the red line.

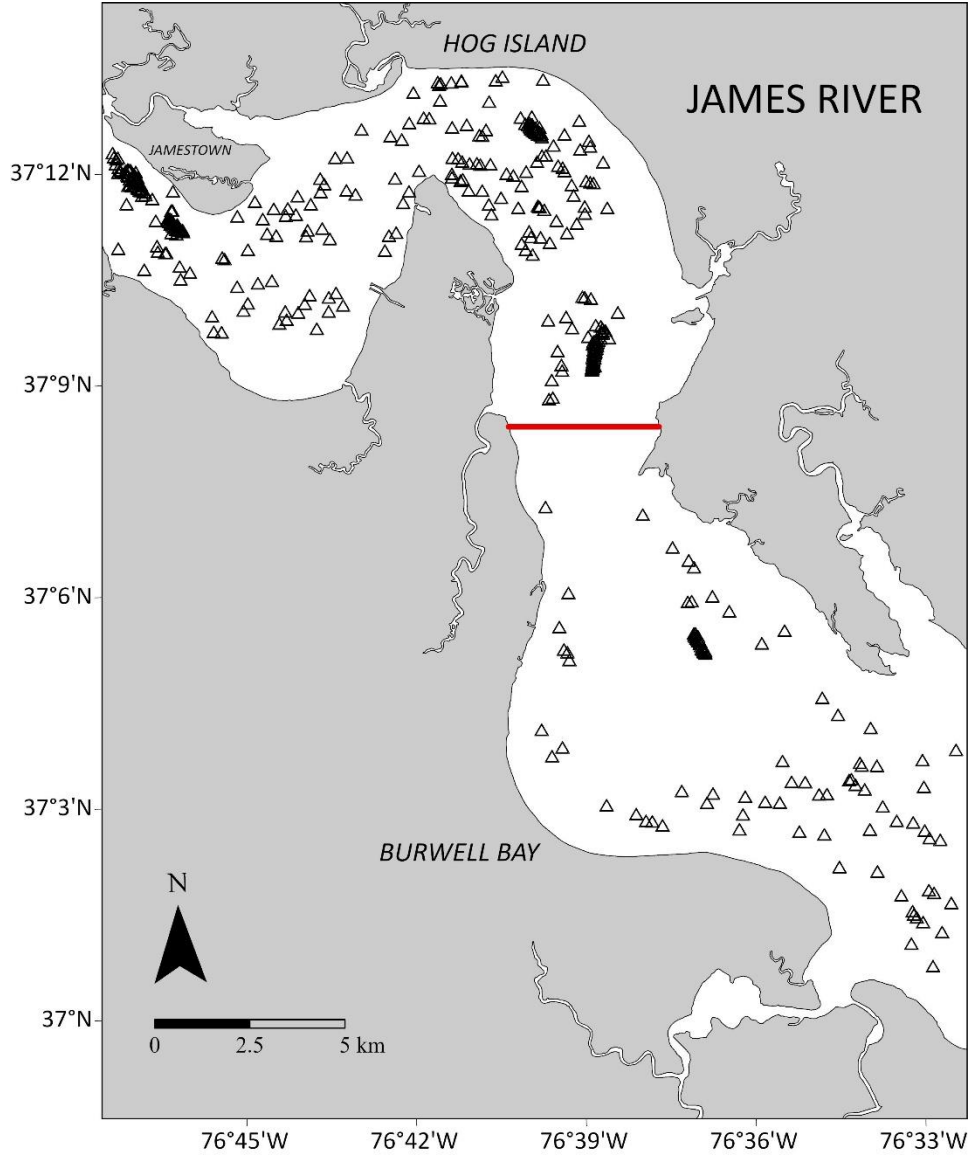


Figure 4. Histogram of fork lengths (mm) of blue catfish that had no prey in their stomach (empty) and those that contained prey. Blue catfish that contained blue crabs in their stomachs are depicted in blue in the lower panel.

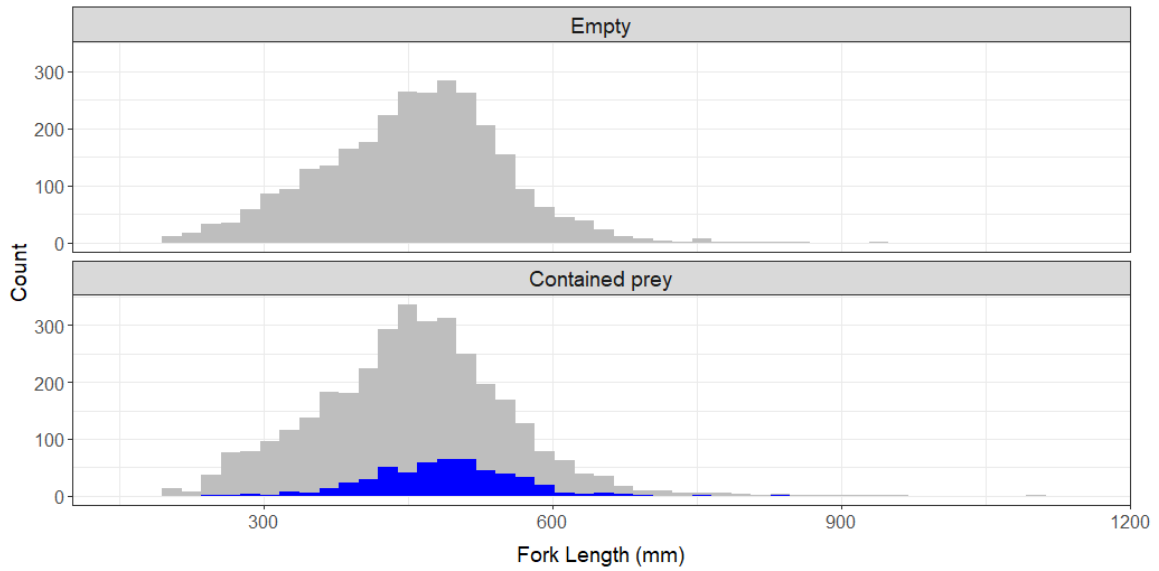
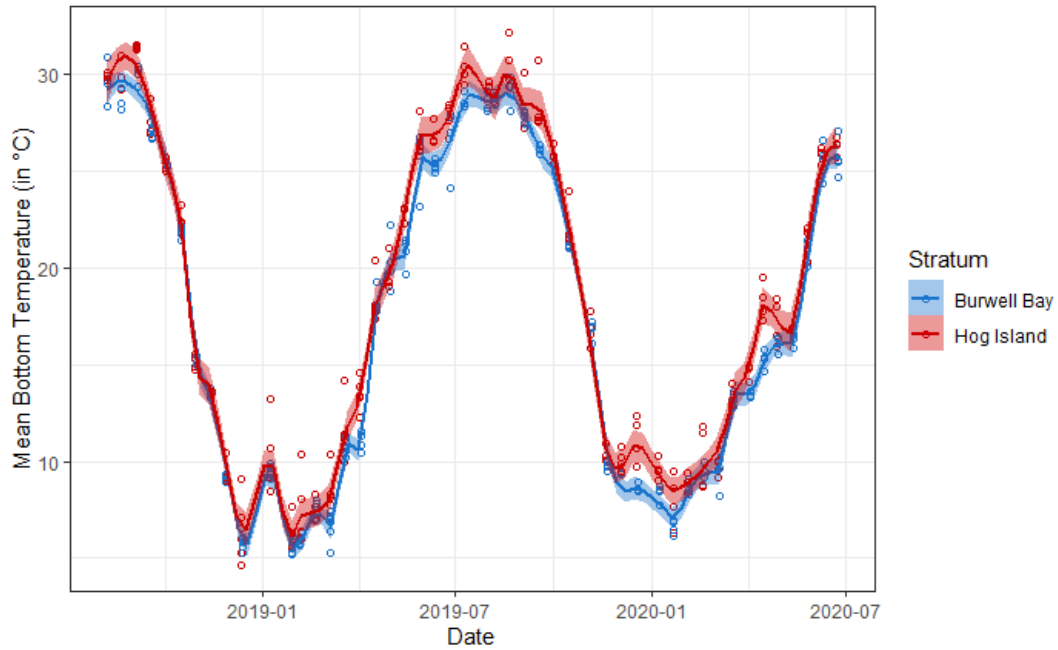


Figure 5. Mean bottom water temperature (°C) at Burwell Bay and Hog Island, August 2018 to June 2020; temperature was recorded hourly with Tidbit dataloggers attached to gillnets. (A) Loess fit to the mean temperature data (smoothing parameter = 0.1). (B) Boxplot of seasonal mean bottom water temperature.

(A)



(B)

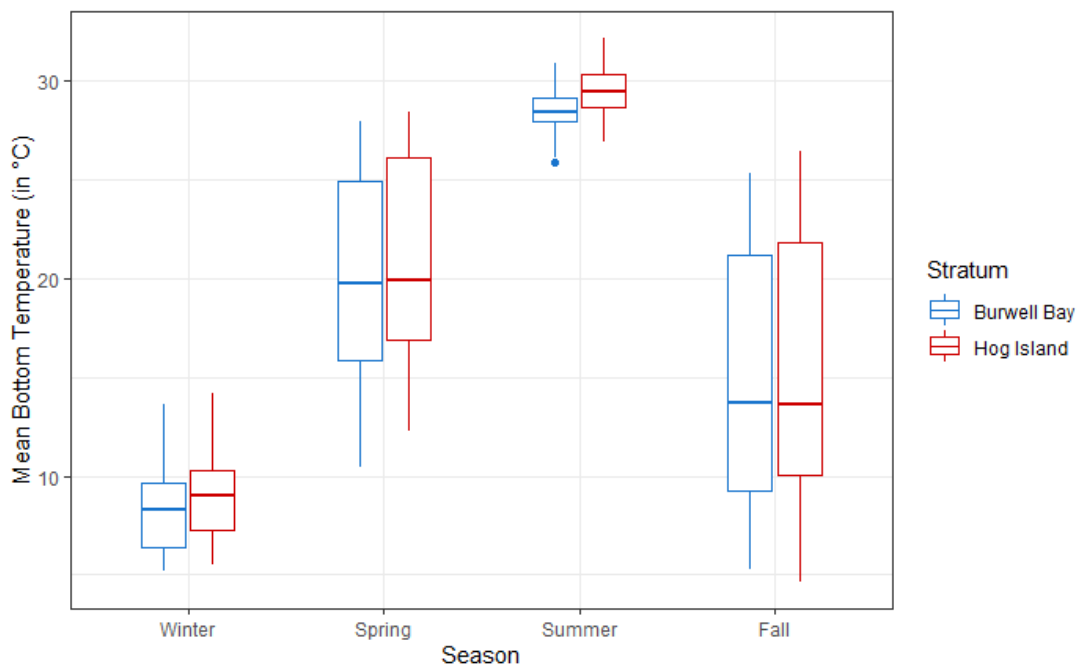
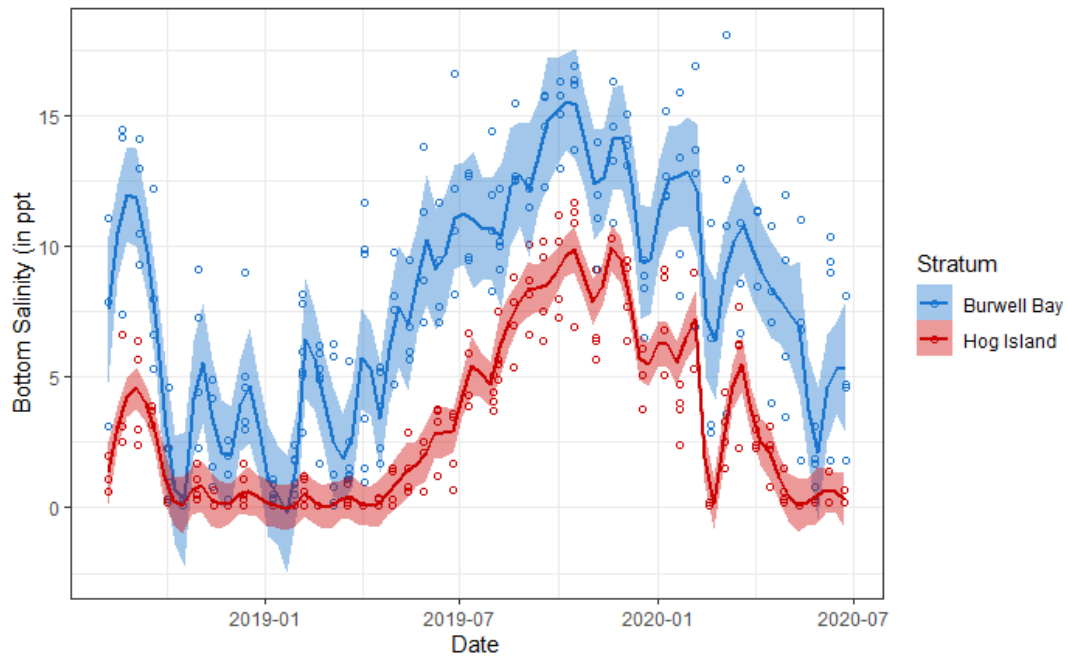


Figure 6. Bottom salinity (psu) for Burwell Bay and Hog Island, August 2018 to June 2020; salinity was recorded at the time of gillnet sampling via a YSI hand-held meter. (A) Loess fit to the data (smoothing parameter = 0.1). (B) Boxplot of seasonal means.

(A)



(B)

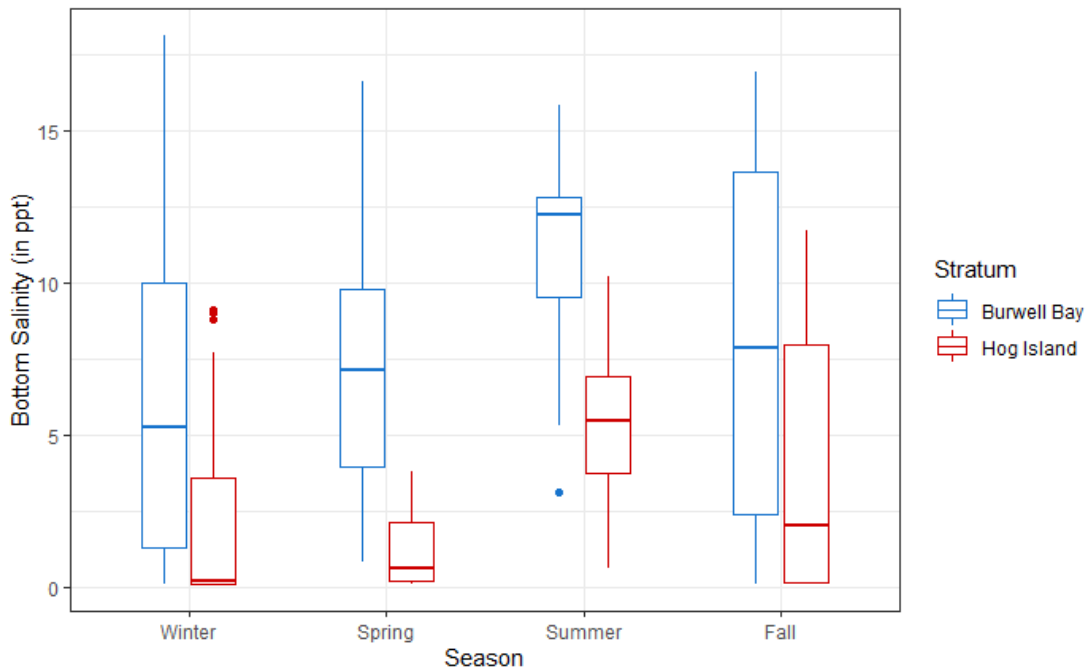


Figure 7. Boxplot of model-based estimates of the probability of observing prey (π_{fed}) in the stomach of blue catfish from Burwell Bay and Hog Island in the lower James River, August 2018 to June 2020. The mean probability associated with blue catfish from Burwell Bay is 0.646 (95% confidence interval: 0.593 – 0.695) and for blue catfish from Hog Island, the mean probability is 0.467 (95% confidence interval: 0.418 – 0.513); because the confidence intervals do not overlap, these differences are significant at the $\alpha=0.05$ level.

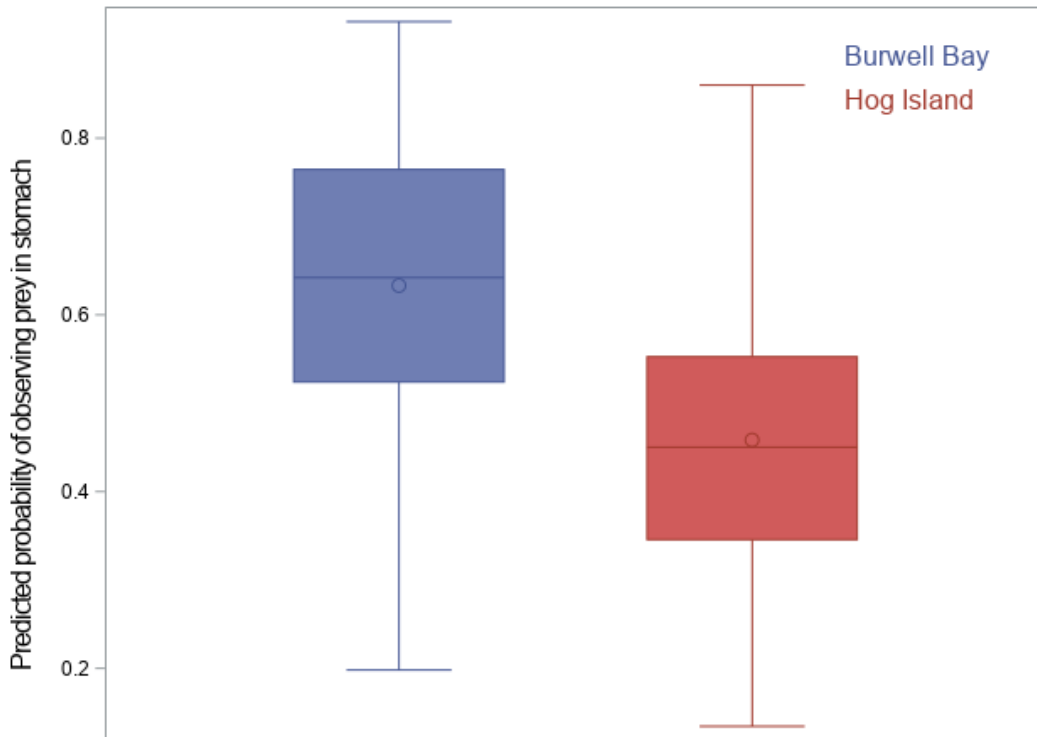


Figure 8. Predicted probability of observing prey in the stomach of blue catfish for a given mean bottom water temperature ($^{\circ}\text{C}$) in the lower James River, August 2018 to June 2020. Filled circles correspond with observations from individual fish; the line, a loess fit with a smoothing parameter of 0.25, depicts the general relationship between the probability of observing prey in the stomach and mean bottom water temperature.

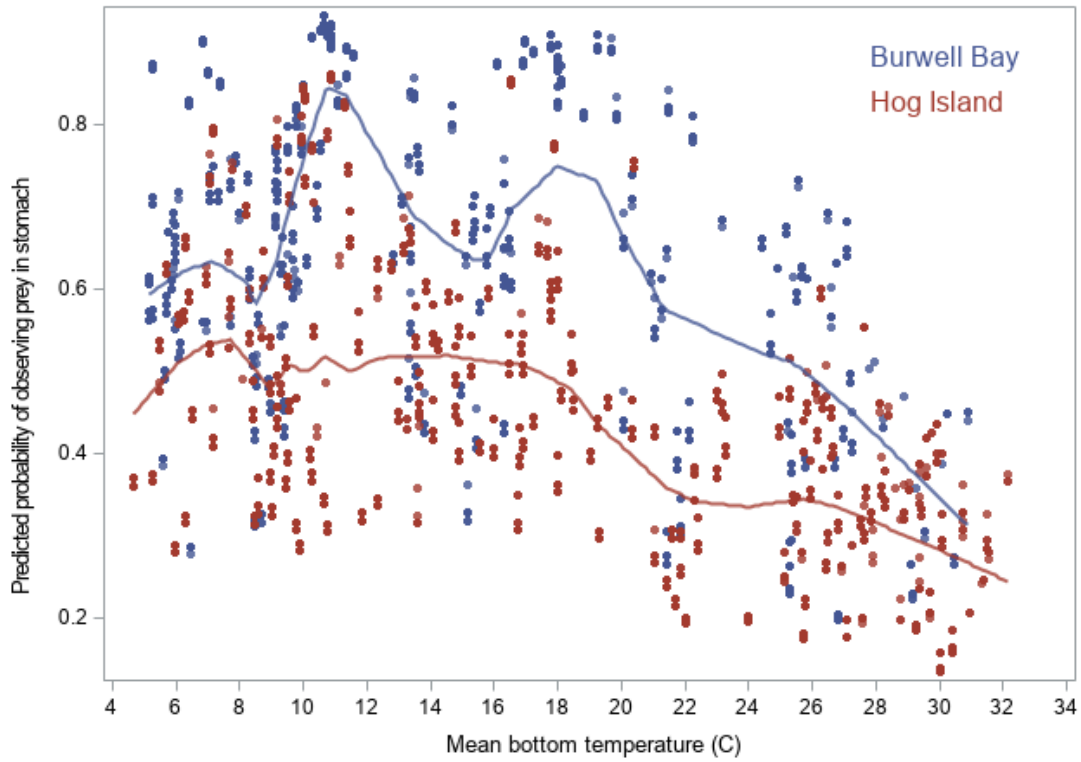
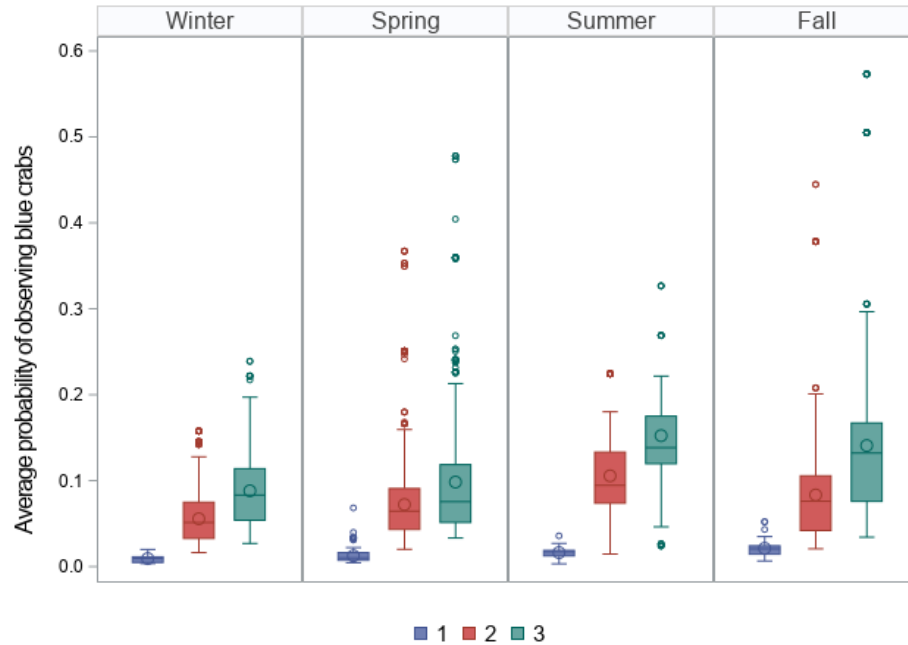


Figure 9. Predicted mean probabilities of observing blue crab in the stomach of blue catfish captured from the lower James River, August 2018 to June 2020. Probabilities are presented in a box plot for each (A) size class and season, (B) by stratum and season, and (C) across time. Blue catfish size classes are: (1) 200 – 300 mm fork length (FL), (2) 301 – 500 mm FL, and (3) \geq 501 mm FL.

(A)



(B)

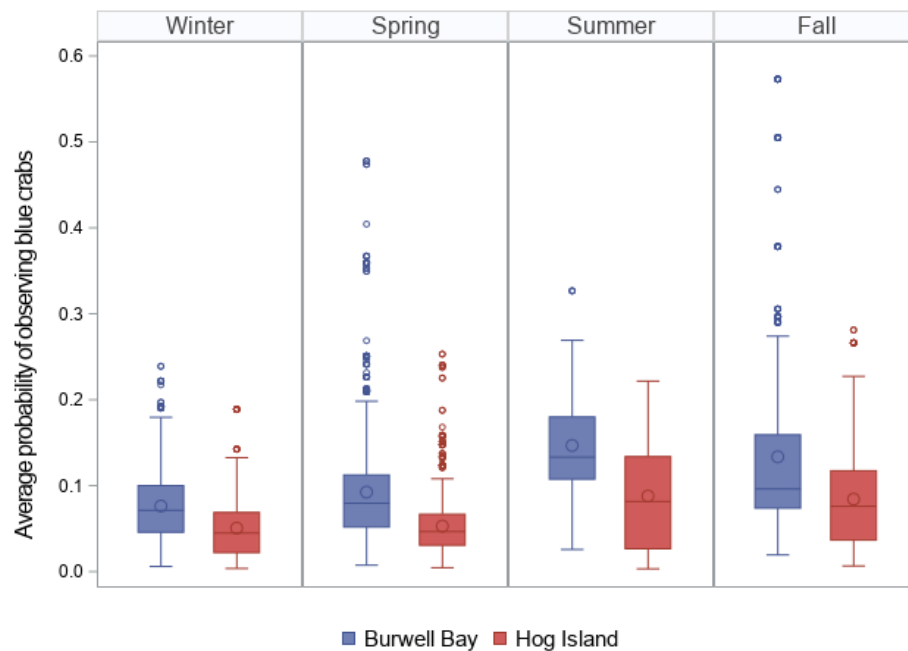


Figure 9, continued.

(C)

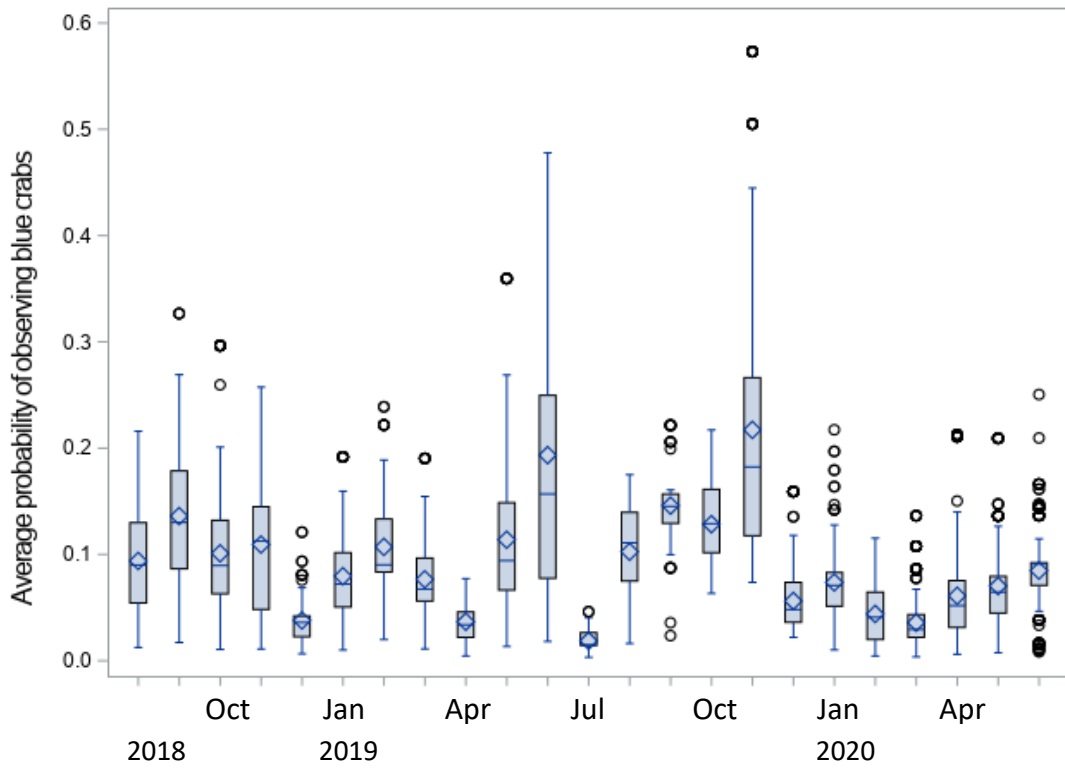


Figure 10. Estimated mean number of blue crabs consumed per day by stratum, blue catfish size, and season from the Poisson model. Blue catfish size classes are: (1) 200 – 300 mm fork length (FL), (2) 301 – 500 mm FL, and (3) ≥ 501 mm FL.

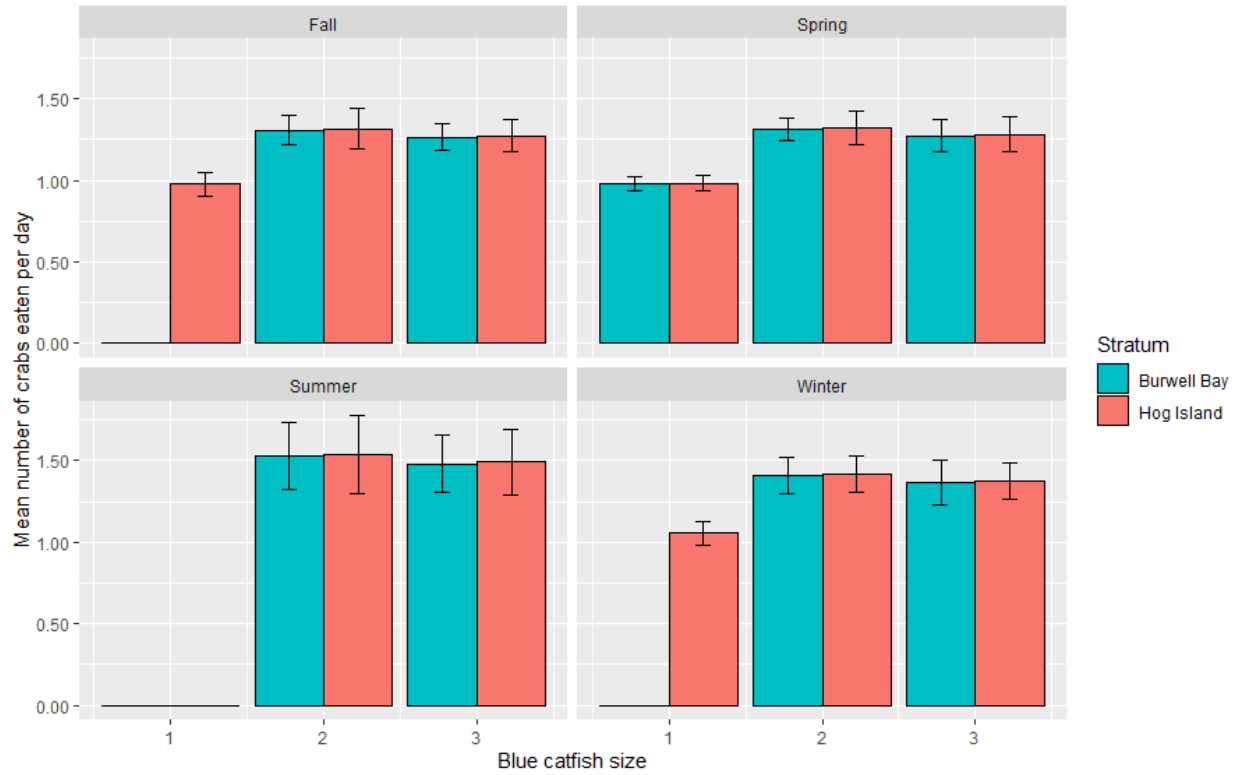


Figure 11. Annual number of blue catfish estimated from the VIMS trawl survey by stratum and season based on the catch of an average tow. Total numbers are based on observations from the VIMS Juvenile Fish Trawl Survey from 2016 to 2020 (and calculated using equations 15 and 16).

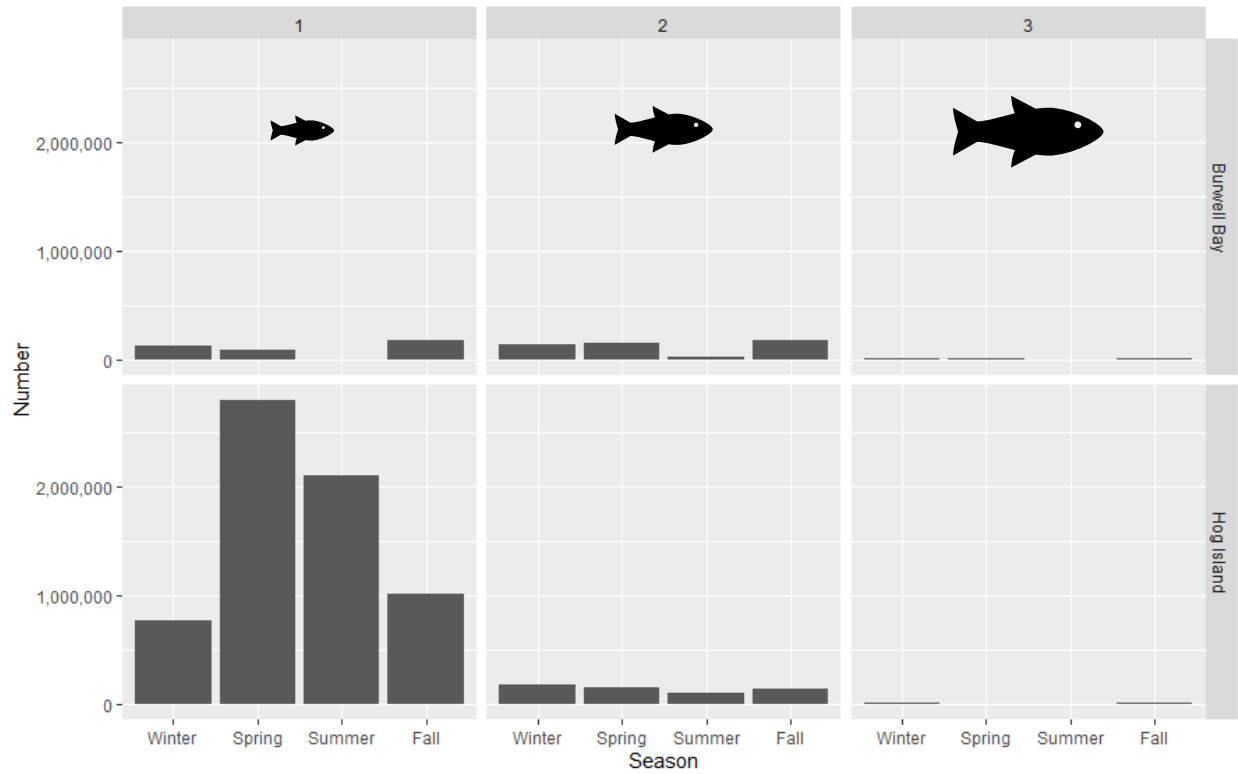


Figure 12. Size (carapace width, mm) frequency histogram of blue crabs observed in the stomachs of blue catfish captured in gillnets (red) during this study and blue crabs collected by the VIMS Juvenile Fish Trawl Survey (blue) between 2016 and 2020. Note that blue crabs less than 25 mm carapace width are not well sampled by the Trawl Survey. The data were binned by 5 mm size intervals.

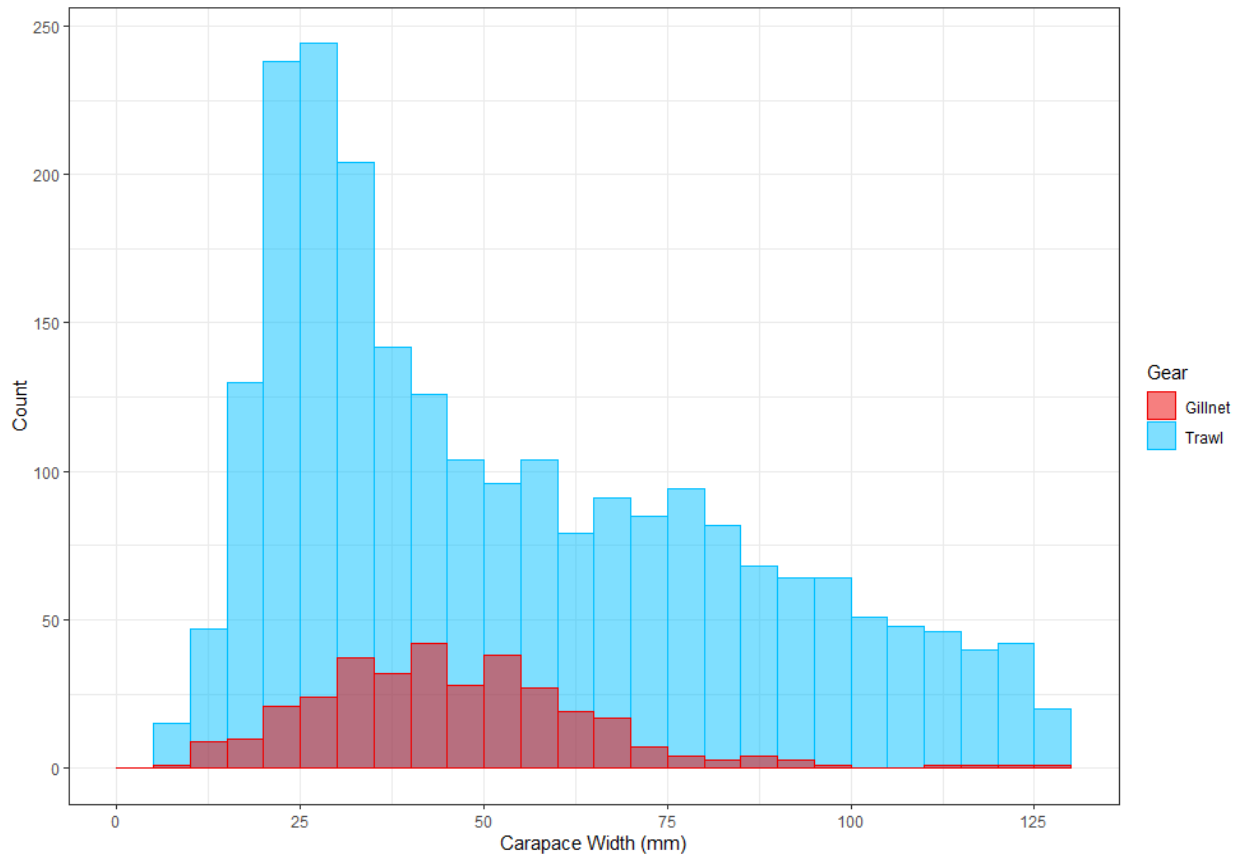


Figure 13. Seasonal percent occurrence (%O) for blue crabs, fishes, and other prey consumed by blue catfish in the lower James River between August 2018 to June 2020. Blue catfish size classes are: (1) 200 – 300 mm fork length (FL), (2) 301 – 500 mm FL, and (3) ≥ 501 mm FL.

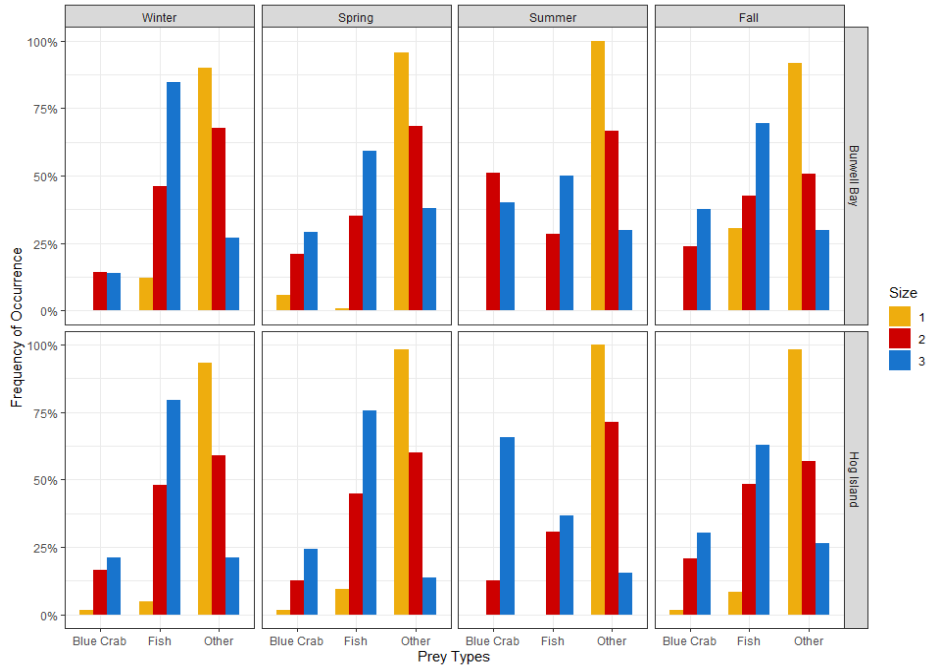


Figure 14. Seasonal percent by number (%N) for blue crabs, fishes, and other prey consumed by blue catfish in the lower James River between August 2018 to June 2020. Blue catfish size classes are: (1) 200 – 300 mm fork length (FL), (2) 301 – 500 mm FL, and (3) ≥ 501 mm FL.

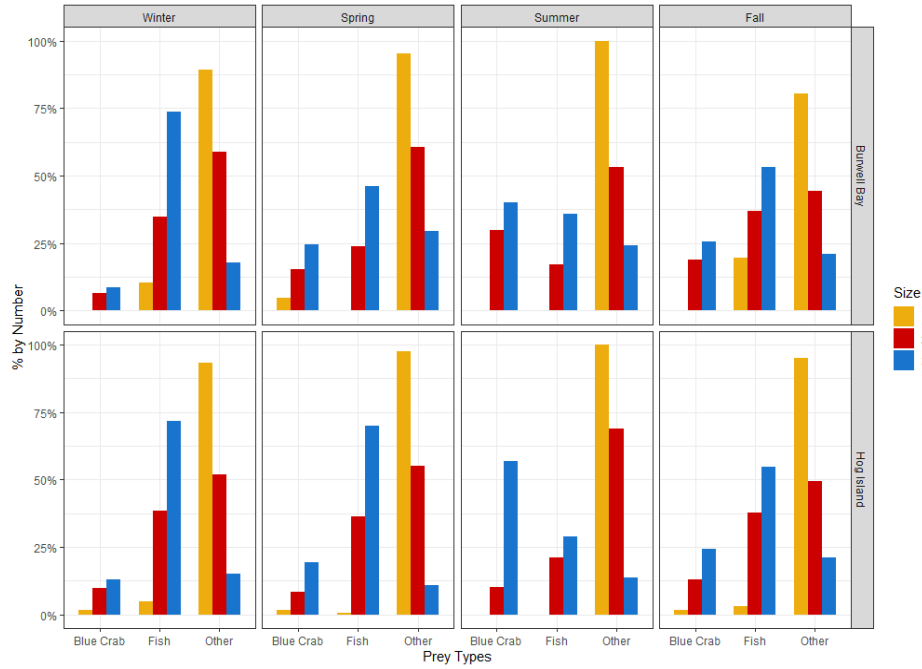


Figure 15. Seasonal percent by weight (%W) for blue crabs, fishes, and other prey consumed by blue catfish in the lower James River between August 2018 to June 2020. Blue catfish size classes are: (1) 200 – 300 mm fork length (FL), (2) 301 – 500 mm FL, and (3) \geq 501 mm FL.

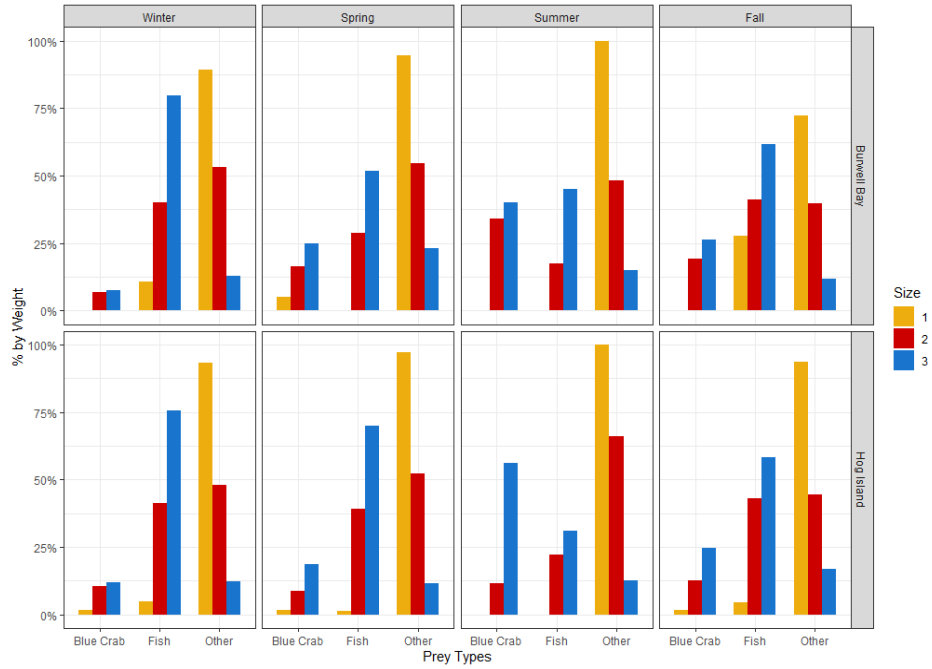


Figure 16. Seasonal prey-specific index of relative importance (PSIRI) for blue crabs, fishes, and other prey consumed by blue catfish in the lower James River between August 2018 and June 2020. Blue catfish size classes are: (1) 200 – 300 mm fork length (FL), (2) 301 – 500 mm FL, and (3) ≥ 501 mm FL.

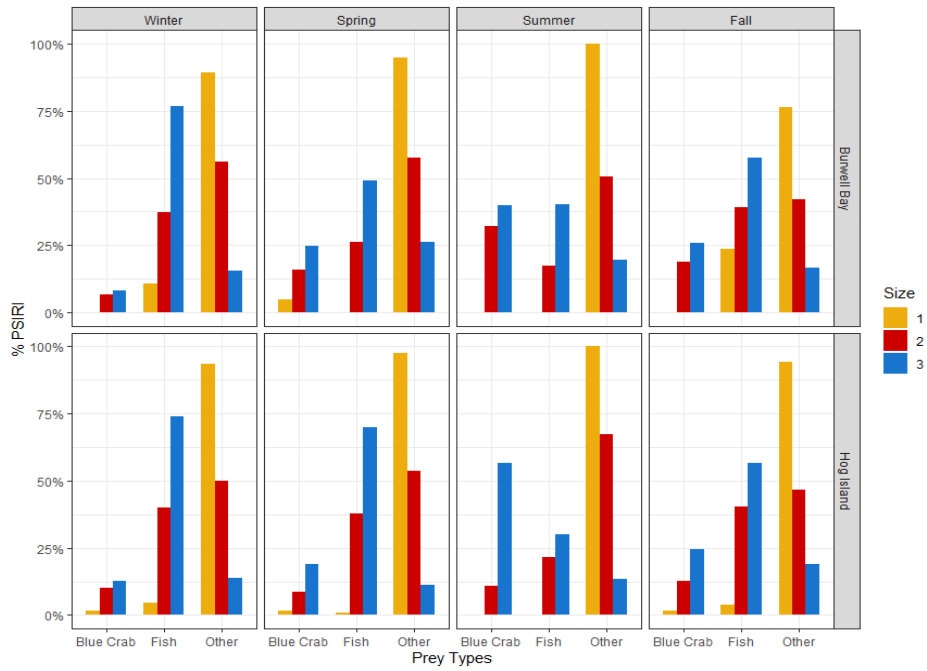


Figure 17. Estimates of seasonal prey selectivity (Chesson's α) \pm 1 standard error for three size classes of blue catfish from the lower James River, August 2018 to June 2020. The dotted line represents the value $1/m$, which indicates neutral selectivity; m is the number of prey types (in this case, 2: either blue crab [green symbol] or fish [yellow symbol]). Values above the line indicate prey was selected, and values below the line indicate the prey was not selected. Blue catfish size classes are: (1) 200 – 300 mm fork length (FL), (2) 301 – 500 mm FL, and (3) \geq 501 mm FL. Symbols are jittered for clarity.

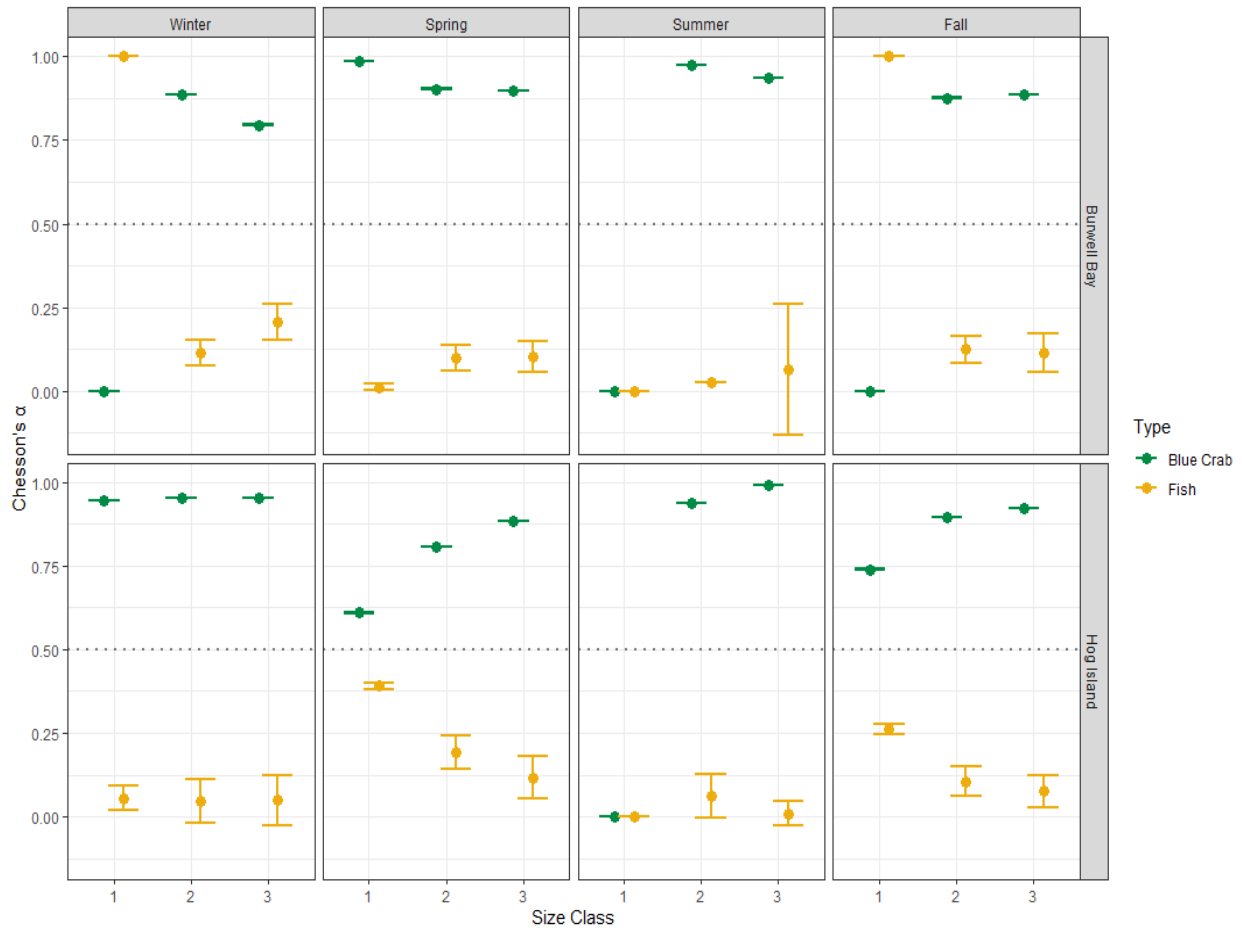


Figure 18. Electivity indices \pm 1 standard error for three size classes of blue catfish on blue crab (green symbols) and fish (yellow symbol) from the lower James River, August 2018 to June 2020; no other prey types were considered for this analysis. Positive values indicate prey was selected, and negative values indicate prey was not selected. The dotted line represents neutral selection. Blue catfish size classes are: (1) 200 – 300 mm fork length (FL), (2) 301 – 500 mm FL, and (3) \geq 501 mm FL. Symbols are jittered for clarity.

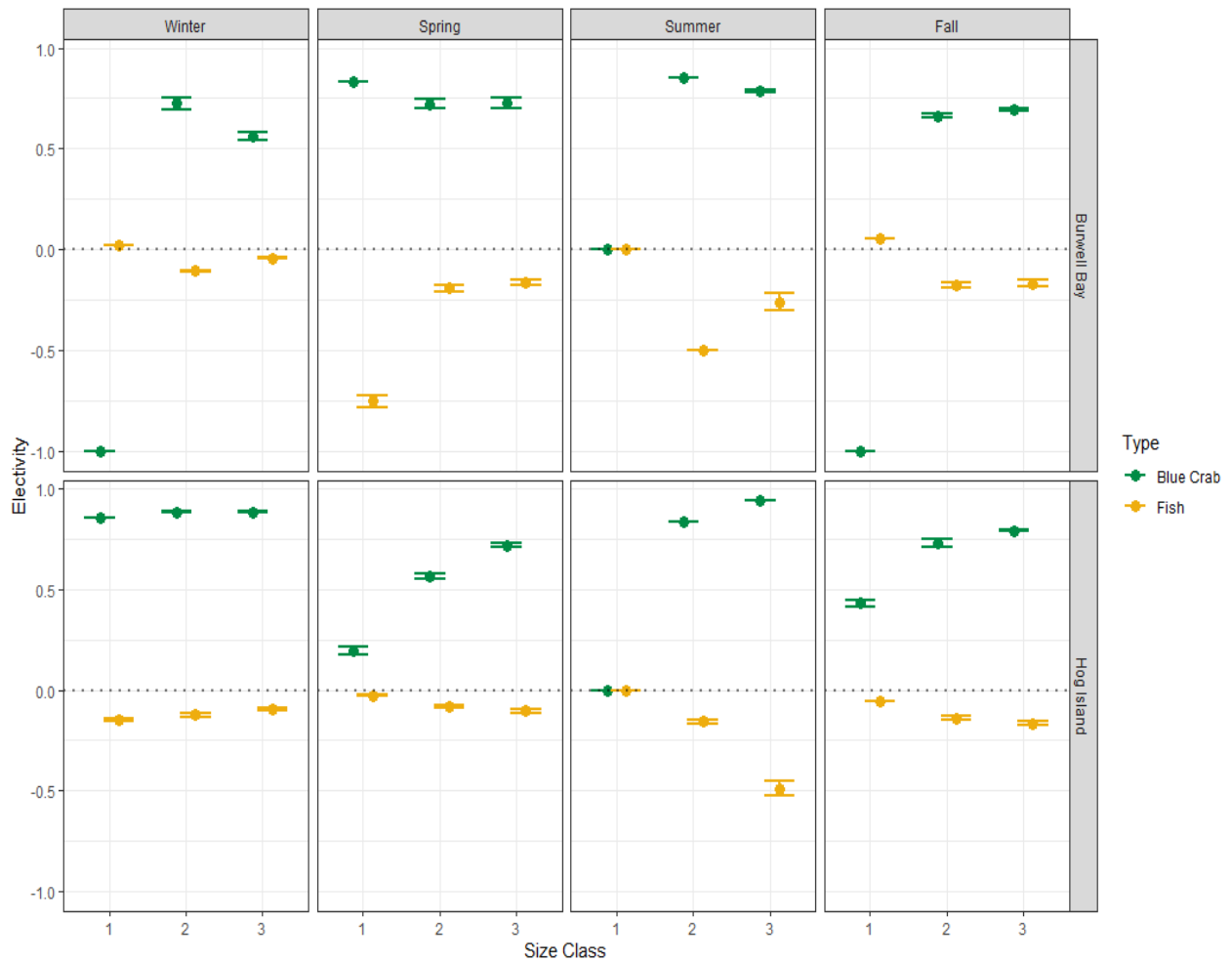


Figure 19. Estimated average total number (\pm one standard error) of blue crabs consumed by blue catfish in Burwell Bay and Hog Island (see Table 4 for values). Blue catfish size classes are: (1) 200 – 300 mm fork length (FL), (2) 301 – 500 mm FL, and (3) \geq 501 mm FL.

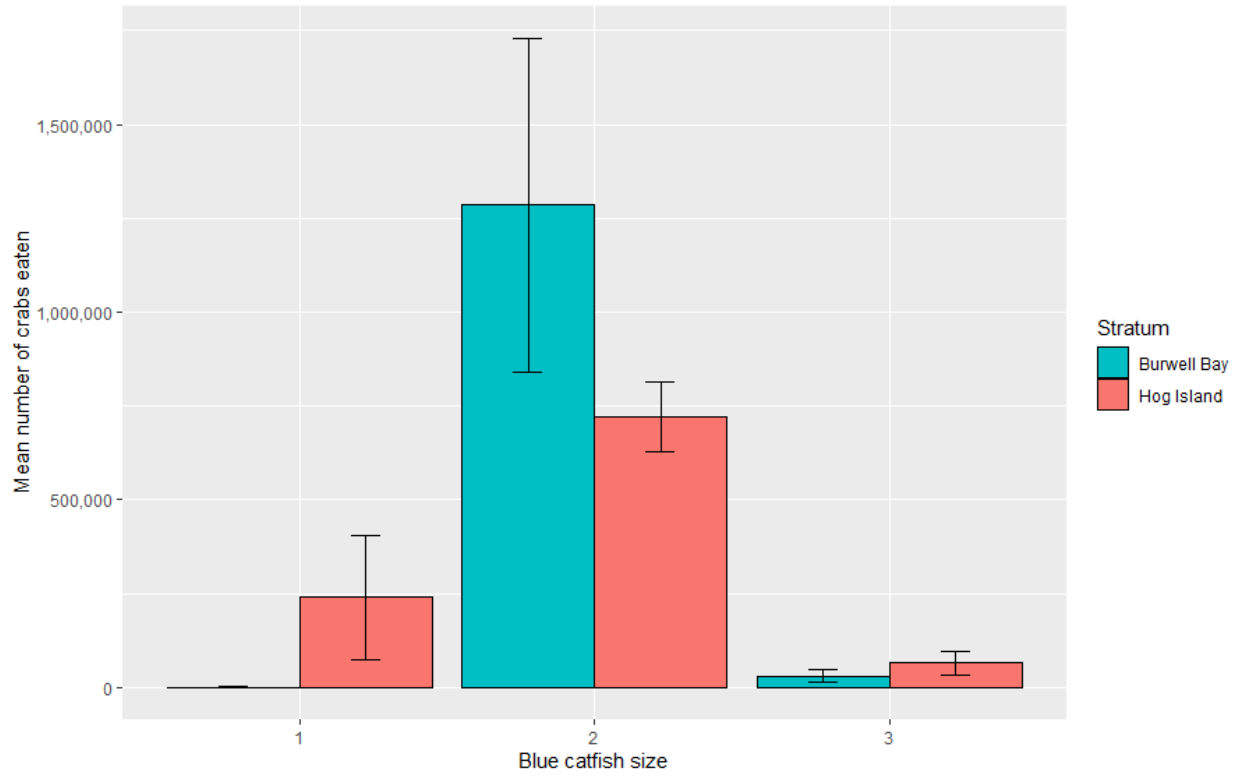
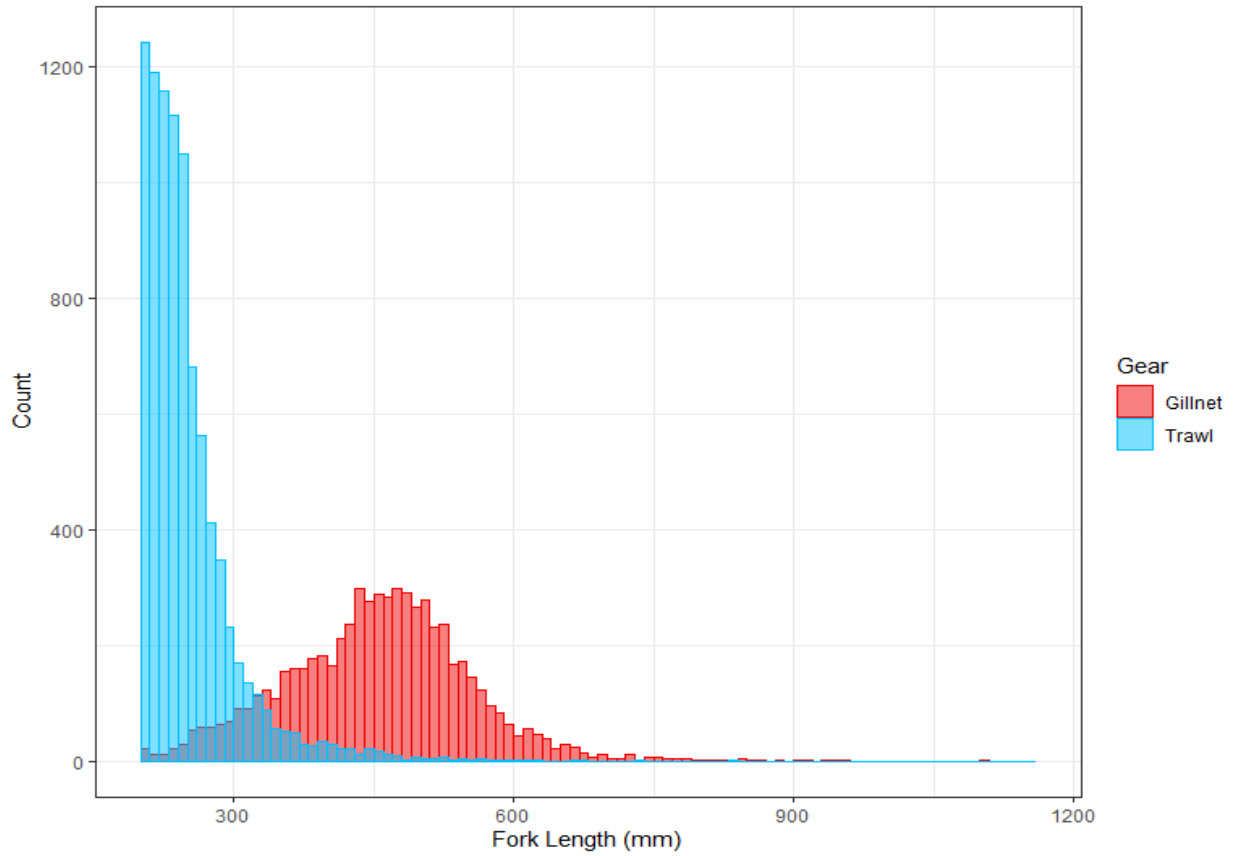


Figure 20. Size (fork length, mm) frequency histogram for blue catfish captured in gillnets from August 2018 to June 2020 (red) and by the VIMS Juvenile Fish Trawl Survey (blue) between 2016 and 2020. Only catfish greater than 200 mm FL are shown; the data were binned by 10 mm size intervals.



APPENDIX

Table A1. Estimated probabilities of observing prey (blue crabs, fish, or other) in the stomach of blue catfish captured from the lower James River, August 2018 to June 2020. The estimated probabilities are least-square means presented by stratum, size class, and month; also shown are the upper and lower 95% confidence intervals on the means. The hierarchical logistic model used to estimate the probabilities was based on 6,314 observations of blue catfish that were examined for stomach contents; about 54.1% (N = 3,418) of stomachs had prey, and the remainder (N = 2,896) were empty. The model accounted for the effect of cluster sampling (multiple fish captured in one net), and included the effect of mean bottom water temperature and bottom salinity in addition to stratum, size, and month.

		Mean probability of observing prey in stomach	Lower 95% confidence interval	Upper 95% confidence interval
Stratum				
	Burwell Bay	0.646	0.593	0.695
	Hog Island	0.467	0.418	0.516
Size (mm fork length)				
	200 – 300	0.586	0.518	0.651
	301 – 500	0.550	0.509	0.589
	≥ 501	0.539	0.495	0.582
Month				
2018	Aug	0.517	0.296	0.731
	Sep	0.487	0.304	0.674
	Oct	0.435	0.337	0.538
	Nov	0.431	0.313	0.558
	Dec	0.328	0.200	0.487
2019	Jan	0.469	0.336	0.607
	Feb	0.527	0.393	0.656
	Mar	0.752	0.640	0.837
	Apr	0.753	0.682	0.812
	May	0.717	0.604	0.808
	Jun	0.655	0.469	0.804
	Jul	0.357	0.142	0.650
	Aug	0.632	0.403	0.814
	Sep	0.620	0.381	0.812
	Oct	0.449	0.279	0.631
	Nov	0.820	0.727	0.886
	Dec	0.357	0.261	0.465
2020	Jan	0.383	0.274	0.505
	Feb	0.562	0.452	0.666
	Mar	0.668	0.574	0.750
	Apr	0.609	0.537	0.676
	May	0.537	0.433	0.637
	Jun	0.652	0.508	0.773

Table A2. Estimated probabilities of observing blue crab in the stomach of blue catfish captured from the lower James River, August 2018 to June 2020. The estimated probabilities are least-square means presented by stratum, size class, and month; also shown are the upper and lower 95% confidence intervals on the means. The hierarchical logistic model used to estimate the probabilities was based on 3,418 observations of blue catfish that had prey in their stomach; about 15.4% (N = 527) of stomachs contained blue crabs, and the remainder (N = 2,891) contained other prey. The model accounted for the effect of cluster sampling (multiple fish captured in one net), and included the effect of mean bottom water temperature and bottom salinity in addition to stratum, size, and month.

		Mean probability of observing blue crabs in stomach	Lower 95% confidence interval	Upper 95% confidence interval
Stratum				
Burwell Bay		0.064	0.044	0.092
Hog Island		0.038	0.026	0.054
Size (mm fork length)				
200 – 300		0.016	0.007	0.035
301 – 500		0.067	0.054	0.084
≥ 501		0.108	0.086	0.134
Month				
2018	Aug	0.053	0.016	0.168
	Sep	0.066	0.025	0.164
	Oct	0.062	0.035	0.107
	Nov	0.078	0.040	0.147
	Dec	0.028	0.010	0.080
2019	Jan	0.051	0.024	0.108
	Feb	0.068	0.033	0.133
	Mar	0.046	0.022	0.091
	Apr	0.023	0.013	0.042
	May	0.059	0.031	0.111
	Jun	0.130	0.054	0.281
	Jul	0.013	0.001	0.113
	Aug	0.066	0.019	0.205
	Sep	0.084	0.026	0.242
	Oct	0.072	0.029	0.166
	Nov	0.126	0.072	0.209
	Dec	0.034	0.018	0.065
2020	Jan	0.057	0.029	0.108
	Feb	0.028	0.014	0.053
	Mar	0.021	0.011	0.040
	Apr	0.038	0.024	0.059
	May	0.039	0.021	0.070
	Jun	0.047	0.021	0.101

Table A3. Estimated mean and standard error (SE) of the number of blue crabs consumed per blue catfish per day by stratum, season, and blue catfish size class. Blue catfish were sampled from the lower James River between August 2018 and June 2020. Blue catfish size classes are: (1) 200 – 300 mm fork length (FL), (2) 301 – 500 mm FL, and (3) \geq 501 mm FL.

Stratum	Season	Size	Mean	SE
Burwell Bay	Winter	1	0	0
Burwell Bay	Spring	1	0.98	0.04
Burwell Bay	Summer	1	0	0
Burwell Bay	Fall	1	0	0
Burwell Bay	Winter	2	0	0
Burwell Bay	Spring	2	1.32	0.07
Burwell Bay	Summer	2	1.56	0.22
Burwell Bay	Fall	2	1.31	0.09
Burwell Bay	Winter	3	1.37	0.14
Burwell Bay	Spring	3	1.28	0.10
Burwell Bay	Summer	3	1.51	0.19
Burwell Bay	Fall	3	1.27	0.09
Hog Island	Winter	1	1.06	0.07
Hog Island	Spring	1	0.99	0.05
Hog Island	Summer	1	0	0
Hog Island	Fall	1	0.98	0.08
Hog Island	Winter	2	1.43	0.11
Hog Island	Spring	2	1.33	0.11
Hog Island	Summer	2	1.57	0.26
Hog Island	Fall	2	1.32	0.13
Hog Island	Winter	3	1.38	0.12
Hog Island	Spring	3	1.29	0.11
Hog Island	Summer	3	1.52	0.22
Hog Island	Fall	3	1.28	0.10

Table A4. Seasonal diet composition for blue catfish in the lower James River between August 2018 and June 2020. Blue catfish size classes are: (1) 200 – 300 mm fork length (FL), (2) 301 – 500 mm FL, and (3) \geq 501 mm FL; frequency of occurrence, %O; frequency by number, %N; frequency by weight, %W; and prey-specific index of relative importance, PSIRI.

Stratum	Season	Size	Prey Type	%O	%W	%N	PSIRI
Burwell Bay	Winter	1	Blue Crab	0.0	0.0	0.0	0.0
Burwell Bay	Winter	1	Fish	12.1	10.8	10.6	10.7
Burwell Bay	Winter	1	Other	90.0	89.2	89.4	89.3
Burwell Bay	Winter	2	Blue Crab	14.2	6.9	6.4	6.6
Burwell Bay	Winter	2	Fish	46.0	40.0	34.7	37.3
Burwell Bay	Winter	2	Other	67.6	53.2	58.9	56.1
Burwell Bay	Winter	3	Blue Crab	14.0	7.4	8.6	8.0
Burwell Bay	Winter	3	Fish	84.8	79.7	73.5	76.6
Burwell Bay	Winter	3	Other	27.0	12.9	17.9	15.4
Burwell Bay	Spring	1	Blue Crab	5.8	5.2	4.7	5.0
Burwell Bay	Spring	1	Fish	0.9	0.1	0.0	0.0
Burwell Bay	Spring	1	Other	95.7	94.7	95.3	95.0
Burwell Bay	Spring	2	Blue Crab	20.9	16.4	15.4	15.9
Burwell Bay	Spring	2	Fish	35.2	28.8	23.9	26.4
Burwell Bay	Spring	2	Other	68.3	54.8	60.7	57.7
Burwell Bay	Spring	3	Blue Crab	29.3	24.9	24.6	24.8
Burwell Bay	Spring	3	Fish	59.2	51.8	46.0	48.9
Burwell Bay	Spring	3	Other	38.0	23.2	29.3	26.3
Burwell Bay	Summer	1	Blue Crab	0.0	0.0	0.0	0.0
Burwell Bay	Summer	1	Fish	0.0	0.0	0.0	0.0
Burwell Bay	Summer	1	Other	100.0	100.0	100.0	100.0
Burwell Bay	Summer	2	Blue Crab	51.1	34.2	29.7	31.9
Burwell Bay	Summer	2	Fish	28.3	17.6	17.1	17.3
Burwell Bay	Summer	2	Other	66.7	48.2	53.2	50.7
Burwell Bay	Summer	3	Blue Crab	40.0	40.0	40.0	40.0
Burwell Bay	Summer	3	Fish	50.0	45.1	35.7	40.4
Burwell Bay	Summer	3	Other	30.0	14.9	24.3	19.6
Burwell Bay	Fall	1	Blue Crab	0.0	0.0	0.0	0.0
Burwell Bay	Fall	1	Fish	30.6	27.8	19.4	23.6
Burwell Bay	Fall	1	Other	91.7	72.2	80.6	76.4
Burwell Bay	Fall	2	Blue Crab	23.7	19.2	18.8	19.0
Burwell Bay	Fall	2	Fish	42.7	41.1	36.9	39.0
Burwell Bay	Fall	2	Other	50.8	39.7	44.3	42.0
Burwell Bay	Fall	3	Blue Crab	37.8	26.3	25.7	26.0
Burwell Bay	Fall	3	Fish	69.5	61.8	53.2	57.5

Burwell Bay	Fall	3	Other	29.9	11.9	21.1	16.5
Hog Island	Winter	1	Blue Crab	1.8	1.8	1.8	1.8
Hog Island	Winter	1	Fish	4.8	4.8	4.8	4.8
Hog Island	Winter	1	Other	93.5	93.5	93.5	93.5
Hog Island	Winter	2	Blue Crab	16.4	10.7	9.9	10.3
Hog Island	Winter	2	Fish	48.0	41.3	38.4	39.8
Hog Island	Winter	2	Other	59.0	48.0	51.8	49.9
Hog Island	Winter	3	Blue Crab	21.2	12.0	13.1	12.6
Hog Island	Winter	3	Fish	79.6	75.7	71.9	73.8
Hog Island	Winter	3	Other	21.0	12.3	15.0	13.7
Hog Island	Spring	1	Blue Crab	1.6	1.6	1.6	1.6
Hog Island	Spring	1	Fish	9.5	1.2	0.8	1.0
Hog Island	Spring	1	Other	98.4	97.2	97.6	97.4
Hog Island	Spring	2	Blue Crab	12.8	8.8	8.5	8.6
Hog Island	Spring	2	Fish	44.7	39.1	36.2	37.6
Hog Island	Spring	2	Other	60.0	52.2	55.3	53.7
Hog Island	Spring	3	Blue Crab	24.4	18.6	19.3	18.9
Hog Island	Spring	3	Fish	75.6	70.0	69.9	70.0
Hog Island	Spring	3	Other	13.6	11.4	10.7	11.1
Hog Island	Summer	1	Blue Crab	0.0	0.0	0.0	0.0
Hog Island	Summer	1	Fish	0.0	0.0	0.0	0.0
Hog Island	Summer	1	Other	100.0	100.0	100.0	100.0
Hog Island	Summer	2	Blue Crab	12.8	11.7	10.1	10.9
Hog Island	Summer	2	Fish	30.7	22.3	21.1	21.7
Hog Island	Summer	2	Other	71.5	66.0	68.8	67.4
Hog Island	Summer	3	Blue Crab	65.6	56.1	57.0	56.6
Hog Island	Summer	3	Fish	36.7	31.1	29.1	30.1
Hog Island	Summer	3	Other	15.6	12.8	13.9	13.3
Hog Island	Fall	1	Blue Crab	1.7	1.7	1.7	1.7
Hog Island	Fall	1	Fish	8.3	4.7	3.1	3.9
Hog Island	Fall	1	Other	98.3	93.6	95.2	94.4
Hog Island	Fall	2	Blue Crab	20.7	12.6	13.0	12.8
Hog Island	Fall	2	Fish	48.3	43.0	37.7	40.3
Hog Island	Fall	2	Other	56.7	44.3	49.3	46.8
Hog Island	Fall	3	Blue Crab	30.3	24.6	24.2	24.4
Hog Island	Fall	3	Fish	63.0	58.4	54.7	56.5
Hog Island	Fall	3	Other	26.5	17.0	21.0	19.0

Table A5. Blue catfish prey selection by stratum, season, type, and size class. Chesson values greater than 0.5 indicate prey were selected, whereas Chesson values less than 0.5 were not selected. Electivity values of -1, 0, and 1 indicate complete prey avoidance, random selection, and complete prey selection, respectively. Hyphens indicate catfish did not consume a prey type and therefore variances and standard errors were not estimable. Blue catfish size classes are: (1) 200-300 mm fork length (FL), (2) 301 – 500 mm FL, and (3) > 501 mm FL.

Stratum	Season	Type	Size	Chesson's α			Electivity		
				Estimate	Variance	Standard error	Estimate	Variance	Standard error
Burwell Bay	Fall	Blue Crab	1	0.000	0.000	0.000	-1.000	0.000	0.000
Burwell Bay	Fall	Fish	1	1.000	0.000	0.000	0.051	0.000	0.000
Burwell Bay	Fall	Blue Crab	2	0.876	0.009	0.002	0.662	0.011	0.002
Burwell Bay	Fall	Fish	2	0.124	0.242	0.040	-0.177	0.015	0.002
Burwell Bay	Fall	Blue Crab	3	0.886	0.003	0.001	0.693	0.009	0.002
Burwell Bay	Fall	Fish	3	0.114	0.331	0.058	-0.168	0.017	0.003
Burwell Bay	Spring	Blue Crab	1	0.987	0.000	0.000	0.833	0.000	0.000
Burwell Bay	Spring	Fish	1	0.013	0.044	0.009	-0.753	0.029	0.006
Burwell Bay	Spring	Blue Crab	2	0.902	0.013	0.002	0.722	0.025	0.003
Burwell Bay	Spring	Fish	2	0.098	0.278	0.037	-0.192	0.017	0.002
Burwell Bay	Spring	Blue Crab	3	0.897	0.009	0.001	0.727	0.028	0.004
Burwell Bay	Spring	Fish	3	0.103	0.316	0.046	-0.161	0.013	0.002
Burwell Bay	Summer	Blue Crab	1	0.000	-	-	0.000	-	-
Burwell Bay	Summer	Fish	1	0.000	-	-	0.000	-	-
Burwell Bay	Summer	Blue Crab	2	0.974	0.001	0.000	0.852	0.002	0.000
Burwell Bay	Summer	Fish	2	0.026	0.000	0.000	-0.497	0.000	0.000
Burwell Bay	Summer	Blue Crab	3	0.935	0.002	0.001	0.788	0.006	0.003
Burwell Bay	Summer	Fish	3	0.065	0.437	0.196	-0.261	0.041	0.019
Burwell Bay	Winter	Blue Crab	1	0.000	0.000	0.000	-1.000	0.000	0.000
Burwell Bay	Winter	Fish	1	1.000	0.000	0.000	0.022	0.000	0.000
Burwell Bay	Winter	Blue Crab	2	0.886	0.009	0.001	0.725	0.030	0.004
Burwell Bay	Winter	Fish	2	0.114	0.283	0.037	-0.107	0.005	0.001
Burwell Bay	Winter	Blue Crab	3	0.795	0.006	0.001	0.562	0.020	0.003
Burwell Bay	Winter	Fish	3	0.205	0.379	0.054	-0.042	0.002	0.000
Hog Island	Fall	Blue Crab	1	0.738	0.006	0.002	0.431	0.018	0.005
Hog Island	Fall	Fish	1	0.262	0.050	0.014	-0.057	0.001	0.000
Hog Island	Fall	Blue Crab	2	0.894	0.007	0.001	0.730	0.022	0.003
Hog Island	Fall	Fish	2	0.106	0.296	0.044	-0.138	0.009	0.001
Hog Island	Fall	Blue Crab	3	0.923	0.002	0.000	0.791	0.006	0.001
Hog Island	Fall	Fish	3	0.077	0.318	0.048	-0.165	0.012	0.002
Hog Island	Spring	Blue Crab	1	0.609	0.008	0.002	0.194	0.020	0.004
Hog Island	Spring	Fish	1	0.391	0.037	0.008	-0.026	0.001	0.000

Hog Island	Spring	Blue Crab	2	0.807	0.005	0.001	0.563	0.014	0.002
Hog Island	Spring	Fish	2	0.193	0.377	0.051	-0.079	0.007	0.001
Hog Island	Spring	Blue Crab	3	0.883	0.003	0.000	0.719	0.008	0.001
Hog Island	Spring	Fish	3	0.117	0.434	0.064	-0.105	0.008	0.001
Hog Island	Summer	Blue Crab	1	0.000	0.000	0.000	0.000	0.000	0.000
Hog Island	Summer	Fish	1	0.000	0.000	0.000	0.000	0.000	0.000
Hog Island	Summer	Blue Crab	2	0.938	0.001	0.000	0.834	0.002	0.001
Hog Island	Summer	Fish	2	0.062	0.320	0.067	-0.156	0.010	0.002
Hog Island	Summer	Blue Crab	3	0.990	0.000	0.000	0.942	0.000	0.000
Hog Island	Summer	Fish	3	0.010	0.140	0.036	-0.490	0.036	0.009
Hog Island	Winter	Blue Crab	1	0.945	0.000	0.000	0.855	0.001	0.000
Hog Island	Winter	Fish	1	0.055	0.137	0.037	-0.147	0.004	0.001
Hog Island	Winter	Blue Crab	2	0.954	0.001	0.000	0.883	0.002	0.000
Hog Island	Winter	Fish	2	0.046	0.455	0.065	-0.125	0.009	0.001
Hog Island	Winter	Blue Crab	3	0.951	0.001	0.000	0.883	0.005	0.001
Hog Island	Winter	Fish	3	0.049	0.533	0.074	-0.097	0.006	0.001