

## **Research** Article

# Black Carp *Mylopharyngodon piceus* (Richardson, 1846) Mouth Gape and Size Preference of a Bivalve Prey

## Patrick T. Kroboth D, Benjamin H. Stahlschmidt D, and Duane C. Chapman D

U.S. Geological Survey, Columbia Environmental Research Center, Columbia, MO 65201, USA

Correspondence should be addressed to Patrick T. Kroboth; pkroboth@usgs.gov

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Black carp Mylopharyngodon piceus (Richardson, 1846) have been widely used as biological control of snails in aquaculture and were imported to the United States in the 1970s and 1980s for this purpose. Prior research emphasizes the species' propensity to control gastropods, but since subsequent escape and establishment of black carp in portions of the Mississippi River Basin, concerns now focus on the numerous endangered and endemic bivalve species upon which black carp may predate. Black carp mouth gape may limit predation on larger bivalves, but bite force is also a factor. We used regression of fish length to mouth gape of wild-caught black carp and compared these results to tank forage size preference trials with bivalve prey Corbicula fluminea clams. Wild-caught black carp ranged from 429 to 1580 mm total length, a size range larger than measured in previous studies. Regression of fish length and mouth gape indicated greater variability among sizes, as expected from wild versus cultured populations. Clam consumption was size-dependent. Black carp commonly engulfed but did not consume the largest clams in tank feeding trials. Shell width was a better predictor of successful consumption than length or height. Predation was restricted at sizes less than the mouth gape of test black carp as observed by individuals engulfing but failing to consume prey. This result indicates that either bite force or the pharyngeal apparatus gape (i.e., the distance between the pharyngeal teeth and keratinous pad) limited successful crushing of engulfed shells. Bivalve predation by black carp is limited by both a fish's ability to engulf prey and the ability to fracture the shell of larger prey items that cannot be broken or swallowed whole. The results of this research may be used to assess potential prey sizes of wild black carp and anticipated effects of predation on bivalve communities.

## 1. Introduction

Freshwater mussels have experienced precipitous declines with both loss of species and reductions in abundance at the global, regional, and local scales [1]. Losses are attributed to documented stressors, such as habitat alteration, drought, non-native species, and over-harvest, with both direct and indirect effects [1]. Non-native and native species potential negative interactions with freshwater mussels include competition for food, space, or host fish; physical fouling; and predation [2].

Black carp *Mylopharyngodon piceus* (Richardson, 1846) have been widely used as biological control of snails in aquaculture [3–6] and were imported to the United States in the 1970s and 1980s for this purpose. These snails serve as

intermediate hosts for digenetic trematodes, which can kill fish or adversely affect their market value [7]. Black carp predation on snails has been studied extensively, including effects of gastropod prey shell size and thickness [8–11]. Because of a molluscivorous diet and large adult size, black carp are thought to be a threat to North America's diverse freshwater mussel assemblage [12], of which many taxa are imperiled [13].

Black carp are highly adapted for durophagy, possessing molariform pharyngeal teeth attached to robust, muscular, and jaw-like pharyngeal arches. Prey items are crushed between these teeth and a keratinous pad positioned at the base of the neurocranium [14]. Together, these structures compose the pharyngeal apparatus, which develops and changes in morphology over the first year of life until reaching the molariform morphology retained throughout adulthood [15]. During this first year, black carp transitions from a diet of zooplankton to chironomids and then finally to a benthic animal-based diet. Gidmark et al. [16] studied limitations of force exerted by the pharyngeal apparatus. The pharyngeal jaw is attached to the skull by five pairs of muscles and an unpaired median muscle directly connecting the two arches [14]. The pharyngeal apparatus exerts the greatest force at intermediate muscle lengths, suggesting that successful predation depends not only on shell thickness but distance between the keratinous pad and pharyngeal jaws [16].

He et al. [17] suggested that most freshwater mussel species are within the theoretical crushable range of black carp. However, limitations in foraging ability vary, and it is not known what size classes of bivalves may be vulnerable to black carp predation [18, 19]. Shelton et al. [18] suggested that mouth gape is the limiting factor for predation. Nico et al. [19] suggested that mouth gape, cleithral distance, or pharyngeal gape may be limitations of black carp predation. Building on prior models comparing fish length and mouth gape measurements from cultured black carp [18, 19], we compared the mouth gape of wild-caught black carp, exceeding total lengths of cultured fish used in prior studies, to assess mouth gape limitations. Most research has focused on black carp foraging upon gastropods or simulated prey [8-11, 16]. Porreca et al. [20] examined both gastropod and bivalve prey fed to age-0 and age-1 black carp, concluding that shell size and strength affect vulnerability to predation. Black carp struggled to consume Corbicula fluminea, which possessed the widest and thickest shells of tested species.

Corbicula fluminea or unidentified Corbicula spp. are reported diet items in the black carp native range of east Asia, where the species co-occur in several large river basins [19]. Corbicula fluminea (hereafter Corbicula) was originally documented on the west coast of the United States in the 1930s and is now the most widespread nonindigenous mollusk in North America, often co-occurring with native freshwater mussels [21]. In general, Corbicula possess a relatively heavy and inflated shell morphology compared to many native bivalves of similar size [22]. We address the following objectives with the goal of assessing large juvenile and adult black carp's ability to consume bivalve prey; (1) we compare the mouth gape and total length of wild black carp for the prediction of predation potential based on size, and (2) we test the foraging ability of large juvenile black carp on a size range of Corbicula. The results of this research may be used to assess potential prey sizes of wild black carp and anticipated effects of predation on bivalve communities.

#### 2. Methods

2.1. Mouth Gape and Length Comparison. We measured mouth gape as the external width of the premaxilla according to the methods described by Nico et al. [19] and Shelton et al. [18]. We measured total length (TL) as the length of the fish from the tip of the snout to the longest caudal fin lobe when the caudal fin is compressed dorsoventrally. Previous mouth gape and total length (TL)

relationships were reported from smaller sample sizes and length ranges of cultured black carp ([18], n = 80 from 120 to 500 mm TL; [19], n = 38, from 123 to 715 mm TL). We measured mouth gape and TL for wild-caught black carp (n = 683; TL 429–1607 mm) from throughout the species current range in the Mississippi River Basin [23]. Prior research indicates that most wild black carp in the Mississippi River Basin are naturally reproduced fish [24], thus should possess minimal potential morphological deformities as can occur in triploids [25]. We used a subsample of cultured diploid age-1 black carp (n = 40; TL 65–223 mm) from Keo Fish Farms (Lonoke, AR) to supplement sizes less than 400 mm TL, which are not commonly reported from the wild.

2.2. Feeding Experiments. We conducted feeding experiments at the U.S. Geological Survey Columbia Environmental Research Center (CERC) in Columbia, Missouri. We procured black carp ~550 mm total length from Keo Fish Farms and maintained indoors, with an initial diet of 4 mm extruded 400 and 450 sinking pellet fish food (Rangen Inc., Buhl, ID). Black carp were transitioned from pelletized food to a diet of *Corbicula* one month prior to testing to allow for adaptation to prey hardness based on the observations of Hung et al. [26]. We assessed black carp size preference for clams using nine 400-liter indoor tanks containing two black carp each. During the transition in diet, initial feeding attempts were unsuccessful with one fish in each tank. We added an additional black carp of similar size to each tank to stimulate competition and encourage feeding.

We recorded water temperature, dissolved oxygen, and pH from each tank with a YSI Professional Plus Multiparameter Instrument (YSI Incorporated, Yellow Springs, OH). A continuous flow of well water removed waste and provided a consistent clean water supply; the addition of compressed air through an air stone maintained dissolved oxygen. Staff were trained regularly and used standard operating procedures approved by the CERC Institutional Animal Care and Use Committee throughout testing, IACUC16-021. The dataset for this project has been archived by the U.S. Geological Survey [27].

We measured prey size preference by presenting four size classes of Corbicula to each pair of black carp. Size classes consisted of small (mean shell length 16.27 mm; sample standard deviation (SD) = 1.7, medium (22.37 mm;SD = 1.68), medium-large (26.46 mm; SD = 1.37), and large (32.38 mm; SD = 1.82). We collected *Corbicula* for this study from the population of Clear Creek in Columbia, MO. We placed a total of 16 clams in each tank including four clams of each size class. We recorded clam size as shell length, a standard method for mollusks [28], as well as shell width and shell height. We measured shell length as the greatest distance between the two valves in the posterior to anterior plane. We measured shell height as the distance from the umbo to the beak of the clam along the dorsal to ventral plane. We measured shell width as the greatest distance between the exterior of the two valves. We grouped clams into size classes and labeled with superficial markings of the periostracum to identify sizes in video observations but not compromise shell structure. GoPro Hero  $4^{R}$  cameras (GoPro, San Mateo, CA) were used to record activity in the tanks for three hours after the clams were added. Cameras recorded video at the mouth level of the fish and just below the water surface. After the first three hours, we removed the remaining clams and measured shell dimensions to identify initial survival. We then placed uneaten clams back into tanks, and 24 hours after the initial feeding, the remaining clams were measured and identified. We cross-referenced video observations of feeding attempts from the two cameras to enumerate the frequency of attempted feeding and successful feeding by size class during the first three-hour period.

2.3. Mouth Gape and Length Analysis. We compared total length and mouth gape by least squares regression with normality assessed prior to model fit by normal probability plots and homoscedasticity by residual plots. We measured model fit by coefficient of determination ( $R^2$ ). We compared the regression slope and intercept to the coefficients estimated by Nico et al. [19] and Shelton et al. [18] with individual paired *t*-tests. We ran all figures and statistics in R statistical software [29] with significance determined at the  $\alpha = 0.05$  level.

2.4. Feeding Preference Analysis. We compared total lengths and weights of black carp pairs among the nine treatment tanks using paired t-tests with the null hypothesis of no significant difference between the weight and length at the  $\alpha = 0.05$  level. We tested Pearson correlations for association among the measurements of shell length and shell width, shell length and shell height, and shell width and shell height. If measurements were correlated, then we ran individual logistic regression models of survival at 3- and 24-hours post-stocking of prey for each measurement. We tested model goodness of fit via the  $\chi^2$  method, comparing the  $\chi^2$ statistic for model deviance to that of the null model [30]. We compared models by change in Akaike Information Criterion scores ( $\Delta$  AIC) [31] for selection of the individually best-fitted model by timeframe. We interpreted selected model slopes by odds ratio, with probability of consumption reported for each of the size classes. We depicted the frequency of feeding attempts from video observations based on prey size in bar graphs and compared the variation in the frequency of observed feeding events among tanks and size classes by  $\chi^2$ . Tanks lacking observations or those without recorded video were excluded from the  $\chi^2$ .

#### 3. Results

3.1. Mouth Gape to Length Comparison. Measurements from wild black carp mouth gapes ranged from 15 to 106 mm and the aquaculture-origin black carp supplementing the smallest lengths had mouth gapes from 3 to 14 mm. The ratio between mouth gape and total length was normally distributed. Error variance was homoscedastic, aside from three residuals identified as potential outliers at 1580, 1130, and

1607 mm TL. These points were retained in the final regression, which possessed an  $R^2$  of 0.82 (Figure 1).

Mouth gape = 
$$0.0481 * \text{Total Length} - 2.048.$$
 (1)

The individual paired *t*-tests of slopes and intercepts of the regression fit by Nico et al. [19] significantly differed from our regression (P < 0.05). The model of Shelton et al. [18] and ours had similar slopes (P = 0.39), but differing intercepts (P < 0.05).

3.2. Feeding Experiments. Mean total length of the 18 black carp used in feeding experiments was 562 mm (SD = 24), and mean weight was 1538 g (SD = 208). Paired *t*-tests indicated similar length (P = 0.33) and weight (P = 0.42) of fish among tanks. Average water temperature among tanks was 17.14°C (SD = 0.15), dissolved oxygen was 7.50 mg/L (SD = 0.67), and pH was 7.85 (SD = 0.10).

Pearson's correlations for comparisons of shell length and shell width, shell length and shell height, and shell width and shell height were all 0.98 (P < 0.05), indicating high correlation among measurements, and thus, individual models were tested. The  $\chi^2$  comparisons of deviance to null model fits suggested individual model parameters were better predictors than null models. Shell width represented the best-fitted model over shell height and shell length (Table 1).

Shell width was the best predictor of consumption, with widths ranging from 7.75 to 22.73 mm. Odds of clam consumption decreased 78% with increasing shell width during the first three hours of feeding. At 24 hrs after feeding, odds of consumption decreased 41% with increasing shell width (Figure 2).

Shell length was the greatest dimension of each clam with a range of 12.31-37.69 mm. Odds of clam consumption decreased by 87% with increasing shell length during the first three hours of feeding. At 24 hrs after feeding, odds of consumption decreased 60% with increasing shell length (Figure 2). At mean shell lengths of each size class, 16.27 (small), 22.37 (medium), 26.46 (medium-large), and 32.38 mm (large), the probability of consumption for a clam was 73%, 53%, 39%, and 22%, respectively, after the first three hours. Probability of consumption for a clam was 100%, 98%, 83%, and 19%, for the respective small-large sizes after 24 hours. The change in the probability of consumption from 39 to 73% at three hours to near complete consumption of 83–100% at 24 hours for the small, medium, and medium-large size classes indicates successful predation within this timeframe, compared to unsuccessful predation of the large size class with consistent 19-22% consumption between 3 and 24 hours.

Videos were recorded among eight of the nine experimental tanks. Combined counts from these cameras of observed feeding in each tank during the first three hours indicated feeding events on small and medium clams were often successful, whereas medium-large and large clams were engulfed but then rejected. We observed from subsequent clam measurements at 24 hours, and most mediumlarge clams were successfully consumed, whereas most large



FIGURE 1: The regression of total length (TL) and mouth gape (MG) for black carp *Mylopharyngodon piceus* fitted from wild-caught fish in the species' current range of the Mississippi River Basin (solid line) and a subset of 40 black carp <400 mm TL of aquaculture origin because of limited wild collections in that size range. The extrapolated regression from Nico et al. [19] is plotted as a dotted line. The extrapolated regression from Shelton et al. [18] is plotted as a dashed line.

TABLE 1: Individual models of *Corbicula* clams survival at 3- and 24-hours after they were placed among nine tank treatments containing pairs of black carp *Mylopharyngodon piceus* and the subsequent coefficients and Akaike Information Criterion (AIC) scores.

Time interval	Model	Intercept	Coefficient	AIC	ΔΑΙΟ
3 hours	Survival~shell length	3.26	-0.14	180.7	0.2
	Survival~shell width	3.66	-0.25	180.5	0
	Survival~shell height	3.35	-0.16	180.6	0.1
24 hours	Survival~shell length	15.32	-0.52	81.5	1.8
	Survival~shell width	16.25	-0.89	79.7	0
	Survival~shell height	13.18	-0.51	89	9.3

clams were engulfed but then rejected. The inability to consume the largest size classes of clams resulted in numerous feeding attempts (Figure 3). Comparison of the frequency of black carp feeding attempts indicated a significant difference ( $\chi^2_{18} = 211.81$ , P < 0.01) among tanks and prey sizes.

#### 4. Discussion

We tested the foraging limitations of large juvenile black carp by first considering the traditional method of mouth gape as a limitation on predation, and second, by measuring size preference of a bivalve prey, *Corbicula*. We estimated the relationship of mouth gape to total length of wild-caught black carp, finding similarity to previous models [18, 19]. In tank experiments of size preference, predation was restricted at sizes less than the mouth gape of test black carp as observed by individuals engulfing but failing to consume prey. This result suggests that either bite force or the pharyngeal apparatus gape (i.e., the distance between the pharyngeal teeth and keratinous pad) limited successful shell crushing.

Our comparison of black carp mouth gape and total length resulted in similar estimated regression models to prior research [18, 19], with only the difference in slope between our model and Shelton et al. [18]. Similarity in intercepts can be attributed to our use of smaller aquaculture fish to supplement a lack of wild reports in the <400 mm TL sizes, which resulted in a similar intercept to previous models. These smaller fish had reduced variability, which may be attributed to aquaculture (<400 mm TL) versus wild (>400 mm TL) fish and expected differences in growth and condition among wild environments. Black carp mouth morphology changes during the transition between these sizes, from an initial terminal to later subterminal position, which appeared to occur between 100 and 200 mm TL from a later subset of aquaculture fish depicted in Figure 4. However, the process and culturing methods (indoor versus pond) may affect the timing and size of this change in morphology. Black carp teeth also change during the first year, shifting morphology to adapt to benthic mollusk-based diet [15]. This transition in mouth position and tooth morphology may influence anticipated mouth gape



FIGURE 2: Odds black carp *Mylopharyngodon piceus* consumed *Corbicula* clams among measurements of shell length (top row), shell height (middle row), and shell width (bottom row) fitted by logistic regression model at 3- (a) and 24-hours (b) postprey stocking.

estimates for smaller size classes. This observation may be less clear in Figure 1 due to the difference in scale as the fullsize range of black carp was measured, and in larger fish, the variability in morphology increases with size.

Our results may be used for the estimation of potential prey size with consideration of the depicted variability (Figure 1) in wild populations and that mouth gape is a relative predictor of potential prey. Estimating mouth gape based on the equation of Nico et al. [19], a 1 m TL fish would possess a mouth gape relative to 57 mm, and a 1.5 m fish would have an approximate gape of 84 mm. Similarly, according to Shelton et al. [18], mouth gape would be estimated at 49 mm (1 m TL) and 72 mm (1.5 m TL). Our estimates are less, at 46 mm (1 m TL) and 70 mm (1.5 m TL). The greatest effect on our model is the variability measured in the 500-1100 mm TL size classes in which most data are present. The variability and deviation of the largest observed specimens (1580 mm and 1607 mm TL with 106 mm mouth gape for both individuals) from the model estimates suggests that models should serve as a base estimate of anticipated mouth gape but not a definitive prediction of potential prey

at a relative size. Additionally, the pharyngeal apparatus, particularly the teeth of black carp, is known to adapt to prey hardness [26], and previously observed morphological plasticity among external characters including mouth gape of wild black carp [32] suggests that variability is to be expected at increasing sizes and among populations.

Measuring the *Corbicula* size preference of black carp, we found that fish were limited by prey size rather than mouth gape. Logistic regression results suggested shell width is a better indicator of consumption than shell length, though differences between the two models were minimal. Video observations documented numerous feeding attempts on large clams in which the clams were engulfed and rejected, whereas smaller-sized clams were typically successfully consumed. Abrasions on the exterior of unconsumed shells and the significance of the shell width model indicate either the carp produced insufficient bite force to crush shells, or the pharyngeal apparatus gape differs from mouth gape, providing another restriction on predation. The ridges present on the exterior of *Corbicula* shells may partially inhibit predation of larger individuals



FIGURE 3: Frequency of feeding attempts on *Corbicula* clams by pairs of black carp *Mylopharyngodon piceus*, enumerated by size class from GoPro Hero 4<sup>R</sup> camera recordings of fish activity within each tank during the first three hours in which prey were provided. No video was recorded in tank five, and no feeding was observed in tank two. Prey size classes consisted of small (mean shell length 16.27 mm), medium (22.37 mm), medium-large (26.46 mm), and large (32.38 mm).

by distributing force across the surface of the valve, breaking before the valve itself, and resulting in a loss of purchase on the shell. Additionally, the globose and inflated shell morphology of Corbicula may inhibit positioning of the shell. Gidmark et al. [16] reported optimum jaw bite forces occur at intermediate size prey and jaw-closing muscle lengths. Our larger engulfed prey items likely remained intact because black carp produced insufficient bite force to crush them. Test black carp were trained on a Corbicula diet prior to experiments, and test animals were larger than age-0 stages when the pharyngeal apparatus adapts to mollusk prey [15]; thus, these results represent limitations of the pharyngeal apparatus. Porreca et al. [20] found similar results, where black carp struggled to crush and consume Corbicula compared to native gastropod and mollusk taxa tested on age-0 and age-1 black carp, attributing prey survival to shell thickness and the strength and gape limitations of the pharyngeal apparatus.

Corbicula possess a globose and inflated shell morphology compared to most North American freshwater mussels. Native mussels range from being elliptically flattened shells to triangular or quadrate shells of variable thicknesses [28], and it is not clear how these shapes might affect limits on black carp prey size. He et al. [17] found most freshwater mussel species are within the theoretical crushable range of black carp, but this range was determined from ceramic tubes intended to simulate prey. Much of the research pertaining to bite forces by black carp [16, 17] has used simulated prey, which may not be representative of natural shell morphologies. Furthermore, research would be needed to determine the actual predation potential of black carp dependent on shell morphology and thickness. Ortmann's law of stream position describes a clinal variation from compressed shells in small streams to inflated shell morphology within the same species in large rivers [28]. This suggests that a mussel species that may be less susceptible to predation by black carp within the currently described range



FIGURE 4: Changes in black carp *Mylopharyngodon piceus* with size depicting the transition from terminal to subterminal mouth position. Relative sizes range from <100 mm TL (a), <200 mm TL (b), and >350 mm TL (c). Images taken by Benjamin Stahlschmidt, U.S. Geological Survey.

in large rivers [23] may be more susceptible to predation in smaller streams and rivers where shells are less inflated (i.e., decreased width to length ratio). Thus, susceptibility to black carp predation may be related to the species general or population-specific shell morphology. Additionally, thinly shelled juveniles or slowly growing species may be more susceptible to predation or population-level effects.

Both Ben-Ami and Heller [8] and Hodgins et al. [33] reported the high feeding rates of small black carp. Hodgins et al. [33] suggested that even low densities of black carp can consume enough prey to affect small or fragmented mollusk populations. The tendency of black carp to consume numerous diet items of a single taxon was documented from wild populations within the species' distribution in the Mississippi River Basin by Poulton et al. [34], of which gastropods and bivalves were commonly consumed. Of the bivalves, a low incidence of Corbicula was reported among samples (<5% incidence among n = 109 diet samples) despite the high abundance and ubiquity of Corbicula in the current range of black carp [35]. One 941 mm TL fish consumed at least 30 Corbicula of similar size, which is determined from shell fragments to be comparable to the smallest size classes examined in this study [27].

The diversity of bivalve species present among habitats occupied by black carp is still unknown, partially due to limited knowledge of black carp habitat and the species' expanding distribution in North America [23]. Variation in prey selection based on shell thickness or morphology of available bivalve prey is also unknown. Ben-Ami and Heller [8] note that black carp with a maximum size of 210 mm TL consumed gastropods with maximum shell sizes of 19 mm shell height (*Melanoides*) and 14 mm shell height (*Melanopsis*), suggesting that these fish were limited by the thickness of *Melanopsis* shells. Hung et al. [36] found that cultured black carp readily consumed *Thiarid* snail species, which possessed a smaller and thinner shell than other test species (Viviparidae). Viviparidae snails represented one of the most common gastropod taxa in wild black carp diets

from North American samples [34]. The relationships revealed in the current study suggest that larger inflated bivalve species might be less affected by black carp predation, at least for adults.

Black carp predation is limited at multiple steps. First, the fish needs to locate their prey. Ben-Ami and Heller [8] found variation in the consumption rate of black carp for gastropods at the surface and 2 cm below substrate over time, attributing this result to learned behavior as the fish developed a search image for their prey. Porreca et al. [20] observed similar foraging efficiency as age-0 and age-1 black carp consistently sampled the substrate in search of buried prey, repeatedly sampling stones within the substrate that resembled mollusks. Next, prey have to be captured and pass through the fish's mouth gape. A fish may only capture prey small enough to be engulfed by the protruded mouth [37]. Our model had lower estimates of mouth gape than prior efforts with smaller aquaculture fish but may be used for the estimation of base potential bivalve prev sizes; because mouth gape is variable, estimates should not be considered definitive limits. Once engulfed, prey have to fit within the pharyngeal apparatus gape allowing enough force to crush the mollusk shell [16] or possess a thickness and shape that allows sections of the shell to be fractured and fragmented until the entire item can be broken and ingested. This fragmentation of prey was observed in Shelton et al. [18], Porreca et al. [20], and here with Corbicula, and may be a technique used to consume thinner shelled species not limited by black carp mouth gape, but by pharyngeal apparatus gape. We also observed black carp expelling a portion of the fragments of shells from the mouth after crushing prey. The ability to engulf, fracture, and reject portions or all of a prey item for additional manipulation and ingestion may assist consumption of oblong or nonuniformly shaped prey and minimize the inefficiencies that result from ingesting nondigestible portions of prey.

## 5. Conclusions

We found fish length and mouth gape measurements resulted in similar estimated regression models to prior research. Due to morphological plasticity in wild populations, models may serve as a base estimate of anticipated mouth gape but not a definitive prediction of potential prey at a relative size. None of the Corbicula in the size preference test exceeded the gape of the test black carp. In our feeding experiments, shell width was a better predictor of predation than the largest measurement, shell length. Bivalve prey consumption by black carp relative to the shell morphology of Corbicula is dependent on the fish's ability to locate, engulf, and exert enough force to break shells and ingest the prey. Furthermore, research would be needed to understand how the diverse shell morphologies of North American freshwater mussel species may limit or aid predation by black carp. The results of this research may be used to assess potential prey sizes of wild black carp and anticipated effects of predation on bivalve communities.

## **Data Availability**

The dataset for this project has been archived by the U.S. Geological Survey [27].

## **Conflicts of Interest**

The authors declare that there are no conflicts of interest regarding the publication of this article. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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