Transactions of the American Fisheries Society 147:1207–1214, 2018

ISSN: 0002-8487 print / 1548-8659 online
DOI: 10.1002/tafs.10117

ARTICLE

Vulnerability of Juvenile Bighead and Silver Carps to Predation by Largemouth Bass

Eric Sanft
Kaskaskia Biological Station, Illinois Natural History Survey, University of Illinois, 1235 CR 1000N Sullivan, Illinois 61951, USA; and Department of Natural Resources and Environmental Sciences, University of Illinois, Champaign, Illinois 61801, USA

Joseph J. Parkos III,* Scott F. Collins, and Anthony P. Porreca
Kaskaskia Biological Station, Illinois Natural History Survey, University of Illinois, 1235 CR 1000N Sullivan, Illinois 61951, USA

David H. Wahl
Kaskaskia Biological Station, Illinois Natural History Survey, University of Illinois, 1235 CR 1000N Sullivan, Illinois 61951, USA; and Department of Natural Resources and Environmental Sciences, University of Illinois, Champaign, Illinois 61801, USA

Abstract
The establishment of Bighead Carp *Hypophthalmichthys nobilis* and Silver Carp *H. molitrix* throughout the Mississippi River basin potentially expands the prey base for native predators. A mechanistic understanding of interactions between nonnative prey and native predators is needed to assess the potential for predator regulation of *Hypophthalmichthys* carp populations and impacts on native predator assemblages. We conducted a series of experiments to quantify the selectivity and efficiency of Largemouth Bass *Micropterus salmoides* predation on juveniles of both of these *Hypophthalmichthys* species and behaviors that potentially influence this selectivity and efficiency. Selectivity was measured over 24 h in 2-m-diameter pools containing one of two prey assemblages consisting of three individuals from each of three species: (1) Bighead Carp with native littoral (Bluegill *Lepomis macrochirus*) and pelagic prey (Golden Shiner *Notemigonus crysoleucas*) or (2) Bighead Carp, Silver Carp, and a morphologically similar native prey (Gizzard Shad *Dorosoma cepedianum*). Foraging efficiency and predator–prey behaviors were quantified in 45-min trials in which Largemouth Bass foraged on 10 individuals of a single prey species inside a 750-L observation tank. All prey species were readily attacked and consumed by Largemouth Bass; Silver Carp were selected less often than Gizzard Shad, and Bighead Carp were selected at a higher rate than any of the other prey species. Of the species tested, Bighead Carp formed the tightest schools and were captured most efficiently by Largemouth Bass. Overall, *Hypophthalmichthys* carps were similar to native prey in their vulnerability to Largemouth Bass; therefore, factors affecting *Hypophthalmichthys* carp availability relative to native prey may shape postinvasion predator–prey interactions.

Consumption of nonnative prey by native predators can influence the course of biological invasions and reshape the ecology and evolution of native predators (Carlsson et al. 2009; Alofs and Jackson 2014; Tablado et al. 2010). As novel prey, invasive organisms can subsidize native predator diets (Magoulick and Lewis 2002; Tablado et al. 2010), and when predation is sufficiently strong, native predators can limit the establishment and

*Corresponding author: parkos@illinois.edu
Received March 26, 2018; accepted August 25, 2018

population growth of invasive species (Alofs and Jackson 2014). A mechanistic understanding of predation on nonnative prey is needed to fully assess the potential for native predators to provide biotic resistance to biological invasions (e.g., Twardochleb et al. 2012). Understanding predator–prey interactions is equally important when nonnative species become hyperabundant and, therefore, unlikely to be regulated by predation mortality, because the ability and tendency to feed on these invaders may be crucial to the postinvasion success of native predators (Carlsson et al. 2009; Tablado et al. 2010; Saul and Jeschke 2015).

The successful establishment and subsequent dominance and expansion of Bighead Carp *Hypophthalmichthys nobilis* and Silver Carp *H. molitrix* populations in the USA is an example of a biological invasion where little is known about interactions with potential predators (Zhang et al. 2016; Lampo et al. 2017). Competition between *Hypophthalmichthys* populations and native planktivores (Kolar et al. 2007; Sampson et al. 2009; Collins and Wahl 2017; Nelson et al. 2017) could reorganize prey communities available to native piscivores. Previous assessments of interspecific interactions between *Hypophthalmichthys* carps and native fishes have focused on competition for limited prey resources (e.g., Kolar et al. 2007; Sampson et al. 2009; Nelson et al. 2017). Few studies have focused on the susceptibility of *Hypophthalmichthys* to predation (Negonovskaya 1980; Wolf and Phelps 2017), and none, to our knowledge, have quantified predator foraging efficiency for either Silver or Bighead carps. Because many piscivores are visual predators, similarities and differences in prey morphologies and behaviors likely affect the rates at which predators detect, attack, and capture prey (Green and Coté 2014; Hansen and Beauchamp 2014). Therefore, there is the potential that native predators in the United States will consume juvenile *Hypophthalmichthys* carps due to morphological and behavioral similarities to common native prey species (Kolar et al. 2007). Relative vulnerability of *Hypophthalmichthys* carps to predators in their invaded range will influence whether these abundant nonnative fishes supplement or decrease prey resources for native predators. What is needed is a behavioral assessment of the vulnerability of *Hypophthalmichthys* carps to native predation that addresses both selectivity and foraging efficiency.

Largemouth Bass *Micropterus salmoides*, a native piscivore found throughout the invaded ranges of Bighead Carp and Silver Carp in North America (Warren 2009; Farrington et al. 2017), is a model species that can be used to address behavioral aspects of *Hypophthalmichthys* vulnerability to native predation. Piscivory by Largemouth Bass has been well described, especially preferences and foraging efficiencies for native prey species that now coexist with Asian carp in the Mississippi River basin (Webb 1986; Hoyle and Keast 1987; Hambright 1991; Einfalt et al. 2015). These previous studies provide the basis for comparing the vulnerability of *Hypophthalmichthys* carps to Largemouth Bass predation relative to native prey species. Among fishes, predation is a size-structured interaction, in which most species are primarily vulnerable as juveniles (Werner and Hall 1988; Olson 1996). Similar to what has been found for Common Carp *Cyprinus carpio* (Bajer et al. 2012), any potential top-down regulation of *Hypophthalmichthys* populations or significant changes to predator ecology is most likely to emerge from the predation on vulnerable, early life stages.

We conducted feeding experiments under controlled environmental conditions to produce baseline assessments of *Hypophthalmichthys* vulnerability to Largemouth Bass predation relative to that of three native prey species. These experiments quantified prey vulnerability from the perspective of predator attack rate, capture efficiency, handling time, and selectivity. We assessed behavioral mechanisms that could affect the vulnerability of juvenile Bighead Carp and Silver Carp to Largemouth Bass predation relative to that of three native prey species: Bluegill *Lepomis macrochirus*, Golden Shiner *Notemigonus crysoleucas*, and Gizzard Shad *Dorosoma cepedianum*. Prey species were chosen to represent a wide range of morphologies and behaviors and are commonly found throughout the invaded range of Bighead Carp and Silver Carp (Koel and Sparks 2002; Sampson et al. 2009; McClelland et al. 2012). We quantified Largemouth Bass selectivity and foraging efficiency for different prey types, as well as predator foraging behaviors and prey antipredator behaviors that could cause differences in selection and efficiency. We hypothesized that differences in morphology and antipredator behaviors would determine the relative vulnerabilities of Bighead Carp, Silver Carp, Bluegill, Gizzard Shad, and Golden Shiner to Largemouth Bass.

Prey morphologies and behaviors, such as schooling and distance maintained from a predator, can affect capture efficiency and handling time, shaping prey vulnerability through predator selectivity and foraging rate (Green and Coté 2014; Einfalt et al. 2015). Sometimes, predators are more likely to select novel prey items from a mixture of familiar and unfamiliar prey (Mills et al. 1987). Under this scenario, Largemouth Bass would be predicted to have higher selection for nonnative prey. If nonnative species are preferred prey, they may also be attacked at higher rates and followed and pursued longer relative to native prey. Conversely, novel prey may have behaviors or morphologies that limit predator effectiveness (Saul and Jeschke 2015), leading to reduced predation efficiency when foraging for nonnative prey. Reduced foraging efficiency could emerge from long handling times and low capture efficiency for nonnative prey. Alternatively, the presence of close native analogs to juvenile *Hypophthalmichthys* morphology and behavior (e.g., Gizzard Shad; Kolar et al. 2007) may indicate Largemouth Bass have preexisting capabilities suitable for capturing invasive carp. The results of these experiments are intended to serve as baseline estimates of vulnerability for future work that would address environmental factors that could influence the vulnerability of *Hypophthalmichthys* carps to native predators.

METHODS

All experiments were conducted in a climate-controlled, indoor laboratory at the Kaskaskia Biological Station, Illinois Natural History Survey, Sullivan, Illinois. The laboratory had lighting programmed to a 12-h light : 12-h dark cycle. For all trials, water was maintained at 22°C, and dissolved oxygen levels ≥8 mg/L. Largemouth Bass, Bluegills, and Gizzard Shad were collected from local lakes, while Golden Shiners were obtained from a local hatchery. Largemouth Bass and Gizzard Shad were collected via boat electrofishing, while Bluegills were captured with beach seines. Bighead Carp and Silver Carp were purchased from a hatchery in Missouri. To ensure that fish used in trials were healthy and adjusted to the laboratory environment, all fish were acclimated for at least 1 month prior to the experiments (Einfalt and Wahl 1997). Prey fish ranged from 45 to 75 mm TL and Largemouth Bass ranged from 160 to 240 mm TL. Each trial matched Largemouth Bass with vulnerable-sized prey close to the predator's optimal prey size in terms of energetic gain (~30% of predator length: Hoyle and Keast 1987; Shoup and Wahl 2009). Largemouth Bass were maintained on a diet of Golden Shiners in the laboratory prior to the experiment. To minimize potential learning bias from the maintenance diet, Largemouth Bass were acclimated to each prey species by allowing them to feed on the prey for 24 h before the experimental trials.

Prey selection.— Prey selection experiments were conducted in 2-m-diameter, polyvinyl pools filled with water to a depth of 45 cm, with no structure added. Previous studies of selection have found that this experimental setting can accurately predict consumption under field conditions (Wahl and Stein 1988; Szendrey and Wahl 1995; Einfalt and Wahl 1997). Five individuals of three different prey species were placed in the tank for a total of 15 prey items. Because of concerns related to limited availability of some prey types and the potential for predator swamping (i.e., the fraction of prey captured that is reduced when prey abundance exceeds the number that a predator can capture and handle per unit time: Ims 1990), prey combinations were restricted to one of two-three-species groups. Prey combinations were designed to address either selection for Bighead Carp against a background of native littoral (Bluegill) and pelagic prey (Golden Shiner) or selection among morphologically similar native (Gizzard Shad) and nonnative (Bighead Carp and Silver Carp) prey species. After a 6-h acclimation period inside an opaque plastic container separated from the prey, an individual Largemouth Bass was released and allowed to forage for 24 h. One Bluegill–Golden Shiner–Bighead Carp trial was terminated early when five Bighead Carp were consumed after 16 h. This trial was halted early to prevent the consumption of more than five prey so as to not confound prey choice with availability (Einfalt and Wahl 1997; Shoup and Wahl 2009). At the end of each trial, fish were removed from the tank and the number of each prey species consumed was counted. A total of 20 different Largemouth Bass were tested once with each prey group in a randomized order.

Prey selection was calculated using Chesson's selectivity index applied to a situation where multiple prey types are offered and consumed individuals are not replaced (Chesson 1983):

$$\widehat{\alpha}_i = \frac{\log_e\left(\frac{n_{i0}-r_i}{n_{i0}}\right)}{\sum_{j=1}^{m}\log_e\left(\frac{n_{j0}-r_j}{n_{j0}}\right)},$$

where n_{i0} is the number of prey type i at the beginning of the experiment, r_i is the number of prey type i consumed by the predator, m is the number of different prey types, and α represents the relative preference for each prey species ranging from values of 0 (avoided) to 1 (strongly preferred). For each prey combination, the effect of prey identity on selection was tested using one-way ANOVA, and if significant, individual species were compared with a post hoc Tukey's mean-separation test. To account for the large number of zeros for some prey types, ANOVA models were constructed as generalized linear models fitted to an exponential distribution, the distribution that provided the best fit to the data.

Prey vulnerability.— Experiments designed to quantify behavioral mechanisms influencing vulnerability of prey to predators were conducted in a 750-L, rectangular, glass, observation tank (180 × 70 × 60 cm: Einfalt and Wahl 1997; Wahl and Stein 1988). The tank was divided with opaque plastic panels into two predator holding compartments (30 × 35 cm) and a foraging arena (150 × 70 cm), and the connection between the compartments was controlled by means of a remotely operated door. Ten individuals of one of the aforementioned prey species were placed in the foraging arena while a single Largemouth Bass was placed inside a predator holding compartment. Before each trial, all fish underwent a 24-h fasting period to standardize hunger and feeding motivation (Webb 1986) and were acclimated to the observation tank for 6 h. Following the acclimation period, the Largemouth Bass was allowed access to prey in the foraging arena by opening the remotely operated door. Trials lasted for 45 min after the introduction of the predator, and predation never was observed after 30 min. Twenty Largemouth Bass were tested once with each prey species, except for Gizzard Shad ($n = 15$) and Silver Carp ($n = 17$), which were tested with fewer Largemouth Bass due to the limited prey availability. To minimize learning bias, individual predators were tested with each prey species in a random order within a 2-week period.

Measurements of predator–prey behaviors were collected from digital video recordings of each trial. Video recordings were processed for frequency and time associated with each behavior using event-recording software (BeastPro 2005 version 2.01A; Windward Technology, Kaneohe, Hawaii). Measurements of distance from the predator and school size were based on a series of dashes spaced at 5-cm intervals on the foraging arena. During the 10-min period following the release of the predator, the number of schooling prey (three or more closely spaced individuals moving in a coordinated manner: Einfalt and Wahl 1997) and two-dimensional school sizes were recorded in 1-min intervals. Distance between the Largemouth Bass and the nearest prey was also recorded in 1-min intervals during the 10-min postrelease period. Time spent on the following mutually exclusive predator behaviors was recorded: follow (moving slowly while oriented towards prey), pursuit (following at burst speed), and handling (period between prey capture and complete ingestion: Einfalt et al. 2015). Attack rate (number of strikes per 45-min trial) and capture efficiency (ratio of total captures to total strikes per trial) were also measured for each trial.

Statistical tests focused on potential differences in Largemouth Bass predatory behavior and capture efficiencies while foraging for different prey species. Attack rate, handling time (min), follow time (min), pursuit time (min), distance from predator (cm), and school area (cm^2) were all transformed as $\ln(x + 1)$ values prior to analyses to meet the assumptions of ANOVA. Repeated-measures ANOVA models tested for an influence of prey species on each variable, with individual predators as the repeatedly sampled subject and degrees of freedom approximated with the Satterthwaite method due to unequal sample sizes across prey types. Variation in capture efficiency among prey types was analyzed with a logistic regression (GLIMMIX procedure; SAS version 9.4) with a random intercept (for each bass). Along with overall capture efficiency, potential differences in capture efficiency were also investigated for dispersed and schooled fish. For all analyses, when prey identity was significant ($P \leq 0.05$), t-tests on least-squares means were conducted to assess which species differed, with a Bonferroni adjustment for multiple comparisons (10 potential species comparisons = 0.005 critical value).

RESULTS

Prey Selection

In both prey combinations, Bighead Carp were the most selected prey species. Each Largemouth Bass captured at least one fish during the trials. Largemouth Bass selection for Bighead Carp was more than three times greater than for Bluegill and Golden Shiner ($F = 12.47$, df = 2, $P < 0.001$), and selection was similarly low for both native species when Bighead Carp were present (Figure 1). In the group of morphologically similar prey, Largemouth Bass selected Bighead Carp more often than

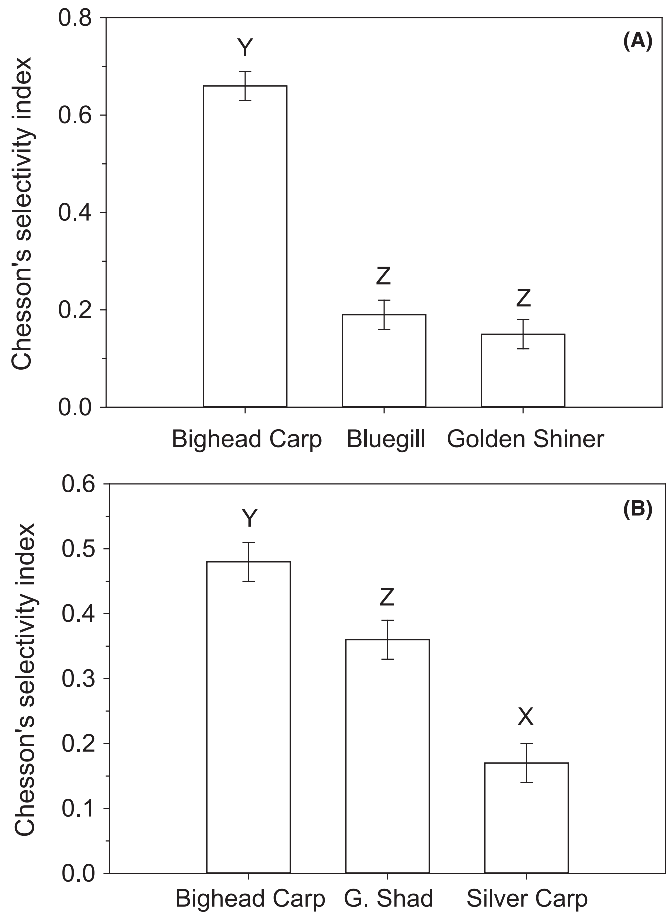

FIGURE 1. Chesson's selectivity values (mean ± SE) for Largemouth Bass foraging on groups of either **(A)** Bighead Carp, Bluegill, and Golden Shiner or **(B)** Bighead Carp, Gizzard Shad (G. Shad), and Silver Carp. Selection increases with Chesson's selectivity index (α) and bars with different letters indicate selection differences among prey types at the 0.05 significance level.

Gizzard Shad and selected more Gizzard Shad than Silver Carp ($F = 8.19$, df = 2, $P < 0.001$; Figure 1).

Prey Vulnerability

Capture efficiency was the primary difference in Largemouth Bass predation on the four prey species. There was little variation in the number of prey captured per trial, with similar numbers captured for each species (total captures ± SE: 1.4 ± 0.15 for Golden Shiner, 1.5 ± 0.17 for Gizzard Shad, 1.3 ± 0.16 for Bluegill, 1.5 ± 0.17 for Bighead Carp, and 1.4 ± 0.15 for Silver Carp). The time spent following and pursuing prey did not differ among prey types (following time: $F = 1.36$, df = 4, $P = 0.26$; pursuit time: $F = 1.73$, df = 4, $P = 0.15$), and handling time for captured prey also did not differ among species ($F = 0.64$, df = 4, $P = 0.63$). Attack rate did vary among prey species ($F = 5.53$, df = 4, $P = 0.0006$), for which there were fewer attacks on Bighead Carp and Gizzard Shad than on other species ($P \leq 0.002$ for all comparisons). These lower attack rates were associated with Largemouth Bass that had their highest capture efficiencies when they attacked these two species ($F = 6.85$, df = 4, $P = 0.0001$; Figure 2).

Differences in capture efficiency were associated with patterns of predator avoidance and schooling behavior. Distances kept between predator and prey varied among prey types ($F = 2.73$, df = 4, $P = 0.04$); Gizzard Shad approached the closest (33.4 ± 2.29 cm [mean ± SE]) and Golden Shiner stayed the farthest away (51.1 ± 3.41 cm) from Largemouth Bass (Gizzard Shad versus Golden Shiner distance from predator: $P = 0.003$). The other prey species maintained similar ($P \geq 0.02$ for all other comparisons), intermediate distances from Largemouth Bass (distance ± SE: 45.9 ± 3.71 cm for Bluegill, 48.2 ± 4.74 cm for Bighead Carp, and 41.6 ± 4.35 cm for Silver Carp). Once a predator entered the foraging arena, the majority of prey, regardless of species, formed schools. School area differed by species ($F = 9.32$, df = 4, $P < 0.0001$); Bighead Carp formed tighter schools than all other prey types (Figure 3). Capture efficiency of Largemouth Bass attacking dispersed individuals was similar across prey species (global mean ± 1 SE = 0.20 ± 0.03; $F = 1.35$, df = 4, $P = 0.26$), but varied for schooled prey ($F = 6.53$, df = 4, $P = 0.0002$; Figure 4), for which capture efficiencies were highest for Bighead Carp and Gizzard Shad (least-squares mean capture efficiency ± SE: −2.78 ± 0.25 for Bluegill, −2.37 ± 0.25 for Golden Shiner, −2.10 ± 0.28 for Gizzard Shad, −2.55 ± 0.26 for Silver Carp, and −1.40 ± 0.26 for Bighead Carp).

DISCUSSION

In terms of predator selectivity and efficiency, both Bighead Carp and Silver Carp were similar to native prey species in their vulnerability to Largemouth Bass predation. Follow and pursuit time of the five prey species did not differ, suggesting that all prey types were easily detected and elicited a foraging response from Largemouth Bass. Attack rates and capture efficiencies for

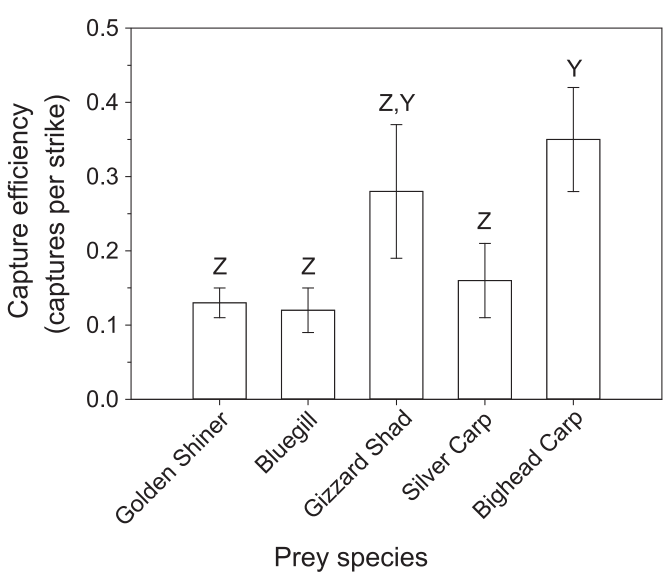

FIGURE 2. Capture efficiency (mean captures per strike ± SE) of Largemouth Bass foraging on Golden Shiner, Bluegill, Gizzard Shad, Silver Carp, and Bighead Carp. Bars with different letters represent differences at the Bonferroni-adjusted 0.005 significance level.

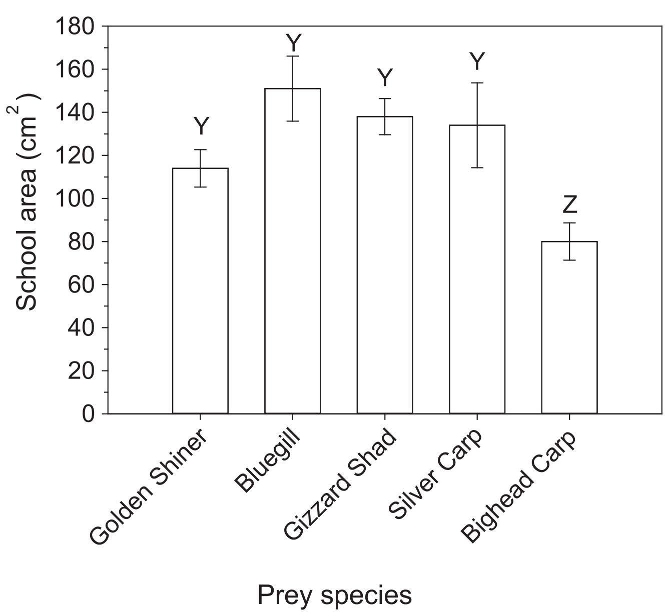

FIGURE 3. School size (mean area [cm^2] ± SE) of Golden Shiner, Bluegill, Gizzard Shad, Silver Carp, and Bighead Carp in the presence of a predator. Bars with different letters represent differences at the Bonferroni-adjusted 0.005 significance level.

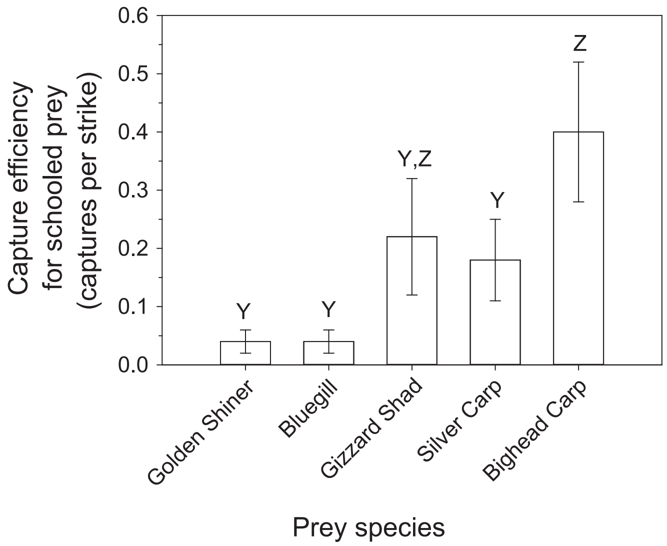

FIGURE 4. Capture efficiency (mean captures per strike ± SE) for schooled prey. Bars with different letters represent differences at the Bonferroni-adjusted 0.005 significance level.

Bighead Carp and Silver Carp were similar to at least one native prey species. Novel prey can pose challenges for naïve predators (Carlsson et al. 2009; Saul and Jeschke 2015), but there are a variety of potential explanations for why vulnerability to predation would be similar between *Hypophthalmichthys* carps and native prey species. Largemouth Bass are opportunistic predators that may have no motivational obstacles to attacking novel prey (Nannini et al. 2015). Considering the wide range of intra- and interspecific variation in morphology and behavior present in the typical prey of Largemouth Bass, *Hypophthalmichthys* carps may also be similar enough in morphology and behavior to native prey familiar to Largemouth Bass to elicit sufficient recognition and capture capabilities by this predator (Saul and Jeschke 2015). Even in novel predator–prey interactions, patterns of prey selection can be predictable from general aspects of prey morphology and behavior (Green and Coté 2014).

Bighead Carp may have been the most preferred prey among all species tested, but the combined evidence from our experiments suggests that the most likely explanation for the difference in selectivity was that Bighead Carp were captured more easily than the other prey. Differences in predator capture efficiencies for Bighead Carp, Gizzard Shad, and Silver Carp in the prey vulnerability experiments were small. Over the foraging time of the selection trials, however, differences in efficiency may have added up to the observed differences in selectivity among the three species. In all cases, variability in preference may actually be attributed to differences in election (sensu Jackson and Underwood 2007) as a result of some prey species being more efficiently consumed by Largemouth Bass. If differences in selectivity were from predator preferences, Largemouth Bass might have selectively consumed Bighead Carp over native prey because of the novelty of nonnative prey items. From a mixture of familiar and unfamiliar prey, predators will sometimes preferentially attack the novel prey type, perhaps to increase diet breadth (Mills et al. 1987). Alternatively, certain prey behaviors can increase either detectability or a predator's assessment of prey vulnerability (Green and Coté 2014). Whether selection was influenced by actual preference or higher foraging efficiencies, prey behavior, specifically schooling, was the main factor influencing selection for Bighead Carp relative to other prey types.

Interspecific patterns of vulnerability were shaped by how prey behaved in the presence of Largemouth Bass. Gizzard Shad approached Largemouth Bass more closely than did the other prey species. The tendency for Gizzard Shad to tolerate a small distance from Largemouth Bass has also been observed with other types of predators (e.g., esocids: Wahl and Stein 1988; Walleye *Sander vitreus*: Einfalt and Wahl 1997). Schooling is a common antipredator behavior and was observed for all prey species exposed to Largemouth Bass. Schooling can provide protection from predators by reducing capture efficiency through a "confusion effect" (Humphries and Driver 1970) or lowering individual risk as the number of potential targets increases (dilution effect: Morgan and Godin 1985). Bighead Carp formed the most closely spaced schools when threatened by Largemouth Bass. The tightness of Bighead Carp schools may have reduced the effectiveness of a confusion effect, as Largemouth Bass were able to successfully attack at least one individual in a school. Nonetheless, schooling should still benefit individual Bighead Carp through risk dilution.

Under conditions free of environmental complexity, the inherent vulnerability of juvenile *Hypophthalmichthys* carps to a common, native predator was similar to native prey. Future research should expand on these results by examining how relative vulnerability may be modified by factors present under more complex conditions, such as spatial overlap and habitat structure. Structurally complex habitats can serve as prey refuge by reducing the foraging efficiency of predators (e.g., Savino and Stein 1982). However, this effect is not universal across all predator types. For example, ambush-predator foraging success is either unaffected or increased in the presence of complex habitats (Eklöv and Diehl 1994; DeBoom and Wahl 2013). Encounter rates were high in our experimental settings, allowing us to assess selection and consumption patterns in the context of contact between predator and prey. Under natural conditions, spatial overlap between predators and prey is an important component of predation risk (Williamson 1993) and can determine predator diets (Hansen et al. 2013). There is an untested expectation that

Hypophthalmichthys juveniles transition from off-channel, low-velocity habitats to river main-stem channels as they grow to adulthood, but there are also records of residence in floodplain lakes and reservoirs (Kolar et al. 2007). Largemouth Bass primarily occupy littoral habitats and commonly reside in lakes and reservoirs (Warren 2009). Although a shift from backwater to main channel habitat by *Hypophthalmichthys* carps would reduce spatial overlap with Largemouth Bass, juveniles remaining in backwater environments would have potentially high encounter rates with this predator. Nonetheless, habitat use by *Hypophthalmichthys* juveniles is not well known and is an important area for future research.

If relative vulnerability of juvenile *Hypophthalmichthys* carps in field settings mirrors our experimental estimates, the availability of these novel prey has implications for both the potential for predator control of these invasive species and native predator–prey dynamics. Silver Carp were neither strongly preferred nor especially vulnerable relative to native prey, and therefore, their populations are unlikely to be regulated by predation from native fishes. Bighead Carp may be more susceptible to predator regulation as they were either preferred or more efficiently consumed by Largemouth Bass. However, Bighead Carp and Silver Carp growth should constrain predation, as both species outgrow their vulnerability to most predators. In the Illinois River, Silver Carp can reach 200 mm TL by age 1 (Stuck et al. 2015), and based on typical Largemouth Bass length frequencies in this system (Raibley et al. 1997), would be too large to be effectively consumed by these predators (i.e., prey > 50% predator TL: Einfalt et al. 2015). The potential effects of *Hypophthalmichthys* carps on piscivore assemblages will depend in part on whether they supplement or decrease prey resources for native predators. Predator growth and survival may be diminished if *Hypophthalmichthys* species cause declines in prey availability via direct competition. Alternatively, successfully established nonnative species sometimes increase the spatiotemporal availability of prey for predators (Dijkstra et al. 2013; Pintor and Byers 2015). In this scenario, *Hypophthalmichthys* carps may be having a relatively unappreciated influence on native food webs through enhancement of prey resources for predator populations.

ACKNOWLEDGMENTS

This study was supported by the Great Lakes Restoration Initiative, and funding was administered through the Illinois Department of Natural Resources. We thank the staff and students of the Kaskaskia and Sam Parr Biological stations, particularly L. Einfalt, for help in gathering and caring for fish in experiments. We are especially grateful to a number of undergraduate research students who helped in behavior analysis and data collection, particularly W. Farhat, B. Rathunde, C. McIntyre, J. Pflederer, R. Lautner, and D. Juiyang. The Illinois Natural History Survey and the Department of Natural Resources and Environmental Sciences, University of Illinois, also provided support. The experiments were conducted following protocols approved by the Institutional Animal Care and Use Committee, University of Illinois Urbana–Champaign (protocol 11053). There is no conflict of interest declared in this article.

ORCID

Anthony P. Porreca http://orcid.org/0000-0002-7401-4902

REFERENCES

Alofs, K. M., and D. A. Jackson. 2014. Meta-analysis suggests biotic resistance in freshwater environments is driven by consumption rather than competition. Ecology 95:3259–3270.

Bajer, P. G., C. J. Chizinski, J. J. Silbernagel, and P. W. Sorenson. 2012. Variation in native micro-predator abundance explains recruitment of a mobile invasive fish, the Common Carp, in a naturally unstable environment. Biological Invasions 14:1919–1929.

Carlsson, N. O. L., O. Sarnelle, and D. L. Strayer. 2009. Native predators and exotic prey–an acquired taste? Frontiers in Ecology and the Environment 7:525–532.

Chesson, J. 1983. The estimation and analysis of preference and its relationship to foraging models. Ecology 64:1297–1304.

Collins, S. F., and D. H. Wahl. 2017. Invasive planktivores as mediators of organic matter exchanges within and across ecosystems. Oecologia 184:521–530.

DeBoom, C. S., and D. H. Wahl. 2013. Effects of coarse woody habitat complexity on predator–prey interactions of four freshwater fish species. Transactions of the American Fisheries Society 142:1602–1614.

Dijkstra, J. A., W. J. Lambert, and L. G. Harris. 2013. Introduced species provide a novel temporal resource that facilitates native predator population growth. Biological Invasions 15:911–919.

Einfalt, L. M., J. J. Parkos III, and D. H. Wahl. 2017. Effect of predator size and prey characteristics on piscivory of juvenile Largemouth Bass. Transactions of the American Fisheries Society 144:2618–2626.

Einfalt, L. M., and D. H. Wahl. 1997. Prey selection by juvenile Walleye as influenced by prey morphology and behavior. Canadian Journal of Fisheries and Aquatic Sciences 54:2618–2626.

Eklöv, P., and S. Diehl. 1994. Piscivore efficiency and refuging prey: the importance of predator search mode. Oecologia 98:344–353.

Farrington, H. L., C. E. Edwards, M. Bartron, and R. F. Lance. 2017. Phylogeography and population genetics of introduced Silver Carp (*Hypophthalmichthyes molitrix*) and Bighead Carp (*H. nobilis*) in North America. Biological Invasions 19:2789–2811.

Green, S. J., and I. M. Coté. 2014. Trait-based diet selection: prey behavior and morphology predict vulnerability to predation in reef fish communities. Journal of Animal Ecology 83:1451–1460.

Hambright, K. D. 1991. Experimental analysis of prey selection by Largemouth Bass: role of predator mouth width and prey body depth. Transactions of the American Fisheries Society 120:500–508.

Hansen, A. G., and D. A. Beauchamp. 2014. Effects of prey abundance, distribution, visual contrast, and morphology on selection by a pelagic piscivore. Freshwater Biology 59:2328–2341.

Hansen, A. G., D. A. Beauchamp, and C. M. Baldwin. 2013. Environmental constraints on piscivory: insights from linking ultrasonic telemetry to a visual foraging model for Cutthroat Trout. Transactions of the American Fisheries Society 142:300–316.

Hoyle, J. A., and A. Keast. 1987. The effect of prey morphology and size on handling time in a piscivore, the Largemouth Bass (*Micropterus salmoides*). Canadian Journal of Zoology 65:1972–1977.

Humphries, D. A., and P. M. Driver. 1970. Protean defense by prey animals. Oecologia 5:285–302.

Ims, R. A. 1990. On the adaptive value of reproductive synchrony as a predator-swamping strategy. American Naturalist 136:485–498.

Jackson, A. C., and A. J. Underwood. 2007. Application of new techniques for the accurate analysis of choice of prey. Journal of Experimental Marine Biology and Ecology 341:1–9.

Koel, T. M., and R. E. Sparks. 2002. Historical patterns of river stage and fish communities as criteria for operations of dams on the Illinois River. River Research and Applications 18:3–19.

Kolar, C. S., D. C. Chapman, W. R. Courtenay Jr., C. M. Housel, D. P. Jennings, and J. D. Williams. 2007. Bigheaded carps: a biological synopsis and environmental risk assessment. American Fisheries Society, Special Publication 33, Bethesda, Maryland.

Lampo, E. G., B. C. Knights, J. M. Vallazza, C. A. Anderson, W. T. Rechkemmer, L. E. Solomon, A. F. Casper, R. M. Pendleton, and J. T. Lamer. 2017. Using pharyngeal teeth and chewing pads to estimate juvenile Silver Carp total length in the La Grange Reach, Illinois River. North American Journal of Fisheries Management 37:1145–1150.

Magoulick, D. D., and L. C. Lewis. 2002. Predation on exotic zebra mussels by native fishes: effects on predator and prey. Freshwater Biology 47:1908–1918.

McClelland, M., G. G. Sass, T. R. Cook, K. S. Irons, N. N. Michaels, T. M. O'Hara, and C. S. Smith. 2012. The long-term Illinois River fish population monitoring program. Fisheries 37:340–350.

Mills, E. L., D. V. Widzowski, and S. R. Jones. 1987. Food conditioning and prey selection by young Yellow Perch (*Perca flavescens*). Canadian Journal of Fisheries and Aquatic Sciences 44:549–555.

Morgan, M. J., and J.-G. J. Godin. 1985. Antipredator benefits of schooling behavior in a cyprinodontid fish, the Banded Killifish (*Fundulus diaphanous*). Ethology 70:236–246.

Nannini, M. A., J. J. Parkos III, and D. H. Wahl. 2015. Do behavioral syndromes affect foraging strategy and risk-taking in a juvenile fish predator? Transactions of the American Fisheries Society 141:26–33.

Negonovskaya, I. T. 1980. On the results and prospects of the introduction of phytophagous fishes into waters of the USSR. Journal of Ichthyology 20:101–111.

Nelson, K. A., S. F. Collins, G. G. Sass, and D. H. Wahl. 2017. A response-surface examination of competition and facilitation between native and invasive juvenile fishes. Functional Ecology 31:2157–2166.

Olson, M. H. 1996. Ontogenetic niche shifts in Largemouth Bass: variability and consequences for first-year growth. Ecology 77:179–190.

Pintor, L. M., and J. E. Byers. 2015. Do native predators benefit from non-native prey? Ecology Letters 18:1174–1180.

Raibley, P. T., T. M. O'Hara, K. S. Irons, K. D. Blodgett, and R. E. Sparks. 1997. Largemouth Bass size distributions under varying hydrological regimes in the Illinois River. Transactions of the American Fisheries Society 126:850–856.

Sampson, S. J., J. H. Chick, and M. A. Pegg. 2009. Diet overlap among two Asian carp and three native fishes in backwater lakes on the Illinois and Mississippi rivers. Biological Invasions 11:483–496.

Saul, W.-C., and J. M. Jeschke. 2015. Eco-evolutionary experience in novel species interactions. Ecology Letters 18:236–245.

Savino, J. F., and R. A. Stein. 1982. Predator-prey interaction between Largemouth Bass and Bluegills as influenced by simulated, submersed vegetation. Transactions of the American Fisheries Society 111:255–266.

Shoup, D. E., and D. H. Wahl. 2009. The effects of turbidity on prey selection by piscivorous Largemouth Bass. Transactions of the American Fisheries Society 138:1018–1027.

Stuck, J. G., A. P. Porreca, D. H. Wahl, and R. E. Colombo. 2015. Contrasting population demographics of invasive Silver Carp between an impounded and free-flowing river. North American Journal of Fisheries Management 35:114–122.

Szendrey, T. A., and D. H. Wahl. 1995. Effect of feeding experience on growth, vulnerability to predation, and survival of esocids. North American Journal of Fisheries Management 15:610–620.

Tablado, Z., J. L. Tella, J. A. Sánchez-Zapata, and F. Hiraldo. 2010. The paradox of the long-term positive effects of a North American crayfish on a European community of predators. Conservation Biology 24:1230–1238.

Twardochleb, L. A., M. Novak, and J. W. Moore. 2012. Using the functional response of a consumer to predict biotic resistance to invasive prey. Ecological Applications 22:1162–1171.

Wahl, D. H., and R. A. Stein. 1988. Selective predation by three esocids: the role of prey behavior and morphology. Transactions of the American Fisheries Society 117:142–151.

Warren, M. L. Jr. 2009. Centrarchid identification and natural history. Pages 375–534 *in* S. J. Cooke and D. P. Philipp, editors. Centrarchid fishes: diversity, biology, and conservation. Wiley-Blackwell, West Sussex, UK.

Webb, P. W. 1986. Effect of body form and response threshold on the vulnerability of four species of teleost prey attacked by Largemouth Bass (*Micropterus salmoides*). Canadian Journal of Fisheries and Aquatic Sciences 43:763–771.

Werner, E. E., and D. J. Hall. 1988. Ontogenetic habitat shifts in Bluegill: the foraging rate-predation risk trade-off. Ecology 69:1352–1366.

Williamson, C. E. 1993. Linking predation risk models with behavioral mechanisms: identifying population bottlenecks. Ecology 74:320–331.

Wolf, M. C., and Q. E. Phelps. 2017. Prey selectivity of common predators on Silver Carp (*Hypophthalmichthys molitrix*): controlled laboratory experiments support field observations. Environmental Biology of Fishes 100:1139–1143.

Zhang, H., E. S. Rutherford, D. M. Mason, J. T. Breck, M. E. Wittman, R. M. Cooke, D. M. Lodge, J. D. Rothlisberger, X. Zhu, and T. B. Johnson. 2016. Forecasting the impacts of Silver and Bighead carp on the Lake Erie food web. Transactions of the American Fisheries Society 145:136–162.