Mechanistic Insight into Gape Limitation and Growth-mediated Competition Among Moronid

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Abstract: Gape limitation is a key mechanism controlling the size of prey a predator can consume, as a fishes gape is intrinsically linked to its body size and changes with growth. Previous studies have shown that gape limitation influences competition among game fishes and helps estimate prey availability. High utilization of shad (*Dorosoma* spp.) by the Moronidae family provides an opportunity to examine gape-limitation theory. Moronids are widely pursued across the United States, with five species present in Oklahoma. This study aimed to determine potential diet overlap among these species using gape-limitation theory and a common forage species, Gizzard Shad (*Dorosoma cepedianum*). Objectives were to: (1) develop equations estimating the proportion of Gizzard Shad vulnerable by size and age to each Moronid species, (2) compare vulnerability among similar-sized Moronids to identify competitive advantages, and (3) assess whether advantages exist when accounting for prey and predator growth trajectories. Results indicate that growth-mediated exploitation occurs among Moronids, allowing individuals that grow faster to achieve a larger gape and better compete for prey. Thus, growth rates and resulting size structures are critical to mediating resource overlap. Managers can apply gap-based vulnerability to estimate forage availability, competition, and exploitation, guiding decisions on whether to manipulate forage or predator populations to meet management goals.

Introduction

Predation is one of the structuring processes in aquatic ecosystems that regulates energy transfer and ecosystem function (Bax 1998; Baxter et al. 2004). Predation is influenced by food-web complexity and the strength of bottom-up and top-down interactions between producers and consumers (Lindeman 1942, Carpenter et al. 1985, McQueen et al. 1986, Power 1992, Pace et al. 1999). Primary mechanisms (e.g., morphological constraints, Mihalitsis and Bellwood 2017) regulated by abiotic and biotic influences (Coutant 2006) within the environment likely control predation. Understanding mechanistic constraints on predation, such as gape lim-

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itation, likely allows for more accurate estimates of consumption and diet overlap and may inform management practices.

Gape limitation is a key mechanism controlling the size of prey a predator can consume (Hill et al. 2004). In theory, the maximum size of prey a predator can consume is based upon the mouth dimensions of said predator (gape width) and the body depth of said prey. Gape limits the breadth of a predator's foraging niche, and therefore influences competition for and consumption of a prey base (Hambright 1991). A fish's gape is intrinsically linked to its size. Therefore, gape-based estimates of prey vulnerability likely vary through time depending on predator and prey growth trajectories (DeVries et al. 1998; Krebs and Turingan 2003). Gape limitation has been shown to be more accurate at predicting consumption relative to other morphometric comparisons between predators and prey (Dennerline and Van Den Avyle 2000). Given its prior use and ecological basis, gape limitation allows for better management of sportfish as it provides insight into potential exploitation and permits the estimation of prey availability.

Gape width has been shown to predict the maximum size of shad (*Dorosoma* spp.) consumed by fishes belonging to the family Moronidae (hereafter Moronids), offering an opportunity for management application of gape-limitation theory (Dennerline and Van Den Avyle 2000). Moronids are some of the most widely pursued sportfish in the United States, and members of this family commonly rank in the top five harvested species within a given state or region (Guy et al. 2002, Bulak et al. 2013). Striped Bass (*Morone saxatillis*), White Bass (*M. chrysops*), and Hybrid Striped Bass (*M. chrysops* × *M. saxatilis*) are sportfish of management interest in Oklahoma (Miller and Robison 2004, Schultz et al. 2013). Competition and resource partitioning among these Moronids have been previously documented, and all three are known to prey upon shad (Gilliland 1978, Rash 2003, Olson 2004).

The amount of food resource exploitation between Moronids of management interest (i.e., Striped Bass, White Bass, and Hybrid Striped Bass) in Oklahoma reservoirs is unknown. However, diet overlap, competition, and resource partitioning among these species has been previously documented (e.g., Rash 2003, Olson 2004). Moronids of management interest in Oklahoma may be further threatened by the invasion of non-native White Perch (*M. americana;* Irons et al. 2002) and possible range expansion of Yellow Bass (*M. mississipiensis)* in the southeastern portion of the state (Snow and Porta 2020). To gain a better understanding of diet overlap, competition, and resource partitioning among these species, the goal of our study was to determine potential diet overlap between Oklahoma Moronids using gape limitation theory and a common forage species (Gizzard Shad; [*Dorosoma cepedianum*]). Given the relation between growth and gape, we compared Gizzard Shad gape vulnerability over similar Moronid size ranges and their potential annual growth trajectories. Specific objectives of our study were to: 1. Develop equations to determine the proportion of Gizzard Shad vulnerable by size and age to five species of Moronids in Oklahoma. 2. Determine potential forage availability overlap among Moronids using gape limitation theory. 3. Determine if advantages exist for a particular species when accounting for prey and predator annual growth trajectories. We then reviewed our findings in the context of managing mixed-Moronid fisheries within the state of Oklahoma.

Methods

Sampling

Fish were collected for this study from nine Oklahoma reservoirs spaced across the state (Table 1). Gizzard Shad were collected in the fall via electrofishing (pulsed DC, high voltage, 7.5 GPP, Smith Root, Vancouver, Washington) from 2018-2021. Moronid species were collected between 2019 and 2022 using experimental gillnets (61 m long x 1.8 m deep and constructed of eight 7.6-m panels [12.7-mm, 15.9-mm, 19.1-mm, 25.4-mm, 38.1-mm, 50.8-mm, 63.5-mm, and 76.2-mm bar mesh]). Gizzard Shad were collected from all nine reservoirs to better estimate variation in fish size and growth across Oklahoma. Striped Bass, White Bass, and Hybrid Striped Bass were collected from 3 of 9 reservoirs (Table

1). Reservoirs for these species were selected based on prior knowledge of growth variability across the state (OFAT 2022). Yellow Bass and White Perch were collected from New Spiro and Sooner reservoirs, respectively (Table 1).

Following collection, fish were euthanized in a 1:1 ice water slurry (Blessing et al. 2010) and returned to the lab where they were measured (TL; mm) and sagittal otoliths were extracted for age estimation. For Moronids, a 150-mm digital caliper (PITTSBURGH 150 mm Digital Caliper, Item #62569, Harbor Freight, Calabasas, CA) was used to measure the horizontal maxillary oral gape (Mihalitsis and Bellwood 2017 and Dennerline and Van Den Avyle 2000) of each individual (0.01 mm).

Estimating Age

Otoliths were cleaned and placed into individually numbered envelopes and allowed to dry for at least 24 h prior to processing (Secor et al. 1992). Sagittal otoliths from Moronid species were broken in the transverse plane and polished using 600-grit wet/dry sandpaper. Clayton and Maceina (1999) suggested that whole otoliths could accurately estimate age of Gizzard Shad under 3 years old. Therefore, sagittal otoliths of Gizzard Shad <3 years old were estimated from whole otoliths and otoliths from older fish were embedded in a 21-cell latex mold (12 mm x 5 mm x 6 mm; Electron Microscopy Sciences, Hatfield, Pennsylvania), immersed in West Systems epoxy (105 resin and 206 harder; Gougeon Brothers Inc., Bay City, Michigan), then cured for more than 12 h. Otoliths were then cut in the sagittal plane using a low-speed Buehler saw (127-mm x 0.4-mm diamond wafering blade; IsoMet®, Buehler, Inc., Lake Bluff, Illinois) and polished using 2000-grit sandpaper (Maceina 1988).

To estimate ages, sectioned otoliths from all species were positioned polished side up in modeling clay and covered with water to reduce glare. Whole otoliths were placed concave side up on the clay. All otoliths were viewed with a variable power stereomicroscope (capable of 130× magnification) using a fiber-optic light and a reflective light source when needed. Annuli were counted to assign an age estimate to each fish. Each otolith was evaluated in random order by two independent readers (Hoff et al. 1997). If there was a disagreement on an estimated age, a concert reading was conducted by both readers and a final age estimate was determined.

Table 1. Reservoirs where Moronid species (Hybrid Striped Bass *Morone saxatilis x M. chrysops* [HSB], Striped Bass *M. saxatilis* [STB], White Bass *M. chrysops* [WHB], White Perch *M. americana* [WHP], Yellow Bass *M. mississippiensis* [YLB]) and Gizzard Shad *Dorosoma cepedianum* (GIS) were collected, including size of reservoirs, sample size (ha), and ranges of TL, weight, gapes, and age estimates. The composition of the Moronid fishery in each reservoir is given in the Moronids column.

				Summary Statistics				
Species	**Reservoir**	**Size (ha)**	**Moronids**	***n***	**TL (mm)**	**Weight (g)**	**Gape (mm)**	**Age (years)**
HSB	Canton	3201	HSB, STB, WHB	161	212-717	120-5445	29-89	1-9
	Sooner	2185	HSB, STB, WHB, WHP	13	408-525	928-2088	46-60	2-7
STB	Canton	3201	HSB, STB, WHB	8	470-659	1180-3220	62-82	3-5
	Texoma	35,612	HSB, STB, WHB	76	194-793	80-6080	23-93	1-7
WHB	Canton	3201	HSB, STB, WHB	114	172-442	13-940	22-57	1-11
	Texoma	35,612	HSB, STB, WHB	24	191-453	80-1170	22-48	1-5
	Sooner	2185	HSB, STB, WHB, WHP	3	306-345	402-600	32-44	2-3
WHP	Sooner	2185	HSB, STB, WHB, WHP	147	191-323	27-496	22-41	2-14
YLB	New Spiro	101	YLB	107	81-302	5-505	10-38	0.5-2.5
GIS	Canton	3201	HSB, STB, WHB	145	65-439	5-810	-	0-8
	Carl Etling	64	HSB	198	45-338	2-280	-	0-12
	Eagle	17	HSB, WHB	34	125-481	10-1450	-	0-7
	Elmer	15	-	110	138-319	10-360	-	1-7
	Guthrie City	83	-	107	81-298	5-270	-	0-6
	New Spiro †	101	YLB	161	108-366	10-530	-	1-6
	Sooner †	2185	HSB, STB, WHB, WHP	76	127-477	10-1210	-	0-12
	Thunderbird	2176	HSB, WHB	127	108-257	10-155	-	0-9
	Texoma †	35,612	HSB, STB, WHB	65	121-471	10-155	-	1-5

†Threadfin shad (*Dorosoma petenense*) also present

Estimating Body Depth or Gape Width from TL

To estimate the mean body depth of each Gizzard Shad present within our samples we used the inverted form of an equation from Lawrence (1957):

$$BD = \frac{(TL - 15.630)}{3.405}$$

where BD and TL represent the estimated mean body depth and observed total length of a Gizzard Shad, respectively. Because this equation is only representative of the mean body-depth to TL relationship, the standard deviation of the regression (SDR = 10.18) reported in Lawrence (1957) was used to estimate the maximum and minimum body-depth of each individual. This was done by adding or subtracting the SDR from the mean estimated body-depth. A small subset (*n* = 17) of Gizzard Shad were used to graphically validate that the equation from Lawrence (1957) captured the variation in body-size to TL relationship by confirming that our observed values fell within the maximum and minimum body-depth estimates.

Gape width to TL relationships were determined independently for each Moronid species. An information theoretic approach was used to determine which of four common morphometric equations best descripted the relationship between gape-width and TL. We selected linear, second-degree polynomial, exponential, and power functions as the most likely morphometric equations (Hill et al. 2004, Slaughter et al. 2008; Dunic and Baum 2017). Morphometric equations were ranked using Akaike's information criterion adjusted for small sample sizes (AICc; Hurvich and Tsai 1989), where lower values of AICc indicate more likely models (Burnham and Anderson 2002). Both root-mean-square error (RMSE) and mean absolute error (MAE) were used to describe the fit of each morphometric equation relative to the data used to estimate the relationships. Because these equations were used to estimate gape-vulnerability for these fishes and we wanted to capture the full potential range of gapes possible at a given length, we also estimated predictive intervals for each equation ($\alpha = 0.01$).

Comparing Gape Vulnerability by TL

To estimate gape vulnerability by TL, the mean, lower, and upper body-depth estimates for Gizzard Shad were compared to the mean, lower, and upper gape estimates for each Moronid. If Gizzard Shad body depth was less than the gape of the Moronid it was considered vulnerable to that species and assigned a one. If it was greater than the Moronid gape it was considered invulnerable and assigned a zero. This resulted in nine estimates of vulnerability for each mm of TL for both the Moronid and Gizzard Shad. These estimates (i.e., the ones and zeros) were averaged to estimate the average vulnerability as a proportion based on variation in shad body depth and Moronid gape. All estimates were restricted to the TLs observed for the shad population and the specific Moronid.

To compare length-based gape-vulnerability between Moronids, we used a binomially distributed generalized linear model (GLM) with a logit-link function. Our data had three categories (i.e., gape-vulnerability advantage for each species being compared [2 categories], and equal gape-vulnerability); however, a binomial model has two categories, specifically "1" and "0". To facilitate this analysis, we grouped one of the species gape-vulnerability advantages with equal gape-vulnerability (scored "0") and compared it to the other species gape-vulnerability advantage (scored "1"). To decide which Moronid to group with equal gape-vulnerability, we grouped both with equal and looked at the ratio of "1's" and "0's" that resulted from each grouping scheme. The grouping scheme that produced the most even ratio of "1's" and "0's" was used for the analysis. Predictive variables for the binomial GLM were shad TL, Moronid TL, and the interaction between both lengths. This allowed us to determine the relationship between gape advantages for each Moronid species relative to the potential size distribution of forage. All models were restricted to the TLs for which average-vulnerability was estimated in each species (e.g., when Hybrid Striped Bass and Striped Bass were compared, the model was restricted between 212 – 717 mm). McFadden's pseudo R^2 estimates were used to estimate the strength of the relationship, with $\rho^2 = 0.20$ used as the threshold for "excellent" model fit (McFadden 1974, 1979). A Hosmer-Lemeshow Goodness of Fit test was also used to determine if models appropriately fit the data ($\alpha = 0.05$).

Growth Modeling

The von Bertalanffy growth model (VBGM) was used to estimate growth trajectories for Gizzard Shad and the five Moronids represented. To better estimate the growth trajectory of each species within Oklahoma, the VBGM was fit using TL measurements and age estimates for each individual within our samples regardless of waterbody. Once a baseline equation was established from the nonlinear modeling function, bootstrapping via second-order Taylor expansion (Wang and Iyer 2005) was used to provide final estimates of mean length at age for the species along with 99% prediction intervals. Because predictive intervals incorporate additional uncertainty associated with the data point being estimated they are inherently wider than a confidence interval. In our application, this increased uncertainty produced estimates that were statistically appropriate but biologically impossible (e.g., the lower 99% PI estimate of TL for an age-0 Gizzard Shad was -60mm). Due to this phenomena, post hoc adjustments were made to nonsensical or unlikely estimates based on available literature data (see Growth Modeling results for specific details).

Comparing Gape-Vulnerability by Age

To estimate the influence of growth on gape-vulnerability comparisons, the same comparison process was used (i.e., Gizzard Shad body-depth estimates were compared to Moronid gape estimates). However, for this comparison TL was based on the mean, lower, and upper estimates generated from the VBGM for each age. These three TL estimates were then fed into either the body-depth equation or the gape equation, resulting in nine estimates of either body-depth or gape for each species. This generated 81 estimates of either vulnerable (1) or invulnerable (0) for each Moronid-shad age group. Estimates were averaged to determine vulnerability at each age. For this analysis, ages were restricted from age-0 to the maximum age observed for each species.

Once average vulnerabilities were attained, we compared vulnerability-by-age between species using a Cochran-Mantel-Haenszel Chi-Squared Test (CMH; $\alpha = 0.05$; Cochran 1954, Mantel and Haenszel 1959). This test is an extension of the Chi-Squared test, allowing for comparisons in three dimensions if no three-way interaction is present (Agresti 2002). Because this test requires counts and not proportions, average vulnerabilities were multiplied by 81 (i.e., the number of original comparisons) to attain an estimate of the frequency of vulnerability within each Moronid-by-Moronid age class. Prior to CMH analysis a log-linear model was fit to detect the presence of a three-way interaction ($\alpha = 0.05$). Similar to ANOVA, the CMH test allowed us to determine if there is a significant difference in vulnerability within one dimension of our matrix. Therefore, if the CMH test detected a significant difference with our three-dimensional matrix a groupwise post hoc test was used to test groups two-dimensions at a time using a modified Chi-squared test for independence ($\alpha = 0.05$) with p-values adjusted to minimize the false discovery rate (Benjamini and Hochberg 1995). We first compared vulnerability of shad at each age group among the Moronids. If no significant differences were detected, we determined if the significant CMH test result was due to shad vulnerability significantly varying by age within one of the species. Because statistical significance is often influenced by sample size, an adjusted estimate of Cramer's V (Bergsma 2013) was used to estimate effect size for each comparison. Cramer's V can be interpreted categorically with $V < 0.30$ suggesting "weak" effects, $V \geq 0.30$ being the threshold for "moderate" effects, and $V \geq 0.50$ begin the threshold for "large" effects (Cohen 1988).

Results

Fish collections for this study spanned nine Oklahoma reservoirs ranging in size from 15 to 35,612 ha (Table 1). Hybrid Striped Bass were the most widely distributed among the reservoirs, with TL ranging from 212-717 mm, weights ranging from 120-5,445 g, gape widths from 29-89 mm, and estimated ages up to 9 years old (Table 1). Striped Bass exhibited the largest size range (194-793 mm TL), weighed up to 6,080 g, and had a gape ranging from 23-93 mm. White Bass were generally smaller (172-453 mm TL) but longer lived (up to 11 years old). White Perch were only sampled from Sooner Lake, ranged 191-323 mm TL, and lived up to 14 years old, making them the longest-lived Moronid observed (Table 1). Yellow Bass collected from New Spiro Lake, were the smallest (81-302 mm TL) and shortest-lived (≤ 2.5 years old). Gizzard Shad were collected from nine reservoirs, with sizes ranging from 45-477 mm TL, and age estimates ranged from 0-12 years old.

Estimating Body-Depth and Gape-Width from TL

The subset of Gizzard Shad used to assess the inverted TL to body-depth equation ranged in TL from 204 to 319 mm and in body depths from 54 to 93 mm. All observed body depths fell within the predicted mean, maximum, and minimum body depths from the inverted Lawrence (1957) equation, suggesting that the equation yielded an appropriate approximation of the variation present in shad body depths.

Gape-TL relationships appeared to vary between species (Figure 1). The relationship between TL and gape for Striped Bass and White Perch was best described by a power equation (Table 2). Hybrid Striped Bass were best described by an exponential equation, Yellow Bass a 2nd-degree polynomial, and White Bass by a linear model (Table 2). Competitive gape-based advantages increased with Moronid size; among species advantages varied based on the size of the individual and variation in the Gape-TL relationship within the species when compared graphically across the size range observed for each species (Figure 2).

Table 2. Mean model parameter estimates, root-mean-square error (RMSE), mean absolute error (MAE), Akaike information criterion adjusted for small sample sizes (AICc), and change in AICc relative to the top ranked model (ΔAICc) for four models predicting the relationship between gape (G) and total length (TL) for each Moronid species (Hybrid Striped Bass *Morone saxatilis x M. chrysops* [HSB], Striped Bass *M. saxatilis* [STB], White Bass *M. chrysops* [WHB], White Perch *M. americana* [WHP], Yellow Bass *M. mississippiensis* [YLB]). The top ranked model used to fit gape-total length relationships has been bolded for interpretability. Mean parameter estimates with values in the hundredths place are presented in reciprocal-power format where "E^{-n}" is equivalent to "×10^{-n}" for uniformity and conciseness. Note: statistics (e.g., RMSE, AICc) are only comparable within a species and should not be compared across species.

Species	Model	RMSE	MAE	AIC$_c$	ΔAIC$_c$
HSB	$\boldsymbol{G = -40.75 + 58.34e^{1.12E^{-3}TL}}$	**2.96**	**2.39**	**879.40**	**0.00**
HSB	$G = 19.10 + 5.43E^{-2}TL + 6.07E^{-5}TL^2$	2.96	2.38	879.48	0.08
HSB	$G = 7.17 + 0.11TL$	3.07	2.44	889.82	10.42
HSB	$G = 0.25TL^{0.88}$	3.13	2.47	896.76	17.36
YLB	$\boldsymbol{G = 3.61 + 7.54E^{-2}TL + 1.27E^{-4}TL^2}$	**1.43**	**1.08**	**389.07**	**0.00**
YLB	$G = -37.33 + 40.50e^{2.06E^{-3}TL}$	1.43	1.08	389.07	<0.01
YLB	$G = 0.12TL^{1.01}$	1.49	1.12	394.53	5.46
WHB	$\boldsymbol{G = 6.93 + 0.10TL}$	**2.73**	**2.12**	**689.58**	**0.00**
WHB	$G = 10.59 + 7.66E^{-2}TL + 4.82E^{-5}TL^2$	2.72	2.11	690.72	1.15
WHB	$G = -80.70 + 90.88e^{8.88E^{-4}TL}$	2.72	2.11	690.75	1.17
WHB	$G = 0.39TL^{0.81}$	2.75	2.14	691.48	1.91
STB	$\boldsymbol{G = 5.07E^{-2}TL^{1.13}}$	**4.11**	**2.97**	**476.44**	**0.00**
STB	$G = -7.09 + 0.13TL$	4.12	3.00	476.85	0.41
STB	$G = -4.09 + 0.12TL + 1.24E^{-5}TL^2$	4.11	2.99	478.87	2.43
STB	$G = -665.50 + 661.00e^{1.78E^{-4}TL}$	4.12	2.99	478.89	2.44
WHP	$\boldsymbol{G = 5.46E^{-2}TL^{1.14}}$	**1.93**	**1.52**	**609.02**	**0.00**
WHP	$G = -3.85 + 0.13TL$	1.94	1.52	609.44	0.42
WHP	$G = -3.21 + 12.02e^{3.90E^{-3}TL}$	1.93	1.51	609.87	0.85
WHP	$G = 13.03 + 1.13E^{-5}TL + 2.50E^{-4}TL^2$	1.93	1.51	609.88	0.85

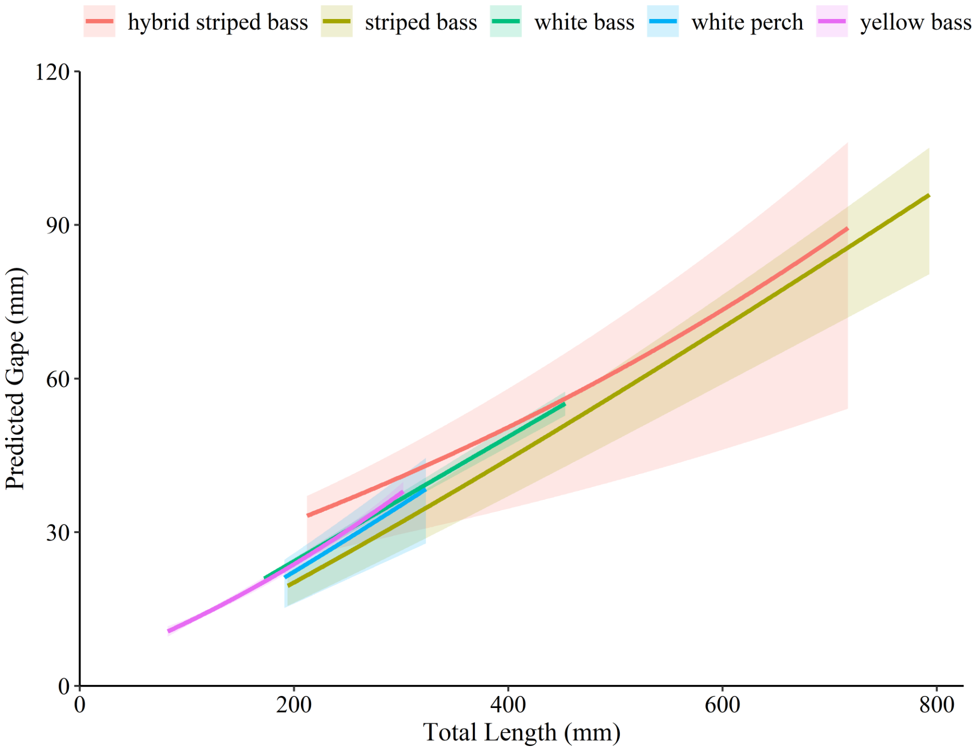

Figure 1. Mean (solid lines) and 99% predictive intervals for the gape-total length relationships observed for Moronids (Hybrid Striped Bass *Morone saxatilis x M. chrysops* [HSB], Striped Bass *M. saxatilis* [STB], White Bass *M. chrysops* [WHB], White Perch *M. americana* [WHP], Yellow Bass *M. mississippiensis* [YLB]) across the sizes observed. Any lines fitted through data points in the figure must be statistically significant and be supported by the mathematical equation and statistical information (P-values and R2 or R values). Keys to the symbols, formulae and regression values can be included in the figure itself or the caption, but not both. The minimum reduction for a figure may be indicated.

Comparing Gape-Vulnerability by TL

This interaction was significant within our binomial models (z range = 5.46-174.40, all P < 0.05), therefore only the interaction was interpreted. McFadden's pseudo R^2 estimates for all models were high (ρ^2 range = 0.20-0.64) indicating strong relationships between gape-based vulnerability and the size of Moronids and shad, suggesting all models fit adequately. This was confirmed by results of the Hosmer-Lemeshow Goodness of Fit tests (X^2 range = 8,539-105,397, df range = 23,815-101,559, all $P > 0.05$).

Several relationships were observed within our binomially distributed GLMs (Figure 3). Our results suggest that small Gizzard Shad were more vulnerable to smaller Hybrid Striped Bass than comparably sized Striped Bass, with vulnerability becoming equal to that of mixed as Moronid TL increased. This suggested that larger Gizzard Shad become more vulnerable to Hybrid Striped Bass than Striped Bass as TL increases. However, this is an artifact of the model detecting that Hybrid Striped Bass's gape-advantage increases to larger sized shad as they grow since vulnerability of the largest Gizzard Shad (i.e., 481 mm TL) plotted was equal. Hybrid Striped Bass had a slight competitive advantage for smaller Gizzard Shad at smaller sizes when compared to White Bass, Yellow Bass, and White Perch, although this decreased with increasing TL. White Bass appeared to have a slight gape advantage over Striped Bass and White Perch for the small-

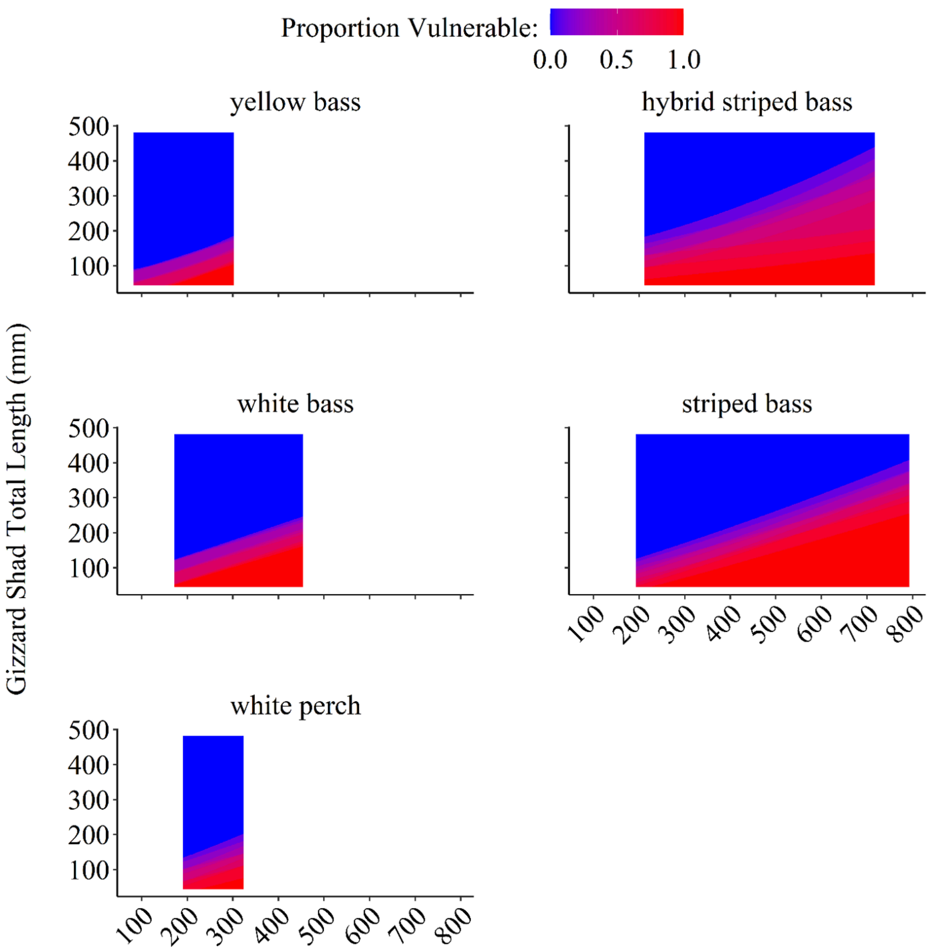

Figure 2. Average gape-based vulnerability of Gizzard Shad (*Dorosoma cepedianum*) to each Moronid (Hybrid Striped Bass *Morone saxatilis x M. chrysops* [HSB], Striped Bass *M. saxatilis* [STB], White Bass *M. chrysops* [WHB], White Perch *M. americana* [WHP], Yellow Bass *M. mississippiensis* [YLB]) predator across the sizes observed.

est Gizzard Shad sizes; however, this advantage decreased with increasing TL. White Bass appeared to have little competitive advantage over Yellow Bass. White Perch had an advantage over Striped Bass of similar size for the smallest sized Gizzard Shad. Small Yellow Bass had a competitive advantage over similarly sized Striped Bass and White Perch when competing for the smallest sized Gizzard Shad. Yellow Bass advantage appears to shift to shad of larger sizes (though still small) as Moronid lengths increased.

Growth Modeling

To make growth trajectories biologically reasonable (i.e., non-negative) the following parameter estimates were adjusted: the lower 0.5% PI for size of an age-0 Yellow Bass was adjusted to 25 mm TL (Burnham 1910), the lower 0.5% PI for size of an age-0 Striped Bass was adjusted to 25 mm TL (Boynton et al. 1981), and the lower 0.5% PI and mean estimated sizes of an age-0 White Bass was adjusted to 46 mm and 51 mm TL, respectively (Bonn 1953). The lower 0.5% PI and mean estimated sizes of an age-0 and age-1 Gizzard Shad were fixed at 25 and 29mm TL (Miller 1960, Michaletz 1997), respectively. Given these estimates were unrealistic, and they impacted a total of 6 observations, we considered this appropriate. To keep growth trajectories feasible, the maximum size a Gizzard Shad

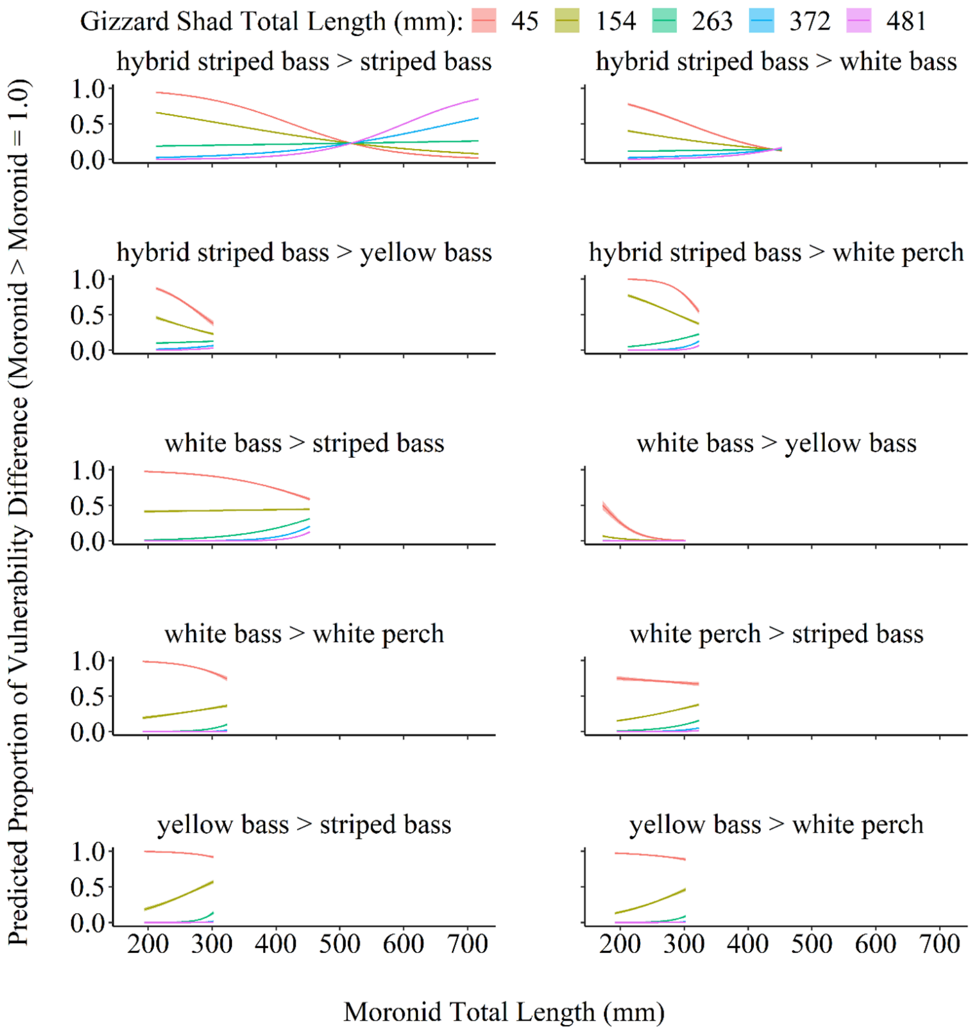

Figure 3. Predictive proportion of vulnerability of Gizzard Shad (*Dorosoma cepedianum*) to each Moronid (Hybrid Striped Bass *Morone saxatilis x M. chrysops* [HSB], Striped Bass *M. saxatilis* [STB], White Bass *M. chrysops* [WHB], White Perch *M. americana* [WHP], Yellow Bass *M. mississippiensis* [YLB]) predator across similar size ranges based on the gape-total length vulnerability relationships. Moronids on the left of the > are scored a "1" and Moronids on the right and equal vulnerability are scored a "0". High estimates can be interpreted as advantages for the Moronid on the left and low estimates can be interpreted as equal or greater advantage for the Moronid on the right.

could attain was set at 521 mm TL (the highest TL ever recorded; Trautman 1981). This affected the upper 99% PI estimates for age-10 to age-13 Gizzard Shad. Given fish of this size are almost completely invulnerable to predation, this did not influence our findings.

Bootstrapped growth trajectories for Gizzard Shad and Moronids appeared to adequately capture the growth trajectories present within our populations, as observed size at age data primarily fell within the estimated 99% PI (Figure 4). Graphical interpretation of bootstrapped growth distributions suggested that Striped Bass had the fastest growth trajectory followed by Hybrid Striped Bass; however, maximum size potential

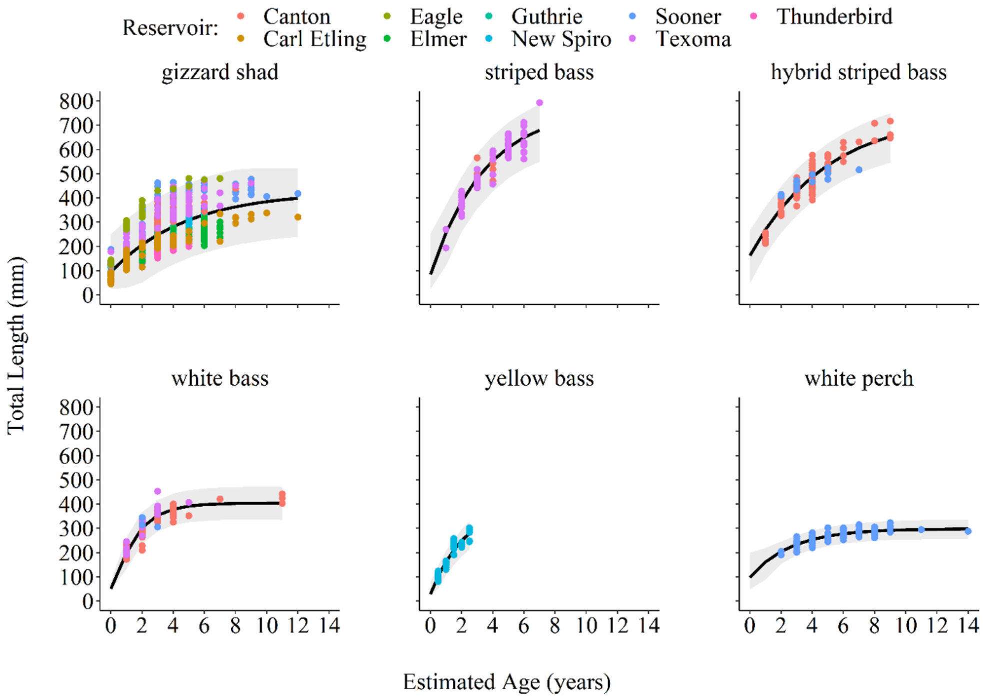

Figure 4. Mean (solid line) and 99% predictive intervals (grey shading) obtained from bootstrapping for Von bertalanffy growth trajectories for each Moronid (Hybrid Striped Bass *Morone saxatilis x M. chrysops* [HSB], Striped Bass *M. saxatilis* [STB], White Bass *M. chrysops* [WHB], White Perch *M. americana* [WHP], Yellow Bass *M. mississippiensis* [YLB]) species. Points indicate individual size at age observations from each population.

of Striped Bass was greater (Figure 2). Likewise, White Bass appeared to have a similar growth trajectory to Yellow Bass; however, they reached a greater theoretical-maximum average length. White Perch exhibited slower early growth and appeared to attain the shortest theoretical maximum lengths of any Moronid.

Gape estimates from growth curve modeling suggest that slow growth results in increased overlap between Moronids, resulting in reduced competitive advantages due to decreased growth (Figure 5). As growth rate increases to the mean rate and above, these estimates deviate from one another. This results in varying competitive advantages for each species based on their growth trajectories. The annular growth of Moronids appeared to allow larger bodied fishes increased access to older and larger shad (Figure 6). For White Perch, and to some degree White Bass, maximum body size appeared to limit access to older and larger shad.

Comparing Gape-Vulnerability by Age

No three-way interactions were detected by log-linear models (all $P > 0.05$). All CMH tests indicated significant variation in the vulnerability estimates of Gizzard Shad across age groups and the age of any two Moronids we compared (M^2 range = 39.2 – 290.7, *df* range = 20 – 132, all $P < 0.05$). Post hoc analyses detected no significant difference in shad vulnerability between ages for Striped Bass, White Bass, and Hybrid Striped Bass (all $P > 0.05$). Likewise, post hoc analyses detected no significant difference in shad vulnerability between ages for Yellow Bass, compared to either White Bass, Striped Bass, or White Perch (all $P > 0.05$). In all the above cases, it was confirmed that the significant result from the CMH test was due to variation in shad vulnerability between ages within one of the species (all $P < 0.05$). Hybrid Striped Bass had a gape-based

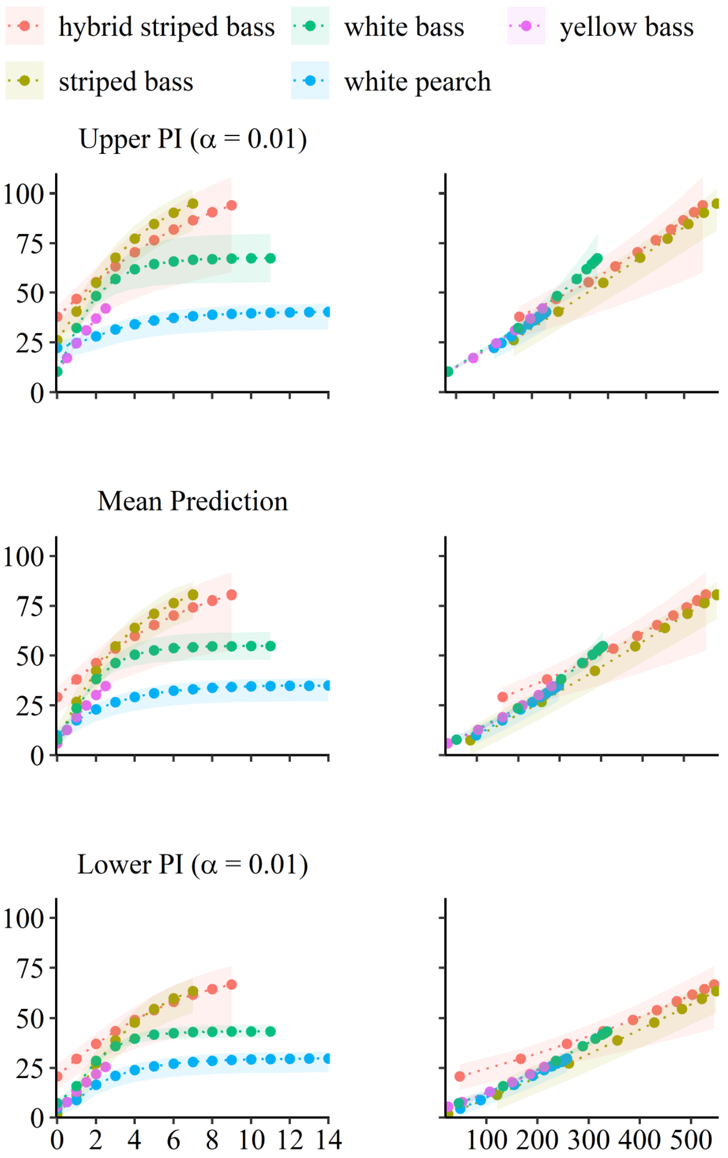

Figure 5. Mean (solid lines) and 99% predictive intervals for the gape-total length relationships observed for Moronids (Hybrid Striped Bass *Morone saxatilis x M. chrysops* [HSB], Striped Bass *M. saxatilis* [STB], White Bass *M. chrysops* [WHB], White Perch *M. americana* [WHP], Yellow Bass *M. mississippiensis* [YLB]) based on the upper, lower, and mean estimates of growth from bootstrapped Von bertalanffy growth trajectories. Comparisons are made based on ages (left) and predicted total lengths (right) for each species to understand how overlap varies relative to growth.

advantage over Yellow Bass across all age ranges compared (all $P < 0.05$); however, this advantage was always weak (V range = 0.18-0.20). We also observed a gape-based advantage for Hybrid Striped Bass over White Perch from age-1 to age-9 (all $P < 0.05$). No advantage was observed at age-0 ($P > 0.05$), a significant but weak advantage was observed from age-1 to age-3 (V = 0.18-

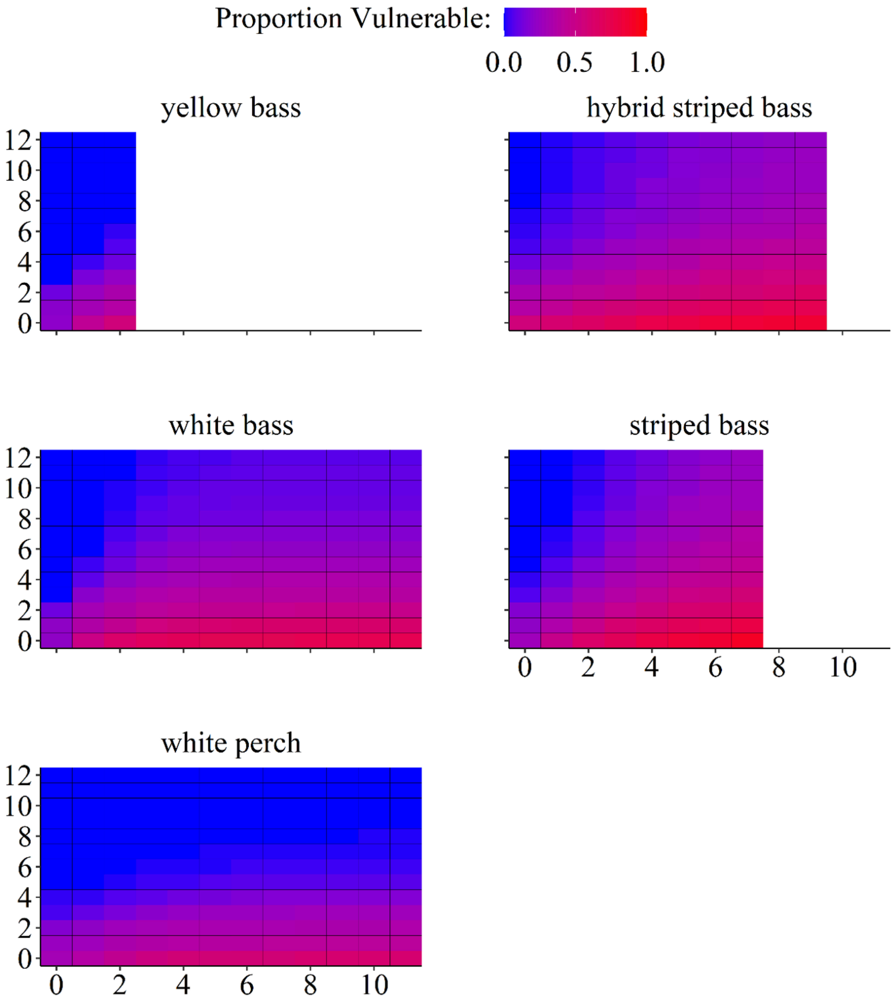

Figure 6. Average gape-based vulnerability of Gizzard Shad (*Dorosoma cepedianum*) to each Moronid (Hybrid Striped Bass *Morone saxatilis x M. chrysops* [HSB], Striped Bass *M. saxatilis* [STB], White Bass *M. chrysops* [WHB], White Perch *M. americana* [WHP], Yellow Bass *M. mississippiensis* [YLB]) predator across the range of age estimates observed.

0.28), and a moderate advantage was observed from age-4 to age-9 (V range = 0.30-0.32), suggesting Hybrid Striped Bass gain increased advantages over White Perch based on their growth trajectories. White Bass also exhibited a varying gape-based competitive advantage over White Perch, with no significant advantage from age-0 to age-2 (all $P > 0.05$) and a weak (V range = 0.23-0.27) significant advantage thereafter to age-11 (all $P < 0.05$). Age-0 and age-1 Striped Bass had no competitive advantage over White Perch (all $P > 0.05$), but a significant advantage from age-3 on (all $P < 0.05$). Their advantage was weak at age-3 and age-4 (V range = 0.21-0.29), then increased to moderate from age-5 on (V ≈ 0.32).

Discussion

Our results collectively demonstrate that gape/TL relationships, vulnerability estimates, and growth trajectories interact to shape competitive foraging advantages among Moronids.

Species differed substantially in their gape/TL allometries, producing size-dependent shifts in the relative vulnerability of Gizzard Shad to each Moronid. GLM analyses showed that these differences translate into variable vulnerability across the size spectrum of both predators and prey, with small-bodied Moronids generally exhibiting greater access to the smallest shad. Growth modeling further revealed that faster-growing species (e.g., Striped Bass, Hybrid Striped Bass) gain increasing gape-based foraging advantages as they age. In contrast, slower-growing or smaller-bodied species (e.g., White Perch, Yellow Bass) are progressively limited to younger, smaller shad. Finally, age-based vulnerability analyses indicated that these competitive hierarchies are reinforced across ontogeny, with some species gaining moderate advantages only after several years of growth. Together, these findings highlight the importance of integrating gape allometry and growth dynamics when evaluating potential diet overlap and forage competition in mixed-Moronid fisheries.

Contrasting results comparing gape-vulnerability suggests accounting for ecological phenomena that confound direct comparisons (e.g., growth trajectories) can better explain diet overlap. Though we were unable to find a similar example of this phenomenon within the Moronid family, size mediated availability for forage has been documented prior in *Lepomis* species, with larger *Lepomis* having reduced niche overlap and likely reduced diet overlap for resources (Mittelbach 1984). Growth-mediated diet overlap appears to be occurring in Moronids, allowing fishes who may not have a competitive advantage at a similar length to reach larger sizes and obtain a larger gape. This allows them to better compete within the conspecifics of their genus. Given the link between gape and forage size (Labropoulou and Eleftheriou 1997, Mihalitsis and Bellwood 2017), these results suggest that growth rates and the resulting size structure of species present within a mixed-Moronid fishery are important in mediating potential overlap in forage availability.

Perhaps most interesting is the advantage of Moronids, which generally reach a smaller maximum size (e.g., Yellow Bass) over those reaching a larger maximum size (e.g., Striped Bass). Though theoretical in nature, the general pattern in TL-gape relationships suggests that smaller bodied Moronids appear to be predisposed to better exploit smaller bodied prey. Apart from Hybrid Striped Bass that appear to inherit the gape-based advantages of White Bass and the growth-based advantages of Striped Bass, smaller bodied Moronids appear to have larger gapes at smaller sizes. This could influence diet overlap, especially in younger Moronids, and impact recruitment, growth, and mortality of gamefish populations (Miller 1960; Michaletz 1997). It is important to note that we investigated the mechanistic potential for diet overlap within these fishes to gain a proper understanding of their ability to exploit the forage base within these systems, and diet studies would be required to measure actual consumption.

Though forage-based competition between Moronids in Oklahoma reservoirs is possible, it can occur only when resources are limited (Polis and Winemiller 1996). By estimating gape-vulnerability, we approximated a theoretical foraging niche (Schoener 2009) for each species. Though this has been documented previously among Moronids (Irons et al. 2002, Olson 2004, Feiner et al. 2013), it may not always occur if species can partition resources among themselves (e.g., Rash 2003). Within the context of our results, the available forage base appears to be a key component of the successful management of Moronids and mixed-Moronid fisheries in particular.

Across the US, *Dorosoma* spp. are an important forage fish and a primary forage source for mature individuals from each of the above mentioned Moronid species (Matthews et al. 1988, Hodson 1989, Bauer 2002, Guy et al. 2002). Large-bodied individuals of the *Dorosoma* genus are associated with negative impacts on sportfish populations (Lyons et al. 2018). Therefore, an inadequate abundance of appropriately sized prey may require manipulation to maintain or enhance Moronid populations and mixed Moronid fisheries. Though shad size structure manipulation may be achieved through predator stocking (Ostrand et al. 2001), abundance appears to be regulated by abiotic factors (e.g., temperature, precipitation, productivity; DiCenzo et al. 1996, Bremigan and Stein 2001). Therefore, it may be important to monitor alternative prey sources used by Moronids (e.g., insects, Snow and Porta 2020) or introduce new forage (e.g., threadfin shad [*Dorosoma petenense*], Maceina and Sammons 2015) if it appears that diet overlap is limiting growth or production. This is especially true at small sizes where gape overlap appears greatest between Moronids.

Assuming that a proper forage base is maintained, competition between Moronids should be reduced; however, predation-based competition is complex and intragenus predation (i.e., the consumption of one Moronid by another; Polis et al. 1989) may occur. For example, White Perch have been documented to eat eggs of other species, which may influence recruitment (Schaeffer and Margraf 1987). On the eastern coast of the United States Hybrid Striped Bass have been hypothesized to compete with native Striped Bass for food and habitat (Patrick and Moser 2001). Therefore, when applying these results, managers should note that competition for food resources may not be the only axis along which these species compete.

Gape based limitation offers managers another tool for managing Moronids and mixed-Moronid fisheries. For example, our results suggest that further invasion of White Perch and range expansion of Yellow Bass in Oklahoma may induce increased forage overlap between Moronids at smaller sizes. Diet compositions from the literature for White Perch and Yellow Bass suggest that White Perch are likely more detrimental to other Moronids (Schaeffer and Margraf 1987, Snow and Porta 2020).

Within our subset of study reservoirs Sooner Lake and Lake Texoma offer a chance to investigate this hypothesis, focusing on mixed-Moronid relationships between Hybrid Striped Bass, Striped Bass, and White Perch. White Perch are established in Sooner Lake, where growth rates of Hybrid Striped Bass are reduced, and Striped Bass are large but in low abundance. Comparatively, no White Perch are present in Lake Texoma, and both Hybrid Striped Bass and Striped Bass exhibit adequate growth (OFAT 2022). Based on our modeled results, a potential cause of these contrasting scenarios is increased competition at smaller size classes by invasive White Perch. Reduced growth potential in Sooner Hybrid Striped Bass and larger sized but low abundance Striped Bass may result from faster growing individuals from each population having higher survival due to reduced competition with White Perch. This may have allowed faster growing Hybrid Striped Bass to mature early, thus stunting the population through density dependent feedbacks (Ylikarjula et al. 1999). The few Striped Bass that survive through this multi-level competition would then be large, but in lower abundance due to the increased biomass of smaller Hybrid Striped Bass. Though diet information would be needed to prove this hypothesis, the lower productivity of Sooner Lake relative to Lake Texoma makes it probable as productivity is tied to Gizzard Shad abundance (OWRB 2019).

We have shown that gape-vulnerability of forage can be easily estimated and compared between size or age structure for Moronids, allowing fisheries managers another tool to assess diet overlap within a system. We documented gape-based advantages to growth rates, and why they should be considered when managing fisheries. This is important as growth effects on competition, though extensively documented, are poorly understood in the fisheries field (Mittelbach 1984; Reed et al. 2019). Given this strong theoretical basis (Mihalitsis and Bellwood 2017; Dennerline and Van Den Avyle 2000), managers concerned with forage availability for Moronids can use gape-based vulnerability to both estimate forage availability and diet overlap between species as well as gauge how growth mediates these interactions. This being said, and caution against blind application. Suppose forage is hypothesized to be limited and exploitation appears likely, as was the case for our Sooner Lake-Lake Texoma comparison. In that case, managers should first estimate diet overlap, prey abundance, and intragenus predation to determine if manipulation of the forage base or Moronid population is warranted. If this is the case, we recommend following standardized fisheries methods (e.g., stocking manipulation, Ostrand et al., 2001; forage introduction, Maceina and Sammons, 2015) to determine whether the population can be manipulated to meet management objectives.

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References

Agresti, A. 2002. An Introduction to Categorical Data Analysis, 2nd edition. Wiley-Interscience, Hoboken, New Jersey.

Bauer, D. L. 2002. White Bass population differences in Nebraska reservoirs with Gizzard Shad or alewife prey bases. North American Journal of Fisheries Management 22:665-670.

Bax, N. J. 1998. The significance and prediction of predation in marine fisheries. ICES Journal of Marine Science 55:997-1030.

Baxter, C. V., K. D. Fausch, M. Murakami, and P. L. Chapman. 2004. Fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. Ecology 85:2656-2663.

Benjamini, Y., and Y. Hochberg. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. Journal of the Royal Statistical Society Series B 57:289-300.

Bergsma, W. 2013. A bias-correction for Ceramer's V and Tschuprow's T. Journal of the Korean Statistical Society 42:323-328.

Blessing, J.J., J.C. Marshall, and S.R. Balcombe. 2010. Humane killing of fish for scientific research: a comparison of two methods. Journal of Fish Biology 76:2571–2577.

Bonn, E. W. 1953. The food and growth rate of young White Bass (*Morone chysops*) in Lake Texoma. Transactions of the American Fisheries Society 82:213-221.

Boynton, W. R., H. Zion, and T. T. Polgar. 1981. Importance of juvenile Striped Bass food habits on the Potomac Estuary. Transactions of the American Fisheries Society 110:56-63.

Bremigan, M. T., and R. A. Stein. 2001. Variable Gizzard Shad recruitment with reservoir productivity: causes and implications for classifying systems. Ecological Applications 11:1425-1437.

Bulak J. S., C. C. Coutant, and J. A. Rice. 2013. Preface. Pages ix-xii *in* J. S. Bulak, C. C. Coutant, J. A. Rice, editors. Biology and management of inland Striped Bass and Hybrid Striped Bass. American Fisheries Society, Bethesda, Maryland.

Burnham, C. W. 1910. Notes on the Yellow Bass. Transactions of the American Fisheries Society 39:103-108.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and inference: A practical information-theoretic approach, 2nd Edition. Springer-Verlag, New York, New York.

Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson 1985. Cascading trophic interactions and lake productivity. Bioscience 35:634-639.

Cochran, W. G. 1954. Some Methods for Strengthening the Common Chi-Squared Tests. Biometrics 10:417–51.

Clayton, D.L., and M.J. Maceina. 1999. Validation of annulus formation in Gizzard Shad otoliths. North American Journal of Fisheries Management. 19:1099-1102.

Cohen, J. 1988. Statistical power analysis for the behavioral sciences. 2nd edition. Routledge. New York, New York.

Coutant, C. C. 2006. Thermal effects on fish ecology. Pages 1146-1151 *in* J. R. Pfafflin JR, and Ziegler EN, editors. Encyclopedia of environmental science and engineering 5th edition. Taylor and Francis

Group, Boca Raton, Florida.

Dennerline, D. E., and M. J. Van Den Avyle. 2000. Sizes of prey consumed by two pelagic predators in US reservoirs: implications for quantifying biomass of available prey. Fisheries Research 45:147-154.

DeVries, D. R., R. A. Stein, and M. T. Bremigan. 1998. Prey selection by larval fishes as influenced by available zooplankton and gape limitation. Transactions of the American Fisheries Society 127:1040-1050.

DiCenzo, V. J., M. J. Maceina, M. R. Stimpert. 1996. Relations between Reservoir tropic state and Gizzard Shad population characteristics in Alabama reservoirs 16:888-895.

Dunic, J. C., and J. K. Baum. 2017. Size structuring and allometric scaling relationships in coral reef fishes. Journal of Animal Ecology 86:577-589.

Feiner Z. S., and J. A. Rice. 2013. Trophic niche and diet overlap between invasive White Perch and resident White Bass in a southeastern reservoir. Transactions of the American Fisheries Society 142:912-919.

Gilliland, E. R. 1978. Food habits of Striped Bass x White Bass hybrids and Largemouth Bass in Sooner Lake, Oklahoma. Master's Thesis, Oklahoma State University, Stillwater, Oklahoma.

Guy, C. S., R. D. Schultz, M. A. Colvin. 2002. Ecology and management of White Bass. North American Journal of Fisheries Management 22:606-608.

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.

Hill, J. E., L. G. Nico, C. E. Cichra, and C. R. Gilbert. 2004. Prey vulnerability to Peacock Cichlids and Largemouth Bass based on predator gape and prey body depth. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 58:47-56.

Hodson, R. G. 1989. Hybrid Striped Bass: biology and life history. Texas Agricultural Extension Service, Southern Regional Aquaculture Center publication no. 300, Texas A&M University, College Station.

Hoff, G.R., D.J. Logen, and M.F. Douglas. 1997. Otolith morphology and increment validation in young Lost River and Shortnose Suckers. Transactions of the American Fisheries Society 126:488-494.

Hurvich, C. M., and C. Tsai. 1989. Regression and time series model selection in small samples. Biometrika 76(2):297-307.

Irons, K. S., T. M. O'Hara, M. A. Mclelland, and M. A. Pegg. 2002. White Perch occurrence, spread, and hybridization in the middle Illinois River, Upper Mississippi River system. Transactions of the Illinois Academy of Science 95:207-214.

Krebs, J. M., and R. G. Turingan. 2003. Intraspecific variation in gape-prey size relationships and feeding success during early ontogeny in Red Drum, Sciaenops ocellatus. Environmental Biology of Fishes 66:75-84.

Labropoulou, M., and A. Eleftheriou. 1997. The foraging ecology of two pairs of cogeneric demersal fish species: Importance of morphological characteristics in prey selection. Journal of Fish Biology 50:324-340.

Lawrence, J. M. 1957. Estimated sizes of various forage fishes Largemouth Bass can swallow. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 11:220-225.

Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. Ecology, 23:399–417.

Lyons, M.T., R.A., Snow, and M.J. Porta. 2018. Population characteristics of Gizzard Shad introduced into a small western Oklahoma impoundment. Proceedings of the Oklahoma Academy of Science 98:25-32.

Maceina, M. J., and S. M. Sammons. 2015. Stocking Threadfin Shad to enhance Largemouth Bass population in two Alabama ponds. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 2:28-34.

Mantel, N., and W. Haenszel. 1959. Statistical

Aspects of the Analysis of Data from Retrospective Studies of Disease. Journal of the National Cancer Institute 22:719–48.

Matthews W. J., L. G. Hill, D. R. Edds, J. J. Hoover, and T. G. Heger. 1988. Trophic ecology of Striped Bass, Morone saxatilis, in a freshwater reservoir (Lake Texoma, U.S.A.). Journal of Fish Biology 33:273-288.

McFadden, D. 1974. Conditional logit analysis of qualitative choice behavior. Pages 105-142 *in* Zarembka, P, editor. Frontiers in econometrics. New York, New York: Academic Press.

McFadden, D. 1979. Quantitative methods for analyzing travel behaviour of individuals: Some recent developments. Pages 279-318. *in* D. A. Henshe, P. R. Stopher, editors. Behavioural Travel Modeling. Croom Helm, London, United Kingdom.

McQueen, D. J., J. R. Post, E. L., and Mills. 1986. Trophic relationships in freshwater pelagic ecosystems. Canadian Journal of Fisheries and Aquatic Sciences 43:1571–1581.

Michaletz, P. H. 1997. Factors affecting abundance, growth, and survival of Age-0 Gizzard Shad. Transactions of the American Fisheries Society 126:84-100.

Mihalitsis, M., and D. R. Bellwood. 2017. A morphological and functional basis for maximum prey size in piscivorous fishes. PLOS One 12:e0184679

Miller, R. R. 1960. Systematics and biology of the Gizzard Shad (*Dorosoma cepedianum*) and related fishes. Fishery Bulletin 173. United States Department of the Interior. United States Fish and Wildlife Service, Washington, DC.

Miller, R. J. and H. W. Robison. 2004. Fishes of Oklahoma. University of Oklahoma Press, Norman, Oklahoma.

Mittelbach, G. G. 1984. Predation and resource partitioning in two sunfishes (Centrarchidae). Ecology 65:499-513.

OFAT (Oklahoma Fishery Analysis Tool). 2022. Oklahoma fishery analysis tool: an R-based application for analysis of standardized fishery samples. Oklahoma Department of Wildlife Conservation. <https://www.odwcfishdata.shinyapps.io/ssp_app/>. Accessed 29 May 2022.

Oklahoma Water Resources Board. 2019. Oklahoma Lakes Report: Beneficial Use Monitoring Program (Bump). <www.owrb.ok.gov>. Accessed 29 May 2022.

Olson, N. W. 2004. Interactions among Hybrid Striped Bass, White Bass, and Walleye in Harlan County Reservoir. Master's Thesis, Montana State University, Bozeman, Montana.

Ostrand, K. G., H. L. Schramm Jr., J. E. Kraai, B. Braeutigam. 2001. Effects of intensive stocking of Hybrid Striped Bass on the population structure of Gizzard Shad in a West Texas impoundment, a Case Study. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 55:324-333.

Pace, M. L., J. J. Cole, S. R. Carpenter, and J. F. Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. Trends in Ecology and Evolution 14:483–488.

Patrick, W. S., and M. L. Moser. 2001. Potential competition between Hybrid Striped Bass (*Morone saxtilis* × *M. americana*) and Striped Bass (*M. saxtilis*) in the Cape Fear River Estuary, North Carolina. Estuaries 24:425-429.

Polis, G. A., C. A. Myers, and R. D. Holt. 1989. The ecology and evolution of intraguild predation: Potential competitors that eat each other. Annual Review of Ecology and Systematics 20:297-330.

Polis, G. A., and K. O. Winemiller. 1996. Food webs: Integration of patterns and dynamics. Springer, New York, New York.

Power, M. E. 1992. Top-down and bottom-up forces in food webs: Do plants have primacy? Ecology 73:733-746.

Rash, J. M. 2003 Comparative ecology of juvenile Striped Bass and juvenile Hybrid Striped Bass in Claytor Lake, Virginia. Master's Thesis, Virginia Polytechnic Institute and State University, Blacksburg, Virginia.

Reed C, R Branconi, J Majoris, C Johnson, and

P Buston. 2019 Competitive growth in a social fish. Biology Letters 15:20180737

Secor, D. H., J. M. Dean, and E. H. Laban. 1992. Otolith removal and preparation for microstructural examination. Pages 19–57 *in* D.K. Stevenson and S.E. Campana, editors. Otolith microstructure examination and analysis. Canadian Special Publication of Fisheries and Aquatic Sciences 117, Ottawa.

Schaeffer, J. S., and F. J. Margraf. 1987. Predation on fish eggs by White Perch, Morone americana, in western Lake Erie. Environmental Biology of Fishes 18:77-80.

Schoener, T. W. 2009. Ecological niche. Pages 3-13 *in* S. A. Levin, S. R. Carpenter, and H. C. Godfray, editors. The Princeton guide to ecology. Princeton University Press, Princeton, New Jersey.

Schultz, R. D., A. L. Fowler, J. M. Goeckler, and M. C. Quist. 2013. Comparisons of growth for Hybrid Striped Bass in North America. Pages 219-227 *in* J. S. Bulak, C. C. Coutant, and J. A. Rice. Editors. Biology and Management of Inland Striped Bass and Hybrid Striped Bass. American Fisheries Society, Symposium 80, Bethesda, Maryland.

Slaughter, J. E., and B. Jacobson. 2008. Gape: Body size relationship of Flathead Catfish. North American Journal of Fisheries Management 28:198-202.

Snow, R. A., and M. J. Porta. 2020. Population dynamics and diets of Yellow Bass in New Spiro Reservoir, Oklahoma. Proceedings of the Oklahoma Academy of Sciences 100:54-61.

Trautman, M. B. 1981. The fishes of Ohio. The Ohio State University Press, Columbus, OH.

Wang, C. J., and H. Iyer. 2005. On higher-order corrections for propagating uncertainties Metrologia 42: 406-410.

Ylikarjula, J., M. Henio, and U. Dieckmann. 1999. Ecology and adaptation of stunted growth in fish. Evolutionary Ecology 13:433-453.