Prey Vulnerability to Peacock Cichlids and Largemouth Bass Based on Predator Gape and Prey Body Depth

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Abstract: The interaction of prey fish body depth and predator gape size may produce prey assemblages dominated by invulnerable prey and excessive prey-to-predator biomass ratios. Peacock cichlids *(Cichla ocellaris)* were stocked into southeast Florida canals to consume excess prey fish biomass, particularly spotted tilapia *(Tilapia mariae).* The ecomorphologically similar largemouth bass *(Micropterus salmoides)* was already present in the canals. We present relations of length-specific gape size for peacock cichlids and largemouth bass. Both predators have broadly overlapping gape size, but largemouth bass ≥126 mm total length have slightly larger gape sizes than peacock cichlids of the same length. Also, we experimentally tested the predictions of maximum prey size for peacock cichlids and determined that a simple method of measuring gape size used for largemouth bass also is appropriate for peacock cichlids. Lastly, we determined relations of body depth and length of prey species to investigate relative vulnerability. Using a simple predator-prey model and length frequencies of predators and bluegill *(Lepomis macrochirus),* redear sunfish *(Lepomis microlophus),* and spotted tilapia prey, we documented that much of the prey biomass in southeast Florida canals is unavailable for largemouth bass and peacock cichlid predation.

Key words: Cichla ocellaris, Micropterus salmoides, gape size, gape limitation

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The dominant predatory fishes of most freshwater assemblages are gape-limited (Zaret 1980a). These predators swallow prey whole, and gape size limits the maximum size of prey consumed (Swingle 1950, Zaret 1980a). The vulnerability of prey larger than predator gape size is reduced to zero (Zaret 1980a, Hambright et al. 1991). Therefore, prey species with a high ratio of body depth-to-body length will be less vulnerable to predation and enter absolute prey size refuges at shorter lengths than species with a low ratio (i.e., large body depth is a morphological antipredator defense) (Hambright et al. 1991, Pettersson et al. 2000).

Prey size refuges based on gape limitation of the predator assemblage can influence the size structure and species composition of fish communities (Hambright et al. 1991, Persson et al. 1996). Indeed, for prey species that grow to large sizes, individuals eventually reach absolute size refuges and become invulnerable to piscivorous fishes. This can lead to domination of fish communities by large- or deep-bodied prey species and populations by large individuals (i.e., invulnerable prey) (Hambright et al. 1991, Persson et al. 1996). A considerable biomass of invulnerable prey fish can lead to excessively high ratios of prey-to-predator biomass (sensu Swingle 1950, see also Jenkins and Morais 1978). Such excessive ratios have occurred in several freshwater systems, including canals in southeast Florida. This canal system has numerous exotic cichlids which rapidly grow to large (i.e., invulnerable) sizes and which may dominate in numerical and biomass abundance (Shafland 1995).

The peacock cichlid *(Cichla ocellaris)* from tropical South America, also known as peacock bass or butterfly peacock, was introduced into southeast Florida canals in 1984 to serve as a biological control over excessive prey fish biomass, particularly the dominant spotted tilapia *(Tilapia mariae)* (Shafland 1995). Largemouth bass *(Micropterus salmoides)* was already present in the canals. Both species also co-occur in Hawaii (Zaret 1980b) and Puerto Rico (Lilyestrom and Churchill 1996), where both were introduced. Based on morphology and feeding mechanics, Norton and Brainerd (1993) concluded that the South America cichlid genus *Cichla* and the North American centrarchid genus *Micropterus* were ecomorphologically similar. Co-occurring predatory fishes with similar gape sizes may feed on the same types and sizes of prey and exert comparable effects on prey assemblages (i.e., prey are equally vulnerable to both predators).

Given the morphological similarity of largemouth bass and peacock cichlids, we predicted that a simple method of estimating gape size used for largemouth bass (i.e., external mouth width; Lawrence 1958, Hambright 1991, Johnson and Post 1996) would also estimate peacock cichlid gape size. Moreover, we predicted that peacock cichlids and largemouth bass would have similar length-specific gape sizes and that prey fish therefore would have similar relative vulnerabilities to predation by both species. In this study, we present the first published model estimating peacock cichlid gape size based on length (see also Hill 2003), and test this model experimentally to determine maximum prey size. We also compared the relations of gape size and length between peacock cichlids and largemouth bass. We developed models predicting body depth given total length for common prey species in southeast Florida canals. Lastly, we used the predator-prey model of Hambright et al. (1991) to estimate vulnerability to predation by largemouth bass and peacock cichlids for important prey species in southeast Florida fish assemblages.

Methods

Regression models describing the relation of gape width (GW) and maximum total length (TL) were calculated for peacock cichlids and largemouth bass (SAS 1985). A Type-I error rate of $\alpha = 0.05$ was used for all statistical procedures in this study. Specimens were obtained from the Florida Museum of Natural History (FLMNH). The method used to measure gape width in this study was chosen because it is simple, requires only commonly available calipers, and has been used in previous studies as an effective means for estimating gape limitation in largemouth bass. Gape width was measured as external mouth width: the external distance across the head, with the mouth closed, from the outside of one maxillary bone to the outside of the other (Lawrence 1958). The actual morphological feature of the predator that limits maximum prey size may vary across taxa, but it is the distance between the cleithral bones in the Centrarchidae (Lawrence 1958, Wainwright and Richard 1995). Although not a direct measure, external mouth width closely approximates intercleithral distance for largemouth bass, and we predicted that it would be an appropriate estimator for peacock cichlid gape size as well.

We conducted a laboratory experiment to determine maximum prey size across a range of peacock cichlid lengths and test the predictions of our gape size model. Twelve peacock cichlids (mean TL ± SD = 293 ± 45 mm; TL range = 222–378 mm) were used, and bluegills *(Lepomis macrochirus)* were used as prey in the experiment. Bluegills were utilized as representative prey rather than spotted tilapia. Both species are morphologically similar and are common peacock cichlid prey items; however, spotted tilapia is a prohibited species in Florida, requiring permits and special precautions against escape. Peacock cichlids were obtained by angling ($N = 6$) in Cutler Drain Canal, Miami-Dade County, Florida, or by donation ($N = 6$) from the Non-Native Fish Research Laboratory, Florida Fish and Wildlife Conservation Commission, Boca Raton, Florida. Bluegills were netted from ponds of the Department of Fisheries and Aquatic Sciences, University of Florida, Gainesville, Florida. The experiment was conducted in indoor fiberglass tanks (1.8 m dia. × 1 m high and 1.5 m dia. × 1 m high) at the U.S. Geological Survey, Florida Integrated Science Center, Gainesville, Florida. Tanks were bare except for a 5-cm diameter central standpipe, two aquarium heaters, and an airstone. Well water was slowly trickled through each tank and water parameters were maintained at 27–30 C, 7.5–8.0 pH, 7.2–7.8 mg/L dissolved oxygen, and near 0 mg/L ammonia nitrogen and nitrite nitrogen. Each peacock cichlid was tested individually following a week of acclimatization to the experimental tank. Each trial was begun by the introduction of a single bluegill with a body depth of about 85% of the peacock cichlid's estimated gape size. Bluegill size was increased daily by about 5% until the predator refused or was unable to eat the prey. If a bluegill was still present after 24 hours, another bluegill of equal size was introduced. The procedure was repeated the third day if neither of the first two bluegills was eaten. If no bluegill of this size was consumed during the three days, a smaller bluegill was added to the tank. The trial was completed when the smaller bluegill was eaten, demonstrating that the predator was not refusing food. Once tested experimentally, the peacock cichlid gape size model was compared to the model developed in the present study for largemouth bass by analysis of covariance (ANCOVA) (SAS 1985).

We developed regression models of body depth versus total length (SAS 1985) to determine the relative vulnerability of common prey species in southeastern Florida—bluegill, largemouth bass, redear sunfish *(Lepomis microlophus),* spotted sunfish *(Lepomis punctatus),* warmouth *(Lepomis gulosus),* black acara *(Cichlasoma bimaculatum),* jewel cichlid *(Hemichromis letourneauxi),* and spotted tilapia. Specimens were obtained from the FLMNH. Other common prey species such as bluefin killifish *(Lucania goodei),* eastern mosquitofish *(Gambusia holbrooki),* and swamp darter *(Etheostoma fusiforme)* (Shafland 1999b, Hill 2003) are small, elongate fishes that are morphologically available to all but the smallest largemouth bass and peacock cichlid predators. Gape-limited piscivores usually swallow a prey fish headfirst after orienting it to lay horizontally (Lawrence 1958, Hoyle and Keast 1987, Reimchen 1991). Therefore, body depth of the prey fish, rather than body length, is the important limiting prey dimension (Swingle 1950, Lawrence 1958, Hambright 1991). Body depth was measured as the maximum depth from dorsal to ventral surfaces of the fish with any intervening fins depressed.

We used length-frequency and abundance data for predators and prey to estimate relative vulnerability of a prey assemblage in a southeastern Florida canal system to predation by largemouth bass and peacock cichlids. Hambright et al. (1991) presented a simple predator-prey model to estimate relative prey vulnerability based

$$V_d = 1 - \sum_{w=0}^{d} W$$

on distributions of predator gape sizes and prey body depths in the fish assemblage, where V is relative vulnerability, *d* is body depth, and W is the frequency of mouth widths *(w)* in the predator population. The index ranges from 0 (prey invulnerable to all predators) to 1 (prey vulnerable to all predators). This model is based on the assumption that predator gape size and prey body depth are the primary determinants of prey sizes consumed by predators (Hambright et al. 1991). Although this model does not include other important factors in predator-prey relations (e.g., prey behavior) and therefore overestimates prey vulnerability, it provides a clear indication of prey that are not vulnerable to predation.

For this analysis, we used data of abundance (number and biomass) and length-frequency distributions for fishes in Black Creek Canal (C-1 and C-1N), Miami-Dade County, Florida (Shafland 1999a, Shafland 1999c). Black Creek Canal is a relatively large (13 km long, 40 ha surface area), artificial waterway draining into Biscayne Bay (Shafland 1999a). This system is well-studied relative to other southeast Florida canals due to several years of pre- and post-introduction quantitative sampling conducted as part of the planned peacock cichlid introduction (Shafland 1995, Shafland 1999a). We chose to include bluegill, redear sunfish, and spotted tilapia in the analysis as representative of the prey assemblage based on the abundance data. These were three of the four most abundant species and together composed 56% by number and 61% of the biomass in 72 concussion blocknet samples

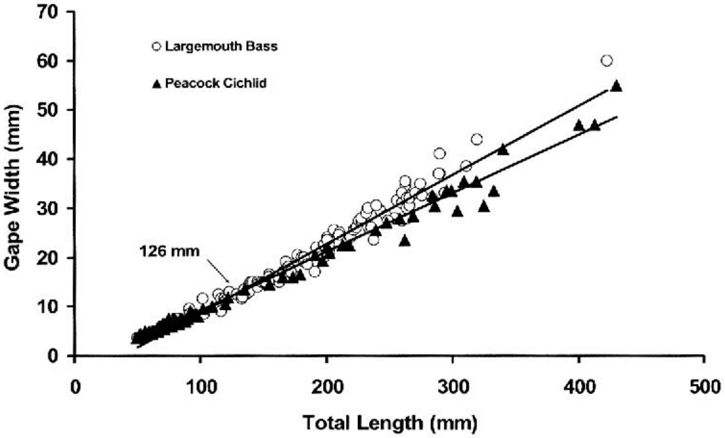

Figure 1. Relationship of gape width (GW) to total length (TL) for largemouth bass (GW = 0.14 TL – 5.59; $r^2 = 0.96$; $N = 121$) and peacock cichlids (GW = 0.12 TL – 2.69; $r^2 = 0.97$; $N = 92$) from southeast Florida. Several data points are hidden. The regression lines cross at 126 mm TL.

conducted over a 10-year period (Shafland 1999a). Largemouth bass and peacock cichlid length distributions from the literature represent electrofishing samples of individuals ≥ 254 mm TL (Shafland 1999c). Length distributions for predators < 254 mm TL were lacking.

Results

Peacock cichlid and largemouth bass gape sizes were strongly correlated linear functions of total length (Fig. 1).

The laboratory experiment, designed to determine maximum consumable prey size, revealed that the largest successfully swallowed bluegills ranged from 88%–104% (mean ± SD = 96.5 ± 5.6%) of the estimates generated in this study (Fig. 2). The probability that a peacock cichlid would eat a bluegill was 100% for prey < 90% of gape size, but fell to about 17% for prey 100%–105%. The observed probability of consumption of prey >105% of estimated gape size was zero.

Largemouth bass and peacock cichlid gape sizes broadly overlapped across the total length range investigated in this study (i.e., about 50–425 mm TL) (Fig. 1). Conversely, ANCOVA revealed that the slopes of the regressions were not equal for the two predators ($F_{1,209} = 62.51$; $P < 0.0001$). The regression lines crossed at 126 mm TL, where both species had an equal gape of about 12.3 mm. Small peacock cichlids (<126 mm TL) had slightly larger gapes than largemouth bass of equal length whereas juvenile and adult largemouth bass (>126 mm TL) had larger gape sizes than peacock cichlids of equal length.

As with predator gape size, prey species body depths also were strongly corre-

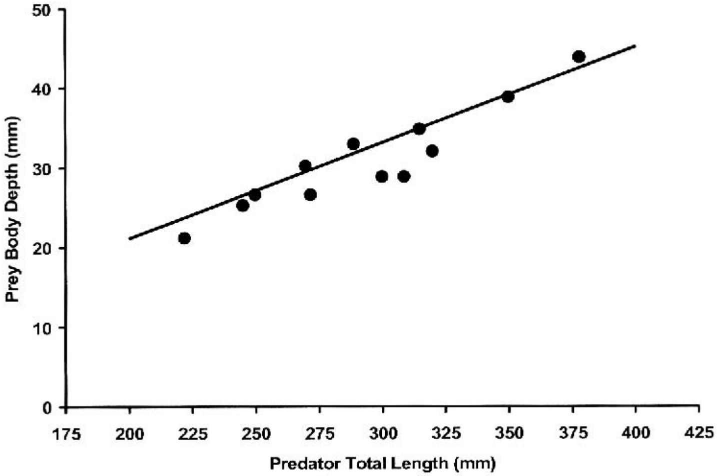

Figure 2. Maximum bluegill size (body depth) eaten by peacock cichlids in laboratory tanks ($N = 12$ trials). The solid line represents maximum prey body depth estimated by the peacock cichlid gape size model.

lated with total length (Table 1). According to these relations, prey varied in morphological vulnerability to predation based on the ratio of body depth-to-body length. Given the results of this study, a peacock cichlid can eat deep-bodied prey of about 30% of its own total length and largemouth bass can eat slightly longer prey (i.e., about 35% of its own length). The analysis of relative vulnerability of prey species based on predator gape sizes and prey body depth distributions showed that a large proportion of the three representative prey species (i.e., bluegill, redear sunfish, and spotted tilapia) was completely invulnerable (i.e., V = 0) to predation by largemouth bass (49%) and peacock cichlids (58%) (Fig. 3).

Discussion

External mouth width has been previously used to describe gape limitation in largemouth bass (Lawrence 1958, Hambright 1991, Johnson and Post 1996) and our investigation provides evidence that external mouth width also is a reliable estimator of prey ingestion limits for the morphologically similar peacock cichlid. The largemouth bass gape size model developed in the present study yielded estimates of maximum prey size similar to models previously described in the literature (e.g., Lawrence 1958, Shireman et al. 1978, Schramm and Maceina 1986).

There was close agreement between observed maximum prey body depths and the predictions of the gape size model in the laboratory experiment. Nevertheless, the laboratory experiment demonstrated that peacock cichlids can consume prey slightly larger than our predictions. Prey vulnerability is greater in the confines of a tank than

Table 1. Relations of body depth (BD) and total length (TL) for nine species of prey fish from southeast Florida canals. All dimensions are in mm.

Species	*N*	TL to BD	r^2	TL range
Centrarchidae				
Bluegill	29	0.46 TL–8.88	0.99	41–206
Largemouth bass	140	0.25 TL–3.38	0.99	17–423
Redear sunfish	28	0.40 TL–6.23	1.00	52–223
Spotted sunfish	81	0.42 TL–3.84	0.99	24–158
Warmouth	117	0.38 TL–5.85	0.99	18–190
Cichlidae				
Black acara	113	0.38 TL–1.15	0.99	21–174
Jewel cichlid	101	0.30 TL–0.25	0.98	27–99
Peacock cichlid	92	0.29 TL–5.13	1.00	49–430
Spotted tilapia	177	0.39 TL–0.84	1.00	14–260

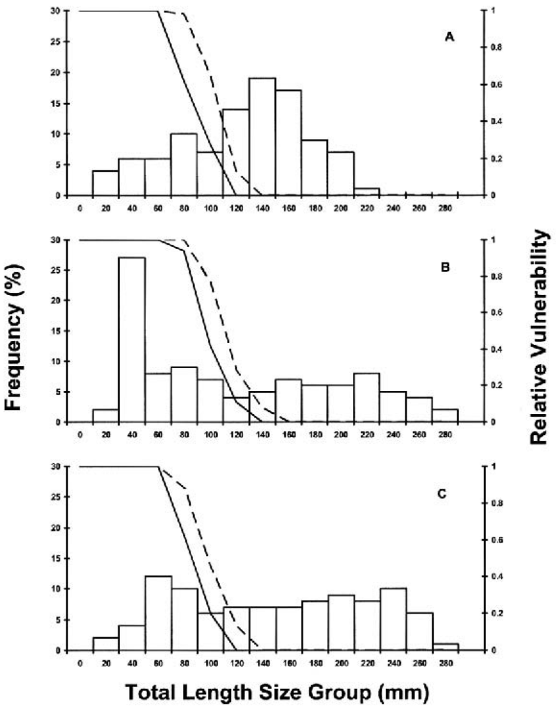

Figure 3. Length-frequency (%) and relative vulnerability (V) of three common prey species in southeast Florida canals: A. bluegill, B. redear sunfish, and C. spotted tilapia. Length-frequency data from fishes collected by concussion blocknet sampling in Black Creek Canal, Miami-Dade County, Florida (Shafland 1999a). Relative vulnerability curves for largemouth bass (broken line) and peacock cichlids (solid line) were generated from predator length-frequency (predators were ≥ 254 mm total length; Shafland 1999c), estimated predator gape sizes, and estimated prey body depths using the relative vulnerability model of Hambright et al. (1991).

in the field (Lewis et al. 1961, Juanes and Conover 1994). In a tank, search time for the predator is small or zero, encounter rates are high, prey antipredator behavior may be constrained (e.g., schooling), structural complexity is lacking (sensu Savino and Stein 1982), prey are unable to leave the vicinity of the predator, and alternative, perhaps more energetically favorable, prey are lacking. These factors of increased vulnerability may enable predators in a tank to successfully eat prey of maximum size on a regular basis.

Our results concur with other studies demonstrating the role of large body depth as an absolute constraint on predation (e.g., Hambright et al. 1991, Nilsson and Bronmark 2000). Several experimental peacock cichlids attempted but failed to eat bluegills exceeding their maximum gape size. Although these prey were killed by the predators in the confines of a tank, it is unlikely that an encounter between the same sizes of these species in the field would have resulted in prey mortality. Experimental peacock cichlids were fed only a single bluegill per day and attacked any relatively small fish added into the tank. Some predators soon gave up on prey too large, or perhaps too difficult, to eat. Others persisted in their attacks for several minutes to hours, finally killing the bluegill. Such long handling times make prey energetically unfavorable and provide ample opportunity for prey to escape in the field.

Largemouth bass and peacock cichlid length-specific gape sizes were broadly similar over the total length range included in this study. However, the estimates for predators over 126 mm TL diverged, with largemouth bass gape size increasing at a faster rate with length than did peacock cichlid gape size. Although, differences in gape width between predators were relatively small, the species-specific gape size differences translated into larger maximum prey size and higher prey relative vulnerability values for largemouth bass. For example, a 400-mm TL largemouth bass can eat a 132-mm TL spotted tilapia whereas a 400-mm TL peacock cichlid can eat a 116-mm TL spotted tilapia. The results imply that prey fish have similar morphological vulnerability to both predators over a broad range of predator sizes but that prey vulnerability to largemouth bass increases at a faster rate with predator size. Indeed, based on morphology alone, prey fish have equal or greater vulnerability to largemouth bass relative to peacock cichlids.

Our results clearly demonstrate that populations of prey fish that are abundant by both number and biomass in a representative southeast Florida canal (i.e., bluegill, redear sunfish, and spotted tilapia) have a high percentage of individuals that are invulnerable to predation. Relative vulnerability of each species rapidly declined over a small size range, indicating that small increases in prey size can have large influences on theoretical prey availability—prey may quickly become morphologically unavailable to the bulk of the piscivorous fish assemblage as they grow out of the theoretical predation window. Therefore, large amounts of potential prey biomass are unavailable for consumption by predatory fishes.

Predatory fishes are often stocked into aquatic systems as a management tool to increase predation pressure on excess prey biomass (Jenkins and Morais 1978, Ney 1990). Prey deficits and surpluses may occur on a size-specific basis for predators (Jenkins and Morais 1978). It is therefore important to consider the antipredator morphology of the prey base as well as the trophic morphology of the intended predators in terms of realistic size distributions. Moreover, species-specific prey use patterns may be influenced by other factors such as predator hunting strategies, prey behavior, and habitat characteristics. Native and exotic prey fishes, including spotted tilapia, remain abundant in southeast Florida canals (Shafland 1999a; L. G. Nico and J. E. Hill, pers. observ.). Nevertheless, the introduction of peacock cichlids has increased the overall biomass of predatory fishes (i.e., peacock cichlid biomass has not replaced largemouth bass biomass; Hill 2003) and thereby decreased prey-to-predator biomass ratios (Shafland 1995, 1999a).

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