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Diet overlap between native bigmouth sleepers (*Gobiomorus dormitor*) and introduced predatory fishes in a Puerto Rico reservoir

Bacheler NM, Neal JW, Noble RL. Diet overlap between native bigmouth sleepers (*Gobiomorus dormitor*) and introduced predatory fishes in a Puerto Rico reservoir.
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Abstract – Native fish species coexist with introduced species in Puerto Rico's freshwater systems, yet competition between these species has not been evaluated. We examined the extent of diet overlap between native bigmouth sleepers *Gobiomorus dormitor* and introduced largemouth bass *Micropterus salmoides* and peacock bass *Cichla ocellaris* in a Puerto Rico reservoir. Bigmouth sleepers and largemouth bass exhibited an ontogenetic shift in feeding habits, whereas peacock bass were exclusively piscivorous at all sizes collected in this study. Biologically significant diet overlap was observed between large bigmouth sleepers and largemouth bass, but not between large bigmouth sleepers and peacock bass, or between large largemouth bass and adult peacock bass. No significant diet overlap in any species combination was observed in small or medium size classes. Better understanding of the ecology of these coexisting predators should lead to improved conservation of bigmouth sleepers, and improved fisheries management for all three predatory species.

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Key words: competition; Puerto Rico; ontogenetic shift

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Un resumen en español se incluye detrás del texto principal de este artículo.

Introduction

The bigmouth sleeper *Gobiomorus dormitor* Lacépède is a euryhaline teleost found in a wide range of tropical and subtropical aquatic environments, including rivers (Darnell 1962; Holmquist et al. 1998), lagoons (Kelso 1965; Nordlie 1981), natural lakes (McKaye 1977; McKaye et al. 1979), and reservoirs (Rivera-Gonzales 1976; Churchill et al. 1995; Neal et al. 1999, 2001; Bacheler 2002). This species is a target for anglers in many areas throughout their native range (Corujo 1989; Corujo 1999), which includes coastal habitats of Florida, the Gulf of Mexico, Caribbean Sea, and northern South America. Recently, population declines have been documented in Florida and Puerto Rico, presumably because of hydrologic alterations (Gilmore 1992; Musick et al. 2000). Consequently, a need exists for improved understanding of bigmouth sleeper ecology and increased conservation efforts for bigmouth sleeper populations.

There is a paucity of information on bigmouth sleeper biology and ecology, especially feeding habits. The earliest published account of bigmouth sleeper diet was given by Hildebrand (1938), who reported that bigmouth sleepers 'feed on crustaceans, fishes, water beetles and apparently any other aquatic animal life of suitable size'. He further stated that, 'they make quick excursions, if hunger prompts them, to seize almost any animal of suitable size that comes near'. Darnell (1955) reported that, of seven

bigmouth sleepers examined from a headwater stream in Mexico, three contained no food, two contained fish, one had aquatic insects, and one had a large tarantula and several unidentified arthropods. Quantitative analysis by Nordlie (1981), based on a sample of five fish from Tortuguero Lagoon, Costa Rica, concluded that shrimp, and to a lesser extent fish, comprised the entire bigmouth sleeper diet. In the same system, more recent and extensive research found that the breadth of diet of bigmouth sleepers was much wider than that previously thought (Winemiller & Ponwith 1998). No studies regarding the diet of bigmouth sleepers in natural lakes or reservoirs have been published.

In Puerto Rico, bigmouth sleepers are primarily a riverine species, but Carite Reservoir supports a substantial reproducing population that coexists with non-native piscivores, largemouth bass *Micropterus salmoides* Lacépède and peacock bass *Cichla ocellaris* Bloch and Schneider (Bacheler 2002). Low productivity in Carite Reservoir limits prey availability (Rivera-Gonzales 1976; Neal et al. 1999, 2001), and low largemouth bass condition reflects this (Neal et al. 2001). If food habits are similar among these species, limitations in prey resources may result in interspecific competition.

The diets of largemouth bass and peacock bass have been quantified in other reservoirs in Puerto Rico. In Guajataca Reservoir, for instance, small largemouth bass (<50 mm total length (TL)) consumed fish, insects, and zooplankton, and switched almost exclusively to piscivory at lengths longer than 200 mm TL (Neal et al. 1999). Alternatively, peacock bass of all sizes fed mainly on fish (Lilyestrom & Churchill 1996).

The degree of diet overlap between bigmouth sleepers, largemouth bass, and peacock bass was unknown in Carite Reservoir. However, given the fact that these species have not coevolved (largemouth bass have been introduced from the USA, and peacock bass from northern South America), and that the total number and abundance of prey species were low (14 total fish species according to Neal et al. 2001), we hypothesized diet overlap between all species could be substantial. An understanding of diet overlap among the predators would facilitate management, allowing production potential of the multispecies fishery to be maximized. In this study, we examined the potential for diet overlap among bigmouth sleepers, largemouth bass, and peacock bass in Carite Reservoir. Our results complement and expand the small body of literature regarding bigmouth sleepers, and provide new information on food utilization of bigmouth sleepers, largemouth bass, and peacock bass from reservoir environments in Puerto Rico.

Materials and methods

Feeding habits of bigmouth sleepers, largemouth bass, and peacock bass were studied from October 1999 to October 2001 in Carite Reservoir, a 124-hectare impoundment located near the town of Cayey in mountainous south-central Puerto Rico. The reservoir is situated at 18°04′N, 66°05′W at an elevation of 543.6 m above sea level. Carite Reservoir was impounded in 1913 by construction of an earthen dam (Erdman 1984), and is the uppermost of a series of impoundments on the La Plata River. Carite Reservoir is one of the least productive reservoirs in Puerto Rico (Carvajal-Zamora 1979), and catch rates of all fishes in the past have been consistently low (Neal et al. 2001). The water level fluctuated 4 m during this study, which is far less than the extreme fluctuations observed in other reservoirs on the island (e.g., up to 17 m annually in Lucchetti Reservoir; Neal et al. 1999).

Sampling for predators was conducted every 3 months between October 1999 and October 2001. Adults were targeted by sampling the littoral zone during daylight hours using a boom-mounted electrofishing unit with 3–4 A and 60 pps DC. All adult fish (>200 mm TL) were collected, measured for TL (mm), and weighed (g) in the field. Stomach samples from adult fish were obtained using esophageal tubes (Van Den Avyle & Roussel 1980) and preserved in 70% ethanol prior to the release of the fish. Juvenile predators were targeted using nighttime electrofishing of the littoral zone with 260-V DC delivered via hand-held probe (Jackson & Noble 1995). All juveniles were euthanized using an anesthetic (MS-222) overdose and kept on ice until processing the following day. In the laboratory, each fish was measured for total length (mm) and weight (±0.01 g). Stomachs were dissected from all juvenile fish and preserved in 70% ethanol.

Stomach contents of juveniles and adults were examined in the laboratory under a binocular microscope at 10× and identified to the lowest recognizable taxon, enumerated, blotted dry, and weighed (± 0.01 g). Because of its relationship to the caloric value of food (Wallace 1981), we used average percentage by weight to describe predator diets. Average percentage by weight was calculated as the sum of proportion by weight of an individual prey type in each stomach divided by the number of stomachs examined.

Diet overlap was determined by two means. We first used Schoener's (1970) index of niche overlap, which is the most commonly used diet overlap index (Wallace 1981). The index is determined using the formula:

$$\alpha = 1 - 0.5\left(\sum |p_{ij} - p_{ij}\right)$$

where α = the degree of overlap, p_{ij} = the proportion of the *i*th resource (in this case, prey type) used by species *j*, and p_{ik} = the proportion of the *i*th prey type used by species *k*. Index values range from 0 to 1; they approach 0 for species that share no prey types and approach 1.0 for species pairs that have completely identical prey utilizations. Values exceeding 0.6 represent 'biologically significant' overlap in resource use (Wallace 1981).

Because of limitations of Schoener's index for arbitrary cutoffs (Feinsinger et al. 1981), we also compared the observed estimate of overlap to an appropriate null model. The distribution of the null model was created from 1000 randomizations of the utilization data using the 'scrambled-zeros' randomization algorithm proposed by Winemiller & Pianka (1990), whereby the entries in each row of the utilization matrix were randomly reshuffled for each iteration. ECOSIM software was used to perform the simulations (Gotelli & Entsminger 2001). Statistical significance was determined by comparing the observed overlap value to the null distribution; an observed value greater than 95% of the simulated values indicated significant overlap at the $\alpha < 0.05$ level (Winemiller & Pianka 1990).

Results

Food habits

We examined the diet composition of 416 bigmouth sleepers (mean = 172 mm TL; SE = 7.8), 93 largemouth bass (mean = 231 mm TL; SE = 9.5), and 25 peacock bass (mean = 211 mm TL; SE = 10.7) during this study. Mean predator weight was higher for peacock bass (mean = 265.4 g; SE = 28.5) than that for largemouth bass (mean = 225.5 g; SE = 22.0) or bigmouth sleepers (mean = 72.2 g; SE = 7.7). The percentage of empty stomachs was higher for bigmouth sleepers (68.0%) than that for largemouth bass (47.3%) or peacock bass (32.0%).

Differences in the diets of similarly sized individuals among these three species were evident. Small (<100 mm TL) bigmouth sleepers principally fed on aquatic insects and zooplankton, whereas small largemouth bass utilized fish, but also aquatic insects and zooplankton (Table 1). Small peacock bass utilized fish exclusively (primarily threadfin

Table 1. Stomach contents of bigmouth sleepers (BMS), largemouth bass (LMB), and peacock bass (PKB) less than 100 mm TL in Carite Reservoir, 1999–2001.

	Predator species		
	BMS	LMB	PKB
Fish			
Threadfin shad (*D. petenense*)	2.2	15.2	29.1
Redbreast sunfish (*L. auritus*)		10.0	
Redbreast tilapia (*T. rendalli*)		10.0	
Mozambique tilapia (*T. mossambica*)	2.2		
Channel catfish (*I. punctatus*)	1.5		
Largemouth bass (*M. salmoides*)	2.2		
Mosquitofish (*G. affinis*)			30.9
Unidentified fish		20.0	40.0
Total fishes	8.1	55.2	100.0
Invertebrates			
Odonata	6.6		
Hemiptera	0		
Diptera	10.0	5.6	
Coleoptera		16.9	
Cladoceran		12.4	
Copopoda	29.0	0.4	
Freshwater crab (*E. sinuatifrons*)	0.7		
Unid. invertebrates	26.0	9.6	
Ostracoda	19.0		
Total invertebrates	91.9	44.8	0
Number containing prey	45	10	5
Mean TL (mm) (SE)	75.2 (2.3)	73.1 (4.3)	79.2 (4.4)
TL range (mm)	38–97	39–89	67–94
Mean weight (g) (SE)	3.7 (0.3)	4.8 (0.6)	6.3 (1.3)

Data are presented as average percentage by weight.

Table 2. Stomach contents of bigmouth sleepers (BMS), largemouth bass (LMB), and peacock bass (PKB) 100–200 mm TL in Carite Reservoir, 1999–2001.

	Predator species		
	BMS	LMB	PKB
Fish			
Threadfin shad (*D. petenense*)	31.3	40.8	40.0
Redear sunfish (*L. microlophus*)	2.6		
Bluegill (*L. macrochirus*)	7.9		
Redbreast sunfish (*L. auritus*)			20.0
Largemouth bass (*M. salmoides*)			16.4
Mosquitofish (*G. affinis*)	2.6		
Unidentified fish	2.6	18.8	23.6
Total fishes	47.1	59.5	100.0
Invertebrates			
Odonata	5.3	25.0	
Hemiptera	5.0	6.3	
Freshwater crab (*E. sinuatifrons*)	11.0		
Unid. invertebrates	20.3	9.2	
Ostracoda	11.0		
Total invertebrates	52.9	40.5	0
Stomachs containing prey	38	8	5
Mean TL (mm) (SE)	157 (5.4)	148.5 (12.4)	158.6 (14.0)
TL range (mm)	101–199	105–195	122–196
Mean weight (g) (SE)	32.9 (3.0)	40.9 (8.8)	55.8 (12.8)

Data are presented as average percentage by weight.

shad *Dorosoma petenense* Günther and mosquitofish *Gambusia affinis* Baird and Girard). Medium sized (100–200 mm TL) bigmouth sleepers consumed fish, aquatic insects, freshwater crabs *Epilobocera sinuatifrons*, and ostracods, while similar-sized largemouth bass only consumed fish and aquatic

Table 3. Stomach contents of bigmouth sleepers (BMS), largemouth bass (LMB), and peacock bass (PKB) larger than 200 mm TL in Carite Reservoir, 1999–2001.

	Predator species		
	BMS	LMB	PKB
Fish			
Threadfin shad (*D. petenense*)	34.0	50.1	43.0
Redear sunfish (*L. microlophus*)		6.5	14.2
Bluegill (*L. macrochirus*)	4.2		4.2
Redbreast sunfish (*L. auritus*)		3.2	38.6
Redbreast tilapia (*T. rendalli*)		9.3	
Mozambique tilapia (*T. mossambica*)		3.2	
Channel catfish (*I. punctatus*)	3.3		
Bigmouth sleeper (*G. dormitor*)	4.9	6.5	
Peacock bass (*C. ocellaris*)		3.2	
Largemouth bass (*M. salmoides*)	9.6		
Unidentified fish	17.0	12.9	
Total fishes	73.0	94.9	100.0
Invertebrates			
Odonata	8.6	2.1	
Hemiptera		3.0	
Freshwater crab (*E. sinuatifrons*)	13.0		
Gastropod	1.2		
Unid. invertebrates	2.1		
Ostracoda	2.1		
Total invertebrates	27.0	5.1	0
Stomachs containing prey	47	31	7
Mean TL (mm) (SE)	271.0 (7.1)	302.6 (10.4)	343.6 (18.9)
TL range (mm)	201–402	202–423	271–411
Mean weight (g) (SE)	165.0 12.6	344.3 (44.9)	600 (95.2)

Data are presented as average percentage by weight.

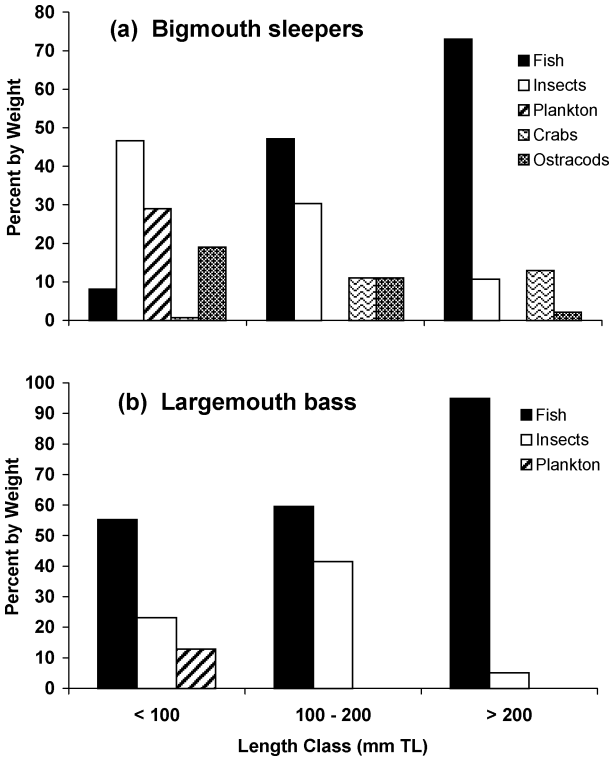

Fig. 1. Ontogenetic shift in prey utilization by bigmouth sleepers (a) and largemouth bass (b) in Carite Reservoir, 1999–2001. Average percentage by weight was calculated as the sum of proportion by weight of an individual prey type in each stomach divided by the number of stomachs examined.

insects; peacock bass fed only on fish (Table 2). Large (>200 mm TL) bigmouth sleepers preyed upon fish, crabs, aquatic insects, zooplankton, and gastropods, while large largemouth bass fed on fish and aquatic insects; large peacock bass fed strictly upon fish (Table 3). There was no significant difference in prey utilization by season for bigmouth sleepers (ANOVA: $F = 0.09$; d.f. $= 3$; $P = 0.96$) or largemouth bass (ANOVA: $F = 0.45$; d.f. $= 3$; $P = 0.45$). Small sample size of peacock bass precluded analyses of differences in prey utilization by season for this species.

The average percentage by weight of prey items differed by length class for bigmouth sleepers and largemouth bass, suggesting an ontogenetic shift in feeding as fish grew. The average weight of fish prey of bigmouth sleeper diets increased with total length (Fig. 1a), increasing from 8.1% in small fish (<100 mm TL) to 73.0% in large fish (>200 mm TL). Conversely, average percentage by weight of insects decreased with size. Average percentage by weight of freshwater crabs was small in bigmouth sleepers less than 100 mm TL (0.7%), but made up a greater average weight in fish between 100 and 200 mm TL (11.0%) and became large in fish longer than 200 mm TL (13%). Average percentage by weight of ostracods was large in fish less than 200 mm TL, yet was very small in fish greater than 200 mm TL.

Largemouth bass displayed a similar ontogenetic shift in diet (Fig. 1b). The degree of piscivory increased with largemouth bass size, increasing from 55.2% in small fish to 94.9% in large ones. Average percentage by weight of insects declined as largemouth bass grew. Zooplankton was important to small largemouth bass (12.8%), but disappeared from the diet after fish grew larger than 100 mm TL. Peacock bass sample size was too small for such analysis.

Diet overlap

Based on Schoener's index and the null model tests, there was significant diet overlap between large (>200 mm TL) bigmouth sleepers and largemouth bass ($\alpha = 0.61$; $P = 0.02$) but not between small

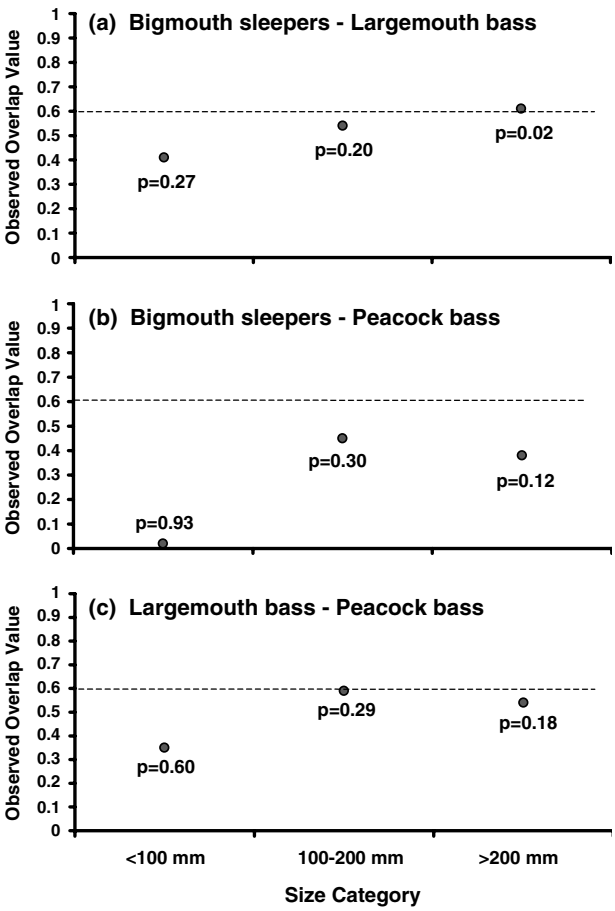

Fig. 2. Observed values of diet overlap between three size classes of bigmouth sleepers and largemouth bass (a), bigmouth sleepers and peacock bass (b), and largemouth bass and peacock bass (c) in Carite Reservoir, 1999–2001. Values above 0.6 (dashed line) are considered biologically significant according to Schoener (1970), while *P*-values indicate significance using the null model test.

($\alpha = 0.41$; $P = 0.27$) or medium sized fish ($\alpha = 0.54$; $P = 0.20$) (Fig. 2a). Diet overlap between bigmouth sleepers and largemouth bass was positively related to fish length. No significant diet overlap was observed between bigmouth sleepers and peacock bass (Fig. 2b) or between largemouth bass and peacock bass (Fig. 2c) in any size category, although the null model tests yielded diet overlap values that were positively related to fish length.

Discussion

This study presents new information on diet of bigmouth sleepers in a lentic environment and diet overlap between bigmouth sleepers and introduced fishes. It further quantifies largemouth bass and peacock bass diets in Puerto Rico. Overall, we found significant diet overlap between large individuals of native bigmouth sleepers and introduced largemouth bass, but not between any other species combination in any size class.

Food habits

Bigmouth sleepers in Carite Reservoir behaved as generalist predators and appeared capable of utilizing a diversity of living organisms of appropriate size. An ontogenetic shift in bigmouth sleeper feeding was apparent. Small bigmouth sleepers fed primarily on small items such as insects, zooplankton, and ostracods, but larger individuals switched to feeding on fish and freshwater crabs. The breadth of diet for bigmouth sleepers was wide; they consumed eight species of fish, as well as aquatic insects, zooplankton, freshwater crabs, gastropods, and ostracods. Additionally, cannibalism was observed, and terrestrial organisms, including a gecko (Gekkonidae), were occasionally recovered from stomach contents, further indicating the opportunistic nature of bigmouth sleeper foraging. Bigmouth sleepers have been reported to forage in terrestrial environments near the water's edge (e.g., Darnell 1955), but we did not observe terrestrial behavior in Carite Reservoir despite sampling over the diel cycle. Hence, we believe that the terrestrial organisms observed in bigmouth sleeper stomachs during our study were consumed after falling into the aquatic environment from overhanging vegetation, not after terrestrial excursions by bigmouth sleepers.

The diet of bigmouth sleepers reported in this study was very different from diets reported from coastal rivers and estuaries elsewhere. Within riverine habitats, postlarvae shrimp dominate the diet, while fish are of lesser importance (Nordlie 1981; Winemiller & Ponwith 1998). As most freshwater shrimp species in Puerto Rico are catadromous and require unimpeded access to marine environments, they are usually not abundant in reservoirs (Holmquist et al. 1998). Hence, landlocked bigmouth sleepers must select prey from available reservoir species, which did not include shrimp in Carite Reservoir.

Largemouth bass displayed a similar ontogenetic shift in feeding. Small individuals consumed aquatic insects, fish, and zooplankton, but switched almost exclusively to fish as adults. Similar results have been found in other reservoirs in Puerto Rico (Lilyestrom & Churchill 1996; Alicea et al. 1997; Neal et al. 1999). The breadth of diet for largemouth bass (seven species of fish, aquatic insects, zooplankton) was large, but not as large as that observed for bigmouth sleepers.

Peacock bass were strictly piscivorous during this study, consuming only six identifiable species of fish: threadfin shad, redbreast sunfish *Lepomis auritus* L., redear sunfish *L. microlophus* Günther, bluegill *L. macrochirus* Rafinesque, largemouth bass, and mosquitofish. Although our sample size of peacock bass stomachs with food was low ($n = 17$), our results agreed with previous studies, which reported that at least 90% of the peacock bass's diet was comprised of piscine prey (Lilyestrom & Churchill 1996; Neal et al. 1999; Shafland 1999). Peacock bass had the most specific diet of any predatory fish studied in Carite Reservoir.

Diet overlap

Two methods of assessing diet overlap were used in this study, the Schoener's (1970) index and the null model test (Winemiller & Pianka 1990). Schoener's index is sensitive to the number of species and prey categories compared, and may give different results as species or prey categories are added or deleted from the data (Feinsinger et al. 1981). On the other hand, the null model test is a statistical model that compares observed values of overlap to a distribution of expected overlap values based on a null model (random overlap). We found agreement between the results of each test in every case.

We found evidence that large bigmouth sleepers and largemouth bass have high diet overlap, with both species feeding mainly on threadfin shad, but also utilizing bigmouth sleepers and aquatic insects. Previous studies from Carite Reservoir have shown the condition of largemouth bass to be consistently low (Neal et al. 2001), indicative of a scarcity of prey, possibly because of interspecific competition with bigmouth sleepers. Habitat use of each species is also likely to be similar. Both largemouth bass and bigmouth sleepers often utilize shoreline structure in the littoral zone (Darnell 1955; McKaye 1977; Nordlie 1981; Annett et al. 1996; Waters 1999), thereby exacerbating the potential for competition. The disappearance of bigmouth sleepers from three reservoirs in

Puerto Rico over the past 10 years (Churchill et al. 1995; Neal et al. 1999, 2001) suggests that they may be at a competitive disadvantage. Given that bigmouth sleepers existed sympatrically with largemouth bass in each reservoir where they ultimately disappeared, interspecific competition between these two species in diet and space may be a possible explanation for the observed bigmouth sleeper disappearances. Further research is required to determine the exact cause of these disappearances.

No biologically significant diet overlap was observed between peacock bass and bigmouth sleepers, consistent with the major differences in prey utilization between these two species. Unlike the generalist bigmouth sleepers, peacock bass were strictly piscivorous. Furthermore, habitat utilization differences effectively separate these two species in space. Peacock bass have large home ranges and move to prey in pelagic areas (Lilyestrom & Churchill 1996), whereas bigmouth sleepers are sedentary ambush predators that hold closely to structure (Darnell 1955; McKaye 1977; Nordlie 1981). Therefore, habitat utilization would not be expected to overlap greatly between bigmouth sleepers and peacock bass. Predation by each of these species on the juveniles of the other was not observed. Given all of the above, coexistence of these two species appears possible without negative interactions.

Diet overlap between largemouth bass and peacock bass was not significant for any size class. While the Schoener's indices of diet overlap between medium and large fish were nearly significant ($\alpha = 0.59$ and $\alpha = 0.54$, respectively), the null model tests yielded P-values that were not even marginally significant ($P = 0.29$ and $P = 0.18$, respectively). Although a negative correlation in abundance exists among largemouth bass and peacock bass in Puerto Rico reservoirs (Neal et al. 1999), no negative interactions between largemouth bass and peacock bass have been identified (e.g., Lilyestrom & Churchill 1996; Shafland 1999).

Future research could help clarify the ecologic requirements of bigmouth sleepers, in both the presence and the absence of largemouth bass. Such experimental work would facilitate management and conservation efforts for this important species in Puerto Rico and elsewhere.

Resumen

1. Especies de peces nativas coexisten con especies introducidas en sistemas de agua dulce de Puerto Rico. Todavía no se han evaluado niveles de competición entre estas especies. En este studio examinamos el solapamiento alimenticio entre la especie nativa *G. dormitor* y las especies introducidas *M. salmoides* y *C. ocellaris*, en un embalse de Puerto Rico.

2. *G. dormitor* y *M. salmoides* mostraron cambios ontogenéticos en los hábitos alimenticios mientras que *C. ocellaris* fue exclusivamente piscívora en todos los tamaños colectados en este estudio. Un solapamiento alimenticio biológicamente significativo fue observado entre *G. Dormitor* y *M. Salmoides* pero no entre *G. Dormitor* y *C. Ocellaris*. El solapamiento alimenticio no fue significativo para ninguna combinación de especies en clases de tamaño pequeñas y medianas.

3. Una mejor comprensión de la ecología de estos predadores que coexisten debería llevar a mejorar la conservación de *G. Dormitor* y a mejorar la gestión pesquera de las tres especies de predadores.

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